Symposium Article

Shifting Thresholds: Rapid Evolution of Migratory Life Histories in Steelhead/Rainbow Trout, *Oncorhynchus mykiss*

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Abstract

Expression of phenotypic plasticity depends on reaction norms adapted to historic selective regimes; anthropogenic changes in these selection regimes necessitate contemporary evolution or declines in productivity and possibly extinction. Adaptation of conditional strategies following a change in the selection regime requires evolution of either the environmentally influenced cue (e.g., size-at-age) or the state (e.g., size threshold) at which an individual switches between alternative tactics. Using a population of steelhead (*Oncorhynchus mykiss*) introduced above a barrier waterfall in 1910, we evaluate how the conditional strategy to migrate evolves in response to selection against migration. We created 9 families and 917 offspring from 14 parents collected from the above- and below-barrier populations. After 1 year of common garden-rearing above-barrier offspring were 11% smaller and 32% lighter than below-barrier offspring. Using a novel analytical approach, we estimate that the mean size at which above-barrier fish switch between the resident and migrant tactic is 43% larger than below-barrier fish. As a result, above-barrier fish were 26% less likely to express the migratory tactic. Our results demonstrate how rapid and opposing changes in size-at-age and threshold size contribute to the contemporary evolution of a conditional strategy and indicate that migratory barriers may elicit rapid evolution toward the resident life history on timescales relevant for conservation and management of conditionally migratory species.

Given on-going environmental changes, it is increasingly important to quantify contemporary evolution (Gienapp et al. 2008; Hansen et al. 2012), which may allow populations to adapt to novel selective pressures (Gonzalez et al. 2012). For example, species that invade novel environments often exhibit rapid phenotypic changes in response to their newly invaded environment (Westley 2011). Indeed, it is now clear that evolution can occur on ecologically relevant timescales (Thompson 1998), particularly due to human-induced selection (Darimont et al. 2009), and in turn may affect population dynamics (Ezard et al. 2009) and other ecological and ecosystem processes (Schoener 2011).

Phenotypic plasticity also influences how organisms respond to novel environments. When environmental cues reliably predict future selective regimes, organisms may maximize fitness by matching their phenotype with a trait optimum (Tufto 2000). Thus, phenotypic plasticity can contribute to population persistence in variable environments, so long as the cue-optimum relationship (reaction norm) is maintained (Reed et al. 2010). However, reaction norms reflect historic selective regimes; changes in the environment, either gradual (e.g., climate change) or abrupt (e.g., habitat alteration), can decouple cues and trait optima, producing maladaptive phenotypes (Mills et al. 2013) with the potential for population extinction (Schlaepfer et al. 2002).

Understanding how conditional strategies respond to selection is particularly important and challenging. Conditional strategies, also called "threshold traits" (Roff 1996) or "polyphenisms" (Stearns 1989), are a type of phenotypic plasticity in which expression of discrete traits depends on a liability trait (a continuously distributed trait describing the organism's condition) relative to some threshold value (Myers and Hutchings 1986; Hazel and Smock 1990; Hutchings and Myers 1994). If heritable genetic variation underlies the threshold of a conditional strategy, novel selective pressures may elicit an evolutionary response, altering frequencies of ecologically important traits. For example, size-selective harvest may drive declining size at maturation in fish populations (Sharpe and Hendry 2009), influencing sustainable harvest levels and recovery plans (Enberg et al. 2009). However, determining the genetic basis of conditional strategies is challenging in nature because an observed shift in phenotypes can be manifested by both plasticity and evolutionary responses of a given trait.

Migration in fishes provides an excellent system for examining the components of conditional strategies and their potential for rapid evolution (Hutchings 2011; Dodson et al. 2013). For example, the salmonid *Oncorhynchus mykiss* exhibits a conditional migratory strategy which produces divergent migratory tactics, including anadromous "steelhead" that migrate to and from the ocean, and resident "rainbow trout" which stay in freshwater. When juvenile salmonids migrate from freshwater to saltwater they undergo a physiological and morphological transformation referred to as "smolting." Individuals that grow faster and achieve larger sizes in freshwater habitat are more likely to undergo the anadromous migration (Beakes et al. 2010). However, this size threshold for migration can vary across populations based on the local freshwater rearing conditions (Satterthwaite et al. 2010, 2012). There is evidence of heritable genetic variation in both the threshold size that triggers smolting in individuals (Thrower et al. 2004; Paez et al. 2010; Buoro et al. 2012; Hecht et al. 2015) and individual size-at-age (Carlson and Seamons 2008). Indeed, recent evidence documents a genetic basis for a number of traits associated with migratory tendency, including development rate (Nichols et al. 2007; Haidle et al. 2008; Easton et al. 2011; Miller et al. 2011; Hecht et al. 2015) and smoltification (Nichols et al. 2008; Martínez et al. 2011; Hecht et al. 2015). Further, even where migration is generally favored, it is more strongly expressed in females (Rundio et al. 2012), and some males forgo migration to mature early, which may conserve genetic variation for the resident life history (Piche et al. 2008). Therefore, the frequency of the smolt phenotype in a population may be influenced by a combination of phenotypic plasticity and selection on the genotypes underlying the conditional strategy for migration (Hutchings and Myers 1994).

Here, we examine a rapid evolutionary shift in life-history expression in a population of *O. mykiss* translocated above a waterfall barrier (Pearse et al. 2009). This presents an opportunity to illuminate the evolutionary processes that drive rapid phenotypic shifts and the response of migratory salmonids to novel barriers (Waples et al. 2008). In a common garden experiment, we compare conditional expression of alternative migratory tactics in offspring of fish from 2 populations: an above-barrier population transplanted above a waterfall approximately 100 years ago (~25 generations) and a below-barrier source population which maintains migratory access to and from the ocean (Pearse et al. 2009). We use a novel model-based approach to ask 3 related questions: 1) Is there evidence of phenotypic evolution in a novel above-barrier environment? 2) If so, is there evidence that the phenotypic changes are adaptive? 3) Does evolution of size-at-age and/or threshold size contribute to the contemporary evolution of conditional migratory strategies? We find evidence for adaptive life history evolution, driven by evolution of both size-at-age and the threshold size that triggers the migratory tactic. Thus, the phenotypic expression and genetic basis of migratory life history in *O. mykiss* can evolve on timescales relevant for conservation and management.

Methods

A Historical Transplant Experiment

Scott Creek is a 70 km² coastal watershed located in central California approximately 100 km south of San Francisco (37°3′43.530″N, 122°13′42.530″W). A waterfall on Big Creek, one of its prominent tributaries, presents a natural barrier to anadromy approximately 6 river km from the creek mouth. Ongoing (Hayes et al. 2004, 2008; Bond et al. 2008) and historical studies (Shapovalov and Taft 1954) in the watershed indicate the below-barrier source population of *O. mykiss* is dominated by the anadromous life history. Above the barrier waterfall a resident population of *O. mykiss* exists, and the landowners' journals document the transfer of below-barrier *O. mykiss* above the barrier in 1910. Genetic data from *O. mykiss* throughout the Scott Creek watershed indicate a recent genetic divergence of the above-barrier population (Pearse et al. 2009), consistent with a 1910 transplantation origin (Anderson and Slatkin 2007).

