

**The evolution, ecology, and restoration of anadromy in
rainbow trout/steelhead *Oncorhynchus mykiss***

by

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Abstract

Evolution can occur on ecologically relevant timescales, creating the potential for a bidirectional link between evolution and ecology. For example, migrating species provide important pulses of resources to recipient ecosystems, but are increasingly subject to intense selection due to ongoing global change. If heritable variation underlies migration, then contemporary evolution may increase non-migratory life histories, thereby increasing population persistence, but at the expense of important ecological processes. I examine contemporary evolution and its consequences of migration in an economically and ecologically important species, the resident and migratory ecotypes of the species *Oncorhynchus mykiss*.

In Chapter 2, I show that a stream barrier has driven the evolutionary loss of the migratory ecotype in only ~25 generations. I estimated the genetic contribution to variation in traits underlying the expression of migration and show that in the above-barrier population there has been a 30% decrease in expression of the migratory ecotype relative to the below-barrier population of origin. In Chapter 3, I examine the ecological consequences of this contemporary evolution. I show that the density decreases associated with loss of anadromy consistently had a greater effect on mesocosm ecosystems than the per-capita effects of the ecotypes. In Chapter 4, I use an analytical model to explore whether a population of *O. mykiss* would evolve toward greater residency in response to increased costs of migration. I find that evolution can rescue isolated populations; populations that persist are those that evolve in response to the changing selection regime on timescales that prevent population extinction. However, when conditions are restored to the pre-disturbance state, the rate of recovery of the migratory ecotype was unpredictable and generally slower than its loss. Finally, in Chapter 5 I review pathways for restoring the migratory ecotype, and how restoration of a life history may differ from restoring a species. Effective restoration of this life history will entail understanding the ecological and genetic mechanisms underpinning the expression of migratory behavior.

Together, these chapters highlight that migratory barriers can drive contemporary evolution of the non-migratory ecotype that increases population persistence, but decreases their ecological impacts. More generally, this research highlights the importance of incorporating evolutionary perspectives in management, conservation, and restoration.

Keywords: Partial migration; contemporary evolution; eco-evolutionary dynamics; threshold traits; salmon

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Chapter 1

Introduction

1.1 Contemporary evolution and the consequences for ecology and conservation

There is increasing appreciation that evolution can occur on timescales relevant to ecological processes (Endler 1986; Thompson 1998; Hendry and Kinnison 1999) and conservation decision-making (Stockwell *et al.* 2003; Rice and Emery 2003; Kinnison and Hairston 2007). While evolution historically was considered a process only observable after “the hand of time has marked the long lapse of ages” (Darwin 1859), long-term studies of wild populations have revealed natural selection can be quite strong (Endler 1986), capable of driving observable evolutionary change in a few centuries or less (“contemporary evolution”) (Thompson 1998; Stockwell *et al.* 2003). Further, contemporary evolution is likely increasing in prevalence due to intense selection by humans (Hendry *et al.* 2008; Darimont *et al.* 2009). Thus, it is becoming increasingly clear that study of ecological systems and management of threatened populations are incomplete without the integration of evolutionary perspectives.

Contemporary evolution has consequences for ecological processes (Schoener 2011). Phenotypes are not only the targets of selection, they are also the agents of ecological interactions, and thus an evolutionary change in phenotype may alter ecological processes. For example, local adaptation by consumers can alter ecological properties of the resource base (e.g. prey size, number, diversity) and ecosystem processes (Palkovacs and Post 2009; Harmon *et al.* 2009). Evolution can also influence demography (Wallace 1975; Kokko and López-Sepulcre 2007; Kinnison and Hairston 2007). In the absence of density dependence, population growth rate will increase if adaptations either increase birth rate or decrease death rate. Alternatively, in the presence of density dependence, adaptations that increase resource acquisition will

increase population size. Thus, the arena of ecology—community ecology, ecosystem ecology, population biology—is made up of dynamic players that both respond to and alter their own ecology.

Contemporary evolution also has consequences for how populations are managed and conserved. Biodiversity loss and contemporary evolution are affected by the same anthropogenic factors (Stockwell *et al.* 2003) and processes (i.e. decreased survival or birth rates relative to undisturbed conditions). When the strength of selection is strong and traits are heritable, evolution may rescue declining populations if adaptations occur rapidly enough to minimize extinction risk from demographic stochasticity (Gomulkiewicz and Holt 1995; Kinnison and Hairston 2007; Carlson *et al.* 2014). This is perhaps most evident where selective practices by fisheries, such as the targeting of larger individuals, induce rapid change in life history trade-offs (e.g. smaller, less fecund females) which reduce population growth rate and harvestable biomass (Conover and Munch 2002). However, affected populations are often slow to recover once fishing has ceased (Hutchings 2000; Hutchings and Reynolds 2004), because natural selection for the life histories favored before fishing (larger, later maturing fish) is often much weaker than selection induced by fishing (smaller, early maturing fish) (Enberg *et al.* 2009). Indeed, modern population management and conservation biology requires incorporating evolutionary perspectives (Stockwell *et al.* 2003; Kinnison and Hairston 2007) with traditional approaches to managing small and declining populations (Caughley 1994).

The objective of this thesis is to explore how populations adapt to anthropogenic disturbances on timescales relevant to conservation and management. Specifically, I investigate contemporary evolution of migration and its consequences in an economically and ecologically important species, the resident and migratory ecotypes of the species *Oncorhynchus mykiss*.

1.2 Anadromy and the salmonid system

Every year millions of salmon return to our rivers, supporting fisheries and controlling ecosystems (Schindler *et al.* 2003). The productive populations and iconic red flesh rich in essential fatty acids make salmon desirable fish for human harvest and terrestrial predators alike. Their large bodies mobilize sediment during nest digging (Moore *et al.* 2007) and upon death provide nutrients that fuel everything from bugs to bears (Cederholm *et al.* 1999). In fact, these various ecosystem functions are all linked by a single important life history: Anadromy. Migration to the productive marine environment enables individuals to quickly reach sizes (and thus fecundities) larger than they could achieve in freshwater. But migration is an inherently difficult behavior that is only becoming more so with ongoing global change (Wilcove and Wikelski 2008), including warming river temperatures (Martins *et al.* 2010), non-native predators (Carey *et al.* 2012), and physical barriers that impede migration (Januchowski-Hartley *et al.* 2013). Thus, long term security of

the important ecosystem services salmon deliver to aquatic, terrestrial, and human systems depends on the resilience of anadromy to increasing selection against migration.

Given the anadromous life history is under both environmental and genetic control (Dodson *et al.* 2013), might we expect the increasing costs of migration to prompt an evolutionary increase in the non-migratory life history that increases population persistence, but does so at the expense of the anadromous life history? And if so, what are the ecological consequences for stream ecosystems that lose anadromy, and how do approaches to restore this important life history differ from restoring a species? I address these questions in the following chapters by integrating lab and field experiments with statistical and analytical methods.

In Chapters 2 and 3 I explore the evolution and ecology of anadromy in a population of *Oncorhynchus mykiss* in Scott Creek, California, USA. First I establish that anadromy is a life history that has evolved over 100 years in response to a migratory barrier (Chapter 2). Next, I test whether the evolutionary loss of the anadromous life history leaves an ecological signature upon stream ecosystems, via either the per-capita effect of the loss of the anadromous life history, or mediated by associated density differences (Chapter 3). Findings from these previous two chapters motivate the following chapters' themes: integrating evolutionary perspectives into managing (Chapter 4) and restoring (Chapter 5) anadromous populations.

Anadromy is a locally adapted, evolved behavior that may be capable of responding on contemporary timescales to increased selection presented by migratory barriers. In Chapter 2 I use a population of steelhead (*Oncorhynchus mykiss*) introduced above a barrier waterfall in 1910 to test whether the alternative life-histories of freshwater residence and ocean migration represent a growth-dependent conditional strategy capable of responding to selection against migration. Common garden-raised offspring of parents from the introduced above-barrier population were 11% smaller and 31% lighter than offspring of parents from the below-barrier source population, as estimated with an 'animal model' (Wilson *et al.* 2010). Using a latent environmental threshold model (Buoro *et al.* 2012), I estimated that the mean size at which above-barrier fish switched between the resident and migrant strategy was 43% larger than below-barrier fish. As a result, above-barrier fish were 30% less likely to express the migratory strategy. These results demonstrate how rapid and opposing changes in growth rate and threshold size contribute to the contemporary evolution of a conditional strategy and indicate that migratory barriers may elicit contemporary evolution towards the resident life-history on timescales relevant for conservation and management of conditionally migratory species.

To test whether this case of contemporary evolution has ecological consequences I performed an instream mesocosm study using the common garden-raised juvenile resident (rainbow trout) and anadromous (steelhead) *O. mykiss* described in Chapter 2. In addition to different migratory strategies, resident and anadromous *O. mykiss* populations achieve different juvenile densities due to the greater fecundity of the anadromous ecotype. Therefore, I stocked mesocosms with either resident (above-barrier origin)

or anadromous (below-barrier origin) fish at high and low densities, with no-fish treatments as controls. I measured community and ecosystem properties over a two month study period and analyzed results with a Bayesian hierarchical model to assess the effects of ecology (presence/absence of fish) and evolution (population of origin and life history associated density). I found that density, regardless of population of origin, had the greatest effect on most ecosystem response measures, including mobilization of fine sediments, which in turn increase rates of algal accrual and carbon cycling. This is an important finding because it suggests juveniles of the anadromous ecotype indirectly alter ecosystem processes by virtue of the greater densities they can achieve relative to the resident ecotype.

Chapters 2 and 3 demonstrate that migratory life-histories can evolve on contemporary timescales and the alternative life-history strategies differentially influence ecosystem processes. In Chapter 4 I take a step back to consider how contemporary evolution may affect an anadromous population's response to, and recovery from, press and pulse disturbances. Using an ecogenetic individual-based model, I explore if and when conditional migration will evolve rapidly enough to prevent population extinction from various disturbance regimes (i.e. "evolutionary rescue," *sensu* Gomulkiewicz and Holt 1995). Simulated populations challenged with pulsed disturbances never went extinct and displayed no signs of an evolutionary response. Conversely, in scenarios similar to press disturbances populations evolved rapidly toward residency, particularly so as the costs of migration increased. The rate of evolution and population persistence were positively correlated with heritability of the trait underlying migration and carrying capacity of the population. When the disturbance was removed, populations recovered anadromy, but at unpredictable and generally slower rates than it took to be lost. This suggests there may be an asymmetry between the evolutionary loss and recovery of anadromy, a finding similar to those for life-history traits before and after a fishing moratorium in harvested fish populations (Dunlop *et al.* 2009; Enberg *et al.* 2009).

I conclude in Chapter 5 by reviewing what we know about the genetic and environmental controls of anadromy and how we can use this information to restore anadromy. I propose there are at least three pathways for restoration of anadromy to proceed: re-colonization, re-expression, and re-evolution. I conclude that while all pathways may operate simultaneously, they do so over different timescales (within generation vs. across (many) generations), and thus success of restoration projects need to be evaluated with an appreciation for the rates the underlying ecological and evolutionary processes are occurring.

Migratory populations are increasingly threatened by ongoing global change (Wilcove and Wikelski 2008); however, evolution of residency may allow populations to avoid extinction, but at the expense of the migratory life history. This thesis documents how a migratory barrier drove the evolutionary loss of anadromy in *Oncorhynchus mykiss* in only 100 years. As a consequence, juvenile population densities are smaller, resulting in a weaker effect on their stream ecosystem. Simulations suggest that if migratory connectivity with the marine environment was re-established, re-evolution of anadromy would proceed at a slow and unpredictable rate. Managing anadromous populations will require incorporating an evolutionary

perspective into the ecology and management of these populations.

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Chapter 2

Shifting thresholds: Contemporary evolution of migratory life histories in steelhead/rainbow trout, *Oncorhynchus mykiss*¹

2.1 Abstract

Expression of phenotypic plasticity depends on reaction norms adapted to historic selective regimes; anthropogenic changes in these selection regimes necessitate contemporary evolution or local extinction. Adaptation of conditional strategies following a change in the selection regime requires evolution of either the environmentally influenced cue (e.g. growth rate) or the state (e.g. size threshold) at which an individual switches between conditional strategies. 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. Common garden-raised offspring of parents from the above-barrier population were 11% smaller and 31% lighter than offspring of parents from the below-barrier source population. Using a novel analytical approach we estimate that the mean size at which

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above-barrier fish switch between the resident and migrant strategy is 43% larger than below-barrier fish. As a result, above-barrier fish were 30% less likely to express the migratory strategy. Our results demonstrate how rapid and opposing changes in growth rate and threshold size contribute to the contemporary evolution of a conditional strategy and indicate that migratory barriers may elicit evolution towards the resident life-history on timescales relevant for conservation and management of conditionally migratory species.

2.2 Introduction

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 an organism’s condition relative to some threshold value (Hazel and Smock 1990; Gross 1996). 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* can exhibit divergent migratory strategies, 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”. Larger smolts are more likely to survive in the marine habitat (Bond *et al.* 2008). 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 switch point size at which an individual smolts (Thrower *et al.* 2004; Paez *et al.* 2010; Buoro *et al.* 2012) and individual growth rate (Carlson and Seamons 2008). Indeed, recent evidence documents a genetic basis for a number of traits associated with smolting, including development rate (Nichols *et al.* 2006; Haidle *et al.* 2008; Easton *et al.* 2011; Miller *et al.* 2011) and smoltification (Nichols *et al.* 2008; Martínez *et al.* 2011). 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 life history variation.

Here we examine a rapid evolutionary shift in life-history expression in a population of *Oncorhynchus mykiss* translocated above a waterfall barrier (Pearse *et al.* 2009). This presents an opportunity to illuminate the evolutionary processes that drive rapid phenological shifts and the response of migratory salmonids to novel barriers (Waples *et al.* 2008). In a common garden experiment, we compare the expression of the migratory life-history strategy in two populations: an above-barrier population transplanted above a waterfall approximately 100 years ago 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 two related questions: 1. Is there adaptive phenotypic evolution to the novel above-barrier environment? 2. Does evolution of growth rate and/or switch point size contribute to the contemporary evolution of alternative migratory strategies? We find evidence for adaptive life history evolution, driven by evolution of both growth rate and switch point size. Thus, the phenotypic expression and genetic basis of migratory life history in *O. mykiss* can evolve on timescales relevant for conservation and management.

2.3 Methods

2.3.1 A historical transplant experiment

Scott Creek is a 70 km² coastal watershed located in central California approximately 100 km south of San Francisco. A waterfall on Big Creek, one of its prominent tributaries, presents a natural barrier to

anadromy approximately six river km from the creek mouth. Ongoing (Hayes *et al.* 2004; 2008; Bond *et al.* 2008) and historic 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 translocation origin (Anderson and Slatkin 2007).

2.3.2 Fish breeding and data collection

In November 2007, juveniles were collected via backpack electrofishing 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, range = 43-90 mm), all individuals were presumed to be less than one year old. In March 2010, 17 mature individuals total were crossed to create over 900 individuals in 9 total pure above- and below-barrier full-sibling families. Number of eggs for each female was enumerated and 20 haphazardly chosen eggs were selected to estimate mean egg diameter. Offspring were reared in common garden conditions for one year. The large number of related offspring allow for precise estimates of population differences provided the sampled parents are representative of their population of origin.

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, Colorado) by intraperitoneal injection with a 12 gauge needle, and small ($\approx 0.3 \text{ cm}^2$) caudal fin clips collected for genetic parentage and gender analysis. We recorded fork length (mm), mass (g), and "smolt condition" of each fish, after which individuals were allowed to recover for at least one week prior to further manipulation. We defined "smolt condition" as a binary trait based on physical appearance (Thrower *et al.* 2004; Nichols *et al.* 2008). "Non-smolts" 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.

2.3.3 Genotyping and parentage analysis

Small ($\approx 0.3 \text{ cm}^2$) 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 gender identification assay consisting of an autosomal and a Y chromosome-linked (Brunelli *et al.* 2008) gene probe was used to determine genetic sex of all genotyped fish. 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.

2.3.4 Seawater challenge and instream movement

We used two 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 x below-barrier and F1 backcrosses) made at the same time as the crosses presented here. First, we tested the hypothesis that non-smolts and smolts would survive equally when moved from freshwater to seawater. A subset of fish (127 non-smolts, 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 every 6-12 hours for 12 days. Second, we tested the null hypothesis that non-smolts 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 six weeks by three instream PIT tag readers and a smolt trap, 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 hours later ($n = 2$).

2.3.5 Statistical analysis

Cross-specific estimates of sex ratio, proportion of smolts, and growth rate (fork length and mass) were generated using generalized linear mixed models implemented in the Bayesian mixed model R package MCMCglmm (Hadfield 2010; R Core Team 2013). The variables 'sex' and 'smolt' were both modeled as binomial responses with 'cross' as a categorical fixed effect (above-barrier or below-barrier). Family

affiliation was included as a random effect to account for maternal effects and initial differences in rearing conditions. Models were run with priors for the family variance set to 1 with a degree of belief of 0.02; the prior on residual variance was fixed at 1. Alternative priors did not influence model estimates. Both models were run for 550,000 iterations, discarding the first 50,000, sampling every remaining 250th iterations to reduce autocorrelation.

A bivariate ‘animal model’ was used to estimate genetic influence on phenotypes and their covariance using relatedness of all individuals in the data set (Wilson *et al.* 2010). Cross-specific estimates for the growth rate parameters ‘fork length’ and ‘mass’ and the covariance between the traits (r_G) were generated using the phenotype of related individuals as a random effect to partition phenotypic variance (V_P) into additive genetic (V_A) and residual (V_R) components. However, estimates of V_A may be upwardly biased by factors (e.g. maternal effects) that could not be separated from the additive genetic effects. Weakly informative priors for the model were generated by equally partitioning the observed V_P in fork length and mass between the V_A and V_R components, with the prior belief parameter set to two. The model was run for 1,020,000 iterations, discarding the first 20,000, and then sampling every 250th iteration. We calculate both trait heritability ($h^2 = \frac{V_A}{V_P}$) and trait evolvability ($I_A = \frac{V_A}{\bar{X}^2}$); where \bar{X} is the mean phenotype), the latter of which is the expected proportional change in the trait under a unit strength of selection (Houle 1992; Hansen *et al.* 2011). We also report the genetic correlation between fork length and mass.

We examined the effects of sex, growth rate, and cross-type on incidence of smolting with a generalized linear (logistic regression) model, including all variables and two-way interactions. To include the effects of both continuous variables (fork length and mass) in model predictions, we estimated the length-mass relationship of the population, as $mass = a \cdot FL^b$. We determined nonlinear least-squares estimates of a and b using the `nls` function in R ($a = 3.73 \cdot 10^{-5}$, $s.e. = 3.46 \cdot 10^{-6}$; $b = 2.75$, $s.e. = 1.89 \cdot 10^{-2}$; $df = 915$). We used coefficient estimates from this model to illustrate the divergence between cross types in the size dependent process of smolting (figure 2.1 d). However, the underlying mechanisms that trigger the expression of the alternative strategies are not observable.

2.3.6 The Latent Environmental Threshold Model

To further investigate the evolution of the underlying threshold trait we utilized the Latent Environmental Threshold Model (LETM; Buoro *et al.* 2012). 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 threshold evolution. In the ETM, switch points are heritable and vary among individuals within a population. The ETM provides a mathematical framework to estimate the switch point; however, quantifying the necessary components is

not straightforward, as the proximate cue and switch point are often not observable. Recently, Buoro *et al.* (2012) addressed this by decomposing the ETM into “observable” and “non-observable” components; the former being the expressed phenotype and an observable environmental cue (e.g. body size), the latter being the switch point and the proximate environmental cue or liability trait (e.g. physiological state). The resulting LETM allows the estimation of genetic variance of the switch point and heritability of the conditional strategy from observations of the phenotypes and the related observable cue.

An additional assumption of the LETM relative to the ETM is that it assumes 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 proximate mechanisms influencing the expression of the phenotype (Tomkins and Hazel 2007). Although η_i is not observable, an observable proxy X_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 X_i with some residual error ε_i (normally distributed with mean 0 and standard deviation σ_η). In their review of alternative migratory strategies in salmonid fishes, Dodson *et al.* (2013) argue that body size is the most commonly (and adequately) reported proxy of the liability trait in salmonids. We use fork length as the observable proxy in the LETM.

Another constraint 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 Hazel and Smock (1990) and Roff (1994). Thus, the standard deviation of switch point 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; i.e., they are sampling thresholds in a multivariate normal distribution depending on the additive genetic relationship matrix and the additive genetic variance.

We apply the LETM framework to compare the switch point for migration between the two populations of *O. mykiss* from above and below the barrier waterfall. We extended this approach combining the analysis for the two populations and introducing three additional modeling constraints:

1. Both populations experienced the same environment (shared proximate cue η_i), given that this was a common garden experiment.
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 two populations separately confirmed that estimates of heritability are similar (results not shown).

3. The means of the threshold (μ_θ) may vary between the two populations.

2.3.7 MCMC conditions and diagnostics

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 non informative or weakly informative to ensure that all information comes from data. More details are available in Buoro *et al.* (2012). Results reported from models are posterior medians and 95% posterior probability intervals. Support for differences between crosses is reported as the percent of the posterior distributions in agreement with the direction of the difference observed.

2.4 Results

Nine families were produced: five pure above-barrier (three females crossed to four males) and four pure below-barrier (three females crossed to four 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 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, and genetic sex was assigned to 853. 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 50% male in above-barrier crosses (43% - 57%; figure 2.1 a), and 43% male in below-barrier crosses (37% - 49%; figure 2.1 a), with 93% 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 population. Frequency of smolts in above-barrier offspring was 54% (40% - 68%; table 2.1; figure 2.1 b), compared

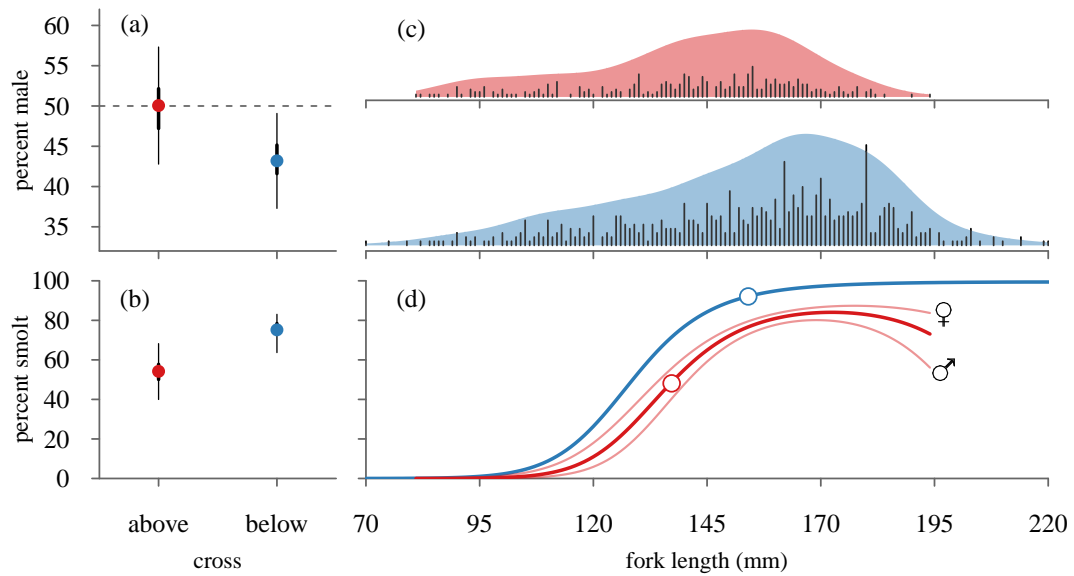


Figure 2.1: Comparison of above-barrier (red) and below-barrier (blue) offspring sex ratio (a), smolt incidence (b), observed fork lengths and data density (c), and predicted smolt incidence from logistic regression (see Methods) (d). In (a) and (b), solid and thin lines represent 50% and 95% posterior probability intervals. In (c), the shaded area represents data density. For (d), fish mass is estimated for a given fork length based on the length-mass relationship as described in the Methods. Open circles in (d) are the predicted incidence of smolts for the median posterior probability fork length 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).

to 75% (64% - 83%; table 2.1; figure 2.1 b) in below-barrier offspring. Support for the lower incidence of smolts in above-barrier offspring was 98% of the posterior distribution. A greater proportion of fish scored as 'smolts' survived the seawater challenge (58 of 71 smolts, 57 of 127 non-smolts, $\chi^2 = 23.9$, $df = 1$, $p < 0.001$; figure 2.2 a), 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 non-smolts (361 of 1038 smolts released, 50 of 541 non-smolts released; $\chi^2 = 136.9$, $df = 1$, $p < 0.001$; figure 2.2 b) and significantly more below-barrier smolts were detected moving downstream than above-barrier smolts (43% to 24%; $\chi^2 = 41.5$, $df = 1$, $p < 0.001$). Fork length (FL) positively influenced these elements of smoltification (GLM, survival: $FL = 0.032, 0.007, s.e., p < 0.001$; detection: $FL = 0.014, 0.006, s.e., p = 0.023$). However, size and smolt state are strongly positively correlated (figure 2.1 d), making it difficult to isolate their individual effects.

