Evolutionary Ecology of Partial Migration: A Case Study from a Pacific Salmonid Fish, *Oncorhynchus mykiss*

By

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A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

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Fall 2018

Abstract

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Intraspecific diversity, or trait differences among individuals of the same species, is important for ecological interactions. Through my dissertation research, I explore the linkages between genotypes, phenotypes, and ecology in nature. I highlight partially migratory populations as systems that are ripe for understanding these linkages. Partially migratory populations are ones that are comprised of migratory and resident individuals – a strong form of intraspecific variation. There is growing appreciation that many migratory populations are in fact comprised of both migratory and resident individuals, including culturally and economically valuable populations of ungulates and salmonid fishes.

I focused on a salmonid fish native to the Pacific Rim, *Oncorhynchus mykiss*. In this system, both migratory and resident forms breed and rear in freshwater. The migratory form ("steelhead trout") then out-migrates to the ocean to feed and grow, returning to freshwater to breed. In contrast, the resident form ("rainbow trout") completes its entire life cycle in freshwater. Recent research by Pearse et al. (2014, Proc. Roy. Soc. B) revealed that the genetic basis of migration in *O. mykiss* is linked to a narrow region of the genome, which opened the door to understanding genotype-phenotype-ecology linkages. My dissertation explores these connections in partially migratory populations of *O. mykiss* in two streams, Fox and Elder Creek, which are tributaries to the South Fork Eel River in coastal Northern California.

In my first chapter, I explored the spatial distribution of migration-linked genetic variation in these streams. I predicted that small natural barriers would limit the upstream distribution of migratory genotypes, and that the effect of these barriers would be greater in dry years when there is less opportunity for adult steelhead passage. In Elder Creek, the largest barrier is a waterfall located 2 km from the mouth of the stream, and is passable under a narrow range of stream flows. In Fox Creek, the largest barrier is at the mouth. I captured fish from pools distributed longitudinally from the mouth to the upper extent of fish in each stream. I conducted RAD-capture on over 3,000 individuals and then classified these individuals as migratory, heterozygous, or resident genotypes using over 400 single nucleotide polymorphisms (SNPs) located on the migration-linked region of the genome. The partial barrier in Elder Creek reduced the frequency of migratory genotypes (migratory allele frequency of 0.60 below the barrier vs. 0.31 above the barrier). In Fox Creek, the proportion of migratory alleles varied greatly among years, ranging from 0.30-0.68. Years when migratory allele frequency was low

were also years when there was not a storm event in February, which is peak breeding season for *O. mykiss* in the South Fork Eel River, suggesting that the frequency of migratory genotypes is tied to adult steelhead access in this creek. Overall, I found that there was spatial variation in migration-linked genotypes, with migratory genotype-fish being more common below the waterfall in Elder Creek, and rare in some years in Fox Creek. Furthermore, inter-annual variation was associated with water year type (dry or wet) and the timing of rainfall events.

In my second chapter, I determined the correlation between life history genotypes and phenotypes at the individual level. I installed stationary antennas at the mouth of Fox and Elder creeks to detect individuals who expressed migration, and assigned individuals to the resident phenotype using a size threshold. I found that resident-phenotype fish were dominated by resident genotypes (55% resident, 39% heterozygous, and 6% migratory genotypes), but migratory-phenotype fish were comprised of a mix of genotypes (25% resident, 45% heterozygous, and 30% migratory genotypes). Females are more likely to express migration in salmonid systems, given that larger females are more fecund. Therefore, I predicted that including information on sex would improve our ability to explain phenotypic variation. Genetic sex typing confirmed that females were more likely to express migration: migratory-phenotype fish were 62% female while resident-phenotype fish were 79% male. This is the first study to use life history genotypes and sex to predict individual phenotypes in partially migratory *O. mykiss*.

In my third chapter, I explored the connections between genotype and aspects of ecology, including population ecology (density and size structure of *O. mykiss*) and community ecology (food chain length and trophic cascades). During fish sampling, I estimated the density and size structure of fish in study pools. I found that stream reaches dominated by migratory genotypes were characterized by double the density of juvenile fish as compared to resident-dominated reaches (0.46 vs 0.26 individuals/m^2), presumably reflecting the higher fecundity of migratory females, but half as many older fish (0.05 vs. 0.13 individuals/m^2). Furthermore, differences in size structure were linked to differences in trophic structure; stable isotope analyses revealed that larger, old fish, were feeding higher on the food web (6.1± 0.62 ‰ δ^{15}N vs for age-0 fish and 7.8 ± 0.83 ‰ δ^{15}N for older fish). Overall, pools within the migratory-dominated region were characterized by many young fish (simple size structure) and a shorter food chain than pools sampled in regions dominated by resident genotypes.

Finally, I explored how inter-annual variation in precipitation influenced two key aspects of *O. mykiss* ecology: downstream migration timing and over-summer growth. My research occurred during the multi-year drought in California and included two dry years (2014 and 2015) and two wet years (2016 and 2017). Despite large differences in overall rainfall magnitudes, out-migration timing and over-summer growth differed little among years, which highlights the value of shaded, groundwater fed streams with a water-storing lithology for the conservation of salmonid fishes in warming river systems.

Overall, my dissertation provides empirical support for linkages among genotypes, phenotypes, and ecology, while also highlighting partially migratory *O. mykiss* populations as a model system for investigating the ecological consequences of intraspecific variation. Partially migratory populations may be common systems where heritable intraspecific variation is associated with ecological change. Migration is on the decline globally, and it is important to understand the ecological consequences of shifting ratios of migratory to resident individuals.

In dedication to:

Jane and Keith Kelson

Thank you for fostering and supporting my curiosity for the natural world.

“When we try to pick out anything by itself, we find it hitched to everything else in the universe” – John Muir

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Acknowledgements

A dissertation is a collaborative effort, and I have many people to thank who have been essential in making the journey worthwhile.

First, I want to thank my adviser Stephanie Carlson. Stephanie, you have been an exceptional advisor in so many ways, and I feel so grateful to have received training from you on how to conduct relevant research in the freshwater world. You are a brilliant editor, and have pushed my writing to be as clear and as concise as possible. You have taught me to think broadly so that my work is relevant to multiple audiences. You have also helped me get the details right (although they aren't all perfect – it's not your fault!), including spending time with me in the field to set up my sampling plan and train me in catching and tagging fish. Beyond scientific training, you have been an incredibly supportive mentor. I appreciated your commitment to your students to ensure they have the resources they need to succeed.

I would also like to thank my committee members. Mary Power, you encouraged me to think beyond *O. mykiss*, and this research would not have been complete without that component. You are a stellar example of how to do field ecology. You demonstrated that it is worth it to wade chest-deep into the river for one last observation, but that it is equally important to look beyond the river and observe natural history in the field. You simultaneously bring humility and scientific curiosity to the table (or streamside invertebrate tray). Ted Grantham, you were essential in informing my work on how stream flows influence fish, and encouraged me to think more quantitatively about stream flows and stream flow management beyond fish. Ian Wang, thank you for providing guidance in the world of landscape genetics. It is a new field with a plethora of novel analyses and methods, and thank you for always encouraging and empowering me to do what I thought was right for my system. Other faculty at UC Berkeley that were essential to this dissertation include Bree Rosenblum, who served on my qualifying exam committee, and encouraged me to question my own understanding of evolution. Matt Kondolf also served on my qualifying exam committee and broadened my interest in the physical and cultural components of river restoration.

My co-authors and collaborators at UC Davis made the genetic component of this research possible. Michael Miller, thank you for your unending excitement about fish genetics, and for encouraging me to catch and analyze so many samples. Sean O'Rourke, thank you for many hours of helping me patiently in the lab. Tasha Thompson, thank you for running the bioinformatics for this project. Thank you all for being so willing to collaborate.

Many undergraduates were essential to this field intensive research project. These students moved up to the Angelo Coast Range Reserve with me for months at a time, leaving their social lives and urban comforts in the dust. We had many days where we returned to the lodge after dark, or left after dark to go night fishing, and I couldn't be more grateful for your willingness and optimism in going along with this field schedule. Cody Schaaf, Katie Kobayashi, Sohil Mali, Terrance Wang, Robbie Gould, Victoria Uva, Robert Spankowski, and Kristen

Shekelle, I could not have done it without you. Other students who helped out with this project include Betty Huang, who was essential in lab work, and Shelley Pneh, who is the bug guru.

The community at the Angelo Coast Range Reserve made field work so much fun. I will treasure the time I spent at the reserve, thanks to the Angelinos. It was invaluable to share excitement in discovering new things in the field. Our community fostered scientific creativity and curiosity. I learned so much about natural history and how various aspects of the food web fit together in the South Fork Eel River watershed thanks to interactions with other researchers at the Angelo. This community of people included Keith Bouma-Gregson, Phil Georgakakos, Gabe Rossi, and Hiromi Uno. Special thanks to Peter Steel, the reserve manager at the Angelo. It is amazing how much you do to steward the land on the reserve. Thank you for allowing a set of solar panels to sit in your view-shed in the meadow. Collin Bode was also a helpful consultant in solar panel installation and Angelo technology.

Carlson lab members and the freshwater community made UC Berkeley a vibrant place to be a freshwater scientist. Sébastien Nusslé was extremely patient in improving my skillset in statistical modelling and R. My time at Berkeley was also enriched by other post docs in the lab, including Laetitia Wilkins, Pablo Rodriguez Lozano, Michael Peterson, Anna Sturrock, and Michael Bogan. Jason Hwan, Kristina Cervantes-Yoshida, Kaua Fraiola, and Cleo Weolfle-Erskine were lab members, mentors and role models in my first few years. I am also thankful for the newer additions to the Carlson lab who have continued the tradition of fun and helped me with field work, including Jordan Wingenroth and Hana Moidu. The community at ESPM also made the graduate student journey so much more fun, and a few important friends include Claire Willing, Emily Kearney, and Joan Dudney.

Last but not least, my family has supported me in every step of my educational career. My parents, Jane and Keith Kelson, thank you for emphasizing and prioritizing the importance of education. My curiosity in natural systems is a result of you exploring the natural world yourselves and taking us outdoors as kids (and adults). Kyle Kelson, my brother, even made time between stitching people up in the hospital to hike up the stream and help sample, giving me a hard time the whole way for not packing enough granola bars. Julia Kelson, my twin sister, you are my best friend and sounding board, and you have provided endless support for so many things, including the graduate students process. Christopher Rhoades, you have been an essential part in my support network. You travelled up the Angelo with me many weekends to help me build fish antennas and solar panels, and even to help me change a flat tire in the middle of a rainy night at the Angelo. You were patient with me when I needed your support and always encouraged me to have fun and enjoy the journey.

This work was supported by a NSF Graduate Research Fellowship. The NSF CZO EAR-1331940, Eel River Critical Zone Observatory, generously funded this project and was an inspiration to connect to scientists across disciplines working in the same watershed. This dissertation was also funded by the UC Berkeley Oliver B. Lyman Wildlife and Fisheries Fund and the UC Natural Reserve System Mildred E. Mathias Award. I was also supported by the Edward A. Colman Watershed Fellowship and the Loker Foundation Graduate Award.

1

Introduction

Populations are comprised of individuals that differ in traits. Accumulating research suggests that such intraspecific variation has ecological consequences (i.e., phenotype-ecology links). For example, guppies that are found in high versus low predation environments are divergent in a suite of traits, from age and size at reproduction to morphology and body size (Travis et al. 2014), and this divergence is also associated with top-down effects on macroinvertebrates and algal standing crop (Bassar et al. 2010, 2015). Intraspecific variation can have implications for population stability (Hilborn et al. 2003, Schindler et al. 2010), food webs (Howeth et al. 2013), species coexistence (Bolnick et al. 2011, Violle et al. 2012, Hart et al. 2016), and cross-ecosystem subsidies (Jackrel and Wootton 2014). In fact, the ecological effects of intraspecific diversity can be as large or larger than species level effects (Des Roches et al. 2018).

Another body of research examines the ecological consequences of genetic variation within populations (i.e., genotype-ecology links) (Whitham et al. 2003). This research has its origins in the ‘extended phenotype’ concept (sensu Dawkins 1982), which recognizes that genotypes have effects beyond the individual level. For example, the behavior of an arboreal ant to bite onto the bottom side of a leaf before dying is the result of its parasitic fungus that positions the ant in a habitat where temperature and humidity are optimal for fungal growth (Andersen et al. 2009). Since the original framing of the extended phenotype, the definition has been expanded to include broad ecological consequences of genetic variation. Most examples of extended phenotypes come from the plant literature (Whitham et al. 2012). For example, genotypes of willows are associated with different insect herbivore communities, and the presence of multiple genotypes increases food web complexity (Barbour et al. 2016).

In this dissertation, I highlight partially migratory populations as systems that are ripe for the study of intraspecific variation and the extended phenotypic effects. Partially migratory populations include a mixture of migratory and resident individuals. Partial migration is common in migratory animals, including ungulates (Hebblewhite and Merrill 2009, Middleton et al. 2013), insects (Odermatt et al. 2017), birds (Boyle 2008, Hegemann et al. 2015), amphibians (Swingland and Lessells 1979, Grayson and Wilbur 2009), and fishes (Chapman et al. 2012). Thus, partial migration is a common form of intraspecific variation in animals, however the ecological consequences of partial migration have rarely been studied. Moreover, in some cases, the genetic underpinnings of migration is known (Liedvogel et al. 2011), opening the door to exploring the extended phenotype of partial migration.

Migration is often associated with a suite of traits, i.e., migratory syndromes (Dingle 2014), which include morphological, behavioral, and physiological traits. Moreover, migration has a suite of ecological consequences because migratory individuals link disparate ecosystems (Bauer and Hoye 2014). For example, migratory individuals can transport other organisms from donor to recipient ecosystems, such as viruses and infectious diseases (Altizer et al. 2011). Additionally, migratory organisms can serve as a prey for predators in the recipient habitat, including migratory mayflies subsidizing stream-dwelling trout (Uno and Power 2015) or migratory moths subsidizing bears (White, Jr. et al. 1998). This body of work suggests that the ratio of migratory individuals in partially migratory populations is likely linked to further ecological effects.

Partial migration is common in salmonid fishes (Jonsson and Jonsson 1993, Dodson et al. 2013). Fully anadromous fish migrate from freshwater juvenile rearing habitats to the ocean to take advantage of productive feeding habitats, and then return to freshwater to breed. Anadromous fish experience high mortality rates during the journey to and from the ocean, but they attain a much larger body size, which leads to elevated fecundity in anadromous females (Fleming and Reynolds 2003). In contrast, resident fish remain in freshwater their entire life, and experience a lower mortality rate but they are much smaller and less fecund (Jonsson and Jonsson 1993). These individual trade-offs between the cost versus benefit of migrating maintain life history polymorphisms in partially migratory populations (Hendry et al. 2003, De Leenheer et al. 2017). Migration in salmonid fishes tends to have a genetic basis (Dodson et al. 2013), which makes salmonids an ideal study system to understand genotype-phenotype-ecology links.

One species, *Oncorhynchus mykiss,* or steelhead/rainbow trout, can express an array of life history strategies, which has long fascinated and confused scientists (Shapovalov and Taft 1954, Hayes et al. 2011), leading to its original classification in the *Salmo* family, since its life history diversity closely resembles that of Atlantic salmon (*Salmo salar*). Life history strategies of *O. mykiss* can be broadly categorized into two types: migratory or resident (Kendall et al. 2014), and these are the categorizations I use throughout this dissertation. Within *O. mykiss,* the heritability of migration has long been suspected (e.g., Neave 1944, Nichols et al. 2008, Hecht et al. 2012, Berejikian et al. 2014). Recently the genetic basis of migration was linked to a narrow region of the genome (Pearse et al. 2014), which opens the door for explicitly linking genotypes to phenotypes to ecology in this system. Through this dissertation, I explore linkages from the molecular level of genotypes to the individual level of ecotypes to the broader level of population and food web ecology within natural streams.

I study these genotype-phenotype-ecology connections within two replicate tributary streams to the South Fork Eel River, Fox Creek and Elder Creek. Both of these streams are located within the UC Angelo Coast Range Reserve on the northern coast of California. They fall within a Mediterranean climate, a hallmark of which is high variability in stream flows among and within years (Cid et al. 2017). More specifically, storm events during the winter months vary greatly in timing and magnitude among years, which results in inter-annual variation in patterns of stream flow in winter. The summer months are dry, with storm events being rare, and aquatic organisms depending on the release of groundwater as summer base flows (Dralle et al. 2016).

In my first chapter, I explored how migration-linked genetic variation in *O. mykiss* is distributed in natural stream systems. I study on the longitudinal (upstream-downstream) distribution of migratory and resident genotypes in these tributary streams, with a focus on how partial barriers interact with annual precipitation patterns to determine the upstream extent of migratory genotype fish. Large barriers are known to completely exclude upstream-migrating fish, but the effect of small partial barriers is less known, despite the fact that they are common across the landscape in the form of small weirs (Newton et al. 2018), road crossings (Benton et al. 2008), or natural cascades (Carlsson and Nilsson 2011). I predicted that in wet years, there would be more opportunities for adult steelhead to make it above partial barriers – i.e., the landscape would be more permeable – and that this would lead to more migratory genotypes upstream of these landscape features. In summary, I predicted that migratory genotypes would be overall more common downstream in these watersheds, but that inter-annual variation in the permeability of partial barriers would lead to inter-annual variation in the in the upstream-distribution of migratory genotypes.

In my second chapter, I determined the relationship between genotypes and phenotypes in two partially migratory populations of *O. mykiss*. Previous research suggested a strong correlation between migratory versus resident genotype frequencies when comparing populations that are short, coastal streams, and predominantly anadromous, with populations that are above impassible barriers (dams or waterfalls) and predominantly resident (Pearse et al. 2014). However, it is unknown how well this region of the genome predicts migration in partially migratory populations. I predicted that the correlation between life history genotype and phenotype would be weaker in populations with co-occurring and intermingling resident and migratory *O. mykiss*. I included another piece of information to improve our ability to explain observed phenotypes: genetic sex. Female-biased migration in *O. mykiss* has been demonstrated in some systems (Ohms et al. 2014), and male-bias residency in others (Rundio et al. 2012). I predicted that the combination of life history genotype and sex would provide the most explanatory power when attempting to explain observed phenotype.

In my third chapter, I linked spatial and annual variation in the distribution of migratory genotypes to population and food web ecology. First, I predicted that in pools and stream regions where migratory genotypes dominated, there would be a high density of juvenile fish as a result of the high fecundity of migratory females. Additionally, I predicted that in regions where resident genotypes dominated, there would be a more complex size structure, including fewer juveniles but more old, large-bodied fish who are presumably resident fish. I predicted that food chain length would be shorter in reaches characterized by a simple size-structure (many juveniles, in the migratory-genotype reaches) and longer in reaches with more complex size structure (mix of juveniles and old fish, in the resident-genotype reaches). Specifically, I predicted that old fish would be feeding higher in the food web, comprising an additional trophic level and ultimately leading to a longer food chain length in reaches dominated by resident fish (4-levels: old fish, young fish, macroinvertebrates, and primary producers). I predicted that this additional trophic level could alter biomass at lower trophic levels via a trophic cascade by limiting biomass of young fish and thereby releasing macroinvertebrates to graze down algae. Overall, the goal of this chapter was to explore the ecological consequences of partial migration, including at the population (density and size structure of fish) and the community (food chain length and trophic level biomass) levels.

In my fourth chapter, I explored the impacts of the multi-year drought on the ecology of *O. mykiss*. Inter-annual variation in precipitation patterns can be extreme in Mediterranean climates, and the years of my field studies (2014-2017) were no exception. This time span included two years (2014 and 2015) that were the tail end of California's most extreme drought in over 21,000 years, based on analyses of tree rings (Robeson 2015, Kwon and Lall 2016), followed by two years that received higher-than-average precipitation ('wet' years), 2016 and 2017. These 'weather whiplashes,' or inter-annual volatility in precipitation patterns, where extreme dry years are followed by extreme wet years, are expected to become more common in California (Swain et al. 2018). I explored the effects of inter-annual variation in precipitation on two components of *O. mykiss* ecology: the timing of their migration in the winter/spring months and their growth in the summer months. I predicted that movement of downstream-migrating fish would coincide with precipitation events, and thus differences in the timing of storms would lead to differences in out-migration timing among years. Second, I predicted that in dry years, *O. mykiss* would have lower growth rates in the summer, which has been observed in previous flow-manipulation experiments in coastal California streams (Harvey et al. 2006).

In summary, through my dissertation research, I aimed to connect genotypes to phenotypes to ecology in nature, using partially migratory *O. mykiss* as the focal system. Partial migration is often associated with strong intraspecific variation in a suite of traits and migration is known to have strong ecological effects, suggesting that partially migratory populations are ideal for studying the ecological consequences of intraspecific variation. Full details can be found in each of the following chapters, with a final conclusion chapter where I discuss the implications of this body of research.

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2

Partial barriers influence the spatial and temporal distribution of migration-linked genotypes in a partially migratory salmonid fish

Abstract

Landscape features shape spatial patterns of animal movement and genetic divergence. While some landscape features are complete barriers to movement, other partial barriers are permeable under some environmental conditions. Such partial barriers are common in rivers in the form of small waterfalls, log jams, or culverts. The permeability of these barriers often varies with river flow and water level, which changes with precipitation. Here we explore the influence of partial barriers on the distribution of migratory genotypes in two tributaries to the South Fork Eel River, northern California, including across years with different rainfall patterns. We study *Oncorhynchus mykiss*, a partially migratory salmonid fish, with co-occurring resident and migratory forms. We genotyped >3,000 individuals using RAD-capture and used loci on the migration-linked region of the genome, Omy5, to classify individuals as resident, heterozygous, or migratory-genotypes. Across the four years of study (2014-2017) the number of days that partial barriers were passable in this system varied, with the largest waterfall on one stream being passable from 4 to 39 days. The proportion of migratory alleles decreased with distance upstream a small (17 km^2) tributary, Elder Creek ($r^2 = 0.47$-0.69 across four years). In this system, partial barriers (waterfalls and tributary confluences) discouraged up-river movement of migratory adult fish, decreasing the number of juvenile migratory alleles found upstream (e.g., 67-75% of the total migratory alleles in the watershed were downstream of the largest barrier across four years). More migratory alleles were concentrated downstream of the waterfall in dry years. In a smaller stream, Fox Creek (3 km^2), there was a high inter-annual variation in migratory allele frequencies (ranging from 30-68% migratory across four years). Overall, our results demonstrate that partial barriers can influence the spatial distribution of migratory genotypes and potential gene flow between life history forms in partially migratory populations, and that the permeability of partial barriers in streams is temporally dynamic with river flow.

Introduction

Landscape features leave a signature on patterns of species composition and genetic diversity. Barriers in the landscape such as roads (Shepard et al. 2008, Holderegger and Di Giulio 2010) or dams (Sheer and Steel 2006, Fullerton et al. 2011) can almost completely impede movement, thereby fragmenting populations, eliminating gene flow, and facilitating genetic divergence between populations (Manel and Holderegger 2013). Small barriers, or partial barriers that are permeable in some conditions, can have a similar, but lesser, effect in shaping patterns of movement and gene flow. For example, in migratory ungulates, partial barriers, like low-density roads or short fences, can reduce connectivity across the landscape by reducing the functionality of stop-overs or resources along the route, and discourage migration (Sawyer et al. 2013). The permeability of such partial barriers can change through time as environmental conditions change. For example, flooding of temporary wetlands can promote movement between otherwise disconnected wetlands for the Australian freshwater turtle (Roe et al. 2009).

Rivers are ideal systems for exploring the effects of temporal variation in barrier permeability because river flows rise and fall in response to precipitation. Partial barriers such as small waterfalls, log jams, and culverts are widespread in river systems (Meixler et al. 2009, Kemp and O'Hanley 2010). Such partial barriers can influence community structure, by limiting the upstream distribution of taxa from invertebrates (Kerby et al. 2005, Blanco and Scatena 2006) to fishes (Fausch et al. 2009), which can result in differences in species composition and abundance above and below barriers (Anderson et al. 2006, Perkin and Gido 2012). Partial barriers can also lead to genetic divergence, reflecting long term patterns of gene flow, in aquatic species, often with reduced genetic diversity above barriers (Yamamoto et al. 2004, Wofford et al. 2005, Carlsson and Nilsson 2011). Moreover, seasonal and inter-annual variation in river flow and water level may inhibit or facilitate animal movement across natural waterfalls and cascades (Powers and Orsborn 1985, Reiser et al. 2006), road culverts (Belford and Gould 1989), and weirs (Russon and Kemp 2011). The movement of up-river migrating organisms may be especially impacted by temporal variation in flow conditions at partial barriers, with low flows often limiting the ability of migratory animals to reach upstream breeding or rearing habitats, such as in the case of diadromous aquatic invertebrates (Resh 2005) and fishes (Rolls 2011).

One migratory fish species common to rivers around the northern Pacific Rim is *Oncorhynchus mykiss*. This species is partially migratory, meaning that some individuals migrate to the ocean (i.e., anadromous "steelhead" trout) whereas others complete their entire life history in freshwater (i.e., resident "rainbow" trout). In general, migratory *O. mykiss* tend to be found in lower elevation streams with easy access to the ocean, while resident *O. mykiss* tend to be found further upstream (Narum et al. 2008, Berejikian et al. 2013, Kendall et al. 2014) and in streams and lakes above impassible barriers (e.g., Thrower and Joyce 2004, Pearse et al. 2009). Migratory salmonids migrate from the ocean to freshwater to breed, and swim upstream to seek out breeding sites where their emergent juveniles will have less competition with other juveniles (Fleming and Reynolds 2003). While large barriers mark step-wise transitions between migratory and resident life history forms, it is less clear how partial barriers influence the distribution of the two forms in streams where they co-occur. The recent discovery of a migration-linked region of the genome in *O. mykiss* (Pearse et al. 2014) opened the door to exploring the influence of landscape features, such as partial barriers, on genetic diversity and distribution of the two life history forms at fine spatial and temporal scales.

Here we explored how migration-linked genetic diversity in *O. mykiss* varies through space and time in tributary streams with partial barriers to up-river migrating adult steelhead. First, we determined to what extent genetic structure reflected migration-associated (i.e., adaptive) loci vs. putatively neutral loci in partially migratory *O. mykiss*. We predicted that the majority of genetic variation within partially migratory populations would reflect migration-linked loci, since previous research has shown that resident and migratory *O. mykiss* in the same basin are closely related (Deiner et al. 2007, Clemento et al. 2009). Second, we determined how migratory vs. resident alleles were distributed longitudinally (downstream-to-upstream) within two streams. In particular, we tested if the proportion of migratory alleles decreased with stream distance, a pattern that has been observed using non-genetic methods in larger watersheds. Third, we explored the influence of partial barriers, including natural waterfalls and tributary confluences, on up-river migrating adults, using the number of juvenile migratory alleles as an indicator of adult upstream passage ability. We predicted that each of partial barriers would reduce the frequency of migratory alleles found upstream. Third, we explored inter-annual variation in the permeability of a suite of partial barriers. We predicted that in dry years with less precipitation and reduced passage opportunities, the spatial distribution of migratory genotypes would be shifted downstream, below barriers and tributary confluences, in comparison to wet years when landscape permeability is higher.

Methods

System and Study Streams

We studied genetic variation in *O. mykiss* in two tributaries to the South Fork Eel River, Fox Creek and Elder Creek (Fig 1), both of which are located within the University of California Angelo Coast Range Reserve. Migratory *O. mykiss* rear for 1-3 years in freshwater, migrate to the ocean for feeding and rearing, and then return to freshwater to breed. Resident *O. mykiss* complete their entire lifecycle in freshwater. *O. mykiss* represent >99% of the fish biomass in these streams, with the remainder represented by the occasional Pacific lamprey (*Entosphenus tridentatus*).

Fox Creek is a small watershed (2.7 km^2 drainage area) with step-pool morphology (Montgomery and Buffington 1997). Elder Creek is a larger watershed, draining 16.8 km^2, with two fish-bearing tributaries, Misery Creek (1.9 km^2 drainage area) and Paralyze Creek (4.9 km^2). Elder Creek is characterized by pool-riffle morphology in the lower reaches and step-pool morphology in the upper reaches, including in both tributaries. The transition from pool-riffle to step-pool morphology occurs near the confluence with Misery Creek, 4.1 km upstream from the Elder Creek mouth.

We explored the influence of four landscape features within Elder Creek and one landscape feature within Fox Creek on patterns of genetic diversity. The most downstream feature in Elder Creek is a large waterfall (3.1 m high from base to crest) that is a barrier to upstream movement of fish at most stream flows, and is located 2 km from the mouth (Fig 1, hereafter referred to as "Elder waterfall"). The second and third features are the two tributary junctions, the mouths of Misery and Paralyze creeks. The final feature is a putative barrier within Paralyze Creek identified by Trush (1989) that is 2.4 m high from base to crest and located 300 m upstream from the confluence with Elder Creek, below - but not above - which steelhead have been observed spawning (Trush 1989). There are no known barriers within Fox Creek, but the creek is elevated from the South Fork Eel River at their confluence, creating a potential barrier to upriver migrating steelhead at the mouth of the creek. While the creek mouth of Elder Creek is also elevated, the larger drainage area and higher flows of Elder Creek renders this step a passable barrier (Trush 1989). The location of the five potential landscape barriers in Fox and Elder creeks are illustrated in Fig 1.

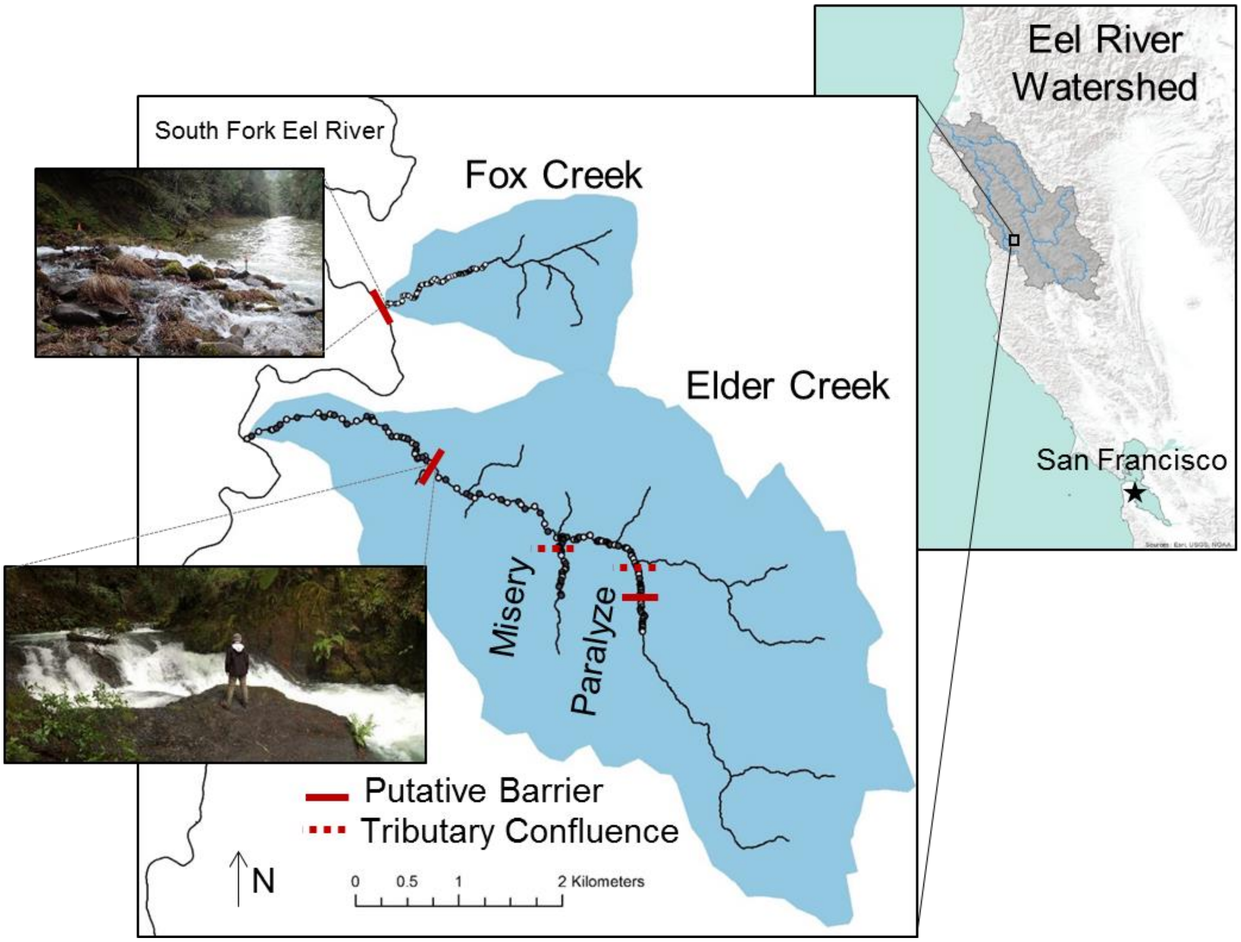

Figure 1. Elder Creek and Fox Creek are tributaries to the South Fork Eel River Watershed in Northern California. Circles represent sample pools, which were spatially stratified to encompass the entire length of the stream occupied by *O. mykiss*. White pools were included in genetic analyses for all years, dark grey pools were included in 2014 only.

