

# Eco-evolutionary vs. habitat contributions to invasion in salmon: experimental evaluation in the wild

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## Abstract

Although trait evolution over contemporary timescales is well documented, its influence on ecological dynamics in the wild has received much less attention particularly compared to traditional ecological and environmental factors. For example, evolution over ecologically relevant timescales is expected in populations that colonize new habitats, where it should theoretically enhance fitness, associated vital rates of survival and reproduction, and population growth potential. Nonetheless, success of exotic species is much more commonly attributed to ecological aspects of habitat quality and 'escape from enemies' in the invaded range. Here, we consider contemporary evolution of vital rates in introduced Chinook salmon (*Oncorhynchus tshawytscha*) that quickly colonized New Zealand and diverged over c. 26 generations. By using experimental translocations, we partitioned the roles of evolution and habitat quality in modifying geographical patterns of vital rates. Variation in habitat quality within the new range had the greatest influence on broad geographical patterns of vital rates, but locally adapted salmon still exhibited more than double the vital rate performance, and hence fitness, of nonlocal counterparts. The scope of this fitness evolution far exceeds the scale of divergence in trait values for these populations, or even the expected fitness effects of particular traits. These results suggest that contemporary evolution can be an important part of the eco-evolutionary dynamics of invasions and highlight the need for studies of the emergent fitness and ecological consequences of such evolution, rather than just changes in trait values.

*Keywords:* eco-evolutionary dynamics, evolutionary rates, fitness, invasiveness, rapid evolution, salmon

Received 8 February 2007; revision received 10 July 2007; accepted 18 July 2007

## Introduction

Numerous studies have shown that evolution can occur over months to decades in the wild, particularly in the face of anthropogenic perturbations (Hendry & Kinnison 1999; Kinnison & Hendry 2001; Reznick & Ghalambor 2001). Such contemporary evolution erases distinctions of ecological and evolutionary timescales and presents an opportunity for evolution to play a role in the short-term dynamics of populations, communities and ecosystems (Thompson 1998; Fussman *et al.* 2007; Kinnison & Hairston 2007). Such eco-evolutionary dynamics have been a concern for some time in the case of pathogens and agricultural

pests subjected to strong anthropogenic selection (Palumbi 2001). In contrast, relatively little is empirically known about the broader importance of adaptive contemporary evolution to ecological dynamics of populations in the wild. This could represent a critical oversight in applied areas of ecology, such as the growing threat of invasive species (Mack *et al.* 2000; Sakai *et al.* 2001; Stockwell *et al.* 2003; Pimentel *et al.* 2005). Here we employ experimental and heuristic approaches to address the practical significance of an eco-evolutionary perspective in a well-characterized case of contemporary evolution – Chinook salmon (*Oncorhynchus tshawytscha*) in New Zealand (NZ).

In the case of biological invasions and other areas of applied ecology, it is not enough to detect the ecological effects of contemporary evolution; we must also be concerned with effect size. Practitioners of conservation

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biology may question whether the small trait changes that characterize most cases of contemporary evolution (Kinnison & Hendry 2001) really merit practical attention (Kinnison *et al.* 2008). In the case of biological invasions, aspects of habitat quality, such as abiotic conditions or 'escape-from-enemies', may be considered more acute concerns (Mack *et al.* 2000; Shea & Chesson 2002). However, a number of theoretical models have provided evidence that evolution may indeed alter the outcome of ecological dynamics, including species interactions (e.g. Abrams & Matsuda 1997), persistence under environmental change (e.g. Burger & Lynch 1995; Gomulkiewicz & Holt 1995), and the spread of invasions (e.g. García-Ramos & Rodríguez 2002; Holt *et al.* 2005). Also important, a few studies have recently found that genotypic variation within and among populations can have a measurable effect on population dynamics, community structure or ecosystem processes in the wild (Bailey *et al.* 2006; Hanski & Saccheri 2006). Finally, recent heuristic analyses and laboratory studies (Yoshida *et al.* 2003; Hairston *et al.* 2005) provide evidence of actual contexts wherein contemporary evolution has likely modified ecological dynamics. We are thus entering a new era of eco-evolutionary integration, but true experimental assessments of evolution's influence on ecological dynamics in the wild are lacking, particularly those that place evolutionary effects into context against other factors (Hairston *et al.* 2005; Kinnison & Hairston 2007).

