



Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process

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Key words: adaptation, contemporary evolution, divergence, introduced population, life history, phenotypic plasticity

Abstract

Chinook salmon, *Oncorhynchus tshawytscha*, from the Sacramento River, California, USA were introduced to New Zealand between 1901 and 1907, and colonized most of their present-day range within about 10 years. The New Zealand populations now vary in phenotypic traits typically used to differentiate salmon populations within their natural range: growth in freshwater and at sea, age at maturity, dates of return to fresh water and reproduction, morphology, and reproductive allocation. This paper reviews a large research program designed to determine the relative contributions of phenotypic plasticity and genetic adaptation to this variation, in an effort to understand the processes underlying the natural evolution of new populations. We found strong evidence of trait divergence between populations within at most 30 generations, particularly in freshwater growth rate, date of return, and reproductive output, with plausible adaptive bases for these differences. Importantly, we also demonstrated not only a genetic basis for post-release survival but higher survival, and hence fitness, of a population released from its established site compared to another population released from the same site. We conclude that divergence of salmon in different rivers probably resulted initially from phenotypic plasticity (e.g., habitat-specific growth rates, and effects of upriver migration on ovarian investment). Philopatry (homing to natal streams) combined with rapid evolution of distinct breeding periods to restrict gene flow, facilitating divergence in other traits. We also suggest that in addition to genetic divergence resulting from random founder effects, divergence may also arise during the very early stages of colonization when the original colonists are a non-random, pre-adapted subset of the source population. This 'favored founders effect' immediately improves the fitness of the new population. Overall, this research reveals the complex interplay of environmental and genetic controls over behavior, physiology and life history that characterize the early stages of population differentiation, a process that has taken place repeatedly during the history of salmon populations.

Introduction

For many years there has been interest in the chronology and mechanisms promoting divergence of populations within species, and the extent to which this divergence represents the early stages of speciation (see reviews in Hendry & Kinnison, 1999, 2001). Researchers have considered the process from various

perspectives, including examination of character displacement as evidence that divergence results from competition (Schluter, 2000), diversification resulting from variation in predation among isolated populations (e.g., three-spine sticklebacks *Gasterosteus aculeatus*: Reimchen, 1994; guppies *Poecilia reticulata*: Endler, 1995), and resource polymorphism in very simple communities with vacant niches (Smith

& Skúlason, 1996). Evolutionary biologists have also considered the processes by which populations diverge after colonization, using translocations of species as research opportunities (e.g., mosquitofish *Gambusia affinis*: Stearns, 1983a, b; guppies: Reznick, Bryga & Endler, 1990; *Anolis* lizards: Losos, Warheit & Schoener, 1997; Reznick et al., 1997). In many cases isolated populations were established by translocation rather than colonization, and few studies have considered evolution following colonization with persistent gene flow. To better understand the evolutionary processes associated with the formation of new populations, we conducted a complex study of chinook salmon in New Zealand (NZ) to investigate the pattern, rate and process of evolution among populations founded by straying from a single introduction site, with continuing genetic interactions.

An enormous body of research has been published on the genetics, ecology, and behavior of salmonid fishes (chiefly the genera *Oncorhynchus*, *Salmo*, and *Salvelinus*), revealing complex factors in the history of the evolution of populations. Salmonids in one river differ from those in other rivers in many traits and these differences typically have some genetic basis, as well as an obvious phenotypic component due to different rearing regimes (see reviews by Ricker, 1972; Taylor, 1991; Wood, 1995; Quinn, 1999). Homing to the natal stream leads to reproductive isolation, allowing genetic drift and the different regimes of selection on heritable traits to produce differentiation. Recognizing this differentiation, salmon management, and conservation is based on the 'distinctness' and 'evolutionary significance' of populations (Waples, 1995).

Studies of the phenotypic traits of salmon populations can document intra-specific differences but reveal little about the rate or process of evolution because the relevant time-scale is usually unknown. Most of the present range of these fishes has been repeatedly glaciated during the millions of years since speciation, most recently on the order of 5000–15,000 years ago (McPhail, 1996). They have thus colonized the myriad river systems of the north Atlantic and Pacific oceans relatively recently, and the process is still taking place in regions where glacial retreat creates new habitat (Milner et al., 2000). Controlled breeding and artificial selection studies can demonstrate the heritability of traits and the upper rates of response to selection (e.g., Siitonen & Gall, 1989; Winkelman & Peterson, 1994), but traits might not evolve as rapidly or in the same manner under natural conditions.

The importance of salmonids to commercial and recreational fisheries has motivated translocation efforts within and beyond their natural ranges since the middle of the 19th century, including many to the southern hemisphere where no salmonids were native (reviewed by McDowall, 1988). The responses of salmonid populations to translocation, and the patterns of population differentiation among native populations, present a paradox. Many phenotypic adaptations of populations, such as breeding date (Brannon, 1987), size, age, and morphology of mature individuals (Beacham & Murray, 1987; Blair, Rogers & Quinn, 1993; Roni & Quinn, 1995), egg size (Quinn, Hendry & Wetzel, 1995), disease resistance (Bower, Withler & Riddell, 1995), and juvenile behavior (Brannon, 1972; Quinn, 1980; Taylor, 1990a) and morphology (Taylor, 1990a) appear to be adaptations to freshwater environments. We would, therefore, expect translocated populations to fail to adapt to the new freshwater conditions. In contrast, salmon at sea feed rather opportunistically in broadly overlapping areas (Groot & Margolis, 1991), so one might expect that marine life would present few problems for new populations. However, freshwater (i.e., non-anadromous) populations have proven extremely easy to establish but translocations within or beyond the natural range of species have almost invariably failed to establish new anadromous populations (Withler, 1982; Fedorenko & Shepherd, 1986; Harache, 1992). The more complex anadromous life history seems to greatly increase the challenge faced by new populations, as they make the transitions to and from seawater.

Against these odds, chinook salmon, *O. tshawytscha*, were successfully transplanted from the Sacramento river system, California, to the South Island of NZ between 1901 and 1907 (McDowall, 1994). All evidence indicates that the source of the transplant was Battle Creek (McDowall, 1994; Quinn et al., 1996) but records were lost in a fire so some details are unknown. By 1915, salmon had colonized rivers to the north along the coast from the transplant site (the Hakataramea river, a tributary of the Waitaki river; Figure 1). Transplants to the Clutha river, to the south, established the only population that involved subsequent human intervention. Transplants to other rivers, notably on the west coast and northern part of the South Island, failed to establish self-sustaining populations. This situation is ideally suited for studying salmon evolution, and we posed the questions: do the salmon in NZ rivers differ in the kinds of traits that define populations in their native range and, if so, did the

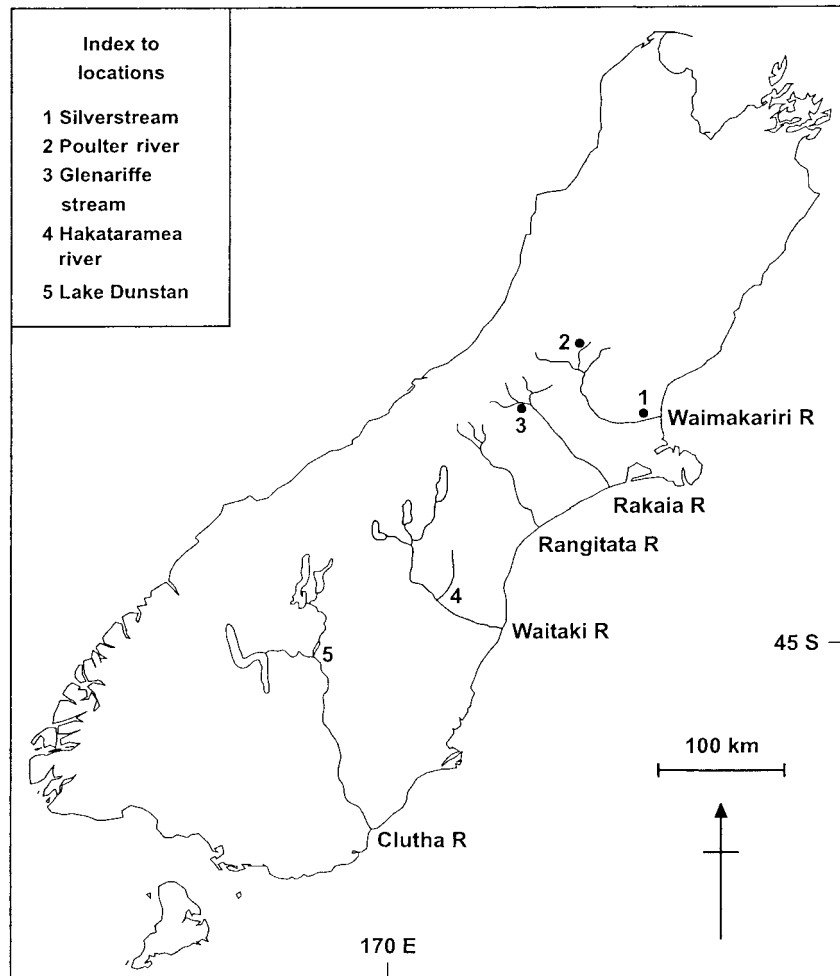


Figure 1. Map of the South Island of New Zealand showing the major salmon rivers and sites mentioned in the text.

differences result from rapid evolution or phenotypic plasticity?

In this paper we review a large, complex research program designed to study the pattern, rate, and process of population divergence in salmon, using the NZ chinook salmon as the focus. We provide some general background on the species and its habitats in NZ, summarize our approach and key results, discuss the results, and describe the process that we believe has taken place in NZ over the past 100 years, and which is likely to have taken place repeatedly as new salmon populations became established within their natural range.

