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QUANTIFYING THE EFFECTS OF NON-NATIVE RAINBOW TROUT (ONCOHYNCHUS MYKISS) HYBRIDIZATION AND ENVIRONMENTAL CONDITIONS ON FITNESSRELATED TRAITS OF WESTSLOPE CUTTHROAT TROUT (ONCORHYNCHUS CLARKII LEWISI)

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By

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ABSTRACT

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Quantifying the effects of non-native rainbow trout (*Oncorhynchus mykiss*) hybridization and environmental conditions on fitness-related traits of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*)

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Human-mediated hybridization is a serious and growing threat to the conservation of biodiversity worldwide. Introgressive hybridization between introduced rainbow trout (*Oncorhynchus mykiss*, RBT) and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*, WCT) is widespread across much of historical range of WCT and is considered one of the top threats to the persistence of remaining WCT populations. The ecological and evolutionary consequences of RBT hybridization and the role of environmental conditions in mediating those consequences is largely unknown but critical for making management decisions. I investigated three fitness-related traits across multiple populations to improve our understanding of the genetic basis of fitness differences due to RBT admixture. Specifically, I asked: how does RBT admixture affect growth, migratory life history, and survival; do environmental conditions mediate the effects of RBT admixture; and does RBT introgression at specific loci explain differences in these traits?

The environmental context in which hybridization occurs influences the outcomes of growth and survival, but not migratory behavior. I found that both growth and survival rates were variable among seasons and populations, likely due to the temporal and spatial environmental variation at these scales. While growth was significantly influenced by RBT admixture, this trait appeared to be less influential for determining the population-level consequences of hybridization as compared to survival and migratory behavior. Effects of RBT admixture on survival was highly variable, and ultimately reflected the population-level admixture. Interestingly, across these populations outbreeding depression was site-dependent and environmental gradients typically used for describing patterns in hybrid zones, such as thermal regimes, did not predict the variation in fitness consequences. A strong genomic association between RBT introgression on chromosome 29 and migratory behavior helps explain the rapid expansion of hybridization in systems through higher dispersal rates of hybrids. Overall, this research demonstrates that even low amounts of RBT admixture can substantially impact growth, survival and migratory behavior - all traits that can have large effects on population demography and evolution. This increases our knowledge of the impacts of RBT admixture on wild populations and provides valuable information regarding factors driving the spread of hybridization and local fitness consequences.

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CHAPTER 1
INTRODUCTION AND OVERVIEW

Human actions have led to novel species interactions, including hybridization between introduced and native flora and fauna (Olden et al. 2004). Human-mediated hybridization (hybridization that is the direct result of human actions via translocations or habitat alterations) threatens biodiversity across the globe (Allendorf et al. 2001; Crispo et al. 2011; Grabenstein & Taylor 2018). Climate change will likely contribute to the continued expansion of human-mediated hybridization and the declines of native taxa in many systems (Kelly, Whiteley, & Tallmon 2010; Muhlfeld et al. 2014; Hunter et al. 2017). While, introgressive hybridization is a powerful evolutionary force that increases genetic diversity and can lead to speciation or adaptive introgression (Nolte & Tautz 2010; Abbott et al. 2013; Hedrick 2013; Jones et al. 2018), human-mediated hybridization can lead to the extinction of native genotypes through the formation of hybrid swarms, loss of locally adapted gene complexes, and outbreeding depression (Rhymer & Simberloff 1996; Abbott, Barton, & Good 2016; Kovach et al. 2016a; Todesco et al. 2016). Genomic extinction can occur if there is complete mixing of a population's (or species') genome, resulting in the irreversible loss of evolutionarily distinct lineages (Allendorf et al. 2001). While there is increasing documentation and quantification of non-native admixture in species of conservation concern, there are typically far fewer studies quantifying the evolutionary and ecological consequences of these events. This lack of scientific data can lead to debate on the urgency of the threat and the most appropriate mitigation actions, ultimately delaying or preventing effective conservation actions (Allendorf et al. 2001).

Outbreeding depression has often been considered a universal phenomenon following human-mediated hybridization events in species that exhibit local adaptation (Rhymer & Simberloff 1996), yet there is increasing evidence that the relative fitness of hybrid genotypes can be environmentally dependent and change over time (Arnold & Martin 2010; Walsh et al. 2016a; Hunter et al. 2017; Zhang et al. 2019). The tension and mosaic hybrid zone models from hybrid zone theory (Arnold 1997) have been used to set expectations of the drivers and consequences of human-mediated hybridization (e.g., Grabenstein & Taylor 2018). Characterizing the model of hybridization in human-mediated events requires quantifying selection on hybrids across a range of environmental conditions to determine the extent of outbreeding depression and the role of environmental context on the outcomes (i.e., are tension or mosaic processes at work?). Such studies help researchers frame expectations regarding the spatial variation in selection, the evolutionary mechanisms driving hybridization and predict the responses to different management actions. Research that quantifies how local environmental conditions influence individual fitness differences in admixed populations is relatively common in plants (e.g., Emms &

Arnold 1997; Campbell & Waser 2001; Gramlich & Hörandl 2016), but extremely rare among vertebrates (Casas et al. 2012; Vallin et al. 2013; Culumber et al. 2015; Walsh, Olsen, et al. 2016a).

Measuring the fitness consequences of human-mediated hybridization in the wild is challenging. Furthermore, the signal of selection on non-native admixture can vary depending on the trait investigated (McGinnity et al. 2004; Muhlfeld et al. 2009a; Ryan, Johnson, & Fitzpatrick 2009; Casas et al. 2012; Drinan et al. 2015; Fukui 2019). Few studies have linked the fitness consequences of human-mediated hybridization to environmental conditions in the wild (Arnold and Martin 2010; Hunter et al. 2017). If environmental conditions influence hybrid fitness, this can confound our ability to make broad conclusions and recommendations from single population or laboratory studies. Because of these challenges, landscape-admixture associations are often used to represent selection gradients or fitness-environment associations in hybrid zones (Culumber et al. 2012; Walsh et al. 2016b). It should be noted that in some studies of natural hybrid zones, researchers have followed up landscape-admixture association studies to confirm genotype-by-environment selection on fitness traits (e.g., Culumber et al. 2015; Walsh et al. 2016a), however, these studies are lacking in human-mediated hybridization events. Landscape patterns are driven by multiple factors including distance from source, dispersal, and selection and as such may not be honest indicators of selection alone. This confounds our ability to use landscape-wide patterns of admixture between native and invasive species across heterogeneous landscapes to understand selection.

The advances of next-generation sequencing techniques have greatly improved our ability to detect, characterize, and manage the rates and patterns of invasive introgression (McFarlane & Pemberton 2019). Genomic approaches are also improving our understanding the evolutionary and ecological consequences of these events (Hedrick 2013; Fraïsse et al. 2014; Christe et al. 2016; Jones et al. 2018) including our understanding of the genetic basis of traits (e.g., the number and effect sizes of genes explaining variation in phenotypic traits; Lindtke et al. 2013; Vestergaard et al. 2015). Salmonids have led in the application of genomic tools for conservation (Waples, Naish, & Primmer 2020), and we have begun to understand the genetic basis of many life history and fitness-related traits (Hecht et al. 2013; Johnston et al. 2014; Gutierrez et al. 2015; Prince et al. 2017; Kodama, Hard, & Naish 2018; Kelson et al. 2019; Ali et al. 2020).

Human-mediated hybridization is particularly common in fishes due to extensive human translocations for sport fishing and harvest (Epifanio & Nielsen 2000; Scribner, Page, &Bartron 2001) and more specifically is among the greatest threat to all cutthroat trout subspecies (*Oncorhynchus clarkii*) in western North America (Shepard, May, & Urie 2005). Rainbow trout (*O. mykiss*, hereafter RBT) is among the world's most widely introduced invasive fish species (Behnke 1992; Halverson 2010), and naturalized populations of RBT hybridize with native cutthroat trout. Westslope cutthroat trout (*O. clarkii*

lewisi, hereafter WCT) have experienced substantial range retractions due to species introductions, land use practices (i.e., logging, mining, grazing), and overexploitation (Shepard, May, & Urie 2005). Rainbow trout having been stocked on many waters across western North America, and many populations of native WCT are experiencing introgressive hybridization with non-native RBT. In areas where their native ranges overlap, admixture is generally lower likely due to the evolution of spatial and temporal isolation of reproduction (Leary, Allendorf, & Sage 1995; Kozfkay et al. 2007). However, in their introduced range, RBT hybridize with WCT and threaten populations with genomic extinction through widespread admixture and the formation of hybrid swarms (Leary et al. 1988; Leary, Allendorf, & Sage 1995; Allendorf et al. 2004). Shepard et al. (2005) estimated that nonhybridized populations of WCT existed at only 10% of their historic distribution, and that number is likely even lower today.

There has been a plethora of research surrounding hybridization between cutthroat and rainbow trout since the mid-1980s (see Table 1.1). However, most of the research on CTxRBT hybridization has focused on characterizing the genetic divergence and quantifying the landscape patterns of hybridization. Fewer have quantified fitness differences between these species and their hybrids. Marker sets have improved greatly since the studies first identifying hybridization and characterizing genetic differences between these species. We have gone from relatively few allozyme or microsatellite loci to thousands of single nucleotide polymorphisms (SNP) mapped to the rainbow trout reference genome (Berthelot et al. 2014). These advancements have fueled our understanding of the patterns and extent of hybridization between these species and also our ability test for and quantify the effects of admixture on fitness-related traits and selection on RBT alleles and hybrids.

The many published studies on CTxRBT hybridization are landscape level analyses describing the landscape patterns of hybridization and testing for associations between site-level admixture and environmental drivers or landscape features (see Table 1.1). Generally, these studies agree in their findings of the environmental factors associated with the patterns and driver of hybridization between these species. Specifically, distance from source populations, site elevation, and stream temperature are positively associated with proportion RBT admixture in many studies and river basins across western North America. These patterns align with known differences in thermal tolerance between these species (Bear, McMahon, & Zale 2007; Yau & Taylor 2014), however, there is considerable variation in the pattern of RBT hybridization unexplained by these environmental predictors (see Muhlfeld et al. 2017).

There are fewer studies quantifying the effects of RBT admixture on fitness related traits (Table 1.1). Many of these studies are limited as they are restricted to F1 generation or early generation backcrosses, laboratory conditions, or a single population. For example, the studies by Leary et al. (1995) and Drinan et al. (2015) show conflicting results of the effect of RBT admixture on embryonic and juvenile survival. Furthermore, the effect of RBT admixture varied from positive to negative depending

on the developmental traits (Drinan et al. 2015). Not only do these data suggest that the fitness effects of admixture likely vary among families and populations, but also caution that we might expect different signals depending on the fitness traits measured in a study.

As with other salmonid studies (Araki, Cooper, & Blouin 2007; Christie, Ford, & Blouin 2014; Glover et al. 2017), Muhlfeld et al. (2009a) found a strong decrease in reproductive success associated with RBT admixture in one wild population (e.g., 50% fewer offspring with only 20% RBT admixture). However, given the landscape studies suggesting there are environmental gradient mediating admixture and its effects on fitness, conclusions from a single population should be taken with caution. To help contextualize data on the fitness effects of hybridization, the landscape patterns, and environmental drivers of admixture it is crucial to quantify the effects of non-native admixture on fitness-related traits in wild populations across a range of environmental conditions.

The work presented in the following three chapters is focused on improving our understanding of the ecological and evolutionary consequences of human-mediated hybridization. Furthermore, this research informs the conservation and management of cutthroat populations threatened by hybridization with rainbow trout. Each chapter is written to be a stand-alone publication and written in the first person plural writing style to reflect the contributions of many persons who will serve as coauthors when these chapters are submitted for publication. This study is not only the first in cutthroat-rainbow hybridization, but one of few in vertebrate taxa that use individual based data to examine fitness by measuring multiple fitness-related traits across multiple populations and environmental conditions. I quantified the effects of individual proportion rainbow trout admixture on multiple fitness-related in three populations that differ substantially in environmental conditions previously shown to influence hybridization.

These chapters add to the body of literature on human-mediated hybridization by: 1) quantifying the effect of admixture on multiple fitness-related traits, 2) testing for the effect of environmental conditions on those fitness outcomes, and 3) investigating the genetic basis of fitness differences by testing for locus-specific effects of introgression on these traits. More specifically, it adds to a body of literature and informs a debate on the fitness consequences and factors driving landscape patterns of hybridization between RBT and WCT. I examined the effect of RBT admixture on seasonal growth rates and life history strategy in Chapter 2. I then quantified the effect of admixture on survival probabilities in Chapter 3. In the final chapter of my dissertation (Chapter 4), I looked for a genetic basis of differences in growth rate and migratory behavior by testing for locus-specific associations between RBT alleles and these traits. Additionally, Chapter 4 includes a power analysis using extensive simulations which is likely to help other researchers and advance the field.

The study populations in my dissertation are all tributaries to the North Fork Flathead River, MT. While the Flathead is still considered a stronghold for large connected populations of WCT, the North and

Middle Forks have experienced substantial and increasing RBT introgression from source populations throughout in the system (Hitt et al. 2003; Boyer, Muhlfeld, & Allendorf 2008; Muhlfeld et al. 2014, 2017). All sampling was conducted in populations Cyclone, Langford, and McGee Creeks. All populations are hybridized but contain nonhybridized WCT as well. Pertinent details concerning sampling and environmental conditions of each population is given in the relevant research chapter(s).

What is the effect of rainbow trout admixture on growth rates and migratory life history? Do the effects differ across streams with varying environmental conditions?

Chapter 2 highlighted that the effect of RBT admixture on growth rates was variable among seasons and populations. We found RBT admixture-by-environment interactions (GxE) at multiple scales; not only did admixture have opposing effects on growth during different seasons but interacted with temperature to influence summer growth rates. Summer growth rates increased positively with RBT admixture, and during warmer summers this relationship was increasingly positive in Cyclone and Langford. However, during the spring season, growth rate was negatively associated with RBT admixture at sites with cooler conditions. These results are consistent with studies showing RBT have a higher thermal tolerance, wider scope for growth, and higher metabolic rates than cutthroat trout (Bear, McMahon, & Zale 2007; Rasmussen, Robinson, & Heath 2010). Overall, the opposing effects of admixture on seasonal growth resulted in neutral effects of admixture on annual growth under cooler conditions. At the warmest site WCT did not have higher spring growth rates, and as a result RBT admixture had a positive effect on annual growth. This has implications for future conservation under climate change as hydrologic and thermal regimes are likely to change. If WCT do not grow faster than hybrids during the spring, this may result in positive effects of RBT admixture on annual growth across much of the landscape.

In contrast to growth, the effect of RBT admixture on the probability of migration was environmentally independent. Migratory life history expression was consistently and positively impacted by RBT admixture (note: McGee was excluded from this analysis due to small sample sizes). These results are consistent with other studies suggesting that hybrids likely have higher dispersal rates that WCT (Boyer, Muhlfeld, & Allendorf 2008; Kovach et al. 2015). In addition to a higher propensity to express a migratory life history, juvenile hybrids were also more likely to emigrate from their natal stream at a smaller size than WCT, again consistent with work from Kovach et al. (2015). This shift in the timing of this trait has potential tradeoffs between river survival, size and age at maturation, and generation interval. Overall, these results offer an explanation for the rapid spread of hybridization in some systems, despite evidence of lower reproductive success. Furthermore, the strong association between RBT

admixture and migratory behavior suggests there is a strong genetic basis affecting differences in the propensity to express a migratory life history between these species. The genetic basis of differences in growth and migratory life history due to hybridization are investigated further in Chapter 4.

What is the effect of rainbow trout admixture on survival rates?
Do the effects differ among populations with varying environmental conditions?

The effects of RBT admixture on survival were variable across our study streams. This supports a mosaic hybrid zone theory as the mechanism influencing landscape patterns of hybridization and is one of few empirical studies demonstrating environmentally dependent fitness consequences in vertebrates (Arnold & Martin 2010; Walsh et al. 2016a; Hunter et al. 2017). Specifically, the effect of RBT admixture on survival varied by season and population. These seasonal effects resulted in different associations between admixture and annual survival probabilities in these populations – there was a positive effect of RBT admixture on juvenile survival at the coldest site, while the warmest site had a negative effect of RBT admixture on survival of all size classes. Interestingly, the effect of admixture on survival reflected the population-level consequences of RBT admixture. The population with the strongest negative effect of admixture on survival also had the lowest population level admixture. Given that all streams reflect negative selection against admixture during early life history stages (Kovach et al. 2015), selection across multiple life history stages may be necessary to prevent a population from becoming highly admixed. This analysis also revealed that significant admixture-environment associations with temperature previously described for these species (e.g., Muhlfeld et al. 2014; Young et al. 2016; Muhlfeld et al. 2017) might not predict the variation in selection across life history stages.

What is the genetic basis of differences in growth and migration due to RBT admixture?

Based on the strong association between genome-wide RBT admixture and the fitness traits investigated in Chapter 2, I further investigated the genetic basis of RBT admixture on these traits. Given the paucity of power analyses in the literature for genomic wide association analyses (GWAA), I initially simulated a river network and the evolution of these populations due to hybridization from a source of non-native alleles. I simulated a locus that had a range of effects sizes on the phenotype and then sampled the populations and tested for associations between loci across the genome and the phenotype. Power was most influenced by the effect size of the locus itself, specifically if the effect size of the locus was relatively high (>0.5; 50% of variation in the phenotype was explained by that locus) there was a high probability the association test would detect it. Power dropped quickly as the effect size of the locus

declined, suggesting that a trait would need to be influenced by a large effect locus in order for the association analysis to detect it with high certainty. These results will help guide other researchers looking to conduct such genome scans for the genetic basis of phenotypic traits in admixed populations.

The results of the GWAA revealed a large effect SNP on chromosome 29 significantly associated with migratory behavior in these populations. Individuals with one of more RBT alleles at this locus had a significantly higher probability of being migratory and this locus better explained migratory behavior than genome-wide admixture alone. These results are consistent with other literature in salmonids, where there is increasing evidence that traits associated with anadromy and migratory are associated with large effect loci (e.g., Johnston et al. 2014; Prince et al. 2017; Kelson et al. 2019; Pearse et al. 2019; Sinclair-Waters et al. 2020). Our association scan of summer growth rate did not detect large effect loci influencing this trait consistently among populations and years. This not surprising for a trait such as growth rate that is environmentally dependent and highlights the challenges of conducting such a study in wild populations where sample size and environmental conditions are not controlled by the researcher. This analysis advances our understanding of the genetic basis of these traits and provides further evidence that hybrids across the landscape will have a higher dispersal rate. This will contribute to the rapid and continued expansion of hybridization regardless of the local fitness consequences.

Contributions to studies of human-mediated hybridization

My dissertation adds to a small but growing body of literature that shows outbreeding depression in vertebrates due to human-mediated hybridization can be mediated by spatial and temporal environmental variation (Arnold & Martin 2010; Walsh et al. 2016a; Hunter et al. 2017). Indeed, human-mediated hybridization of closely related taxa likely operates under mosaic hybrid zone patterns and processes, especially when strong physiological differences exist among the parental species. The differences in the effect of non-native admixture on fitness-related traits and across environmental conditions highlights the need for careful research design and the importance of long-term studies – for example, what traits are most important for fitness, how many populations should be studied, and what environmental conditions should be monitor? The contrasting results between admixture-environment associations and the fitness consequences of admixture in my study populations bring up hypotheses for other important selective forces influencing evolution in human-mediated hybrid zones. Populations that appear as outliers in admixture-environment associations might demonstrate other important selective forces at work such as density or frequency dependent processes (i.e., soft selection; Wallace 1975).

Contributions to westslope cutthroat trout conservation

My dissertation also informs the conservation and management of westslope cutthroat trout by informing debates over the threat of widespread admixture and genomic extinction as well as genetic thresholds for conservation status (Allendorf et al. 2004). WCT were denied U.S. Endangered Species Act (ESA) listing in 2002 (Shepard, May, & Urie 2005); the relatively wide distribution of WCT and uncertainty regarding the prevalence of RBT admixture and its fitness consequences played a large role in this decision. Allendorf et al. (2004) were critical of the inconsistency to which these policies have been applied to cutthroat trout conservation. Demonstrating this point, arbitrary levels of 10% or 20% RBT admixture have been used as thresholds for determining a populations conservation status at the state and federal levels. Since the ESA ruling in 2002, genetic marker panels have improved as has our ability to precisely determine both individual and population levels of RBT admixture. My work shows that there are significant evolutionary and ecological differences between nonhybrid WCT and hybrid individuals in populations with < 20% RBT admixture.

Furthermore, my dissertation shows that while stream temperature and distance to source population are important for predicting broad landscape patterns, they may not reflect the evolutionary processes at work within populations. I found further evidence that the spread of hybridization is driven by increased dispersal associated with RBT introgression, suggesting that admixture will continue to spread regardless of the fitness consequences. Populations that appear to resist admixture over many generations might represent unique ecological or evolutionary processes and understanding these would help managers better focus conservation efforts. Cyclone Creek was the only population to show strong selection against admixture across all life stages, however, it differs in many other ways from Langford and McGee Creeks. First, Cyclone Creek has the strongest resident life history form (e.g., the highest proportion of adult residents) which might help resist admixture from migratory hybrids dispersing from other populations. Secondly, it has the highest density of fish and might represent a population where the high density of WCT and low frequency of hybrids allows selection to act most efficiently on non-native admixture (i.e., soft selection). Further investigation of these “outlier” populations might allow managers to understand the factors that prevent widespread admixture. Overall, my dissertation fills critical gaps in knowledge of the fitness consequences and drivers of hybridization across a heterogeneous landscape and will aid efforts to conserve westslope cutthroat trout threatened by rainbow trout hybridization.

Table 1.1: A summary of major studies in cutthroat x rainbow trout hybridization. These studies represent work that has advanced our understanding of hybridization between these species by: 1) describing genetic divergence and identifying molecular markers diagnostic purposes, 2) describing landscape patterns of hybridization and environmental drivers of admixture, and 3) laboratory and field based studies quantifying differences in developmental, life history, and fitness-related traits. These studies have helped improve our understanding of the factors driving hybridization/admixture across the range of WCT and the evolutionary and ecological consequences of hybridization between these species. These studies have helped inform conservation and management actions and inform the debate on the urgency of the threat of hybridization and has implications for future ESA listing.

Area of investigation	Description of advancement	Peer-reviewed study
Genetic tool development	genetic diversity & divergence in RBT/CT	Leary et al. 1987; Leary et al. 1988; Allendorf & Leary 1988
	genomic patterns of RBT introgression	Hohenlohe et al. 2013
	identify and map RAD markers	Amish et al. 2012; Hand et al. 2015
Patterns/extent of hybridization	environmental drivers	Weigel et al. 2003 (Clearwater, ID)
	environmental drivers	Bennet et al. 2010 (Kootenay, BC, CA)
	environmental drivers	Rasmussen et al. 2010 (Oldman, AB, CA)
	environmental drivers	Muhlfeld et al. 2009b, 2014 (Flathead, MT)
	environmental drivers	Muhlfeld et al. 2017 (MT - ID)
	pattern/extent	Hitt et al. 2003; Boyer et al. 2008 (Flathead, MT)
	pattern/extent	McKelvey et al. 2016 (MT - ID)
	environmental drivers	Young et al. 2016 (MT - ID)
	environmental drivers	Yau & Taylor 2013 (BC - AB, CA)
	environmental drivers	Carim et al. 2013 (Blackfoot, MT)
	environmental drivers	Corsi et al. 2013 (Jocko, MT)
	selection across landscape	Kovach et al. 2016b (Flathead, MT)
	environmental drivers	Mandeville et al. 2019 (Shoshone, WY)[Y]
	pattern/extent	Kovach et al. 2011 (Snake, WY)[Y]
	pattern/extent	Loxterman et al. 2014 (Salmon, ID)
	pattern/extent	Rubidge & Taylor 2004 (Kootenay, BC, CA)
	environmental drivers	Rubidge &Taylor 2005 (Kootenay, BC, CA)
	pattern/extent	Kozfkay et al. 2007 (Salmon, ID)
Laboratory studies	developmental traits	Leary et al. 1995; Drinan et al. 2015
	thermal tolerance, scope for growth	Bear et al. 2007**
	Growth, morphology, performance	Seiler & Keeley 2007[Y;], 2009[Y F1]
	thermal tolerance	Yau & Taylor 2014
	gene expression in growth related genes	Ostberg et al. 2015 [Y BC]
	growth and survival	Allendorf & Leary 1988 [F1]; Leary et al. 1995[F1]
Field Based studies	Growth*, fecundity, migration timing	Corsi et al. 2013 (Jocko, MT)
	migration timing	Muhfeld et al 2009c (Flathead, MT)
	juvenile migration timing, selection	Kovach et al 2015 (Flathead, MT)
	reproductive success	Mulhfeld et al 2009a (Flathead, MT)
	phenology & spawning location	Heim et al 2019 (Lamar, MT)
	developmental traits, MTDNA-DNA associations	Forbes & Allendorf 1991a, 1991b
	metabolic traits, life history traits	Rasmussen et al. 2010 (Oldman, AB, CA)

*Otolith-based growth; Y = Yellowstone cutthroat trout; F1 = F1s only ** parental species only – no hybrids

CHAPTER 2
INTROGRESSIVE HYBRIDIZATION ALTERS GROWTH AND LIFE HISTORY EXPRESSION OF WESTSLOPE CUTHROAT TROUT

Abstract

Human-mediated hybridization threatens many native species, but the effects of introgressive hybridization on life history expression are rarely quantified, especially in vertebrates. We quantified the effects of non-native rainbow trout admixture on important life history traits including seasonal growth, annual growth, and migratory behavior in three populations of native cutthroat trout over five years. Rainbow trout admixture increased summer growth rates in all populations, and decreased spring growth rates in two populations with cooler spring temperatures. These results show that non-native admixture may increase growth under warm conditions, but cutthroat trout have higher growth rates during cooler periods. Non-native admixture consistently increased the expression of migratory behavior in all populations, suggesting genomic differences in life history strategy between these species, despite environmental and growth differences among populations. Our results show the effects of interspecific hybridization on fitness traits can be the product of genotype-by-environment interactions even when there are only slight differences in environmental optima among hybridizing species. While environmentally mediated traits like growth may play a role in population-level consequences of admixture, strong genomic control of migratory life history differences among these species likely explains the continued spread of non-native alleles at the landscape-level despite selection against hybrids at the population-level.

Introduction

Hybridization with introduced species is a serious and growing threat to the conservation of biodiversity and native species worldwide (Rhymer & Simberloff 1996; Allendorf et al. 2001; Olden et al. 2004; Crispo et al. 2011; Grabenstein & Taylor 2018). Although natural hybridization can lead to evolutionary novelty and speciation (Abbott et al., 2013; Nolte & Tautz, 2010), human-mediated hybridization and introgression can lead to the extinction of native genotypes, loss of locally adapted gene complexes and outbreeding depression (Rhymer & Simberloff 1996; Einum & Fleming 1997; Araki, Cooper, & Blouin 2007; Todesco et al. 2016). Climate change will likely contribute to the continued expansion of human-mediated hybridization and the declines of native taxa (Kelly, Whiteley, & Tallmon 2010; Muhlfeld et al. 2014). Therefore, understanding the ecological and evolutionary consequences of introgression is critical for conservation of native species experiencing or threatened with non-native hybridization. However, data demonstrating the effects of hybridization on ecologically and evolutionarily important traits are limited for native species in the wild and this lack of scientific data can delay or prevent effective conservation and management (Allendorf et al. 2001).

Understanding the consequences of hybridization in wild populations is challenging as genomic (G) and environmental (E) factors, as well as their interactions (GxE) can lead to fitness differences among parental and hybrid individuals (Arnold 1997; Arnold & Martin 2010; Hunter et al. 2017; Zhang et al. 2019). The impacts of human-mediated hybridization vary depending on the taxa and the phenotypic traits examined by researchers (McGinnity et al. 2004; Muhlfeld et al. 2009a; Ryan, Johnson, & Fitzpatrick 2009; Casas et al. 2012; Fukui 2019). While laboratory studies can be key for isolating the effects of ancestral differences in phenotypic traits, these studies are often limited to early generation hybrid crosses and often lack environmental variation to assess environmental or GxE interactions on phenotypic traits (Leary, Allendorf, & Sage 1995; Seiler & Keeley 2007, 2009; Drinan et al. 2015). Studies of GxE interactions in vertebrate hybrid zones are often limited to association analyses between genotypes and environmental variables or coarse habitat classifications (Culumber et al. 2012; Walsh et al. 2016b). And of the relatively few studies that demonstrate the effects of non-native hybridization on fitness-related traits, few have linked these consequences in multiple populations to differences in ecologically important environmental conditions in the wild (Arnold & Martin 2010; Hunter et al. 2017). This lack of understanding limits our understanding of the factors (G, E, or GxE) that drive landscape-wide patterns of introgression between native and invasive species across heterogeneous landscapes.

Interspecific hybridization is particularly common in fishes due to limited pre- or postzygotic barriers to interbreeding among closely related species; and humans have translocated many non-native fish species for sportfishing and harvest (Scribner, Page, & Bartron 2001). Rainbow trout (*Oncorhynchus*

mykiss, RBT) is among the world's most widely introduced invasive fish species (Behnke 1992; Halverson 2010), and readily hybridize with native cutthroat trout subspecies (*O. clarkii spp.*) throughout their native ranges. Hybridization is one of the greatest threats to all cutthroat trout subspecies in western North America, including remaining populations of westslope cutthroat trout (*O. clarkii lewisi*, WCT; Shepard, May, and Urie 2005). Hybridization between WCT and non-native RBT is widespread in populations inhabiting a range of environmental conditions despite strong selection against non-native alleles (Kovach et al. 2015; Lowe, Muhlfeld, & Allendorf 2015; Kovach et al. 2016). However, many non-hybridized populations persist in cooler headwater streams (Mckelvey et al. 2016; Young et al. 2016; Muhlfeld et al. 2017), and this genotypic gradient is likely due to historic stocking locations and environmental variation regulating spread thereafter (Muhlfeld et al. 2017). Similar environmental gradients have been observed in other hybrid zones (Culumber et al. 2012; Walsh et al. 2016b; Abbott 2017)(Walsh, Rowe, et al. 2016; R. J. Abbott et al. 2018), suggesting that environmental variation may partly explain the distribution of admixture across space, but the underlying mechanisms that produce these patterns are rarely understood. Examining the effects on non-native admixture on multiple individual fitness traits and across a range of environmental conditions is needed to gain a more complete understanding of the consequences of hybridization on native biota.

Hybridization between RBT and WCT provides an excellent model to study the effects of hybridization and environmental conditions on fitness outcomes due to the strong environmental differences that can exist among nearby populations and the known contributions of both genomic and environmental factors on fitness traits like growth and migratory life history strategy. Growth and migratory life history expression are important fitness traits in salmonids influencing survival and fecundity (e.g., Sogard 1997; Thompson & Beauchamp 2016; Janowicz et al. 2018). Furthermore, both traits can be influenced by genomic (Hecht et al. 2013; Kelson et al. 2019; Pearse et al. 2019; Ali et al. 2020), environmental (Olsson et al. 2006; Vøllestad & Olsen 2008; Kanno et al. 2015; Thompson & Beauchamp 2016), and GxE factors (Bærum et al. 2013; Yates et al. 2015; Nater et al. 2018). Growth is influenced by a suite of environmental condition (Kovach et al. 2016c), and the effects of temperature on growth and interspecific differences in temperature tolerance have been well described in these species (Bear, McMahon, & Zale 2007). This suggests there are likely differences in seasonal growth rates between these species and their hybrids in wild populations. Increased migratory behavior and dispersal of hybrids have been hypothesized mechanisms to explain the landscape patterns of differentiation among WCT populations and the rate of spread of RBT admixture (e.g., Boyer, Muhlfeld, & Allendorf 2008). In many taxa, partial migration is thought to be a conditional strategy where genetics, relative body conditions, and environmental context influence the threshold of the reaction norm for migration (Sloat et al. 2014; Kendall et al. 2015; Berg et al. 2019). Partial migration in salmonids refers to populations where

some portion of individuals mature within their natal stream as residents while others migrate to larger rivers or lakes for at least one year before returning as much larger migratory adults to spawn. Since fecundity increases exponentially with length in salmonids (Downs, White, & Shepard 1997; Janowicz et al. 2018), there are large fitness tradeoffs associated with migratory life history strategy. Therefore, hybridization and local environment likely mediate individual growth and life history expression leading to variable fitness outcomes across a heterogeneous landscape.

Here, we examine how individual growth rate and migratory life history expression are influenced by proportion RBT admixture (pRBT; G), environmental conditions (E), and the interaction of pRBT and environment (GxE) in three native WCT populations inhabiting streams with varying thermal and hydrologic conditions. Specifically, we addressed two main questions: 1) Does pRBT affect individual seasonal and annual growth rates and do environmental conditions influence these genetic effects? and 2) Does pRBT affect the propensity to express a migratory life history strategy and do environmental conditions influence these genetic effects?

Methods

Study Sites

We sampled populations of WCT in Cyclone, Langford, and McGee creeks in the North Fork Flathead River in northwestern Montana, USA (Figure 2.1a; 2013-2017). These sites were selected because they were known to contain both non-admixed WCT and a wide range of admixed individuals (Figure 2.1b), and despite being geographically close, the streams differ in key environmental drivers (temperature and flow) thought to influence growth and the rate of spread of RBT admixture (Figure 2.2, Table S2.1; Hitt et al. 2003; Muhlfeld et al. 2009; Muhlfeld et al. 2014). Admixture was first detected in Langford in the 1980's, but RBT alleles were not detected in Cyclone and McGee until the late 1990s (Muhlfeld et al. 2014). Genetic admixture has been occurring in each population for at least five to ten generations, allowing substantial time for backcrossing and recombination.

Environmental Data Collection

To test for environmental effects and their interactions with pRBT on growth rates, we collected data on factors known to affect growth in salmonids (i.e., temperature, stream flow, and *Oncorhynchus spp.* density). We used Onset HOBO Water Temperature Pro v2 Data Loggers to measure hourly water temperatures from March through November each year. To characterize the growing conditions during the spring and summer periods, we calculated both median daily temperature and growing-degree-days (GDD) for each year and season (summer – suGDD, spring - spGDD). For each annual growth period we

calculated GDD (aGDD) to characterize growing conditions. We calculated spGDD and aGDD by assuming the growing season begins on the first day of the week in which mean daily water temperature reaches and remains above 5°C and ends at the end of the week in which mean daily water temperature drops below 4°C and remains below this threshold (Coleman & Fausch 2007). Langford was the coldest site and least variable among years (see Figure 2.2a-c, Table S2.1). Given the strong snowmelt hydrology in Cyclone and McGee, these sites had warmer and more variable median summer temperatures than Langford. While McGee was the warmest site, Cyclone had much warmer spring conditions than McGee (Figure 2.2b, Table S2.1).

Stream flow was determined with several measures. First, stage gauges were present at each site and stage height was recorded daily from April through July every year. Second, Onset HOBO Water Level Data Loggers were added to each site in 2015, recording in-stream and atmospheric pressure every hour throughout the sampling season. Finally, stream discharge was measured using a SonTek FlowTracker2 at regular intervals (at least once a week) within a sampling season from April through October. Using the stage gauge or water pressure measures, we created discharge rating curves to quantify seasonal stream discharge. Discharge rating curves were created for each year by fitting a polynomial regression to the stage height (or HOBO water level data loggers) and flow (m^3/s) measures. From these stream discharge data, we computed average summer base flow (~July 1 - November 1), maximum spring flow, and average spring flow (~April 1 - July 1; Table S2.1). Due to equipment malfunctions, we did not have spring discharge data from 2017, so stream flow was not included in the modelling of spring growth rates. Being groundwater influenced, Langford had the lowest spring peak flows, but similar base flows to McGee (Figure 2.2d & 2.2e, Table S2.1). Cyclone had the highest mean spring flow, however, McGee had a higher mean peak spring flow.

The abundance of *Oncorhynchus spp.* was estimated using the model of constant effort developed by (Otis et al., 1978) and implemented in the *Fishmethods* package (Nelson 2016) in Program R. We calculated average wetted stream width at base flow (measured every 50m longitudinally along study reach). The average density of *Oncorhynchus spp.* in each study reach for each year was estimated by dividing the mean abundance estimate by the average wetted width at base flow (# fish/m^2). Densities were highest in Cyclone and lowest in McGee (Figure 2.2f; Table S2.1). These characteristics demonstrate the differences in seasonal growing conditions among our study populations.

Genetic Analyses

To estimate genome wide proportion RBT admixture (pRBT) for each individual, we extracted DNA using the SPRI bead extraction protocol described in Ali et al. (2016). DNA quality (260/280 ratio) and quantity were measured using a Nanodrop 2000 Spectrophotometer (Thermo Scientific, Waltham

MA). The concentration of double stranded DNA was measured using QuantIt Picogreen assays (Thermo Fisher Scientific, Waltham, Massachusetts) after diluting samples to less than 20ng/ul.

Sequencing libraries were prepared using the bestRAD and Rapture (RAD-capture) protocols (O. A. Ali et al. 2016) using 50 nanograms of input DNA for each sample. RAD libraries were sheared to an average fragment size of 350 base pairs using a Covaris E220 Ultrasonicator (Covaris Inc., Woburn, Massachusetts). Libraries were amplified for 12 cycles using a plate specific indexing primer, purified using Ampure XP beads, and quantified using Quantit Picogreen assays. Plates were pooled in groups of 6 (83ng from each library) before enriching for 3015 RAD loci previously found to be informative for estimating admixture coefficients. Enrichment was performed using a custom Mybaits target enrichment kit (V3., *Arbor Biosciences, Ann Arbor, Michigan)*. This panel included a combination of baits complementary to RAD loci containing WCT polymorphic SNPs and WCT, YCT, and RBT species diagnostic SNPs (Amish et al. 2012; Hohenlohe et al. 2013; Hand et al. 2015; Kovach et al. 2016b). Loci were chosen for capture based on their genotyping quality, reliability for distinguishing each (sub)species and even distribution across the assembled rainbow trout genome (Amish et al. 2012; Berthelot et al. 2014; Hand et al. 2015; Kovach et al. 2016b). Pooled libraries were amplified post-capture for 10-12 cycles and quantified using Quantit Picogreen assays before being sequenced 6 libraries/lane on an Illumina HiSeq X (Novogene Corporation, *Sacramento, CA*).

Bioinformatics and Genotype Calling

Read quality was assessed using FASTQC v0.11.5 and duplicates reads were removed using the clone_filter program from Stacks v1.44 (Catchen et al. 2011). Sequencing adapter contamination was removed from reads using Trimmomatic and reads were truncated whenever the mean Phred score across a window of 4 nucleotides dropped below q15. We further required reads to be greater than 60 bp after applying the trimming steps above. We then used a custom script to exchange reads between read 1 and read 2 fastq files whenever the inline index for an individual was found at the beginning of read 2. Properly oriented fastq files were demultiplexed by individual barcode using process_radtags v1.44. Reads were mapped to the RBT reference genome (Berthelot et al. 2014) using bwa-mem and resulting sam files were sorted, converted to bam format, and indexed using samtools v1.4. We then used HaplotypeCaller v3.7 to generate gVCF files for each individual, combined gVCF files across individuals using CombineGVCFs v3.7, and called genotypes using GenotypeGVCFs v3.7 (McKenna et al. 2010). The resulting VCF file was filtered using vcftools (LGPLv3; Danecek et al. 2011).

RBT diagnostic loci were separated from WCT polymorphic loci and only diagnostic markers were used in the following analyses. Genotypes were set to missing if the genotype quality score was less than 30 and minimum read depth was less than 7. In addition, an allele balance between 0.25 – 0.75 and a

minimum read depth of 10 was required for all heterozygote genotypes. Loci were removed if they were missing genotypes in more than 10% of individuals and individuals were dropped from the analysis if they did not have genotypes at greater than 20% of remaining loci after filtering. Proportion RBT admixture (pRBT) was estimated for each individual as the number of RBT alleles / (2 * number of genotyped diagnostic loci).

We genotyped over 3,245 individuals across all sites. We retained 650 RBT diagnostic loci after filtering. The median number of loci per individual was 536, and individuals were genotyped at a minimum of 160 RBT diagnostic loci. While each population contained non-admixed WCT individuals, the proportion of the population that was non-admixed varied greatly among the populations (Figure 2.1b, Table 2.1). The distribution of pRBT in Cyclone was skewed strongly towards WCT with a median of 0.013 pRBT. Langford and McGee had higher median pRBT (Langford = 0.34; McGee = 0.39) and less skewed distributions of pRBT than Cyclone.

Field Sampling: Growth Rates

We used a mark-recapture in each tributary to quantify seasonal and annual growth rates across five years (2013-2017). Reaches of each tributary were sampled via electrofishing twice annually (July and October). We completed a single electrofishing pass of each study reach (~2km) and collected as many individuals as possible. In addition to this single pass, we conducted two 150-meter three-pass depletions in July of each year to estimate trout abundance/density. For each individual we measured total length (TL, mm) and mass (g), and collected a tissue sample for genetic analysis. Fish >70mm TL were implanted with a unique PIT tag (passive integrated transponder) at first capture and, if previously tagged, their tag number was recorded. Each study reach had PIT-tag antennae at the downstream end of the reach and two of the three study reaches also had a PIT tag antennae at the upstream end. Antennae were active from early April through November. This allowed us to measure movement out of the study reach to exclude individuals that left the system from our growth analyses. Electrofishing twice annually allowed us to estimate daily growth over three distinct intervals: summer (July – October), winter/spring (October to July), and annually. We obtained growth and genotypic data from 918 individuals with a total of 1,262 growth measurements (Table 2.1).

Field Sampling: Life History Strategies

To capture individuals expressing a migratory life history strategy, we installed migrant fish traps each spring in Cyclone and Langford for four year (2013-2016). These traps captured immigrating adults moving upstream to spawn and emigrating juveniles moving downstream (presumably moving to the mainstem river to carry out a migratory life history strategy). Traps were checked daily from early April

through July (until traps failed to catch any individuals for two weeks) and were removed for the remainder of the year. For each individual caught in the traps, we followed the same sampling protocol for individuals captured via electrofishing. Fish captured migrating upstream allowed us to examine how introgression influenced migratory fish coming into the system to spawn. We used samples from the migrant trap and the downstream fixed PIT-tag antennae to estimate emigration from the creeks.

Data Analyses:

Effect of pRBT on Growth Rate

To test for the effects of pRBT, environmental conditions, and their interactions on seasonal growth rates, we analyzed growth rate in both length (mm/day) and weight (g/day) during the summer ($July_t$ - $October_t$), winter/spring ($October_t$ - $July_{t+1}$; hereafter, spring), and annual intervals ($July_t$ - $July_{t+1}$ or $October_t$ - $October_{t+1}$). This analysis included four years of summer, spring, and annual growth. We modeled growth separately in each population using multiple linear regression to avoid differences in the distributions of pRBT, sample sizes, and growth rates among populations from influencing model results.

Since these populations are partially migratory, we excluded putative adults from the analyses to reduce effects of individuals that have slowed somatic growth. We assumed individuals over 160mm TL are likely to be mature resident fish (Downs, White, & Shepard, 1997; Janowicz et al., 2018). For each individual (i) captured in stream j and at time t, we calculated growth rate as:

G_{ijt} (mm/days) = total length t_2 (TL_2) - total length t_1 (TL_1) / days(t_2-t_1)

G_{ijt} (g/days) = weight t_2 (W_2) - weight t_1 (W_1) / days(t_2-t_1)

In addition to proportion RBT admixture (pRBT), we considered both abiotic and biotic factors known to impact growth rate as potential covariates in our global model. Biotic conditions included individual size at first capture (TL_1 or W_1), individual body condition at first capture (K), and the density of *Oncorhynchus spp* (Table S2.1). Size at first capture (TL) was included to correct for any size-based biases in growth due to energy allocation toward gametes instead of somatic growth in mature individuals. K was estimated as an individual's residual value from a population length-weight regression (as in Al-Chokhachy et al., 2019). Abiotic conditions included metrics to characterize seasonal temperature and stream flow (Figure 2.2; Table S2.1).

