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ARTICLE

Differences in growth and condition of juvenile *Oncorhynchus mykiss* related to sex and a migration-associated genomic region

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Abstract: The expression of anadromy in partially migratory salmonid populations is influenced by sex-specific interactions among an individual's genotype, condition, and environment, but genotype–phenotype relationships prior to the expression of migratory type are poorly understood. We examined whether juvenile growth and condition differed with respect to sex and a migration-associated genomic region (Omy05) in a coastal California population of steelhead and rainbow trout (*Oncorhynchus mykiss*). Sex and Omy05 genotype had additive effects on annual growth from age 0+ to age 1+ (~6–18 months old), with higher growth in males and individuals with copies of the rearranged–resident haplotype. Condition at age 1+ increased with the number of copies of the rearranged–resident haplotype, with similar support for additive or interactive effects with sex; additive effects suggested that genotype differences occurred in both sexes and also that condition was slightly higher in males, while interactive effects suggested that the genotype differences occurred only in males. Our results indicate that phenotypic differences related to sex and Omy05 genotype occur well in advance of anadromous migration or freshwater maturation in this southern *O. mykiss* population.

Résumé : Si l'expression de l'anadromie dans les populations de salmonidés partiellement migratrices est influencée par des interactions propres au sexe entre le génotype, l'embonpoint et le milieu d'un individu, les relations entre génotype et phénotype précédant l'expression du type migratoire ne sont pas bien comprises. Nous tentons de déterminer si la croissance et l'embonpoint de juvéniles diffèrent selon le sexe et une région génomique associée à la migration (Omy05) dans une population côtière de saumons–truites arc-en-ciel (*Oncorhynchus mykiss*). Le sexe et le génotype Omy05 ont des effets additifs sur la croissance annuelle de 0+ an à 1+ an (~6 à 18 mois), des taux de croissance plus grands étant observés chez les mâles et les spécimens présentant des copies de l'haplotype réarrangé–résident. L'embonpoint à 1+ an augmente parallèlement au nombre de copies de l'haplotype réarrangé–résident, et les données appuient aussi des effets additifs ou interactifs associés au sexe; les effets additifs indiqueraient que des différences de génotype sont présentes chez les deux sexes et que l'embonpoint est aussi légèrement plus grand chez les mâles, alors que les effets interactifs semblent indiquer que les différences de génotype ne se retrouvent que chez les mâles. Nos résultats indiquent que les différences phénotypiques associées au sexe et au génotype Omy05 se produisent bien avant la migration anadrome ou la maturation en eau douce au sein de cette population méridionale d'*O. mykiss*. [Traduit par la Rédaction]

Introduction

Many fishes have populations in which some individuals migrate but others do not, a phenomenon known as partial migration (Chapman et al. 2012). Partial migration is widespread in many salmonid species, with well-known examples including Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and rainbow trout (*Oncorhynchus mykiss*) (reviewed in Jonsson and Jonsson 1993; Hendry et al. 2004; Dodson et al. 2013). In salmonids, partial migration often occurs in the form of populations composed of both anadromous (migrating to the ocean for growth prior to maturation and reproduction) and nonanadromous or resident (maturing in fresh water) individuals. In partially migratory populations, anadromy typically is more common in females than in males, due to differences in size and fecundity between migratory and nonmigratory individuals (Jonsson and Jonsson 1993; Fleming and Reynolds 2004; Hendry et al. 2004). Expression of anadromy is genetically influenced and highly heritable, but also subject to large phenotypic plasticity in response to environmental conditions affecting fitness-related traits such as growth, development, and survival (Thrower et al. 2004; Aubin-Horth et al. 2005; Thériault et al. 2007; Dodson et al. 2013; Doctor et al. 2014). As such, expression of anadromy versus freshwater maturation appears to be a threshold trait involving sex-specific interactions among an individual's genotype, condition, and environment (Dodson et al. 2013; Sloat et al. 2014; Phillis et al. 2016; Ferguson et al. 2019; Pearse et al. 2019).