Fish from above-barrier crosses grew slower than fish from below-barrier crosses; above-barrier fish

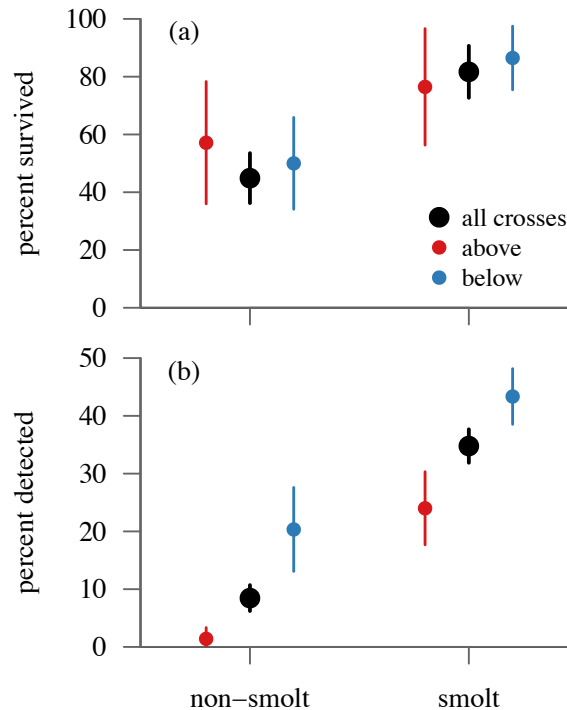


Figure 2.2: Relationships between different metrics of smoltification. ‘Smolt score’ and (a) the survival of individuals in seawater and (b) the probability of being detected migrating downstream. General assessment of our ‘smolt’ scoring criteria was independent of the effect of cross type, and include offspring of additional crosses (above-barrier \times below-barrier and F1 backcrosses) made at the same time as the crosses presented here (‘All crosses’, black circles; Methods for further details). Estimates for above-barrier (red circles) and below-barrier (blue circles) crosses are also presented. Error bars represent 2 s.e.).

had smaller mean fork length (137 mm; 116 - 158 mm) and mass (28.9; 14.7 – 42.1 g) than below-barrier fish (FL: 154 mm; 132 – 173 mm; mass: 43.5 g; 28.4 – 54.7 g) (table 2.1; figure 2.1 c). Probabilities that above-barrier fish were smaller in length and mass were 86.8% and 90.9%, respectively. For both metrics of growth, V_A accounted for a majority of the total V_P (FL: $h^2 = 0.73$; 0.41 – 0.96; mass: $h^2 = 0.74$; 0.42 – 0.96; table 2.1). Expected proportional changes in fork length and mass under a unit strength of selection were 2.9% (1.0 – 5.0%) and 15.7% (4.1 – 36.9%), respectively for the below-barrier population. There was strong statistical support for a positive genetic correlation between the two measures of growth rate ($r_G = 0.97$; 0.94 – 0.99). Logistic regression supported migration as a size-dependent process that is also influenced by cross and sex (figure 2.1 d).

Threshold fork length also differed substantially between the divergent populations. The above-barrier threshold was larger than the below-barrier threshold (difference estimated of 0.60; 0.28 - 0.91 with > 99% of support). The mean threshold for the above-barrier population is 43% (25% - 61%) larger than

Table 2.1: Estimates and Bayesian 95% credible intervals from the bivariate animal model for the observable environmental cues (fork length and mass) and switch point size. 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.

	fork length (mm)	mass (g)	switch point
Above	137 (116 - 158)	28.9 (14.7 - 42.1)	128 (121 - 135)
Below	154 (132 - 173)	43.5 (28.4 - 54.7)	112 (104 - 120)
P	86.8%	90.9%	> 99.9%
V_A	701 (268 - 1082)	286.1 (124.5 - 451.8)	—
V_P	954 (730 - 1174)	389.2 (293.3 - 471.1)	—
I_A	2.9% (1.0 - 5.0%)	15.7% (4.1 - 36.9%)	—
h^2	0.73 (0.41 - 0.96)	0.74 (0.42 - 0.96)	—
d	-1156 (-3247 - 922)	-3695 (-10552 - 1842)	1381 (674 - 2159)

the below-barrier population. In the LETM, the scale of the proximate cue is arbitrary and the link between proximate and observable cues is an undefined function (equation 3 in Buoro *et al.* 2012). For the sake of illustration, we scale the proximate cue to the observable cue such that the two cues share a 1:1 relationship (i.e., a one millimeter increase in fork length 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 fork length is 42 mm less than the mean fork length. In contrast, the mean threshold is only 9 mm less than the mean fork length in above-barrier offspring. Thus, a much larger proportion of the fork length and threshold size distributions overlap in the above-barrier population (figure 2.3), reducing expression of the migratory behavior.

2.5 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 *Oncorhynchus mykiss* isolated above a barrier waterfall for ~100 years. The migratory phenotype at age-1 was reduced by 30% (18 – 40%) in the above-barrier families, consistent with evolutionary adaptation to selection for the non-migratory strategy. This rapid evolution was driven by changes in growth rate as well as evolution of the underlying size threshold.

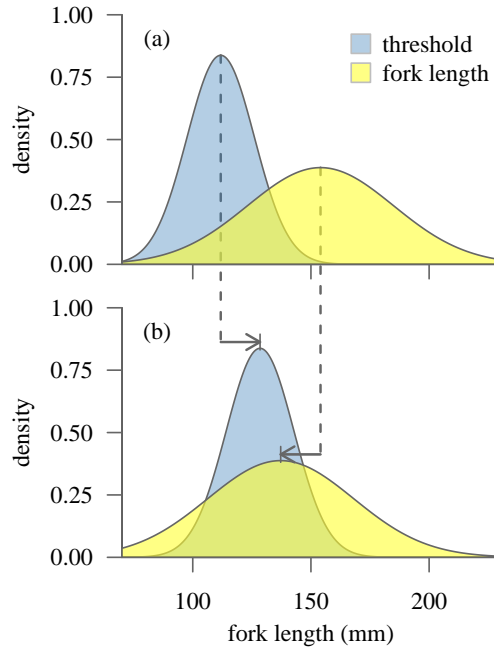


Figure 2.3: A comparison of distributions of thresholds (in blue) and fork lengths (in yellow) for (a) the below-barrier source population, and (b) the derived above-barrier population. Dashed lines and arrows indicate the direction and magnitude of the response to selection against downstream migration in the above-barrier population.

These changes in fish length represent a rapid evolutionary rate of change of 1,156 ‘Darwins’ (the natural logarithm of the trait values in each population, differenced, and divided by time the populations have been isolated in millions of years; Haldane 1949). The estimated fork length threshold value changed at a rate of 1,381 Darwins. Both rates are similar to those observed for populations introduced to novel habitats (Hendry *et al.* 2008). More generally, our results indicate that migratory behavior has a heritable genetic basis that can evolve rapidly.

The rapid evolutionary change in the frequency of the migratory life history strategy is mediated by a shift in the distribution of the switch point relative to the cues that trigger migration (figure 2.3), 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 proximate cue (Wright 1934; Falconer 1965) or the switch point (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 switch point and proximate cue (body size) to identify evolutionary shifts in their distributions (figure 2.3). Simultaneous evolution

of these two aspects enabled shifts in migratory behavior (figure 2.1 b).

This study represents a relatively rare example of the evolution of switch points (Roff 2011). Genetic variation has been reported in the switch point underlying the expression of many threshold traits, including male morphologies (Moczek 2003; Buzatto *et al.* 2012), reproductive strategies (Piche *et al.* 2008), and migratory tactics (Beakes *et al.* 2010; Paez *et al.* 2010). However, there are few examples of the switch point trait actually responding to selection in a natural population (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 non-fighter morph, Tomkins *et al.* (2011) were able to induce an evolutionary increase in the mean size at which males express the alternative fighter morph. Thus, switch points can evolve over a few generations when faced with strong directional selection.

Body size of salmonid fishes is a key trait that is heritable and that selection acts upon. Carlson and Seamons (2008) found the median estimates for length-at-age and mass-at-age heritability to be 0.29 (range -0.10 to 0.73) and 0.32 (range 0 to 1), respectively. In the present study, above-barrier offspring reared in a common-garden environment were 11% and 31% smaller than below-barrier offspring in fork length and mass, respectively, and heritability was high for both traits (table 2.1). 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 2.1 d). 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. However, while our results suggest the frequency of the migratory phenotype is significantly reduced in the above-barrier population, the incidence of migrants (54.2%) is still quite high. Why would the migrant phenotype remain so common? One possibility is 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 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 one year of growth (Hayes *et al.* 2008), well below the mean threshold size estimated here.

Gender-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 occurs 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 fork lengths in figure 2.1 d). 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 (S. Hayes; pers. obs.), 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, while males and females were found in equal proportion in the above-barrier families, females significantly outnumbered males in progeny of below-barrier parents (figure 2.1 a). 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. For instance, 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, with a limited number of parents represented in the breeding design, may not be representative of all 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), 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 migration is highly heritable ($h^2 = 0.91$; $s.d. = 0.09$) and can evolve rapidly in response to selection. On the other hand, *O. mykiss* isolated for many decades still produce some smolts with the capacity to osmoregulate in seawater (see also Thrower *et al.* 2004). This suggests conservation of physiological and behavioral components of smoltification in isolated *O. mykiss* populations via cryptic 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. 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 variation interact to promote rapid adaptation to ongoing environmental change.

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Chapter 3

Density-mediates effects of steelhead/rainbow trout on stream ecosystems²

3.1 Abstract

Recent evidence for contemporary evolution has generated interest in how shifts in consumer phenotype may directly affect prey communities. However, ecological effects could be the result of changes in population density associated with phenotype divergence, an eco-evolutionary pathway that remains understudied. Previously we found that stream barriers have driven contemporary evolutionary loss of the migratory ecotype of *Oncorhynchus mykiss* in a coastal California watershed. Here we test whether density or migratory ecotype mediates these changes. We used a mesocosm with juvenile *O.mykiss* produced from above- and below-barrier parents, to compare the relative importance of density- vs. phenotype-mediated effects on stream ecosystems. High density treatments consistently had a greater effect than *O. mykiss* ecotype, including decreasing invertebrate biomass and diversity, and increasing rates of sediment export, leaf litter break down, and algal accrual. Thus, differences in density, not the per-capita effect of the ecotype itself, results in a divergence in community structure and ecosystem processes. Field surveys of *O.mykiss* densities indicated that above-barrier populations were associated with a 82% reduction in

²A version of this chapter is in review as:
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juvenile density compared to below-barrier populations. If the observed density differences are fully or partly due to evolution, these results suggest density-mediated effects could potentially be an important eco-evolutionary pathway shaping stream ecosystems.

3.2 Introduction

There is increasing appreciation that ecology not only shapes the evolutionary trajectory of populations and species (Endler 1986; Schluter 2000), but that evolution also shapes ecology (Pelletier *et al.* 2009; Schoener 2011). This interaction has the potential for creating an eco-evolutionary feed-back loop if the ecological response results in further evolutionary change (Post and Palkovacs 2009). Contemporary evolutionary responses to natural and anthropogenic selection may generate ecological consequences across a range of organizational levels (Bailey 2010). Adaptation to local conditions by populations that occupy different habitats, particularly in foraging traits which maximize extraction of resources, can reciprocate back to the community and ecosystem level (Kokko and López-Sepulcre 2007; Ezard *et al.* 2009; Post and Palkovacs 2009). However, evolutionary shifts in adaptive traits can alter population equilibrium density (Kokko and López-Sepulcre 2007), which could drive ecological responses. For instance, selection that acts on demographic traits such as survival, recruitment (Pelletier *et al.* 2007) or dispersal (Hanski and Mononen 2011) can alter population dynamics, in some cases to a greater degree than the ecological and environmental drivers alone (Hairston *et al.* 2005; Pelletier *et al.* 2007; Ezard *et al.* 2009). This indirect pathway—where evolutionary change of the phenotype of the consumer influences its population size, with cascading effects on lower trophic levels and ecosystem processes—has been alluded to in the literature (Hendry *et al.* 2011), but empirically remains largely unexplored (Bassar *et al.* 2010; 2012). Here we examine the impacts of contemporary ecotype divergence on ecosystems through changes in per capita effects and/or density.

The top-down role fish play in structuring aquatic food webs is well studied (Power *et al.* 1996); however, the sensitivity of this ecological role to contemporary evolutionary divergence is less well understood. Recently, research on a few well-studied examples of ecotype divergence has experimentally tested for eco-evolutionary effects of fish on community structure (Harmon *et al.* 2009; Palkovacs and Post 2009; Bassar *et al.* 2010). These studies have generally found that adaptive divergence in consumers can leave ecological signatures on aquatic ecosystems via top-down control, ecosystem engineering, and/or nutrient excretion. For example, landlocked populations of alewife (*Alosa pseudoharengus*) exhibit narrower gape width and smaller gill raker spacing relative to the anadromous populations that founded them in the past 300-5000 years (Palkovacs *et al.* 2008; Post *et al.* 2008; Palkovacs and Post 2008). In a mesocosm experiment, Palkovacs and Post (2009) found anadromous alewives selectively preyed on large-bodied zooplankton reducing total biomass, body size, diversity, and species richness relative to the

less size-selective predation of landlocked alewife. Similarly, in a study of Trinidadian guppies (*Poecilia reticulata*), Bassar *et al.* (2010) found the phenotypes and population densities associated with low- and high-predation habitats affected ecosystem processes, with high density treatments increasing benthic organic matter, biomass-specific gross primary production, and total flux of dissolved nitrogen. In this case phenotype divergence and population dynamics are intimately coupled, as the predation that regulates guppy density also selects for earlier age at maturity, greater reproductive effort, and smaller, more numerous offspring (Reznick *et al.* 1990). However, many of these traits also exhibit phenotypic plasticity in response to demographic, social, and maternal environments and resource availability, sometimes equal in magnitude to evolved differences (Rodd *et al.* 1997; Bashey 2006). This highlights a challenge of all eco-evolutionary experiments to date involving fish: the ecological effects due to phenotypic differences in field-collected specimens cannot isolate evolutionary differences from plastic responses to the maternal environment or the environment from which they were collected.

Partially migratory fishes provide a potentially important system in which to compare the trait- and density-mediated consequences of evolutionary divergence. For example, tradeoffs between foraging efficiently in low-growth freshwater environments and accessing high-growth marine habitats may lead to adaptive divergence in resident and anadromous traits (Bell and Andrews 1997). In salmonids, the transition from freshwater to seawater requires a morphological, physiological, and osmoregulatory transformation called smoltification. In addition, anadromous individuals experience strong size-selective mortality upon ocean entry (Bond *et al.* 2008). Adaptations to the energetically costly demands of smoltification and selection for size-at-age may explain the observation that anadromous juveniles have higher consumption rates at the expense of lower growth efficiency, relative to their resident counterparts (Morinville and Rasmussen 2003; Sloat and Reeves 2014). Different fish ecotypes could also impact ecosystems differently via differences in the densities they can achieve. Due to the dramatically larger sizes and much higher fecundity of migratory individuals, potential offspring density of the migratory ecotype can greatly exceed that of the resident ecotype when costs of migration are minimized (e.g. short migration distance, low elevation gain) (Hendry *et al.* 2003). As a result, where migration is favored, but impossible due to migration barriers, offspring density can be lower than expected due to the lost reproductive potential of the migratory ecotype (Bohlin *et al.* 2001).

The anadromous and resident ecotypes of *Oncorhynchus mykiss* present an ideal system to study ecological consequences of contemporary evolution. Isolation of formerly anadromous steelhead above impassible barriers, either by fish transplantation or construction of dams, has led to the contemporary parallel evolution of genetically distinct resident rainbow trout populations across the species' range (Clemento *et al.* 2009; Pearse *et al.* 2014). Genetic divergence of above barrier populations is the result of selection acting against traits associated with anadromy. As these barriers only allow one-way (downstream) gene flow, populations persist only where there is variation in individual propensity to migrate. To the extent that there is a heritable genetic basis underlying this variation, populations

above barriers can be expected to rapidly evolve reduced expression of the juvenile migrant phenotype (Thrower *et al.* 2004; Phillis *et al.* 2014) and exhibit smaller equilibrium population density. Understanding the ecological consequences of selection against anadromy requires distinguishing between two potential causal pathways, the shift in phenotype (migrant to resident) and the associated reduction in density.

Here we use the resident and migratory forms of the species *Oncorhynchus mykiss* to test the ecological consequences of contemporary ecotypic divergence against density differences that may emerge from ecotype divergence (figure 3.1). We take advantage of a historical translocation of *O. mykiss* above a barrier waterfall in the coastal watershed of Scott Creek, California (Pearse *et al.* 2009; Hayes *et al.* 2012). Following their introduction in 1910, genetically distinct, resident populations have rapidly diverged from the below-barrier anadromous form (Pearse *et al.* 2009), including evolving a lower propensity to express traits associated with the migratory phenotype (Phillis *et al.* 2014). We use juvenile *O. mykiss* produced from crosses of above- and below-barrier parents in a mesocosm experiment to ask two questions: 1) What is the impact of *O. mykiss* density compared to *O. mykiss* ecotype on stream communities and ecosystems? 2) How do these effects compare to the presence or absence of fish?

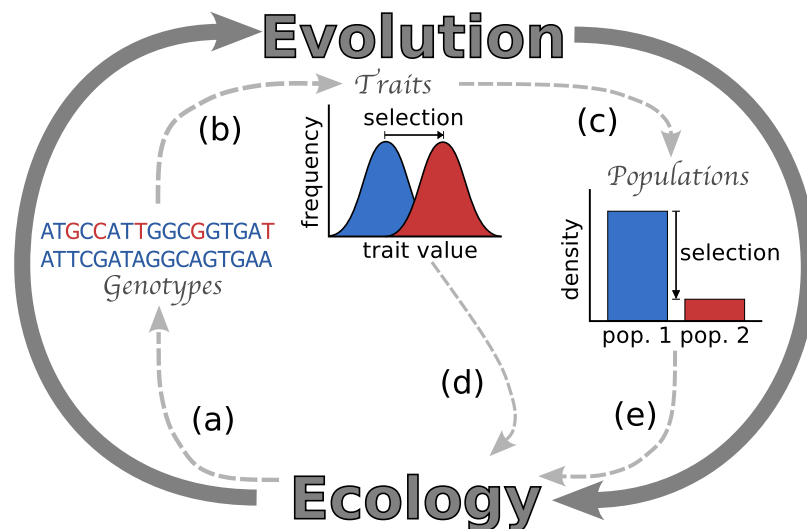


Figure 3.1: Ecological and evolutionary processes can occur on overlapping timescales producing the potential for eco-evolutionary dynamics. (a) Pearse *et al.* (2009) have previously shown that *O. mykiss* above impassable barriers in the Scott Creek watershed have genetically diverged from the below-barrier source populations in only 100 years (~25 generations); a pattern of divergence that has recently been documented in 21 populations in 10 watersheds in California and Oregon (Pearse *et al.* 2014). (b) Subsequently Phillis *et al.* (2014) demonstrated that *O. mykiss* of above-barrier genetic origin have diverged in several heritable traits, including reduced growth rates and an increase in the threshold size required to smolt, leading to an overall reduction in rates of anadromy. Here we test whether (c) population densities are reduced in the above-barrier populations following the loss of anadromy (figure 3.2), and if an ecological signature can be detected from (d) the divergence in the traits associated with anadromy (figures 3.3 and 3.4), or (e) a change in population density (figures 3.3 and 3.4).

3.3 Methods

3.3.1 *O. mykiss* Density field survey

We performed 26 snorkel surveys in the 1 km reaches above and below two barrier waterfalls in the Scott Creek watershed (104 surveys total) to estimate *O. mykiss* density. Surveys occurred in small off channel areas (0.56 to 23.92 m²) characteristic of young-of-year *O. mykiss* rearing habitat. Surveys were performed early in the summer to estimate initial young-of-year densities prior to the onset of severe over-summer mortality (Hayes *et al.* 2008; Sogard *et al.* 2012). We used a hurdle model (Zeileis *et al.* 2008) to 1) estimate the probability of encountering a fish in a surveyed area above and below the barrier waterfall on each tributary (zero model with binomial errors and a logit link function), and 2) estimate the number of fish in cases where fish were observed (count model with negative binomial errors and a log link function).

3.3.2 Fish origin

To test the ecological effects of contemporary evolution, it was important to isolate the genetic differences between the two ecotypes from differences due to the divergent environments anadromous and resident mothers experience. To minimize these maternal effects we first captured juveniles above and below the barrier waterfall on the Big Creek tributary of Scott Creek, CA and raised them to maturity in Big Creek Hatchery, under common conditions. Reproductively mature individuals were then used to make pure crosses (i.e. within-ecotype), and offspring of these crosses were similarly raised in common garden conditions at the hatchery for three months before a subset of fish were haphazardly selected for outplanting into the mesocosms (length = 46 mm, 3.6 s.d.; mass = 1.07 g, 0.29 s.d.). On average, the below-barrier genetic origin fish were 1.6 mm longer (-0.2-3.4 95% C.I., $t = 1.73$, d.f. = 55.97, $p = 0.089$) and 0.25 g heavier (0.1-0.4 95% C.I., $t = 3.64$, d.f. = 58, $p = 0.001$) than the above-barrier genetic origin fish. These differences are likely early evidence of divergent growth rates between the genetic stocks; (Phillis *et al.* 2014) found that above-barrier genetic origin fish from these crosses were 11% shorter and 31% lighter than below-barrier genetic origin fish at the end of one year of growth in common garden.

3.3.3 Mesocosm experiment

Flow-through mesocosms were constructed by cutting three ~10 x 40 cm holes in both the upstream and downstream ends of 0.6 m² plastic totes and covering them with ~1 mm insect screening. The

mesocosms were secured in two stream side channels adjacent to the hatchery on the Big Creek tributary of Scott Creek. Gravel collected from the study area was mixed to homogenize sediment size and the initial invertebrate community before redistributing $\sim 0.038 \text{ m}^3$ to each mesocosm. Five cobble-sized rocks were selected from the study area, macro fauna dislodged by hand, and added to each mesocosm for habitat complexity. Mesocosms were situated in five blocks of five (total number of mesocosms = 25), standardized at approximately equal depths ($\sim 14 \text{ cm}$), and left in the creek for 33 days (May 27 – July 1) to establish the algal and benthic invertebrate communities prior to the introduction of fish into the mesocosms. Each block consisted of one no fish treatment (“control”) and four fish treatments stocked at low and high density with progeny of either below- or above-barrier genetic origin. Estimates from the count component of the hurdle model were then used to inform the number fish to use in low (1 fish) and high (5 fish) density mesocosm treatments. After adding fish, wire mesh (20 gauge, 2.54 cm opening, galvanized steel) was secured to the top of all mesocosms to allow terrestrial infall of insects, but exclude piscivorous predators. Over the course of the experiment, densities were maintained by removing mortalities, and replacing them with new fish from the appropriate genetic origin. The experiment was allowed to run for 42 days (July 2 – August 13), over which time we monitored ecological and environmental response variables in the mesocosms including algal accrual, leaf litter decay, benthic invertebrate abundance, nutrients, fine benthic organic matter (FBOM), and silt cover. For each mesocosm, stream flow within and canopy cover above, estimated with a handheld densiometer, were estimated for inclusion as covariates in the multilevel model.

