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ARTICLE

Do genomics and sex predict migration in a partially migratory salmonid fish, *Oncorhynchus mykiss*?

Suzanne J. Kelson, Michael R. Miller, Tasha Q. Thompson, Sean M. O'Rourke, and Stephanie M. Carlson

Abstract: Partial migration is a common phenomenon wherein populations include migratory and resident individuals. Whether an individual migrates or not has important ecological and management implications, particularly within protected populations. Within partially migratory populations of *Oncorhynchus mykiss*, migration is highly correlated with a specific genomic region, but it is unclear how well this region predicts migration at the individual level. Here, we relate sex and life history genotype, determined using >400 single nucleotide polymorphisms (SNPs) on the migratory-linked genomic region, to life history expression of marked juvenile *O. mykiss* from two tributaries to the South Fork Eel River, northern California. Most resident fish were resident genotypes (57% resident, 37% heterozygous, 6% migratory genotype) and male (78%). Most migratory fish were female (62%), but were a mixture of genotypes (30% resident, 45% heterozygous, 25% migratory genotype). Sex was more strongly correlated with life history expression than genotype, but the best-supported model included both. Resident genotypes regularly migrated, highlighting the importance of conserving the full suite of life history and genetic diversity in partially migratory populations.

Résumé : La migration partielle est un phénomène répandu dans lequel des populations comptent des individus migrateurs et résidents. Le fait pour un individu de migrer ou non a d'importantes conséquences écologiques et en matière de gestion, en particulier au sein de populations protégées. Au sein de populations partiellement migratrices de truites arc-en-ciel (*Oncorhynchus mykiss*), la migration est fortement corrélée à une région précise du génome, mais la mesure dans laquelle cette région peut prédire la migration au niveau individuel n'est pas bien établie. Nous relions le sexe et le génotype du cycle biologique, déterminé en utilisant >400 polymorphismes mononucléotidiques (SNPs) sur la région du génome associée à la migration, à l'expression du cycle biologique d'*O. mykiss* juvéniles marqués issus de deux affluents de la rivière South Fork Eel, dans le nord de la Californie. La plupart des poissons résidents présentent des génotypes de résident (57 %, 37 % et 6 %, respectivement, de génotypes de résident, d'hétérozygote et de migrateur) et sont des mâles (78 %). La plupart des poissons migrateurs sont des femelles (62 %), mais ils présentent un mélange de génotypes (30 % résident, 45 % hétérozygote, 25 % migrateur). Le sexe présente une plus forte corrélation avec l'expression du cycle biologique que le génotype, mais le modèle qui a le plus d'appui comprend les deux. Les individus de génotype résident migrent régulièrement, soulignant l'importance de conserver toute la gamme de diversité génétique et du cycle biologique dans les populations partiellement migratrices. [Traduit par la Rédaction]

Introduction

Animal migration is an important phenomenon that allows populations to exploit different habitats throughout their life history (Dingle 2014). Many migratory populations are partially migratory, meaning they include a mix of individuals who do and do not migrate (Chapman et al. 2011). Partial migration has been observed across a 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). However, migration is on the decline globally because migratory animals depend on multiple habitats and the landscape connectivity needed to access them (Wilcove and Wikelski 2008; Shuter et al. 2011). This pattern is especially striking within partially migratory populations of salmonid fish, where the migratory form is often on the decline and protected (e.g., *Salmo salar* and *Salmo trutta*, Jonsson and Jonsson 2009; *Salvelinus fontinalis*, Scribner et al. 2012), 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 cross-ecosystem subsidies 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 many populations with short coastal migrations are fully anadromous (steelhead trout), and inland populations are fully resident (rainbow trout), some populations include both forms. Migratory steelhead are federally protected throughout the southern end of their range in California under the Endangered Species Act (Williams et al. 2016), but resident rainbow trout in the same populations are not. 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 showed high divergence between populations below barriers (dominated by anadromous fish) versus populations above barriers (domi-

