

SYNTHESIS

A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change

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Abstract

Salmonine fishes are commonly subjected to strong, novel selective pressures due to anthropogenic activities and global climate change, often resulting in population extinction. Consequently, there is considerable interest in predicting the long-term evolutionary trajectories of extant populations. Knowledge of the genetic architecture of fitness traits is integral to making these predictions. We reviewed the published, peer-reviewed literature for estimates of heritability and genetic correlation for fitness traits in salmonine fishes with two broad goals in mind: summarization of published data and testing for differences among categorical variables (e.g., species, life history type, experimental conditions). Balanced coverage of variables was lacking and estimates for wild populations and behavioral traits were nearly absent. Distributions of heritability estimates were skewed toward low values and distributions of genetic correlations toward large, positive values, suggesting that significant potential for evolution of traits exists. Furthermore, experimental conditions had a direct effect on h^2 estimates, and other variables had more complex effects on h^2 and r_G estimates, suggesting that available estimates may be insufficient for use in models to predict evolutionary change in wild populations. Given this and other inherent complicating factors, making accurate predictions of the evolutionary trajectories of salmonine fishes will be a difficult task.

Introduction

Salmonine fishes are experiencing many anthropogenic disturbances and may need to adapt if they are to persist. In their native range, for instance, many populations are extinct or threatened with extinction, typically due to human activities (e.g., Gustafson et al. 2007). Consequently, there is considerable interest in predicting whether and how populations (or more specifically, traits within populations) will evolve in response to these perturbations (e.g., Crozier et al. 2008). Understanding the adaptive potential of these fishes requires information on quantitative genetic parameters, which is the goal of this paper. Specifically, we reviewed estimates of two quantitative genetic parameters, heritability (h^2) and genetic correlation (r_G), for fitness traits for Pacific salmon and trout (*Oncorhynchus* spp.), Atlantic salmon (*Salmo salar*

Linnaeus) and brown trout (*Salmo trutta* Linnaeus), and the circumpolar charr (*Salvelinus* spp.).

Salmonids vary in a number of important traits, linked to their use of diverse aquatic habitats, the timing of breeding, iteroparity, and anadromy. For example, the Pacific salmon are almost invariably semelparous and anadromous and spawn in fall whereas the congeneric Pacific trout spawn in spring, are iteroparous and facultatively anadromous (Groot and Margolis 1991; Quinn 2005). Atlantic salmon are similar to Pacific salmon in many regards but are iteroparous, as are brown trout but the latter are more often nonanadromous than the salmon of the same genus. The charrs are all iteroparous and facultatively anadromous. This diversity suggests that variability in quantitative genetic parameter estimates is likely and yet this has not been evaluated systematically.

A review of heritabilities and genetic correlations is appropriate because these parameters are related to the rate and direction of evolution of a population. Heritability generally describes the fraction of phenotypic variation explained by genetic variation (e.g., Falconer and Mackay 1996; Roff 1997). Heritability estimates are often used as evidence that there is some genetic basis for a trait that is under selection, but the more common use is for making predictions about how traits will evolve under selection. This prediction is accomplished through the theoretical relationship between genetic variation and selection, commonly known as the breeder's equation, where the response to selection (change in the trait) is equal to the narrow-sense heritability multiplied by the selection differential. Genetic correlation describes the degree to which two traits are influenced by the same genes (pleiotropy, Roff 1997). This relationship means that selection on one trait may indirectly drive evolution on any correlated trait(s). The magnitude and sign of the genetic correlation together determine the nature of the relationship. Thus, to some degree, one may predict the evolutionary trajectory of a population if one knows the values of these quantitative genetic parameters (e.g., Grant and Grant 1995).

Several reviews of heritability in salmonine fishes have already been written, the first in 1975 (Gjedrem 1975). In the 30+ years since then, there has been an explosion of studies estimating trait heritabilities as well as genetic correlations among traits. Although several more recent reviews of heritability estimates in salmonids already exist, they focused on production-related traits (e.g., Gjedrem 2000) or on a focal species (e.g., *Salmo salar*, Garcia de Leaniz et al. 2007). To date, there has been no comprehensive review of the literature examining quantitative genetic components of fitness traits in salmonine fishes. Herein, we undertook this task.

Objectives

In this paper, our objectives were to answer the following general questions. How extensive is our knowledge of quantitative genetic parameters in salmon, trout, and charr? How is that knowledge distributed among species, genera, trait classes, traits, life history stages, or populations? We will also address the following specific questions:

Quantitative genetic parameters are difficult to estimate, especially for wild populations. Thus, parameter estimates for a trait from one group [e.g., species, life history stage (age), life history type (e.g., iteroparous)] are often cited as evidence of genetic variation of the same magnitude for the same trait in another group. Is there any support for doing this, that is, are there differ-

ences in parameter estimates for traits among species? Among genera? Among life history stages? Among life history types (e.g., between among anadromous and nonanadromous species or between iteroparous and semelparous species)?

Quantitative genetic parameters are most often measured on populations that are reared in experimental settings, like hatcheries, where the environment can be controlled and/or measured on captive-bred broodstock (derived from farmed or hatchery populations), which are often the subject of intentional artificial selection on important fitness-related traits. Parameters for traits measured under these circumstances are often cited as evidence of genetic variance in the same traits in wild populations. Is there any support for this practice or are there differences in parameter estimates for traits among experimental treatments and/or broodstock sources?

Methods

Literature search

We limited our review to the peer-reviewed literature. Consequently, data included in unpublished studies, data published in book chapters, technical reports, or theses/dissertations were not included. We did not limit studies included in our review any further. Published literature was found by performing searches of three online databases, BIOSYS, ASFA, and Web of Science. We searched using different combinations of the following keywords: trout, salmon, char, charr, *Salmo*, *Oncorhynchus*, *Salvelinus*, heritability, genetic correlation, quantitative genetic parameters, and genetic architecture. As our goal was to include all peer-reviewed published works on the subject, we also scanned the literature cited from books (e.g., Tave 1993), previously published reviews (e.g., Gjedrem 2000), or other published works (e.g., papers estimating quantitative genetic parameters). We included all papers published before and up to April 2007, when the literature search was performed.

Dataset compilation

For each estimate of heritability (h^2) or genetic correlation (r_G) from each study included in our dataset, we recorded the following data: species, sex (when reported), trait (as described in original study), age (when reported), broodstock source (described below), treatment (described below), source population, mating design, and statistical method used to calculate the estimate (Table S1, for information on studies included in the h^2 and/or r_G datasets). We also recorded standard errors and P -values when these data were reported. Where data were available only in graphical format, the digitizing software

ENGAUGE DIGITIZER v4.1 (<http://digitizer.sourceforge.net>) was used to determine estimates and standard errors.

We found a total of 182 different sources reporting 3150 different estimates of heritability (hereafter 'complete h^2 dataset', Table S2). Heritability estimates were categorized by the quality of estimate, that is, how closely it estimated additive genetic variance (i.e., narrow-sense). For later analysis of h^2 values, we restricted our dataset to only those considered to be narrow-sense or realized heritability estimates. To be considered narrow-sense, the heritability estimate had to be derived from population with a mating design (or system) that included full-sib families nested within half-sib families or from mid-parent or sire offspring regression (Roff 1997). Although h^2 estimates calculated from dam-offspring regression included some environmental variance (maternal effects, Falconer and Mackay 1996), these estimates were included for traits specific to females, e.g., fecundity. If we could not determine the category of h^2 estimate from the description of the experimental design included in the paper, the estimate was recorded as an unknown type and was excluded from further analysis. Our dataset of narrow-sense heritabilities consisted of 164 sources, which yielded 2049 h^2 estimates of quality suitable for further analysis (hereafter 'reduced h^2 dataset', Table S3).

We found a total of 108 different sources reporting 2284 different estimates of genetic correlations (hereafter 'complete r_G dataset', Table S5). Genetic correlation estimates were categorized by quality of the estimate. When the quality of the estimate could not be determined from the description of the analysis in the paper, inclusion was based on the quality of the h^2 estimates based on the same data and the experimental design. For example, if the h^2 estimate was considered broad-sense because it was based solely on full-sib family data, then any associated r_G estimates were excluded from further analysis. Our dataset of 'narrow-sense' genetic correlations consisted of 81 sources which presented 1548 estimates of quality suitable for further analysis (hereafter 'reduced r_G dataset', Table S6).

