

Migratory costs and contemporary evolution of reproductive allocation in male chinook salmon

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Abstract

Energetically demanding migrations may impact the resources available for reproductive trait development and activity, and hence favour evolution of new investment strategies for remaining resources. We conducted a large-scale experiment to evaluate the proximate cost of migration on male reproductive investment in chinook salmon (*Oncorhynchus tshawytscha*) and contemporary evolution of reproductive allocation. Experimentally induced differences in migratory costs (17 km inland and 17 m elevation vs. 100 km and 430 m) influenced dorsal hump size and upper jaw length, two traits influencing male mating success that are developed during migration. Longer migration also reduced tissue energy reserves available for competition and length of breeding life. Corresponding shifts in the balance between natural and sexual selection appear to have been responsible for heritable population divergence in secondary sexual trait investment, in approximately 26 generations, following colonization of spawning sites with different migratory demands.

Introduction

Sexually selected traits (e.g. morphology, colour, mating displays and mate competition behaviours) evolve in response to intrasexual competition, mate choice or a combination of these forces (Darwin, 1871; Andersson, 1994). The exaggeration of secondary sexual traits related to reproductive success may arise by direct benefits to the possessor in mate competition (e.g. intrasexual combat or display), as cues of mate quality (i.e. 'good genes'), via linkage to genes associated with mate preference (i.e. Fisherian runaway process) or as a means of exploiting a sensory bias in mate choice. Such sexual selection for increased development of secondary sexual traits, however, is likely limited by trade-offs associated with other components of fitness under natural selection. Depending on the nature of the trait, secondary trait development may be inhibited by countervailing selective pressures from predation (Endler, 1980; Ryan *et al.*, 1981, 1982; Houde, 1997), constraints on locomotion (Buchanan & Evans, 2000), or

physiological constraints such as nutrition (Brown, 1990; see Andersson, 1994 for a general review). In this paper, we provide evidence for contemporary evolution of secondary sexual traits resulting from proximate trade-offs with energetic constraints related to migration and mating activity. This divergence occurred in less than a century following colonization of habitats with different migratory requirements.

Extensive migrations are metabolically expensive and often occur as a prerequisite to mating (e.g. Blem, 1980; Brett, 1995; Sandberg & Moore, 1996; Hendry & Berg, 1999; reviewed by Dingle, 1996). When migration occurs prior to, or concurrent with, reproductive development or reproduction itself, increases in the metabolic cost of migration may reduce the likelihood of successful migration or impose a deficit on other components of reproductive investment within a finite resource budget. Life-history theory suggests that other attributes of migratory animals (e.g. provisioning, body size, maturation timing, iteroparity) will coevolve to maximize lifetime reproductive success under a given set of migratory conditions (e.g. Leggett & Carscadden, 1978; Leggett, 1985; Roff, 1988; Snyder & Dingle, 1989; Sandberg & Moore, 1996; Kinnison *et al.*, 2001). Ultimately, selection is expected to favour (1) the evolution of features that improve the likelihood and efficiency of

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successful migration, (2) the evolution of increased resource acquisition or (3) re-distribution of migratory deficits among other components of reproductive investment in a way that maximizes fitness.

In males of many species, migratory costs may be expected to reduce residual resources available for survival, development of secondary sexual traits and mate competition. Presumably, when reserves used in active competition are more closely linked to fitness, secondary sexual traits may be sacrificed, especially if they reduce the efficiency or probability of successful migration. Additionally, if increased migratory rigour reduces the intensity of mate competition, selection acting against secondary sexual trait development may prevail. One way this may occur is if migratory rigour reduces operational sex ratios (OSRs) (Emlen & Oring, 1977) by limiting the abundance (i.e. relative survival) or duration of breeding life of males relative to females. Conversely, a shorter migration may result in excess reserve energy, stronger sexual selection (due to increased male survival, OSRs and competition) and a greater marginal value of investment into secondary sexual traits. Ultimately, altered phenotypic expression of secondary sexual traits in migrants may reflect both the proximate availability of energy used to construct such traits and genetic adaptation to divert more or less energy to develop those traits.

Anadromous Pacific salmon (*Oncorhynchus* species) are useful subjects for studying the evolution and expression of sexually selected traits in response to migratory arduousness for several reasons. First, their strong homing tendency (Dittman & Quinn, 1996) produces reproductively isolated populations with widely varying migratory challenges (upstream migration may vary from <1 to 3200 km). Pacific salmon are also semelparous, capital breeders (*sensu* Jönsson, 1997; Hendry *et al.*, 1999) that cease feeding upon return to fresh water, where they migrate to breeding sites and die following a single reproductive season (Groot & Margolis, 1991). Hence, post-reproductive investment (into survival and reproduction) and ongoing acquisition of resources need not be considered. Investment during the freshwater phase, including migration, the bulk of gonad and secondary trait development, and mating activities, thus occurs within a finite and closed energy budget.

Male salmon invest far less into gamete production than females (egg production may exceed 20% of female mass) but reproduction in both sexes is exhaustive (Hendry & Berg, 1999), due to more extensive investment into mate competition in males. Variation in male investment and reproductive success largely surrounds features that enhance their ability to acquire mates, such as longevity, display and combative ability (Fleming & Gross, 1994; Quinn & Foote, 1994). Biased OSRs (more males than females) often result in high levels of competition (Fleming & Gross, 1994; Quinn *et al.*, 1996) and strong sexual dimorphism arises near maturity. Males

show greater elongation of the jaws and a dorsal hump along the ridge of the back, but there is considerable variation in the degree of development of secondary sexual traits among populations (e.g. Beacham & Murray, 1987; Beacham *et al.*, 1988; Quinn *et al.*, 2001a).

Given the hypothesized influences of migratory costs on reproductive allocation and reproductive investment in Pacific salmon, we formulated and tested the following predictions:

Prediction 1: There is a cost to migration – a longer migration imposed on similar genotypes will decrease energy reserves and secondary sexual trait size, relative to a less challenging migration.

Prediction 2: There are trade-offs among components of reproductive success – all else being equal, individuals arriving at the breeding site with larger than average secondary sexual traits will possess lower than average tissue energy reserves available for allocation to other components of reproductive investment.

Prediction 3: Heritable variation exists as a target for selection – genetic variation exists in the development of secondary sexual traits on which selection may act in response to allocation constraints imposed by migration.

Prediction 4: Secondary sexual traits have evolved – introduced populations with common ancestors will show evidence of genetic divergence in secondary sexual trait size consistent with migration patterns. Specifically, secondary sexual traits will tend to be reduced in populations with more arduous migrations.

The first three predictions above set the stage for evolution of secondary sexual traits in response to migratory conditions, and the fourth involves demonstration of actual contemporary evolution. We made use of rearing and translocation experiments to test these predictions.