Algal accrual

We quantified algal accrual on 48 by 48 mm square unglazed ceramic tiles. Eight tiles were placed in each mesocosm at the beginning of the experiment and then removed in pairs after 10, 20, 31, and 41 days. Algae from the tiles was recovered by scrubbing with a small brush and water and filtering a known fraction of the filtrate through 47 mm GF/F silica filters (pore size 0.7 μm). Filters were frozen and later solubilized in methanol and the concentration of chlorophyll-a was determined with fluorometry (Hauer and Lamberti 2007). A linear relationship between tile soak time (days) and algal biomass consistently fit better than an exponential relationship. Further, estimates of algal accrual rate using only the tiles from day 41 converged with rates estimated from the slope of the linear relationship over all dates. Thus, for simplicity we use estimated algal accrual rates from tiles collected on day 41 as our index of algal biomass accrual.

Leaf litter breakdown

To quantify leaf litter breakdown rates in each mesocosm we used coarse mesh bags containing ~5 g dry red alder leaves. Eight leaf litter bags were deployed at the beginning of the experiment and then removed in pairs after 12, 21, 32, and 42 days. Data inspection revealed inconsistent decay rates over time, perhaps due to interference from silt deposition or differential breakdown rates between tissue and veins. Thus, we estimated leaf breakdown rate (k) according to exponential decay from litter bags collected on day 42 (Hauer and Lamberti 2007).

Benthic invertebrates

We collected two benthic invertebrate samples from each mesocosm at the end of the experiment using a small Surber sampler (0.02 m² in area, mesh size = 0.5 mm). Paired samples were later pooled and invertebrates were identified to at least family level, and where possible functional feeding group and vulnerability to predation by juvenile *O. mykiss* was categorized. The first 20 individuals from each unique taxa were measured for total length, which was converted to mass using length-weight regressions (Benke *et al.* 1999; Sabo *et al.* 2002). We calculated the Simpson diversity index (D) using the `vegan` package (Oksanen *et al.* 2013) in R (R Core Team 2013).

Nutrients

We sampled nutrients in each mesocosm prior to fish being added (day 0) and after 11, 21, 32, and 42 days. Water samples for nutrients were collected in acid-washed polyethylene bottles, filtered through a pre-ashed 47 mm GF/F silica filter (pore size = 0.7 μ m), and frozen for subsequent analyses. Nitrate, phosphate, and ammonium concentrations were quantified at the University of California, Santa Barbara with a QuikChem 8000 flow injection analyzer. There was not a consistent temporal pattern in the data, thus we estimated proportional change in nutrients between the beginning (day 0) and end (day 42) of the experiment.

Fine benthic organic matter

We collected fine particulate matter in each mesocosm at the end of the experiment by agitating the sediment within a PVC tube (2.5 cm radius, to a depth of 7 cm) and filtering the suspended sediment through a 47 mm GF/F silica filter of known weight (pore size = 0.7 μ m) and weighing the filter again after drying at 80 C for at least 24 hours. Filters were combusted at 550 C and weighed again to quantify

fine benthic organic matter (FBOM).

Silt cover

At the end of the experiment we visually surveyed the proportion of substrate covered in silt within each mesocosm. A point transect of seven systematically spaced observations was haphazardly placed in the upstream, middle, and downstream third of the mesocosm for 21 observations total. At each point observation substrate was scored as either covered (1) or not covered (0) in silt.

3.3.4 Multilevel model

We used a Bayesian approach to fit multilevel models that contrast the ecological signature of evolutionary divergence with the ecological signature of going from a fish absent to fish present state. This approach has the advantage of, in a single model, simultaneously contrasting the effects of fish, density, and genetic origin on the mesocosm ecosystem. The model thus quantifies the impact of density and genetic origin relative to the effect fish have on the mesocosm ecosystem. For benthic invertebrate (biomass and diversity), organic matter, algal accrual, and leaf decay, observed data y_i in mesocosm i is drawn from a log-normal distribution, with a mean μ_i and variance σ^2 :

$$y_i \sim \log \mathcal{N}(\mu_i, \sigma^2) \quad (3.1)$$

The mean response in a mesocosm (μ_i) is estimated from the linear function:

$$\mu_i = \beta_k + \beta_c * canopy_i + \beta_f * flow_i + \phi_i * fish_i \quad (3.2)$$

where β_k is the intercept for block k , and β_c and β_f are coefficients for the covariates canopy and flow, respectively. ϕ_i is a binary variable for fish presence (1) or absence (0) such that $fish_i$ is the effect of fish at the different levels of origin ($origin_i$; above-barrier = 0, below-barrier = 1) and density ($density_i$; low = 0, high = 1) estimated from the linear function:

$$fish_i = \gamma_{f_k} * \phi_i + \gamma_o * origin_i + \gamma_d * density_i \quad (3.3)$$

Here γ_{f_k} is the effect of fish in an above-barrier, low density mesocosm (defined here as the “base case”) and γ_o and γ_d are the effects of modifying origin (below-barrier genetic origin) and or density (five

fish per mesocosm) from the base case. For nutrient data, y_i in equation (3.1) was drawn from a normal distribution. For silt cover data, y_i in equation (3.1) was drawn from a binomial distribution with 21 trials, and $\text{logit}(\mu_i)$ was modeled in equation (3.2). In both cases equation (3.3) remained unchanged.

Joint posterior probability distributions for the parameters of interest were obtained by Markov chain Monte Carlo (MCMC) sampling using JAGS implemented in R with `rjags` (Plummer 2003). Three MCMC chains were initiated from parameter values drawn randomly from the range of the uninformative priors and allowed to map the parameter space for 2,010,000 iterations. The first 10,000 iterations of each chain were discarded as burn-in to avoid bias of initial chain conditions, after which every 250th sample was retained to reduce autocorrelation between MCMC samples. Visual inspection of all models showed evidence of well mixed stationary chains with low levels of autocorrelation; Gelman and Rubin's potential scale reduction factor (Gelman and Rubin 1992; Gelman *et al.* 2003) was 1 for all parameters indicating output from chains were indistinguishable.

We present the mean and 95% highest posterior density Bayesian credible interval from posterior probability distributions for the coefficients of interest (γ_f , γ_o , and γ_d) after accounting for the effect of the base case. Posterior distributions were exponentiated for all response variables with the exception of nutrient data which were drawn from a normal distribution in equation (3.1) and their coefficients are presented on the original scale. For exponentiated posterior distributions, coefficient estimates of 1/2 and 2 are effects of equal size but represent a decline and increase in the response variable, respectively. The proportion of a posterior distribution, P , that is lower (alternatively, higher) than 1 is the posterior probability that the treatment decreases (e.g. $P_{trt < bc}$; alternatively, increases $P_{trt > bc}$) the response variable relative to the base case.

3.4 Results

3.4.1 *O. mykiss* Density field survey

The low and high densities used in the mesocosm experiment were similar to those observed in the above and below-barrier genetic origin source populations. Densities observed below the barriers ranged from 0 to 11.43 fish·m⁻²; above the barrier densities ranged from 0 to 1.56 fish·m⁻² (figure 3.2). Whether a survey location was above or below a barrier significantly predicted the probability of observing fish (zero model, barrier = 2.4, 1.36 - 3.44 95% CI; $p = 5.9 \cdot 10^{-6}$), but area and tributary did not (area, $p = 0.72$; tributary, $p = 0.32$). Location above or below the barrier and surveyed area both significantly predicted counts when fish were present (count model, barrier = 1.72, 1.11 - 2.33 95% CI, $p = 3 \cdot 10^{-8}$; area = 0.04, 0 - 0.08 95% CI, $p = 0.043$), but tributary did not ($p = 0.89$). For a given sized area, there were 5.61

times more fish in surveys below the barrier waterfalls compared to above the barrier.

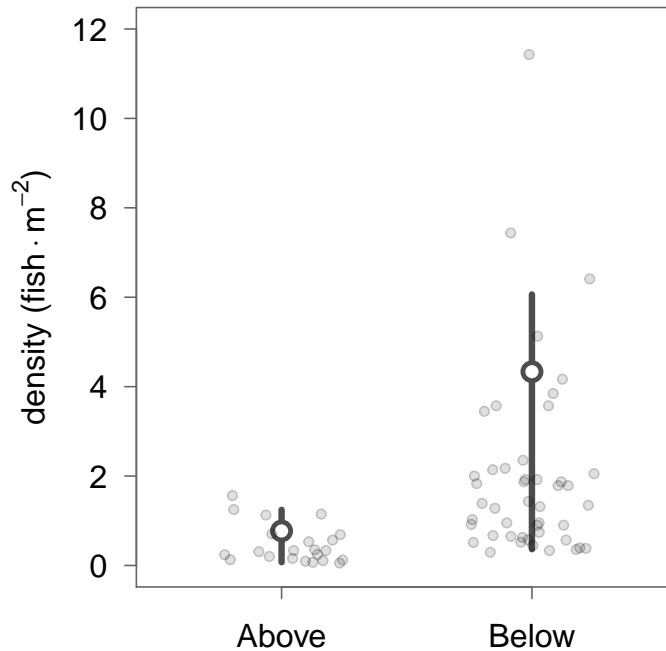


Figure 3.2: Predicted fish density (large open circles) and observed 5th and 95th quantiles (solid lines) above and below two barrier waterfalls in the Scott Creek watershed where fish were present ($n = 68$ of 104 surveys; small grey circles).

3.4.2 Mesocosm experiment

Fish

The presence of fish in mesocosms had an effect on several ecological and environmental response variables (figure 3.3). Mesocosms without fish had 2.1 times greater total invertebrate biomass ($P_{ctrl>bc} = 0.97$) and 1.15 times greater benthic invertebrate diversity (Simpson's D) ($P_{ctrl>bc} = 0.93$) than mesocosms with a single above-barrier genetic origin fish (figure 3.4, table A.1). Similar patterns were seen for biomass of predator, prey, *O. mykiss* vulnerable, and invulnerable invertebrates (figure A.1, table A.1). Mesocosms without fish also had 1.35 times greater fine benthic organic matter ($P_{ctrl>bc} = 0.85$) and were 1.93 more likely to have silt covering the substrate ($P_{ctrl>bc} = 0.88$). No effect of fish was detected for leaf litter decay rate, algal accrual rate, or relative change in nitrate, phosphate, or ammonium concentrations, as

all mesocosms without fish had posterior distributions centered around one for these variables (or zero in the case of the nutrient data), suggesting they were indistinguishable from the above-barrier, low density “base case” (figures 3.4 and A.1, table A.1).

Origin

There was some evidence that recently diverged *O. mykiss* impact stream ecosystems differently. Below-barrier genetic origin fish exerted less top-down control on the benthic invertebrates than above-barrier genetic origin fish (figure 3.3). Invertebrate biomass was 1.23 times greater in below-barrier genetic origin mesocosms than above-barrier genetic origin mesocosms, specifically in invertebrate prey taxa such as midges in the family Chironomidae (figure 3.4, table A.1), however support for these effects was weak (total invertebrate biomass, $P_{o>bc} = 0.83$, prey invertebrate biomass, $P_{o>bc} = 0.85$). Below-barrier genetic origin mesocosms also had 1.25 times greater silt cover ($P_{o>bc} = 0.81$); conversely benthic organic matter in the mesocosms was 0.78 times less than the base case ($P_{bc>o} = 0.91$). There was little support for an effect of genetic origin on the other response variables (algal accrual rate, invertebrate diversity, nutrients, and leaf litter decay) (figures 3.4 and A.1, table A.1).

Density

High density mesocosms were markedly different than mesocosms with only a single fish (figure 3.3). At high densities, fish suppressed invertebrate biomass and diversity (figure 3.4, table A.1). Total invertebrate biomass in high density treatments was less than half (0.43) that of the low density base case ($P_{d<bc} > 0.99$). Similar patterns were seen for predator, prey, vulnerable, and invulnerable invertebrate biomass (figure A.1, table A.1). Benthic invertebrate diversity (Simpson’s D) was only 0.91 times that of the base case ($P_{d<bc} = 0.95$). Algal accrual rate was 1.2 times higher in high density mesocosms as would be predicted in a trophic cascade, but there was high uncertainty in this estimate ($P_{d>bc} = 0.81$). Despite the reduction in invertebrate biomass, including the shredder functional group (data not shown), rates of leaf decay were 1.27 times higher in high density mesocosms ($P_{d>bc} = 0.97$). One explanation is reduced silt cover on the leaf packs, making them more accessible to shredding invertebrates; high density mesocosms had only 0.14 times the silt cover as base case mesocosms ($P_{d<bc} > 0.99$). Fine benthic organic matter was also 0.63 times lower than the base case ($P_{d<bc} = 0.99$). While density had a clear effect on many response variables, there was little support for density altering nutrient cycling (figure A.1, table A.1).

All fish in low density treatments survived the duration of the experiment, regardless of genetic origin. However, in high density treatments, mortality in the above-barrier genetic origin mesocosms was higher than in all but one below-barrier genetic origin mesocosm (4 and 2 median mortalities per mesocosm of

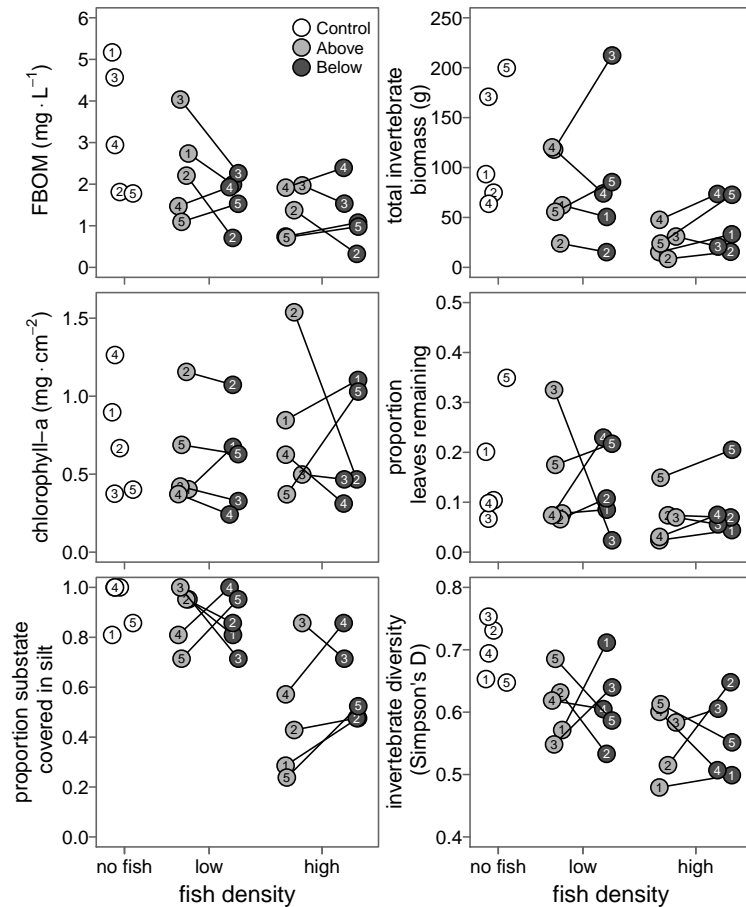


Figure 3.3: Measured response variables in each mesocosm for control treatments (white circles) and above- (grey circles) and below-barrier (black circles) genetic origin fish at low and high density. Numbers correspond to blocks; within a block the origin treatments for a density are connected by a line.

above and below-barrier genetic origin, respectively; figure A.2). Mortalities occurred on average every 12.8 days in high density above-barrier mesocosms compared to 35.9 days in below-barrier mesocosms; however, this difference was only marginally significant ($p = 0.09$).

3.5 Discussion

Our results suggest juvenile *O. mykiss* density alters stream communities and ecosystems to a far greater degree than the per capita effects of contemporary evolution. Higher densities of fish increased the effects of fish in the mesocosms in most cases. Mesocosms with high densities of *O. mykiss* had lower invertebrate diversity and biomass, silt cover, and fine benthic organic matter, and higher leaf litter decay

and algal accrual rates than low density mesocosms. Conversely, in most cases the per capita effect of fish did not differ between the above- and below-barrier genetic origin treatments. We also observed different juvenile *O. mykiss* densities associated with the resident and migratory ecotypes. Above barrier waterfalls in the Scott Creek watershed, juvenile *O. mykiss* were present in fewer surveyed sites and at significantly lower densities than were observed in the below-barrier sites, consistent with predictions from life-history theory and findings from other salmonid systems (Bohlin *et al.* 2001). Combined, the field and mesocosm results highlight that juvenile density can be greatly reduced in populations that have lost the migratory ecotype, and the lower equilibrium density may indirectly constrain the effects these fish can have on freshwater ecosystems (Figures 3.4 and 3.4).

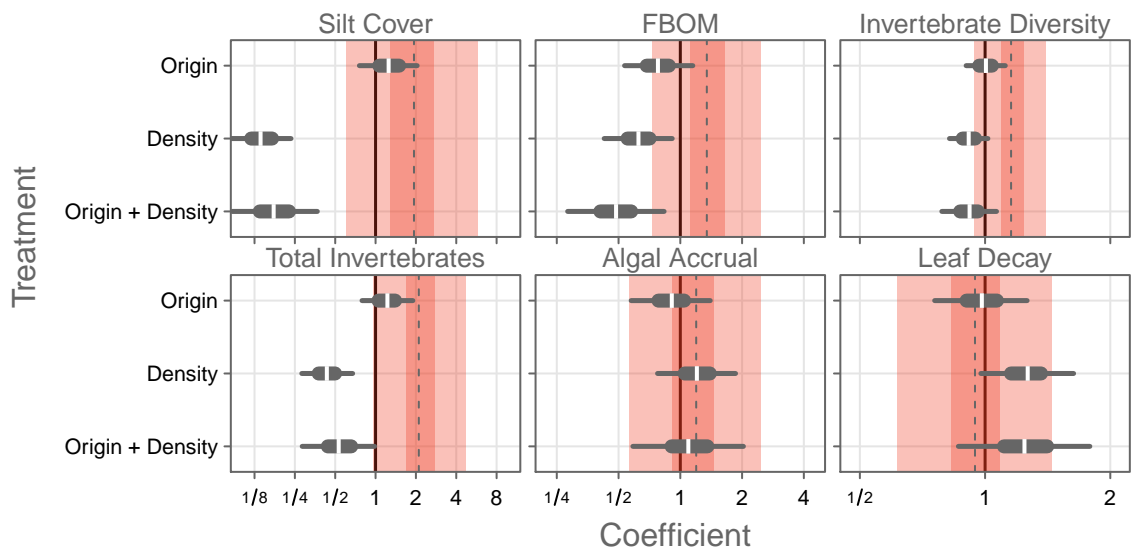


Figure 3.4: Fish, genetic origin, and fish density effects on response variables measured in the mesocosm experiment as estimated by the Bayesian multilevel model. Estimates are relative to the base case state (above-barrier genetic origin at low density; vertical solid black line) such that a treatment coefficient of 1 signifies no difference from the base case, and coefficients 1/2 and 2 are a decrease and increase, respectively, of equal magnitude in the response variable relative to the base case. The ecological effect of fish can be seen by comparing the posterior mean of the no fish treatments (vertical dashed black line) and 50% and 95% highest posterior density (HPD) credible intervals (dark and light red area, respectively) to the base case. There is strong support for an ecological effect of fish where there is little or no overlap between the light red shaded region and the solid black vertical line. The posterior mean (white line) and 50% and 95% HPD credible intervals (thick and thin black lines, respectively) are presented for genetic origin, density, and their combined effect (Origin + Density). Ecological effects of evolution are present where there is little or no overlap between the 95% HPD credible interval (thin horizontal black line) and 1 (vertical solid black line). Similarly, the ecological effects of genetic origin, density, and their combined effect (Origin + Density) can be compared to the 95% HPD credible interval of no fish treatments (light red shaded region). Posterior support for differences shown here are presented in Table A.1.)

Fish modified mesocosm ecosystems to the greatest effect in high density treatments. In particular, silt and FBOM were greatly reduced, which likely affected invertebrate biomass, leaf litter decay, and

algal accrual rates. Fine sediments have been shown to impair juvenile *O. mykiss* growth and survival (Suttle *et al.* 2004), but our results here suggest juveniles may also help prevent the accumulation of fines at fine spatial scales particularly when at high density. Based on observations during the experiment, we speculate competition in high density treatments resulted in greater bioturbation and remobilization of fine sediments, facilitating their export from the mesocosm. When fish were at low density or absent, silt covered 75-100% of the sediment in the mesocosm and there was substantially more FBOM (Figure 3.3). These mesocosms were characterized by a thick layer of fine sediment that supported high densities of burrowing invertebrates inaccessible to juvenile *O. mykiss*. The negative effect fish density had on invertebrate biomass is likely due to both direct consumption and bioturbation limiting the accumulation of invertebrate habitat. In contrast to other studies that have reported reduced decay rates due to top-down control of detritivore density by stream fish (Greig and McIntosh 2006; Woodward *et al.* 2008), decay rates of leaf litter were higher in high density mesocosms, likely because leaf packs became more inaccessible to detritivores in low density and no fish mesocosms due to accumulation of sediment. There was weak support for an increased rate of algal accrual in high density mesocosms suggestive of either a trophic cascade or bioturbation keeping tiles clear of silt; however, this result is incongruent with no fish treatments which also experienced a 20% increase in algal accrual rate relative to the base case.

The differences in per capita effects between the genetic origins of *O. mykiss* were modest relative to the effects of fish in general. Mesocosms with fish had less benthic invertebrate biomass, silt cover, and FBOM than control mesocosm, but the size of these effects differed between above- and below-barrier genetic origin treatments. Relative to above-barrier genetic origin treatments, below-barrier genetic origin treatments had greater benthic invertebrate biomass and silt cover, but less FBOM (Figures 3.3 and 3.4). This could be due to adaptive behavioral differences generated by the divergent selection regimes anadromous and resident *O. mykiss* encounter during development. In the Scott Creek watershed (Bond *et al.* 2008), as elsewhere (Ward *et al.* 1989), early marine survival of anadromous *O. mykiss* is strongly size selective. This should favor not only alleles for fast growth (Phillis *et al.* 2014), but also bold behaviors that maximize foraging opportunities at fine scales (Morinville and Rasmussen 2003; 2006) such as maximizing net energy gain through use of profitable riffle microhabitat (Fausch 1984; Hill and Grossman 1993). Increased benthic invertebrate biomass in below-barrier genetic origin mesocosms may reflect a preference for drift prey. For instance, Morinville and Rasmussen (2003) found pre-migratory anadromous brook trout (*Salvelinus fontinalis*) have higher consumption rates and metabolic demands than resident brook trout due to their preference for foraging for drift invertebrates in riffle habitats (Morinville and Rasmussen 2006). A similar foraging preference in below-barrier genetic origin *O. mykiss* may have resulted in the decrease in FBOM due to localized bioturbation in fast waters where (re-)suspended sediments would be most efficiently exported. Thus, contemporary evolutionary divergence appears to have ecological consequences, primarily mediated by density rather than phenotype change.

The possibility that reduction in juvenile *O. mykiss* density is an evolved response to life above the

barrier waterfall is intriguing (Hendry *et al.* 2011), particularly in light of the density effects on the mesocosm ecosystem relative to the per capita effects of ecotype divergence. However, the contribution of evolutionary divergence to changes in density, relative to ecological factors, is unknown here, and challenging to assess in general (Pelletier *et al.* 2007). The densities used in the mesocosm experiment can be considered an upper bound on a density-mediated eco-evolutionary pathway. Future eco-evolutionary studies should explore how small the density-mediated effects of evolution could be and still be equal to or greater than the direct per capita effects of trait divergence on community and ecosystem conditions.

The effects of density we observed will have consequences at different scales outside the experimental mesocosm ecosystem. First, The density-dependent mortality would diminish density-mediated effects on stream ecosystems through time. Second, in natural systems fish are not confined to mesocosms and can be expected to emigrate to new habitat when competition increases (Keeley 2001; Einum *et al.* 2006). However, we note that the densities we used were based on observed densities of fish from this system. We also note that the ecological effects of *O. mykiss* will be localized to the microhabitat that fish occupy at higher densities. In addition, there were mortalities in the high density mesocosms (Figure A.2). These patterns of young of year mortality mirror observations of *O. mykiss* in the study watershed; previous studies have found strong evidence of food limitation and severe over-summer mortality of young of year *O. mykiss* (Hayes *et al.* 2008; Sogard *et al.* 2012). Interestingly, the greater incidence of mortality observed in the high density above barrier genetic origin mesocosm treatments hint at the possibility that above barrier populations may be constrained by not just the loss of anadromy reducing innate growth rate, but also by greater sensitivity to the effects of density on juvenile survival.