How then do we quantify the effect size of contemporary evolution in an ecologically relevant fashion? Ideally, we would want an integrative measure of evolution's influences that (i) incorporates the effects of the entire phenotype (not just a few traits), and (ii) that is implicitly ecological in nature to allow comparisons with nonevolutionary factors. In the case of population ecology, vital rates of survival (i.e.  $l_x$ ) and offspring production (i.e.  $m_x$ ) provide natural units for eco-evolutionary comparison. In evolutionary biology, these measures are considered the closest and most integrative correlates of fitness. In population ecology, they are the fundamental variables controlling population growth potential (i.e.  $\sum l_x m_x$ ). Classic theory on the 'evolution of fitness' (Fisher 1930; Burt 1995) also tells us that a population's net fitness (and growth potential) is a product of positive contributions to fitness by natural selection and either positive or deteriorating effects on fitness from the environment. A translocation experiment that controls for environmental or genotypic effects on vital rates, in the wild, should theoretically provide a means to isolate the effects of contemporary evolution and environmental factors.

Evaluation of the broader fitness and ecological consequences of contemporary evolution in this fashion would represent a distinct departure from prior studies

that have focused on just trait change. Hence, we suggest it would be useful to assess how rates of fitness evolution, measured by vital rates, compare with rates of trait evolution.

We adopt the following conceptual framework that integrates contemporary evolution into the population ecology of invasion. Following initial introduction, an exotic species may spread to occupy a range of habitats that differ in suitability, as measured by the vital rates regulating the growth potential of a particular set of genotypes. Habitats that allow greater population productivity or growth potential are characterized as having greater 'invasibility'. Examples of factors that might enhance invasibility would include amenable abiotic conditions and escape from limiting competitors or predators (Mack *et al.* 2000; Shea & Chesson 2002). Populations that face selection in new habitats undergo contemporary evolution (Kinnison & Hendry 2001; Stockwell *et al.* 2003; Reznick *et al.* 2004) which enhances local fitness, as measured by vital rates of local genotypes compared to counterparts from ancestral or diverged populations. Increases in population fitness and vital rates may be considered contributions to 'local invasiveness', because these demographic rates have the potential to influence invasive characteristics like the local abundance of various life stages, rebound or resilience in the face of control measures, and ecological (e.g. numeric) impacts on other species. Theory even suggests that such local adaptation may contribute importantly to the spread of invasions (García-Ramos & Rodríguez 2002; Holt *et al.* 2005).

The specific objectives of this study on NZ salmon were (i) to experimentally assess contemporary evolution of fitness in the wild as reflected in vital rates of performance; (ii) to heuristically compare evolution of population fitness/vital rates with potential fitness contributions from adaptive trait divergence; and (iii) to contrast evolutionary contributions to population vital rates with the more widely regarded influences of habitat quality in a real ecological context – invasion of an exotic species. We addressed these objectives by employing large-scale translocation experiments in the wild. By addressing these objectives in a well-characterized study system, we provide one of the first experimental assessments of the eco-evolutionary consequences of contemporary evolution and how they compare with commonly regarded environmental determinants of population performance.

## Methods

### *Study system and experimental groups*

Between 1901 and 1907, fall-run Chinook salmon from Battle Creek (Sacramento River system, California, USA), were introduced into a single river system on the South Island of New Zealand (NZ) (McDowall 1994). The exact

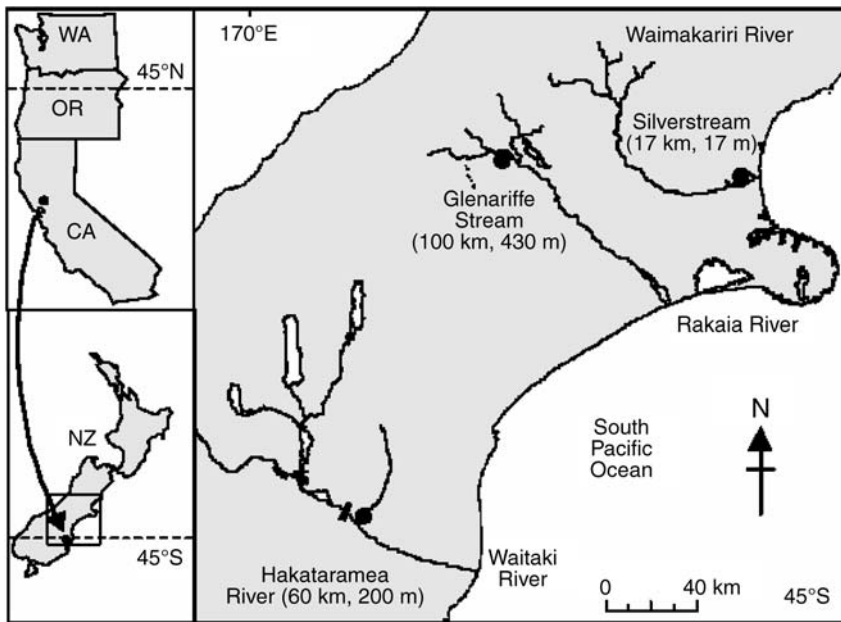


Fig. 1 Central South Island of New Zealand. Panels on the left show introduction of salmon into Waitaki/Hakataramea River system, relative latitudes of originating and established populations, and area detailed in larger map. River systems studied are shown on right, with populations and experimental sites marked with filled circles (river distance, altitude).