To reduce the number of correlated environmental covariates (Tables S2.2 & S2.3), we explored linear regressions of each environmental metric to growth rate. First, we chose the temperature metric with the lowest AICc to include in our model, as we expected temperature would have a stronger effect on growth. For summer growth our temperature metric with the lowest AICc was median daily

temperature (compared with suGDD or maximum seven-day average), and for the spring modelling it was spGDD (compared to mean daily temperature). In the annual growth modelling we used aGDD as our temperature covariate. We then tested for collinearity between our top temperature metric and potential flow and density metrics and only included metrics that were not correlated with temperature ($r^2 < 0.6$).

We used the *nlme* package in Program R (Pinheiro et al. 2017) to conduct linear modelling following the model selection protocol of (Zuur et al. 2009). We modelled growth (both length and mass) in each population and season separately. We first found the best supported variance structure correcting for pRBT and/or year as there was evidence of heteroscedasticity in the residuals plotted against pRBT. Next, we tested for the significance of a random intercept model (year), however, this was never supported. We then performed top-down model selection beginning with a saturated global model (all hypothesized covariates and interactions), removing the least significant term at each step until only the intercept remained. In addition to these hypothesized models, we tested several null models (model selection without pRBT covariate). To avoid selecting models with spurious associations and uninformative parameters (Arnold 2010), we used a p-value threshold of 0.05 and only considered models that contained all supported parameters (Tables S2.4 – S2.12).

Effect of pRBT on Migratory Life History Strategy

To test for the effect of pRBT on life history expression, we used a combination of migratory trap and electrofishing datasets collected from 2013-2016. We evaluated the influence of RBT admixture on the probability of expressing a migratory life history versus a resident life history. We used migratory traps and fixed PIT tag stations to identify immigrating adults (hereafter, migratory adults) and emigrating juveniles (hereafter migratory juveniles) moving into and out of our study tributaries between April 1 and July 1 of each year. Catch data from annual summer electrofishing surveys of each tributary (June 20 - July 31) were used to identify resident individuals each year. To assign individuals as adults or juveniles, we used a total length threshold of 160mm (juveniles $\leq$ 160; adults > 160mm; Downs et al. 1997; Janowicz et al. 2018). We captured and genotyped 206 and 129 immigrating adults and 107 and 192 emigrating juveniles from 2013-2016 in Cyclone and Langford, respectively (Table 2.1). We then used generalized linear modelling (GLM) with a logit link function to test for an effect of pRBT on migratory life history strategy separately in the adult and juvenile classes (1 = migratory, 0 = resident).

In addition to pRBT, we considered other biotic and abiotic factors thought to influence life history strategy in salmonids. We included total length (TL) and individual condition (K) in our global model as both have been shown to influence propensity for migration (Kendall et al. 2015; Ferguson et al. 2019)(Ferguson et al. 2019; Kendall et al. 2015). We then included capture year in our model as a

blocking factor to account for any environmental conditions that might lead to variation migratory behavior over time.

We used the *lme4* package in Program R (Bates et al. 2015; *nlme* cannot perform a logit-link) to conduct generalized linear modelling with a logit link for both life stage classes (adult versus juvenile) and population. McGee was excluded due to insufficient effectiveness of the migrant trap. We performed the similar model selection process as described in the previous selection and compared supported models using AICc (Tables S2.13 & S2.14).

Results

Effect of RBT Admixture on Growth Rate

Growth was highest during the spring season in all populations, and mean spring growth was similar among populations (Figure 2.3). McGee had the highest mean spring growth (1.2x Cyclone & 1.05x Langford). Mean summer growth was more variable among populations. Langford had the highest mean summer (1.8x Cyclone & 1.2x McGee) and annual growth rates (1.4x Cyclone & 1.02x McGee). Cyclone had the lowest mean growth rates across all seasons. Regardless of whether we considered length or mass we found that the effects of pRBT on growth rate were largely consistent (except for spring growth in McGee) and so we focus on results for length (mm/d). Results for mass are available in Appendix A.

We found strong evidence of GxE interactions influencing summer growth. Both within a season and among seasons, RBT admixture had a positive effect on growth rates under warmer environmental conditions and negative effects under cooler conditions. During summer, pRBT was positively associated with growth rates in all populations (Figures 2.4a, 2.4c, & 2.4e). Additionally, in Langford and Cyclone, higher admixture led to a significantly greater increase in growth during higher median summer temperatures than WCT (Figures 2.4b & 2.4d; Tables S2.4a & S2.5a). Only in one stream (McGee) was density supported in a top model (Table S2.6b). In both Cyclone and Langford our top models remained unchanged when testing these additional density models (Tables S2.4 & S2.5).

There were significant negative effects of pRBT on spring growth rates in Langford, but not in Cyclone or McGee (Figure 2.5b; Tables S2.7 – S2.9). Spring growth was also explained by a significant positive effect of temperature in Langford. It is worth noting that in McGee while pRBT did not have a significant effect on growth in length, there was a significantly negative effect of pRBT on growth in mass (Table S2.9). In the McGee length model, spring growth was only explained by a negative effect of starting size. There was no evidence of a significant effect of pRBT on growth rates in CYC. Instead, growth was explained only by size, condition and temperature.

On an annual basis, pRBT had a significant positive effect on growth rates in Cyclone only (Figure 2.5a; Tables S2.10 – S2.12). In addition to pRBT, annual growth in Cyclone was explained by starting size and body condition as well as an interaction between pRBT and condition (Table S2.10). Langford and McGee showed no evidence of pRBT on annual growth rates. Growth was only explained by size in McGee. In addition to size, growth in Langford was explained by negative effects of body condition and temperature.

Effect of RBT Admixture on Migratory Life History Strategy

The probability of migration was consistently and positively associated with pRBT for juvenile and adult trout (Figure 2.6). In fact, within a reproductive class (i.e., juveniles or adults), both populations supported identical covariate structure (Tables S2.13 & S2.14). The covariate structure for the juveniles and adults included condition (K), total length (TL), pRBT, and year effects. Generally, coefficients had the same direction of effect (positive or negative), although the magnitude of effect sizes differed slightly among populations. For example, in Langford adult migration probability increases ~20% for an individual with pRBT=0.4 versus a non-admixed WCT. The increase in Cyclone was ~31%. Juvenile migration probability was also influenced by a significant interaction between pRBT and total length (Figure 2.6a & 2.6c). More specifically, the probability of emigration increases with total length for non-admixed WCT and individuals with low levels of admixture. For moderately or highly admixed hybrids, the probability of emigration decreases as total length increases. This relationship indicates that hybrids are more likely to emigrate at smaller sizes than WCT, however the strength of this relationship differs between Cyclone and Langford.

Discussion

Our study was the first to evaluate how non-native hybridization and the environment interact (GxE) to affect individual fitness traits in wild populations. We found that non-native admixture influenced both seasonal growth rates and migratory life history expression. Environmental conditions worked to mediate the effects of admixture on seasonal growth rates, but not migratory behavior. Our analysis of seasonal growth rates revealed RBT admixture x environment interactions (GxE) at multiple scales; not only did RBT admixture interacted with temperature to influence summer growth rates, but it had varying effects on growth by season. Migratory life history expression was consistently and positively impacted by admixture. Non-native hybridization clearly impacts ecologically and evolutionarily important traits in native trout, and these results highlight how environmental differences

among populations can influence these outcomes. These impacts have the potential to disrupt locally-adapted phenotypic optima in traits with strong impacts on local fitness outcomes.

Admixture x Environment Interactions on Growth Rates

Non-native admixture led to increasingly higher summer growth rates for hybrids across a range of temperatures suitable for WCT growth. From 2013-2016, median summer temperature at our study sites ranged from 10.2 ºC to 14.3 ºC, a range that is well within the limits of growth for WCT and RBT which were found to have very similar thermal optima for growth (Bear, McMahon, & Zale, 2007; WCT = 13.7 ºC, RBT = 13.2 ºC) . Given that pRBT positively interacted with temperature across this range, it is likely that RBT and hybrids have an advantage in growth during the summer across much of the Flathead River basin. Even at our coldest site (Langford), where average median summer temperatures did not exceed 10.7 ºC in any year, hybrids still grew faster than WCT. Higher growth rates even under cooler summer conditions supports the hypothesis that hybrids may have metabolic or physiological advantages over WCT (Morinville & Rasmussen 2003; Rasmussen et al. 2012) that may lead to competitive advantages over cutthroat (Seiler & Keeley 2007, 2009).

Lower summer growth rates may be inconsequential to the fitness outcomes of hybridization if WCT are able to make up this lag in growth during the more favorable spring growing season. In the populations with cooler spring conditions (Langford and McGee), pRBT was negatively associated with growth rates. In these same populations, there was no annual impact of pRBT on growth. This suggests that a pRBT x season interaction could exist in many populations across the landscape. In the population that did not show any evidence of a negative effect of admixture on spring growth (Cyclone), this site accumulated on average 27% and 48% more growing-degree-days than McGee and Langford during the spring. Although we did not detect a pRBT x temperature interaction during the spring, if cooler water temperatures are contributing to higher WCT growth rates in the spring, it is not surprising that WCT are unable to grow faster than hybrids given the drastically warmer conditions in Cyclone.

Climate change induced shifts in thermal and hydrologic regimes will likely only lead to more favorable conditions for RBT and hybrids in the Flathead River basin (Jones et al. 2014). Altered thermal and hydrologic conditions over the last three decades have already been associated with increased expansion of hybridization in the Flathead River (Muhlfeld et al. 2014). Increasing summer water temperatures should only exacerbate the positive effects of pRBT on summer growth rate as RBT have a wider scope-for-growth and can continue to grow at water temperatures over 20 ºC (Bear, McMahon, & Zale 2007). These climatic shifts could alter the growth patterns seen in other seasons as well. As spring conditions warm, WCT might begin to experience a larger portion of this season where they grow more

slowly than sympatric RBT and hybrids; seasonal and annual growth patterns like those seen in Cyclone might become more common across the region.

Not only do differences in annual growth have potential implications for fitness differences among WCT and hybrids, but patterns the seasonal growth play an equally important role in fitness, even in cases where there are no net annual differences in growth. Consistently higher annual growth may lead to differences in life history traits such as age at maturation, migration versus residency, and fecundity (Kendall et al. 2015; Janowicz et al. 2018). However, differences in seasonal growth rate might have important implications for survival, such as size-selective overwinter survival (Sogard 1997; Carlson, Olsen, & Vøllestad 2008), that might favor individuals going into winter at larger sizes or better condition (Uthe et al. 2016; Al-Chokhachy et al. 2019). If seasonal growth and survival are linked, not knowing the survival outcomes in these systems means we are potentially underestimating the effect of RBT admixture differences in seasonal growth rates. Investigating the effects of non-native admixture on seasonal survival rates is a critical next step in understanding the complex interactions between these fitness traits and the environment.

Genetic Driver of Partial Migration

The consistent effect of admixture probability of migration adds critical knowledge to a rich list of literature on life history differences among these species (Muhlfeld et al. 2009c; Corsi, Eby, & Barfoot 2013; Kovach et al. 2015). Our results add further evidence to the findings of Boyer et al. (2008) that dispersal of hybrids is likely higher than that of WCT. Our results also confirm those found by Kovach et al. (2015) showing juvenile hybrids tend to emigrate out of natal streams at a smaller size (earlier age) than WCT. By showing that RBT admixture not only influences the phenology of life history events, but leads to a higher expression of migratory behavior we begin to understand a mechanism behind the continued expansion of RBT admixture in this system and others. Given the size differences that typically exist between resident and migratory trout (Downs, White, & Shepard 1997), this represents a life history trade-off with potentially massive consequences for reproductive success and fitness.

Our conclusions of a strong genomic driver of life history variation align with recent findings from salmonids (Hecht et al. 2013; Prince et al. 2017; Kelson et al. 2019; Pearse et al. 2019) and other vertebrate taxa (mammals - McDevitt et al. 2009; Berg et al. 2019; birds - Delmore & Irwin 2014; Delmore et al. 2016; Ralston et al. 2019). Interestingly, many studies of partially migratory populations suggest the slowest growing individuals are most likely to adopt the migratory strategy as they cannot acquire enough energy in local food sources and must seek more productive areas to grow large enough to mature (e.g., Yates et al. 2015; Berg et al. 2019; Ferguson et al. 2019). Our results do not indicate a connection between non-native admixture effects on growth rates and its effects on migration. While

Cyclone and Langford creeks differed in their effect of RBT admixture on annual growth, pRBT had consistent effects on the probability of migration. Our study is one of a few across vertebrate taxa to demonstrate effects of hybridization on partially migration behavior. Furthermore, our findings parallel those of Yates et al. (2015) where genetic differences explained more variation in the probability of freshwater maturation in Atlantic salmon (*Salmo salar*) than environmental treatments. Determining the true mechanisms underlying migratory life history expression is challenging (Kendall et al. 2015; Berg et al. 2019); perhaps the genetic association with migration in hybrid zones represent interspecific differences in the threshold reaction norm associated with the switch point from migratory to residency (Sloat et al. 2014). Using new genomic techniques (i.e., admixture mapping, genome-wide association analyses) we might gain insight into the genomic structure of partial migration life history and the effects hybridization has on it.

While juvenile growth is generally considered an important fitness trait linked to competition, survival, maturation and life history strategy (Sogard 1997; Seiler & Keeley 2009; Berg et al. 2019; Ferguson et al. 2019), our study demonstrates its complex nature might make it uninformative or misleading when trying to predict fitness outcomes and the spread of non-native admixture in this system. Interestingly, Cyclone, which shows positive effects of pRBT on annual growth rates and probability of migration has the lowest population level pRBT. This suggests there are factors other than stream temperature and growth rates influencing invasion and admixture by RBT in this system. Reproductive success and survival across life stages may play an important role in regulating introgression. These data provide further evidence that hybrid dispersal is the critical mechanism driving the spread of introgressive hybridization between these species, not necessarily species-specific differences in thermal performance (Kovach et al. 2015; Lowe, Muhlfeld, & Allendorf 2015). Our study provides important supporting evidence of these hypotheses explaining the patterns of fitness and hybrid zone expansion.

Implications:

Knowing the fitness consequences of human-mediated hybridization and whether environment mediates these effects is critical to understanding and predicting the future expansion of hybrid zones. Studies demonstrating how environment influences the effects of non-native hybridization on important phenotypic traits in wild populations are rare. This limits our understanding of drivers of introgression across a heterogeneous landscape and may hinder our ability to make appropriate conservation actions. Changes in the seasonal growth patterns and migratory proportion might represent disruption of locally adapted phenotypic optima and have unforeseen consequences on long-term evolutionary trajectories and population persistence. While environmentally dependent (or mediated) traits maybe important for

determining local fitness dynamics and introgression, they maybe inconsequential for the spread of non-native alleles compared to traits with consistent effects under stronger genomic control.

Table 2.1: Sample size by year and population for individual growth (2013-2017) and life history analyses (2013-2016). The sample sizes and mean proportion RBT admixture (pRBT) for each year and season of the growth rate dataset are on the left half of the table. The right half shows the sample sizes and mean pRBT for the adult and juvenile datasets in the migratory life history behavior analyses.

		growth rate analysis				Adults		life history analysis		Juveniles			
population	year	summer	spring	annual	pRBT	number migrants	number residents	pRBT migrants	pRBT residents	number migrants	number residents	pRBT migrants	pRBT residents
Cyclone	**2013**	24	-	-	0.11	51	44	0.17	0.10	10	129	0.20	0.06
	2014	20	10	15	0.11	39	64	0.18	0.04	4	187	0.07	0.12
	2015	129	33	51	0.12	65	183	0.22	0.08	33	484	0.16	0.11
	2016	105	52	69	0.14	52	157	0.20	0.06	60	546	0.21	0.11
	2017	-	50	106	0.14	-	-	-	-	-	-	-	-
	total	278	145	244	NA	206	448	NA	NA	107	1346	NA	NA
Langford	**2013**	34	-	-	0.41	26	5	0.37	0.43	42	105	0.40	0.21
	2014	18	15	16	0.32	15	18	0.59	0.38	113	134	0.36	0.26
	2015	43	18	30	0.37	27	40	0.41	0.22	6	131	0.43	0.41
	2016	47	27	27	0.37	61	39	0.47	0.39	31	191	0.45	0.35
	2017	-	15	21	0.36	-	-	-	-	-	-	-	-
	total	142	75	94	NA	129	102	NA	NA	192	561	NA	NA
McGee	**2013**	-	-	-	-								
	2014	29	-	-	0.41								
	2015	70	21	27	0.40								
	2016	47	17	18	0.32								
	2017	-	23	32	0.38								
	total	146	61	77	NA								

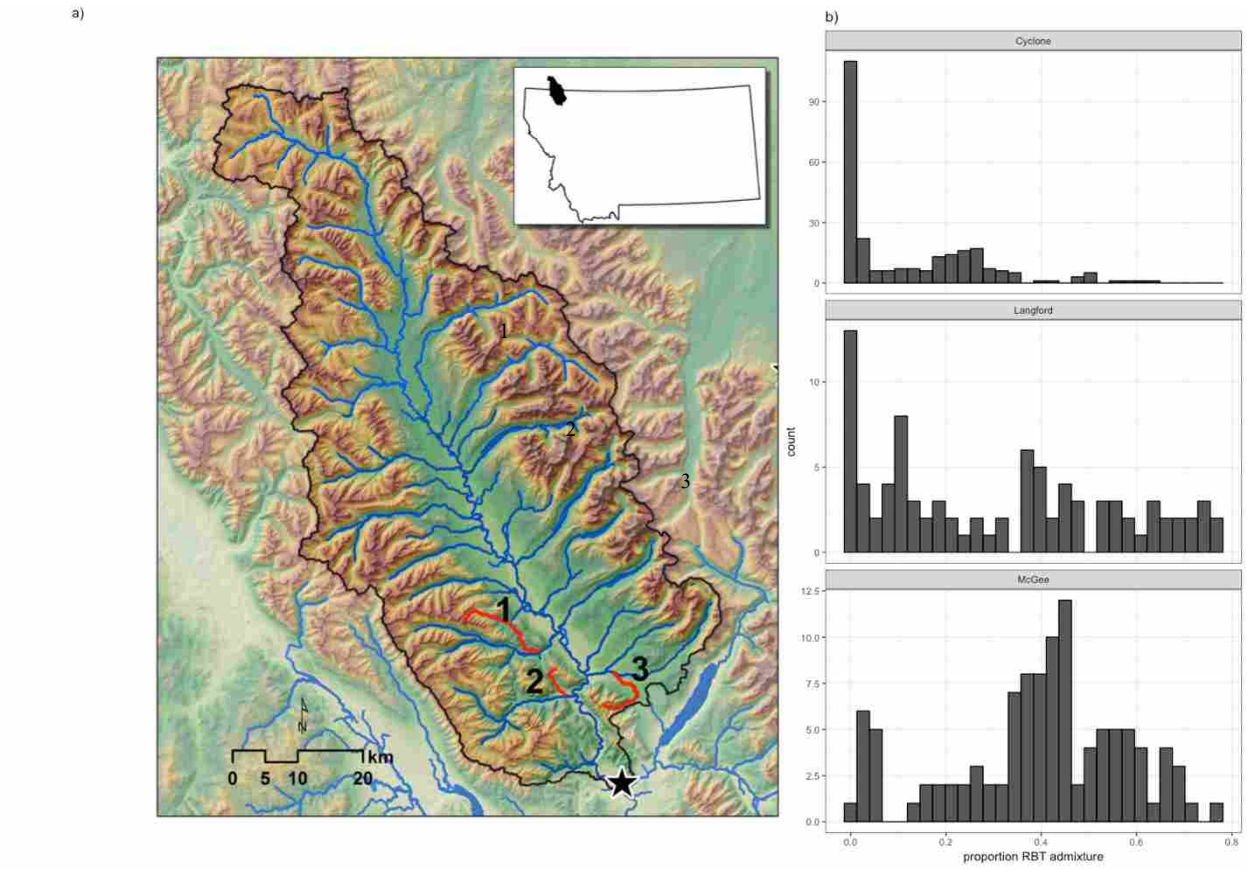

Figure 2.1: Map of our study system, the North Fork Flathead River in Northwestern Montana, USA (a). We sampled Cyclone (1), Langford (2), and McGee (3) creeks using migrant fish traps and seasonal backpack electrofishing surveys to capture, tag, and recaptured Oncorhynchus ssp. from 2013 – 2017. These populations contain WCT and hybrids but differ in their distributions of individual proportion RBT admixture (pRBT). Panel b) shows the distributions of pRBT from 2015 sampling efforts. These distributions are typical of the distributions within each population throughout the entire study. See Appendix A, Figure S2.1 for distributions of RBT admixture within each population by sampling year.

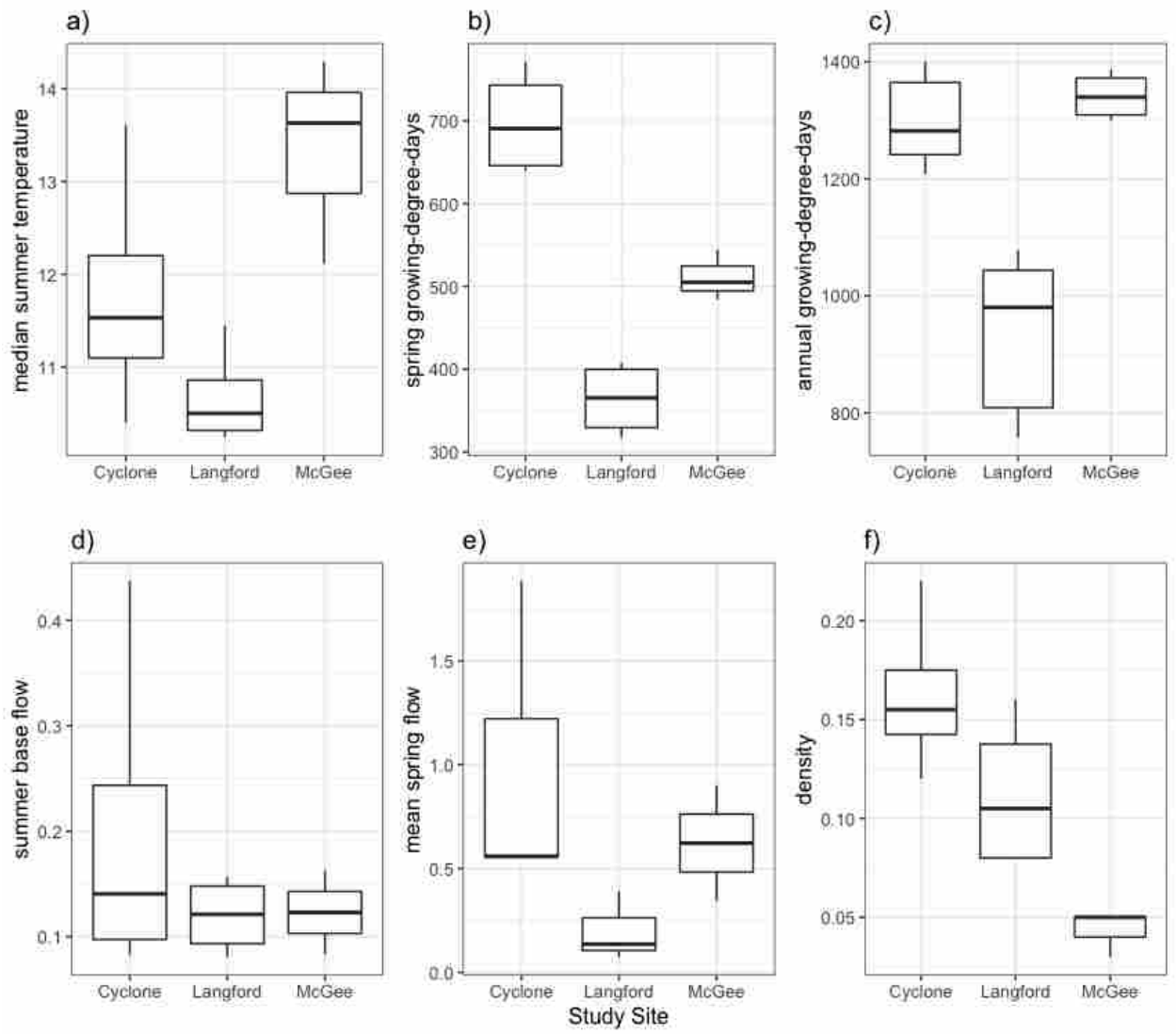

Figure 2.2: Boxplots of key environmental variables: median summer temperature (ºC; a; ANOVA p = 0.031), growing-degree-days accumulated during the spring season (b; ANOVA $p < 0.00005$) and annually (c; ANOVA $p < 0.00005$), summer base flow (m^3/sec; d; ANOVA p = 0.51), mean spring flow (m^3/sec; e; ANOVA p = 0.27), and *Oncorhynchus spp.* density (fish/m^2; f; ANOVA $p < 0.0077$). See Appendix A, Table S2.2 for full environmental data.

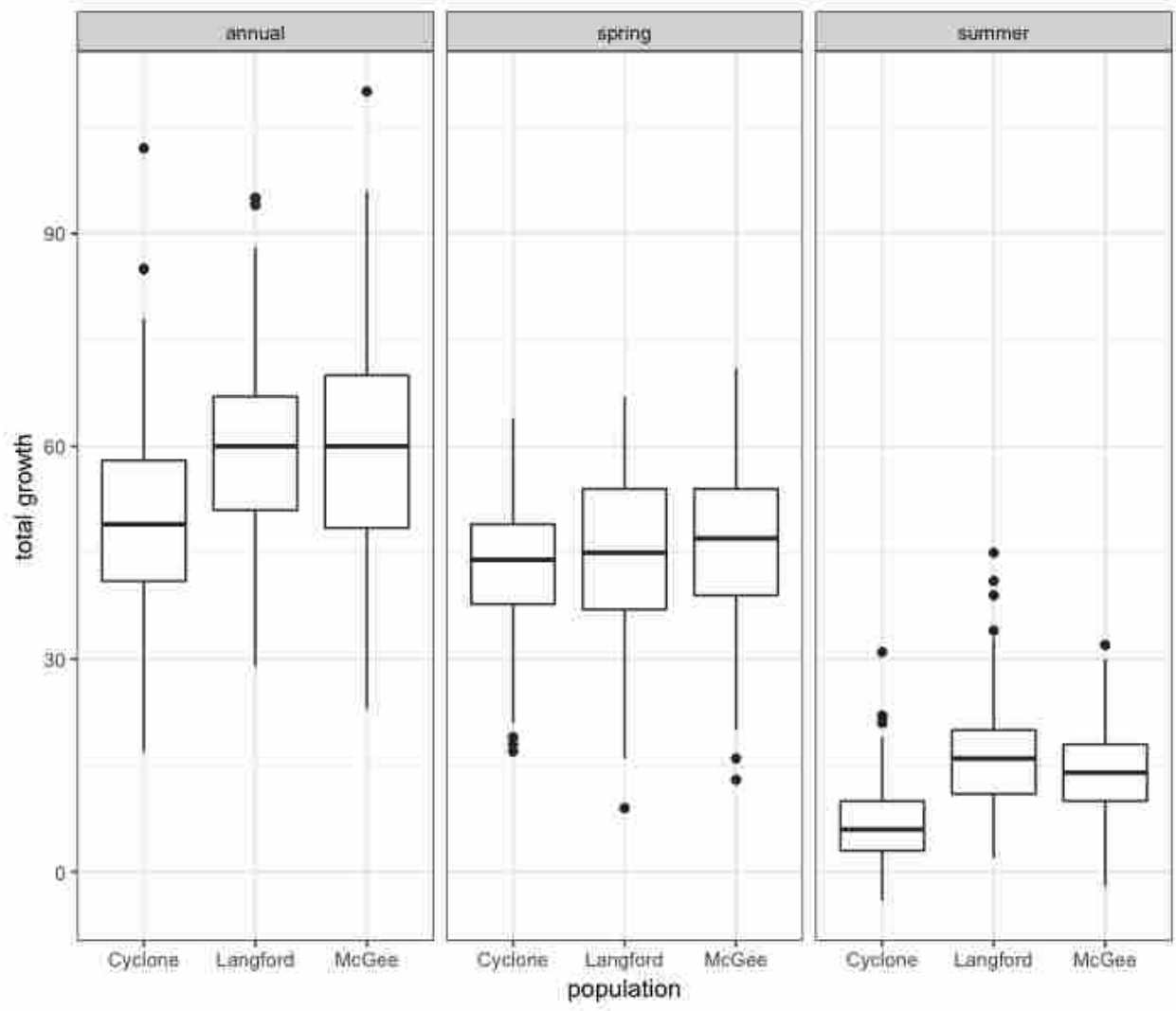

Figure 2.3: Boxplots of annual, spring, and summer growth in length (mm, top) for each population. Growth during the spring season is significantly higher than summer growth in all populations (t-test, $p < 0.00001$). Summer and annual growth in Cyclone is lower than growth in Langford or McGee ($p < 0.00001$), however, there are no significant differences in growth among populations during the spring season.

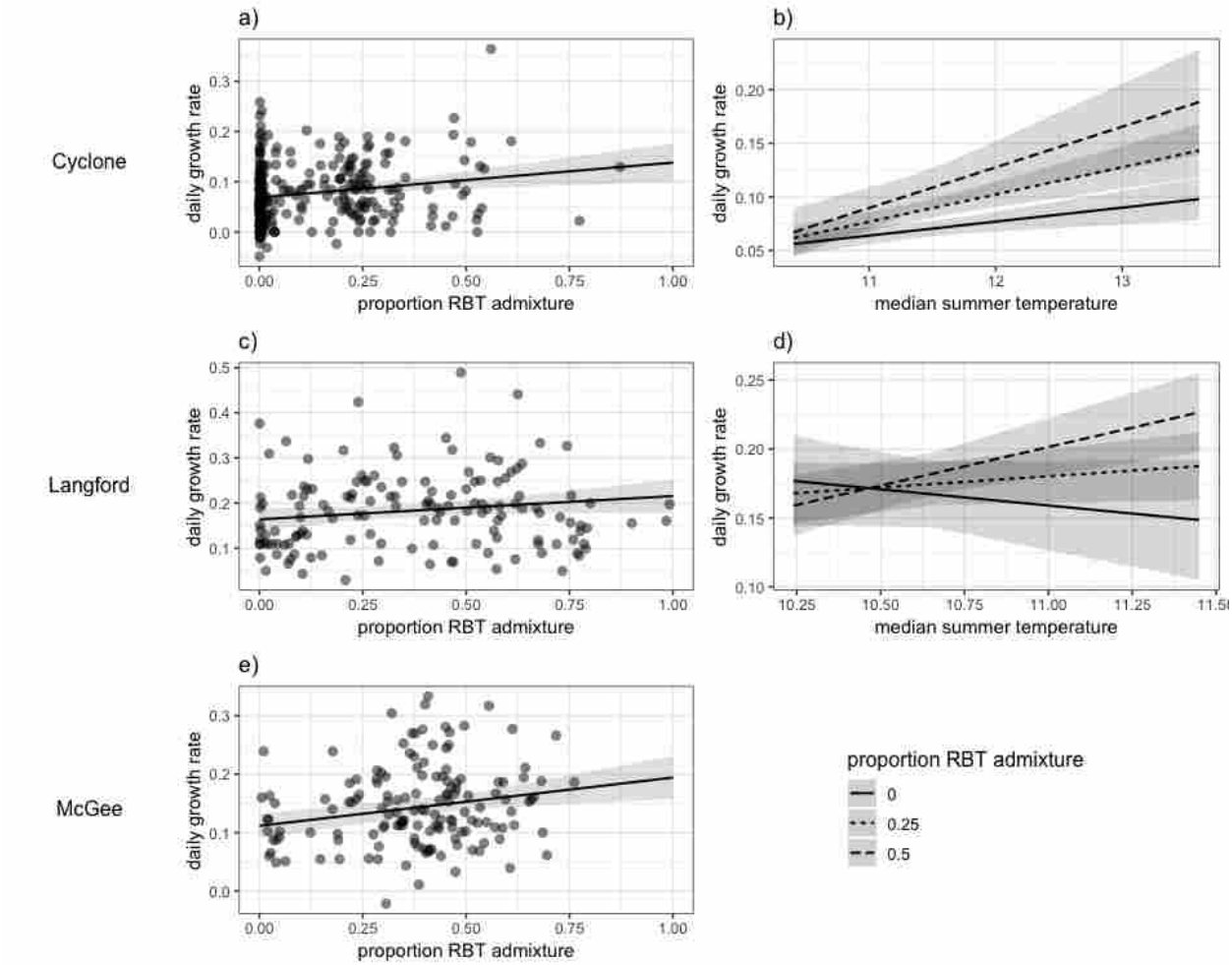

Figure 2.4: The left column shows the predicted relationship between pRBT and daily growth rate from the top supported models of summer growth rate (mm/d) in each population: Cyclone (a), Langford (c), McGee Creeks (e). The right column shows the interaction between pRBT and median summer temperature on growth rates for Cyclone (b) and Langford Creeks (d), where the different lines depict different RBT admixture (non-admixed WCT - solid, 0.25 RBT admixture - dotted, and 0.5 RBT admixture - dashed).

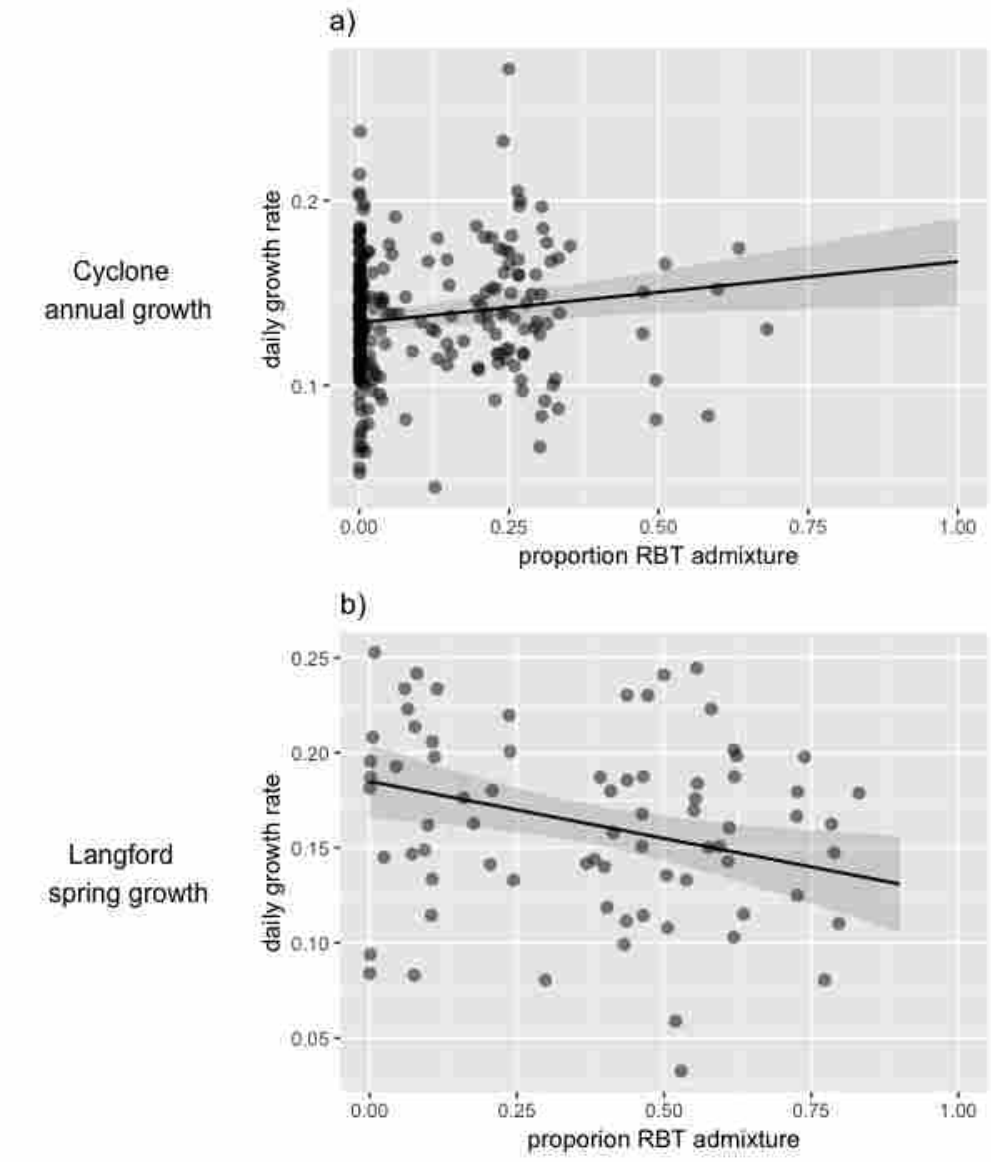

Figure 2.5: Predicted relationship between pRBT and daily growth rate (mm/d). On an annual basis, only Cyclone had a positive effect of pRBT on growth rate (a). During the spring, Langford had a negative effect of pRBT on daily growth on length (b), however, McGee had a negative effect of pRBT on daily growth in mass (see Appendix A, Table S2.9b).

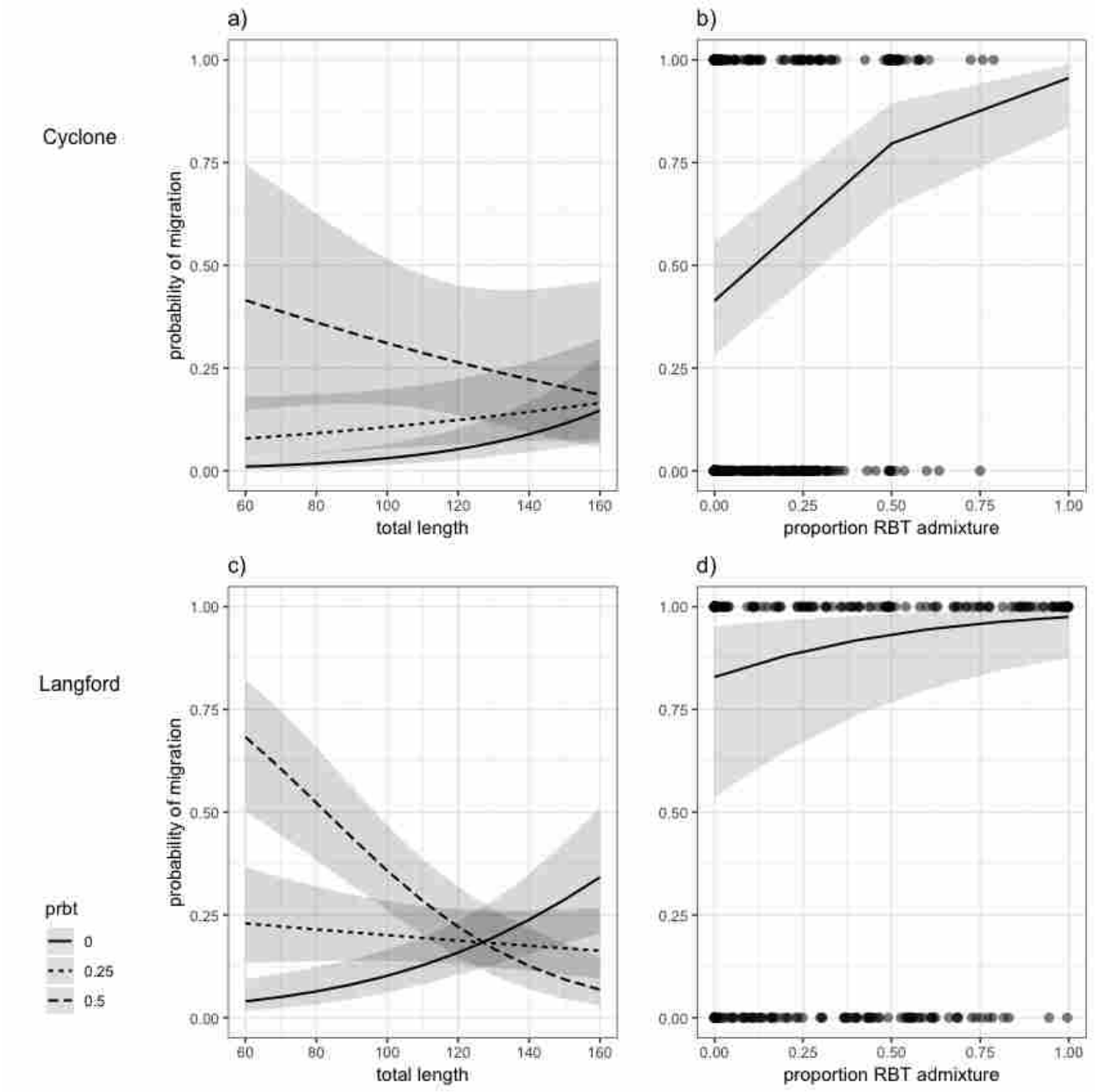

Figure 2.6: Predicted relationship between pRBT and the probability of expressing a migratory life history strategy in CYC and LAN for juveniles (left column) and adults sampled (right column). Plots a) and c) show the negative effect of pRBT on probability of emigration as total length increases for a non-admixed WCT (solid), 0.25 admixed individual (dotted), and 0.5 admixed individual (dashed). Plots b) and d) show the positive effect of pRBT on the probability of captured adults being migratory.

CHAPTER 3
NON-NATIVE HYBRIDIZATION HAS VARIABLE EFFECTS ON SURVIVAL IN DIFFERENT SALMONID POPULATIONS

Abstract

Human-induced hybridization increasingly threatens global biodiversity. However, variation in fitness consequences of human-mediated hybridization across heterogeneous landscapes is poorly understood. Introgressive hybridization with introduced rainbow trout (*Oncorhynchus mykiss*) threatens all subspecies of cutthroat trout (*O. clarkii*) and environmental conditions are thought to influence hybridization. We used mark-recapture of over 5,200 individuals in three wild populations of westslope cutthroat trout (*O. clarkii lewisi*) to parameterize a multistate mark-recapture survival model. We quantified the effects of non-native rainbow trout genetic admixture (measured with >500 species diagnostic-SNPs) and environmental variation (season, temperature, and population density) on survival rates. Summer survival was positively associated with non-native hybridization at two sites, however, overwinter survival was negatively associated with non-native admixture at the warmest site. Site-level variation in temperature and density did not interact with admixture to influence survival rates. Annual survival was negatively associated with rainbow trout admixture at the warmest site, while positively associated with admixture at the coldest site. These results show that outbreeding depression in the wild is context-dependent, and that environmental gradients typically used for describing patterns in hybrid zones, such as thermal regimes, may poorly predict variation in fitness consequences across the landscape.

Introduction

Non-native hybridization is a serious and growing conservation problem threatening numerous species worldwide (Allendorf et al. 2001; Crispo et al. 2011; Grabenstein and Taylor 2018). Human-mediated hybridization (hybridization that is the direct result of human actions via translocations or habitat alterations) can lead to the extinction of native genotypes (hybrid swarms), loss of locally adapted gene complexes, and outbreeding depression (Rhymer & Simberloff 1996; Abbott, Barton, & Good 2016; Todesco et al. 2016). Outbreeding depression has typically been considered a universal phenomenon following human-mediated hybridization events in species that exhibit local adaptation (Rhymer and Simberloff 1996), yet there is increasing evidence that the relative fitness of hybrid genotypes can be environmentally dependent and change over time (Arnold & Martin 2010; Walsh et al. 2016a; Hunter et al. 2017; Zhang et al. 2019). The tension and mosaic hybrid zone models from hybrid zone theory (Arnold 1997) have been used to set expectations of the drivers and consequences of human-mediated hybridization (e.g., Grabenstein & Taylor 2018). Research that quantifies how local environmental conditions regulate individual fitness differences in admixed populations is relatively common in plants (e.g., Emms & Arnold 1997; Campbell & Waser 2001; Gramlich & Hörandl 2016), but extremely rare in vertebrates (e.g., Culumber et al. 2015; Walsh et al. 2016a). Indeed, there are only a few studies that quantify the fitness consequences of human-mediated hybridization in wild vertebrate populations (e.g., Casas et al. 2012), and there is a lack of research on the interaction between environmental variation and admixture on fitness-related traits in these populations (but see Hunter et al. 2017).