Materials and methods

Experimental organisms and study sites

Anadromous chinook salmon (*Oncorhynchus tshawytscha* Walbaum) were established in New Zealand (NZ) from releases to a single river system (the Waitaki) between 1901 and 1907 (Fig. 1; McDowall, 1994). NZ salmon were derived from Sacramento River sources, most likely a Battle Creek population that returned to fresh water in the fall of their spawning year (McDowall, 1994; Quinn *et al.*, 1996). 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 east coast of the South Island where spawning occurs today (McDowall, 1990). Analyses of population structure based on DNA micro-satellite variation indicated that salmon in different drainages are now partly reproductively isolated (Kinnison *et al.*, 2002), consistent with the high degree of philopatry characteristic of the species (Unwin &

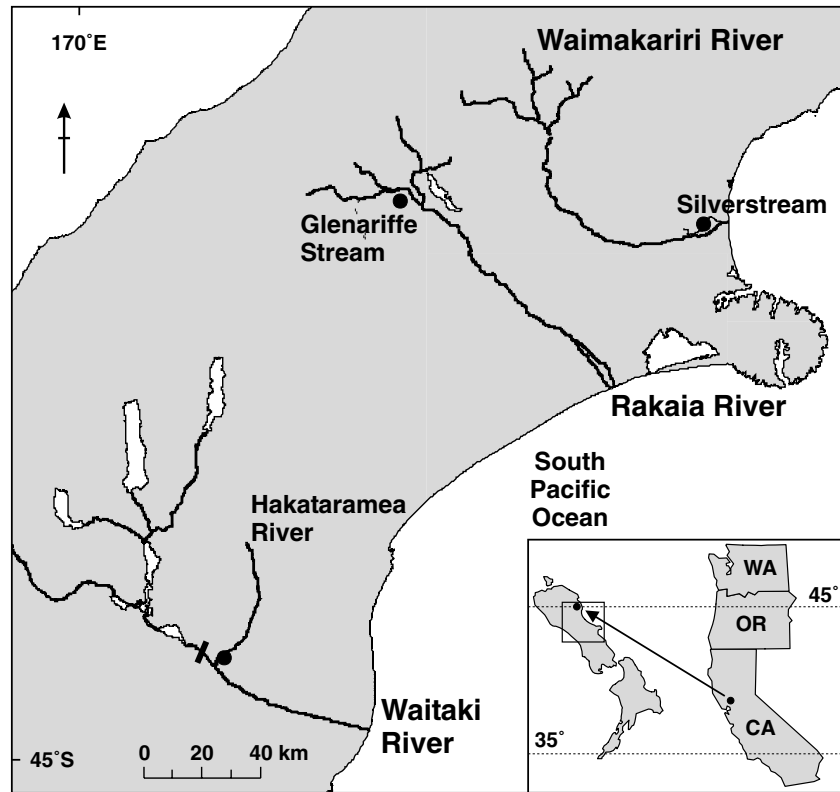


Fig. 1 Map of the South Island of New Zealand showing natal sites of experimental populations and experimental release sites. Inset depicts translocation of chinook salmon from an upper Sacramento River tributary to the Waitaki drainage on the East Coast of the South Island. Note that New Zealand has been inverted in the inset to show relative latitudes encountered by indigenous and translocated populations.

Quinn, 1993). Populations of NZ salmon now show phenotypic differences in morphometric, life history and reproductive traits (Quinn & Bloomberg, 1992; Quinn & Unwin, 1993; Kinnison *et al.*, 1998a,b,c). A genetic basis for population variation in ovarian traits of females was established by Kinnison *et al.* (2001), but the genetic and environmental basis for variation in male secondary sexual trait morphology has not been examined, nor have any estimates been made of the heritability of secondary sexual traits in salmon.

Experimental fish in this study were bred from wild adults returning to spawn in two populations. One population spawns in the Hakataramea River and the other spawns in the Glenariffe Stream, a headwater tributary of the Rakaia River (Fig. 1). The Hakataramea joins the Waitaki River 60 km from the sea at approximately 200 m elevation, whereas the Glenariffe joins the Rakaia River at approximately twice the distance and elevation (100 km above the mouth at an altitude of 430 m – Unwin, 1986). Very little spawning habitat exists downstream of either of these tributaries and a dam prevents spawning farther upriver in the Waitaki. Most spawning takes place from mid-April to early June (austral fall) in the lower few km of both tributaries.

To experimentally examine the costs of migration on morphological development, we released and recovered tagged salmon from both populations from two sites: Glenariffe Stream and the Silverstream experimental

hatchery on the Kaiapoi River. The latter site was located in the Waimakariri River system at only 17 km from the coast and 17 m elevation (Fig. 1). These release–recovery sites maximized the difference in migratory rigour between experimental groups, and permanent fish traps enabled us to recapture nearly all salmon that returned.

On 22 and 23 April 1994, 29 full-sib families nested within 15 half-sib families were produced via half-sib matings (two females to each male) within each population. Two families from different populations were accidentally mixed before marking and were excluded from the design, resulting in one full-sib family without half-sib relatives in each population. Prior to combining all families into fully mixed captive groups or releases, measures were taken to control for rearing variation. These measures included randomly pairing families in tanks without respect to population or half-sib pair (one family marked by adipose fin excision) and equalizing tank densities via culling or addition of marked ‘filler’ fry (from other families).

Two experimental release groups were ultimately created from these matings, each including juveniles from all families: a ‘Glenariffe release’ group (117 824 Glenariffe fry and 23 655 Hakataramea fry released on 19 July 1995) and a ‘Silverstream release’ group (13 709 fish on 31 July 1995, equally distributed among populations). More fish were released from the Glenariffe site because they represented the focal part of a larger

research programme (Quinn *et al.*, 2001a) and because survival rates tend to be significantly lower than at Silverstream. All juveniles in the release groups were marked to the family level with coded-wire micro-tags inserted into their cranial cartilage, except the Hakataramea fry in the Glenariffe release group. These fish could only be marked as a population owing to other constraints. An additional 50 fish were randomly selected from each family to create a 'captive rearing' group marked with individually encoded passive integrated transponder (PIT) tags (Peterson *et al.*, 1994). They were combined in a large raceway at Glenariffe, and reared to maturity in fresh water.

In 1995 a second release programme was initiated using a full-sib mating design to create 12 families of Hakataramea origin and 13 of Glenariffe origin (on 1–3 May 1995). We followed similar protocols for collecting gametes, incubating embryos, marking and rearing of these fish, but no representatives were retained for captive rearing. These fish were released on 16–20 August 1996 from the Glenariffe and Silverstream sites (average 630 per family from Silverstream and 2742 per family from Glenariffe). Additional details of the production, rearing and release of experimental fish are provided in Kinnison *et al.* (1998c, 2001).