number of introduced salmon is not known, but within only a couple generations salmon were observed to colonize other major drainages along the eastern seaboard where they formed self-sustaining populations that seasonally dominate the local fish fauna (Fig. 1). Like indigenous Chinook salmon in North America and Asia, NZ salmon migrate to sea as juveniles in their first or second year of life, and reproduce semelparously in their natal streams after spending up to 3 years feeding in the marine environment (Quinn *et al.* 2001). Strong natal homing has resulted in partial reproductive isolation among spawning populations (Kinnison *et al.* 2002), facilitating local adaptation. As in their natural range, salmon habitats in NZ differ importantly in features correlated with migratory rigour (i.e. altitude and distance from the sea) that can in turn influence migratory success (Kinnison *et al.* 2001, 2003). Our research has focused primarily on divergence between the population spawning in the initial introduction drainage, the Hakataramea River, and the Glenariffe Stream population that descended from it (Fig. 1). The unambiguous relationship of these populations assures that any trait or performance differences reflect the role of environment or evolution acting over *c.* 26 generations (3.2 years per generation).

Central to all aspects of the study, we created two experimental cohorts of juvenile salmon in 1994 and 1995, using wild parents from the Hakataramea (ancestral) and Glenariffe (derived) populations. Gametes used in generating the experimental fish were obtained from a large number of wild Hakataramea and Glenariffe adults in both years (1994:  $n = 45$  adults each; 1995:  $n = 24$ –26 adults

each) (Unwin *et al.* 2003). A half-sib breeding design (one male to two females) was implemented in the 1994 cohort to allow estimation of quantitative genetic parameters and to control for dominance and maternal effects. One-to-one matings were used in 1995 (not used for quantitative genetics). Following embryonic and larval development, juvenile salmon from both populations were initially reared under shared conditions in captivity and marked by population with coded wire microtags inserted into their cranial cartilage (Quinn *et al.* 2000, 2001). The 1994 cohort was subdivided into three groups. One group consisted of individuals from both populations reared to maturity in captivity for the purpose of estimating heritable divergence and genetic variances under common-garden conditions. The other groups, also consisting of individuals from both populations, were released from two river sites (Fig. 1), the Glenariffe stream site and the Silverstream site, in July 1995 (Glenariffe = 141 479; Silverstream = 13 709). The 1995 cohort was subdivided into only two groups that were released into the two stream sites in August 1996 (Glenariffe = 68 747, Silverstream = 15 753; no fish held in captivity). Fish were free to imprint on their release sites and undertake their anadromous life cycle, spending 1–3 years at sea. Because siblings were represented in releases from both sites, we controlled for genetic background in our assessment of habitat-related performance. Conversely, fish released in common from the same site likely experienced the same migratory environment, controlling for the influence of habitat variation in our estimates of divergence in migratory timing and vital rates.

**Table 1** Divergence between Hakataramea and Glenariffe populations of Chinook salmon after *c.* 26 generations ( $Q_{ST}$ , quantitative trait structuring; SD/gen, standard deviations per generation; % diff., percentage difference in trait values; Con. *I*, conservative estimate of standardized selection differential required to produce observed divergence; Lib. *I*, liberal estimate of standardized selection differential; con.  $\Delta\omega$  or lib.  $\Delta\omega$  estimates of change in mean relative fitness given Con. *I* or Lib. *I*, respectively.  $Q_{ST}$ , selection intensities and fitness changes only estimated for traits showing evidence of detectable divergence)

Trait	Divergence‡		Haldanes					
	Glen–Haka	% diff.	(SD/gen)	$Q_{ST}$	Con. <i>I</i>	Lib. <i>I</i>	Con. $\Delta\omega$	Lib. $\Delta\omega$
Hatch time (°C-days @ 5 °C)	491.4–487.2	0.9%	0.019	—	—	—	—	—
Growth (%/day; 5–10 months)	1.26–1.17*	7.4%	0.032	0.121	0.054	0.142	4.5%	11.8%
Salinity tolerance† (min. @ 43 ppt)	406.9–415.9	2.2%	0.013	—	—	—	—	—
Return date	22 Apr–27 Apr**	NA	0.023	0.029	–0.030	–0.097	1.8%	5.8%
Mature date	6 May–9 May*	NA	0.021	0.019	–0.028	–0.090	1.5%	4.9%
Ova mass (g)†	415.9–390.8**	6.4%	0.038	0.099	0.053	0.161	5.3%	15.9%
Egg number†	2642–2535*	4.2%	0.020	0.088	0.035	0.086	1.8%	4.5%
Egg size (mg)†	158.1–154.9	2.1%	0.011	—	—	—	—	—
Hump depth (mm)†	43.89–45.31**	3.3%	0.045	0.092	–0.065	–0.189	7.5%	21.9%
Snout length (mm)†	31.73–31.54	0.6%	0.002	—	—	—	—	—

\* $P \leq 0.10$ ; \*\* $P < 0.01$ ; NA, not applicable.