Partial migration is common in *O. mykiss*, in which many populations include both nonanadromous (resident rainbow trout) and anadromous (steelhead) life-history forms, and recent research has provided a better understanding of how sex, genotype, and environment interact to influence the expression of anadromy in this species (Ohms et al. 2014; Kendall et al. 2015; Kelson et al. 2019; Pearse et al. 2019). Multiple genomic regions on several chromosomes have been associated with a variety of phenotypic and developmental traits related to anadromy and migration (e.g., Nichols et al. 2008; Miller et al. 2012; Hecht et al. 2012, 2013, 2015; Hale et al. 2014). Among these, the strongest association has been found with a single genomic region containing a large double-inversion on chromosome Omy05 (Pearse et al. 2019; hereinafter Omy05 genotype). However, the influence of Omy05 genotype relative to other

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genomic regions appears to vary across a broad latitudinal gradient in temperature and environmental conditions. In southern *O. mykiss* populations, migration is strongly and consistently associated with Omy05 genotype in both anadromous and above-barrier adfluvial populations (Martínez et al. 2011; Pearse et al. 2014; Leitwein et al. 2017; Pearse and Campbell 2018; Abadía-Cardoso et al. 2019; Kelson et al. 2020*b*). In contrast, the genetic basis of migration appears more complex and polygenic in northern and inland populations in colder environments, with Omy05 playing a reduced role and additional genes on multiple chromosomes being involved (Arostegui et al. 2019; Pearse et al. 2019; Weinstein et al. 2019). Recent studies from two southern *O. mykiss* populations in California were able, for the first time, to assess the sex-specific relationships between Omy05 genotype and expression of anadromy by individuals by genotyping uniquely tagged wild fish (Kelson et al. 2019; Pearse et al. 2019). Both studies showed that the probability of migrating was greater for individuals with the ancestral–anadromous (AA) genotype than those with the rearranged–resident (RR) genotype and greater for females than for males. Pearse et al. (2019) further demonstrated a sex × genotype interaction whereby sex-dependent dominance determined the migratory phenotype of heterozygotes, highlighting the importance of a detailed understanding of the relationships between genotype and phenotype.

Differences in expression of migratory behavior between male and female *O. mykiss* may be expected to involve corresponding sex × genotype differences in juvenile development, such as in growth, size, or condition, but whether and how this occurs is unclear. Rearing of anadromous and resident *O. mykiss* lines and crosses under laboratory conditions has revealed differential gene expression between sexes and life-history types beginning as early as hatching and continuing during the first 1–2 years of development (McKinney et al. 2015; Hale et al. 2018). Phenotypic differences in growth, size, and condition between life-history types also have been detected 9–12 months prior to displaying signs of smoltification or maturation in some cases; however, results have varied across studies and most did not address sex (reviewed in Kendall et al. 2015). Of the studies that did, sex and life-history type usually have been evaluated separately rather than in combination (i.e., as independent rather than interactive factors), and these studies, too, have found inconsistent results. Nichols et al. (2008) and Hecht et al. (2012) examined sex and life-history differences in growth and condition of age 1+ *O. mykiss* under laboratory conditions. Nichols et al. (2008) found no significant differences in growth or condition between sexes or life-history types among immature fish, while Hecht et al. (2012) found complex, time-dependent differences. In that latter study, females had higher growth and lower condition than males at 15 to 24 months of age but not at 12 to 15 months. Also, fish that eventually displayed signs of smoltification had lower growth at 12–15 months but higher growth at 15–24 months than fish that showed signs of maturation. Finally, fish that showed signs of smoltification had lower condition at 15 and 24 months but not at 12 months. Sloat and Reeves (2014) found considerably higher growth rates in females than in males based on mass-at-age trajectories for fish reared for a year in the laboratory and also found smaller differences between fish that smolted versus fish that matured, with slightly higher growth for fish that matured in most cases. They also found higher lipid content in maturing versus smolting females but no difference in lipid content between life-history types in males. In studies of wild populations, Ohms et al. (2014) found no difference between sexes in sizes of smolts, and McMillan et al. (2012) found no difference in size of age 1+ males and females but did find that maturing males were larger and had higher lipid content than nonmaturing males. Finally, in a population in northern California, Kelson et al. (2020*a*) found that age 0+ *O. mykiss* with the RR Omy05 genotype were larger in late summer than fish with the AA genotype, suggesting higher growth rate, but they did not evaluate whether sexes differed. Thus, data to evaluate sex-specific phenotypic differences in development related to the expression of anadromy in *O. mykiss* are limited and inconsistent.