Inter-annual variation in stream passage conditions

Fox and Elder creeks both experience Mediterranean seasonality, which is characterized by high variability in precipitation among years and hence high variability in river flows (Cid et al. 2017). Consequently, we expected the permeability of partial barriers within these streams to vary among years. We classified our four study years (2014-2017) as "dry" or "wet" using the Drought Severity Classification Index (DSCI) data on the South Fork Eel River watershed from the National Drought Monitor (https://droughtmonitor.unl.edu). We calculated the average DSCI for each year during the steelhead breeding season (January-May) (Trush 1989, Brown 1990), and considered years with a DSCI score of over 300 (out of 500) as "dry" and years with a DSCI score of under 200 as "wet." We also used stream flow records from the USGS gage on Elder Creek (gage no. 11475560) to estimate inter-annual differences in stream flow and differences in the opportunities for adult steelhead to ascend the aforementioned partial barriers. Prior research by Trush (1989) revealed that adult steelhead can ascend the largest waterfall in Elder Creek when flows are between 1.7-4.8 cubic meters per second (cms). This information allowed us to estimate the number of days that the Elder waterfall was passable to adult steelhead during the breeding season in each of our four study years. The mouth of Fox Creek and tributary confluences are likely passable at a broader range of stream flows.

Study Pools

To collect tissue samples for genetic analyses, we sampled fish longitudinally in each creek in each year (2014-2017, details below). In 2014, the entire fish-bearing extent of each stream was mapped onto a 10-m DEM in the field, including numbering each pool sequentially in each stream. We sampled fish from approximately 20% of the pools in each stream, selecting study pools using a spatially stratified random sampling approach to ensure that sample pools extended from the mouth to the upper extent of fish in both streams. The surface area (m^2) of each unit was measured within two weeks of fish sampling, and was estimated as pool length × average pool width, based on 5 evenly-spaced width measurements. We calculated the stream distance from the pool to the mouth of the creek (Fox or Elder) in ArcGIS. The same pools were revisited each year, with only a few exceptions due to natural alterations in the stream channel that made some pools inaccessible in later years. When this occurred, we replaced the original pool with the next upstream pool. This sampling scheme allowed us to compare changes in genotype frequencies among years and locations.

Fish Sampling

We sampled fish using three pass backpack electrofishing in each pool. Pools were blocked with nets prior to sampling and effort (seconds) was recorded for each pass. Using this method, we captured the majority of fish in most study pools. We used the fish abundance estimate combined with the pool surface area to estimate fish density (fish/m^2). We estimated abundance using the Leslie-K three-pass depletion method (Leslie and Davis 1939, Ogle 2016), and found that the total count of fish was highly correlated with three-pass depletion estimate except for pools with very small numbers, which led to unreliable depletion estimates (details in

Kelson et al. CH4, Appendix 1). For this reason, we present the total fish counts instead of depletion estimates.

At capture, we removed a small tissue sample (caudal fin clip), which was stored on Whatman filter paper in a coin envelope for later genetic analyses. At the same time, fish were measured for fork length (FL, in mm) and mass (to the nearest 0.01 g). We collected additional tissue samples from trout collected in the South Fork Eel River during sampling for other studies (e.g., Schaaf et al. 2017), and a subset of those samples were included here as a reference to the tributary sites in a principal component analysis (see below).

DNA Extraction and Genotyping

We conducted genetic analyses on all of the tissue samples collected in 2014. For 2015-2017 samples, we included a subset of approximately 50% of the samples, where every-other pool was included in the final analysis. We chose to subset the samples in the later years after preliminary analyses from 2014 revealed consistent results with a smaller number of samples. In total, we analyzed n = 3129 fish, with a breakdown by year, location, sample pool, and age class reported in Table 1.

Table 1. Number of pools and fish that were included in genetic samples in 2014-2017 by sample location.

Year	Location	Num. Pools	Num. Fish Incl.	Num. Age-0 Fish
2014	Fox Creek	41	71	14
	Elder – Below	36	751	580
	Elder – Above	49	412	219
	Elder - Misery	29	87	33
	Elder - Paralyze	34	199	122
2015	Fox Creek	26	111	84
	Elder – Below	17	242	190
	Elder – Above	24	156	87
	Elder - Misery	11	26	11
	Elder - Paralyze	16	76	33
2016	Fox Creek	24	89	50
	Elder – Below	17	157	124
	Elder – Above	25	180	90
	Elder - Misery	14	23	8
	Elder - Paralyze	16	85	26
2017	Fox Creek	26	127	69
	Elder – Below	14	148	86
	Elder – Above	23	108	39
	Elder - Misery	13	29	12
	Elder - Paralyze	15	72	21

We conducted DNA extractions and RAD capture (RAPTURE) using methods in Ali et al. (2016). We used an Illumina HiSeq 2500 to sequence libraries using paired-end 100-basepair (2014) or 150-basepair reads (2015-2017).We de-multiplexed sequence data using custom scripts

(Ali et al 2016) and used the MEM algorithm (Li and Durbin 2009) to align sequences to a rainbow trout genome assembly (https://www.ncbi.nlm.nih.gov/assembly/GCF_002163495.1/). We used SAMtools (Li et al. 2009) to filter alignments for proper pairs, sort alignments, remove PCR duplicates and index binary alignment map files. We also removed PCR duplicates using Picard tools.

We used Analysis of Next Generation Sequencing Data (ANGSD) for all RAPTURE sequencing data analyses (Korneliussen et al. 2014). We inferred major and minor alleles of sites with a high probability of being variable (SNP p-value 1e-6) from genotype likelihoods. We estimated allele frequencies assuming affixed major but unknown minor allele (Kim et al. 2011), and a uniform prior. Sites were included if they had a minor allele frequency > 0.05, and had data at a minimum of 50% of the samples. From here, we created two genotype files for analyses. First, we used a single read sampling approach, where a single base from each individual was randomly sampled and used for downstream analyses. This approach ('single-read SNP genotypes') was used in analyses to include the largest number of individuals and to mediate the effect of coverage differences (number of sequence reads) between individuals. Second, we called genotypes using a posterior probability cutoff of 0.95 for sites that were located on the RAPTURE baits, and refer to this approach as 'called genotypes.'

We used a discriminant analysis of principle components (DAPC, Jombart et al. 2010) on the single-read genotypes for SNPs on Omy5 (n = 415 SNPs) to assign individuals to migratory, heterozygous, or resident genotype groups (described further in Kelson et al., CH2).

Genetic Structure with and without Migration-Linked Loci

We calculated observed vs. expected heterozygosity for each SNP in the called genotypes (n = 473 SNPs) in the R package 'adegenet' (Jombart and Ahmed 2011). We found that Omy5 SNPs were characterized by lower heterozygosity than expected (Hobs = 0.43, Hexp = 0.46, P < 0.01 in a paired t-test), and this was the only chromosome where this was true (Fig S1), which is consistent with the description of this region as an inversion with highly linked loci (Pearse et al. 2014).

Next, to explore how migration-linked loci altered population structure within these streams, we conducted a principle component analysis (PCA) on single-read genotypes. For this analysis, we excluded individuals missing >20% of data (min. n = 586 SNPs per individual). We conducted PCAs using "adegenet" package in R. To test for the influence of the migration-linked region of the genome (Omy5) on genetic structure, we ran PCAs including all SNPs (n = 732 SNPs) and excluding SNPs on Omy5 (n = 699 SNPs). PCA visualization was done using ggplot2 (Wickham 2009). We also calculated pairwise F_{ST} values between Fox Creek and the regions of Elder Creek using called genotypes in "hierfstat" (Goudet and Jombart 2017) in R.

Data Analysis: Spatial Variation in Migration-Linked Genetic Diversity

We explored how migratory allele frequencies changed longitudinally in each stream. First, we were interested if there was a relationship with the overall proportion of migratory alleles and stream distance, which has been observed at larger geographic scales (e.g., Narum et al. 2004, Berejikian et al. 2013)(Narum et al. 2004, Berejikian et al. 2013). We addressed this question by relating the proportion of migratory alleles per study pool with distance upstream from the confluence with the South Fork Eel River, and predicted that there would be a negative relationship between the two. For each pool, we calculated the proportion of migratory alleles (individuals assigned a migratory genotype = 2 alleles, heterozygote = 1 allele, and resident = 0 alleles, divided by the total number of alleles, 2 per fish). We conducted a generalized linear regression, using a binomial distribution for proportions (response variable ranged from 0 to 1), with the proportion of migratory alleles as the response variable and distance-upstream as the predictor variable. We calculated regressions separately for each year (n=4) and creek (n=2) combination, for a total of 8 regressions.

Next, we explored the influence of partial barriers on up-river migrating adults in Elder Creek. For this analysis, we focus on the abundance of migratory alleles in juvenile fish, with the idea that, moving upstream from the mouth of the creek, the spatial distribution of the number of migratory juveniles should be consistent until a partial barrier to adult steelhead is reached, at which point there will be a decrease in the number of migratory alleles per sample pool. We classified individuals as young-of-year fish, hereafter referred to as 'juveniles,' if they were < 85 mm in fork length (see Kelson et al. CH 3). High spatial correlation between parents and juveniles < 4 months old was demonstrated for another salmonid fish (*Salvelinus fontinalis*, Hudy et al. 2010), suggesting that the location of young fish reflects the location of where their parents spawned, and hence a proxy for the upstream passage ability of anadromous adults the previous winter, rather than juvenile dispersal.

To explore the effects of the four partial barriers, we asked where "breakpoints" existed in the number of migratory alleles of juvenile fish per pool, moving from downstream to upstream. For each pool, we calculated the cumulative number of migratory alleles per m^2 by summing alleles/m^2 in that pool and all downstream pools. Each pool was assigned a pool number based on its location from downstream to upstream, with 1 being the most downstream pool at the mouth of Elder Creek. We used pool number rather than upstream distance to avoid spatial autocorrelation between pool location and distances between pools (e.g., pools in Misery and Paralyze were closer together than elsewhere in the watershed, due to shorter pool lengths). Here, if there was no influence of partial barriers on up-river migrating adults, then the number of migratory alleles per pool would be consistent throughout the watershed, and the relationship between cumulative sum of migratory alleles and stream distance would be best represented by a single linear regression. We then tested if this relationship between cumulative sum of migratory alleles and stream distance would be better represented by multiple linear regressions, with the slope of the relationship changing at "breakpoints," representing locations in the watershed where there is a change in the pattern in the number of migratory alleles per pool or partial barriers. We used the package "segmented" (Muggeo 2008) to determine the number and location of breakpoints. We conducted the analysis twice for Elder Creek, once including pools in Paralyze and all of the pools downstream of its confluence with Elder Creek, and a second analysis including pools in Misery and all of the pools downstream of its confluence. For both analyses, we set the possible number of breakpoints as up to the number of predicted breakpoints plus one additional break to allow for identification of unknown potential barriers. This approach resulted in up to four potential breakpoints in Paralyze (Elder waterfall, Paralyze confluence, barrier within Paralyze, and one additional break) and three in Misery (Elder waterfall, Misery confluence, and one additional break). We then compared models including 1-4 or 1-3 breaks for Paralyze and Misery, respectively, using the Akaike Information Criteria (AIC) and report results from the model with the lowest AIC score.

Data Analysis: Inter-Annual Variation in Spatial Distribution of Genotypes

After determining the location of partial barriers using the breakpoint analysis, we explored their influence in years with different rainfall magnitudes and timing. Here, we were specifically interested in testing if these partial barriers were less permeable to upriver migrating anadromous steelhead in dry years, that is, if they were more effective at reducing the number of upstream migratory-alleles in dry years as compared to wet years. We tested this hypothesis again using data from juvenile fish as a reflection of where their parents spawned.

Within Elder Creek, we explored the inter-annual variation in genotype patterns at the four putative barriers (Elder waterfall, two tributary confluences, small barrier in Paralyze), which aligned with our results from the breakpoint analysis (see Results). To test for the effect of tributary confluences, we compared the number of migratory alleles per pool in the tributary vs. the reach of Elder Creek above the waterfall (i.e., excluding pools downstream of the large barrier, which showed a different pattern than above the waterfall, see Results). For each downstream vs. upstream comparison, we conducted a generalized linear model (Poisson distribution) with the number of migratory alleles per sample pool as the response variable and, with sample location – downstream or upstream of the landscape feature – and year and surface area (m^2) of the pool as predictor variables. We tested for an interaction effect with sample location (downstream versus upstream of the landscape feature) and year. A significant interaction indicates that the difference in migratory alleles per pool downstream versus upstream of each feature depends on the year.

Within Fox Creek, the major putative barrier is located at the creek mouth, so we explored inter-annual variation in the number of migratory alleles per pool for the entire creek. Here, we conducted a generalized linear model (Poisson distribution) with number of migratory alleles per pool as the response variable, and including sample year and pool surface area (m^2) as predictor variables.

Results

Inter-annual Variation in Stream Flow and Barrier Passage

Our study encompassed two dry years (2014, 2015) and two wet years (2016, 2017), based on the average Drought Severity Classification Index (DSCI) in the South Fork Eel River watershed during the steelhead breeding window (DSCI score of 392 and 324 in 2014 and 2015, 120 and 0 in 2016 and 2017). Beyond differences in total precipitation, there were differences in the magnitude and timing of high flow events during the adult steelhead breeding season. In 2014, stream flows were elevated in March and April, while in 2015 the only major flow event occurred in February (Fig 2). Both 2016 and 2017 were characterized by higher stream flows overall during the adult steelhead spawning season, with the highest flows in 2016 in January and March and several high flow events in 2017 (Fig 2). Using the estimated flow passage window based on results of Trush (1989), the waterfall on Elder Creek was passable for 7 days in 2014, 4 days in 2015, 37 days in 2016, and 39 days in 2017.

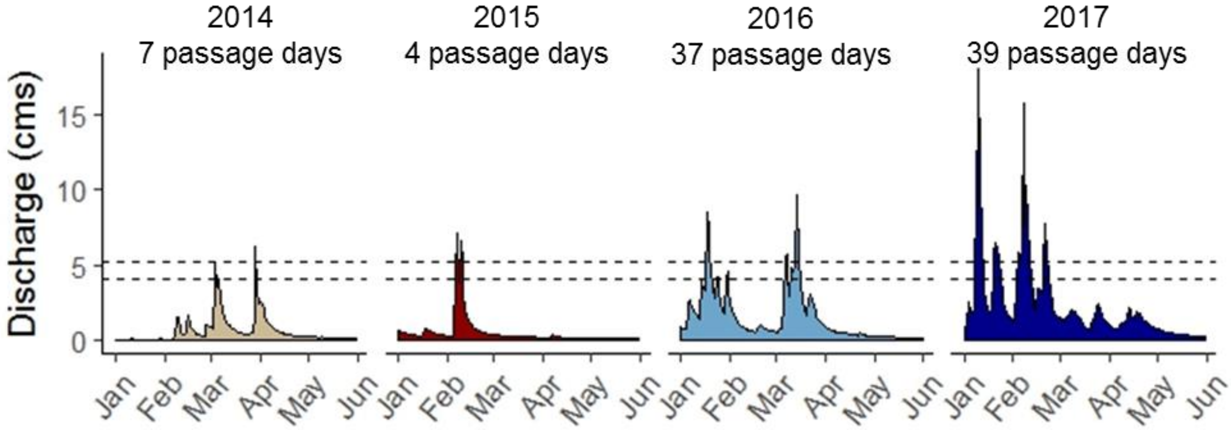

Figure 2. Stream flow patterns in Elder Creek from 2014-2017 during the steelhead breeding window, which included two dry years (2014-2015) and two wet years (2016-2017). Dotted lines indicate the flow window when the waterfall in Elder Creek is estimated to be passable to adult steelhead. Passage days are when stream flows fall within the passage flow window.

Genetic Structure at Omy5 Exceeds Background Structure

To explore the relative influence of neutral versus migration-linked loci on genetic clustering, we conducted two PCAs using all samples collected in both streams and the South Fork Eel River, one including all SNPs (n = 732 SNPs), and one excluding SNPs on Omy5, the migration-linked region (n = 699 SNPs). In a PCA with all SNPs, grouping mostly occurred on the first PC axis (Fig 3), which explained 2.4% of the variance (twice as much variation as the next two PCs, Fig S2). The first PC separated individuals into 3 groups, corresponding to migratory, heterozygous, and resident-genotype groups, and there was no strong pattern that separated sampling locations (including samples from the South Fork Eel River, Fig 3a). Loading for all principle components were dominated by SNPs on Omy5 (Fig 3b). In the PCA that excluded SNPs on Omy5, there was no strong clustering, with 80% of the samples falling in a center cluster and no clustering based on sample location, including samples collected from the South Fork Eel River (Fig S2). Loadings for the PCs were distributed across many SNPs throughout the genome (Fig S2). Additionally, F_{ST} comparisons between the streams (within regions of Elder Creek) and Fox Creek were all < 0.02 and not statistically significant. Together these results suggest little genetic divergence among *O. mykiss* captured from neighboring locations.

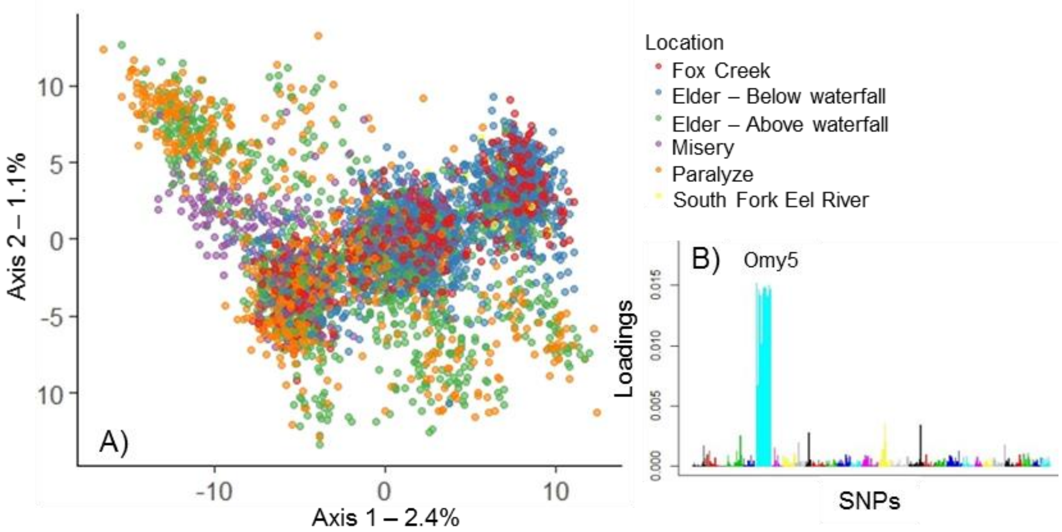

Figure 3. A) A PCA demonstrates that SNPs on Omy5 contribute to most of the genetic clustering in these streams, with no groups forming between sample locations (Fox Creek, regions within Elder Creek, and South Fork Eel River). The visualized PCA used all SNPS (n = 726 SNPs in total, including n=34 SNPs on Omy5). B) Loading plot averaging over the all principal components indicate that most of the variance is attributed to SNPs on Omy5. SNPs are color coded by their chromosome.

Spatial Variation in Migratory Allele Frequency

First we explored the longitudinal (upstream-downstream) distribution of migratory allele frequency. Within Elder Creek, the proportion of migratory alleles per pool decreased with upstream-distance; there was a strong, linear relationship between the proportion of migratory alleles per pool and the distance upstream in each year (2014: $r^2 = 0.47$, z = -14.3, P < 0.001, 2015: $r^2 = 0.69$, z = -11.6, P < 0.001, 2016: $r^2 = 0.65$, z = -11.5, P < 0.001, 2017: $r^2 = 0.55$, z = -7.8, P < 0.001) (Fig 4a). Within Fox Creek, there was a weak, but significant, linear relationship between the proportion of migratory alleles per pool and upstream-distance in 2015-2017 (Fig 4b, 2015: $r^2 = 0.20$, z=-2.8, P < 0.01, 2016: $r^2 = 0.11$, z = -1.9; P = 0.05, 2017: $r^2 = 0.25$, z=-3.7, P < 0.01), and no relationship in 2014 (P = 0.40).

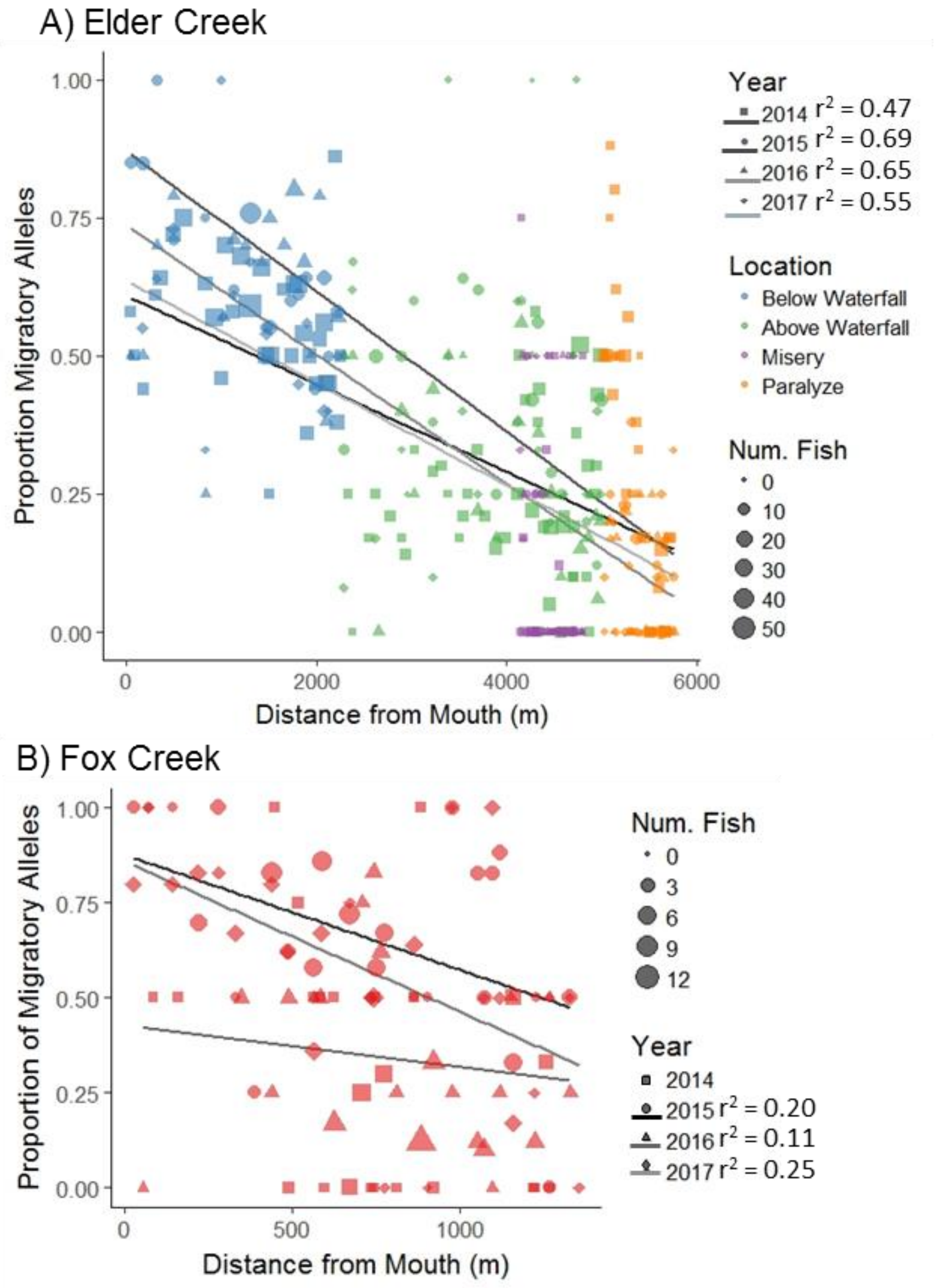

Figure 4. A) The proportion of migratory alleles per pool decreases with distance upstream in Elder Creek in 2014-2017. B) The proportion of migratory alleles per pool shows a weaker, negative relationship with distance upstream in Fox Creek.

Next we explored locations in the Elder Creek watershed that were obstacles to upstream-migrating adult steelhead by conducting a breakpoint analysis to determine if and where there were shifts in the number of migratory alleles per pool (per m^2) for juvenile fish. We predicted that these breakpoints would coincide spatially with our a priori knowledge of landscape features in the watershed (the Elder Creek waterfall, confluences with Misery and Paralyze, and the barrier within Paralyze), but the analysis is agnostic with respect to these predictions. For the analysis including Paralyze and all pools downstream, the breakpoint model with the lowest AIC score included 4 breakpoints in 2014 and 2015 and 3 breakpoints in 2016 and 2017 (Table S1). For the analysis including Misery and all pools downstream, the breakpoint model with the lowest AIC score included 3 breakpoints in all years (Table S1). The breakpoint at the largest waterfall in Elder was included in all models (Fig 5), and the breakpoint at (or very near) the tributary confluences were included in models for 3 of the 4 years (Fig 5). Other breakpoints that were included in the best supported (lowest AIC) models included breakpoints in lower Elder below the waterfall, which fell at no consistent location, and a breakpoint within Paralyze canyon, which coincided with the description of a barrier to adult steelhead in Trush (1989). Based on these breakpoint analyses, we included four main breakpoints, the Elder Creek waterfall, confluences with Misery and Paralyze, and the barrier within Paralyze, in further analyses comparing the number of migratory alleles downstream vs. upstream of each feature.

Inter-Annual Variation in Spatial Distribution of Genotypes

Within Elder Creek, the number of migratory alleles per pool was higher downstream in comparison to upstream for each of the four partial barriers (Fig 6 and Fig 7). We found some evidence that the effect of each landscape feature depended on the year, as the interaction between location (downstream versus upstream of the feature) and year was significant in some cases (Fig 7). For the largest waterfall in Elder, the difference in the number of migratory alleles per study pool between the downstream and upstream regions was highest in 2014 and 2016 (Fig 6), and correspondingly the coefficient for the interaction between year and upstream-location was significant and positive in 2015 and 2017 (Fig 7), indicating that proportionally fewer migratory alleles were found in the upper watershed in those years. At the barrier within Paralyze, the difference between the number of migratory alleles upstream and downstream of the features was smaller in 2016 (wet year) in comparison to other years (Fig 6, Fig 7). There was also evidence that the Misery confluence was less of a barrier in 2017 (wet year) than in other years, when there were higher densities of migratory alleles upstream of the feature in comparison to the other years (Fig 6, Fig 7). The driest winter, 2014, was the most extreme year in that there were more migratory alleles downstream of each landscape feature than upstream (Fig 6). The one exception to this pattern was the Paralyze confluence, where the number of migratory alleles was similar downstream and upstream of the confluence in 2014 (Fig 6), but reduced upstream in other years (there was a significant, negative interaction between year and upstream-location in 2015-2017, Fig 7). This pattern appears to be driven by the fact that there were more migratory alleles upstream of the confluence in Paralyze in 2014 than in any other year (Fig 6), and the influence of the barrier within the stream was stronger than the influence of the confluence (Fig 6).

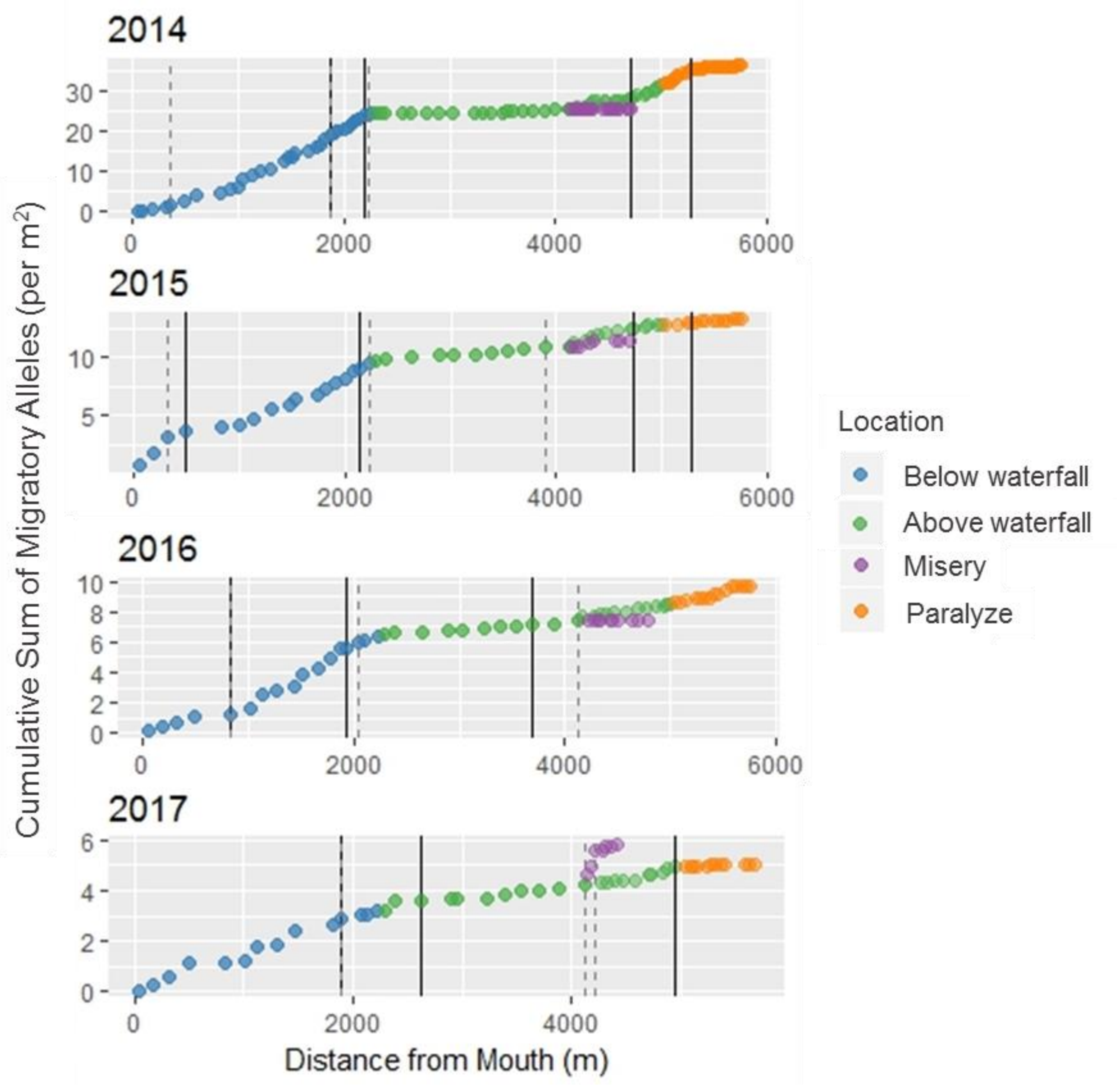

Figure 5. A-priori breakpoints in the cumulative sum of migratory alleles per m^2 in Elder Creek, indicating where shifts in the spatial distribution of migratory alleles occur. Dark lines indicate breakpoints in the analyses that includes Paralyze and all pools downstream, and grey dotted lines indicate breakpoints in the analyses that includes Misery and all pools downstream. The Elder waterfall is a significant breakpoint in all 4 years and in both sets of analyses. The confluence with Paralyze and the confluence with Misery is a breakpoint in 3 of the four years (2014, 2015, and 2017, and 2015-2017, respectively).

