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(*Oncorhynchus mykiss*)**

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2016-0175.R1
Manuscript Type:	Article
Date Submitted by the Author:	01-Jul-2016
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Keyword:	heritability, domestication selection, SMOLTIFICATION < General, size- selective mortality, fitness

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Rearing strategies alter patterns of size-selective mortality and heritable size variation in steelhead trout (*Oncorhynchus mykiss*)

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Key words: heritability, growth rate, hatchery, domestication selection, seawater challenge, osmoregulation, smoltification

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Abstract

Steelhead trout (*Oncorhynchus mykiss*) reared under two different regimes: high food ration for one year (S_1 ; typical strategy) or low ration for two years (S_2) were subjected to a seawater challenge during the corresponding spring outmigration period. The S_1 smolts were smaller, suffered greater seawater challenge mortality (23.9% compared to 0.7% for the S_2 smolts) that was significantly and negatively related to body size. Heritability of body size was similar for the two treatments during the parr stage (fork length: $S_1 = 0.181$, $S_2 = 0.245$; mass: $S_1 = 0.372$; $S_2 = 0.447$), but higher for the S_1 treatment during the smolt stage for length ($S_1 = 0.212$, $S_2 = 0.002$) and body mass ($S_1 = 0.145$, $S_2 = 0.015$). Strong family effects for both traits and significant family by environment interactions for parr mass and smolt length indicated significant phenotypic plasticity. A genetic response to size-selective mortality caused by insufficient growth opportunity in the S_1 treatment is plausible and may affect fitness in the natural environment through effects on correlated traits.

41 Introduction

42 Captive breeding programs can cause changes in phenotypic traits related to fitness in
43 just a few generations (Frankham 2008, Fraser 2008). Genetic divergence in important life
44 history traits can occur even where genetic management protocols are strictly followed for
45 conservation purposes (Waters et al. 2015), although the effects of such changes on fitness in
46 the natural environment can be difficult to predict (Charge et al. 2014). In other cases, genetic
47 fitness loss can be substantial and occur within one or two generations (Araki et al. 2009),
48 although identifying the mechanisms has been elusive (Blouin et al. 2010, Christie et al. 2014).
49 Fitness loss in salmonid fish populations is currently considered an unavoidable consequence of
50 captive breeding. The predominant management response has been to limit the productivity
51 drag on natural populations by quantitatively controlling gene flow between hatchery and
52 natural populations (Baskett and Waples 2013). However, the ability to effectively manage
53 gene flow in the natural environment to minimize interbreeding between hatchery and natural
54 populations is largely uncertain (Lorenzen et al. 2012), and population viability models suggest
55 that even a low level of fitness loss (e.g., 15%) can reduce productivity over the long term
56 (Bowlby and Gibson 2011). Far less attention has been paid to changes in culture strategies
57 (separate from breeding practices) that might reduce genetic changes in key phenotypic traits
58 contributing to fitness variation between hatchery and natural populations.

59 Reduced genetic fitness of hatchery salmon and steelhead populations may stem from
60 inherited effects of relaxed sexual and natural selection pressures, unintentional selection
61 during artificial spawning, or selection on traits that reduce the viability of offspring in the
62 natural environment (e.g., growth rate, predator avoidance, competition). There are massive

differences between environments experienced by hatchery- and natural-origin fish during egg incubation, emergence from gravel nests, and juvenile development, which cannot be mimicked in hatchery environments. One way to minimize the impact of culture environments may be to minimize time in captivity (Christie et al. 2014), but this partially offsets the primary benefit of supportive breeding (high survival), because fish released at a younger age and smaller body size suffer lower post-release survival (Berejikian et al. 2004, Leber et al. 2005). Because survival during captivity is typically very high and post release survival is very low, selection on phenotypic variation may be much stronger in the post-release environment, but likely acts on traits that fish develop in the culture environment (Waples 1999, Quinn 2005).

Most anadromous *Oncorhynchus mykiss* inhabit freshwater systems for 1 to 4 years. Individuals adopting an anadromous life history (steelhead) undergo a series of coordinated morphological, behavioral, and physiological changes (smoltification) to adapt to and survive in the marine environment. Many of these changes are growth/size-related, including development of hypo-osmoregulatory capacity, which is one of the most critical for seawater survival (Hill et al. 2006). Body size appears to be a threshold trait that influences migratory propensity; a minimum size is required to trigger seaward migration (Kendall et al. 2015). Age-at smoltification in natural populations is determined by a number of proximate factors related to growth rate and adiposity, including temperature and food availability (Kendall et al. 2015). The modal age-at-smoltification is age-2 throughout much of the species' southern range where hatchery production is greatest. Nevertheless, hatchery-reared steelhead are almost ubiquitously reared on accelerated growth regimes and released at age-1, primarily to increase production and minimize costs. Steelhead populations reared under this approach have

diverged from wild progenitors for a number of juvenile traits related to fitness including competitive and predator avoidance abilities (Berejikian 1995, Berejikian et al. 1996). Atlantic salmon (*Salmo salar*), which share a similar life history trajectory (typically age-2 smolts), show divergence in juvenile growth rate with just one generation of captive rearing (Wilke et al. 2015). Selection favoring large body size in released hatchery steelhead is evident from studies showing size-biased seaward migration (Reisenbichler 2004, Tatara et al. in review) and marine survival (Osterback et al. 2013). Thus, understanding how changes to conventional hatchery culture environments influence the viability of released fish is an important step in minimizing domestication selection.