Measurement of experimental fish

Most male salmon returned from sea or matured in captivity in 1996 and 1997, and most females in 1997 and 1998 (Quinn *et al.*, 2000). Coded-wire-tagged individuals were captured alive and fully matured within a few weeks at the Glenariffe and Silverstream sites. A few months prior to the spawning season, captive fish were sorted into two groups on the basis of early indicators of maturation (primarily colour). Immature fish were retained and examined in subsequent years. Maturing individuals from the release or captive groups that were not at peak reproductive readiness were held and checked at approximately weekly intervals. Fully mature individuals from both the wild and captive groups (as indicated by the ability to express eggs or milt) were killed and processed for trait data.

Each fish was laid on its side on a photographic background with nose and tail aligned along a straight axis. A rectangle of white paper with the individual's ID number was positioned so that its upper edge lay along the lateral line immediately ventral to the insertion of the dorsal fin. Large white pinheads were used to mark the location of the hypural flexure (end of the spinal column) and posterior extreme of the maxilla. A second slip of white paper was inserted into the top edge of the operculum to distinguish its dorsal terminus. A lateral profile photo was then taken using a mounted fixed focal length camera. Landmark points were later digitized from each photograph using a CalComp™ digitizing tablet (GTCO CalComp, Inc., Columbia, MD, USA) and a

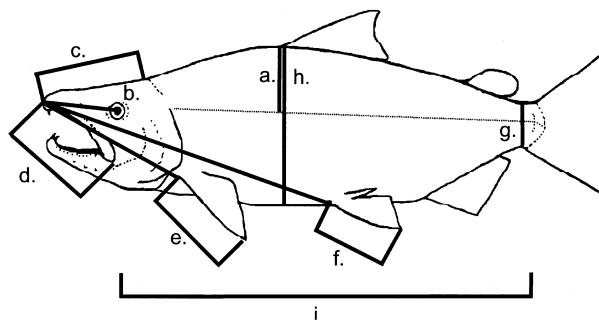


Fig. 2 Morphometric measures recorded on New Zealand chinook salmon. *a*, hump depth (HUMP); *b*, snout length (SNOUT); *c*, head length (HEAD); *d*, upper jaw length (JAW); *e*, pectoral fin length (PECF); *f*, pelvic fin length (PELV); *g*, caudal peduncle depth (CPD); *h*, body depth (BD – re-analysis of Kinnison *et al.*, 1998a only); *i*, mid-eye to hypural flexure (MEH) length.

cross-hair stylus. A series of length measurements (Fig. 2) were then computed by Pythagorean theorem, including hump depth (HUMP, distance from lateral line to the apex of the hump at the front insertion of the dorsal fin), and snout length (SNOUT, from the middle of the eye to the tip of the upper jaw). Analogous measures have been employed in other studies of reproductive success in salmon (Fleming & Gross, 1994; Quinn & Foote, 1994). We also extracted length measurements associated with head length (HEAD), jaw length (JAW), snout to pectoral fin length (SNAP), snout to pelvic fin length (SNAPE), pectoral fin length (PECF), pelvic fin length (PELV), and caudal peduncle depth (CPD) for additional multivariate analyses. A size variate, mid-eye-to-hypural-flexure length (MEH), was extracted from each photograph. MEH is preferable to total length, fork length or mass for analyses of morphological variation in maturing salmon (e.g. Quinn & Foote, 1994; Hendry & Berg, 1999) because it is not confounded with snout and hump development (or fin erosion).

After obtaining morphometric data, testes were weighed, and a sample of muscle tissue (ca. 10–15 g without skin or subcutaneous fat) was cut from the dorsal muscle surface on the fish, anterior and ventral to the dorsal fin and ridge of the back (Hendry & Berg, 1999). Tissue was frozen in a Whirl-Pack™ bag (Nasco, Fort Atkinson, WI, USA), weighed to 0.0001 g, dried at 95 °C for 24 h, and then re-weighed to estimate the per cent dry mass (% muscle solids). This percentage is highly correlated with fat content in NZ salmon ($r = 0.87$, Kinnison *et al.*, 2001, see also Unwin *et al.*, 1999) and dry weight is highly correlated with energy density in fish ($r = 0.97$, Hartman & Brandt, 1995). These energy stores reflect relative reserves available to these fish for mating activities and competition (see also Kinnison *et al.*, 2001). Finally, coded-wire tags were dissected from snouts to identify population and family origin.

Analysis of experimental data

Analyses were performed using SPSS v. 8.0, except genetic correlations and evolutionary rates, which were estimated using S-Plus v. 6.0. Analysis of trade-offs can be confounded if one does not account for trait variation resulting directly from variation in body size (cf. Roff, 1992). Because all of our morphometric measures tended to increase allometrically with body size, trait variation was examined by ANCOVA of $\log_{10}(\text{trait values})$ with $\log_{10}(\text{MEH})$ as the covariate. Alternatively, size-standardized values were computed from these allometric relationships for subsequent analyses. To determine the cost of migration on secondary sexual traits (i.e. HUMP and SNOUT), testes and energy reserves, the following ANCOVA model was employed for each character (Y):

$$Y_{ijkl} = \mu + M_i + O_j + A_k + L_l + \text{interactions} + \varepsilon_{ijkl}$$

where M_i is the size covariate (MEH), O_j is the population effect (fixed), A_k is the age effect (fixed) and L_l is the release site effect (fixed) for evaluating the influence of migratory costs. Only two-way interactions were examined. Factor effects were tested in the absence of interaction effects when interaction effects were not significant. In cases where there was a significant interaction between age and another factor, a reduced model was evaluated for each age. We also performed pairwise t -tests between family mean values of fish that returned to the two release sites to ensure that migratory costs were not artefacts of the relative abundances of certain families or populations. The per cent difference in the anti-logged estimated means ($\Delta\bar{X}$) or marginal means ($\Delta\bar{X}_m$; means when all other factors and covariates are standardized) were computed as an indication of the effect size.

Heritable population divergence and trait inheritance were examined with the captive fish data. Initial analyses used a model analogous to that shown above but without a site effect (no L_l) to test for interactions among the major factors (particularly age and MEH). A nested model incorporating full-sib and half-sib relationships was then used for further analyses of divergence and heritability. The full ANCOVA model may be written as:

$$Y_{ijklm} = \mu + M_i + O_j + A_k + S(O)_{l(j)} + D(S(O))_{m(l(j))} + \text{interactions} + \varepsilon_{ijklm},$$

where M_i , O_j and A_k are as defined above, $S(O)_{l(j)}$ is the effect of a given sire (random) within a population, and $D(S(O))_{m(l(j))}$ is the effect of a given dam (random). Again, when age showed a significant interaction effect separate ANCOVAs were performed for each age class.