Chinook salmon and their habitats in New Zealand

Healey (1991) reviewed the basic biology of chinook salmon. Briefly, spawning populations are broadly

distributed along the Pacific coasts of North America and Asia. Adults leave the ocean and enter fresh water from spring through fall but typically spawn in fall. As in other salmonids, females select, prepare and guard nest sites and males compete for access to ripe females. The eggs (which are very large for teleost fishes) are fertilized and buried in gravel-bedded streams where they develop during the winter. The hatchlings, termed alevins, remain buried until their yolk sac is absorbed and they emerge in spring. In slow-growth environments (e.g., northern latitudes and higher elevations) the juveniles tend to remain in streams, feeding chiefly on insects, for 1 year prior to seaward migration in spring. At lower elevations and in southern areas juveniles tend to migrate to sea in their first year of life, from spring through early fall, often feeding in estuaries for weeks or months before entering the ocean. These life history variants

are termed stream-type and ocean-type, respectively (Taylor, 1990b; Healey, 1991). Both forms are characteristically anadromous, though some males from stream-type populations mature in fresh water without going to sea. Chinook salmon attain the largest size among salmon and spend 1–5 years at sea (Roni & Quinn, 1995) before returning to fresh water where they spawn in medium to large rivers, displaying a high degree of philopatry. Populations migrating into the continental interior (typically stream-type as juveniles) often do so in spring or summer, whereas ocean-type populations typically spawn nearer the coast and enter in fall.

The rivers supporting most NZ chinook salmon (Waitaki, Rangitata, Rakaia, and Waimakariri) are primarily fed by snow and ice melt from the Southern Alps flowing east to the South Pacific Ocean. Floods from heavy rainfall can occur at any time of year, but peak flows tend to occur in spring and low flows in winter. The rivers have unstable, braided, gravel-rich beds as they flow down U-shaped valleys often more than a kilometer wide. Our research program focused on tributaries of two of these rivers, the Waitaki (mean discharge: $350\text{ m}^3\text{ s}^{-1}$) and Rakaia ($196\text{ m}^3\text{ s}^{-1}$). In the Waitaki system, salmon spawn in the margins of the river below an impassable dam (built in 1932) and in the Hakataramea river, which enters 60 km from the mouth at 200 m elevation. In the Rakaia river, most salmon spawn in stable streams fed by groundwater in the upper catchment's flood plain (river km 90–120), including the study site, Glenariffe stream (river km 100, elevation 430 m) and the nearby Hydra waters. We also conducted experiments on chinook salmon from the Poulter river, a 30 km long rain- and snow-fed river flowing into the upper Waimakariri river 95 km above the mouth at an elevation of 600 m (Figure 1). None of the NZ rivers producing chinook salmon have estuaries, a marked difference from the Sacramento river. Battle Creek enters the Sacramento river at river km 418, at 106 m above sea level with a mean annual discharge of $13.5\text{ m}^3\text{ s}^{-1}$. The Sacramento is largely unbraided, heavily modified by human activities, and flows into the very large estuarine San Francisco Bay.

Methodological approaches

In 1992 we began the first phase of our program, to identify phenotypic differences among salmon from several NZ rivers and to evaluate the degree of philo-

patry (i.e., homing) in NZ salmon. Our initial approach in both efforts was to examine archival datasets on life history traits and tagging studies. Data had been collected on the life history traits of chinook salmon for many years prior to our investigations but not for the purpose of examining population-specific traits or the rate of evolution. We found data on two age-related traits (the proportion of adults with ocean-type and stream-type juvenile life histories, and the number of years spent at sea prior to maturity), three size-related traits (length at age, weight at length, and fecundity at length), and two behavioral traits (timing of entry into fresh water by maturing adults and the timing of spawning). These data revealed differences between at least some populations in all traits (Quinn & Unwin, 1993), justifying further research.

Straying was an essential part of the initial spread of salmon in NZ and is a contemporary source of gene flow so we wanted to learn about this trait in the NZ fish. Patterns of homing and straying were inferred from releases of smolts from Glenariffe Stream that were marked with coded-wire micro-tags injected into the nasal cartilage. Tags were coded with population and year and individuals possessing them were identifiable because their adipose fin was clipped prior to release. Salmon homing to Glenariffe Stream at maturity were recovered at a permanent weir; strays were recovered in other parts of the Rakaia River system and in the other rivers of the South Island during spawning ground surveys or from fishermen (Unwin & Quinn, 1993). Levels of straying varied with date of release from the hatchery but releases at about the time when migration of ocean-type chinook would naturally occur produced 4.2% strays.

In 1994 we initiated the second phase of the program: dedicated sampling to augment the 'archival' dataset. We standardized and coordinated measurements to avoid problems with data collected by different researchers in different years. Specifically, we sampled adults from the Hakataramea River (henceforth 'Haka') and Glenariffe Stream ('GA') that were the parental generation for controlled breeding and rearing studies initiated in 1994 and 1995. These salmon were caught at weirs to minimize bias with respect to size and age of the fish and were measured by the same people. We also obtained data from NZ angler competitions, held in rivers, from 1984 to 1995. These fish were weighed and measured in a standard manner, largely by the same person. There is no directed salmon fishing at sea so the age and size distribution of salmon entering the rivers represents

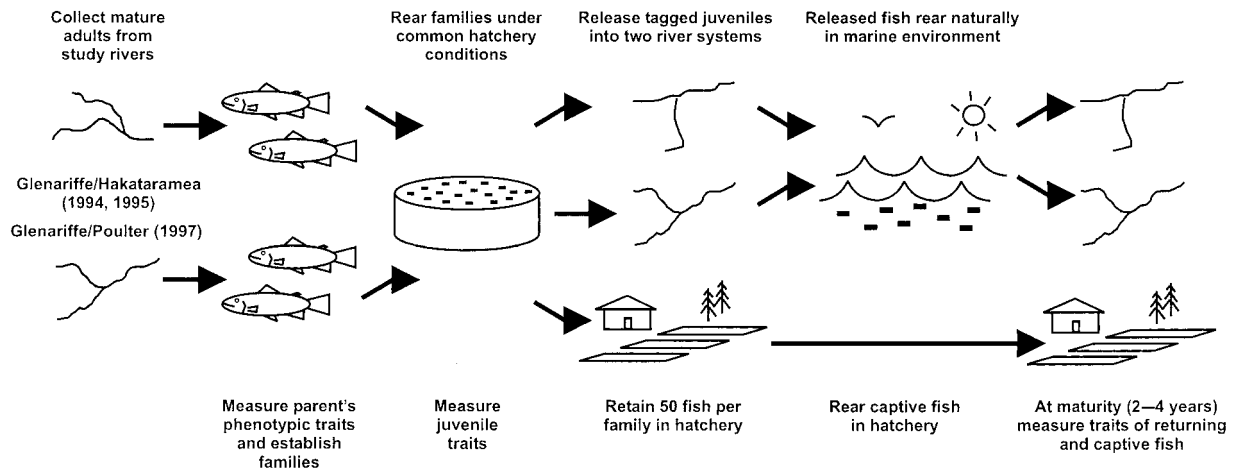


Figure 2. Diagrammatic description of the experimental design for comparing the phenotypic and genotypic traits of New Zealand chinook salmon populations.

their true distributions, without the biases introduced by size- or age-selective fisheries that would confound such a study in North America. Mature and maturing fish (from the fishing competitions) were measured for a suite of morphological features; gonad weight, average egg weight, and egg number were determined for each female. Similar size, shape and gonad measurements were taken in 1994 and 1995 on adult salmon from the Coleman National Fish Hatchery in California, where the Battle Creek population is propagated (Kinnison et al., 1998a).

After the measurements on adults in 1994, we initiated the third and largest phase of the research program, a controlled breeding and rearing study to reveal the blend of environmental and genetic factors shaping trait variation in NZ (Figure 2). This work consisted of two primary elements: a large, multi-year controlled breeding, rearing and release experiment, and a detailed examination of the genetic history and current structure of the populations based on analysis of neutral molecular variation. The controlled breeding, rearing and release experiments, referred to hereafter as the 'experimental program', consisted of comparisons of Haka and GA salmon under 'common garden' conditions, analysis of additive genetic variance/covariance of traits, and comparisons of representatives from the same families released to the ocean from two different river systems (Figure 2). These studies allowed detailed investigation of the genetic and environmental factors shaping trait variation in NZ salmon.

We chose a conservative design for the experimental program. GA and Haka fish were spawned

on consecutive dates and virtually all parents were age 3 ocean-type fish. The similarity in phenotype between the experimental populations' founders was our effort to minimize differences in progeny that might arise from maternal effects or traits that were heritable but did not differ between populations. Salmonid fishes show many interconnected life history traits (Figure 3). For example, differences in spawning date or female size (affecting egg size) between the founders would have created differences in fry size at emergence, which might have influenced growth when reared together. The resultant size differences would have affected seawater tolerance, post-release survival and maturity schedule.

In 1994 we established 72 experimental families by spawning salmon from the two study populations (Figure 2). Milt from each male fertilized egg from two females from its own population, creating 32 full-sib Haka families nested within 16 half-sib families, and 40 full-sib GA families nested within 20 half-sib families. The Haka population was represented by fewer progeny per family than GA because we were not permitted to take all the eggs from each female. All fish were initially incubated and reared at the Silverstream Research Station, on a tributary of the lower Waimakariri river (Figure 1). As they grew and rearing facilities became more limited the number of families was reduced to 28 per population.

