

EVOLUTION OF TEMPORAL ISOLATION IN THE WILD: GENETIC DIVERGENCE IN TIMING OF MIGRATION AND BREEDING BY INTRODUCED CHINOOK SALMON POPULATIONS

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Abstract.—The timing of migration and breeding are key life-history traits; they are not only adaptations of populations to their environments, but can serve to increase reproductive isolation, facilitating further divergence among populations. As part of a study of divergence of chinook salmon, *Oncorhynchus tshawytscha*, populations, established in New Zealand from a common source in the early 1900s, we tested the hypotheses that the timing of migration and breeding are under genetic control and that the populations genetically differ in these traits despite phenotypic overlap in timing in the wild. Representatives of families from two populations were collected within a day or two of each other, reared in a common environment, and then released to sea from each of two different rivers, while other family representatives were retained in fresh water to maturity. The date of maturation of fish held in fresh water and the dates of return from the ocean and maturation of fish released to sea all showed significant differences between the two populations and among families within populations. The very high heritabilities and genetic correlations estimated for migration and maturation date indicated that these traits would respond rapidly to selection. Combined with the results of related studies on these chinook salmon populations, it appears that spawning time may not only evolve during the initial phases of divergence, but it may play an important role in accelerating divergence in other traits.

Key words.—Breeding time, divergence, migration time, rapid evolution, reproductive isolation.

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Individuals who breed at unfavorable times may experience lower relative fitness, as evidenced by differential reproductive success of parents breeding within a given season. Variance in fitness may result from variation in environmental conditions, competition, predation, and other factors including parental quality (e.g., insects: Ohgushi 1991; birds: Hatchwell 1991; Norris 1993; Wiggins et al. 1994; Verhulst et al. 1995; fishes: Hayes 1987; Schultz 1993; Warlen 1994; Secor and Houde 1995; Cargnelli and Gross 1996). Many animals also undertake lengthy seasonal migrations between feeding habitats and breeding grounds, and the timing of these movements is often adapted to prevailing environmental conditions encountered along the migratory route (Dingle 1996).

Many populations experience partial reproductive isolation because adults home to breed at their natal site (philopatry) or because dispersal occurs only over a limited geographic scale. This isolation allows selection on heritable traits to improve fitness via local adaptations. If site-specific selective factors also influence the timing of reproduction, either directly or indirectly, prezygotic isolation associated with geographic isolation is strengthened by temporal isolation as the populations evolve locally appropriate breeding periods. Thus, although breeding time is only one of many traits that may differ among populations, its evolution may be pivotal in controlling divergence in other traits. Prezygotic isolating mechanisms, such as differences in breeding time, are thought to evolve via genetic correlations with other life-history traits (Rice and Hostert 1993), and the potential for differences in

breeding time to evolve via correlated selection has been shown in laboratory populations (Miyatake and Shimizu 1999). Convincing evidence has been presented for the genetic divergence of reproductive timing among populations, or “races,” that have been isolated over geological time scales (e.g., classic work of Clausen et al. 1940). Likewise, temporal traits other than actual breeding time (e.g., post-diapause eclosion time) may be important in contributing to recent population isolation and divergence in insect host interactions (e.g., Smith 1988). However, evidence for the development of genetic divergence in annual breeding time has remained largely unexplored over short time scales in the wild. Such a demonstration would help evaluate its importance as a prezygotic isolating mechanism during initial population establishment and divergence.

Populations of anadromous Pacific (*Oncorhynchus* spp.) and Atlantic (*Salmo salar*) salmon are excellent model systems for the study of local adaptation and evolutionary processes associated with the timing of migration and breeding. Migration and breeding dates are under stronger genetic control and are less responsive to environmental conditions in salmonids than in most fishes (e.g., clupeid fishes such as American shad, *Alosa sapidissima*: Leggett and Whitney 1972; Quinn and Adams 1996). Migration and spawning dates vary greatly among salmon populations, but only slightly within populations among years (Killick 1955; Ricker 1972; Brannon 1987; see reviews in Groot and Margolis 1991). Such variation in migration and spawning timing is thought to have evolved to accommodate environmental conditions such as temperature and flow that affect returning adults (Gilhousen 1990; Quinn and Adams 1996). Spawning date is also the primary mechanism controlling the date when offspring emerge from the gravel (months later), and is adapt-

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ed to the local thermal conditions during incubation and patterns of food availability and other factors influencing juvenile survival (Beacham and Murray 1987; Brannon 1987; Webb and McLay 1996). Where water is relatively warm during the incubation period, adults spawn later than in systems with cooler water (Brannon 1987).

The homing tendency of salmon (Quinn 1993) ensures that local populations remain spatially isolated. The myriad local adaptations presently observed (Ricker 1972; Taylor 1991) presumably evolved following postglacial colonization and isolation, but the early stages of the divergence process are unclear because they took place long ago. However, animal populations introduced to new habitats provide opportunities to study the "microevolutionary" phenotypic and genotypic changes during initial population formation and divergence (for review, see Hendry and Kinnison 1999). Salmon and trout have been transplanted to freshwater habitats throughout the world but poor records or complex ancestry often make it difficult to determine if present life-history patterns have resulted from recent diversification or the existence of multiple lineages (e.g., variation in spawning date in Great Lakes rainbow trout, *O. mykiss*: Biette et al. 1981). The longest standing introduction of anadromous Pacific salmon has occurred in New Zealand, where chinook salmon (*O. tshawytscha*) from the Sacramento River system in California were liberated in a single river system in the early 1900s. By 1915, these introductions had produced offspring that thrived, rapidly colonized suitable habitat in other rivers on New Zealand's South Island, and have sustained themselves to the present (McDowall 1994). Wild salmon from different rivers show phenotypic differences in various life-history traits, including timing of return migration and date of entry to the spawning grounds (Quinn and Unwin 1993). These differences indicate that local adaptation to New Zealand rivers may have evolved within about 30 generations, making this an ideal system in which to study the early stages of divergence.

This paper presents the results of controlled breeding and rearing experiments to determine the roles of genetic and environmental factors controlling reproductive timing in the newly established New Zealand chinook salmon populations. We tested the null hypotheses that migration and maturation timing did not genetically differ between populations for families collected at the same time in both systems and then reared under common environmental conditions and did not differ between environments (i.e., return locations) for fish from two study populations. We also derived quantitative genetic estimates of inheritance for return and maturation timing so that we could evaluate the potential for evolution of this trait given sufficient selection.

MATERIALS AND METHODS

Study Populations

The two study populations, Glenariffe Stream, a headwater tributary of the Rakaia River, and the Hakataramea River, a tributary of the Waitaki River (Fig. 1), differ in migratory timing by about a month. Quinn and Unwin (1993) reported that 69% of the chinook salmon caught by anglers at the mouth of the Rakaia River were taken in January and Feb-

ruary, whereas 48% of the Waitaki River catch were taken in March. Median capture dates were 7 February in the Rakaia River and 9 March in the Waitaki River. Both rivers have several distinct spawning areas, although a precise measure of run timing (median date of entry) is available only for Glenariffe Stream (Quinn and Unwin 1993). However, the one month difference in migration timing between the two river systems (as evidenced by angler catches) does not appear to be mirrored by a similar difference in peak spawning date, which occurs in late April/early May in both populations.