Selection on phenotypic traits such as body size will not necessarily produce a detectable evolutionary response in the same traits. Estimating heritability of important traits in hatchery-raised steelhead can provide a greater understanding of the potential for hatchery-induced (i.e., domestication) selection to reduce fitness of fish released to the wild. Heritability estimates the amount of expressed trait variation that is attributable to genetic factors (Falconer and Mackay 1996, Roff 1997), and it provides one indication of whether selection on a phenotypic trait (if detectable) is likely to result in adaptive evolution (Lynch and Walsh 1998). Phenotypic plasticity refers to the ability of a single genotype, or sometimes a group of closely related individuals, to produce different phenotypes under different environmental conditions; it represents an adaptive response to the environment that sometimes involves genetic change (Roff 1997, Schlichting and Pigliucci 1998). In the present study, we compare two hatchery rearing regimes designed to produce age-1 and age-2 smolts, and 1) test whether rearing treatments cause differences in seawater mortality of hatchery steelhead during the parr-smolt

transformation, 2) test whether mortality is size-dependent, 3) estimate the heritabilities of body size (as a proxy for growth rate) and condition in two different hatchery rearing treatments at two developmental stages (parr and smolt), and 4) test for evidence of phenotypic plasticity and maternal effects on size.

Methods

Study population and Crosses

A total of 14 female and 20 male adult steelhead of both hatchery and natural-origin returning to the upper Methow River (near Winthrop, WA: 48° 28' 25.1796" N 120° 11' 21.6852" W) were used to create 28 full-sib families. Twelve of the full sib families represented six maternal half-sibs (six mothers each crossed with two unique males). The other 16 full-sib families represented 4 2x2 factorial matings (8 males and 8 females); each male and female was crossed with two mates. Steelhead production in the Methow River Basin has been dominated by hatchery-origin fish since the 1940s. Adult steelhead genotyped for 15 microsatellite DNA loci indicate that the hatchery- and natural-origin adults spawned in this study belong to a single panmictic population (Blankenship et al. 2011). Artificial matings were performed between 17 April and 12 May 2012. Incubation temperatures at the Winthrop National Fish Hatchery (WNFH) were manipulated to synchronize emergence timing to minimize effects of emergence timing on feeding and growth performance after exogenous feeding. Eyed embryos were transferred from the WNFH to the NOAA Fisheries Manchester Research Station (Manchester, WA) on 14 June 2012 and placed into the same style embryo incubators (vertical incubators; MariSource, Fife, WA) used at WNFH. The remainder of the experiment was carried out at the Manchester Research Station (MRS).

129 Rearing treatments

130 The study included two hatchery rearing regimes. Four tanks were allocated to a high
131 ration treatment designed to produce smolts in one year (hereafter 'S₁'), and the other four
132 tanks were allocated to a low ration treatment designed to produce smolts in two years
133 (hereafter 'S₂'). The rearing system consisted of an array of tanks plumbed to a freshwater
134 recirculation system. Average monthly water temperatures were maintained between 6.7 °C
135 and 12.7 °C and fluctuated seasonally, averaging approximately 11.9 °C during summer and 7.1
136 °C during winter. Temperatures were selected in an attempt to match the average monthly
137 rearing temperature profile and average annual rearing temperature for steelhead rearing at
138 WNFH (8.4 °C). The average annual water temperature at the MRS was 9.4 °C. On 11 July 2012,
139 all emergent fry were removed from the incubators and 476 (17 fish per family) were stocked
140 into each of eight tanks (1.8 m diameter x 0.6 m deep). The 28 full-sib families were initially
141 equally represented in each of the 8 tanks. Both rearing treatments were initially fed to excess
142 on a daily basis for the first 3 weeks. The S₁ fish were then fed to satiation five days per week,
143 and S₂ fish were fed to achieve a body size at smoltification similar to the target size for WNFH
144 (195 mm fork length, 90 g body mass), which is based on Federal guidelines for steelhead
145 hatchery programs. Feed rations for each treatment were calculated as daily percentage of
146 body mass using a temperature-based growth model (Iwama and Tautz 1981) that was re-
147 calculated weekly to reflect modeled growth. Some losses occurred in some tanks associated
148 with water overflow early in the rearing period. To obtain a direct count and equalize density
149 among the tanks, the fish within each rearing treatment were combined and then redistributed

equally among the four S_1 tanks (404 fish per tank) and the four S_2 tanks (407 fish per tank) on 13 August 2012.

Tagging and size sampling

The S_1 rearing group was initially sampled for fork length (nearest mm) and body mass (nearest 0.1 g) on 29 November 2012, and 154 to 170 fish from each tank were implanted with 9-mm Passive Integrated Transponder (PIT) tags (Biomark, Boise, ID), allowing for individual identification throughout the study. The S_2 rearing group was similarly sampled and tagged on 22 January 2013. The timing of PIT-tagging was planned so that the two groups would be approximately the same size at tagging and so that the smallest fish in each group would be large enough to tag (i.e., “parr” in Figure 1b). Each PIT-tagged fish had a small portion of its pelvic fin removed. Fin tissues were dried on filter paper and DNA was extracted from subsamples. Subsequent size samplings occurred periodically for the S_1 group (6 February 2013) and the S_2 group (5 June 2013 and 4 November 2013). Final sampling for both the S_1 and S_2 groups occurred on several dates associated with the spring seawater challenges in 2013 (S_1) and 2014 (S_2 , Table 1). Survival from tagging to final sampling was 96.0% for the S_1 group and 95.2% for the S_2 group.

Pedigree assignments

A total of 943 offspring were genotyped to determine family of origin. Parent-pairs (the most likely father and mother) for 916 offspring were determined from a likelihood-based parentage analysis using the program FRANz (Riester et al. 2009), using the default genotyping error rate of 1%. The remaining 37 offspring were not assigned to a parent-pair, due either to

poor DNA quality (fewer than 8 loci genotyped) or uncertain parentage assignments (posterior probability $P < 0.900$).