Species were categorized as anadromous or nonanadromous. For salmon species, this was relatively simple; although they can often be held in freshwater for their entire lives, they are almost always naturally anadromous. For trout and charr species that may be facultatively anadromous, this was more difficult as it is entirely possible that the original broodstock was derived from a population with a life history that differed from the current/selected life history, but this information was rarely noted. Consequently, we categorized trout and charr populations as nonanadromous if they were held in freshwater their entire lives, or as anadromous if they were transferred to brackish or salt water for rearing.

Because of the huge variability in the traits studied, we added a field in which we combined related traits into summary categories (hereafter 'traits', Table S8). For instance, the two traits originally described as length at 100 days post emergence and length at 150 days post emergence were both labeled 'length-at-age'. Following Mousseau and Roff (1987), we then categorized each trait into one of the following trait classes: (i) behavior, (ii) life history, (iii) morphological, and (iv) physiological. Many of the estimates of quantitative genetic parameters were made for the purpose of 'genetic improvement' of populations used for commercial farming. As such, many of the traits for which these parameters were estimated were traits of no obvious fitness importance to natural populations (e.g., 'cutlet width'). For these traits, we added a fifth class which was not included in the review by Mousseau and Roff (1987), production-related traits. Again following Mousseau and Roff (1987), we defined life history traits to be the subset of traits closely linked to fitness (e.g., age-at-maturity).

Many traits were measured at multiple ages (sometimes just days or months apart), both among and within studies, and so we added a field which combined specific age data into a more general category termed 'life history stage'. This category included the following stages: egg, alevin, juvenile, smolt, immature adult, and mature adult. Our decision rules for each life history stage were as follows: egg stage (specifically noted as such), alevin (noted as such or <1 month posthatching), smolt (regardless of age, noted as such, or traits measured at time of transfer to saltwater), mature adults (regardless of age, traits measured on mature adults or traits that included mature adult at the end of the focal interval, e.g., growth or survival). The juvenile and immature adult stages were slightly more complicated and our classification rules were as follows. For anadromous fish, any fish still in freshwater but not undergoing the smolt transformation were classified as juveniles whereas these fish were categorized as immature adults once they entered saltwater. For nonanadromous fish, we classified all fish less than 1 year of age as juveniles and all fish greater than 1 year of age as immature adults. Occasionally, parameters were estimated for a combined life history stage that included individuals of more than one life history stage (e.g., immature/mature adults).

We designated two fields to describe the history of the populations used in each study – broodstock source and treatment. The field 'broodstock source' described the recent history of the population used in the experiment, or a measure of the genetic background of the population under experiment; 'treatment' described how the population was treated during the experiment, or the environment in which the population was tested. We designated

each population in terms of the treatment and broodstock source using the following descriptors: farmed, hatchery, sea-ranched, wild, mixed, and unknown. Each of these was defined for both fields as follows. *Farmed* meant the population was reared in salt water net-pens at some time in its life. *Hatchery* meant the population was reared in captivity in freshwater its entire life. *Sea-ranched* meant the population was reared in captivity in freshwater and subsequently released to open salt water. *Wild* meant the population spawned and reared in the wild over the entire life history (regardless of whether it was anadromous or nonanadromous). *Mixed* meant that the broodstock source or treatment consisted of more than one category. *Unknown* meant that not enough information was provided to determine the status of the population. Thus, an experimental population with the parents taken directly from a wild population, mated in a hatchery, offspring reared in the hatchery until final rearing in a net-pen in saltwater where the traits of interest were measured would be designated as a wild broodstock source and farmed treatment.

Statistical analysis

Many of the published studies reported many estimates of h^2 or r_G for the same trait using the same or similarly related data. In cases where h^2 estimates for both observed and liability scales were reported, we used only h^2 estimate on the observed scale (observed = raw, untransformed data; liability = transformed to underlying continuous scale, Roff 1997). For the rest, median values of h^2 or r_G estimates were calculated for traits within studies when the following conditions were met: (i) when multiple, different statistical models were used, (ii) when the trait was measured in different environments (e.g., hatchery versus farmed, but with the same populations/families), (iii) when parameters were estimated for multiple ages within a life history stage, (iv) when the traits were measured on individuals from multiple, but unknown source populations; (v) when parameter estimates were calculated for lengths or weights of different parts of the same fish (e.g., gutted weight/ungutted weight/visceral weight), (vi) and when multiple regression-based estimates for the same trait were calculated (e.g., mid-parent and sire-offspring). When parameter estimates calculated from data pooled among strains or lines of the same broodstock source were available, the estimate from the pooled data was used instead of calculating a median value, and individual estimates were discarded. After calculating median values and after removing production-related traits, the final 'medianized h^2 dataset' included 706 h^2 estimates (Table S4) and the final 'medianized r_G dataset'

included 532 r_G estimates (Table S7), after removing pseudo-replication due to the above issues and were used in all analyses comparing values of parameter estimates among groups.

Data were analyzed using univariate ANOVA tests with fixed factors as implemented in the GLM analysis of SPSS 12.0 (SPSS Inc., Chicago, IL, USA) unless otherwise noted. Negative h^2 estimates were changed to 0 and h^2 estimates >1 were changed to 1 and were arcsine square root transformed prior to analysis. Any factor with fewer than three data points was omitted from analysis. Any sample with 'mixed' or 'unknown' factor values were omitted from analysis of those factors, but were included in other tests where factor values were known or unmixed. When comparing h^2 values of anadromous versus nonanadromous populations, traits specific to smolts or smolt transformation were removed from analysis. When comparing h^2 estimates among life history types, traits specific to life histories stages were removed from analysis. Significance levels of *post hoc* tests and multiple pair-wise comparisons were adjusted to minimize type I errors using sequential Bonferroni corrections (Holm 1979) and a correction promoted by Verhoeven et al. (2005). The two methods yielded identical conclusions and so we present only the results of the more conservative correction (i.e., Bonferroni corrected α values).

Results

Heritability estimates

Distribution of counts among factors

The number of h^2 estimates was unevenly distributed among species (Fig. S1A) – nearly 50% of the estimates were reported for two species, *Oncorhynchus mykiss* Walbaum and *S. salar*, whereas no estimates were reported for four others (*Oncorhynchus clarki* Richardson, *Salvelinus malma* Walbaum, *Salvelinus namaycush* Walbaum, and *Salvelinus confluentus* Suckley). Within species, contributions also differed among the life history stages, trait classes, and broodstock sources (Table S9). Four species had h^2 estimates for nearly all categories (*Oncorhynchus kisutch* Walbaum, *Oncorhynchus mykiss*, *Oncorhynchus tshawytscha* Walbaum, *S. salar*); others were missing estimates for many categories (Table S9).

Numbers of h^2 estimates were also unevenly distributed among trait classes (morphological and life history traits together comprised 87% of the estimates, Fig. S1B) and among life history stages (juveniles and immature adults together comprised 72% of the estimates, Fig. S1C). Finally, the number of h^2 estimates was unevenly distributed among broodstock sources (Fig. S1D) and treatment groups (Fig. S1E). Most estimates were derived from

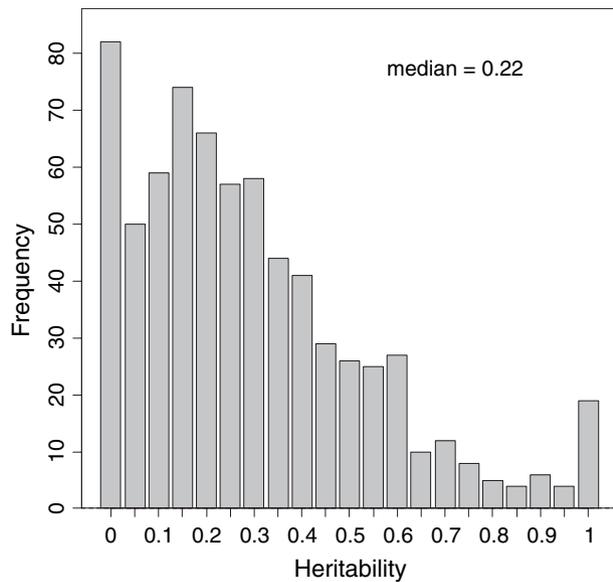


Figure 1 Distribution of h^2 estimates pooled across groups. These data were generated based on the ‘medianized h^2 dataset’ (see Methods and Table S4).

farmed (27%) or hatchery broodstock (26%), and estimates based on wild broodstock comprised only 20% of the estimates. When the fish were maintained in a farm-

ing, hatchery, or sea-ranching operation to estimate heritabilities, the fish were derived from a range of broodstock sources including wild broodstock (Fig. S2).