Restricted maximum likelihood (REML) was used to obtain estimates of sire and dam variance components and their associated sampling variances for age 2 males. The number of families for each population represented a modest quantitative genetic design, hence variance

components were estimated for captive males using separate ANCOVAs for both populations, as well as a mixed ANCOVA model in which population was treated as a fixed factor. Heritabilities were estimated from variance components using techniques described in Becker (1984) and Lynch & Walsh (1998). Genetic correlations among traits were estimated by pairwise covariance of half-sib family means (Lynch & Walsh, 1998) using residuals from an ANCOVA model with MEH as the covariate, a population effect, and an age effect where appropriate. The significance of the correlations were inferred from the P -values of the covariance of the traits across half-sib pairs (Lynch & Walsh, 1998). Divergence rates in darwins and haldanes, with 95% confidence bounds, were estimated from the adjusted sire means for captive fish by bootstrapping (Kinnison & Hendry, 2001) and assuming a time scale of 84 years or 26.25 generations (estimated generation time = 3.2 years).

Phenotypic trade-offs were examined with Spearman correlations among HUMP, SNOUT and tissue energy using standardized residuals from ANCOVA models incorporating MEH, population of origin and age. Trade-offs were examined for the Glenariffe site returns, the Silverstream returns, and captive salmon. We also performed a PCA analysis on the full set of size-standardized morphometric measures extracted from captive fish photographs in order to (1) validate the presence of orthogonal snout and hump components of variation, (2) show that such factors differed between populations at a multivariate level, and (3) provide factors for comparison with results from a previous dataset on multivariate phenotypic variation of NZ salmon (Kinnison *et al.*, 1998a).

Finally, we performed a subset of similar analyses on the morphology of female salmon from the study populations. Hump and snout features develop less in females than males, but female salmon morphology does change from the immature form. The magnitude of secondary sexual trait development in females is expected to impose minimal costs to migratory efficiency or to require major construction costs, but may nonetheless be impacted by a reduction in total energy reserves available under migration. Females thus pose an interesting contrast to males with regard to the cost of migration on sexually selected features.

Results

Experimental effect of migration on morphology

All male morphometric traits increased with body size ($P < 0.001$ for all tests), with allometric coefficients for hump depth and snout length averaging 1.16 and 1.06, respectively (averaged across ages and rearing/release groups). Summary statistics for raw and size-adjusted trait values (by age) are shown in Table 1. ANCOVA detected slight interactions between MEH and age for hump depth

Trait	Age	Cost of migration		Genetic divergence	
		Glen (long)	Silver (short)	Glen (long)	Haka (short)
Raw trait values					
MEH (mm)	2	369.5 ± 3.5 (56)	359.6 ± 2.1 (150)	298.1 ± 2.7 (15)	293.9 ± 3.5 (15)
	3	582.4 ± 3.3 (120)	550.2 ± 8.3 (18)	440.2 ± 6.1 (14)	437.0 ± 7.3 (11)
Hump (mm)	2	50.3 ± 0.7 (56)	50.2 ± 0.5 (150)	43.1 ± 0.6 (15)	43.5 ± 0.8 (15)
	3	71.0 ± 0.6 (119)	71.1 ± 1.6 (17)	62.3 ± 1.0 (14)	65.6 ± 1.5 (11)
Snout (mm)	2	41.2 ± 0.6 (56)	42.08 ± 0.4 (150)	29.3 ± 0.4 (15)	28.8 ± 0.5 (15)
	3	67.0 ± 0.6 (120)	65.6 ± 1.6 (18)	46.1 ± 0.6 (14)	46.3 ± 1.4 (11)
% Dry tissue	2	23.8 ± 0.3 (35)	26.1 ± 0.2 (141)	24.1 ± 0.2 (15)	24.1 ± 0.2 (15)
	3	21.2 ± 0.2 (39)	23.5 ± 0.5 (16)	24.8 ± 0.3 (14)	25.1 ± 0.4 (11)
Testes (g)	2	71.5 ± 3.0 (56)	70.4 ± 1.9 (145)	59.8 ± 3.3 (15)	56.0 ± 2.6 (15)
	3	149.4 ± 2.8 (119)	143.4 ± 6.9 (18)	123.5 ± 5.3 (14)	128.1 ± 6.0 (11)
Size-adjusted†					
Hump (mm)	2	49.1 ± 0.4 (56)	50.6 ± 0.31 (150)	42.7 ± 0.3 (15)	43.8 ± 0.4 (15)
	3	70.5 ± 0.5 (119)	75.0 ± 1.6 (17)	61.6 ± 0.7 (14)	65.4 ± 0.7 (11)
Snout (mm)	2	40.4 ± 0.4 (56)	42.4 ± 0.3 (150)	29.1 ± 0.2 (15)	29.0 ± 0.3 (15)
	3	66.4 ± 0.5 (120)	69.2 ± 1.5 (18)	45.6 ± 0.5 (14)	46.2 ± 0.7 (11)
% Dry tissue	2	23.7 ± 0.2 (35)	26.2 ± 0.2 (141)	24.1 ± 0.2 (15)	24.1 ± 0.2 (15)
	3	21.3 ± 0.2 (39)	23.3 ± 0.5 (16)	24.4 ± 0.2 (14)	24.6 ± 0.2 (11)
Testes (g)	2	67.2 ± 2.0 (56)	71.3 ± 1.7 (145)	55.1 ± 1.8 (15)	54.5 ± 1.4 (15)
	3	146.6 ± 2.5 (119)	156.0 ± 6.2 (18)	117.7 ± 3.0 (14)	126.0 ± 2.9 (11)

*Sample size per sire and age ranged from 1 to 38 individuals.

†Adjusted to following MEH: migratory costs: age 2 = 362 mm, age 3 = 578 mm; divergence: age 2 = 296 mm, age 3 = 436 mm.