Spawning records indicated that two females and three males that were potential parents for these offspring were not sampled for DNA analyses, and thus could not be included in the pool of potential parents for the parentage analysis. All families that were created had at least one sampled parent. Therefore, juveniles could be assigned as offspring of the non-sampled parents because the offspring matched one sampled parent in all cases. We separated the offspring into full sibling groups using the program COLONY (Jones and Wang 2010), and added them to the results of the parentage analysis to improve the power to estimate relatedness, an advantage when constructing a full relationship matrix used in an animal-model approach.

Seawater challenges

Development of hypo-osmoregulatory capacity is one of the critical physiological changes during smoltification and is required for juvenile salmonids to survive in seawater (Stefansson et al. 2008). In this study, survival of transfer from freshwater to seawater was used to characterize how completely individual steelhead had undergone smoltification (Blackburn and Clarke 1987), and how they might survive in seawater in the natural environment. In the spring of 2013 (S_1) and spring of 2014 (S_2) when each group was expected to develop salinity tolerance, all PIT tag implanted fish were weighed (to nearest 0.1 g), measured (fork length to nearest mm), and allocated to one of three groups: 33 parts per thousand (ppt) seawater challenge, 28 ppt seawater challenge, or lethal sampling for physiological assessment as part of another study (Swanson et al. unpublished data). Three sequential 33 ppt seawater challenges

were conducted at weekly intervals ($n = 35$ per trial) in 2013 (brood year 2012; S_1) and 2014 (brood year 2012; S_2). For each trial fish were stocked directly into two tanks (1.8 m diameter x 0.6 m deep) equipped with aeration and filled with ambient seawater from Puget Sound (approximately 28 ppt) that was adjusted upward to a salinity of 33 ppt with Crystal Sea Bioassay Marinemix (Baltimore, MD) to simulate Pacific Ocean salinities. The first 48 hours of the seawater challenge were static exposures at 33 ppt. After 48 hours, Puget Sound seawater (28 ppt) was added at $19.0 \text{ L} \cdot \text{min}^{-1}$ for the purpose of restoring a flow-through water supply. The tanks were monitored and data on mortalities, temperature, dissolved oxygen, and salinity were recorded twice daily for the first 14 days (fish were not fed during this period) and daily afterward. The PIT tag number, mass (g), fork length (mm), and sex were recorded for each mortality. After 14 days in the SW exposure tanks, all surviving fish were transferred to a common tank (4.6 m diameter x 1.2 m deep) supplied with $114 \text{ L} \cdot \text{min}^{-1}$ of ambient 28 ppt seawater for extended rearing. The procedure for conducting the 28 ppt seawater challenges was the same as for the 33 ppt seawater challenges, except that the two replicate vessels were larger (4.6 m diameter x 1.2 m deep) and were supplied with ambient Puget Sound seawater at a rate of $114 \text{ L} \cdot \text{min}^{-1}$.

Statistical analyses

Analyses pertaining to body size and condition focused on two distinct life stages. The term 'parr' refers to measurements taken at the time of PIT-tag implantation, which was approximately 4.5 or 6.5 months post-emergence for S_1 and S_2 groups, respectively (Table 1). The 'smolt stage' or 'during smoltification' refers to the time when fish were seawater-challenged, approximately 9.5 or 21.5 months post-emergence for S_1 and S_2 groups,

respectively (Table 1). The timing of the seawater challenges for both S_1 and S_2 corresponded to the season (spring) when smoltification occurs in natural populations and the age at which hatchery fish from each rearing treatment would be released. To test whether body size affected seawater challenge survival, we conducted a logistic regression analysis to estimate the conditional probability of surviving a seawater challenge as a function of fork length. Data from the 28 ppt challenges and 33 ppt challenges were analyzed separately. The analysis was repeated on data from both challenges combined.

Heritability of size, condition, and challenge mortality

We assessed variability in body size (fork length and mass), condition (Fulton's condition factor: $K = 100 \times \text{mass} \div \text{fork length}^3$) and seawater challenge mortality within and among families to estimate the phenotypic and genetic variance components for each trait with univariate animal models (Kruuk 2004) as implemented with the package 'MCMCglmm' in R v 3.0.3 (Hadfield 2010; RDCT 2014). The form of the animal model was:

$y_{ijk} = \mu + a_i + s_j + t_{k(j)} + e_{ijk}$, where y_{ijk} is the phenotype (e.g., fork length) of individual i in treatment j and tank k , μ is the population mean phenotype, a_i is the breeding value of individual i (a random family effect estimated from the contribution of individual i to the distribution of y relative to μ , as estimated from the deviations of its relatives' phenotypes from the population mean), s_j is the fixed effect of rearing treatment j (S_1 or S_2), t_k is the random effect of tank k nested within treatment j , and e_{ijk} is the residual term. Size of parr and smolts, and corresponding condition were analyzed as Gaussian traits. Seawater challenge mortality was analyzed as an ordinal trait because we were interested in when individuals died and

whether time to death was heritable. Deviance information criterion (DIC) values were used to evaluate the fit of alternative models to the data.

The narrow-sense heritability (h^2) of each trait was estimated as the ratio of the additive genetic variance (V_A) to the total phenotypic variance (V_P), where V_P is the sum of V_A and the residual variance V_R , which includes environmental variance unaccounted for by additional fixed or random effects in the model, non-additive genetic variance, and error variance (Falconer and Mackay 1996). Estimates of heritability from models that include specified fixed or random effects are conditioned on these effects (Wilson et al. 2010). The estimate of heritability of mortality between relatives was adjusted by adding a factor of $\pi^2/3$ to the estimate's denominator to account for the logit scale used for the binary trait distribution. Several weakly informative priors were evaluated to ensure that their effects on the posterior estimates were minimal. We used parameter-expanded priors (Gelman 2006) based on the inverse Wishart or the inverse Gamma distributions for the analyses of the Gaussian traits; alternative priors, including a parameter-expanded prior based on the chi-square distribution, was used to estimate heritability of mortality (de Villemereuil et al. 2013).