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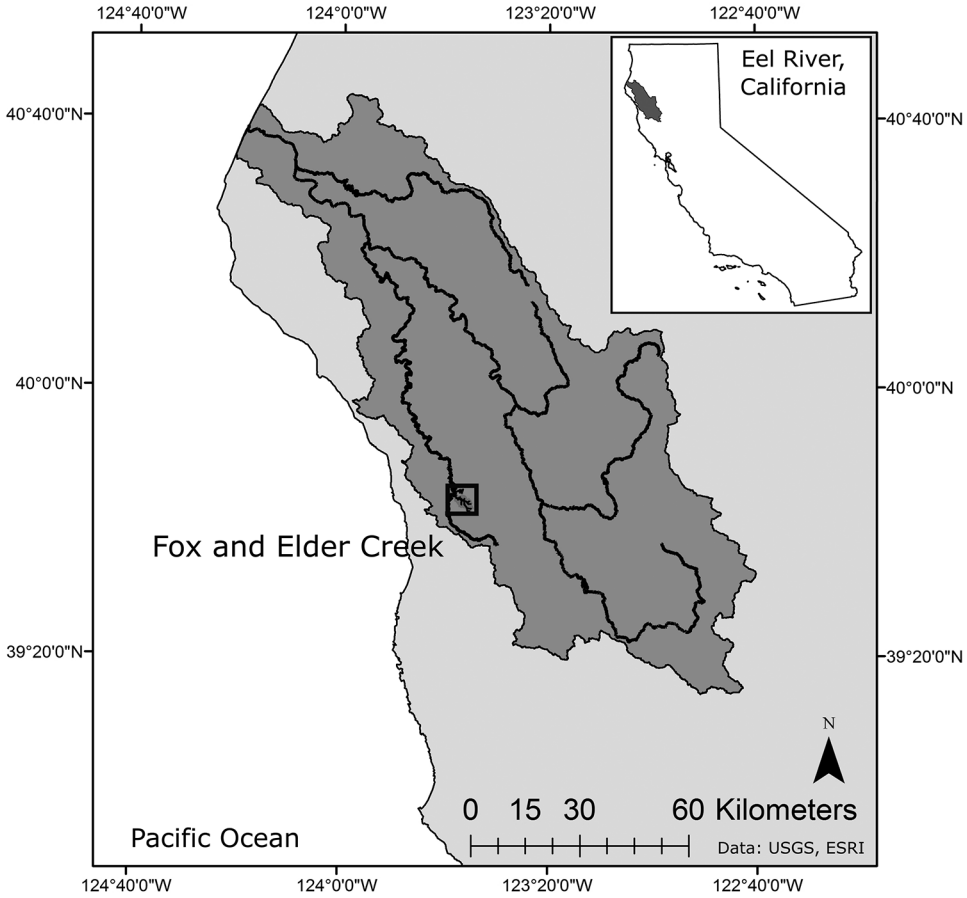
Fig. 1. Fox and Elder creeks are headwater tributaries to the South Fork Eel River in the Eel River watershed in coastal northern California.



nated 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. Together, these studies suggest that life history genotyping, using loci on *Omy5*, may be a powerful approach for predicting migration behavior of individuals in partially migratory populations of *O. mykiss*.

Sex is another factor that can influence migration strategy in partially migratory animals (Chapman et al. 2011). Theory suggests that female-biased migration should arise in salmonids because fecundity (i.e., egg production) increases with body size, and females achieve a larger body size at sea than in fresh water (Fleming and Reynolds 2003; Hendry et al. 2004). 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 nonlethal 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 that combining information on sex and life history genotype might improve our ability to predict migration at the individual level within partially migratory populations.

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

Methods

Study site and fish sampling

We studied partially migratory populations of *O. mykiss* in two tributaries of the South Fork Eel River, Elder and Fox creeks, both located within the University of California Angelo Coast Range Reserve (Mendocino County, California; 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). *Oncorhynchus 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 three-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 2 g and 60 mm FL were tagged with a 2 mm 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 remeasured for length and mass.

DNA extraction, sequencing, and single nucleotide polymorphism (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 subsample from 2015–2017, where every other sample pool was included in the genetic analyses. We conducted restriction site-associated DNA (RAD) capture (Rapture) following the methods and bait set described in Ali et al. (2016). Briefly, the bait set targets 500 SbfI RAD tags that are distributed across all chromosomes. While the capture enriches coverage at the targeted loci, many other RAD tags are also sequenced at lower coverage. This approach facilitates analyses that require high coverage using the targeted loci while also providing a larger amount of data for analyses that do not require high coverage (e.g., discriminant analysis of principal components (DAPC) analysis from single-read sampling; see below). Libraries were sequenced using paired-end 100-base pair (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 (Li and Durbin 2009) with default parameters. SAMtools (Li et al. 2009) was used to filter alignments for proper pairs, sort alignments, remove polymerase chain reaction (PCR) duplicates, and index binary alignment map files.