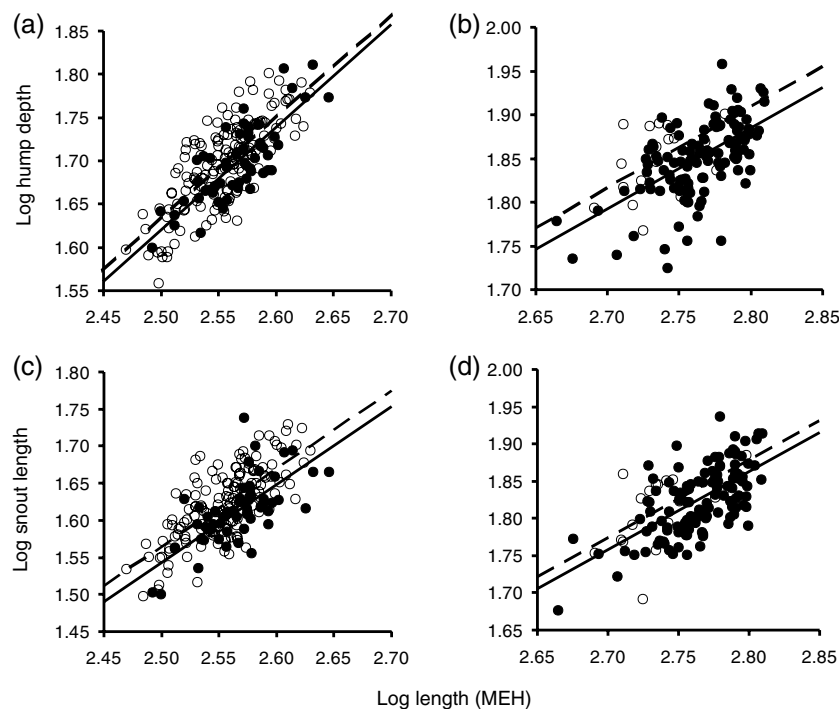


Table 1 Mean ± SE by treatment for analyses of migratory costs and genetic divergence in male chinook salmon including raw trait values (top) and values adjusted to accommodate slight variation in mid-eye to hypural flexure length (MEH – bottom). Values in parenthesis represent sample sizes (total N for cost of migration; number of sires for genetic divergence*). Note that differences indicated here approximate but do not fully capture results of formal ANCOVA analyses that simultaneously considered additional factors (e.g. population, age, dam effects).

Fig. 3 Migratory effects on hump depth and snout length by age. Lines represent predicted regressions of log values from ANCOVA analyses including age and origin factors with log MEH length as covariate. Open circles and dashed lines are for Silverstream releases and filled circles and solid lines are for Glenariffe releases. Statistical analyses indicated an interaction effect between years for hump depth, but not for snout length. Salmon returning to Silverstream tended to have larger humps ($P < 0.05$ for both ages) and longer snouts ($F_{1,358} = 16.50$, $P < 0.001$) for their body size. *a*, Age 2 hump depth; *b*, age 3 hump depth; *c*, age 2 snout length; *d*, age 3 snout length.

and per cent tissue dry mass. For both ages, salmon released and recovered at Silverstream had larger humps at a given MEH than those returning to Glenariffe (Fig. 3;

$P < 0.05$ for both ages; age 2: $\Delta\bar{X}_m = 2.7\%$; age 3: $\Delta\bar{X}_m = 5.8\%$) and also larger snouts (Fig. 3; $F_{1,358} = 16.50$, $P < 0.001$; $\Delta\bar{X}_m = 4.5\%$). Salmon migrating to

Glenariffe also possessed less energy in their muscle, as indicated by differences in per cent dry tissue mass ($P < 0.001$ for both ages; age 2: $\Delta\bar{X}_m = 10.2\%$; age 3: $\Delta\bar{X}_m = 10.4\%$). However, there was no detectable influence of migratory costs on testes size ($F_{1,333} = 1.050$, n.s.). For females, there was no difference between salmon migrating to Glenariffe or Silverstream in hump depth ($F_{1,211} = 0.697$, n.s.) but Silverstream salmon had longer snouts ($F_{1,215} = 84.08$, $P < 0.001$). Previous analysis of tissue dry mass in these females showed a significant reduction in energy reserves associated with the longer migration (Kinnison *et al.*, 2001).

The above results were based on analyses treating individuals as fully independent. This approach is justified because the salmon released from both sites consisted of the same populations and families and the proximate effects of migration are expected to act irrespective of genetic group. To further test whether migratory costs accounted for the observed differences (rather than differences in the representation of families or populations returning to the two sites), we compared size-adjusted mean trait values for individuals from the same families of the same age at both sites. Pairwise *t*-tests confirmed that Silverstream males of a given age had 4.3% larger humps ($t_{36} = 3.162$, $P < 0.01$), 6.7% longer snouts ($t_{36} = 4.698$, $P < 0.001$) and 10.2% greater tissue energy reserves ($t_{28} = 5.560$, $P < 0.001$) than their siblings migrating the longer distance to Glenariffe Stream.

Evolutionary divergence and trait inheritance

Nested ANCOVA of males reared in a (shared) captive environment showed no indication of significant interaction effects for hump depth, but did show an age by MEH interaction effect for snout size. Formal analyses of the latter trait were thus performed using separate models for each age. Hakataramea males had significantly larger humps than Glenariffe males (Fig. 4; $F_{1,28.1} = 11.07$, $P < 0.01$; $\Delta\bar{X}_m = 3.3\%$), but neither snout length (age 2: $F_{1,29.1} = 0.048$, n.s.; age 3: $F_{1,27.7} = 0.069$, n.s.) nor testes size ($F_{1,40.7} = 1.243$, n.s.) differed between the populations in captivity. There was also no difference between populations in per cent dry mass of tissue energy samples ($F_{1,47.2} = 0.166$, n.s.). Analysis of female hump and snout development showed a similar pattern. Hakataramea females had larger humps but the populations did not differ in snout length (HUMP: $F_{1,28.7} = 9.821$, $P < 0.01$; SNOUT age 3: $F_{1,30.3} = 0.074$, n.s.; SNOUT age 4: $F_{1,38.1} = 0.685$, n.s.). There was also no detectable difference between populations in tissue energy in captive females (see Kinnison *et al.*, 2001).

Inheritance was estimated using data from captive males maturing in 1996 because a significant year interaction was detected for snout length and too few males matured in 1997 for us to estimate quantitative genetic parameters. Significant sire and dam effects