The number of Markov chain Monte Carlo (MCMC) iterations run for each chain was 500,000 to 750,000 with a burn in of 50,000 to 75,000 iterations and a thinning rate of 1 in 50 to 75, which ensured that the effective MCMC sample size evaluated from each chain was between 8,000 and 10,000 after accounting for lag autocorrelation, which was generally $< 5\%$ across the chain. Heidelberg and Welch MCMC diagnostics that included half-width and stationarity tests were conducted to confirm chain convergence. The 95% credible intervals for each estimate were obtained from the 2.5% and 97.5% quantiles of the posterior densities.

Significance of estimates was tested by comparing fits of animal models with and without the random animal term using DIC values.

We also estimated heritability of challenge mortality using a modification of Falconer's (1965) proband method (Reich et al. 1972). For an overall level of mortality, this method, based on a liability model, provides a test of observed incidence of mortality among affected relatives against that expected if mortality occurred at random in the experiment. Heritability estimated in this way does not depend upon the incidence of mortality, unlike some other approaches (Lynch and Walsh 1998). Dispersions around the estimates were computed from equations given in Lynch and Walsh (1998).

Family effects and phenotypic plasticity

It is important to note that differences in body size, size-at-age (reflecting growth), and condition between rearing treatments reflected the combined effects of feed ration and rearing duration (age). S_1 groups were fed high rations and sampled at approximately 4.5 months (parr) and 9.5 months (smolt), and S_2 groups were fed low rations sampled at approximately 6.5 months (parr) and 21.5 months (smolt) post-stocking and exogenous feeding. Thus, body size at age provides a proxy for growth rate within treatment groups, but not between.

We compared general linear mixed models to test the significance of variation in size and condition at the family or parental level and to estimate the level of family/parent by treatment (rearing treatment, S_1 or S_2) interaction effects on size. The form of the saturated general linear model was: $y_{ij} = \mu + f_i + t_j + ft_{ij} + v_{k(ij)} + e_{ij}$, where y_{ij} is the phenotype (e.g., fork length, mass, condition) for an individual from a particular family/parent and treatment, μ is the overall mean phenotype, f_i is the random effect of family, sire, or dam i ,

t_j is the fixed effect of treatment j , ft_{ij} is the interaction between the family/sire/dam and treatment (i.e., family x environment interaction, a measure of phenotypic plasticity), $v_{k(j)}$ is the effect of rearing tank nested within treatment, and e_{ij} is the residual error associated with y_{ij} . Parr and smolt data were analyzed separately. Both analyses used the same GLM outlined above. For each trait we compared the fit of this model to a model that excluded the interaction term, and used likelihood-ratio tests from an ANOVA and the Akaike information criterion (AIC) to test the significance of the best fit model. All analyses were run in R v3.0.3 (RDCT 2014) using the 'glm' and 'hglm' package.

Results

Growth and body size

The S_1 (high ration) treatment caused higher growth rates than the S_2 (low ration) treatment during the first 9.5 months of rearing (Figure 1). However, the additional year of rearing for the slower growing S_2 treatment resulted in fish with a larger mean ($\pm$ SD) fork length (209.9 mm $\pm$ 18.5) and mass (99.0 g $\pm$ 25.4) during the spring smolt window than the S_1 treatment (fork length: 153.6 mm $\pm$ 21.9; mass: 39.0 g $\pm$ 14.7; Figure 1).

In the S_1 treatment at smoltification, there were no significant body size differences among tanks in general linear models that included a family x treatment interaction (final fork length: $t_{912} = 0.397$, $P = 0.691$; mass ($t_{911} = -0.150$, $P = 0.881$) or those that did not (fork length: $t_{911} = 0.483$, $P = 0.629$; mass: $t_{910} = -0.099$, $P = 0.921$). In the S_2 treatment at smoltification (21.5 months), there were small but significant differences in body size among tanks indicated by models that included a family x treatment interaction (fork length: $t_{912} = -3.455$, $P < 0.001$; mass: $t_{911} = -4.217$, $P < 0.001$) and those that did not (fork length: $t_{911} = -3.476$, $P < 0.001$; mass:

$t_{910} = -4.226$, $P < 0.001$). The largest relative difference in mean body mass among the four S_2 tanks was 10.9% and the largest difference in mean fork length was 5.1%. An ANOVA and corresponding likelihood-ratio tests comparing the fits of the two models indicated that the model including family by treatment interaction was superior for fork length ($\chi^2_1 = 6.70$, $P < 0.009$) but not for mass ($\chi^2_1 = 2.50$, $P = 0.114$).

Seawater survival

A significantly greater proportion of S_1 steelhead (0.14) than S_2 steelhead (0.00) died within 21 days of transfer to 28 ppt seawater ($P < 0.001$), after transfer to 33 ppt seawater ($P < 0.001$, $S_1 = 0.38$, $S_2 = 0.018$), and for both salinities combined ($P < 0.001$, $S_1 = 0.24$, $S_2 = 0.01$; Table 1). Only two steelhead died in the S_2 treatment (both in the 33 ppt challenge); therefore, the logistic regression analysis was only applied to the S_1 treatment ($n = 284$). In the S_1 treatment, fork length was positively related to probability of surviving transfer to seawater at both 28 ppt ($\chi^2 = 46.57$, $P < 0.001$) and 33 ppt ($\chi^2 = 67.20$, $P < 0.001$; Figure 2).

