

ORIGINAL ARTICLE

Correlated contemporary evolution of life history traits in New Zealand Chinook salmon, *Oncorhynchus tshawytscha*MT Kinnison^{1,4}, TP Quinn^{2,4} and MJ Unwin^{3,4}¹School of Biology and Ecology, University of Maine, Orono, ME, USA; ²National Institute of Water and Atmospheric Research Ltd., Christchurch, New Zealand and ³School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA

Size at age and age at maturity are important life history traits, affecting individual fitness and population demography. In salmon and other organisms, size and growth rate are commonly considered cues for maturation and thus age at maturity may or may not evolve independently of these features. Recent concerns surrounding the potential phenotypic and demographic responses of populations facing anthropogenic disturbances, such as climate change and harvest, place a premium on understanding the evolutionary genetic basis for evolution in size at age and age at maturity. In this study, we present the findings from a set of common-garden rearing experiments that empirically assess the heritable basis of phenotypic divergence in size at age and age at maturity in Chinook salmon (*Oncorhynchus tshawytscha*) populations introduced to

New Zealand. We found consistent evidence of heritable differences among populations in both size at age and age at maturity, often corresponding to patterns observed in the wild. Populations diverged in size and growth profiles, even when accounting for eventual age at maturation. By contrast, most, but not all, cases of divergence in age at maturity were driven by the differences in size or growth rate rather than differences in the threshold relationship linking growth rate and probability of maturation. These findings help us understand how life histories may evolve through trait interactions in populations exposed to natural and anthropogenic disturbances, and how we might best detect such evolution.

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Introduction

Age at maturity and size at age are fundamental life history traits that are ultimately shaped by age- and size-specific patterns of mortality and offspring production (Roff, 1992; Stearns, 1992). Other things being equal, earlier maturity increases the probability of survival to reproduction, but larger size, often associated with delayed maturity, confers greater individual reproductive success through increased number or quality of offspring or enhanced competitive ability. Age at maturity and size at age are also linked at a more proximate level, because previous growth or size often provides a physiological cue for maturation (for example, Stearns and Koella, 1986; Thorpe *et al.*, 1998; Morita and Fukuwaka, 2006). These proximate and ultimate relationships raise fundamental questions concerning the degree to which such life history traits evolve independently or in conjunction.

More formally, the proximate relationship between age at maturity and size at age can be described by a threshold trait model relating the odds of surpassing a maturation threshold at a given age to an underlying continuous 'liability' trait that serves as the maturation trigger, in this case size or growth rate (Falconer, 1960; Myers and Hutchings, 1986; Thorpe *et al.*, 1998; Heino *et al.*, 2002). Although some component of variation in liability is often environmentally determined, liability traits are also presumed to possess a heritable component that can in turn serve as a basis for evolution of threshold traits, such as age at maturation. However, this is not the only means by which threshold characters might theoretically evolve; the sensitivity of the threshold relating phenotypes to liability could also change. For maturation, such threshold evolution has recently been conceptualized as a shift in the probabilistic norm of reaction relating maturation odds at a given age to observed size or growth (*sensu* Heino *et al.*, 2002). Overall, this framework presents a complex set of alternative explanations for life history variation in nature. Differences in age at maturity might be attributed to environmental effects on growth, evolutionary changes in growth profiles (that is, liability trait evolution), or evolutionary changes in the probabilistic maturation reaction norm (PMRN) defining age-specific maturation thresholds. In this study, we conducted two

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large-scale common-garden experiments to examine the processes controlling early divergence in size at age and age at maturity in naturalized populations of salmon.

Studies on patterns of age and size at maturity in salmonids have a long history (Ricker, 1972; Gardner, 1976), with many examples of population-specific variation (reviewed in Groot and Margolis, 1991; Quinn, 2005; Garcia de Leaniz *et al.*, 2007). Indeed, such patterns provided some of the earliest evidence for the discreteness of salmon populations (Rich, 1939). Age at maturity is under genetic as well as environmental influences, as shown by controlled breeding studies on various salmonids (reviewed in Carlson and Seamons, 2008). However, these experiments neither directly reveal how rapidly age at maturity can evolve in response to natural or anthropogenic disturbances, nor whether evolution of age at maturity owes largely to liability or threshold evolution. Understanding the basis for life history variation may be important for many species facing natural or anthropogenic stressors, given that age at maturity and size at age also strongly affect demography. However, such knowledge is a particular concern for harvested species, such as salmon, because of questions of resource sustainability in the face of exceptionally rapid trait change (Conover and Munch, 2002; Darimont *et al.*, 2009; Sharpe and Hendry, 2009).

Salmon populations introduced into new habitats provide opportunities to investigate the evolutionary genetics of size at age and age maturity. The establishment of Chinook salmon populations in New Zealand (NZ), from a shared Sacramento River (USA) source, is among the best characterized examples of such an introduction (McDowall, 1994). Phenotypic information collected on adults migrating up several rivers revealed significant differences in life history traits, including age at maturity and size at age (Quinn and Unwin, 1993). A subsequent, large-scale experimental program demonstrated a genetic basis for differences between a subset of populations (Quinn *et al.*, 2001), including the growth of juveniles (Unwin *et al.*, 2000), timing of return migration and spawning (Quinn *et al.*, 2000), egg size and fecundity in females (Kinnison *et al.*, 2001) and morphology of mature males (Kinnison *et al.*, 2003). Overall, population divergence in NZ confers local adaptation in the form of differential survival and reproductive output (Unwin *et al.*, 2003; Kinnison *et al.*, 2008).

This study reports further results from these experiments, testing the primary hypothesis that recently (<100 years) diverged populations display heritable differences in life histories under controlled rearing conditions as well as the subsidiary mechanism by which such divergence might arise. Specifically, our experiments were designed to distinguish among the following scenarios.

- (1) Under shared rearing conditions, the populations do not differ in size, growth profiles or age structure. This outcome would indicate that the phenotypic differences between wild populations in age and size are controlled solely by environmental conditions.
- (2) The populations differ in growth profiles and age at maturation under common rearing but divergence in the traits is linked. For example, divergence in age at maturity might be explained by the liability trait consequences of divergence in size and growth profiles.

- (3) The populations show evidence of heritable divergence in growth profiles or maturation age even after controlling for divergent expression in the other trait. In the case of age at maturation this would occur under evolution of the thresholds defining PMRNs.

Materials and methods

Experimental organisms and sources

Chinook salmon populations in NZ were ancestrally derived from the fall-run Battle Creek stock (Sacramento River system, CA, USA), brought to the Waitaki River system between 1901 and 1907 (McDowall, 1994; Quinn *et al.*, 1996; Kinnison *et al.*, 2002; O'Malley *et al.*, 2007). Spawning salmon were observed in a tributary of the Waitaki system (the Hakataramea River) within a few years, and within 10 years in the other large, glacier-fed rivers on the eastern coast of the South Island. Analyses of population structure based on DNA microsatellite variation indicates that salmon in different drainages now show evidence of partial reproductive isolation (Kinnison *et al.*, 2002; O'Malley *et al.*, 2007), consistent with a high degree of philopatry.