We recorded embryo development rates (Kinnison et al., 1998b), growth rates, and seawater tolerance (Kinnison, Unwin & Quinn, 1998) among families and between the populations. Representatives of both populations and all families were reared in fresh wa-

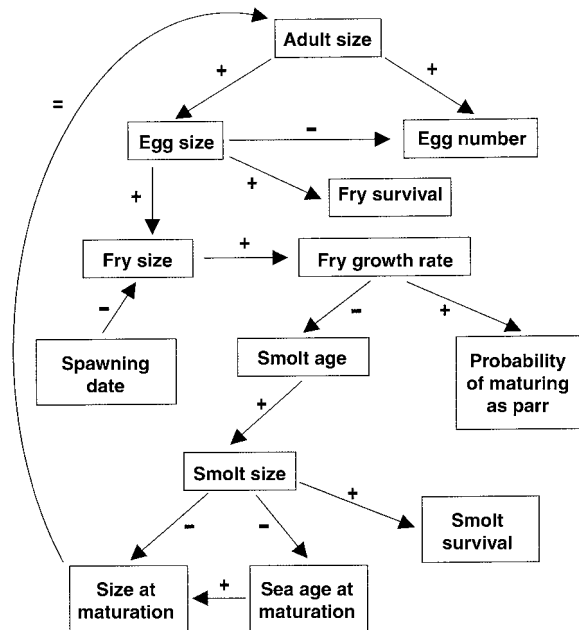


Figure 3. Diagrammatic description of connections among life history traits observed or hypothesized in salmonid fishes, with special reference to chinook salmon. Arrows indicate the direction of control and signs indicate the nature of the influence. For example, female size has a positive influence on egg size and egg number (i.e., larger females tend to have larger and more numerous eggs) but egg size and egg number are negatively correlated with each other. Smolt size has a negative influence on size at maturity (i.e., larger smolts tend to mature at a younger age than smaller smolts). Modified from Marschall et al. (1998).

ter, marked with coded-wire tags to the family level (except Haka fry spawned in 1994 which were tagged to the population level), and then released to sea from two different hatcheries, one at Glenariffe and the other at Silverstream, in July 1995 (Figure 2). This reduced the risk of ambiguous results because of poor returns to one site, and also provided a valuable environmental contrast. Silverstream is very close to the ocean at low elevation (17 m) whereas Glenariffe is farther inland and at higher elevation. Migration to Glenariffe might require more time and energy, affecting expression of other traits. We also reared representatives of all families (50 fish per family) to maturity under common, controlled conditions in fresh water at Glenariffe. These salmon received passive integrated transponder (PIT) tags, allowing us to repeatedly measure individuals and to relate patterns of maturity to growth trajectories (Kinnison, Unwin & Quinn, 1998; Unwin, Kinnison & Quinn, 1999). When adults from the three groups returned or matured we measured egg weight, egg number, age, length, weight,

morphology, date of return, date of maturation, and tissue energy reserves.

To estimate the level of interannual variation in phenotypic traits and to further guard against the possibility of poor marine survival for the 1994 brood, we repeated the spawning program in fall 1995 with a reduced design. Full-sib matings created 12 Haka and 13 GA families on 1 and 3 May, respectively, following the protocols of the 1994 brood year Glenariffe release group, including releases from Silverstream and Glenariffe.

The GA–Haka comparison was designed to minimize the effects of spawning date on subsequent trait variation. However, in 1997 we initiated another comparison, between GA salmon and ones from the Poulter River ('PR') in the Waimakariri River system (Figure 1; Unwin et al., 2000) that, in addition to investigating population divergence, sought to investigate the implications of spawning date. Stream surveys indicate that most spawning in the Poulter River is in late May, 3–4 weeks later than in Glenariffe Stream. The Poulter River is also substantially colder than Glenariffe during the summer growing season and scale analyses indicate that stream-type fish made up 89 out of 92 (95%) of the PR spawners examined prior to this study (Unwin et al., 2000). This contrast thus offered an opportunity to consider both (1) the influence of spawning date on traits (a factor removed in our previous comparison), and (2) systems where extreme differences in life history patterns suggested substantial divergence. In fall 1997 we established two groups of full-sib families from each population over three dates in total, representing peak spawning for GA (1 May), late spawning for GA and peak spawning for PR (18 May), and late spawning for PR (29 May). Husbandry procedures during incubation largely followed those described above and mean weights were measured for each family in November 1997 and at approximately 6-week intervals thereafter until 5 March 1998.

Our final approach in the study was to consider the genetic history and population structure of the NZ salmon using a suite of variable genetic markers including polymorphic proteins and mitochondrial DNA (Quinn et al., 1996) and nuclear DNA microsatellites (Kinnison, 1999). These analyses included comparisons with populations from the Sacramento river system to consider possible founder and bottleneck events, detect recently evolved population structure, and estimate population size and structure. Juvenile salmon were collected from the Waima-

Table 1. Fork length at seawater entry (in millimeter, ± 1 SE, back-calculated from scale radius measurements of adults) of Rakaia and Waitaki chinook salmon, by juvenile life history type and number of years spent at sea

| Life history | Sea age | Fork length (mm) | | Percentage of the population | |
|--------------|---------|------------------|-----------------|------------------------------|---------|
| | | Rakaia | Waitaki | Rakaia | Waitaki |
| Ocean-type | 2 | 85.5 \pm 1.3 | 66.2 \pm 3.1 | 17.9 | 3.0 |
| | 3 | 80.6 \pm 0.5 | 69.3 \pm 0.8 | 73.3 | 79.2 |
| | 4 | 80.2 \pm 1.6 | 70.8 \pm 1.7 | 8.8 | 17.8 |
| Total | | <i>N</i> = 637 | <i>N</i> = 202 | 60.1 | 43.6 |
| Stream-type | 1 | 105.4 \pm 3.9 | 101.6 \pm 4.9 | 3.5 | 3.4 |
| | 2 | 100.4 \pm 1.1 | 91.5 \pm 1.5 | 65.0 | 44.8 |
| | 3 | 105.4 \pm 1.4 | 94.6 \pm 1.4 | 31.0 | 51.3 |
| | 4 | 108.8 \pm 1.0 | 99.9 | 0.5 | 0.4 |
| Total | | <i>N</i> = 423 | <i>N</i> = 261 | 39.9 | 56.4 |

The percentage of each population and life history type composed of those age groups is also presented. Note that ocean-type fish made up a larger proportion of the Rakaia than the Waitaki population, that Rakaia river salmon of both life history types were larger when they went to sea, and that the Waitaki river fish spent more time at sea.

kariri, Rakaia, and Waitaki rivers and landlocked adults were sampled from Lake Dunstan, an impoundment in the upper Clutha river formed in 1992. These samples were the basis for comparisons within NZ at 24 polymorphic protein-coding loci, and for comparison with published allelic data on Sacramento river populations. In addition, 172 individuals were examined for mtDNA sequence frequencies and were compared with mtDNA variation from Sacramento river samples. Finally, 11 microsatellite loci were amplified from the initial set of NZ samples (excluding the landlocked fish), supplemented with additional samples from the mainstems and tributaries of the Waimakariri, Rakaia, and Waitaki river systems in 1997 and 1998. These samples allowed us to consider temporal variation in population structure within NZ, estimate effective population sizes within drainages and simulate the effective numbers of migrants.

Patterns of divergence

Phenotypic comparisons of wild salmon

Analysis of archival data (Quinn & Bloomberg, 1992; Quinn & Unwin, 1993) revealed significant differences in all traits measured, and standardized comparisons of fish collected in 1994 and 1995 to initiate the experimental program supported these findings.

Scale pattern analyses indicated that the populations were mixtures of stream-type and ocean-type juveniles, with an overall modal age of 3, but that age at seawater entry and maturation varied significantly among years and rivers. The length of time spent in fresh water and at sea were linked; fish going to sea in their first year of life (ocean-type) were smaller at seawater entry than stream-type fish (Unwin & Lucas, 1993), and tended to compensate for this by spending an extra year at sea before maturing (Table 1). For example, most ocean-type fish spent 3 years at sea, whereas stream-type fish often spent only 2 years at sea and rarely remained for more than 3 years. Length at seawater entry differed between populations, Rakaia fry of both life history types being about 10–15 mm larger than Waitaki fry, and this was apparently connected to the difference in years at sea between the populations (Table 1).

We documented significant differences among rivers in size at age within sexes. Waitaki river fish (largely the Haka spawning population) were old, long for their age, and also heavy for their length compared to most other populations (Quinn & Unwin, 1993; Kinnison et al., 1998a). However, as with the patterns in age at maturity, the populations varied in growth among years. For example, age 3 ocean-type fish of Rakaia and Waitaki origin varied approximately four times more in mean length among years (c. 100 mm) than the mean difference between the two populations (c. 24 mm, $p = 0.002$; Figure 4). The

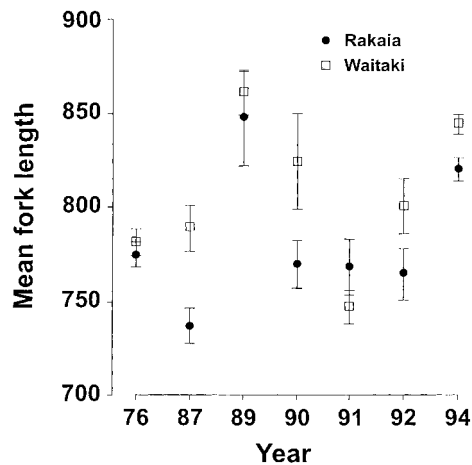


Figure 4. Average fork length of age-3 ocean-type chinook salmon from the Rakaia and Waitaki rivers. Note both the inter-annual variation and the larger size of the Waitaki river fish.

environmental contribution to size at age was also evident from the strong correlation ($r = 0.76$) between mean lengths of Waitaki and Rakaia angler-caught fish over 7 years of common record. The two NZ populations differed in morphology (involving primarily fin and tail dimensions) and in weight at a given length (Kinnison et al., 1998a). Fecundity data were available for only two populations in the archival dataset (Quinn & Bloomberg, 1992) but they indicated that Haka females had fewer eggs for a given size than GA females. More extensive data collected in 1994 and 1995 revealed that Haka females had larger ovaries and eggs but did not differ from GA females in fecundity at a standard length (Table 2).