In the emerging field of eco-evolutionary dynamics, ours is a rare study that has measured effects of divergent ecotypes with a known genetic basis (Hendry 2013). Previous studies have found divergence in fish phenotype can alter rates of biological processes and shift the size, biomass, and identity of the prey community in aquatic systems (Palkovacs and Post 2009; Harmon *et al.* 2009; Bassar *et al.* 2010); however, these studies have relied on field-captured fish which may either mask or amplify evolutionary trait divergence by ignoring plasticity and maternal effects. In our mesocosm study we isolated the ecological consequences of heritable phenotypic divergence from environmental or non-genetic maternal effects by using offspring of parents captured from the wild as juveniles and raised to maturity under common conditions. Thus, effects we see in our study are specifically the result of differences in additive genetic variance between the two ecotypes. In fact, the true difference between the effects of juvenile anadromous and resident *O. mykiss* on aquatic systems is likely not realized in our study. Ultimately, genetic, environmental, and maternal effects underlie the phenotypes that directly affect ecological processes. Given resident and anadromous salmon rear in vastly different habitats as adults, it is possible the non-genetic maternal effects on phenotypes produce divergent ecological effects that equal or surpass those with a genetic basis. In addition to producing more offspring than their resident counterparts, leading to increased juvenile densities, anadromous mothers also produce larger eggs that are linked to

advantages in early life-history growth and survival (Chernoff and Curry 2007; Liberoff *et al.* 2013), which may translate into per-capita differences in their ecological effects relative to resident juveniles. Future studies may wish to consider systems such as this one where it is possible to experimentally disentangle the contribution of genetic and plastic effects in eco-evolutionary dynamics.

3.6 Conclusions

Over the past century *O. mykiss* throughout their natural range have been repeatedly isolated from the marine environment by construction of artificial barriers to anadromy and translocations above natural barriers. Population persistence in these cases has required rapid evolution to the novel environment. Perhaps it is not surprising then from these multiple replicate “selection experiments” that we are seeing an accumulation of evidence supporting phenotypic and genetic divergence from migratory to non-migratory phenotypes over only a few dozen generations (Thrower *et al.* 2004; Phillis *et al.* 2014; Pearse *et al.* 2014). If reduced juvenile population densities are a consistent byproduct of adaptation to freshwater residency, our results suggest we can expect consequences of this evolution to propagate throughout freshwater ecosystems. More generally, it highlights the need in studies of eco-evolutionary dynamics to focus on populations responses, not just traits.

3.7 References

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Chapter 4

Dam evolution: an individual-based model of the evolution of anadromy in a steelhead/rainbow trout population³

4.1 Abstract

Ongoing global change is threatening populations of migratory animals generally, and anadromous fishes, including salmonids specifically. Partially migratory populations, like resident rainbow trout and anadromous steelhead (*Oncorhynchus mykiss*), consist of both migratory and non-migratory breeding individuals. When the migration decision is under genetic control, population persistence may be buffered from environmental change if increased selection on migratory individuals drives an evolutionary increase in residency. We used an eco-genetic model to explore whether a population of interbreeding resident and anadromous *O. mykiss* would evolve toward greater residency in response to three different disturbance scenarios: the construction and subsequent removal of an impassable dam, increased spawning migration mortality, and decadal-scale regime shifts in the marine environment that affect survival of migratory individuals. We found little support for pulse disturbances to result in directional selection, suggesting that decadal-scale regime shifts may not drive evolutionary responses detectable on the background of natural

³J.W. Moore is a coauthor on this chapter, which is currently in preparation for journal submission.

population stochasticity. Conversely, in scenarios similar to press disturbances populations were capable of evolving rapidly toward residency, particularly so as the costs of migration increased. However, population resilience to this disturbance is greatly reduced when either controls on population size (juvenile carrying capacity) or genetic contribution to migration (heritability) are decreased. When conditions are restored to the pre-disturbance state, the rate of recovery of the migratory ecotype was unpredictable and generally slower than its loss. Rapid evolution of residency may rescue declining populations impacted by migratory barriers, but do so at the expense of the ecologically important anadromous life history. How fast the anadromous life history recovers in these populations will vary and may in fact take longer than it took for the life history to be lost.

4.2 Introduction

There is growing concern that the migratory phenomenon is threatened by ongoing global change which has increased the costs of migration (Wilcove and Wikelski 2008). Dams and roadways disrupt aquatic and terrestrial migrations (Larinier 2001; Forman *et al.* 2002). Climate change can alter the conditions that once reliably predicted when (or if) to migrate to the foraging habitat, and vice versa (Reed *et al.* 2010). For example, in a comparison of 30 pairs of closely related migrating and non-migrating European birds Sanderson *et al.* (2006) found the migrating populations have declined significantly over a 30-year period during which time non-migrant populations were stable or increasing. The fate of populations affected by increasing costs of migration will depend on the capacity of populations to respond adaptively to a changing environment. One possible outcome is evolutionary rescue (Gomulkiewicz and Holt 1995; Gonzalez *et al.* 2012). In the case of migratory organisms, declining populations may be “rescued” if an evolutionary shift toward resident phenotypes occurs rapidly enough to prevent extinction.

Populations that have partial migration—consisting of both migratory and non-migratory breeding individuals—may respond to changing selection pressures that disproportionately affect the migratory phenotype on timescales that will prevent population extinction. The phenomenon of partial migration is found across many taxa, including insects, birds, fish, and mammals and likely reflects an evolutionary intermediary between resident and migratory states (Roff and Fairbairn 2007; Salewski and Bruderer 2007; Cagnacci *et al.* 2011; Chapman *et al.* 2012). Thus, partially migratory populations exhibit variation in migratory behavior, some of which may have an underlying genetic basis, suggesting adaptive responses may buffer populations against changing costs of migration.

An individual’s decision to migrate can be described by the threshold model of migration (Pulido 2011). The expression of the discrete migratory behavior (stay vs. go) is informed by a continuously distributed liability trait and a related threshold for migration. If an individual’s liability trait exceeds

their threshold value at decision time, then the migratory behavior will be expressed. Further, one or both of the threshold and liability trait may be heritable and selection that favors a discrete phenotype will also favor the underlying liability trait and individual threshold that trigger the phenotype. For example, migratory timing and intensity in the blackcap (*Sylvia atricapilla*) has been shown to be highly correlated with the heritable trait migratory activity (nocturnal restlessness, or *zugunruhe*), that expression of the dichotomous migrant-non-migrant trait is determined by an individual's migratory restlessness relative to a threshold, and that selection on lower migratory activity can drive evolution of residency (Berthold and Pulido 1994; Pulido *et al.* 1996; Pulido and Berthold 2010). Thus, under the threshold model of migration, an evolutionary gain or loss of migratory propensity may occur in a population when the distribution of the liability trait or threshold trait evolves.

Eco-genetic individual-based models are useful tools for predicting demographic and evolutionary fates of natural populations under different environmental regimes or resource management scenarios (Dunlop *et al.* 2009; Bauer and Klaassen 2013). The models combine features of population dynamics, life-history tradeoffs, and, importantly, quantitative genetics, including genetic variance and heritability. Further, when coupled with empirical data, the models can have practical implications by providing predictions about how populations may respond, both demographically and evolutionarily, to various disturbances (Thériault *et al.* 2008; Dunlop *et al.* 2009; Wang and Höök 2009; Kuparinen *et al.* 2014). For example, using an ecogenetic model Reed *et al.* (2011) predict that, given modest amounts of heritable variation in run timing, sockeye populations have the evolutionary potential to advance migration timing by 10 days in response to the 2°C river warming predicted for the Fraser River by end of the next century, and, by doing so, reduce their extinction probability relative to simulated populations without heritable variation in run timing.

Here we use an ecogenetic individual-based model to test whether rapid evolution of the threshold trait in response to changing costs of migration can rescue a partially migratory salmonid population from extinction. While many salmonids exhibit some degree of partial anadromy, it is largely the anadromous contingent of the population that return in large enough numbers to support fisheries and deliver marine derived nutrients that fuel freshwater and terrestrial ecosystems. Within these populations, migratory individuals can experience elevated risks of natural and anthropogenic sources of mortality including dams, harvest, and variable marine survival (Ruckelshaus *et al.* 2002; Hendry *et al.* 2003). Yet, evidence of heritable variation underlying an individual's decision to migrate (Thériault and Dodson 2003; Paez *et al.* 2010; Phillis *et al.* 2014) suggests populations may be resilient to changing selection regimes if thresholds for the expression of residency evolve rapidly. Here we ask whether increased selection against migration under three disturbance scenarios will drive evolution of residency fast enough to prevent population extinction. Each scenario approximates a real example of increased costs to migration with applied consequences, but may also be generalized as press or pulse disturbances on evolutionary timescales (Lake 2000). The three scenarios are 1) The construction and subsequent removal of an impassable

dam (a press disturbance followed by reversal and recovery), 2) Increased spawning migration mortality, such as due to fishing mortality or inefficient fish passage around a novel barrier (a press disturbance without reversal), and 3) Decadal-scale regime shifts in the marine environment that affect survival of migratory individuals (pulse disturbance). In each disturbance scenario we monitor the response of three variables, 1) the population mean of the heritable threshold trait, 2) the percent of a population that is anadromous, and 3) the percent of populations that persist for the entire simulation. We find that pulse disturbances and press disturbances of low intensity (i.e. weak selection) have only modest effects on the demographic and evolutionary trajectory of the populations, but press disturbances of high intensity (i.e. strong selection) can drive the rapid evolution of residency, buffering the population from extinction; however, reversing the disturbance does not result in predictable evolutionary recovery of anadromy. These findings have important applied implications, particularly with respect to aligning restoration goals with evolutionary timelines.

4.3 Methods

To test the potential for selection to drive evolution of residency in a partially migratory salmonid, we built an ecogenetic individual-based model of a rainbow trout/steelhead (*Oncorhynchus mykiss*) population, parameterizing the model where possible with empirical data from current and historical studies of the Scott Creek and Waddell Creek coastal watersheds in Central California (table 4.1; Shapovalov and Taft 1954; Bond *et al.* 2008; Hayes *et al.* 2008; Phillis *et al.* 2014). In Scott Creek, steelhead typically rear in freshwater for 1-3 years as juveniles before undergoing anadromous migrations to sea, returning to spawn after 1-4 years (Hayes *et al.* 2013). Rainbow trout complete their full life cycle in freshwater. The decision whether to migrate to sea or to mature in freshwater is controlled by both genetic and environmental factors (Dodson *et al.* 2013; Sloat *et al.* 2014). In particular, critical threshold body sizes for migration are commonly reported for many salmonids, including *O. mykiss* (Dodson *et al.* 2013), and the threshold size is a heritable trait capable of evolving (Thrower *et al.* 2004b; Phillis *et al.* 2014). Given expression of the migratory tactic is under some genetic control, it is possible the highly altered landscape migrating salmon encounter will prompt an evolutionary response in migratory life histories (Williams *et al.* 2008).

4.3.1 Model description

Our model tracks individual traits and population demography over 175 generations (or 700 years, assuming a four year life cycle) in 30 populations initialized from the same starting conditions. For simplicity we assume a closed population with no overlapping generations. There are three phases of a generation in the model: the migration decision, survival, and reproduction. The latter two are conditional on the

Table 4.1: Parameters used in the ecogenetic individual-based model

Symbol	Definition	Value or Function	Justification
L, σ_L^2	distribution of fork lengths at decision	196, 28	fall size distribution in Scott Creek estuary reported by Bond <i>et al.</i> (2008)
z_o, σ_z^2	initial distribution of threshold sizes	183, 18	initial conditions tuned to produce a population at equilibrium that is anadromy-dominated. z is allowed to evolve
M	migration switch: 1=migrate, 0=stay	$M_i = \begin{cases} \text{migrate if } L_i \geq z_i \\ \text{resident if } L_i < z_i \end{cases}$	
h^2	threshold heritability	0.75	Thrower <i>et al.</i> (2004b); Paez <i>et al.</i> (2010); Buoro <i>et al.</i> (2012)
S_0	young-of-year survival	0.0381	egg-to-fry times fry-to-smolt survival from Table 15-1 in (Quinn 2005)
S_M	size-specific marine survival	$0.84 \frac{e^{(-8.657+0.0369 \cdot L \cdot b)}}{1+e^{(-8.657+0.0369 \cdot L \cdot b)}}$	modified size-specific survival function from Satterthwaite <i>et al.</i> (2009)
S_R	annual resident survival	0.4	tuned to keep resident population above replacement

first (i.e. survival and reproductive success are specific to the migratory tactic), and thus determine the fitness of the heritable threshold trait underlying the migration decision. Within a generation we track an individual's body size, additive and phenotypic threshold size at the time of the migration decision, whether they migrate, size-and-migration-dependent expected survival and recruits per spawner, and fate. We also track the percent of a population that is anadromous, as measured after the migration decision (but prior to migratory tactic-specific mortality), and the percent of the populations that remain extant in each generation.

Migration decision

The threshold model of migration requires individuals express a continuously distributed liability trait and associated threshold switch point for migration. We use individual size as a proxy for the liability trait in our model because it is a commonly measured trait that adequately predicts alternative migratory tactics in many salmonids, including *O. mykiss* (Dodson *et al.* 2013). Heritable genetic variation underlies both individual size and threshold switch point size (Thrower *et al.* 2004b; Carlson and Seamons 2008; Paez *et al.* 2010; Phillis *et al.* 2014); however, for simplicity we focus only on evolution of the threshold trait in this model.

Initially a population of 400 individuals is generated at the time of the migration decision. Individual fork length L_i is drawn from a normal distribution that remains constant during the simulation (i.e. no

evolution or plasticity; mean, μ_L and variance σ_L^2 are static):

$$L_i = N(\mu_L, \sigma_L^2) \quad (4.1)$$

Threshold body size z_i is modeled as a heritable trait composed of additive (a_i) and environmental (e_i) components:

$$z_i = a_i + e_i, \quad (4.2)$$

where the additive genetic component, a_i of an individual's threshold phenotype is drawn from a normal distribution with a mean of μ_a in the initial generation, but is allowed to evolve in subsequent generations (described more below), and variance σ_a^2 that remains constant across generations:

$$a_i = N(\mu_a, \sigma_a^2), \quad (4.3)$$

The non-heritable residual effect, e_i of an individual's threshold phenotype is drawn from a normal distribution with mean 0 and variance σ_e^2 , both of which remain constant across generations:

$$e_i = N(0, \sigma_e^2). \quad (4.4)$$

Individuals are classified as migrants if their body size exceeds their threshold size and classified residents if their body size is less than their threshold size:

$$M_i = \begin{cases} \text{migrate if } L_i \geq z_i \\ \text{resident if } L_i < z_i \end{cases} \quad (4.5)$$

In the initial generation, threshold sizes are drawn from a normal distribution with mean threshold, μ_a equal to 183 mm and variance σ_a^2 set equal to half the variance of the liability trait. This yields a stable population that is approximately 65% anadromous prior to the onset of a scenario's disturbance regime. In subsequent generations an individual's threshold size is determined as in equation (4.2), but with the midpoint of the parents additive component, a , used as the mean, μ_a , in equation (4.3). We adjust σ_a^2 and σ_e^2 to set heritability of the threshold trait in the model equal to approximately 0.75, similar to the heritability of the migratory tactic reported for *O. mykiss* in Southeast Alaska and Atlantic salmon (*Salmo salar*) in Europe and Atlantic Canada (Paez *et al.* 2010; Buoro *et al.* 2012). In addition, we evaluate the sensitivity of our findings under a range of heritabilities (see below).

Juvenile-to-adult survival

Fish length at ocean entry has been shown to be positively associated with marine survival in the Scott Creek watershed [Bond *et al.* (2008); Osterback *et al.*, in review] as well as elsewhere (Ward *et al.* 1989). We assign marine survival probabilities of the migrants in our model according to a modified version of the logistic function fit by Satterthwaite *et al.* (2009) to smolt to adult survival data in Bond *et al.* (2008):

$$S_M = 0.84 \frac{e^{-8.6568+0.0369 \cdot L \cdot b}}{1 + e^{-8.6568+0.0369 \cdot L \cdot b}} \quad (4.6)$$

We include the additional parameter b to modify survival such that mean marine survival for migrant-sized individuals is approximately 4% under initial model conditions ($b = 0.7$) and 0.2% during the periods of poor marine survival in Scenario 2 ($b = 0.3$, more details below; figure 4.1), reflecting a range in marine survival similar to what has been observed in the Scott Creek watershed (Hayes *et al.* 2013). Annual resident size-independent survival is 40%, with survival through all three possible resident spawning years (details below) equal to 6.4%. This is greater than the annual survival estimated previously (14% age 1+ annual survival; Satterthwaite *et al.* 2009), but necessary in this model to produce a self-sustaining population in the absence of anadromous fish. An individual lives if their survival probability is greater than a number drawn from a random uniform distribution between 0 and 1.

Reproduction

Migratory and resident individuals are assigned separate reproductive outputs to account for the enhanced productivity and growth potential of the marine environment relative to freshwater habitats. As a result of their much larger size at spawning, fecundity of anadromous mothers can be 2-35 times greater than resident mothers (Hendry and Stearns 2003). Conversely, if resident mothers can reach maturity early, they may be able to spawn in multiple years before anadromous mothers first return to spawn. In our model migratory individuals are allowed to spawn once at the end of a generation, whereas resident individuals are allowed to reproduce up to three times. However, for simplicity there are no overlapping generations; at the end of a generation resident mothers are credited with offspring produced in up to three spawning years where the mother was alive and above a minimum size for maturation.

The number of recruits per spawner (here defined as number of offspring to survive to the migration decision window) an individual is capable of producing is their fecundity, ϕ , which differs between resident and migrant fish, and an egg-to-migration-decision survival parameter, S_0 , that is constant for both

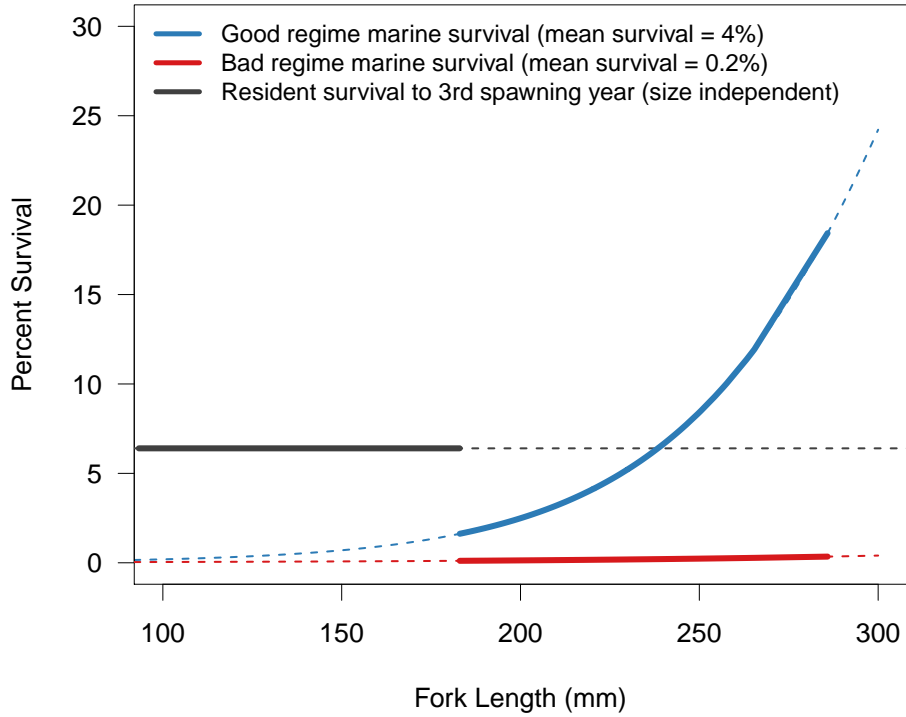


Figure 4.1: Size-independent resident three year freshwater survival (dashed black line) and size-dependent marine migrant survival functions (modified from Satterthwaite *et al.* (2009)) during good (dashed blue line) and poor (dashed red line) marine conditions. Solid lines correspond to the range of sizes from equation (4.1) that are below (black solid line) and above (red and blue solid lines) the initial threshold size. Mean marine survival is calculated for the range of sizes above the threshold size only.

resident and migratory ecotypes:

$$RPS = \phi \cdot S_0 \quad (4.7)$$

We assign anadromous mothers a fecundity of 7100 eggs based on estimates generated from the nearby Waddell Creek population (Shapovalov and Taft 1954; Satterthwaite *et al.* 2009). While body size strongly correlates with fecundity in fish, we assume a size-independent fecundity for our model because size at outmigration is a poor predictor of size at spawning (Satterthwaite *et al.* 2009). Conversely, we use the size-dependent fecundity function for resident mothers (Shapovalov and Taft 1954):

$$\phi_r = 0.0974 \cdot (L_S/10)^{2.1169} \quad (4.8)$$

Where length at spawning, L_S , is estimated from size at decision by the von Bertalanffy growth equation. First we estimate the Brody growth coefficient, k given an individual's size at decision:

$$k = \ln\left(\frac{L + L_\infty}{L_\infty - L_0}\right) \quad (4.9)$$

Setting length at emergence L_0 to 27 mm to correspond to the minimum size *O. mykiss* are observed in the Scott Creek watershed (Hayes *et al.* 2008) and maximum length, L_∞ , at 300 mm. Next we estimate length at spawning event t given our estimate of k :

$$L_{S_t} = L_\infty \cdot (1 - e^{(-k \cdot t)}) + L_0 \quad (4.10)$$

Thus, a resident individual's growth trajectory is set by the length drawn from equation (4.1) (i.e. no compensatory growth).

If there are 2 or fewer surviving individuals at spawning we consider the population extinct. Otherwise, we randomly sample and pair up all individuals that survive to spawning, up to a carrying capacity of 100 individuals. Thus, there was no assortative mating incorporated into the model. The first individual in a pair is considered the female, which produces a number of offspring corresponding to her RPS (equation (4.7)), rounded to the nearest integer. All spawning pairs are allowed to reproduce once. If the number of offspring exceed a carrying capacity of 400, then a subset of offspring are randomly sampled. In addition, we evaluate the sensitivity of our findings under a range of juvenile carrying capacities.

4.3.2 Testing model sensitivity

Population density, available genetic variation, and the degree of maladaptation post-disturbance contribute to determining if evolutionary rescue can prevent population extinction (Gomulkiewicz and Holt 1995; Bell and Gonzalez 2009; Gonzalez and Bell 2012). We explore how degree of maladaptation contributes to evolutionary rescue in Scenario 2 (details below) by varying the costs of migration (pre-spawn mortality). To evaluate how population density and genetic variation contributes to evolutionary rescue we re-ran Scenario 1 (details below), varying either juvenile carrying capacity or heritability of the threshold trait.

Juvenile carrying capacity

To evaluate sensitivity of the model predictions we re-ran Scenario 1 using juvenile carrying capacities at 5%, 10%, 25%, 50% and 200% of the original 400 individuals. In the model juvenile carrying capacity adjusts the size of the population prior to the migration decision. As this parameter increases we should expect reduced influences of demographic and genetic stochasticity on population persistence.

Heritability

To evaluate sensitivity of the model predictions to the threshold heritability parameter, we re-ran Scenario 1 using a range of heritability estimates. Estimates of the heritability of migration in salmon often come from individuals reared in a controlled environment, such as in a lab or hatchery. Because these controlled conditions could reduce the contribution of environmental variance V_E on variance of the phenotype V_P , and narrow-sense heritability (h^2) is the ratio of additive genetic variance (V_A) to phenotypic variance, $h^2 = \frac{V_A}{V_P}$, it is commonly hypothesized heritability is overestimated in laboratory experiments (though evidence supporting this is equivocal at best, Weigensberg and Roff 1996; Roff and Simons 1997). Therefore, we adjust V_E to produce four new initial heritabilities of approximately 0.10, 0.25, 0.50 and 0.90. The highest heritability, 0.90, corresponds with that reported by Phillis *et al.* (2014), who estimated heritability of the threshold, whereas most studies have estimated the heritability of the binary migratory tactic. Increasing genetic variance and associated heritability the population should increase the rate of the adaptive response to the disturbance, thereby increasing the likelihood of population persistence by evolutionary rescue (Gomulkiewicz and Holt 1995; Barrett and Hendry 2012).