Fish Breeding and Data Collection

In November 2007, juveniles were collected via backpack electro-fishing above and below the Big Creek barrier falls, and brought to a small hatchery facility below the falls for rearing. Based on their size (above-barrier mean = 68.9 mm, range 51–90 mm; below-barrier mean = 60.3 mm, range = 43–90 mm), all individuals were presumed to be from brood year 2006 or 2007. It is possible that some individuals from the 2006 brood year had grown fast enough to exceed their threshold for migration in the previous spring, upwardly biasing the threshold distribution of the sampled individuals; however, given the moderate growth rates in the upper watershed reported by Hayes et al. (2008) we assume this effect is minimal.

In the spring of subsequent years we assessed development of the broodstock and released fish to maintain approximately equal rearing densities between the above- and below-barrier broodstocks. In spring of 2009, 71 of 97 fish in the below-barrier broodstock had the physical appearance of smolts (silver streamlined body and lack of parr marks), whereas only 1 of 25 above-barrier broodstock fish were smolts. At this time we released 43 below-barrier fish (36 smolts, 7 non-smolts) to equalize the rearing densities between the above- and below-barrier broodstocks. In early March of 2010, fish were assessed for readiness to spawn. At this time 16 of 41 below-barrier fish were still expressing the smolt phenotype, whereas none of the above-barrier fish were smolts.

On 23 March 2010, 14 mature individuals were crossed to create over 900 individuals in 9 families: 5 pure above-barrier (3 females crossed to 4 males) and 4 pure below-barrier (3 females crossed to 4 males). Number of eggs for each female was enumerated and 20 haphazardly chosen eggs were selected to estimate mean egg diameter. The large numbers of related offspring allow for precise estimates of family differences; however, due to the limited number of families, generalizing to population differences assumes sampled parents are representative of their population of origin.

Offspring were reared for 1 year at the Monterey Bay Salmon and Trout Project's Kingfisher Flat Hatchery on Big Creek. Families of fertilized eggs and alevin were reared inside the hatchery in incubator jars and trays, respectively. After yolk absorption, fish were transferred to flow-through troughs where some families were combined to maintain approximately equal densities across the troughs. At 5 months all fish were transferred outside to a single round holding tank (6.1 m diameter) supplied with unfiltered water drawn from Big Creek and supplemental air to provide a current and prevent oxygen depletion. Throughout the rearing period fish were fed rations following standard hatchery practices (~4–5% of body weight while in the troughs, ad libitum twice daily while in the holding tank). These practices are intended to increase growth and expression of the smolt phenotype (see Discussion).

During peak outmigration timing in the Scott Creek watershed (March; Hayes et al. 2011), all fish were lightly anesthetized using MS222, implanted with a uniquely identifiable passive integrated transponder (PIT) tag (11.5 mm FDX-B Glass Transponder, Allflex, Boulder, CO) by intraperitoneal injection with a 12-gauge needle, and small (≈0.3 cm²) caudal fin clips collected for genetic parentage and sex analysis. We recorded fork length (FL; mm), mass (g), and "smolt status" of each fish and noted mature male parr if milt was extruded during tagging, after which individuals were allowed to recover for at least 1 week prior to further manipulation. We defined "smolt status" as a binary trait based on physical appearance (Thrower et al. 2004; Nichols et al. 2008). "Nonsmolts" retained parr marks, cryptic stream coloration, and a rounded caudal fin, including mature male parr. "Smolts" had silvery and countershaded appearance, faint or complete loss of parr marks, streamlined body, and sharp pointed caudal fin typical of juvenile salmonids undergoing an ocean migration. Scoring was done without knowledge of cross-type.

Genotyping and Parentage Analysis

Small (≈0.3 cm²) caudal fin clips were collected from all juveniles for genetic parentage analysis. Tissue samples were digested with proteinase K, followed by DNA extraction with a semi-automated filter-based system (DNeasy 96 Tissue Kit) on a BioRobot 3000 (QIAGEN, Inc.). A panel of 95 single nucleotide polymorphisms (SNPs) was genotyped for all individuals (Abadia-Cardoso et al. 2013), and a sex identification assay consisting of an autosomal and a Y chromosome-linked gene probe was used to determine genetic sex of all genotyped fish (Brunelli et al. 2008). Phenotypic sex was determined by dissection on a subset of 63 fish following the seawater challenge (below), of which there was a mismatch between phenotypic and genetic sex in only 2 individuals. Genotyping was conducted using TaqMan assays (Applied Biosystems, Inc.) on 96.96 Dynamic Genotyping Arrays with the EP1 Genotyping System (Fluidigm Corporation). Two negative controls were included in each array and genotypes were scored using SNP Genotyping Analysis Software v3.1.1 (Fluidigm). Individual SNP genotypes were used for parentage analysis with the program SNPPit (Anderson 2012), following Abadia-Cardoso et al. (2013), and the accuracy of the inferred parentage assignments was assessed by comparing the genetic parentage results with the known family crosses.

Seawater Challenge and Instream Movement

We used 2 experiments to evaluate whether our visual "smolt" scoring corresponded with the capacity to osmoregulate in saltwater and downstream migration characteristics of smoltification. These assessments of our "smolt" scoring criteria were independent of the effect of cross type, and we therefore increased sample size by including offspring of additional crosses (above-barrier × below-barrier and F1 backcrosses) made at the same time as the crosses presented here. First, we tested the null hypothesis that nonsmolts and smolts would survive equally when moved from freshwater to seawater. A subset of fish (127 nonsmolts, 71 smolts) was haphazardly selected and a seawater challenge performed following (Beakes et al. 2010). Fish were introduced into a large seawater-fed tank (salinity 35‰) at the approximate time of peak downstream migration (March–April) and monitored for mortalities every 6–12 h for 12 days. Second, we tested the null hypothesis that nonsmolts and smolts would be detected migrating downstream in equal proportions following release. All fish not included in the seawater challenge were released into Big Creek approximately 0.5 km downstream of the barrier waterfall and 5.5 km upstream of the ocean. Movement was monitored over 6 weeks by 3 instream PIT tag readers and a smolt trap (a fixed-panel-and-pipe trap with 2 chamber live box, monitored daily) all located downstream of the release site (Bond et al. 2007; Hayes et al. 2011). All detections and recaptures were interpreted as movement downstream unless the individual was detected again at the same site more than 24 h later ($n = 2$).

Statistical Analysis

We used the Bayesian mixed model R package *MCMCglmm* (Hadfield 2010; R Core Team 2013) to estimate sex ratio, proportion of smolts, and growth rate (FL and mass) conditional on the categorical fixed effect "*cross*" (above-barrier or below-barrier). Family affiliation was included as a random effect to account for initial differences in rearing conditions. The variables "*sex*" (male or female) and "*smolt status*" (nonsmolt or smolt) were both modeled as binomial responses with a probit link. Because there is no individual variation in the expression of the binomial traits, we fixed the prior on the residual variance at 1 (de Villemereuil et al. 2013). We used a χ^2 distribution with 1 degree of freedom as a prior for the random variance components as recommended by de Villemereuil et al. (2013). A bivariate "animal model" (Wilson et al. 2010) was implemented in *MCMCglmm* to generate cross-specific estimates of "*fork length*" and "*mass*" at age 1. We used an inverse-Wishart matrix distribution

with 2 degrees of freedom as a prior for the residual variance; for the variance components we use a parameter expanded prior composed of an inverse-gamma distribution with 2 degrees of freedom and a normal distribution with mean 0 and variance 625 (Gelman 2006). We attempted to estimate heritability of FL and mass at age 1, but posteriors were heavily biased by the prior which tended to pull heritability estimates toward the margins (i.e., $h^2 = 0$ or 1). All models were run as a single chain for 5 010 000 iterations, discarding the first 10 000, sampling every remaining 1000th iterations to reduce autocorrelation. Convergence of MCMC sampling was visually inspected and assessed by Brooks–Gelman–Rubin diagnostics (Brooks and Gelman 1998). Results reported from the models are Bayesian posterior medians and 95% credible intervals. Support for differences between crosses is reported as the percent of the posterior distributions in agreement with the direction of the difference observed.