Our study involved two experimental comparisons: between the Glenariffe Stream and Hakataramea River populations, and between the Glenariffe Stream and Poulter River populations. Glenariffe Stream, a spring-fed tributary, joins the Rakaia River 100 km from the sea, the rain-fed Hakataramea River joins the Waitaki River 60 km from the sea and the Poulter River, a rain and snow fed stream, joins the Waimakariri River 95 km from the sea. NZ Chinook salmon show both juvenile life history patterns typical of this species (Healey, 1991); stream-type individuals migrate to sea after a full year of residence in the river system, whereas ocean-type individuals migrate in their first year of life. Examination of scale samples from returning adults indicates that the Glenariffe Stream population is dominated by ocean-type fish (typical of the Battle Creek population), the Hakataramea River population has a mix of the two forms and the Poulter River is dominated by stream-type fish (Quinn and Unwin, 1993; Unwin and Lucas, 1993 and NIWA unpublished data). Importantly, previous studies of spawning age fish in the wild revealed that Hakataramea River salmon tend to be slightly older and larger for their age than the Glenariffe Stream population (Quinn and Unwin, 1993), consistent with general size and age patterns for the overall Waitaki and Rakaia systems, respectively (Quinn *et al.*, 2001). Previous analyses also suggested that older spawners were somewhat more common in samples of Poulter River fish than fish from the Glenariffe population (Unwin *et al.*, 2000).

Glenariffe–Hakataramea experiment

On April 22–23 1994, we spawned salmon from the Hakataramea and Glenariffe study populations and took the gametes to the Silverstream Research Station on the lower Waimakariri River. We used milt from each male to fertilize ova from two females, creating 58 full-sib families within 29 half-sib families, evenly divided between the two populations. Unless otherwise specified, the term 'family' refers to a full-sib family. Age and life history type (ocean or stream type) were determined for all parents by scale pattern analysis (Unwin and

Lucas, 1993) and we preferentially used ocean-type adults of age 3 years (the modal life history type in both populations). All 29 females and 15 males from the Hakataramea River were at the age of 3 years, as were all but two of the Glenariffe females who were at age 4. This conservative design reduced the likelihood of detecting a genetic difference between populations in size and age at maturity but minimized confounding effects associated with variation in parental age. Nevertheless, the Hakataramea fish of both sexes tended to be larger than the Glenariffe fish of the same age (males: 888.7 versus 843.3 mm mean length, $t = 2.62$, $P = 0.013$, two-tailed test; females: 840.8 versus 811.0 mm, $t = 2.16$, $P = 0.036$).

All families were incubated and reared at the Silverstream Research Station (Kinnison *et al.*, 1998), and were progressively culled (randomly) to 400 fish per family. In October 1994 (spring), 6 months after fertilization, all fry were marked with family-specific sequential coded-wire micro-tags inserted into the cranial cartilage. At 12 months after fertilization (April 1995), 50 randomly selected fish from each family at Silverstream were measured (fork length to ± 1 mm), weighed (to ± 0.1 g), and marked with individual passive integrated transponder tags. They were then transferred to Glenariffe and pooled in a single large raceway for long-term rearing and repeated length and weight measurements at 4–5 month intervals for the next 3 years (12, 16, 19, 24, 28, 31 and 36 months). Fish maturation status was assessed annually (and confirmed by spawning or internal examination).

Glenariffe–Poulter experiment

We established full-sib families of Glenariffe and Poulter origin in May (autumn) 1997 by spawning fish from one or both populations on three different dates (Unwin *et al.*, 2000). These dates approximated the peak of spawning in Glenariffe Stream (1 May), late spawning in Glenariffe Stream and peak spawning in the Poulter River (18 May) and late spawning in the Poulter River (29 May). We spawned the fish in this manner, rather than simply spawning all fish at the same time as we did in the Glenariffe–Hakataramea River experiment, because the Poulter River population spawns significantly later than the Glenariffe Stream population and we were concerned that sampling from a single common date might be unrepresentative. We established 14 Glenariffe families on 1 May and another 14 on 18 May, 12 Poulter families on 18 May and 7 more Poulter families on 29 May. Many scales from the Poulter parents were unreadable, so we could not determine their specific age distribution, but Poulter River fish of both sexes tended to be larger than the Glenariffe Stream fish, consistent with an older age distribution (males: 876.1 versus 821.7 mm mean length, $t = 2.35$, $P = 0.023$, two-tailed test; females: 825.0 versus 802.3 mm, $t = 1.16$, $P = 0.251$).

About 500–600 ova from each female were fertilized with milt from a paired male from the same population, and the embryos were incubated at Glenariffe Stream hatchery. The families reared at Glenariffe were eventually culled to 500, 250 and ultimately 55 individuals per family by May 1998, when they were ~12 months of age, passive integrated transponder tagged, measured and pooled in a hatchery raceway for common rearing to maturity. Again, over the next 2 years (that is, their second and third years of life), we examined and

measured all fish at 4–5 months intervals (12, 16, 19, 24, 28, 31 and 36 months). We conducted a final examination at the end of the fourth year of life (30 March 2001), foregoing the 4-monthly sampling regime to minimize handling mortalities and maximize the number of 4-year-old fish available for data collection.

Data analysis

We used contingency tables and χ^2 -tests to compare frequencies of age at maturity between populations, pooling cells as necessary to avoid problems with sparsely represented age classes. We used repeated measures analysis of variance to compare growth trajectories between and within populations for the captive groups in each experiment, based on collated measurements of fork length and weight (log transformed), and for growth rate (percentage body weight per day) for individually passive-integrated transponder-tagged fish during their second and third year of life. Males and females were analyzed separately, and only the two dominant age classes for each sex, (ages 3 and 4 for females, and 2 and 3 for males) were analyzed because few families included 2-year-old females, 4-year old males or 5-year-olds of either sex.

For the Glenariffe–Hakataramea experiment, the most general model we used was

$$Y_{ijkmn} = \mu + \text{date}_i + \text{origin}_j + \text{age}_k + \text{origin}_j \\ \times \text{age}_k + \text{sire}_{m(j)} + \text{dam}_{n(m(j))} + \varepsilon_{ijkmn} \quad (1)$$

where Y is the response variable of interest; date_i denotes calendar date of measurement; origin_j denotes population of origin; age_k denotes age at maturity; $\text{sire}_{m(j)}$ denotes sire nested within population of origin; $\text{dam}_{n(m(j))}$ denotes dam nested within sire within population; and μ , ε denote mean and error terms, respectively. For data sets including only one age class, terms in age_k were deleted. For the Glenariffe–Poulter experiment, our most general model was

$$Y_{ijkop} = \mu + \text{date}_i + \text{origin}_j + \text{age}_k + \text{origin}_j \\ \times \text{age}_k + \text{spawn}_{o(j)} + \text{Fam}_{p(o(j))} + \varepsilon_{ijkop} \quad (2)$$

where sire and dam are dropped from the model, $\text{spawn}_{o(j)}$ denotes spawning date nested within population and $\text{Fam}_{p(o(j))}$ denotes family nested within spawning date. When interpreting the results, our primary concern was the significance of the main factors, the origin \times age interaction, and the temporal trends for successive repeated measures in relation to population and age at maturity.