In this study, we used mark–recapture methods and genetic markers for sex and Omy05 genotype to investigate sex-by-genotype specific juvenile growth and condition of wild *O. mykiss* in a coastal population in central California. Pearse et al. (2019) found sex-dependent dominance in the probability of anadromous migration in this population, and expression of migratory life history appears to occur after 2–3 years of rearing in the stream when fish have reached >150 mm in length (Hanson 2008; Rundio et al. 2012; Pearse et al. 2019). Our objective was to determine whether these sex-specific differences in migratory behavior among genotypes are preceded by phenotypic differences earlier during development, prior to expression of life history. Specifically, we tested for differences in growth and condition with respect to sex and Omy05 genotype in eight young-of-year (YOY) *O. mykiss* cohorts from their first fall (age 0+) to the following fall (age 1+) after accounting for other factors potentially affecting development, including density and temperature.

Methods

Study area

Big Creek is a small basin (58 km^2) that drains the Santa Lucia Mountains on the Big Sur coast in central California (Fig. 1). The lower portion of the basin, including our study area, is within the University of California Landels-Hill Big Creek Natural Reserve, and the upper portion is within the Los Padres National Forest Ventana Wilderness Area. The basin has high topographic relief, with constrained stream channels and relatively narrow riparian zones set in steep hillsides. The region has a coastal Mediterranean climate, with warm, dry but foggy summers and cool, wet winters. The major stream channels and tributaries have perennial flow and moderate water temperatures; a 5-year drought (water years 2012–2016) occurred in California during the study and caused reduced flows and slightly higher temperatures (Table 1; also refer to online Supplementary Materials Fig. S1[1]). The stream flows directly into the Pacific Ocean year-round over a short riffle, and there is ~7 km of habitat accessible to anadromous fish in the basin downstream of natural waterfall barriers.

Our study area was the first 2.6 km upstream from the ocean and consisted of three reaches: 1.2 km of mainstem Big Creek and the first 700 m of the two main tributaries, upper Big Creek and Devils Creek (Fig. 1). Habitat in these reaches is a mixture of pools and rapids in relatively high-gradient (3%–8%) step-pool and cascade channels. Stream width (wetted) averages 5–6 m during summer, with mean depths of about 35 cm and maximum depths ~1.75 m. Habitat is generally similar among the reaches, although gradient is lower in the main stem (3%) than in Devils Creek (6%) and upper Big Creek (8%), and streambed travertine (calcium carbonate) deposition occurs during the summer dry season in Devils Creek but usually is absent in the other reaches. The most abundant riparian trees are redwood (*Sequoia sempervirens*), white alder (*Alnus rhombifolia*), and bigleaf maple (*Acer macrophyllum*), and the canopy is almost fully closed over most of the study reaches during the leafing period for deciduous trees from February–March to October–November. See Rundio and Lindley (2008) for additional details about the study area.

The *O. mykiss* population in Big Creek is partially migratory, and anadromous and nonanadromous (resident) life-history types are sympatric in all three reaches. Spawning occurs in winter (typically January–April but ranging from November to May),

[1]Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0073.

Fig. 1. Map of the study area in the Big Creek watershed on the Big Sur coast of central California, USA. Big Creek enters the Pacific Ocean at 36°4′10″N, 121°36′2″W. Map was created using ArcGIS software by ESRI with data from the National Hydrography Dataset Plus (USEPA and USGS 2006).