We examined the effects of sex, size-at-age, and cross-type on smolt status with a generalized linear (logistic regression) model, including all variables and 2-way interactions. To plot the effects of both continuous variables (FL and mass), we estimated the length–mass relationship of the population, as mass = $a \times FL^b$. We determined nonlinear least-squares estimates of a and b using the *nls* function in R ($a = 3.73 \times 10^{-5}$, standard error [SE] = 3.46×10^{-6}; $b = 2.75$, SE = 1.89×10^{-2}; df = 915). We used coefficient estimates from this model to illustrate the divergence between cross types in the size dependent process of smolting (Figure 1d). However, the underlying mechanisms that trigger the expression of the alternative strategies are not observable.

The Latent Environmental Threshold Model

We apply the Latent Environmental Threshold Model (LETM; Buoro et al. 2012) to compare the threshold size that triggers expression of the migratory tactic between the 2 populations of *O. mykiss* from above and below the barrier waterfall. The environmental threshold model (ETM; Hazel and Smock 1990; Roff 1994; Tomkins and Hazel 2007) enables assessment of selection on conditional strategies under a single framework that accommodates both phenotypic plasticity and evolution of a threshold trait. In the ETM, thresholds for adopting alternative tactics are heritable and vary among individuals within a population. The ETM provides a mathematical framework to estimate the threshold; however, quantifying the necessary components is not straightforward, as both the threshold for adopting a tactic and the proximate cue that triggers the expression of the tactic are often not observable. Recently, Buoro et al. (2012) addressed this by decomposing the ETM into "observable" and "nonobservable" components; the former being the expressed tactic or phenotype (e.g., smolt vs. nonsmolt) and an observable proxy for the liability trait (e.g., body size), the latter being the threshold for adopting a tactic, and the proximate cue (e.g., physiological state). The resulting LETM allows the estimation of genetic variance of the threshold and heritability of the conditional strategy from observations of the phenotypes and the related observable cue.

An assumption of the LETM relative to the ETM is that the proximate cue (η_i) varies among individuals as a function of the environment, but is unobservable. Little biological knowledge is often available regarding the precise proximate mechanisms influencing the expression of the phenotype (Tomkins and Hazel 2007). Although η_i is not observable, an observable proxy $\chi_{i,}$ which is correlated with η_i, can be measured. For example, growth rate and/or size at a given age in fish are known to be strongly influenced by the environment and are thus considered as integrating various

environmental factors (Dieckmann and Heino 2007). The distribution of η_i can be expressed conditional on χ_i with some residual error ε_i (normally distributed with mean 0 and standard deviation σ_{η_i}). In their review of alternative migratory strategies in salmonid fishes, Dodson et al. (2013) argue that body size in salmonids is the most commonly (and adequately) reported proxy of the liability trait. We use FL as the observable liability trait in the LETM.

An additional assumption of the LETM is that there can be a unique threshold for each genotype and thus the threshold of individual i (θ_i) is a polygenic quantitative trait which is normally distributed with mean μ_θ and standard deviation σ_θ, as typically assumed in quantitative genetics, following Myers and Hutchings (1986), Hazel et al. (1990), and Roff (1994). Thus, the standard deviation of the threshold σ_θ is a measure of genetic variability. In the LETM, we assume that the individual thresholds θ_i covary according to the individual relatedness; that is, they are sampling thresholds in a multivariate normal distribution depending on the additive genetic relationship matrix and the additive genetic variance.

We extended the LETM approach by combining the analysis for the 2 cross-types and introducing 3 additional modeling constraints:

(1) Because both cross-types experienced the same environment, we sample the proximate cue (η_i) from the same distribution. In other words, we consider the relationship between the size and the proximate cue of individuals to be the same in both populations.

(2) Both populations are characterized by similar genetic variance and heritability of the conditional strategy, so that they are characterized by the same propensity to respond to selection (shared θ_i). Analyses of the 2 cross-types separately confirmed that estimates of heritability are similar (results not shown). Thus, we sample individual thresholds (θ_i) from the same distributional form considering that the variance of the threshold (i.e., genetic variance) is similar between the 2 cross-types.

(3) The means of the threshold (μ_θ) may vary between the 2 cross-types.

Further information on how the LETM is fit to data is provided in the Supplemental Materials online and in Buoro et al. (2012).

Bayesian Markov chain Monte Carlo (MCMC) algorithms provide a flexible framework for analyzing latent variable models and their conditional structure (Clark 2004). We used this approach to fit the LETM to data. Joint posterior distributions of model parameters of interest were obtained by MCMC sampling implemented for the LETM in the R package *rjags* (Plummer 2003). Convergence of MCMC sampling was assessed by Brooks-Gelman-Rubin diagnostics (Brooks and Gelman 1998).

Bayesian analyses require specifying prior probability distributions for model parameters. Here, all priors were noninformative or weakly informative to ensure that all information comes from data. For the LETM, we did not fix a uniform prior on the standard deviations directly as is usual. Instead, priors on the standard deviations σ_θ and σ_η were defined on the total variance σ_P^2 and the heritability h^2. Because there is a one-to-one transformation relating these parameters to the standard deviations, assigning a prior to them (σ_P^2, h^2) induces a prior on (σ_θ, σ_η) as well (as suggested by Gelman et al. 2003). We used a scaled inverse-χ^2 with one degree of freedom for σ_P^2 (as recommended by Gelman 2006), a uniform distribution between 0 and 1 for the heritability h^2 and a normal distribution with mean 0 and a large variance (1000) on the mean of the threshold distribution μ_θ.

Results reported from the LETM model are Bayesian posterior medians and 95% credible intervals. Support for differences between crosses is reported as the percent of the posterior distributions in agreement with the direction of the difference observed. In addition, we report the rate of trait evolution (*d*) and trait evolvability (*I*$_A$). We measure trait evolution in Darwins (Haldane 1949):

$$d = \frac{\ln(\mu_{\theta,b}) - \ln(\mu_{\theta,b})}{t}$$

where $\mu_{\theta,b}$ and $\mu_{\theta,a}$ are the posterior mean threshold estimates for the below- and above-barrier crosses, and *t* is the time since population divergence (100 years) in millions of years. Threshold evolvability is the expected proportional change in the trait under a unit strength of selection (Houle 1992; Hansen et al. 2011) and is presented with respect to the source population (i.e., below-barrier cross):

$$I_A = \frac{\sigma_\theta^2}{\mu_{\theta,b}^2}$$

Evolvability has the advantage of being less susceptible to experimental studies that minimize environmental variation resulting in upwardly biased estimates of heritability (Houle 1992).

Data Availability

In fulfillment of data archiving guidelines (Baker 2013), the primary data underlying all analyses described here have been deposited in Dryad.

Results

Nine families were produced: 5 pure above-barrier (3 females crossed to 4 males) and 4 pure below-barrier (3 females crossed to 4 males). Number of eggs per female varied considerably (range: 301–832) but egg diameters were similar (range: 4.5–5.0 mm); there were no significant differences between above- and below-barrier females, suggesting that maternal environmental effects were minimal, perhaps not surprising given parents were raised from young-of-year to maturity in the same hatchery environment.