To assess the possible roles of liability trait (growth history) or threshold (PMRN) evolution as the basis for divergence in mean age at maturation, we constructed logistic regression models describing the odds of maturing at the modal maturation age in both males (age 2) and females (age 3). For each sex and experiment, we first assessed logistic models containing only the effect of population (or population and spawning date for the Glenariffe versus Poulter study). We then also assessed full models that further incorporated the size and growth histories of all individuals over the year preceding maturation. Because it is unclear whether length, weight or growth rate provides the proximate cue(s) for maturation, we included comprehensive length, weight

and growth rate histories in our models. The basic form for these logistic models was:

$$\begin{aligned} \text{logit}(p) &= \log_e \left(\frac{p}{1-p} \right) \\ &= c_0 + c_1 \text{Pop} + c_n \text{size}_t + c_{n+1} \text{growth}_{t-1,t} \end{aligned} \quad (3)$$

where p is the probability of maturation at the focal age, c_0 is a constant, c_1 is the coefficient for the population effect, and c_n and c_{n+1} are coefficients for the n th size (length or weight) and intervening growth parameters at various times t , or time intervals $t-1$ to t , respectively. An additional term, $c_2 \text{date}$ was included to account for differences in the creation date of different families in the Glenariffe versus Poulter experiment. For males, full models included lengths and weights at 12, 16 and 19 months of age, as well as growth rates in length and weight from 12 to 16 months and 16 to 19 months. For females, the full models included lengths and weights at 24, 28 and 31 months, as well as growth rates from 24 to 28 and 28 to 31 months. We did not include the final sizes of individuals at maturation (24 months for males and 36 months for females) or their growth during the final period preceding maturation because (1) maturation is primarily determined by growth or size characteristics during the preceding spring and fall (Thorpe, 1986; Silverstein *et al.*, 1998), and (2) size and growth become themselves dependent on physiological and morphological preparations for reproduction in the months immediately preceding maturation (for example, migration, gonad development, secondary sexual trait development, anorexia—for example, Hendry *et al.*, 2000; Kinnison *et al.*, 2001, Kinnison *et al.*, 2003). Statistical significance of model terms was evaluated using Wald χ^2 ($df = 1$).

Size and growth attributes are often highly correlated, hence, we further performed backward stepwise regressions ($P \geq 0.05$ for removal), starting with the full models, to obtain more parsimonious solutions with less multicollinearity. These stepwise models were compared with identical models in which population of origin was either added or subtracted, depending on the stepwise solution. The performance of alternate logistic models was assessed on the basis of changes in Akaike's information criterion (AIC) and the amount of error variance in maturation explained by size and growth histories was inferred from Nagelkerke's pseudo- R^2 ($N-R^2$). Models that differed from the best stepwise solution by $\Delta \text{AIC} < 2.0$ were considered to have effectively equivalent support, whereas ΔAIC values of ≥ 4.0 or ≥ 10.0 were considered modest to strong support for differences in model plausibility, respectively.

The nested mating design in the Hakataramea versus Glenariffe experiment permitted estimation of genetic variances and covariances for computation of quantitative genetic parameters. We focused our variance components analyses on length and incidence of maturation at age 2 in males and age 3 in females, for the reasons outlined above. We estimated heritabilities (h^2) for size at age and age at maturity from the sire-variance components obtained using restricted maximum likelihood. To maximize our power for estimating variances and covariances, we used estimation models that included population and maturity status (mature/not-mature) as fixed effects. The linear model was thus as

follows:

$$Y_{jmnq} = \mu + \text{origin}_j + \text{sire}_{m(j)} + \text{dam}_{n(m(j))} + \text{Mat}_q + \varepsilon_{jmnq} \quad (4)$$

where origin_j , $\text{sire}_{m(j)}$ and $\text{dam}_{n(m(j))}$ are as defined for equation 1 and Mat_q is a bivariate factor defining maturation status at that age (0 = immature, 1 = mature). In the case of age at maturation, h^2 values were initially estimated on the observed scale but were then converted to values on the underlying liability scale (equation 25.8b of Lynch and Walsh, 1998).

We estimated the genetic correlation between male length at age 2 and female length at age 3 from the covariance of mean family length residuals of half-sib families (Lynch and Walsh, 1998). Although we did not estimate genetic correlations between the sexes on the liability scale for age at maturity, we did estimate the correlation of residual (accounting for population effects) arcsin square-root-transformed incidences of male and female maturation across all half-sib family pairs (averaging the reciprocal correlations). We assessed potential genetic correlations between size at maturation and age at maturation by considering correlations of family means for both rearing experiments, and, in the case of the Hakataramea–Glenariffe comparison by further assessing the relative correspondence of half-sib family values in size and age space.

Results

Glenariffe–Hakataramea experiment

Of the fish with passive-integrated transponder tags, 2331 provided information on age at maturity, which ranged from 2 to 5 years (Table 1). Glenariffe males held in captivity tended to mature at an older age than their Hakataramea counterparts ($\chi^2 = 14.42$, $df = 2$, $P < 0.001$) but females displayed the opposite pattern (Glenariffe females matured at a younger age: $\chi^2 = 11.43$, $df = 2$, $P = 0.003$; Table 1).

Immature and maturing fish of a given age differed markedly in size. Males maturing in April 1996 at age 2 were 19.9 ± 3.0 mm (Glenariffe) to 27.3 ± 3.2 mm (Hakataramea) longer at this time than males destined to mature at age 3 (Figure 1a), and females destined to mature at age 3 were 13.7 ± 1.8 – 16.4 ± 1.9 mm longer at this time than females that would mature at age 4. The following year, females maturing at age 3 were 74.7 ± 3.1 – 76.3 ± 3.0 mm longer than those which did not mature until age 4 (Figure 1b). Glenariffe fish were generally larger than Hakataramea fish of the same age, at virtually all stages of the experiment, even after controlling for differences in eventual age at maturation. These differences were apparent in both sexes, but were of variable significance ($P < 0.001$ to $P = 0.55$). During

Table 1 Age at maturity, expressed as % of the sample, of Chinook salmon from the Glenariffe Stream and Hakataramea River populations, held in captivity until they matured

Sex	Population	Age				Sample
		2	3	4	5	
Female	Glenariffe	0.7	70.4	27.4	1.5	547
	Hakataramea	0.9	60.5	37.0	1.5	527
Male	Glenariffe	81.2	16.6	1.5	0.7	613
	Hakataramea	88.0	11.5	0.2	0.3	644