Among the most dramatic inter-population differences were patterns of entry into fresh water from the ocean, inferred from catches by anglers in the lower portions of the rivers (Figure 5). Anglers are certainly imperfect samplers but chinook salmon are sufficiently prized that catches broadly reflect periods of availability. Median date of capture varied by nearly 7 weeks, ranging from 20 January in the Rangitata river to 8 March in the Waitaki river (Figure 5; see also Quinn & Unwin, 1993).

Taken together, the results clearly indicated that chinook salmon in the major NZ rivers differ in a suite of inter-related life history traits (Figure 3), despite environmental influences. The NZ salmon differed to an even greater degree from the Battle Creek population in most traits. For example, NZ salmon tended to be longer for their age than Battle Creek salmon (Kinnison et al., 1998a), but Battle Creek females had

a larger investment in gonads (with a smaller number of large eggs) than the NZ females (Kinnison et al., 1998b). We found the evidence of phenotypic divergence in NZ salmon, and other studies (e.g., Lake Washington sockeye salmon, Hendry & Quinn, 1997; see also Hendry, 2001), compelling enough to warrant a large-scale controlled breeding, rearing and release program to determine the genetic (and environmental) basis of divergence among the NZ populations.

Experimental breeding, rearing, and release program

Developmental rate and growth

Detailed measurements of temperature-specific rate and pattern of embryonic development revealed no differences between the GA and Haka populations (Kinnison et al., 1998b). The number of degree-days to hatching did not differ between populations at the ambient incubation temperature (mean = 480.3 for both populations; Table 2) or in colder water (Haka = 487 and GA = 490 degree days). At hatching, Haka alevins had more yolk and were heavier than GA alevins through the fry stage because they were produced from larger eggs. Haka alevins grew somewhat faster ($p = 0.055$), consistent with larger yolks, but yolk conversion efficiencies did not differ between any of the consecutive collections or over the entire collection period ($p > 0.05$ in all cases; Table 2). Consistent with these results, we found no differences between incubation rates of GA and PR embryos (Unwin et al., 2000).

GA fry were initially smaller than Haka fry (1.01 v.s. 1.19 g, $p < 0.001$) but over time differences in mean weights largely disappeared (Kinnison, Unwin & Quinn, 1998). GA fry grew more rapidly from August to October ($p = 0.05$) and from October to February ($p = 0.02$), but not over the remaining 2 months ($p = 0.36$) of study. Initial fry weight varied among families and was correlated with egg weight ($r = 0.43$) but the correlation degraded over longer intervals and weight at the end of the study was not correlated with either egg or initial fry weight. The higher growth rate of GA fry, compared to Haka fry reared under the same conditions, implied a genetic difference between the two populations, albeit small. In contrast, GA fish grew much faster than PR fish in the subsequent experiment (Unwin et al., 2000). Spawning date had a substantial effect on size at a given date early in life but intrinsic growth differences soon overcame this effect. The early and late GA families were similar in size and both were much larger

Table 2. Comparisons between chinook salmon of Glenariffe (GA), Hakataramea (HK), and Poulter River origin for selected life history traits (± 1 SE) under common rearing conditions

| Trait/comparison | Year(s) | Group/treatment | Glenariffe | HK/Poulter | Sig. |
|--|-----------|---|-----------------------------|------------------|-------------------|
| Total ova mass (g) ^a | 1994 | 1994–1995 parent stock | 1211 \pm 49 | 1496 \pm 56 | $p < 0.001$ |
| | 1995 | | 1224 \pm 51 | 1583 \pm 94 | $p < 0.001$ |
| Mean ova weight (mg, size-adjusted) ^a | 1994 | 1994–1995 parent stock | 185 \pm 3 | 258 \pm 5 | $p < 0.001$ |
| | 1995 | | 177 \pm 4 | 236 \pm 3 | $p < 0.001$ |
| Fecundity (size-adjusted) ^a | 1994 | 1994–1995 parent stock | 6577 \pm 162 | 6724 \pm 174 | ($p \geq 0.05$) |
| | 1995 | | 6792 \pm 189 | 6490 \pm 332 | ($p \geq 0.05$) |
| Hatching time (days at 12.4°C) ^a | 1994 | 1994–1995 parent stock | 38.74 \pm 0.03 | 38.73 \pm 0.06 | n.s. |
| Specific growth rate (%/day) ^a | 1994 | 40–73 days post-fertilisation | 4.9 \pm 0.2 | 5.4 \pm 0.1 | ($p = 0.055$) |
| Specific growth rate (%/day) ^b | 1994 | 3–10 weeks post-hatch | 2.72 \pm 0.05 | 2.56 \pm 0.04 | $p = 0.04$ |
| | 1994 | 14–24 weeks post-hatch | 0.93 \pm 0.02 | 0.86 \pm 0.02 | ($p = 0.06$) |
| | 1994 | 26–32 weeks post-hatch | 1.23 \pm 0.03 | 1.19 \pm 0.03 | n.s. |
| Hypersalinity tolerance ^b | 1994 | 4, 6, and 10 months-post-hatch | | | n.s. |
| Migration and maturation timing ^c | 1994–1995 | Upriver migration (mean date of angler capture) | GA 10 days earlier than HK | | $p = 0.04$ |
| | | Spawning ground entry | GA 4.6 days earlier than HK | | $p = 0.004$ |
| | | Maturation date (ocean release group) | GA 3.6 days earlier than HK | | $p = 0.03$ |
| | | Maturation date (captive group) | GA 2.8 days earlier than HK | | $p = 0.006$ |
| Mature male parr (%) ^d | 1994 | GA v.s. Hakataramea | | | n.s. |
| Marine survival (%) ^e | 1994 | Glenariffe release | 0.34 \pm 0.02 | 0.20 \pm 0.03 | $p < 0.001$ |
| | 1995 | Glenariffe release | 0.32 \pm 0.03 | 0.11 \pm 0.02 | $p < 0.001$ |
| | 1994 | Silverstream release | 1.89 \pm 0.16 | 2.22 \pm 0.18 | n.s. |
| | 1995 | Silverstream release | 0.97 \pm 0.12 | 0.73 \pm 0.09 | n.s. |
| Total ova mass (g) ^f | 1994 | Freshwater (captive-reared) group | 416 \pm 4 | 392 \pm 5 | $p = 0.004$ |
| Mean ova weight (mg, size-adjusted) ^f | 1994 | Freshwater (captive-reared) group | 153.7 \pm 2.3 | 152.9 \pm 2.2 | n.s. |
| Fecundity (size-adjusted) ^f | 1994 | Freshwater (captive-reared) group | 2753 \pm 48 | 2614 \pm 35 | $p = 0.072$ |
| Muscle solids (%) ^f | 1994 | Freshwater (captive-reared) group | 21.9 \pm 0.2 | 21.8 \pm 0.2 | n.s. |
| Hatching time (d) ^g | 1997 | at 12.2°C | 40.01 \pm 0.16 | 40.10 \pm 0.12 | $p = 0.06$ |
| | | at 7.3°C | 63.18 \pm 0.14 | 63.52 \pm 0.16 | |
| Weight at age (g) ^g | 1997 | After 1 year | 53.2 \pm 1.1 | 27.9 \pm 1.1 | $p < 0.001$ |
| | | After 2 years | 499.3 \pm 1.1 | 362.5 \pm 1.1 | $p < 0.001$ |

Refs: ^aKinnison et al. (1998b); ^bKinnison, Unwin and Quinn (1998); ^cQuinn, Unwin and Kinnison (2000); ^dUnwin, Kinnison and Quinn (1999); ^eUnwin et al. (unpublished data); ^fKinnison et al. (2001); ^gUnwin et al. (2000).

Year(s) refers to brood year (i.e., year of spawning); data for Hakataramea fish are for the 1994 and 1995 broods only, and data for Poulter fish are for the 1997 brood only.

Reproductive traits were size-adjusted to facilitate comparisons between study populations.

Significance levels (Sig.) were for the comparison in question, and were not adjusted for multiple comparisons; n.s. indicates $p > 0.10$.

than either the early or late PR group. In particular, GA families were larger than PR families ($p < 0.001$) spawned on the same date (18 May, 1997), confirming that the observed inter-population difference in growth trajectory was not simply an artefact of different spawning dates (Unwin et al., 2000). GA families were 60–76% heavier than PR families during their first year of life, and 53–123% heavier during their

second year of life, with final mean weights of 519 g (GA) and 338 g (PR).