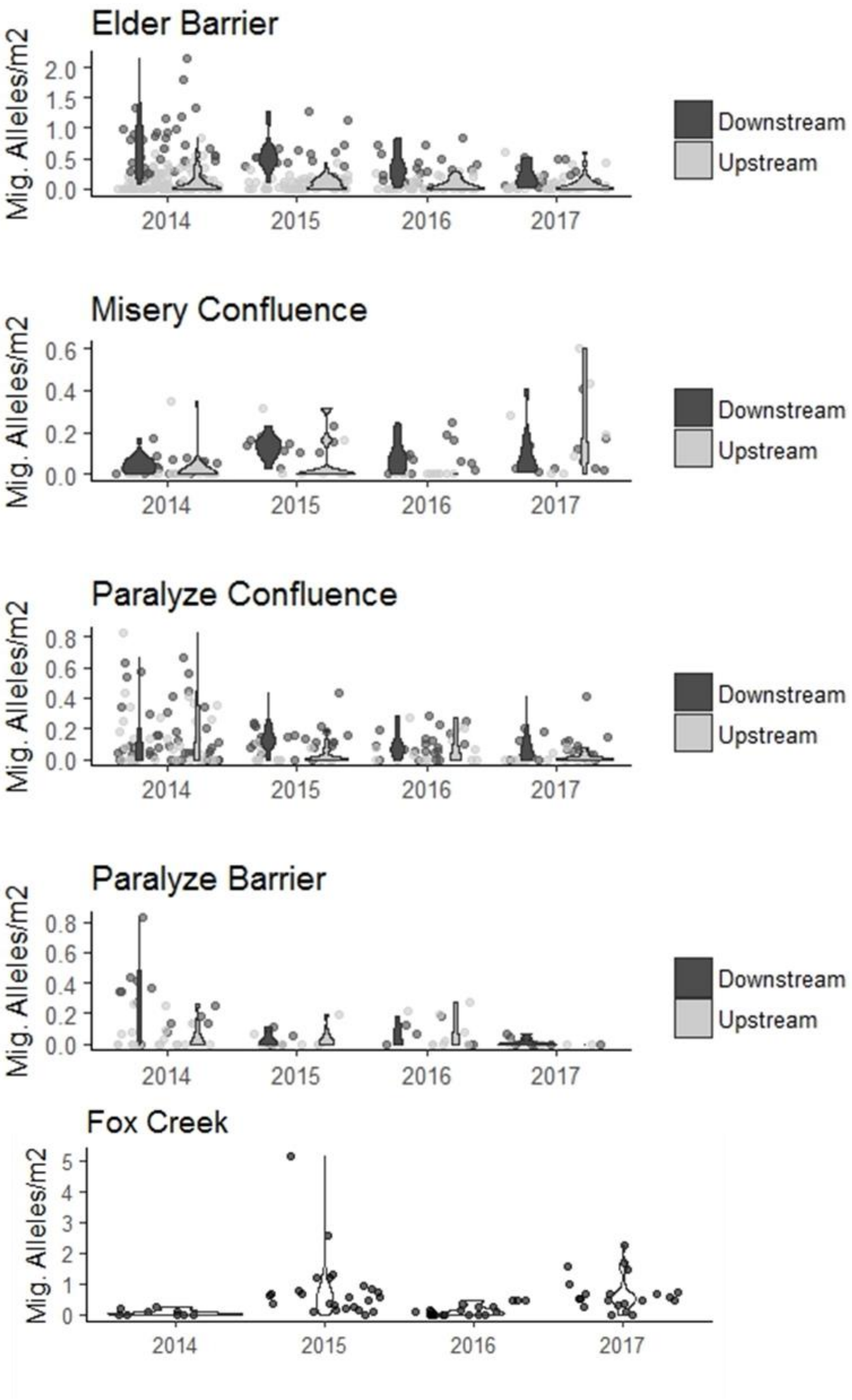

Figure 6. Distribution of migratory alleles per m^2 downstream versus upstream of each landscape feature in Elder Creek and in Fox Creek across 4 years of sampling, 2014-2017.

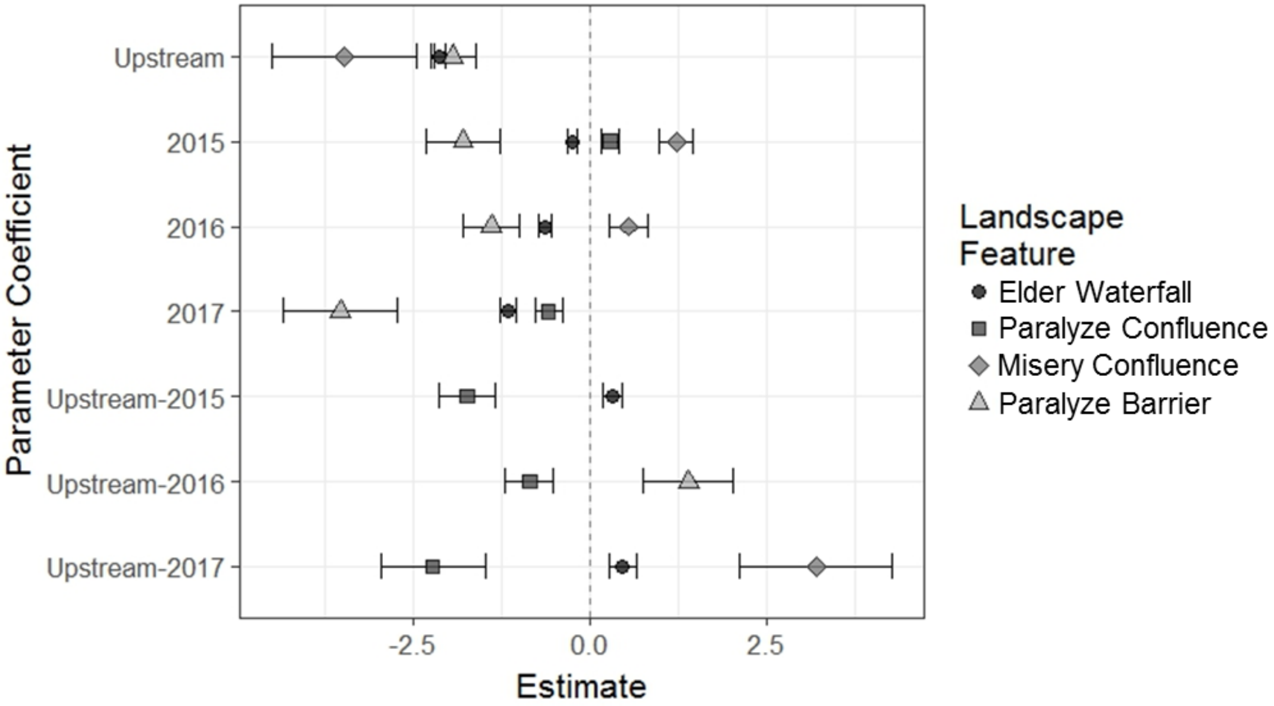

Figure 7. Parameter coefficients estimated from a generalized linear model with the number of migratory alleles per pool as the response variable. "Upstream" coefficient is contrasting the number of migratory alleles per pool upstream from number downstream of each feature. Each year parameter (2104-2017) is in contrast from 2014. "Upstream-year" year parameters are interaction effects between upstream and year. Surface area (m^2) of each pool was also included in the model (not shown). Coefficients that are greater than zero and plotted represent a significant increase in the number of migratory alleles for that feature/year. Non-significant parameter coefficients ($P>0.05$) are not plotted.

For Fox Creek, the strongest pattern in migratory alleles was across years, rather than spatially within the watershed. We found strong inter-annual variation in the number of migratory alleles per pool, with year explaining 35% of the deviance (318.5 out of a total 909.6) in an ANOVA of the generalized linear model. There was a strong increase in migratory alleles per pool in the years of 2015 and 2017, in comparison to 2014 (2015 estimate ± std. error = 4.7 ± 1.1, t=4.1, $P < 0.01$; 2017 estimate ± std. error = 4.6 ± 1.2, t = 4.0, $P < 0.01$, see also Fig 6). There was no increase in the number of migratory alleles per pool in 2016 in comparison to 2014 (estimate ± std. error = 0.6 ± 1.2, t =0.5, P=0.62). The migratory allele frequency varied among years, and was 30.0% in 2014, 68.4% in 2015, 30.3% in 2016, and 60.3% in 2017 (Fig 1).

Discussion

Overall, the proportion of migratory alleles decreased with upstream-distance in two streams. Inter-annual variation in rainfall patterns led to variation in the permeability of the streams, with landscape features becoming more permeable in years with more rainfall. These temporal dynamics were translated into inter-annual variation in the spatial distribution of migratory genotypes. In particular, migratory alleles in juveniles were more concentrated downstream of partial barriers in dry years in Elder Creek, and were reduced by over 50% in Fox Creek in two years (one dry, one wet). In summary, the influence of partial barriers varies among years, with consequences for spatial distribution of genotypes, including the distribution of resident and migratory genotypes in partially migratory populations of a salmonid fish.

Distance and permeable barriers influence distribution of migratory genotypes

Theory suggests that migration in salmonids should decrease with an increased cost of migration, which is often estimated as distance traveled or elevation gained (Jonsson and Jonsson 1993, Hendry et al. 2003). In alignment with theoretical predictions, prior research from large watersheds has documented the general pattern that anadromous *O. mykiss* tend to be distributed further downstream than resident trout (McMillan et al. 2007, Narum et al. 2008, Berejikian et al. 2013). The same pattern was demonstrated in brown trout (*Salmo trutta)*, where juvenile density of migratory fish declined with altitude, and resident fish became proportionally more common in upper headwaters (Bohlin et al. 2001). Our study expands on previous research to highlight that stream distance can be important even within a small watershed with a long zone of co-occurrence, i.e., within 6 km of stream in Elder Creek, and to a lesser extent within 2 km of stream in Fox Creek.

Beyond patterns with upstream distance, partial barriers influenced the spatial distribution of migratory alleles in juvenile fish. Within Elder Creek, the reduction in migratory allele frequencies was greatest at the largest partial barrier, a waterfall located relatively low within the watershed (approximately 2 km from the mouth). This barrier was more influential in reducing the migratory allele frequency upstream of it than the tributary confluences, suggesting that barrier permeability is relatively more important than the drainage area in determining the distribution of migratory alleles in river systems. While other studies have documented that complete barriers select against anadromy, leading to divergence in *O. mykiss* populations distributed above and below barriers (Pearse et al. 2009, Leitwein et al. 2017), our study provides an example of the lesser-studied effects of small, partial barriers on the distribution of migratory genotypes in *O. mykiss.* Small barriers are common across the landscape (Januchowski-Hartley et al. 2013), and include natural features, such as tributary confluences or waterfalls like those studied here, but also include unnatural landscape features, such as road crossings (Benton et al. 2008), and weirs, or small diversion dams (Weigel et al. 2013b, Newton et al. 2018). Apgar et al. (2017) showed that many small barriers can have a cumulative effect that is equal to large, impassible barriers, and be just as effective at reducing the migratory allele frequency upstream in *O. mykiss*. Together these results suggest more attention is needed on the influence of partial barriers in streams on organismal distributions and patterns of gene flow, particularly for partially migratory populations.

Inter-annual variation in migratory allele frequencies and landscape permeability

Beyond the winnowing influence of partial barriers, we documented inter-annual variation in their permeability. This pattern was most pronounced in Fox Creek, where in two years (2014 and 2016), the migratory allele frequency was reduced by more than 50%, presumably due to the inability of migratory fish to access the creek in those years. This pattern was more extreme in 2014, when only 1.2% (1 out of n=82 age-0 fish sampled) juveniles were migratory-genotypes. In both of these years there were no high flow events in February, which is the peak breeding season for steelhead in the Eel River watershed (Trush 1989, Brown 1990). We observed a similar pattern when focusing on the largest waterfall in Elder Creek, when migratory alleles were concentrated downstream of the waterfall in 2014 and 2016, suggesting the waterfall inhibited the upstream movement of adult steelhead in those years. These results emphasize that the influence of partial barriers on distributions and gene flow is dynamic, with passage of migratory individuals depending on the timing and magnitude of high flow conditions that facilitate their upstream movement.

In our study system, inter-annual variation in rainfall lead to temporal differences in landscape permeability. Temporal variability in landscape permeability for the movement of animals has been demonstrated in other systems, for example in the Canadian Rockies where seasonal variation in the number of vehicles per day on major highways effects large mammal crossings (Alexander et al. 2005), or in temporary river systems where dry riverbeds become a movement corridor for terrestrial animals and insects (Steward et al. 2012). However, the influence of inter-annual variation in environmental conditions is not often explored in terms of its influence on barrier permeability in studies of genetic diversity and gene flow. Some exceptions include studies that compare genetic diversity in historical samples with contemporary samples (e.g., Heath et al. 2002, Martínez-Cruz et al. 2007) or long-term gene flow estimates (F_{ST} values) with contemporary movement (e.g., Epps et al. 2013). Studies that use individual-based, spatially and temporally explicitly sampling, or modeling (Landguth et al. 2010, 2011), may be a powerful approach for disentangling the influence of among year variation in the environment and landscape features, as well as their interaction, on patterns of gene flow and local adaptation.

Non-neutral loci shape genetic structure in partially migratory populations

We found that there was no genetic divergence between streams or above vs. below permeable barriers within a stream when using putatively neutral loci (F_{ST} values < 0.02). Apgar et al. (2017) also found that migration-linked loci frequencies showed greater divergence than neutral loci in *O. mykiss*, and Van Doornik et al. (2013) reported high rates of gene flow between sympatric anadromous and resident *O. mykiss*. The result also aligns with evidence that anadromous and resident *O. mykiss* within a watershed are more closely related to each other than to fish with the same life history in neighboring watersheds (Olsen et al. 2006, Clemento et al. 2009, Leitwein et al. 2017). Our results suggest that resident and migratory individuals are interbreeding and gene flow is maintained between the two life history strategies. Additionally, the lack of divergence between the two streams, Fox and Elder Creek, suggests that steelhead are not necessarily returning to their natal creek to breed in the South Fork Eel River watershed.

Conclusions

Overall, our results emphasize the dynamic nature of partial barriers in influencing patterns of abundance and gene flow in a partially migratory fish. Permeability of partial barriers was mediated by river flow conditions; in general, partial barriers were less permeable during dry years. Up-river migrating adults expanded their range upstream of partial barriers when conditions allowed. Similar results of upstream range expansion have been observed following dam removal (Kiffney et al. 2008, Weigel et al. 2013a, McMillan et al. 2015), when upstream migrating fish have recolonized former habitat following barrier removal. Like many diadromous fishes, the distribution of migratory *O. mykiss* has been reduced by dams, and restoring migration is a major goal where this life history has been lost (Limburg and Waldman 2009, Quiñones et al. 2014), and these results suggest that upstream range expansion of the migratory life history is possible. More generally, the spatial distribution of resident and migratory individuals and the potential for gene flow between forms in partially migratory populations is likely to be dynamic and to be strongly influenced by landscape features and environmental variability.

Acknowledgements

This study was co-authored by Michael R. Miller, Tasha Q. Thompson, Sean M. O'Rourke, and Stephanie M. Carlson. This work was supported by a NSF Graduate Research Fellowship to SJK and by and the Eel River Critical Zone Observatory, NSF CZO EAR-1331940. The work was also funded by the UC Berkeley Wildlife Fund and the UC Natural Reserve System Mildred E. Mathias Award. We would also like to acknowledge Peter Steele for supporting this research at the UC Angelo Coast Range Reserve.

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Supplemental Tables and Figures

Table S1. AIC score for the number of breaks in the linear fit between the cumulative number of migratory alleles per m^2 and the sample pool number (from downstream to upstream). For the analysis including Misery pools, we tested for a maximum of 3 breakpoints (waterfall, Misery confluence, and one extra). For the analysis including Paralyze pols, we tested for a maximum of 4 breakpoints (waterfall, Paralyze confluence, and barrier within Paralyze, and one extra). The AIC score for the number of breaks displayed in Fig 4 is in bold.

Num.	**Misery**				**Paralyze**			
Breaks	**2014**	**2015**	**2016**	**2017**	**2014**	**2015**	**2016**	**2017**
1	101.2	7.7	-12.8	5.9	292.6	48.4	-53.2	-34.3
2	62.5	44.1	-26.8	-24.1	254.6	-9.6	-53.6	-95.2
3	**-16.8**	**-48.0**	**-25.0**	**-47.1**	139.6	-70.7	**-89.7**	**-101.3**
4	**-**	**-**	**-**	**-**	**127.1**	**-80.6**	-74.4	-92.0

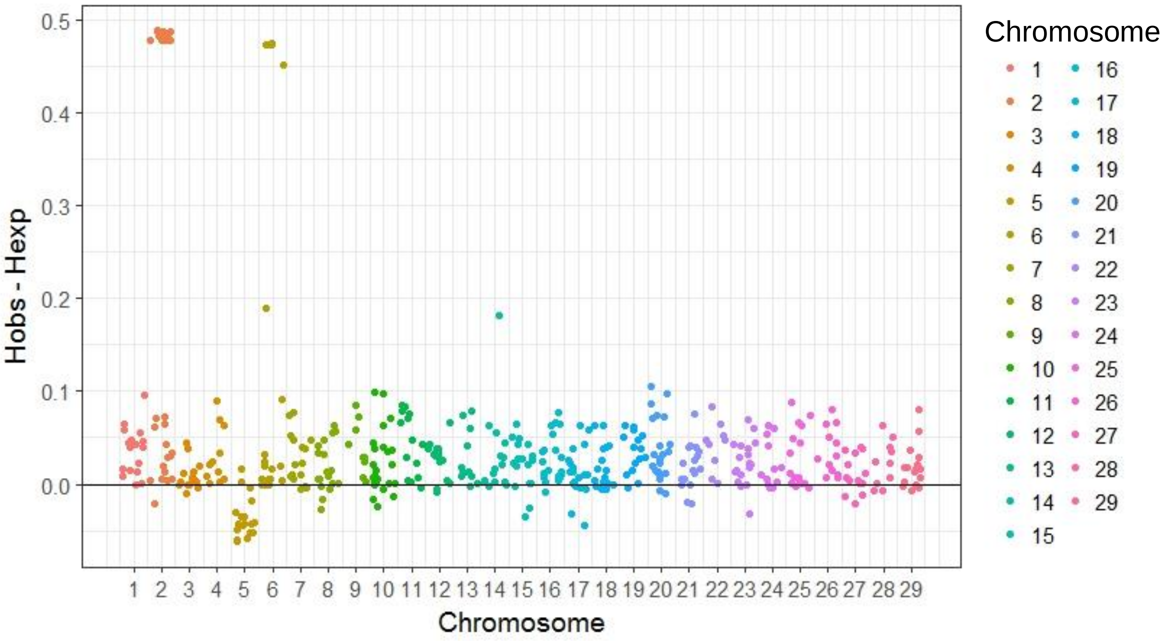

Figure S1. Loci on Omy5 were less heterozygous than expected, and this pattern was more extreme for loci on Omy5 than for loci that were not on Omy5.

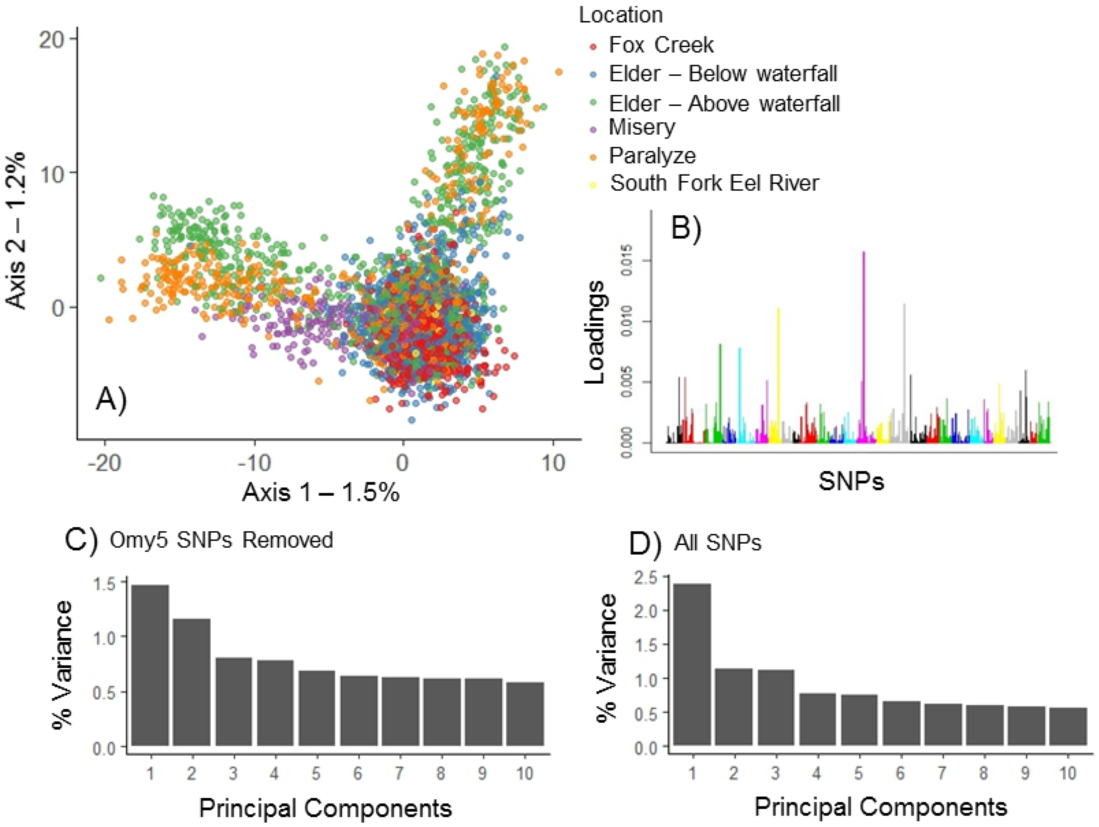

Figure S2. PCAs demonstrate that SNPs on Omy5 contribute to most of the genetic variation in these streams, with no groups forming between sample locations (Fox Creek and regions within Elder Creek). A) PCA excluding SNPs on Omy5 (n = 692 SNPs). B) Loading plot averaging over the all principal components for PCAs excluding Omy5 SNPs, demonstrate that variance is distributed evenly across chromosomes once Omy5 is excluded. Colors represent chromosomes. Plots C) and D) show the percent variance explained by each principal component for the PCA that excludes SNPs on Omy5 and that includes all SNPs, respectively.

3

Do genomics and sex predict life history ecotype in partially migratory populations of a salmonid fish, *Oncorhynchus mykiss*?

Abstract

Migratory populations commonly include a mixture of migratory and resident individuals, a phenomenon called partial migration. Whether an individual migrates or not has important ecological and management implications. *Oncorhynchus mykiss* is a partially migratory salmonid fish endemic in coastal north Pacific streams, but in California only the migratory form is protected under state and federal endangered species acts. Recent research revealed a region of the genome that is highly correlated with migration across populations of *O. mykiss* (Pearse et al 2014), but it is unclear how well genetic markers from this region correlate with observed life history – migratory or resident – at the individual level, especially in partially migratory populations. Moreover, females are more likely to express migration because of the significant fecundity gain associated with increased growth at sea as compared to freshwater, but it is difficult to sex fish as juveniles. Here, we relate genetic sex and life history genotype, determined using over 400 single nucleotide polymorphisms (SNPs) on the migratory-linked region of the genome, to life history expression of individual *O. mykiss* from two tributaries to the South Fork Eel River, Mendocino County, California. Fish that adopted the resident life history strategy were likely to have the resident-genotype (55% of resident fish were resident-genotype, 39% are heterozygous, and 6% are migratory-genotype), and residency was strongly male-biased (79% male). Out-migrating individuals tended to be female (62% female) and included a mixture of all genotypes (25% resident-, 45% heterozygous, and 30% migratory-genotype). In general, sex was more strongly correlated with life history expression than life history genotype ($r^2 = 0.31$ vs. $r^2 = 0.20$), but the best-supported model included both sex and life history genotype ($r^2 = 0.45$). We used life history genotype and genetic sex frequencies of the resident and out-migrating fish in a simple model to estimate the percent of the population that expresses migration, which revealed that these populations are dominated by migratory fish (70-88%). However, resident genotypes regularly adopted the migratory ecotype, highlighting the importance of conserving the full suite of life history diversity in partially migratory populations.

Introduction

Animal migration is an important phenomenon that allows populations to exploit different habitats throughout their life history (Dingle 2014). An accumulating body of research suggests that many migratory populations are partially migratory, meaning that they include a mix of individuals who do and do not migrate (Chapman et al. 2011). Partial migration has been observed across a diverse range of taxa, including large ungulates (Fryxell and Sinclair 1988, Hebblewhite and Merrill 2009), passerine birds (Smith and Nilsson 1987, Hegemann et al. 2015), and fishes (Chapman et al. 2012).

Migration connects disparate ecosystems with numerous ecological consequences (Bauer and Hoye 2014). For example, migratory animals can subsidize receiving ecosystems. A classic example is salmon that subsidize the freshwater and riparian ecosystems where they breed through the decomposition of their carcasses (Wipfli et al. 1998, Naiman et al. 2002), providing marine-derived nitrogen and phosphorous to otherwise nutrient-poor temperate freshwater lakes and streams (Gresh et al. 2000). Because they depend on multiple habitats, however, migration is on the decline globally (Wilcove and Wikelski 2008, Shuter et al. 2011). This pattern is especially striking within partially migratory populations of salmonids, where the migratory form is on the decline (*e.g., Salmo salar and S. trutta,* Jonsson and Jonsson 2009, *S. fontinalis,* Scribner et al. 2012), and commonly have protected status, while the resident form is not. Managing partially migratory populations and partially protected population complexes is difficult in part because of challenges in identifying migrants, yet the preservation of the migratory life form is essential for sustaining subsidies to freshwater ecosystems among other cultural and economic interests.

One animal that commonly expresses partial migration is *Oncorhynchus mykiss*, a salmonid fish native to the north Pacific Rim. While some populations with short coastal migrations are fully anadromous (“steelhead trout”), and other inland populations are fully resident (“rainbow trout”), some populations include both forms. Recent research by Pearse et al. (2014) revealed that a region of the genome in *O. mykiss* (on chromosome 5, or Omy5) is closely associated with anadromy. This region consists of a large block of strong linkage disequilibrium that is likely maintained by a chromosomal inversion (Leitwein et al. 2017). Pearse et al. (2014) demonstrated that loci in this region on Omy5 showed high divergence between populations below barriers (dominated by anadromous fish) versus populations above barriers (dominated by resident fish) in watersheds from central California to southern Oregon. Moreover, other life-history-linked traits, including embryonic development rate (Robison et al. 2001, Miller et al. 2012), growth (Nichols et al. 2008), and maturation timing (O’Malley et al. 2003), have all mapped to the same migration-linked genomic region. These studies together suggest that life-history genotyping, using loci on Omy5, may be a powerful approach for predicting migration behavior of individuals in partially migratory *O. mykiss* populations.

Sex is another factor that can be important in determining migration strategy in partially migratory animals (Chapman et al. 2011). Theory suggests that female-biased migration should arise in animals where fecundity is linked to body size (reviewed in Hendry et al. 2004), including in salmonids where females who migrate to ocean feeding grounds reach larger sizes and produce more eggs (Fleming and Reynolds 2003). In support of this prediction, empirical studies have documented female-biased migration in several salmonid fishes (Jonsson and Jonsson 1993, Dodson et al. 2013). A genetic method to determine the sex of *O. mykiss* (Brunelli et al. 2008) allows the ability to determine the sex of a large number of juvenile fish using non-lethal methods. Using this approach, Ohms et al. (2014) calculated the sex ratio of *O. mykiss* smolts across several streams in the Pacific Northwest and found that migrants tended to be female-biased. Similarly, Rundio et al. (2012) calculated the sex ratio of resident *O. mykiss*, and found a male-bias among resident-ecotype fish. These results suggest combining information on sex and life-history genotype might improve our ability to predict migration at the individual level.

Here, we explore the relationship between life history genotype, genetic sex, and life history expression of individual *O. mykiss* from two streams with partially migratory fish. We predicted that most migratory individuals would be migratory-genotypes and females, whereas most resident individuals would be resident-genotypes and males. Overall, we predicted that life history ecotype would be best predicted with the combination of life history-genotype and sex information in partially migratory populations.

Methods

System

Here, we focus on partially migratory populations of *O. mykiss.* In this system, the migratory ecotype rears in freshwater for 1-2 years, migrates to the ocean for feeding and growth, and then returns to freshwater to breed. In contrast, the resident ecotype completes its entire life cycle in freshwater. While migratory steelhead are federally protected throughout their range in California under the Endangered Species Act (Williams et al. 2016), resident rainbow trout in the same populations are not.

Study Site and Fish Sampling

We studied partially migratory populations of *O. mykiss* in two tributaries to the South Fork Eel River, Elder and Fox creeks, both located within the University of California Angelo Coast Range Reserve (Mendocino County, CA; Fig. 1). Elder Creek drains 16.8 km^2 and Fox Creek drains 2.7 km^2, and both are steep, shaded streams. There is a waterfall located 2 km from the mouth of Elder Creek that is passable to adult steelhead under some stream flow conditions, and steelhead have been observed spawning above this barrier (Trush 1989). *O. mykiss* represent >99% of the fish biomass in these streams. The only other fish species encountered is the occasional Pacific lamprey (*Entosphenus tridentatus*).

We sampled fish in Fox and Elder creeks from late-July to early August in 2014-2017. Fish were collected using 3 pass backpack electrofishing. We sampled approximately 20% of the pools in each stream, with sample pools distributed longitudinally from the mouth to the upper extent of fish in each stream. Sample pools were selected using spatially stratified random sampling in 2014 and the same sites were revisited in 2015-2017. At capture, fish were measured for fork length (FL, mm) and mass (0.01 g) and a small tissue sample was removed from the caudal fin for genetic analyses. Fish that exceeded 2g and 60 mm FL were tagged with a 2mm passive integrated transponder (PIT) tag, which allowed us to track life history expression. All fish were scanned for PIT tags prior to tagging, and any recaptures were noted and re-measured for length and mass.

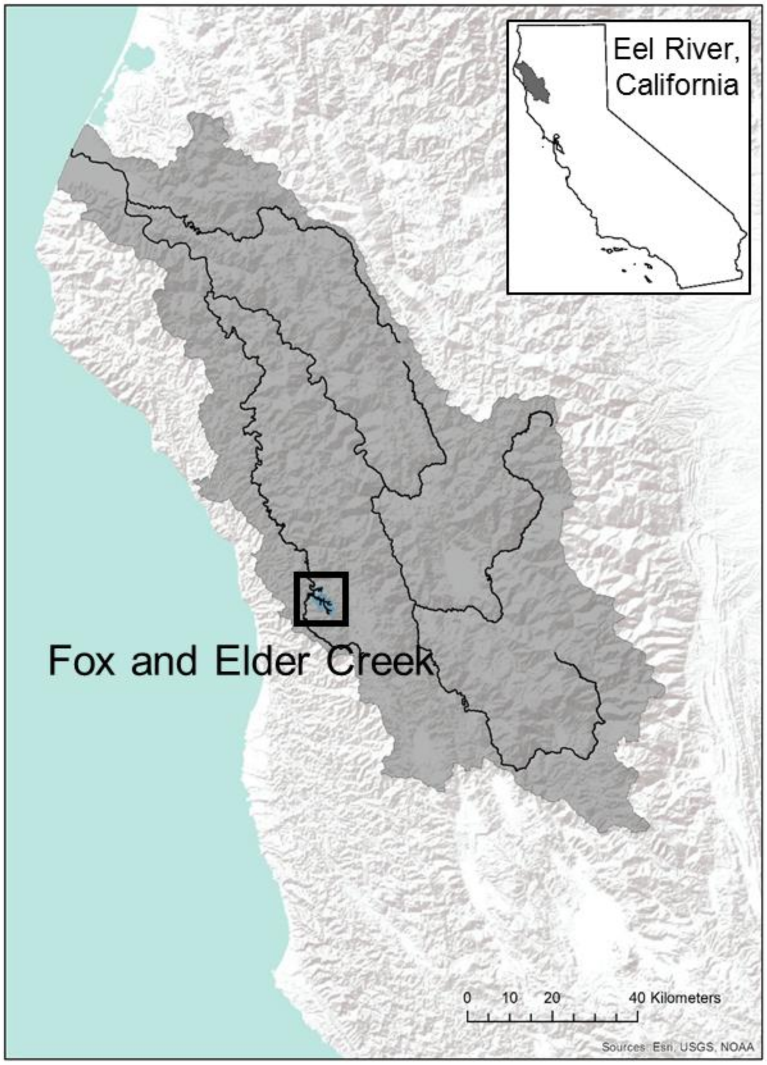

Figure 1. Fox and Elder Creek are headwater tributaries to the South Fork Eel River in the Eel River watershed in coastal Northern California.

DNA Extraction and Sequencing and SNP Discovery

We extracted DNA from caudal fin samples as described by Ali et al (2016). We included all of the samples collected in 2014 and a sub-sample from 2015-2017, where every-other sample pool was included in the genetic analyses. We conducted RAD capture (Rapture) following methods of Ali et al (2016). Libraries were sequenced using paired-end 100-bp (samples collected in 2014) or 150-bp (all other sample years) reads on Illumina HiSeq 2500 or HiSeq 4000 machines. Demultiplexing of sequence data was performed by requiring a perfect barcode (unique to each sample) and partial restriction site match (Ali et al. 2016). Sequences were aligned to a recent rainbow trout genome assembly (https://www.ncbi.nlm.nih.gov/assembly/GCF_002163495.1/) using the MEM algorithm of Burrows-Wheeler Aligner (BWA) (Li and Durbin 2009) with default parameters. SAMtools (Li et al. 2009) was used to filter alignments for proper pairs, sort alignments, remove PCR duplicates, and index binary alignment map (BAM) files. Picard was used to remove PCR duplicates **(**http://broadinstitute.github.io/picard).

All Rapture sequencing data analyses were performed using Analysis of Next Generation Sequencing Data (ANGSD) (Korneliussen et al. 2014) with a minimum mapping quality score of 20, and a minimum base quality score of 20. To select sites (single nucleotide polymorphisms, or SNPs) appropriate for downstream analyses, the following steps were applied. Major and minor alleles were inferred for sites with a high probability of being variable (SNP-p-value < 1e-6) from genotype likelihoods using the SAMtools genotype likelihood model (Li et al. 2009). Allele frequencies were estimated assuming a fixed major but unknown minor allele (Kim et al. 2011) and a uniform prior. Sites with a minor allele frequency less than 0.05 and sites missing data in more than half of individuals were excluded.

Assigning Migratory vs Resident Genotypes

To determine life history genotype groups, we sampled a single base from each position on Omy5, the chromosome with the migration-associated block of linkage disequilibrium (Pearse et al. 2014), that passed the filtering described above (415 total) and conducted a discriminant analysis of principal components (DAPC) (Jombart et al. 2010) with the allelic information. Single read sampling mediates the effects of coverage differences between individuals and allows the inclusion of data from positions and samples with low coverage, facilitating the inclusion of a larger number of samples than would be possible with called genotypes (Korneliussen et al. 2014). Due to its large size and high divergence, the variation in the migration-associated region dominates the discriminate analysis of Omy5 (Fig. 2).