Heritabilities of body size, condition, and challenge mortality

The number of individuals assigned to each full-sib family ranged from 22 to 43. The number of offspring produced by individual males ranged from 12 to 83. The number of offspring produced by individual females ranged from 51 to 83. To estimate genetic contributions to observed variation in smolt fork length, mass, condition, and challenge mortality, we first conducted a series of analyses with animal models conditioned on rearing treatment as a fixed effect. At smoltification, low heritabilities for fork length were estimated to be on the order of 4 to 5%, and those for mass were on the order of 17 to 18% (Table 2). Heritability for condition factor was less than 0.1%. As expected, length and mass were highly

correlated phenotypically ($r_p = +0.691$; 95% credible interval, 0.643 to 0.717). There was no detectable phenotypic correlation between length or mass and condition. We could not estimate the magnitude of the genetic correlation between these traits reliably, but it was positive as well, as was the correlation of family trait means.

When analyzed separately for each rearing treatment, heritability estimates for body size at the parr stage were similar in the S_1 and S_2 treatments. Heritabilities for fork length were on the order of 20%, and those for mass were on the order of 40% (Table 2). During the smolt window, the separate estimates suggested that heritabilities were 10 (mass) to 100 (fork length) times greater in the S_1 than the S_2 treatment, but their 95% credible intervals overlapped (Table 2). Estimates of heritability for smolt condition factor were very low for both rearing treatments (S_1 : 0.001, 95% credible interval, <0.001 to 0.177; S_2 : <0.001, 95% credible interval, <0.001 to 0.067). A comparison of DIC values for animal models estimating condition factor heritability with and without an animal term also indicated that the estimates were not significantly different from zero.

Heritability of seawater challenge mortality (both salinities) was estimated only for the S_1 treatment because of the low mortality in the S_2 treatment. In the S_1 treatment, the heritability of challenge mortality was very low whether size was included as a fixed factor or not. Heritability estimates from the animal model were near zero (Table 2). Estimates based on the proband method varied from 0.024 to 0.027, depending on the number of days of exposure considered (<21 days or the full duration of the challenge, indicating no detectable variation among families (Table 2). By contrast, estimates of heritability for days to death in S_1 were substantially higher (0.805 to 0.930), depending on the number of days in exposure considered,

indicating appreciable variation among families in endurance during the challenge (Table 2). This endurance is positively correlated with body size ($r_p = +0.346$; 95% confidence interval, $+0.145$ to 0.547). A simple linear regression analysis was performed to provide another measure of family effects on challenge mortality. The full-sibling, family-specific percentage of S_1 steelhead surviving the seawater challenge ranged from a low of 50% (three families) to a high of 100% (three families). The proportion of S_1 smolts from each full-sib family that survived the seawater challenge was positively correlated with mean family fork length (Figure 3).

Maternal effects

Evaluating animal models that incorporated an additional random effect of dam on length and mass at the parr or smolt stage indicated no significant maternal effects on these traits (95% credible intervals ranged from <0.0001 to 0.0023), and consequently they had no detectable effect on the heritability estimates. When evaluated separately for each rearing treatment, maternal effects were not detectable in the S_1 treatment for length or mass (95% credible intervals, <0.0001 to 0.0013). Similarly, no maternal effects were detectable in the S_2 treatment for length or mass (95% credible intervals, 0.0001 to 0.0049).

Family effects and phenotypic plasticity

Using general linear models and likelihood ratio tests, we evaluated the effect of plastic responses on body size and condition at both the parr and smolt stages by comparing the fit of hierarchical linear models to analyze variation in each trait that included or excluded an interaction term between the random effect of family and the fixed effect of rearing treatment. These comparisons were done with the 'glm' package in R v 3.0.3 (RDCT 2014). We detected evidence for weak effects of family x environment (rearing treatment) interaction (hereafter 'F

x T') on the expression of smolt length and parr mass. For smolt length, these analyses indicated highly significant effects of both family ($t = -3.46$, $P = 0.0003$) and treatment ($t = -3.48$, $P = 0.0005$) (Table 3; Figure 4). We also detected a highly significant influence of family x treatment interaction (F x T) on smolt length ($t = 2.58$, $P = 0.0099$). Both AIC and likelihood-ratio tests comparing the fit of the two models (with or without the interaction term) provided weak support for the model of smolt length that incorporates F x T (Table 3). The results for parr length were somewhat similar except that plasticity was not clearly evident: there was a highly significant effect of family ($t = -3.66$, $P = 0.0003$) but not treatment ($t = -1.60$, $P = 0.1096$); the effect of F x T was marginally non-significant ($t = 1.73$, $P = 0.0845$), and the more complex model was not adequately supported (Table 3).

For smolt mass, there was a highly significant effect of treatment ($t = 9.22$, $P < 0.0001$) but no detectable family effect ($t = -2.34$, $P = 0.2180$) in the simpler model without F x T. In the more complex model that incorporated F x T, a significant family effect was detectable ($t = -1.99$, $P = 0.0465$) but an effect of F x T was not ($t = 1.58$, $P = 0.2551$). Neither AIC nor a likelihood-ratio test comparing the fit of the two models provided greater support for the model of mass that included F x T (Table 3). For parr mass, we detected a highly significant effect of family ($t = -3.69$, $P < 0.0003$) but not treatment ($t = -1.25$, $P = 0.2109$); there was a significant effect of F x T ($t = 1.98$, $P = 0.0479$). However, the more complex model incorporating F x T was not adequately supported (Table 3, Figure 4).

For smolt condition factor, there was no significant effect of treatment ($t = -0.37$, $P = 0.7121$) and only a marginally significant family effect ($t = 1.91$, $P = 0.0564$) in the simple model without F x T. In the more complex model that incorporated F x T, no significant effect of family

($t = 0.29$, $P = 0.7760$) or treatment ($t = -0.65$, $P = 0.5130$) was detectable, nor was an effect of $F \times T$ ($t = 1.42$, $P = 0.1570$). Comparison of the fit of the two models indicated that they had equivalent support (Table 3). The results for parr condition were considerably different: there was no significant effect of family ($t = -1.01$, $P = 0.3110$), but in both models there was a highly significant effect of treatment ($t = -4.02$, $P < 0.0001$) but no detectable effect of $F \times T$ ($t = -0.96$, $P = 0.3370$). The more complex model incorporating $F \times T$ was not supported (Table 3).