Parentage was determined for 917 offspring that survived the duration of the experiment (312 above-barrier; 605 below-barrier). Family sizes ranged from 1 to 265 individuals (excluding 2 families represented by less than 5 individuals did not qualitatively change our results). We were able to assign genetic sex to 853 individuals. As there was no apparent bias in which fish could not be assigned sex, we use the reduced dataset only in models where sex is included as a variable. Offspring sex ratio was estimated as 49% male in above-barrier crosses (41–58%; Figure 1a), and 43% male in below-barrier crosses (37–50%; Figure 1a), with 90% of the posterior distribution supporting the lower incidence of males in the below-barrier crosses. Incidence of maturity among males differed significantly between crosses ($\chi^2 = 36.6$, df = 1, $P < 0.001$): mature males accounted for 27.8% of all above-barrier males (14.0% of all fish), but only 5.4% of below-barrier males (2.3% of all fish).

Expression of the migratory life history was substantially reduced in the above-barrier crosses. Frequency of smolts in above-barrier offspring was 54% (39–68%; Table 1; Figure 1b) and ranged among families from 48% to 56% compared with 73% in below-barrier offspring (61–84%; Table 1; Figure 1b) with a range of 50–81% among families. Support for the lower incidence of smolts in above-barrier offspring was 96% of the posterior distribution. A greater proportion of fish scored as "smolts" survived the

seawater challenge (58 of 71 smolts, 57 of 127 nonsmolts, $\chi^2 = 23.9$, df = 1, $P < 0.001$; Figure 2a), but survival of fish scored "smolts" did not differ between the crosses ($\chi^2 = 0.27$, df = 1, $P = 0.60$). A higher proportion of smolts were detected migrating downstream than nonsmolts (361 of 1038 smolts released, 50 of 541 nonsmolts released; $\chi^2 = 136.9$, df = 1, $P < 0.001$; Figure 2b) and significantly more below-barrier smolts were detected moving downstream than above-barrier smolts (43% to 24%; $\chi^2 = 41.5$, df = 1, $P < 0.001$). FL positively influenced these elements of smoltification (GLM, survival: FL = 0.032, 0.007 SE, $P < 0.001$; detection: FL = 0.014, 0.006 SE, $P = 0.023$). However, size and smolt state are strongly positively correlated (Figure 1d), making it difficult to isolate their individual effects.

Fish from above-barrier crosses grew slower than fish from below-barrier crosses; above-barrier fish had smaller mean FL (134 mm; 116–152 mm) and mass (24.3 g; 15.9–34.5 g) than below-barrier fish (FL: 151 mm; 132–173 mm; mass: 35.6 g; 23.3–51.0 g) (Table 1; Figure 1c). Probabilities that above-barrier fish were smaller in length and mass were 91% and 93%, respectively. Logistic regression supported smolting as a size-dependent process that is also influenced by cross and sex (Figure 1d).

The threshold for smolting exhibited high heritability ($h^2 = 0.91$; 95% credible interval = 0.72–0.99), but only modest evolvability ($I_A = 1.6\%$; 1.3–2.1%). Threshold size differed substantially between the 2 cross-types. The above-barrier threshold was larger than the below-barrier threshold (estimated difference of 0.60; 0.28–0.91 with >99% of support). The mean threshold for offspring of above-barrier crosses is 43% (25–61%) larger than below-barrier crosses. In the LETM, the proximate cue is on an arbitrary scale; however, the proximate cue and the observable liability trait are linked by an undefined function (equation 3 in Buoro et al. 2012). For the sake of illustration, we scale the proximate cue to the observable liability trait such that the 2 cues share a 1:1 relationship (i.e., a 1 mm increase in FL corresponds to a one unit increase in the proximate cue). On this scale the median posterior difference in thresholds would be 17 mm (8–25 mm). In below-barrier offspring, the mean threshold FL is 39 mm less than the mean FL. In contrast, this difference in mean threshold and mean FL in above-barrier offspring is only 5 mm. Thus, a much larger proportion of the FL and threshold size distributions overlap in the offspring of above-barrier crosses (Figure 3), reducing expression of the migratory behavior.

Discussion

Human activities increasingly threaten migratory species by presenting barriers to movement (Wilcove and Wikelski 2008). Dams in particular have been responsible for large declines in the distribution and diversity (Gustafson et al. 2007) of migratory salmonids in the United States. We investigated the response to selection against migration in a population of *O. mykiss* isolated above a barrier waterfall for 100 years (~25 generations). The migratory phenotype at age-1 was reduced by 26% in the above-barrier families, consistent with evolutionary adaptation to selection for the nonmigratory tactic. This rapid evolution was driven by changes in size-at-age as well as evolution of the underlying size threshold. These changes in fish length represent a rapid evolutionary rate of change of 1195 "Darwins" (Haldane 1949). The estimated FL threshold value changed at a rate of 1381 Darwins. Both rates are similar to those observed for populations introduced to novel habitats (Hendry et al. 2008). More generally, our results indicate that
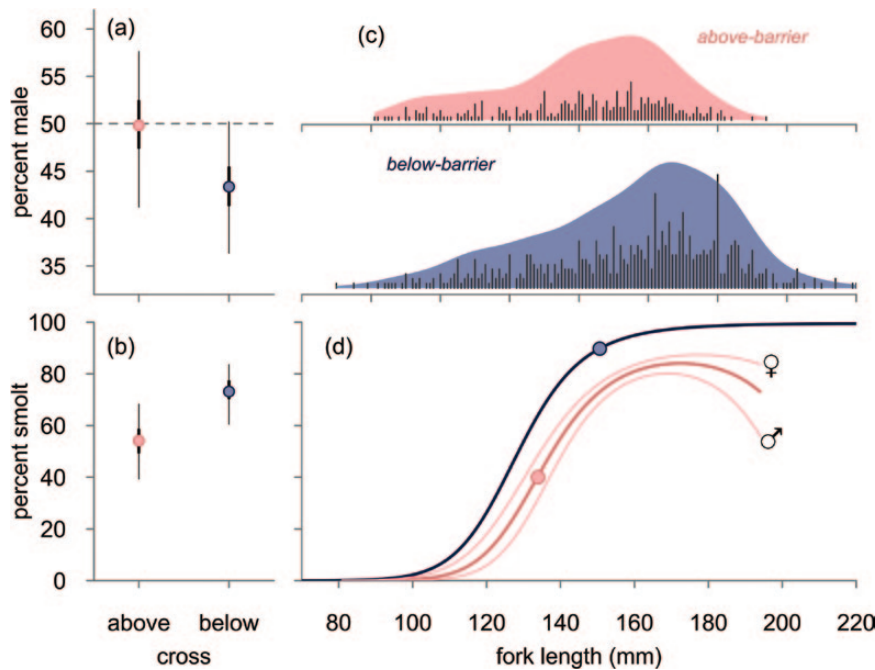
Figure 1. Comparison of above-barrier (red; light gray in print) and below-barrier (blue; dark gray in print) offspring sex ratio (**a**), smolt incidence (**b**), observed FLs and data density (**c**), and predicted smolt incidence from logistic regression (see Methods) (**d**). In (a) and (b), solid and thin lines represent Bayesian 50% and 95% posterior credible intervals. In (c), the shaded area represents data density and vertical bars are counts of individuals in 1 mm bins. For (d), fish mass is estimated for a given FL based on the length-mass relationship as described in the Methods. Circles in (d) are the predicted incidence of smolts for the median posterior probability FL of the given cross and assuming the mean effect of sex. Lighter red lines indicate female (♀) and male (♂) specific predictions. Sex specific predictions for below-barrier offspring are indistinguishable from the mean. Logistic curves decline for above-barrier fish at larger body sizes due to the incidence of early maturing males (see Results).