Glenariffe Stream and the Hakataramea River differ in flow and temperature regimes, both of which might affect the evolution of migration or spawning timing. The Hakataramea is a 60-km, rain-fed river that joins the Waitaki River at river km 60 and approximately 200 m elevation, but most spawning takes place in the lower 10–15 km of the river. Mean daily discharge is $6.0 \text{ m}^3\text{s}^{-1}$, but the river is prone to sudden and severe flooding, with a mean annual flood of $105 \text{ m}^3\text{s}^{-1}$ (daily mean discharge) and a maximum recorded discharge of $1350 \text{ m}^3\text{s}^{-1}$. Glenariffe Stream is a stable, spring-fed stream joining the Rakaia River 100 km above the mouth at an altitude of 430 m (Unwin 1986). It is smaller (daily mean discharge $3.4 \text{ m}^3\text{s}^{-1}$) and much more stable than the Hakataramea River, with a mean annual flood and maximum recorded discharge of only $7.9 \text{ m}^3\text{s}^{-1}$ and $16.0 \text{ m}^3\text{s}^{-1}$, respectively. The Hakataramea River is warmer ($7\text{--}12^\circ\text{C}$) during the spawning and juvenile incubation period (about May–September) than Glenariffe Stream ($6.5\text{--}9.5^\circ\text{C}$). This difference in temperature regimes would result in a four- to six-week difference in emergence date of juveniles from the gravel for parents spawning on the same date, based on observed temperature-specific rates of embryonic development for these populations (Kinnison et al. 1998a).

A fundamental assumption of our study is that population-specific differences demonstrated under common rearing conditions constitute evidence of genetic divergence, irrespective of the magnitude of the phenotypic differences in the wild (which may be only approximately known). Our primary goal was to determine whether there were genetically based differences between the two populations in the timing of migration and breeding and to elucidate how environmental variation may contribute to phenotypic variation, rather than to attempt the more elusive task of partitioning variation in the wild into genetic and environmental components. This contrasts with our approach in an earlier study (Quinn and Unwin 1993), which demonstrated phenotypic differences in the wild, but did not directly address the question of their genetic basis.

Experimental Families

In 1994 we established 72 experimental families by spawning salmon from the two study populations on consecutive days (Fig. 2; 22 April for Hakataramea and 23 April for Glenariffe). This conservative design minimized the chance of detecting a genetic difference between populations in timing because the experimental parents had all matured within several days of each other. For both populations, mature fish were intercepted at weirs near the river mouths and were

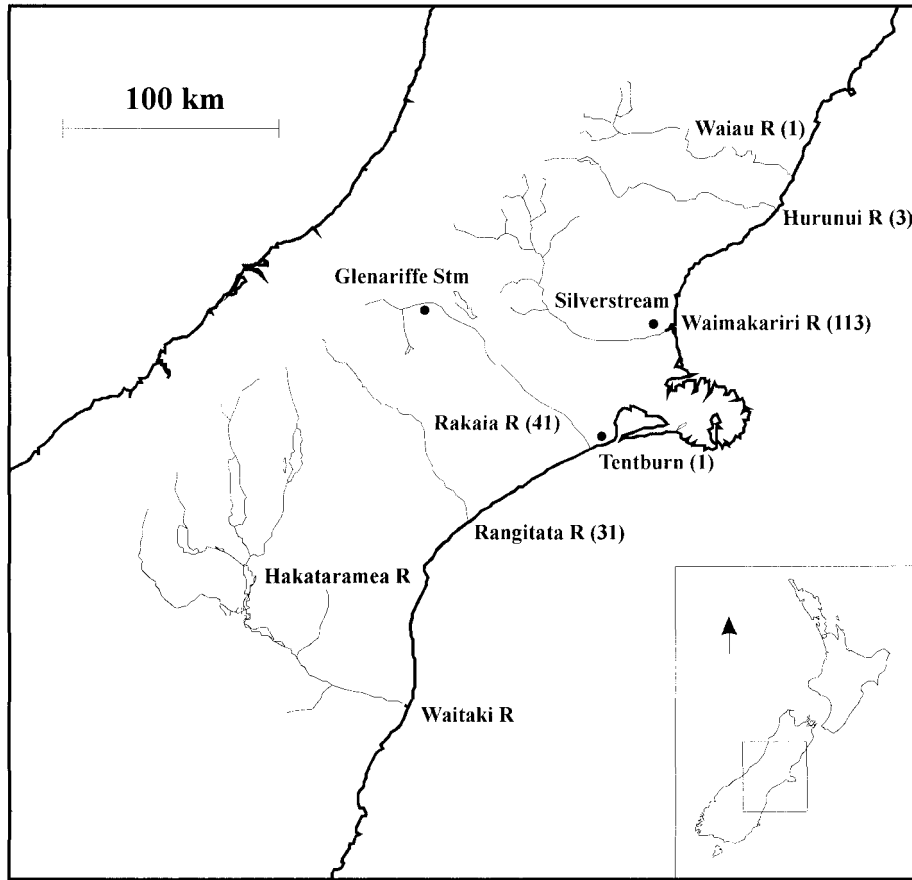


FIG. 1. The central regions of the South Island, New Zealand, showing locations referred to in this study. Figures in parentheses along river names refer to the number of marked adult chinook from the two study populations taken by anglers between 1996 and 1998.

accumulated for up to seven days prior to spawning, giving preference (at Glenariffe Stream) to individuals of natural rather than hatchery origin on the basis of point of interception (Unwin and Glova 1997) and scale pattern analysis (Unwin and Lucas 1993). We used a half-sib mating design (milt from each male fertilized ova from two females), initially creating 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. All available ova (about 5000 per female) were taken from Glenariffe fish, but only 2000 ova were collected from each Hakataramea female.

All families were incubated and reared at the National Institute of Water and Atmospheric Research's Silverstream Research Station, on a tributary of the lower Waimakariri River (Figs. 1, 2). On 17 May we reduced the number of families to 60, comprising 30 full-sib families within 15 half-sib families per population (Kinnison et al. 1998a), by discarding half-sib family pairs with poor fertilization or survival rates. After hatching (early July) each family was reared individually and was progressively culled to 700 individuals per family (for further details, see Kinnison et al. 1998b). All surplus Glenariffe embryos (initially about 3000 per family) were also incubated and reared as separate families. Space limitations prevented us from holding culled fry of Hakataramea origin in family-specific groups, so they were

accumulated in two 2000-L circular tanks and reared as a single population-specific group. All fry were fed to satiation with a standard commercially produced dry diet.

In October 1994 (spring), six months after fertilization, all fry were marked with sequential coded-wire microtags (CWTs) inserted into the cranial cartilage, and assigned to one of two groups. Those in one group, consisting of all surplus Glenariffe and Hakataramea fry, were marked externally by excision of the adipose fin and tagged to either population level (Hakataramea fry) or family level (Glenariffe fry). They were trucked to the hatchery on Glenariffe Stream and pooled into a single production raceway for common rearing until 19 July 1995, when they were released to sea via the upper Rakaia River at average weights of 59 g (Glenariffe) and 60 g (Hakataramea). We released 117,824 fish of Glenariffe origin (averaging 3927 individuals per family) and 23,655 of Hakataramea origin (divided evenly between two CWT codes, which served as replicates for subsequent analyses). We refer to this group as the "1994 Glenariffe release" (Fig. 2), where 1994 indicates the brood year rather than the year of release. Fish in the second group (400 fry per family) were given family-specific tags and reared on well water, under natural photoperiod, at Silverstream in 3000-L circular tanks, with two families (one marked by removal of the adipose fin) drawn randomly from the combined populations assigned to each tank. Two families were