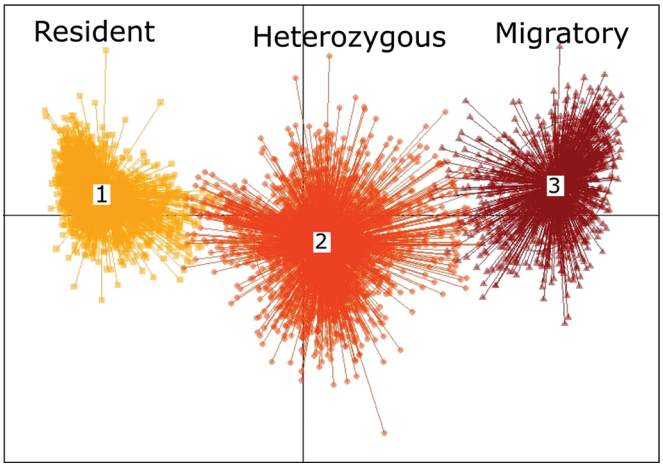
All Rapture sequencing data analyses were performed using analysis of next generation sequencing data (Korneliussen et al. 2014) with a minimum mapping quality score of 20 and a minimum base quality score of 20. To select sites (SNPs) appropriate for downstream analyses, the following steps were applied. Using all samples, 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 the individuals were excluded.

After establishing loci that met the above filtering criteria, for each individual, we sampled a single sequencing read at each locus on *Omy5* (415 total), the chromosome with the migration-associated block of linkage disequilibrium (Pearse et al. 2014), and used the base call from that read as input data for downstream analyses (see below). In other words, for each individual, one read was sampled at each SNP passing the filtering step regardless of sequencing depth at that SNP. The single-read sampling approach 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 other approaches, such as calling genotypes (Korneliussen et al. 2014). The single-read base calls were used to generate an individual-by-loci matrix, where 1 represented the major allele and 0 represented the minor allele. Missing data were replaced with the mean allele call at the locus, which corresponds to the major allele frequency, to conduct DPAC, which requires a full numeric matrix (Jombart et al. 2011; see below).

Assigning migratory versus resident genotypes

To determine life history genotype groups, we conducted a DAPC (Jombart et al. 2010) with the matrix described above. Owing to its large size and high divergence, the variation in the *Omy5* region dominates the discriminate analysis (Fig. 2). We used the "find.cluster" method implemented in R package "adegenet"

Fig. 2. Discriminant analysis on principal component group individuals into three clusters, which are used to assign individuals to resident (1, light grey – yellow squares), heterozygous (2, dark grey – orange circles), or migratory (3, black – red triangles) genotypes. [Colour online.]



(Jombart et al. 2011), 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 (major allele frequency) at each locus, which led to individuals with large amounts of missing data being grouped into the heterozygote group. To avoid false heterozygotes, we included individuals who had data at a minimum of 165 SNPs (assignment to the heterozygote group increases substantially among individuals who are missing more than this number of SNPs; see also Appendix A). 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, California). PCRs were done in a 10 μL volume containing Taqman GT Master Mix and custom Taqman probes and primers for OMY1–2SEXY and an autosomal locus 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 min hold at 95 °C and then 40 cycles of 15 s at 95 °C and 1 min 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, California. We also calculated the sex ratios for a random subset of juvenile, age-0 fish (<85 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, Oregon), 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 200 and 350 m upstream of the mouth in Elder Creek and 175 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 to 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 h, 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 detections also represented fish moving downstream (n = 175). 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 during the outmigration window (98.2% of fish detected were less than 155 mm FL). Second, mark–recapture data (Kelson and Carlson 2019) and length frequency plots (refer to online Supplementary material, Fig. S1[1]) 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, California; 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 also compared the genotype frequency of migratory ecotype fish and resident ecotype fish against the "baseline" genotype frequency of juvenile fish (less than 85 mm FL) using a χ^2 test in R.

Next, 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 creeks 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).

Table 1. Summary table of the number of fish who were assigned ecotypes and successfully genotyped for life history and sex.

	Migratory ecotype			Resident ecotype		
Genotype	Female	Male	Unknown	Female	Male	Unknown
Migratory	18	18	6	0	2	2
Heterozygote	38	28	11	4	16	3
Resident	33	9	9	9	22	5
Unknown	7	4	32	0	5	3

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 premigration aged 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:

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

where P is the proportion of migrants, m is the migratory allele frequency of migratory ecotype fish, b is the baseline migratory allele frequency of premigration-aged fish, and r is the migratory allele frequency of resident fish.