Seawater tolerance and early maturity

The GA and Haka fish were subjected to experimental hypersalinity challenges in November, January, and May. Salinity tolerance increased with body size, consistent with investigations using other techniques

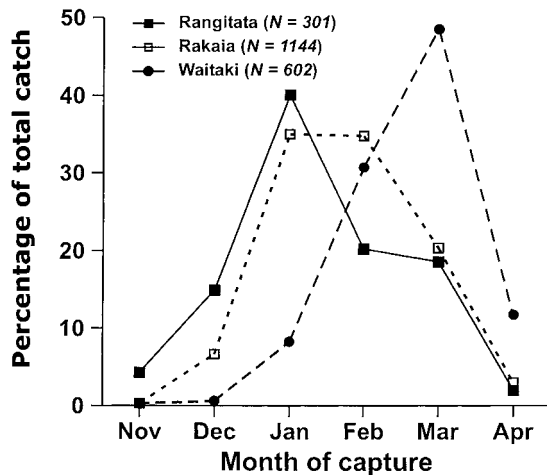


Figure 5. Percentages of chinook salmon caught each month by anglers in three New Zealand rivers.

(reviewed in Hoar, 1976), and family variation was apparent. Fish from the two populations did not differ in tolerance at any of the three experimental periods, even after adjustment for the effects of body size (Table 2).

The growth experiments provided an opportunity to examine the incidence of sexually mature male parr (in their first year of life) as a component of the age distribution pattern among and within populations (Unwin, Kinnison & Quinn, 1999). Of the 58 families examined in the GA-Haka experiment, based on examination of c. 300 fish per family, 28 had fewer than five mature parr but 15 families produced more than 15, including one GA family with 97 (69% of the estimated males). Despite this family variation, nested ANOVA did not indicate significant sire ($p = 0.23$) or population ($p = 0.12$) effects on the incidence of mature parr. The initial breeding design of the study did not involve parr but in subsequent matings the incidence of mature parr in families produced using parr as sires was similar to that among their parent stock, further indicating that genetic influence over parr maturation was weak (Unwin, Kinnison & Quinn, 1999). The incidence of mature parr was not correlated with mean family weight at any time during the first year of life, with growth rate, or with mean weight of alevins or eggs, indicating absence of size related maternal effects.

The GA-PR experiment did not produce mature age 1 parr but 577 males matured at age 2. The incidence of maturation varied from 0 to 57%, with five families exceeding 50% or virtually all the males. The incidence of maturation was positively correlated with

family mean body mass at the end of the second year of life ($r = 0.81$). PR families had less than half the incidence of early maturation than GA families (15% v.s. 35%) but this difference appeared to be solely related to the size difference between the two populations. Analysis of covariance showed no interaction between population and the relation between incidence of maturation and mean weight ('homogeneity of slopes', $p = 0.77$), and no effect associated with population ($p = 0.82$) or spawning date ($p = 0.99$).

Reproductive timing and investment

Chinook salmon from both release groups that survived natural mortality matured and returned to fresh water in autumn 1996–1998, representing 2-, 3-, and 4-year-old from the 1994 brood, and 2- and 3-year old from the 1995 brood (Quinn, Unwin & Kinnison, 2000). One hundred ninety salmon were caught by anglers, 450 returned to spawn at Glenariffe stream, and 311 returned to Silverstream. We used capture date as a measure of migration timing for angler-caught fish, and date of arrival at the hatchery weirs as a measure of date of entry to their respective spawning grounds. We tagged fish when they arrived at the Glenariffe stream weir and thereafter checked them for maturity every 3–6 days, allowing us to determine individual maturation date to within ± 3 day. We used a similar protocol to record maturation date for all captive females. Most captive males were mature upon first inspection each year, precluding useful information on maturation date.

Population-level effects on return and maturation date were obvious and consistent among brood years and sites (Table 2). Mean date of capture by anglers for GA origin fish was 10 day earlier than Haka fish, and did not differ between the two return locations. Mean date of spawning ground entry differed consistently between the populations (GA returned first) and sexes (males returned first) but there were no effects of return site (hatchery), age or brood year. GA fish preceded Haka fish in 12 of the 14 available subsets of data, tabulated by year of return, brood year, sex, and point of return. GA salmon also matured before Haka fish after returning from the ocean. Finally, the captive salmon showed the same pattern as those rearing at sea. GA females matured before Haka females ($p = 0.006$), with significant differences among sires ($p < 0.001$). This pattern is consistent with the observed pattern in wild Rakaia River salmon (including GA) returning to fresh water nearly a month before Waitaki River (chiefly Haka, Figure 5). It is also

consistent with the relationship between river temperature, latitude and spawning date found for North American populations of *Oncorhynchus* (e.g., Brannon, 1987); the Hakataramea River is farther south and warmer during spawning and incubation period (Kinnison et al., 1998a).

The salmon that returned from the ocean revealed a significant 'environmental' cost of migration for ovarian investment ($p < 0.001$) based on ANCOVA of logged trait values relative to log somatic weight (weight of body minus ovarian mass). Those making the much shorter migration to Silverstream had 13% heavier ovaries, 19% heavier eggs and 6% more muscle solids (a measure of muscle energy density), but slightly (<5%) fewer eggs at a given somatic weight than females migrating to Glenariffe (Kinnison et al., 2001). Analyses based on size-adjusted means for the same families at both sites using paired t -tests (controlling for variation in genetic background of returns) also indicated significant site effects for all traits ($p < 0.007$). In contrast, under common rearing conditions, ovary weight at a given somatic weight was larger for GA than Haka fish ($p = 0.004$) and egg number was the primary character accounting for the difference (Table 2; Kinnison et al., 2001). Genetic divergence thus appeared to run counter to the environmental effect of migration on ovarian investment.

Rate of divergence

Assuming that most NZ populations became established in about 1910 (1–2 generations after the first salmon returned), with an average age at maturity of 3.2 years (Kinnison et al., 1998a), the differences among NZ salmon populations have arisen in fewer than 30 generations. Although the differences in some traits are modest at present, evolution must still have been rapid. However, the term 'rapid evolution' must be evaluated relative to some scale (Hendry & Kinnison, 1999; Kinnison & Hendry, 2001). Many recent studies, from a broad range of taxa, have detected divergence over short time frames so 'rapid' may actually be the typical rate of initial evolution. In this section we consider the statistical significance of evolutionary rates in NZ salmon, compare rates and trait types, and compare the NZ salmon results with other studies of contemporary microevolution.

All rates we discuss here are in haldanes (Gingerich, 1993; Hendry & Kinnison, 1999), which express the divergence between populations in standard

deviation units per generation. By using bootstrapping and randomization methods (Kinnison & Hendry, 2001) based on family mean values we estimated confidence bounds for haldane rates and performed one-tailed tests of whether the rates were significantly greater than zero. Confidence bounds on our evolutionary rate measures were very large but the significance of rates and statistical significance in other analyses (mostly ANOVA) used to detect population divergence were consistent (Table 3). Divergence rates calculated among wild populations were comparable to rates detected among populations under common rearing, though use of phenotypic differences can be misleading because of environmental differences such as the effect of migration on ovarian mass and egg weight.

Time has an inordinately strong effect on estimates of evolutionary rates (Gingerich, 1983, 2001). The general result is decreasing rates with longer time intervals. Trait divergence in NZ has been slow in terms of calendar time; only modest differences are evident in some traits nearly a century after the introduction. However, when scaled for generation length and trait variability, the NZ rates under common rearing are as representative of 'rapid' evolution as rates documented in studies with other organisms over similar time scales (NZ rates 0.009–0.066, others under common rearing over 20–40 generations 0.001–0.081; rates compiled by Kinnison & Hendry, 2001). Furthermore, the divergence of these salmon has arisen in the face of continued gene flow and in an organism with a long and complex life history, as discussed below.

The process of divergence

Given that NZ salmon have diverged in a wide range of traits, what processes have been responsible for these changes, and how can investigation of these processes advance our general understanding of evolution? In this section we consider the processes leading to the patterns we have described by considering the quantitative genetic basis for the traits, evidence for adaptive value of the traits, and population structure.

Inheritance of quantitative traits and adaptation

One would expect that the traits showing genetic divergence would have substantial amounts of genetic variation available for selection to act on, unless such variation has been depleted by sustained strong selection. Quantitative genetic analyses indicated primarily

Table 3. Estimated evolutionary rates (haldanes) for specified phenotypic traits in wild and captive New Zealand chinook salmon, with 2.5–97.5% confidence bounds and significance (*P*-values) of rate tests

| Trait | 2.5% | Haldanes | 97.5% | <i>P</i> -values | Difference |
|--------------------------------|--------|----------|-------|------------------|------------|
| Wild | | | | | |
| Male fin factor | −0.13 | 0.010 | 0.031 | 0.190 | No |
| Female fin factor | 0.005 | 0.031 | 0.066 | 0.004 | Yes |
| Gonadosomatic index | 0.010 | 0.026 | 0.043 | 0.001 | Yes |
| Egg size ^a | 0.027 | 0.048 | 0.076 | <0.001 | Yes |
| Fecundity ^a | −0.011 | 0.012 | 0.044 | 0.815 | No |
| Captive | | | | | |
| Time to hatch | −0.008 | 0.020 | 0.050 | 0.122 | No |
| Growth – H v.s. G ^b | 0.013 | 0.032 | 0.053 | 0.009 | Yes |
| Growth – P v.s. G ^c | 0.039 | 0.066 | 0.112 | <0.001 | Yes |
| Gonad weight ^a | 0.020 | 0.038 | 0.059 | 0.001 | Yes |
| Egg size ^a | −0.009 | 0.011 | 0.030 | 0.176 | No |
| Fecundity ^a | 0.002 | 0.020 | 0.042 | 0.036 | Yes |
| Day of maturation | 0.003 | 0.021 | 0.043 | 0.022 | Yes |

^aAdjusted for body size.