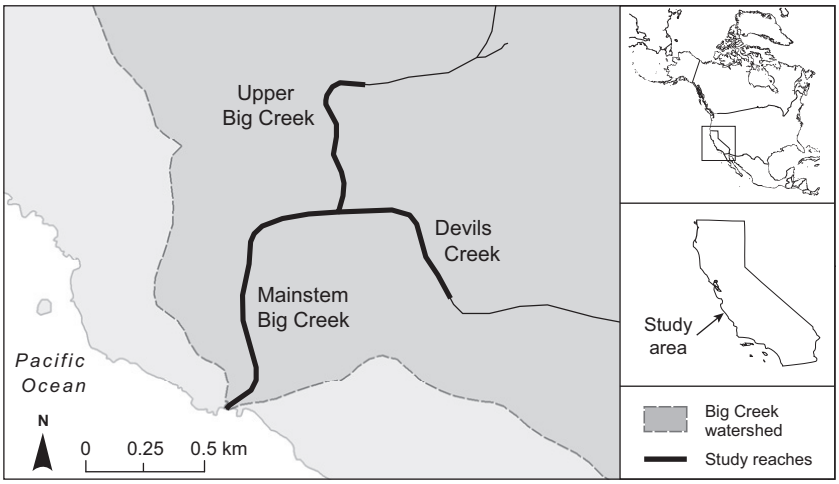


Table 1. Summary of sample size, mean water temperature, and density of age 0+ *O. mykiss* by cohort and stream reach.

	Sample size				Mean water temperature (°C)			Density of age 0+ *O. mykiss* (no.·m^{-2})		
Cohort	MS	DC	UB	Total	MS	DC	UB	MS	DC	UB
2008	16	27	14	56	12.66	12.37	13.30	0.76	0.61	0.84
2009	31	23	16	71	12.41	12.25	12.74	0.35	0.22	0.12
2010	61	48	37	146	12.50	12.32	12.75	0.33	0.30	0.26
2011	27	29	14	70	12.28	11.98	12.90	0.24	0.19	0.22
2012	14	18	16	48	12.83	12.55	13.39	0.49	0.67	0.35
2013	19	8	25	52	13.03	12.56	13.95	0.56	0.30	0.28
2014	15	11	22	48	13.64	13.26	14.34	0.41	0.43	0.25
2015	27	24	30	81	13.09	12.87	13.56	0.18	0.25	0.08
Total or mean	210	188	174	572	12.81	12.52	13.37	0.42	0.37	0.30

Note: MS, main stem; DC, Devils Creek; UB, upper Big Creek.

and age 0 fish emerge in spring and typically are 50–95 mm fork length (FL) by September–October. Juvenile steelhead rear in the stream for 2–3 years before smolting at an average size of 150 mm FL (Hanson 2008). Fish larger than this appear to be primarily nonanadromous individuals and are strongly male-biased (Rundio et al. 2012). Total *O. mykiss* density (juveniles and nonanadromous adults) in the study area in fall ranged from 0.25 to 0.88 m^{-2} during 2008–2015 (unpublished data from preliminary analysis of mark–recapture sampling using electrofishing and PIT tagging). Coastrange sculpin (*Cottus aleuticus*) was the only other fish species present and occurred in the lower 800 m of mainstem Big Creek.

Field sampling

For this analysis we used data for eight YOY cohorts (2008–2015) that were sampled as part of a mark–recapture study of *O. mykiss* population dynamics in which the entire study area was sampled annually by backpack electrofishing in late September – early October. During each survey, two electrofishing passes (mark and recapture) were completed 1 week apart. Captured fish were measured for FL (nearest mm), weighed (to 0.1 g), and scanned for a passive integrated transponder (PIT) tag. Untagged fish ≥ 65 mm FL were injected with a 12-mm PIT tag using a 12-gauge needle. Tissue samples were collected by taking a small clip from the upper caudal fin with scissors. Fin clip samples were placed on filter paper in individual envelopes, air-dried, and stored until DNA extraction. In 2009–2015, tissue samples were collected from all fish captured, while in 2008 tissues were collected from about 5% of fish captured and targeted toward sampling YOY fish throughout the study area. After handling, all fish were released to their point of capture.