†Analysed relative to body size (and other covariates as appropriate).

‡All traits compared in captive common-garden except return date (released fish).

Although this design does not constitute a full reciprocal transplant because Glenariffe and Hakataramea genotypes were not released from the Hakataramea River (due to logistical constraints), the comparison of fish released from the Glenariffe and Silverstream sites offers its own advantages. Namely, the Glenariffe Stream site requires one of the most rigorous migrations in NZ and the Silverstream site requires almost no freshwater migration (Fig. 1). This allowed us to estimate the *maximum* influence of a major habitat quality variable on salmon performance, and compare it to the relative performance consequences of recent adaptation.

### Trait divergence

Divergence between the Hakataramea (ancestral) and Glenariffe (derived) populations and estimation of quantitative genetic parameters are described in prior work (i.e. Kinnison *et al.* 2001, 2003; Quinn *et al.* 2001), but are summarized in Table 1 (*divergence* column). Ten phenotypic traits were examined for divergence: (i) cumulative number of degree (°C) days to hatching, (ii) growth rate from 5 to 10 months post-fertilization, (iii) juvenile survival time under hypersaline (43 ppt) conditions, (iv) date of adult return to breeding sites, (v) date of full maturation (expression of mature eggs), (vi) total ovarian mass, (vii) total egg number, (viii) average female egg size, (ix) dorsal hump size of males (from dorsal fin insertion to lateral line), and (x) length of male snouts (from tip of snout to centre of eye orbit). We used mixed-model ANOVA

and ANCOVA approaches to estimate trait divergence, and restricted maximum likelihood to estimate variance components for quantitative genetic parameter estimation. Covariates of egg or individual size were used where appropriate to further control for any maternal or allometric effects. Narrow-sense heritability estimates based on sire variance components were often high (approaching 1.0), perhaps reflecting an influence of reduced environmental variation within captivity during early juvenile or lifetime rearing. Thus, we also employed more conservative heritability values in some of our heuristic analyses (see below).

Building on prior work, evolutionary rates were estimated in haldanes, the average generational change in mean trait values in standard deviation (SD) units (Hendry & Kinnison 1999; Kinnison & Hendry 2001). Estimates of standardized selection differentials ( $I = S/\sigma_s$ ) required to produce observed trait divergence were obtained using a recursion approach that incorporates trait heritability and migration (Hendry *et al.* 2001). To bracket a reasonable range of selection conditions, we first obtained conservative values using high estimates of heritability (i.e. our actual estimates: 0.76–1.0) and an immigration rate of only 0.023 (pairwise  $mNe$  from microsatellite analysis of Kinnison *et al.* 2002). We had no direct heritability estimate for juvenile growth, so we used  $h^2 = 0.80$  to be consistent with other estimates. We also obtained more liberal selection estimates for all traits using a lower heritability estimate, closer to the norm for salmonids and other organisms [ $h^2 = 0.40$ –e.g. (Mousseau & Roff 1987)]

and a larger immigration rate (twice the value: 0.046). For simplicity, all evolution was assumed to occur in the Glenariffe population and all gene flow was from the Hakataramea into the Glenariffe system (consistent with predominant patterns of migration Unwin & Quinn 1993). The recursion approach assumed that migration occurred before selection in adult traits (e.g. egg number, hump depth, etc.) and after selection in juvenile traits (i.e. growth) (Hendry *et al.* 2001).

Quantitative trait structuring ( $Q_{ST}$ ) was estimated from our common-garden comparisons using the formula:

$$Q_{ST} = \sigma_{GB}^2 / (\sigma_{GB}^2 + 2\sigma_{GW}^2)$$

where  $\sigma_{GB}^2$  and  $\sigma_{GW}^2$  are the additive genetic variances between and within populations, respectively.  $Q_{ST}$  values were then compared with neutral population structuring estimated from nine microsatellite loci ( $F_{ST} = \theta = 0.008$ : Kinnison *et al.* 2002) as an indirect test of divergence by natural selection.

Finally, we wished to assess the maximum fitness contributions of each case of trait evolution to provide an evaluation of how important various characters might be to population performance. Expected changes in mean relative fitness ( $\Delta\bar{\omega}$ ) for each case of trait evolution were obtained using estimates of  $I$ , and the following equation we derived from the Robertson–Price identity (Price 1970):

$$\Delta\bar{\omega} = \Delta\bar{z} \cdot \frac{S}{\sigma_z^2} = \frac{\Delta\bar{z}}{\sigma_z} \cdot \frac{S}{\sigma_z} = (\text{haldanes} \cdot \text{gens}) \cdot I$$

where  $\Delta\bar{z}$  is the change in mean trait value, and  $S$  is the covariance of trait values and relative fitness (i.e. non-standardized selection differential). In the case of evolution within a single population the resulting value would represent the proportional change in mean population fitness relative to the ancestral condition. In the current case of two populations, the actual fitness effects driving divergence would be lower (split between the two), and thus this value represents a heuristic maximum had all of the divergence been due to evolution in one population of the diverging pair.