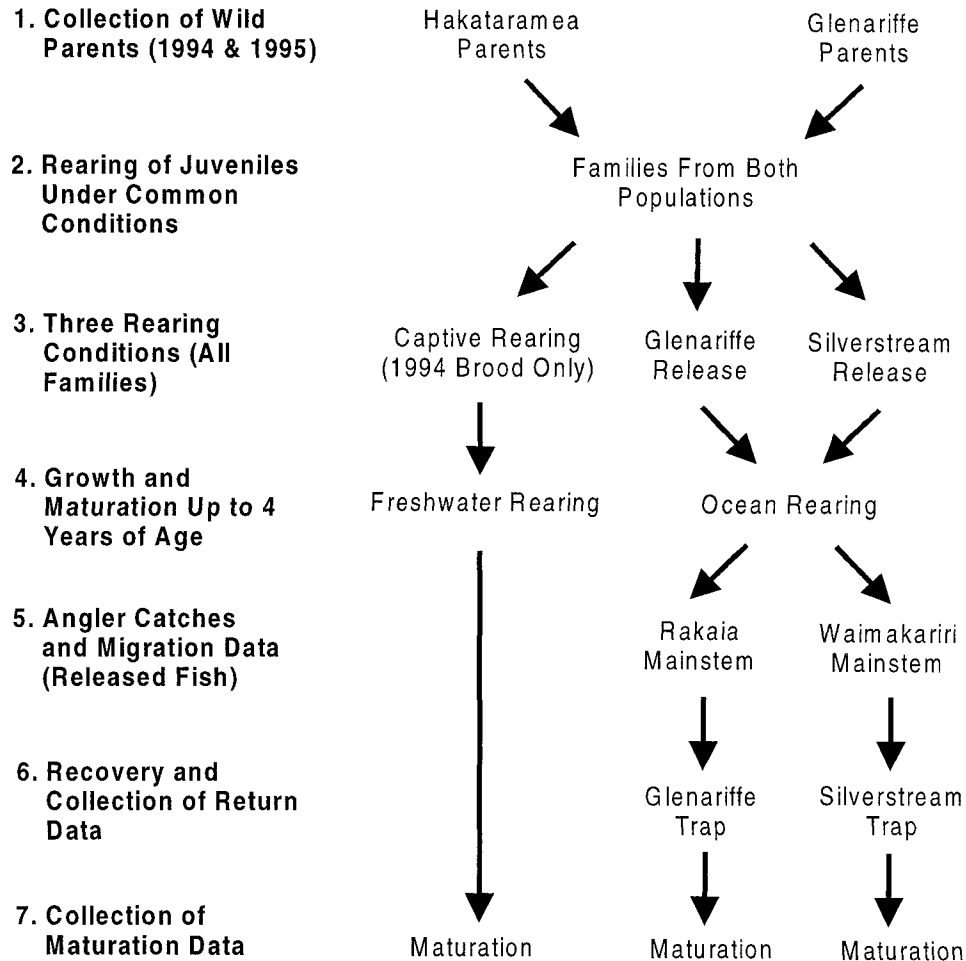


FIG. 2. Experimental design used to study divergence in migration, return, and maturation timing of New Zealand chinook salmon. Inheritance of return and maturation timing were examined with data from half-sib families created in the 1994 brood year and held captive or recovered at Glenariffe Stream.

inadvertently mixed prior to marking, reducing the number of usable families to 58.

In April 1995 (12 months after fertilization), 50 randomly selected fish from each family at Silverstream were marked with individual passive integrated transponder (PIT) tags, transferred to Glenariffe, and pooled in a large raceway for long-term rearing in a captive freshwater environment. The PIT tags allowed us to identify individuals in this group (the "captive rearing" group; Fig. 2) without having to sacrifice them. All remaining fish at Silverstream (13,709 fish, averaging 232 per family) were pooled, reared for a further three months in an external raceway, and released to sea on 31 July 1995 at an average weight (for both populations) of 94 g. These fish constituted the "1994 Silverstream release" (Fig. 2).

To replicate the Glenariffe and Silverstream release groups and to protect the experiment against the possibility of a weak return from the 1994 brood year, we initiated a partial repeat of the 1994 spawning program in autumn 1995. We used a full-sib mating design to create 12 families of Hakataramea origin (on 1 May 1995) and 13 of Glenariffe origin (on 3 May 1995), following the same protocols for collecting gam-

etes, incubation, initial rearing at Silverstream, marking with CWTs, and additional rearing at Glenariffe, as for the 1994 brood year Glenariffe release group. In July 1996, 15,753 (average 630 per family) of these fish were transferred back to Silverstream and released on 16 August. The remaining fish (68,547, averaging 2742 per family) were released from Glenariffe Stream on 20 August 1996. Average weight at release at both locations was 114 g (Glenariffe) and 101 g (Hakataramea). We refer to these groups as the "1995 Silverstream release" and the "1995 Glenariffe release," respectively.

Data Collection

Chinook salmon from all release groups that survived natural mortality matured and returned to fresh water in autumn 1996 to 1998, representing two, three, and four year olds from the 1994 brood, and two and three year olds from the 1995 brood. There is no marine commercial or recreational salmon fishery in New Zealand, but some returning fish were caught by anglers in the Rakaia, Waimakariri, and other east coast rivers. The remainder (all of which homed to their point

of release) were intercepted at the Glenariffe Stream and Silverstream counting fences. We used capture date as a measure of migration timing for angler-caught fish and date of arrival at the counting fence as a measure of date of entry to their respective spawning grounds. We also recorded the maturation state of fish returning to Glenariffe Stream in 1997 and 1998, judging them to be fully mature if they freely expressed milt or ova when squeezed gently around the vent. Fish that had not fully matured were marked with a unique external tag and transferred to a holding pond where they were inspected regularly, allowing their maturation date to be estimated with a temporal resolution of ± 3 days. After the fish were spawned, we recovered the CWTs and determined the family or population for all fish.

Fish from the captive group also matured from 1996 to 1998; most males matured in 1996 and 1997 and most females in 1997 and 1998. In early April, all fish were inspected and any maturing individuals (based on color and body form) were transferred to a holding pond. Almost all males were mature when first inspected, precluding an estimate of their maturation date. Females matured more gradually, over a period of six to eight weeks, allowing us to record maturation date (along with family and population identification) for 1028 individuals over three years.

Data Analysis

We analyzed family variation and inheritance of maturation timing of captive females and of return time, maturation time, and the interval between return and maturation for CWT males and females released from Glenariffe Stream. The latter dataset was constrained by variation in survival rates (thus the number of available fish) among families, so that some half-sib families were poorly represented. Restricted maximum likelihood (REML, vers. 7.5; SPSS, Inc., Chicago, IL) was used to obtain estimates of sire and dam variance components and their associated sampling errors for estimation of narrow-sense heritability (h^2). In all inheritance analyses only families for which half-sibs were available were considered. Variance components were estimated for captive females using two models, one in which the populations were analyzed separately and one in which population was added as a fixed factor (this model was also used to test for a population effect) for an additional level of nesting (containing sire and dam random effects). Each model contained a fixed factor for age of maturation; for separate populations:

$$T_{ijkl} = T_0 + \text{Age}_i + \text{Sire}_j + \text{Dam}_{k(j)} + \epsilon_{l(ijk)} \quad (1)$$

and for population as a factor:

$$T_{ijklm} = T_0 + \text{Age}_i + \text{Pop}_j + \text{Sire}_{k(j)} + \text{Dam}_{l(k(j))} + \epsilon_{m(ijkl)} \quad (2)$$

When estimating variance components for return timing, maturation timing, and delay period of released fish, sex was added as an additional fixed factor. However, because only fish from the Glenariffe population had family-specific CWTs for the 1994 Glenariffe release, population was dropped from the model. The most general model used for this analysis was:

$$T_{ijklm} = T_0 + \text{Age}_i + \text{Sex}_j + \text{Sire}_k + \text{Dam}_{l(k)} + \epsilon_{m(ijkl)} \quad (3)$$

Heritabilities were then estimated as four times the sire variance component divided by the total phenotypic variance and the associated standard errors were estimated using the techniques described in Becker (1984). A test for significant additive genetic effects (sire effect) was also performed (Lynch and Walsh 1998). Genetic correlations among traits were estimated by pairwise comparison of half-sib families using residuals from an analysis of variance (ANOVA) with age and sex as fixed effects. The significance of the correlations were inferred from the average P -values for the covariance of the traits across half-sibs (Lynch and Walsh 1998).