In contrast, a large body of literature has examined landscape patterns of human-mediated hybridization relative to environmental gradients, and these efforts typically invoke differences in fitness as one explanation for environmental-admixture correlations (Culumber et al. 2012; Walsh et al. 2016b; Muhlfeld et al. 2017). Studies of landscape patterns are rarely followed by more intensive studies of fitness traits to confirm if fitness differences are environmentally influenced in wild populations (see Walsh et al. 2016b & Walsh et al. 2016a). Therefore, studies linking fitness consequences of non-native hybridization with environmental variation (temporally and spatially) are key to understanding the prevalence of outbreeding depression and the factors driving the spread of non-native hybridization across heterogeneous landscapes.

Human-mediated hybridization is particularly common in fishes due extensive human translocations for sport fishing and harvest (Epifanio & Nielsen 2000; Scribner, Page, & Bartron 2001). Decreased reproductive success associated with human-mediated hybridization is well documented in salmonids (Araki, Cooper, & Blouin 2007; Christie, Ford, & Blouin 2014; Glover et al. 2017). These studies often assume outbreeding depression to be independent of environmental conditions (as typically

described in tension zones rather than mosaic hybrid zones). Furthermore, few studies have looked beyond the early life history to the effects of hybridization on fitness-related traits in juvenile through adult life histories (but see Fukui 2019; *Chapter 1*).

Hybridization is among the greatest threats to cutthroat trout in western North America, including remaining populations of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*, hereafter WCT; Shepard, May, & Urie 2005). Rainbow trout (*O. mykiss*, hereafter RBT) is among the world's most widely introduced fish species (Behnke 1992; Halverson 2010), and naturalized populations of RBT hybridize with native cutthroat trout. RBT admixture has continued to expand across the landscape despite decreased reproductive success across a range of different environmental conditions (Muhlfeld et al. 2009a; Kovach et al. 2015; Kovach et al. 2016; Muhlfeld et al. 2017)(R. P. Kovach et al. 2015; Ryan P. Kovach, Hand, et al. 2016; Muhlfeld, Kalinowski, et al. 2009; Muhlfeld et al. 2017). Furthermore, the expansion of RBT hybridization and population-level admixture has been associated with stream temperature and other environmental features (Weigel, Peterson, a& Spruell 2003; Boyer, Muhlfeld, & Allendorf 2008; Bennett et al. 2010; Rasmussen, Robinson, & Heath 2010; Muhlfeld et al. 2014; Carim, Eby, & Pierce 2015; Young et al. 2016; Muhlfeld et al. 2017). These hybridization patterns align with known differences in thermal tolerance between these species (Bear, McMahon, & Zale 2007; Yau & Taylor 2014), however, there is considerable variation in the pattern of RBT hybridization unexplained by these environmental predictors (see Muhlfeld et al. 2017). To better understand variation in landscape patterns of admixture it is crucial to understand if non-native admixture influences survival, and if differences in survival (i.e., selection) is environmentally-independent (tension zone model) or -dependent (mosaic model).

Here, we quantified the effects of proportion RBT admixture (pRBT) on seasonal survival rates in three populations of WCT. Specifically, we asked the following questions: (1) how does RBT admixture affect seasonal survival probabilities and do environmental factors influence these effects; (2) if there are significant relationships between admixture and survival, do they correlate with observed population-level admixture; and (3) do they align with landscape patterns previously described for these species (e.g., admixture increases with stream temperature)? These results fill a critical void in the literature by demonstrating the effects of human-mediated hybridization can vary substantially as a function of spatial and interannual environmental variation. Furthermore, previously published environmental associations do not seem to predict the strength of selection against non-native admixture.

Methods

Study Sites

We sampled populations of WCT in Cyclone, Langford, and McGee Creeks on the North Fork Flathead River in northwestern Montana, USA (Figure 3.1). These sites were selected because they were known to contain both non-hybridized WCT and individuals with a range of admixture (Figure 3.2). The sites, while geographically close, differ in key environmental drivers (temperature, flow, density) that influence salmonid survival (Vøllestad & Olsen 2008) and are associated with landscape patterns of non-native admixture (Bear, McMahon, & Zale 2007; Muhlfeld et al. 2017; *Chapter 2;* Table S3.1). Genetic admixture has been occurring in each population for at least five to ten generations, allowing substantial time for backcrossing and recombination.

Mark-Recapture Field Sampling

We used a seasonal mark-recapture design in each tributary to quantify seasonal survival rates across five years (2013-2017). We completed a single electrofishing pass of each study reach (~2km) twice annually (July and October). For each individual > 70mm total length (TL, mm), we measured TL, collected a tissue sample for genetic analysis, and double-marked each with a unique PIT tag (passive integrated transponder) and an external adipose fin clip. Recaptures were identified visually by the absence of an adipose fin, and then by detecting PIT tags previously implanted. If a fish's adipose was clipped but it did not register a PIT tag, it was assumed to have shed its PIT tag; this occurred for < 1% of released tags (see Table 3.1).

In addition to recapturing tagged individuals via electrofishing, we used mobile PIT tag surveys to relocate tagged fish. We searched for PIT tag detections using a single pass across the entire study reach. Upon detection of a PIT tag, we determined whether the signal was from a live, tagged fish or if the tag was shed (i.e., due to mortality, live shedding of tag through the incision, or spawning). We determined this by agitating the water around the detected tag, forcing the fish to move from its current position. We called a tag as "live" if the tag signal moved positions after agitation. We called a tag "shed" if the signal failed to move after sufficient attempts to agitate the fish.

We installed duel PIT-tag antennae at the downstream end of all study reaches and at the upstream end of two study reaches. We ran these antennae from early April through November allowing us to detect the direction of movement and measure movement rates out of the study reaches (i.e., permanent emigration). We obtained capture and genotypic data from 5,249 individuals in our study populations (Table 3.1).

Environmental Data Collection

Since survival in salmonids is influenced by individual size and environmental conditions (Hokanson, Kleiner, & Thorslund 1977; Henderson & Cass 1991; Meyer & Griffith 1997; Sogard 1997; Vøllestad & Olsen 2008), we accounted for all their impacts in addition to testing for effects of individual proportion RBT admixture (pRBT) on survival probability. To test for environmental effects and their interactions with pRBT on seasonal survival rates, we collected data for factors known to affect survival in salmonids: stream temperature (Bear, McMahon, & Zale 2007) and *Oncorhynchus spp.* density (Vøllestad & Olsen 2008). We measured water temperature and density as detailed in Strait et al. (*in prep*). To characterize the severity of the summer conditions we calculated the maximum seven-day average temperature each year. We estimated growing-degree-days (GDD; Coleman & Fausch 2007) to characterize the winter/spring conditions (as in *Chapter 2*). Langford was the coldest site and least variable among years (Table S3.1). Cyclone and McGee had warmer and more variable summer temperatures. *Oncorhynchus spp.* densities were highest in Cyclone and lowest in McGee (Table S3.1).

Laboratory and Bioinformatic Analyses

To estimate genome wide proportion RBT admixture for each individual, we followed the laboratory analyses in Strait et al. (*Chapter 2*). We extracted and quantified DNA prior to RAD-capture procedures. Genetic samples were prepared and sequenced according to the bestRAD protocol and Rapture (RAD-capture) for genotyping (Ali et al. 2016). The capture was performed with the same 3015 customized *mybaits* produced by *Arbor Biosciences* to capture RAD-tags that contain any combination of WCT polymorphic SNPs or WCT, YCT, and RBT species diagnostic SNPs. SNP loci were chosen for capture based on their genotyping quality, reliability for distinguishing each subspecies or species (i.e., subspecies- or species-diagnostic), and even distribution across the assembled rainbow trout genome (see Amish et al. 2012; Berthelot et al. 2014; Hand et al. 2015). We followed the same bioinformatic steps and quality control thresholds and the same set of RBT diagnostic loci as in Strait et al. (*Chapter 2*); on average all individuals were genotyped at 512 RBT diagnostic markers. Proportion RBT admixture (pRBT) was estimated for each individual as the number of RBT alleles / (2 * number of loci).

We genotyped 5,249 individuals across all sites. While each population contained non-admixed WCT individuals, the proportion of the population that was non-admixed varied greatly among the populations (Figure 3. 2). The distribution of pRBT in Cyclone was skewed strongly towards WCT with a median of 0.013 pRBT. Langford and McGee had higher median pRBT (Langford = 0.34; McGee = 0.39) and less skewed distributions of pRBT than Cyclone.

Data Preparation and Model Development

To quantify the effects of RBT admixture on survival rates, we developed a Bayesian multistate Cormack-Jolly-Seber capture recapture modeling framework for each population independently (hereafter MSCJS; Lebreton et al. 2009). This framework has been used in stream salmonids to account for size structure (size classes), permanent emigration from study areas, and movement across space within a study area (Letcher & Horton 2008; Horton, Letcher, & Kendall 2011)(Horton, Letcher, and Kendall 2011; Letcher and Horton 2008). We made novel use of this framework by incorporating size-based-states (hereafter size classes) to deal with unknown sizes of individuals redetected with a mobile PIT reader as well as emigration (Figure 3.3). We developed and ran our MSCJS models in JAGS (Plummer 2013). JAGS runs Bayesian hierarchical models using Markov Chain Monte Carlo (MCMC) simulations to generate the posterior probability distributions for all parameters and model covariates. We formulated all models and tested each using the *jagsUI* package in Program R (Kellner 2015). Our formulation of the MSCJS allowed us to test for the effect of pRBT on seasonal survival (S_s) and transition ($\Psi_{s\text{-}s+1}$) probabilities for each of s size classes.

We chose the multistate formulation of the CJS capture-recapture model because this framework allowed us to achieve three key goals: 1) account for permanent emigration for the study reach, 2) divide each population into distinct life history stages that we hypothesized would have significantly different survival and emigration rates, and 3) reduce bias in our ability to accurately estimate the sizes of individuals resampled via mobile PIT tag reader when true size was unknown. Like many taxa, survival rates in salmonids vary across life history stages and furthermore, variation in environmental conditions can have different impacts on the survival of different size classes (Xu, Letcher, & Nislow 2010; Kanno et al. 2015) And finally, because a large proportion of our recaptures came from mobile PIT tag detections (Table 3.1), grouping individuals into size classes reduced potential bias associated with our imprecision when estimating unknown sizes.

We considered two key features of data collected using a mobile PIT tag unit when we chose our modeling framework: 1) unknown lengths of resampled live individuals and 2) shed tag detections. When an individual's length was unknown, we estimated its length based on Von Bertalanffy (VB) growth curves estimated from individuals in each population separately (Table S3.3). We estimated each individual's age at first capture using the VB growth curves, which allowed us to estimate its age throughout the duration of the study. For any individual i resampled via mobile PIT tag reader at time t, we then estimated $\text{length}_{i,t}$ at a given $\text{age}_{i,t}$ from the VB equation. Finally, we adjusted $\text{length}_{i,t}$ by adding residual_i from the mean size at age of the growth curve to adjust its estimated lengths across time. This ensured that imprecision in our estimates of length did not cause individuals to shrink over time (i.e., estimated $\text{length}_{i,t}$ is greater than a known $\text{length}_{i,t+1}$). Since there was uncertainty whether a shed tag was

due to mortality or tag loss from a live individual, we censored individuals from the model at the occasion they were first detected as a shed.

Our multistate CJS model consisted of four states, three size classes (juvenile, sub-adult, and adult) and one permanent emigration state (*E,* Figure 3.3). In addition to the assumptions of CJS models (Lebreton et al. 1992), we assumed emigration was permanent, occurred prior to mortality, and was perfectly detected. We recoded all encounter histories from measured or estimated total lengths to the size classes. If an individual was captured at a total length < 120 mm it was assigned to the juvenile class (*juv*), individuals at lengths > 120 mm and < 180 mm were assigned to the sub-adult class (*sub*), and individuals at lengths > 180 mm were assigned to the adult class (*ad*). These size classes were taken from life history work within WCT which found females to generally be mature at 180 mm TL (Downs, White, & Shepard 1997; Janowicz et al. 2018)(Janowicz et al. 2018; Downs, White, and Shepard 1997). We assumed released individuals survived with a size-class-specific probability S_s. We allowed individuals to transition across size class between any consecutive sampling occasions. It was assumed that individuals survived in their current size class and transitions occurred just prior to capture or detection. Individuals were not allowed to move from *juv* to *ad* without first moving into *sub* for at least one period and individuals could never transition back to smaller size classes. Transition probabilities for the *juv* and *sub* size classes were estimated from a multinomial distribution. We estimated the probability an individual remained in its current class ($\Psi_{juv\text{-}juv}$, $\Psi_{sub\text{-}sub}$), transitioned to the next larger class ($\Psi_{juv\text{-}sub}$, $\Psi_{sub\text{-}ad}$), or emigrate permanently from the system ($\Psi_{juv\text{-}E}$, $\Psi_{sub\text{-}E}$) between sampling occasions. Adult emigration probability was estimated from a binomial distribution ($\Psi_{ad\text{-}E}$). Once an individual emigrated from the system, its probability of detection and transition probability out of state *E* was fixed to zero (emigration is permanent).

Model Parameterization and Testing

We built and tested MSCJS models for each population by the following steps: 1) we determined the most appropriate covariate structure on probability of detection (p_s), 2) we tested our null and hypothesized covariate structure on survival (S_s), 3) we tested our null and hypothesized covariate structures on transitions ($\Psi_{s\text{-}s+t}$), and 4) we ran each full model with supported structure on p, S, and Ψ. Our goal was to parameterize final MSCJS models that minimized the number of necessary covariates for p and included only supported covariates for S and Ψ. We tested the covariate structure for p under a fully saturated (time-varying) covariate structure for S_s to avoid variability in S_s over time being partitioned into variability in p_s. We tested for state-specific, fully time-varying, and crew effects on p_s. We used slightly informative priors to increase the speed of MCMC chain convergence by informing the prior distributions based on probability of detection estimates from the multiple pass depletion conducted every

July at each site (Table S3.2). After setting the covariate structure on p_s, we tested several hypothesized covariate structures on S_s and then $\Psi_{s1\text{-}s2}$. We tested a fully-time varying structure, seasonal effects, pRBT effects, and a pRBT*season interaction on state-specific S_s and $\Psi_{s1\text{-}s2}$. Additionally, we tested for the effect of seasonal temperatures and densities on S_s (Table S3.8).

We tested the covariate structure on all parameters using uninformative (uniform) prior distributions on all coefficients and ran three parallel MCMC chains for a minimum of 10,000 repetitions. In some cases, we used slightly informative priors to speed up chain convergence (see Appendix B). We assessed Markov chain convergence by inspecting the Gelman-Rubin diagnostic ($\hat{R}$) for each parameter and through visual inspection of the Markov chain trace plots (Tables S3.4-S3.6). We considered a covariate to be supported if the 95% credible interval (C.I.) of the posterior distribution did not overlap zero. In order for an environmental covariate to be considered supported, we required 1) that its 95% C.I.'s did not overlap zero, and 2) it demonstrated consistent effects across size classes and seasons (i.e., never switch from positive to negative in different size classes or seasons). After we determined the supported covariate structure on p_i, S_i, and $\Psi_{i\text{-}j}$, we ran all final models for a minimum of 50,000 MCMC repetitions, with 10,000 burn-in repetitions and 5,000 adaptive steps to estimate our final posterior distributions for all parameters (Tables S3.3-S3.5).

Results

Probability of Detection

We found support for size class-specific probability of detection, but there was not support for time varying or crew effects on probability of detection. There was substantial overlap between the posterior distributions of detection probabilities among some size classes in each population (e.g., juvenile and subadult probability of detection was not different). As a result, we parameterized constant detection probability for the juveniles and subadults ($p_{juv/sub}$), and separately for adults (p_{ad}) in Langford and McGee Creeks (Tables S3.4 & S3.5). In Cyclone Creek we parameterized constant detection probability for juveniles (p_{juv}) and a separate detection probability for sub-adults and adults ($p_{sub/ad}$, Table S3.3).

We found significant differences in seasonal emigration and size class transition probabilities in all populations, however, as these results are not the focus of this paper and have been previously described in these populations (*Chapter 2*), we do not discuss these any further. All results for emigration and transition probabilities are discussed further in the Appendix B (section S3.1.1)

Effects of pRBT and Season on Survival Probabilities

Monthly survival probabilities varied among summer and winter seasons and each population had a unique pattern of season survival differences (Figures S3.1 & S3.4; Tables S3.4 – S3.6). For example, monthly survival probability was higher during the winter in all size classes in Cyclone Creek (Table 3.2). However, fish of all size classes in McGee Creek had a higher monthly survival probability during the summer. And in Langford there was no difference in seasonal monthly survival probabilities for the juvenile or subadult size classes, but the adult size class higher monthly survival probability during the summer.

The effect of pRBT on survival probabilities also varied among populations and seasons (Table 3.2). In populations where pRBT significantly influenced survival, there was a positive effect on summer survival and a negative effect on winter survival. In Cyclone, pRBT positively influenced summer survival in subadults and adults and negatively influenced winter survival in all size classes (Figure 3.5a-c). In Langford only juvenile summer survival probability was positively affected by pRBT (Figure 3.4a). We found no evidence that RBT admixture affected survival probabilities in McGee Creek (all posterior distributions for coefficients of pRBT overlapped zero).

In Cyclone and Langford Creeks, the impacts of pRBT on seasonal survival rates, led to differences in annual survival probabilities associated with RBT admixture (Table 3.2). In Langford, the positive effect of pRBT on juvenile summer survival resulted in 20% higher annual survival for individuals with a hybrid score of 0.3 pRBT relative to a nonhybridized WCT (Figure 3.4b). In Cyclone Creek, despite the positive effect of pRBT on summer survival, the negative effect during the winter resulted in lower annual survival for individuals with increasing pRBT (Figure 3.5d-f). For example, in all size classes nonhybridized WCT had ~25% higher annual survival probability than individuals with hybrid scores of 0.25 pRBT.

Effects of Temperature and Density on Survival

While seasonal variation in environmental conditions generally had strong impacts on survival and interacted with pRBT, we found no evidence that interannual variation in temperatures or fish densities interacted with pRBT to influence survival. The effect of pRBT on survival was not influenced by inter-annual variation in temperature or density consistently in any population (Table S3.7). However, variation in summer temperatures did positively influence survival in all juvenile and subadult classes (Table S3.7) and in Cyclone, adult summer survival was also positively associated with temperature. There was little evidence that pRBT interacted with summer temperature to influence survival as only one (of nine) coefficients estimating this interaction had a posterior distribution that did not overlap zero (Table S3.7).

There was weak evidence that winter temperature (GDD) affected survival as only three (of eighteen) coefficients' posterior distributions did not overlap zero. Furthermore, these effects did not impact the same size class and did not have the same direction of effect. For example, in Cyclone, winter temperature negatively affected adult survival, while it positively affected sub-adult survival in McGee, and in Langford there was a positive interaction between winter temperature and pRBT on survival probability.

Density only had significant effects on survival in Cyclone Creek. Density had significant negative effects on juvenile and sub-adult survival, additionally there was a negative interaction between density and pRBT on sub-adult summer survival (Table S3.7). Winter survival was less consistent; juvenile survival was negatively affected by density, while sub-adult and adult survival was positively affected by density. There was also a positive interaction between pRBT and density on juvenile winter survival. In Langford, all twelve coefficients of density on survival overlapped zero and only one coefficient did not in McGee.

Survival, Population-level pRBT, and Landscape Patterns

Variation in the effect of pRBT on survival reflected the variation in population-level pRBT among our study sites (Figure 3.2; Table 3.2). Populations that displayed neutral or positive effects of pRBT on annual survival probabilities had much higher site-level pRBT. There was no significant effect of pRBT on survival in McGee Creek and this population had the highest pRBT admixture (mean pRBT = 0.34). There was a positive effect of pRBT on juvenile annual survival in Langford Creek and while there were still many nonhybridized WCT, there was a high proportion of hybrids in this populations (mean pRBT = 0.31). Finally, Cyclone Creek had the lowest population-level pRBT (mean pRBT = 0.11) and was the only population to have significant negative effects of pRBT on annual survival.

Population-level pRBT and its effects on survival did not align with previous associations between environmental variation and population pRBT (Table 3.2). Although, positive associations between stream temperature and site pRBT has been documented in numerous studies (Muhlfeld et al. 2014; Carim, Eby, & Pierce 2015; Young et al. 2016; Muhlfeld et al. 2017), our sites did not follow this pattern. First, the site with coolest summer temperatures (mean August temperature 11.3ºC) had a positive effect of pRBT on juvenile survival and high population pRBT (Table S3.1). Moreover, at the site with the warmest conditions (mean August temperature 14.1ºC), there were strong negative effects of pRBT on survival and low population-level admixture. While density has not been shown to predict landscape patterns of hybridization, we found density was negatively correlated with pRBT at our sites (Table 3.2). Cyclone Creek had the highest and most variable fish density while McGee had the lowest and least variable fish density (Table S3.1).

Discussion

Our study is among the first in vertebrate taxa to quantify the effects of non-native hybridization and environmental conditions on a trait directly influencing fitness in wild populations. We found that the effect of non-native admixture on survival varied by season and among populations, ranging from strongly negative to positive. There is evidence that spatial variation in environmental conditions mediated the effects of RBT admixture on survival rates, but not as predicted from landscape patterns previously described for these species (Table 3.2). Interestingly, the differences in annual survival due to proportion RBT admixture reflected the population level admixture at each site. This indicates that selection against hybrids at later life-stages might be a necessary mechanism to prevent widespread admixture from occurring.

Human-mediated hybridization is often documented to result in wide-spread admixture (Allendorf et al. 2001; Grabenstein & Taylor 2018), yet this is not uniform across the landscape as variation in the extent of RBT admixture is attributed to landscape patterns of introductions and environmental conditions (Muhlfeld et al. 2017). Previous research in the Flathead River, MT has demonstrated that extensive admixture can occur despite decreased reproductive success and selection against hybrids (Muhlfeld et al. 2009a; Kovach et al. 2015); Cyclone and Langford Creeks have been extensively studied for over two decades. Previous research found strong signals of selection against hybrids in Langford and Cyclone during early life history stages, yet population-level admixture is high in Langford (pRBT = 0.34) and remains relatively low in Cyclone (pRBT = 0.11). This suggests that selection during the early life history alone may not prevent admixture from reaching a high level, particularly in highly fecund taxa that produce 100s or 1000s of offspring. In such species, strong reductions in survival of later life history stages (juvenile-adult) are likely necessary to limit non-native admixture in the face of continuous gene flow from source populations.

The variation in the effect of non-native admixture on survival and the population-level consequences found in this study were different from the previous described trends of higher site-level pRBT associated with warmer stream temperatures (Muhlfeld et al. 2014; Young et al. 2016; Muhlfeld et al. 2017; Table 3.2). However, the strength of selection on RBT hybridization did match the site-level admixture. This has important implications for a wide body of research that documents association between environmental variation and hybridizations (e.g., Culumber et al. 2012; Walsh et al. 2016b). Specifically, significant environment-admixture associations may be extremely poor predictors of spatial variation in fitness and natural selection.

Although density-dependent growth and survival is well documented in a wide range of taxa (Clutton-Brock et al. 1987; Vøllestad & Olsen 2008), density has not been shown to explain the landscape patterns of hybridization (Weigel, Peterson, & Spruell 2003; Muhlfeld et al. 2009b; Rasmussen, Robinson, & Heath 2010; Mckelvey et al. 2016; Young et al. 2016; Muhlfeld et al. 2017). However, this could be due to the collinearity between density and other landscape features (i.e., stream width and elevation). Moreover, density itself may not be the mechanism responsible for differences in growth, survival, or landscape patterns of hybridization, but density relative to the carrying capacity of the local environment (e.g., Bowyer et al. 2014). We found density-dependent effects on survival only in the population with the highest (1.3-3.2x higher) and most variable density (Cyclone, Table S3.1). The lack of evidence for density-dependent survival in the other populations could be due to a lack of interannual variation in density or that density is not near the carry-capacity of that site. This suggest the strength of selection against non-native admixture could be both density and frequency dependent (i.e., soft selection; Wallace 1975). Under the soft selection hypothesis, selection against hybrids should be strongest when density is high and the frequency of hybrids is low, and this is exactly what we observed in this study.

The number of generations that admixture has been occurring might also explain the variable effects of RBT admixture on survival rates. RBT admixture was detected in Langford about two generations before it was detected in Cyclone. Recombination and selection during that period, would result in small chromosomal segments than a more recently admixed population and result in potentially weaker selection against hybrids. Similarly, once a population is nearly a hybrid swarm (few or no parental species; as in McGee Creek) detecting selection due to genome-wide admixture might be very difficult. First, selection is likely to have removed the most deleterious alleles from the population, and due to recombination, individuals of approximately the same hybrid index may have very different chromosomal admixture.

Quantifying fitness consequences of human-mediated hybridization in vertebrates is challenging. This challenge is further complicated since the relative fitness of hybrids can depend on temporal or spatially varying factors and the fitness-related trait(s) measured. This works adds to a small but growing body of literature that shows outbreeding depression due to human-mediated hybridization is context-dependent. Our data confirm that non-native hybridization can reduce survival of juvenile through adult life histories and prevent extensive admixture in some populations despite constant invasion from hybrids. Our work also cautions that previously reported environmental gradients in human-mediated, mosaic hybrid zones may not reflect the factors mediating the fitness consequences of hybridization. Studies reporting landscape patterns of hybridization should also attempt to quantify the fitness consequences to pull apart propagule pressure from selection. Populations that resist non-native

admixture might represent the robust populations where (soft) selection is most efficient at removing non-native alleles from the population.

Table 3.1: Mark-recapture sample sizes used in the multistate Cormack-Jolly-Seber models for each population. Reported for each population, 1) the number of uniquely tagged individuals, 2) total number of live recaptures (electrofishing or mobile PIT unit), 3) unique fish recaptured via electrofishing surveys, 4) unique individuals recaptured via electrofishing surveys at least twice, 5) unique fish recaptured via mobile PIT surveys, 6) unique fish recaptured via mobile survey at least twice, 7) permanent emigrants detected via stationary PIT arrays, 8) unique fish detected as "shed" via mobile PIT surveys, and 9) the number of unique fish found to have "shed" their original PIT tag via electrofishing survey recaptures.

		Langford	Cyclone	McGee
1	Number of unique tags deployed	1220	2913	1116
2	total live recaptured	472	1207	493
3	tags recaptured via electrofishing	375	987	434
4	tags recaptured via electrofishing > 1 time	302	768	353
5	tags recaptured via mobile survey	312	960	219
6	tags recaptured via mobile survey > 1 time	237	676	180
7	permanent emigrants	29	185	72
8	tags detected as shed vua mobile survey	37	118	31
9	fish found to have shed original PIT tag	8	34	2

Table 3.2: Summary of the hypothesized versus detected population-level proportion RBT admixture (pRBT) based on landscape correlations between stream temperature and pRBT. Cyclone and McGee Creeks are relatively warm sites (mean August temperature > 13.8 C; mean annual growing-degree-days > 1250). Langford Creek is on average much colder (mean August temperature < 11.3 C; mean annual GDD < 940). These differences in stream temperature should correlate with lower site-level pRBT in Langford than either Cyclone or McGee. Additionally, we predicted that the effect of individual pRBT on survival rates would be positive at the warmer sites and negative at the colder site. However, we detected similarly high site-level pRBT at Langford and McGee (L = 0.31; M = 0.34), while Cyclone had relatively low admixture (CYC = 0.11). Furthermore, we found strong positive effects of pRBT on juvenile survival at the coldest site and strong negative effects of pRBT on survival at the warmest site.

			population-level admixture		Hypothesized effect of pRBT on survival			detected effect of pRBT on survival		
population	density	temperature	hypothesized	detected	sum	win	ann	sum	win	ann
Cyclone	high	warmest	high	low	+	+	+	+	-	-
Langford	medium	cold	low	high	- / N	-	-	+	N	+
McGee	low	warm	high	high	+	+	+	N	N	N

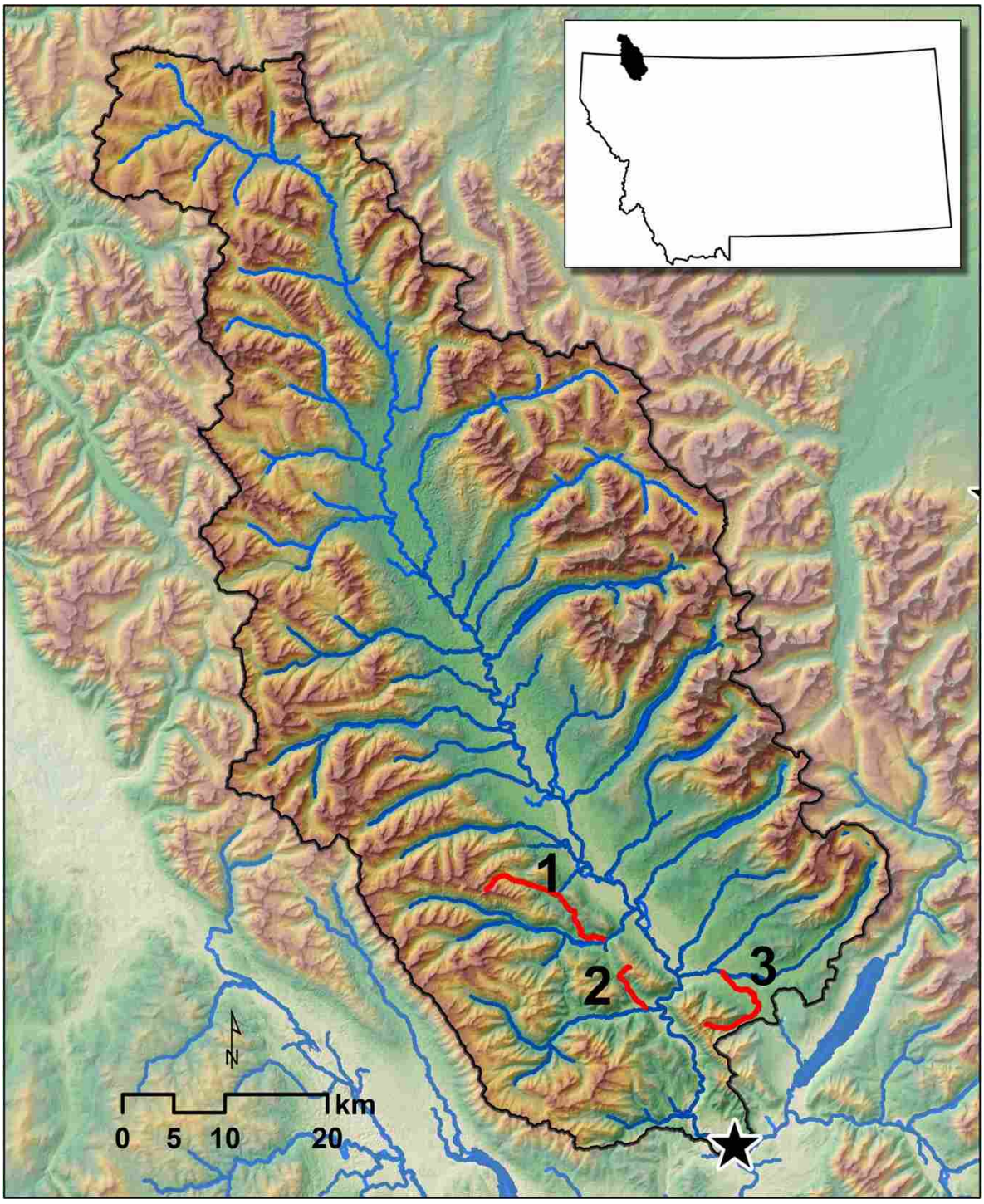

Figure 3.1: Map of our study system (study tributaries in red) in the North Fork Flathead River in Northwestern Montana, USA. We sampled Cyclone (1), Langford (2), and McGee (3) Creeks using a combination of seasonal backpack electrofishing and mobile PIT tag surveys to capture, tag, and recapture *Oncorhynchus ssp*. from 2013 – 2017. These tributaries differed in key environmental factors that we hypothesized would influence the extent of RBT admixture and the effects of RBT admixture on fitness traits (see Appendix B, Table S3.1).

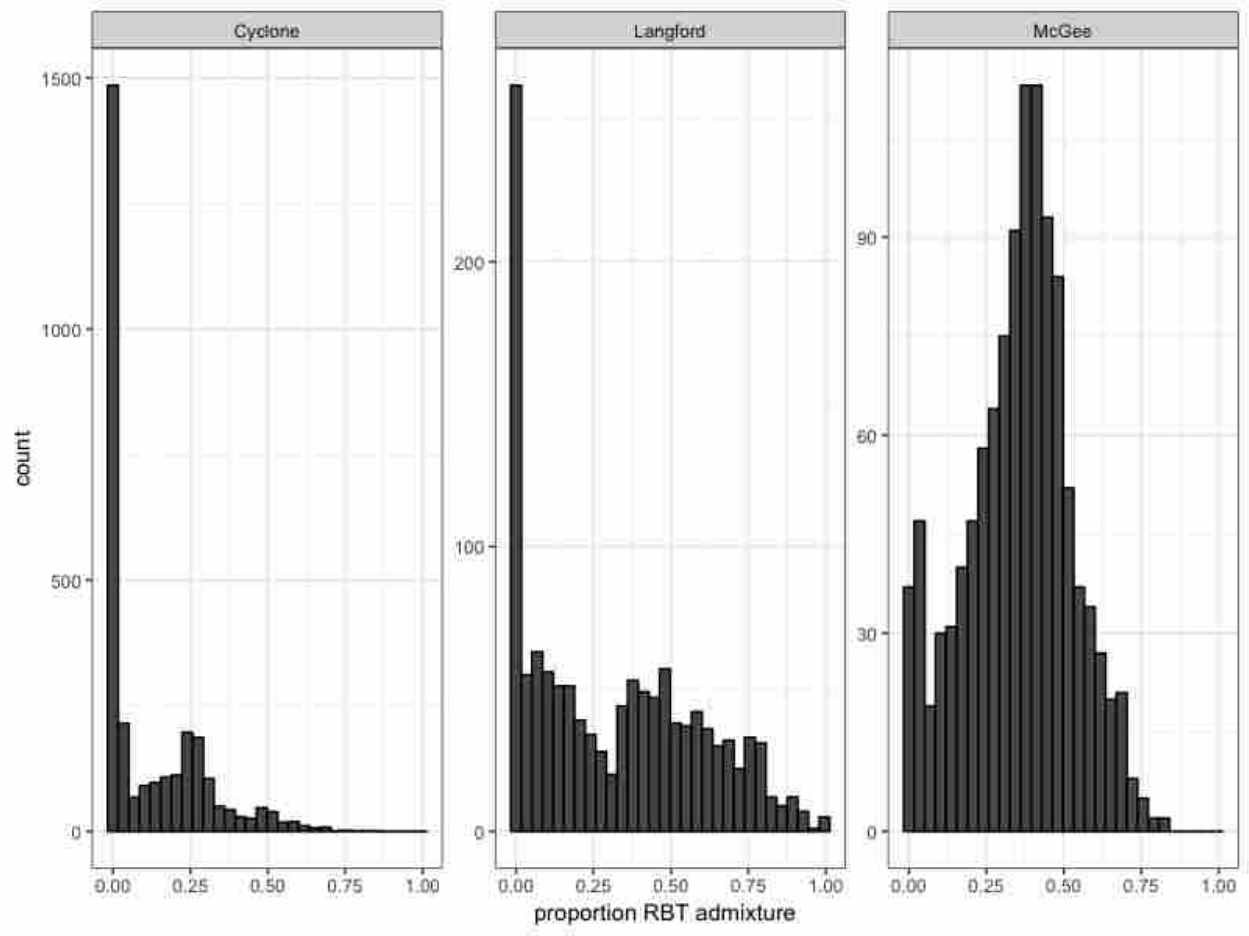

Figure 3.2: The distributions of proportion RBT admixture (pRBT) among individuals in Cyclone, Langford, and McGee Creeks. These populations contain non-admixed WCT and hybrids, but differ in their distributions of pRBT. Cyclone Creek is predominantly WCT with relatively few hybrids above 0.5 pRBT (mean pRBT = 0.11). Langford and McGee Creeks both have WCT, but have a much higher mean proportion RBT admixture (Langford = 0.31, McGee = 0.34).

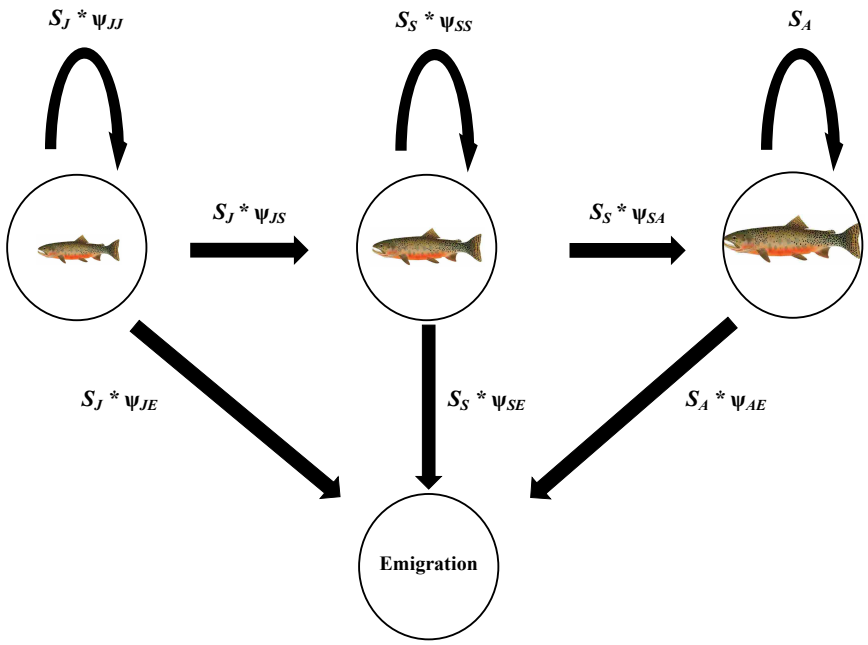

Figure 3.3: Formulation of a multistate Cormack-Jolly-Seber capture recapture model. States represent distinct life history stages separated by total length: juveniles < 120 mm TL, sub-adults > 120mm TL < 180mm TL, adults > 180 mm TL. The fourth state represents permanent emigration from the study area (*E*). We estimated state-specific survival probabilities (S_s) and transition probabilities ($\Psi_{s1\text{-}s2}$) and the effect of proportion RBT admixture on each survival and transition probability.

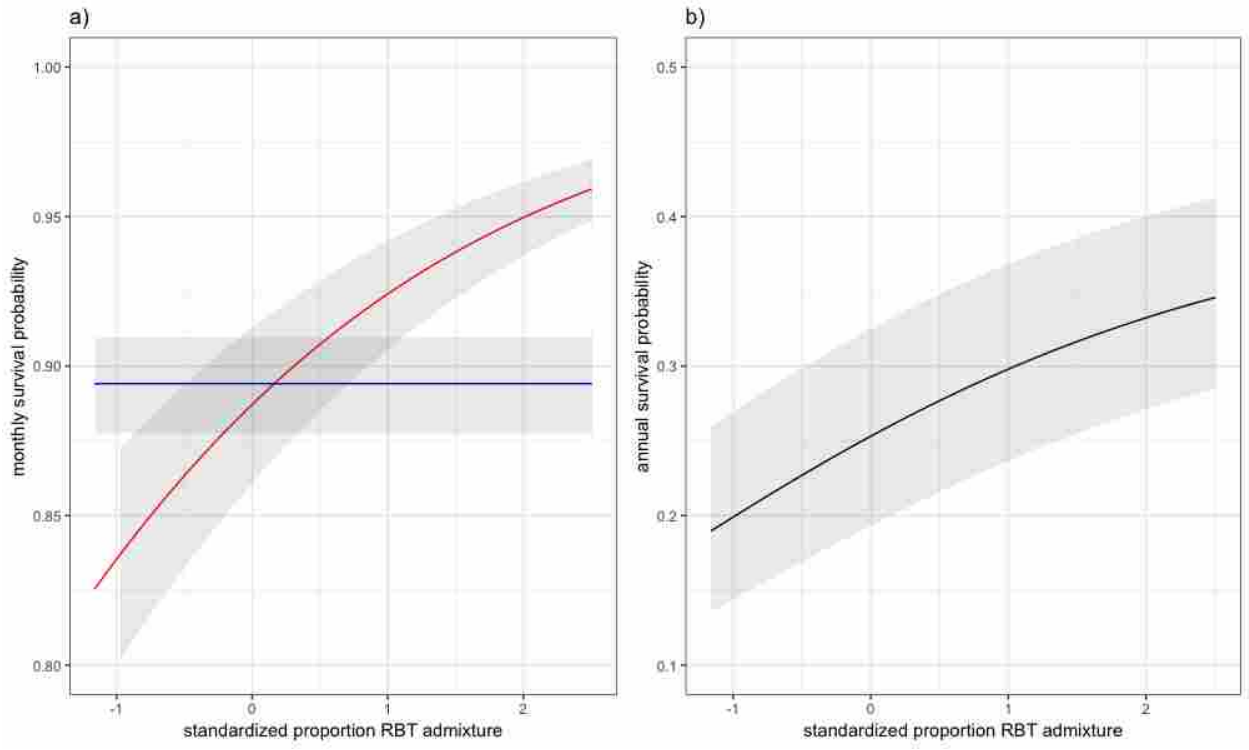

Figure 3.4: The predicted probabilities of proportion RBT admixture (pRBT) on monthly (a) and annual survival probabilities (b) for Langford. The red and blue lines indicate summer and winter/spring relationships respectively. (a) Juvenile summer survival was positively associated with proportion RBT admixture in Langford Creek during the summer. (b) Combined, the seasonal influence of pRBT on survival resulted in a net positive effect of pRBT on annual juvenile survival probabilities in Langford.