Distribution of values among factors

Overall, h^2 estimates spanned the entire range from 0 to 1; however the distribution was skewed toward lower values (Fig. 1). The majority (90%) of h^2 estimates fell between 0.00 and 0.60 (median = 0.22, 25th % = 0.09, 75th % = 0.40; Fig. 1). Median values for traits within trait classes ranged from 0.06 to 0.51, but most were between 0.20 and 0.30 (life history traits, Fig. 3; morphological traits, Fig. 4; and physiological traits, Fig. 5). The distribution of h^2 for life history traits and physiological traits were more skewed to lower h^2 values than the distribution of h^2 for morphological traits (Fig. 2, Two-sample Kolmogorov–Smirnov test: life history, $Z = 3.490$, $P < 0.001$; physiological, $Z = 2.228$, $P = 0.0001$; Bonferoni-corrected $\alpha = 0.008$).

Variation among groups

Heritability estimates differed among traits nested within trait classes ($F_{0.05(1),22,702} = 5.438$, $P < 0.001$), but not among trait classes ($F_{0.05(1),3,702} = 1.742$, $P = 0.157$). The estimate of h^2 of a trait depended on the species although no clear pattern emerged (Table 1, median values for each

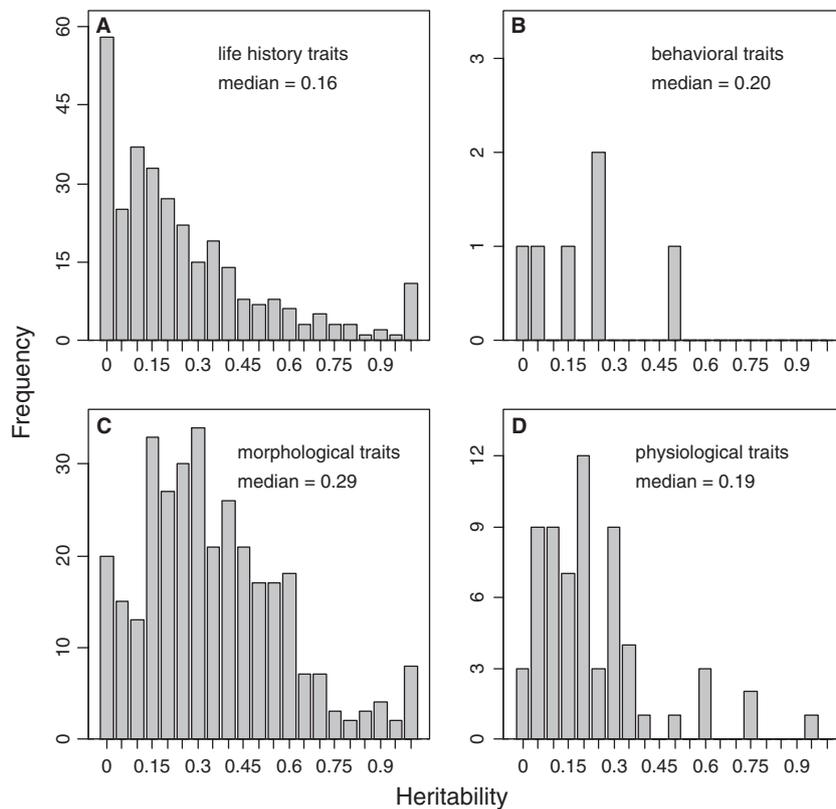


Figure 2 Distributions of heritability estimates for the following trait classes: life history traits (A), behavioral traits (B), morphological traits (C), and physiological traits (D). These data were generated based on the ‘medianized h^2 dataset’ (see Methods and Table S4).

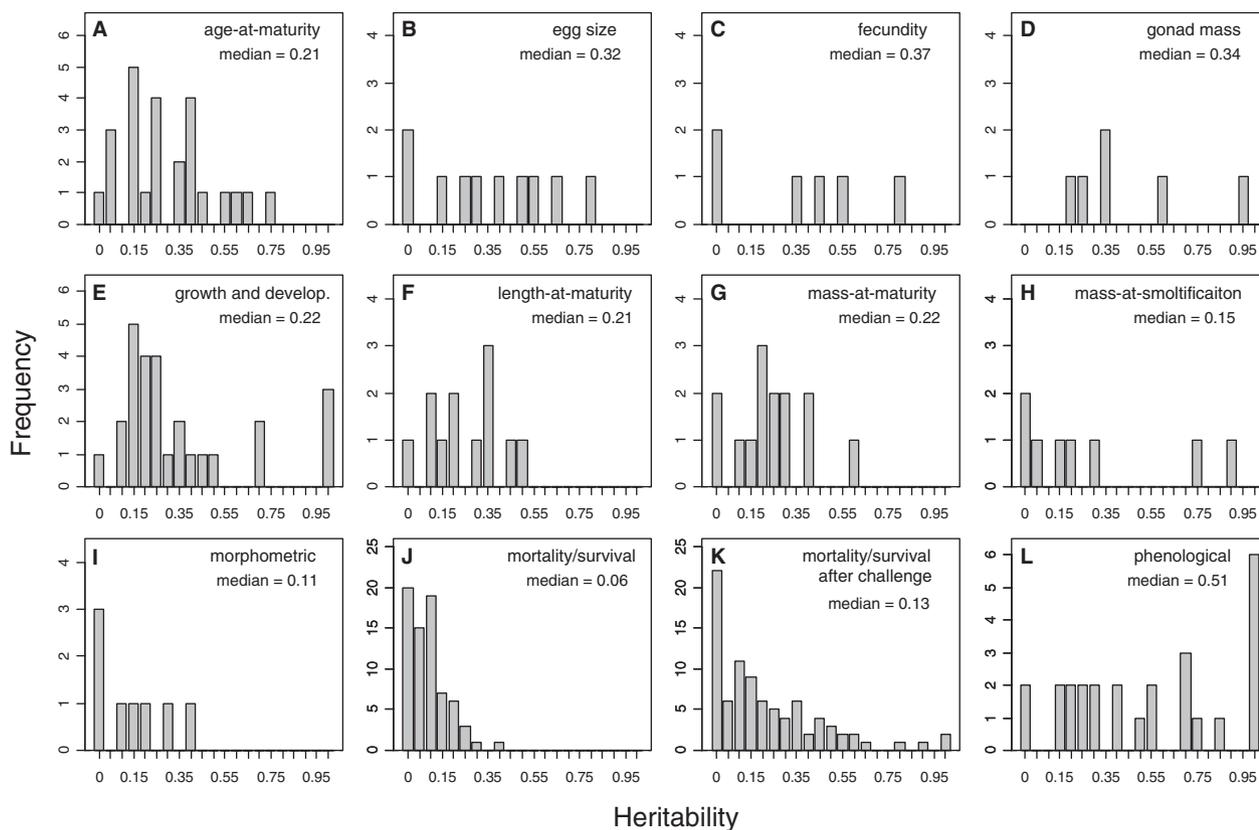


Figure 3 Distributions of heritability estimates for the following life history traits: (A) age-at-maturity, (B) egg size, (C) fecundity, (D) gonad mass, (E) growth and development, (F) length-at-maturity, (G) mass-at-maturity, (H) mass-at-smoltification, (I) morphometric traits including snout length-at-maturity and body depth-at-maturity, (J) mortality/survival, (K) mortality/survival after challenge, and (L) phenological traits. These data were generated based on the 'medianized h^2 dataset' (see Methods and Table S4).

species pooled across traits are presented in Table S9). Moreover, the h^2 estimate of a trait depended on the life history stage (excluding life history stage-specific traits, e.g., egg size), on the diadromous life history type (median h^2 : anadromous, 0.20; nonanadromous species, 0.32; Table S4), and on parity (median h^2 : semelparous, 0.21; iteroparous, 0.23; Table S4), as revealed by a significant two-way interaction between trait and these other factors (Table 1). The h^2 estimate of a trait did not depend on genera (median h^2 : *Oncorhynchus*, 0.24; *Salmo*, 0.16; *Salvelinus*, 0.27), as revealed by a nonsignificant interaction between these two factors.