Because fewer families were represented from the 1994 Glenariffe population brood among the returns to Silverstream, a detailed estimate of the cross-environment correlation and/or genotype-by-environment interaction could not be made using half-sibs. However, we performed a regression of full-sib family values between release sites. This regression underestimates any cross-environment correlation, providing a conservative significance test for this effect (Lynch and Walsh 1998). Likewise, the slope and intercept of this relationship provide useful information regarding the nature of the environmental effect on the traits considered.

The study design also permitted a hierarchical analysis of the genetic and environmental influences on return and maturation timing for marked fish from the CWT groups returning to Glenariffe and Silverstream. The broadest experimental unit was the population, and we used ANOVA models to estimate population-level differences relative to return site, sex (a fixed factor known to influence timing; e.g. Quinn and Unwin 1993), and three additional secondary factors (related to annual variation) that might further influence timing. These factors were brood year (a random genetic effect), return year (a random environmental effect), and age at maturity (treated as a fixed effect). These factors were not all independent (any one of them is a simple linear function of the other two), so we focussed our analysis on identifying which factors were most useful for characterizing annual variation in timing between populations and release locations. We used means for each half-sib family (rather than data for individual fish nested within sires and dams) for these analyses, to avoid problems with missing data for families with low survival rates and to maintain consistency between the 1994 and 1995 brood years. Data for Hakataramea fish in the 1994 Glenariffe release (which were tagged to population level only) were included by treating the two replicate CWT groups as surrogate "families" (a conservative measure because degrees of freedom are much smaller than for the actual number of families). Although mean release weight differed between release groups, we did not include it as a factor that might have influenced migration and maturation timing because our study was not designed to measure any such effects independently of brood year and location. However, preliminary analysis of return and maturation timing for the 1994 Glenariffe release showed no evidence of a correlation between either timing index and mean family weight at release ($P > 0.15$ in both cases).

To assess their influences on migration timing (T), we used

ANOVA models including population of origin (P), return site (S), sex, and one additional factor (F , representing either year of return, brood year, or age at return), of the form

$$T_{ijklm} = T_0 + P_i + S_j + \text{Sex}_k + F_l + (P \times S)_{ij} + (P \times F)_{il} + (S \times F)_{jl} + \epsilon_{ijklm} \quad (4)$$

to determine whether significant ($P < 0.1$) secondary or interaction effects were present. For analysis of maturation date, only fish returning to Glenariffe were considered in a reduced model. Given the number of possible combinations of secondary effects, we did not consider all interactions but focussed our analysis on testing our primary hypotheses concerning variation between populations and between return sites. We then reestimated each model after deleting any non-significant interactions (pooling these into the error term ϵ), so as to isolate the main effects and interactions. We exhibited results for each model in terms of multiple r (as an index of goodness of fit), along with significance levels for each effect (adjusted as necessary for fixed and random effects), and the magnitude of all main effects based on comparisons of marginal means. For females from the 1994 brood year families, we also compared maturation date (using family means) between populations (for the captive group) and between families of Glenariffe origin (for the captive and CWT groups).

RESULTS

A total of 190 tagged adult chinook with a known date of capture were recovered from the sports fishery between 1996 and 1998. Most were caught in the Waimakariri and Rakaia Rivers, but 36 fish (all from Glenariffe releases) were caught in four other rivers from the Rangitata River to the Waiau River (Fig. 1). Mean migration date did not differ for strays and fish released and recaptured in the same river (t -test, $P = 0.57$). For all rivers, return years, and brood years combined, date of capture ranged 5.5 months, from 14 November (late spring) to 29 April (late autumn). Date of return (arrival at the counting fence) was recorded for 450 fish at Glenariffe Stream (Glenariffe origin: 375, Hakataramea origin: 75), and 311 fish at Silverstream (Glenariffe origin: 148, Hakataramea origin: 163). The most abundant age classes were two-year-old fish (predominantly males) from the 1994 and 1995 brood years, returning in 1996 and 1997 respectively, and three-year-old fish from the 1994 brood. Date of maturation was recorded for 347 chinook returning to Glenariffe Stream in 1997 and 1998 (292 of Glenariffe and 55 of Hakataramea origin; 164 females and 183 males) and for 160 fish returning to Silverstream (77 of Glenariffe and 83 of Hakataramea origin; 85 females and 75 males). We recorded date of maturation for 1028 captive females (532 fish of Glenariffe and 496 of Hakataramea origin). Most captive females (698) matured in 1997 at age 3, but 325 matured at age 4, and five matured at age 2. The number of females per family averaged 18 and ranged from seven to 29.

Inheritance of Return and Maturation Timing

There were significant additive genetic (sire) effects on timing of return and maturation for released fish ($P = 0.001$ and $P = 0.02$, respectively), as illustrated by the significant

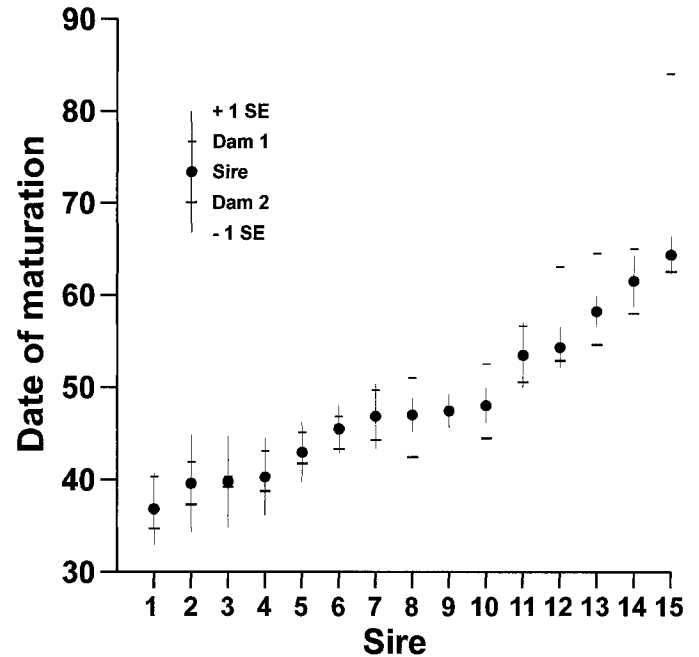


Fig. 3. Sire influence on maturation date (days since 1 March) for 1994 brood year coded-wire tagged chinook salmon returning to Glenariffe Stream. The figure shows mean maturation date ± 1 SE with mean maturation date for each dam (i.e., half-sib family). Sires have been arbitrarily ordered by maturation date to aid comparison of variation among and within families.

association of families with the same sire (Fig. 3). The estimated heritability (controlling for age and sex, ± 1 SE) was 1.26 ± 0.40 . Similarly, the heritability for timing of maturation of released fish of Glenariffe origin was estimated at 1.06 ± 0.42 . The delay period between dates of return and maturation had a lower but still significant heritability (0.67 ± 0.31 ; sire effect $P = 0.002$).

For captive females inheritance of maturation timing (controlling for age) was also high. There was a very strong association between half-sib families (Fig. 4); both Hakataramea and Glenariffe families showed strong additive genetic effects ($P \leq 0.002$ in both cases). Heritability estimates for maturation times of captive females were 1.28 ± 0.43 for Glenariffe females and 0.82 ± 0.34 for Hakataramea females based on 14 half-sib families per population. The combined estimate for the two populations was 1.08 ± 0.28 ; sire effect $P < 0.001$.

For the 1994 brood CWT Glenariffe fish there was a large, positive, genetic correlation (controlling for age and sex) between timing of return and maturation ($r_G = 0.92$, $P \leq 0.035$). Delay period (the interval between return and maturation) showed a negative genetic correlation with return date ($r_G = -0.85$, $P \leq 0.044$) and a negative correlation with maturation date ($r_G = -0.59$, $P \leq 0.365$), indicating that later return or maturation were associated with less time between return and maturation. The cross-environment regressions (Glenariffe = x , Silverstream = y) for full-sib families (controlling for age and sex) were positive and significant for return day ($y = 0.524x + 30.19$, $P < 0.001$) and maturation day ($y = 0.853x + 17.29$, $P = 0.041$) but not for delay period ($y = -0.562x + 9.78$, $P = 0.79$).