Discussion

Several results from the present study indicate that after release from hatcheries, selection favoring large body size is more likely to occur in the S_1 rearing and release strategy than in the S_2 strategy. First, significantly more S_1 than S_2 fish died during the seawater challenges conducted during the spring smolt window, and mortality in the S_1 treatment was strongly negatively correlated with body size. Second, heritability estimates of fork length and body mass at smolting were higher in the S_1 treatment than in the S_2 treatment (although 95% credible intervals overlapped for fork length). Third, there were significant family effects on fork length and body mass within the S_1 treatment, and a significant positive correlation between mean family body size and the proportion of survivors within families. Furthermore, a significant family $\times$ treatment interaction on smolt body length (and on parr body mass) indicates that within-family growth performance could vary under different rearing regimes, although this was a weak effect.

The two approaches to producing hatchery-reared steelhead smolts (S_1 : high ration for one year; S_2 : low ration for two years) resulted in significant differences in seawater challenge mortality that were strongly dependent on body size. Nearly all fish (99%) in the S_2 treatment,

which averaged 209 mm fork length, survived the 21 d seawater challenge (both salinities combined), suggesting no evidence for size-selective mortality within this treatment. Survival in the S_1 treatment (76%; average fork length = 154 mm) was significantly lower overall and strongly influenced by size. The positive correlation between body size and endurance in the challenge indicated that larger fish took longer to succumb to osmoregulatory stress. The effect of size on days to death varied little among families, suggesting little genetic variation was available to cope with selection on endurance which responded simply to body size. The average fork length ($164 \text{ mm} \pm 15.8$) of S_1 survivors was very similar to the size of natural-origin steelhead smolts outmigrating from the Methow and Okanogan rivers (158 mm at age-1, 168 mm at age-2, and 172 mm at age-3; Peven et al. 1994); consistent with the assumption that the seawater challenges provided a reasonable proxy for a suite of physiological and behavioral processes involved in smoltification (see Hill et al. 2006).

Steelhead released from hatcheries that have not undergone smoltification and are unprepared for survival in the marine environment may remain in fresh water (residualize) and have opportunities to grow and outmigrate in the following year(s) at a more optimal size and condition. However, S_1 smolts released from the Winthrop National Fish Hatchery over four years (2011 to 2014) exhibited size biased downstream migration, and those that did not migrate in the year of release were rarely detected migrating in subsequent years (0.04% to 0.53%; Tatara et al. in review). This is consistent with a number of other cases in Washington and British Columbia, where residuals outmigrating the year following release (age-2) account for about 1% of the number of fish released the previous spring (Sharpe et al. 2007). Together, these data suggest that in S_1 steelhead, body size, and thus, physiological and behavioral traits

that regulate or influence growth rate, are under selection after release from the hatchery.

However, the degree to which hatchery-induced selection modulates changes in growth rate in hatchery steelhead populations depends in large part on heritability of the traits.

Our study quantified the genetic basis for variation in seawater challenge survival and in size-at-age (growth rate). The family-specific proportion of S_1 smolts surviving the seawater challenged ranged from 50% to 100%, but we did not detect significant family variation in challenge mortality in the S_1 treatment. Neither length nor mass had an influence on the heritability of challenge mortality. Based on the heritability estimates for seawater challenge mortality alone, a response to direct selection on this trait in the short term is expected to be weak unless mean size at smoltification varies substantially among families in the same cohort. The sample sizes available to inform the heritability estimates for challenge mortality in S_1 fish were less ($n = 284$) than for body size ($n = 476$). Significant body size differences among families not manifesting in significant evidence of heritability for challenge mortality could also reflect among-family variation in thresholds for smoltification, or combined random variation in both the size-survival relationship and other family-specific effects on survival.

We detected modest heritability estimates in length and mass under the S_1 rearing treatment, some evidence for phenotypic plasticity in smolt length and parr mass across treatments, and no evidence for maternal effects influencing expression of these traits in either S_1 or S_2 . The S_1 heritability estimates for fork length (0.212) and body mass (0.145) during the smolt window are comparable to other salmonid populations where domestication selection was evident. For example, (Solberg et al. 2013) raised Atlantic salmon under common culture conditions for 4.5 months, and estimated heritabilities for body mass (using the animal model)

to be 0.14 for farmed, 0.14 for hybrid, and 0.29 for wild salmon. Past domestication selection (over 10 generations) was indicated by strong differences in growth rate among the three types. The heritability estimates in our study are also consistent with farmed *O. mykiss* populations that have also been subjected to intentional domestication. Carlson and Seamons (2008) summarized narrow-sense heritabilities for size-at-age data in *O. mykiss* and reported estimates for hatchery fish between 1 and 2 years old that ranged from < 0.1 to 0.46. Across all species, although still heavily weighted by studies of *O. mykiss*, median narrow-estimates for length-at-age (0.29), mass at smoltification (0.15), and mortality (0.06) were also quite comparable to the present study. Applying an animal model to an extensive pedigree of Alaskan hatchery steelhead recently derived from wild broodstock, Hecht et al. (2015) estimated heritabilities for parr length and mass of 0.16 and 0.10, respectively, and for smolt length and mass of 0.37 and 0.21, respectively. Doctor et al. (2015) estimated heritabilities that were much higher than in the present study using an animal model to evaluate variation in length and mass in wild juvenile steelhead removed from gravel nests as embryos and reared in similar-sized hatchery tanks. In that study, the parents were not sampled, pedigrees were reconstructed from relatedness values, and the juveniles were reared at much lower densities.