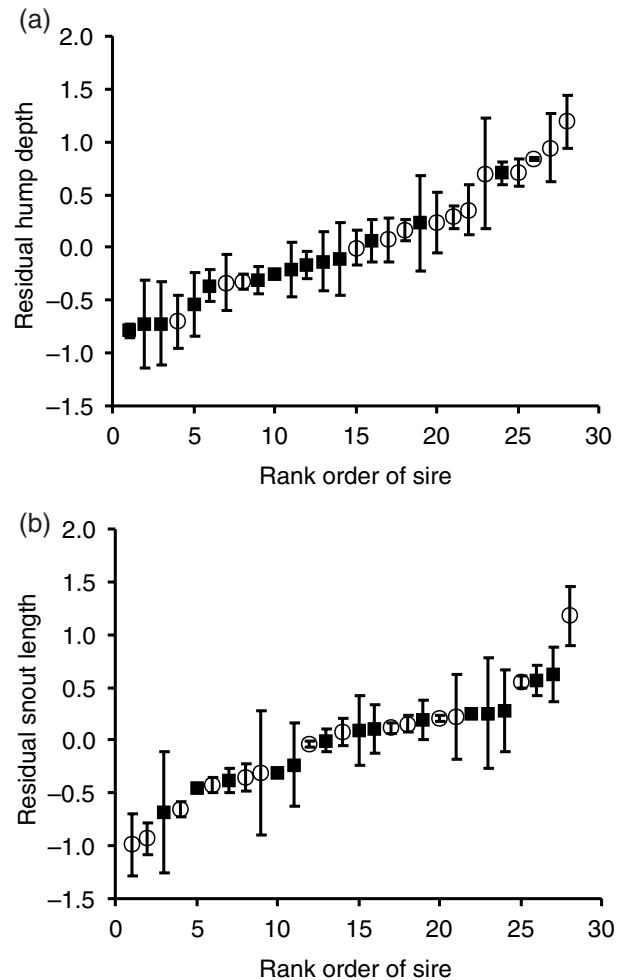


Fig. 4 Inheritance and genetic divergence of hump depth (a) and snout length (b) in New Zealand salmon. Observations (circle = Hakataramea or squares = Glenariffe) represent median residual trait values between the means for two half-sib families produced by different dams (dam values = endpoints of bars) but a single sire. Sire contributions are ranked from smallest to largest values. Substantially greater variation among sires than among dams (within sires) indicates a strong heritable component of each trait. Preponderance of Hakataramea families with larger hump sizes reflects genetic difference between populations (as found in formal analyses). Residuals: Hump, residuals from analysis on mid-eye to hypural flexure length (MEH) and age; snout, residuals on MEH, age and MEH by age interaction.

($P < 0.001$ for both effects) were detected for both hump depth and snout length in our nested ANCOVA models. Consistent with the magnitude of sire effects (Fig. 4) heritabilities ($h^2 \pm SE$) for both traits relative to MEH were significantly greater than zero (hump depth: 0.91 ± 0.27 ; snout length: 0.76 ± 0.36). Separate estimates by population varied widely around these combined population estimates, but their confidence bounds overlapped. (Hakataramea: hump = 1.13 ± 0.40 ,

snout = 1.03 ± 0.35 ; Glenariffe: hump = 0.56 ± 0.36 , snout = 0.35 ± 0.34). This variation was likely due to the smaller number of half-sib pairs limiting power of parameter estimation in the separate population estimates. The estimated genetic correlation between hump depth and snout length at a given age, a measure of potential evolutionary trade-off, was very low (-0.16), and covariances across half-sib pairs were not significant.

Within-site phenotypic trade-offs and multivariate validation

Males that had large humps tended to have long snouts at a given body size (MEH), for fish returning to Glenariffe Stream ($r = 0.360$, $n = 178$, $P < 0.001$), to Silverstream ($r = 0.392$, $n = 168$, $P < 0.001$), and the captive males ($r = 0.112$, $n = 822$, $P < 0.001$). Males returning to Glenariffe Stream also showed negative correlations between tissue energy density (measured by per cent dry mass) and size of both hump ($r = -0.236$, $n = 75$, $P < 0.05$) and snout ($r = -0.223$, $n = 76$, $P = 0.053$). At Silverstream, there was a slight positive correlation between muscle energy and hump size ($r = 0.146$, $n = 146$, $P = 0.068$) but no correlation with snout length. Captive males showed a very similar pattern of correlation to that found for salmon returning to Silverstream: a positive correlation between muscle energy and hump depth ($r = 0.279$, $n = 93$, $P < 0.01$) and little if any correlation between muscle energy and snout length ($r = -0.182$, $n = 93$, $P = 0.080$).

Principal components analyses (PCA: with varimax rotation) on HUMP, SNOUT, and seven other morphometric measures extracted from our captive males (adjusted for MEH) provided similar factor solutions for age 2 and age 3 males (Table 2). The first factor in both cases was associated with snout and head length features (SNOUT having the highest loading at both ages). The second factor described hump and body depth, with loadings largely from HUMP and CPD. The third factor involved paired fin lengths (PECF and PELF). MANOVA on combined PCA scores for both years showed no evi-

dence of a year effect (Wilk's λ : $F_{3,982} = 0.176$, n.s.) but a difference between the populations (Wilk's λ : $F_{3,982} = 32.29$, $P < 0.001$), primarily related to the hump factor.

Re-analysis of morphometric data collected by Kinnison *et al.* (1998a), focusing on the same NZ populations and characters similar to those in the present study, indicated that hump size of wild Hakataramea fish was larger than for Glenariffe salmon (univariate: $F_{1,77} = 5.118$, $P < 0.05$; multivariate hump factor: $F_{1,74} = 6.680$, $P < 0.05$, Table 2). Snout size alone did not significantly differ between populations ($F_{1,74} = 1.218$, n.s.), and the multivariate snout/head size factor (Table 2) suggested smaller values for Hakataramea fish ($F_{1,74} = 14.75$, $P < 0.001$).