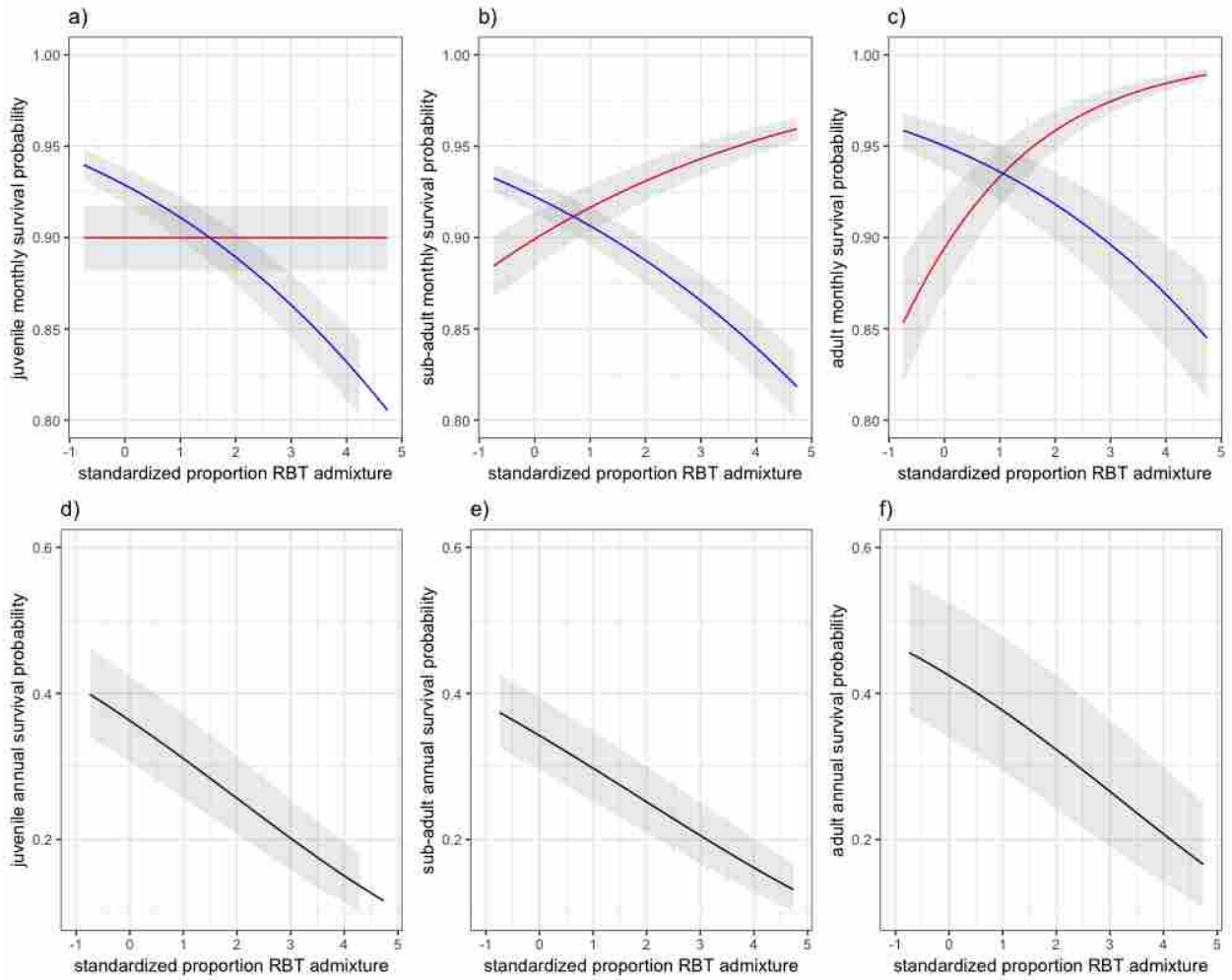

Figure 3.5: The predicted relationships between proportion RBT admixture (pRBT) and monthly survival (top row) and annual survival (bottom row) probabilities for Cyclone. In Cyclone there were positive effects of pRBT on monthly summer survival probabilities (red lines) in the sub-adult (b) and adult size classes (c). During the winter/spring season (a-c, blue lines) pRBT had negative effects on monthly survival in all size classes. Combined, the seasonal influence of pRBT on survival resulted in a net negative effect of pRBT on annual for juveniles (d), sub-adults (e), and adult (f) survival probabilities in Cyclone.

CHAPTER 4

GENOME-WIDE SNP ANALYSIS REVEALS LOCI LINKED TO FITNESS-RELATED TRAITS IN A SALMONID HYBRID ZONE

Abstract

Introgressive hybridization due to anthropogenic factors is a growing conservation concern. Understanding the genetic basis of fitness traits associated with hybridization will help manage and predict long-term consequences of hybridization. Hybridization with introduced rainbow trout (*Oncorhynchus mykiss*) threatens all subspecies of cutthroat trout (*O. clarkii*) across their native ranges. We investigated the genetic basis of individual growth rate and migratory behavior in three hybridized populations in northwest Montana (2013-2016). We conducted a genome-wide association analysis (GWAA) using >2000 polymorphic and species-diagnostic single nucleotide polymorphisms (SNPs) to identify loci associated with growth and migratory behavior. Power analysis suggested we had high power (>0.8) to identify large effect loci (effect size >0.5) but lower power (<0.8) to detect multiple small effect loci associated with a phenotypic trait (growth or migration). We expected multiple loci of small effect to underly growth rates but predicted that migratory behavior would have loci of large effect. Consistent with these expectations, we found no SNPs associated with growth, however we found rainbow trout diagnostic alleles on chromosome 29 strongly associated with migratory behavior. The genetic basis of differences in migratory behavior between cutthroat trout and hybrids could help explain the rapid expansion of hybridization in systems where hybrid dispersal appears to be a mechanism leading to hybrid swarm formation. If this genomic association persists in many populations, managers may have a way to target the suppression of individuals and populations (with highest frequency of these alleles) to reduce the spread of hybridization across the landscape. This study illustrates how genomic approaches in hybridized populations can potentially improve understanding and management of spread of invasive hybridization.

Introduction

Human-mediated hybridization is a serious conservation problem threatening both plant and animal taxa and has been increasing due to factors such species introductions, land use practices and climate change (Allendorf et al. 2001; Kelly, Whiteley, & Tallmon 2010; Crispo et al. 2011; Grabenstein and Taylor 2018). Fortunately, genomics has greatly improved our ability to detect, characterize, and manage the rates and patterns of invasive introgression (McFarlane & Pemberton 2019). Genomic approaches are also improving our understanding the evolutionary and ecological consequences of these events (Hedrick 2013; Fraïsse et al. 2014; Christe et al. 2016; Jones et al. 2018) including our understanding of the genetic basis of traits (e.g., the number and effect sizes of genes explaining variation in phenotypic traits; Lindtke et al. 2013; Vestergaard et al. 2015).

The rapid expansion of some introduced species has led researchers to investigate the evolutionary mechanisms for this phenomenon. The hybridization-invasion hypothesis suggests an evolutionary advantage due to introgressive hybridization with the native taxon which allows non-native alleles to spread (Ellstrand & Schierenbeck 2000). The hybridization-invasion hypothesis (hereafter, H-I) suggests that introgressive hybridization enhances invasiveness of species by creating novel genotypic or phenotypic variation that increases the fitness of these individuals relative to the parental species or by masking deleterious alleles in the native populations (Hovick and Whitney 2014). Most of the research on H-I has focused on understanding if non-native hybridization positively impacts traits associated with individual fitness and population growth rate (i.e., fecundity, growth, or survival; Ryan, Johnson, and Fitzpatrick 2009; Whitney et al. 2015). However, few studies and tests of the H-I hypothesis have looked at traits directly related to migration and dispersal rates (see Lowe, Muhlfeld, & Allendorf 2015). Another evolutionary mechanism by which invasive hybridization might expand across the landscape is through spatial sorting (Shine, Brown, & Phillips 2011; Lowe, Muhlfeld, & Allendorf 2015). Spatial sorting suggests the genotypes associated with higher dispersal rates should be more frequent at the range edge of an expanding species and can fuel the spread of invasive hybridization regardless of the fitness consequences (e.g., decreased reproductive success or survival). Understanding the evolutionary mechanisms by which invasive hybridization spreads and the genetic basis of traits related to fitness and dispersal will aid our conservation efforts and our understanding of evolutionary consequences of hybridization.

The genomic era has ushered in many recent advances in our understanding of the genetic basis of fitness traits and the consequences of introgressive hybridization (Abbott, Barton, & Good 2016; Gompert, Mandeville, & Buerkle 2017), including the genomic mechanisms underlying reproductive isolation (Payseur & Rieseberg 2016; Schumer et al. 2017; Baiz, Tucker, & Cortés-Ortiz 2019; Knief et

al. 2019) and adaptive introgression (e.g., Hedrick 2013), and patterns of selection in hybrid zones (Payseur 2010; Fraïsse et al. 2014; Schumer & Brandvain 2016; Walsh et al. 2016c; Ryan et al. 2017; Schumer et al. 2018). Searching for evidence of adaptive introgression in cases of natural and human-mediated hybridization is of great interest (Hedrick 2013; Abbott, Barton, & Good 2016), but it remains difficult to identify underlying genes associated with phenotypic variation (Rieseberg 2011; Song et al. 2011; Jones et al. 2018). Hybrid zones are useful for identifying genomic regions underlying phenotypic differences between the hybridizing taxa as linkage disequilibrium extends long distances early in the admixture process and so detecting these genomic regions can be done with relatively few loci (Gompert, Mandeville, & Buerkle 2017). Not only have these advances fueled evolutionary biology, but they can also inform conservation questions in a broad range of taxa (Allendorf, Hohenlohe, &Luikart 2010; Harrisson et al. 2014; Shafer et al. 2015; Garner et al. 2016; Supple & Shapiro 2018).

Salmonids have led in the application of genomic tools for conservation (Waples, Naish, & Primmer 2020), and we have begun to understand the genetic basis of many fitness related traits such as growth, development, and maturation (e.g., Johnston et al. 2014; Gutierrez et al. 2015; Kodama, Hard, & Naish 2018; Ali et al. 2020) and migratory behaviors such as phenology and partial migration/anadromy (Hecht et al. 2013; Barson et al. 2015; Hess et al. 2016; Prince et al. 2017; Kelson et al. 2019; Pearse et al. 2019). Growth and migratory life history behavior are important traits in salmonids that influence individual fitness and the spread of hybridization (e.g., Sogard 1997; Thompson & Beauchamp 2016; Janowicz et al. 2018). Growth is likely influenced by many genes of small effect as factors such as maternal effects, conspecific density, and abiotic conditions influence growth rates (Vøllestad & Olsen 2008; Xu, Letcher, & Nislow 2010; Bærum et al. 2013; Falica et al. 2017). Due to a long history of aquaculture in rainbow trout (*Oncorhynchus mykiss*) we have discovered numerous growth related genes (Wringe et al. 2010; Gonzalez-Pena et al. 2016; Reis Neto et al. 2019; Ali et al. 2020). In contrast, there is accumulating evidence across salmonid species that traits associated with discrete migratory phenotypes are controlled by few large effect loci (Prince et al. 2017; Pearse et al. 2019), and likely many small effect loci as well (Sinclair-Waters et al. 2020). Similarly, fewer genomic factors might play a role in partially migratory freshwater salmonid populations (Arostegui et al. 2019). Understanding the genetic basis of traits that influence fitness or the rate of spread of human-mediated hybridization, which includes both growth and migration, would be valuable for conservation by improving our understanding, and our ability mitigate and predict long-term consequences of hybridization.

Invasive hybridization is among the greatest threats to all cutthroat trout subspecies (*O. clarkii*) in western North America, including remaining populations of westslope cutthroat trout (*O. clarkii lewisi*, hereafter WCT; Shepard, May, and Urie 2005). Rainbow trout (*Oncorhynchus mykiss*, hereafter RBT) is among the world's most widely introduced invasive fish species (Behnke 1992; Halverson 2010), and

naturalized populations of RBT hybridize with native cutthroat trout. Despite evidence of lower reproductive success and selection against hybrids, RBT admixture has continued to spread and threatens many of the remaining populations of WCT with hybridization (Muhlfeld et al. 2009a; Kovach et al. 2015; Kovach et al. 2016b; Muhlfeld et al. 2017). Multiple studies have found evidence that RBT and hybrids have higher dispersal rates (i.e., a lack of natal site-fidelity) than WCT (e.g., Boyer, Muhlfeld, & Allendorf 2008; Kovach et al. 2015; Bourret et al., *unpublished*). In stream-spawning freshwater fishes, migrants have a higher probability of dispersal (i.e., spawning in a non-natal site) than residents due to their migrations from natal sites and their larger body size (Radinger & Wolter 2014). Furthermore, Strait et al. (*Chapter 2*) found positive associations between genome-wide proportion RBT admixture and daily summer growth rates and migratory behavior. Understanding the genetic basis of these two traits would help us better understand the evolutionary mechanism(s) (i.e., H-I, spatial sorting) leading to the spread of RBT alleles in some systems.

Our objectives were to test for locus-specific effects of RBT introgression on growth rates and migratory behavior in WCT. First, we conducted a power analysis to quantify our ability to detect RBT alleles associated with growth and migratory behavior. Specifically, we asked 1) What is the statistical power for detecting large-effect loci (and small-effect loci) influencing pehnotypes using our sample sizes of individuals and loci? We used our empirical data to ask 2) are there specific RBT alleles associated with higher summer growth rates in hybrids and RBT, and 3) are there specific RBT alleles associated with expression of migratory life history behavior?

Methods

Study Sites and Sample Collection

We sampled populations of WCT in Cyclone, Langford, and McGee Creeks on the North Fork Flathead River, Montana, USA (2013-2016; Figure S4.1). Hybridization has been occurring in each population for at least five to ten generations, allowing substantial time for backcrossing and recombination. Admixture was first detected in Langford in the 1980's, but was not detected in Cyclone and McGee until the late 1990s (Muhlfeld et al. 2014). These sites were selected because they differ in mean RBT admixture as well as the distribution of individual RBT admixture (Figure S4.2). Cyclone Creek is predominantly non-admixed WCT, while Langford and McGee are both highly admixed populations. We expected stronger linkage disequilibrium and therefore higher power to detect genotype-phenotype associations in the more recently admixed populations.

We used both migrant fish traps and backpack electrofishing to capture individuals; detailed field methods can be found in Strait et al. (*Chapter 2*). For each individual captured, we measure total length

(TL, mm), implanted each individual with a unique PIT tag (passive integrated transponder), and took a tissue sample for genetic analysis. We sampled each tributary via backpack electrofishing in July and October for resident adult and juvenile trout. For all fish collected, we assigned individuals as adults or juveniles using a total length threshold of 160mm (juveniles ≤ 160; adults > 160mm; Downs, White, & Shepard 1997; Janowicz et al. 2018). For resident juvenile trout (< 160mm TL) captured in the stream in July and October of the same year, we measure daily summer growth rate (daily growth rate = $TL_2 - TL_1$ / # days; mm/d). We also trapped migratory (fluvial) adults entering each tributary to spawn using migrant traps during the spring (~April 1 – July 1) of each year. In addition to the metrics taken above, sex of migratory adults was determined visually before release. To identify loci associated with migratory behavior, we contrasted the genotypes of migratory adults against putatively resident adults captured via electrofishing during July electrofishing surveys. Each study reach had PIT-tag antennae at the downstream end to detect movement of tagged individuals from the study reach. Any individuals tagged during electrofishing surveys that were detected emigrating from the stream were not included in the growth or migratory behavior analysis.

Laboratory and Bioinformatic Analyses

We extracted DNA from tissue samples using the SPRI bead extraction protocol described in Ali et al. (2016). DNA quality (260/280 ratio) and quantity were measured using a Nanodrop 2000 Spectrophotometer (Thermo Scientific, Waltham MA). The concentration of double stranded DNA was measured using QuantIt Picogreen assays (Thermo Fisher Scientific, Waltham, Massachusetts) after diluting samples to less than 20ng/ul. Sequencing libraries were prepared using the bestRAD and Rapture (RAD-capture) protocols (Ali et al. 2016) using 50 nanograms of input DNA for each sample. RAD libraries were sheared to an average fragment size of 350 base pairs using a Covaris E220 Ultrasonicator (Covaris Inc., Woburn, Massachusetts). Libraries were amplified for 12 cycles using a plate specific indexing primer, purified using Ampure XP beads, and quantified using Quantit Picogreen assays. Plates were pooled in groups of 6 (83ng from each library) before enriching for 3015 RAD loci previously found to be informative for estimating admixture coefficients. Enrichment was performed using a custom Mybaits target enrichment kit (V3, *Arbor Biosciences, Ann Arbor, Michigan)*. This panel included a combination of baits complementary to RAD loci containing WCT/RBT polymorphic SNPs and WCT, YCT, and RBT species diagnostic SNPs (Amish et al. 2012; Hohenlohe et al. 2013; Hand et al. 2015; Kovach et al. 2016b; Figure S4.3). Loci were chosen for capture based on their genotyping quality, reliability for distinguishing each (sub)species and even distribution across the assembled rainbow trout genome. Pooled libraries were amplified post-capture for 10-12 cycles and quantified using Quantit Picogreen assays before being sequenced 6 libraries/lane on an Illumina HiSeq X (Novogene Corporation,

Sacramento, CA).

Read quality was assessed using FASTQC v0.11.5 and duplicates reads were removed using the clone_filter program from Stacks v1.44 (Catchen et al. 2011). Sequencing adapter contamination was removed from reads using Trimmomatic and reads were truncated whenever the mean Phred score across a window of 4 nucleotides dropped below q15. We further required reads to be greater than 60 bp after applying the trimming steps above. We then used a custom script to exchange reads between read 1 and read 2 fastq files whenever the inline index for an individual was found at the beginning of read 2. Properly oriented fastq files were demultiplexed by individual barcode using process_radtags v1.44. Reads were mapped to the RBT reference genome (Berthelot et al. 2014) using bwa-mem and resulting sam files were sorted, converted to bam format, and indexed using samtools v1.4. We then used HaplotypeCaller v3.7 to generate gVCF files for each individual, combined gVCF files across individuals using CombineGVCFs v3.7, and called genotypes using GenotypeGVCFs v3.7 (McKenna et al. 2010). The resulting VCF file was filtered using vcftools (LGPLv3; Danecek et al. 2011).

We performed an initial quality control on loci and individuals. Genotypes were set to missing if the genotype quality score was less than 30 and minimum read depth was less than 7. In addition, an allele balance between 0.25 – 0.75 and a minimum read depth of 10 was required for all heterozygote genotypes. Loci were removed if they were missing genotypes in more than 10% of individuals and individuals were dropped from the analysis if they did not have genotypes at greater than 20% of remaining loci after filtering. Species diagnostic loci were separated from WCT/RBT polymorphic loci. Proportion RBT admixture (pRBT) was estimated for each individual as the number of RBT alleles / (2 * number of genotyped diagnostic loci). After sub-sampling our entire sequencing dataset to the individuals presented in this paper, we filtered the individuals and loci to have < 30% missing genotypes.

Power Analysis

We used simulations to assess our power to detect a QTL with varying effects sizes on survival across a range of marker densities and sample sizes of individuals. We quantified changes in power at relatively low, medium, and high marker density and over a range of individual sample sizes. All scripts are available in the supplemental materials. We ran individual-based simulations of three populations of native fish in a river network for eight generations using a package written in Program R (Figure S4.4; package available in supplemental materials). For the first six generations, 500 non-native fish were stocked at the bottom of the river network. To allow hybridization to occur and spread during the simulation, dispersal probability had a mean of 0.1 and maximum of 0.4 for all individuals. Random mating among individuals within a population occurred each generation and the population size was held constant at 2000 individuals per population. Individuals matured at age 1, lived to a maximum of 2 years

(Table S4.4) and the age structure of each population was held constant at 0.5 age zero, 0.3 age one, and 0.2 age two.

For simplicity and efficient computing, we simulated one QTL that was randomly placed on one of two chromosomes, each 100 centiMorgans (cM) long. We then sampled 50, 75, or 100 loci per chromosome. We varied the QTL effect size on survival directly, ranging from slightly deleterious (20% reduction in survival) to strongly deleterious (80% reduction in survival). This allowed the evolution of these systems to resemble those found in the wild with a range of non-native admixture in different populations (Figure S4.4). We also varied the number of individuals sampled in each population from 200 to 1000. We then simulated 500 repetitions of each level of a full factorial design of QTL effect size, marker density, and sample size. We simulated 84 combinations of QTL effect size, marker density, and individual sample sizes each for 500 independent repetitions (Table S4.4). After each simulation repetition, we performed a genome wide association study using the programs Plink (Purcell et al. 2007) and GCTA (Yang et al. 2011a) and recorded if the QTL was detected in the GWAA. To estimate power, we calculated the number of independent simulations in which the GWAA successfully detected the QTL divided by the total number of simulation repetitions. This framework allowed us to explore the effects of QTL effect size, marker density, and sample size on our ability to detect a locus-specific effect of RBT introgression on fitness traits in wild populations.

Genome-wide Association Analyses

We conducted all GWAA using the package *GenABEL* (Aulchenko et al. 2007) in Program R. We used the same approach for identifying potential loci underlying differences in growth rate and migratory behavior in admixed populations. For each phenotypic trait, we conducted GWAA using data from the three populations combined, and then analyzing data from each population independently. We then compared the top supported loci from each approach as in Hecht et al. (2013). The mixed effects models accounted for population structure and factors known to affect growth rates and migratory behavior in salmonids, as well as relatedness among individuals. We fitted and tested mixed effects models with the following forms for 1) daily summer growth rate and 2) migratory life history behavior:

1) $\text{Growth} \sim \beta_{TL}\, TL + \beta_{SNP} SNP + \beta_{pop}\, Pop + \; G + \; \varepsilon$

2) $\text{Migration} \sim \beta_{TL}\, TL + \beta_{SNP} SNP + \beta_{pop}\, Pop + \; G + \; \varepsilon$

where TL is a vector of fixed-effects of the total length (mm, TL) of each individual and β_{TL} is the coefficient on TL. Previous analysis showed that TL was an important predictor of growth rate and

migratory behavior in these populations (*Chapter 2*). *SNP* is the design matrix of the SNP genotypes (coded as 0, 1, or 2) and β_{SNP} is the matrix of SNP coefficients. *G* is the random genetic effect controlling for relatedness and population structure and ε is the error term. *Pop* is a vector of fix-effects of each individual's population of capture and β_{pop} is the corresponding coefficient for population (note: a fixed-effect of population was only included in models when data from all populations were combined). For a list of all models tested, see the Appendix C (Table S4.5).

Controlling for Genomic Inflation and Multiple Testing

We assessed the results of our GWAA using *P*-values that were corrected for genomic inflation and multiple testing. We tested multiple methods for accounting for population structure and relatedness provided within *GenABEL* including: 1) eigenstrat method (Price et al. 2006; *eg.score()* function) , and 2) genomic kinship matrix (*ibs()* function). The Eigenstrat method combines structured association and genomic kinship by creating principle components from the genomic kinship matrix and thus accounts for structured associations among larger strata (i.e., populations), as well as, more subtle structure through the genomic kinship matrix. Ultimately, we used the method of controlling for relatedness that best reduced the genomic inflation (λ), however, inflation of the test statistic is expected in polygenic traits even after accounting for population structure (Yang et al. 2011b). Before interpreting results from the GWAA, we corrected *P*-values for genomic inflation, by dividing the test statistic by the genomic inflation factor and used a false discovery rate (FDR, *p.adjust()* function) to prevent Type I error.

Further Investigation of Migratory Behavior

We followed the GWAA with several other analyses to further investigate our finding of an RBT allele on chromosome 29 associated with migration. First, we checked the allele frequencies of all loci on this chromosome. We split the data set by phenotype (migrants and residents) to determine which species diagnostic allele was associated with migratory behavior and to confirm that all populations displayed the same pattern. Since we did not know sex of all individuals in this analysis, we then checked for sex bias in our migrant dataset, as there is evidence of female-biased migratory behavior in partially migratory salmonids (e.g., Koizumi, Yamamoto, & Maekawa 2006). We did not have a sex-diagnostic marker on our Rapture marker set, and so we confirmed sex visually in the field where possible.

Since chromosome 29 is known to be the location of the sex-determining genes in rainbow and cutthroat trout (Yano et al. 2013; Berthelot et al. 2014), we checked for a sex bias in our results. We looked at the sex ratio of the migratory fish and ultimately removed all known females (n = 112) and reran the GWAA on males only. Our final step to confirm these results, we re-analyzed the generalized linear models for predicting probability of migration from Strait et al. (*Chapter 2*). We performed the

same top down model selection with three sets of global models: 1) including a fixed effect for genome-wide proportion RBT admixture (pRBT), 2) including fixed effects for pRBT and the genotypes at the putative QTL on chromosome 29 for migration phenotype, 3) including only the genotypes at the putative QTL on chromosome 29. We then performed model selection based on Akaike's Information Criterion corrected for small sample sizes (AICc).

Results

Power Analysis of GWAA Via Simulations

Power was most improved by increasing the locus effect size on survival. Power ranged from less than 0.1 to nearly 1.0 as the effect size increased (Figure 4.1, Table S4.5). Even at the highest sample size of individuals (n = 1000), power rapidly dropped below 80% as the QTL effect size on the survival dropped below 0.45 (i.e., the locus explained 45% of the variation in the phenotype). These results clearly demonstrate that a locus must control a large proportion of the phenotypic variance (> 0.5) in order to avoid false negative results in our GWAA of growth rate and migratory life history behavior. It is important to note that since we simulated a marker that directly impacted survival probability, power in our simulation decreased as the effect size of the QTL increased about ~0.7. While this was necessary to allow evolution the simulated populations, we did not expect the same decrease in power at larger QTL effect sizes because our phenotypes of growth and migratory behavior do not directly influence survival.

Power was also strongly affected by sample size of individuals. The maximum power to detect the locus associated survival differences was ~ 60% if we sampled 200 individuals. Power increased to ~87% if the sample size was increased to 500 individuals, and to ~100% if we sampled 1000 individuals. Power was minimally affected by marker density. For example, in simulations where we sampled 500 individuals maximum power ranged from 0.82 (50 loci/chromosome) to 0.84 (100 loci/chromosome). Overall, these estimates suggest that our empirical sample sizes should give us adequate power to detect large effect loci associated with growth and migration.

No Evidence for a Large Effect Locus on Growth Rate

We obtained growth and genotypic data from 435 juvenile trout that passed the quality control (QC) and filtering steps for genotype calling (Table S4.1). Through the QC filtering, we retained a total of 2,140 SNPs distributed across the RBT genome assembly, including 1,264 polymorphic SNPs and 876 species diagnostic SNPs for estimating relatedness and conducting the genome-wide association analyses (Table S4.3).

None of the 2,140 SNPs were statistically significantly associated with growth rates in our GWAA of all populations combined or when analyzed within each population separately (Figure S4.5). When all populations were combined, the model that best accounted for genomic relatedness included fixed effects for total length and population as well as a random genetic effect using the *eigenstrat* method (Table S4.6). The model of all populations combined had genomic inflation of the test statistics (λ) was 1.03 and the genomic estimate of the heritability was $h^2 = 0.007$.

GWAA Discovers SNPs Associated with Migratory Behavior

We captured and genotyped 364 migratory adults and 510 resident adults (Table S4.2). After QC filtering this migratory dataset, we retained a total of 2,292 SNPs distributed across the RBT genome assembly, including 1,323 polymorphic SNPs and 969 species diagnostic SNPs for estimating relatedness and genome-wide association analyses (Table S4.3).

Our GWAA of all populations revealed a RBT diagnostic SNP on chromosome 29 significantly associated with migratory behavior (omy_29_28901336; *FDR p* = 0.03; Figure 4.2). The model that minimized genomic inflation included total length, population, and relatedness using the genomic kinship matrix. There was evidence of genomic inflation of the test statistics (λ = 1.32, Figure S4.6 Table S4.7) and the genomic estimate of the heritability was $h^2 = 0.220$. Closer examination of chromosome 29 revealed a large region, including SNP omy_29_28901336, where the frequency of the RBT diagnostic allele was at higher frequency in the migrants than the residents (Figure 4.3a).

There was no evidence that female bias drove the association between migratory behavior and omy_29_28901336. Specifically, the RBT allele was similarly associated with migratory behavior in males and females. We found no evidence for difference in the allele frequencies on chromosome 29 between males and females (Figure 4.3b). After removing the 112 known females from the dataset, our GWAA results showed the same association between migratory behavior and the RBT allele at omy_29_28901336 (*FDR p* = 0.0597, Figure S4.6).

Model selection of generalized linear models explaining migratory behavior showed that models including the genotypes at locus omy_29_28901336 had lower AICc than models with only genome-wide proportion RBT admixture. The probability of migration was positively affected by RBT introgression at locus omy_29_28901336 (Figure 4.4). Our generalized linear models showed positive effects of RBT alleles at omy_29_28901336 in a mixed effects framework (with random population intercept), and Cyclone and Langford when we modelled each population separately. McGee did not have a significant effect of genotypes at omy_29_28901336 or genome-wide proportion RBT admixture on migratory behavior (Figure 4.4c, Table S4.8c), however, the RBT allele was at much higher frequency in the migrants than the residents (a pattern consistent among all populations; Figure 4.3a), suggesting that this

effect may also be present in McGee but undetected due to low power. The top supported model in Cyclone and Langford included condition (K), total length (TL), pRBT, and year effects (Table S4.8a & b). The effect of RBT alleles on migratory behavior was strongest in Cyclone Creek, individuals that were heterozygous and homozygous for the RBT allele had 34% and 99% higher probability (respectively) of being migratory over individuals that were homozygous for the WCT allele. In Langford, the probability of migration was 3.5% and 4.7% higher for heterozygotes and homozygotes for the RBT allele, respectively.

Discussion

Our results substantially advance our understanding of the genetic basis of fitness-related traits associated with hybridization with a non-native species in multiple wild populations. Although summer growth rate was positively affected by genome-wide non-native admixture (*Chapter 2*), our power analysis and genome-wide association study suggest the trait is not likely impacted by large-effect loci. On the other hand, migratory behavior was positively affected by a large-effect locus on chromosome 29. The presence of a large effect locus underlying the genetic basis of a trait linked to dispersal likely contributes to the rapid expansion of hybridization is some systems (Boyer, Muhlfeld, & Allendorf 2008; Kovach et al. 2015).

Few studies provide a power analysis before conducting GWAA, yet other studies warn researchers about the dangers of interpreting negative results from GWAA without inspecting the probability of type II error (Kardos et al. 2015). We cannot overstate the benefit of conducting a power analysis a priori to aid study design and guide expectations and interpretation of results. Our power analysis showed that even in admixed populations where linkage disequilibrium among loci is high, detecting SNPs that have a small effect size on the phenotype was very low. Power analyses should be done during study design to inform the sample sizes and marker density necessary to achieve acceptable power. Since we were dealing with fairly-recently admixed populations, marker density within the range we expected to achieve from our multipurpose Rapture array unlikely had a substantial impact on power.

Using our genotyping Rapture array with > 2000 loci we expected our largest sample sizes from field work could not achieve power greater than 80% to identify small effect loci for polygenic traits (like growth rate). These limitations supported our decision to combine populations during GWAA of growth rate and migratory behavior (to maximize power). For example, in the growth analyses if we ran each population separately, we did not even have power to detect a large effect locus with certainty and so we opted to run all the populations together to improve power. However, combining populations in this way is not problematic since we corrected for population substructure with random genetic effects, chose the

model that most reduced genomic inflation of the test statistic, and corrected p-values for genomic inflation. And even though there was evidence of genomic inflation in the GWAA models for growth rate and migratory behavior, genomic inflation is expected in polygenic traits even if population structure is perfectly accounted for with random genetic effects (see Yang et al. 2011b).

Our inability to detect any RBT alleles associated with summer growth rates has several potential explanations. First, this suggests that growth is not likely influenced by large effect loci (> 0.5). However, given the additive effect of genome-wide admixture on this phenotype (*Chapter 2*), there are likely smaller effect loci that we did not have the power to detect in this study. Secondly, Strait et al. (*Chapter 2*) also found substantial variation in growth rates among populations and years associated with environmental variation. The low estimated heritability of summer growth rate ($h^2 = 0.007$) supports the hypothesis that both genome-wide admixture and environmental conditions driver variation in this trait. This estimate is on the lower end of the distribution of heritability for life history and growth traits in salmonids (Carlson & Seamons 2008), but is not surprising since those estimates predominantly come from controlled crosses and laboratory studies where environmental conditions are held constant. We grouped multiple populations and years of data together for this analysis, and both interannual and spatial variation in environmental conditions (i.e., temperature, flow, density, productivity) likely reduced the estimate of heritability as well as our ability to detect a strong association between growth rates and any SNP locus.

While the impact of RBT admixture on other fitness traits is variable among populations and influenced by environmental conditions (i.e., growth rate and survival), increased migratory behavior has been consistently and positively associated with RBT admixture (Boyer, Muhlfeld, & Allendorf 2008; Kovach et al. 2015; *Chapter 2*). Higher propensity to migrate in RBT and hybrids can explain the patterns of continued expansion of hybridization despite selection against RBT alleles in many populations. The large effect locus influencing migration might reflect a relatively simple genetic basis for differences in the propensity to migrate between these species. This is also consistent with other literature in salmonids and other species that have found large effect loci controlling traits related to migration and anadromy (Johnston et al. 2014; Barson et al. 2015; Prince et al. 2017; Kelson et al. 2019; Pearse et al. 2019; Sinclair-Waters et al. 2020). Multiple studies have reported the presence of a large inversion on chromosome 5 associated with the expression of anadromy in RBT/steelhead populations (Arostegui et al. 2019; Kelson et al. 2019). We found no evidence of SNPs on chromosome 5 influencing migratory and resident behaviors in our system. This could be due to different genetic bases of anadromy and fluvial behaviors or due to the hatchery origin of the rainbow trout that founded these populations; indeed, we found no evidence that this inversion was segregating in our populations.

The variation in the strength of the RBT allele at omy_29_28901336 on migratory behavior when we investigated each population separately is likely due in part to differences in the proportion of migrants and the distribution and recombination of alleles in each population. Both Cyclone and Langford had highly significant effects of the RBT allele at omy_29_28901336 on migratory behavior, yet in Cyclone there was approximately a 99% increase in the probability of migration for homozygotes for the RBT allele while in Langford this was only about 4.8% increase (Figure 4.4). These differences are likely mostly due to differences among populations in the proportion of migratory versus resident adults. For example, Langford Creek supports almost an entirely migratory adult population, while Cyclone has a large resident (non-migratory) adult population (see C*hapter 2*).

While McGee did not show the same strength of this association as Cyclone or Langford Creeks in the GLMs, the RBT allele was still at higher frequency in the migrants in this population (Figure 4.3a). This weaker signal between RBT alleles and migration could be due to the distribution of admixture in this population. McGee is essentially a hybrid swarm; there were very few nonhybridized WCT and no RBT present in our samples from this population. Unlike Cyclone and Langford which both have substantially more WCT, there is no WCT population segment to compare the effect of RBT alleles on migratory behavior in McGee (i.e., all migrants and residents are hybrids). Furthermore, extensive recombination of the parental genomes in this population likely means that linkage disequilibrium between omy_29_28901336 and the casual locus/loci are potentially very low and therefore difficult to detect. The fact that we did not detect a significant association between alleles at omy_29_28901336 and migration in McGee Creek is of little consequence to conservation since essentially any disperser from this population would be a hybrid of some form and contribute to the spread of hybridization.

There has been great interest in documenting and describing adaptive introgression, however we hesitate to speculate that adaptive RBT alleles are linked to migratory behavior. Increased migratory life history expression is not likely to be adaptive across an entire river basin, as the selective pressures acting on migration likely vary spatially as well as temporally. Instead, migration is an effective invasive behavior allowing for widespread admixture regardless of the consequences for other fitness traits such as reproductive success, growth, and survival.

Conclusions and Implications

Our results suggest that RBT hybridization and invasion success is in partly due to the higher migration rate of non-native RBT and hybrids due to genetic variation at a single genomic region on chromosome 29. This supports hybridization as a mechanism through which invasive species and their genes can rapidly spread (i.e., hybridization-invasion hypothesis – H-I; spatial sorting) by demonstrating a direct link between an invasive hybridization and higher movement rates in hybrids. While most of the

evidence for H-I focuses on increased fitness of hybrids and population growth rate, spatial sorting suggests genotypes and phenotypes associated with dispersal should be at higher frequency on the range edge of a species. Our work shows that both hypotheses provide valuable insight to the evolutionary mechanisms by which invasive species spread in novel systems. First, our work shows that the effects of hybridization on fitness-related traits can be environmentally mediated, traits related to movement and dispersal can consistently lead to higher rates of migration in hybrids (regardless of the local fitness consequences). Second, our work suggests that positive effects of hybridization on dispersal might not be limited to the leading edge of an expanding invasive species but can promote movement and the spread in populations within the hybrid zone that have been experiencing admixture for many generations. Furthermore, we add to a growing body of literature demonstrating large effect loci impact traits associated with differences in migratory life history expression (Diopere et al. 2013; Liedvogel, Åkesson, & Bensch 2011; Saastamoinen et al. 2018; Sinclair-Waters et al. 2020).

Invasive introgression in this study is not necessarily linked to adaptive behaviors and provides a mechanism for non-native admixture to continue to spread despite selection against non-native alleles. Evidence for a large effect locus positively affecting migratory behavior adds to the urgency of conservation actions to mitigate and prevent the further spread of non-native alleles among native populations as recombination across the rest of the genome will have a minimal impact on the portion of phenotypic variation associated with this locus. Individuals with a wide range of non-native admixture are still likely to possess this allele and therefore be more likely to migrate and disperse. Researchers studying human-mediated hybridization should not only consider the effects of admixture on traits related to local fitness outcomes but should consider how admixture itself might influence traits related to movement and dispersal of hybrids. This study illustrates how genomic approaches in hybridized populations could improve understanding and management of spread of invasive hybridization and alleles driving invasion.

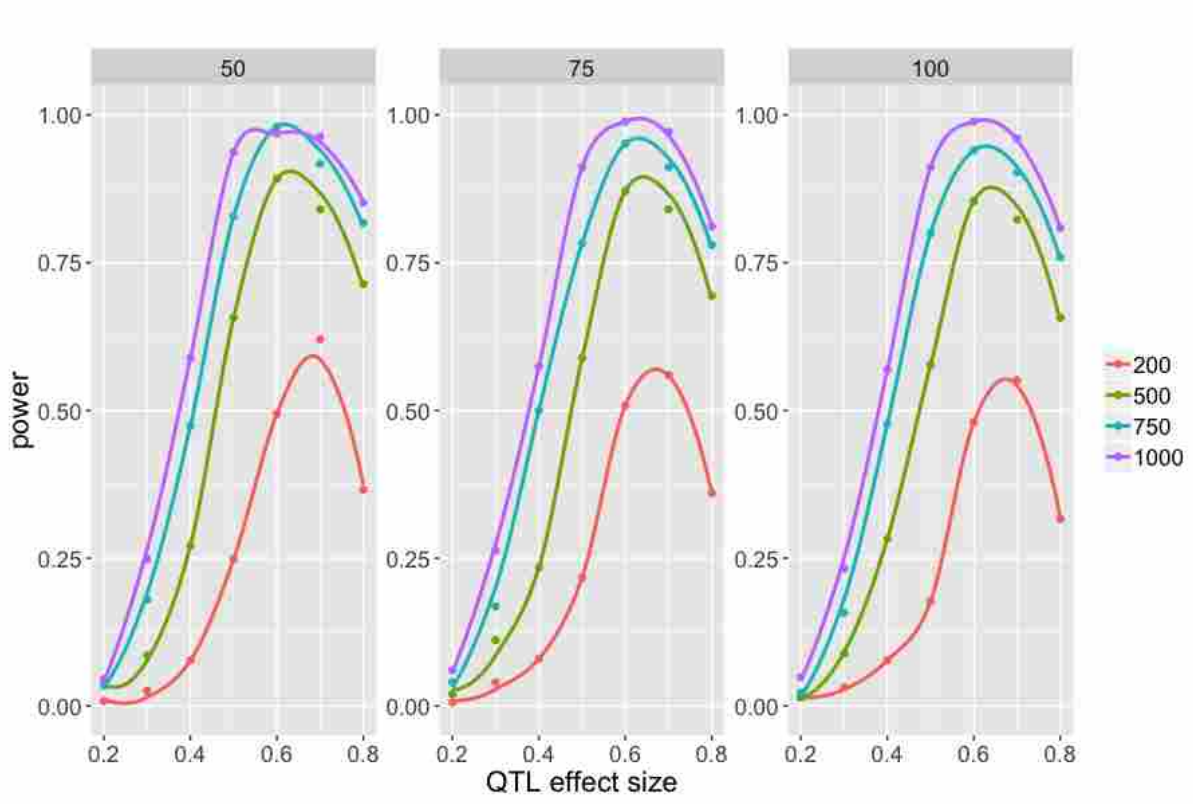

Figure 4.1: Results of a GWAS power analysis from a simulated river network using the program *admixRiver* in Program R. Each panel displays the proportion of independent simulations where the QTL impacting survival was detected (power) as the effect size of the locus is increased from weakly negative to strongly negative (20% to 80% reduction in survival, respectively). Colored lines represent different sample sizes of individuals in the simulated populations, and each panel represents different marker densities from 50, 75, to 100 SNPs per chromosome. Generally, power was most affected by QTL effect size and sample size impact power more than marker density. Power was high (>0.8) if the QTL had greater than a 50% impact on survival and we sampled greater than 500 individuals. Power greatly declined as QTL effect size dropped below 0.4. These results show that power is low to detect a QTL with a small effect size on the phenotype (i.e., highly polygenic traits), but high for traits controlled by a large effect locus.

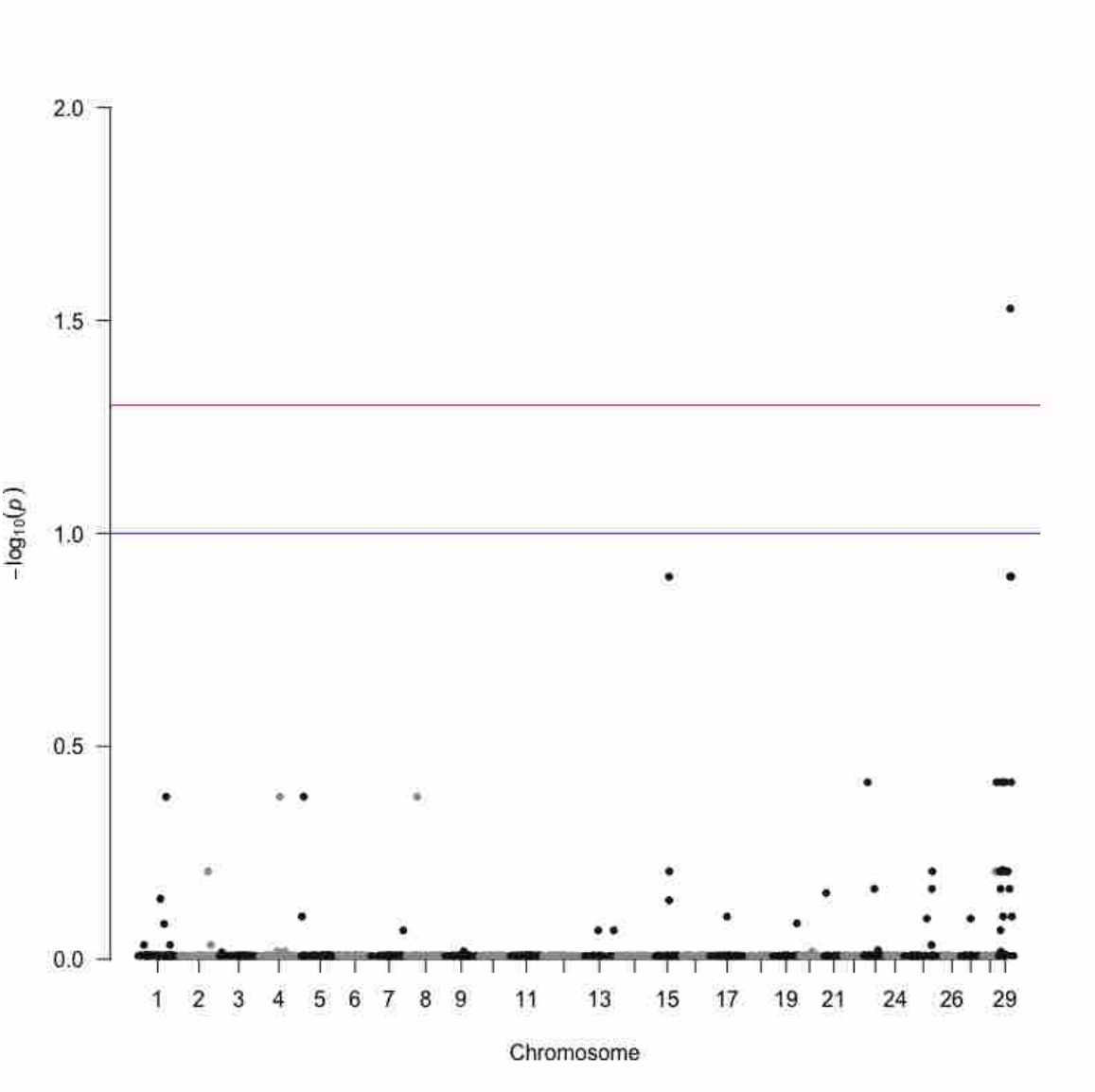

Figure 4.2: Manhattan plot of the genome-wide association scan of adult life history behavior (migratory versus resident) after correcting for population substructure using a kinship matrix. *P*-values were corrected for multiple testing using a false discovery rate (FDR). The red and blue lines indicate genome-wide significance levels equivalent to $p = 0.05$ and $p = 0.10$, respectively, after the FDR was applied to p-values. Point colors alternate by chromosome. There is one RBT-diagnostic SNP on chromosome 29 (locus omy_29_28901336) that meets the genome-wide significance threshold associated with migratory behavior in these populations. A second adjacent locus approaches the significance threshold of $p = 0.1$.