Because treatment and broodstock source for any h^2 estimate were correlated (Spearman's rank test, $r = 0.420$, $P < 0.001$), we compared h^2 estimates of traits while considering treatment and broodstock source simultaneously. Heritability estimates differed among treatments ($F_{0.05(1),3,573} = 6.409$, $P < 0.001$) and among traits ($F_{0.05(1),24,573} = 3.798$, $P < 0.001$). Moreover, the effect of trait on h^2 depended upon broodstock source, as revealed by a significant interaction between these factors

($F_{0.05(1),30,573} = 2.529$, $P < 0.001$), but not upon treatment, as revealed by a nonsignificant trait \times treatment interaction ($F_{0.05(1),20,573} = 0.663$, $P = 0.863$). *Post hoc* tests of treatments failed to reveal any significant differences among treatments (for all tests, $P > 0.246$).

Genetic correlations

Distribution of counts among factors

As with h^2 estimates, numbers of r_G estimates were unevenly distributed among species (Fig. S3A) – most estimates were reported for three species, *O. mykiss* (37%), *S. salar* (25%), and *O. kisutch* (18%), while no estimates were found for four others (*O. clarki*, *Sv. malma*, *Sv. namaycush*, and *Sv. confluentus*) (see also Table S10). Numbers of r_G estimates were also unevenly distributed among trait classes (Fig. S3B) – most r_G estimates were within trait types (66%), with combinations of morphological traits with other morphological traits being the most numerous (39%, Fig. 7). Finally, numbers of r_G estimates were also unevenly distributed among life

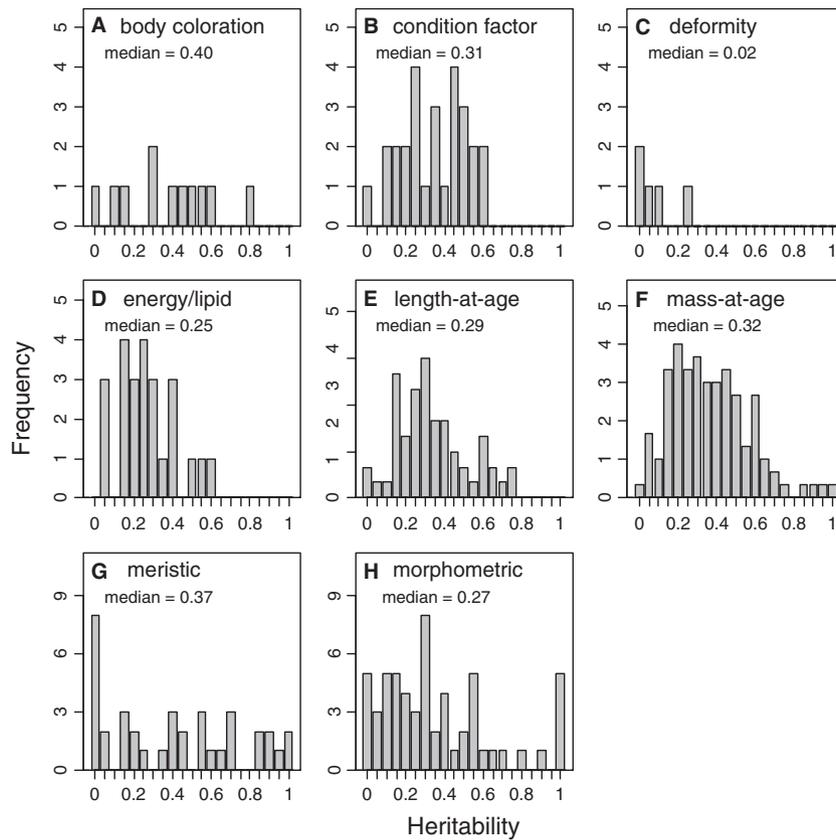


Figure 4 Distributions of heritability estimates for the following morphological traits: (A) body coloration, (B) condition factor, (C) deformity, (D) energy/lipid, (E) length-at-age, (F) mass-at-age, (G) meristic traits, and (H) morphometric traits. These data were generated based on the ‘medianized h^2 dataset’ (see Methods and Table S4).

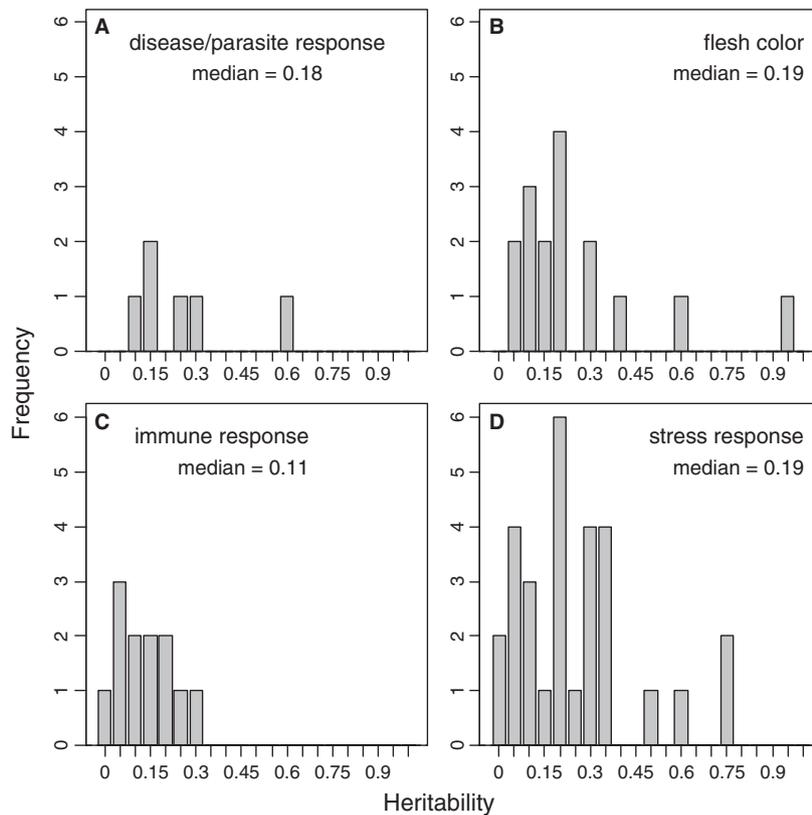


Figure 5 Distributions of heritability estimates for the following physiological traits: (A) disease/parasite response, (B) flesh color, (C) immune response, (D) stress response. These data were generated based on the ‘medianized h^2 dataset’ (see Methods and Table S4).

Table 1. ANOVA statistics for two-way models seeking to explain variation in h^2 estimates by including the factor 'trait' and one other factor (species, life history stage, diadromous life history types, or parity types) as independent variables.

	Factor	Trait	Interaction (trait × factor)
	<i>F</i> (d.f.) <i>P</i>	<i>F</i> (d.f.) <i>P</i>	<i>F</i> (d.f.) <i>P</i>
Species	1.269 (10, 700) <i>P</i> = 0.245	3.562 (24, 700) <i>P</i> < 0.001	1.918 (81, 700) <i>P</i> < 0.001
Genus	0.753 (2, 702) <i>P</i> = 0.471	2.737 (24, 702) <i>P</i> < 0.001	0.989 (26, 702) <i>P</i> = 0.480
Life history stage*	0.707 (5, 580) <i>P</i> = 0.619	4.483 (15, 580) <i>P</i> < 0.001	2.650 (24, 580) <i>P</i> < 0.001
Diadromous life history types† (andadromous versus nonandadromous)	4.478 (1, 679) <i>P</i> = 0.035	2.766 (23, 679) <i>P</i> < 0.0011	1.947 (17, 679) <i>P</i> = 0.012
Parity types (semelparity versus iteroparity)	0.380 (1, 702) <i>P</i> = 0.538	5.494 (24, 702) <i>P</i> < 0.001	2.012 (19, 702) <i>P</i> = 0.007

Listed is the *F*-statistic, associated degrees of freedom and *P*-value for each factor separately and for their interaction. The data used in these analyses were based on the "medianized h^2 dataset" (see Methods and Table S4).

*For the life history stage analysis, we excluded all traits that were life history stage-specific including age-at-maturity, age-at-smoltification, egg size, fecundity, flesh color, gonad mass, GSI, length-at-maturity, length-at-smoltification, mass-at-maturity, mass-at-smoltification, and reproductive success.