DNA extraction and genetic analysis

Total DNA was extracted from dried fin clips using the DNeasy 96 filter-based nucleic acid extraction system on a BioRobot 3000 (Qiagen, Inc.), following the manufacturer's protocols. DNA extractions were diluted 2:1 with distilled water and used for polymerase chain reaction pre-amplification. Genotyping of a 96 SNP locus panel described by Abadía-Cardoso et al. (2013) was conducted using TaqMan (Thermo Fisher Scientific, Inc.) and SNP Type (Fluidigm, Inc.) assays and 96.96 SNP Dynamic Array IFCs for Genotyping on an EP1 system (Fluidigm, Inc.). Two negative controls were included in each array, and genotypes were called using Fluidigm SNP Genotyping Analysis software. The SNP loci included a sex identification assay (Brunelli et al. 2008) and three SNPs on chromosome Omy05 that are associated with migratory life-history traits in southern *O. mykiss* populations (Pearse et al. 2014; Pearse and Garza 2015; Apgar et al. 2017; Leitwein et al. 2017). Alleles at

these loci are tightly linked and can be characterized as being part of either ancestral–anadromous (A) or rearranged–resident (R) haplotypes of the Omy05 chromosomal inversion (Pearse et al. 2019). Thus, on these genotype data, each individual was categorized as male or female and as having an AA, AR, or RR genotype at Omy05.

To consider the potential effects of family structure, which might confound the analysis for sex and Omy05 effects, the neutral SNP loci in the genotyping panel were used to identify siblings among the sampled individuals. Identification of full siblings was conducted with the software COLONY (Jones and Wang 2010), using the full likelihood model with both male and female polygamy and the default parameters. The results indicated that family effects likely did not confound the analysis; the 572 individuals included in the COLONY analysis were assigned to 293 full-sibling families with a range of one (singletons) to 12 members. The sample was dominated by small families: 80% of families were one to two siblings, and 72% of individual fish were from families of ≤4 siblings. There were large numbers of families per year (26–68) and per reach (104–124). Within larger families, siblings were distributed across sexes and genotypes; this was true for all families of five or more and for most families of three or four. Finally, growth did not differ among families ($P > 0.1$, ANOVAs by year and reach for all families of four or more siblings). Therefore, based on these results, family effects did not appear to interfere with assessing effects of sex and Omy05 and were not considered further.

Data analysis

We assessed whether growth and condition during early life stages differed by sex and Omy05 genotype after accounting for other covariates. We classified fish in each fall sample as YOY based on length criteria by choosing a cut-off (≤95 or ≤99 mm) for each cohort that was exceeded by ≥90% of the fish from the prior cohort; for five of the cohorts the cut-off was ≤95 mm and for three it was ≤99 mm (2008, 2010, and 2015). Using different cut-offs maximized sample size by accounting for differences in growth among years while still being conservative to minimize the possibility of misassigning age 1+ fish as YOY. We analyzed annual growth for the eight cohorts from their first fall (age 0+) to the following fall (age 1+), corresponding to when fish were ~6 to 18 months old. Growth in length was calculated as

$$\text{growth}_{\text{FL}} = (\text{FL}_{1+} - \text{FL}_{0+}) \cdot \text{days}^{-1}$$

and growth in weight as

$$\text{growth}_{\text{WT}} = \log_e\left[(\text{WT}_{1+} - \text{WT}_{0+}) \cdot \text{days}^{-1}\right]$$

where days is the number of days between captures (mean = 364 days, range = 356–372 days). Growth in weight was $\log_e$-transformed prior to analysis to meet assumptions of normality, but no transformation was needed for growth in length. Condition was expressed as the linear relationship of weight as a function of length on $\log_e$-transformed data at both age 0+ and age 1+. Specifically, condition at age 0+ (condition_{0+}) was expressed as

$$\log_e(\text{WT}_{0+}) = \beta_0 + \beta_1 \cdot \log_e(\text{FL}_{0+}) + \ldots$$

and condition at age 1+ (condition_{1+}) as

$$\log_e(\text{WT}_{1+}) = \beta_0 + \beta_1 \cdot \log_e(\text{FL}_{1+}) + \ldots$$