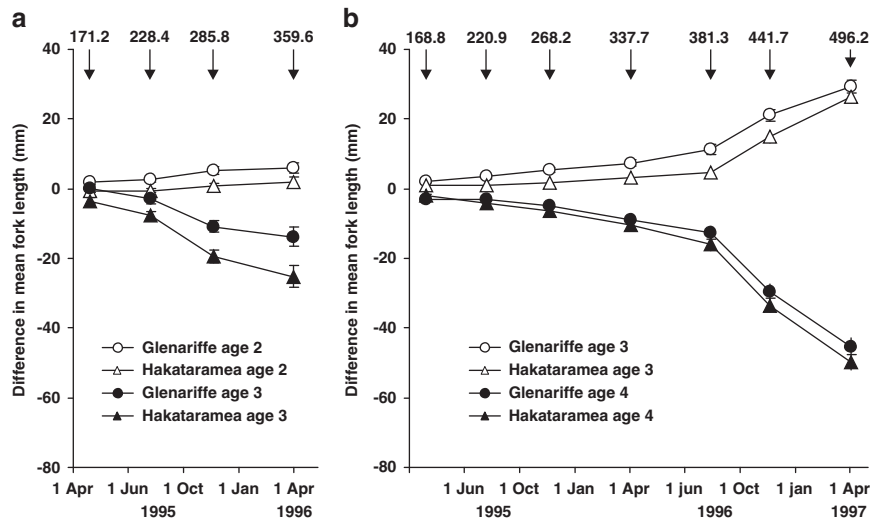


Figure 1 Size at age trajectories for captive reared Chinook in the Glenariffe versus Hakataramea experiment, based on repeated FL measures of individually tagged fish at 3–4 month intervals. Results shown are for 2- and 3-year-old males during the second year of life (a), and 3- and 4-year-old females during the second and third year of life (b). Results are shown as the difference (\pm s.e.) between the trajectory for each population \times age class and the grand mean for each sampling period (as shown on the horizontal axis above each plot), thus emphasizing the differences between trajectories rather than the trajectories themselves. For example, in April 1995, Hakataramea males destined to mature at age 3 averaged 3.5 ± 1.0 mm less than the grand mean for this period (171.2 mm), that is, 167.7 ± 1.0 mm.

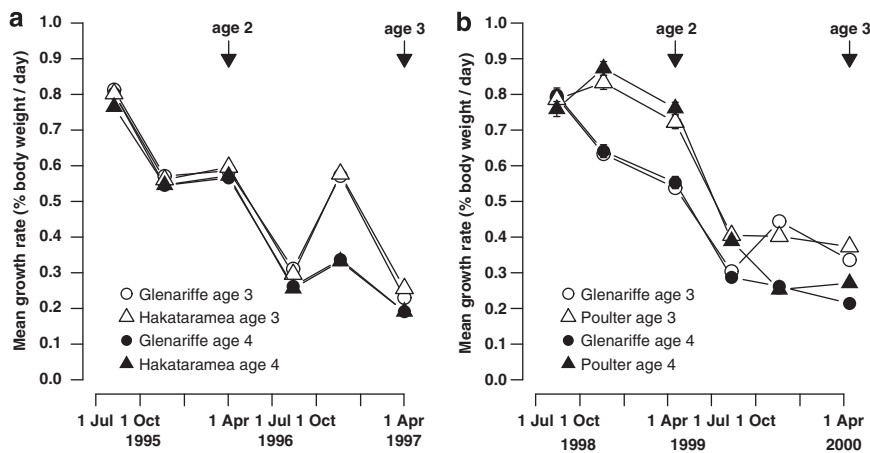


Figure 2 Age-specific growth trajectories for captive reared Chinook in the Glenariffe versus Hakataramea experiment (a) and Glenariffe versus Poulter experiment (b), based on repeated measures of individually tagged females at 3–4 month intervals during their second and third year of life. The dates along the horizontal axis indicate the end of the period to which each growth rate datum refers; thus the data for April 1996 represent average growth rates since the previous (November 1995) measure. Vertical bars denote 1 s.e.

their second year of life, Glenariffe males were longer than Hakataramea males by an average of 2.6 ± 0.6 – 4.5 ± 1.2 mm for individuals maturing at age 2, and 3.5 ± 1.4 – 11.5 ± 4.0 mm for individuals maturing at age 3 (Figure 1a). For females during their second and third years, the corresponding figures were 1.3 ± 0.6 – 6.4 ± 1.9 mm for individuals maturing at age 3, and 1.1 ± 1.1 – 4.6 ± 3.3 mm for individuals maturing at age 4 (Figure 1b). The sole exception to this trend occurred at the start of the experiment in May 1995, when 1-year-old Hakataramea females destined to mature at age 4 were 0.8 ± 0.9 mm longer than their Glenariffe counterparts. Population level differences of similar magnitude were also apparent in analyses of actual size at maturation, after controlling for age (males maturing at age 3 and females maturing at age 4), and for analyses based on weight rather than length.

Comparisons of growth rates based on repeated measures analysis suggest that growth rate differences

between populations were modest in contrast to differences in size (Figure 2a). Population \times age interactions were not significant ($F_{1, 857} \leq 1.53$, $P \geq 0.17$) in any analyses involving multiple age classes, nor were population effects for repeated measures comparisons involving males ($F_{1, 560} \leq 0.81$, $P \geq 0.52$). Population level effects on growth were detected in females ($F_{1, 4430} = 3.82$, $P = 0.002$), although less pronounced than those associated with age at maturity (Figure 2; $P < 0.001$ in all available polynomial contrasts for both males (linear, quadratic and cubic) and females (up to sixth degree)). Family level (sire and dam) effects were also highly significant in all repeated measures analyses (for example, 3-year-old males: $F_{80, 560} = 2.07$, $P < 0.001$; 3- and 4-year-old females, $F_{125, 4430} = 5.92$, $P < 0.001$).

Consistent with differences in frequencies of maturation by age, logistic models containing only population effects indicated that Glenariffe males were less likely ($P < 0.001$; odds ratio: 0.59 ± 0.09) to mature at a younger

Table 2 Logistic model outcomes describing the odds of early maturation (age 2 in males and age 3 in females) for Glenariffe versus Hakataramea contrasts

Model	Glenariffe versus Hakataramea Terms (<i>P</i> -values and odds effects)	N-R ²	AIC	ΔAIC
<i>Males</i>				
Population	<i>Pop</i> < 0.001	0.017	1232.87	495.15
Full model	<i>Pop</i> < 0.001, <i>F</i> 12 < 0.001, <i>F</i> 16 = 0.131, F19 = 0.053 , W12 = 0.003 , W16 = 0.929 , <i>W</i> 19 = 0.490, <i>GF</i> 16 < 0.001, <i>GF</i> 19 = 0.023, GW16 = 0.001 , GW19 = 0.003	0.534	739.55	1.83
Backwards+population ^a	<i>Pop</i> = 0.018, <i>F</i> 12 < 0.001, F19 < 0.001 , W12 < 0.001 , <i>GF</i> 16 < 0.001, <i>GF</i> 19 < 0.001, GW16 < 0.001 , GW19 < 0.001	0.531	737.72	—
Backwards–population	<i>FL</i> 12 < 0.001, FL19 < 0.001 , W12 < 0.001 , <i>GF</i> 16 < 0.001, <i>GF</i> 19 < 0.001, GW16 < 0.001 , GW19 < 0.001	0.523	741.39	3.67
<i>Females</i>				
Population	Pop < 0.001	0.015	1356.53	1189.25
Full model	Pop = 0.133 , <i>F</i> 24 = 0.496, <i>F</i> 28 = 0.873, F31 = 0.460 , W24 = 0.633 , W28 = 0.210 , <i>W</i> 31 = 0.118, <i>GF</i> 28 = 0.391, <i>GF</i> 31 = 0.467, GW28 = 0.238 , GW31 = 0.001	0.940	176.48	9.20
Backwards+population	Pop = 0.204 , W28 = 0.002 , <i>GF</i> 28 = 0.002, GW28 < 0.001 , GW31 < 0.001	0.939	167.64	0.36
Backwards–population ^a	W28 = 0.003 , <i>GF</i> 28 = 0.003, GW28 < 0.001 , GW31 < 0.001	0.938	167.28	—