^bHakataramea v.s. Glenariffe.

^cPoulter v.s. Glenariffe.

The final column indicates whether significant interpopulation differences were detected using ANOVA and related analyses.

maternal effects and low heritabilities for incubation-related traits, though we found sire effects for alevin growth rate and conversion efficiencies. The lack of divergence in early development rates was not surprising, given the relatively modest amount of variation seen among natural populations that have been isolated for thousands of years. Differences in fry emergence dates among North American salmon populations are more strongly affected by spawning date than developmental rate but both factors operate (Tallman, 1986; Brannon, 1987). Perhaps a hybridization experiment such as Wood and Foote (1990) conducted with anadromous and non-anadromous sockeye salmon would have revealed differences between the NZ populations. NZ chinook developed rapidly compared to North American populations (Beacham & Murray, 1989) but the absence of data on the development rate of Battle Creek chinook prevents us from knowing if this trait has changed since the transplant.

Although genetic divergence was not evident in developmental rate, this does not necessarily mean that actual developmental rates are identical in the wild. Selection during the developmental period may still be important in contributing to genetic divergence in other traits. Glenariffe Stream's flow regime is exceptionally stable, with very little tendency to flood. In contrast, floods are common in the Hakataramea river,

which is also warmer than Glenariffe over most of the year (Kinnison et al., 1998b). The observed difference of 2.3°C between these rivers during the incubation period would have resulted in emergence dates differing by about 4 weeks in 1994 and 6 weeks in 1995, had the fish spawned at the same date. The slightly later spawning by Haka fish would reduce the difference in emergence dates somewhat, perhaps synchronizing emergence with food resources, and also reduce exposure to winter floods.

Despite similar developmental rates, growth rates of fry from the three study populations differed under controlled conditions. Fast growth of GA fry might be an adaptive compensation for the population's smaller eggs and colder water temperatures of Glenariffe Stream and the Rakaia River compared to the Hakataramea and Waitaki rivers (unpublished data, National Institute of Water and Atmospheric Research, NZ). If body size is under common selection among NZ populations (e.g., for seawater adaptation or marine survival), then compensatory mechanisms may have evolved to promote faster growth in GA fry. The Rakaia River produces a larger proportion of ocean-type juveniles than the Waitaki (Quinn & Unwin, 1993), so selection would favor more rapid growth to reach critical sizes for seawater tolerance and marine survival.

Why then do PR salmon grow so slowly? Under the late spawning and poor growing conditions faced by the PR population, it may not be possible to grow large enough to produce ocean-type smolts with sufficient survival rates, thus the fastest growing members of the population may actually have been initially selected against. The population thus shows slow growth and most individuals spend a full year in fresh water before going to sea. This raises the question of why the PR salmon spawn so late in the season, when earlier spawning would provide a longer growing period for the offspring. The growth rate of Haka fish was intermediate between the GA and PR populations, and they also showed intermediate proportions of stream- and ocean-type fish.

Although families varied in seawater tolerance, sire effects were not detected, nor did the populations vary in this trait, despite the significant role of transition to the ocean in the lives of salmon and the presence of such differences among some North American populations (Kreeger, 1995). The mainstem Rakaia and Waitaki rivers have relatively similar environmental conditions compared to the range of habitats encountered in North America. Both rivers are short, have high gradients, synchronous flow regimes, and lack estuaries. Variation in seawater tolerance may have a genetic basis (directly, or as correlated with growth) but insufficient selective differences to cause the populations to diverge. Studies of smolt timing and tolerance in anadromous and non-anadromous sockeye salmon populations suggest that smolt transformation may be strongly conserved in salmonids (Foote et al., 1994; Wood, 1995) so the parsimonious conclusion is that no divergence has taken place in tolerance per se. However, size increases seawater tolerance so selection on tolerance may have manifested itself in patterns of growth and juvenile life history. In addition, the large size of our experimental fish, relative to wild salmon of the same age, may have obscured possible differences in tolerance.

The proportions of males maturing as parr in the GA-Haka experiment, and at age 2 in the GA-PR experiment, varied greatly among families. However, the lack of significant sire or population effects and the similar proportions of mature parr in broods sired by parr and older males (Unwin, Kinnison & Quinn, 1999) indicated that any additive genetic effects (and consequently heritability) were weak. Studies with North American salmon have indicated some genetic influence over age at maturity for older (migratory) fish (e.g., Hard et al., 1985). However, maturation in

freshwater parr may be a different phenomenon and most studies report strong environmental effects (Silverstein & Hershberger, 1992; Hankin, Nicholas & Downey, 1993; Heath et al., 1994; Heath, Iwama & Devlin, 1994). Salmon show an inverse relationship between growth rate and age at maturity. Fast-growing individuals within a brood are more likely to mature than slower-growing ones, and in years when salmon are growing rapidly they tend to mature at a younger age than when growth is slow (Figure 3).

The significant additive genetic (sire) effects ($p \leq 0.02$) and high heritability estimates for timing of return and maturation for released fish ($h^2 = 1.26 \pm 0.40$ and 1.06 ± 0.42 , respectively) and for maturation timing in captive fish ($h^2 = 1.08 \pm 0.28$) were consistent with work on other salmonids (e.g., Siitonen & Gall, 1989; Smoker, Gharrett & Stekoll, 1998). Not only were return and maturation timing highly heritable, they were also genetically correlated ($r_G = 0.92$), and both were negatively correlated with the length of time females delayed between spawning ground entry and maturation ($r_G = -0.85$ and -0.59 , respectively). If evolution occurred along genetic lines of least resistance (Schluter, 1996), then we would expect the population that returns later to both mature later and show a shorter delay between return and maturation. This is exactly the genetic pattern we found in GA and Haka salmon.

The timing of migration and reproduction are under very strong genetic control in salmonids, and this is the primary way they control the date when juveniles emerge from the gravel in spring. Spawning may take place later in the Hakataramea River than Glenariffe Stream but the populations overlap considerably. This similarity of spawning dates is noteworthy given the substantial differences in their respective temperature and flow regimes. Higher temperatures are generally associated with later spawning among salmonids (Brannon, 1987; Webb & McLay, 1996), so Haka chinook should spawn later than GA fish if emergence is to be synchronized. However, timing in the Hakataramea may also be influenced by the flow regime if the river's tendency to flood in August, harming pre-emergent fish, selects for earlier spawning.

The heritabilities of female reproductive traits (gonad size, egg weight, and egg number) were high (ca. $h^2 = 0.70$), especially for GA fish (Kinnison et al., 2001). The patterns observed in GA and Haka fish migrating to their respective natal streams at first appear inconsistent with our results under controlled

conditions. Wild salmon migrating to GA had smaller ovaries and eggs than Haka fish at a given body size, but when reared in captivity (i.e., no migratory challenge at all), the GA fish grew larger ovaries with more eggs than captive Haka females. Migration to the Hakataramea River is about half the distance and elevation to Glenariffe Stream so the pattern among wild salmon is consistent with the environmental cost of migration seen in our experiment (i.e., bigger gonads in fish migrating to Silverstream compared to Glenariffe). Egg number is apparently determined earlier in life than egg size, and the phenotypic effect of a challenging migration is primarily a reduction in egg size rather than number. Egg size is initially correlated with offspring size and offspring size is generally correlated with survival (e.g., Einum & Fleming, 2000), and thus with parental fitness. Therefore, the genetic pattern revealed under captive rearing at Glenariffe likely reflects a greater investment in gonads of the longer migrating GA population to counter fitness costs of migration. Our experimental results were supported by an examination of data on egg size and number among North American salmon populations. Those with more arduous migrations generally have smaller eggs, relative to egg number, than populations with easier migrations (Kinnison et al., 2001). Fecundity is phenotypically plastic, in addition to having a genetic basis, and fish that grow quickly have more eggs for a given body size than those growing slowly (e.g., Jonsson, Jonsson & Fleming, 1996; Quinn et al., 1998). This may explain why the NZ chinook salmon are both large for their age and fecund for their length compared to North American populations (Healey & Heard, 1984; Roni & Quinn, 1995).

Perhaps the most striking insights into the adaptation of chinook salmon populations came not from any single trait but from the integration of traits into survival from release to return. GA origin salmon were released from their natal stream (Glenariffe) and from a 'foreign' location (Silverstream), whereas Haka salmon were released from two different foreign locations (Glenariffe and Silverstream). When 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 ($p < 0.001$ overall) whereas when released from Silverstream, GA fish had a lower survival rate in 1994 and a higher rate in 1995 but in neither year was the difference significant ($p = 0.75$ overall, Figure 6). We do not know what properties or traits conferred the higher survival rate on GA fish when released from the upper Rakaia River. Sur-

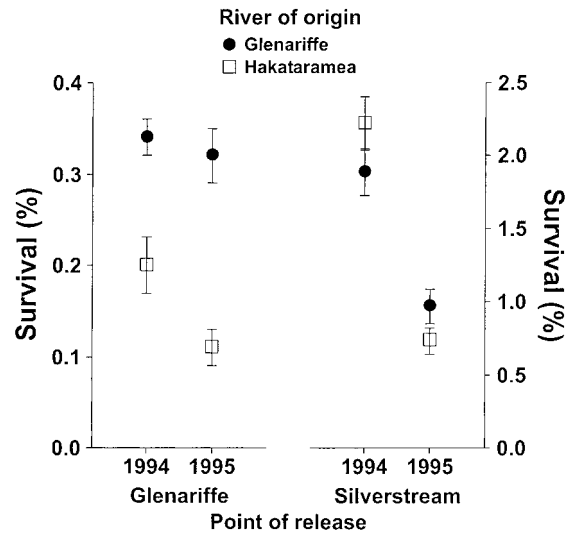


Figure 6. Mean survival (± 1 s.e.) for two populations of chinook salmon (Glenariffe and Hakataramea) released to sea from two different locations (Glenariffe and Silverstream) in 1994 and 1995.

vival is not a trait in itself but a result of many traits including migratory timing and orientation, predator avoidance, foraging behavior, and others, and it interacts with environmental conditions in complex ways. However, the basic result (a 'home court' advantage) is consistent with comparisons between survival rates of local and transplanted salmon in their native range (reviewed by Ricker, 1972; Reisenbichler, 1988), and we show that such an advantage may evolve quickly.