†For the diadromous life history types analysis, we excluded all traits that were smolt-specific including age-at-smoltification, length-at-smoltification and mass-at-smoltification.

history stages (Fig. S3C) – most genetic correlation estimates reported were for traits within a life history stage (78%). Estimates for combinations between the youngest (egg and alevin) and oldest life history stages (smolt, immature adult and mature adult) were absent (Fig. S3C).

Distribution of values among factors

Overall, r_G estimates spanned the entire range of values, from -1 to $+1$, however the distribution was skewed toward positive values (Fig. 6). The majority (81%) of estimates fell between 0 and $+1$ (median = 0.40 , 25th% = 0.08 , 75th% = 0.79 ; Fig. 6). Genetic correlations of all combinations of trait class were more likely to be positive than negative (chi-square tests, $P < 0.05$ all tests; Fig. 7A–E) except the life history × physiology r_G estimates (chi-square test, $P = 0.180$; Fig. 7F). The distribution of r_G between morphological traits (Fig. 7A) differed significantly (after corrections for multiple tests) from all other trait class combinations (Two-sample Kolmogorov–Smirnov test, $P < 0.003$, all tests) except physiological × physiological ($P = 0.058$). The distribution of r_G for combinations of life history and physiological traits differed from that of combinations of life history traits ($P = 0.035$), life history × morphological ($P = 0.034$) and combinations of physiological traits ($P = 0.038$), although none of these tests were significant after Bonferroni corrections for multiple tests.

Greater than 60% of comparisons of mass-at-age or length-at-age were with other morphological traits. Distributions of values of genetic correlation estimates for mass- and length-at-age (Fig. 8) were more likely to be

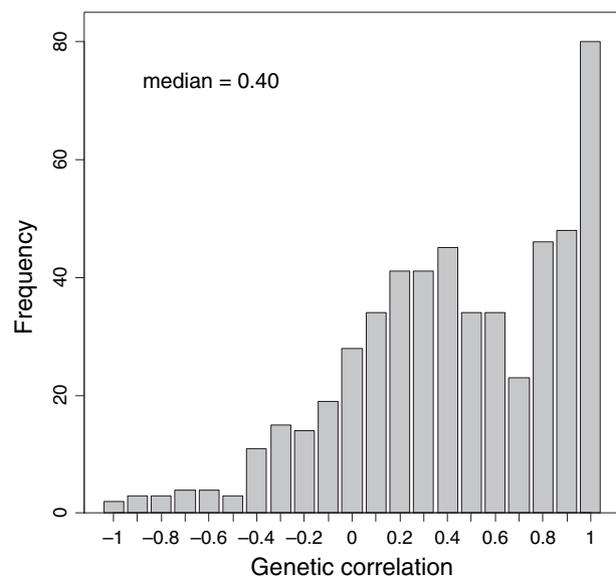


Figure 6 Distribution of r_G estimates pooled across groups. These data were generated based on the 'medianized r_G dataset' (see Methods and Table S7).

positive (chi-square tests, $P < 0.05$, all tests except length-at-age × physiological traits, which was excluded from this analysis due to small sample size), were positively skewed, and had positive medians (Fig. 8A–F).

Variation among groups

Genetic correlations differed among trait type comparisons (ANOVA, $F_{0.05(1),5,532} = 11.591$, $P < 0.001$). Genetic

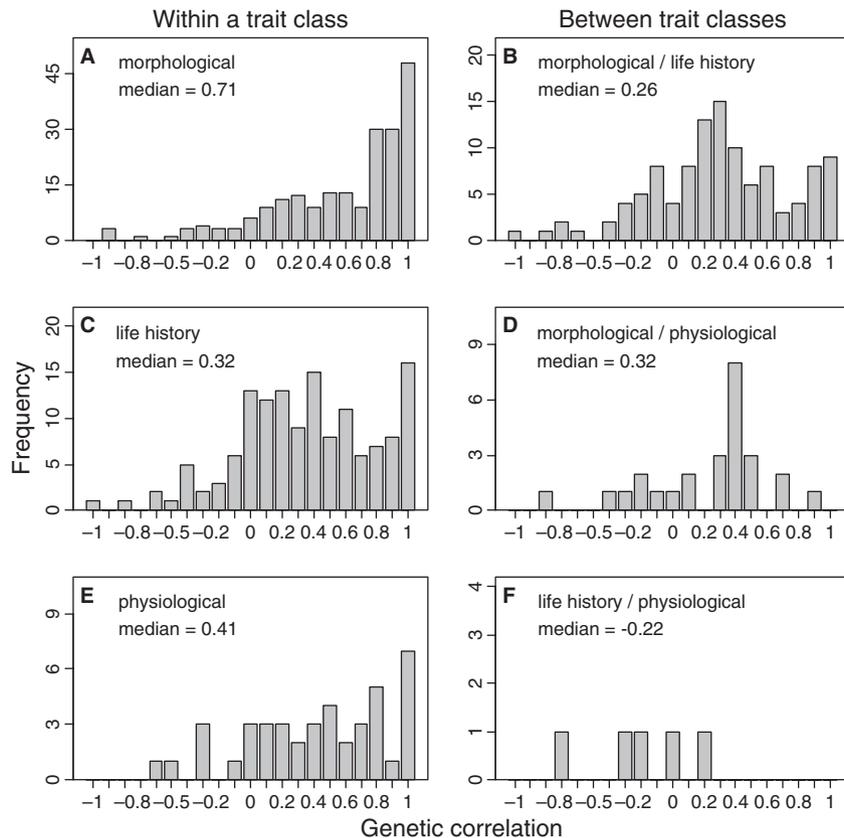


Figure 7 Distributions of genetic correlations within (left panel) and between (right panel) trait classes. These data were generated based on the 'medianized r_G dataset' (see Methods and Table S7).

correlations between morphological traits were larger than those within life history, morphological \times life history, and morphological \times physiological (Tamhane's *post hoc* test, $P < 0.002$, Bonferroni-corrected $\alpha = 0.003$). The effect of trait class combination on r_G depended on species and on genus (median r_G : *Oncorhynchus*, 0.46; *Salmo*, 0.32; *Salvelinus*, 0.48), as shown by a significant interaction term between trait class combination and these other factors (Table 2).

Because treatment and broodstock source were correlated for any r_G estimate (Spearman's rank test, $r = 0.736$, $P < 0.001$), we compared r_G estimates of trait class combination while considering treatment and broodstock source simultaneously. Estimates differed among trait class combinations ($F_{0.05(1),5,464} = 6.310$, $P < 0.001$). Moreover, the r_G estimates of trait class combinations depended upon broodstock source and combinations of treatment and broodstock source, as shown by a significant trait class combination \times broodstock source interaction ($F_{0.05(1),7,464} = 3.031$, $P = 0.004$) and a significant treatment \times broodstock source interaction ($F_{0.05(1),3,464} = 3.423$, $P = 0.017$). The interaction between treatment and trait class combination was not significant ($F_{0.05(1),6,464} = 1.319$, $P = 0.247$), nor was the interaction between trait class combination, treatment, and broodstock source ($F_{0.05(1),2,464} = 0.169$, $P = 0.917$).

Genetic correlations between length- or mass-at-age and other morphological traits (Fig. 8A,B) were higher than correlations between these same traits and either life history traits (Fig. 8C,D) or physiological traits (Fig. 8E, no statistical test for length-at-age \times physiological traits due to small sample size) (ANOVA, $P < 0.002$; Tamhane's *post hoc* test, $P < 0.001$, Bonferroni-corrected $\alpha = 0.016$).