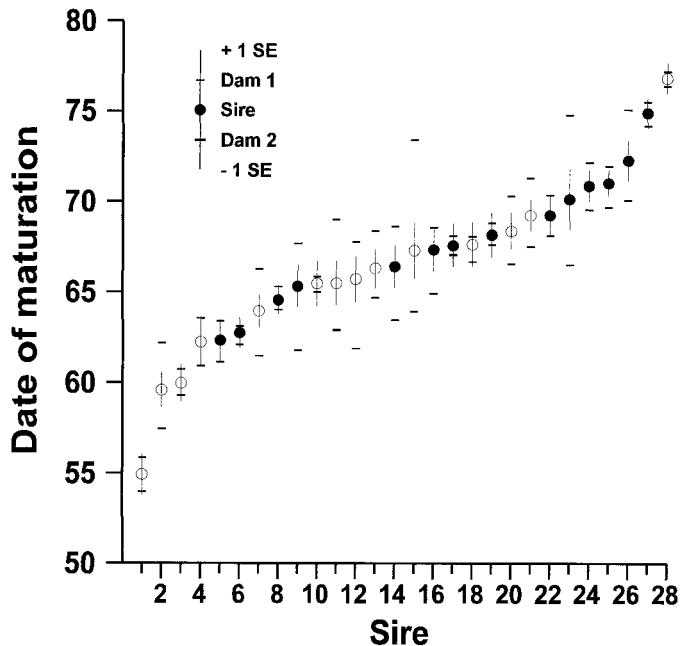


FIG. 4. Influence of sire and population on maturation date (days since 1 March) for female chinook salmon of Glenariffe Stream (○) and Hakataramea River (●) origin reared to maturity in fresh water. For each sire, the figure shows mean maturation date \pm 1 SE, together with mean maturation date for each dam (i.e., half-sib family). Sires have been arbitrarily ordered by maturation date to aid comparison of variation among and within families and populations.

Upriver Migration

Mean date of capture by anglers for fish of Glenariffe origin was 10 days earlier than for fish of Hakataramea origin (12 February; $N = 136$ vs. 22 February; $N = 54$; t -test, $P = 0.04$; Fig. 5a), and did not differ for fish (from both populations combined) returning to the two release locations (Waimakariri River: 19 February, $N = 113$; Rakaia River: 10 February, $N = 41$, t -test, $P = 0.13$). This trend persisted when effects taking annual variation into account were included, although at slightly reduced levels of significance. Two factor ANOVAs including population and either year of return, brood year, or age at return, indicated population effects ranging from 9.4 days to 10.1 days ($0.044 < P < 0.086$), but no consistent differences related to annual variation, brood year, or age at return ($0.06 < P < 0.83$). For fish from the Silverstream release groups taken in the sports fishery in the lower Waimakariri River (which provide a measure of migration date unconfounded by any possible factors associated with straying to other rivers), mean capture date for fish of Glenariffe origin was seven days earlier than for Hakataramea fish (Glenariffe: 17 February, $N = 66$; Hakataramea: 24 February, $N = 47$; t -test, $P = 0.19$), which is consistent with the general trend. Only two tagged fish of Hakataramea origin were caught by anglers in the Rakaia River, thus precluding analysis of capture date by population at this location.

Spawning Ground Entry

With annual variation and point-of-return effects accounted for as in model 1 (Table 1), mean date of entry differed

consistently between the two study populations and between sexes. Fish of Glenariffe origin preceded those of Hakataramea origin by an average of 4.6 days ($P = 0.004$), and males preceded females by 3.9 days ($P = 0.010$). There was no evidence of interaction between population of origin and point of return ($P > 0.47$ in all models), so this effect was dropped. Addition of age or brood year to model 1 did not improve the fit to the data; neither effect was significant ($P > 0.84$ in both cases), and did not reduce residual variation enough to justify the lost degrees of freedom.

Mean date of entry for fish returning to Glenariffe and Silverstream varied by up to 10 days (18 to 28 April) among the various release groups (Tables 1 and 2). Annual variation was most readily described in terms of year of return (model 1; $r = 0.487$), rather than age at return (model 2; $r = 0.373$) or brood year (model 3; $r = 0.332$). Results for model 1 suggested that date of return did not differ consistently between Glenariffe and Silverstream ($P = 0.53$), but that there was a strong interaction ($P < 0.0001$) between point of return and year of return. Inspection of marginal means for this interaction showed that, compared to Silverstream, fish returned to Glenariffe 10.4 days later in 1996, 9.8 days earlier in 1997, and 3.7 days earlier in 1998.

To further characterize variation in date of return between the different populations and experimental groups, we tabulated mean date of entry for 14 groups of fish subdivided by year of return, brood year, sex, and point of return (Table 2). Fish of Glenariffe origin preceded those of Hakataramea origin for 12 of the 14 available subsets of data. Notwithstanding the small sample sizes for some groups, the appearance of the same trend (Glenariffe earlier than Hakataramea) for all but two groups is far beyond expectations based on chance and supports the conclusion that date of return was subject to a consistent population-level effect.

Maturation Date (Glenariffe Release Group)

A model including both age and year of return provided the best fit to the data (Table 3, model 4, $r = 0.729$) and indicated that maturation date was influenced by population of origin (Glenariffe preceded Hakataramea by 3.6 days; $P = 0.03$) and by sex (males preceded females by 8.6 days; $P < 0.0001$). Compared to date of entry, population effects associated with date of maturation were both smaller (in absolute terms) and weaker (in terms of statistical significance), although our power to detect such effects was limited by the absence of family-level data for the 1994 Hakataramea fish. However, mean maturation dates for specific year, age, and sex combinations (Table 4), were generally consistent with this trend, with fish of Glenariffe origin maturing earlier than those of Hakataramea origin for five of six paired comparisons.

Most chinook (72%) entered Glenariffe Stream before they were fully mature, as much as six to eight weeks in advance of spawning (Fig. 6). Males were more likely than females to be mature at the time of entry; 60% of males matured within five days of entry compared to 30% of females. Conversely, 40% of females did not mature until at least 15 days after entry to Glenariffe Stream, compared to 15% of males. Dates of maturation and entry were moderately correlated (r