#### Vital rates and fitness metrics

Our three measures of vital rates and relative fitness for the release experiments were: (i) the ability to survive and return to each release location; (ii) the same, but adjusted for variation in juvenile size at release; and (iii) the mean number of eggs returned to a site per original female released. This latter measure incorporates the joint effects of survival and offspring number. Significance tests and 95% confidence bounds of performance were obtained based on returns of all population and site marked salmon using logit–loglinear analyses and  $\chi^2$  (i and ii), or via a

bootstrapping-simulation approach (iii – using actual egg number data for all females). Because our 1995 cohort salmon were also marked to family, we ran  $t$ -tests based on family mean survival for 1995 salmon that provided nearly identical results to log-linear analyses of total survival by population and site (Glen/Haka = 2.6 at Glen site,  $P = 0.002$ ; Glen = Haka at Silverstream,  $P = 0.828$ , Glen/Silver for Glen genotypes = 0.41,  $P = 0.017$ ; Glen/Silver for Haka genotypes = 0.17,  $P = 0.002$ ). Hence, we present the 2005 analyses in the same format as 2004 to be consistent.

Size-at-release effects were corrected for in the case of (ii) by using a known relationship between juvenile size and return probability ( $\log \text{Survival} \propto 1.34 \log \text{Mass}$ ) (Unwin *et al.* 2003). In one case (1994 Silverstream releases), size data was only available for the two populations in combination, and thus a size-adjusted comparison of Glenariffe and Hakataramea genotypes was not performed. Prior analyses show that the populations do not differ in their homing precision when released from these sites, so return rates reflect relative survival (Unwin *et al.* 2003).

## Results and discussion

### Trait evolution

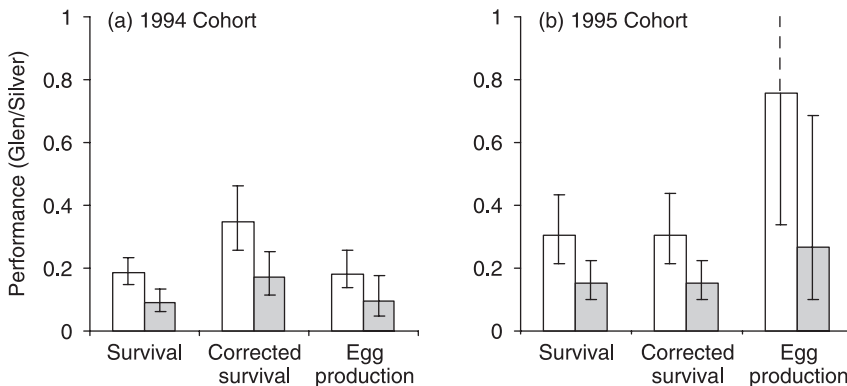
The trait differences that we noted in prior work (Table 1) are consistent with adaptive expectations and habitat associations of Pacific salmon in their indigenous range (Kinnison *et al.* 2001, 2003; Quinn *et al.* 2001). The adaptive significance of this trait divergence is further demonstrated in the present study by contrasting additive genetic population structuring,  $Q_{ST}$  (based on quantitative traits), with molecular genetic structuring ( $\theta$ ) at presumed neutral loci (Merilä & Crnokrak 2001). Average  $Q_{ST}$  between the Glenariffe and Hakataramea populations was 2.3–15.1 times the multilocus neutral estimator of structure ( $\theta = 0.008$ ), a highly significant difference (Tables 1,  $t_{(1)5d.f.} = 3.98$ ,  $P = 0.005$ ). This pattern exists despite persistent gene flow. Though such  $Q_{ST}$  comparisons are somewhat controversial (e.g. Hendry 2002), results like ours have been used by a number of studies as indirect evidence that divergence is too large to be explained by neutral processes like genetic drift (Merilä & Crnokrak 2001; Koskinen *et al.* 2002).