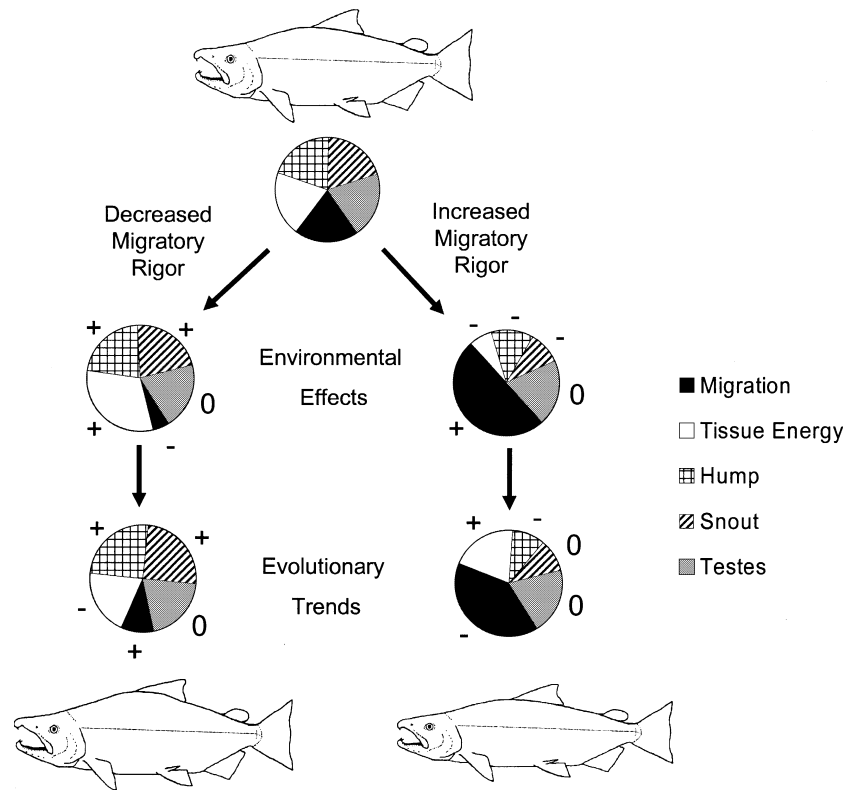
Discussion

The results of this large-scale experiment provided support for our four predictions regarding migratory rigour, reproductive investment and evolution of secondary sexual traits. A schematic of environmental and evolutionary impacts on bins of reproductive investment, consistent with theory and our findings, is shown in Fig. 5. First, we predicted that salmon completing a more challenging migration would show reduced development of morphological features and energy reserves related to breeding. Males of the same populations and families had smaller humps and snouts after making the more arduous migration to Glenariffe Stream than to Silverstream (100 vs. 17 km upriver and 430 vs. 17 m elevation). This conclusion was independent of the family composition of returns. We did not detect a difference in hump depth in females but they vary much less than males in this trait. However, the same pattern seen in snout length of males was seen in females. Furthermore, survival rates from release as juveniles to return as adults are significantly lower at Glenariffe Stream than at Silverstream (for the same families and populations), suggesting potential impacts of migratory rigour on probability of successful migration (Unwin *et al.*, 2003).

Factor	Captive age 2			Captive age 3			Wild males		
	% Var	Variables	Loadings	% Var	Variables	Loadings	% Var	Variables	Loadings
Hump/body Depth	17.8	HUMP	0.90	17.1	HUMP	0.79	21.3	HUMP	0.93
		CPD	0.77		CPD	0.83		BD	0.72
Snout/head Length	38.5	SNOUT	0.92	41.9	SNOUT	0.94	30.5	SNOUT	0.74
		SNAP	0.90		SNAP	0.87		SNAP	0.86
		SNAPE	0.71		SNAPE	0.94		SNAPE	0.84
		HEAD	0.71		HEAD	0.85			
		JAW	0.85	JAW	0.84				
Paired fin Size	15.2	PECF	0.82	14.5	PECF	0.82	22.3	PECF	0.73
		PELF	0.74		PELF	0.71		PELF	0.84
							CPD	0.59	

Table 2 Principle components of shape variation (rotated factor solutions). Highest loading variables are listed for each factor and the percentage of total variation described by each factor is provided. 'Captive' solutions represent fish from the current study and the 'Wild' solution represents data from Kinnison *et al.* (1998a). Loadings between any given variable and remaining factors are not shown but in every case are much smaller than those listed. Variables are defined in Fig. 2.

Fig. 5 Schematic of environmental and evolutionary effects of altered migratory costs on reproductive allocation in male salmon. Exact sizes of wedges are not known or of direct significance. Rather, figure conveys changes in bin sizes associated with environmental effects and net evolutionary trends (i.e. evolutionary impact on top of environmental variation) expected under a given migratory alteration. +, increase in bin size; -, decrease in bin size; 0, no change in bin size. Morphology of male salmon conveys the related influence on morphology, but is not meant to be representative of morphological divergence recorded in the present study.



These results corroborate our previous findings on the cost of migration on female reproductive traits for these same families and populations (Kinnison *et al.*, 2001). Females migrating farther to Glenariffe Stream had smaller ovarian mass, for their length, than those migrating to Silverstream. Thus, both males and females showed phenotypic costs of migration in traits related to reproduction. In contrast to females, there was no evidence of a cost of migration on gonad development in males but testes are both smaller than ovaries and lower in energy density.

Our results are also consistent with observations of variation in body depth of males from indigenous salmon populations differing in migration. Fraser River sockeye salmon (*O. nerka* Walbaum) with long migrations tend to be less deep-bodied than those with shorter migrations (Moore, 1996; G. T. Crossin, S. G. Hinch, A. P. Farrell, D. Higgs, A. Lotto, J. Oakes & M. C. Healey, in review). However, the amount of this variation that is due to proximate migratory costs vs. genetic divergence is unknown and the length of migration may not be the only source of selection on reproductive trait values in these populations. For example, populations with similar migrations show strong correlations between egg size and the size of gravels in which the eggs develop (Quinn *et al.*, 1995), and between water depth at the breeding site and the body depth of males (Quinn *et al.*, 2001b). Our experimental approach avoided the confounding effects

of such factors and allowed us to focus more directly on migratory costs.

Interestingly, males appear to have suffered a substantially greater cost to tissue energy reserves than females for the same migration. Females travelling to Silverstream possessed ca. 6.0% greater tissue dry mass relative to those returning to Glenariffe but the difference for males was over 10%. After accounting for an estimated 14% unmetabolizable dry mass at death in salmon (estimated conservatively from Hendry & Berg, 1999), the difference between migrating to Glenariffe and Silverstream would represent approximately a 30% difference in metabolically useable energy reserves available for spawning males. Kinnison *et al.* (2001) estimated the same difference to be about 17% for females. Although males on average possessed more energy than females at return to both release sites ($P < 0.001$ for both sites), males were estimated to have 27.9% more metabolically useable energy than females at Silverstream but only 14.3% more at Glenariffe. These results are consistent with greater deviation from a hydrodynamically efficient fusiform shape in males and with other studies suggesting less efficient migration in male salmon (electromyogram telemetry: Hinch & Rand, 1998; respirometry: Williams, 1986).

A greater cost of migration in energy reserves of males could affect *en route* survival, duration of breeding life, or intensity of reproductive competition, relative to males

with shorter migrations. The ratio of returning males to females was somewhat smaller for Glenariffe Stream releases than Silverstream releases (Fisher's exact test: $n = 777$, $P = 0.062$), consistent with a greater impact of migration on male survival as well as energy. If the proportion of males and duration of male breeding life decline relative to female numbers and breeding life, then the OSR and intensity of male competition would tend to decrease as well, reducing selection for exaggerated secondary sexual traits. We propose that future studies attempt to evaluate the hypothesis that variation in breeding life or sex ratios is linked to migration costs experienced by indigenous populations with implications for sexual selection.

One would expect that morphological analyses on wild Hakataramea and Glenariffe salmon, or other populations returning to their respective spawning sites, would show patterns of variation consistent with the genetic and environmental trends we have demonstrated here. Re-analysis of morphometric data collected by Kinnison *et al.* (1998a), focusing on wild adults from the same NZ populations and similar characters supported this contention for hump size, but a consistent pattern was not found for snout development. Unlike the current study, fish in our previous investigation were not processed at a standardized stage of maturation. We believe this inconsistency in pattern of snout variation may reflect variation in senescence, a factor known to impact secondary sexual trait values (e.g. Quinn & Blair, 1992).