Discussion

Quantitative genetic parameter estimates are generally calculated for two purposes. First, they are calculated for use as evidence that a trait under study is heritable (a 'virtually certain' outcome, Lynch and Walsh 1998). Second, parameters are estimated for use in models to make predictions about changes in a trait value with a given level of selection. Both points are important for the focus of this special issue of Evolutionary Applications – scientists interested in predicting the evolutionary trajectory of salmonine fishes may want to use previously published quantitative genetic parameter estimates, both as evidence that the trait can/will evolve and for use in predictive models to estimate the rate of response to changing conditions, which determines the likelihood of population persistence in response to environmental change (e.g.,

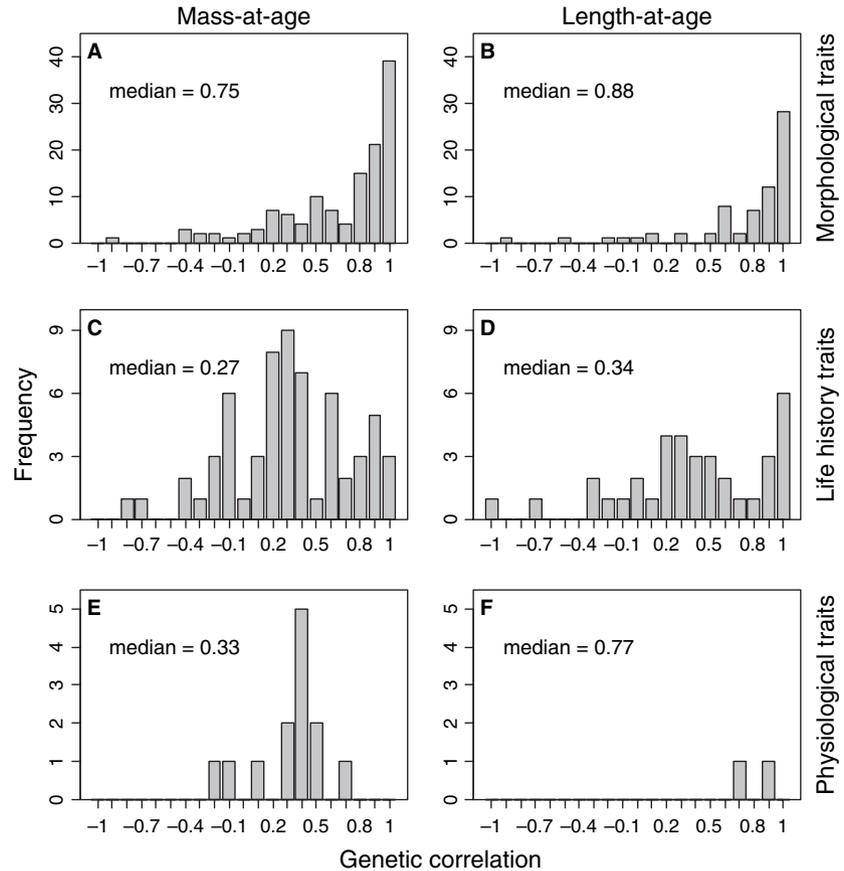


Figure 8 Distributions of genetic correlations between either mass-at-age (left column) or length-at-age (right column) and morphological traits (top row), life history traits (middle row), or physiological traits (bottom row). These data were generated based on the ‘medianized r_G dataset’ (see Methods and Table S7).

Table 2. ANOVA statistics for two-way models seeking to explain variation in r_G estimates by including the factor ‘‘trait’’ and one other factor (species, life history stage, diadromous life history types, or parity types) as independent variables.

	Factor <i>F</i> (d.f.) <i>P</i>	Trait class combination <i>F</i> (d.f.) <i>P</i>	Interaction (trait class combination × factor) <i>F</i> (d.f.) <i>P</i>
Species	3.734 (8, 529) <i>P</i> < 0.001	4.268 (5, 529) <i>P</i> = 0.001	2.918 (19, 529) <i>P</i> < 0.001
Genus	0.413 (2, 532) <i>P</i> = 0.662	7.839 (5, 532) <i>P</i> < 0.001	2.403 (7, 532) <i>P</i> = 0.020
Life history stage	1.059 (18, 514) <i>P</i> = 0.392	6.656(5, 514) <i>P</i> < 0.001	0.601 (22, 514) <i>P</i> = 0.924
Diadromous life history types (andadromous versus nonandadromous)	0.015 (1, 518) <i>P</i> = 0.904	6.273(5, 518) <i>P</i> < 0.001	2.523 (3, 518) <i>P</i> = 0.057
Parity types (semelparity versus iteroparity)	0.240 (1, 532) <i>P</i> = 0.625	10.014(5, 532) <i>P</i> < 0.001	1.795 (4, 532) <i>P</i> = 0.129

Listed is the *F*-statistic, associated degrees of freedom and *P*-value for each factor separately and for their interaction. The data used in these analyses were based on the ‘‘medianized r_G dataset’’ (see Methods and Table S7).

Gomulkiewicz and Holt 1995). Thus, our objectives in conducting this review were to address both of these topics. It is important to bear in mind, however, that these were seldom the goals of the studies that we reviewed, most of which were conducted for the purposes of estimating responses to selection for aquaculture or other

production goals. Thus the distribution of studies was very uneven with respect to species and traits under study and did not necessarily reflect the distribution of species at risk of extinction, traits essential for survival or adaptation of wild populations, or other conservation goals.

How is knowledge of quantitative genetic parameters distributed in salmonine fishes?

No matter which category we examined, the distribution of quantitative genetic parameters was unequal. These inequalities highlighted where data were lacking. The most obvious lack was that of parameter estimates for many species, especially those in the genus *Salvelinus* (h^2 : Fig. S1A; r_G : Fig. S3A). The species for which there were few estimates were generally those for which information in general is relatively scarce (Quinn 2005). They also tended to be species which are not extensively used in aquaculture (farmed, hatchery or sea-ranched), the groups for which many estimates were available (Fig. S1D). These biases in the data are only a problem if there is evidence that quantitative genetic parameter estimates for different traits differ among categories – and they do differ. Specifically, h^2 and r_G estimates for a given trait differed among species, life history stages, and life history types, as revealed by significant two-way interactions between trait and these other factors (Tables 1 and 2). This suggests that parameter estimates for one group may not be representative of those from another, and that scientists must use caution when making such comparisons.

Environmental variation and heritability

Estimates of genetic parameters are influenced by the environment in which parents and offspring are reared. Heritability estimates as ratios of genotypic variance over phenotypic variance are directly affected by the influence of the environment on total phenotypic variance in a trait. Heritability and genetic correlation estimates may also be influenced by the quality of the environment (i.e., whether or not it is 'favorable' to the trait; Hoffman and Merilä 1999). For both parameters, the value (and in the case of correlations, the sign) of the estimate may change under the influence of varying environmental quality (Hoffman and Merilä 1999; Sgrò and Hoffman 2004). Moreover, the class of traits (e.g., life history, morphological) may not be equally affected (Charmanier and Garant 2005). This becomes important when evaluating the results of this review both because the majority of published estimates were generated from experiments conducted under farmed or hatchery conditions ('treatment', Fig. S1E) and because, contrary to a previously published review (Weigensberg and Roff 1996), we found direct effects of treatment and more complex effects of the source population on estimates of genetic parameters. Each of the potential treatment settings (hatchery, farmed, sea-ranched, wild) is associated with a unique set of advantages and disadvantages in terms of estimating quantitative genetic parameters and on the traits mea-

sured themselves. For instance, highly controlled operations such as hatcheries or fish farms, allow maximum control over many aspects of the rearing conditions (e.g., temperature, density): a highly domesticated stock may find the hatchery conditions favorable, while a wild stock would find them stressful. Thus, the quantitative genetic parameters estimated may not have relevance for wild populations.

Ideally, information on quantitative genetic parameters used to guide the restoration and conservation of salmonids would be derived from estimates generated on wild-reared populations and yet such estimates are exceedingly rare. Indeed, h^2 estimates from wild fish that were reared in the wild comprised only 2% of the total number of h^2 estimates (58 of 2389 h^2 estimates, Fig. S2). Moreover, there were no r_G estimates for wild fish that were reared in the wild (Table S6). This lack of estimates reflects the difficulties associated with estimating quantitative genetic parameters for wild salmonid populations. Although new methods of reconstructing and analyzing pedigrees of wild populations have improved our ability to estimate quantitative genetic parameters for wild populations (Jones and Ardren 2003; Garant and Kruuk 2005), difficulties persist, due in part to characteristics inherent to salmonid populations such as the difficulty in sampling all or most of the individuals in a large population, the cost of processing so many samples, the relatively long life span or generation times (especially in some charr species), overlapping generations, straying (emigration, immigration), and the variable environmental conditions from year to year. The largest obstacle facing scientists interested in estimating parameters for wild salmonid populations is the difficulty sampling all (or even most) breeding individuals and their offspring, i.e., difficulty obtaining the samples with which to reconstruct the pedigree (e.g., Dickerson et al. 2005). Many different families (as opposed to offspring per family) are needed to precisely estimate genetic parameters, especially genetic correlations (Lynch and Walsh 1998). While pedigrees can be reconstructed without sampling parents, the power to infer half-sib families is less than that to infer full-sib families, and sufficient numbers of offspring must be collected to sample half-sib families suggesting that often only broad-sense genetic parameters can be estimated.