Adaptation aside, the absolute magnitudes of trait divergence were relatively modest ( $\bar{x} = 5.3\%$ ,  $SD = 1.9\%$ ). Indeed, these changes correspond to evolutionary rates (haldanes) of less than 0.05 SD per generation (Table 1), consistent with other studies of contemporary evolution (reviewed in Kinnison & Hendry 2001). Such evolution would be achievable with even modest selection intensities. For example, the mean selection intensities required to produce Glenariffe phenotypes from Hakataramea-like

**Table 2** Survival and egg production for Chinook salmon relative to release site (Glenariffe Stream and Silverstream), cohort and population of origin. Egg production reflects the mean number of eggs produced per female originally released, including females that did not survive and return to their release site

	Cohort	Population	Glenariffe Stream		Silverstream	
			Released	Survival percentage (SE)	Released	Survival percentage (SE)
Survival	1994	Glen	117 824	0.259 (0.015)	6892	1.378 (0.141)
	1994	Haka	23 655	0.156 (0.026)	6617	1.678 (0.158)
	1995	Glen	29113	0.258 (0.028)	6671	0.840 (0.112)
	1995	Haka	39 634	0.098 (0.016)	9082	0.650 (0.084)
	Cohort	Population	Released	Mean # (SE)	Released	Mean # (SE)
Egg production	1994	Glen	58 912	11.01 (0.93)	3446	60.06 (8.09)
	1994	Haka	11 828	4.37 (1.23)	3309	45.21 (7.23)
	1995	Glen	14 557	5.98 (1.32)	3336	7.87 (3.01)
	1995	Haka	19 817	2.14 (0.68)	4541	8.05 (2.57)

Glen, Glenariffe; Haka, Hakataramea.



**Fig. 2** Influence of habitat quality on vital rates of Glenariffe (white bars) and Hakataramea genotypes (grey bars). The lower quality of the Glenariffe Stream habitat is depicted as the ratio of Glenariffe Stream (Glen) to Silverstream (Silver) values for survival, survival adjusted for mass of offspring at release, and total egg production (controlling for original numbers released). Error bars represent 95% confidence bounds (dashed lines exceed chart area).

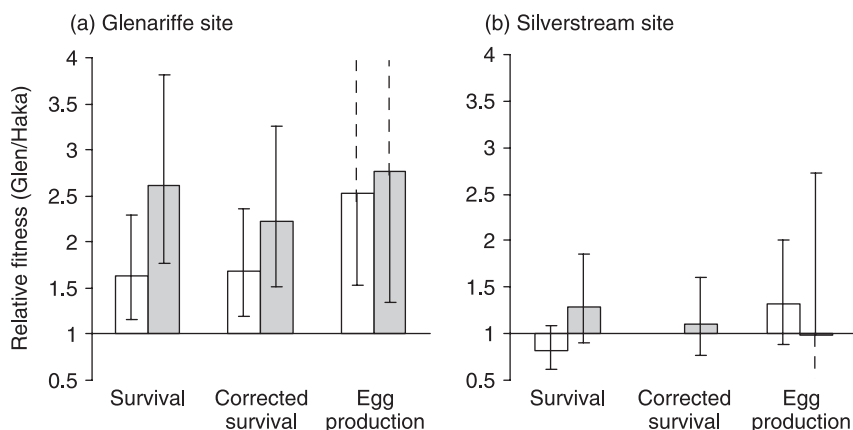
ancestors (Con. *I* and Lib. *I* in Table 1) would fall within the lower 61% of values measured in the wild (Kingsolver *et al.* 2001), even given high rates of immigration and conservative heritability estimates.

Such selection intensities, which essentially represent correlations between trait values and fitness, might imply that contemporary evolution of any given trait makes little individual contribution to variation in population fitness and productivity. To assess this, we can heuristically consider upper estimates of the fitness effects underlying each observed case of divergence using our evolutionary rate estimates and our estimates of divergent selection. With liberal parameterization (i.e. favouring larger fitness effects), individual traits would increase initial fitness over the entire interval by at most 4.5–21.9%, or an average of less than 0.8% of the ancestral value per generation (see lib.  $\Delta\omega$  in Table 1). Under more conservative parameterization, the range of fitness effects would be reduced to 1.5–7.5% (less than 0.2% per generation: con.  $\Delta\omega$  in Table 1).

Such influences on fitness might be considered modest, although they are probably not inconsequential. After all, it is presumed that they would act in some combination to influence overall fitness, vital rates and population ecology. So then, how does evolution of population vital rates, which integrates fitness effects over the full phenotype, compare?

#### *Evolutionary and habitat effects on vital rates*

In total, 777 mature salmon were recovered from our release groups between 1996 and 1998 as they arrived at their respective release sites to reproduce. Survival rates ranged from 0.16 to 1.68% and the number of returned eggs per released female ranged from 2.14 to 60.06, depending on year, site and population (Table 2). Both populations tended to have about one-fifth the survival and egg production when released from the longer-migration Glenariffe Stream site than when released from the Silverstream site (Fig. 2). Given that these two release



**Fig. 3** Relative fitness of Glenariffe and Hakataramea genotypes released from two experimental sites (Glenariffe Stream and Silverstream). (a) Glenariffe genotypes (Glen) outperform Hakataramea genotypes (Haka) when both are released from the Glenariffe Stream site. 1994 (white bars) and 1995 (grey bars) cohorts provide replicate tests of relative performance. Error bars represent 95% confidence bounds (dashed exceed chart area). (b) Glenariffe and Hakataramea genotypes perform similarly when released from the Silverstream site where neither has had the opportunity to adapt and where relative migratory (habitat) effects are minimized. Separate population size data not available for 1994 Silverstream release.

sites span the range of migratory habitats in NZ, this fivefold difference suggests that habitat quality, and thus invasibility, remains a major determinant of geographical variation in population vital rates. This is consistent with prior studies showing a substantial influence of migratory costs on tissue energy reserves and reproductive investment in these salmon (Kinnison *et al.* 2001, 2003).