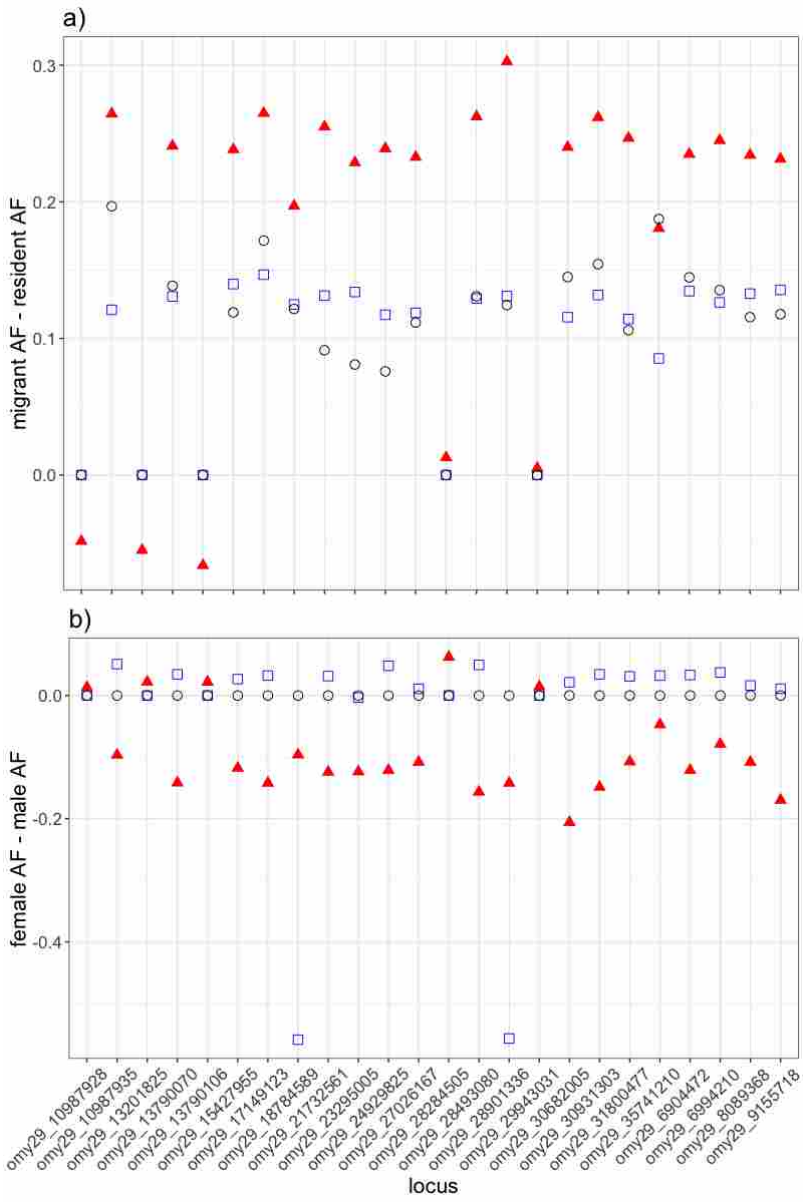

Figure 4.3: a) The differences in RBT allele frequencies between migrants and residents at species diagnostic loci on CHR 29. The loci are order by position along CHR 29 and the difference in frequency is shown separately for individuals captured in Cyclone (blue squares), Langford (red triangles), and McGee (black circles) creeks. Positive y values indicate the RBT allele is at higher frequency in the migratory fish (than the resident adults). Panel b) shows the differences in RBT allele frequencies between migratory females and males at the same loci. The difference in allele frequencies is shown for each population as in panel a) and the results show at most loci the difference in RBT allele frequency between migratory females and males is very small. These results show that migratory fish do have higher frequencies of RBT alleles at loci on CHR 29 and that there is no difference in allele frequencies between females and males that might be influencing these results.

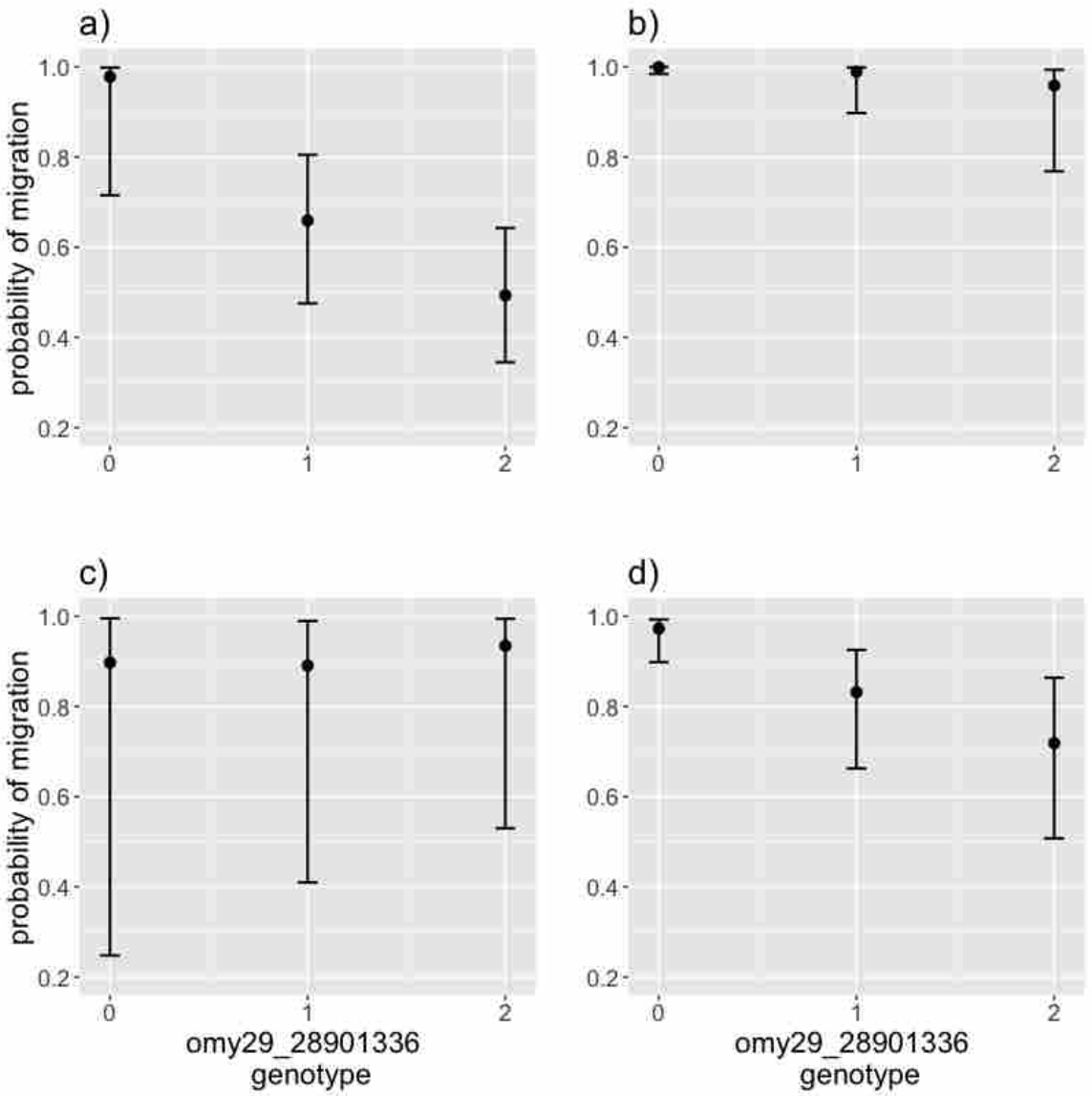

Figure 4.4: Predicted relationship between the genotypes at locus omy_29_28901336 and the probability of being migratory from generalized linear models in (a) Cyclone, (b) Langford, and (c) McGee creeks. In Cyclone and Langford Creeks, the probability of migration is highest for homozygotes for the RBT allele (0), intermediate for the heterozygotes (1), and lowest for the homozygotes for the WCT allele (2). McGee Creek showed no evidence of an increased probability of being migratory in the homozygotes or heterozygotes for the RBT allele. (d) Is the full data set (three creeks), where we included a random effect of population in the generalized mixed-effects model.

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APPENDIX A

CHAPTER 2 SUPPLEMENTAL MATERIALS

Section S2.1 Supplemental Figures and Tables

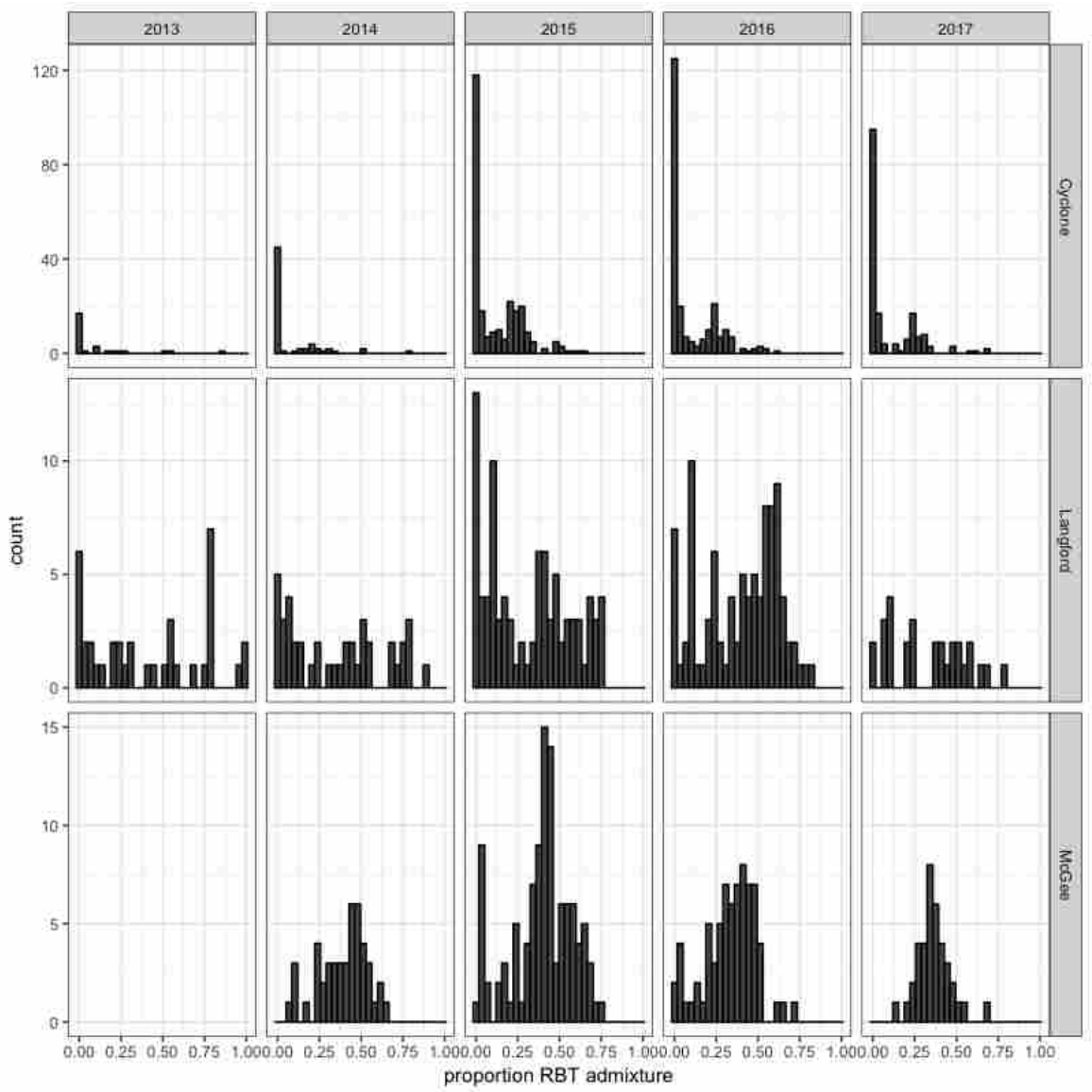

Figure S2.1**:** Distributions of proportion RBT admixture in each population across the study period (2013-2017). Distributions within each population remain relatively stable across the study period.

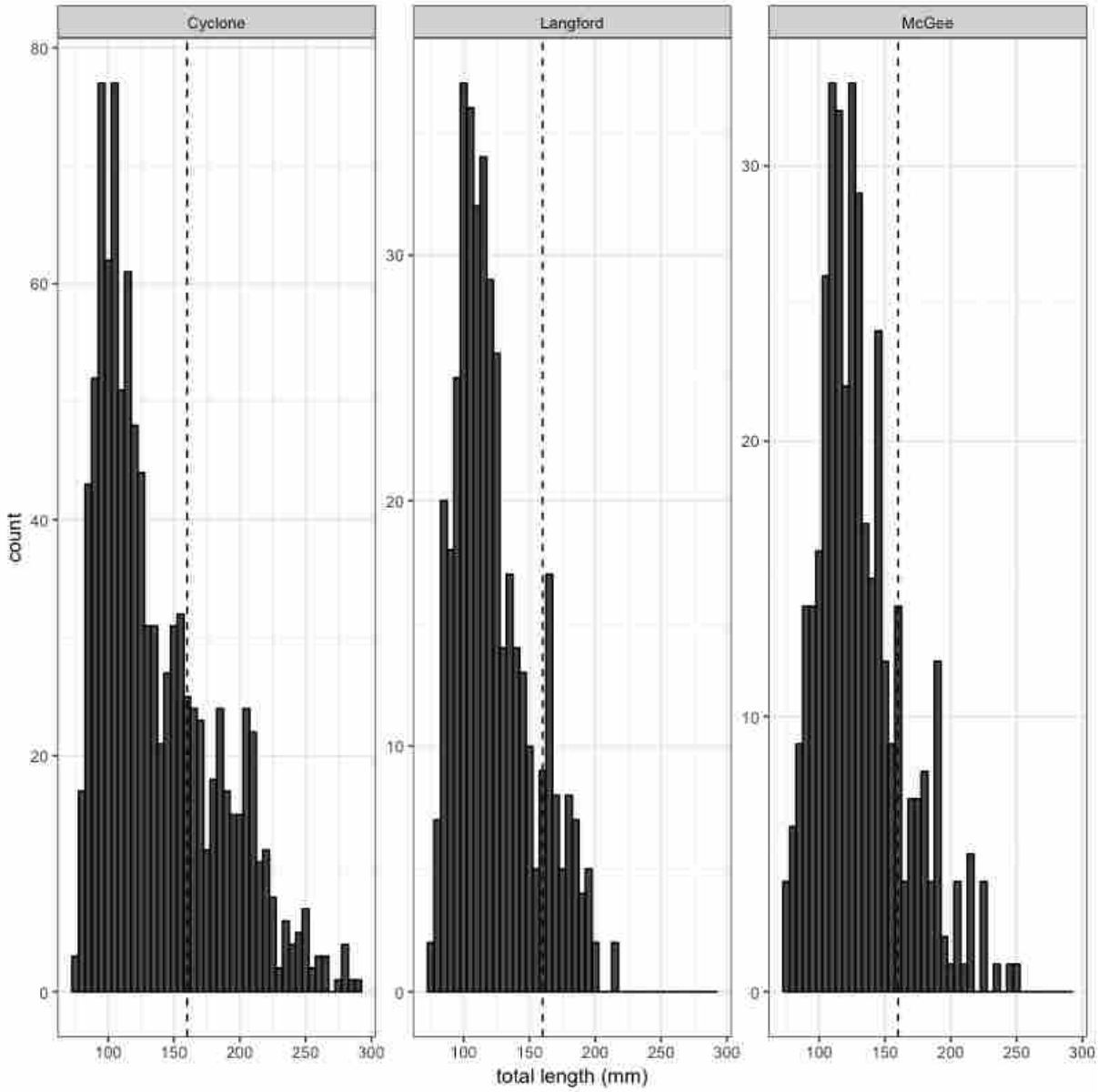

Figure S2.2: Length frequency distributions for each population. The vertical dashed line at 160mm total length was the maximum starting length allowed for individuals in growth analyses. This was done to remove the influence of mature resident adults on growth rates.

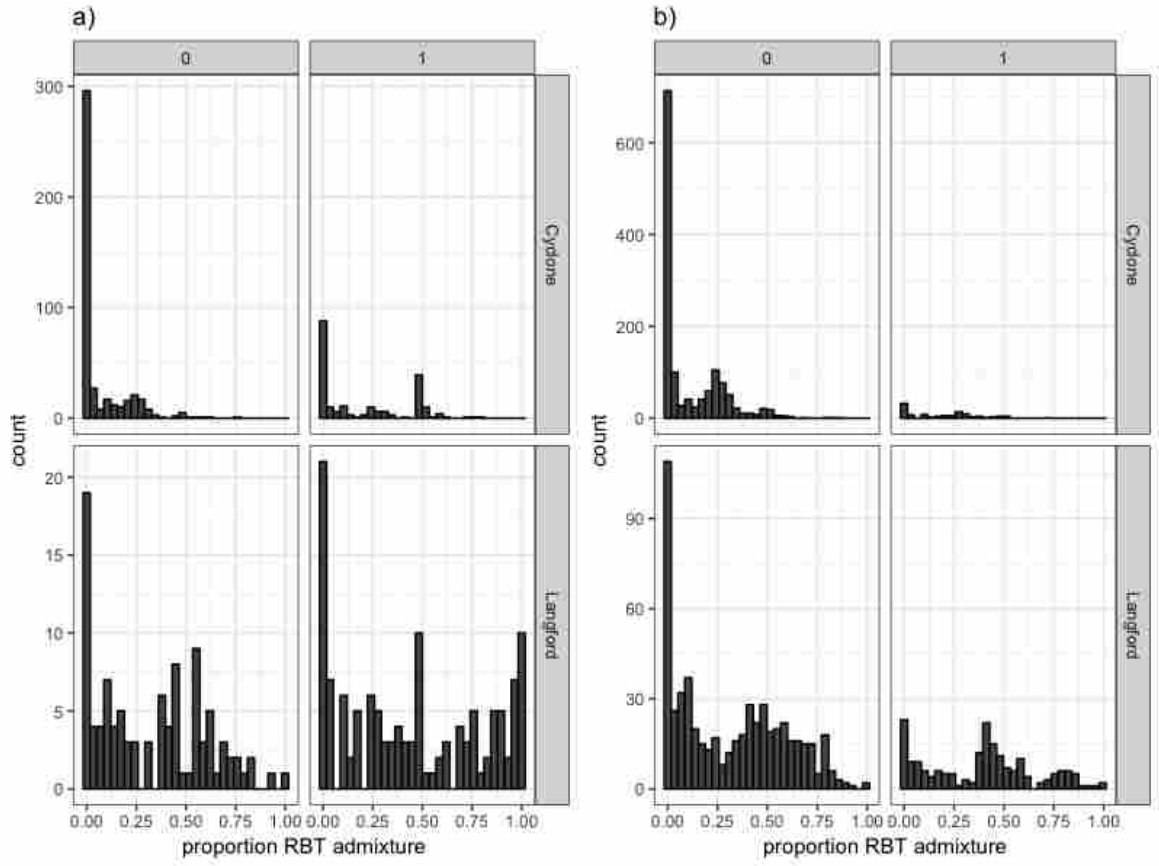

Figure S2.3**:** The distributions of proportion RBT admixture (pRBT) in adults (a) and juvenile datasets (b) sampled between 2013-2016 in Cyclone and Langford Creeks. Resident individuals (0) were sampled via electrofishing during July surveys and migratory individuals (1) were sampled via migrant fish traps from April-July.

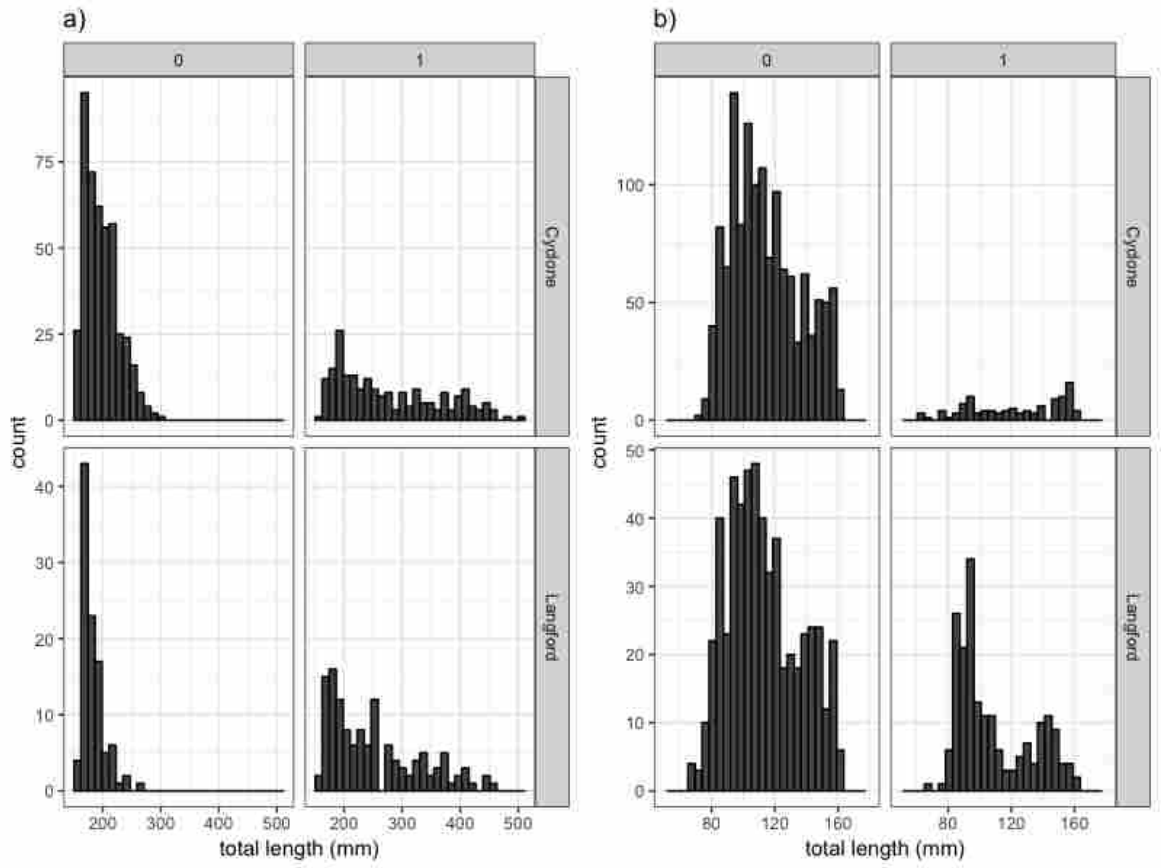

Figure S2.4: The length frequency distributions (TL, mm) of adults (a) and juveniles (b) sampled between 2013-2016 in Cyclone and Langford Creeks. Resident individuals (0) were sampled via electrofishing during July surveys and migratory individuals (1) were sampled via migrant fish traps from April-July.

Table S2.1: Summary statistics of environmental data collected at each study site from 2013-2017. We measured stream temperature using HOBO dataloggers and then estimated summer daily median temperature (ºC), spring growing-degree-days (GDD), and annual GDD for each population and year. We also measured stream flow (m^3/s) through the year at each site and estimated summer base flow, mean spring flow, and maximum spring flow. Finally, we estimated *Oncorhynchus ssp.* density (# fish/m^2) from multi-pass depletion estimates of abundance and stream width measurements from each population taken every July.

		seasonal temperature metrics			flow metrics (m^3/sec)			
population	**year**	**summer median**	**spring GDD**	**annual GDD**	**summer base**	**spring mean**	**spring max**	**summer density**
Cyclone	**2013**	13.61	-	-	0.179	-	-	0.12
	2014	11.33	640	1250.5	0.437	1.884	2.837	0.16
	2015	11.73	733.6	1367.2	0.0828	0.559	1.126	0.15
	2016	10.4	771.5	1380.1	0.1023	0.552	1.124	0.22
	2017	-	648	1210.8	-	-	-	-
Langford	**2013**	10.34	-	-	0.157	-	-	0.16
	2014	10.24	333.4	771.7	0.145	0.389	0.729	0.13
	2015	10.66	317.5	897	0.081	0.136	0.223	0.08
	2016	11.45	407.2	1034.4	0.0976	0.075	0.174	0.08
	2017		397.3	1063.8	-	-	-	-
McGee	**2013**	-	-	-	-	-	-	-
	2014	12.11	-	-	0.123	-	-	0.05
	2015	13.63	544.5	1385.2	0.0833	0.343	0.667	0.05
	2016	14.29	504.9	1340.7	0.1628	0.902	3.714	0.03
	2017	-	484.3	1300.5	-	-	-	-

Table S2.2**:** Correlation matrix of environmental covariates considered in the linear modelling of summer growth rates.

	stdmedianT	stdd7maxT	stdgdd	stdflow	stdflow.d	stddensity
stdmedianT	1					
stdd7maxT	0.51	1				
stdgdd	**0.872**	0.535	1			
stdflow	0.051	0.102	-0.052	1		
stdflow.d	-0.333	0.24	-0.318	-0.167	1	
stddensity	**-0.74**	-0.37	**-0.74**	0.034	0.388	1

Table S2.3: Correlation matrix of environmental covariates considered in the linear modelling of spring growth rates.

	std.total.gdd	std.meanT	std.max.meanT	std.med.flow	std.max.flow
std.total.gdd	1				
std.meanT	**0.904**	1			
std.max.meanT	**0.914**	**0.978**	1		
std.med.flow	0.397	0.517	0.46	1	
std.max.flow	0.214	0.286	0.191	**0.751**	1

Table S2.4: Supported models considered in our AICc model selection for summer growth rates for length (a) and mass (b) in Cyclone Creek. We only considered models that contained only significant parameters (p = 0.05). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for stream flow (flow), relative condition factor (K), median summer temperature (MedT), proportion RBT admixture (pRBT), total length (TL), weight (W), density (D), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

a)

Cyclone Length	INT	flow	K	MedT	pRBT	TL	pRBT * MedT	pRBT * TL	D	PAR	logLik	AICc	delta	weight
1	**0.098**	**0.011**	**0.013**	**0.033**	**0.032**	**0.005**	**0.015**	**0.024**		**13**	**454.535**	**-881.691**	**0.000**	**0.776**
2	0.092	0.011	0.013	0.023	0.024	0.004		0.022		12	452.081	-878.984	2.707	0.201
3	0.086	0.010	0.013	0.023	0.014	-0.012				11	448.589	-874.186	7.505	0.018
4	0.090	0.011	0.015	0.023	0.012					10	445.965	-871.105	10.586	0.004
5	0.082	0.011	0.017	0.022						9	442.822	-866.972	14.720	0.000
10	0.102		0.014		0.023	0.002		0.021	-0.025	11	444.867	-866.741	14.951	0.000
11	0.097		0.014		0.014	-0.013			-0.026	10	441.796	-862.768	18.923	0.000
12	0.101		0.016		0.011				-0.025	9	438.510	-858.348	23.343	0.000
6	0.080		0.018	0.023						8	436.862	-857.189	24.503	0.000
9	0.083	0.010	0.017	0.023						5	433.593	-856.966	24.725	0.000
13	0.092		0.019						-0.023	8	435.838	-855.141	26.551	0.000
7	0.070		0.021							7	425.908	-837.400	44.291	0.000
14	0.070		0.021							7	425.908	-837.400	44.291	0.000
8	0.068									6	407.171	-802.031	79.660	0.000

b)

Cyclone Weight	INT	K	pRBT	W	pRBT * W	MedT	D	PAR	logLik	AICc	delta	weight
1	**0.031**	**-0.006**	**0.037**	**0.034**	**0.055**			**10**	**609.154**	**-1197.483**	**0.000**	**0.963**
2	0.031		0.034	0.035	0.054			9	604.818	-1190.965	6.519	0.037
4	0.017		0.011					7	586.006	-1157.598	39.886	0.000
3	0.015		0.011	-0.003				8	586.190	-1155.844	41.639	0.000
5	0.009							6	578.968	-1145.627	51.857	0.000
6	0.005					-0.011		3	559.340	-1112.592	84.891	0.000
7	0.002						0.007	3	553.249	-1100.410	97.074	0.000

Table S2.5: Supported models considered in our AICc model selection for summer growth rates for length (a) and mass (b) in Langford Creek. We only considered models that contained only significant parameters (p = 0.05). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for stream flow (flow), relative condition factor (K), median summer temperature (MedT), proportion RBT admixture (pRBT), total length (TL), weight (W), density (D), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

a)

Langford Length	INT	MedT	pRBT	pRBT * MedT	PAR	logLik	AICc	delta	weight
1	**0.186**	**0.011**	**0.048**	**0.048**	**9**	**163.632**	**-307.900**	**0.000**	**0.583**
4	0.173				6	159.448	-306.273	1.626	0.258
3	0.187	0.015			7	159.763	-304.689	3.210	0.117
2	0.188	0.019	0.003		8	159.865	-302.647	5.252	0.042

b)

Langford Weight	INT	flow	K	MedT	pRBT	W	pRBT * flow	pRBT * MedT	D	PAR	logLik	AICc	delta	weight
1	**0.079**	**-0.039**	**-0.007**	**-0.001**	**0.048**	**0.041**	**0.022**	**0.053**		**13**	**232.637**	**-436.431**	**0.000**	**0.398**
12	0.074		-0.007			0.050			-0.027	9	227.420	-435.476	0.955	0.247
2	0.073	-0.043		-0.008	0.048	0.038	0.025	0.054		12	230.663	-434.907	1.524	0.186
13	0.074					0.050			-0.025	8	225.177	-433.272	3.159	0.082
3	0.092	-0.017		0.009	0.027	0.054		0.029		11	227.984	-431.937	4.493	0.042
4	0.105			0.023	0.035	0.056		0.036		10	226.803	-431.927	4.503	0.042
6	0.105			0.027		0.052				8	221.714	-426.345	10.086	0.003
5	0.107			0.030	0.003	0.055				9	222.036	-424.708	11.723	0.001
7	0.084					0.053				7	219.405	-423.973	12.457	0.001
9	0.086	-0.036				0.054				4	210.798	-413.304	23.127	0.000
8	0.058									6	211.550	-410.478	25.952	0.000
10	0.093					0.064				3	204.992	-403.809	32.621	0.000
11	0.063	-0.044								3	203.921	-401.669	34.762	0.000

Table S2.6: Supported models considered in our AICc model selection for summer growth rates for length (a) and mass (b) in McGee Creek. We only considered models that contained only significant parameters (p = 0.05). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for stream flow (flow), relative condition factor (K), median summer temperature (MedT), proportion RBT admixture (pRBT), total length (TL), weight (W), density (D), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

a)

McGee Length	INT	pRBT	year	PAR	logLik	AICc	delta	weight
1	**0.132**	**0.019**		**6**	**192.556**	**-372.507**	**0.000**	**0.948**
2	0.142			5	188.424	-366.420	6.087	0.045
3	0.157		+	4	185.494	-362.704	9.803	0.007

b)

McGee Weight	INT	MedT	pRBT	flow	D	PAR	logLik	AICc	delta	weight
6	-0.078		0.011		-0.087	7	257.303	-499.795	0.000	0.761
1	**0.005**	**0.019**	**0.011**			**7**	**255.709**	**-496.607**	**3.188**	**0.155**
7	-0.067				-0.081	6	253.778	-494.951	4.843	0.068
2	0.030		0.010			6	251.513	-490.422	9.373	0.007
4	0.015	0.018		0.012		4	248.942	-489.600	10.195	0.005
5	0.010	0.021				3	247.619	-489.070	10.725	0.004
3	0.034					5	249.072	-487.715	12.080	0.002

Table S2.7: Supported models considered in our AICc model selection for spring growth rates for length (a) and mass (b) in Cyclone Creek. We only considered models that contained only significant parameters (p = 0.05). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for relative condition factor (K), spring growing-degree-days (GDD), proportion RBT admixture (pRBT), total length (TL), weight (W), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

a)

Cyclone length	INT	K	GDD	TL	PAR	logLik	AICc	delta	weight
1	**0.131**	**-0.005**	**0.016**	**-0.023**	**5**	**289.766**	**-569.101**	**0.000**	**0.667**
2	0.145	-0.004		-0.022	4	287.522	-566.758	2.343	0.207
3	0.145			-0.022	3	285.976	-565.781	3.320	0.127
4	0.155				2	276.292	-548.500	20.600	0.000

b)

Cyclone weight	INT	K	W	PAR	logLik	AICc	delta	weight
1	**0.105**	**-0.009**	**0.052**	**4**	**317.573**	**-626.861**	**0.000**	**0.999**
2	0.103		0.045	3	308.461	-610.752	16.109	0.000
4	0.085	-0.006		3	296.417	-586.664	40.197	0.000
3	0.085			2	293.107	-582.130	44.731	0.000

Table S2.8: Supported models considered in our AICc model selection for spring growth rates for length (a) and mass (b) in Langford Creek. We only considered models that contained only significant parameters (p = 0.05). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for relative condition factor (K), spring growing-degree-days (GDD), proportion RBT admixture (pRBT), total length (TL), weight (W), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

a)

Langford length	INT	pRBT	GDD	PAR	logLik	AICc	delta	weight
1	**0.263**	**-0.013**	**0.065**	**4**	**127.627**	**-246.683**	**0.000**	**0.822**
2	0.222		0.042	3	124.102	-241.866	4.817	0.074
3	0.162			2	122.119	-240.071	6.612	0.030

b)

Langford weight	INT	K	pRBT	GDD	W	PAR	logLik	AICc	delta	weight
1	**0.268**	**-0.016**	**-0.011**	**0.085**	**0.090**	**6**	**140.225**	**-267.216**	**0.000**	**0.890**
2	0.239	-0.018		0.069	0.094	5	136.927	-262.984	4.232	0.107
3	0.141	-0.010			0.090	4	131.306	-254.040	13.176	0.001
6	0.141	-0.010			0.090	4	131.306	-254.040	13.176	0.001
4	0.136				0.078	3	129.115	-251.892	15.324	0.000
7	0.136				0.078	3	129.115	-251.892	15.324	0.000
8	0.175			0.047		3	121.504	-236.671	30.545	0.000
5	0.110					2	119.266	-234.365	32.851	0.000

Table S2.9: Supported models considered in our AICc model selection for spring growth rates for length (a) and mass (b) in McGee Creek. We only considered models that contained only significant parameters (p = 0.05). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for relative condition factor (K), spring growing-degree-days (GDD), proportion RBT admixture (pRBT), total length (TL), weight (W), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

a)

McGee length	INT	TL	PAR	logLik	AICc	delta	weight
1	**0.161**	**-0.021**	**5**	**108.544**	**-205.998**	**0.000**	**0.923**
2	0.167		4	104.877	-201.040	4.958	0.077

b)

McGee weight	INT	pRBT	W	K	PAR	logLik	AICc	delta	weight
1	**0.146**	**-0.019**	**0.061**		**4**	**113.244**	**-217.775**	**0.000**	**0.520**
4	0.132		0.063	-0.015	6	115.202	-216.849	0.925	0.328
2	0.132		0.060		3	110.864	-215.308	2.467	0.152
3	0.116				2	104.157	-204.106	13.668	0.001

Table S2.10: Supported models considered in our AICc model selection for annual growth rates for length (a) and mass (b) in Cyclone Creek. We only considered models that contained only significant parameters (p = 0.05). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for year, relative condition factor (K), annual growing-degree-days (GDD), proportion RBT admixture (pRBT), total length (TL), weight (W), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

a)

Cyclone length	INT	K	pRBT	TL	year	pRBT * K	PAR	logLik	AICc	delta	weight
1	**0.149**	**-0.007**	**0.008**	**-0.024**	**+**	**-0.012**	**9**	**513.648**	**-1008.516**	**0.000**	**1.000**
7	0.146			-0.023	+		6	501.167	-989.975	18.541	0.000
2	0.129	-0.009	0.008	-0.025		-0.014	6	500.201	-988.042	20.474	0.000
4	0.127		0.005	-0.024			4	486.561	-964.953	43.563	0.000
3	0.127	-0.002	0.006	-0.025			5	487.326	-964.396	44.120	0.000
5	0.125			-0.024			3	484.969	-963.837	44.679	0.000
6	0.137						2	471.112	-938.174	70.342	0.000

b)

Cyclone weight	INT	GDD	pRBT	W	year	pRBT * GDD	PAR	logLik	AICc	delta	weight
1	**0.123**	**-0.024**	**0.001**	**0.063**	**+**	**0.022**	**9**	**535.797**	**-1052.814**	**0.000**	**0.958**
2	0.099	0.023	0.000	0.061		0.024	6	529.316	-1046.273	6.541	0.036
7	0.123	-0.039		0.065	+		7	528.024	-1041.567	11.247	0.003
8	0.118			0.065	+		6	525.929	-1039.498	13.316	0.001
3	0.103	0.012	0.006	0.061			5	523.740	-1037.226	15.589	0.000
4	0.101	0.013		0.063			4	520.786	-1033.403	19.411	0.000
5	0.105			0.064			3	517.381	-1028.660	24.154	0.000
6	0.075						2	487.638	-971.225	81.590	0.000

Table S2.11: Supported models considered in our AICc model selection for annual growth rates for length (a) and mass (b) in Langford Creek. We only considered models that contained only significant parameters (p = 0.05). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for year, relative condition factor (K), annual growing-degree-days (GDD), proportion RBT admixture (pRBT), total length (TL), weight (W), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

a)

Langford length	INT	GDD	K	TL	year	PAR	logLik	AICc	delta	weight
1	**0.000**	**-0.063**	**-0.012**	**-0.030**	**+**	**8**	**186.084**	**-354.473**	**0.000**	**0.578**
4	0.149			-0.027		3	179.224	-352.181	2.293	0.184
3	0.160	0.009		-0.028		4	179.937	-351.425	3.048	0.126
2	0.060	-0.038		-0.027	+	7	183.202	-351.102	3.371	0.107
5	0.164					2	174.747	-345.362	9.111	0.006

b)

Langford weight	INT	GDD	K	W	year	PAR	logLik	AICc	delta	weight
1	**-0.016**	**-0.070**	**-0.019**	**0.087**	**+**	**11**	**194.143**	**-363.067**	**0.000**	**0.931**
2	0.128		-0.014	0.086	+	10	190.228	-357.806	5.261	0.067
3	0.149		-0.006	0.094		7	182.457	-349.612	13.455	0.001
4	0.150			0.093		6	181.196	-349.426	13.641	0.001
5	0.102					5	171.328	-331.974	31.093	0.000

Table S2.12: Supported models considered in our AICc model selection for annual growth rates for length (a) and mass (b) in McGee Creek. We only considered models that contained only significant parameters (p = 0.05). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for year, relative condition factor (K), annual growing-degree-days (GDD), proportion RBT admixture (pRBT), total length (TL), weight (W), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

a)

McGee length	INT	TL	year	PAR	logLik	AICc	delta	weight
1	**0.153**	**-0.024**		**3**	**138.919**	**-271.509**	**0.000**	**0.755**
3	0.157		+	4	138.349	-268.143	3.366	0.140
2	0.164			2	135.856	-267.550	3.959	0.104

b)

McGee weight	INT	W	PAR	logLik	AICc	delta	weight
1	**0.153**	**0.107**	**3**	**147.371**	**-288.413**	**0.000**	**1.000**
2	0.105		2	134.069	-263.975	24.438	0.000

Table S2.13: Supported models considered in our AICc model selection for the GLM analysis of migratory life history strategy of juvenile *Oncorhynchus spp.* in Cyclone and Langford Creeks. We only considered models that contained only significant parameters ($p = 0.05$). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for year, relative condition factor (K), annual growing-degree-days (GDD), proportion RBT admixture (pRBT), total length (TL), weight (W), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

Cyclone Juveniles	**INT**	**K**	**pRBT**	**TL**	**year**	**pRBT * TL**	**PAR**	**logLik**	**AICc**	**delta**	**weight**
1	**-1.688**	**-0.912**	**0.279**	**1.118**	**+**	**-0.737**	**8**	**-340.110**	**696.321**	**0.000**	**0.964**
2	-1.615	-0.901	0.624	1.018	+		7	-344.434	702.945	6.624	0.035
3	-2.015	-0.939	0.620	0.975			4	-351.577	711.181	14.861	0.001
4	-2.428	-1.006	0.590				3	-357.962	721.941	25.620	0.000
6	-1.863	-0.474		0.883	+		6	-363.580	739.218	42.897	0.000
5	-2.612		0.441				2	-370.606	745.220	48.899	0.000
10	-2.046	-0.562		0.812			3	-370.978	747.972	51.651	0.000
8	-2.106			0.943			2	-375.229	754.467	58.146	0.000
7	-2.557				+		4	-373.775	755.577	59.257	0.000
9	-2.394	-0.646					2	-375.930	755.868	59.548	0.000
Langford Juveniles	**INT**	**K**	**pRBT**	**TL**	**year**	**pRBT * TL**	**PAR**	**logLik**	**AICc**	**delta**	**weight**
1	**-1.437**	**-0.732**	**-0.247**	**-0.820**	**+**	**-1.771**	**8**	**-306.403**	**629.000**	**0.000**	**1.000**
3	-0.921	-0.752	0.530		+		6	-331.278	674.669	45.669	0.000
2	-1.056	-0.739	0.505	-0.274	+		7	-330.591	675.333	46.333	0.000
6	-1.282	-0.694		-0.497	+		6	-342.112	696.336	67.336	0.000
4	-1.039	-0.711			+		5	-344.599	699.278	70.278	0.000
5	-0.916				+		4	-372.652	753.357	124.357	0.000
9	-1.137	-0.769		-0.334			3	-388.899	783.829	154.829	0.000
8	-0.989	-0.782					2	-390.221	784.457	155.457	0.000
7	-1.284			-0.471			2	-424.629	853.274	224.274	0.000

Table S2.14: Supported models considered in our AICc model selection for the GLM analysis of migratory life history strategy of adult *Oncorhynchus spp.* in Cyclone and Langford Creeks. We only considered models that contained only significant parameters ($p = 0.05$). The models below are ranked by AICc and the coefficients for these competing models are shown. Coefficients are shown for models that contain covariates for year, relative condition factor (K), annual growing-degree-days (GDD), proportion RBT admixture (pRBT), total length (TL), weight (W), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

Cyclone Adults	**INT**	**K**	**pRBT**	**TL**	**year**	**PAR**	**logLik**	**AICc**	**delta**	**weight**
1	**-1.446**	**-2.078**	**0.545**	**1.482**	**+**	**7**	**-234.219**	**482.611**	**0.000**	**1.000**
2	-1.527	-1.872		1.598	+	6	-243.773	499.675	17.064	0.000
6	-2.698	-1.661		1.635		3	-260.450	526.938	44.326	0.000
4	-2.784			1.504		2	-298.566	601.150	118.539	0.000
5	-0.568	-1.226				2	-377.384	758.785	276.174	0.000
3	0.148				+	4	-392.434	792.929	310.318	0.000
Langford Adults	**INT**	**K**	**pRBT**	**TL**	**year**	**PAR**	**logLik**	**AICc**	**delta**	**weight**
1	**-0.485**	**-2.075**	**0.597**	**1.968**	**+**	**7**	**-75.103**	**164.708**	**0.000**	**0.968**
3	-0.135	-1.971		1.751	+	6	-80.077	172.528	7.820	0.019
2	-1.818	-1.873	0.601	1.905		4	-82.619	173.414	8.706	0.012
7	-1.514	-1.785		1.696		3	-88.500	183.107	18.399	0.000
6	0.724	-2.157				2	-113.537	231.126	66.418	0.000
5	-2.223			1.928		2	-114.145	232.342	67.634	0.000
4	1.649				+	4	-148.480	305.136	140.428	0.000

APPENDIX B

CHAPTER 3 SUPPLEMENTAL MATERIALS

Section S3.1 Supplemental Results

S3.1.1 Effects of pRBT and season on emigration and size class transition probabilities

We found strong seasonal differences in emigration and size class transition probabilities in all populations, however the effect of pRBT on these probabilities was inconsistent. Emigration rates were lower than previously described (Strait et al. *in prep*), less than 8% of tagged individuals emigrated from any study stream (Table 1). In all populations, mean emigration probabilities for juvenile ($\Psi_{juv\text{-}E}$) and subadult ($\Psi_{sub\text{-}E}$) classes was highest during the spring/winter period (Figs S3 & S6). In addition to this mean effect, emigration during the spring for sub-adults in Langford negatively interacted with pRBT. Adult emigration did not vary by season in Langford or McGee, however, in Cyclone adult emigration was higher during the spring and positively interacted with pRBT (Fig S6c).