Results

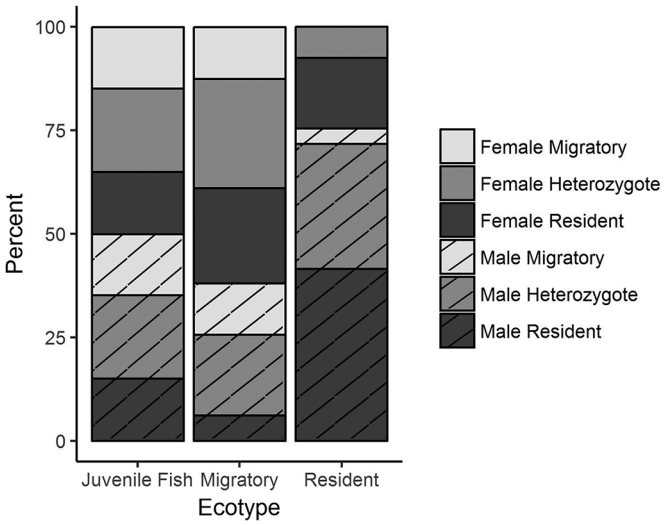
Resident and migratory genotypes

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[1]), which aligned with our prediction of three groups (resident, heterozygous, and migratory) corresponding to each genotype. We used group membership (k = 3) to call individuals as resident, heterozygous, or migratory genotypes (Fig. 2). Herein, 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.

We obtained genotype data from n = 4303 out of 4332 (99.3%) fish. We then assigned life history genotypes to n = 3450 fish (80.1% of those that were genotyped), with individuals being excluded due to missing data at many SNPs on *Omy5* (see above; Appendix A). See Table S1[1] for a summary table of life history genotypes by year and age class. Across 4 years of sampling (2014–2017), the overall genotype frequency for juvenile fish (<85 mm FL, n = 2485) in these streams was 29.6% migratory, 40.2% heterozygotes, and 30.2% resident. We successfully assigned life history ecotypes and genotypes to 284 fish, which are summarized by genotype and sex (Table 1), and the data set is available on Dryad Digital Repository (Kelson et al. 2019).

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0394.

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 with juvenile fish, which are assumed to have an even sex ratio for visualization.



We found that migratory genotype fish were unlikely to remain in the streams as resident fish, as resident ecotypes were composed of 57.1% resident genotypes, 36.5% heterozygous genotypes, and only 6.3% migratory genotypes (Fig. 3). This frequency of genotypes differed from the frequency of genotypes in juvenile fish in a χ^2 test for given probabilities (χ^2 = 27.0, p < 0.001). 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. 4*a*), 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. The genotype frequencies in the migratory ecotypes (24.7% migratory, 45.3% heterozygote, and 30.0% resident genotypes) were very similar to the baseline juvenile genotype frequencies and did not differ in a χ^2 test (χ^2 = 2.5, p > 0.1; Fig. 3). Similarly, we found that migratory ecotype fish did not always include a higher proportion of migratory alleles when compared with all the fish caught the previous summer (the baseline for that year; Fig. 4*b*).

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), 77.6% 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 30.4% to 46.2%).

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 (Table 1; 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 2). The probability of out-migrating increased with the addition of migratory alleles; migratory genotypes were the most likely to out-migrate (probability for males = 0.91 and for female = 0.99), followed by heterozygotes (male = 0.62, female = 0.92), and then resident genotypes (male = 0.31, female = 0.77; Fig. 5*a*). Based on effect sizes of parameters, sex was more important than genotype in explaining variation in ecotype (Fig. 5*b*, 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).

Table 2. We used Bayesian information criteria (BIC) to compare models to predict life history ecotype from sex, genotype, and capture location, listed in order of highest to lowest BIC.

Predictor variable(s)	BIC
Sex + genotype	200.1
Sex + genotype + location	209.2
Sex × genotype	209.8
Sex × genotype + location	218.5
Sex	232.7
Genotype	269.4

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 69.9% of the population migrated. Using migratory allele frequencies in the migratory versus resident ecotypes, we estimated that 88.3% of the population migrated.