We used the “find.cluster” method implemented in R package “adegenet,” a method that uses model selection to infer genetic groups by partitioning genetic variation into between- and within-group variation. We calculated Bayesian Information Criteria (BIC) for cluster models including k=1 to k=10 clusters, and calculated the decrease in BIC between models to identify the optimal number of clusters (Jombart et al. 2010), methods akin to choosing the number of clusters in STRUCTURE (Evanno et al. 2005). Missing data were replaced with the mean value at each locus, which led to individuals with missing data being grouped into the heterozygote group. To avoid false heterozygotes, we included individuals who had data at a minimum of 165 SNPs (heterozygosity increases among individuals who are missing more than this number of SNPs, see also Appendix 1). This decision resulted in excluding life history genotype classifications for 54 individuals, 41 of which were assigned heterozygote-genotypes.

Genetic Sex Determination

We conducted additional analyses on a subset of samples to determine their genotypic sex using presence/absence of a Y chromosome-linked marker, using sequences described by Brunelli et al. (2008). We used 1-10 ng of DNA as a template for a Taqman SNP genotyping assay (Life Technologies Corporation, Carlsbad, CA). PCR reactions were done in a 10 uL volume containing Taqman GT Master Mix, and custom Taqman probes and primers for OMY1-2SEXY and an autosomal SNP to distinguish between a lack of template and lack of Y-chromosome. The amplification was conducted on a QuantStudio3 (ThermoFisher Scientific) and consisted of a 10 minute hold at 95°C and then 40 cycles of 15 seconds at 95°C and 1 minute at 60°C. Each plate included one male and one female control in addition to two blanks. Control samples for each sex were collected from known-sex adult *O. mykiss* at the Warm Springs Hatchery in Santa Rosa, CA. We also calculated the sex ratios for a random subset of juvenile, age-0 fish (< 80 mm FL, n = 239), to confirm a 1:1 sex ratio at the juvenile life stage.

Assigning Life History Ecotypes at an Individual Level

We assigned observed life history ecotypes based on mark-recapture histories of individual fish and body size. In brief, individuals were assigned “migratory” if they were detected moving downstream during the spring smolt outmigration window, and were assigned “resident” if they exceeded a size threshold (described below). To detect downstream movement, we installed stationary antennas at the mouths of each creek. We used multiplex readers from Oregon RFID (Portland, OR), and antennas were operated from November 2014 through May 2018 in Elder and Fox creeks (installation November 2014 in Elder and May 2015 in Fox). Antennas were located 200m and 350m upstream of the mouth in Elder Creek and 175 m and 195 m upstream of the mouth in Fox Creek. We attempted to operate antennas continuously, but high-flow events dislodged the antenna wires for periods during the wet season (up to 19 consecutive days). Here we focus on detections during the smolt migration window, from February-May, which is the period when *O. mykiss* smolts have been observed migrating in the Eel River watershed (Brown 1990). Individuals were assigned a “migratory” ecotype if they were detected moving downstream past the antenna arrays during these months (first detected at the upstream antenna and then at the downstream antenna). A subset of fish (n=30) were removed due to detection histories that suggested persistent local movement and/or shed tags (i.e., detected moving both upstream and downstream, and were detected at the antenna over a span of time >36 hours, with 9-6571 detections per tag). There was a subset of individuals who were only detected once in the migration time frame, which only occurred when one antenna was functioning. Because all of the directional detections (n = 98) that occurred during the smolt outmigration period were in the downstream direction, we assumed that these single-movements also represented fish moving downstream (n = 175). See Kelson et al. Chapter 4 for further description of antenna efficiencies and movement categorizations. It is important to note here that we are assigning individuals to ‘migratory’ ecotypes, rather than ‘anadromous,’ and some individuals who are moving out of these headwater tributaries may be migrating to another part of the watershed rather than to the ocean.

We assigned individuals to a resident ecotype if they were >160 mm FL in July based on several lines of evidence. First, no individuals larger than 160 mm were detected moving downstream past the antennas in during the outmigration window (98.2% of fish detected were less than 155 mm FL). Second, mark recapture data (Kelson et al., Chapter 4) and length frequency plots (Fig S1) indicate that a fish of 160 mm FL in the summer months is typically 2+ years old. The dominance of age-0+ and age-1+ fish in the out-migrants has been noted previously from *O. mykiss* smolt trapping in the South Fork Eel River (Brown 1990), and from a smolt trap operated in nearby Pudding Creek (Mendocino County, CA; Ohms et al. 2014). Finally, this size cut-off is larger (i.e., more conservative) than the size threshold of 150 mm that was applied in nearby populations of *O. mykiss* to assign "resident" fish (streams in central California, Rundio et al. 2012).

Data Analyses

To determine if sex ratios differed from 1:1 in juvenile fish, out-migrating fish, and resident fish, we used exact binomial tests, computed in R (R Core Team 2017).

We modeled the relationship between life history genotype, genotypic sex, and life history ecotype using generalized linear models in R. Specifically, we used binomial models, with migratory fish assigned a value of 1 and resident fish assigned a value of 0. We calculated BIC for six models with different combinations of predictor variables: 1) sex, 2) life history genotypes, 3) sex and life history genotypes, 4) sex, life history genotype, and their interaction, 5) sex, life history genotype, and sample location, and 6) sex, life history genotype, their interaction, and sample location. We also calculated r^2 using the "rsq" package (Zhang 2018) for models including sex, genotype, and the combination of the two (models 1-3 listed above) to compare the ability of these factors to predict life history expression independently and in combination.

We combine data from Fox and Elder creek in the results below for two reasons. First, we had limited sample sizes from Fox Creek (n = 38 individuals out of a total of 284 assigned a life history ecotype were from Fox). Second, the best fit generalized linear binomial model did not include capture location (see Results).

Predicting proportion of resident fish from sex and genomic data

We used an equation from Ohms et al. 2014 to estimate the proportion of the combined population that migrates, given the sex ratios in the out-migrating fish, the resident fish, and the juvenile (baseline) fish. In this model, if sex ratios are skewed for only the resident fish, but close to 1:1 for the out-migrating fish, then the number of individuals expressing residency is a small proportion of the total population (see also Ohms et al. 2014). We applied the same equation, substituting migratory allele frequencies for sex ratios, where:

$P = (r-b)/(r-m)$

If *P* is the proportion of migrants, *m* is the migratory allele frequency of migratory ecotype fish, *b* is the baseline migratory allele frequency of pre-migrating-aged fish, and *r* is the migratory allele frequency of resident fish.

Results

Resident and Migratory Genotypes

When grouping individuals into clusters based on Omy5 SNPs, we found the largest reduction in BIC occurred between models with k=2 and k=3 clusters (Fig S2), which aligned with our prediction of 3 groups (resident, heterozygous, and migratory) corresponding to each genotype. We used group membership to call individuals as resident, heterozygous, or migratory genotypes (Fig 2). Hereafter, we refer to the group assignment as "genotype," where the "migratory genotype" means homozygous for the haplotype associated with the migratory life history, "resident genotype" means homozygous for the haplotype associated with the resident life history, and "heterozygous" means one copy of each haplotype. Across 4 years of sampling (2014-2017), the overall genotype frequency for juvenile fish (n = 3930) in these streams was 24.9% migratory, 39.8% heterozygotes, and 35.1% resident.

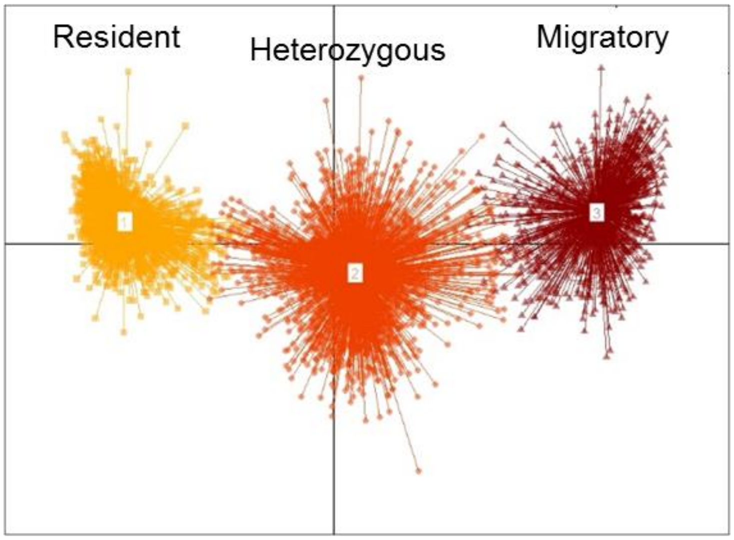

Figure 2. A discriminant analysis on principle components of Omy5 SNPs groups individuals into three clusters, which are used to assign individuals to resident (1, yellow), heterozygous (2, orange), or migratory (3, dark red) genotypes.

We found that migratory-genotype fish were unlikely to remain in the streams as resident fish, as resident-ecotypes were comprised of 55.2% resident genotypes, 38.8% heterozygous genotypes, and only 6% migratory genotypes (Fig 3). Similarly, we found that the proportion of migratory alleles decreased in a cohort of fish from age-0 to age-2+ (i.e., as the cohort aged, Fig 4a), also indicating that migratory-genotype fish were less likely to remain in the stream as older fish.

In contrast, we found that resident-genotype fish often expressed the migratory ecotype, and the genotype frequencies in the migratory-ecotypes (30% migratory, 45.3% heterozygote, and 24.7% resident genotypes) were very similar to the baseline juvenile genotype frequencies (Fig 3). Similarly, we found that migratory-ecotype fish did not always include a higher proportion of migratory alleles when compared to all the fish caught the previous summer (the baseline for that year, Fig 4b).

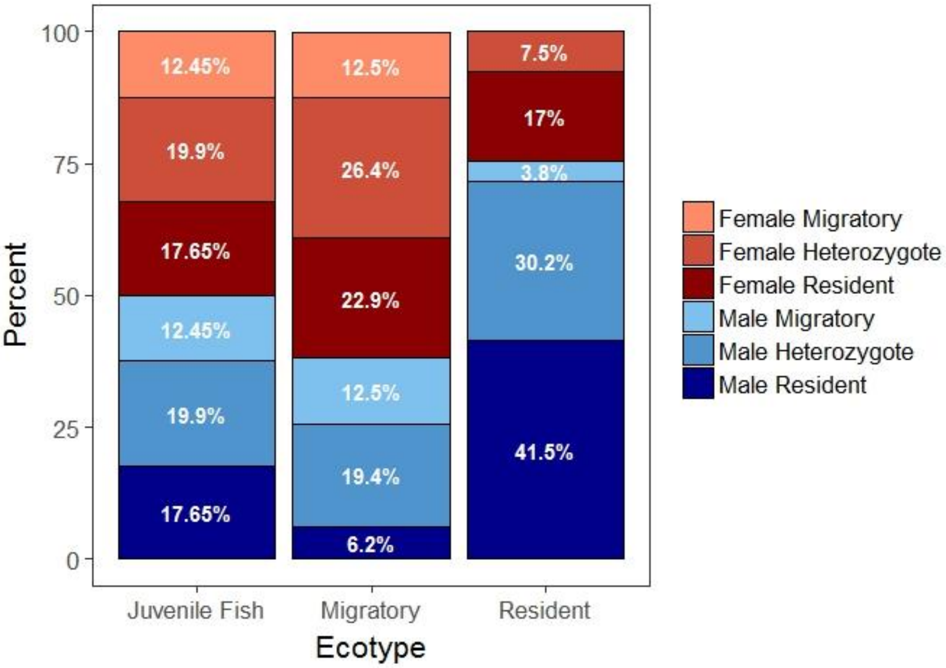

Fig 3. Bar chart showing the life history genotype and genetic sex for fish assigned to the migratory ecotype (n = 213 fish) or resident ecotype (n = 71 fish) in comparison to juvenile fish, which are assumed to have an even sex ratio for visualization.

Genetic Sex Determination

For juvenile fish (i.e., age-0, <85 mm FL, n = 252), 48.8% were male and 51.2% were female, which was not significantly different from a 1:1 ratio (binomial test, P = 0.75). For fish assigned a resident ecotype (n=58 with sex data), 78.7% were male (binomial test, P < 0.01, 95% confidence interval from 64.7% to 87.5%). In contrast, migratory ecotype fish (n=153 with sex data) were 38.1% male, which differed significantly from an even sex ratio (binomial test, P <0.01, 95% confidence interval from 30.3% to 46.2%).

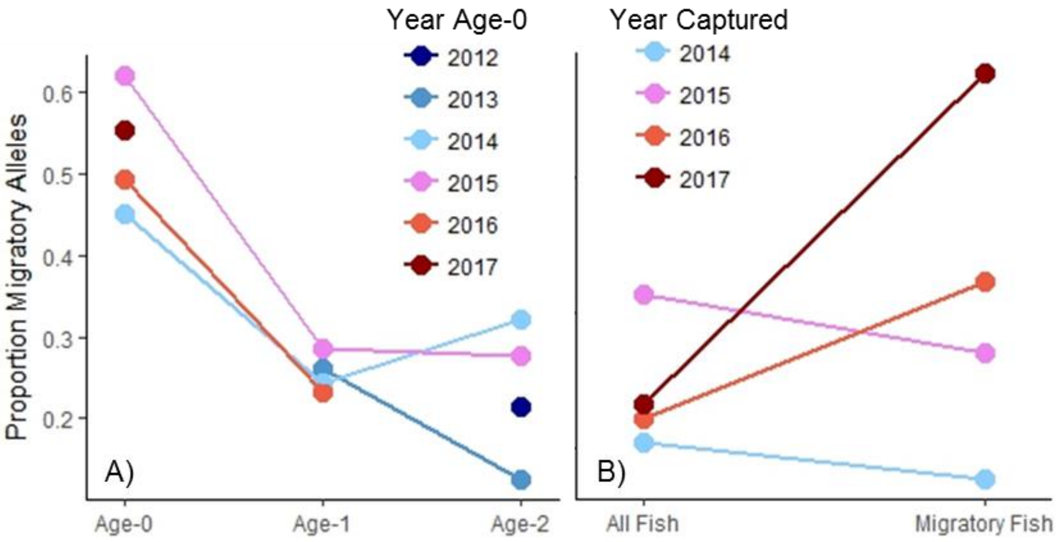

Fig 4. A) The proportion of migratory alleles in year-class remaining in freshwater decreases with time (age) of fish. B) The difference in proportion of migratory alleles for all fish vs. fish out-migrating fish depends on the year.

Table 1. We used BIC to compare models to predict life history ecotype from sex, genotype, and capture location, listed in order of highest to lowest BIC.

Predictor variables	**BIC**
Sex + Genotype	200.1
Sex + Genotype+ Location	209.2
Sex * Genotype	209.8
Sex	232.7
Sex * Genotype+ Location	218.5
Genotype	269.4

Combining life history genotype and sex to predict ecotype

Migratory ecotypes consisted of fish from every life history genotype (migratory, resident, and heterozygous) but were female-biased (Fig 3). In contrast, resident ecotypes consisted primarily of resident genotypes and were male-biased (Fig 3). Notably, there were no female migratory-genotype fish who expressed the resident ecotype, and correspondingly, there were very few male resident-genotype fish who expressed the migratory ecotype (Fig 3).

We found that the best model (lowest BIC) describing whether individuals expressed a migratory or resident ecotype included life history genotype and sex (Table 1). The probability of out-migrating increased with the addition of migratory alleles: migratory genotypes were the most likely to out-migrate (probability for males = 0.88 and for female = 0.98), followed by heterozygotes (male = 0.62, female = 0.92), and then resident genotypes (male = 0.35, female = 0.79) (Fig 5a). Based on effect sizes of parameters, sex was more important than genotype in explaining variation in ecotype (Fig 5b, with heterozygote-female as the intercept, z = 6.0, P <

0.01, migratory-genotype, z = 2.4, $P < 0.05$, resident-genotype, z = -3.2, $P < 0.01$, and male z = -4.9, $P < 0.01$). Similarly, the correlation between genotype and life history ecotype ($r^2 = 0.20$) was lower than the correlation between sex and life history ecotype ($r^2 = 0.31$), but including both factors had the highest correlation ($r^2 = 0.45$).

Using Sex and Allele Frequencies to Estimate Proportion Residency

Using the sex ratio data from our system as input data to the equation from Ohms et al. (2014), we estimated that 70.7% of the population migrated. Using migratory allele frequencies in the migratory vs. resident ecotypes, we estimated that 88.3% of the population migrated.

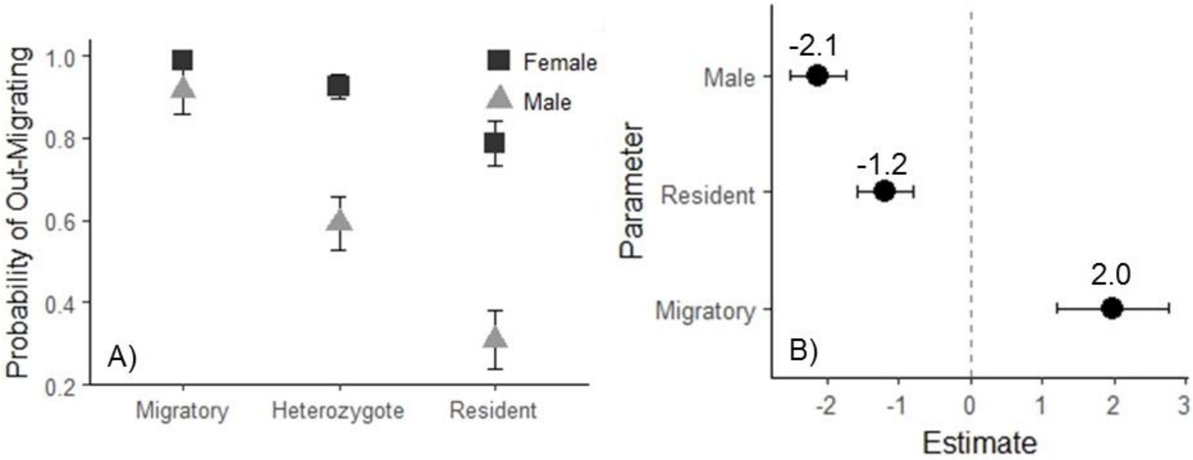

Fig 5. A) Predictions from a binomial model for the probability of out-migrating given an individuals' life history genotype and genetic sex. **B)** Coefficient estimates and standard error for parameters predicting the outmigration probability of a fish. Parameters are calculated in contrast from a female heterozygote.

Discussion

Overall, we found that genetic sex and life history genotype are useful for estimating life history ecotype in partially migratory *O. mykiss*, especially when used in combination. Migratory-genotype fish were more likely to leave the streams, and this pattern was most pronounced for females. Moreover, the large, resident fish in these streams were comprised of resident and heterozygous-genotypes, and were male-dominated. The model that included sex and life history genotype to predict ecotype explained more variation than including each variable alone ($r^2 = 0.45$, in comparison to sex alone, $r^2 = 0.30$, or life history alone, $r^2 = 0.20$). Over half of the variation in life history ecotype was unexplained by life history genotype and genotypic sex, suggesting a strong role of the environment, or unidentified genetic differences, in determining migratory ecotype in partially migratory populations. This result indicates that in these systems there is value in conserving genetic diversity. Specifically, resident-genotypes have potential to express migration, and thus have value in conserving life history diversity in partially migratory populations.

Sex-linked Freshwater Maturation and Migration

In our system, genetic sex was correlated with observed life history, with resident-ecotypes dominated by males and migratory-ecotypes dominated by females (Fig 3, Fig 5a). The male-biased sex ratio in large, resident fish that we observed (79%) was close to the ratio observed (83%) in Big Creek (Monterey County, Rundio et al. 2012). In contrast, approximately 800 miles north, in the South Fork John Day River (Oregon), there was a 1:1 sex ratio among older fish (Ohms et al. 2014). This variation among systems suggests that the propensity for male-bias in resident fish may depend on the environmental context. Overall, favorable freshwater growth conditions lead to a higher likelihood of freshwater maturation in male *O. mykiss* (McMillan et al. 2007, Doctor et al. 2014, Kendall et al. 2014), with males tending to be more plastic than females in exploiting freshwater resources in partially migratory populations (Berejikian et al. 2014). The pattern of male-maturation in high growth conditions has been observed across salmonid systems (Jonsson and Jonsson 1993, Hendry et al. 2003), including widespread precocial maturation of age-0 male *Salmo salar* following a flood-induced pulse of food resources (Letcher and Terrick 1998). Additionally, the decision to mature in freshwater for males may be driven by access to mates (Gross 1985, Fleming and Reynolds 2003, Sloat et al. 2014).

Similarly, female-bias in migrating fish also has been documented in salmonid systems. For example, Ohms et al. 2014 reported female-bias is *O. mykiss* out-migrants, with females representing 56%-76% of out-migrants in streams from Northern California, Washington, Oregon, and Idaho, comparable to our results (61.9% females in the out-migrants). Long-term studies on Atlantic salmon also reported that out-migrants can be female biased; across 7 years in the Saint Marguerite River, Quebec, Canada, females represented 50%-64% of the out-migrants (overall mean = 59%) (Páez et al. 2011). Similarly, females represented 51-76% (overall mean = 64%) of out migrating *S. salar* across 11 years in the River Imsa, Norway (Jonsson et al. 1998). This pattern is consistent with the theory that females are more likely to benefit from migration due to enhanced growth opportunities and, hence, fecundity (Jonsson and Jonsson 1993, Fleming and Reynolds 2003, Hendry et al. 2003). Together these studies suggest that across salmonids females are more likely to undertake ocean-migration than males, but, similar to male-bias maturation, this tendency may vary among populations (experiencing different growth conditions) or within populations (experiencing temporal variation in growth conditions).

It is important to note that male-bias in residents does not necessarily imply female-bias in out-migrants. When one life history strategy makes up a relatively small proportion of the overall population, sex ratios of the two life history forms become decoupled (Ohms et al. 2014). In our system, for example, the female-skew we observed in out-migrants (61.9% female) was not as extreme as the male-bias observed in freshwater residents (78.7% male). That sex ratios can be decoupled highlights the importance of estimating sex ratios in both the out-migrants and residents to understand the propensity of each sex to migrate within a given system, and accordingly the utility of genetic sex for predicting life history ecotype.

The Role of the Environment: Resident-Genotype Fish Can Express Both Life Histories

We found that including information about both life history genotype and sex was the strongest predictor for individual life history decision, however 55% of the variation remained unexplained. The decision to migrate is often considered a threshold trait, with individuals who reach a large enough body size by a certain time out-migrating the following spring (Satterthwaite et al. 2009, 2012). Beyond growth rates, the propensity to migrate can be influenced by body condition (Sloat and Reeves 2014), epigenetic regulation (Baerwald et al. 2015), and indirectly by maternal history (Liberoff et al. 2014), all of which we did not quantify in this study. Further research could identify if gene expression differs at the Omy5 loci for resident versus migratory ecotypes. Given that migration is a partially plastic trait, it is not surprising that life history strategy did not correlate perfectly with genotypic assignment in partially migratory populations.

Migratory-ecotype individuals included a mixture of genotypes that was similar to the juvenile, or "baseline," frequencies, including both resident- and heterozygous-genotype fish. This result emphasizes the importance of maintaining resident-genotype fish in partially migratory populations because they are a source of migrants. Conservation of genetic diversity may buffer phenotypic variability in partially migratory populations. This result builds on a suite of earlier studies using otolith microchemistry to reveal that both resident and anadromous mothers can produce anadromous offspring (Zimmerman and Reeves 2000, Riva-Rossi et al. 2007, Zimmerman et al. 2009, Hodge et al. 2016). Similarly, studies from a population of *O. mykiss* isolated above a barrier for over 70 years revealed that the fish are still able to undergo smoltification, though with reduced fitness (Thrower and Joyce 2004, Thrower et al. 2004). In general, this body of work emphasizes the plastic nature of life history ecotypes in partially migratory populations of *O. mykiss*, further demonstrating the importance of conserving the full suite of diversity.

Management Implications

A vexing management problem for partially migratory populations such as *O. mykiss* is determining the proportion of the population expressing the migratory ecotype of conservation concern. We suggest that genotyping at Omy5 is more useful at the population level (as demonstrated by Abadía-Cardoso et al. 2011, Pearse et al. 2014, Apgar et al. 2017), than at the individual level given the influence of the environment. We generated two estimates for the percent of the population expressing migration, the first based on sex ratios (estimated 70.7% migration) and the second based on migratory allele frequencies (estimated 88.3% migration) in these streams. Both approaches suggest that most of the population out-migrates from these creeks. The mathematical models used to generate these estimates included simplifying assumptions such as an assumption of equal mortality rates between sexes or genotypes before the life history decision window or before the samples are collected in wild fish. We suggest that using the sex ratios, rather than migratory allele frequency, are less likely to violate these assumptions. This is because other traits that have been linked to Omy5, including development rate (Miller et al. 2012) and growth (Nichols et al. 2008), could be related to age-specific mortality. Future studies could test the assumptions of these models by estimating sex-specific and genotype-specific juvenile mortality rates in freshwater for wild *O. mykiss* to further evaluate the utility of this approach for estimating the proportion of the population that is migratory.

For predicting ecotype at the individual level using genetic information, our results indicate that genetic sex provides more explanatory power than life history genotype. Determining genetic sex is a relatively easy and inexpensive procedure, and can be done using qPCR to genotype at two SNPs (one autosomal control and one Y-chromosome SNP), which further highlights the value of this genetic tool for informing management and conservation decisions (see also Rundio et al. 2012).

Conclusions

Within partially migratory populations of *O. mykiss* and other salmonid fishes, there is interest in conserving and restoring migration where it has been lost. Evaluating the success of conservation and restoration efforts requires an understanding of the proportion of the population expressing migration, which can be tackled at the population level (by estimating genotype frequencies or the proportion of fish expressing each life history) or the individual level (by correlating life history ecotype with life history genotype, as we did here). Our results suggest that genetic tools, especially when combining information on genetic sex and life history-genotype, can be useful in estimating life history ecotype in partially migratory populations. However, 55% of the variation in life history ecotype remained unexplained after accounting for genetic sex and life history genotype. Our results suggests that using these tools at the population level is more appropriate for management decisions because life history genotype does not perfectly predict life history expression at the individual level. More generally, our results emphasize the importance of conserving genetic diversity in protected partially migratory populations, including conserving resident fish in addition to migratory fish, because resident genotypes can give rise to migratory ecotypes.

Acknowledgements

This study was co-authored by Michael R. Miller, Tasha Q. Thompson, Sean M. O’Rourke, and Stephanie M. Carlson. We thank Peter Steel, the reserve manager at the UC Angelo Coast Range Reserve, for facilitating several aspects of this research. This work was funded in part by a National Science Foundation Graduate Research Fellowship to SJK and the NSF CZO EAR-1331940, Eel River Critical Zone Observatory. Additionally, SJK was supported by the Wildlife Fund at UC-Berkeley and the UC Natural Reserve System Mildred E. Mathias Award.

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Supplemental Figures

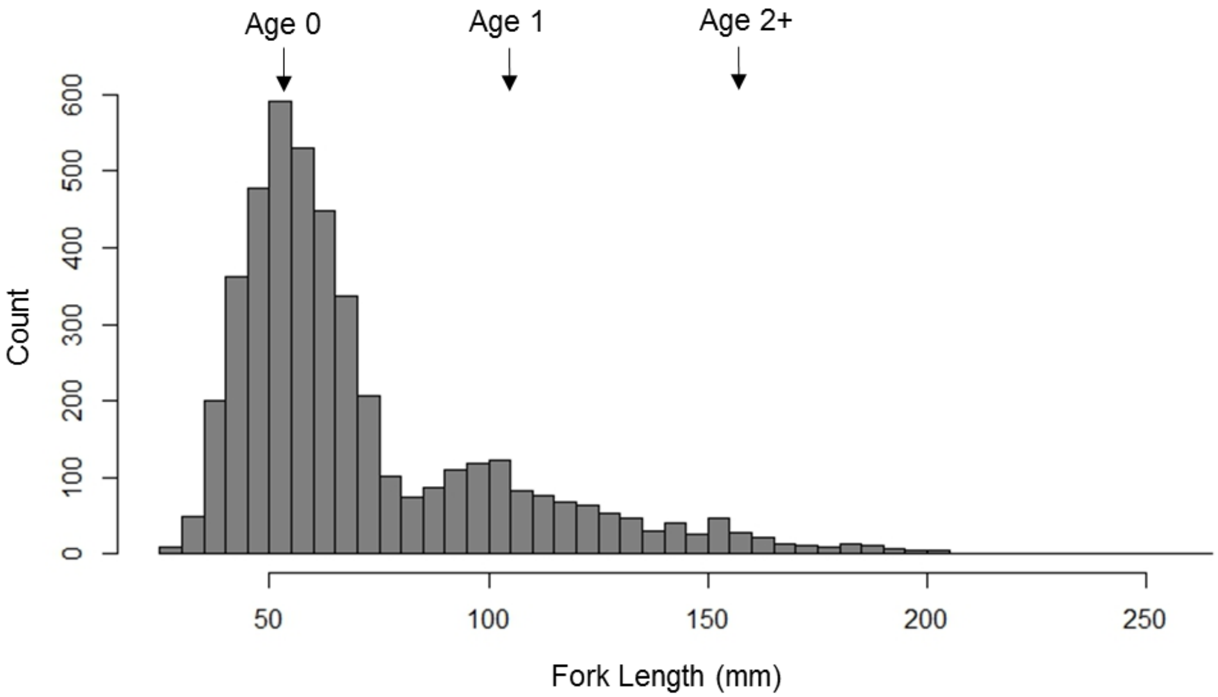

Figure S1. Fork-length histograms for all fish captured in mid-summer (July – August), including sampling from 2014-2017, indicate that fish over 160 mm FL are likely 2+ years old.

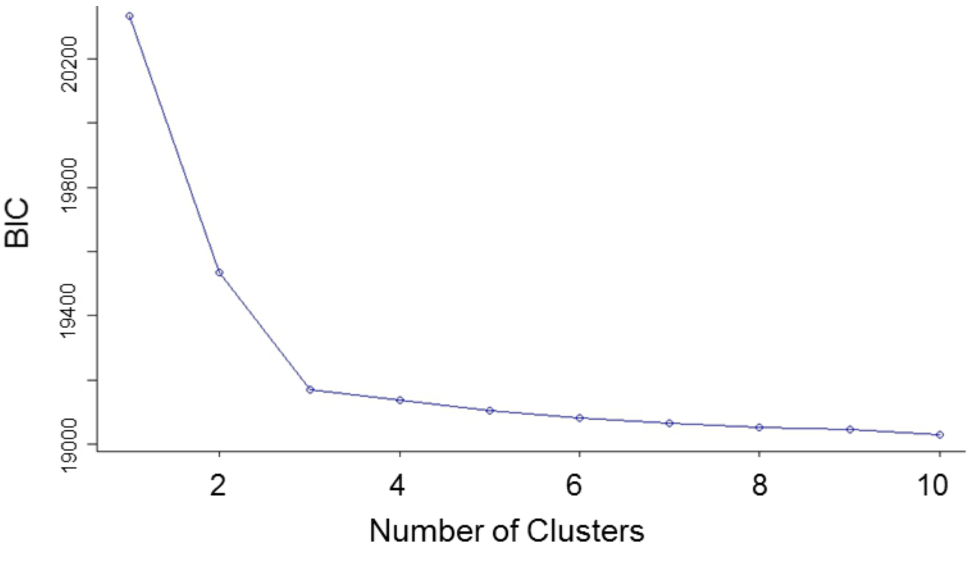

Figure S2. Bayesian Information Criteria for k=1-10 clusters describing the variance of SNPs on Omy5. The largest reduction in BIC occurred between k=2 and k=3 clusters, aligning with our prediction of 3 genotype groups (resident, heterozygous, and migratory) on Omy5.

Appendix 1. Minimum number of SNPs per individual to be assigned a genotype

We chose to exclude genetic data from Omy5 for individuals who were missing data at 250 out of 415 SNPs (60%). Heterozygosity is higher among individuals who are missing more than 60% of SNPs, compared to individuals who are missing less than 60% (Fig A1). In order to conduct the DAPC, missing data was replaced with the mean allele frequency for each loci, which lead to individuals who were missing data at over half of the loci to be categorized within the middle group, or as heterozygotes (Fig A2, Fig A3). Individuals who were missing this amount of SNPs were more likely to be categorized as 'heterozygotes,' or grouped into the middle group, because we replaced missing SNPs with the mean allele frequency.