4.3.3 Disturbance scenarios

Scenario 1: Dam construction & removal

Dams are a ubiquitous feature on the landscape in the natural range of *O. mykiss*. Since the beginning of the 20th century, construction of dams have eliminated 55% of historical habitat in the Columbia River Basin (National Research Council 1996) and 80% in the California Central Valley (Lindley *et al.* 2006). Many populations have become isolated from the marine environment following dam construction. Dam removal is a proposed means to restore anadromy to watersheds where this migratory life history has been extirpated. This scenario aims to approximate a situation where a dam is built without migration passage facilities (i.e., fish ladders) and removed after 100 years, a timeline that corresponds to the ages of many dams in North America (Doyle *et al.* 2003). In the model a dam is built in generation 50 at which point all migrants have a survival probability of zero, regardless of size. The dam is subsequently removed in

generation 75. after which expected marine survival of migrants is again determined by equation (4.6) and anadromy is once again viable migratory tactic in the population.

Scenario 2: Spawning migration mortality

In many cases, disturbances will decrease survival, but not select against migration completely. For example fishing mortality, migratory habitat degradation, or inefficient fish passage design will all reduce migrant survival, but not necessarily to zero. Scenario 2 is similar to the first, except 1) the strength of selection is reduced, and 2) once implemented, the press disturbance is maintained for the duration of the simulation. The disturbance begins in generation 50, after which migrant survival is reduced by an additional size-independent survival parameter. We explore responses to a range of increasing costs of migration (0%, 25%, 50%, 75%, and 100% pre-spawn mortality).

Scenario 3: Variable marine survival

Decadal-scale patterns in adult salmon returns may be caused by cyclical climatic phenomena like the Pacific Decadal Oscillation which cause regime shifts between 'good' and 'poor' ocean conditions, affecting marine survival (Mantua *et al.* 1997; Ward 2000). The regime shifts can be thought of as disturbance pulses, but on timescales that encompass multiple generations, and thus potentially elicit an evolutionary response by alternately selecting for and against anadromy. Unlike Scenarios 1 & 2, Scenario 3 is a natural disturbance. Understanding whether these natural perturbations could drive evolution of anadromy could provide insight into fisheries management and assessment. In our model, marine survival cycles between good and poor regimes every 30 years or 7.5 generations. We modify the parameter b in equation (4.6) for size-dependent expected marine survival such that mean survival of individuals larger than the initial threshold is only 4% of that during the good regime (figure 4.1). To test if marine regime has an effect on either percent of a population that is anadromous or the mean threshold size in a population, we fit a linear model to generation, regime, and their interaction. Response variables were calculated with the median of the population means for percent anadromy and threshold size ($n = 30$) and standardized to simulations with a constant marine survival (Scenario 2; 0% pre-spawn mortality) by taking either the log ratio (mean percent anadromy) or absolute difference (mean threshold size).

4.4 Results

4.4.1 Scenario 1: Dam construction & removal

Rapid evolution toward residency allowed some populations to persist despite being blocked completely from the marine environment. About half (53%) of the populations survived the duration of the simulation in Scenario 1, with the majority of extinctions occurring shortly after dam construction (figure 4.2). Populations that persisted were those where the threshold trait evolved rapidly toward larger values, generally in excess of two standard deviations from the population mean fork length (the liability trait). As a result, fewer individual's fork length exceeded their threshold value for expressing the migratory tactic and populations that persisted were only 3% anadromous when the dam was removed (median occurrence of anadromy in extant populations, range 0-22%). Following dam removal the threshold trait rapidly evolved back to the mean value prior to dam construction in most populations. However, some populations were slower to recover, including some that became fixed for the resident tactic for the duration of the simulation (figure 4.2). These populations were characterized by threshold distributions that had evolved well outside the range of the fork length distribution in the population. The large threshold sizes, combined with the smaller equilibrium population size for resident-only populations, meant few individuals expressed the migratory trait—and, importantly, the heritable threshold value underlying it—that selection favors when anadromy is permitted in the model.

When we decreased either freshwater carrying capacity (figure 4.3) or threshold trait heritability (figure 4.4) the number of populations that persisted for the duration of the simulations decreased. Due to demographic stochasticity, no populations survived to the “dam in” period when carrying capacity was 5% of the baseline (baseline $K = 400$; results not shown). In simulations where carrying capacity was 10% of the baseline or threshold heritability was 0.10, populations that survived the initial disturbance at “dam in” went extinct prior to or upon the removal of the dam (figure 4.3 a, b; figure 4.4 a, b). In all other simulations of carrying capacity and heritability some populations survived the duration of the disturbance period (figure 4.3 c–j; figure 4.4 c–j). With increasing carrying capacities or heritabilities there was a larger range in times to recover the pre-dam states of percent anadromy in a populations and mean threshold size. This response diversity may simply reflect the greater number of populations that survived the disturbance period, rather than resulting strictly from the carrying capacity or heritability conditions.

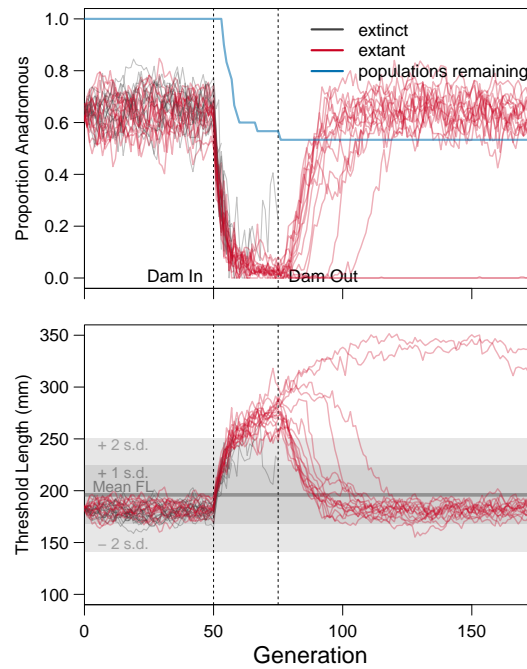


Figure 4.2: Demographic and evolutionary responses to the construction and removal of an impassable dam (Scenario 1). Panel (a): Each line represents the percent of an individual population that has adopted the anadromous life history in a generation, measured prior to marine and resident-specific mortality. Red lines indicate populations that persist for the full simulation, those going extinct before the end of the simulation are in dark grey. The blue line tracks the proportion of the original populations remaining each generation. Dashed vertical line at generation 50 indicates the construction of a dam (Dam In), following which survival for the migratory tactic is zero. Dashed vertical line at generation 75 represents the removal of the dam (Dam Out), at which point survival for the migratory tactic is again determined by the size-dependent function described in equation (4.6). Panel (b): Lines follow the evolution of a population’s mean threshold length. The distribution of the fork length trait (liability), which remains constant throughout the simulation, is represented by the horizontal grey line (mean), and dark (1 s.d.) and light (2. s.d.) grey boxes. Line color and vertical dashed lines are same as described in the top panel.

4.4.2 Scenario 2: Spawning migration mortality

Populations were surprisingly resilient to a large range of pre-spawning mortality rates. All populations survived the duration of the simulation when pre-spawn mortality for migrants was less than 100% (figure 4.5). When pre-spawn mortality was 100% only 33% of the populations survived the first 40 generations post-disturbance, after which the remaining populations persisted for the duration of the simulation. The threshold trait evolved rapidly—and, consequently, the percent of the population that was anadromous—following the disturbance in all cases, with the magnitude of the response corresponding to the rate of pre-spawn mortality for migrants. Mean threshold values and percent anadromy in a population stabilized within the first 25 generations following the disturbance in all cases with the exception of simulations

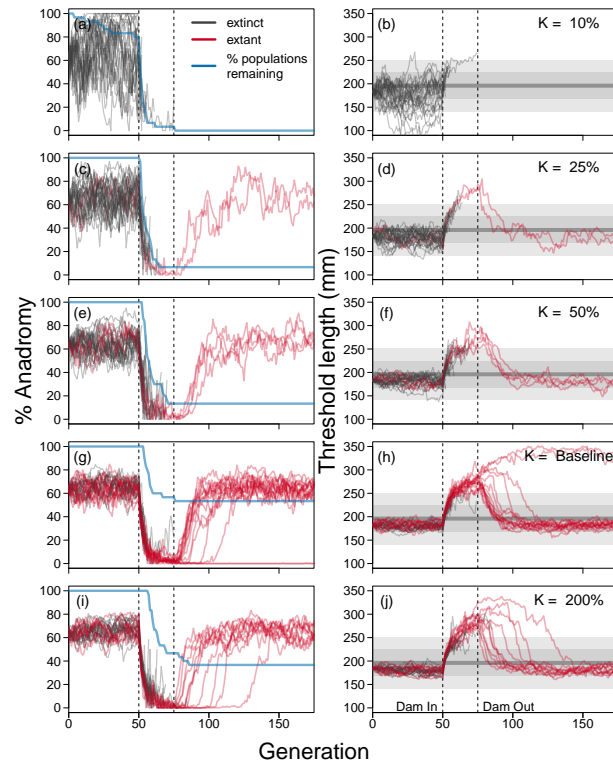


Figure 4.3: Demographic and evolutionary responses to the construction and removal of an impassable dam (Scenario 1) at a range of juvenile carrying capacities relative to the baseline of 400 individuals.

with pre-spawn mortality of 100% which continued to evolve away from the pre-disturbance state. While rapid evolution allowed populations to persist despite high migration mortality, anadromy was rapidly lost in populations. In these cases the percent of a population that was anadromous went to near zero within 25 generations following the disturbance, but the threshold trait continued to evolve away from the fork length distribution to the point where, at the end of the simulation, the median 10th percentile threshold value was 2.5 standard deviations from the population mean fork length.

4.4.3 Scenario 3: Variable marine survival

There was no discernible effect of variable marine survival on the demographic or evolutionary trajectory of the populations relative to simulations with constant marine survival (Scenario 2; 0% pre-spawn mortality; figure 4.6). All populations survived the duration of the simulation. Despite mean marine survival of only 0.16% during poor marine regimes, mean percent population anadromy declined by only 0.6% relative to scenarios with constant marine survival and the difference in mean threshold size was only 0.4 mm.

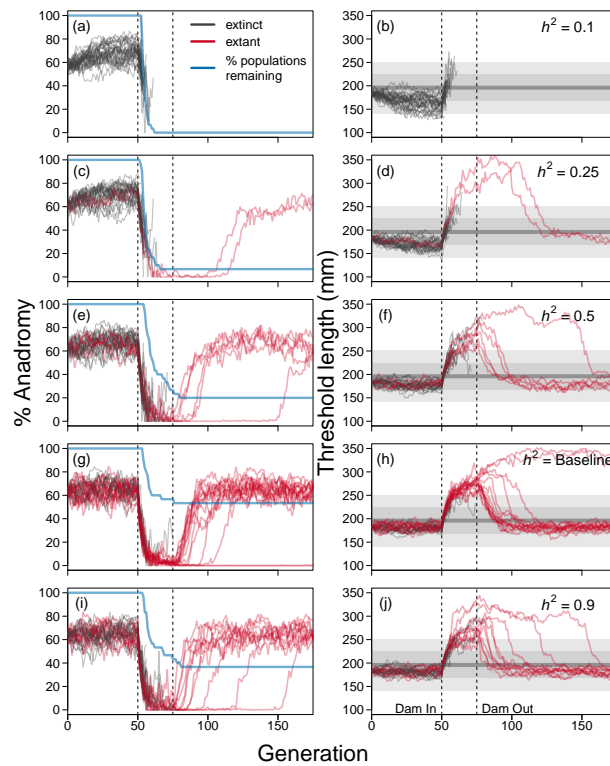


Figure 4.4: Demographic and evolutionary responses to the construction and removal of an impassable dam (Scenario 1) at a range of threshold heritabilities. See figure 4.1.

In neither case was the trait statistically different from a scenario with constant marine survival (regime: $F_{2,171} = 0.81$, $P = 0.45$; regime-generation interaction: $F_{1,171} = 1.23$, $P = 0.27$) or mean threshold size (regime: $F_{2,171} = 0.5$, $P = 0.61$; regime-generation interaction: $F_{1,171} = 1.24$, $P = 0.27$).

4.5 Discussion

Results from our simulated populations of steelhead/rainbow trout reveal conditions in which selection against the migratory form will result in rapid evolution of residency that may rescue the population from extinction. In particular, following a disturbance that increased the costs of migration, median anadromy in populations that avoided extinction declined from $\sim 65\%$ before the disturbance to 50% anadromous 25 generations after the disturbance when selection was weak (25% pre-spawn mortality) and 3% anadromous when selection was very strong (100% pre-spawn mortality). This was achieved when evolution shifted the distribution of migration thresholds within a population to sizes that regularly exceeded an individual's fork length at decision time (figure 4.2). Median threshold sizes were 5% and

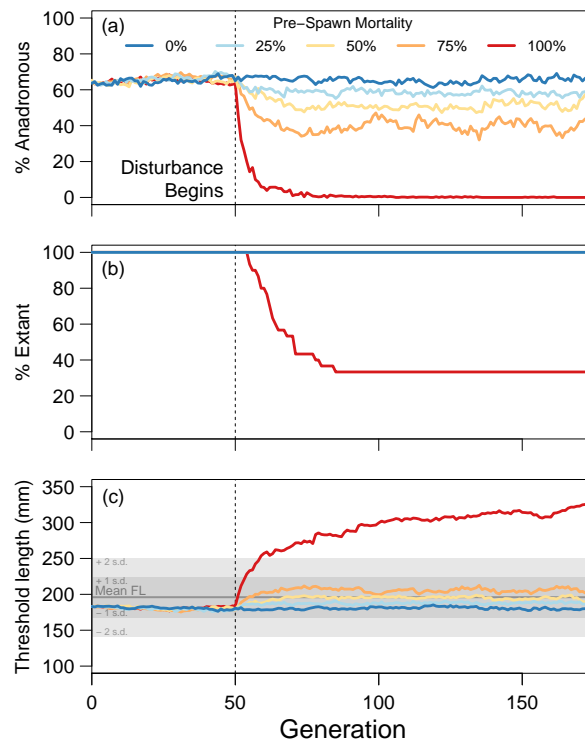


Figure 4.5: Demographic and evolutionary responses to a range of pre-spawn mortality for anadromous individuals, such as that driven by harvest, predation, or migration corridor degradation (Scenario 2). Dashed vertical line at generation 25 indicates the beginning of the disturbance regime. Unlike Scenario 1, the disturbance is maintained for the duration of the simulation. Panel (a): Lines are median percent anadromy in each generation for simulations using the five pre-spawn mortality values. (see legend). Panel (b): Median percent of the original populations remaining each generation. Panel (c): Median of population mean threshold fork length.

50% larger 25 generations after the disturbance, respectively, for the weak and strong selection scenarios described above. However, we found that the fate of populations depend on both the magnitude and type of disturbance. When the costs of migration varied episodically, an evolutionary response was not distinguishable from the stochastic behavior of populations experiencing constant survival (figure 4.6). Conversely, disturbances that were permanent and selected completely against the migratory phenotype required rates of evolution of the threshold trait that could not be achieved before most populations went extinct (figure 4.5). Further, populations were more likely to go extinct when population growth or available genetic variation was limited (figures 4.3 and 4.4). When the disturbance was removed, populations recovered anadromy, but at unpredictable and generally slower rates than it took to be lost.

Evolutionary rescue occurs when adaptation to a changed environment arrest or reverse a population's decline. Evidence for evolutionary rescue, in the form of population persistence was greatest in our

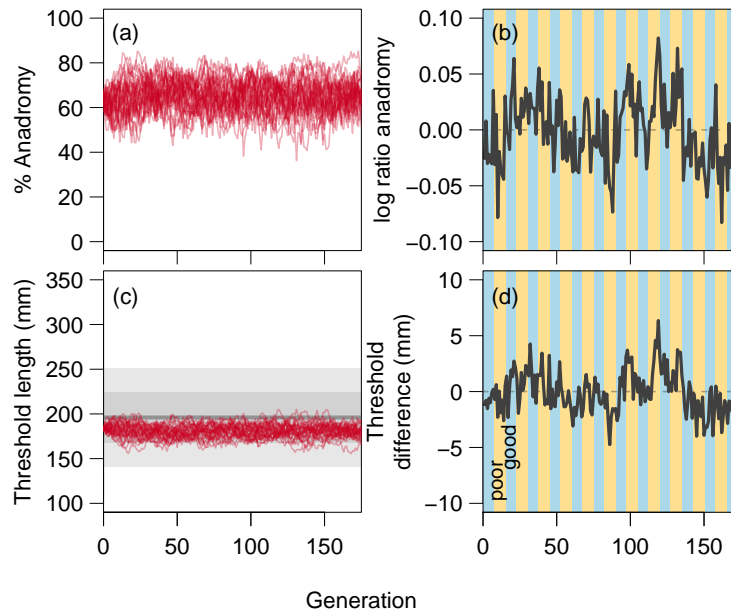


Figure 4.6: Demographic and evolutionary responses to decadal-scale oscillations in marine survival. Panel (a): Lines trace the percent of an individual population that has adopted the anadromous life history in a generation, measured prior to marine and resident-specific mortality. 100% of the populations persisted for the duration of the simulation. Panel (b): The log ratio of mean percent anadromy for simulations with variable marine survival (Scenario 3) to simulations with constant marine survival (Scenario 2, 0% pre-spawn mortality). Positive values indicate the incidence of anadromy is greater in simulations with variable marine survival. Panel (c): Lines follow the evolution of a population's mean threshold length. The distribution of the fork length trait (liability), which remains constant throughout the simulation, is represented by the horizontal grey line (mean), and dark (1 s.d) and light (2. s.d) grey boxes. Panel (d): Difference between mean threshold size for simulations with variable marine survival and simulations with constant survival. Positive values indicate mean thresholds are larger in simulations with variable marine survival. Survival regimes shift every 7.5 generations between periods of good marine survival in blue (4% mean marine survival; figure 4.1) and poor marine survival in yellow (0.2% mean marine survival; figure 4.1). The effect of marine regime is not significant in either case (see Results)

simulations when the conditions that favor evolutionary rescue (available genetic variation, large population size, and limited degree of maladaptation) allowed populations to respond rapidly to the Scenario's disturbance. The process of evolutionary rescue in partially migratory populations differs somewhat from the theoretical models and experiments performed to date. Namely, the latter have focused on whether rates of mutation and accumulation of resistant genotypes can occur rapidly enough to prevent population extinction (Bell and Gonzalez 2009; Gonzalez and Bell 2012). However, what makes evolutionary rescue in partially migratory populations an intriguing possibility is that the necessary genetic variation for evolutionary transitions between resident and migratory forms is already present in all individuals within the population. Under a threshold model of migration, an evolutionary shift between discrete resident and migratory phenotypes is actually the result of directional selection on the underlying threshold trait which is continuously distributed within the population (Tomkins and Hazel 2007; Pulido 2011). Given

the necessary genetic variation is already present in the population, rapid evolution of the threshold trait may reduce the likelihood of population extinction even in cases of strong selection against the migratory life history (figures 4.2 and 4.5). Indeed, our simulations here and results from empirical studies (Thrower *et al.* 2004b; Phillis *et al.* 2014) suggest evolutionary rescue following major disturbances may not be uncommon in *O. mykiss*

Evolutionary rescue of the population and evolutionary recovery of anadromy are two processes that may operate on different timescales. In Scenario 1 we explored how the populations would respond to removing a dam after 25 generations. While populations predictably evolved rapidly toward greater residency following the disturbance, populations were less predictable in how they responded when conditions were restored to their pre-disturbance state. In many cases, populations rapidly returned to the state they were in prior to when the dam was constructed. However, some populations took as long, or longer, than the period of time the dam was in place to return to its pre-dam state (figures 4.2, 4.3 g-i, 4.4 e-i). The recovery process after dam removal is similar to the process of evolutionary rescue when the dam goes in, with one important distinction: following dam removal populations that do not evolve rapidly enough back to the original state are not at risk of extinction like they are when the dam goes in. As a result, some populations can become fixed for the resident life history for tens of generations before they recover the anadromous life history. In these cases, the threshold trait has evolved well beyond the range of the liability trait (fork length) in the population and anadromy does not evolve because it is rarely expressed. The cryptic genetic variation (Ghalambor *et al.* 2007) for anadromy will be 're-discovered' either by genetic drift in the threshold trait or when the liability trait increases (e.g. larger fork lengths due to a change in the juvenile rearing environment). The asymmetry in the loss and recovery of anadromy is similar to that described for life-history traits before and after a fishing moratorium in harvested fish populations (Dunlop *et al.* 2009; Enberg *et al.* 2009). This symmetry may be a general phenomenon when the strength of anthropogenic selection far exceeds the strength of natural selection that shapes the life history prior to and after the disturbance (Enberg *et al.* 2009).

Population size and available genetic variation contributed to determining if evolutionary rescue would prevent population extinction in Scenario 1. The number of populations that survived the duration of the simulations in Scenario 1 markedly declined when either juvenile carrying capacity or available genetic variation were decreased, consistent with our understanding of the roles of demographic and genetic processes in population extinctions (Lande 1993; Frankham 2005). Most populations that went extinct following the construction of the dam did so despite evolution toward larger threshold traits within the population, suggesting the disturbance reduced populations to sizes that were susceptible to demographic stochasticity (Lande 1993). Assuming a disturbance affects the relative population size (as was the case here) and not the absolute population size, then populations beginning at a larger equilibrium size would be more likely to adapt fast enough to prevent extinction and avoid the demographic and genetic sampling errors that doom smaller populations. Increasing heritability increases the potential for

evolutionary rescue by limiting the non-genetic influence over phenotype expression. For wild populations, differences in heritabilities between two environments are more often explained by differences in residual or environmental variation, not additive genetic variation (Charmantier and Garant 2005). To our knowledge it is relatively unknown how non-genetic contributions to heritability of the threshold trait vary between environments. However, if the liability trait responds to changes in the environment, then we would expect the relative expression of the migratory life history to vary without differences in the threshold trait distribution. For instance, in *O. mykiss*, poor or variable growth conditions may decrease the average size of fish at the migratory decision window, but also increase the variability of sizes in the population. Whereas under favorable growth conditions, environmental effects would be diminished relative to the genetic contributions to growth.

Management actions may increase the potential for evolutionary rescue by increasing population size or diminishing the environmental influence on heritability. For example, increasing freshwater rearing habitat would improve a population's potential for evolutionary rescue following a large disturbance by increasing the population size and limiting the influence of demographic and genetic sampling errors. Likewise, if stressful rearing environments decrease heritability (Charmantier and Garant 2005), improving habitat quality could also improve potential for evolutionary rescue by limiting the non-genetic influence on phenotype expression. Fortunately, both improving capacity and quality of juvenile *O. mykiss* rearing habitat are already common goals of restoration actions intended to limit the effects of demographic and environmental stochasticity. Our results suggest these management actions additionally promote population persistence by increasing potential for evolutionary rescue.

A pulsed disturbance did not drive rapid evolution of migration in our simulations, in contrast to the press disturbances of Scenarios 1 and 2 (figure 4.6). There is growing appreciation that climate forcing drives decadal-scale switches in marine survival (Mantua *et al.* 1997; Ward 2000). Our simulations suggest that the time-scale of these disturbances are too short to drive discernible signs of evolution.