Table 1. Estimates and Bayesian 95% credible intervals for the observable environmental cues (FL- and mass-at-age 1) estimated from the bivariate animal model and threshold size estimated from the LETM

	FL (mm)	Mass (g)	Threshold
Above	134 (116–152)	24.3 (15.9–34.6)	128 (121–135)
Below	150 (132–173)	35.6 (23.3–51.0)	112 (104–120)
P	91%	93%	>99%
V_A	—	—	204 (180–230)
V_P	—	—	209 (191–233)
I_A	—	—	1.6% (1.3–2.1%)
h^2	—	—	0.91 (0.72–0.99)
d	−1195 (−3095 to 720)	−3861 (−9409 to 1750)	1381 (674–2159)

P, posterior density supporting above-barrier fall offspring are smaller than below-barrier offspring. I_A, evolvability, defined as the additive genetic variation divided by mean phenotype squared (here, mean of below-barrier offspring). See Hansen et al. (2011). d, Darwins, the change in the trait by a factor of *e* per one million years. Other abbreviations defined in text.

alternative migratory tactics have a heritable genetic basis that can evolve rapidly.

The rapid evolutionary change in the tactics expressed by the migratory life history strategy is mediated by a shift in the threshold size distribution relative to the cues that trigger the migratory tactic (Figure 3), consistent with the view of migration as a threshold trait (Pulido 2011; Dodson et al. 2013). Previous theoretical models of threshold traits assumed that the expression of the discrete states are under polygenic control, either by genetic variation in the liability trait (Wright 1934, Falconer 1965) or the threshold (Hazel and Smock 1990; Roff 1994; Hazel et al. 2004), but could not examine the potential for both (Roff 2011). The LETM (Buoro et al. 2012) allowed us to separately estimate the threshold and liability trait to identify evolutionary shifts in their distributions (Figure 3).

Simultaneous evolution of these 2 aspects of the conditional strategy resulted in divergence in migratory tactic expression (Figure 1b).

This study represents a relatively rare example of threshold evolution in conditional strategy (Roff 2011). Genetic variation has been reported in the threshold value that triggers alternative phenotype expression in many conditional strategies, including male morphologies (Moczek 2003; Buzatto et al. 2012), reproductive tactics (Piche et al. 2008), and migratory tactics (Beakes et al. 2010, Paez et al. 2010). However, there are few examples of the distribution of threshold values in a natural population actually responding to selection (but see Moczek 2003; Tomkins and Brown 2004). Perhaps, the best example comes from an artificial selection experiment on alternative male morphs of a mite (*Rhizoglyphus echinopus*). By increasing the hiding places available to (and presumably the fitness of) a nonfighter morph, (Tomkins et al.
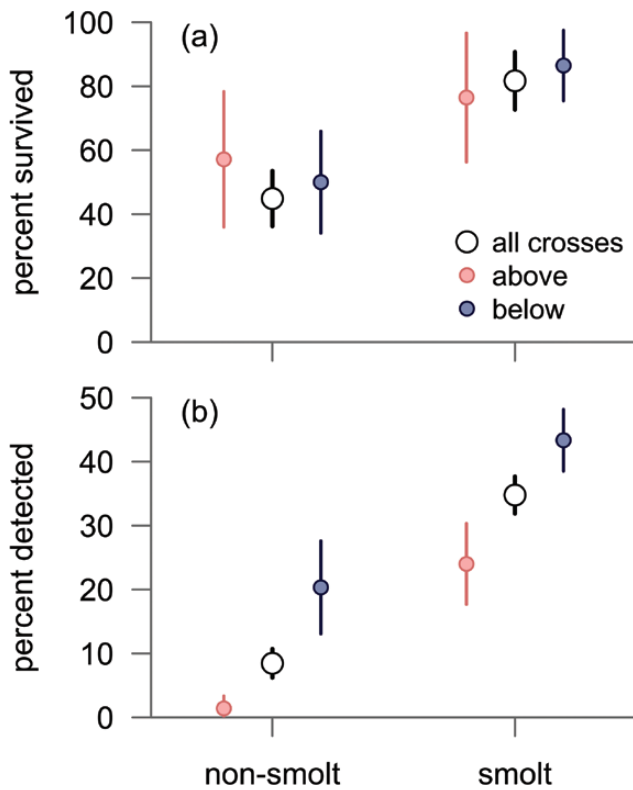
Figure 2. Relationships between different metrics of smoltification. "Smolt score" and (**a**) the survival of individuals in seawater and (**b**) the probability of being detected migrating downstream. General assessment of our "smolt" scoring criteria was independent of the effect of cross type, and include offspring of additional crosses (above-barrier × below-barrier and F1 backcrosses) made at the same time as the crosses presented here ("All crosses," white circles). Estimates for above-barrier (red circles; light gray in print) and below-barrier (blue circles; dark gray in print) crosses are also presented. Error bars represent 2 SE.

Figure 3. A comparison of distributions of thresholds (in blue; dark gray in print) and FLs (in yellow; light gray in print) for (**a**) the below-barrier source population, and (**b**) the derived above-barrier population. Dashed lines and arrows indicate the direction and magnitude of the response to selection against downstream migration in the above-barrier population. Distributions are idealized (normal, no skew) based on the estimated means and variances from the LETM and animal model.

2011) were able to induce an evolutionary increase in the mean size at which males express the alternative fighter morph. Thus, thresholds for phenotype expression in alternative strategies can evolve over a few generations when faced with strong directional selection.

Body size is a heritable trait in salmonids capable of responding to selection (Carlson and Seamons 2008). In the present study, above-barrier offspring reared in a common-garden environment were 11% and 32% smaller than below-barrier offspring in FL and mass, respectively. In the below-barrier source population, selection favors larger fish due to the strong size-selective mortality migrants experience at sea (Bond et al. 2008). Following transplantation above the barrier waterfall, genetic variants conferring faster growth would be quickly lost due to the relationship between size and smolting (Figure 1d). Thus, above the barrier waterfall, high-risk foraging behaviors that increase growth opportunities could decrease relative fitness by increasing both predation risk (Biro et al. 2006) and the likelihood of exceeding the environmentally cued threshold to migrate over the waterfall.