Selection and heritability

By favoring certain alleles or allele combinations, selection erodes genetic variation (Roff 1997). Thus, one might expect traits that have been subject to consistent and strong directional selection (e.g., life history traits) to have lower heritabilities than traits subject to weaker or less consistent selection (e.g., morphological traits). Some

theoretical and empirical evidence supports this view (Mousseau and Roff 1987). Our review also provides support for this hypothesis – within the salmonine fishes, the heritabilities of life history traits were significantly lower than for morphological traits, and the estimates for behavioral and physiological traits were intermediate (Fig. 2). Further support may be found in our examination of broodstock source. Artificial selection acting on farmed and hatchery-produced fish may also influence estimates of quantitative genetic parameters. Such populations often have been subject to many generations of artificial selection – both intentional and unintentional – that may be consistent in strength, direction, and form. Wild populations, in contrast, are subject to natural selection that is inconsistent in strength, direction, and form (Grant and Grant 2002; Seamons et al. 2007). Thus, we might expect h^2 estimates to be higher when based on wild broodstock relative to captive-produced broodstock (farmed, hatchery, sea-ranched). In contradiction, no direct effect of broodstock source was revealed, and we found that h^2 estimates of traits generated for wild fish were slightly lower (nonsignificant) from captive-produced fish. Although we did find that h^2 estimates of traits depended on broodstock source (significant interaction term), the lack of strong support for the selection hypothesis may be due to the more complex genetic relationships among traits and environments (Hoffman and Merilä 1999) as well as limitations of using heritabilities and correlations as the measure of genetic variance (Merilä et al. 2001) (see also Limitations and recommendations section below).

Genetic correlations

Genetic correlations between traits are generally thought to arise through pleiotropy, that is, the same genes having effects on multiple traits. Genetic correlations may also arise through linkage disequilibrium, but such correlations may be less meaningful for evolution of fitness traits (Roff 1997 and citations within). *A priori* expectations of the values and distributions of genetic correlations are difficult to formulate (Price and Schluter 1991; Roff 1996). Consistently strong directional selection on two genetically correlated traits should produce negative genetic correlations due to fixation of alleles that maximize the traits. The remaining variable alleles would be only those which have a positive effect on one trait and a negative effect on the other (Roff 1997 and citations within). Correlational selection may also produce genetic correlations, although without consistent and strong correlational selection, the correlations will disappear (Sinervo and Svensson 2002). In his review of genetic correlations, Roff (1996) found a preponderance of posi-

tive genetic correlation estimates for all trait type combinations, consistent with our analysis (Fig. 6). Interestingly, our results differed from Roff (1996) in that the median r_G estimate for morphological trait combinations was much higher than that of any other combination (Fig. 7). Negative genetic correlations, often interpreted as evidence of life history trade-offs (Reznick 1985), were rare in our dataset. Some pairs of traits hypothesized to be involved in life history trade-offs had mostly negative genetic correlations (e.g., egg size and fecundity, three of four estimates were negative, Table S6), but there was no obvious pattern within trait or trait type combinations that had negative genetic correlations. A prevalence of positive values might occur because of environmental effects associated with novel experimental settings (reviewed in Roff 1996). This may explain the pattern seen here because pleiotropic genetic correlations would have evolved over many generations in the wild and most of the experimental conditions found in the studies reviewed here were relatively novel and non-natural.

Estimates of genetic correlations may be necessary for accurate predictions (Grant and Grant 1995) but are difficult to estimate mainly because of the large number of families required to obtain a reasonably small standard error (Roff 1997; Lynch and Walsh 1998). With each trait analyzed, more families are required to obtain reasonably small standard errors. Each additional trait included also adds more pairwise comparisons, which are not independent of one another, requiring adjustment of Type I error levels further making it difficult to obtain statistical significance. In addition, all analyses will suffer from the influence of correlations with unmeasured traits that may also be under selection. Making matters more difficult, even in the same population genetic correlations may change with a changing environment (Sgrò and Hoffman 2004). Because adaptive evolution may be limited by genetic correlations in the opposite direction to the direction of selection (Falconer and Mackay 1996; Etersson and Shaw 2001) and because our estimates may depend on the source population, caution must be used when applying published r_G estimates to predict evolution in wild populations.

Implications for adaptation in a changing global environment

Predicting the response of organisms to future anthropogenic disturbance and climate change is a challenging yet critical goal of contemporary evolutionary ecology. Previous work has demonstrated that evolution can sometimes (Grant and Grant 1995), but not always (Merilä et al. 2001), be predicted in the short-term with knowledge about the strength of selection acting on traits combined with estimates of genetic parameters for those traits.

Predicting evolution over the long-term, however, is a far more difficult task because of the influence of unpredictable changes in the environment, which hinder efforts to predict selection (Grant and Grant 2002, 2006). To make accurate predictions, information about how the strength and form of selection varies as the environment varies is required and yet this information is rarely known (but see Grant and Grant 2002; Réale et al. 2003; Carlson and Quinn 2007). Phenotypic plasticity in response to selection may also hinder accurately predicting evolutionary trajectories. Recent evidence suggests that many examples of microevolution and increased rates of microevolution due to anthropogenic disturbance may in fact be phenotypic changes due to plasticity (Gienapp et al. 2008; Hendry et al. 2008). Adaptive plasticity may move populations closer to phenotypic optima while nonadaptive plasticity may increase phenotypic variance or move populations away from optima (Ghalambor et al. 2007). Clearly, predicting evolutionary change will be a difficult task.

Global climate change could conceivably affect all species. Indeed, changes in phenological traits have already been documented for a variety of taxa (Bradshaw and Holzapfel 2008). Temperature is one of the primary selective forces shaping the timing of breeding, hatching, and emergence of salmonine fishes (Quinn 2005) and climate models predict continued warming of the earth's surface over the next century (Δ 2–5°C by 2100, Intergovernmental Panel on Climate Change). Similarly, river flow regime affects run timing for both adults and out-migrating smolts (Quinn 2005) and recent research has revealed that patterns and the form of precipitation (i.e., rainfall versus snowfall) are changing as well (Stewart et al. 2005; Mote 2006). Will salmon populations adapt to these changing conditions quickly enough to avoid extirpation? Heritability estimates exist for some but not all of the above phenological traits (reviewed in McClure et al. 2008). The median h^2 estimate for phenological traits is quite high (0.51, Table S8) but the range is large (effectively 0–1, Table S8) and the sample size low (only 26 estimates, Table S8). Of the 31 traits considered in this review, phenological traits had the highest median h^2 value suggesting that phenological traits are likely to evolve in response to changing temperature and flow regimes. Indeed, introduction of Chinook salmon (*O. tshawytscha*) from the Sacramento River (California, USA) to New Zealand confirm that phenological traits evolve rapidly in response to novel selection pressures (e.g., Quinn et al. 2000).

Many other life history traits also have clear links to environmental conditions, and these conditions are already changing. For instance, for the anadromous species with some period of freshwater residency, age- and length-at-smoltification are influenced by freshwater growth opportunities where faster growth in freshwaters

is associated with an earlier age-at-smoltification and a larger size at that age (e.g., Hutchings and Jones 1998; Hutchings 2004). However, whether these two traits are likely to evolve in response to changing freshwater growth conditions is difficult to predict because only a single, relatively high h^2 estimate exists for each of these two traits [0.51 (age) and 0.30 (length), Table S8]. Similarly, age- and length-at-maturity are influenced by growth opportunities in the marine environment (or the freshwater environment for nonanadromous species), where faster growth is again associated with an earlier age-at-maturity and a larger size at that age (e.g., Parker and Larkin 1959). Both are associated with moderate h^2 values (median = 0.21 in both cases) suggesting the potential to adapt to changing conditions.