The estimates of heritability suggest that response to selection on body size might be higher in fish exposed to hatchery environments with high feed rations intended to increase growth rates and reduce age-at-release. The heritabilities for fork length and body mass declined from the parr to the smolt stage in the S_2 treatment (after an additional 15 months of rearing), and to a lesser degree for mass in the S_1 treatment (5 months of additional rearing); no decline was evident for fork length in the S_1 treatment. The declining genetic influence on

body size in the S_2 treatment may reflect diminishing effects of common environment as the fish develop over an extended rearing period. In the S_2 treatment, the ability of larger, possibly more aggressive and dominant, parr to gain resources necessary to maintain their size advantages may have declined over the course of the study. The heritability estimates relied heavily on single pair matings, and the declining heritabilities are likely to reflect small paternal contributions. Our attempts to discern an effect of dam indicated no evidence for significant maternal effects on length or mass at any age, and they had no detectable influence on the heritability estimates. The lack of detectable maternal effects on parr or smolt size is not surprising since these typically occur early in life when maternal genotype or phenotype (e.g. yolk quality or quantity) influence offspring development (Heath et al. 1999, Van Leeuwen et al. 2016), and our size measurements of parr stage were greater than 4 months after first feeding.

The typically high survival during culture in salmon and steelhead hatcheries, followed by low survival after release, has suggested that adaptation to the hatchery environment (i.e., domestication selection) may result from selection on that occurs on phenotypic traits after release (Waples 1999, Reisenbichler 2004). Substantial evidence exists for divergence in behavioral, physiological, and morphological traits between intentionally domesticated (farmed) and wild salmon stocks (briefly summarized by Solberg et al. 2013). Evidence is mounting for unintentional divergence in hatchery populations where released smolts are released into the natural environment for harvest or conservation (reviewed by Fraser 2008). Efforts to investigate mechanisms causing adaptive genetic divergence of hatchery from wild stocks have most recently focused on how hatchery rearing affects maturation schedules (Harstad et al. 2014, Ford et al. 2012), how features of hatchery environments might promote

heritable variation in body size (Thompson and Blouin 2015), and exploring patterns of differential gene expression (Christie et al. 2016). Christie et al. (2012) found an inverse relationship between the reproductive success of hatchery-spawned steelhead broodstock and reproductive success of their offspring spawning in nature, providing evidence of domestication selection. They hypothesized that rearing density may have contributed variation in fitness among families. In a follow up study on a different population, smolt size (considered as a surrogate for viability in the study) varied significantly between high and low densities and among families, but high density did not increase among-family variance in body size (Thompson and Blouin 2015). Our analyses provided a direct measure of viability (seawater challenge) and indicated significant family-level variation in body size as well as significant interactions between family-specific size (smolt length and parr mass) and rearing treatment. The interaction between family and treatment suggests that smolt size could evolve in response to hatchery-induced selection on growth rate. This response is likely to influence the fate of hatchery smolts upon seawater entry; families with a propensity to produce larger smolts in an accelerated age-1 release program are likely to have higher survival during early ocean residence and be further subjected to size-selective mortality during their marine lifetime (Thompson and Beauchamp 2014, Ward et al. 1989)

To the extent there is selection favoring rapid growth rate in hatchery populations, negative fitness consequences for offspring of naturally spawning hatchery fish may stem from correlated traits, such as standard metabolic rate (Rosenfeld et al. 2015) agonistic behavior (Metcalf et al. 1995), and response to predation risk (Johnsson et al. 1996) that have different optima or trade-offs in natural streams than in hatchery environments. Hatchery populations

that have undergone selection for growth rate may perform poorly in a natural (food-poor) environment where standard metabolic rate can be negatively correlated with survival (Alvarez and Nicieza 2005). Hatchery populations of coho salmon and steelhead show less interspecific variation in metabolic rate and growth rate than wild populations, suggesting some convergent adaptation to hatchery conditions (Van Leeuwen 2011), which may limit the expression of life history diversity in natural habitats (Kendall et al. 2015). High-growth-selected salmon populations have been shown to experience greater predation mortality under natural (lake) conditions associated with risky foraging behavior (Biro et al. 2004). Farmed Atlantic salmon selected for rapid growth grew moderately faster in a quasi-natural stream but had lower survival (heritability estimates for size at age-1 ranged between 0.08 and 0.21, similar to the S_1 steelhead in the present study, Reed et al. 2015). In steelhead, offspring of hatchery parents were more aggressive than offspring from the founding wild population, but only under natural conditions or low hatchery rations (Berejikian et al. 1996), and the higher levels of aggression in the hatchery offspring were accompanied by reduced ability to survive predation by a naturally occurring predator (Berejikian 1995).

The results of the present study together with evidence of size-biased downstream migration (Reisenbichler 2004, Tatara et al. in review) suggests that hatchery programs can alter evolutionary trajectories of size at smolting and subsequent marine survival for steelhead trout. Because this species harbors some plasticity in size at smolting as well, this source of diversity could help facilitate rapid adaptation of these traits to hatchery rearing regimes. The S_2 strategy could substantially alleviate the potential for selection on body size and growth rate because this strategy resulted in no evidence of size-selective seawater challenge mortality and

very low heritability for body size at smolting. Other mechanisms of domestication selection in S_2 rearing programs have not been investigated but are possible because downstream migratory and marine mortality are greater (and the factors more complex) in the natural environment than in our seawater challenges. The results of the present study are most relevant to S_1 programs that use broodstock with natural spawn timing and rear juveniles on cold water sources. In those cases, or in similar situations for other species, growth rate-selected hatchery populations may be partially mismatched for the natural environment, and may explain a portion of the fitness loss in hatchery populations.