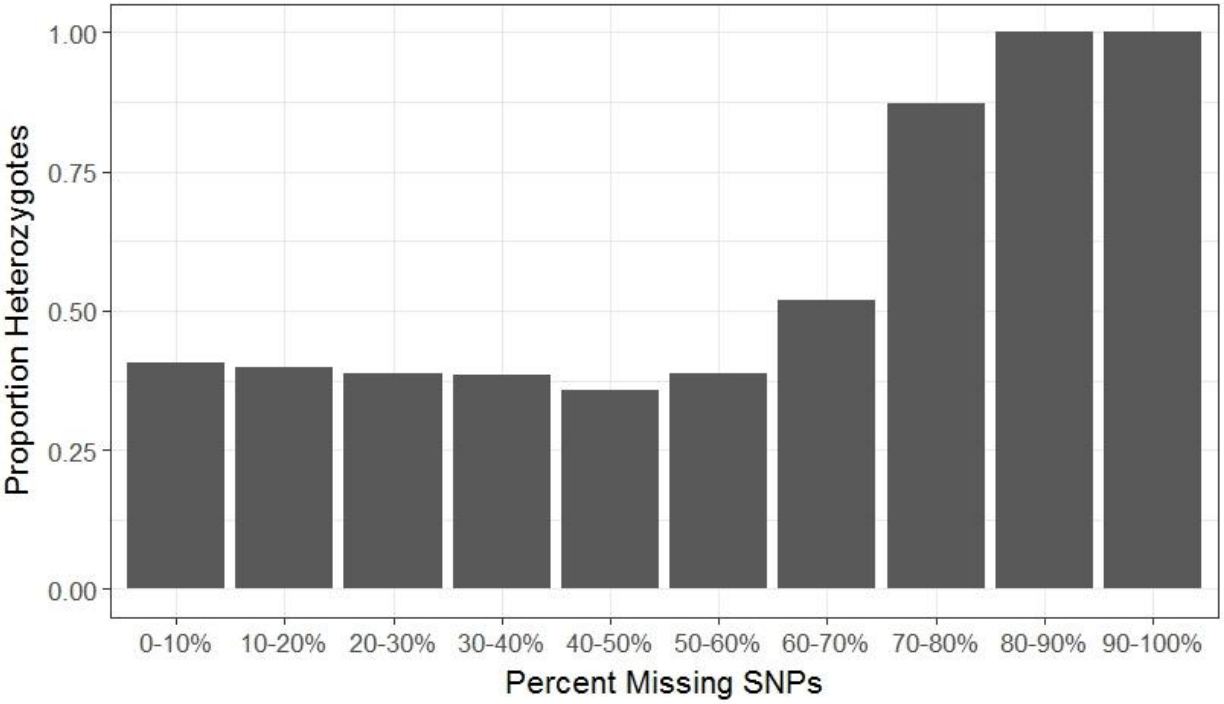

Fig A1. Heterozygosity is higher among individuals who were missing data at more than 165, or 60% of SNPs, so these individuals were excluded from analyses.

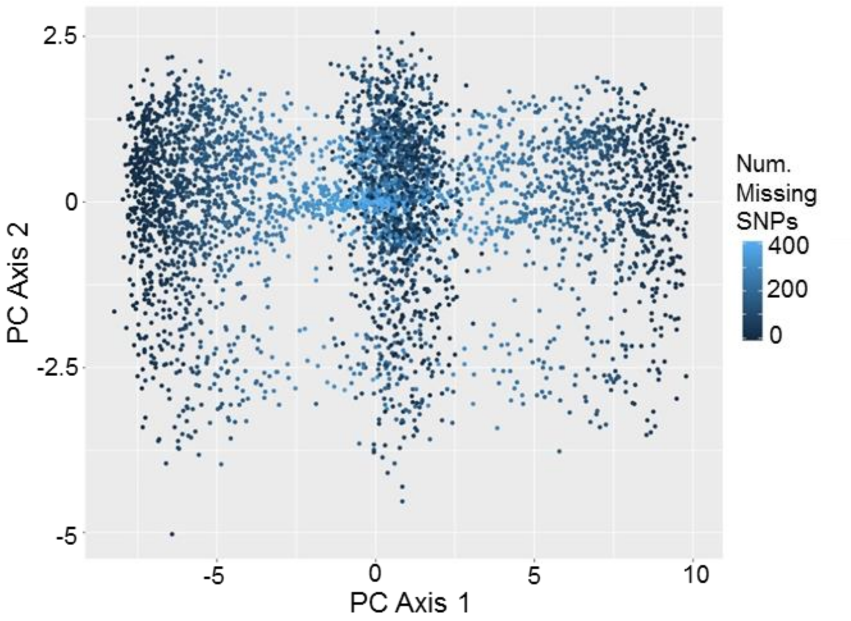

Figure A2. Individuals who are missing data at many SNPs tend to fall between the main three clusters or are classified within the middle, or heterozygote cluster.

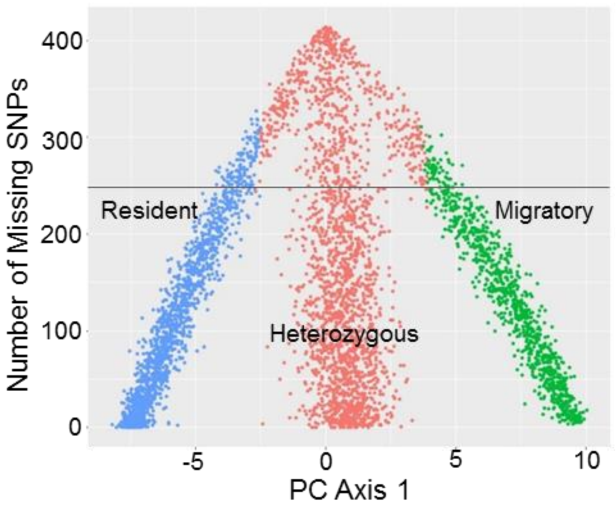

Figure A3. A plot of score one the first principal component against the number of missing SNPs per individual indicates that individuals who are missing data at many SNPs (i.e., over 250 SNPs) have a score on the first PC that falls between genotype groups, and are more likely to be called heterozygotes.

4

Ecological effects of partial migration: evidence from a salmonid fish

Abstract

Genetic variation among individuals within the same species can be associated with a suite of traits that have ecological consequences. We suggest that partially migratory populations, which are comprised of a mixture of resident and migratory individuals, may be excellent systems for studying genotype-phenotype-ecology linkages. In particular, we highlight partial migration in a salmonid fish, *Oncorhynchus mykiss*, in small coastal streams in Northern California. In this system, steelhead trout migrate to the ocean, whereas resident rainbow trout spend their entire life in freshwater, and the tendency to migrate has a strong genetic basis. We demonstrate that there are spatial differences in the frequency of migration-linked genotypes above and below a natural waterfall barrier (migratory allele frequency of 60% below the barrier vs. 31% above the barrier). Downstream, in the migratory-dominated region, juvenile fish in their first year of life were twice as dense compared to the resident-dominated region above the waterfall (0.46 vs 0.26 individuals/m^2, respectively), presumably reflecting the higher fecundity of migratory females. Additionally, upstream of the waterfall, there were twice as many older fish (0.13 vs 0.05 individuals/m^2). In summary, pools dominated by fish with migratory genotypes had higher densities of young and lower densities of older trout, and a simpler size structure than pools dominated by resident genotypes. Older resident trout had more enriched δ^{15}N, suggesting that they fed at a higher trophic level (6.1± 0.62 ‰ δ^{15}N versus for juvenile fish and 7.8 ± 0.83 ‰ δ^{15}N for older fish). We did not, however, detect evidence for a trophic cascade in biomass of primary consumers sampled above and below the waterfall. Phenotypic divergence between individuals adopting a resident versus migratory life history strategy is a common feature of partially migratory populations, suggesting considerable potential for ecological effects arising from this intraspecific variation.

Introduction

Intraspecific variation, or phenotypic variation among individuals of the same species, can have a strong ecological consequences, including on community structure (Bolnick et al. 2011) and ecosystem processes (Des Roches et al. 2018). For example, divergence in foraging traits in a predatory fish drives changes in the average body size and species richness of lake zooplankton prey communities (Palkovacs and Post 2009). In some systems, intraspecific variation can have an ecological effect that is of similar magnitude to interspecific variation (Des Roches et al. 2018).

When heritable intraspecific variation leads to ecological change, it is often considered an ‘extended phenotype’ of a genotype (Whitham et al. 2003). These genotype-ecological interactions have been studied extensively in plants, revealing that genetic variation can be associated with a suite of ecological changes. For example, genetic variation alters the functional response curve of seed predators on herbs (Abdala-Roberts and Mooney 2014), indirectly effects trophic interactions between herbivores and their insect parasitoids in coastal willows (Barbour et al. 2016), and determines the composition of root fungal communities in pine trees, which can lead to drought tolerance (Gehring et al. 2017).

Here we suggest that partial migration is a form of intraspecific variation with likely large ecological consequences. Partial migration describes the phenomenon where a subset of individuals within a population migrate, while others do not. Partial migration is common across migratory animals (Chapman et al 2011), including examples from ungulates (Ball et al. 2001, Cagnacci et al. 2011), fishes (Chapman et al. 2012), birds (Boyle 2008, Jahn et al. 2010, Sanz-Aguilar et al. 2012), and insects (Attisano et al. 2013, Odermatt et al. 2017). While much research on partially migratory animals has focused on understanding trade-offs between life history strategies (i.e., migrating or not, reviewed in Chapman et al. 2011) or exploring the evolutionary stability of this polymorphism (e.g., Lundberg 2013, De Leenheer et al. 2017), there has been less focus on the ecological consequences of this form of intraspecific variation (e.g., Fryxell and Sinclair 1988, Palkovacs and Post 2009).

By linking disparate ecosystems, migration has a suite of ecological consequences (Lundberg and Moberg 2003, Bauer and Hoye 2014). For example, migratory animals can transport other organisms, such as aquatic invertebrates and plant seeds in waterfowl guts (van Leeuwen et al. 2012). Migrants can also provide food subsidies for resident predators, such as the subsidy of waterfowl for Arctic foxes (Giroux et al. 2012) or of adult mayflies for stream-dwelling trout (Uno and Power 2015). Thus, it is likely that partial migration also has strong ecological effects through life-history associated trait differences. For example, across partially migratory animals, migratory and resident conspecifics often differ in body size (Chapman et al. 2011) with consequences for size-dependent thermal tolerance (Ketterson and Nolan 1976, Belthoff and Gauthreaux 1991), predation risk (Hansson and Hylander 2009), metabolism (Sloat and Reeves 2014), or diet specialization (Dobson 2009). Body size can influence fecundity (Blueweiss et al. 1978), feeding preferences (Wilson 1975, Werner and Gilliam 1984), and per capita nutrient cycling (Torres and Vanni 2016). Additionally, the contrast between individuals with long, uninterrupted residency periods and migratory individuals that have pulsed, often seasonal arrivals has large consequences for the dynamics of trophic structure in the natal/resident habitat (Fryxell and Sinclair 1988, Brodersen et al. 2008).

Partial migration is common among salmonid fishes (Jonsson and Jonsson 1993, Dodson et al. 2013), and the genetic basis of migration is well-established within the Salmonidae family (Northcote 2010, Dodson et al. 2013). In the case of *Oncorhynchus mykiss*, or steelhead/rainbow trout, migration tendency has been linked to a specific region of the genome (Thrower et al. 2004, Hecht et al. 2012, Pearse et al. 2014), which opens the door to exploring the ecological effects of partial migration in this species.

Migratory and resident *O. mykiss* commonly co-occur in coastal streams, including our study sites in Northern California, allowing us to explore links between genotypes and population and community ecology. In particular, we characterize migratory genotypes of *O. mykiss* within two streams and then explore the population (density and size structure) and community (food chain length and lower trophic level biomass) effects. At the population level, we predicted that pools and regions where the migratory genotype dominates would be characterized by a high density of juvenile (young of year) fish due to the high fecundity of large, migratory females. Likewise, we predicted that pools and regions where the resident genotype dominates would be characterized by reduced density and more complex size structure due to the addition of older, larger resident fish. At the community level, we predicted a 4-level food web in regions dominated by resident fish with large resident fish comprising an additional trophic level. In contrast, we predicted a 3-level food web in regions dominated by migratory-genotypes, due to the smaller body size and simpler size structure overall. Finally, we predicted that in regions where the food web is characterized by 3-levels (primary producers, benthic macroinvertebrates, fish), the biomass of benthic macroinvertebrates would be reduced due to top-down predation by small fish. On the other hand, in the 4-level food web, we predicted that benthic macroinvertebrates would be released from predation by small fish due to the addition of large fish. We also predicted that because some large macroinvertebrates could escape in size from a small-gaped predator (juvenile fish) but not from a larger-gaped predator (older fish), macroinvertebrates in the upstream habitats might shift towards smaller size distributions.

Methods

Study system and streams

In partially migratory *O. mykiss*, the migratory form (“steelhead trout”) spends 1-3 years in freshwater before migrating to the ocean where they spend another 1-3 years feeding and growing, finally returning to freshwater to breed. In contrast, the resident form (“rainbow trout”) remains in freshwater for its entire life history. Migratory fish grow larger than resident fish, and are consequently much more fecund (e.g., ~5000 eggs for migratory females (Quinn 2005) vs. <1000 eggs for resident females (Moyle 2011)).

Our study focuses on Fox Creek and Elder Creek, both tributaries of the South Fork Eel River (Fig. 1), within the University of California Angelo Coast Range Reserve (39°44017.7″ N, 123°37048.8″ W). In these streams, *O. mykiss* is the dominant fish species, representing >99% of the fish biomass (the only other fish species is Pacific lamprey, *Entosphenus tridentatus*). Both creeks are mostly shaded: Elder Creek has a canopy cover of 88% ± standard deviation (std. dev.) 5%, measured with a spherical densitometer in 2014 at 142 study pools, and Fox Creek has a canopy cover of 92% ± 3%, measured at 57 study pools). Fox Creek drains 2.7 km^2 and is characterized by step-pool morphology (Montgomery and Buffington 1997). Elder Creek drains 16.8 km^2, and is characterized by riffle-pool morphology in lower reaches and step-pool morphology in upper reaches (Montgomery and Buffington 1997). Elder Creek has a large waterfall (3 m high from the pool floor to crest) 2.5 km upstream from the confluence with the South Fork Eel River (Fig. 1). This waterfall is a partial barrier to upstream-migrating adult steelhead, meaning that adult steelhead can pass the waterfall under some flow conditions (see Trush 1989, Kelson et al. CH1). This barrier provides an opportunity to examine stream ecology in regions of the stream that are easily accessible versus less accessible to migratory *O. mykiss*, hereafter referred to as ‘below’ versus ‘above’ the waterfall. We also included two fish-bearing tributaries to Elder Creek, Misery (drainage area of 1.9 km^2) and Paralyze (4.9 km^2), both upstream of the large waterfall (Fig 1).

Fish Sampling to Estimate Density and Size Structure

Before fish sampling commenced in June 2014, pools in Fox Creek and Elder Creek were numbered and mapped in the field by hand onto a topographic map. After mapping, study pools were randomly chosen using a spatially stratified design, so that study units ranged from the confluence with the South Fork Eel River to the upper extent occupied by fish. Our survey excluded the pools that were too deep for electrofishing (i.e., when maximum depth exceeded 1 m). We estimated the surface area of each pool within one week of sampling fish (see below), by measuring the length and average width, estimated from 5 width transects spaced evenly along the length transect.

To estimate density and size structure, we captured fish from study pools in late July to early August in each of four years (2014-2017). In 2014, we sampled fish from 142 study pools in Elder Creek and 57 study pools in Fox Creek. In the following years, we returned to the same pools, with some exceptions due to shifting of the stream channel and input of large woody debris (2015: n = 143 pools in Elder, n = 56 pools in Fox, 2016: n = 142 pools in Elder, n = 57 pools in Fox, 2017: n = 140 pools in Elder and n = 55 pools in Fox). When a pool was no longer accessible, we sampled the next upstream pool. We captured fish from study pools using standard three-pass electrofishing methods (Hauer and Lamberti 2006), with block nets set at the upstream and downstream ends of the pool to prevent emigration during sampling. Fish from each pool were counted, measured for fork length (mm), and weighed to the nearest 0.01g. We also removed a small sample of the caudal fin for genetic and isotopic analyses.

We estimated the number of fish in each pool using Leslie-K depletion methods (Leslie and Davis 1939, Ogle 2016). We found a high correlation between depletion estimates and the total catch for each pool (count data), and present the count data here (see Kelson et al, CH4). We present fish density as the count data divided by the surface area of each pool (abundance/surface area, or fish/m^2). We used the length data to characterize size/age structure of fish. We classified fish under 85 mm fork length (FL) at capture in July as juvenile fish, based on visual examination of the length-frequency histogram and determining the size where the two primary size modes intersect (Fig. 5) (Hall et al. 2016). This classification was problematic for the small subset of fish (n = 253 or 5% of the total sample) between 80 and 90 mm FL.

Summarizing Variation in Migratory vs. Resident Allele Frequencies

We extracted DNA from the tissue samples (total n = 3149 individuals). Genotyping methods are described in Kelson et al. (CH1 and CH2). In short, we conducted RAD capture (Ali et al. 2016), and sequenced libraries using Illumina HiSeq and then randomly sampled a single read at each single nucleotide polymorphism (SNP) per individual to create a 'single read' genotype dataset. We then conducted a discriminant analysis on the principle components (Jombart et al. 2010) from n= 415 SNPs on the migration-linked region of the genome (Pearse et al. 2014), which allowed us to group individuals into clusters of migratory, heterozygous, or resident genotypes.

We summarized the life history genotype data by calculating the number of fish that were assigned to each genotype in each study pool. We then calculated the migratory allele frequency, or proportion of migratory alleles, for each pool as a single quantitative variable to summarize the dominant life history genotype. Specifically, we calculated the proportion of migratory alleles by summing the number of migratory alleles (2 per migratory-genotype fish and 1 per heterozygote-genotype fish), and then dividing by the total number of alleles (2 per fish). In addition to summarizing the migratory allele frequency for each pool, we summarized the migratory allele frequency for Fox and Elder creeks as a whole. For Elder Creek, the largest differences in allele frequencies occurred among regions in the stream (see Results, and Kelson et al. CH1), so we summarize migratory allele frequencies for each major region of Elder Creek ('below' the waterfall, 'above' the waterfall, Misery, and Paralyze). For Fox Creek, we observed differences in the migratory allele frequency among years, with little spatial differentiation within the stream (see Results, and Kelson et al. CH1), so we highlight inter-annual differences in migratory allele frequencies.

Data Analyses to Understand Relationships between Genotype, Density, and Size Structure

We conducted a series of analyses to explore the relationship between migratory genotype and the density and size structure of fish. We characterize density and size structure of fish using three metrics: the density of young fish, density of older fish, and proportion of young fish. We analyzed density of fish by size/age class because exploratory analyses demonstrated that they differed in density patterns.

We explored the relationship between the frequency of migratory alleles and density/size structure at the smallest spatial scale that we sampled, i.e., at the level of individual study pools. We predicted a linear relationship between the proportion of migratory alleles per pool and the density of young fish (positive), the density of older fish (negative), and the proportion of young fish per pool (positive). For each of these three response variables, we conducted a linear mixed effects model, with the proportion of migratory alleles per pool as a predictor variable, and also including sample year and sample location (Fox Creek, and regions within Elder Creek, below the waterfall, above the waterfall, Misery, or Paralyze) as predictor variables (random effects). All linear mixed models were fit by maximum likelihood using the R package ‘lme4’ (Bates et al. 2015), and parameter significance was assessed using the Satterthwaite approximations to degrees of freedom implemented in the package ‘lmerTest’ (Kuznetsova et al. 2016).

Our exploration of density and size structure at the pool level revealed spatial patterns in density and size structure in Elder Creek, and temporal patterns in Fox Creek (see Results). To test if these changes in density and size structure were linked with differences in stream carrying capacity, we explored variation in the total biomass of fish (g) (standardized by surface area of the study pool, m^2)(Randall and Minns 2000). In Elder Creek, we conducted a linear mixed effects model with fish biomass per m^2 as the response variable, and the location within the stream (below the waterfall, above the waterfall, Misery, or Paralyze) as a predictor variable (fixed effect) and included sample year as another predictor variable (random effect) to account for repeated measures in four years. The model was constructed to calculate parameter estimates as contrasts against the below-waterfall region. In Fox Creek, we found strong inter-annual variation in genotype frequencies rather than spatial variation (see Results, and Kelson et al. CH1), so we tested for the effect of year on fish biomass, with models constructed to contrast against 2014.

Trophic Position

We used stable isotope analyses to estimate the trophic position of *O. mykiss* to test the prediction of a longer food chain in regions dominated by resident fish. For these analyses, we focused on a subset of fish from two distinct size classes: young fish (40 – 70 mm FL) and older fish (>150 mm FL). For young fish, we combined tissue samples from 1-3 fish in order to meet the minimum sample weight requirements for stable isotope analysis. Tissue samples (caudal fin clip) were desiccated in glass vials for 24 hours at 60˚C, weighed to the nearest 0.001mg, and wrapped in tin capsules. Samples were analyzed at the UC Berkeley Center for Stable Isotope Biogeochemistry, with continuous flow (CF) dual isotope analysis on a CHNOS Elemental Analyzer interfaced to an IsoPrime100 mass spectrometer. The facility reports long-term precision rates for $\delta^{15}N$ of ± 0.15‰, and $\delta^{15}N$ is reported in relation to atmospheric nitrogen ($\delta^{15}N = 0$ ‰), the international standard. Because $\delta^{15}N$ is enriched through the food web, estimated at 3.4‰ for each step in trophic level (Post 2002), we used $\delta^{15}N$ to estimate relative food web position for *O. mykiss* for each size class. We also report the mean and standard deviation of $\delta^{13}C$ enrichment for young vs. old fish. For *O. mykiss*, isotopic enrichment in the caudal fin reflects diet over the past 30 days (Heady and Moore 2013).

To examine evidence of trophic enrichment via isotopic enrichment of $\delta^{15}N$, we compared the $\delta^{15}N$ enrichment of young fish vs. old fish using an analysis of variance (ANOVA), with isotopic enrichment as the response variable and age class as the predictor variable. Most older fish for which we have both isotopic and genetic data for were resident or heterozygote genotype (see Results), but we also conducted the ANOVA excluding migratory-and heterozygote-genotype older fish to test if the relationship held true when only resident-genotype fish were included. We report the mean $\delta^{15}N$ enrichment for older fish of each genotype. We were only able to link genotype data to a few isotopic samples for young fish, because most stable isotope samples combined multiple individuals.

Food Web Sampling

We explored whether differences in fish density and size structure influence macroinvertebrate abundance and size. Specifically, we predicted that the expected 3-level food web in the migratory-genotype region would have a lower biomass of macroinvertebrates, with young fish having a top-down effect on invertebrates, but that this effect would be lessened where older fish limited the abundance of young fish, releasing macroinvertebrates in a 4-level trophic cascade. Additionally, we predicted that the shift in fish size structure would reduce the size of benthic macroinvertebrates, as larger fish can eat larger macroinvertebrates that might escape from smaller fish. We tested these predictions by sampling macroinvertebrates in Elder Creek in June-August of 2015. To reduce the impact of longitudinal variation on ecological covariates, we conducted our food web sampling over a short reach of Elder Creek, sampling in 3 pools downstream and 3 pools upstream of the waterfall, the point at which we observed a sharp change in fish densities and size structure (see Results).

We sampled benthic macroinvertebrates to estimate of the standing crop of biomass and also sampled drift to provide an estimate of the rate of macroinvertebrate flux in each stream region. To collect benthic macroinvertebrates, we removed invertebrates from 4-6 cobbles within each study pool. Specifically, we quickly rolled individual cobbles into a 1mm-mesh dip net and collected all invertebrates in the net and on the cobble. To standardize samples by surface area, we estimated the surface area of each cobble by wrapping it in foil and then weighing the foil (Bergey and Getty 2006). To test for differences in flux of invertebrates in reaches dominated by resident or migratory fish, we deployed drift nets overnight from 18h-10h twice during the summer of 2015, once in June (6-7, 2015) and August (26-27, 2015). The biomass of each drift net sample was standardized by the area of the drift net that was submerged and the length of time it was deployed.

Using a dissecting scope, we identified all collected aquatic invertebrates to the family level, or to genus or species when possible. Terrestrial invertebrates were identified to the nearest order. Biomass of invertebrates was estimated by weight-length regressions, matching the lowest taxonomic level possible (Benke et al. 1999, Sabo et al. 2002). Invertebrates were then classified into one of the three categories: armored, unarmored, or terrestrial, to represent the prey types that are available to fish. We predicted that unarmored taxa were more likely to show a response to top-down predation of fish. Armored taxa included Coleoptera, Gastropoda, cased Trichoptera, and Hemiptera (Gerridae spp.), cased Diptera (i.e., *Rheotanytarsus*). Unarmored taxa included Ephemeroptera, Plecoptera, uncased Trichoptera, Acari, Collembola, unarmored Diptera, Nematoda, Megaloptera, Odonata and Oligochaeta.

To test for differences in the biomass of benthic macroinvertebrates and biomass of drifting invertebrates, we conducted a series of nested ANOVAs. For the benthic invertebrates, we summed the biomass of each invertebrate by type (armored, unarmored, terrestrial) that was found on each cobble sample. We then used an ANOVA to test whether biomass of benthic invertebrates (response variable) was explained by location (above vs. below the waterfall, predictor variable, included as a fixed effect), with sample pool nested within each location (i.e., pool is included as predictor variable/random effect to account for repeated measures on multiple cobbles). To test whether benthic invertebrates were smaller in the resident-dominated region above the waterfall, we conducted a similar nested ANOVA with length as the response variable. Next, we used an ANOVA to test whether biomass of drifting invertebrates (response variable) was explained by location (above vs. below the waterfall, predictor variable, fixed effect). Drifting invertebrates were only measured once at each pool, precluding the need to include pool as a random effect in this model.

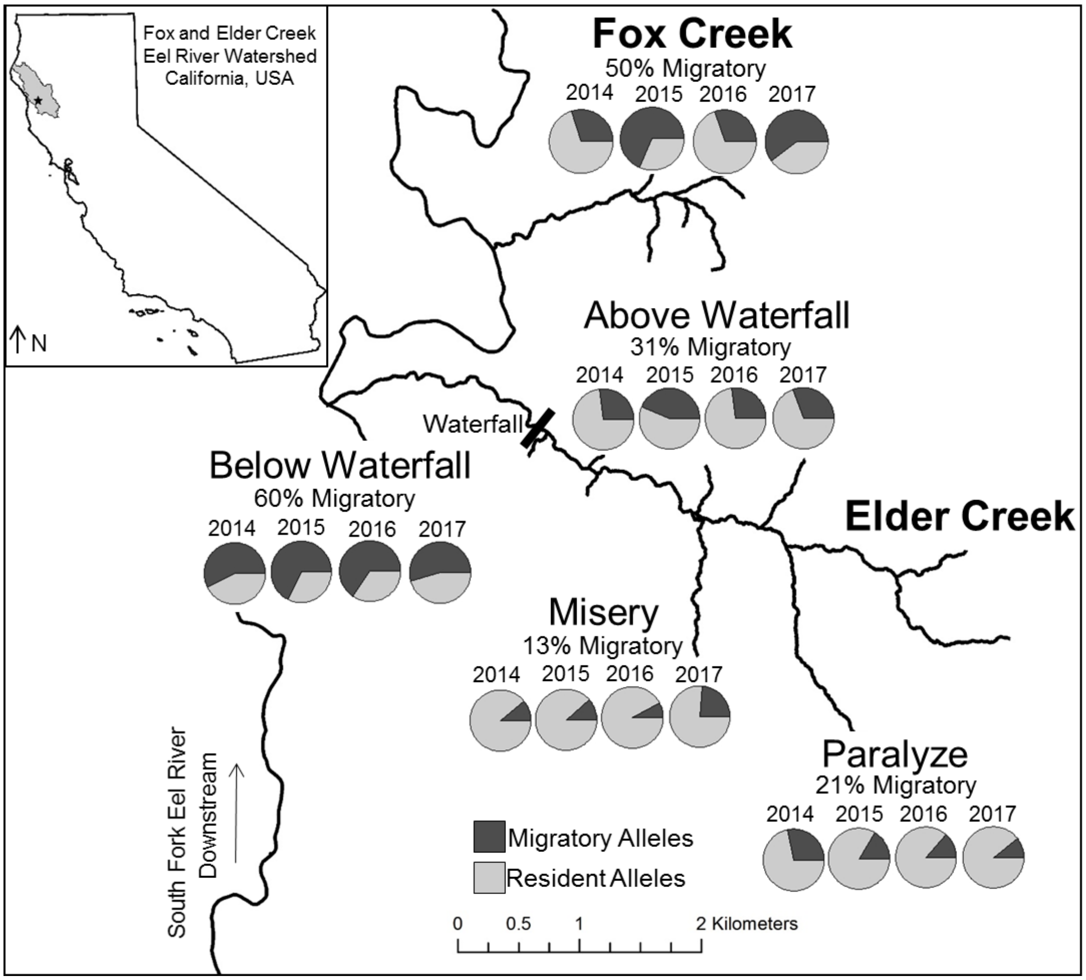

Figure 1. The proportion of migratory alleles is lower below the waterfall than in the upper watershed of Elder Creek, including above the waterfall and in tributaries Misery and Paralyze, in 2014-2017. The proportion of migratory alleles in Fox Creek varies among years.

Results

Distribution of Resident vs. Migratory Allele Frequencies

The region of Elder Creek below the large waterfall was dominated by migratory genotypes (60% migratory alleles), while regions above the waterfall were dominated by resident genotypes (69%, 87% and 79% resident alleles in the region above the waterfall, Misery, and Paralyze, respectively), and this trend was consistent across years (Fig 1). In Fox Creek, genotype frequencies varied through time rather than through space (Fig 1). In particular, Fox Creek was dominated by resident alleles in two years (70% resident in both 2014 and 2016) and by migratory alleles in two different years (68% and 60% migratory in 2015 and 2017). Rates of heterozygosity for all four years combined ranged from low in Misery and Paralyze (0.23 and 0.26, respectively) to intermediate in Elder above the waterfall (0.38) and Fox Creek (0.39), and were highest in Elder Creek below the waterfall (0.50) (Table S1), suggesting the highest level of life history-linked genetic diversity in the lower region of the Elder Creek watershed.

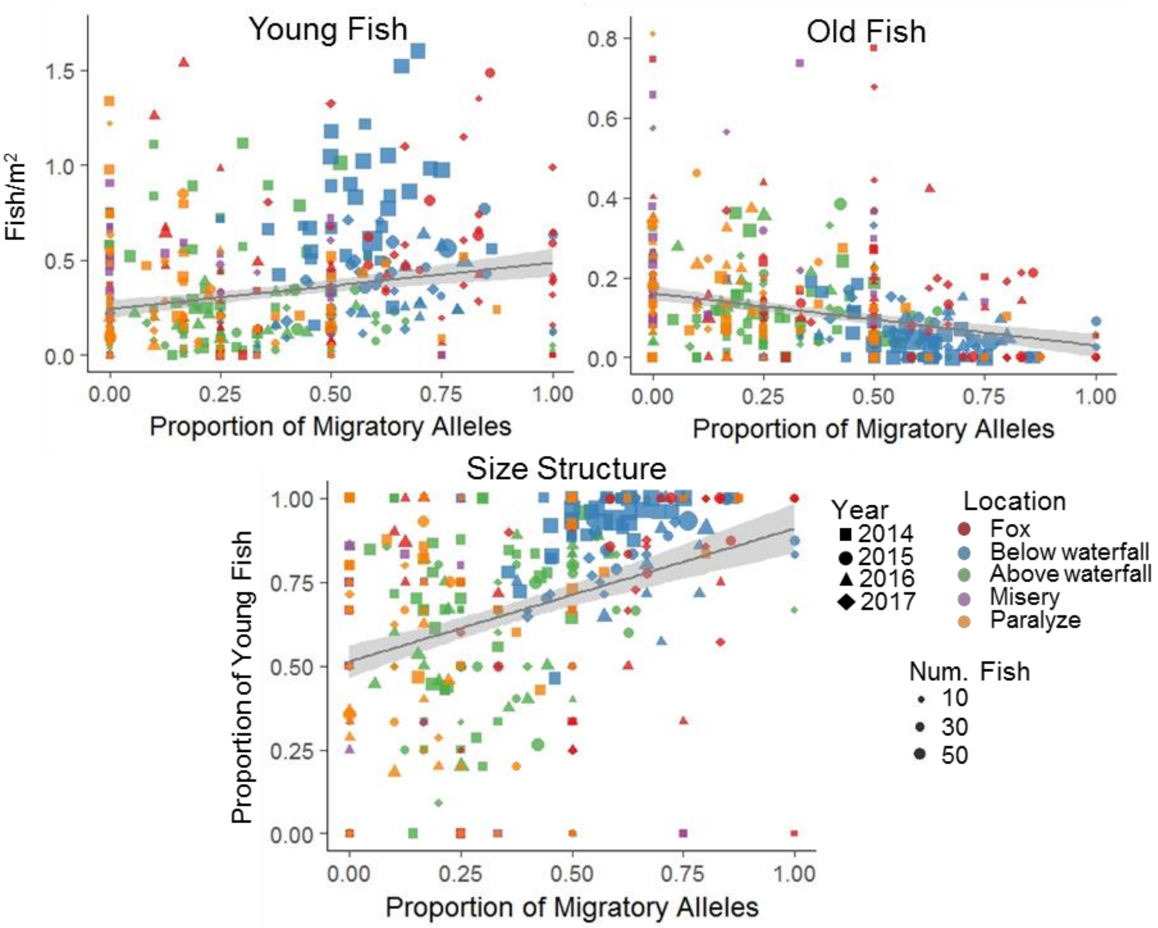

Figure 2. The proportion of migratory alleles per pool has a strong relationship with density of young fish, density of older fish, and size structure (proportion of young fish).