In our effort to understand how a population of *O. mykiss* might respond to various disturbance scenarios, we employed several simplifying assumptions in our model. Our model assumes non-overlapping generations and that a single decision determines the migratory fate of an individual. In reality, *O. mykiss* can express a range of life-history strategies in terms of the age-at-migration and number of years spent at sea—a staggering 36 such life histories were reported for populations from two British Columbia watersheds (Moore *et al.* 2014)—which can buffer populations from short-term variability. However, this life-history diversity likely does not provide resilience to longer-term perturbations that persist longer than one generation, and thus likely would not quantitatively influence our results. Secondly, we assumed matings were non-assortative (i.e. random) which should slow the rate of evolution by allowing gene flow between adaptive and maladaptive genotypes during the disturbance period. We also did not allow migration in from other populations. This simplification allowed us to isolate the process of evolutionary

rescue from demographic (Hanski 1998) or genetic (Tallmon *et al.* 2004) rescue effects. Yet, salmonid populations exhibit many of the features of metapopulations (Schtickzelle and Quinn 2007); a natural extension of our model would be the incorporation of immigration and gene flow between populations, which we predict would facilitate the recovery of anadromy when effects of a disturbance are reversed, such as the dam removal simulated in Scenario 1. Lastly, we assumed that only the threshold trait evolves in the population. An alternative evolutionary solution to increased selection against migration is a slower individual growth rate that reduces the probability of surpassing a static threshold trait. Alternatively, both the threshold and individual growth rate could evolve. Indeed, this appears to be what has happened in a population of *O. mykiss* transplanted above a barrier waterfall in the Scott Creek watershed (Phillis *et al.* 2014). We anticipate allowing for the evolution of growth rate would increase model complexity and perhaps allow populations to evolve more rapidly.

4.6 Conclusion

There is an ongoing call for conservation biology and fisheries management to consider contemporary evolution (Stockwell *et al.* 2003; Rice and Emery 2003; Kinnison and Hairston 2007; Hendry *et al.* 2011; Palkovacs 2011). In the case of partially migratory populations this includes recognizing that resident and migratory individuals experience different environments and selection regimes over their life. Specifically, common threats to biodiversity (e.g. habitat loss, harvest) may non-randomly affect the migratory forms of these species. For example, Pacific salmon have experienced dramatic population declines, local extinction, and lost genetic and life-history diversity due largely to construction of impassable dams (National Research Council 1996; Gustafson *et al.* 2007). However, behind many of these dams and above natural barriers exist isolated resident populations (Thrower *et al.* 2004a; Clemento *et al.* 2009; Godbout *et al.* 2011; Holecek *et al.* 2012) which have been identified as potentially important for the recovery of the threatened anadromous forms (Thrower *et al.* 2008). Success of this approach will depend, in part, on evolutionary processes, including potential outbreeding depression (reduced fitness of offspring between anadromous and resident parents) and the rate at which anadromy re-evolves, which we have shown can be slower and less predictable than the evolutionary loss of anadromy (figures 4.2–4.4). Anadromous populations may also be exposed to higher rates of fishing-induced selection which can drive evolution of residency (figure 4.5; Thériault *et al.* 2008), an outcome that should not be ignored by fishery managers. Failing to account for similar fisheries-induced evolution of life histories has resulted in collapsed fisheries that are slow to recover even when fishing is suspended (Olsen *et al.* 2004; Hutchings and Rangeley 2011).

Evolutionary rescue may play an important role in the persistence of partially migratory populations on a landscape where the costs of migration are increasing (Wilcove and Wikelski 2008). In *O. mykiss*,

evolution toward residency will prevent population extinction, but will come at the cost of anadromy which provides ecosystem services unique to its life history. Steelhead will be lost, but rainbow trout may persist. Restoring anadromy is an increasingly common restoration goal (Chapter 5), but managers will need to consider that partially migratory populations are constantly adapting to the migratory landscape, particularly those that have persisted behind barriers by evolving residency. The rate of recovery of the anadromous life history will be somewhat unpredictable and likely slower than its loss. Exercises such as this provide insights into the limits and potential for evolution to provide resilience to populations.

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Chapter 5

Restoration of Anadromy⁴

5.1 Abstract

Migration can link habitats and drive ecosystem services, yet may predispose populations to being degraded by human activities. Given losses of this migratory life-history, restoration is increasingly called upon to recover not just a species, but rather the expression of this life-history. For instance, the removal of migratory barriers is a common tool in the recovery of anadromous fish population. However, migratory life histories are controlled by genetic and environmental factors and simply removing a barrier may restore connectivity, but fail to recover lost phenotypic diversity. For restoration to be effective we must have a greater understanding of the ecological and genetic mechanisms underpinning the expression of migratory behavior. Here we review the theory of migration and explore three pathways through which anadromy may be restored: re-colonization, re-expression, and re-evolution. Because these pathways act simultaneously, but on different timescales, we highlight the importance of aligning temporal scales of management and restoration.

5.2 Introduction

Whether it is two million wildebeest making a 3,000 km journey across Africa's Serengeti or monarch butterflies completing four generations in a single migration across North America, animal migrations

⁴J.W. Moore, M.P. Beakes, C. Favaro, H. Nesbitt, E. Palkovacs, and G. Pess are coauthors on this chapter, which is currently in preparation for submission.

can inspire cultures and fundamentally alter ecosystems. These migrations connect otherwise disparate habitats, providing physical and functional linkages between communities and ecosystems. However, the migratory life history may predispose populations to being degraded by human activities (Wilcove and Wikelski 2008). Physical barriers or degradation of corridor habitats can impede or block migrations, thus breaking the vital connection between recipient ecosystems. Indeed, migration of animals is an increasingly threatened phenomenon over a global scale (Wilcove and Wikelski 2008).

In this paper we examine the restoration of a common form of migration in fishes—*anadromy*. *Anadromy* is a migration characterized by movement of adult fish from marine ecosystems to fresh-water for spawning (panel 5.1). *Anadromous* fishes utilize more types of habitat and thus are exposed to more potential sources of habitat degradation than resident counterparts. Habitat degradation anywhere along the migratory corridor or blockage of passage can impact *anadromous* populations by altering the costs of an already physiologically challenging migration (McDowall 1999; Reynolds *et al.* 2005; Limburg and Waldman 2009). Indeed, many *anadromous* populations have been declining due to a variety of impacts (Reynolds *et al.* 2005; Gustafson *et al.* 2007; Jelks *et al.* 2008; Limburg and Waldman 2009) leading to an increasing reliance on invasive restoration actions to rebuild populations of migratory fishes. However, *anadromy* may be either a fixed behavior, occurring in all individuals of a population, or a flexible behavior, expressed only by some individuals of a population and sometimes only under specific conditions. Thus, restoration is being asked to restore a *life-history strategy* (Watters *et al.* 2003). We postulate that understanding the mechanistic causes of *anadromy* can guide restoration of this important and valuable migratory life-history. Furthermore, we suggest that on-going restoration activities act as large-scale experiments that can continue to illuminate the ecology and evolutionary causes and consequences of *anadromy*. While we focus specifically on *anadromous* fishes, we hope that insights gained from our framework and the data available from these relatively well-studied systems may be applicable to other migratory animals worldwide.

Panel 5.1: Why migrate?

Gross (1987) proposed a mathematical framework that captures the costs and benefits of migration to predict when anadromy should evolve. Building from a simple model of fitness as the product of survival and breeding success, and given fitness of anadromy is relative to fitness of residency, Gross states that anadromy should occur when the following expression is satisfied:

$$\frac{T_O(G_O * S_O) + T_M(G_M * S_M)}{T_O + T_M} > 1 \quad (5.1)$$

Where ocean growth and survival (G_O and S_O) and growth and survival during up-and-downstream migration (G_M and S_M) are relative to growth and survival in freshwater, and these parameters are scaled to the time spent in the ocean and migrating (T_O and T_M). Here growth is used as a proxy for breeding success (fecundity scales with body size in many fish). When this expression is greater than 1 the fitness of the anadromous life

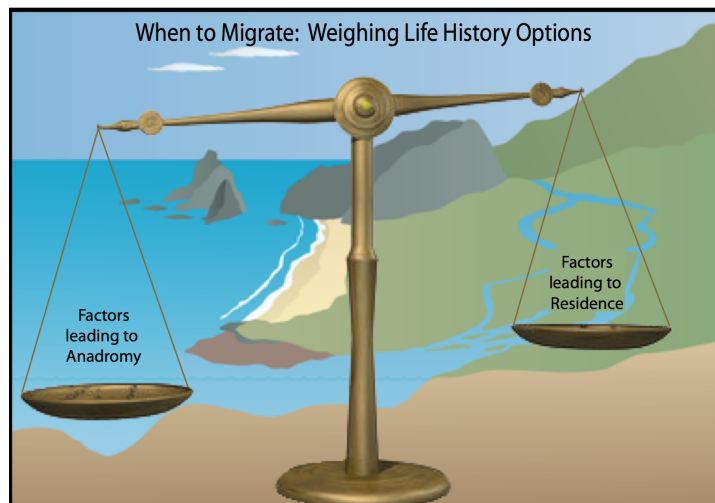


Figure 5.1: An heuristic model of the environmental conditions favoring anadromy. Art courtesy of Steve Sharron.

history is greater than the relative fitness of the resident life history, and the evolutionary endpoint will be the anadromous life history. Subsequent work has expanded and built off this framework (Thorpe *et al.* 1998; Mangel and Satterthwaite 2008), including recent work that has incorporated individual state-dependence (e.g. size at age) to predict life history strategies (Satterthwaite *et al.* 2009; 2010). These mathematical approaches provide a useful framework for predicting how anadromous populations will respond to anthropogenic change—construction or removal of a dam will change the migration survival parameter in expression 5.1 and the fate of the anadromous strategy in a population will depend on the sensitivity of relative anadromous fitness to changes in migration survival.

5.2.1 What is anadromy?

Anadromous species spend much of their life at sea before returning to freshwater to spawn. While Pacific salmon (*Oncorhynchus* spp.) are the archetype of anadromous species, there is a diverse array of fishes that exhibit anadromy (Chapman *et al.* 2012). Anadromy has evolved multiple times across a phylogenetically diverse set of fish taxa, including sturgeon (*Acipenseridae*), herring (*Clupeidae*), white perch and striped bass (*Moronidae*), smelts (*Osmeridae*), lampreys (*Petromyzontidae*), and salmon and trout (*Salmonidae*). We choose to focus on the anadromous life history because it is the dominant diadromous life history (McDowall 1988) and many anadromous species are of ecological, commercial, and cultural importance (Limburg and Waldman 2009).

A wide range of migration strategies can be expressed within a closely related group. The Pacific salmon and trout (*Oncorhynchus* spp.) in their native range are particularly illustrative of this life-history diversity. Pink (*O. gorbuscha*) and chum salmon (*O. keta*) are exclusively anadromous (Groot and Margolis 1991). Chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon are almost always also anadromous, but if blocked by a barrier such as a dam, individuals can reach maturity without making the migration to the ocean. Other species commonly have sympatric anadromous and resident populations, including *O. nerka* (sockeye and kokanee) and *O. mykiss* (steelhead and rainbow trout). Lastly, many subspecies of rainbow trout (*O. mykiss*) and cutthroat trout (*O. clarki*) are nominally non-migratory, though their evolution is owed to their anadromous ancestors colonizing freshwaters and then being isolated from the marine habitat during the repeated glacial cycles of the Pleistocene (Waples *et al.* 2008; Wilson and Turner 2009). Thus, within this single genus there are examples of fixed anadromy (pink and chum salmon), fixed residency (many subspecies of rainbow and cutthroat trout), and partial anadromy (kokanee and sockeye, rainbow trout and steelhead).

To preserve or restore anadromy requires an understanding of why anadromy exists (panel 5.1). Anadromous individuals can experience elevated life-time reproductive output by capitalizing on the enhanced productivity, and growth potential, in the marine environment relative to freshwaters. Thus, for anadromy to evolve, the benefits of the marine environment—relative to freshwater residency—must exceed the costs of migrating across the sea-freshwater boundary (Gross 1987; Gross *et al.* 1988; Hendry *et al.* 2003). The expression of anadromy is in part influenced by the cost of migration. Specifically, when migration distance, elevation gained, or risk of mortality is high in the migration, the route anadromous contingents within a species become rarer (Bohlin *et al.* 2001; Secor *et al.* 2001; Sahashi and Morita 2013; Finstad and Hein 2012). Even where latitude and migratory difficulty are approximately equal, differences in habitat characteristics and growing conditions of adjacent watersheds can generate divergent rates of anadromy (Pavlov *et al.* 2011; Finstad and Hein 2012; Berejikian *et al.* 2013). Thus, the patterns of aquatic productivity and physical challenges of migration (e.g. gradient, flow, temperature, predation risk) provide an adaptive landscape on which anadromy evolves.

This adaptive landscape has driven the local adaptation of many different anadromous life-history strategies (e.g., Quinn 2005). Heritable differences in traits associated with migration (e.g. size-at-migration, age-at-migration, timing of migration, morphology of migrants) have been documented for many populations (Carlson and Seamons 2008), including heritability of migration (e.g. steelhead populations in Alaska, $h^2 = 0.73$ (Thrower *et al.* 2004) and California, $h^2 = 0.91$ (Phillis *et al.* 2014); brook charr in Quebec, $h^2 = 0.52-0.56$ (Thériault *et al.* 2007); Atlantic salmon populations in Quebec, $h^2 = 0.77$ (Paez *et al.* 2010) and Brittany, $h^2 = 0.77$ (Buoro *et al.* 2012)). Thus, anadromy is influenced by genetics.

Environmental conditions can influence the expression of anadromy in partially anadromous populations. For example, in some populations anadromy is likely only when resources become growth-limiting due to competition or increasing metabolic demands of the individual, thus favoring migration over freshwater residency. In laboratory experiments, Olsson *et al.* (2006) found that brown trout (*Salmo trutta*) were more likely to express the migratory body morphology when reared in growth limiting conditions. In a natural environment we expect that the growth opportunity for an individual is a function of food availability, metabolic demands, and interspecific and intraspecific competition. When competition is strong, food restricted, or habitat availability sparse, the environment is more likely to provide poor growing conditions, thus increasing the potential benefit of seaward migration. This prediction may help explain the positive association between density and anadromy observed in several studies (Morita *et al.* 2000; Olsson *et al.* 2006; O'Neal and Stanford 2011). Thus, anadromy can also be influenced by environmental conditions.

In reality, the expression of anadromy in partially migratory populations is the product of interactions between genetic and environmental controls (panel 5.2). Partial migration can be described as a reaction norm wherein the migratory tactic expressed is dependent on an individual's status (the integration of the environment experienced) relative to a genetically-controlled threshold state (Tomkins and Hazel 2007; Hutchings 2011; Pulido 2011; Dodson *et al.* 2013). Growth rate and body-size thresholds above which emigration takes place have been described theoretically (Thorpe *et al.* 1998; Rikardsen *et al.* 2004; Mangel and Satterthwaite 2008) and documented empirically for several salmonid species, including steelhead (Thrower *et al.* 2004; Beakes *et al.* 2010; Satterthwaite *et al.* 2010; Phillis *et al.* 2014), brook charr (Thériault *et al.* 2007), Arctic charr (Rikardsen 2000), and Atlantic salmon (Paez *et al.* 2010). Less is known about what triggers migration in non-salmonids, but it is likely to be under similar genotype-environment control. For example, early life history environment and larval growth rates appear to determine resident and dispersive individuals in white perch (Kerr and Secor 2009). The outcome of these genotype-environment interactions will vary from species to species—and from population to population—with the costs and benefits of seaward migration versus freshwater residency for any given system.

Panel 5.2: The environmental threshold model of partial anadromy.

Partial anadromy as a threshold trait (adapted from Hazel and Smock 1990). (a) The decision to migrate is determined by an individual's environment or status (here inferred from body size) relative to a threshold switch point (vertical lines). (b) Genotypes for the threshold vary continuously within a population following a normal distribution. Individuals will migrate if their threshold size is less than their body size. Body size varies with the environment (dashed vertical lines), therefore, the number of individuals that migrate in environment 1 (\bar{e}_1) is a subset of those individuals that migrate in environment 2 (\bar{e}_2). (c) Selection against seaward migration (e.g. increased fishing pressure at sea or dams that block upstream migration) will favor individuals with larger threshold sizes (blue lines in (a)) resulting in fewer migrants in each environment. (d) The number of migrants in a population takes on a cumulative frequency distribution.

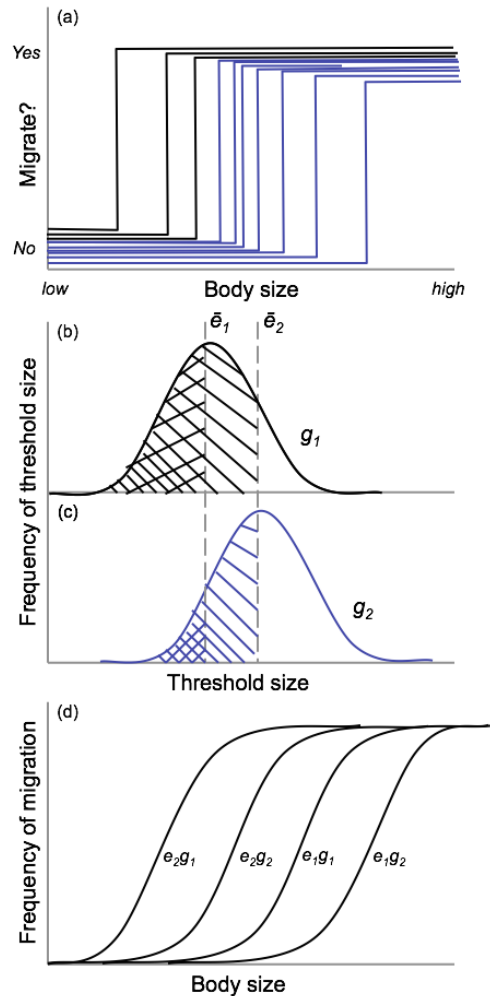


Figure 5.2: The environmental threshold model of migration. Adapted from Tomkins and Hazel (2007)

5.3 Tipping the scales of anadromy

Between 1990 and 2004 at least 14 billion dollars were spent in the U.S. on river restoration projects, yet there has been limited post-project monitoring for the vast majority of restoration actions (Bernhardt *et al.* 2005). Ongoing restoration efforts should be viewed as large-scale “experiments” that can evaluate

success and guide further restoration (i.e., adaptive management). When restoring anadromy is the goal, monitoring the results of a restoration activity can be performed within the context of expression 5.1 (panel 5.1). For example, fish ladders have long been used at dams to increase survival during migration to spawning grounds, yet in many instances the target populations continues to decline or fail to recover because, as post-project monitoring reveals, the ladders do not increase upstream survival as intended (Brown *et al.* 2013). Further, restoration of anadromy can be achieved via at least three pathways: re-colonization, re-expression, and re-evolution. Successful restoration projects will be ones that identify the pathway(s) appropriate for the species or system and sets goals and time lines congruent with the underlying ecological and evolutionary mechanisms (Anderson *et al.* 2014; Pess *et al.* 2014).

5.3.1 Re-colonization

Anadromy can be restored when anadromous fish from elsewhere colonize the habitat. For fixed anadromous species, re-colonization is the only viable pathway to restore anadromy. While salmonids in particular are well known for their homing, a small but variable proportion of fish “stray” to new spawning habitats (Quinn 2005). Natural re-colonization by salmonids has been observed to occur fairly rapidly; on the order of years to decades (Milner *et al.* 2011; Pess *et al.* 2012). The location of the newly opened habitat in relation to potential source populations will influence colonization rates—presumably the probability of straying is a function of distance to a source population (Hamann and Kennedy 2012) as well as the size of the source population (Pess *et al.* 2012). It should be noted that these colonizing individuals may not have the suite of local adaptations that predispose them to flourish in the newly accessible habitat. Although these first colonists will experience little density-dependence and thus have the potential for extremely high fitness, they also may not have key traits such as the timing of life-history events that match well with the new environment. Thus, re-colonization will go in concert with re-evolution of associated locally adapted traits (Kinnison *et al.* 2008). It may be possible to speed the re-colonization process by reintroducing anadromous individuals from adjacent populations into the new habitat, thereby artificially increasing the natural “straying rate”. However, this strategy risks delaying local adaptation of the new populations, and evidence for the success of this method is mixed at best (box 5.1; Withler 1982; Kallio-Nyberg *et al.* 2010; Griffiths *et al.* 2011; Anderson *et al.* 2014).

In partially anadromous populations, re-colonization can also occur via the production of anadromous offspring by resident individuals. For example, freshwater maternal origin for successfully spawning anadromous adults in populations of *O. mykiss* has been inferred using otolith microchemistry (Zimmerman and Reeves 2000; Courter *et al.* 2013). Indeed, such bet-hedging strategies by mothers and partial anadromy in general may have originated in freshwater systems that regularly experience disturbances such as landslides or intermittent flows that temporarily disconnect an upstream population from the ocean. How the two sources of colonists—downstream and out of basin anadromous strays or anadromous offspring

of resident mothers—contribute to a successful recolonization event is not well known, in part because determining origin of colonists often requires molecular or otolith techniques. Dam removals, such as the recent removals of the Elwha and Glines Canyon Dams on the Elwha River (Service 2011), will present valuable opportunities to study the source of successful colonists during the re-colonization process.

5.3.2 Re-expression

The onset of migration is cued by an organism's environment; if these cues change migration may be delayed or abandoned. An individual will benefit from moving between habitats if cues reliably forecast future resource availability. External (environmental) cues influence the internal cues (e.g. hormone levels) that initiate the morphological and physiological preparations for migration. While some external cues such as photoperiod and magnetic fields are stable, many others (temperature, flow, conspecific density) are susceptible to human disturbance. Thus, in some cases restoring anadromy may require resetting the environmental conditions that induce the expression of the migratory phenotype.

A current challenge in restoring anadromy is anticipating how oncoming climate change will alter the expression of anadromy via changes in water temperature and freshwater productivity (Crozier *et al.* 2008; Lassalle *et al.* 2008; Finstad and Hein 2012; Crozier and Hutchings 2014). Predictive models may be useful for identifying how populations and life-histories will respond to the changes in the environment. Using a regression approach to model climatic predictors of current anadromous Arctic charr (*Salvelinus alpinus*) occurrence in Norwegian lakes, Finstad and Hein (2012) projected increasing lake productivity, driven by catchment-wide terrestrial primary productivity, will increase freshwater growth opportunities leading to a reduction in the occurrence of anadromous populations by the end of the century. Conversely, in simulations from coupled state-dependent and bioenergetic models, Benjamin *et al.* (2013) predicted an increase in the anadromous life-history trajectory of a Washington (USA) population of *O. mykiss* under all but the most extreme scenarios of warming stream temperatures. However, when prey availability is increased with temperature (as is assumed under the climate scenarios in Finstad and Hein 2012) Benjamin *et al.* (2013) also predict a decrease in occurrence of the anadromous life-history. These studies and others (Kerr and Secor 2010; Satterthwaite *et al.* 2010; McMillan *et al.* 2011; Sloat and Reeves 2014) suggest mitigating for climate change by manipulating the freshwater environment to promote (re-)expression of anadromy would entail understanding the complex dynamics between climate change and stream temperature, primary productivity, and density of conspecific competitors. Further, approaches predicting future adaptive life-history responses to changes in the freshwater environment do so assuming the population has reached an evolutionary end-point, but do not capture the transition between freshwater environmental states or consider concomitant change in the marine environment. Thus, recognizing populations are expected to respond differently to climate change across their range (Beer and Anderson 2013), best practices for managing (re-)expression of anadromy will require preserving and

restoring a diverse portfolio of habitats and populations capable of supporting anadromy (Anderson *et al.* 2014; Sloat *et al.* 2014).

There are some scenarios where re-expression may be a viable restoration pathway. Indeed, it is common in hatcheries to increase growth conditions for salmonids, thereby maximizing juvenile growth rates and promoting the expression of anadromy earlier in their development (though this may also increase early maturity; Dodson *et al.* 2013). Where landscapes have been modified, restoring or subsidizing ecosystem processes to natural systems may permit re-expression of anadromy. This may be occurring in Alouette Lake, British Columbia. A population of kokanee, the resident form of sockeye, became established after dams constructed in the 1920's excluded all anadromous fish. Beginning in 1998, nitrogen and phosphorous additions have been made in an effort to boost lake productivity by replacing the marine-derived nutrients anadromous fish would have imported before they were excluded. Subsequently, kokanee density has increased six-fold (Shannon Harris, Ministry of the Environment, unpublished data). In 2005 and 2006, out-migrating juveniles were recorded down stream of the dam following experimental water releases, and in 2008 anadromous adults were observed for the first time since the construction of the dams (Godbout *et al.* 2011), suggesting recent nutrient restoration efforts in the lake may be responsible for the re-expression of anadromy. While the return of anadromous adults to Alouette lake is promising, their relatively low marine survival is a reminder that plastic responses to the environment, such as the re-expression of downstream migration, may not be adaptive. The Alouette Lake system will serve as an important case study for understanding how re-expression of anadromy in reservoir populations can contribute to restoration of migratory life histories in modified systems (Thrower *et al.* 2008).