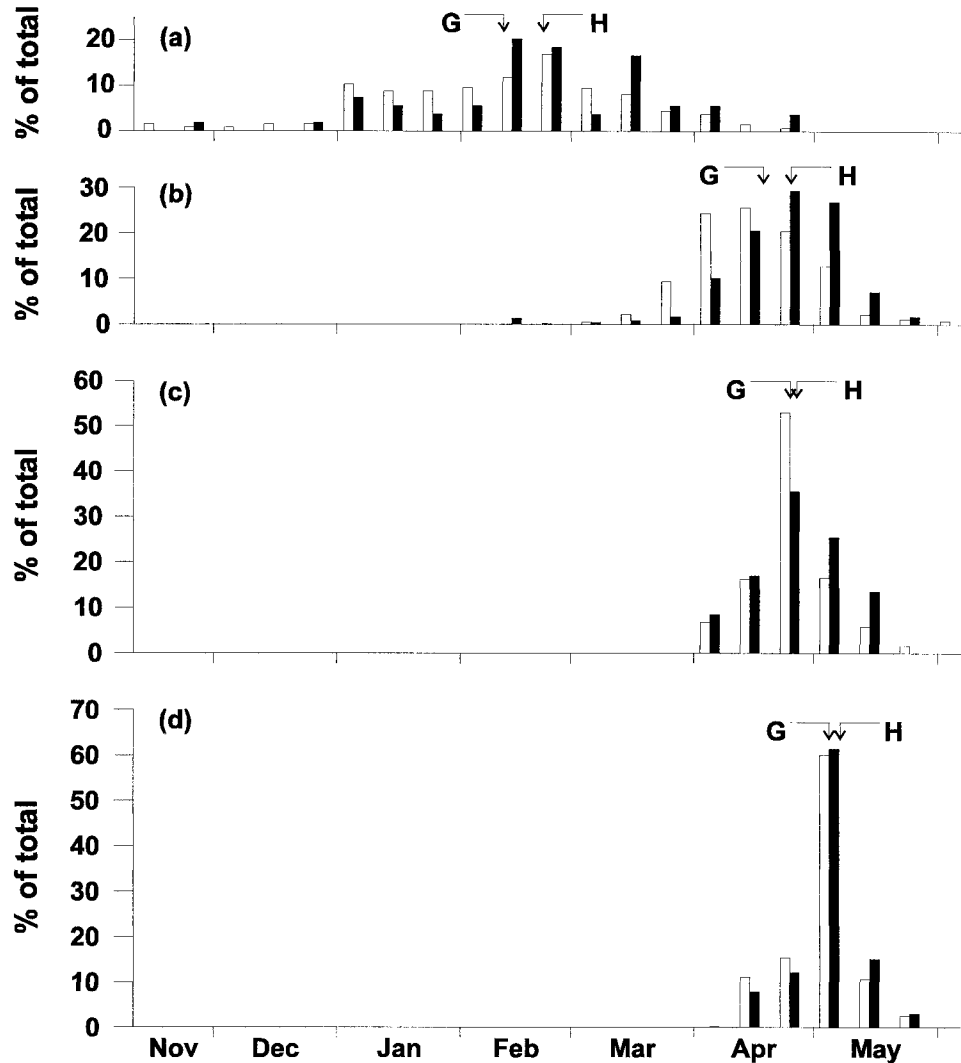


FIG. 5. Seasonal migration and maturation timing for 1994 and 1995 brood year adult chinook salmon of Glenariffe Stream origin (open bars) and Hakataramea River origin (solid bars), grouped over 10-day intervals from November to May. Successive histograms show (a) date of capture in the sports fishery; (b) date of entry to Glenariffe Stream or Silverstream; (c) date of maturation for fish returning to Glenariffe Stream; and (d) date of maturation for females from the captive group. Mean dates for each population are indicated by arrows.

= 0.54), as expected by the constraint that late entering fish cannot mature early in the season.

Maturation Date (Captive Females)

A two-factor ANOVA model of maturation date versus population, including age as the secondary effect, showed no evidence of an interaction between population and age ($P = 0.92$) and no variation among ages ($P = 0.09$). Glenariffe females matured an average of 2.8 days before Hakataramea females ($P = 0.006$; Fig. 5d). Mean maturation date for the captive females was 5.7 days later than for their female counterparts from the Glenariffe release group (two factor ANOVA of population and group effects, $P < 0.0001$). The significance of the population effect may have been inflated by using family means, a necessary limitation for comparing maturation dates between the captive and CWT groups. How-

ever, we were able to include sire and dam effects in a nested design for captive females. This showed significant differences among sires ($P < 0.001$), along with a 2.8-day difference between the two populations (Glenariffe preceding Hakataramea) but the decrease in degrees of freedom for the population effect (only 14 sires per population) reduced the significance of this effect to $P = 0.11$.

DISCUSSION

Evidence indicated that the timing of migration, maturation, and breeding of New Zealand chinook salmon have undergone genetic divergence in approximately 30 generations since their introduction, suggesting that these timing traits can evolve during the early periods of population evolution in the wild. Previous tagging (Unwin and Quinn 1993) and genetic studies (Quinn et al. 1996) suggested that phil-

TABLE 1. Significance of population of origin (Glenariffe [G] vs. Hakataramea [H]) and secondary effects (location, sex, year of return, age, and brood year) on mean date of entry to Glenariffe Stream and Silverstream Hatchery (S), for 80 families of coded-wire tagged chinook from the 1994 and 1995 broods, based on ANOVA models incorporating origin and the specified secondary effects. Interaction terms are shown only when significant ($P < 0.1$). Multiple r (goodness of fit) for each model is also shown, as are marginal means (days since 1 March) for all single-factor effects.

Model	Multiple r	Effect	Significance (P)	Effect means
1	0.486	Origin	0.003	G: 52.2 ± 0.9 H: 56.5 ± 1.3
		Location	0.85	G: 53.7 ± 1.2 S: 55.0 ± 1.1
		Sex	0.008	F: 56.3 ± 1.3 M: 52.4 ± 0.9
		Year	<0.0001	1996: 59.2 ± 1.7 1997: 49.8 ± 0.9 1998: 54.1 ± 1.5
		Location × year	<0.0001	
2	0.369	Origin	0.024	G: 51.3 ± 1.0 H: 58.1 ± 2.8
		Location	0.003	G: 52.4 ± 1.7 S: 57.0 ± 1.7
		Sex	0.024	F: 56.7 ± 1.8 M: 52.7 ± 1.6
		Age	0.16	2: 53.7 ± 1.5 3: 51.5 ± 1.1 4: 59.8 ± 4.2
		Origin × age	0.011	
3	0.329	Origin	0.004	G: 49.8 ± 1.0 H: 54.6 ± 1.3
		Location	0.33	G: 49.2 ± 1.2 S: 55.2 ± 1.1
		Sex	0.073	F: 53.5 ± 1.3 M: 50.8 ± 0.9
		Brood year	0.56	1994: 52.6 ± 0.9 1995: 51.7 ± 1.4
		Location × brood year	0.032	

opatry and population structuring are present among New Zealand chinook, although some straying and gene flow occur. The absolute magnitude of the genetic divergence, amounting to about a three- to five-day difference in maturation time for families collected at the same time from the two runs, is modest. However, the result is significant, given

the relatively small temporal and spatial (about 200 km) scales involved and the conservative experimental design (parents collected on the same day within both runs). The difference represents a divergence rate of 0.021 haldanes (average number of standard deviations per generation; 95% CI = 0.003–0.043 haldanes) for an estimated 26.2 generations

TABLE 2. Mean date of entry (days since 1 March ± 1 SE) to Glenariffe Stream (GA) and Silverstream Hatchery (SS) by year of return, age, and sex, for coded-wire tagged chinook of Glenariffe and Hakataramea origin from the 1994 and 1995 brood year experimental families. Sample sizes (number of families/number of fish) are in parentheses. The difference in mean entry date between the two populations (Hakataramea – Glenariffe) is also shown.

Year of return	Brood year	Age	Sex	Point of return	Population		Difference (days)
					Glenariffe	Hakataramea	
1996	1994	2	M	GA	60.7 ± 4.3 (17/38)	59.6 ± 4.4 (—/12)	–1.1
1996	1994	2	M	SS	52.5 ± 1.6 (17/29)	53.8 ± 1.3 (22/64)	1.3
1997	1994	3	F	GA	44.4 ± 1.8 (26/116)	52.4 ± 3.1 (—/13)	8.0
1997	1994	3	F	SS	55.4 ± 2.5 (21/52)	58.8 ± 2.6 (17/37)	3.4
1997	1994	3	M	GA	43.7 ± 2.2 (24/100)	46.3 ± 4.8 (—/10)	2.6
1997	1994	3	M	SS	41.9 ± 1.4 (8/10)	53.2 ± 2.1 (3/5)	11.3
1997	1995	2	M	GA	35.0 ± 2.2 (9/38)	43.7 ± 4.2 (9/18)	8.7
1997	1995	2	M	SS	53.3 ± 1.1 (12/42)	57.0 ± 2.3 (12/44)	3.7
1998	1994	4	F	SS	50.3 ± 8.8 (3/3)	72.0 (1/1)	21.7
1998	1994	4	M	GA	50.5 ± 2.8 (13/18)	59.5 ± 3.5 (—/2)	9.0
1998	1995	3	F	GA	52.9 ± 4.2 (7/22)	58.4 ± 4.4 (4/9)	5.5
1998	1995	3	F	SS	52.2 ± 4.2 (3/5)	70.5 ± 1.8 (3/4)	18.3
1998	1995	3	M	GA	43.1 ± 3.6 (7/16)	54.1 ± 6.2 (6/11)	11.0
1998	1995	3	M	SS	53.4 ± 9.9 (4/5)	50.5 ± 7.2 (4/4)	–2.9

TABLE 3. Significance of population of origin (Glenariffe [G] vs. Hakataramea [H]) and secondary effects (sex, year of return, age, and brood year) on mean date of maturation for 76 families of coded-wire tagged chinook from the 1994 and 1995 broods returning to Glenariffe Stream, based on ANOVA models incorporating origin and the specified secondary effects. Interaction terms are shown only when significant ($P < 0.1$). Multiple r and marginal means (days since 1 March) are shown as for Table 1.