Proportion of Migratory Alleles Correlates with Density and Size Structure of Fish

The proportion of migratory alleles within a study pool was correlated with fish density and size structure. For young fish, this was a positive relationship, with the density of young fish increasing with proportion of migratory alleles (linear mixed effects model was significant, $F_{1,258} = 8.8$, $P<0.01$, slope = 0.20 ± 0.06 std. error, Fig 2). Pools that were dominated by migratory alleles (>50% migratory alleles) were characterized by nearly twice as many young fish on average than pools dominated by resident alleles (mean ± std. dev.: 0.52 ± 0.42 juvenile/m^2 vs 0.28 ± 0.28 juvenile/m^2, respectively). In contrast, for older fish, there was a negative relationship between proportion migratory alleles in a pool and density (linear mixed effects model was significant, $F_{1,242}=20.6$, $P < 0.01$, slope = -0.11 ± 0.02 std. error, Fig 2). The number of older fish was on average nearly three times as high in pools dominated by resident alleles compared to pools dominated by migratory alleles (mean ± std. dev.: 0.14 ± 0.13 fish/m^2 vs 0.05 ± 0.07 fish/m^2, respectively). Similarly, we found that the proportion of juvenile fish was nearly 50% higher in pools with a higher proportion of migratory alleles (mean ± std. dev: 0.87 ± 0.20) compared to pools dominated by resident alleles (0.68 ± 0.31), and this was significant in the linear mixed effects model ($F_{1,314}=27.3$, $P < 0.01$, slope estimate = 0.33 ± 0.06 std. error, Fig 2).

Because migratory alleles dominated in the reach below the waterfall, and because the proportion of migratory alleles was correlated with density and size structure, spatial patterns emerged in the density and size structure of fish in Elder Creek (Fig 3). More specifically young fish were twice as dense in the migratory-dominated region, below the waterfall, as in upstream regions (mean ± std. dev.: 0.46 ± 0.31 fish/m^2 below the waterfall, in comparison to 0.20 ± 0.22 fish/m^2 above the waterfall, 0.21 ± 0.23 fish/m^2 in Misery, and 0.27 ± 0.26 fish/m^2 in Paralyze). In contrast, resident genotype fish were more common above the waterfall, where there were higher densities of older fish (Fig 3). Densities of older fish in the migratory-dominated region were approximately half those in the resident-dominated region (mean ± std. dev.: 0.05 ± 0.06 fish/m^2 below the waterfall, in comparison to 0.09 ± 0.08 fish/m^2 above the waterfall, 0.16 ± 0.16 fish/m^2 in Misery, and 0.14 ± 0.13 fish/m^2 in Paralyze). Densities of heterozygous genotypes demonstrated a pattern intermediate between those of resident and migratory genotypes (Fig S4). Across all four years, the mean proportion of young fish in pools in the migratory-dominated reach was 0.87 ± 0.15, whereas above the waterfall the proportion was lower (0.62 ± 0.26 Elder Creek above the waterfall, 0.49 ± 0.39 in Misery, and 0.61 ± 0.30 in Paralyze). In the migratory-dominated region (below the waterfall), size structure was simple, and dominated by many small fish (unimodal length-frequency histogram, Fig 5), while the resident-dominated regions (above the waterfall) have a more complex size structure and the length-frequency histogram was bimodal with a second peak representing older fish (Fig 5).

While density and size structure varied spatially in Elder Creek, this was not the case in Fox Creek, where the largest barrier is located at the mouth. In Fox Creek, we found differences among years in migratory allele frequencies which corresponded with changes in fish density and size structure. When densities of migratory genotypes were low, densities of young fish were also low (Fig 4). The density of young fish was lowest in 2014, with young fish only being captured in the most upstream pools in the creek and second lowest in 2016, another year when resident-genotypes dominated (mean ± std. dev in 2014: 0.02 ± 0.07 fish/m^2, 2015: 0.57 ± 0.60 fish/m^2, 2016: 0.30 ± 0.39 fish/m^2, 2017: 0.43 ± 0.47 fish/m^2). When resident genotypes dominated in 2014, there was also a lower proportion of young fish (mean std. ± dev. of proportion of young fish in 2014: 0.16 ± 0.30), compared to migratory-dominated years (2015: 0.91 ± 0.19, 2017 0.58 ± 0.38, Fig 5). Densities of older fish also varied among years, with densities being slightly higher in 2016, a resident-dominated year, than in other years (Fig 4). The density of heterozygous genotypes was similar among years in Fox Creek (Fig S5).

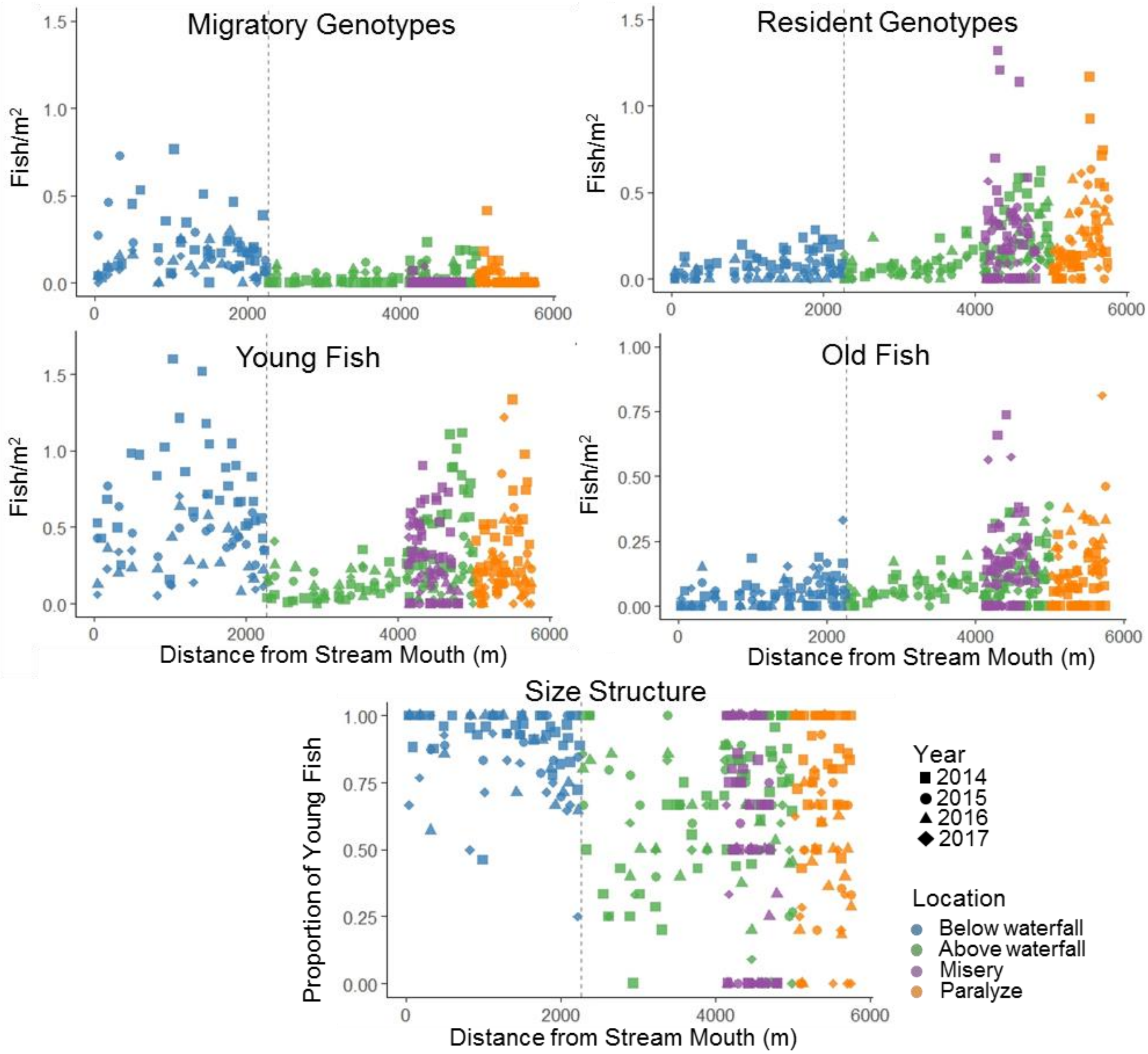

Figure 3. Migratory genotypes are more abundant below the waterfall (grey dashed line), while resident genotypes are more abundant above the waterfall. Similarly, density of young fish is higher below the waterfall, while density of old fish is higher above the waterfall. As follows, the proportion of young fish is lower below the waterfall.

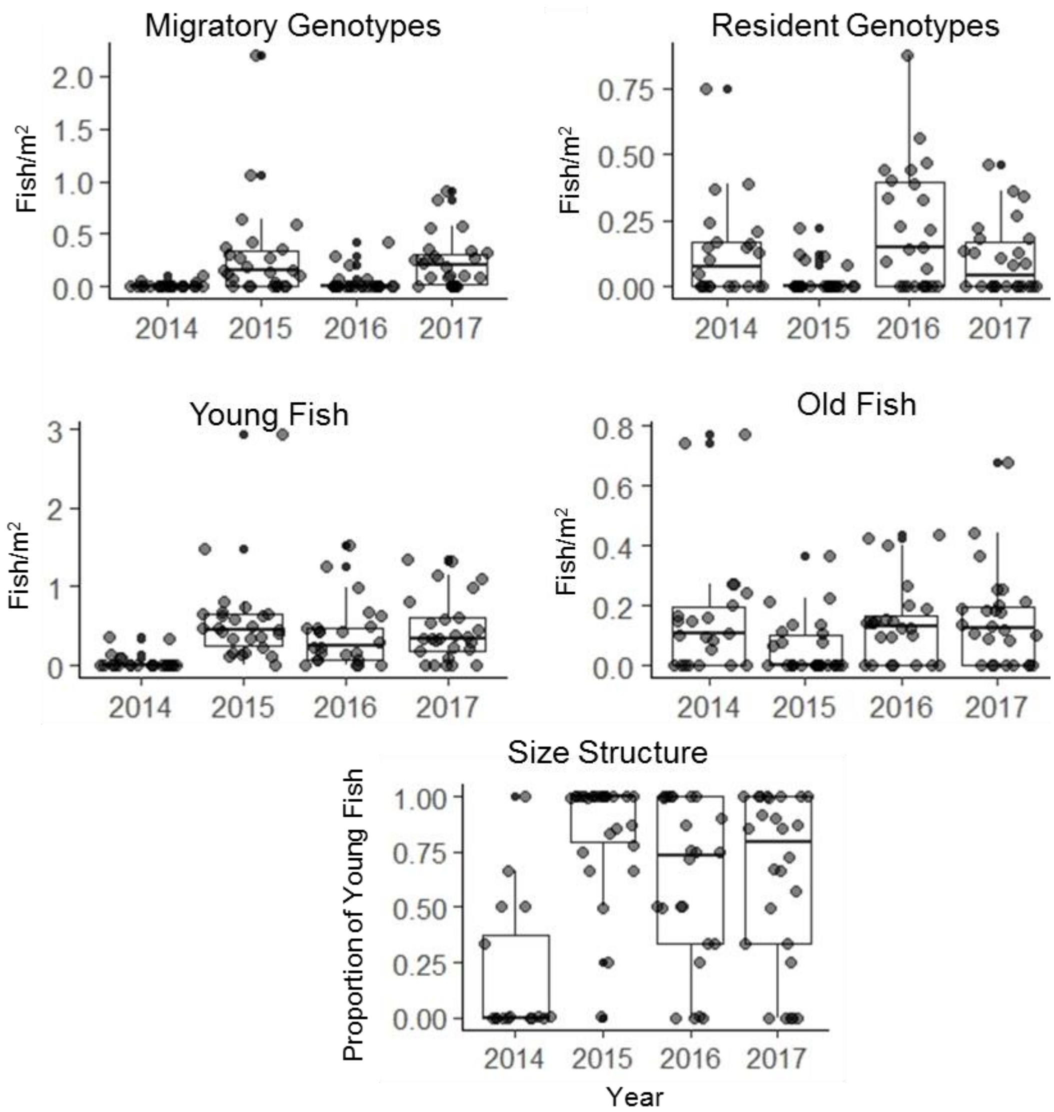

Figure 4. The density of young of year fish is lower in year in Fox Creek when migratory allele frequencies are also low (2014 and 2016). Similarly, the proportion of young fish per pool is low in these years.

We analyzed trends in total fish biomass as an estimate of overall ecosystem productivity in each stream. Fish biomass per m^2 varied among regions in Elder Creek ($F_{3,559} = 7.6$, $P < 0.01$), but there was no difference in total biomass of fish above versus below the waterfall in Elder Creek ($P > 0.05$, Table S2), despite the large shift in density at this point in the stream. Instead, we found that trout biomass was higher in Misery, the smallest tributary by drainage area, than elsewhere in the Elder Creek watershed (Table S2), suggesting no strong pattern between stream summer carrying capacity (biomass of fish per pool surface area) and drainage area in Elder Creek. The increase in biomass per m^2 is likely due to the small size of pools in Misery Creek. In Fox Creek there was inter-annual variation in total estimated biomass ($F_{3,221} = 3.8$, $P = 0.01$), with biomass being higher in 2016 and 2017 than in 2014 and 2015 (Table S2).

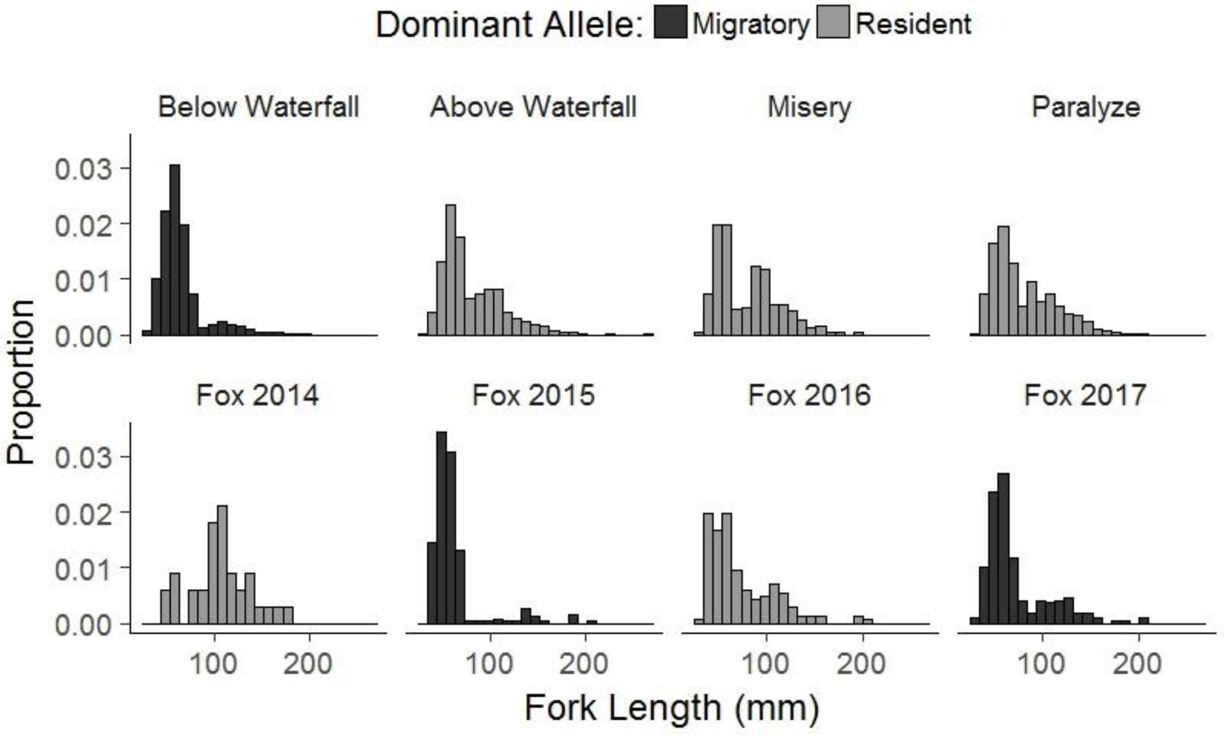

Figure 5. Histograms reveal different distributions of fish size (FL, in mm) in migratory-dominated regions (below waterfall) and resident-dominated regions (above waterfall, Misery and Paralyze) for all four years combined (2014-2017), and in migratory-dominated years (2015 and 2017) versus resident-dominated years (2014 and 2016) in Fox Creek.

Trophic Position of Large vs. Small Fish and Food Web Effects

Larger *O. mykiss* were more enriched for δ^{15}N than young of year fish (age class was statistically significant in an ANOVA, $F_{1,164} = 176.7$, $P < 0.01$, Fig 6), but their isotopic differences were less than the 3.4‰ expected had they fed on distinctly different trophic levels. The mean ± std. dev. δ^{15}N for young trout was 6.2 ± 0.7 ‰ versus 7.9 ± 0.8 ‰ for older fish (Fig 6). This pattern held when heterozygote (n = 30 out of 82) and migratory-genotype (n = 4) older fish were excluded ($F_{1,104}=147.8$, $P < 0.01$), suggesting that age/size rather than genotype controls trophic enrichment. The mean ± std. dev. δ^{15}N was 7.9 ±0.8 ‰ for large resident-genotype fish (n = 48), 7.8 ± 0.9 ‰ for large heterozygote-genotype fish, and 7.5 ±0.6 ‰ for large migratory-genotype fish. Young and old fish also differed in their isotopic fractionation of carbon (mean ± std. dev. δ^{13}C -25.3 ±1.19 ‰ versus -22.7 ± 0.9 ‰, respectively, Fig S1).

We predicted that if large fish had produced a 4-level trophic cascade, they would suppress (by cannibalism) juvenile fish, releasing aquatic macroinvertebrates. However, we did not find differences in the biomass of benthic invertebrates below versus above the waterfall for each macroinvertebrate type (armored, unarmored, terrestrial) (P>0.1 for all comparisons, Fig S2). Additionally, we detected no difference in the size of macroinvertebrates in below versus above waterfall in Elder Creek (P>0.1 for comparisons of each invertebrate type, Fig S2), suggesting that fish gape size did not influence macroinvertebrate size structure. Similarly, we found no difference in drifting invertebrate biomass in the pools above versus below the waterfall for unarmored invertebrates (P > 0.1, Fig S2). The pools above the waterfall did have marginally higher rates of drift of armored invertebrates (F=3.7, P =0.09), which was driven by a large number of adult Elmidae beetles and significantly higher rates of drifting terrestrial invertebrates (F=6.5, P=0.03; Fig S3), but these differences are unlikely to be linked to fish size structure.

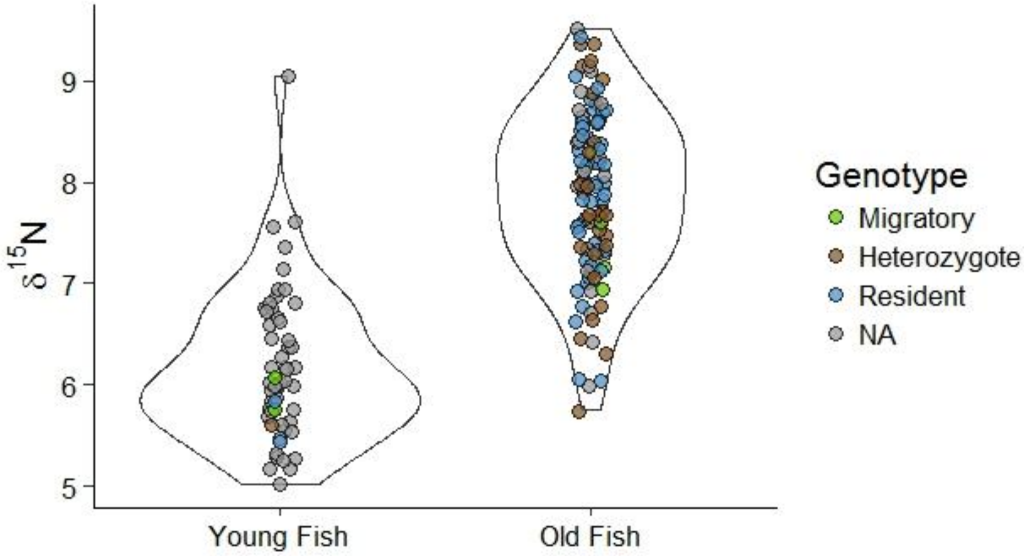

Figure 6. Young fish are less isotopically enriched than older fish for δ^{15}N. Most old fish (over 150 mm FL) are resident (58.5%) or heterozygote (36.6%) genotype.

Discussion

The spatial distribution of migratory and resident genotypes in partially migratory *O. mykiss* was associated with differences in density of juvenile fish, size structure, and trophic structure. In pools where migratory genotypes dominated, juvenile densities were high and size structure was simple. In contrast, pools dominated by resident genotypes were characterized by lower densities of juvenile fish and more complex size structure. Because pools dominated by migratory genotypes were downstream, below the waterfall, and pools dominated by resident genotypes were above the waterfall, the pool-specific patterns in density and size structure resulted in reach-scale differences in density of young fish (twice as high below the waterfall than above) and size structure (simple below the waterfall, comprised of many young fish versus complex above the waterfall, comprised of both young and old fish). Larger, resident fish were more isotopically enriched in δ^{15}N, but not enough to clearly add a fourth trophic level. We saw no change in the biomass or size structure of lower trophic levels (benthic macroinvertebrates) between regions dominated by resident versus migratory genotypes.

Density in partially migratory populations

The distribution of migratory genotypes in partially migratory population is likely to have ecological consequences across taxa. In our system, we found that high density of young fish was associated with migratory genotypes, and increased juvenile density may have secondary effects. High densities of juvenile fish in association with migratory *O. mykiss* has been documented in other streams (Phillis 2014, McMillan et al. 2015), and in other salmonid species including *Salmo trutta* (Bohlin et al. 2001, Olsson and Greenberg 2004). A number of vital rates in salmonid populations are density dependent, including juvenile growth rates (Jenkins et al. 1999, Grant and Imre 2005). Additionally, high densities can increase variation in body size of age-matched rearing juveniles (Keeley 2001, Jacobson et al. 2015). More broadly, density can affect social and feeding behavior across taxa, from foraging specialization in largemouth bass (Schindler et al. 1997) to feeding-path lengths of *Drosophila* (Sokolowski et al. 1997) to diet choice of alpine sheep (Kausrud et al. 2006).

Density-mediated ecological changes may be common across partially migratory populations where one life history strategy is associated with higher fecundity or reproductive success than the other. Ocean-migrating female salmonids are much larger and more fecund than resident trout (Fleming and Reynolds 2003), and can greatly increase juvenile densities where and when they are able to spawn. In other partially migratory systems, there are also likely differences in density of juveniles that accompany the divergent reproductive success or fecundity of resident versus migratory individuals. However, which life history strategy produces more offspring, resident or migratory, depends on the system. For example, in other fish systems, migration also leads to increased juveniles in the population (Kerr et al. 2009), but examples from newts suggest that resident individuals have higher reproductive success (Grayson et al. 2011). In birds, increased population size is linked to migratory individuals in blue tits (Nilsson et al. 2006), but resident American dippers are more likely to have larger brood sizes or double brood (Gillis et al. 2008).

Density-dependence is often cited as a cause – rather than a consequence - of migration from theoretical studies (Kaitala et al. 1993, Taylor and Norris 2007, De Leenheer et al. 2017). This “competitive release” hypothesis, in which individuals migrate from high-density habitats to escape competition (Chapman et al. 2011), has considerable empirical support including in in birds (Hegemann et al. 2015), ungulates (Mysterud et al. 2011), and fish (Olsson et al. 2006). For example, red-spotted newts were more likely to migrate from experimental high-density enclosures (Grayson and Wilbur 2009). However, the two may be linked in a feedback loop in *O. mykiss* and other species, such that migratory juveniles are present in a higher density due to the increased fecundity of migratory adults, which then leads to higher competition and lower growth rates for juveniles (Grant and Imre 2005), encouraging migration via density dependence. This link between intraspecific variation in migration behavior and ecology, and the persistence of migration as an evolutionary stable strategy in partially migratory animals (De Leenheer et al. 2017) may be prevalent across partially migratory individuals.

Body size in partially migratory populations

Body size is often linked to a migratory vs resident life history strategy (Chapman et al. 2011). Within anadromous fishes, including salmonids, the migratory form attains a larger body size overall, but the resident form that stays in freshwater attains a much larger body size while in freshwater. In our system, these larger, resident fish become top predators. In fact, the largest individuals were enriched in $\delta^{15}N$ and comprised an additional trophic level, leading to a 4-level food web in regions where resident-genotypes were common. The difference in isotopic enrichment is less than 3.4‰ (mean 6.1‰ vs. 7.8‰ $\delta^{15}N$), or the difference in trophic fractionation that would be expected if older fish were an entire trophic level higher than young of year fish (Minagawa and Wada 1984, Post 2002), suggesting that the largest individuals had a diet including a range of prey items including primary and secondary consumers. The higher $\delta^{15}N$ enrichment suggests that the larger fish are feeding higher in the food web, with a diet that likely includes some fish. Diet changes throughout ontogeny of an organism are common (Werner and Gilliam 1984), and so body size linked differences in diet in partially migratory populations may have implications for the whole food web.

Most prior research on body size in partially migratory populations has focused on the effect of body size on the decision to migrate or not (Chapman et al. 2011). In some fish systems, large-bodied individuals are more likely to migrate (e.g., bull trout, Monnot et al. 2008, and pelagic coregonids, Mehner and Kasprzak 2011). In birds, the body size-dependent migration is often linked to 'thermal tolerance' hypothesis (Chapman et al. 2011), where small-bodied individuals are more likely to migrate because they cannot withstand cold winters (Ketterson and Nolan 1976, Belthoff and Gauthreaux 1991), and large-bodied individuals migrate to avoid overheating in the summer (e.g., Alonso et al. 2009). However, size-biased migration has implications beyond the decision to migrate; it also influences the size structure of the remaining (resident) population. This result is very general in partially migratory populations, suggesting that this form of intraspecific variation commonly has community level consequences.

Density and size-structure can mediate food web effects

We observed that larger-bodied, resident individuals fed at a higher trophic level, but this change did not drive a trophic cascade. Previous research in the South Fork Eel River demonstrated that *O. mykiss* have a top-down effect (Power 1990), however these studies took place in the open, sunny mainstem (South Fork Eel River), rather than in steep, shaded tributary streams. In the tributary streams, benthic macroinvertebrate production may be instead limited by primary productivity, which is supported by the observation that algal blooms developed in Elder Creek following the removal of algivorous armored caddisflies (McNeely et al. 2007). Additionally, previous research on salmonid diet has found that larger fish include even the smallest items in their diet (Keeley and Grant 1997), which may have contributed to the lack of decrease in size and biomass of benthic macroinvertebrates where large fish exist. However, in an experimental manipulation of juvenile *O. mykiss*, Phillis (2014) found that high-densities of juvenile *O. mykiss* reduced invertebrate biomass, and increased sediment export and algal accrual, suggesting that density-mediated ecosystem impacts occur under some conditions.

Density and size-structure mediated food web effects have been observed in other systems. One example is provided by research on *Poecilia reticulata*, where guppy density and size structure altered prey communities, standing stock of algal biomass, and decomposition rates in tropical streams (Bassar et al. 2010). Similarly, the continual presence of resident ungulates (i.e., temporary increase in density that would not occur if individuals had migrated) had a top-down effect on the regeneration rates and standing crop of forage vegetation, due to their intense grazing pressure (Fryxell and Sinclair 1988). Across partially migratory animals, density and size-structure mediated food web effects are likely.

Summary

Migratory versus resident life history strategies represent an extreme form of intraspecific variation in partially migratory animals. Previously explored ‘migratory syndromes’ suggest that migration is linked with a suite of individual traits (Dingle and Drake 2007), and we expand on these syndromes to suggest migration may also be linked to a suite of ecological changes in partially migratory populations. Migration itself, along with traits that commonly differ between migratory and resident individuals, such as body size, fecundity, and reproductive success (Chapman et al. 2011), may generate ecosystem effects in other systems (e.g., Bassar et al. 2010, El-Sabaawi et al. 2015a, 2015b).

Animal migration is on the decline globally (Wilcove and Wikelski 2008) as migrants are excluded from many habitats where they were historically present (Januchowski-Hartley et al. 2013, Beyer et al. 2016). This may tip the balance toward resident life histories in partially migratory populations (e.g., White et al. 2007), with many likely secondary effects for the ecology of these systems. As follows, restoring or removing migratory corridors of partially migratory populations may have ramifying ecological consequences beyond the impacts on life history diversity of the focal population.

Acknowledgements

This study was co-authored by Mary E. Power and Stephanie M. Carlson. This study was funded by a NSF Graduate Research Fellowship to SJK and the NSF CZO EAR-1331940, Eel River Critical Zone Observatory. Research was also funded by the UC Berkeley Wildlife Fund and the UC Natural Reserve System Mildred E. Mathias Award to SJK.

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Supplemental Tables and Figures

Table S1. Number of fish assigned to each genotype in Fox and each region of Elder Creek from 2014-2017.

Year	Location	Num. Resident Genotypes	Num. Migratory Genotypes	Num. Heterozygous Genotypes
2014	Below waterfall	113	207	316
	Above waterfall	188	33	115
	Misery	47	1	11
	Paralyze	91	21	50
	Fox	29	5	26
2015	Below waterfall	24	98	85
	Above waterfall	48	31	56
	Misery	17	0	5
	Paralyze	42	1	18
	Fox	8	43	44
2016	Below waterfall	12	56	73
	Above waterfall	86	12	63
	Misery	16	0	3
	Paralyze	51	2	14
	Fox	36	8	27
2017	Below waterfall	20	31	67
	Above waterfall	38	7	35
	Misery	13	1	9
	Paralyze	42	1	9
	Fox	24	44	29

Table S2. Summary of statistical analyses exploring variation in biomass among regions in Elder Creek and years in Fox Creek. In Elder Creek, the parameter estimates from the linear mixed effects model are contrasted from the migratory-dominated below waterfall region, and a random effect of year is included in each model. In Fox Creek, parameter estimates from the linear model are contrasted from 2014. Non-significant parameters are italicized.

Stream	Fixed effect	Estimate ± std. error	t-value	P-value
Elder Creek	Intercept	0.87 ± 0.05	16.7	<0.01
	Above	-0.25 ± 0.03	-8.2	<0.01
	Misery	-0.38 ± 0.04	-10.9	<0.01
	Paralyze	-0.26 ± 0.03	-7.7	<0.01
Fox Creek	Intercept	1.47 ± 0.42	3.5	<0.01
	2015	0.79 ± 0.60	1.3	0.19
	2016	1.49 ± 0.59	2.5	0.01
	2017	1.86 ± 0.60	3.1	<0.01

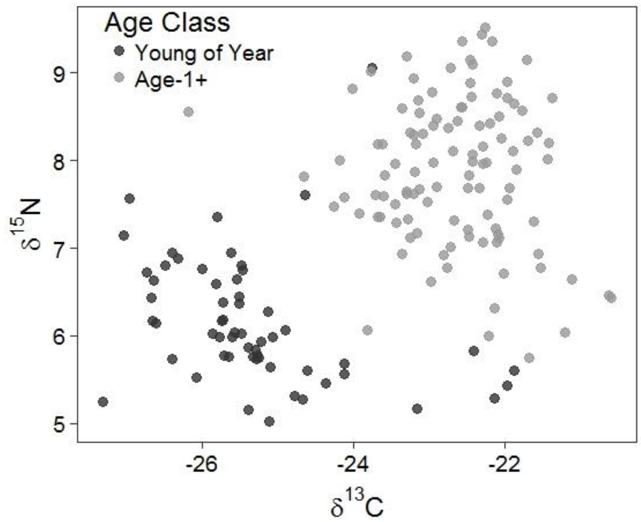

Figure S1. Carbon-Nitrogen bi-plot for young and old fish demonstrates that young fish are less enriched for $\delta^{15}N$ and $\delta^{13}C$ than older fish.