Size class transition probabilities varied significantly among seasons in all populations and interacted with pRBT in Cyclone and Langford Creeks. In all populations, juvenile-subadult ($\Psi_{juv\text{-}sub}$) and subadult-adult ($\Psi_{sub\text{-}ad}$) transition probabilities were higher during the spring than the during the summer (Figs S4 & S7). In Cyclone creek, we found a significant, positive interaction between pRBT and juvenile-subadult transition probability ($\Psi_{juv\text{-}sub}$). In Langford, we found negative effects of pRBT on the spring juvenile-subadult and subadult-adult transitions.

Section S3.2: Supplemental Materials: JAGS models

S3.2.1: Final JAGS model for Cyclone Creek

```
model {
    # ------------------------------------------------
    # Parameters:
    # phiA: survival probability in size class A (juveniles)
    # phiB: survival probability in size class B (subadults)
    # phiC: survival probability in size class C (adults)

    # psiA[1]: probability of remaining in class A
    # psiA[2]: probability of transitioning from class A to class B
    # psiA[3]: probability of individuals in class A emigrating permanently
    # psiB[1]: probability of remaining in class B
    # psiB[2]: probability of transitioning from class B to class C
    # psiB[3]: probability of individuals in class B emigrating permanently
    # psiCE: probability of individuals in class C emigrating permanently

    # pA: recapture probability in for A class
    # pBC: recapture probability in for larger sizes (B and C)
    # pE: Set this to 1.0 (assuming perfect detection of migrants)
    # ------------------------------------------------
    # States (S):
    # 1 alive in A
    # 2 alive in B
    # 3 alive in C
    # 4 recent emigrant
    # 5 old emigrant
    # 6 dead
    # ------------------------------------------------
    # Observations (O):
    # 1 seen in A
    # 2 seen in B
    # 3 seen in C
    # 4 seen recent emigrant
    # 5 not seen
    # ------------------------------------------------

   # Priors and constraints for probability of detection
    for( t in 1:( n.occasions-1 ) ){
      pA[t] <- mean.pA
      pBC[t] <- mean.pBC
    }
      mean.pA ~ dunif(0.1, 0.9)      # Priors for mean state-spec. recapture
      mean.pBC ~ dunif(0.1, 0.9)      # Priors for mean state-spec. recapture

  # priors for state-specific survival
 # priors for state-specific survival
   b0.phiA ~ dnorm( 0, 0.001 )T(-10,10)
   b0.phiB ~ dnorm( 0, 0.001 )T(-10,10)
   b0.phiC ~ dnorm( 0, 0.001 )T(-10,10)
   b1.phiA ~ dnorm( 0, 0.001 )T(-10,10)
   b1.phiB ~ dnorm( 0, 0.001 )T(-10,10)
   b1.phiC ~ dnorm( 0, 0.001 )T(-10,10)
   b2.phiA ~ dnorm( 0, 0.001 )T(-5,5)
```

```
  b2.phiB ~ dnorm( 0, 0.001 )T(-5,5)
  b2.phiC ~ dnorm( 0, 0.001 )T(-5,5)
  b3.phiA ~ dnorm( 0, 0.001 )T(-5,5)
  b3.phiB ~ dnorm( 0, 0.001 )T(-5,5)
  b3.phiC ~ dnorm( 0, 0.001 )T(-5,5)

 # Priors for mean transitions from C to E
          # just mean CE, no season or pRBT effect
  b0.psiCE ~ dnorm( 0, 0.001 )T(-10,10)
  b1.psiCE ~ dnorm( 0, 0.001 )T(-10,10)
  b2.psiCE ~ dnorm( 0, 0.001 )T(-10,10)
  b3.psiCE ~ dnorm( 0, 0.001 )T(-10,10)

# Transitions: multinomial logit
# Normal priors on logit of all but one transition probability
   b0.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b0.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiAE ~ dnorm(0, 0.001)T(-10,10)

   b0.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b0.lpsiBE ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiBE ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiBE ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiBE ~ dnorm(0, 0.001)T(-10,10)

# logit transformations of all priors
# phi's
# derive period survival estimates
  summer.phiA <- ilogit(b0.phiA)^4
  winter.phiA <- ilogit(b1.phiA)^8
  summer.phiB <- ilogit(b0.phiB)^4
  winter.phiB <- ilogit(b1.phiB)^8
  summer.phiC <- ilogit(b0.phiC)^4
  winter.phiC <- ilogit(b1.phiC)^8

# monthly survivals
  m.summer.phiA <- ilogit(b0.phiA)
  m.summer.phiB <- ilogit(b0.phiB)
  m.summer.phiC <- ilogit(b0.phiC)

  m.winter.phiA <- ilogit(b1.phiA)
  m.winter.phiB <- ilogit(b1.phiB)
  m.winter.phiC <- ilogit(b1.phiC)

# psi's
  logit(summer.psiCE) <- b0.psiCE
  logit(winter.psiCE) <- b2.psiCE
```

```
 # Derive summer and winter estimates fo movement probabilities
 # Constrain the transitions such that their sum is <1
     # Psi A transitions for summer and winter and pRBT
      psiAB.sum <- exp(b0.lpsiAB ) / (1 + exp(b0.lpsiAB ) + exp(b0.lpsiAE ) )
      psiAE.sum <- exp(b0.lpsiAE ) / (1 + exp(b0.lpsiAB ) + exp(b0.lpsiAE ) )
      psiAB.win <- exp(b2.lpsiAB ) / (1 + exp(b2.lpsiAB ) + exp(b2.lpsiAE ) )
      psiAE.win <- exp(b2.lpsiAE ) / (1 + exp(b2.lpsiAB ) + exp(b2.lpsiAE ) )

     # Psi B transitions for summer and winter and pRBT
           psiBC.sum <- exp(b0.lpsiBC ) / (1 + exp(b0.lpsiBC ) + exp(b0.lpsiBE ) )
           psiBE.sum <- exp(b0.lpsiBE ) / (1 + exp(b0.lpsiBC ) + exp(b0.lpsiBE ) )
           psiBC.win <- exp(b2.lpsiBC ) / (1 + exp(b2.lpsiBC ) + exp(b2.lpsiBE ) )
           psiBE.win <- exp(b2.lpsiBE ) / (1 + exp(b2.lpsiBC ) + exp(b2.lpsiBE ) )

   # calculate the last transition probability
      psiAA.sum <- ( 1 - psiAB.sum - psiAE.sum )
      psiAA.win <- ( 1 - psiAB.win - psiAE.win )
      psiBB.sum <- ( 1 - psiBC.sum - psiBE.sum )
      psiBB.win <- ( 1 - psiBC.win - psiBE.win )

   for( i in 1:nind ){
     for( t in f[i]:(when.cens[i]-1) ){

       phiA[i,t] <- ilogit( b0.phiA*summer[t] + b1.phiA*winter[t] + b2.phiA*summer[t]*prbt[i] +
b3.phiA*winter[t]*prbt[i] )^power[t]
       phiB[i,t] <- ilogit( b0.phiB*summer[t] + b1.phiB*winter[t] + b2.phiB*summer[t]*prbt[i] +
b3.phiB*winter[t]*prbt[i] )^power[t]
       phiC[i,t] <- ilogit( b0.phiC*summer[t] + b1.phiC*winter[t] + b2.phiC*summer[t]*prbt[i] +
b3.phiC*winter[t]*prbt[i] )^power[t]

    # Psi's for state C
       logit(psiCE[i,t]) <- b0.psiCE*summer[t] + b1.psiCE*summer[t]*prbt[i] + b2.psiCE*winter[t] +
b3.psiCE*winter[t]*prbt[i]

            # Psi's for state A
       psiAB[i,t] <- exp( b0.lpsiAB*summer[t] + b2.lpsiAB*winter[t] + b1.lpsiAB*summer[t]*prbt[i] +
b3.lpsiAB*winter[t]*prbt[i] ) /
       (1 + exp(b0.lpsiAB*summer[t] + b2.lpsiAB*winter[t] + b1.lpsiAB*summer[t]*prbt[i] +
b3.lpsiAB*winter[t]*prbt[i]) +
       exp(b0.lpsiAE*summer[t] + b2.lpsiAE*winter[t] + b1.lpsiAE*summer[t]*prbt[i] +
b3.lpsiAE*winter[t]*prbt[i]) )

       psiAE[i,t] <- exp(b0.lpsiAE*summer[t] + b2.lpsiAE*winter[t] + b1.lpsiAE*summer[t]*prbt[i] +
b3.lpsiAE*winter[t]*prbt[i]) /
       (1 + exp(b0.lpsiAB*summer[t] + b2.lpsiAB*winter[t] + b1.lpsiAB*summer[t]*prbt[i] +
b3.lpsiAB*winter[t]*prbt[i]) +
       exp(b0.lpsiAE*summer[t] + b2.lpsiAE*winter[t] + b1.lpsiAE*summer[t]*prbt[i] +
b3.lpsiAE*winter[t]*prbt[i]) )

       psiAA[i,t] <- ( 1 - psiAB[i,t] - psiAE[i,t])

             # Psi's for state B
       psiBC[i,t] <- exp( b0.lpsiBC*summer[t] + b2.lpsiBC*winter[t] + b1.lpsiBC*summer[t]*prbt[i] +
b3.lpsiBC*winter[t]*prbt[i] ) /
       (1 + exp(b0.lpsiBC*summer[t] + b2.lpsiBC*winter[t] + b1.lpsiBC*summer[t]*prbt[i] +
b3.lpsiBC*winter[t]*prbt[i]) +
```

```
    exp(b0.lpsiBE*summer[t] + b2.lpsiBE*winter[t] + b1.lpsiBE*summer[t]*prbt[i] + b3.lpsiBE*winter[t]*prbt[i]))

      psiBE[i,t] <- exp(b0.lpsiBE*summer[t] + b2.lpsiBE*winter[t] + b1.lpsiBE*summer[t]*prbt[i] +
b3.lpsiBE*winter[t]*prbt[i]) /
      (1 + exp(b0.lpsiBC*summer[t] + b2.lpsiBC*winter[t] + b1.lpsiBC*summer[t]*prbt[i] +
b3.lpsiBC*winter[t]*prbt[i]) +
    exp(b0.lpsiBE*summer[t] + b2.lpsiBE*winter[t] + b1.lpsiBE*summer[t]*prbt[i] + b3.lpsiBE*winter[t]*prbt[i]))

      psiBB[i,t] <- ( 1 - psiBC[i,t] - psiBE[i,t])
    }
  }

    # Define state-transition and observation matrices
    for (i in 1:nind){
    # Define probabilities of state S(t+1) given S(t)
     for (t in f[i]:(when.cens[i]-1)){

       ps[1,i,t,1] <- phiA[i,t] * psiAA[i,t]
       ps[1,i,t,2] <- phiA[i,t] * psiAB[i,t]
       ps[1,i,t,3] <- 0
       ps[1,i,t,4] <- phiA[i,t] * psiAE[i,t]
       ps[1,i,t,5] <- 0
       ps[1,i,t,6] <- 1-phiA[i,t]

       ps[2,i,t,1] <- 0
       ps[2,i,t,2] <- phiB[i,t] * psiBB[i,t]
       ps[2,i,t,3] <- phiB[i,t] * psiBC[i,t]
       ps[2,i,t,4] <- phiB[i,t] * psiBE[i,t]
       ps[2,i,t,5] <- 0
       ps[2,i,t,6] <- 1-phiB[i,t]

       ps[3,i,t,1] <- 0
       ps[3,i,t,2] <- 0
       ps[3,i,t,3] <- phiC[i,t] * (1-psiCE[i,t])
       ps[3,i,t,4] <- phiC[i,t] * psiCE[i,t]
       ps[3,i,t,5] <- 0
       ps[3,i,t,6] <- 1-phiC[i,t]

       ps[4,i,t,1] <- 0
       ps[4,i,t,2] <- 0
       ps[4,i,t,3] <- 0
       ps[4,i,t,4] <- 0
       ps[4,i,t,5] <- 1
       ps[4,i,t,6] <- 0

       ps[5,i,t,1] <- 0
       ps[5,i,t,2] <- 0
       ps[5,i,t,3] <- 0
       ps[5,i,t,4] <- 0
       ps[5,i,t,5] <- 1
       ps[5,i,t,6] <- 0

       ps[6,i,t,1] <- 0
       ps[6,i,t,2] <- 0
       ps[6,i,t,3] <- 0
       ps[6,i,t,4] <- 0
```

```
      ps[6,i,t,5] <- 0
      ps[6,i,t,6] <- 1

      # Define probabilities of O(t) given S(t)
      po[1,i,t,1] <- pA[t]
      po[1,i,t,2] <- 0
      po[1,i,t,3] <- 0
      po[1,i,t,4] <- 0
      po[1,i,t,5] <- 1-pA[t]

      po[2,i,t,1] <- 0
      po[2,i,t,2] <- pBC[t]
      po[2,i,t,3] <- 0
      po[2,i,t,4] <- 0
      po[2,i,t,5] <- 1-pBC[t]

      po[3,i,t,1] <- 0
      po[3,i,t,2] <- 0
      po[3,i,t,3] <- pBC[t]
      po[3,i,t,4] <- 0
      po[3,i,t,5] <- 1-pBC[t]

      po[4,i,t,1] <- 0
      po[4,i,t,2] <- 0
      po[4,i,t,3] <- 0
      po[4,i,t,4] <- 1
      po[4,i,t,5] <- 0

      po[5,i,t,1] <- 0
      po[5,i,t,2] <- 0
      po[5,i,t,3] <- 0
      po[5,i,t,4] <- 0
      po[5,i,t,5] <- 1

      po[6,i,t,1] <- 0
      po[6,i,t,2] <- 0
      po[6,i,t,3] <- 0
      po[6,i,t,4] <- 0
      po[6,i,t,5] <- 1
    } #t
  } #i
  # Likelihood
  for (i in 1:nind){
    # Define latent state at first capture
    z[i,f[i]] <- y[i,f[i]]
    for (t in (f[i]+1):when.cens[i]){
      # State process: draw S(t) given S(t-1)
      z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
      # Observation process: draw O(t) given S(t)
      y[i,t] ~ dcat(po[z[i,t], i, t-1,])
    } #t
  } #i
}
```

S3.2.2: Final JAGS model for Langford Creek

```
model {
    # -----------------------------------------------
    # Parameters:
    # phiA: survival probability in size class A (juveniles)
    # phiB: survival probability in size class B (subadults)
    # phiC: survival probability in size class C (adults)

    # psiA[1]: probability of remaining in class A
    # psiA[2]: probability of transitioning from class A to class B
    # psiA[3]: probability of individuals in class A emigrating permanently
    # psiB[1]: probability of remaining in class B
    # psiB[2]: probability of transitioning from class B to class C
    # psiB[3]: probability of individuals in class B emigrating permanently
    # psiCE: probability of individuals in class C emigrating permanently

    # pAB: recapture probability in for A and B classes
    # pC: recapture probability in for largest size
    # pE: Set this to 1.0 (assuming perfect detection of migrants)
    # -----------------------------------------------
    # States (S):
    # 1 alive in A
    # 2 alive in B
    # 3 alive in C
    # 4 recent emigrant
    # 5 old emigrant
    # 6 dead
    # -----------------------------------------------
    # Observations (O):
    # 1 seen in A
    # 2 seen in B
    # 3 seen in C
    # 4 seen recent emigrant
    # 5 not seen
    # -----------------------------------------------

   # Priors and constraints for probability of detection
    for( t in 1:( n.occasions-1 ) ){
      pAB[t] <- mean.pAB
      pC[t] <- mean.pC
    }
      mean.pAB ~ dunif(0.2, 0.8)      # Priors for mean state-spec. recapture
      mean.pC ~ dunif(0.2, 0.8)      # Priors for mean state-spec. recapture

  # priors for state-specific survival
 # priors for state-specific survival
   b0.phiA ~ dnorm( 0, 0.001 )T(-10,10)
   b0.phiB ~ dnorm( 0, 0.001 )T(-10,10)
   b0.phiC ~ dnorm( 0, 0.001 )T(-10,10)
   b1.phiA ~ dnorm( 0, 0.001 )T(-10,10)
   b1.phiB ~ dnorm( 0, 0.001 )T(-10,10)
   b1.phiC ~ dnorm( 0, 0.001 )T(-10,10)
   b2.phiA ~ dnorm( 0, 0.001 )T(-10,10)
   b2.phiB ~ dnorm( 0, 0.001 )T(-10,10)
   b2.phiC ~ dnorm( 0, 0.001 )T(-10,10)
```

```
  b3.phiA ~ dnorm( 0, 0.001 )T(-10,10)
  b3.phiB ~ dnorm( 0, 0.001 )T(-10,10)
  b3.phiC ~ dnorm( 0, 0.001 )T(-10,10)

 # Priors for mean transitions from C to E
          # just mean CE, no season or pRBT effect
  b0.psiCE ~ dnorm( 0, 0.001 )T(-10,10)
  b1.psiCE ~ dnorm( 0, 0.001 )T(-10,10)
  b2.psiCE ~ dnorm( 0, 0.001 )T(-10,10)
  b3.psiCE ~ dnorm( 0, 0.001 )T(-10,10)

# Transitions: multinomial logit
# Normal priors on logit of all but one transition probability
   b0.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b0.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b0.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b0.lpsiBE ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiBE ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiBE ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiBE ~ dnorm(0, 0.001)T(-10,10)

# logit transformations of all priors
# phi's
# derive period survival estimates
  summer.phiA <- ilogit(b0.phiA)^4
  winter.phiA <- ilogit(b1.phiA)^8
  summer.phiB <- ilogit(b0.phiB)^4
  winter.phiB <- ilogit(b1.phiB)^8
  summer.phiC <- ilogit(b0.phiC)^4
  winter.phiC <- ilogit(b1.phiC)^8

# monthly survivals
  m.summer.phiA <- ilogit(b0.phiA)
  m.summer.phiB <- ilogit(b0.phiB)
  m.summer.phiC <- ilogit(b0.phiC)

  m.winter.phiA <- ilogit(b1.phiA)
  m.winter.phiB <- ilogit(b1.phiB)
  m.winter.phiC <- ilogit(b1.phiC)

# psi's
  logit(summer.psiCE) <- b0.psiCE
  logit(winter.psiCE) <- b2.psiCE

# Derive summer and winter estimates fo movement probabilities
# Constrain the transitions such that their sum is <1
     # Psi A transitions for summer and winter and pRBT
```

```
      psiAB.sum <- exp(b0.lpsiAB ) / (1 + exp(b0.lpsiAB ) + exp(b0.lpsiAE ) )
      psiAE.sum <- exp(b0.lpsiAE ) / (1 + exp(b0.lpsiAB ) + exp(b0.lpsiAE ) )
      psiAB.win <- exp(b2.lpsiAB ) / (1 + exp(b2.lpsiAB ) + exp(b2.lpsiAE ) )
      psiAE.win <- exp(b2.lpsiAE ) / (1 + exp(b2.lpsiAB ) + exp(b2.lpsiAE ) )

     # Psi B transitions for summer and winter and pRBT
          psiBC.sum <- exp(b0.lpsiBC ) / (1 + exp(b0.lpsiBC ) + exp(b0.lpsiBE ) )
          psiBE.sum <- exp(b0.lpsiBE ) / (1 + exp(b0.lpsiBC ) + exp(b0.lpsiBE ) )
          psiBC.win <- exp(b2.lpsiBC ) / (1 + exp(b2.lpsiBC ) + exp(b2.lpsiBE ) )
          psiBE.win <- exp(b2.lpsiBE ) / (1 + exp(b2.lpsiBC ) + exp(b2.lpsiBE ) )

   # calculate the last transition probability
      psiAA.sum <- ( 1 - psiAB.sum - psiAE.sum )
      psiAA.win <- ( 1 - psiAB.win - psiAE.win )
      psiBB.sum <- ( 1 - psiBC.sum - psiBE.sum )
      psiBB.win <- ( 1 - psiBC.win - psiBE.win )

   for( i in 1:nind ){
     for( t in f[i]:(when.cens[i]-1) ){

phiA[i,t] <- ilogit( b0.phiA*summer[t] + b1.phiA*winter[t] + b2.phiA*summer[t]*prbt[i] +
      b3.phiA*winter[t]*prbt[i] )^power[t]
phiB[i,t] <- ilogit( b0.phiB*summer[t] + b1.phiB*winter[t] + b2.phiB*summer[t]*prbt[i] +
      b3.phiB*winter[t]*prbt[i] )^power[t]
phiC[i,t] <- ilogit( b0.phiC*summer[t] + b1.phiC*winter[t] + b2.phiC*summer[t]*prbt[i] +
      b3.phiC*winter[t]*prbt[i] )^power[t]

# Psi's for state C
logit(psiCE[i,t]) <- b0.psiCE*summer[t] + b1.psiCE*summer[t]*prbt[i] + b2.psiCE*winter[t] +
      b3.psiCE*winter[t]*prbt[i]

# Psi's for state A
psiAB[i,t] <- exp( b0.lpsiAB*summer[t] + b2.lpsiAB*winter[t] + b1.lpsiAB*summer[t]*prbt[i] +
      b3.lpsiAB*winter[t]*prbt[i] ) /
 (1 + exp(b0.lpsiAB*summer[t] + b2.lpsiAB*winter[t] + b1.lpsiAB*summer[t]*prbt[i] +
      b3.lpsiAB*winter[t]*prbt[i]) +
exp(b0.lpsiAE*summer[t] + b2.lpsiAE*winter[t] + b1.lpsiAE*summer[t]*prbt[i] + b3.lpsiAE*winter[t]*prbt[i]))

psiAE[i,t] <- exp(b0.lpsiAE*summer[t] + b2.lpsiAE*winter[t] + b1.lpsiAE*summer[t]*prbt[i] +
      b3.lpsiAE*winter[t]*prbt[i]) /
(1 + exp(b0.lpsiAB*summer[t] + b2.lpsiAB*winter[t] + b1.lpsiAB*summer[t]*prbt[i] +
      b3.lpsiAB*winter[t]*prbt[i]) +
exp(b0.lpsiAE*summer[t] + b2.lpsiAE*winter[t] + b1.lpsiAE*summer[t]*prbt[i] + b3.lpsiAE*winter[t]*prbt[i]) )

psiAA[i,t] <- ( 1 - psiAB[i,t] - psiAE[i,t])

       # Psi's for state B
psiBC[i,t] <- exp( b0.lpsiBC*summer[t] + b2.lpsiBC*winter[t] + b1.lpsiBC*summer[t]*prbt[i] +
      b3.lpsiBC*winter[t]*prbt[i] ) /
 (1 + exp(b0.lpsiBC*summer[t] + b2.lpsiBC*winter[t] + b1.lpsiBC*summer[t]*prbt[i] +
      b3.lpsiBC*winter[t]*prbt[i]) +
exp(b0.lpsiBE*summer[t] + b2.lpsiBE*winter[t] + b1.lpsiBE*summer[t]*prbt[i] + b3.lpsiBE*winter[t]*prbt[i]))

      psiBE[i,t] <- exp(b0.lpsiBE*summer[t] + b2.lpsiBE*winter[t] + b1.lpsiBE*summer[t]*prbt[i] +
b3.lpsiBE*winter[t]*prbt[i]) /
```

```
 (1 + exp(b0.lpsiBC*summer[t] + b2.lpsiBC*winter[t] + b1.lpsiBC*summer[t]*prbt[i] +
b3.lpsiBC*winter[t]*prbt[i]) +
exp(b0.lpsiBE*summer[t] + b2.lpsiBE*winter[t] + b1.lpsiBE*summer[t]*prbt[i] + b3.lpsiBE*winter[t]*prbt[i]))

psiBB[i,t] <- ( 1 - psiBC[i,t] - psiBE[i,t])
     }
   }
     # Define state-transition and observation matrices
     for (i in 1:nind){
     # Define probabilities of state S(t+1) given S(t)
       for (t in f[i]:(when.cens[i]-1)){

         ps[1,i,t,1] <- phiA[i,t] * psiAA[i,t]
         ps[1,i,t,2] <- phiA[i,t] * psiAB[i,t]
         ps[1,i,t,3] <- 0
         ps[1,i,t,4] <- phiA[i,t] * psiAE[i,t]
         ps[1,i,t,5] <- 0
         ps[1,i,t,6] <- 1-phiA[i,t]

         ps[2,i,t,1] <- 0
         ps[2,i,t,2] <- phiB[i,t] * psiBB[i,t]
         ps[2,i,t,3] <- phiB[i,t] * psiBC[i,t]
         ps[2,i,t,4] <- phiB[i,t] * psiBE[i,t]
         ps[2,i,t,5] <- 0
         ps[2,i,t,6] <- 1-phiB[i,t]

         ps[3,i,t,1] <- 0
         ps[3,i,t,2] <- 0
         ps[3,i,t,3] <- phiC[i,t] * (1-psiCE[i,t])
         ps[3,i,t,4] <- phiC[i,t] * psiCE[i,t]
         ps[3,i,t,5] <- 0
         ps[3,i,t,6] <- 1-phiC[i,t]

         ps[4,i,t,1] <- 0
         ps[4,i,t,2] <- 0
         ps[4,i,t,3] <- 0
         ps[4,i,t,4] <- 0
         ps[4,i,t,5] <- 1
         ps[4,i,t,6] <- 0

         ps[5,i,t,1] <- 0
         ps[5,i,t,2] <- 0
         ps[5,i,t,3] <- 0
         ps[5,i,t,4] <- 0
         ps[5,i,t,5] <- 1
         ps[5,i,t,6] <- 0

         ps[6,i,t,1] <- 0
         ps[6,i,t,2] <- 0
         ps[6,i,t,3] <- 0
         ps[6,i,t,4] <- 0
         ps[6,i,t,5] <- 0
         ps[6,i,t,6] <- 1

         # Define probabilities of O(t) given S(t)
         po[1,i,t,1] <- pAB[t]
```

```
      po[1,i,t,2] <- 0
      po[1,i,t,3] <- 0
      po[1,i,t,4] <- 0
      po[1,i,t,5] <- 1-pAB[t]

      po[2,i,t,1] <- 0
      po[2,i,t,2] <- pAB[t]
      po[2,i,t,3] <- 0
      po[2,i,t,4] <- 0
      po[2,i,t,5] <- 1-pAB[t]

      po[3,i,t,1] <- 0
      po[3,i,t,2] <- 0
      po[3,i,t,3] <- pC[t]
      po[3,i,t,4] <- 0
      po[3,i,t,5] <- 1-pC[t]

      po[4,i,t,1] <- 0
      po[4,i,t,2] <- 0
      po[4,i,t,3] <- 0
      po[4,i,t,4] <- 1
      po[4,i,t,5] <- 0

      po[5,i,t,1] <- 0
      po[5,i,t,2] <- 0
      po[5,i,t,3] <- 0
      po[5,i,t,4] <- 0
      po[5,i,t,5] <- 1

      po[6,i,t,1] <- 0
      po[6,i,t,2] <- 0
      po[6,i,t,3] <- 0
      po[6,i,t,4] <- 0
      po[6,i,t,5] <- 1

    } #t
  } #i

  # Likelihood
  for (i in 1:nind){
    # Define latent state at first capture
    z[i,f[i]] <- y[i,f[i]]
    for (t in (f[i]+1):when.cens[i]){
      # State process: draw S(t) given S(t-1)
      z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
      # Observation process: draw O(t) given S(t)
      y[i,t] ~ dcat(po[z[i,t], i, t-1,])
    } #t
  } #i
}
```

S3.2.3: Final JAGS model for McGee Creek

```
model {
    # ------------------------------------------------
    # Parameters:
    # phiA: survival probability in size class A (juveniles)
    # phiB: survival probability in size class B (subadults)
    # phiC: survival probability in size class C (adults)

    # psiA[1]: probability of remaining in class A
    # psiA[2]: probability of transitioning from class A to class B
    # psiA[3]: probability of individuals in class A emigrating permanently
    # psiB[1]: probability of remaining in class B
    # psiB[2]: probability of transitioning from class B to class C
    # psiB[3]: probability of individuals in class B emigrating permanently
    # psiCE: probability of individuals in class C emigrating permanently

    # pAB: recapture probability in for A and B classes
    # pC: recapture probability in for largest size
    # pE: Set this to 1.0 (assuming perfect detection of migrants)
    # ------------------------------------------------
    # States (S):
    # 1 alive in A
    # 2 alive in B
    # 3 alive in C
    # 4 recent emigrant
    # 5 old emigrant
    # 6 dead
    # ------------------------------------------------
    # Observations (O):
    # 1 seen in A
    # 2 seen in B
    # 3 seen in C
    # 4 seen recent emigrant
    # 5 not seen
    # ------------------------------------------------

   # Priors and constraints for probability of detection
    for( t in 1:( n.occasions-1 ) ){
      pAB[t] <- mean.pAB
      pC[t] <- mean.pC
    }
      mean.pAB ~ dunif(0.2, 0.9)      # Priors for mean state-spec. recapture
      mean.pC ~ dunif(0.2, 0.9)      # Priors for mean state-spec. recapture

  # priors for state-specific survival
 # priors for state-specific survival
   b0.phiA ~ dnorm( 0, 0.001 )T(-10,10)
   b0.phiB ~ dnorm( 0, 0.001 )T(-5,5)    # adjusted priors based off first run
   b0.phiC ~ dnorm( 0, 0.001 )T(-5,5)    # adjusted priors based off first run
   b1.phiA ~ dnorm( 0, 0.001 )T(-10,10)
   b1.phiB ~ dnorm( 0, 0.001 )T(-10,10)
   b1.phiC ~ dnorm( 0, 0.001 )T(-10,10)
   b2.phiA ~ dnorm( 0, 0.001 )T(-10,10)
   b2.phiB ~ dnorm( 0, 0.001 )T(-5,5)    # adjusted priors based off first run
   b2.phiC ~ dnorm( 0, 0.001 )T(-5,5)    # adjusted priors based off first run
```

```
  b3.phiA ~ dnorm( 0, 0.001 )T(-10,10)
  b3.phiB ~ dnorm( 0, 0.001 )T(-10,10)
  b3.phiC ~ dnorm( 0, 0.001 )T(-10,10)

 # Priors for mean transitions from C to E
          # just mean CE, no season or pRBT effect
  b0.psiCE ~ dnorm( 0, 0.001 )T(-10,10)
  b1.psiCE ~ dnorm( 0, 0.001 )T(-10,10)
  b2.psiCE ~ dnorm( 0, 0.001 )T(-10,10)
  b3.psiCE ~ dnorm( 0, 0.001 )T(-10,10)

# Transitions: multinomial logit
# Normal priors on logit of all but one transition probability
   b0.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b0.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiAB ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiAE ~ dnorm(0, 0.001)T(-10,10)
   b0.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b0.lpsiBE ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b1.lpsiBE ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b2.lpsiBE ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiBC ~ dnorm(0, 0.001)T(-10,10)
   b3.lpsiBE ~ dnorm(0, 0.001)T(-10,10)

# logit transformations of all priors
# phi's
# derive period survival estimates
  summer.phiA <- ilogit(b0.phiA)^4
  winter.phiA <- ilogit(b1.phiA)^8
  summer.phiB <- ilogit(b0.phiB)^4
  winter.phiB <- ilogit(b1.phiB)^8
  summer.phiC <- ilogit(b0.phiC)^4
  winter.phiC <- ilogit(b1.phiC)^8

# monthly survivals
  m.summer.phiA <- ilogit(b0.phiA)
  m.summer.phiB <- ilogit(b0.phiB)
  m.summer.phiC <- ilogit(b0.phiC)
  m.winter.phiA <- ilogit(b1.phiA)
  m.winter.phiB <- ilogit(b1.phiB)
  m.winter.phiC <- ilogit(b1.phiC)

# psi's
  logit(summer.psiCE) <- b0.psiCE
  logit(winter.psiCE) <- b2.psiCE

# Derive summer and winter estimates fo movement probabilities
# Constrain the transitions such that their sum is <1
     # Psi A transitions for summer and winter and pRBT
      psiAB.sum <- exp(b0.lpsiAB ) / (1 + exp(b0.lpsiAB ) + exp(b0.lpsiAE ) )
```

```
      psiAE.sum <- exp(b0.lpsiAE ) / (1 + exp(b0.lpsiAB ) + exp(b0.lpsiAE ) )
      psiAB.win <- exp(b2.lpsiAB ) / (1 + exp(b2.lpsiAB ) + exp(b2.lpsiAE ) )
      psiAE.win <- exp(b2.lpsiAE ) / (1 + exp(b2.lpsiAB ) + exp(b2.lpsiAE ) )

     # Psi B transitions for summer and winter and pRBT
      psiBC.sum <- exp(b0.lpsiBC ) / (1 + exp(b0.lpsiBC ) + exp(b0.lpsiBE ) )
               psiBE.sum <- exp(b0.lpsiBE ) / (1 + exp(b0.lpsiBC ) + exp(b0.lpsiBE ) )
      psiBC.win <- exp(b2.lpsiBC ) / (1 + exp(b2.lpsiBC ) + exp(b2.lpsiBE ) )
               psiBE.win <- exp(b2.lpsiBE ) / (1 + exp(b2.lpsiBC ) + exp(b2.lpsiBE ) )

   # calculate the last transition probability
      psiAA.sum <- ( 1 - psiAB.sum - psiAE.sum )
      psiAA.win <- ( 1 - psiAB.win - psiAE.win )
      psiBB.sum <- ( 1 - psiBC.sum - psiBE.sum )
      psiBB.win <- ( 1 - psiBC.win - psiBE.win )

   for( i in 1:nind ){
     for( t in f[i]:(when.cens[i]-1) ){

phiA[i,t] <- ilogit( b0.phiA*summer[t] + b1.phiA*winter[t] + b2.phiA*summer[t]*prbt[i] +
      b3.phiA*winter[t]*prbt[i] )^power[t]
phiB[i,t] <- ilogit( b0.phiB*summer[t] + b1.phiB*winter[t] + b2.phiB*summer[t]*prbt[i] +
      b3.phiB*winter[t]*prbt[i] )^power[t]
phiC[i,t] <- ilogit( b0.phiC*summer[t] + b1.phiC*winter[t] + b2.phiC*summer[t]*prbt[i] +
      b3.phiC*winter[t]*prbt[i] )^power[t]

    # Psi's for state C
logit(psiCE[i,t]) <- b0.psiCE*summer[t] + b1.psiCE*summer[t]*prbt[i] + b2.psiCE*winter[t] +
      b3.psiCE*winter[t]*prbt[i]

      # Psi's for state A
psiAB[i,t] <- exp( b0.lpsiAB*summer[t] + b2.lpsiAB*winter[t] + b1.lpsiAB*summer[t]*prbt[i] +
      b3.lpsiAB*winter[t]*prbt[i] ) /
 (1 + exp(b0.lpsiAB*summer[t] + b2.lpsiAB*winter[t] + b1.lpsiAB*summer[t]*prbt[i] +
      b3.lpsiAB*winter[t]*prbt[i]) +
exp(b0.lpsiAE*summer[t] + b2.lpsiAE*winter[t] + b1.lpsiAE*summer[t]*prbt[i] + b3.lpsiAE*winter[t]*prbt[i]) )

psiAE[i,t] <- exp(b0.lpsiAE*summer[t] + b2.lpsiAE*winter[t] + b1.lpsiAE*summer[t]*prbt[i] +
      b3.lpsiAE*winter[t]*prbt[i]) /
(1 + exp(b0.lpsiAB*summer[t] + b2.lpsiAB*winter[t] + b1.lpsiAB*summer[t]*prbt[i] +
      b3.lpsiAB*winter[t]*prbt[i]) +
exp(b0.lpsiAE*summer[t] + b2.lpsiAE*winter[t] + b1.lpsiAE*summer[t]*prbt[i] + b3.lpsiAE*winter[t]*prbt[i]) )

psiAA[i,t] <- ( 1 - psiAB[i,t] - psiAE[i,t])

       # Psi's for state B
psiBC[i,t] <- exp( b0.lpsiBC*summer[t] + b2.lpsiBC*winter[t] + b1.lpsiBC*summer[t]*prbt[i] +
      b3.lpsiBC*winter[t]*prbt[i] ) /
 (1 + exp(b0.lpsiBC*summer[t] + b2.lpsiBC*winter[t] + b1.lpsiBC*summer[t]*prbt[i] +
      b3.lpsiBC*winter[t]*prbt[i]) +
exp(b0.lpsiBE*summer[t] + b2.lpsiBE*winter[t] + b1.lpsiBE*summer[t]*prbt[i] + b3.lpsiBE*winter[t]*prbt[i]))

      psiBE[i,t] <- exp(b0.lpsiBE*summer[t] + b2.lpsiBE*winter[t] + b1.lpsiBE*summer[t]*prbt[i] +
      b3.lpsiBE*winter[t]*prbt[i]) /
      (1 + exp(b0.lpsiBC*summer[t] + b2.lpsiBC*winter[t] + b1.lpsiBC*summer[t]*prbt[i] +
      b3.lpsiBC*winter[t]*prbt[i]) +
```

```
exp(b0.lpsiBE*summer[t] + b2.lpsiBE*winter[t] + b1.lpsiBE*summer[t]*prbt[i] + b3.lpsiBE*winter[t]*prbt[i]))

psiBB[i,t] <- ( 1 - psiBC[i,t] - psiBE[i,t])
    }
   }
    # Define state-transition and observation matrices
    for (i in 1:nind){
    # Define probabilities of state S(t+1) given S(t)
     for (t in f[i]:(when.cens[i]-1)){

       ps[1,i,t,1] <- phiA[i,t] * psiAA[i,t]
       ps[1,i,t,2] <- phiA[i,t] * psiAB[i,t]
       ps[1,i,t,3] <- 0
       ps[1,i,t,4] <- phiA[i,t] * psiAE[i,t]
       ps[1,i,t,5] <- 0
       ps[1,i,t,6] <- 1-phiA[i,t]

       ps[2,i,t,1] <- 0
       ps[2,i,t,2] <- phiB[i,t] * psiBB[i,t]
       ps[2,i,t,3] <- phiB[i,t] * psiBC[i,t]
       ps[2,i,t,4] <- phiB[i,t] * psiBE[i,t]
       ps[2,i,t,5] <- 0
       ps[2,i,t,6] <- 1-phiB[i,t]

       ps[3,i,t,1] <- 0
       ps[3,i,t,2] <- 0
       ps[3,i,t,3] <- phiC[i,t] * (1-psiCE[i,t])
       ps[3,i,t,4] <- phiC[i,t] * psiCE[i,t]
       ps[3,i,t,5] <- 0
       ps[3,i,t,6] <- 1-phiC[i,t]

       ps[4,i,t,1] <- 0
       ps[4,i,t,2] <- 0
       ps[4,i,t,3] <- 0
       ps[4,i,t,4] <- 0
       ps[4,i,t,5] <- 1
       ps[4,i,t,6] <- 0

       ps[5,i,t,1] <- 0
       ps[5,i,t,2] <- 0
       ps[5,i,t,3] <- 0
       ps[5,i,t,4] <- 0
       ps[5,i,t,5] <- 1
       ps[5,i,t,6] <- 0

       ps[6,i,t,1] <- 0
       ps[6,i,t,2] <- 0
       ps[6,i,t,3] <- 0
       ps[6,i,t,4] <- 0
       ps[6,i,t,5] <- 0
       ps[6,i,t,6] <- 1

       # Define probabilities of O(t) given S(t)
       po[1,i,t,1] <- pAB[t]
       po[1,i,t,2] <- 0
       po[1,i,t,3] <- 0
```

```
      po[1,i,t,4] <- 0
      po[1,i,t,5] <- 1-pAB[t]

      po[2,i,t,1] <- 0
      po[2,i,t,2] <- pAB[t]
      po[2,i,t,3] <- 0
      po[2,i,t,4] <- 0
      po[2,i,t,5] <- 1-pAB[t]

      po[3,i,t,1] <- 0
      po[3,i,t,2] <- 0
      po[3,i,t,3] <- pC[t]
      po[3,i,t,4] <- 0
      po[3,i,t,5] <- 1-pC[t]

      po[4,i,t,1] <- 0
      po[4,i,t,2] <- 0
      po[4,i,t,3] <- 0
      po[4,i,t,4] <- 1
      po[4,i,t,5] <- 0

      po[5,i,t,1] <- 0
      po[5,i,t,2] <- 0
      po[5,i,t,3] <- 0
      po[5,i,t,4] <- 0
      po[5,i,t,5] <- 1

      po[6,i,t,1] <- 0
      po[6,i,t,2] <- 0
      po[6,i,t,3] <- 0
      po[6,i,t,4] <- 0
      po[6,i,t,5] <- 1

    } #t
  } #i

  # Likelihood
  for (i in 1:nind){
    # Define latent state at first capture
    z[i,f[i]] <- y[i,f[i]]
    for (t in (f[i]+1):when.cens[i]){
      # State process: draw S(t) given S(t-1)
      z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
      # Observation process: draw O(t) given S(t)
      y[i,t] ~ dcat(po[z[i,t], i, t-1,])
    } #t
  } #i
}
```

Section S3.3 Supplemental Figures and Tables

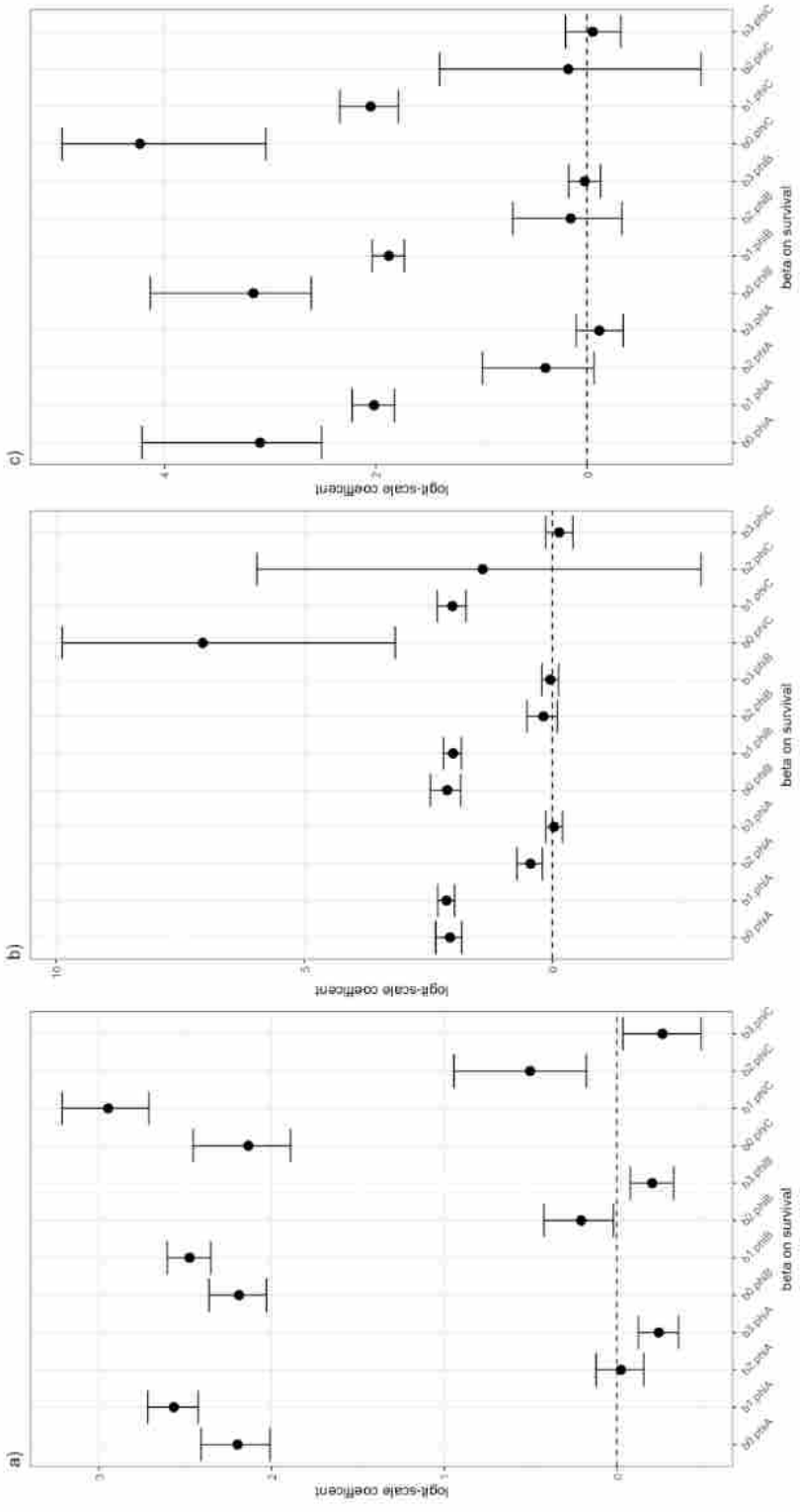

Figure S3.1: Forest plots of the mean and 95% credible intervals for coefficients on survival probabilities estimated by a Bayesian multistate Cormack-Jolly-Seber model in Cyclone (a), Langford (b), and McGee (c) creeks. Beta coefficients b0 and b1 refer to the mean summer and winter/spring monthly survival probabilities (respectively) for juveniles (PhiA), sub-adults (PhiB), and adults (PhiC). Beta coefficients b2 and b3 are the estimated effect of individual proportion RBT admixture (pRBT) on summer and winter/spring monthly survival, respectively, for each size class. If the 95% CI's on b2 or b3 overlap zero (dashed line), they were not considered significant and it was interpreted as no effect of pRBT on survival in that population/size class. In terms of pRBT effects, only b2.PhiA overlapped zero in Cyclone. In Langford, only b2.PhiA did not overlap zero, and in McGee all pRBT coefficients overlapped zero.