Acknowledgments

We thank Jeff Atkins (NOAA), Rob Endicott (NOAA), Mollie Middleton (University of Washington, UW), and Jon Dickey (UW) for their assistance in conducting the experiments. Krista Nichols (NOAA) provided valuable input on the experimental design and analyses. We thank the USFWS Winthrop National Fish Hatchery Staff for providing eyed embryos. Funding was provided by the Bonneville Power Administration (Project # 1993-056-00).

Table 1. Sample dates, sample sizes, and mortalities associated with seawater transfer for S_1 and S_2 rearing treatments. Trials were conducted in 2013 (S_1) and 2014 (S_2) using the same protocols and very similar time schedules. Data include mortalities that occurred within three weeks of seawater transfer.

Challenge	S_1 (2013)			S_2 (2014)		
	Dates	N	Mortalities	Dates	N	Mortalities
28 ppt	May 2	169	24	May 6	176	0
33 ppt	April 23 – May 7	115	44	April 22 - May 6	109	2
Lethal	April 17	192	--	April 17	193	--
Total		476			478	

Table 2. Heritability (h^2) estimates for parr and smolt fork length (FL) and mass, and for seawater challenge mortality and challenge days to death for smolts in the S_1 and S_2 rearing treatments. Most estimates were computed from animal model analyses. Two of the estimates of heritability of seawater challenge mortality used a modification of Falconer's proband method (Reich et al. 1972; see text). $P < 0.05$ (*), not significant (ns), based on DIC (see text).

Response	Model terms		Heritability	
	Random effects	Fixed effects	h^2	95% HPD/CI
Parr				
FL	Animal	None (S_1 only)	0.181	0.054-0.394*
FL	Animal	None (S_2 only)	0.245	0.101-0.565*
Mass	Animal	None (S_1 only)	0.372	0.187-0.712*
Mass	Animal	None (S_2 only)	0.447	0.231-0.770*
Smolt				
FL	Animal, tank	Rearing treatment (S_1, S_2)	0.047	0.017-0.097*
FL	Animal	Rearing treatment (S_1, S_2)	0.051	0.018-0.099*
Mass	Animal, tank	Rearing treatment (S_1, S_2)	0.179	0.078-0.306*
Mass	Animal	Rearing treatment (S_1, S_2)	0.168	0.078-0.305*
FL	Animal	None (S_1 only)	0.212	0.056-0.531*
FL	Animal	None (S_2 only)	0.002	0.001-0.457 ^{ns}
Mass	Animal	None (S_1 only)	0.145	0.035-0.299*
Mass	Animal	None (S_2 only)	0.015	0.010-0.025 ^{ns}
Mortality	Animal	Rearing treatment (S_1, S_2)	0.002	0.001-0.589 ^{ns}
Mortality ^a	--	None (S_1 only, all days)	0.027	-0.208-0.266 ^{ns}
Mortality ^a	--	None (S_1 only, ≤ 21 days)	0.024	-0.212-0.255 ^{ns}
Days to death	Animal, tank	None (S_1 only, all days)	0.805	0.567-0.907*
Days to death	Animal, tank	None (S_1 only, ≤ 21 days)	0.930	0.903-0.948*

^a proband est.

Table 3. General linear model selection results for parr and smolt fork length (FL), mass, and condition factor (K) in the S₁ and S₂ rearing treatments. Likelihood-ratio tests were used to test the significance of the F, T, and F x T interaction terms (see text for results); the table gives the Akaike Information Criterion (AIC) and change in AIC from the saturated model (ΔAIC). Significance levels: P < 0.10 (°), P < 0.05 (*), P < 0.01 (**), P < 0.001 (***), P < 0.0001 (****).

Response	Model parameters	Significance of terms	AIC	ΔAIC
Parr				
FL	Family, treatment, F x T	F***, F x T°	7560.8	--
FL	Family, treatment	F***	7562.8	1.0
Mass	Family, treatment, F x T	F***, F x T*	5097.3	--
Mass	Family, treatment	F***	5099.2	1.9
K	Family, treatment, F x T	T****	-2145.4	--
K	Family treatment	T****	-2144.1	0.3
Smolt				
FL	Family, treatment, F x T	F***, T***, F x T**	8092.5	--
FL	Family, treatment	F***, T***	8097.0	4.5
Mass	Family, treatment, F x T	F*, T****	8166.3	--
Mass	Family, treatment	T****	8166.7	0.4
K	Family, treatment, F x T	--	-88.09	--
K	Family treatment	F°, T**	-88.04	0.05

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Figure 1. A) Size frequency distributions for fish in the S_1 (gray bars) and S_2 (black bars) rearing treatments during the respective spring smolt period. B) Mean ($\pm$ SD) fork length for S_1 (gray squares) and S_2 (black triangle) treatments. The multiple means at spring sampling reflect that the sampling for the 28 ppt seawater challenge, 33 ppt seawater challenge, and lethally sampled groups occurred over a three-week period.

Figure 2. Probabilities of surviving seawater challenges at 28 ppt (A) and 33 ppt (B) and for both salinities combined (C) as a function of fork length during spring for age-1 (S_1) steelhead smolts. Individual data points for mortalities (0) and survivors (1) for the combined dataset are shown slightly offset from those values for presentation.

Figure 3. The significant positive relationship between the proportion of survivors from each family during the seawater challenges conducted at 28 and 33 ppt (combined data) and family mean fork length ($r^2 = 0.225$, $P = 0.011$).

Figure 4. A) Mean ($\pm$ 95% CI) fork length and B) body mass for each of the 28 full-sib families at the spring smolt window prior to seawater challenge. The S_1 families are indicated by the grey bars, overlapped by the same family reared in the S_2 environment (open bars). To better display the range and variation within the S_1 treatment, family number refers to the ranked means of the S_1 families within each panel; thus, the numbers do not necessarily correspond to the same families between the two panels (fork length and body mass).

Figure 1.

Figure 2

Figure 3.

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