Water temperature and YOY density were included as covariates potentially influencing growth and condition. Hourly water temperature was recorded from data loggers (Onset HOBO Water Temperature Pro v2) in each reach. For growth and condition at age 1+, mean water temperature for each cohort was calculated from 1 October of the first fall (age 0+) to 30 September of the second fall (age 1+) for each reach; for condition at age 0+, mean temperature was calculated from 1 May (roughly time of emergence) to 1 October of the first fall. Densities of YOY in each reach were estimated using closed robust design mark–recapture models in the program MARK version 8.2 (White and Burnham 1999). In each year there were some YOY that were too small to tag (i.e., <65 mm FL), so we estimated their abundance by dividing the number of these small fish by the reach- and year-specific capture probabilities for the tagged YOY. We then added the estimates for tagged and untagged fish to produce an estimate of the total abundance of each YOY cohort. We converted these abundances to densities to account for differences in habitat area among the reaches. Densities of YOY were highly correlated with total densities of all age classes ($r = 0.98$).

We used linear mixed models (LMM) to assess whether growth and condition differed with respect to sex and Omy05 genotype as fixed effects while accounting for other potentially important covariates as fixed effects and cohort as a random effect. We fit models for each of four responses: growth in length ($\text{growth}_{\text{FL}}$), growth in weight ($\text{growth}_{\text{WT}}$), condition at age 0+ ($\text{condition}_{0+}$), and condition at age 1+ (condition_{1+}). Models were fit following the two-step approach of Zuur et al. (2009). First, to select the random effects structure to account for variability among cohorts, we fit a series of models having the same full fixed effects structure (see below) but ranging from no to increasingly complex random effects and used AIC_c to identify the model with most support from the data. The random effects we considered were cohort (i.e., random intercept) and interactions between cohort and the main fixed effects (i.e., random intercept and slope); for interactions, we included both correlated and uncorrelated intercept and slope. Models were fit by restricted maximum likelihood (REML) in this step; models with no random effect were fit by generalized least squares (GLS), and models with random effects were fit as LMM. Models that failed to converge, had random effects with zero variance, or had random effects with perfect correlations were dropped from consideration. Second, we then compared a set of models that all used this best random structure but differed in fixed effect structures to identify variables related to differences in growth and condition. We considered 20 candidate models that included different combinations of sex, Omy05, sex × Omy05, density, and temperature, ranging from a null model with none of these effects to a full model with all five variables. Models also included a term for FL, either as a covariate to account for differences in initial size in the models for growth or as a predictor of weight in the models for condition. Finally, all of these candidate models also included stream reach as a blocking variable to account for other differences in habitat conditions between reaches. Continuous predictor variables were centered, and models were fit by maximum likelihood (ML) during this step and ranked by AIC_c. Plausible models ($\Delta\text{AIC}_c < 4$) were then refit with REML for parameter estimation and prediction. Diagnostic plots and simulated interquartile ranges indicated adequate model fits. Analyses were carried out in R version 3.5.0 (R Core Team 2018) using the packages lme4 version 1.1–17 (for LMM; Bates et al. 2015), nlme version 3.1–137 (for GLS; Pinheiro et al. 2018), AICcmodavg version 2.1–1 (for AIC_c; Mazerolle 2017), and effects version 4.1–0 (for predicted values; Fox and Weisberg 2019).