Although our results suggest that the frequency of the migratory phenotype is significantly reduced in the above-barrier population, the incidence of migrants (54%) is still quite high. Why would the migrant phenotype remain so common? One possibility is that the migratory behavior has become decoupled from the morphological and physiological traits that make up the migratory syndrome
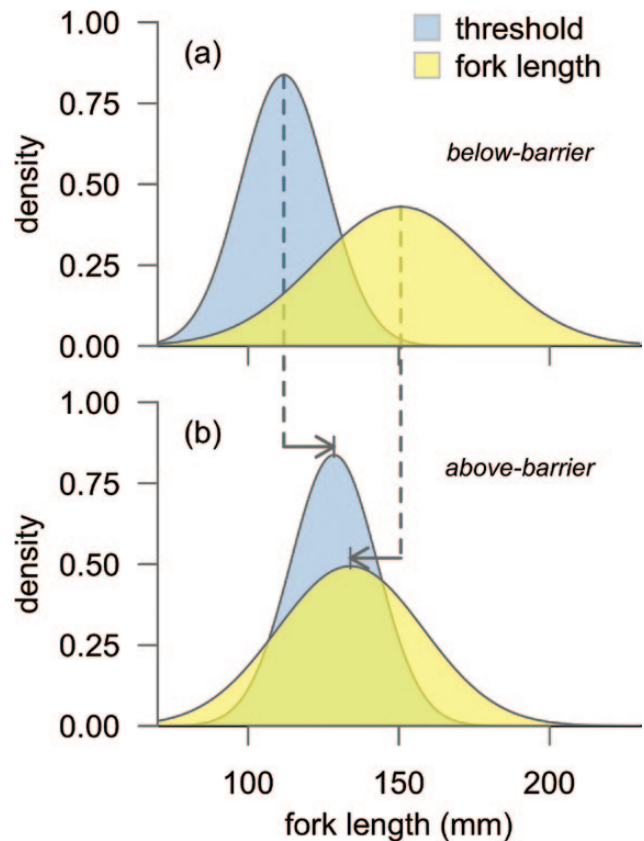
(Dingle and Drake 2007), as suggested by the lower downstream movement probability of above-barrier smolts relative to below-barrier smolts (24% vs. 43%; Figure 2b). A second possibility is the presence of strong genetic covariance between the migratory phenotype and other traits influenced by growth rate, such as maturation (Thrower et al. 2004). Finally, it is possible that the short time since the transplantation occurred has not given selection sufficient opportunity to remove the migratory phenotype. This is consistent with the results of (Pearse et al. 2014), who found that specific genomic regions had significantly lower frequency of alleles associated with anadromy in long-established resident populations compared with recently established above-barrier populations. However, the high growth rate of our experimental fish, which is typical for salmonid hatcheries intent on maximizing the number of fish that migrate upon release (Hayes et al. 2004), likely also contributed. In fact, in situ incidence of smolts in the above-barrier population is likely much lower; 95% of fish rearing in the upper watershed are <100 mm in length after 1 year of growth (Hayes et al. 2008), well below the mean threshold size estimated here.

Sex-specific differences in maturation schedules appear to play an important role in the rapid evolution of the resident life history described here. Early maturity is also a threshold trait (Piche et al. 2008), but the decision-window is thought to occur prior to that

of smoltification (Mangel and Satterthwaite 2008). Our study did not explicitly quantify the maturation threshold; rather, the LETM subsumes variation produced by multiple development pathways. Smaller thresholds for early maturity may achieve the same outcome as larger thresholds for migration (lower probability of migration), but are constrained by the minimum energetic state necessary to mature. Due to the greater energetic requirements and associated fecundity advantage, rates of anadromy in salmonid populations are often female biased (Ohms et al. 2014). Males, on the other hand, can reach maturity in a single year of freshwater growth. We found males were less likely to smolt at a given size, particularly in above-barrier families, and more likely to mature at larger body sizes (illustrated by the decline in the male logistic curve at larger FLs in Figure 1d). The higher incidence of mature males in above-barrier offspring is consistent with the strong negative genetic correlation between smolting and early maturation documented by Thrower et al. (2004). The 2.3% rate of early male maturity in below-barrier offspring is consistent with the ~3% observed annually in the Big Creek Hatchery steelhead stock (Hayes S, personal observation), suggesting the phenotype was also segregating in the founding population prior to introduction above the barrier waterfall. Further, alleles conferring early maturity should rapidly accumulate in this population as these males have earlier, and potentially more numerous, reproductive bouts. Interestingly, although males and females were found in equal proportion in the above-barrier families, females significantly outnumbered males in progeny of below-barrier parents (Figure 1a). The cause of this difference is unclear, as an equal sex-ratio in juvenile *O. mykiss* was found in a nearby population (Rundio et al. 2012).

Contrasting traits of introduced and source populations following biological invasions can provide valuable insight into contemporary evolution (Westley 2011). However, such studies are often opportunistic, as in the present case, and thus consideration of the results must be done within the context of a possibly imperfect study design. Here, generalizing from sample to population should be done cautiously as the limited number of parents represented in the breeding design may not be representative of their populations of origin. In particular, the below-barrier parents used here represent only the small fraction of below-barrier broodstock that matured in their third year, when the experimental crosses took place. Conversely, all above-barrier broodstock were mature and available for breeding (see Fish Breeding and Data Collection). This suggests that resident genotypes were oversampled in the below-barrier broodstock, meaning genetic differences for the liability and threshold traits between the above- and below-barrier populations in the wild may be larger than we observed. Additionally, although unlikely, it is impossible to rule out the presence of a previously established, genetically divergent *O. mykiss* population above the barrier before the human-mediated introduction in 1910 (Pearse et al. 2009). Further, our results from a single above- and below-barrier population pair may not be representative of other, unsampled populations. However, given that *O. mykiss* have been widely introduced above barriers there is a unique opportunity to test predictions from our study in independent populations. Recently, Pearse et al. (2014) found parallel adaptive genomic evolution in multiple above-barrier populations, including Big Creek, with the degree of evolution consistent with time since isolation from the paired below-barrier populations. Thus, Big Creek appears representative of many populations undergoing similar genomic evolution following recent isolation above barriers.

A growing body of literature highlights the complicated interplay between resident and anadromous forms of *O. mykiss* (Zimmerman and Reeves 2000; Thrower et al. 2004; Pearse et al. 2009; Hayes et al. 2012; Courter et al. 2013; reviewed in Sloat et al. 2014; Kendall et al. 2015), and the challenges and opportunities for management and conservation of species with conditional migration. However, the US Endangered Species Act (NMFS 2006) protects listed steelhead populations, but protects only "naturally spawned anadromous *O. mykiss* (steelhead) populations below natural and manmade impassable barriers," while excluding the resident forms that they are connected to. In addition, fragmentation of aquatic migratory corridors and on-going introductions are likely causing contemporary evolution throughout the range of *O. mykiss*. We found that the conditional migration strategy is highly heritable (h^2 = 0.91; SD = 0.09) and can evolve rapidly in response to selection. However, evolvability (I_A = 1.6%; 1.3–2.1%) is modest relative to life-history traits reported by Hansen et al. (2011), suggesting strong selection, here in the form of the barrier waterfall, is necessary to produce the evolutionary response we observed. Further, *O. mykiss* isolated for many decades still produce some smolts with the capacity to osmoregulate in seawater (Thrower et al. 2004). This suggests conservation of physiological and behavioral components of smoltification in isolated *O. mykiss* populations via adaptive genetic variation, and that isolated *O. mykiss* populations could contribute to the recovery of genetically similar endangered migratory populations downstream, but will likely be sensitive to the strength and duration of selection experienced during isolation (Pearse et al. 2014). Additionally, recovery of the migratory phenotype will be slowed if smolt survival to spawning is reduced in the isolated population, as observed by Thrower and Hard (2008). Thus, our study demonstrates that evolution of key life-history traits can occur on timescales relevant for management and conservation and provides insight into how ecological and genetic variations interact to promote rapid adaptation to ongoing environmental change.

Supplementary Material

Supplementary material can be found at http://www.jhered.oxford-journals.org/

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References

Abadia-Cardoso A, Anderson EC, Pearse DE, Carlos Garza J. 2013. Large-scale parentage analysis reveals reproductive patterns and heritability of spawn timing in a hatchery population of steelhead (*Oncorhynchus mykiss*). *Mol Ecol*. 22:4733–4746.