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 composed 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 with sex alone: r^2 = 0.30, or life history alone: r^2 = 0.20). In brief, resident genotypes have potential to express migration and thus have value in conserving life history diversity in partially migratory populations, but this is not the whole story. Approximately 50% of the variation in life history expression was unexplained, suggesting that environment context and (or) other unidentified genetic variation also play a role in maintaining life history diversity within partially migratory populations. Owing to this large amount of unexplained variation, unidentified genetic variation may also be of conservation value.

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. 5*a*). The male-biased sex ratio in large, resident fish that we observed (78%) was close to the ratio observed (83%) in Big Creek (Monterey County, California; Rundio et al. 2012). In contrast, approximately 1280 km 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

Fig. 4. (A) The proportion of migratory alleles in each year class remaining in fresh water decreases with time (age) of fish. (B) The change in proportion of migratory alleles for all fish versus migratory fish depends on the year.

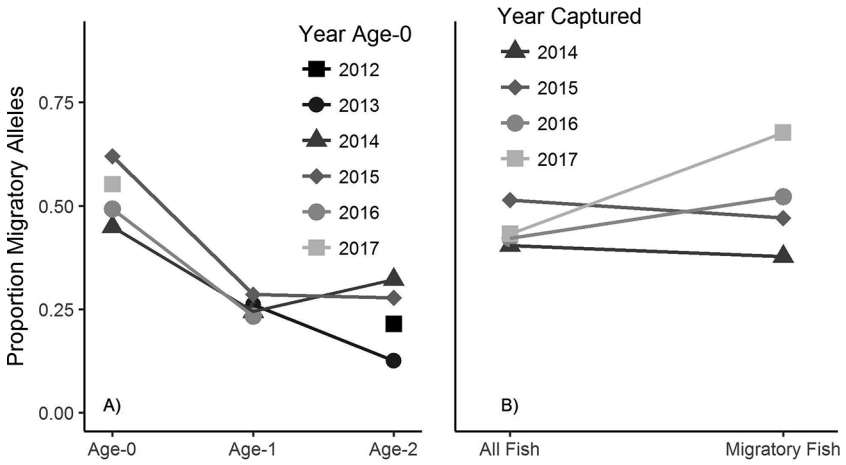
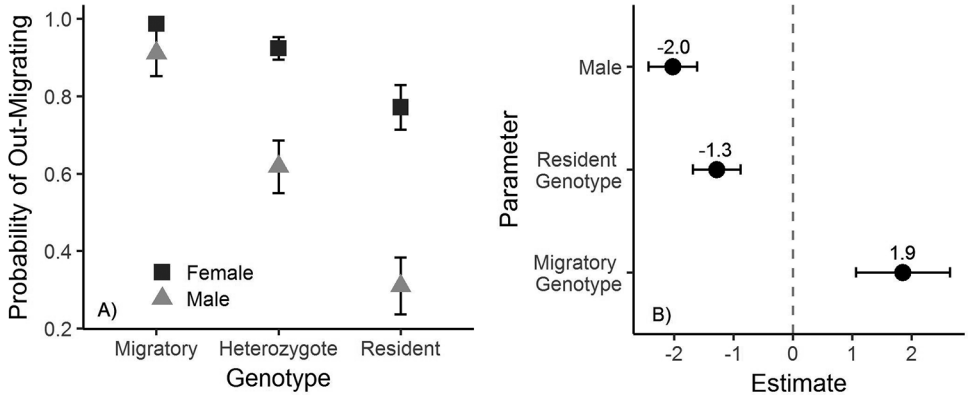


Fig. 5. (A) Predictions from a binomial model for the probability of out-migrating given an individuals' life history genotype and genetic sex. (B) Estimates and standard error of parameters predicting the outmigration probability of a fish. Parameters are calculated in contrast from a female heterozygote.



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 *S. salar* following a flood-induced pulse of food resources (Letcher and Terrick 1998). Additionally, the decision to mature in fresh water 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 (62% 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 resident fish 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 (62% female) was not as extreme as the male skew observed in freshwater residents (78% 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 a model including both life history genotype and sex received the most support in terms of explaining 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 mater-

nal 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, although with reduced fitness (Thrower and Joyce 2004; Thrower et al. 2004). In general, this body of work emphasizes the plastic nature of life history expression 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. In this study we present two genetic tools, genotyping at *Omy5* and sex-genotyping, both of which are useful for understanding migration behavior within partially migratory populations. 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 that 55% of the variation in life history expression was unexplained by genetic sex and life history genotype. Our results indicate that genetic sex provides more explanatory power than life history genotype at the individual level. Furthermore, determining genetic sex is a relatively easy and inexpensive procedure and can be done using nonlethal tissue samples and qPCR to genotype at two SNPs (one autosomal control and one Y-chromosome SNP).