Model	Multiple r	Effect	Significance (P)	Effect means
1	0.688	Origin	0.087	G: 57.1 \pm 0.7 H: 59.9 \pm 1.4
		Sex	<0.0001	F: 63.4 \pm 1.1 M: 53.5 \pm 0.9
		Year	<0.0001	1997: 54.9 \pm 1.0
				1998: 62.1 \pm 1.1
2	0.671	Origin	0.0005	G: 54.0 \pm 0.9 H: 60.2 \pm 1.5
		Sex	<0.0001	F: 61.4 \pm 1.3 M: 52.9 \pm 1.0
		Age	<0.0001	2: 50.7 \pm 1.9
				3: 59.6 \pm 1.0
4: 62.0 \pm 1.6				
G: 56.8 \pm 0.9 H: 59.5 \pm 1.7				
3	0.568	Sex	<0.0001	F: 63.5 \pm 1.3 M: 52.9 \pm 1.0
		Brood year	0.42	1994: 57.5 \pm 1.2 1995: 58.9 \pm 1.3
		Origin	0.033	G: 55.1 \pm 0.9 H: 58.8 \pm 1.5
4	0.729	Sex	<0.0001	F: 61.3 \pm 1.2 M: 52.7 \pm 0.9
		Year	<0.0001	1997: 53.3 \pm 1.2 1998: 60.6 \pm 1.2
		Age	0.002	2: 53.5 \pm 2.0
				3: 60.2 \pm 0.9 4: 57.2 \pm 1.8

of divergence. Confidence bounds for this estimate overlap with those observed for other phenotypic traits in New Zealand chinook salmon (e.g., juvenile growth: 0.036 haldanes, gonadosomatic index: 0.026 haldanes) and are consistent with rates for traits measured in other taxa over similar periods of divergence (for examples, see Hendry and Kinnison 1999). The temporal isolating effect of divergence in return and breeding time could create a feedback mechanism, with divergence resulting in lower reproductive success of strays and reduced gene flow (c.f., Tallman and Healey 1994), thus accelerating further divergence in breeding time and other characters (Rice and Hostert 1993).

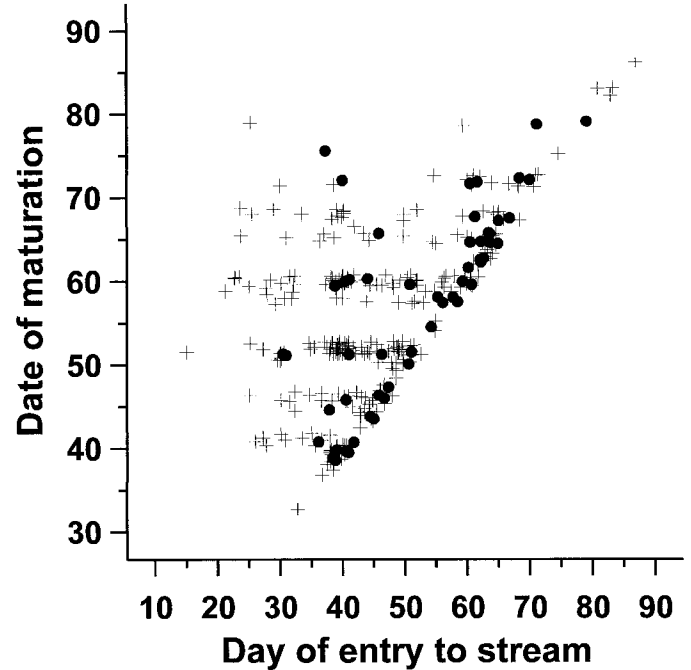


FIG. 6. Date of maturation versus date of entry to Glenariffe Stream (days from 1 March) for adult chinook salmon of Glenariffe Stream (+) and Hakataramea River (•) origin maturing in 1997 and 1998. The tendency for maturation dates to cluster in horizontal bands is an artifact of the weekly sampling protocol.

Glenariffe Stream chinook returned before Hakataramea River chinook in our experiment, based on angler catches and arrivals at the hatcheries, to a greater or lesser extent for all brood and return years at each site. This is consistent with Rakaia River salmon (including Glenariffe Stream) returning to fresh water nearly a month earlier than Waitaki River (chiefly Hakataramea River) chinook (Quinn and Unwin 1993). We have no way of knowing when the parental individuals returned (only when they matured and were spawned), but we assume they were representative of their populations with respect to migration and return date. In addition, Glenariffe fish consistently tended to mature earlier than Hakataramea fish under all levels of experimental control (kept in captivity vs. released to sea, returns to Glenariffe vs. returns to Silverstream, and two brood years). In the absence of counting facilities on the Hakataramea River spawning grounds, comparable to those on Glenariffe Stream, we

TABLE 4. Mean date of maturation (days since 1 March \pm 1 SE) by year of return, brood year, age, and sex, for coded-wire tagged chinook of Glenariffe and Hakataramea origin from the 1994 and 1995 experimental families returning to Glenariffe Stream. Sample sizes and the difference in mean entry date between the two populations (Hakataramea - Glenariffe) are shown as for Table 2.

Year of return	Brood year	Age	Sex	Population		Difference (days)
				Glenariffe	Hakataramea	
1997	1995	2	M	42.3 \pm 3.4 (7/21)	48.6 \pm 6.4 (8/14)	6.3
1997	1994	3	F	59.5 \pm 4.9 (25/101)	62.3 \pm 1.2 (—/13)	2.8
1998	1995	3	F	66.8 \pm 4.6 (7/21)	70.3 \pm 4.5 (4/7)	3.5
1997	1994	3	M	50.4 \pm 4.3 (23/92)	48.6 \pm 7.9 (—/8)	-1.8
1998	1995	3	M	57.4 \pm 9.2 (7/15)	60.9 \pm 10.5 (6/11)	3.5
1998	1994	4	F	62.0 \pm 8.3 (12/22)		
1998	1994	4	M	55.9 \pm 9.3 (12/17)	61.5 (1/2)	5.6

cannot present detailed estimates of phenotypic differences in natural timing of spawning for the two populations. Fortnightly aerial surveys of the Hakataramea River indicate considerable overlap with spawning dates in Glenariffe Stream, but local sources indicate a somewhat later date of peak spawning in the Hakataramea (M. Webb, Central South Island Fish and Game Region, pers. comm.). Such a later date is consistent with the relationship between river temperature (Hakataramea is warmer during spawning and incubation period; Kinnison et al. 1998a) and spawning date found for North American populations of *Oncorhynchus* (e.g., Brannon 1987) and thus with life-history predictions.