Consistent with our second prediction, individual salmon returning to Glenariffe Stream showed a negative correlation between tissue energy reserves and secondary sexual trait development. This result supports the contention that morphology itself affects the efficiency of migration. This hypothesis is consistent with the absence of a negative correlation between hump development and tissue energy reserves in males making the negligible migration to Silverstream or reared in captivity. In the latter cases, efficiency costs are minimal and thus hump size and tissue energy may be positively correlated due to individual variation in overall energy condition. Under longer migrations, evolutionary reduction in hump depth may be favoured under direct selection for survival and mating energy, due to both the energy freed from hump construction and the potentially greater energy associated with efficiency of migration (Fig. 5).

Our third prediction was that development of secondary sexual traits is under genetic control, providing a heritable basis for selection in response to constraints imposed by migration or other factors. Under common-garden rearing, Hakataramea males had larger humps than Glenariffe males, but there were no significant differences in snout size. Quantitative genetic analyses indicated ample heritability for both hump and snout size in captivity (even after accounting for body size). Although these heritabilities may overestimate values

in the wild (because environmental variation is reduced under captivity), it is clear that a significant heritable component exists for both characters. This is an important finding because it demonstrates the scope for selection to promote evolution in these traits. Heritability has not previously been estimated for secondary sexual characters of salmonids. We do not regard the presence of a substantial heritable component as surprising, but it provides credence to other studies that have suggested an adaptive and heritable basis to population divergence in these features (e.g. Beacham & Murray, 1987; Beacham *et al.*, 1988; Blair *et al.*, 1993; Hendry *et al.*, 2000; Hendry, 2001; Quinn *et al.*, 2001b).

Interestingly, the genetic correlation between hump and snout size was nominally negative and close to zero. These traits are often regarded as elements of a secondary sexual trait complex in salmon (e.g. Fleming & Gross, 1994; Quinn & Foote, 1994). The jaws of mature male salmon are used in direct aggression, and a male with sufficiently large jaws may inflict significant wounds on a combatant. The hump may serve as a 'shield' to prevent this kind of attack, but it is also used in displays to other males and females. In general, populations of salmon that are deep-bodied for their length tend to have long snouts (Blair *et al.*, 1993; Quinn, unpublished data), although considerable variation exists around this trend. The small genetic correlation and evolutionary response of only one trait (hump depth) in NZ salmon suggests that snout and hump correlations may be due to correlated selection (e.g. an arms race between weapons and shields) more than correlated inheritance (i.e. pleiotropy).

Our fourth prediction was that the NZ salmon populations, derived from a common ancestral introduction <30 generations before our experiment, would show evidence of heritable divergence favouring smaller secondary sexual trait development in populations with more arduous migrations. This prediction was supported for hump depth but not for snout size, despite the proximate impact that migration appears to have on the latter trait. Evidence of slight evolutionary divergence in hump size in female NZ chinook is interesting. It may indicate correlated evolution arising from a cross-sex genetic correlation (*sensu* Lande, 1987) or perhaps a parallel pattern of selection on females (*sensu* Fleming & Gross, 1989). The role of migration in parallel selection would seem minimal given the likely minor impact of hump development on female migratory efficiency.

One might expect that evolutionary reduction in either hump size or snout size would be impeded if the corresponding 'weapon' or 'shield' did not change. However, investment into a weapon or a shield is not exclusively determined by the scale of its foil, but is also shaped by trade-offs with additional aspects of fitness. For example, in the native range of Pacific salmon, body size and hump depth face additional selection from size-selective predation from bears (Quinn & Kinnison, 1999) and difficulty in accessing very shallow streams (Quinn &

Buck, 2001; Quinn *et al.*, 2001b). Selection from predation, stream access and hydrodynamics may ultimately mean that hump size is often less than it would optimally be under selection from snout size alone. Indeed, especially deep-bodied salmon are found in indigenous populations of salmon that are freed from such constraints by spawning off lake beaches (Blair *et al.*, 1993; Quinn *et al.*, 2001b). In addition, a disproportionately large environmental effect of migration on the length of snouts, or energy available for launching biting attacks, would also theoretically reduce the intensity of selection preserving large hump size. Our results support both patterns: the proximate impact of migration on snout size was somewhat larger than the impact on hump depth, and migration clearly reduced energy reserves available for mating activities.

The contemporary divergence we have described is remarkable, given that it has occurred in the face of continued straying (Unwin & Quinn, 1993) and gene flow (Kinnison *et al.*, 2002) among NZ populations. This divergence can be added to evidence for modest but heritable differences in a range of other traits, including juvenile growth rates (Unwin *et al.*, 2000), timing of migration and maturation (Quinn *et al.*, 2000) and ovarian investment (Kinnison *et al.*, 2001; multiple traits reviewed by Quinn *et al.*, 2001a). The rate of divergence in hump depth between the NZ populations of 0.045 haldanes (95% CI: 0.018–0.076) or 393.1 darwins (95% CI: 159.7–626.2) is comparable with rates we have estimated for other divergent features of NZ salmon (Quinn *et al.*, 2001a), suggesting that selection on hump development is consistent with the broader suite of selection shaping contemporary evolution in these populations. However, our demonstration of heritable divergence in hump size not only represents the first evidence of divergence in a sexually selected trait in New Zealand salmon, but also the first formal evidence (i.e. using a common-garden design) of heritable variation and divergence in the secondary sexual traits of salmon. We find it remarkable that such variation has not been demonstrated before in salmon, given that these features have been discussed as examples of sexual selection since Darwin's (1871) treatise on the topic.

Conclusions

We propose that evolution of hump size in NZ salmon has been driven by trade-offs with *en route* survival and mating activity/longevity on the spawning grounds. When new populations are established the balance in such trade-offs is altered, at least in part, by the strong proximate effects of migration on survival and components of reproductive trait investment. Evolution of new allocation strategies is expected over even short time scales given heritable variation in investment traits and such patterns may persist over thousands of years to shape patterns of indigenous population variation.

Populations of other migratory species may have faced similar trade-offs when colonizing new habitats. Although other studies have provided evidence of contemporary evolution of secondary sexual traits in response to trade-offs with predation (e.g. Endler, 1980; Magurran *et al.*, 1992), we have provided evidence of contemporary evolution driven by trade-offs with an abiotic component of the environment. However, this evolutionary process is not inherently restricted to colonization. Alterations to *in situ* costs of migration, such as those imposed by dramatic anthropogenic influences (e.g. temperature or flow regimes – Quinn & Adams, 1996), may have significant implications for contemporary evolution of many extant populations.

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