Salmonids are well known for migratory behavior, however parameter estimates for this and other behavioral traits were nearly absent from the published data. Only six h^2 estimates for behavioral traits were found (no r_G estimates, counts based on the 'reduced datasets', Tables S3 and S6, h^2 and r_G data, respectively), all were for measures of agonistic behaviors in one life history stage (juvenile) of just one species (coho salmon). Anadromous salmonids migrate to and around the oceans and all salmonids (anadromous and nonanadromous) make spawning migrations, characteristically to the same location where they were born ('homing' or 'philopatry'). There is evidence that population-specific differences in migration patterns exist (Kallio-Nyberg and Ikonen 1992; Pascual and Quinn 1994), suggesting a genetic component (see also a recent paper containing pertinent h^2 estimates by Thériault et al. 2007). Migration patterns are influenced by and may change with a changing environment (Quinn and Dittman 1990). For example, a warming climate will likely cause new habitat to open for colonization by salmonine (and other) fishes, as is currently happening in Glacier Bay, Alaska, USA (Milner et al. 2000). Colonization of new habitat requires 'straying' (i.e., dispersal), that is, individuals that do not display homing behavior. Populations show differences in homing/straying rates (see Appendix 1 in Hendry and Stearns 2004), suggesting a genetic component. Both homing and straying are thought to be important adaptations for the long-term persistence of salmon species (Hendry et al. 2004) and yet we know virtually nothing about the likelihood that these traits will evolve in response to selective pressures exerted by a changing environment.

Limitations and recommendations

Palmer (2000) noted that h^2 estimates less than zero are under-reported. In several papers included in our dataset, the authors noted that they had calculated negative h^2 estimates, but as negative values made no sense, they

reported the estimates as zero. And for our analyses, h^2 estimates below zero were rounded up to zero, and estimates above one were rounded down to one. The consequence of this action may be a bias in our distribution of h^2 estimates (Palmer 2000). We suggest that authors report the estimated values, which can subsequently be rounded or not depending on the specific application.

In many cases, we could not determine the value of a factor (e.g., life history stage, treatment) from the description in the paper. In most cases, it was the broodstock source which could not be determined (368 h^2 estimates from 25 different papers included in the ‘complete h^2 dataset’, Table S2; 233 r_G estimates from 11 different papers included in the ‘complete r_G dataset’, Table S5). The broodstock source represents the genetic baseline upon which experiments were conducted. Our data analysis revealed differences in parameter estimates among broodstock source types, thus we recommend that authors clearly state the type of population upon which they experiment.

Nearly a third of all parameter estimates were reported without standard errors ($h^2 = 1040$, $r_G = 829$; based on ‘complete datasets’, Tables S2 and S5, respectively) and more than half without a P -value ($h^2 = 2905$, $r_G = 1857$; based on ‘complete datasets’, Tables S2 and S5, respectively) (a lack also noted earlier by Mousseau and Roff 1987). Instead, authors often just stated whether the estimate was significantly different from zero. We recommend that authors publish standard errors and P -values along with their parameter estimates so that analyses of bias (sensu Roff 1996) can be performed.

Heritabilities and genetic correlations may not be the most appropriate measure of genetic variance when comparing across trait classes as these estimates may be biased by environmental variance (Price and Schluter 1991). Houle (1992) suggested that a measure of trait ‘evolvability’ can be described by the ratio of additive genetic variance to the mean phenotypic value, V_a/\bar{X} , or the coefficient of genetic variation, CV_a . Studies where these measures have been compared have often found low h^2 estimates, but high CV_a estimates at traits closely linked to fitness, the differences mainly being a difference in residual variance (Merilä and Sheldon 2000, Coltman et al. 2005). Most of the studies used in our review failed to report V_a or \bar{X} . We suggest that authors present three pieces of information – phenotypic variance (V_p), additive genetic variance (V_a), and the mean phenotype (\bar{X}) – from which it is possible to calculate both the trait $h^2(V_a/V_p)$ and the trait evolvability (V_a/\bar{X}) (see also Houle 1992; Lynch and Walsh 1998).

Future directions

Despite a large body of research documenting the strength and form of selection in nature (reviewed in

Endler 1986; Kingsolver et al. 2001), the mechanism of selection is seldom understood. Selection is context-specific and the context is the environment. Future research is needed to illuminate relationships between the strength and form of selection and the environment (e.g., Grant and Grant 2002; Carlson and Quinn 2007). This information, combined with information on quantitative genetic parameters, will greatly improve our ability to predict how organisms will respond to changing conditions.

Our data suggest that the experimental environment (‘treatment’) and source population (‘broodstock source’) both have an effect on h^2 estimates, which limits their utility. In part because of the environmental specificity of h^2 and r_G , the field is moving towards more use of the G-matrix (the matrix of genetic variance and covariance among traits, McGuigan 2006), which may only be useful for short-term predictions, and may change generation to generation, but is more comparable among populations or experiments because it is not environment-specific.

Finally, quantitative genetic parameters tell us something about the general way phenotypic traits are related to genes at the population level, but they tell us nothing about the actual genes involved in determining phenotypic trait values. Genome mapping projects, underway for many salmonine species (e.g., Lindner et al. 2000; Danzmann et al. 2005; McClelland and Naish, 2008) provide the structure for placing phenotypic traits on the genome (quantitative trait locus [QTL] mapping; e.g., Martyniuk et al. 2003, Reid et al. 2005; Leder et al. 2006), a step closer to finding the actual genes that determine phenotypes. Once specific genes are known, the diversity within and among populations could be quantified, and specific responses to selective events could be predicted.

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Supplementary material

The following supplementary material is available for this article online:

Figure S1 Number of heritability estimates partitioned by: (a) species, (b) trait class, (c) life history stage, (d) broodstock source, and (e) treatment group. These data were generated based on the ‘reduced h^2 dataset’ (see Methods and Table S3).

Figure S2 The number of heritability estimates available for each broodstock source presented for each of the following treatment groups: (a) farmed, (b) hatchery, (c) sea-ranch, and (d) wild. These data were generated

based on the 'reduced h^2 dataset' (see Methods and Table S3).

Figure S3 Number of genetic correlation estimates partitioned by: (a) species, (b) trait class combination, and (c) life history stage combination. When genetic correlations were estimated within a trait class combination or within a life history stage combination, the trait class or life history stage was only listed once along the x -axis. These data were generated based on the 'reduced r_G dataset' (see Methods and Table S6).

Table S1. List of references that had data which was included in the heritability or genetic correlation datasets, also including information on the species studied and the location of the parameter estimates within the reference.

Table S2. Complete list of all published heritability estimates and associated categorical data. Referred to as 'complete h^2 dataset'.

Table S3. List of all narrow-sense heritability estimates and associated categorical data. A subset of the 'complete h^2 dataset' referred to as 'reduced h^2 dataset'.

Table S4. List of narrow-sense heritability estimates where pseudo-replication was eliminated by calculating median heritability values within references (see Methods). A subset of the 'reduced h^2 dataset' referred to as 'medianized h^2 dataset'.

Table S5. Complete list of all published genetic correlation estimates and associated categorical data. Referred to as 'complete r_G dataset'.

Table S6. List of all "narrow-sense" genetic correlation estimates and associated categorical data. A subset of the 'complete r_G dataset' referred to as 'reduced r_G dataset'.

Table S7. List of "narrow-sense" genetic correlation estimates where pseudo-replication was eliminated by calculating median genetic correlation values within references (see Methods). A subset of the 'reduced r_G dataset' referred to as 'medianized r_G dataset'.

Table S8. List of traits included within each of the trait classes as well as associated summary information for the h^2 estimates including the count as well as the median, minimum, and maximum h^2 estimate reported by trait. This summary information was generated from the 'medianized h^2 dataset' (see Methods and Table S4).

Table S9. Median h^2 values presented by species \times factor combination (where 'factor' includes life history stage, trait class, broodstock source, and treatment groups). Additionally, we present the median h^2 value pooled within a species and ignoring the other factors (top row) as well as pooled within each factor and ignoring species (left column). This summary information was generated from the 'medianized h^2 dataset' (see Methods and Table S4).

Table S10. Median r_G values presented by species \times factor combination (where 'factor' includes life history stage, trait class combination, broodstock source, and treatment groups). Additionally, we present the median r_G value pooled within a species and ignoring the other factors (top row) as well as pooled within each factor and ignoring species (left column). This summary information was generated from the 'medianized r_G dataset' (see Methods and Table S7).

Studies Included in the Heritability and/or Genetic Correlation Databases.

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