Abbreviations: AIC, Aikiake’s information criterion; Pop, population; F no. or W no., fork length or weight at the specified month number; GF no. or GW no., growth in fork length or growth in weight during the interval leading up to the specified month number; N-R², Nagelkerke’s R².

Model terms, *P*-values, N-R², AIC and deviations in AIC (that is, ΔAIC) from the model with lowest AIC score are presented for each model and sex. Backwards stepwise models are depicted with and without population effects to better assess contribution to model performance. Model terms depicted in bold had positive marginal effects on odds of early maturation, those presented in italics had negative marginal effects on early maturation. Population effect reflects influence of a fish being of Glenariffe origin as opposed to Hakataramea origin.

^aMost parsimonious model identified under backwards stepwise regression.

age and females more likely (*P* < 0.001; odds ratio: 1.55 ± 0.20) to mature at a younger age, than their Hakataramea counterparts (Table 2). That said, these models explained < 2% of the variation in probability of maturation. Addition of individual growth profiles improved the explanatory power of maturation models (that is, lower AIC, large ΔAIC values), to roughly 53% in males and 94% in females (Table 2). Importantly, however, addition of individual growth histories eliminated the statistical significance of the population effect for females, causing it to be dropped from the most parsimonious stepwise model. Conversely, the addition of individual growth histories did not eliminate population effects on maturation in males (*P* = 0.018; odds ratio: 0.63 ± 0.12), a result consistent with divergence in the probabilistic norm for maturation. In both sexes, stepwise models suggested positive effects of weight or growth rate in weight, and negative effects of length (except F19 in males) or growth rate in length on odds of maturation (Table 2). Given that these partial coefficients must be interpreted with respect to one another, this pattern suggests that individual condition factor and changes in condition had particularly important roles in maturation during this experiment (see also Uusi-Heikkiä *et al.*, 2010).

Heritabilities for all traits were relatively large, but consistent with values for other traits in NZ salmon (Kinnison *et al.*, 2008). For male length at age 2 and female length at age 3, estimates of *h*² (± s.e.) were 0.680 ± 0.277 and 0.599 ± 0.234, respectively. The genetic correlation for size at age in the two sexes was statistically significant and quite large (0.821; *F*_{1, 26} ≥ 5.80, *P* ≤ 0.024), despite sex differences in modal age of maturation. Heritabilities on the liability scale for maturation at age 2 (versus older) in males and at age 3 (versus older) in females were 0.408 ± 0.319 and 1.239 ± 0.512, respectively. The latter estimate exceeds unity and thus suggests some overestimation bias, but the associated

confidence interval (0.727–1.851) is biologically meaningful and consistent with the trait being strongly heritable. The genetic correlation (0.594) for incidence of male (age 2 versus older) and female (age 3 versus older) maturation on the observed scale (not liability scale) was not statistically significant (*F*_{1, 26} ≤ 2.75, *P* ≥ 0.109).

Supporting the logistic models, an inverse relationship between age at maturity and body size was apparent from a scatter plot of family specific means for females (Figure 3a), with a moderate negative correlation (*r* = −0.409) between mean length at age 2 and mean age at maturity. No such relationship was apparent for males (*r* = 0.069; Figure 3b). Mean ages at maturity for males and females from the same family were relatively weakly correlated (*r* = 0.303; Figure 3c). However, all three scatter plots relating size and age at maturity for families from the same half-sib pair suggest some tendency for each pair to lie close to each other in age × size space (Figures 3a and b) and age × age space (Figure 3c). A bootstrap analysis, in which we compared the mean spatial separation between all 28 half-sib pairs (based on standardized means for length and age at maturity) with the mean separation for 10 000 sets of 28 randomly chosen pairs from the same data set was consistent with this tendency, with the actual pairs lying closer together than the randomly chosen pairs in 99.79, 99.82 and 99.46% of the simulations corresponding to Figures 3a, b and c, respectively. Such half-sib associations support a heritable correlation between size at age and odds of maturation in these fish.

Glenariffe–Poulter experiment

A greater proportion of Poulter population salmon matured at an older age than the Glenariffe population for both males ($\chi^2 = 78.56$, *df* = 2, *P* < 0.001) and females ($\chi^2 = 55.38$, *df* = 2, *P* < 0.001). Specifically, Glenariffe