Individual level life history decisions scale up to population level patterns, and quantifying these patterns may be of interest to managers seeking to restore or monitor anadromy in partially migratory populations. Using genetic tools, we generated two estimates for the percentage of the population expressing migration, the first based on sex ratios (estimated 70% migration) and the second based on migratory allele frequencies (estimated 88% migration) in these streams. Both approaches suggest that most of the population migrates from these streams. The mathematical models used to generate these estimates included simplifying assumptions such as that of equal mortality rates between sexes or genotypes before the life history decision window or before the samples are collected. We suggest that using the sex ratios, rather than migratory allele frequency, may be 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 fresh water for wild *O. mykiss* to further evaluate the utility of this approach for estimating the proportion of the population that is migratory. If these assumptions are robust, then determining the sex ratios of different groups in a population (smolts versus residents) may be a cost-effective way to estimate the proportion of a population that out-migrates. Furthermore, this tool may be useful for understanding population-level responses in migration behavior to restoration projects (e.g., dam removals, habitat improvements projects).

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 suggest 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.

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Appendix A. Excluding genetic assignment for individuals missing data at many SNPs

We chose to exclude genetic data from *Omy5* for individuals who were missing data at 250 or more out of 415 SNPs (60%). Heterozygosity is higher among individuals who are missing more than 60% of SNPs, compared with individuals who are missing less than 60% (Fig. A1). To conduct the DAPC, we replaced missing data 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 number 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.

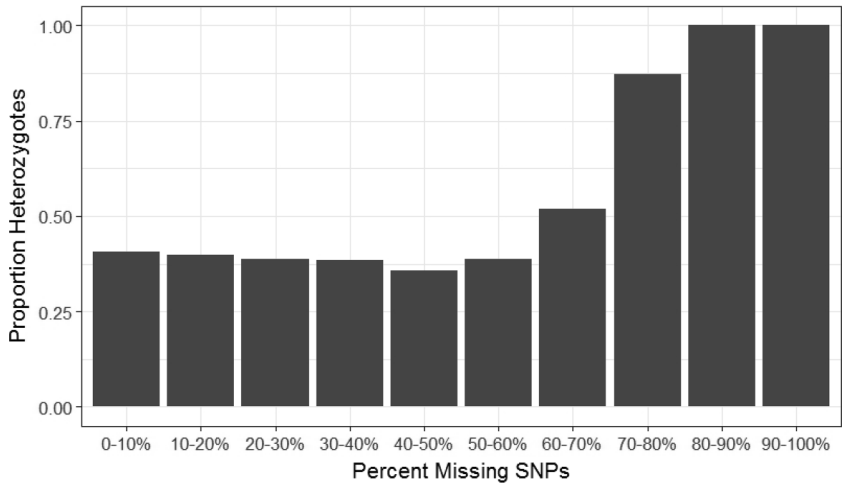

Fig. A2. Individuals who are missing data at many SNPs tend to fall between the main three clusters or are classified within the middle, or heterozygote, cluster. [Colour online.]

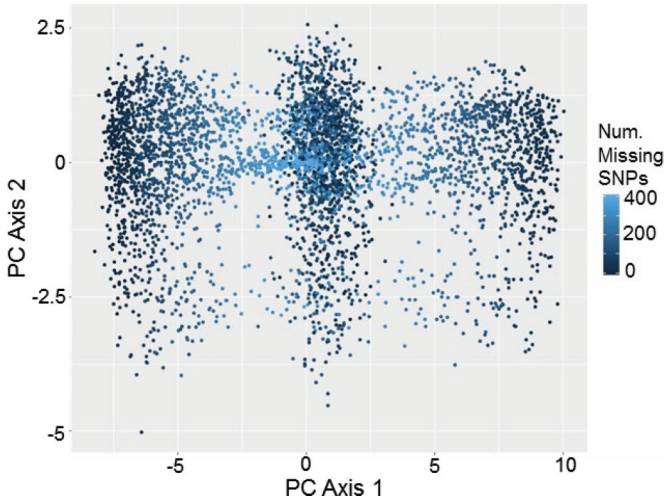

Fig. A3. A plot of score one, the first principal component (PC), against the number of missing SNPs per individual indicates that individuals who are missing data at many SNPs (i.e., over 250 SNPs, indicated by the black line) have a score on the first PC that falls between genotype groups and are more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