5.3.3 Re-evolution

Re-evolution is an intriguing potential pathway toward restoring anadromy. There is increasing appreciation that evolution occurs rapidly, and several examples of evolution on contemporary timescales (a few centuries or less) come from anadromous fishes (Kinnison and Hendry 2004). To date several studies have documented the contemporary loss of migratory phenotypes due to selection against anadromy (e.g. Thrower *et al.* 2004; Palkovacs *et al.* 2008; Pearse *et al.* 2009). Promoting re-evolution of anadromy in these populations and others like them requires identifying and reversing the conditions that have favored residency.

Evolution can happen quickly when traits have high heritability and selection is strong. The clearest example of this occurs when a migration corridor is completely blocked to upstream migration (i.e. migratory survival is zero), such as by a dam or transplanted above an impassable migratory barrier such as a waterfall. For example, populations of *O. mykiss* isolated above migration barriers have repeatedly shown molecular divergence (Hecht *et al.* 2012; Pearse *et al.* 2014) and reduced expression of the migratory

phenotype (Thrower *et al.* 2004; Phillis *et al.* 2014), including osmoregulatory capacity and downstream movement behavior (Aykanat *et al.* 2011; Wilzbach *et al.* 2012; Phillis *et al.* 2014) in 100 years or less. Similarly, Palkovacs *et al.* (2008) show that dams constructed on coastal streams of Connecticut in the 1700's likely led to the repeated loss of anadromy in multiple independently landlocked alewife populations. Alternatively, if a migration corridor is opened there can be selection for anadromy. However, we know of no studies to unequivocally document the (re)evolution of anadromy (but see Pascual *et al.* 2001, for a possible case involving *O. mykiss*). This may be due to an asymmetry in the transitions between anadromy and residency and vice versa. For instance, where barriers block upstream migration, residency can evolve because anadromous alleles will be quickly lost from the population if migrating individuals are allowed to move downstream of the barrier; conversely, when a barrier is removed in a system that favors anadromy, resident phenotypes retain a non-zero absolute fitness and thus gene flow between life-history types may retard the rate the anadromous phenotype re-evolves. Indeed, results from simulated populations support asymmetry in the transition between anadromy and residency. In an ecogenetic model, anadromous populations confronted with an impassable dam either rapidly evolved residency or went extinct. However, when the dam was subsequently removed in the simulation, most populations re-evolved anadromy, but at rates that were unpredictable and on average slower than the rate anadromy was lost (Chapter 4).

While barriers select for resident forms by excluding anadromous phenotypes, there are many other cases where migratory phenotypes persist, but experience disproportionate reductions in survival and reproductive success as a consequence of anthropogenic activity. Fishing pressure in the ocean is a source of mortality that anadromous populations historically evolved in the absence of, and many commercially exploited marine fish stocks show evidence of phenotypic change (Kuparinen and Merilä 2007), including in heritable life-history traits capable of responding to selection (Conover and Munch 2002; Sharpe and Hendry 2009). In simulations of anadromous and resident brook charr (*Salvelinus fontinalis*), Thériault *et al.* (2008) show that populations exposed to increasing levels of fishing mortality targeting anadromous individuals leads to the rapid decrease in the average probability of migration, suggesting selective fisheries may generate evolutionary responses similar to those observed in systems with migration barriers (Phillis *et al.* 2014). Selection against anadromy may also result from conditions that reduce reproductive success. Migration is physiologically challenging and energy reserves are limited. Shifts in river temperatures and timing of peak flow due to climate change, emerging infectious diseases, and poorly designed fishways can compromise an individual's physiological state. Energy expended migrating upstream will reduce reproductive success if it comes at the expense of energy needed during breeding. To date we lack empirical evidence of evolutionary responses but it has been hypothesized these selective forces may shift threshold switch points in anadromous populations toward states that trigger earlier maturity or the outright adoption of the resident life-history (Hutchings 2011). However, detecting evolutionary changes from standard population monitoring is challenging (Kuparinen and Merilä 2007), yet important given the

growing realization that ignoring evolutionary processes can result in inefficient management of fisheries (Sharpe and Hendry 2009; Palkovacs 2011; Kuparinen *et al.* 2014).

5.4 Restoration in practice

5.4.1 Integrating pathways

In reality restoration of anadromy will be achieved through a combination of the above pathways. For example, the mechanisms of re-evolution and re-expression are not an either / or scenario—traits are simultaneously under genetic and environmental control, and thus trait evolution is the evolution of plasticity. Additionally, in many scenarios re-colonization will be a facilitated (box 5.1) or natural (boxes 5.2 & 5.3) complementary component of the restoration effort.

The re-colonization, re-expression, and re-evolution pathways operate simultaneously in recovering anadromy, but the timescales over which they operate differ. The process of re-expression is controlled by phenotypic plasticity, the individual's response to its environment, and will occur within a generation. Re-colonization will occur across generations, with recent evidence from salmonid systems suggesting self-sustaining populations can become (re-)established in only 10-20 generations (Milner *et al.* 2011; Pess *et al.* 2012). Re-evolution too will proceed over multiple generations, and theoretically could occur very rapidly if genetic variation for the migratory behavior is present and relative fitness strongly favors anadromy (Chapter 4). Thus, it is important that the temporal scales of management and restoration align. Indeed, restoration efforts meant to increase anadromy may appear counterproductive initially due to phenotypic plasticity, but yield expected results following multiple generations of selection on the underlying reaction norm (figure 5.3). Thus, evaluating success of restoration projects will need to occur on the relevant ecological and evolutionary timescales the pathways operate.

5.4.2 The role of resident populations

It is relatively unknown what role resident populations will play in the recovery of the anadromous life history. Genetic admixture upon secondary contact between resident and anadromous life-history types could slow the re-evolution of anadromy. In *O. mykiss*, pure resident and anadromous-resident crosses can produce anadromous offspring (Zimmerman and Reeves 2000; Courter *et al.* 2013), but their marine survival tend to be much lower, particularly in cases where the resident population has been isolated from the marine environment for many generations (Thrower and Joyce 2004; Thrower *et al.* 2008; Weigel *et al.* 2013a). This suggests selection on traits favored during marine migrations is relaxed or opposed during

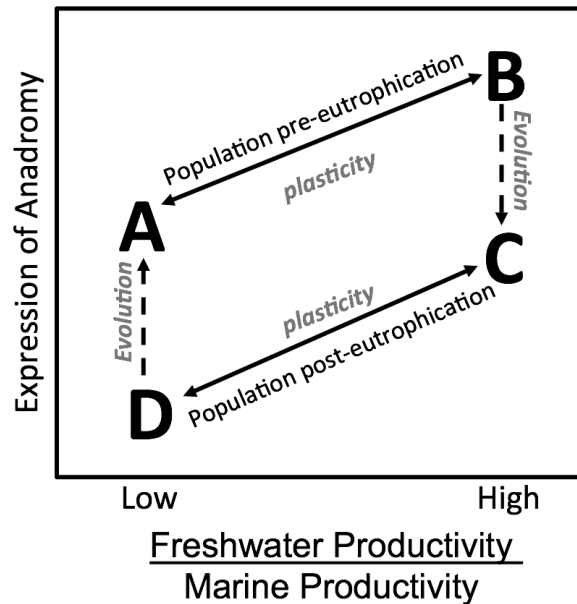


Figure 5.3: An illustration of a partially anadromous population under simultaneous environmental and evolutionary control. Initially (A) approximately 50% of the population expresses anadromy due to low freshwater productivity relative to marine productivity. Cultural eutrophication increases the expression of anadromy as individuals' growth exceeds their threshold size (A to B). If cultural eutrophication persists, freshwater growth opportunities favor residency (B to C) and mean population threshold sizes will increase, decreasing anadromy. Because the relative difference between freshwater and marine productivity is now smaller, the evolutionary endpoint at C predicts less anadromy than the evolutionary endpoint at A. Restoring the system to its pre-cultural eutrophication state will initially decrease the proportion of the population that expresses anadromy (C to D) as growth conditions will be too poor to exceed the now larger threshold sizes. Over subsequent generations the rate of anadromy will increase (D to A) as smaller threshold sizes are again favored. Solid lines represent plastic responses to changes in the environment that occur within a generation. Dashed lines represent evolutionary changes that occur across many generations. Properly evaluating success of restoration projects requires recognizing that plastic and evolutionary responses occur on different timelines.

adaptation to a complete freshwater life-cycle, though low genetic diversity due to founder effects may also be responsible in recently isolated populations (Thrower and Joyce 2004). Certain systems, such as those with large rivers or lakes and reservoirs that allow fluvial and adfluvial migrations, respectively, may favor the retention of migratory alleles (Thrower *et al.* 2008). For instance, following a barrier removal in a small stream, Weigel *et al.* (2013b) found migratory parents (both anadromous and fluvial) produced juveniles later detected migrating downstream and returning as adult steelhead, whereas non-migratory resident parents did not. Thus, gene flow from resident populations may be useful for restoring the anadromous life history, but may decrease population productivity.

In some cases gene flow could be limited if reproductive barriers have evolved during isolation. For

example, Pearse *et al.* (2009) found that a resident *O. mykiss* population was reproductively isolated from the ancestral anadromous population upon secondary contact after only 100 years. Reproductive isolation may come about if traits such as spawn timing, habitat requirements, or mate size preference are traits correlated with migratory life-history. This is often the case where reproductively isolated resident and anadromous populations have been reported to occur in sympatry, including spatial and temporal reproductive isolation in steelhead and rainbow trout (Zimmerman and Reeves 2000), sockeye and kokanee (Wood and Foote 1996), and anadromous and freshwater stickleback (Hagen 1967; Karve *et al.* 2008). A period of allopatry, either due to natural or human barriers, are likely responsible for the initial divergences in these populations which are maintained in sympatry by pre-zygotic (assortative mating) and post-zygotic (reduced hybrid life-history fitness) isolating mechanisms. These cases suggest outcomes of barrier removal projects intended to reconnect resident and anadromous populations will depend on whether reproductive isolation is maintained in sympatry. For example, recent installations of fishways will soon allow anadromous alewives access to Rogers Lake, CT, where they will encounter land-locked alewives that evolved residency when colonial dams isolated them from the marine environment (Palkovacs *et al.* 2008). In adapting to a full life-cycle in lakes, resident alewives have diverged from anadromous alewives in a number of foraging traits (gape width and gill raker spacing; Palkovacs and Post 2008; Palkovacs *et al.* 2008) and reproductive traits (spawn timing; E.P.P, *pers. obs*) suggesting the possibility that pre- and post-zygotic isolating mechanisms may maintain the divergent life-history types even in sympatry.

5.4.3 Unintended consequences of restoring anadromy

Restoring anadromy may have unintended or undesired ecological and cultural consequences. Anadromous fishes may deliver nutrients to already nutrient-rich ecosystems, increasing the risk of eutrophication or other problems with drinking water. As healthy anadromous alewife runs are restored to Connecticut lakes, alewives are expected to switch from net exporters to net importers of phosphorous, furthering nutrient-loading in lakes already experiencing cultural eutrophication (box 5.2; West *et al.* 2010). Similarly, the restoration of threatened anadromous salmon populations in Cedar River, Washington, has excluded sockeye salmon out of concern their high spawning abundance could lead to eutrophication of Seattle's source of drinking water (box 5.3; City of Seattle 2000). Also of concern, anadromous fish have been shown to transport contaminants to freshwater ecosystems (Ewald *et al.* 1998; Krümmel *et al.* 2003) which bioaccumulate in consumers, including resident fish (Gregory-Eaves *et al.* 2007) and grizzly bears (Christensen *et al.* 2005). As always, post-project monitoring of the intended *and unintended* consequences of restoration will be critical.

5.5 Frontiers in restoration of anadromy

5.5.1 Eco-evolutionary feedback loops

Given anadromous fish can strongly impact ecosystems, and ecosystem conditions can control rates of anadromy, there is a strong possibility that there are either positive or negative eco-evolutionary feedback loops operating in anadromous systems. Anadromy is both a response and a driver of ecosystems. In other words, rates of anadromy may control future rates of anadromy. These feedback loops can be mediated either through direct selective pressures exerted by anadromy itself (e.g., the density of conspecific competitors) or indirectly through the modification of environmental conditions (e.g., increased ecosystem productivity mediated by nutrient excretion) that influence the expression of anadromy. These feedback loops could either be positive (anadromy modifies the environment, thereby selecting for anadromy) or negative (anadromy modifies the environment, thereby selecting against anadromy). These feedbacks could exist within species or across species. One such feedback involves the impact of anadromous alewife predation on life history evolution in *Daphnia ambigua* (Walsh and Post 2011), which in turn may have further impacts on trophic interactions and ecosystem function (Walsh *et al.* 2012). Another example is the hypothesized feedback loop whereby nutrients deposited by adult salmon increase productivity and future carrying capacity of fresh waters, thereby altering the trajectory of evolution for both salmon and the other species in the watershed.

5.5.2 Ecosystem hysteresis

It is possible that feedback loops could drive hysteresis (Beisner *et al.* 2003) whereby it becomes difficult to restore anadromy without intervention. Successful restoration of anadromy may require restoration of the ecosystem to the prior 'anadromous state,' in order to re-establish the anadromous life history. One example could be the restoration of anadromous alewife populations that require large-bodied zooplankton to be present in a lake in early spring. Landlocked populations eliminate these large-bodied prey items and may, therefore, put the ecosystem into an alternate state that makes anadromy difficult or even impossible to restore without an ecological manipulation. Restoring the environment to an 'anadromous state' is really just one facet of manipulating the environment to shape the costs and benefits of anadromy, tipping the scales from residency back to anadromy. This is commonly done with restoring connectivity such as fish passage and dam removal, but should also be considered for diverse ecological processes, including those driven by anadromous fishes themselves.

5.5.3 Learning from large scale experiments

Efforts to restore anadromy often represent large-scale experiments that can inform questions that are fundamental to ecology and evolution as well as important applied issues. Much of what we know about anadromy comes from large-scale perturbations. Large-scale perturbations can make new habitat accessible, isolate previously contiguous habitat, or restore connectivity between previously isolated habitats. Colonization of new habitat both within and outside the native range of salmonids provides insight into the emergence of anadromy (O'Neal and Stanford 2011), rapid evolution to the costs of migration (Kinnison *et al.* 2001), and the ecological consequences of the anadromous life-history (Milner *et al.* 2011; O'Neal and Stanford 2011). Isolation of closely related anadromous and resident populations have contributed substantially to our understanding of adaptation, including leading the way in the exploration of genomics of adaptation (e.g. Hohenlohe *et al.* 2010; Martínez *et al.* 2011; Czesny *et al.* 2012). Additionally, anadromous-resident systems are well-suited for study of evolutionary divergence and speciation questions (Wood and Foote 1996; Taylor and McPhail 1999). Removing barriers that isolate populations of resident and anadromous individuals of a partially anadromous species can inform which pathways (re-colonization, re-expression, and re-evolution) are most important and or complementary in the process of restoring anadromy. Unfortunately, restoration efforts are often poorly monitored, thus our understanding of past “large-scale experiments” has been greatly limited. As such, a greater emphasis on pre-and-post-restoration monitoring will provide valuable information that cannot be gained from small-scale manipulations (Roni *et al.* 2010).

5.6 Conclusions

Here we outlined the conceptual basis for anadromy as it relates to the application of restoring this important migratory phenotype. While anadromous fishes have declined in many regions due to anthropogenic pressures, there are enormous on-going efforts to restore populations of anadromous fishes. These restoration efforts serve as large-scale experiments that can illuminate the ecological and evolutionary causes and consequences of life-history expression. Recent and on-going restoration efforts offer spectacular success stories as well as surprising failures. Thus, these restoration efforts should be well-monitored so that they can inform the adaptive management cycle (*sensu* Walters and Hilborn 1978), thereby guiding future restoration efforts.

Recent papers have called for restoration to focus on restoring “processes” rather than “patterns” (Beechie *et al.* 2010). This concept applies to the restoration of anadromy as well—the goal of restoring anadromy should not be singularly focused on increasing the abundance of a migratory life-history, but rather preserving and restoring the diversity of habitats that support it (Sloat *et al.* 2014) thus maintaining

the processes that drive the evolution and expression of anadromy. Further, restoration often focuses on a specific population or location, but these efforts can contribute to larger-scale patterns of resilience. Decision frameworks that prioritize restoration projects across regional landscapes (e.g., Anderson *et al.* 2014) will be useful tools for identifying projects that increase anadromy at the local scale and life-history and population diversity on the metapopulation scale.

Finally, there is a unique opportunity to restore anadromy now. Dams have isolated partially anadromous populations, but locally-adapted anadromous genes may persist for tens of generations in the resident population (Thrower *et al.* 2004; Phillis *et al.* 2014). Re-evolution is a promising but under-appreciated pathway to restoring anadromy; restoring the costs and benefits of migration to their natural state may return the favor to the anadromous form if it occurs before reproductive isolation can evolve. Fortunately the window of opportunity for removal and re-evolution may overlap with the time horizon of dam removals. (Chapter 4) Over 85% of dams in the US will require upgrades or decommissioning by the year 2020 (Doyle *et al.* 2003). Given that most dams are relatively recent but aging rapidly, there is a closing window of opportunity for preserving this ecologically, culturally, and commercially important life history.

Box 5.1: Anadromous brown trout in Finland

The past century has seen a dramatic decline in brown trout (*Salmo trutta*) in the coastal rivers of Finland that drain to the Baltic Sea. The cause of the declines are multiple (e.g. overharvest, damming, loss of habitat), but have disproportionately affected the migratory stocks. Only a fraction of the of the estimated 60 historical anadromous stocks (“sea trout”) in Finland persist, all of which are declining or endangered. Although the IUCN lists brown trout as “Least Concern,” they recognize that the migratory variants have markedly declined (IUCN 2011) . It follows that Finland is faced with empty rivers that once accommodated migratory forms of this important fish for recreational fishers. On the other hand, resident brown trout forms still remain in approximately 30 rivers (Kallio-Nyberg *et al.* 2010). Managers have questioned whether anadromy could be induced from these resident forms to “rescue” the threatened migratory types.

The best populations for a migratory “rescue” strategy was explored in a study (Kallio-Nyberg *et al.* 2010) in which different resident populations were released in two rivers to determine which had the greatest potential to behave like migratory trout. It was previously shown that residents released in fjords are able to survive and behave in migratory fashion (Jonsson *et al.* 1995). This pathway to restoration uses on two mechanism: recolonization which is assisted by outplanting and use of hatcheries, and plasticity to a changing environment (trait variation, behavioral plasticity). In one river, the tendency to choose a particular life history was largely genetically controlled– meaning that residents remained residents 70% of the time. However in the other river, residents behaved the same as migrants and, even the same as crosses of the two. This suggested an environmental effect that superseded the genetic effect. The results also show that adoption of migratory behavior can occur quickly (within a generation).

These results suggest the potential of using residents to stock empty rivers and evolve anadromous fish. Important genetic considerations include evaluating the genetic similarity of fish being introduced to previous migratory fish (DeHaan *et al.* 2011). Additionally, the environmental considerations must include similarity of new river to resident river, and appropriate selection of the release site. Whether this life history choice is retained in subsequent populations remains unanswered.

Box 5.2: Alewives in Connecticut, USA

The alewife (*Alosa pseudoharengus*) can be considered the 'Jekyll and Hyde' of fisheries management. Its anadromous form was once an important fishery resource along the Atlantic Coast of North America; however, anadromous alewife populations have declined significantly, especially since the mid-1960s (Limburg and Waldman 2009; ASMFC 2012). Abundances are now so low that the anadromous alewife has been considered for protection under the US Endangered Species Act. In contrast, the landlocked alewife, most famous for its colonization of the Laurentian Great Lakes, is widely considered to be a harmful invasive species due to its negative impacts on water quality and native fish diversity (Stewart *et al.* 1981; Mills *et al.* 1995).

In Connecticut, USA, where the two life history forms co-occur, the anadromous form is considered to be 'native' while the landlocked form is considered to be 'invasive' (Jacobs and O'Donnell 2002). Therefore, management efforts directed towards anadromous alewife runs focus on restoration and recovery, whereas management efforts directed towards landlocked populations focus on population control and limiting their spread to other lakes. Despite being managed as a separate species, genetic data show that landlocked alewives in coastal Connecticut lakes are recently diverged from their downstream anadromous ancestors, likely as a result of human constructed dams (Palkovacs *et al.* 2008).

To restore anadromous fish populations throughout the state, Connecticut has made fishway construction a mandatory part of dam relicensing on streams with anadromous fish runs. Interestingly, many dams that could be targets for restoration projects separate above-dam landlocked alewives from their below-dam anadromous progenitors. One such project involves a series of fishways being constructed on three dams on Mill Brook, a tributary of the Connecticut River with a landlocked population at its headwaters in Rogers Lake. When anadromous alewives had access to Rogers Lake, this system likely supported one of the largest anadromous alewife runs in the state. The goal for this project is to restore anadromous alewife access to the spawning and juvenile rearing habitat available in the lake.

The final fishway on Mill Brook, at the outlet to Rogers Lake, was completed in 2014. With this fishway built, anadromous alewives again have access to Rogers Lake. The outcome of the re-invasion of anadromous alewives into the lake will be monitored closely. Several outcomes are possible: (1) the anadromous population may successfully recolonize the lake, replacing the landlocked population due to greater fecundity, (2) the two populations may introgress and the resulting population may display an anadromous or mixed life history strategy, (3) the two populations may coexist as separate breeding populations (i.e., speciation), or (4) the ecology of the lake may have shifted, potentially due to the effects of the landlocked population itself (Post *et al.* 2008; Palkovacs and

Post 2009), preventing successful re-colonization by anadromous alewives. This project provides an example of how restoration can be used as a large-scale experiment to learn about the ecology and evolution of anadromy and freshwater residency in a natural ecosystem.



Figure 5.4: A fishway was completed on Rogers Lake Dam in Old Lyme CT, USA in 2014 (above). This fishway is the final piece of a restoration project begun in 1998 and involving fishways on three dams on Mill Brook, a tributary of the Connecticut River. This final fishway will allow anadromous alewives (inset, top) from Mill Brook to access the spawning habitat in Rogers Lake, which is currently inhabited by landlocked alewives (inset, bottom) that became residualized in the lake when the dams were constructed. The outcome of this restoration project of will be monitored closely. Photo credits: Steve Gephard, David Post (inset).

Box 5.3: Pacific salmon in Cedar Creek, Washington, USA

The Landsburg Diversion Dam on the Cedar River, Washington, USA, was constructed to supply water to the city of Seattle in 1901, cutting off 33 km of anadromous Pacific salmon habitat until fish passage facilities were built in 2003. These fish passage facilities allow coho salmon (*Oncorhynchus kisutch*), Chinook salmon (*O. tshawytscha*), and steelhead (*O. mykiss*) to access the Cedar River above Landsburg and its tributaries (Anderson and Quinn 2007), but not sockeye salmon due to concerns about excess nutrient inputs to the watershed. Historic fish populations above the dam included resident rainbow trout, mountain whitefish, cutthroat trout, speckled dace, and several sculpins. The goal of the project was to mitigate migration blockage for the recovery of listed species (Chinook salmon, steelhead, and bull trout) while safely managing the drinking water of the city.

Restoration of anadromy above Landsburg has been through the natural straying of adult salmon from below the diversion (Kiffney *et al.* 2009). The number of Chinook and coho salmon passing above Landsburg ranged between 50 and 200 between 2003 and 2006, increasing each year (Kiffney *et al.* 2009). Furthermore, the reproductive success of first generation coho salmon, defined as the number of returning adult offspring from an initial female colonizer, was consistently above replacement (Anderson *et al.* 2010). Spatial expansion of anadromous salmon was also due to juvenile salmon dispersal (Anderson *et al.* 2008; Pess *et al.* 2011). Juvenile coho salmon migrated after emergence and entered the closest tributary to the main spawning area (Anderson *et al.* 2008).