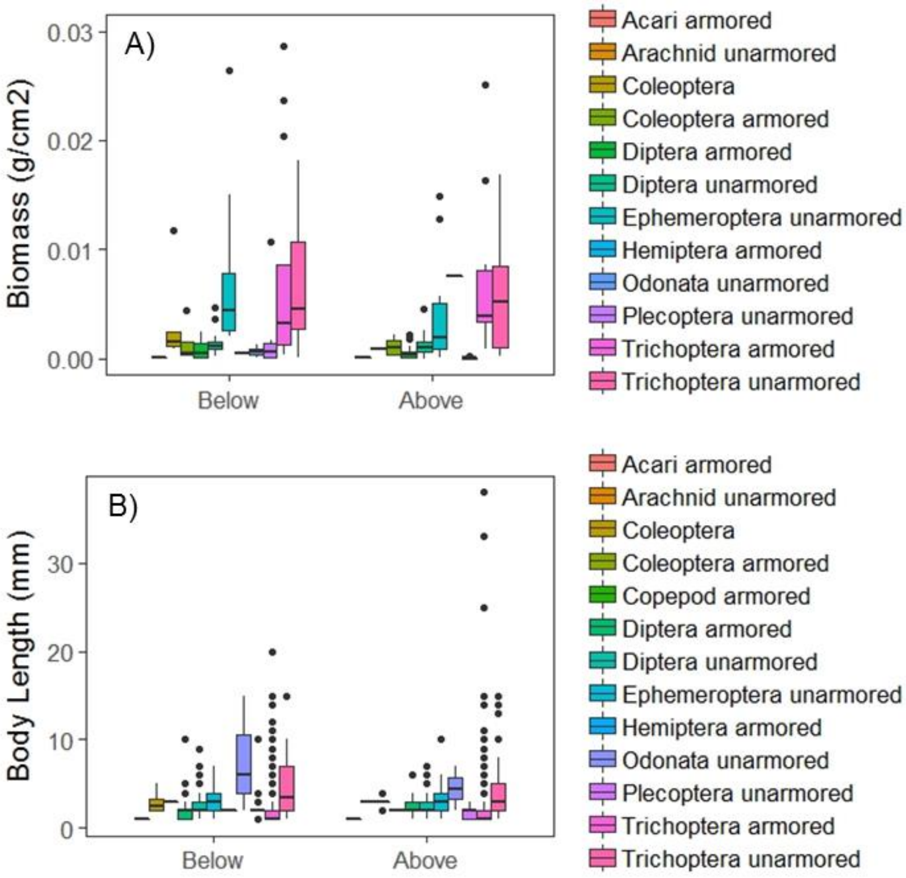

Figure S2. A) Biomass and B) size of benthic invertebrates do not differ below vs. above the waterfall in Elder Creek.

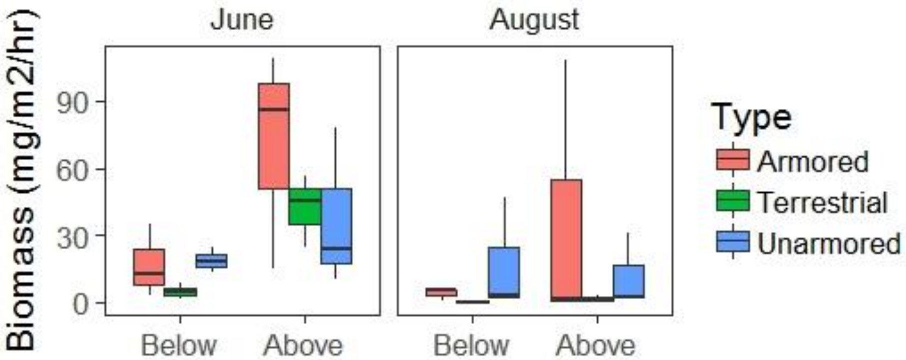

Figure S3. Biomass of invertebrates collected in 14-hr drift net samples (7pm – 9am) at the head of pools below versus above the waterfall in Elder Creek (n = 3 pools in each region).

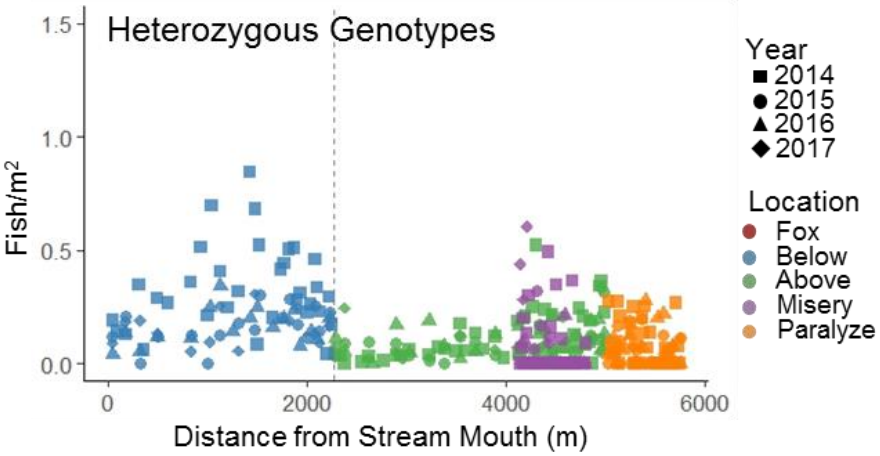

Figure S4. The spatial distribution of heterozygous-genotype fish in Elder Creek.

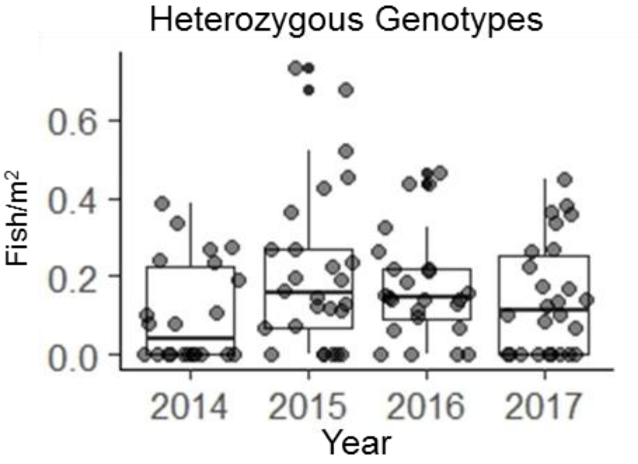

Figure S5. The density of heterozygous-genotype fish is similar among years in Fox Creek.

5

Growth and out-migration timing of *O. mykiss* across precipitation extremes in Mediterranean-climate California streams

Abstract

Climate change is expected to bring weather extremes and variability, and for California these changes include ‘weather whiplashes,’ with the increased likelihood of severe drought years immediately followed by super flood years (Swain et al. 2018). Fluctuations in precipitation patterns will alter stream flow regimes, affecting critical life history stages of sensitive aquatic organisms. Understanding how threatened fish species, such as steelhead/rainbow trout (*Oncorhynchus mykiss*), are affected by stream flows in wet versus dry years is important for their conservation. In this study we observed how extreme wet and dry years, from 2015-2018, affected stream flow patterns in two tributaries to the South Fork Eel River, California, and aspects of *O. mykiss* ecology, including over-summer fish growth and body condition, and spring out-migration timing. We found that stream flow patterns differed across years in the timing and magnitude of winter-spring flow events, and in summer base flows. We were surprised to find that differences in stream flows did not impact growth, body condition, or timing of out-migration of *O. mykiss* ecology. Fish growth was limited in the late summer in these streams (average of 0.02 ± 0.05 mm/day), but was similar across dry and wet years, and so was body condition. Similarly, *O. mykiss* migrated out of tributaries during the last week of March/first week of April regardless of the timing of spring flow events. We suggest that this lack of response to inter-annual hydrologic variability is due to the high quality of habitat provided by these unimpaired, groundwater fed tributaries. Similar streams that are likely to maintain cool temperatures and sufficient base flow, even in the driest years, should be a high priority for conservation and restoration efforts.

Introduction

Drought can have complex effects on stream ecosystems and the ecology of the aquatic species who depend on them (Matthews and Marsh-Matthews 2003). The recent multi-year drought in California (2012-2016) may be the most severe drought in over 21,000 years, based on analyses of tree rings (Robeson 2015, Kwon and Lall 2016). It was immediately followed by a series of extremely wet years. Such “weather whiplash” (*sensu* Swain et al. 2018) is expected to become increasingly common in California, including more frequent and severe droughts and floods (Cook et al. 2015, Diffenbaugh et al. 2015). It is unclear how precipitation extremes influence the ecology of aquatic species in this region, particularly sensitive species, but understanding these stream flow-ecology relationships has large conservation implications.

Much of California experiences a Mediterranean climate, with most precipitation occurring between October and April, followed by warm, dry summers (Gasith and Resh 1999, Bonada and Resh 2013). Beyond pronounced seasonality, another defining characteristic of Mediterranean climate systems is strong inter-annual variation in precipitation, which alters stream flow patterns in both the wet (winter) and dry (summer) seasons. In winter, stream flow varies considerably both in timing and magnitude of peak flows (Kondolf et al. 2012, Cid et al. 2017). In summer, stream flow varies both in the rate of recession from winter to summer base flows and the magnitude of base flows (Dralle et al. 2016). Across-season flow variation is thus a hallmark of Mediterranean streams, and this variation in flow was on display when California abruptly shifted between weather extremes from drought conditions in 2012-15 to extremely wet conditions in 2016-17.

Pacific salmonids (*Oncorhynchus spp.*) are distributed in streams around the Pacific Rim, and California represents the southern end of the range for all anadromous (ocean-migrating) forms. Many population complexes in California are protected under federal and state Endangered Species Acts (Williams et al. 2016) and climate change, including changes to stream flows, is a threat to their persistence (Wenger et al. 2011, Katz et al. 2013). Life histories of *O. mykiss* are tightly coupled to stream flow patterns across the seasons. Winter stream flows cue anadromous adult upstream migration and spawning (Trush 1989, Brown 1990), and out-migration of smolts (ocean-bound juveniles) is often linked to timing of spring flow events (McCormick et al. 1998, Achord et al. 2007, Roni et al. 2012, Hall et al. 2016). The low-flow summer season is often limiting for growth and survival of *O. mykiss* in California (Hayes et al. 2008, Sogard et al. 2009, Grantham et al. 2012, Hwan et al. 2018) and other arid and semi-arid regions, such as parts of Oregon and Washington (Ebersole et al. 2009). Growth during the dry season can later affect over-winter survival (Ebersole et al. 2006) and life history decisions on the timing of age at out-migration (Satterthwaite et al. 2009, 2012), making summer an important period in the salmonid life history. When stream flow is experimentally reduced during the dry season, growth of *O. mykiss* is also reduced (Harvey et al 2006). However, how growth varies during the dry season following extreme dry (drought) and wet winters is unknown.

Here we explore how precipitation extremes influence the ecology of threatened *Oncorhynchus mykiss* in tributary streams by comparing over-summer growth rates and the timing of spring outmigration among years with different stream flow patterns including extreme drought and wet conditions. First, we use long term flow records to characterize flow conditions at our study site during the three focal years in the context of the longer-term record. Second, we quantify over-summer growth rates and condition of juvenile *O. mykiss* across three summers including during the weather extremes. Finally, we quantify differences in the timing of seasonal movements of *O. mykiss* during years with extreme differences in rainfall magnitudes and, to a lesser degree, timing.

Methods

Study Site

We studied growth and movement of *O. mykiss* in two tributaries to the South Fork Eel River, Elder Creek (16.8 km^2 in drainage area) and Fox Creek (2.7 km^2 in drainage area), located within the University of California Angelo Coast Range Reserve in Mendocino County, California (Fig 1). Both tributaries are well-shaded and groundwater fed (Lovill et al. 2015, Dralle et al. 2016), maintaining cool water temperatures throughout the summer months. Both resident and anadromous forms of *O. mykiss* are present in these streams, and *O. mykiss* is the dominant fish species, representing >99% of our catches (the only other fish species present was the occasional adult Pacific lamprey, *Entosphenus tridentatus*).

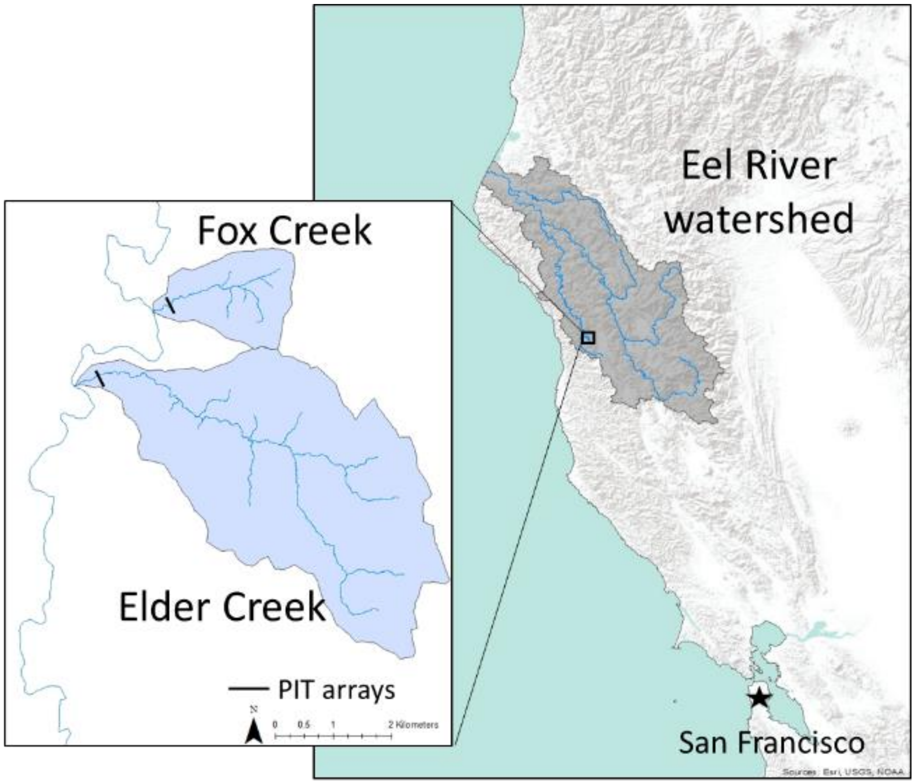

Figure 1. Fox and Elder Creek are located within the Eel River watershed in Northern California, USA.

Characterizing Flow Conditions

Elder Creek is the site of a U.S. Geological Survey (USGS) stream gauge (no. 11475560). We used the USGS mean daily discharge to characterize patterns in streamflow during the 2015-2018 water years (where Oct 1, 2014 – Sept 30, 2015 corresponds to the 2015 "water year"). Stream flow data have been collected at this station since 1967, providing an opportunity to explore stream flow patterns in relation to the long-term record at this site. Specifically, we calculated the cumulative mean daily discharge for each year on record, and then calculated quantiles for the annual cumulative discharge, categorizing years as "very dry" (1st quintile), "dry" (2nd quintile), "normal" (3rd quintile), "wet" (4th quintile), and "very wet" (5th quintile), (e.g., Kiernan et al. 2012, Hwan and Carlson 2016). Next we calculated, for each day, the percent difference in discharge from the long-term average for that day, and then calculated the monthly average percent difference in discharge. Fox Creek is ungauged but it is adjacent to Elder Creek (the mouths of the two streams are approximately 2.5 km apart), and both drain similar geology, so we assumed similar stream flow patterns.

Fish Sampling

We captured *O. mykiss* from ~ 20% of the pools in both Elder (n = 140-143 total pools surveyed per year) and Fox creeks (n = 46-57 pools per year) from 2014-2017. Pools were initially surveyed and mapped onto a 10 m digital elevation map by hand in the field, and then survey pools were selected using spatially stratified random sampling to encompass all of the habitat occupied by *O. mykiss*. We sampled the same pools every year, with the exception of when winter stream channel dynamics rendered pools inaccessible, in which case we sampled the next upstream pool instead. We blocked the pools with nets at the upstream and downstream ends, and then sampled the fish using three pass backpack electrofishing, recording effort (number of seconds) for each pass. After fish sampling, the surface area of each pool was estimated by multiplying the maximum length of the unit by the average wetted width (calculated from five width measurements spaced equally along the length of the pool).

Fish were sampled twice during each summer, once in late-July to early-August ("mid-summer sampling," Jul 15 – Aug 5, 2015; Jul 16 – Aug 5, 2016; Jul 13 – Aug 3, 2017), and again in mid-September ("late summer sampling," Sept 25-28, 2015; Sept 9-11, 2016; Sept 8-10, 2017). Fish were initially captured and marked in the first sampling event when most encountered young of year were large enough to implant with a passive integrated transponder (PIT) tag (over 60 mm in FL and 2 g in weight). At capture, fish were measured for fork length (FL, mm) and mass (0.01 g), and tagged if large enough. We then returned to a subset of the pools in September to recapture fish, returning to pools where the most fish were PIT-tagged in the July sampling to maximize the possible number of known recaptured fish in three-four days of sampling. All recaptured fish were re-measured for length and mass, allowing us to estimate end-of-summer growth (hereafter 'summer growth') in each year.

Analyses of Fish Growth and Condition in Summer Season

We tested for differences in summer growth among years via a series of ANOVAs, with growth rate (mm/day) as the response variable and both year and stream (Elder vs. Fox Creek) as predictor variables. All ANOVAs were conducted in R. Additionally, we recaptured a small number of fish during other seasons in sampling for other studies, and we recaptured some individuals across multiple years. For both of these groups of recaptures, we calculated growth rate as before and qualitatively compared growth rates in other periods with summer growth.

Additionally, we compared fish condition among years for all the fish that were captured during electrofishing surveys in September (n = 1022). Specifically, we used ANCOVAs with log mass as the response variable, log length as the covariate, and year as the fixed grouping factor. We first tested for heterogeneity in slopes relating log mass and log length (i.e., the interaction term). If this term was not-significant, it was removed and the model was fitted again to explore the influence of the grouping factor (year) and line elevations (i.e., intercepts). When the interaction term was significant, it could not be removed. In these cases, we concluded that condition in one year differed from condition in other years if the log mass of one year was consistently above or below those from the other years. ANCOVA is the preferred method to test for differences in condition factor to appropriately calculate the degrees of freedom and regression coefficients (Garcia-Berthou 2001).

Additional Environmental Covariates: Temperature and Fish Density

We explored two environmental correlates of fish growth and condition, water temperature and fish density, because both can influence fish growth. In particular, water temperature can have a strong influence on salmonid growth rates (e.g., Myrick and Cech 2005, Boughton et al. 2007). Stream temperatures for Elder Creek (obtained from the USGS gauge, and independently measured water temperatures throughout both streams followed the same temporal patterns, (S. Kelson, unpublished data) and were similar across all three summers (June – Sept, Fig 2d), ranging from a daily mean from 10.6 to 19.1 °C, with an absolute range from 9.7 - 21.1 °C during summer months. The mean water temperatures were slightly higher in 2017, due to a week of warming in September (Table 1, Fig 2d). Although at times the difference in mean daily temperature was large between years (max. difference of 6 °C), the mean difference was low (2.0 ± 1.2 °C standard deviation, Fig 2). The temperatures for all years were well within tolerated thermal ranges (Wurtsbaugh and Davis 1977, Sloat and Osterback 2013), so we do not analyze temperature as a correlate with fish growth or condition among years.

Table 1. Mean density of *O. mykiss* did not differ among three years, 2015-2017, in Fox or Elder Creek. Stream temperatures from July 15 – Sept 30 (growth window) were slightly warmer in 2017. 95% confidence intervals are in parenthesis.

Year	Density in Elder Creek (fish/m^2)	Density in Fox Creek (fish/m^2)	Stream Temperature (°C)
2015	0.36 (0.31-0.41)	0.59 (0.43-0.75)	15.5 (15.1-16.0)
2016	0.31 (0.27-0.35)	0.44 (0.34-0.54)	15.2 (14.8-15.6)
2017	0.28 (0.24-0.32)	0.55 (0.42-0.68)	16.3 (15.8-16.8)

Density of juvenile salmonids can also have a strong influence on their growth (Grant and Kramer 1990, Jenkins et al. 1999), so we report density estimates from each stream (Fox and Elder Creek) and year (2015-2017) from our July sampling event. We estimated the number of fish per pool using two methods, the total count of fish captured and the Leslie-K method of estimating population size from depletion estimates (Leslie and Davis 1939, Ogle 2016). Differences between these methods were slight (summarized in Appendix 1), so we present count data. We found that there was no difference in the density of fish captured per pool (fish/m^2) among years in Fox or Elder Creek in ANOVA (overlapping 95% confidence intervals, Table 1). Because we did not find inter-annual variation in densities in our sampling reaches, we do not further explore the influence of density on fish growth and condition.

Fish Movements during Spring Months

To characterize the downstream movements of PIT-tagged fish, we installed stationary antennas that spanned the wetted channel near the mouth of Elder Creek in November 2014 and at the mouth of Fox Creek in May 2015. At Elder Creek, we installed antennas 200 m and 350 m upstream of the mouth. At Fox Creek, we installed antennas 175 m and 195 m upstream of the mouth. Test tags, which exposed a PIT-tag to the antenna every 30 minutes, were installed at each antenna to monitor antenna efficiency. For every fish that was detected at the antenna, we received data on the date and time of detection, allowing us to quantify differences in movement patterns across years with different flow conditions. While some movement was detected in most months of the year, we focus here on the spring movements (Feb 01 – May 31), which coincide with the typical outmigration season for anadromous *O. mykiss* in this region (Brown 1990) and when smolt traps are operated in nearby watersheds (Gallagher et al. 2014, Obedzinski et al. 2017).

We grouped detection records from each antenna array into three categories. The first category represents the "perfect detections," or fish that were detected at both upstream and downstream antennas within a 36-hour window, signaling directional downstream movement (n = 98 fish in the spring at Elder, and n= 29 in other months, and n = 0 at Fox). The second category represents fish that were detected multiple times at one or both antennas, but with a long (>36-hour) gap between detections, suggesting local movement in the vicinity of the antenna array (n = 16 at the Elder array, and n = 8 fish at the Fox array in spring months, and n = 15 and n = 3 in other months, respectively). To be conservative, these individuals were removed from our analyses on outmigration timing. The third category represents fish that were only detected at one antenna, or "single detections." Due to technical difficulties with antenna operation (e.g., elevated stream flows, debris, shed tags masking the ability of other tags) many of our data points are single detections (n = 142 at Elder and n = 33 at Fox in the spring, and n = 55 and n = 13 in other months). We assumed that these spring-season single detections were associated with down-stream movement for several reasons. First, all 'perfect detections' during the out-migration time period were documented swimming in a downstream direction through the array. Second, all of the 'single detections' occurred when only one antenna was functioning. Third, there was no difference in the body length or capture location for single detections and perfect detections.

To test for differences in timing of spring (Feb 01 – May 31) fish movement among years, we conducted an ANOVA with Julian date of detection at the antenna array as the response variable and year as the explanatory factor. Additionally, we tested whether fish moved during only a subset of the flows, e.g., during high flows (e.g., Raymond 1988, Jager and Rose 2003). We found that fish moved during both spring and fall (see Results), so we tested for movement-flow preferences separately in each season. To test for flow preferences, we compared the flows when fish were moving vs. flows available to the fish during the outmigration season, excluding days when the antenna was not operating (at least 50% detection efficiency of the marker tag in order to be designated an operating day). To test for flow preference, we conducted an ANOVA between movement flows and all flows, nested within each year (i.e., year is included as a random effect), separately for both the spring and fall.

Results

Weather extremes and inter-annual variation in stream flow

This study spanned years with substantial variation in annual precipitation in California, with conditions in the South Fork Eel River watershed ranging from extreme drought conditions (2015 summer, in “exceptional drought”) and extreme wet conditions (2017 summer, with “no” drought conditions) according to the United States Drought monitor (http://droughtmonitor.unl.edu/). Stream flow in Elder Creek reflected these weather extremes. The 2015 water year was classified as “dry” (0.22 percentile), the 2016 water year as “wet” (0.68 percentile), the 2017 water year as “very wet” (0.94 percentile), and the 2018 water year as “dry” (0.24 percentile). Flow differences among these years were greatest in the winter season, from October – April. During the dry 2015 water year, for example, the only month that experienced above-long-term-average flows was December, meaning that flows were below-average for the entire out-migration season (February – May, Fig 2a, Fig 2b). In the second dry year, 2018, the only month that experienced above-average flows was April, which coincided with the outmigration season (Fig2a, Fig 2b). In the wet year, 2016, only three months experienced above-average long-term flows, December, January, and March, meaning flows were below-average for most of the out-migration season (Fig 2a, Fig 2b). In the very wet year, 2017, flows were above average for almost the entire wet season, and exceeded the long-term average in February by nearly 200%, then dropped just-below average (-4%) only in March (Fig 2b).

There were also differences in summer flows among years, though the differences were muted compared to wet season differences. For the three years that we monitored summer growth rates (2015-2017), the summer flows (June – September) were lower than the monthly-long term average (Fig 2b), except for September 2017, when flows were slightly higher than the long-term average (+3% difference). Stream flows at the start of summer (on June 1) differed among years, ranging from 0.05 cubic meters per second (cms) in 2015 to 0.2 cms in 2017, with 2016 intermediate at 0.11 cms (Fig 2c). In 2017, discharge did not decrease to 0.05 cms until July 23. Early season differences persisted through the mid-summer: on August 1, discharge was 0.02 cms, 0.03 cms, and 0.04 cms, in 2015, 2016, and 2017, respectively. However, by the end of summer, on September 1, discharge had converged to 0.02 cms in all years (Fig 2c).

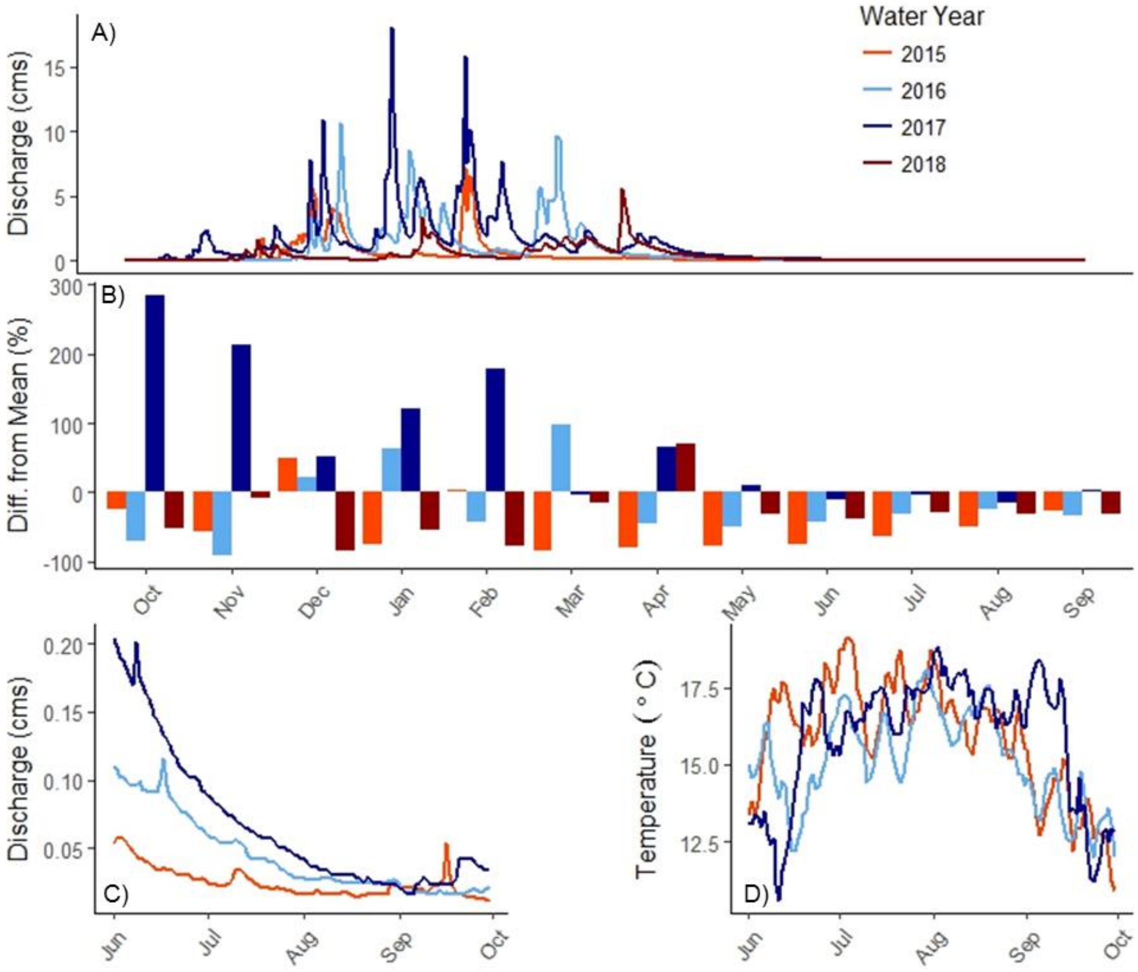

Figure 2. Differences in winter stream flow for 2015-2018 (when fish migration was monitored) and summer stream flow and temperature for water years 2015-2017 (when fish growth and condition was monitored). A) Discharge (cms) for the entire year for each year B) monthly mean percent difference from the long-term (51 years) daily mean discharge, C) zoom-in view of discharge in summer months and D) mean daily temperature during the summer months. Data are from USGS Elder Creek Gage (no. 11475560).

O. mykiss Growth Rates

We recaptured a total of 217 individuals (n = 63, 85, and 69 in 2015, 2016, and 2017, respectively; length and weight histograms in Fig S2 and Fig S3) from which we were able to calculate late-summer growth. Overall, *O. mykiss* grew little, and some even lost weight, during late summer regardless of large differences in antecedent flow conditions (Fig 3, Fig 4). Mean growth rate across all years during this time period was 0.02 ± 0.05 mm/day. Growth rates did not differ between Fox and Elder creeks (site was not a significant effect in a two-way ANOVA within a given year, $P > 0.10$), so growth data from both streams were combined for analyses. There were no differences in growth rates among years (i.e., year was not statistically significant in an ANOVA, $F_2 = 1.81$, $P > 0.10$, Fig 3), despite marked differences in winter rainfall magnitudes and timing as well as initial summer flows across years (Fig 2c).

Based on a small sample of recaptures at other times of the year (n = 119), we found that positive growth occurred outside of the summer season, with the mean growth rate for the entire year of 0.09 ± 0.04 mm/day. Data from 3 fish captured in Fox Creek indicated that growth was very high in the spring and early summer (0.24 ± 0.02 mm per day, from Apr 29, 2017 – Jul 14, 2017). We also found that growth rates were high in the early summer (June-July: average of 0.08 ± 0.07 mm per day based on 20 fish from Elder Creek) and high in the winter (0.12 ± 0.10 mm per day, based on 4 fish captured Jan 24, 2015, 3 of which were recaptured on Jul 16, 2015, 1 of which was recaptured on Jun 17, 2015). A spaghetti plot showing growth histories for all recaptured individuals further highlights that later summer is generally a period of slow growth compared to other seasons, though the observations from other seasons are limited (Fig 4).

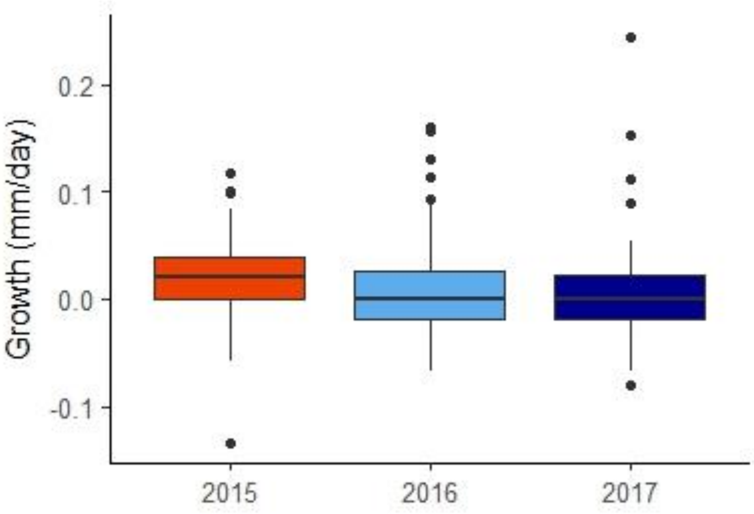

Figure 3. Individual growth rates from mid-summer (July) to end of summer (September) is close to zero and does not differ between dry (2015), intermediate (2016), and wet years (2017).

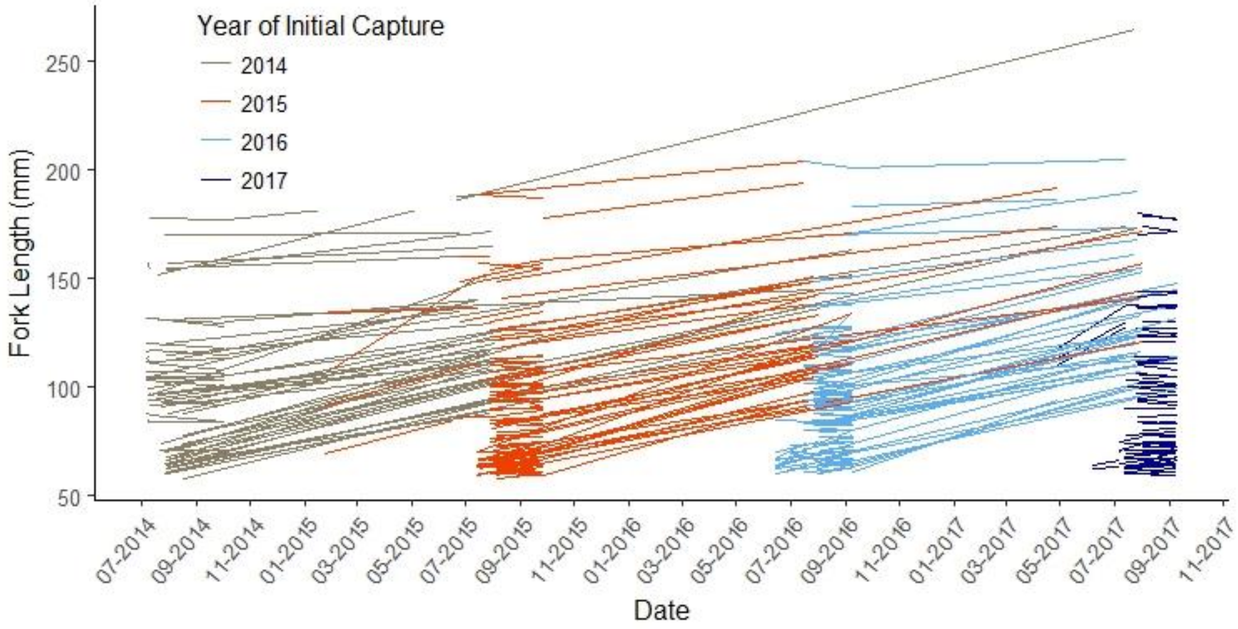

Figure 4. In Fox and Elder Creek, *O. mykiss* grew over the year between captures over the summer, but did not grow between mid-summer (July-Aug) and late-summer (Sept). Each line is an individual fish. A positive slope indicates growth, a flat or negative slope indicates no growth.