The Hakataramea parents were spawned one day earlier than Glenariffe fish in 1994 and two days earlier in 1995, so their offspring would be expected to spawn one to two days earlier if genetic differences alone controlled maturation timing. We infer that some environmental influences act counter to the genetic pattern of reproductive timing in the wild, resulting in hidden genetic variation (countergradient variation) among fish from different populations showing similar timing in the wild. Under natural conditions, the different genotypes of the two populations would interact with the different river-specific environmental conditions such as temperature and migration distance. If genetic and environmental effects are in some manner additive, then strays (adapted for spawning at a date appropriate to their natal system, but experiencing the environmental conditions of the nonnatal river) could mature at dates even more disparate than those observed under common rearing. The tendency for mean maturation date in our study to differ more under natural conditions (5.1 days) than under artificial hatchery conditions (2.8 days) is consistent with this hypothesis.

Our results clearly indicated genetic control over migration and maturation date in chinook salmon. Families returning early to Silverstream also tended to return early to Glenariffe, and offspring sired by the same male tended to return and mature on a similar date. In addition, there was evidence of genetic control over the interval between return and maturation. Heritability estimates greater than 1.0 generally reflect the imprecision of estimation methods, and indeed the confidence bounds for very high estimates in this study clearly overlap with 1.0. However, maturation in male salmon also extends over a longer time period than in females and is more difficult to pinpoint, so the males in the parental groups may have represented a wider range of maturation dates than the females. Thus, sire effects may have been larger than expected relative to dam variation in the offspring of half-sib matings, biasing heritabilities upward. Nonetheless, our evidence for very high heritabilities in these traits and for substantial genetic correlations among them is consistent with results for artificial selection on maturation date in *O. mykiss* (Ayerst 1977; Siitonen and Gall 1989) and with the high estimates for maturation timing in other salmonid species (Su et al. 1997; Smoker et al. 1998). Given the high heritabilities of these traits, divergence of the magnitude observed in this study would not be unexpected within 30 generations, given even modest selection differentials (for range of values in the wild, see Endler 1986).

Evolutionary theory suggests that divergence in breeding time and subsequent prezygotic isolation can evolve via plei-

otropy and/or genetic hitchhiking with other selected life-history traits, even in the presence of gene flow (Rice and Hostert 1993). Laboratory studies with the melon fly (*Bactrocera cucurbitae*) have shown that divergent selection enacted on developmental period, a life-history trait genetically correlated with breeding time, can result in the divergence of breeding time and an increase in prezygotic reproductive isolation (Miyatake and Shimizu 1999). Genetic correlation may also have played an important role in the divergence of New Zealand salmon populations. The positive genetic correlation between return date and maturation date and the negative correlation between return date and the delay until maturation indicate that these traits are not independent. Divergence in any one of these characters could therefore result from selection on another trait or from the combined effects of selection on the entire suite of characters. For example, selection for a shorter delay between spawning stream entry and maturation would tend to favor later returning fish and vice versa.

The analogy with the theory and results of Miyatake and Shimizu (1999) may be even more direct with regard to a possible role of juvenile development. Embryonic development rates for our two study populations, measured for the same families used in this study, showed no evidence of divergence (Kinnison et al. 1998a). Because we initiated these families from parents spawned at the same time in both populations, any influence of spawning date on development was removed and we ascertained that this trait shows little additive genetic variation ($h^2 = 0.05$ to 0.23 depending on temperature, $SE = 0.34$ for both cases; Kinnison et al. 1998a). In the wild, however, spawning date and thermal regimes vary and are the primary mechanisms controlling juvenile development and emergence (Brannon 1987; Tallman and Healey 1991). Thus juvenile development is almost certainly pleiotropically correlated with spawning time in New Zealand due to temporal developmental constraints, and breeding date would be expected to evolve due to selection on juveniles as well as adults.

We have no direct field evidence that salmon spawning on different dates experience different survival rates as adults or juveniles, but ecological processes related to survival of adults, embryos, and free-swimming juveniles might cause this to occur. Warmer temperatures, as might be experienced if adult salmon returned early, affect the efficiency of energy use prior to death and the rate at which senescence develops, which may in turn detrimentally influence nest (redd) preparation and defense (van den Berghe and Gross 1989). Second, embryo mortality is temperature related (Murray and McPhail 1988). Third, progeny of early-spawning fish or of fish spawning under warmer thermal regimes may emerge in spring prior to peak food availability and may face predators (Brännäs 1995). Conversely the progeny of late spawners or of fish spawning under cooler incubation conditions may spend a protracted period in development and, on emergence, be unable to compete for feeding territories with established, larger competitors (Rhodes and Quinn 1998), miss out on growth opportunities, and experience size-selective mortality (Quinn and Peterson 1996). Thus, there are a number of selective factors interacting with thermal regimes that may promote later spawning in the Hakataramea and/or earlier spawn-

ing in Glenariffe Stream, in a pattern consistent with that found among salmon populations in North America.

Although we believe that selection is the most likely explanation for divergence in timing between the New Zealand populations, other mechanisms may be responsible or have played an additional role. During the recent colonization of Glenariffe Stream, by what must have been genotypes derived either directly or indirectly from the Waitaki/Hakataramea system, a founder effect may have occurred. Likewise, if periods of demographically small population size existed in either system, random genetic drift may have shifted genotype frequencies. For these effects to obtain and persist, there must be some combination of small effective population size, little countervailing selection, and/or very restricted gene flow. Examination of DNA microsatellite variation suggests, however, that effective population sizes are fairly large (about 500 fish at present) and gene flow is relatively high (at least five to 10 individuals per generation) among the major river drainages (M. T. Kinnison, P. Bentzen, and M. J. Unwin, unpubl. data). This suggests that the influence of drift or founder effects would not persist. Nonetheless, drift-migration-selection equilibrium is by no means assured on such a short evolutionary time scale and the quantitative genetic characteristics of gene flow and random genetic processes are poorly defined (particularly for nonequilibrium conditions).

Environmental influences were detected in several ways. In general, fish held in captivity matured later in the season than the comparable group released to sea. In addition, return and maturation timing varied among return years and sites. For example, mean capture date by anglers in the Rakaia River was earlier (although not significantly so) than in the Waimakariri River. For the 1994 Glenariffe populations, most of which returned in 1996 and 1997, return and maturation date showed a positive cross-environment correlation among families, but varied less for returns to Silverstream than for returns to Glenariffe. A number of environmental factors, notably temperature, influence reproductive timing in fishes (Stacey 1984), and it is not clear when such factors might have influenced migration and maturation timing. Migration timing is affected by conditions at sea (Burgner 1980; Blackbourn 1987) and in rivers (Banks 1969; Jonsson 1991; Smith et al. 1994; Quinn and Adams 1996), but different study designs would have been required to differentiate between these influences.

The present results notwithstanding, the importance of reproductive timing in the development and maintenance of prezygotic isolation in the wild remains poorly understood. Although we present evidence that some of its component conditions can develop on short time scales, further studies of the process and its prevalence are clearly needed. The mechanisms leading to divergence of timing under high gene flow rates are unclear, but the work of Tallman and Healey (1994) indicated differential reproductive success of stray salmon. In addition to being important in the early stages of population differentiation, timing related traits may limit gene flow between wild and hatchery-produced populations of salmonids (Leider et al. 1984) or among natural populations and thus play a large role in the conservation of populations.

In summary, a strong genetic basis exists for the inheritance of return and maturation time in populations of chinook salmon introduced to New Zealand. When genotypes were sampled from these populations and compared under a range of common rearing and release conditions, strong evidence was found for the genetic divergence of these populations in the timing of their migration, spawning stream entry, and maturation. These differences were consistent with observed trends in the wild and are hypothesized to reflect adaptation to different spawning environments rather than genetic drift or founder effects. The differences were also consistent with the relationship between temperature and spawning time in natural populations of *Oncorhynchus* (Brannon 1987). Given that these differences arose within approximately 30 generations in the wild, this study presents evidence that populations can diverge in reproductive timing over short time frames. This has important implications for the evolution of locally adapted populations, because divergence in reproductive timing strengthens prezygotic isolation and thus affects rates of genetic and phenotypic divergence.

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