Several factors are contributing to the initial success. First, natural recolonization of salmon can occur rapidly. This is due to a nearby source population, high habitat quality in the newly available habitats, and low densities of resident populations (Kiffney *et al.* 2009). Second, resident populations have responded positively to anadromy, suggesting novel subsidies. The presence of anadromous salmon above Landsburg has resulted in distribution and abundance shifts of resident trout. Before recolonization, the majority of resident trout occurred towards their upstream distribution extent (Kiffney *et al.* 2009). Today higher densities of trout occur just upstream of the Landsburg diversion in close proximity to high coho spawning density. Third, there has been evidence of selection on breeding data and body size during colonization (Anderson *et al.* 2010).

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Chapter 6

Conclusion

Migratory species are increasingly threatened by barriers to movement (Wilcove and Wikelski 2008). Pacific salmon, in particular, have been affected: Gustafson *et al.* (2007) estimate 29% of 1,400 historical populations in the Pacific Northwest have gone extinct since the late 1700's, largely due to construction of impassable dams (National Research Council 1996). Further, dams have extirpated a non-random subset of species, life histories, and genetic diversity (Lindley *et al.* 2006; Gustafson *et al.* 2007) and continue to drive genetic and phenotypic trait change in the remaining populations (McClure *et al.* 2008). There is, however, a growing interest in removing dams (Service 2011) and otherwise restoring connectivity between freshwater and marine habitats for migratory populations. Doing so would attempt to reverse an anthropogenic selection regime that has shaped the evolutionary trajectory of salmonid populations for tens to hundreds of generations, a timescale that has proven more than sufficient for significant evolutionary changes to occur in many species (Hendry and Kinnison 1999), including salmon (Kinnison and Hendry 2004). My dissertation has been motivated by the challenge now facing salmon biologists and managers: How do we integrate our growing appreciation for contemporary evolution into the established practices of conservation biology and restoration science?

In Chapter 2 I established that migratory behavior has a heritable genetic basis that can evolve in 100 years or less. By estimating the switch point and proximate cue (body size) underlying the migratory decision, I was able to identify evolutionary shifts in their distributions. The simultaneous evolution of these two traits, in opposite direction, highlight that with strong directional selection, migratory tendency can evolve over only a few generations. This represents a rather novel finding across species and threshold traits (Roff 2011). Several studies have documented heritable variation in either the threshold switch point or proximate cue (Moczek 2003; Piche *et al.* 2008; Buzatto *et al.* 2012), but few examples exist of the traits evolving in response to selection (Tomkins *et al.* 2011). I suspect the

lack of evidence is not for a lack of examples—indeed, humans are in the process of increasing the prevalence of contemporary evolution (Hendry *et al.* 2008; Darimont *et al.* 2009)—but rather reflect two conditions. First, our ability to establish pedigrees in non-model organisms and wild populations has provided data that would have historically been impossible or prohibitively expensive to collect; this data is then leveraged with quantitative genetic models (e.g., Wilson *et al.* 2010; Buoro *et al.* 2012) that have grown in utility with the increase in computational power available to the modern researcher⁵. This is a promising development for managers: assessing evolutionary potential (heritable genetic variation) and history (evolutionary divergence of isolated populations) prior to restoration efforts should facilitate managing the (re-)evolution of anadromy in concert with population recovery.

The second explanation for the lack of examples of contemporary evolution of threshold traits is the role phenotypic plasticity may play in modifying trait expression. The migratory behavior is clearly under both genetic and environmental control (Chapman *et al.* 2011; 2012; Dodson *et al.* 2013), but the results from Chapter 2 can only speak to the genetic controls of migration under a single environment (and a rather contrived, growth maximizing environment at that)⁶. Indeed, there is conflicting evidence and debate over whether increasing growth conditions will increase or decrease an individual's probability to adopt the anadromous life history (Dodson *et al.* 2013; Sloat *et al.* 2014). This is a pressing question should we hope to adaptively manage anadromous populations in the face of oncoming climate change. Chapter 2 does not offer a resolution; however, I argue my results agree with the explanation proposed by Dodson *et al.* (2013). The authors argue that the fastest growing fish early in life adopt a development trajectory that prepares them for migration, while among the slower growing fish a decision is made at a later date, with larger males opting to mature, and females and smaller males delaying their development decision (Paez *et al.* 2010; 2011). This explanation is appealing because it satisfactorily explains how the larger fish in a cohort can be made up of both smolts and mature parr (Figure 2.1 d). There is valuable research still to be done here: a study that follows individual growth across multiple environments from early development to expression of the migratory behavior would help resolve how and when growth environment influences the decision to migrate. Nevertheless, it is clear from the findings in Chapter 2 that evolution of migratory behavior is likely to have occurred in populations isolated by migratory barriers and that restoring these populations will require special consideration of their evolutionary history.

The results in Chapter 3 highlight the consequences contemporary evolution can have on ecological systems. I show that evolutionary loss of anadromy in above barrier *O. mykiss* populations is associated with lower juvenile densities, which indirectly reduce the effects these populations have on many

⁵As an aside, can you imagine what R.A. Fisher would have accomplished if he had access to the computers ecologists and evolutionary biologists now consider indispensable tools of the trade?

⁶This is not to say I did not try to test for plasticity. A component of Chapter 2 included an experiment raising the above- and below-barrier offspring at low and medium rations. Unfortunately, this experiment ultimately demonstrated that *O. mykiss* are cannibals: many of the tanks that began the experiment with 30 fish ended with one fat fish. Subsequent discussions with hatchery managers and fish culturists confirmed that my discovery was far from novel.

community and ecosystem processes. Several studies have tested the ecological effects of intra-specific trait divergence (Harmon *et al.* 2009; Palkovacs and Post 2009), but few have considered how population density changes with trait divergence and what consequences this may have on ecological systems (Bassar *et al.* 2010; 2012). It is perhaps not a surprise that the effect size fish have on stream ecosystems depends on density, but nonetheless this is additional and novel evidence suggesting anadromous salmonids play a role in stream ecosystems that cannot be replicated by resident forms of the same species (Schindler *et al.* 2003). Further, an intriguing, but untested possibility is that an eco-evolutionary feedback loop (Post and Palkovacs 2009) could drive hysteresis (Beisner *et al.* 2003) whereby anadromy modifies the environment in a way that further selects for anadromy (Chapter 5). For example, nutrients deposited by salmon carcasses may boost productivity and carrying capacity of fresh waters, which promotes further evolution of the anadromous life history. Consequently, restoring anadromy may require manipulating the environment to favor migration, as may be the case in Alouette Lake where nutrient additions preceded the return of anadromous sockeye to the population following a century of isolation in the reservoir (Chapter 5; Godbout *et al.* 2011).

Two possible eco-evolutionary feedbacks may emerge in the resident and anadromous *O. mykiss* system. First, in the mesocosm experiment, results suggest fish density promotes a positive feedback between sediment cover and invertebrate biomass, the consequence, I argue, of bioturbation caused by intra-specific competition. May it be possible that *O. mykiss* densities associated with anadromy modify juvenile habitat in a way that increases available invertebrate biomass, favoring growth conditions and future anadromy? And does this feedback inhibit the evolutionary transition between residency and anadromy? Second, are resident populations adapted to local densities as suggested in Chapter 3 (see also Figure A.2)? And does this greater sensitivity to the effects of density on juvenile survival further constrain population growth rate? Answering these questions requires integrating ecological and evolutionary perspectives. In general, the emerging field of eco-evolutionary dynamics stand to play a large role in conservation biology wherever ecological and evolutionary processes are coupled.

6.1 Future directions

In this section I consider the limitations of chapters 2, 3, and 4 and directions forward to address these limitations.

6.1.1 Is Scott Creek special?

Isolation of *O. mykiss* populations above impassable barriers has been quite common across their range and subsequent evolutionary divergence surprisingly predictable (Pearse *et al.* 2014). Nevertheless, Chapters 2 and 3 represent the outcome of isolation only in the Scott Creek watershed and therefore some findings may be the product of local conditions or the experimental design rather than generalities that can be applied wherever *O. mykiss* have been isolated above impassable barriers. For instance, though unlikely, it is possible that an *O. mykiss* population existed undetected above the barrier waterfall prior to the 1910 introduction of the below-barrier individuals. It is also impossible to assess the roles of genetic drift and founder effects in evolutionary divergence of the above-barrier population. Founder effects occur when a small number of colonizing individuals are not representative of their original population, which may have been the case if the juvenile *O. mykiss* used in the above-barrier introduction were below-barrier juveniles that had not yet migrated downstream. Likewise, juveniles collected from the field and brought to the hatchery for the breeding experiment may not have been representative of their original population. A second instance of founder effects surely did occur during the breeding experiment designed to test for adaptive phenotypic evolution to the novel above-barrier environment. The number of families were determined by the number of parents that matured, with females being the limiting factor. A greater number of families would have ruled out the possibility that the findings in Chapter 2 were the result of parents not representative of the sampled population. Further, females from the below-barrier sampled population were far less likely to be mature than above-barrier females (most below-barrier origin fish were still smolting at age-3+). Anecdotally this supports our conclusion that above-barrier populations have adapted to the novel impassable barrier, but it also suggests below-barrier mothers were not representative of the sampled populations (more likely to mature in freshwater) and that our results may underestimate the migratory tendency of below-barrier offspring. Determining whether the results in Chapter 2 are the product of the Scott Creek isolation event or experimental design will require repeating the experiment with more families (10's to 100's ideally) in multiple watersheds where *O. mykiss* have been isolated by an impassable barrier.

The juvenile density differences between the above- and below-barrier populations reported in Chapter 2 are suggestive of an outcome of the evolutionary loss of anadromy; however, there are other explanations that cannot be ruled out. While subjectively the habitats sampled above and below the barrier waterfalls appeared similar, there is no data to assess the extent to which environmental differences contributed to the juvenile densities observed. Additionally, *O. mykiss* biomass may better reflect population differences given the above-barrier, resident populations consist of both young-of-year offspring and the older, larger age classes, whereas in below-barrier populations the older age classes predominately migrate to sea. It also worth considering that density surveys occurred prior to the severe over-summer mortality that is common in this system (Hayes *et al.* 2008; Sogard *et al.* 2012) which may diminish any density

or biomass differences that appear shortly after fry emergence, particularly if over-summer mortality is density dependent. Nevertheless, the possibility that reduction in juvenile *O. mykiss* density is an evolved response to life above the barrier waterfall is intriguing, particularly in light of the results of the mesocosm experiment that demonstrate the large effects fish density can have on stream ecosystems. A broad survey of juvenile *O. mykiss* densities and environmental metrics in systems with above and below barrier populations, coupled with new genetic markers for ecotype divergence (Martínez *et al.* 2011; Pearse *et al.* 2014) would improve our understanding of if (or how much) evolutionary loss of anadromy contributes to reductions in juvenile density.

6.1.2 Extensions of the Individual-Based Model

The environment plays an important role in the expression of life-histories generally (Stearns 1989), and salmonid migration specifically (Hutchings 2011; Dodson *et al.* 2013; Ohms *et al.* 2014; Sloat and Reeves 2014). However, controlling for environmental effects in natural systems is notoriously difficult (particularly if the unit of replication is considered a watershed, as would be the case in Chapters 2 and 3) and controlled experiments produce unintended results (see footnote 2). Computer simulations, such as the Individual-Based Model built for Chapter 4, can be useful here for exploring questions about the role of the environment in the expression and evolution of anadromy. For instance, in Chapter 4 by using a constant normal distribution from which to draw fish lengths (equation 4.1) I assumed the freshwater environment was spatially and temporally invariant, which is an oversimplification. Future extensions of the Individual-Based Model could allow for the freshwater environment to become more or less productive over time (change μ_L) to reflect predicted changes in the freshwater environment due to climate change, or incorporate multiple freshwater habitats of different quality (each habitat would have an equation 4.1, with individual's length a function of time spent in each habitat) to reflect the ability of individuals to redistribute themselves to take advantage of freshwater habitat heterogeneity (e.g. pools vs. riffles, upstream vs. downstream vs. lagoon rearing). The Individual-Based Model could also incorporate sex of the individual into the migration decision to better represent the how the different genders respond to environmental cues (Figure 2.1 d; Ohms *et al.* 2014).

Multiple traits may evolve in response to selection against anadromy. Two such traits are the threshold size at which individuals migrate and the growth rate of individuals. However, for simplicity only the former was allowed to evolve in the Individual-Based Model, despite evidence both had evolved and exhibited high genetic correlation (Table 2.1). Updating the Individual-Based Model to allow both to evolve, with and without genetic correlation, would improve the reality of the model and make it possible to test whether the correlated and opposing changes in growth rate and threshold size speed the evolutionary loss or recovery of anadromy.

6.1.3 Concluding remarks

Partially anadromous populations present unique challenges for managers, particularly in light of contemporary evolution. Evolution in response to disturbances may promote population resilience in partially migratory species like *O. mykiss*, but will do so at the expense of the commercially and ecologically important anadromous life history. The obvious solution for managers tasked with restoring the anadromous life history is to remove the disturbance; however, the time it takes to recover anadromy following removal of the disturbance may be longer than it took to be lost (Chapter 4). This has important implications for how managers evaluate success of restoration projects, particularly large-scale projects involving significant investment of time and political capital, such as dam removals. Evaluating the recovery of anadromy on timescales not aligned with the evolutionary processes at work risks concluding the dam removal failed to deliver on the goal of restoring anadromy, possibly jeopardizing approval of future large-scale restoration projects. However, the greater risk is inaction. Pacific salmon are a weedy species on a geologically dynamic landscape (Montgomery 2003). They have (re-)colonized much of western North America's watersheds since the last glaciation cycles of the Pleistocene (Waples *et al.* 2008; Wilson and Turner 2009), and continue to (re-)colonize and adapt to native (Milner *et al.* 2011; Pess *et al.* 2012) and non-native rivers (Kinnison *et al.* 2001; Pascual *et al.* 2001) on contemporary timescales. By maintaining and restoring the habitats and genetic diversity that promote anadromy, restoration of this commercially and ecologically important migratory life history should be successful.

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Appendix A

Supplemental tables and figures for Chapter 3

Table A.1: Multilevel model results. Posterior means and 95% highest posterior density (HPD) credible intervals are reported. $P_{trt < bc}$, posterior probability the treatment decreases the response variable relative to the base case (low density, above-barrier genetic origin); $P_{trt < nofish}$, posterior probability the genetic origin or density treatment decreases the response variable relative to the no fish treatment; $P_{d < o}$, posterior probability the density treatment decreases the response variable relative to the origin treatment.

Response Variable	Treatment	Mean (95% CI)	$P_{trt < bc}$	$P_{trt < nofish}$	$P_{d < o}$
Algal Accrual	No Fish	1.20 (0.56-2.46)	0.30	—	—
Algal Accrual	Origin	0.91 (0.58-1.40)	0.67	0.78	—
Algal Accrual	Density	1.20 (0.77-1.86)	0.19	0.49	0.17
Algal Accrual	Origin+Density	1.09 (0.59-2.03)	0.38	0.60	—
Silt Cover	No Fish	1.93 (0.61-5.81)	0.12	—	—
Silt Cover	Origin	1.25 (0.76-2.04)	0.19	0.78	—
Silt Cover	Density	0.14 (0.08-0.23)	>0.99	>0.99	>0.99
Silt Cover	Origin+Density	0.17 (0.09-0.37)	>0.99	>0.99	—

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Table A.1 – continued from previous page

Response Variable	Treatment	Mean (95% CI)	$P_{trt < bc}$	$P_{trt < nofish}$	$P_{d < o}$
FBOM	No Fish	1.35 (0.73-2.47)	0.15	—	—
FBOM	Origin	0.78 (0.53-1.15)	0.91	0.96	—
FBOM	Density	0.63 (0.43-0.91)	0.99	0.99	0.80
FBOM	Origin+Density	0.49 (0.28-0.83)	0.99	>0.99	—
Leaf Decay	No Fish	0.95 (0.61-1.44)	0.61	—	—
Leaf Decay	Origin	0.98 (0.76-1.26)	0.56	0.43	—
Leaf Decay	Density	1.27 (0.98-1.63)	0.03	0.08	0.08
Leaf Decay	Origin+Density	1.24 (0.86-1.79)	0.11	0.09	—
Total Invertebrates	No Fish	2.10 (0.96-4.71)	0.03	—	—
Total Invertebrates	Origin	1.23 (0.79-1.90)	0.17	0.92	—
Total Invertebrates	Density	0.43 (0.28-0.67)	>0.99	>0.99	>0.99
Total Invertebrates	Origin+Density	0.53 (0.28-0.98)	0.98	>0.99	—
Predator Invertebrates	No Fish	3.83 (1.46-10.95)	0.01	—	—
Predator Invertebrates	Origin	1.04 (0.62-1.80)	0.44	0.99	—
Predator Invertebrates	Density	0.52 (0.30-0.86)	0.99	>0.99	0.97
Predator Invertebrates	Origin+Density	0.54 (0.26-1.11)	0.95	>0.99	—
Prey Invertebrates	No Fish	2.00 (0.88-4.55)	0.05	—	—
Prey Invertebrates	Origin	1.26 (0.81-2.02)	0.15	0.88	—
Prey Invertebrates	Density	0.43 (0.27-0.68)	>0.99	>0.99	>0.99
Prey Invertebrates	Origin+Density	0.54 (0.28-1.01)	0.97	>0.99	—
Invulnerable Invertebrates	No Fish	2.27 (0.42-13.21)	0.16	—	—
Invulnerable Invertebrates	Origin	1.28 (0.44-3.86)	0.32	0.76	—

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Response Variable	Treatment	Mean (95% CI)	$P_{trt < bc}$	$P_{trt < nofish}$	$P_{d < o}$
Invulnerable Invertebrates	Density	0.51 (0.18-1.53)	0.90	0.96	0.89
Invulnerable Invertebrates	Origin+Density	0.65 (0.14-2.94)	0.72	0.93	—
Vulnerable Invertebrates	No Fish	2.05 (0.93-4.40)	0.03	—	—
Vulnerable Invertebrates	Origin	1.11 (0.71-1.72)	0.30	0.94	—
Vulnerable Invertebrates	Density	0.43 (0.28-0.68)	>0.99	>0.99	>0.99
Vulnerable Invertebrates	Origin+Density	0.48 (0.26-0.89)	0.99	>0.99	—
Invertebrate Diversity	No Fish	1.15 (0.94-1.40)	0.07	—	—
Invertebrate Diversity	Origin	1.00 (0.90-1.12)	0.46	0.92	—
Invertebrate Diversity	Density	0.91 (0.82-1.02)	0.95	0.99	0.90
Invertebrate Diversity	Origin+Density	0.92 (0.79-1.07)	0.88	0.99	—
Phosphate	No Fish	-0.05 (-0.39-0.27)	0.64	—	—
Phosphate	Origin	0.03 (-0.14-0.21)	0.36	0.29	—
Phosphate	Density	0.05 (-0.12-0.22)	0.28	0.25	0.44
Phosphate	Origin+Density	0.07 (-0.17-0.30)	0.26	0.20	—
Nitrate	No Fish	-0.01 (-0.17-0.13)	0.59	—	—
Nitrate	Origin	0.01 (-0.04-0.06)	0.36	0.36	—
Nitrate	Density	-0.01 (-0.06-0.05)	0.59	0.45	0.66
Nitrate	Origin+Density	0.00 (-0.07-0.07)	0.47	0.39	—
Ammonium	No Fish	-0.02 (-0.32-0.26)	0.57	—	—
Ammonium	Origin	0.06 (-0.09-0.20)	0.20	0.27	—
Ammonium	Density	-0.05 (-0.20-0.10)	0.77	0.58	0.86
Ammonium	Origin+Density	0.01 (-0.20-0.21)	0.47	0.41	—

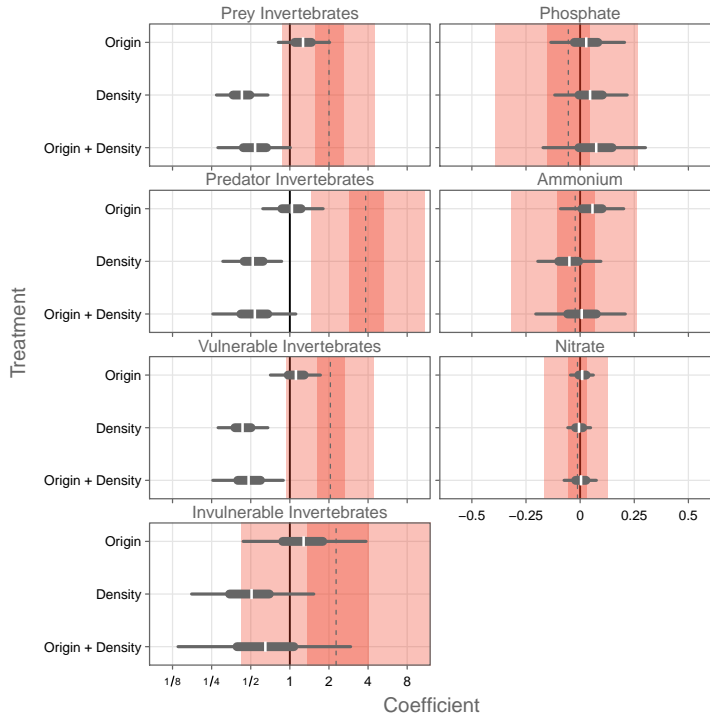


Figure A.1: Fish, genetic origin, and fish density effects on response variables measured in the mesocosm experiment as estimated by the Bayesian multilevel model. Estimates are relative to the base case state (above-barrier genetic origin at low density; vertical solid black line). Coefficients in the left column are interpreted as they are in Figure 4. Nutrient data (right column) were drawn from a normal distribution and thus the coefficients are plotted on the original scale, where 0 is no change from the base case. The ecological effect of fish can be seen by comparing the posterior mean of the no fish treatments (vertical dashed black line) and 50% and 95% highest posterior density (HPD) credible intervals (dark and light red area, respectively) to the base case. There is strong support for an ecological effect of fish where there is little or no overlap between the light red shaded region and the solid black vertical line. The posterior mean (white line) and 50% and 95% HPD credible intervals (thick and thin black lines, respectively) are presented for genetic origin, density, and their combined effect (Origin + Density). Ecological effects of evolution are present where there is little or no overlap between the 95% HPD credible interval (thin horizontal black line) and 1 (vertical solid black line). Similarly, the ecological effects of genetic origin, density, and their combined effect (Origin + Density) can be compared to the 95% HPD credible interval of no fish treatments (light red shaded region). Posterior support for differences shown here are presented in Table A.1.

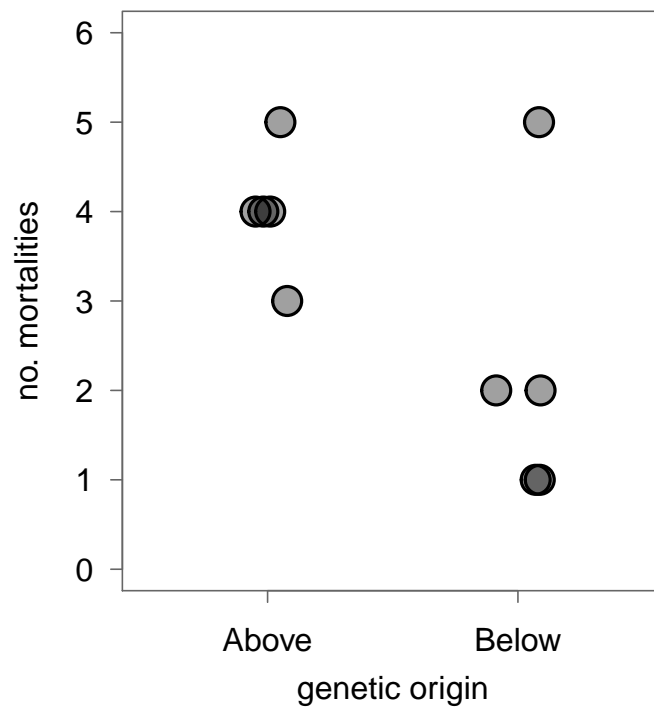


Figure A.2: Number of mortalities by genetic origin in the high density mesocosm treatments