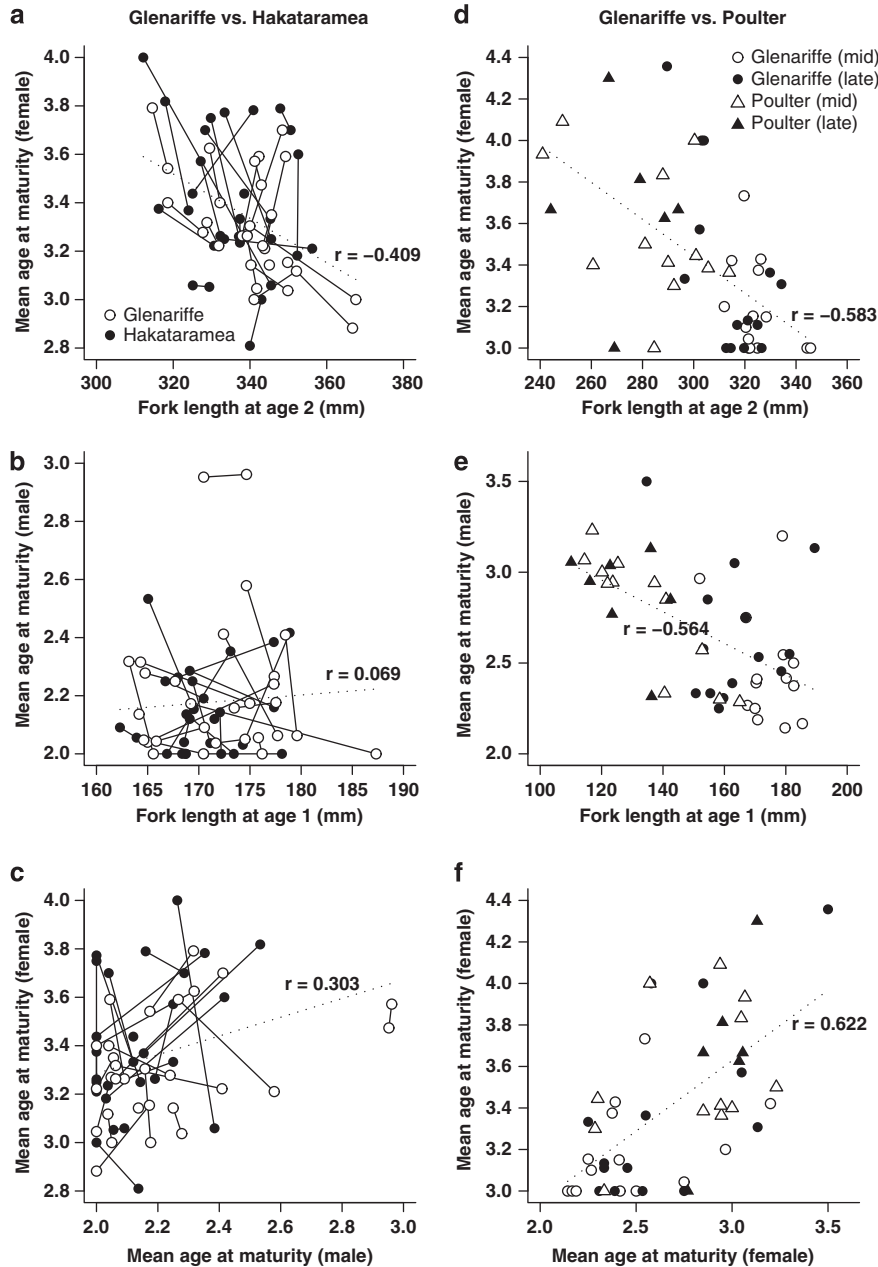


Figure 3 Correlations between family specific mean age at maturity, and mean fork length at age 2 (for females) or age 1 (for males), and between mean age at maturity for males and females from the same family, for captive reared Chinook from the Glenariffe versus Hakataramea experiment (a–c), and the Glenariffe versus Poulter experiment (d–f). Linear regressions for each plot are indicated by dashed lines, and families from the same half-sib pair in the Glenariffe versus Hakataramea experiment are connected by solid lines.

males were evenly split between ages 2 and 3, whereas the great majority of Poulter males matured at age 3. Glenariffe females matured primarily at age 3 with a smaller proportion at age 4, whereas more Poulter females matured at age 4 than age 3 (Table 3). We also detected an effect of date when parents were spawned (to create the experimental groups) on their offspring's frequency of maturation at different ages. For both populations, a higher proportion of progeny of salmon spawned early in the season matured at a younger age than the progeny of parents of the same population spawned later (Poulter females: $\chi^2 = 5.43$, $df = 2$, $P = 0.066$, Poulter males: $\chi^2 = 5.75$, $df = 2$, $P = 0.056$,

Glenariffe females: $\chi^2 = 20.05$, $df = 2$, $P < 0.001$, Glenariffe males: $\chi^2 = 13.88$, $df = 2$, $P = 0.001$).

Glenariffe fish were larger (both longer and heavier) than Poulter fish of the same age at all stages of the experiment, for both sexes (Figure 4a). In contrast to the Hakataramea–Glenariffe results, these size differences were strikingly large, and were of similar magnitude to those associated with different maturation ages within populations. For the purposes of presenting these results in detail, we focused on 3- and 4-year-old females during their second and third year of life, as these analyses (which include a population \times age interaction) encapsulate all the major trends we observed over the longest

period (Figures 2b and 4). Glenariffe females were larger at maturity than Poulter females throughout the study period, by 23–45 mm for fish maturing at age 3, and 30–51 mm for fish maturing at age 4 (Figure 4a). These differences were well established by the first sampling period (at age 12 months), and became increasingly apparent in all subsequent samples. At the end of their second year of life (April 1999), Glenariffe females destined to mature at age 3 were, on average, 30.8 ± 3.3 mm larger than their Poulter counterparts. At the end of their third year, maturing Glenariffe females were 24.7 ± 4.8 mm larger than maturing Poulter females, and among females destined to mature at age 4 those of Glenariffe origin were 30.2 ± 5.1 mm larger than those of Poulter origin. However, a strong ($F_{6,2910} = 176.2$, $P < 0.001$) population \times age interaction was also apparent, indicating that size (and hence growth) trajectories differed between the two populations. In the context of Figure 4a, this difference appears as a strong tendency, consistent in both age classes, for the size difference between Glenariffe and Poulter fish of the same age to reach a maximum (45.3 ± 3.4 – 52.2 ± 4.2 mm) in August 1998, midway through the second year of life, but to decline steadily over the next 12 months (to August 1999) and change little thereafter. In terms of growth rates, Glenariffe and Poulter fish grew at similar rates from age 12 to 16 months (April to August 1998), after which Poulter fish of both age classes grew markedly faster than their Glenariffe equivalents until August 1999 that is, austral winter), at the beginning of their third year of life (Figure 2b). Subsequent growth

rates were strongly influenced by whether or not fish matured at the end of their third year, but were similar for both populations within each age class.

The date on which parental fish were spawned to create our experimental groups had a significant ($F_{12, 2910} = 5.62$, $P < 0.001$) and consistent effect on size at age in both populations (Figure 4b), but this effect was much smaller than the effects of population and age at maturity. Averaged across both age classes, fish from the later spawning group within each population were typically about 10 mm shorter (range 6–14 mm) than those from the earlier group.

The logistic model assessments for the Glenariffe versus Poulter captive comparison provided somewhat analogous findings to females under the Glenariffe versus Hakataramea comparison, but there were some noteworthy differences (Table 4). Population only models again supported χ^2 analyses in showing higher odds of early maturation of Glenariffe males and females ($P < 0.001$; male odds ratio: 4.09 ± 0.68 ; female odds ratio: 3.92 ± 0.74). In this case, population alone explained more variation in maturation odds (~12–13%) than witnessed in the Hakataramea–Glenariffe experiment. Likewise, the addition of information on when these fish were produced (that is, parental spawning date) further improved these base models, with later spawning date having a significant negative effect on odds of early maturation ($P \leq 0.003$). Again, addition of individual size and growth histories provided much improved models (Table 4) that explained 78–82% of fish maturation. As with females in the previous experiment, the addition of individual size and growth histories also resulted in loss of significance of the population term and exclusion of the term from the most parsimonious stepwise models (Table 4). The same was true of the parental spawning date term. Unlike the previous experiment, the effects of length or growth in length were less consistently negative and effects of weight or growth in weight were less consistently positive (weight) or included in the stepwise models (growth in weight).

Family level effects were significant in all repeated measures analyses of growth profiles (for example, 3- and 4-year-old females: $F_{210, 2910} = 3.38$, $P < 0.001$).