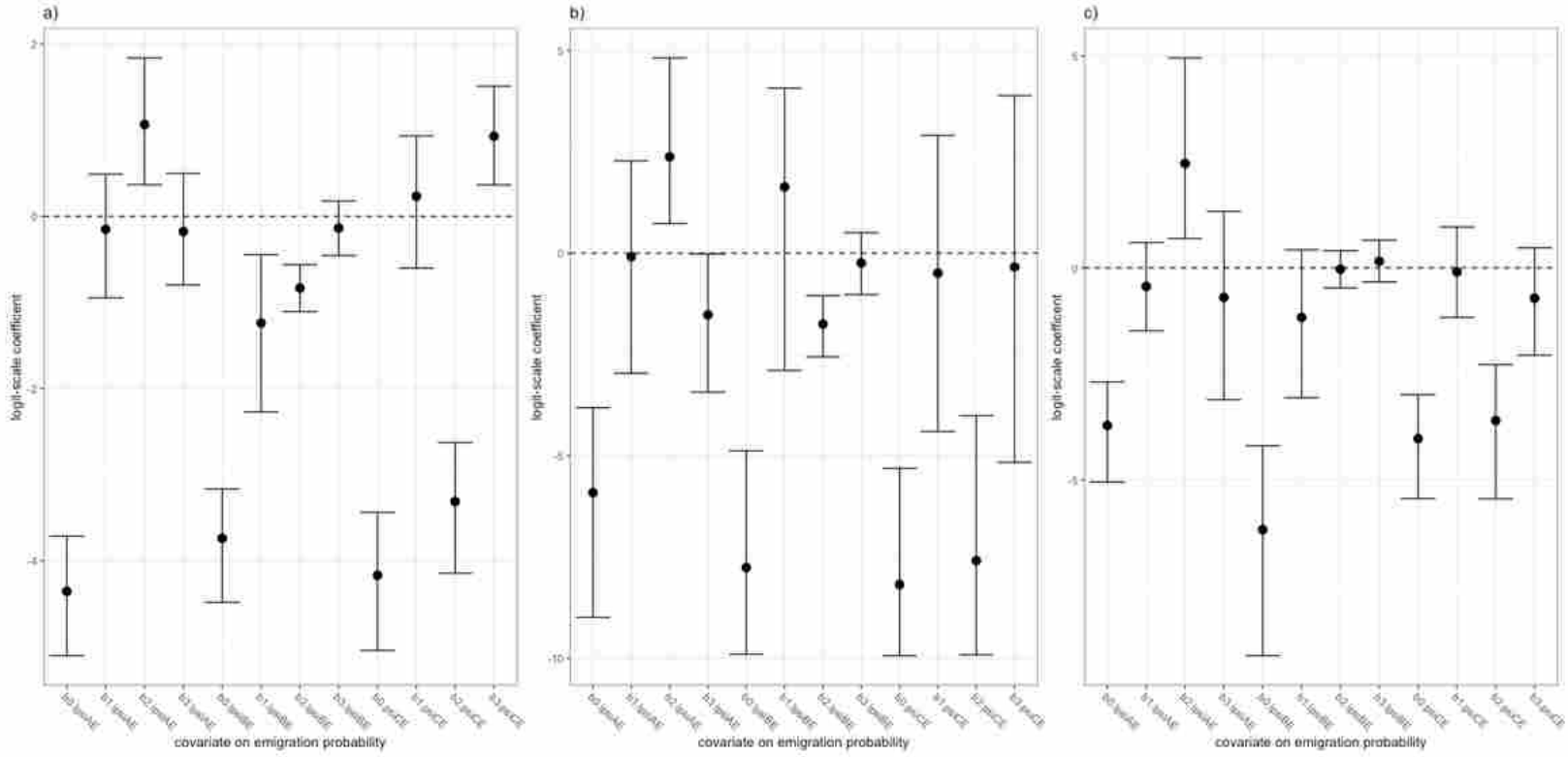

Figure S3.2: Forest plots of the mean and 95% credible intervals for coefficients on emigration probabilities estimated by a Bayesian multistate Cormack-Jolly-Seber model in Cyclone (a), Langford (b), and McGee (c) creeks. Beta coefficients b0 and b2 refer to the mean summer and winter/spring emigration probabilities (respectively) for juveniles (psiAE), sub-adults (psiBE), and adults (psiCE). Beta coefficients b1 and b3 are the estimated effect of individual proportion RBT admixture (pRBT) on summer and winter/spring emigration probability, respectively, for each size class. If the 95% CI's on b1 or b3 overlap zero (dashed line), they were not considered significant and it was interpreted as no effect of pRBT on survival in that population/size class. In terms of pRBT effects, b1.psiAE and b3.psiCE did not overlap zero in Cyclone. In Langford, only b3.psiAE did not overlap zero, and in McGee all pRBT coefficients overlapped zero.

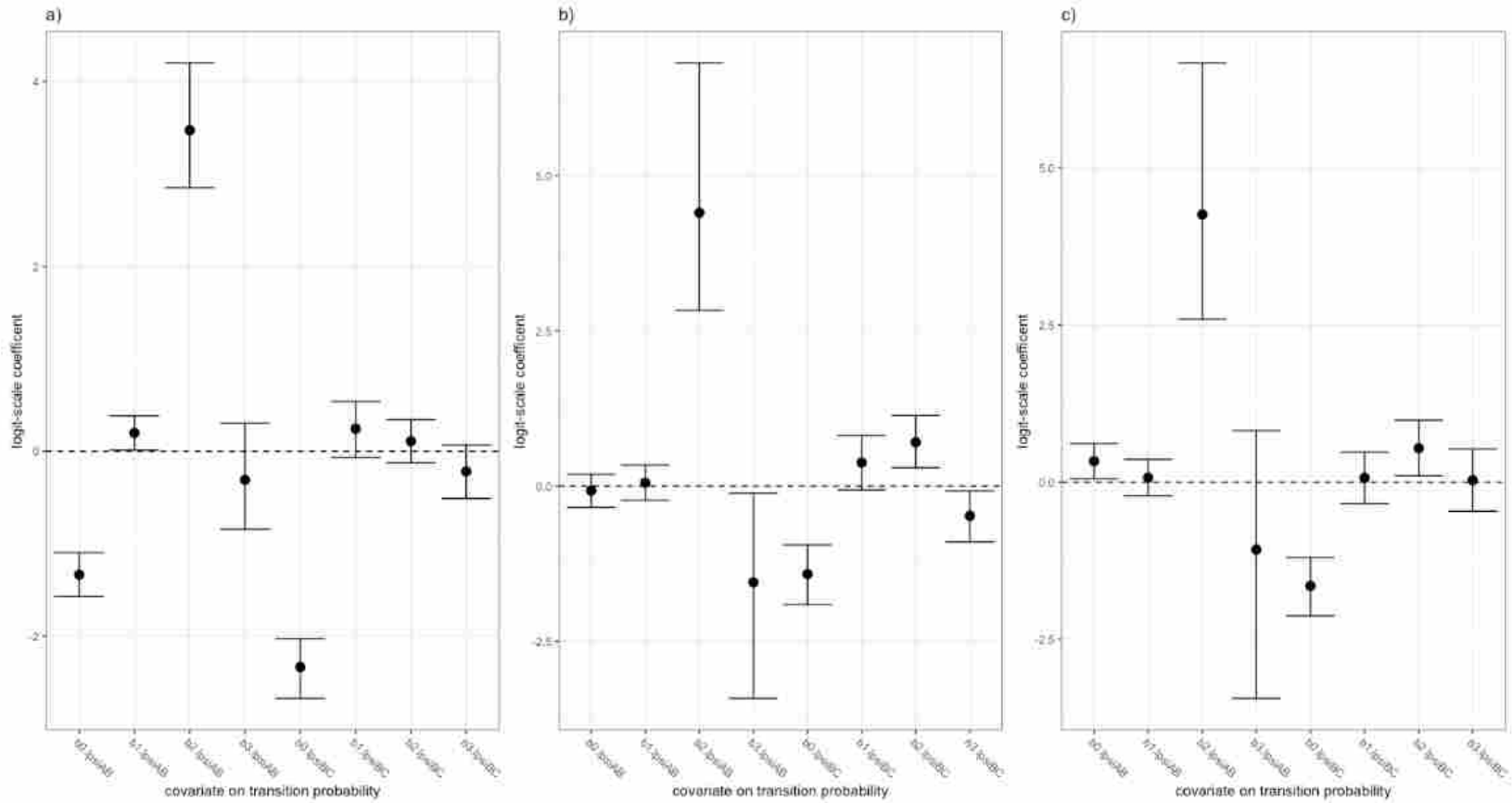

Figure S3.3: Forest plots of the mean and 95% credible intervals for coefficients on size class transition probabilities estimated by a Bayesian multistate Cormack-Jolly-Seber model in Cyclone (a), Langford (b), and McGee (c) creeks. Beta coefficients b0 and b2 refer to the mean summer and winter/spring transition probabilities (respectively) from juvenile to sub-adult (psiAB) size class and sub-adult to adult (psiBC) size class. Beta coefficients b1 and b3 are the estimated effect of individual proportion RBT admixture (pRBT) on summer and winter/spring transition probability, respectively, for each size class. If the 95% CI's on b1 or b3 overlap zero (dashed line), they were not considered significant and it was interpreted as no effect of pRBT on survival in that population/size class. In terms of pRBT effects, only b1.psiAB did not overlap zero in Cyclone. In Langford, only b3.psiAB and b3.psiBC did not overlap zero, and in McGee all pRBT coefficients overlapped zero.

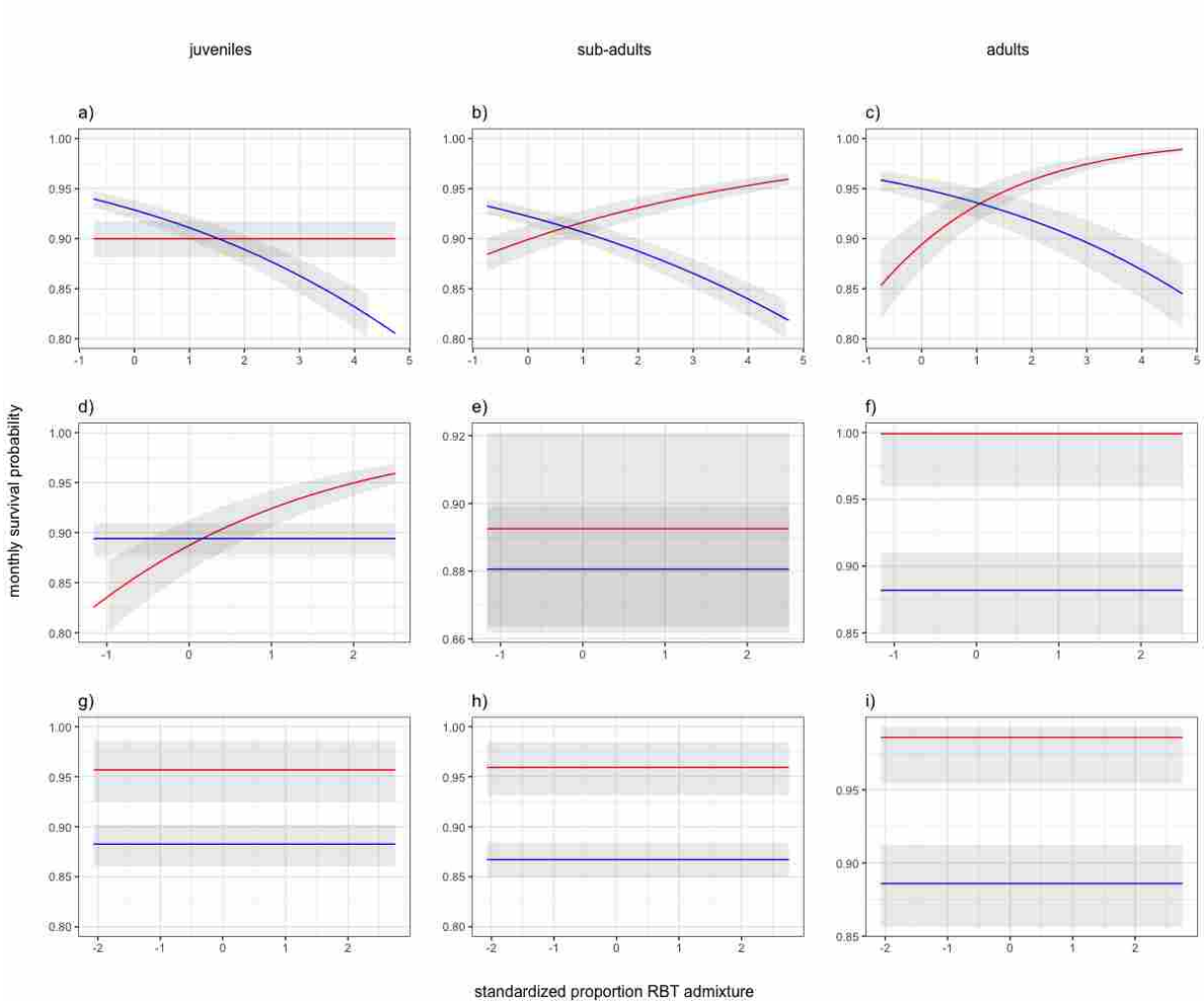

Figure S3.4: The predicted probabilities of individual proportion RBT admixture (pRBT) on monthly survival probabilities for each size class in Cyclone (top row), Langford (middle row), and McGee (bottom row) Creeks. The red and blue lines indicate summer and winter/spring relationships, respectively.

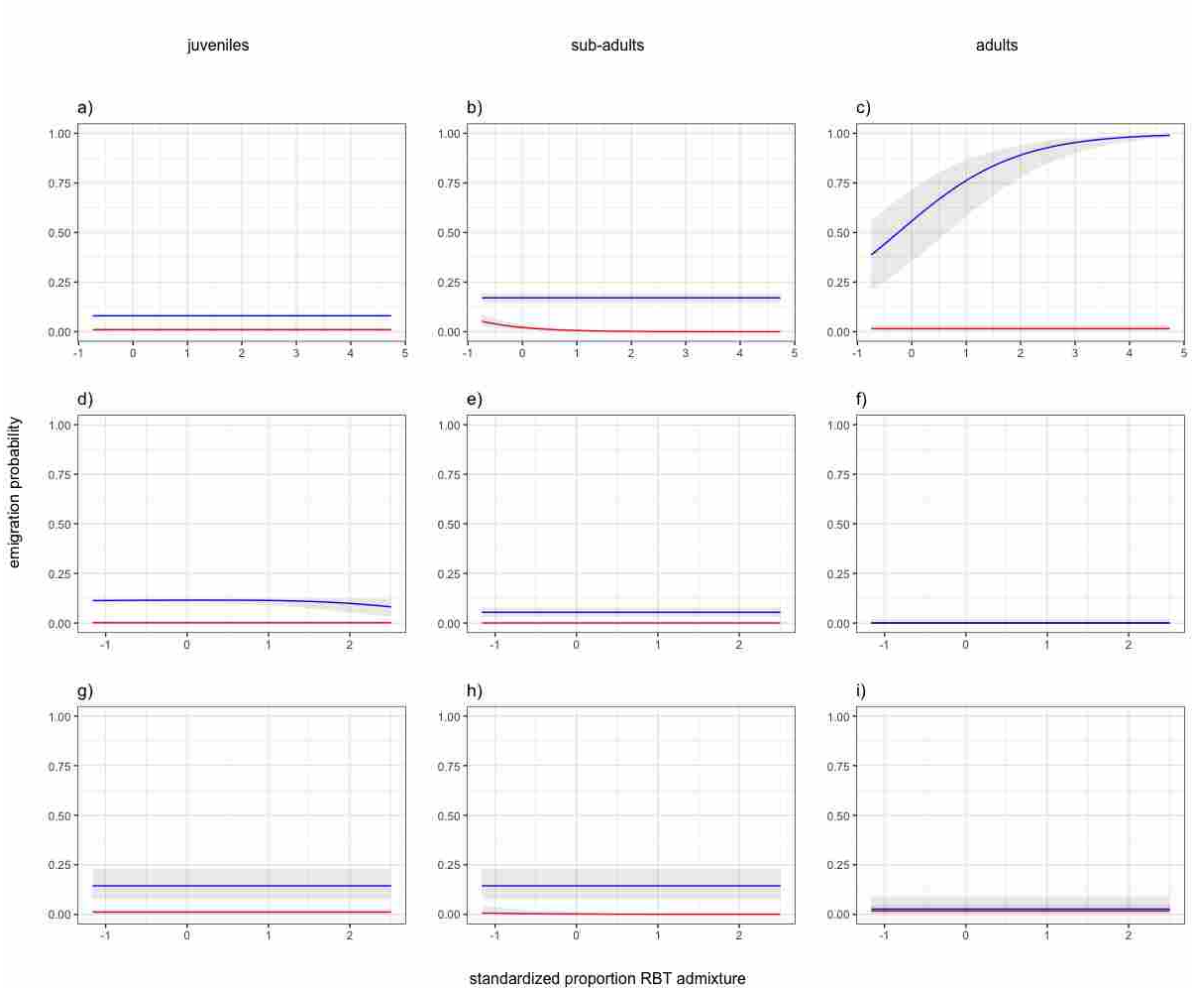

Figure S3.5: The predicted probabilities of individual proportion RBT admixture (pRBT) on emigration probabilities for each size class in Cyclone (top row), Langford (middle row), and McGee (bottom row) Creeks. The red and blue lines indicate summer and winter/spring relationships, respectively.

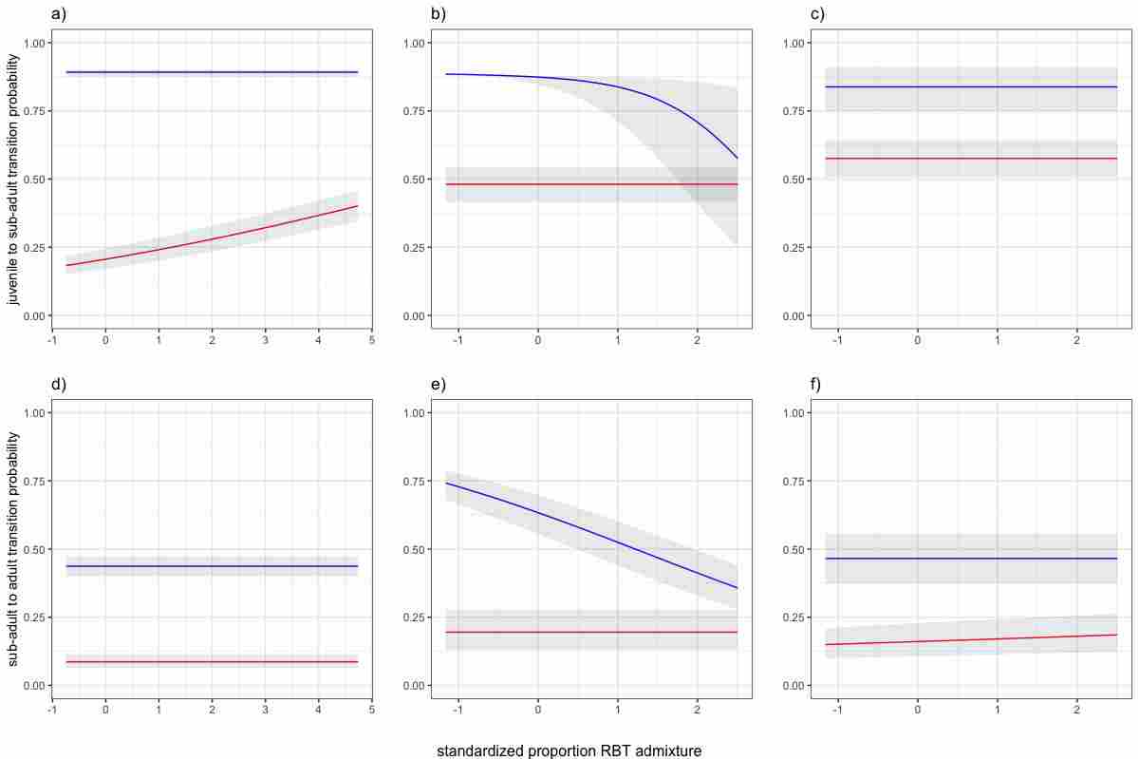

Figure S3.6: The predicted probabilities of individual proportion RBT admixture (pRBT) on size class transition probabilities for each size class in Cyclone (left column, a & d), Langford (middle column, b & e)), and McGee (right column, c & f) Creeks. The red and blue lines indicate summer and winter/spring relationships, respectively.

Table S3.1: Environmental metrics collected from 2013-2017. We measured temperature using HOBO dataloggers deployed at each study site and then calculated mean daily temperature, weekly mean temperature, growing-degree-days (GDD) during the summer, and GDD during the winter/spring period. During out MSCJS modelling, we tested for the effects of maximum weekly mean temperature on summer survival and spring GDD on winter/spring survival. In addition to temperature metrics, we estimated *Oncorhynchus spp.* abundance using multi-pass depletions and measured stream width (m) every 50m to estimate density (# fish/m^2).

population	year	Mean August temp	summer median temp	summer maximum weekly mean temp	summer GDD	spring GDD	density
Cyclone	2013	15.15	13.61	19.43	607.6	-	0.12
	2014	14.88	11.33	20.28	611.9	640	0.16
	2015	13.37	11.73	19.05	620.8	733.6	0.15
	2016	13.86	10.4	13.35	532.2	771.5	0.22
	2017	13.31	12.03	15.63	544.85	647.99	0.14
Langford	2013	19.65	10.34	15.51	407.4	-	0.16
	2014	10.58	10.24	15.08	432.1	333.4	0.13
	2015	10.99	10.66	16.32	557.2	317.5	0.08
	2016	12.28	11.45	13.26	599.4	407.2	0.08
	2017	12.10	11.9	13.31	559.75	397.3	0.13
McGee	2013	14.75	9.3*	16.76*	285.28	-	0.05
	2014	-	12.11	19.97	762.13	491.2	0.05
	2015	12.54	13.63	20.48	813.1	544.5	0.05
	2016	14.18	14.29	15.104	803.2	504.9	0.03
	2017	-	12.62	17.02	766	484.29	0.06

*HOBO Datalogger deployed in August 2013, not in July as all other measurements

Table S3.2: Estimates of abundance of *Oncorhynchus spp.* (N), standard error (se), and probability of detection (*p*) from multi-pass depletions conducted each July from 2013-2017 in each population.

population	**year**	**N**	**se**	***p***
Cyclone	2013	63.43	27.41	0.26
	2014	82.11	2.41	0.69
	2015	79.46	3.54	0.68
	2016	117.12	2.81	0.69
	2017	75.3	2.84	0.67
Langford	2013	54.3	1.17	0.75
	2014	44.6	2.56	0.61
	2015	28.74	1.77	0.57
	2016	27.59	1.21	0.74
	2017	64.82	1.23	0.77
McGee	2013	34.37	2.15	0.62
	2014	28	1.17	0.78
	2015	28.81	2.43	0.67
	2016	20.5	0.79	0.83
	2017	33.91	1.38	0.72

Table S3.3: Summary of Von Bertallanfy growth curve equation statistics (Formula: $TL \sim S_{inf} * (1 - \exp(-(K * (age - t_0))))$).

population	parameter	Estimate	Std. Error	t value	p-value
Cyclone	S_{inf}	937.456	364.529	2.572	0.010
	K	0.055	0.025	2.197	0.028
	t_0	-0.893	0.094	-9.552	<2e-16
Langford	S_{inf}	475.720	274.930	1.730	0.084
	K	0.161	0.129	1.254	0.211
	t_0	-0.397	0.213	-1.866	0.063
McGee	S_{inf}	269.381	51.222	5.259	0.000
	K	0.349	0.134	2.609	0.010
	t_0	-0.332	0.194	-1.714	0.088

Table S3.4: Summary of final MSCJS model for the final model structure tested in Cyclone Creek. The table includes the parameter means, 2.5% and 97.5% credible intervals, Gelman-Rubin diagnostic ($\widehat{R}$), effective number of estimates, an indicator if the 95% CI of the posterior distribution overlapped 0, and the proportion of the posterior distribution that shared the same sign as the mean for each covariate tested in the final model.

parameter	covariate	effect	mean	2.5%	97.5%	Rhat	n.eff	overlap0	f
p	pA	Mean	0.579	0.516	0.643	1	3851	0	1
	pBC	Mean	0.638	0.609	0.667	1	7200	0	1
$S_{juvenile}$	Beta0	Summer	2.199	2.008	2.412	1.001	2060	0	1
	Beta1	Winter	2.565	2.425	2.713	1	7200	0	1
	Beta2	pRBT (summer)	-0.022	-0.16	0.124	1.001	2409	1	0.631
	Beta3	pRBT(winter)	**-0.241**	**-0.356**	**-0.128**	**1**	**7200**	**0**	**1**
$S_{sub\text{-}adult}$	Beta0	Summer	2.189	2.028	2.361	1	7200	0	1
	Beta1	Winter	2.475	2.351	2.603	1.001	1374	0	1
	Beta2	pRBT (summer)	**0.207**	**0.021**	**0.432**	**1**	**5433**	**0**	**0.985**
	Beta3	pRBT(winter)	**-0.206**	**-0.327**	**-0.078**	**1**	**7200**	**0**	**0.999**
S_{adult}	Beta0	Summer	2.132	1.888	2.428	1	7200	0	1
	Beta1	Winter	2.946	2.71	3.214	1	7200	0	1
	Beta2	pRBT (summer)	**0.5**	**0.177**	**0.914**	**1**	**7200**	**0**	**0.999**
	Beta3	pRBT(winter)	**-0.265**	**-0.489**	**-0.036**	**1**	**7200**	**0**	**0.988**
$\Psi_{ad\text{-}E}$	Beta0	Summer	-4.17	-5.036	-3.432	1	5485	0	1
	Beta1	pRBT (summer)	0.229	-0.61	0.937	1.001	2171	1	0.74
	Beta2	winter	-3.305	-4.153	-2.619	1	6455	0	1
	Beta3	pRBT(winter)	**0.924**	**0.377**	**1.518**	**1**	**7200**	**0**	**0.999**
$\Psi_{juv\text{-}sub}$	Beta0	Summer	-1.336	-1.57	-1.097	1	7200	0	1
	Beta1	pRBT (summer)	**0.199**	**0.015**	**0.383**	**1**	**5478**	**0**	**0.983**
	Beta2	winter	3.481	2.851	4.217	1.002	6013	0	1
	Beta3	pRBT(winter)	-0.315	-0.857	0.313	1.001	4039	1	0.859
$\Psi_{juv\text{-}E}$	Beta0	Summer	-4.361	-5.135	-3.717	1.001	3784	0	1
	Beta1	pRBT (summer)	-0.143	-0.939	0.481	1	7200	1	0.63
	Beta2	winter	1.076	0.383	1.865	1.001	5611	0	0.999
	Beta3	pRBT(winter)	-0.179	-0.798	0.503	1.001	2778	1	0.716
$\Psi_{sub\text{-}ad}$	Beta0	Summer	-2.337	-2.671	-2.029	1.001	3407	0	1
	Beta1	pRBT (summer)	0.246	-0.075	0.542	1	7200	1	0.939
	Beta2	winter	0.109	-0.129	0.333	1.001	2278	1	0.819
	Beta3	pRBT(winter)	-0.218	-0.508	0.069	1	7200	1	0.933
$\Psi_{sub\text{-}E}$	Beta0	Summer	-3.751	-4.499	-3.168	1	7200	0	1
	Beta1	pRBT (summer)	**-1.252**	**-2.296**	**-0.453**	**1**	**7200**	**0**	**1**
	Beta2	winter	-0.836	-1.106	-0.562	1.001	2630	0	1
	Beta3	pRBT(winter)	-0.135	-0.46	0.181	1	7200	1	0.8

Table S3.5: Summary of final MSCJS model for the final model structure tested in Langford Creek. The table includes the parameter means, 2.5% and 97.5% credible intervals, Gelman-Rubin diagnostic ($\widehat{R}$), effective number of estimates, an indicator if the 95% CI of the posterior distribution overlapped 0, and the proportion of the posterior distribution that shared the same sign as the mean for each covariate tested in the final model.

parameter	covariate	effect	mean	2.5%	97.5%	$\widehat{R}$	n.eff	overlap0	f
p	pAB	Mean	0.734	0.672	0.789	1	7401	0	1
	pC	Mean	0.423	0.343	0.505	1.002	1343	0	1
$S_{juvenile}$	β_0	Summer	2.062	1.822	2.348	1	24000	0	1
	β_1	Winter	2.134	1.97	2.307	1	24000	0	1
	Beta2	pRBT (summer)	**0.438**	**0.199**	**0.712**	**1**	**24000**	**0**	**1**
	Beta3	pRBT(winter)	-0.036	-0.203	0.128	1	22946	1	0.664
$S_{sub\text{-}adult}$	Beta0	Summer	2.117	1.846	2.455	1.001	3745	0	1
	Beta1	Winter	1.998	1.83	2.188	1.001	1598	0	1
	Beta2	pRBT (summer)	0.177	-0.1	0.51	1	13718	1	0.885
	Beta3	pRBT(winter)	0.04	-0.127	0.206	1	4345	1	0.685
S_{adult}	Beta0	Summer	7.044	3.163	9.88	1.002	872	0	1
	Beta1	Winter	2.011	1.735	2.321	1	8849	0	1
	Beta2	pRBT (summer)	1.404	-2.997	5.951	1.001	3785	1	0.688
	Beta3	pRBT(winter)	-0.143	-0.42	0.131	1	9093	1	0.849
$\Psi_{ad\text{-}E}$	Beta0	Summer	-8.178	-9.935	-5.308	1	24000	0	1
	Beta1	pRBT (summer)	-0.493	-4.404	2.908	1	24000	1	0.573
	Beta2	winter	-7.59	-9.911	-4.011	1	9026	0	1
	Beta3	pRBT(winter)	-0.343	-5.165	3.887	1	24000	1	0.527
$\Psi_{juv\text{-}sub}$	Beta0	Summer	-0.074	-0.343	0.191	1	24000	1	0.706
	Beta1	pRBT (summer)	0.053	-0.229	0.339	1	24000	1	0.644
	Beta2	winter	4.399	2.826	6.81	1.004	1394	0	1
	Beta3	pRBT(winter)	**-1.55**	**-3.418**	**-0.118**	**1.003**	**1309**	**0**	**0.984**
$\Psi_{juv\text{-}E}$	Beta0	Summer	-5.911	-8.99	-3.815	1	24000	0	1
	Beta1	pRBT (summer)	-0.086	-2.966	2.278	1	24000	1	0.5
	Beta2	winter	2.377	0.729	4.816	1.003	1499	0	1
	Beta3	pRBT(winter)	**-1.523**	**-3.431**	**-0.019**	**1.003**	**1350**	**0**	**0.977**
$\Psi_{sub\text{-}ad}$	Beta0	Summer	-1.417	-1.907	-0.948	1	6868	0	1
	Beta1	pRBT (summer)	0.377	-0.062	0.813	1	24000	1	0.957
	Beta2	winter	0.705	0.295	1.134	1.001	1722	0	1
	Beta3	pRBT(winter)	**-0.48**	**-0.899**	**-0.079**	**1**	**7377**	**0**	**0.991**
$\Psi_{sub\text{-}E}$	Beta0	Summer	-7.76	-9.9	-4.879	1	23157	0	1
	Beta1	pRBT (summer)	1.634	-2.897	4.07	1	22439	1	0.862
	Beta2	winter	-1.751	-2.56	-1.051	1	24000	0	1
	Beta3	pRBT(winter)	-0.242	-1.023	0.506	1	24000	1	0.737

Table S3.6: Summary of final MSCJS model for the final model structure tested in McGee Creek. The table includes the parameter means, 2.5% and 97.5% credible intervals, Gelman-Rubin diagnostic ($\widehat{R}$), effective number of estimates, an indicator if the 95% CI of the posterior distribution overlapped 0, and the proportion of the posterior distribution that shared the same sign as the mean for each covariate tested in the final model.

parameter	covariate	effect	mean	2.5%	97.5%	Rhat	n.eff	overlap0	f
p	pAB	Mean	0.704	0.631	0.771	1.001	2958	0	1
	pC	Mean	0.423	0.344	0.506	1	24000	0	1
$S_{juvenile}$	Beta0	Summer	**3.096**	**2.514**	**4.214**	**1.005**	**1608**	**0**	**1**
	Beta1	Winter	**2.017**	**1.82**	**2.225**	**1**	**6860**	**0**	**1**
	Beta2	pRBT (summer)	0.393	-0.068	0.99	1.002	2538	1	0.955
	Beta3	pRBT(winter)	-0.118	-0.343	0.102	1	24000	1	0.85
$S_{sub-adult}$	Beta0	Summer	**3.16**	**2.611**	**4.134**	**1**	**24000**	**0**	**1**
	Beta1	Winter	**1.876**	**1.729**	**2.032**	**1**	**18080**	**0**	**1**
	Beta2	pRBT (summer)	0.155	-0.332	0.703	1	12897	1	0.739
	Beta3	pRBT(winter)	0.022	-0.129	0.172	1	7353	1	0.61
S_{adult}	Beta0	Summer	**4.234**	**3.042**	**4.97**	**1**	**5051**	**0**	**1**
	Beta1	Winter	**2.05**	**1.786**	**2.341**	**1**	**17926**	**0**	**1**
	Beta2	pRBT (summer)	0.177	-1.079	1.395	1	24000	1	0.6
	Beta3	pRBT(winter)	-0.054	-0.319	0.203	1	14400	1	0.657
Ψ_{ad-E}	Beta0	Summer	-4.03	-5.44	-2.994	1.001	4436	0	1
	Beta1	pRBT (summer)	-0.095	-1.171	0.963	1	24000	1	0.571
	Beta2	winter	-3.603	-5.448	-2.285	1	24000	0	1
	Beta3	pRBT(winter)	-0.717	-2.064	0.471	1	24000	1	0.874
$\Psi_{juv-sub}$	Beta0	Summer	0.333	0.052	0.616	1	24000	0	0.99
	Beta1	pRBT (summer)	0.071	-0.216	0.362	1	13767	1	0.685
	Beta2	winter	4.258	2.592	6.671	1.004	759	0	1
	Beta3	pRBT(winter)	-1.075	-3.442	0.82	1.003	935	1	0.835
Ψ_{juv-E}	Beta0	Summer	-3.718	-5.05	-2.692	1	18463	0	1
	Beta1	pRBT (summer)	-0.439	-1.487	0.592	1	24000	1	0.802
	Beta2	winter	2.46	0.692	4.948	1.004	734	0	0.998
	Beta3	pRBT(winter)	-0.699	-3.112	1.328	1.003	1019	1	0.721
Ψ_{sub-ad}	Beta0	Summer	-1.651	-2.128	-1.202	1	5233	0	1
	Beta1	pRBT (summer)	0.068	-0.339	0.479	1	24000	1	0.629
	Beta2	winter	0.541	0.099	0.984	1	24000	0	0.991
	Beta3	pRBT(winter)	0.029	-0.464	0.526	1	7215	1	0.543
Ψ_{sub-E}	Beta0	Summer	-6.174	-9.148	-4.196	1	5509	0	1
	Beta1	pRBT (summer)	-1.169	-3.064	0.423	1	8124	1	0.92
	Beta2	winter	-0.036	-0.476	0.404	1	10059	1	0.564
	Beta3	pRBT(winter)	0.153	-0.335	0.652	1	24000	1	0.727

Table S3.7: Coefficient estimates from the Bayesian multistate Cormack-Jolly-Seber model (MSCJS). Beta coefficient's that had a posterior distribution that overlapped 0 are represented by dashes (-). Values in the table represent coefficients with posterior distributions that did not overlap zero. We tested for effects of temperature and density on summer and winter monthly survival. Overall temperature had a positive effect on survival probabilities, but did not interact with proportion RBT admixture (except in the Cyclone sub-adults). Winter temperature was not supported by our MSCJS modelling.

			Cyclone		Langford		McGee	
size class	**season**	**environmental covariate**	**coefficient**	**pRBT interaction**	**coefficient**	**pRBT interaction**	**coefficient**	**pRBT interaction**
juveniles	summer	temperature	**0.446**	-	**0.557**	-	**1.075**	-
sub-adults			**0.705**	**0.405**	**0.745**	-	**1.031**	-
adults			**0.326**	-	-	-	-	-
juveniles	winter	temperature	-	-	-	-	-	-
sub-adults			-	-	-	**0.311**	**0.214**	-
adults			**-1.326**	-	-	-	-	-
juveniles	summer	density	**-0.259**	-	-	-	-	-
sub-adults			**-0.527**	**-0.398**	-	-	**0.851**	-
adults			-	-	-	-	-	-
juveniles	winter	density	**-0.237**	**0.149**	-	-	-	-
sub-adults			**0.19**	-	-	-	-	-
adults			**0.71**	-	-	-	-	-

Table S3.8: Model covariate structures tested for each parameter using a multistate Cormack-Jolly-Seber framework in *JAGS.* We tested the following covariate structures on detection probabilities (p), survival probabilities (S), and transition probabilities (Ψ) for each size class (s) and time (t).

parameter	**covariate structure**	**hypothesis**
p	$p_s \sim \text{mean}.p_s$	state-specific
	$p_{st} \sim p_{s2} + p_{s3} .. + .. p_{s10}$	time-varying
	$p_{st} \sim p_{s2013/2014} + p_{s2015\text{-}2017}$	crew effect
S	$\text{logit}(S_s) \sim S_{mean\ s}$	state-specific
	$\text{logit}(S_s) \sim S_{s1} + S_{s2} + S_{s3} .. + .. S_{s9}$	time-varying
	$\text{logit}(S_s) \sim S_{s\ summer} + S_{s\ winter}$	season
	$\text{logit}(S_s) \sim S_{mean\ s} + S_{pRBT\ s}$	pRBT
	$\text{logit}(S_s) \sim S_{s\ summer} + S_{s\ winter} + S_{s\ summer} * \text{pRBT} + S_{s\ winter} * \text{pRBT}$	season*pRBT
Ψ	$\text{logit}(\Psi_{s\text{-}s+1}) \sim \Psi_{\text{mean } s\text{-}s+1}$	state-specific
	$\text{logit}(\Psi_{s\text{-}s+1}) \sim \Psi_{\text{summer } s\text{-}s+1} + \Psi_{\text{winter } (s\text{-}s+1)}$	season
	$\text{logit}(\Psi_{s\text{-}s+1}) \sim \Psi_{\text{mean } s\text{-}s+1} + \Psi_{\text{pRBT } s\text{-}s+1}$	pRBT
	$\text{logit}(\Psi_{s\text{-}s+1}) \sim \Psi_{\text{summer } (s\text{-}s+1)} + \Psi_{\text{winter } (s\text{-}s+1)} + \Psi_{\text{summer } (s\text{-}s+1)} * \text{pRBT} + \Psi_{\text{winter } (s\text{-}s+1)} * \text{pRBT}$	season*pRBT

APPENDIX C

CHAPTER 4 SUPPLEMENTAL MATERIALS

Section S4.1 Supplemental Figures and Tables

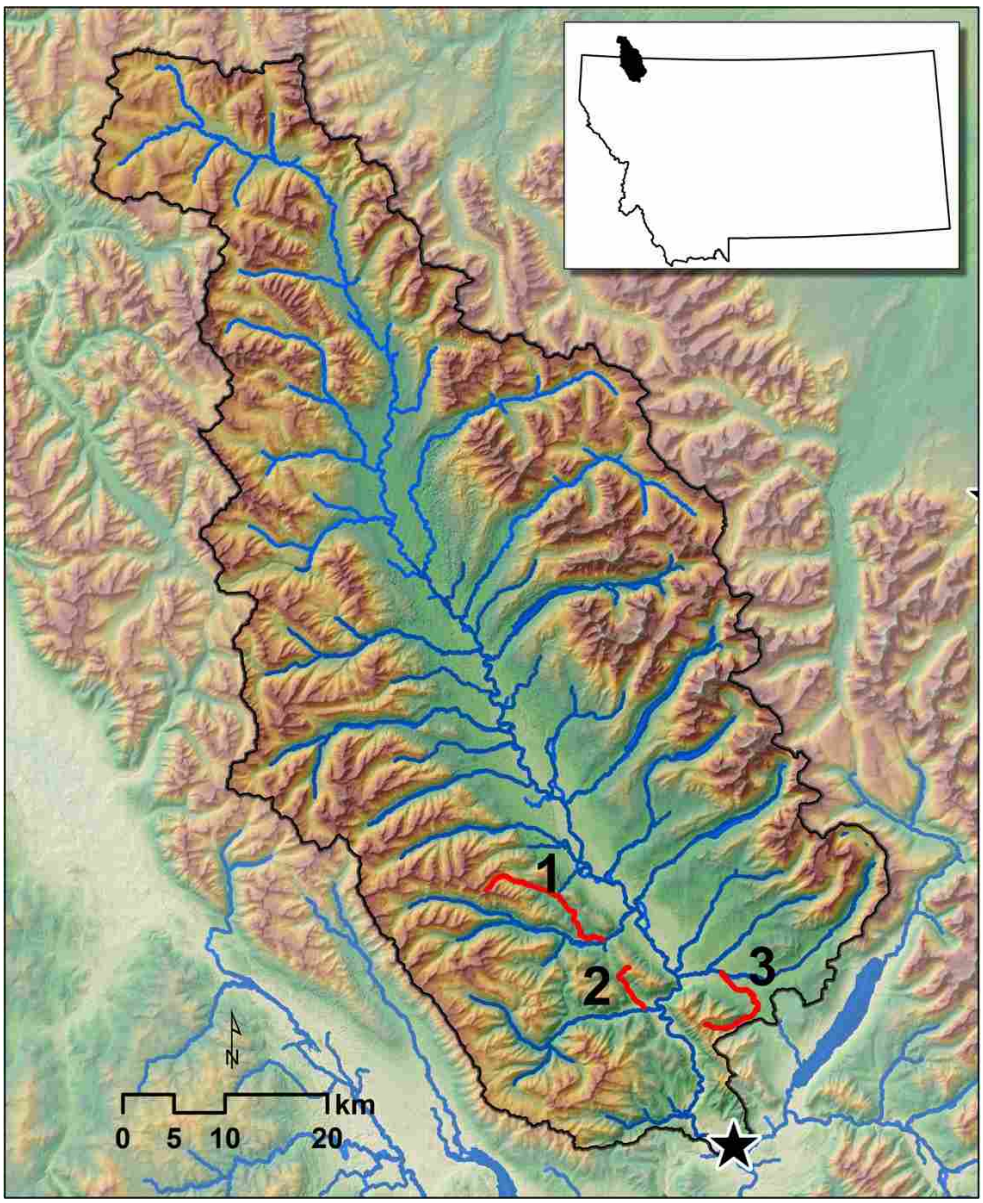

Figure S4.1: Map of our study system, the North Fork Flathead River in Northwestern Montana, USA. Study tributaries are colored red, while second order tributaries and the main stem river are blue. The black outline is the boundary of the North Fork watershed. We sampled Cyclone (1), Langford (2), and McGee (3) Creeks using a combination of seasonal backpack electrofishing and migrant fish traps to capture, tag, and recapture *Oncorhynchus ssp*. from 2013 – 2016.