Anderson EC. 2012. Large-scale parentage inference with snps: an efficient algorithm for statistical confidence of parent pair allocations. *Stat Appl Genet Mol Biol*. 11:1544–6115.

Anderson EC, Slatkin M. 2007. Estimation of the number of individuals founding colonized populations. *Evolution*. 61:972–983.

Baker CS. 2013. Journal of heredity adopts joint data archiving policy. *J Hered*. 104:1.

Beakes MP, Satterthwaite WH, Collins EM, Swank DR, Merz JE, Titus RG, Sogard SM, Mangel M. 2010. Smolt transformation in two California steelhead populations: effects of temporal variability in growth. *Trans Am Fish Soc*. 139:1263–1275.

Biro PA, Abrahams MV, Post JR, Parkinson EA. 2006. Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *J Anim Ecol*. 75:1165–1171.

Bond MH, Hanson CV, Baertsch R, Hayes SA, MacFarlane RB. 2007. A new low-cost instream antenna system for tracking passive integrated transponder (PIT)-tagged fish in small streams. *Trans Am Fish Soc*. 136:562–566.

Bond MH, Hayes SA, Hanson CV, MacFarlane RB. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. *Can J Fish Aquat Sci*. 65:2242–2252.

Brooks SP, Gelman A. 1998. General methods for monitoring convergence of iterative simulations. *J Comput Graph Stat*. 7:434–455.

Brunelli JP, Wertzler KJ, Sundin K, Thorgaard GH. 2008. Y-specific sequences and polymorphisms in rainbow trout and Chinook salmon. *Genome*. 51:739–748.

Buoro M, Gimenez O, Prévost E. 2012. Assessing adaptive phenotypic plasticity by means of conditional strategies from empirical data: the latent environmental threshold model. *Evolution*. 66:996–1009.

Buzatto BA, Simmons LW, Tomkins JL. 2012. Genetic variation underlying the expression of a polyphenism. *J Evol Biol*. 25:748–758.

Carlson SM, Seamons TR. 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. *Evol Appl*. 1:222–238.

Clark JS. 2004. Why environmental scientists are becoming Bayesians. *Ecol Lett*. 8:2–14.

Courter II, Child DB, Hobbs JA, Garrison TM, Glessner JJG, Duery S, Fraser D. 2013. Resident rainbow trout produce anadromous offspring in a large interior watershed. *Can J Fish Aquatic Sci*. 70:701–710.

Darimont CT, Carlson SM, Kinnison MT, Paquet PC, Reimchen TE, Wilmers CC. 2009. Human predators outpace other agents of trait change in the wild. *Proc Natl Acad Sci U S A*. 106:952–954.

de Villemereuil P, Gimenez O, Doligez B. 2013. Comparing parent-offspring regression with frequentist and Bayesian animal models to estimate heritability in wild populations: a simulation study for Gaussian and binary traits. *Methods Ecol Evol*. 4:260–275.

Dieckmann U, Heino M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Mar Ecol Prog Ser*. 335:253–269.

Dingle H, Drake VA. 2007. What is migration? *BioScience*. 57:113.

Dodson JJ, Aubin-Horth N, Thériault V, Páez DJ. 2013. The evolutionary ecology of alternative migratory tactics in salmonid fishes. *Biol Rev*. 88:602–625.

Easton AA, Moghadam HK, Danzmann RG, Ferguson MM. 2011. The genetic architecture of embryonic developmental rate and genetic covariation with age at maturation in rainbow trout *Oncorhynchus mykiss*. *J Fish Biol*. 78:602–623.

Enberg K, Jørgensen C, Dunlop ES, Heino M, Dieckmann U. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evol Appl*. 2:394–414.

Ezard TH, Côté SD, Pelletier F. 2009. Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. *Philos Trans R Soc Lond B Biol Sci*. 364:1491–1498.

Falconer DS. 1965. The inheritance of liability to certain diseases, estimated from the incidence among relatives. *Ann Hum Genet*. 29:51–76.

Gelman A. 2006. Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Anal*. 1:515–534.

Gelman A, Carlin JB, Stern HS, Rubin DB. 2003. *Bayesian data analysis*. 2nd ed. London (UK): Chapman and Hall/CRC.

Gienapp P, Teplitsky C, Alho JS, Mills JA, Merilä J. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Mol Ecol*. 17:167–178.

Gonzalez A, Ronce O, Ferriere R, Hochberg ME. 2012. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. *Philos Trans R Soc Lond B Biol Sci*. 368:20120404.

Gustafson RG, Waples RS, Myers JM, Weitkamp LA, Bryant GJ, Johnson OW, Hard JJ. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. *Conserv Biol*. 21:1009–1020.

Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J Stat Softw*. 33:1–22.

Haidle L, Janssen JE, Gharbi K, Moghadam HK, Ferguson MM, Danzmann RG. 2008. Determination of quantitative trait loci (QTL) for early maturation in rainbow trout (*Oncorhynchus mykiss*). *Mar Biotechnol (NY)*. 10:579–592.

Haldane JB. 1949. Suggestions as to quantitative measurement of rates of evolution. *Evolution*. 3:51–56.

Hansen MM, Olivieri I, Waller DM, Nielsen EE, The GeM Working Group. 2012. Monitoring adaptive genetic responses to environmental change. *Mol Ecol*. 21:1311–1329.

Hansen TF, Pélabon C, Houle D. 2011. Heritability is not evolvability. *Evol Biol*. 38:258–277.

Hayes SA, Bond MH, Hanson CV, Freund EV, Smith JJ, Anderson EC, Ammann AJ, MacFarlane RB. 2008. Steelhead growth in a small Central California watershed: upstream and estuarine rearing patterns. *Trans Am Fish Soc*. 137:114–128.

Hayes SA, Bond MH, Hanson CV, Jones AW, Ammann AJ, Harding JA, Collins AL, Perez J, MacFarlane RB, Bradford M. 2011. Down, up, down and "smolting" twice? Seasonal movement patterns by juvenile steelhead (*Oncorhynchus mykiss*) in a coastal watershed with a bar closing estuary. *Can J Fish Aquat Sci*. 68:1341–1350.

Hayes SA, Bond MH, Hanson CV, MacFarlane RB. 2004. Interactions between endangered wild and hatchery salmonids: can the pitfalls of artificial propagation be avoided in small coastal streams? *J Fish Biol*. 65:101–121.

Hayes SA, Hanson CV, Pearse DE, Bond MH, Garza JC, MacFarlane RB. 2012. Should I stay or should I go? The influence of genetic origin on emigration behavior and physiology of resident and anadromous juvenile *Oncorhynchus mykiss*. *N Am J Fish Manage*. 32:772–780.

Hazel WN, Smock R. 1990. A polygenic model for the evolution and maintenance of conditional strategies. *Proc R Soc Lond B Biol Sci*. 242:181–187.

Hazel W, Smock R, Lively CM. 2004. The ecological genetics of conditional strategies. *Am Nat*. 163:888–900.

Hecht BC, Hard JJ, Thrower FP, Nichols KM. 2015. Quantitative genetics of migration-related traits in rainbow and steelhead trout. *G3*. 5:873–889.

Hendry AP, Farrugia TJ, Kinnison MT. 2008. Human influences on rates of phenotypic change in wild animal populations. *Mol Ecol*. 17:20–29.

Houle D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics*. 130:195–204.

Hutchings JA. 2011. Old wine in new bottles: reaction norms in salmonid fishes. *Heredity*. 106:421–437.