However, vital rate differences between sites were far less for Glenariffe genotypes than for Hakataramea genotypes in both replicates of the design (i.e. site-by-population loglinear interactions:  $P < 0.005$ ). Given that there were no differences between populations when released from Silverstream ( $\chi^2_{1.d.f.} \leq 2.01$ ;  $P \geq 0.178$ ; Fig. 3), this pattern clearly resulted from a substantial advantage of locally adapted Glenariffe genotypes at the Glenariffe site ( $\chi^2_{1.d.f.} \geq 8.57$ ;  $P \leq 0.004$ ). Averaged over both cohorts, this difference amounted to approximately 120% greater lifetime performance for the derived Glenariffe genotypes (95 to 164% depending on vital rate measures). This would equate with an approximately 5% (3.7–6.5% depending on vital rate) generational increase in Glenariffe fitness relative to an ancestral condition approximated by their Hakataramea counterparts. These per cent differences are much larger than the estimated fitness contributions associated with evolution of individual traits (Table 1), and are thus truly 'rapid' (Hendry & Kinnison 1999; Kinnison & Hendry 2001).

How important was contemporary evolution relative to habitat quality? Our results suggest that adaptation to longer migratory conditions (Glenariffe) did not come with an apparent vital rate trade-off in the more benign habitat (Silverstream). Performance of fish released from Silverstream might thus be taken as an upper estimate of vital rates expected for salmon in NZ. Performance costs associated with less optimal habitats (e.g. Glenariffe site) might thus be expressed as a proportion of that ideal

value, and the role of contemporary evolution estimated as the per cent reduction of habitat-dependent costs by adapted genotypes relative to the cost experienced by their nonadapted counterparts over the same habitat gradient. Hakataramea genotypes released from Glenariffe suffered an average (across cohorts) survival cost of 87.8% ( $\pm 4.1$  SD; adjusted survival =  $84.0\% \pm 1.3$  SD) and an egg production cost of 81.8% ( $\pm 12.0$  SD) relative to their performance at Silverstream. On the other hand, locally adapted Glenariffe salmon faced only a 75.5% ( $\pm 8.4$  SD; adjusted survival =  $67.5\% \pm 3.0$  SD) cost of survival and a 52.9% (SD = 40.6%) cost in egg production. Thus, evolution can be conservatively estimated to mitigate habitat dependent costs on vital rates by 12–29% (survival =  $12.3\% \pm 4.3$  SD; adjusted survival =  $16.5\% \pm 1.7$ ; egg production =  $28.9\% \pm 28.6$ ).

These results emphasize that habitat quality (invasibility) remains a foremost determinant of geographical variation in vital rates in NZ salmon. However, contemporary evolution still contributed substantially to local vital rates.

#### *Conservation and theoretical implications*

Our findings show that local adaptation can appreciably increase population vital rates of survival and egg production relative to a nonlocal population, supporting the idea of contemporary evolution as an eco-evolutionary component of invasion and colonization. Interestingly, most prior works on invasions, particularly in plants, have emphasized a different eco-evolutionary problem. Namely, they have focused on comparing invaders with populations from their native ranges to identify initial innovations of 'weedy' or 'general-purpose' genotypes that may exploit many habitats in the invaded range (Sakai *et al.* 2001; Parker *et al.* 2003). Evolution of such forms is sometimes invoked to explain apparent lag times

in invasions (Sakai *et al.* 2001). Theoretically, the eco-evolutionary threat of local adaptation arising during and after the wave of invasion should be relevant with or without initial innovation of a weedy form or a lag time (Kinnison & Hairston 2007). Salmon very quickly invaded NZ once the right source was introduced (McDowall 1994) and it is not apparent that this required initial evolution of a more invasive form, but it is clear that substantial local adaptation has arisen in the interim. Likewise, studies on the intercontinental evolution of weedy forms have occasionally noted geographical variation in fitness-related traits within the invaded range, even if they have not focused as much on its eco-evolutionary significance (e.g. Blair & Wolfe 2004).