In addition to site and population effects, marine survival varied considerably among families, consistent with the results of Geiger et al. (1997) for pink salmon and Jónasson (1996) for Atlantic salmon. For the 1994 brood, survival ranged from 0.04 to 0.89% for families released from Glenariffe and from 0.0 to 5.8% from Silverstream (ANOVA, $p < 0.001$ at both locations). Corresponding figures for the 1995 brood were 0.0–0.58% from Glenariffe Stream ($p < 0.001$) and 0.15–2.02% from Silverstream ($p = 0.07$). Within each brood year, survival rates of families from the two release sites were positively correlated ($r = 0.45$ – 0.47 , $p = 0.02$). Family-specific survival tended to increase with weight at release, though size did not determine the differences between the two study populations. The marine survival advantage of larger salmon is consistent with earlier work on NZ chinook salmon (Unwin, 1997), as well as results for other salmonids including chum, *O. keta* (Healey, 1982), coho, *O. kisutch* (Holby, Anderson & Kadowaki, 1990), and sockeye salmon, *O. nerka* (Henderson &

Cass, 1991), steelhead, *O. mykiss* (Ward et al., 1989) and cutthroat trout, *O. clarki* (Tipping & Blankenship, 1993), and white-spotted char, *Salvelinus leucomaenis* (Yamamoto, Morita & Goto, 1999). This widespread pattern probably underlies the distinction between ocean-type and stream-type chinook salmon. Populations whose growth is comparatively rapid can enter the ocean with acceptable survival rates in their first year of life but in growth-limiting environments the juveniles would be at such a disadvantage that they stay in fresh water and leave the following spring.

Population structure and genetic diversity

Analysis of traits assumed to be selectively neutral provided complementary insights to the results from our experimental program. Allozyme data indicated that Sacramento River chinook had higher levels of genetic variation than NZ chinook, with more alleles per locus, more polymorphic loci, and 22% greater mean heterozygosity. Likewise, allele frequencies given by Quinn et al. (1996) suggested that in the NZ fish, mtDNA haplotypes were both less numerous (by 41%), and less diverse, than in Sacramento fish. A similar trend was apparent in analyses of microsatellite variation; NZ salmon had fewer alleles per locus and 5% lower mean heterozygosity than Battle Creek fish (Kinnison, 1999). We cannot compare the present NZ fish to their ancestors (i.e., the Sacramento river salmon of the early 1900's), only to their modern descendants, and the Battle Creek population may have undergone changes in gene frequency over the past 100 years. Notwithstanding this drawback, our results indicate that modest founder effects or bottlenecks may have occurred but were evidently not great enough to prevent subsequent phenotypic divergence among NZ populations.

Allele frequencies at 24 polymorphic, protein-coding loci revealed that the Sacramento and NZ populations formed two distinct subgroups, and that the NZ populations were grouped more closely than the Sacramento River populations (Quinn et al., 1996). The matrix of Cavalli-Sforza and Edwards (1967) distances revealed comparable UPGM and neighbor-joining trees separating the NZ and Sacramento River populations. However, the level of variation seen among populations within NZ was of the same order as that seen among years within populations from California. Analysis of the nine microsatellite loci out of 11 that followed Hardy-Weinberg proportions, run on a much larger array of samples over space and

time in NZ, supported the conclusion that interannual variation was substantial among years (AMOVA, $p < 0.02$; Kinnison, 1999). However, significant interannual variation does not preclude significant population structuring; 11 out of 12 samples from different sites and years in NZ clustered into expected drainage clades in a neighbor-joining tree of Weir and Cockerham's (1984) θ values (Figure 7). Thus the variation in gene frequencies among years may reflect the limited sampling of these large populations rather than lack of population structure. The NZ drainages were weakly structured in space, tending to follow an isolation-by-distance pattern ($p < 0.07$ via Mantel test; Kinnison, 1999).

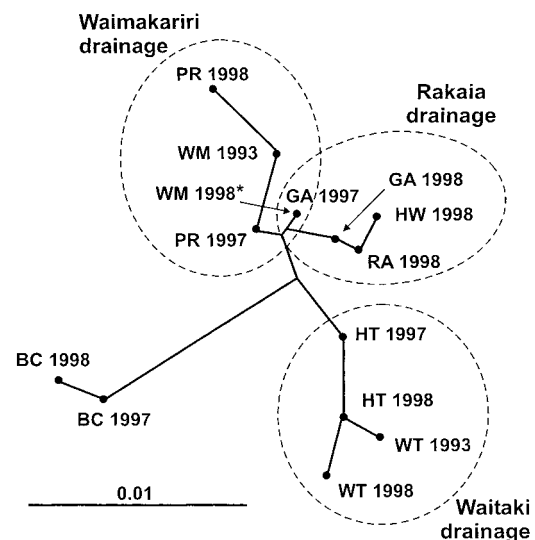


Figure 7. Neighbor-joining tree of θ values for temporal and spatial samples from three major NZ salmon drainages and their nearest North American relatives. Dashed lines indicate the subsets of samples derived from each of the drainages. Samples are abbreviated by letter code and year: Battle Creek, California – BC; Waitaki mainstem – WT; Hakataramea – HT; Rakaia mainstem – RA; Glenariffe stream – GA; Hydra waters – HW; Waimakariri mainstem – WM; Poulter river – PR. Note that WM 1998 (which coincides with the Glenariffe 1997 node) was the only sample that failed to cluster inside the 'true' drainage.

Current census populations (including catch) are on the order of 10,000 adults in each of the four major rivers, including the three sampled in this study. By examining interannual variation in allele frequencies from 1993 to 1998 we estimated that the effective population size in each drainage was about 600 fish (Kinnison, 1999). Using simulations based on this figure and non-equilibrium we estimated gene flow at about 14 migrants per population per generation (M.T. Kinnison, unpubl. data). We do not know if such effective

population sizes and gene flow are large enough to preclude substantial effects of drift on neutral or adaptive traits (at least at present). In any case, the divergence in adaptive traits has taken place despite some straying (Unwin & Quinn, 1993) and apparent gene flow, implying considerable selection against introgression in these recently diverged populations (see also Hendry et al., 2000).

The establishment of salmon populations: conclusions and hypotheses

Our results demonstrate that salmon populations are capable of 'rapid' divergence as they adapt to new environments. How might this process have occurred in NZ, in the range of salmon in the Northern Hemisphere, and among colonizing organisms in general? Our results can be discussed in the context of four key elements: (1) initial founding, (2) interactions between plastic and genetically controlled life history traits, (3) building reproductive isolation, and (4) divergence versus convergence.

Initial founding

Salmon are famous for their philopatry, the tendency and ability to return as mature adults to their natal site, but such homing is obviously initially incompatible with colonization. Some straying takes place in salmon and it may be more frequent when densities are low (Quinn, 1993). Pink salmon (*O. gorbuscha*) spread out rapidly after they were inadvertently released into the Great Lakes (Emery, 1981), and straying levels were probably quite high. Similarly, the proportion of salmon straying from the Hakataramea (site of the transplant) in the first few generations may have been higher than is presently observed. In the early stages of colonization at low population densities, strays may face positive or negative Allee effects, such as high productivity from negligible competition or decreased productivity associated with difficulty in finding mates or predation. Salmon colonized north from the Waitaki River (McDowall, 1994), consistent with the northward distribution of strays seen recently (Unwin & Quinn, 1993). Such directionally biased straying also occurs within the natural range of salmon (e.g., Pascual & Quinn, 1994).

After the first generation, however, the general tendency of salmon to home (notwithstanding the behavior of their parents) will restrict gene flow with the

donor population(s). Sufficient reproductive isolation and selection on heritable traits will cause the new population to diverge from the founding population. It is also reasonable to expect that the genotype of the colonists may strongly affect the ultimate characteristics of the population via founder effects. However, founder effects need not be limited to random deviations of founders from the mean of the donor population. Colonists may be a highly selected, non-random sample of the ancestral population. We refer to this as a 'favored-founders effect'. The key feature of this phenomenon (in contrast to random founder effects) is that it not only promotes divergence between populations in some heritable characters in the 'zero' generation, before a self-sustaining population is even established, but can also improve the fitness of the new population relative to a random sample from the donor population.

The favored-founders effect can be illustrated with salmon traits we have studied. Take, as an example, a new population of salmon formed from individuals that strayed upriver past their natal site to colonize new habitat. Colonists that attained the more distant location are likely to have had more energy reserves, greater investment in ovarian mass or differed in size or morphology from the average of the donor population. If these traits were heritable, as they apparently are, the colonists would have a significantly different mean genetic trait value, conferring higher fitness in the new environment, than would be found in a random sample of salmon from the donor population. Conversely, if an experimental transplant study were to use randomly chosen groups of colonists to initiate a new population, then some elements of a favored founders scenario may be artificially excluded.