Table 3 Age at maturity, expressed as % of the sample, of Chinook salmon from the Glenariffe Stream and Poulter River populations, held in captivity until they matured

Sex	Population	Age				Sample
		2	3	4	5	
Female	Glenariffe	0.0	80.0	20.6	1.4	368
	Poulter	0.0	46.5	52.3	1.2	172
Male	Glenariffe	48.3	48.3	3.4	0.0	447
	Poulter	17.8	77.5	4.8	0.0	337

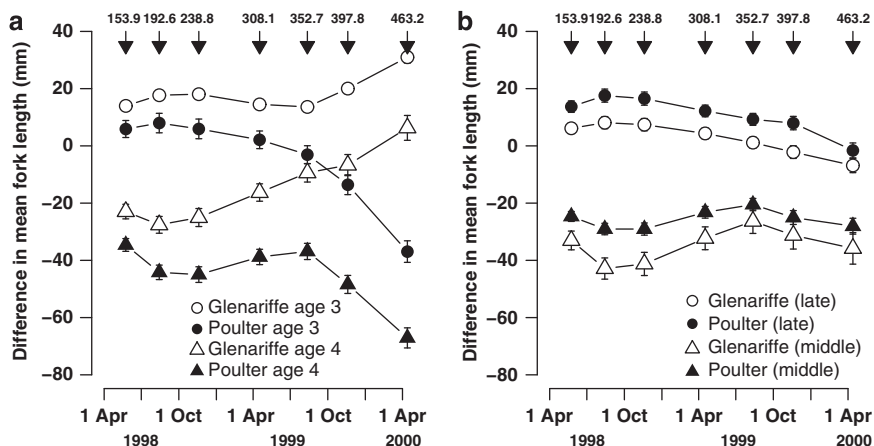


Figure 4 Relative growth trajectories for captive reared Chinook in the Glenariffe versus Poulter experiment, based on repeated fork length measures of individually tagged fish at 3–4 month intervals. Results shown are for 3- and 4-year-old females during the second and third year of life, showing the population \times age interaction (a), and the influence of spawning date within each population (b). The convention used to plot each datum is described in the caption to Figure 1.

Table 4 Logistic model outcomes describing the odds of early maturation (age 2 in males and age 3 in females) for Glenariffe versus Poulter contrasts

Model	Glenariffe versus Poulter Terms (P-values and odds effects)	N-R ²	AIC	ΔAIC
<i>Males</i>				
Population	Pop < 0.001	0.129	971.04	631.62
Population+date	Pop < 0.001, Date = 0.003	0.142	964.31	624.89
Full model	Pop = 0.143, Date = 0.587, F12 < 0.001, F16 = 0.263, <i>F19 = 0.039, W12 = 0.031, W16 = 0.006, W19 < 0.001,</i> GF16 = 0.155, GF19 = 0.416, GW16 = 0.693, GW19 = 0.774	0.815	344.98	5.56
Backwards+population	Pop = 0.178, F12 < 0.001, F16 = 0.006, F19 < 0.001, W12 = 0.003, <i>W16 < 0.001, W19 < 0.001, GF16 = 0.016, GF19 = 0.010</i>	0.813	339.66	0.24
Backwards–population ^a	F12 < 0.001, F16 = 0.003, F19 < 0.001, W12 = 0.002, <i>W16 < 0.001, W19 < 0.001, GF16 = 0.032, GF19 = 0.009</i>	0.813	339.42	—
<i>Females</i>				
Population	Pop < 0.001	0.123	700.19	433.54
Population+date	Pop = 0.008, Date < 0.001	0.177	676.94	410.29
Full model	<i>Pop = 0.082, Date = 0.376, F24 < 0.049, F28 = 0.096,</i> <i>F31 = 0.557, W24 = 0.059, W28 = 0.030, W31 < 0.500,</i> <i>GF28 = 0.049, GF31 = 0.446, GW28 = 0.032, GW31 = 0.337</i>	0.788	271.29	4.64
Backwards+population	<i>Pop = 0.133, F24 = 0.049, F28 = 0.025, W24 = 0.047, W28 = 0.021,</i> <i>GF28 = 0.045, GF31 = 0.029, GW28 = 0.018, GW31 < 0.001</i>	0.787	266.65	—
Backwards–population ^a	<i>F24 = 0.037, F28 = 0.018, W24 = 0.038, W28 = 0.016,</i> <i>GF28 = 0.037, GF31 = 0.023, GW28 = 0.014, GW31 < 0.001</i>	0.784	266.97	0.32

Abbreviations: AIC, Aikake's information criterion; Pop, population; date, parental spawning date; F no. or W no., fork length or weight at the specified month number; GF no. or GW no., growth in fork length or growth in weight during the interval leading up to the specified month number; N-R², Nagelkerke's R².

Model terms, P-values, N-R², AIC and deviations in AIC (that is, ΔAIC) from the model with lowest AIC score are presented for each model and sex. Backwards stepwise models are depicted with and without population effects to better assess contribution to model performance. Model terms depicted in bold had positive marginal effects on odds of early maturation, those presented in italics had negative marginal effects on early maturation. Population effect reflects influence of a fish being of Glenariffe origin as opposed to Poulter origin.

^aMost parsimonious model identified under backwards stepwise regression.

Negative correlations between family means for age at maturity and body size at age were also significant for both sexes (females: $r = -0.583$, $N = 47$, $P < 0.001$; males: $r = -0.564$, $N = 47$, $P < 0.001$), but were strongly influenced by population level effects (Figures 3d and e). Likewise, mean age at maturity for males and females from the same family were strongly correlated ($r = 0.622$, $N = 47$, $P < 0.001$), largely because of the underlying population effect (Figure 3f). However, these plots also show considerable differences between families within each population and spawning date.

Discussion

Our primary objective was to determine whether population differences in life histories observed in wild NZ Chinook salmon (Quinn and Unwin, 1993) result from environmental plasticity or heritable divergence since the species was introduced in the early 1900s (~26 generations). Two consecutive, controlled-rearing studies revealed heritable population differences in age at maturity and size at age, especially between the Glenariffe and Poulter River populations. These findings refute the first scenario presented in the introduction. Population effects often accounted for a relatively modest proportion of total variation in size or age at maturity, but this is not unexpected given the contemporary nature of divergence, family-level variation (see also Unwin *et al.*, 2000) and environmental influences. Indeed, population level variation often compared favorably with other sources, such as the date when individuals were produced.

A subsidiary objective of our study was to assess the relative independence of evolution of size at age and age at maturation, and in so doing the relative importance of alternate evolutionary pathways underlying life history divergence (that is, scenario 2 versus scenario 3). Whereas divergence in size at age was commonly apparent after controlling for age at maturation, only male salmon in the Hakataramea–Glenariffe comparison showed evidence of divergence in age at maturation after controlling for individual growth histories (that is, support for scenario 3). All other contrasts suggested that divergence in age at maturity resulted largely from correlated divergence in size and growth trajectories, consistent with a scenario of liability trait evolution (that is, scenario 2).