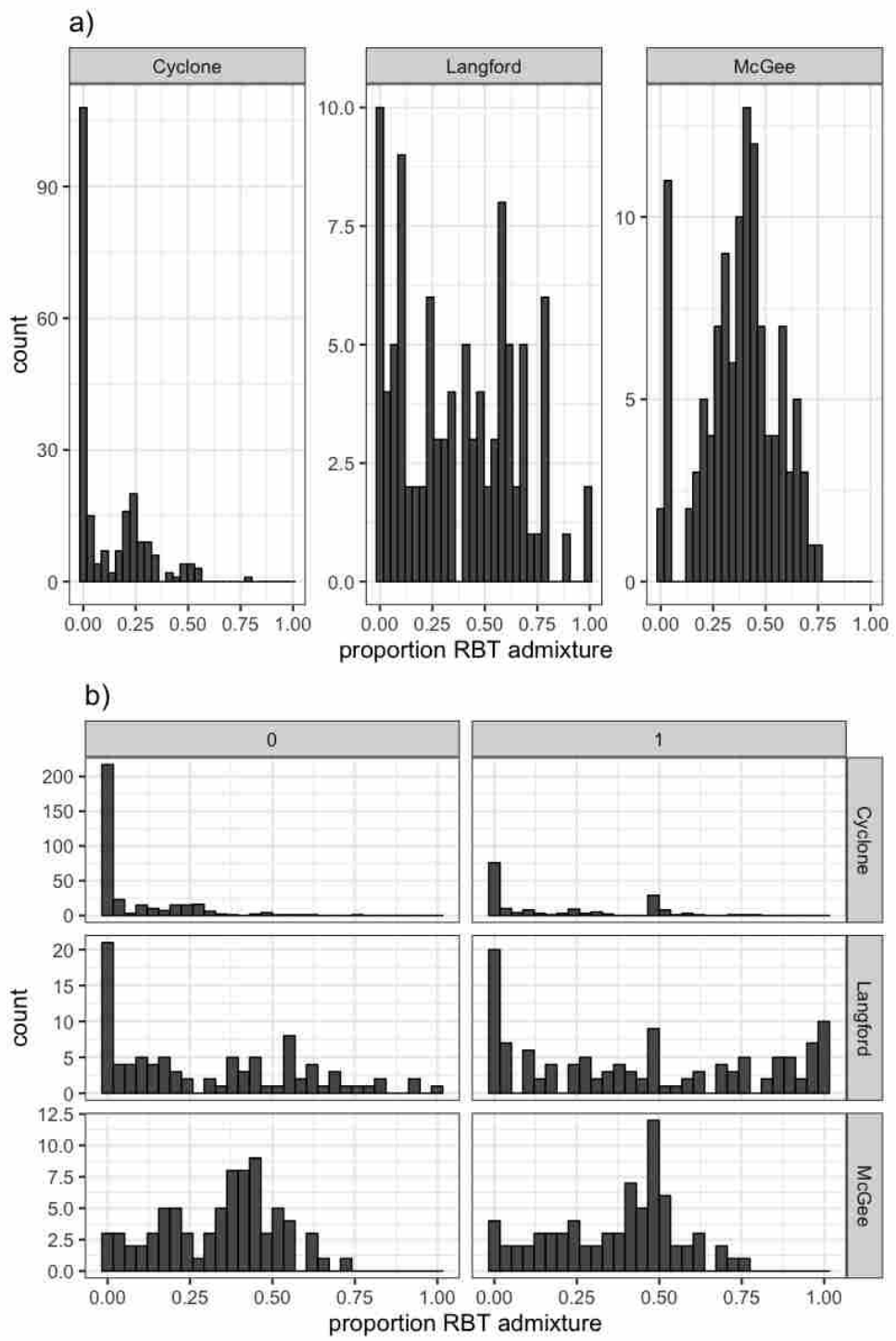

Figure S4.2: Distribution of individual proportion RBT admixture in the samples for the growth rate (a) and migratory behavior (b) genome-wide association studies for each population sampled. b) for the samples of individuals included in the migratory behavior analyses, the samples are separated by residents (0) and migrants (1).

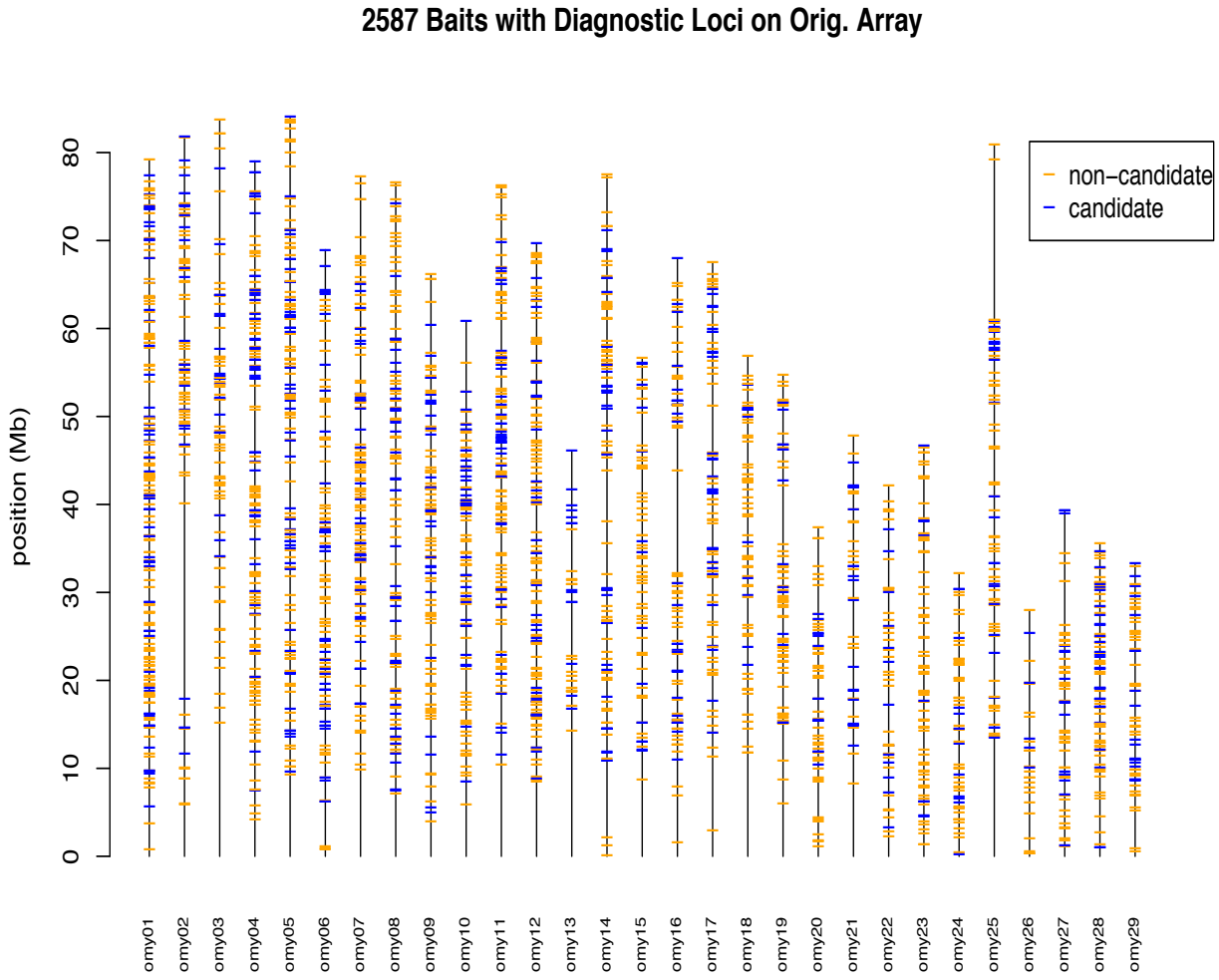

Figure S4.3: Distribution of Rapture RAD locus bait set across the rainbow trout (*Oncorhynchus mykiss*) genome assembly. The 29 chromosomes are along the x-axis and position along each chromosome on the y-axis.

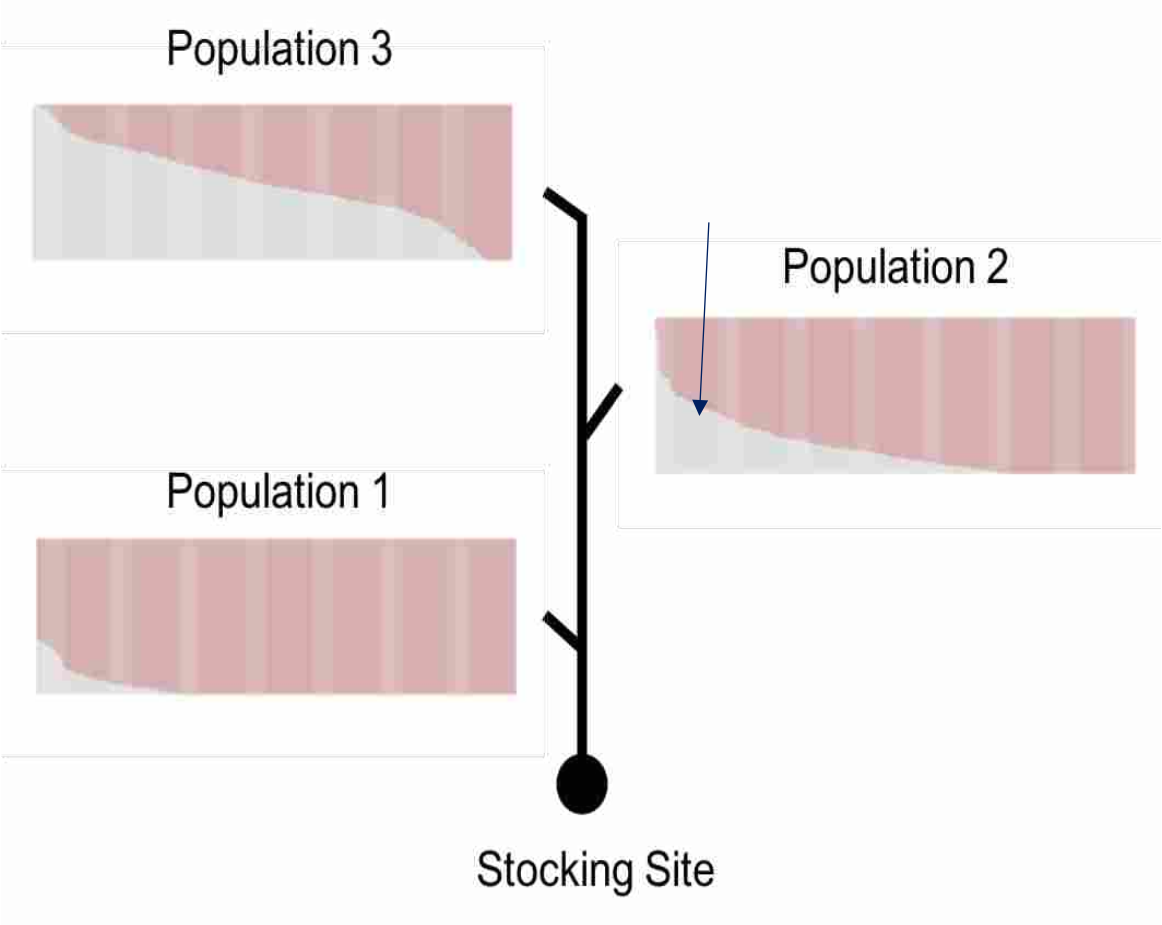

Figure S4.4: Map of simulated river system from *admixRiver* package (Kardos, unpublished). A visual representation of the simulated river network, demonstrating the admixture between native and non-native alleles after 8 generations. Each population had 2000 individuals with varying levels of admixture, represented by the histogram. Each vertical bar (see arrow) is an individual's genome, where the red portion is due to non-native fish ancestry, and grey represents native genetic ancestry. The arrow shows an individual with approximately 50% rainbow (red) and 50% WCT (grey).

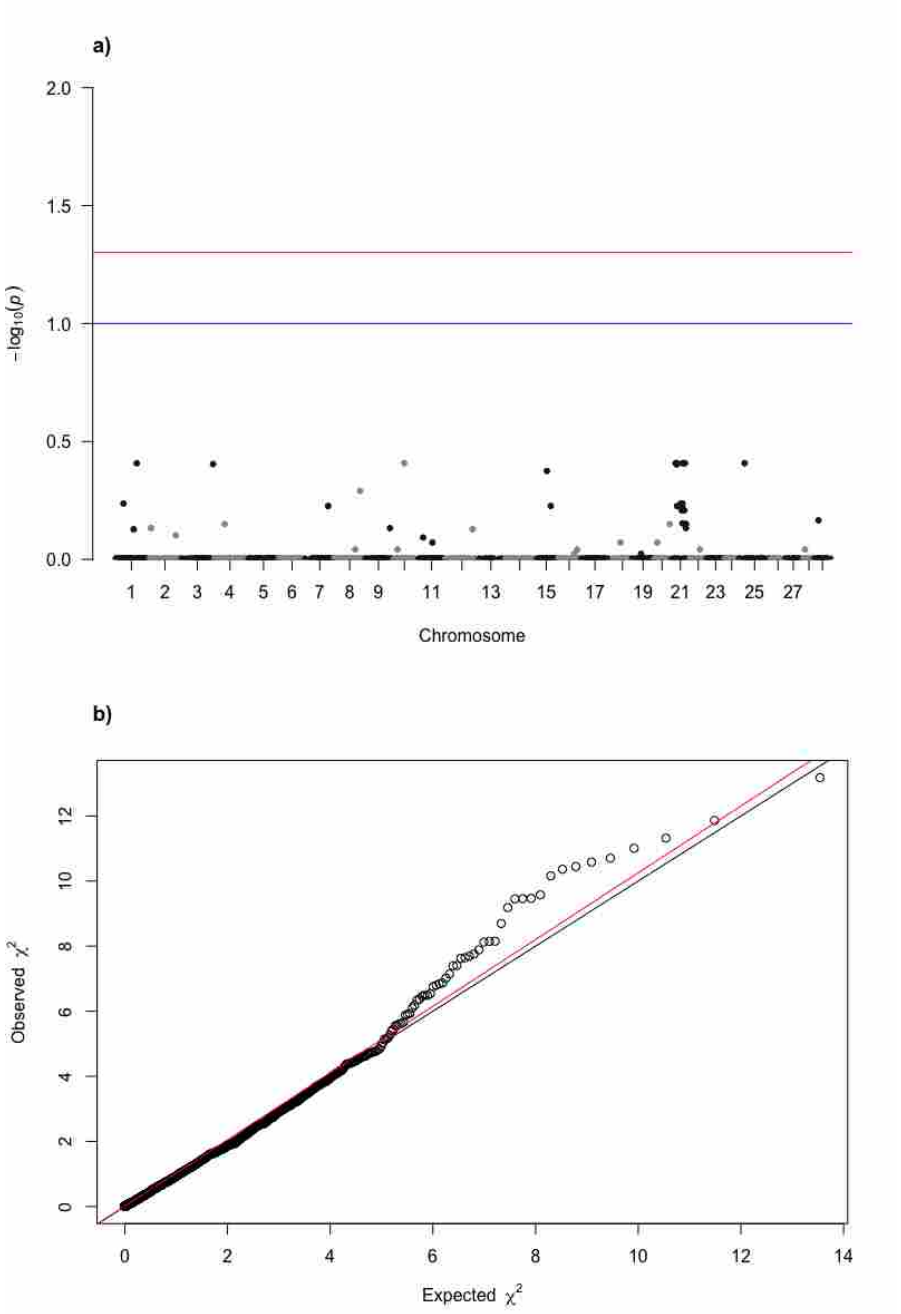

Figure S4.5: (a) Manhattan plot of the genome-wide association scan for loci associated with growth rate after correcting for population substructure using the eigenstrat method (Price et al. 2006) from a genomic kinship matrix. P-values were corrected for multiple testing using a false discovery rate (FDR) for the 2142 loci. The red and blue lines indicate genome-wide significance levels equivalent to $p = 0.05$ and p = 0.10, respectively, after the FDR was applied to p-values. Point colors alternate by chromosome. (b) The distribution of the observed test statistic (χ^2) over the expected χ^2 if growth was not affected by variation at any loci. The slope of this relationship is the estimate of genomic ($\lambda = 1.03$).

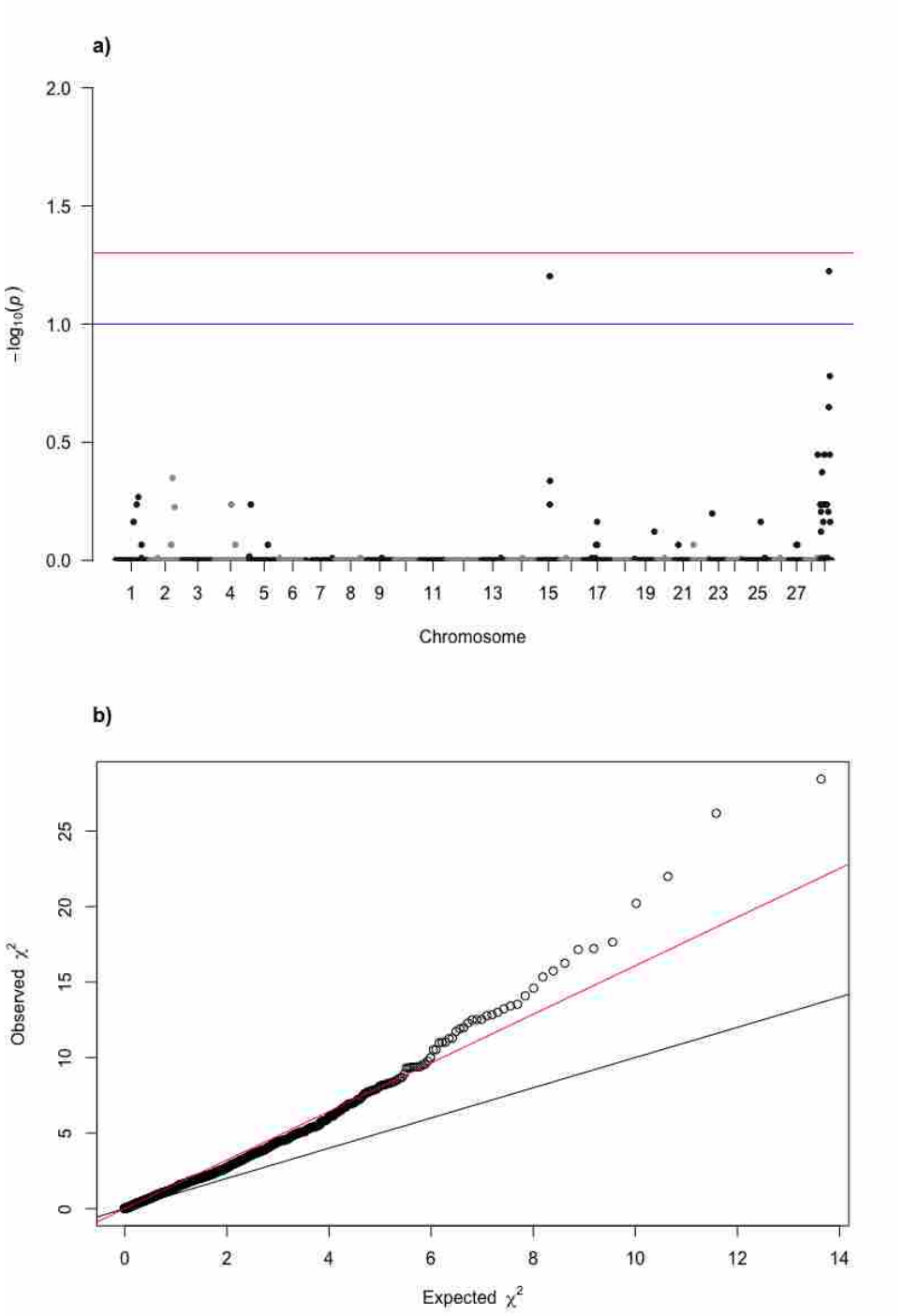

Figure S4.6: Manhattan plot of genome-wide association scan for loci (dots) associated with migratory life history behavior after removing all known females (n =112). (b) The distribution of the observed test statistic (χ^2) over the expected χ^2 if migratory behavior was not affected by variation at any loci. The slope of this relationship is the estimate of genomic (λ = 1.61).

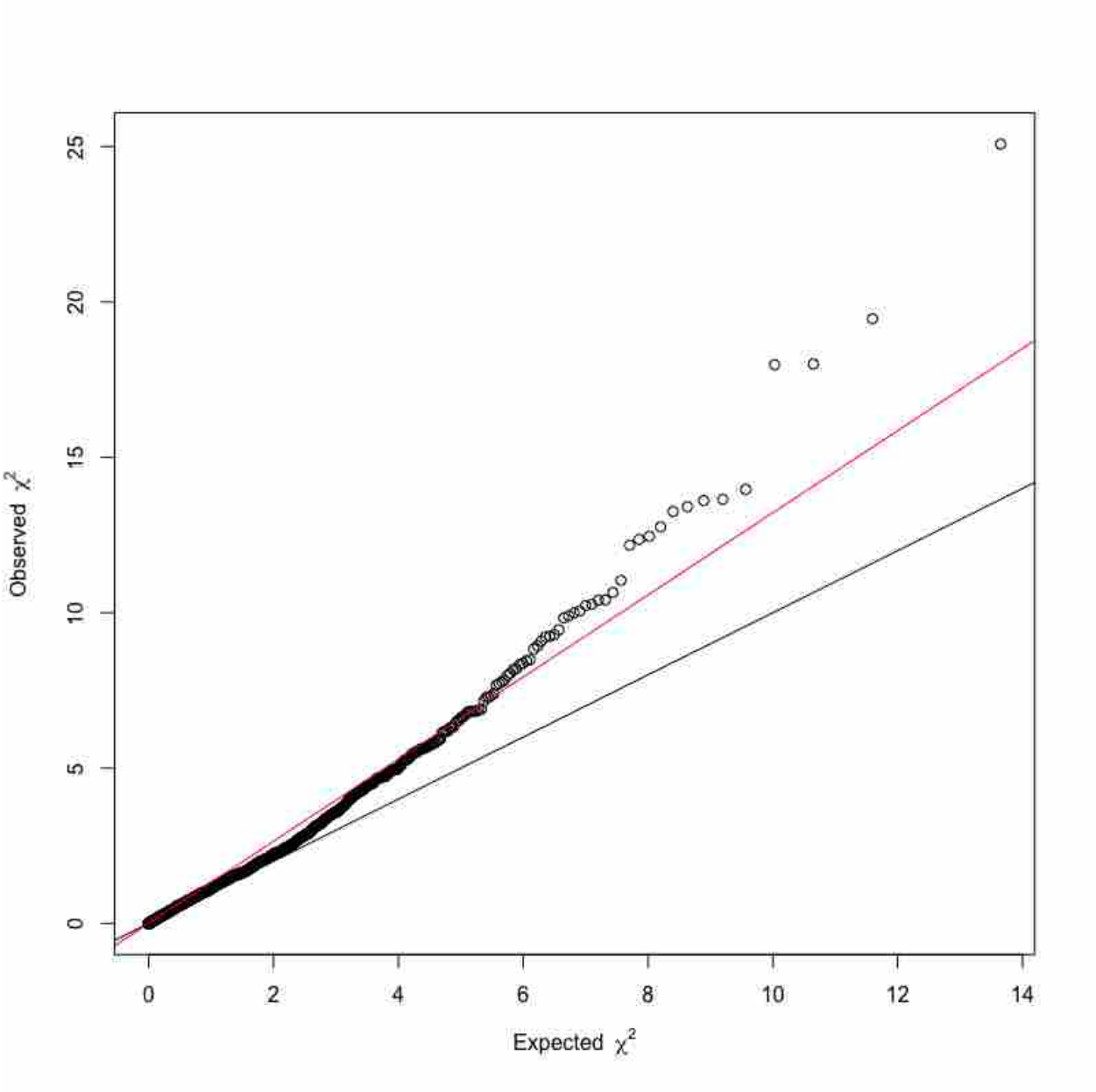

Figure S4.7: The distribution of the observed test statistic (χ^2) over the expected χ^2 if migratory behavior was not affected by variation at any loci. The slope of this relationship is the estimate of genomic (λ = 1.32).

Table S4.1: Sample sizes of individuals (n) in growth GWAS and the mean (standard deviation) daily growth rate (mm/d; growth rate), length at first capture (length), and proportion RBT admixture (pRBT) for each populations and the whole combined dataset.

population	n	growth rate	length	pRBT
Cyclone	218	0.007 (0.035)	114.05 (21.5)	0.12 (0.156)
Langford	98	0.183 (0.084)	117.43 (21.14)	0.37 (0.27)
McGee	119	0.145 (0.065)	122.38 (18.58)	0.374 (0.181)
All	435	0.119 (0.081)	117.08 (20.91)	0.246 (0.231)

Table S2: Total sample sizes of individuals (n), migrants, and residents in migratory behavior GWAS and the mean (standard deviation) of total length at capture (mm, length), weight at capture (g, weight), and proportion RBT admixture (pRBT) for each population and the whole combined dataset.

population	n	migrants	residents	length	weight	pRBT
Cyclone	510	169	341	219.61 (65.23)	127.31 (157.96)	0.11 (0.18)
Langford	213	121	92	219.49 (150.06)	134.64 (150.06)	0.39 (0.33)
McGee	151	74	77	212.09 (61.15)	111.71 (123.48)	0.35 (0.18)
ALL	874	364	510	218.29 (65.59)	126.35 (150.7)	0.22 (0.26)

Table S4.3: Numbers of loci distributed on each chromosome (CHR) for growth and migratory analyses. Poly is polymorphic loci (used for relatedness assessment), RBT, WCT, and YCT are rainbow-, westslope-, and Yellowstone cutthroat trout diagnostic loci.

	Migratory life history behavior					Daily summer growth rate				
CHR	**TOTAL**	**POLY**	**RBT**	**WCT**	**YCT**	**TOTAL**	**POLY**	**RBT**	**WCT**	**YCT**
1	**179**	108	31	20	20	**165**	102	30	19	14
2	**91**	52	19	9	11	**83**	48	18	7	10
3	**88**	58	18	8	4	**85**	56	18	8	3
4	**112**	73	24	9	6	**110**	72	23	9	6
5	**134**	84	34	11	5	**128**	82	33	11	2
6	**118**	71	30	13	4	**108**	66	28	13	1
7	**97**	57	20	11	9	**89**	54	20	11	4
8	**127**	75	35	12	5	**113**	70	31	12	NA
9	**89**	56	22	6	5	**80**	51	21	5	3
10	**86**	41	32	9	4	**84**	40	31	9	4
11	**105**	62	25	12	6	**96**	57	23	10	6
12	**97**	50	34	10	3	**90**	48	32	10	NA
13	**35**	19	7	6	3	**31**	18	5	6	2
14	**70**	41	18	8	3	**68**	40	18	7	3
15	**65**	37	17	7	4	**58**	33	16	7	2
16	**83**	44	20	9	10	**81**	44	20	9	8
17	**79**	48	21	6	4	**75**	44	21	6	4
18	**50**	29	13	6	2	**43**	24	13	6	NA
19	**58**	36	16	4	2	**54**	33	16	3	2
20	**61**	33	18	6	4	**57**	30	17	6	4
21	**40**	23	12	4	1	**38**	21	12	4	1
22	**46**	32	7	3	4	**41**	31	7	3	NA
23	**69**	42	19	4	4	**63**	39	17	4	3
24	**53**	30	13	7	3	**49**	27	12	7	3
25	**86**	50	19	9	8	**79**	47	18	9	5
26	**38**	19	7	6	6	**34**	19	7	6	2
27	**50**	21	19	6	4	**45**	20	18	5	2
28	**52**	22	19	7	4	**46**	22	17	6	1
29	**34**	10	17	2	5	**47**	26	16	2	3
TOTAL	**2292**	**1323**	**586**	**230**	**153**	**2140**	**1264**	**558**	**220**	**98**

Table S4.4: Parameters and values used in simulation of admixed populations in a river network from *admixRiver* package (Kardos, unpublished).

Simulation parameter	**Set value**
n populations	3
population size	2000
N stocked fish	500
n generations	8
n stocking generations	6
mean dispersal prob	0.1
max dispersal prob	0.4
age at maturity	1
maximum age	2
population age structure	0.5 : 0.3 : 0.2
n QTLs	1
n chromosomes	2
chromosome length	100 cM

Table S4.5: Power analysis results table. 500 reps of each factorial level of effect sizes, marker density, and sample sizes. The QTL affect size represents the reduction in survival probability resulting from an individual having the causal allele at the QTL. We also varied the number of fish sampled in each population (n individuals), the number of randomly sampled loci on each chromosome (n loci) in each independent simulation repetition. We then estimated the proportion of independent simulations repetitions where the QTL was successfully detected by a genome-wide association study, and the mean pRBT and QTL frequency in the simulated population after 8 generations of evolution and random mating.

QTL effect size	n individuals	n loci	Proportion detected	Mean pRBT	Mean QTL frequency	Simulation reps
-0.8	200	50	0.37	0.06	0.04	350
-0.8	200	75	0.36	0.06	0.04	350
-0.8	200	100	0.32	0.06	0.04	350
-0.8	500	50	0.71	0.06	0.04	350
-0.8	500	75	0.69	0.06	0.04	350
-0.8	500	100	0.66	0.06	0.04	350
-0.8	750	50	0.82	0.06	0.04	350
-0.8	750	75	0.78	0.06	0.04	350
-0.8	750	100	0.76	0.06	0.04	349
-0.8	1000	50	0.85	0.06	0.04	350
-0.8	1000	75	0.81	0.06	0.04	350
-0.8	1000	100	0.81	0.06	0.04	350
-0.7	200	50	0.62	0.14	0.12	350
-0.7	200	75	0.56	0.14	0.12	350
-0.7	200	100	0.55	0.14	0.12	350
-0.7	500	50	0.84	0.14	0.12	350
-0.7	500	75	0.84	0.14	0.12	350
-0.7	500	100	0.82	0.14	0.12	350
-0.7	750	50	0.92	0.14	0.12	350
-0.7	750	75	0.91	0.14	0.12	350
-0.7	750	100	0.90	0.15	0.12	350
-0.7	1000	50	0.96	0.14	0.12	349
-0.7	1000	75	0.97	0.14	0.12	349
-0.7	1000	100	0.96	0.14	0.12	349
-0.6	200	50	0.49	0.25	0.22	350
-0.6	200	75	0.51	0.25	0.22	350
-0.6	200	100	0.48	0.26	0.22	350
-0.6	500	50	0.89	0.25	0.22	350
-0.6	500	75	0.87	0.25	0.22	350
-0.6	500	100	0.85	0.25	0.22	350
-0.6	750	50	0.98	0.25	0.22	350
-0.6	750	75	0.95	0.25	0.22	350
-0.6	750	100	0.94	0.25	0.22	350
-0.6	1000	50	0.97	0.25	0.22	349
-0.6	1000	75	0.99	0.25	0.22	350
-0.6	1000	100	0.99	0.25	0.22	349
-0.5	200	50	0.25	0.35	0.32	350
-0.5	200	75	0.22	0.35	0.32	350
-0.5	200	100	0.18	0.36	0.32	350
-0.5	500	50	0.66	0.36	0.32	350
-0.5	500	75	0.59	0.36	0.32	350
-0.5	500	100	0.58	0.36	0.32	350
-0.5	750	50	0.83	0.35	0.32	350
-0.5	750	75	0.78	0.35	0.32	350
-0.5	750	100	0.80	0.36	0.32	350
-0.5	1000	50	0.94	0.36	0.32	350
-0.5	1000	75	0.91	0.36	0.32	350
-0.5	1000	100	0.91	0.36	0.32	350
-0.4	200	50	0.08	0.44	0.41	350
-0.4	200	75	0.08	0.44	0.41	350
-0.4	200	100	0.08	0.44	0.41	350
-0.4	500	50	0.27	0.44	0.41	350
-0.4	500	75	0.23	0.44	0.41	350
-0.4	500	100	0.28	0.44	0.41	350
-0.4	750	50	0.47	0.44	0.41	350

-0.4	750	75	0.50	0.44	0.41	350
-0.4	750	100	0.48	0.44	0.41	350
-0.4	1000	50	0.59	0.44	0.41	350
-0.4	1000	75	0.57	0.44	0.41	350
-0.4	1000	100	0.57	0.44	0.41	350
-0.3	200	50	0.03	0.51	0.48	350
-0.3	200	75	0.04	0.51	0.48	350
-0.3	200	100	0.03	0.51	0.49	350
-0.3	500	50	0.09	0.51	0.48	350
-0.3	500	75	0.11	0.51	0.48	350
-0.3	500	100	0.09	0.51	0.49	350
-0.3	750	50	0.18	0.51	0.49	350
-0.3	750	75	0.17	0.51	0.48	350
-0.3	750	100	0.16	0.51	0.48	350
-0.3	1000	50	0.25	0.51	0.48	350
-0.3	1000	75	0.26	0.51	0.49	349
-0.3	1000	100	0.23	0.51	0.48	348
-0.2	200	50	0.01	0.56	0.55	350
-0.2	200	75	0.01	0.56	0.55	350
-0.2	200	100	0.01	0.56	0.55	350
-0.2	500	50	0.03	0.56	0.55	350
-0.2	500	75	0.02	0.56	0.54	350
-0.2	500	100	0.01	0.56	0.54	350
-0.2	750	50	0.03	0.56	0.55	350
-0.2	750	75	0.04	0.56	0.55	350
-0.2	750	100	0.02	0.56	0.55	350
-0.2	1000	50	0.05	0.56	0.55	350
-0.2	1000	75	0.06	0.56	0.55	349
-0.2	1000	100	0.05	0.56	0.55	349

Table S4.6: Model structures tested and the genomic inflation of the test statistic from each model in the GWAS of growth rate. We tested model structures that included fixed effects for individual total length (TL, mm), year of capture (year), and population of capture. We ran GWAS in each population independently and all populations together (ALL). Finally, we tested different genomic random effects structures using the *eigenstrat* method (Price et al. 2006) or the full genomic kinship matrix. We considered the results from the model (bold and underlined) that best reduced the genomic inflation factor (λ).

population	model form	random genetic effect	λ	notes
Cyclone	growth ~ TL	none	1.84	
	growth ~ TL + year	none	2.5	
	growth ~ TL	eigenstrat	1.66	
	growth ~ TL + year	eigenstrat	1.34	
	growth ~ TL	genomic kinship	1.46	
	growth ~ TL + |year	genomic kinship	1.84	
Langford	growth ~ TL	none	1	lambda < 1
	growth ~ TL + year	none	1	lambda < 1
	growth ~ TL	eigenstrat	1	lambda < 1
	growth ~ TL + year	eigenstrat	1	lambda < 1
	growth ~ TL	genomic kinship	1	lambda < 1
	growth ~ TL + year	genomic kinship	1	lambda < 1
McGee	growth ~ TL	none	1.13	
	growth ~ TL + year	none	1.12	
	growth ~ TL	eigenstrat	1	lambda < 1
	growth ~ TL + year	eigenstrat	1	lambda < 1
	growth ~ TL	genomic kinship		lambda < 1
	growth ~ TL + year	genomic kinship	1	lambda < 1
ALL	growth ~ TL + population	none	1.51	
	growth ~ TL + year + population	none	1.44	
	growth ~ TL + population	**eigenstrat**	**1.03**	
	growth ~ TL + year + population	**eigenstrat**	**1.03**	
	growth ~ TL + population	genomic kinship	1.17	
	growth ~ TL + year + population	genomic kinship	1.23	

Table S4.7: Model structures tested and the genomic inflation of the test statistic from each model in the GWAS of migratory behavior. We tested model structures that included fixed effects for individual total length (mm), weight (g), and population of capture. We ran GWAS in each population independently and all populations together (ALL). Finally, we tested different genomic random effects structures using the *eigenstrat* method (Price et al. 2006) or the full genomic kinship matrix. We considered the results from the model (bold and underlined) that best reduced the genomic inflation factor (λ).

population	model form	random genetic effect	λ	notes
Cyclone	mig ~ total length	none	3.18	
	mig ~ weight	none	3.22	
	mig ~ total length	eigenstrat	1	lambda < 1
	mig ~ weight	eigenstrat	1	lambda < 1
	mig ~ total length	genomic kinship	2.17	
	mig ~ weight	genomic kinship	2.51	
Langford	mig ~ total length	none	2.49	
	mig ~ weight	none	1.95	
	mig ~ total length	eigenstrat	1.25	
	mig ~ weight	eigenstrat	1.23	
	mig ~ total length	genomic kinship	1.06	
	mig ~ weight	genomic kinship	1.01	
McGee	mig ~ total length	none	1	lambda < 1
	mig ~ weight	none	1.16	
	mig ~ total length	eigenstrat	1	lambda < 1
	mig ~ weight	eigenstrat	1	lambda < 1
	mig ~ total length	genomic kinship	1	lambda < 1
	mig ~ weight	genomic kinship	1.02	
ALL	mig ~ total length + population	none	3.2	
	mig ~ weight + population	none	3.56	
	mig ~ total length + population	eigenstrat	1.65	
	mig ~ weight + population	eigenstrat	1.71	
	mig ~ total length + population	**genomic kinship**	**1.32**	
	mig ~ weight + population	genomic kinship	1.37	

Table S4.8: Supported models considered in our AICc model selection for migratory life history expression in Cyclone (a), Langford (b), and McGee (c) creeks. Models are ranked by AICc. We also tested a mixed-effects framework, where we included a random effect of population (d). The models below are ranked by AICc. Coefficients are shown for models that contain covariates for year, relative condition factor (K), proportion RBT admixture (pRBT), total length (TL), and any combination of interactions between these covariates that were supported. The coefficient for the intercepts are also shown (INT) and the number of parameters (PAR) for each model. The top model is bold and underlined.

a)

INT	K	pRBT	TL	year	K * pRBT	TL * pRBT	omy29 28901336	PAR	logLik	AICc	delta	weight
3.795	**-1.176**		**1.755**	**+**			**+**	**8**	**-190.499**	**397.294**	**0.000**	**0.370**
2.821	-1.221	0.294	1.724	+			+	9	-189.823	398.017	0.723	0.258
3.697	-1.229	0.247	1.735	+		0.311	+	10	-189.029	398.512	1.218	0.201
3.881	-1.255	0.329	1.773	+	-0.183	0.424	+	11	-188.581	399.707	2.413	0.111
-0.019	-1.267	0.527	1.663	+				7	-194.469	403.162	5.868	0.020
-0.019	-1.267	0.527	1.663	+				7	-194.469	403.162	5.868	0.020
0.058	-1.276	0.557	1.683	+	-0.171			8	-193.954	404.197	6.903	0.012
0.098	-1.313	0.599	1.711	+	-0.292	0.350		9	-193.050	404.461	7.167	0.010

b)

INT	K	pRBT	TL	year	K * pRBT	TL * pRBT	omy29 28901336	PAR	logLik	AICc	delta	weight
7.774	-1.580	-0.920	3.612	+		-1.603	+	10	-45.714	112.678	0.000	0.551
7.118	**-1.502**		**3.780**	**+**			**+**	**8**	**-48.760**	**114.328**	**1.650**	**0.242**
7.847	-1.657	-0.917	3.563	+	-0.213	-1.490	+	11	-45.562	114.634	1.955	0.207
2.813	-1.604	0.230	3.570	+		-1.025		8	-64.000	144.747	32.068	0.000
2.729	-1.588	0.634	3.450	+				7	-65.700	145.977	33.299	0.000
2.812	-1.635	0.258	3.549	+	-0.150	-0.932		9	-63.887	146.711	34.033	0.000

c)

INT	K	pRBT	TL	year	K * pRBT	TL * pRBT	omy29 28901336	PAR	logLik	AICc	delta	weight
0.540	**-3.553**		**3.925**					**3**	**-35.589**	**77.350**	**0.000**	**0.303**
2.512	-3.891		4.593	+				5	-33.595	77.624	0.274	0.264
2.779	-3.961	-0.376	4.969	+				6	-32.928	78.469	1.119	0.173
0.546	-3.517		3.867				+	5	-34.671	79.804	2.454	0.089
2.706	-3.956	-0.209	4.875	+		0.384		7	-32.864	80.552	3.202	0.061
0.843	-3.554	-0.248	3.970				+	6	-34.431	81.513	4.163	0.038
2.671	-3.882	-0.313	4.722	+			+	8	-32.247	81.628	4.278	0.036
2.678	-3.927	-0.182	4.834	+	0.185	0.333		8	-32.831	82.730	5.380	0.021
2.407	-3.869	-0.057	4.633	+		0.564	+	9	-32.105	83.639	6.289	0.013
2.385	-3.843	-0.034	4.600	+	0.184	0.503	+	10	-32.073	85.906	8.556	0.004

d)

INT	K	pRBT	TL	year	K * pRBT	TL * pRBT	omy29 28901336	PAR	logLik	AICc	delta	weight
3.564	**-1.374**		**2.123**	**+**			**+**	**9**	**-300.790**	**619.803**	**0.000**	**0.601**
3.430	-1.382	0.070	2.119	+			+	10	-300.692	621.656	1.853	0.238
3.412	-1.398	0.085	2.129	+	-0.102		+	11	-300.436	623.199	3.397	0.110
3.470	-1.412	0.115	2.143	+	-0.147	0.155	+	12	-300.172	624.732	4.929	0.051
1.077	-1.444	0.407	2.105	+				8	-323.704	663.579	43.776	0.000
1.132	-1.458	0.414	2.122	+	-0.149			9	-323.111	664.435	44.632	0.000
1.139	-1.475	0.452	2.132	+	-0.206	0.186		10	-322.675	665.610	45.808	0.000