Hutchings JA, Myers RA. 1994. The evolution of alternative mating strategies in variable environments. *Evol Ecol*. 8:256–268.

Kendall NW, McMillan JR, Sloat MR, Buehrens TW, Quinn TP, Pess GR, Kuzishchin KV, McClure MM, Zabel RW, Bradford M. 2015. Anadromy and residency in steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of the processes and patterns. *Can J Fish Aquat Sci*. 72:319–342.

Mangel M, Satterthwaite WH. 2008. Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. *Bull Mar Sci*. 83:107–130.

Martínez A, Garza JC, Pearse DE. 2011. A microsatellite genome screen identifies chromosomal regions under differential selection in steelhead and rainbow trout. *Trans Am Fish Soc*. 140:829–842.

Miller MR, Brunelli JP, Wheeler PA, Liu S, Rexroad CE III, Palti Y, Doe CQ, Thorgaard GH. 2011. A conserved haplotype controls parallel adaptation in geographically distant salmonid populations. *Mol Ecol*. 21:237–249.

Mills LS, Zimova M, Oyler J, Running S, Abatzoglou JT, Lukacs PM. 2013. Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proc Natl Acad Sci U S A*. 110:7360–7365.

Moczek AP. 2003. The behavioral ecology of threshold evolution in a polyphenic beetle. *Behav Ecol*. 14:841–854.

Myers RA, Hutchings JA. 1986. Selection against parr maturation in Atlantic salmon. *Aquaculture*. 1986:313–320.

Nichols KM, Broman KW, Sundin K, Young JM, Wheeler PA, Thorgaard GH. 2007. Quantitative trait loci × maternal cytoplasmic environment interaction for development rate in *Oncorhynchus mykiss*. *Genetics*. 175:335–347.

Nichols KM, Edo AF, Wheeler PA, Thorgaard GH. 2008. The genetic basis of smoltification-related traits in *Oncorhynchus mykiss*. *Genetics*. 179:1559–1575.

NMFS. 2006. Endangered and threatened species: final listing determinations for 10 distinct population segments of West Coast steelhead. *Fed Reg*. 71:834–862.

Ohms HA, Sloat MR, Reeves GH, Jordan CE, Dunham JB. 2014. Influence of sex, migration distance, and latitude on life history expression in steelhead and rainbow trout (*Oncorhynchus mykiss*). *Can J Fish Aquat Sci*. 71:70–80.

Paez DJ, Brisson-Bonenfant C, Rossignol O, Guderley HE, Bernatchez L, Dodson JJ. 2010. Alternative developmental pathways and the propensity to migrate: a case study in the Atlantic salmon. *J Evol Biol*. 24:245–255.

Pearse DE, Hayes SA, Bond MH, Hanson CV, Anderson EC, Macfarlane RB, Garza JC. 2009. Over the falls? Rapid evolution of ecotypic differentiation in steelhead/rainbow trout (*Oncorhynchus mykiss*). *J Hered*. 100:515–525.

Pearse DE, Miller MR, Abadia-Cardoso A, Garza JC. 2014. Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in steelhead/rainbow trout. *Proc Roy Soc Lond B Biol Sci*. 281:20140012.

Piche J, Hutchings JA, Blanchard W. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. *Proc R Soc Lond B Biol Sci*. 275:1571–1575.

Plummer M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*. p. 20–22.

Pulido F. 2011. Evolutionary genetics of partial migration—the threshold model of migration revis(it)ed. *Oikos*. 120:1776–1783.

R Core Team. 2013. *R: a language and environment for statistical computing*. Vienna (Austria).

Reed TE, Waples RS, Schindler DE, Hard JJ, Kinnison MT. 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. *Proc R Soc Lond B Biol Sci*. 277:3391–3400.

Roff DA. 1994. The evolution of dimorphic traits: predicting the genetic correlation between environments. *Genetics*. 136:395–401.

Roff DA. 1996. The evolution of threshold traits in animals. *Q Rev Biol*. 1996:3–35.

Roff DA. 2011. Alternative strategies: the evolution of switch points. *Curr Biol*. 21:R285–R287.

Rundio DE, Williams TH, Pearse DE, Lindley ST. 2012. Male-biased sex ratio of nonanadromous *Oncorhynchus mykiss* in a partially migratory population in California. *Ecol Freshw Fish*. 21:293–299.

Satterthwaite WH, Beakes MP, Collins EM, Swank DR, Merz JE, Titus RG, Sogard SM, Mangel M. 2010. State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley. *Evol Appl*. 3:221–243.

Satterthwaite WH, Hayes SA, Merz JE, Sogard SM, Frechette DM, Mangel M. 2012. State-dependent migration timing and use of multiple habitat types in anadromous salmonids. *Trans Am Fish Soc*. 141:781–794.

Schlaepfer MA, Runge MC, Sherman PW. 2002. Ecological and evolutionary traps. *Trends Ecol Evol*. 17:474–480.

Schoener TW. 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science*. 331:426–429.

Shapovalov L, Taft AC. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Department of Fish and Game.

Sharpe DMT, Hendry AP. 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evol Appl*. 2:260–275.

Sloat MR, Fraser DJ, Dunham JB, Falke JA, Jordan CE, McMillan JR, Ohms HA. 2014. Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. *Rev Fish Biol Fish*.

Stearns SC. 1989. The evolutionary significance of phenotypic plasticity—phenotypic sources of variation among organisms can be described by developmental switches and reaction norms. *BioScience*. 39:436–445.

Thompson JN. 1998. Rapid evolution as an ecological process. *Trends Ecol Evol*. 13:329–332.

Thrower FP, Hard JJ. 2008. Effects of a single event of close inbreeding on growth and survival in steelhead. *Conserv Genet*. 10:1299–1307.

Thrower FP, Hard JJ, Joyce JE. 2004. Genetic architecture of growth and early life-history transitions in anadromous and derived freshwater populations of steelhead. *J Fish Biol*. 65:286–307.

Tomkins JL, Brown GS. 2004. Population density drives the local evolution of a threshold dimorphism. *Nature*. 431:1099–1103.

Tomkins JL, Hazel W. 2007. The status of the conditional evolutionarily stable strategy. *Trends Ecol Evol*. 22:522–528.

Tomkins JL, Hazel WN, Penrose MA, Radwan JW, LeBas NR. 2011. Habitat complexity drives experimental evolution of a conditionally expressed secondary sexual trait. *Curr Biol*. 21:569–573.

Tufto J. 2000. The evolution of plasticity and nonplastic spatial and temporal adaptations in the presence of imperfect environmental cues. *Am Nat*. 156:121–130.

Waples RS, Zabel RW, Scheuerell MD, Sanderson BL. 2008. Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific Salmon in the Columbia River hydropower system. *Mol Ecol*. 17:84–96.

Westley PAH. 2011. What invasive species reveal about the rate and form of contemporary phenotypic change in nature. *Am Nat*. 177:496–509.

Wilcove DS, Wikelski M. 2008. Going, going, gone: is animal migration disappearing. *PLoS Biol*. 6:e188.

Wilson AJ, Réale D, Clements MN, Morrissey MM, Postma E, Walling CA, Kruuk LEB, Nussey DH. 2010. An ecologist's guide to the animal model. *J Anim Ecol*. 79:13–26.

Wright S. 1934. An analysis of variability in number of digits in an inbred strain of guinea pigs. *Genetics*. 19:506–536.

Zimmerman CE, Reeves GH. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. *Can J Fish Aquat Sci*. 57:2152–2162.