The implications of widespread local adaptation throughout the invaded range may extend beyond effects on current abundance, to aspects of invasiveness associated with the ability of local invaders to resist or rebound in the face of control measures, to dominate in interactions with local communities (e.g. numeric effects) or to expand to new habitats. Each of these aspects of invasion is at least in part influenced by the vital rates underlying population adaptation and growth potential. In the case of invasion expansion, local adaptation could demographically convert marginal habitats to sources in a spreading metapopulation (García-Ramos & Rodríguez 2002), or provide evolutionary bridges that create genotypes capable of seeding previously unsuitable sites (Holt *et al.* 2005). Most of these threats remain to be empirically tested in the wild. However, an evolutionary bridging process, by which salmon colonized, adapted, and spread to spawning sites progressively up river, may account for the ability of salmon to postglacially colonize habitats thousands of kilometres up rivers like the Yukon of North America.

Unfortunately, the eco-evolutionary consequences of local adaptation by invaders may make it much more difficult to predict the scope or impact of invasions from simple ecologically based envelope models (Holt *et al.* 2005). This challenge is perhaps nowhere better demonstrated than by the costs of virulence and resistance evolution in pathogens and pests (Palumbi 2001). Although subject to extreme anthropogenic selection, evolution in these organisms clearly emphasizes how local adaptation can contribute to widespread eco-evolutionary dilemmas. Indeed, we might heed warnings from attempts to deal with these problems. Could delays in eradicating local 'infestations' of invaders increase their ability to become evolutionarily entrenched in susceptible sites? Might partial control impose selection favouring control-resistant forms? Planned gene flow from maladapted sources has been considered a tool to slow the evolution of pesticide resistance (Mallet & Porter 1992). Could this strategy be used to slow adaptation in invasions (Stockwell *et al.* 2003) or are the risks of supplementing adaptive genetic variation

too high? Although the disparities of fitness that we detected in NZ salmon are consistent with the early stages of ecologically mediated isolation (Schluter 2000; Hendry 2004), they also suggest some scope for migrants to potentially depress the mean fitness of recently diverged populations (Holt & Gomulkiewicz 1997; Tufto 2001).

If our results are considered representative, many studies of contemporary evolution that focus on trait change alone may 'miss the forest for the trees'. Theoretically, changes in overall fitness and vital rates wrought by contemporary evolution should generally be greater than changes in trait values or the fitness effects of particular characters, simply because the former integrate over the latter. Our results show that this disparity can be quite large (orders of magnitude). There is also no reason to believe that the fitness/ecological effects documented in this study are extraordinary. Indeed, we estimated the change in fitness due to natural selection in the derived Glenariffe environment at approximately 5% per generation (3.7–6.5%, depending on vital rate metric) which falls within suggested theoretical bounds (1–10% per generation – Burt 1995). Although Fisher (1930) predicted that environmental deterioration of fitness should ultimately nearly offset fitness gains from natural selection, many of the problems that confront conservation biology, including invasions, involve perturbations to such a balance. Under these conditions, contemporary evolution might have profound implications for the fate of populations (Kinnison & Hairston 2007). Still, ours is just one study, and analogous estimates will be needed to empirically appreciate the broader scope for eco-evolutionary consequences of contemporary evolution in the wild.

In conclusion, our experimental findings support that we cannot afford to overlook evolution of fitness as a factor in the short-term eco-evolutionary dynamics of populations in the wild. This is all the more true in applied areas of ecology like biological invasions. A broader understanding of the ecological consequences of contemporary evolution has the potential to precipitate a new level of synthesis between the fields of ecology, evolution and conservation biology. This synthesis may not only erase outdated perceptions of evolution as a slow process separate from the concerns of ecology; it may be critical to our ability to understand how populations, communities and ecosystems will respond in a world where both ecological and evolutionary landscapes are facing unprecedented rates of human alteration.

## Acknowledgements

We thank A. Blair, A. Hendry, D. Reznick, L. Wolfe and anonymous reviewers for constructive comments. We are especially grateful to B. Beckman, P. Bentzen, N. Boustead, K. Burton, T. Gough, J. Griffith, L. Hawke, S. Hawke, A. Hendry, L. Lehman, F.

Lucas and M. Tawa for their extensive technical support. Funding was provided by a consortium of Pacific Northwest utilities, the New Zealand Foundation for Research, Science and Technology (Contracts Co1417 and Co1501), the H. Mason Keeler Endowment (University of Washington), the Hannah T. Croasdale Fellowship (Dartmouth College) and the Maine Agricultural and Forestry Experiment Station. Experiments were conducted under animal care approval from the University of Washington.

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This study represents a culmination of more than 15 years of international collaboration on the contemporary evolution and genetics of New Zealand salmon. Michael Kinnison is an Associate Professor of Biology and ecology at the University of Maine, where he conducts both basic and applied research at the interface of contemporary evolution and ecology. Martin Unwin is a scientist at the National Institute of Water and Atmospheric Research, where he studies the ecology and management of NZ fishes. Thomas Quinn is the H. Mason Keeler Professor in Fisheries at the University of Washington and he studies the behaviour, ecology and evolution of salmonids.

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