Complex plastic and genetic life history interactions

The many traits we measured (and others as well) are linked in complex ways through cascading developmental, environmental, and simple chronological connections (Figure 3), and all are influenced by varying amounts of genetic and environmental influences. The challenge in understanding the initial process of population evolution and adaptation is sorting through this tangle of interactions and influences. Selection is focused on the genotypes of a population through the lens of the phenotypes. Thus the phenotypic responses of the organism (with its ancestral genotype) to new environmental conditions may determine the success of the first generation, and subsequently the

novel selection agents can modify the genotype. For example, optimal egg and smolt sizes may be similar among many NZ populations. If so, environmental effects would cause populations experiencing different growth opportunities or migratory distances to express different phenotypes and to evolve different genotypic profiles in response to similar patterns of selection.

Interactions among life history traits (Figure 3) can make it difficult to demonstrate the associations between particular selective factors and the organism's responses. As an example, consider selection favoring larger progeny at a given age (clearly linked to survival in our work and that of others) in a novel population. Several 'pathways' are open to address this 'evolutionary problem' in salmon (Figure 8). First, selection may favor increased egg size, because egg size strongly influences fry size (e.g., our results) and fitness in the wild (Einum & Fleming, 2000). The wild NZ populations now differ in egg size but this seems to primarily reflect variation in the arduousness of the migration, and hence a phenotypically plastic effect with fitness implications. Nonetheless, under controlled conditions, the longer migrating GA

population invested more in ovarian mass, suggesting an adaptive genetic compensation for environmental impacts on egg and progeny size.

Second, the date of spawning may evolve, altering emergence time and hence growing opportunities. Our data and other studies indicate a strong genetic control over adult timing, relative to environmental controls, and relative to other fishes (e.g., Quinn & Adams, 1996), so this is a viable means of controlling juvenile size at age. Third, selection for size at age may result in a change in the rate at which embryos develop but our data revealed no divergence. North American populations differ in developmental rate but it seems to be secondary to spawning date as the mechanism controlling fry emergence time.

Finally, progeny size can be affected by the evolution of growth rate and, despite obvious environmental effects, this trait is heritable and varies among populations. In the hatchery environment, growth rate differences between GA and PR populations were more important than egg size or even emergence date in controlling juvenile size after several months, though the extent to which wild populations would perform similarly is unknown. As in North America, NZ seems to be evolving slow-growing populations (e.g., the Poulter River) whose 'stream-type' juvenile life history is adapted to their slow-growth environments (Taylor, 1990b). Growth of juveniles is strongly related to environmental conditions (chiefly food and temperature) and the observation of stream-type juveniles shortly after colonization by ocean-type parents (Parrott, 1971; reporting data from the late 1920's and early 1930's) suggest an early phenotypic response to factors controlling juvenile growth and life history type. We hypothesized that conditions do not permit PR fry to grow large enough in their first year of life to overcome size-selective mortality at sea, and so they tend to remain in fresh water for a full year (Unwin, Kinnison & Quinn, 1999). Correlated with this pattern of selection they seem to have evolved a slower growth rate (through some unknown behavioral or physiological mechanism). There are trade-offs between foraging, territoriality and predation risk (e.g., Godin, 1990), so this population may be attempting to maximize survival at the expense of growth in fresh water, while the GA population may be under selection for faster growth and earlier migration to sea. Selection has apparently begun to reinforce the juvenile growth and life history patterns initially set by environmental conditions.

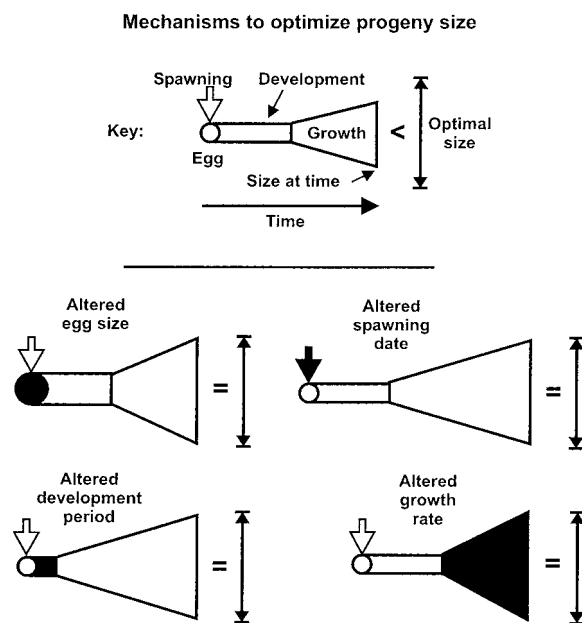


Figure 8. Conceptual model for possible evolutionary approaches to the challenge of increasing progeny size. Any of four traits can be modified: egg size ('egg'), date of spawning ('spawning'), rate of embryonic development ('development') and progeny growth rate ('growth'). The vertical axis represents progeny size and the horizontal axis is time. Each panel illustrates how changing one trait, shown in black, increases future progeny size.

Building reproductive isolation

The timing of adult migration and spawning were consistently different between populations and had high heritabilities. We believe that spawning timing is a key trait in the divergence of many populations because it (1) reflects adaptation, (2) strongly influences other traits, and (3) augments spatial isolation of populations to facilitate and accelerate divergence in other traits. Salmonids vary greatly in migration and spawning dates in their native range; these attributes seem to reflect selection on adult passage (Quinn & Adams, 1996) and juvenile incubation conditions (Brannon, 1987; Webb & McLay, 1996). Spawning date also provides a strong phenotypic link to size and growth of progeny in spring because it determines when they emerge from the gravel in the spring: too early and they have little to eat but too late and they miss growing opportunities or fail to acquire feeding territories. Perhaps most importantly, the divergence of spawning dates among populations will reinforce the reproductive isolation provided by homing, accelerating the evolution of other traits. Studies with sockeye salmon in Lake Washington indicated that partial genetic isolation and divergence in various traits can arise very quickly (Hendry et al., 2000; Hendry, 2001).

Divergence and convergence

Does initial population evolution reflect primarily phenotypic diversification or convergence? If one looks at population establishment as the first stage in speciation, the tendency is to look for processes favoring divergence. However, ecological factors characterizing certain types of habitats (e.g., streams, lakes, estuaries) and connections among life history traits (egg size, progeny size, competition, and growth) may produce similar phenotypes in isolated populations. The tendency to successfully colonize similar habitat types and exploit similar resources promoting common selection regimes, and complex life history interactions (as described above) may constrain selective patterns and evolutionary responses during initial population evolution. The tendency of many species to repeatedly produce similar sets of eco-phenotypes suggests a finite number of general 'types' and evolutionary trends within species. Repeated evolution of certain 'types' within Arctic char (Skúlason et al., 1996; Gíslason et al., 1999), guppies (Reznick et al., 1997), sockeye salmon (Wood, 1995; Wood & Foote, 1996), threespine sticklebacks (Bell, 2001), and other species (Taylor, 1999) argues strongly for factors favoring

population convergence. Similarly, Johnson and Belk (2001) pointed out that different, geographically isolated livebearing fish species (guppies in Trinidad and *Brachyrhaphis rhabdophora* in Pacific drainages of Costa Rica) have evolved strikingly similar life history responses to predation intensity.

Anadromous salmon have proven much more difficult to transplant than non-anadromous populations, suggesting that their complex life history limits their adaptive potential. Our studies provided evidence of genetic differentiation resulting in both phenotypic divergence (e.g., juvenile growth patterns), and phenotypic convergence toward more similar trait values (e.g., ovarian investment). However, even the cases of divergence appeared to follow patterns seen in the natural range of the species (e.g., life-history types such as 'stream' and 'ocean' chinook salmon, and patterns of ovarian allocation with migratory distance), consistent with genetic variance and covariance (i.e., genetic lines of least resistance; Schluter, 1996). The tendency of populations to evolve along similar lines within species should be considered in evaluating population structure for conservation purposes, and planning reintroduction or recovery efforts of extirpated or depleted populations (c.f. Crandall et al., 2000).

In conclusion, the kinds of processes we have described have presumably taken place repeatedly during the evolution of salmonid fishes but are not unique to them. Some degree of site fidelity or philopatry is common among animals but environmental conditions periodically render sites uninhabitable, create new habitats, or facilitate dispersal. These might be slow processes such as glaciation and sea level change, rapid and dramatic ones such as volcanic eruptions and earthquakes, or anthropogenic processes such as the construction or breaching of dams. In each case, organisms are extirpated or virgin territory is made available for colonization. The life history patterns of the species and the mix of biotic and abiotic factors affecting their survival and evolution will vary, but the role founders play in setting the stage for subsequent evolution, the interplay of genotype, plasticity and environment in contributing to selection patterns, the enhancement of isolation, and the potential for both evolutionary diversification and convergence are likely to be universal.

Acknowledgements

Many individuals assisted with the lab and field work and fish culture for this study but we thank especially

Nelson Boustead, Lindsay Hawke, Selwyn Hawke, Fred Lucas, Carole Steele, William Hershberger, Andrew Hendry, Jason Griffith, Brian Beckman, Karl Burton, and Larry Lehman, and the NZ Fish and Game Council. Bob McDowall, Fred Allendorf, Michael Bell, Andrew Hendry, and Chris Wood provided editorial assistance. This study was funded by the Foundation for Research, Science and Technology via Contracts CO1417 and CO1501 (in NZ), and a consortium of utilities, coordinated by Puget Power and Light Company and the H. Mason Keeler Endowment (in the US). Casy Feldmann was instrumental in helping us obtain and maintain financial support.

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