Correspondence of wild and captive patterns

In most cases, patterns of divergence in age at maturity in captivity mirrored patterns observed or inferred in wild populations. Similar to wild fish, female Glenariffe Stream salmon had higher odds of maturing at younger ages than their Hakataramea River counterparts. An exception to such correspondence was noted for male fish in the Glenariffe–Hakataramea experiment. Captive Glenariffe males tended to mature at a slightly older age than Hakataramea males, in contrast to the phenotypic expression of this trait in the wild (Quinn and Unwin, 1993). Patterns of size at age under captive rearing for this population contrast were also counter to patterns observed at maturity in the wild, where Glenariffe fish tend to be smaller at a given age of maturity than Hakataramea fish.

Differences in expression of age at maturity and size in captivity and in the wild suggest the presence of

important environmental effects that interact with heritable population differences to mediate trait expression in nature. It is beyond the scope of this study to assess the full suite of local environmental factors and life history interactions that might complicate population differences in the wild. However, even without such comprehensive insights, our use of common-garden rearing experiments makes it amply apparent that life history evolution has occurred in these populations as they diverged from a recent common ancestral source.

In contrast to the Glenariffe versus Hakataramea study, the Glenariffe Stream and Poulter River fish of both sexes showed patterns of divergence in captivity that were more fully consistent with their wild counterparts. The colder and less productive conditions of the Poulter River are expected to slow juvenile growth, and we have previously suggested that natural selection has favoured the slower growing stream-type life history under these growth-limited conditions (Unwin *et al.*, 2000). Maturity at age 4 was also more common in samples of wild Poulter River fish compared with Glenariffe fish (Unwin *et al.*, 2000). Hence, evolutionary and environmental effects seem to function in accordance in this population contrast.

Mechanisms of life history divergence

A relationship between growth or size and age at maturation has been recognized in fishes, including Chinook salmon, for decades (for example, Parker and Larkin, 1959) and has often been depicted in a threshold framework (for example, Myers and Hutchings, 1986; Thorpe *et al.*, 1998). Although terminology has sometimes varied, the central premise is that size or growth function as proximate 'liability' cues to determine the physiological decision to mature at some evolutionarily determined threshold. In practice, such thresholds are not discrete but probabilistic across a range of age, size and growth values (Heino *et al.*, 2002). Inclusion of detailed growth histories eliminated the effect of population in most logistic models in this study (that is, Hakataramea versus Glenariffe females and both sexes for Poulter versus Glenariffe), suggesting that liability trait evolution predominated as the mechanism accounting for divergence in age at maturity. In each of these population contrasts, the population with higher odds of early maturation was also the population that tended to show larger size at age or faster growth in the preceding year. The high h^2 for size and age at maturity in both sexes suggest that these traits should respond readily to selection. A correlated evolutionary response between divergence in size profiles and divergence in age at maturity is also expected on the basis of negative genetic correlations implied by most of our half-sib and full-sib association analyses.

The results from the differently timed groups of Poulter and Glenariffe families further support the role of size and growth on maturation rather than differences in maturation thresholds. Families spawned earlier began to feed earlier and were consistently larger at a given date than those spawned later, and consequently tended to mature at a younger age. This finding contributes to the growing literature emphasizing the importance of parental breeding date for reproductive success in wild populations (Anderson *et al.*, 2010, and references therein).

Several lines of evidence support a different outcome for male salmon in the Hakataramea–Glenariffe experiment. Population effects remained significant in the most parsimonious stepwise model linking maturation odds and growth history. This indicated that evolutionary divergence in age of maturity involved a change in probabilistic maturation thresholds independent of liability trait evolution (scenario 3). The Glenariffe males were larger at age but had lower odds of early maturation, contrary to the pattern predicted under a liability model, and the pattern found in other combinations of sex and population. The negative genetic correlation between size and age at maturation observed in other groups was not apparent in these males. Likewise, although there was a strong genetic correlation for size at age in males and females, the genetic correlation for size and age at maturity was not statistically significant, implying more opportunity for maturation thresholds to evolve independently in the two sexes.

The question remains as to specifically why contemporary evolution took the form of divergence in the PMRN for males in this population contrast. However, such evolution is likely not unprecedented in salmon. Within their native range, Chinook salmon vary greatly in the age and size at maturity (Roni and Quinn, 1995; Quinn, 2005). In Chinook, as with other species of salmon, there is evidence that wild populations differ in not only growth rate at sea but in the relationship between growth and maturation at various ages (Quinn *et al.*, 2009). Given enough time, or the right suite of selective conditions, threshold evolution may take on greater importance.

Broader implications

The PMRN approach has received considerable attention as a way to discern evolutionary changes in wild fish populations facing size- and age-selective harvest (for example, Olsen *et al.*, 2004; Hutchings, 2005; but see Morita and Fukuwaka, 2006; Morita *et al.*, 2009), although it has received less attention in salmonids than other fishes (see Hutchings, 2011). The premise of such work is that changes in PMRNs are more likely than raw phenotypic differences to reflect evolution, independent of plastic factors that affect growth or size (for example, reduced competition, climate variation and so on). Because we used the same logistic regression approach used to define PMRNs in wild populations, we can begin to assess the power of the PMRN approach to detect contemporary evolution under a 'best case scenario'—a common-garden experiment with comprehensive accounting of individual size and growth profiles.

Our findings support that significant evolution of age at maturity can occur that would likely not be detected by a classical PMRN approach. Liability trait (size and growth) evolution was a far more frequent cause of contemporary evolution of age at maturity. One might thus infer that the PMRN approach is conservative for detecting contemporary evolution (high risk of type II error). However, surveys of wild populations rarely if ever achieve the high-resolution multivariate size and growth data afforded by our experiments. Our logistic models explained upwards of 94% of variation in the odds of maturation, and always indicated complex marginal contributions of length, weight and growth rates at various time points. Less detailed size and

growth data could be expected to lead to more variable inferences, including type I errors. As it turns out, such errors were common for inferences of PMRN divergence in supporting logistic analyses based on length or weight at single ages (MT Kinnison, unpublished data). This study thus joins others (for example, Morita and Fukuwaka, 2006, Morita *et al.*, 2009, Uusi-Heikki *et al.*, 2010) in suggesting some caution in application of PMRN approaches to detect and characterize contemporary evolution in the wild.

This study contributes to a growing body of research demonstrating marked evolution resulting from anthropogenic disturbance (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001; Hendry *et al.*, 2008). Such anthropogenic disturbances may accelerate trait changes in nature relative to natural background rates, particularly for life history traits, such as size at age and age at maturity (Hendry *et al.*, 2008; Darimont *et al.*, 2009). With such dramatic trait changes already wrought by humans, and anticipated for the future (for example, global climate change), the obvious question becomes one of emergent ecological consequences (Stockwell *et al.*, 2003; Kinnison and Hairston, 2007; Post and Palkovacs, 2009; Carlson *et al.*, 2011) and the ongoing sustainability of anthropogenic trait changes (Carlson and Seamons, 2008; Hendry *et al.*, 2008). The evolution of life history traits we have observed in NZ seems thus far sustainable with respect to persistence of these exotic populations, but it remains for future studies to assess the importance of correlated evolution, as evidenced here, in aiding or impeding sustainable evolutionary outcomes.

Conflict of interest

The authors declare no conflict of interest.

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