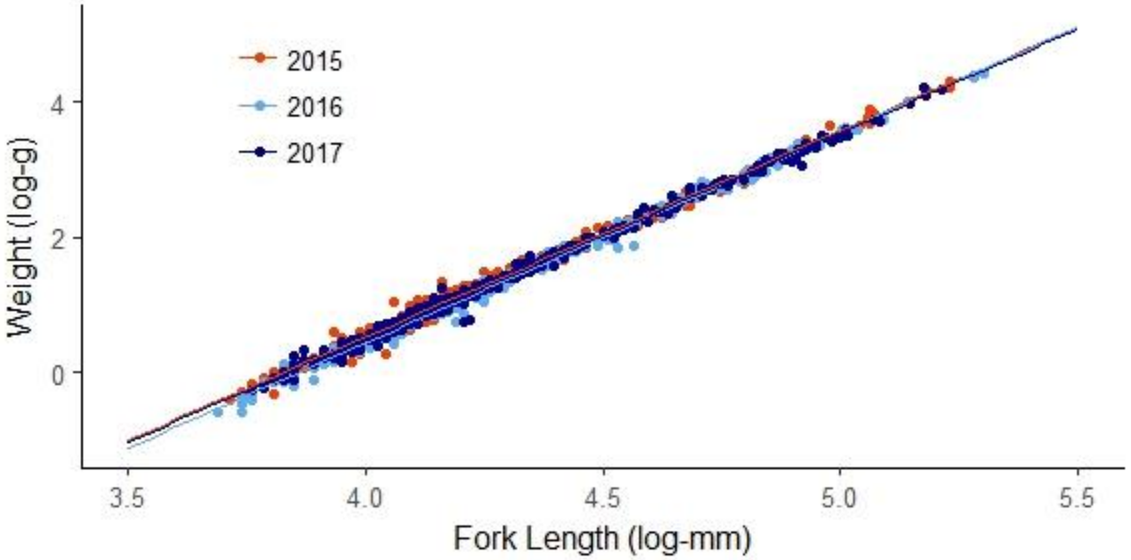

Figure 5. Length-by-weight relationship (condition factor) for fish caught September.

O. mykiss Condition Factor

We found that fish condition in September differed among years (year was significant in an ANCOVA as well as a main effect of year and fork length-year interaction; main effect: $F_2 = 81.9$, $P < 0.001$, interaction: $F_2 = 7.7$, $P < 0.01$). We found that the fish sampled in 2016 were lighter in weight (in worse condition) than the fish sampled in 2015 within the entire size range of fish that we observed (Fig 5), and they were lighter than the fish sampled in 2017 for most of our observed size range (up to 142 mm, which includes 96.1% of the sampled fish). In the ANCOVA model, fish sampled in 2015 were always heavier than the fish sampled in 2017 within the size range that we observed, but the predicted estimates for weights were very similar between these two years (overlapping lines, Fig 5), indicating that condition was similar for fish between these two years.

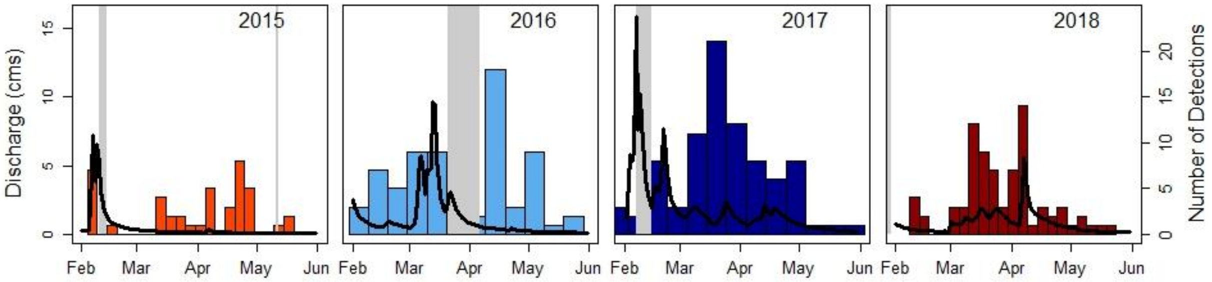

Figure 6. Peak spring out-migration of juvenile *O. mykiss* occurs at the same date across dry and wet years, from February – May for each water year, 2015-2017. Grey bars indicate when antenna was not operating. Bars are the number of detected fish, black lines are stream flows.

Spring Movements and Selecting Flows for Movement

The mean date of all spring movements (defined here as antenna detections between Feb 01 – May 31) did not differ among years ($F_3 = 0.66$, $P > 0.1$ in an ANOVA, mean date April 1, 2015, March 28, 2016, March 25, 2017, and March 27, 2018, Fig 6) despite extreme differences in flow conditions during this window (Fig 1, Fig 6). In general, movements were detected from February through May, with most movement detected in March and April (Fig 6, 73.8%, 63.2%, 76.5%, and 84.6% in 2015, 2016, 2017, and 2018, respectively).

Stream flow on the days in which fish were detected moving was significantly higher than the flows available to the fish across the entire spring outmigration season (ANOVA, nested within water year, $t_{711}=5.3$, $P < 0.01$, Fig 7). However, the difference in flow was small, and the mean flow when fish were moving was only slightly higher than the mean available flow in any given year (Table 2).

Table 2. Mean flows (± sd) when fish were detected moving past stationary antenna vs. mean of all flows (± sd) when antennas were operating.

Year	Movement Flows (cms)	All Flows (cms)
2015	1.00 (1.94)	0.41 (1.05)
2016	1.15 (1.65)	1.10 (1.75)
2017	1.74 (1.39)	1.61 (1.92)
2018	1.38 (0.96)	0.82 (0.80)

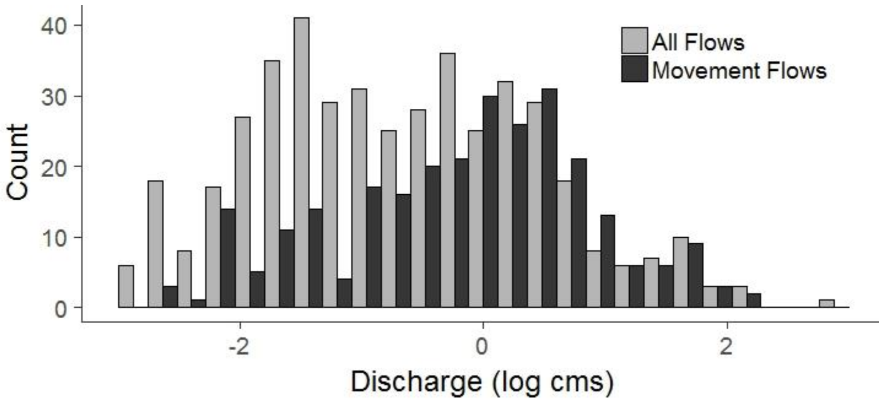

Figure 7. *O. mykiss* were detected moving at flows that were slightly higher than all the flows for the spring seasons. Flows that fish are detected moving at are in black, and all flows for the season are in grey.

Movements outside the Spring Window

Detections at the stationary antenna revealed an additional pulse of downstream-movement outside the spring outmigration season. Most (73.8%) detections at the stationary antenna occurred in the spring months, from February – May. However, during fall 2016, there was an additional pulse of movement, with 41 fish being detected at the antenna between September and November. These fish were smaller than fish that moved out in the spring ($t_{86} = -4.06$, $p < 0.01$ in a Welch two-sample t-test), and 93% of these fish were originally captured low in the system (within 0.5 km from the mouth), which differed from the spring detections, 50% of which were originally captured in the upper watershed. Additionally, fall movements were strongly related to stream flow; the stream flow on days when fish were detected moving was significantly higher than the stream flows available to the fish during the fall season (ANOVA, $F = 22.18$, $P < 0.01$, Fig S1).

Discussion

California experienced a weather whiplash in 2015-2018 with extreme swings in annual precipitation over a short time span, a phenomenon that is expected to become more common in the future (Swain et al. 2018). In the wettest year (2017), stream flow in Elder Creek in the mid-summer was nearly three times higher than during the driest year (2015). Given the differences in total rainfall among years, we expected that trout growth would differ as well, especially considering that period of summer that we monitored can be an especially harsh period for salmonids rearing in streams (Hwan et al. 2018). Regardless, we found little difference in growth rates in dry and very wet years. Additionally, spring out-migration timing differed little between drought and wet years, despite large differences in stream flow during out-migration months. These results suggest that groundwater-fed tributary streams with lithology that tends to store rather than shed water through the "critical zone," such as Elder Creek (Rempe and Dietrich 2014, 2018), may be buffered against inter-annual variation in rainfall relative to streams that become even drier in the driest of years. As follows, these groundwater-fed streams with storing lithology may be important sites for conservation of salmonids, especially near the southern end of their range.

Shaded, ground-water fed tributary streams as high-quality habitat across years

Our result that *O. mykiss* summer growth differed little following wet versus dry winters is surprising given that previous studies have documented that drought and reduced stream flow can be limiting for salmonids (Elliott et al. 1997, Deegan et al. 1999, Harvey et al. 2006). Harvey et al. 2006 experimentally reduced stream flow by 75-80% during summer months and found a concomitant decrease in the growth of juvenile *O. mykiss*. Moreover, in our study, trout condition varied minimally among years. We found that condition factor in one year, 2016, was slightly lower in September than in other years, but this was not linked to a drought year or differences in stream flow or fish density. One possible explanation for these results is that stream flow at the end of the time period (September) was very similar for all three years, despite flows being elevated earlier in the season. These conditions contrast with the experimental manipulation in Harvey et al. (2006), where flows were reduced for an entire 6-week period in the summer when growth was measured, not just the beginning of the sampling period. In addition, across all years in our streams, temperatures were similar and remained largely within a suitable range for *O. mykiss* (e.g., 17- 19°C, Wurtsbaugh and Davis 1977, Myrick and Cech 2005). The convergence of stream conditions at the end of the summer following both dry and wet winters suggests that in some lithologic settings, groundwater fed, shaded tributary habitats can produce sufficient stream flow and cool temperatures to support stream-dwelling salmonids rearing during the summer drought season, regardless of the previous winters' precipitation patterns (Rempe and Dietrich 2018). These results further highlight the importance of such habitats as the envelope of suitable conditions for salmonids in California shrinks with climate change (Wenger et al. 2011). Many of these upper headwater tributary sites are disconnected from each other and mainstem habitats, and restoring access to these sites, by barrier removal or re-design (Kemp and O'Hanley 2010, Martens and Connolly 2010), for example, could allow stream salmonids to access high quality habitat (Fausch et al. 2002b, Sheer and Steel 2006, Fausch et al. 2009).

Summer growth is slow in Mediterranean-climate California streams

Our finding that growth is slow during the summer season in Mediterranean-climate California streams is in agreement with other studies that have measured growth rates of *O. mykiss* in coastal California streams (Harvey et al. 2005, Hayes et al. 2008, Sogard et al. 2009). Our study is also consistent with the results of Hayes et al. (2008), who also found little to no growth between August-September and that growth rates did not increase until November in Scott Creek, California (Santa Cruz County). Similarly, Harvey et al. (2005) found low specific growth rates of *O. mykiss*, between -0.2% and 0.6%, in the summer in Jacoby Creek, California (Humboldt County). In another stream in Santa Cruz county, Soquel Creek, the fastest growth rates for *O. mykiss* were observed in winter (Sogard et al. 2009). There, over-summer growth rates were much higher than our estimates (0.11 mm/day vs. 0.02 mm/day), but they measured growth during summer over a longer period, including June – October, and it is possible that fast growth in early summer or fall wet-up contributed to the high average summer growth. These studies, together with the data we present on a few individuals who were recaptured during the early summer period, suggest that the early summer (June – July) may be a time of elevated growth and productivity, which also coincides with a mayfly subsidy in Fox Creek (Uno and Power 2015), but that growth slows as the summer progresses.

Reduced growth at the end of the summer for salmonids rearing in Mediterranean-climate streams may be linked to food web phenology during this season. In the Eel River, food web productivity, including invertebrate biomass, peaks early in the summer, often from June - July (S. Kelson, unpublished data, McNeely and Power 2007, Power et al. 2008), a pattern that is common among semi-arid streams that experience reliably dry summers (Rundio and Lindley 2008). The reduction in invertebrate biomass, in addition to the reliable reduction in stream flows (even in summers following extreme wet years, such as 2017), may result in limited opportunities for drift feeding during this period, which is one of the primary feeding behaviors exhibited by rearing juveniles salmonids (Fausch 1984, Nielsen 1992, Nakano and Kaeiryama 1995). Experimental manipulations of food availability in other systems have greatly increased growth rates, by up to 0.9% per day in *O. kisutch* (Rosenfeld et al. 2005) and up to 2.3% per day in *O. mykiss* (Boughton et al. 2007), suggesting that food availability is limiting in natural streams, and may be a cause of reduced growth. However, subsidies from the mainstem, even if they are temporally short pulse subsidies (Uno and Power 2015), or the terrestrial environment (Nakano and Murakami 2001, Fausch et al. 2002a) may compensate for reduced instream production.

Stream Flow and Timing of O. mykiss Movements

Beyond limited differences in growth, we found that the timing of when juvenile *O. mykiss* moved downstream in spring was similar among years (Fig 5). Fish moved during all flow conditions available during the spring, showing only slight (but significant) preference for higher flows. These results suggest that juvenile trout out migrating from Elder and Fox creeks are not limited by flow during the spring outmigration window, even during the recent drought. These results contrast with results of other research indicating that high flow events can be cues for fish migrations (Jonsson 1991). However, we should note that the antennas were often not functional during the highest flows, and we could have missed movement pulses during those highest flows. Previous studies have found that juvenile salmonids likely initiate migrations in response to various cues, including photoperiod and stream temperature (Bjornn 1971, Achord et al. 2007, Spence et al. 2014) and lunar cycles (Grau et al. 1981, DeVries et al. 2004), and these factors may be at play for *O. mykiss* here. In summary, spring flows were not limiting to movement in these groundwater-fed tributaries, even during drought years.

While we did not find flow-initiated migrations in the spring season, we did find a pulse of downstream movement during elevated flows in the fall. Across our three years of study, there were several early season storms in only one year (fall 2016), and in this year, we also detected individuals moving past stationary antenna. Fall movements have been previously documented for juvenile *O. mykiss* (Brown 1990, Tattam et al. 2013) and other anadromous salmonids

(Riddell and Leggett 1981, Roni et al. 2012). In Washington state, these fall movements were associated with the larger, faster growing individuals who were moving into higher-order streams (Tattam et al. 2013), likely because these individuals did not have the lipid storage to remain in the cold tributaries over the winter. Here, we found that these individuals who were detected moving in the fall were smaller on average than those moving in the spring, and they originated from the lower watershed in Elder, below the waterfall. This suggests that the fall movers may be subdominant to those who are moving in the spring (Sloat and Reeves 2014), and either shuffling habitat unit within the creek, volitionally moving downstream to rear in the mainstem, or being displaced with the high flow pulses (Young et al. 2011).

Drought, weather whiplashes, and O. mykiss ecology

Although we did not find a large effect of drought flow conditions on *O. mykiss* summer growth or spring out-migration timing, there may have been changes to steelhead juvenile ecology and performance that we did not measure. For example, we did not quantify survival in this study, and it is possible that there were changes in survival across the drought and wet years. While we found little difference in end of summer density among years, it is possible that this reflects earlier self-thinning or significant mortality differences among years, and thus improved growth opportunities for survivors (Dunham and Vinyard 1997, Keeley 2003). Additionally, nearby habitats that are also used by juvenile *O. mykiss*, such as the mainstem South Fork of the Eel River, can be quite warm during the summer (up to 28°C), and those warmer conditions are associated with higher incidence of black spot disease (Schaaf et al. 2017). Moreover, drought years without a scouring flood event produce a food web that is less favorable for salmonids feeding in the mainstem South Fork Eel River (Power et al. 2008, 2013). In other streams, and especially further south in the range of anadromous *O. mykiss*, reduced flows are often correlated with increased stream temperatures that create physiologically stressful conditions for cold-water salmonids (Mantua et al. 2010, Wenger et al. 2011, Boughton et al. 2015). Finally, differences in flow conditions in the winter in association with the drought may impact migration timing for adults returning from the ocean and their ability to access spawning habitats, including tributaries in the upper watershed (Carlson et al. in prep).

Conclusions

Overall, we report that *O. mykiss* growth and movement did not differ across years, despite an abrupt transition from extreme drought to wet years. These results highlight the importance of upper headwater, groundwater fed streams that maintain cool temperatures and sufficient base flow (Wiley et al. 1997), including streams that are characterized by a lithology that allows for over-summer storage and slow draining of groundwater (Salve et al. 2012, Rempe and Dietrich 2014). Near the southern end of the range of salmonids, these habitats may be especially important, making them a high priority for conservation and restoration efforts (Wenger et al. 2011, Katz et al. 2013).

Acknowledgements

This study was co-authored by Stephanie M. Carlson. We thank Peter Steel for his stewardship of the UC Angelo Coast Range Reserve and support for our research there. This work was partially funded by a National Science Foundation (NSF) Graduate Research Fellowship and UC Berkeley Wildlife Grant to S.J.K, and by the NSF CZP EAR-1331940, Eel River Critical Zone Observatory.

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Supplemental Tables and Figures

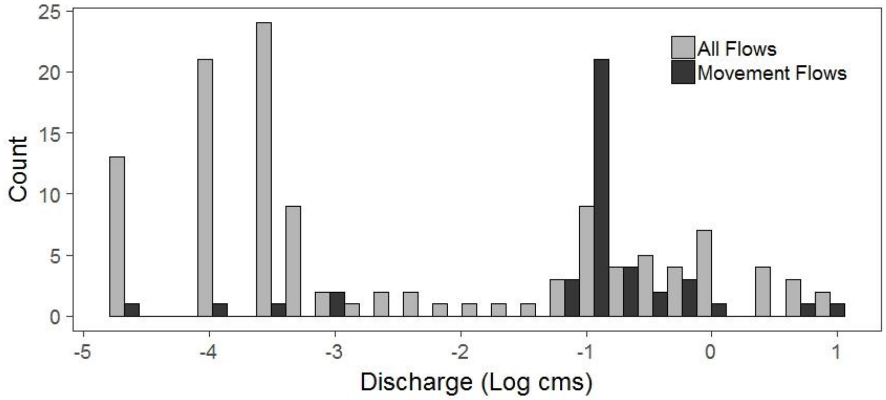

Figure S1. Fish movements in the fall only occurred during elevated flow events. Flows that fish are detected moving at are in black, and all flows for the season are in grey.

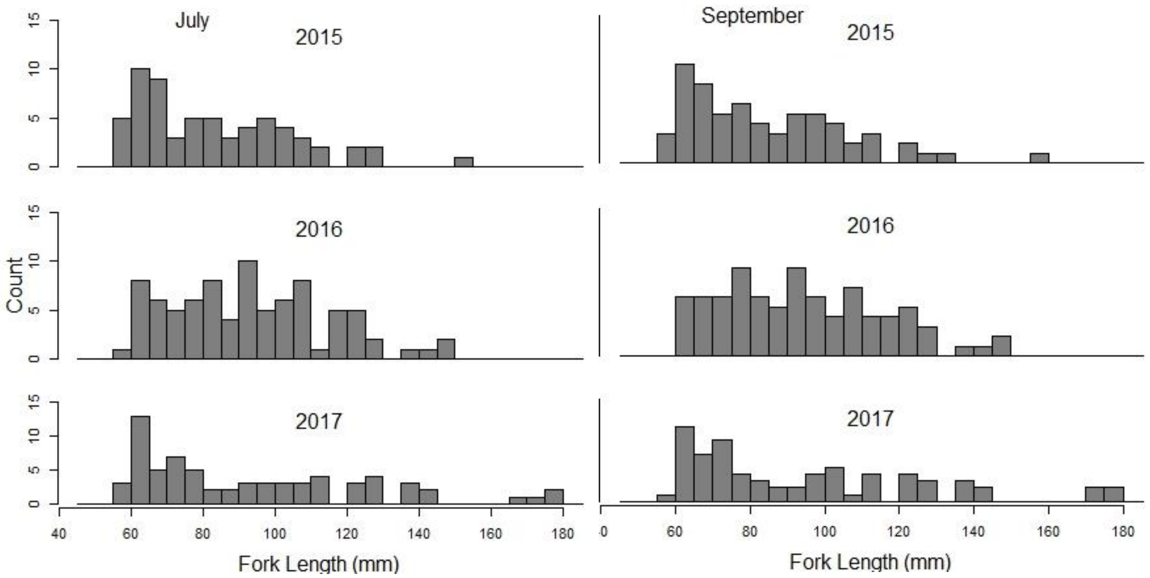

Figure S2. Histograms of length of recaptured fish at initial capture in July and recaptured in September.

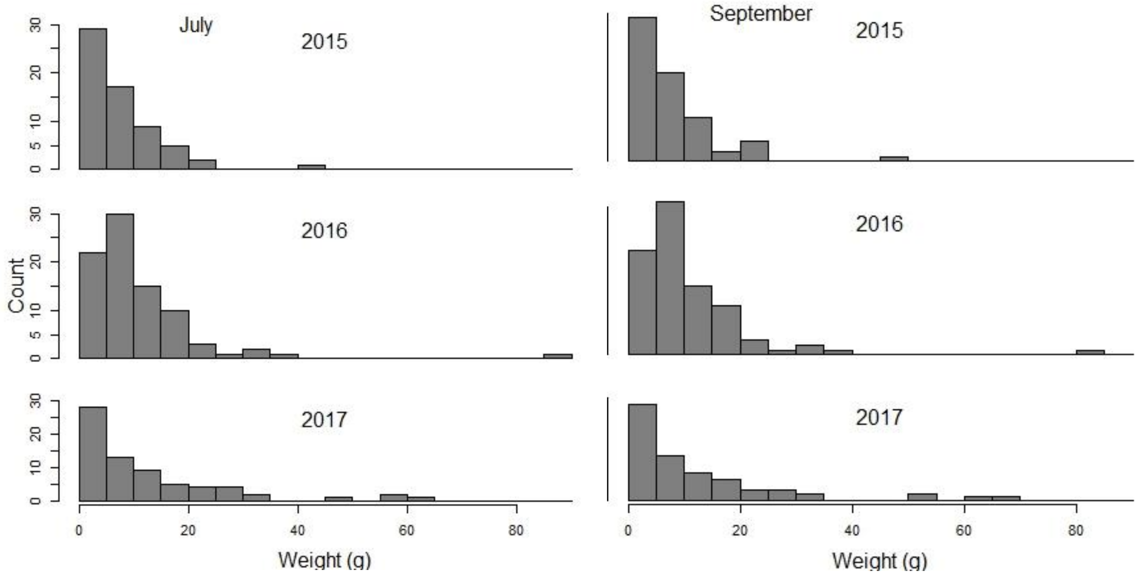

Figure S3. Histograms of weight of recaptured fish at initial capture in July and recapture in September.

Appendix 1: Approximating population size with Leslie-K method vs. total counts

We found that the Leslie-K method of approximating population size tended to be inaccurate for pools with a small total catch (<10 individuals). In these cases, the pools were more likely to violate the assumption of the model that catch per unit effort decreases with each pass, which lead to erroneous population estimates, including some negative estimates (Figure S1). When we excluded pools where we caught less than 10 fish, the confidence interval for the slope of relationship between the count of fish and Leslie-K estimated number of fish included one (Table S1), suggesting that the two were returning similar results when the Leslie-K assumptions were not violated. For this reason, we used the total counts to estimate fish density as this allowed us to include pools with small total catches.

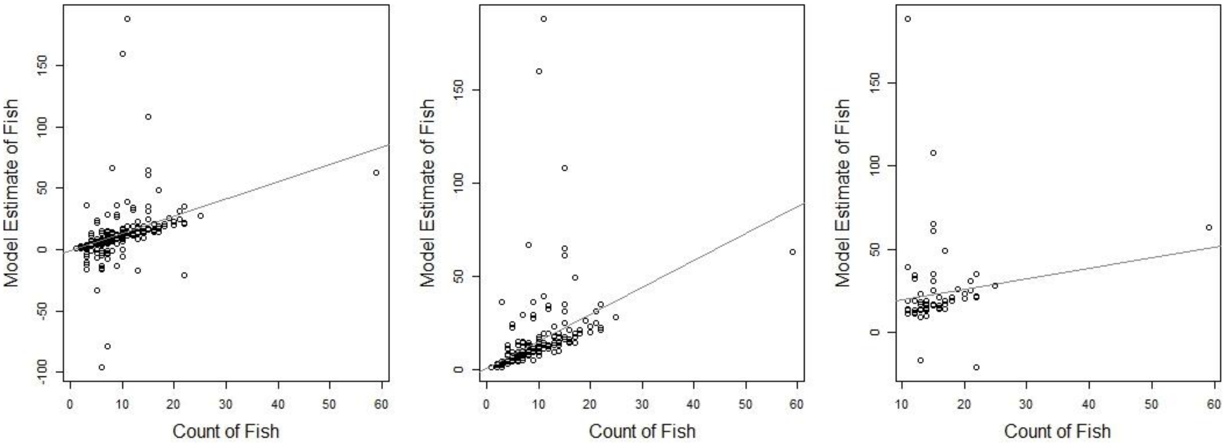

Figure A1. Relationship between estimated number of fish per pool using Leslie-K methods and sum of fish caught per pool for a) all pools and b) only pools that met the assumption have having a decaying catch per unit effort and c) only for pools that had >10 fish in the total counts. Grey lines are a linear regression, parameters in Table S1.

Table A1. Model parameters for the linear regression between the count of fish and the estimated number of fish using Leslie-K methods. Results are reported as estimate with 95% confidence intervals in parenthesis.

Pools Included	**Intercept**	**Slope**	**r^2**
All Pools	-1.33 (-4.02-1.36)	1.41 (1.11-1.72)	0.18
Pools Meet Assumptions	0.22 (-2.22-2.67)	1.46 (1.18-1.73)	0.27
Pools with over 10 fish in count	13.44 (-2.6, 29.5)	0.62 (-0.35, 1.60)	0.20

6

Conclusions and Future Research

My dissertation research highlights partially migratory populations as ideal systems for exploring linkages across multiple levels of biological organization: from genotypes to phenotypes to ecology. Partial migration is common in nature and is a strong form of intraspecific variation. Moreover, migration is known to have large ecological consequences, suggesting that partially migratory populations are ideal for studying the ecological consequences of intraspecific variation (phenotype-ecology). In some cases, including my study system, the genetic underpinnings of migration are known, paving the way to studying the extended phenotype of partial migration (genotypes-phenotypes-ecology).

I studied partially migratory populations of *O. mykiss* in two northern California streams. I found spatial variation in migration-linked genotypes in replicate tributary streams, such that the frequency of migratory genotype fish was higher downstream of partial barriers, and increased above partial barriers in wet years when stream permeability was higher. This genetic variation was associated with changes in populations and food web effects. In particular, I found differences in density (higher in regions dominated by migratory genotypes) and size structure (more complex, including older fish in regions dominated by resident genotypes). These differences in population ecology had food web effects, and in particular the presence of large fish was accompanied by an increase in the food chain length, as these old fish were feeding higher on the food web.

The trait differences associated with resident vs. migratory fish in *O. mykiss* are traits that are commonly associated with life history divergence in other partially migratory taxa. For example, resident and migratory individuals commonly differ in body size (Chapman et al. 2011). Body size is a critical trait in ecology (Wilson 1975), and may be linked to further differences in fecundity (Honěk 1993), feeding preferences (Cohen et al. 1993), including the ability of predators to limit their prey (Borcherding et al. 2010), and social hierarchies (Keeley and Grant 1995). Furthermore, fecundity and reproductive success often differs between resident and migratory individuals (Gillis et al. 2008, Middleton et al. 2013), and these differences may be associated with population density in the natal habitat. Previously, population density has been explored as a *cause* of migration, with individuals being more likely to migrate from high-density habitats (e.g., Grayson and Wilbur 2009). However, it is possible that migration and density are linked in a feedback loop, such that migratory individuals create high-density habitats via to their increased fecundity, which then leads to a tendency to migrate due to density-dependent competition. Future research could explore his possibility by manipulation the density or size structure (Bassar et al. 2010, Phillis 2014) and asking how this effects competition and growth among individuals and among other trophic levels. Future research is needed to understand the relative fitness of migratory and resident individuals in high-density environments, to determine if migratory animals create an environment where they are also more successful than their resident counterparts, thereby creating a feedback loop. Finally, by definition, resident individuals remain in one habitat for extended periods of time when migratory individuals are absent. This year-round presence of resident individuals may have further ecological consequences, such as top-down pressure on lower trophic levels, similar to resident ungulates foraging on grasses (Fryxell and Sinclair 1988) or resident alewives foraging on zooplankton communities (Palkovacs and Post 2008). Partial migration is an extreme form of intraspecific variation that is linked to body size and habitat use, and future research could explore the ecological effects of these traits in other partially migratory animals.

My dissertation also demonstrates that partial barriers influence patterns of genetic variation across the landscape. I found that partial barriers reduced the frequency of migratory genotypes in stream reaches above barriers, and this was true for natural waterfalls and tributary confluences. While impassible barriers in stream systems are associated with genetic divergence above and below barriers (e.g., Deiner et al. 2007, Pearse et al. 2009, Clemento et al. 2009), divergence associated with partial barriers is less frequently studied. However, small, partial barriers are ubiquitous features of landscapes and streamscapes (Meixler et al. 2009, Kemp and O'Hanley 2010), and the cumulative influence of multiple, small barriers may equal that of larger, impassible barriers (Apgar et al. 2017). Importantly, I found that the permeability of partial barriers varied among years due to variation in precipitation events that raised stream flow levels and facilitated passage. Such temporal variation in permeability across the landscape, including at partial barriers, may also be common. In terrestrial systems, roads rarely act as complete barriers (Holderegger and Di Giulio 2010) and, in some cases, vehicle traffic changes seasonally with tourism (Alexander et al. 2005). Understanding the factors that influence temporal variation in barrier permeability should be a key target of future research on the ecological and evolutionary effects of partial barriers.

This body of work also has implications for the conservation and management of partially migratory *O. mykiss*. The migratory form of *O. mykiss* is federally protected (Williams et al. 2016), but the resident form is not, and as a consequence many conservation efforts are aimed at restoring migration in *O. mykiss* where it has been lost. In this context, it is valuable to understand the conditions that lead to the expression of migration within partially migratory populations. Furthermore, it is useful for managers to be able to predict the proportion of a population migrating using molecular tools. I found that sex ratios in the out-migrating fish versus resident fish is a low-cost method of approximating of the proportion of the population that migrates, building off a model proposed by Ohms et al. (2014). Similarly, there is growing interest in restoring connectivity in aquatic systems by removing large dams (Quiñones et al. 2014) and small barriers (Kemp and O'Hanley 2010). One question that arises in these systems is if it will be necessary to transplant migratory fish into the previously disconnected upper watersheds in order to restore migration. The finding from my research that migratory adults extended their distribution upstream of partial barriers in wet years suggests that migratory fish have the ability to expand their range upstream rapidly. This upstream range expansion has been observed following the removal or remediation of small barriers (Wood et al. 2018) and larger dams such as the Elwha in Washington state (McMillan et al. 2015). Moreover, I found that resident-genotype fish do sometimes migrate from their natal streams, which suggests that resident fish are another potential source of migrants. However, it is unclear whether those migratory fish with resident-genotypes have the same fitness as migratory fish with migratory-genotypes, but this could be an important avenue of future research (see also Hale et al. 2013). To restore migration is to restore a complex life history trait, and understanding ecological and evolutionary causes and consequences of this life history variation will help inform conservation efforts.

Migratory animals are often threatened in part due to their reliance on connectivity across the landscape to complete their life history and take advantage of spatially and temporally disparate resources (Dingle and Drake 2007). Understanding how landscape connectivity influences the ability of migratory animals to undertake their migration is key to informing conservation strategies (Wilcove and Wikelski 2008). Additionally, understanding the ecological effects of migration are important in predicting ecological change that may follow with the loss of migration. My body of dissertation research contributes to our understanding of the evolutionary and ecological dynamics of migration in partially migratory animals, including how they are influenced by landscape connectivity under different environmental conditions.

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