Results

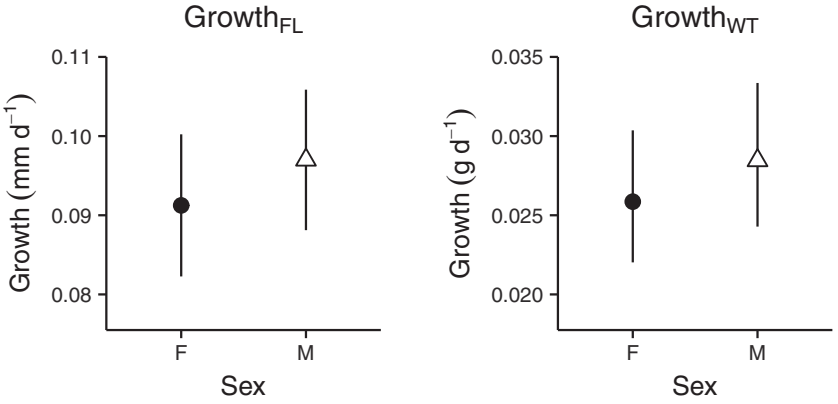
We analyzed a total of 572 fish from the eight YOY cohorts, with samples ranging from 48 to 146 fish per cohort (Table 1). The sample was relatively balanced with respect to sex (46% female, 54% male) and stream reach (37% main stem, 33% Devils Creek, 30% upper Big Creek). The proportions by Omy05 genotype were 0.13 AA, 0.54 AR, and 0.33 RR. Environmental conditions and

Table 2. Ranking of plausible ($\Delta AIC_c < 4$) linear mixed models of juvenile *O. mykiss* growth in length ($growth_{FL}$, top) and weight ($growth_{WT}$, bottom) from age 0+ to age 1+ as a function of fixed effects variables.

Model	Sex	Omy05	Density	Temp.	*K*	AIC_c	ΔAIC_c	AIC_c wt
$Growth_{FL}$								
14	+		+		13	−2481.07	0	0.43
13	+		+	+	14	−2479.30	1.77	0.18
7	+	+	+		15	−2478.67	2.40	0.13
$Growth_{WT}$								
14	+		+		13	761.90	0	0.41
7	+	+	+		15	763.47	1.57	0.19
13	+		+	+	14	763.94	2.05	0.15
5	+	+	+	+	16	765.50	3.60	0.07

Note: All models also included initial size (FL_{0+}) and stream reach as fixed effects and a (Stream|Cohort) random effect. $Growth_{WT}$ data were log_e-transformed. Plus (+) symbols indicate that a variable is included in a particular model. *K* is the number of parameters in the model, and AIC_c wt is model selection weight. None of the plausible models included Omy05 × Sex. Full model selection results for all candidate models are shown in Supplementary Materials Tables S1 ($growth_{FL}$) and S4 ($growth_{WT}$).[1]

Fig. 2. Predicted annual growth rate (with 95% confidence interval) from age 0+ to age 1+ for male and female juvenile *O. mykiss* from the top linear mixed model (M14). Growth is shown in terms of both length ($growth_{FL}$, left) and weight ($growth_{WT}$, right). Predicted values are at the population level of the random effects for the mean-sized fish (FL_{0+} = 80 mm) and averaged over the levels of stream reach.



O. mykiss densities varied considerably across years (Table 1; Supplementary Material Fig. S1[1]).

There was strong evidence that annual growth from age 0+ to age 1+ differed by sex, as this variable was included in the top models for $growth_{FL}$ and $growth_{WT}$ and in all plausible models ($\Delta AIC_c < 4$; Table 2 and Supplementary Material Tables S1 and S4[1]). Males grew 6% more than females in terms of length and 10% more in terms of weight (Fig. 2; Supplementary Material Tables S2 and S5[1]). Models that also included Omy05 genotype were plausible but had less support from the data (AIC_c weights two to three times lower than the top models; Table 2). Fish with RR and AR genotypes grew about 4%–5% more by length and 10% more by weight than fish with AA genotypes (Fig. 3; Supplementary Material Tables S2 and S5[1]). There was no evidence of an interaction between sex and Omy05 (models with an interaction had $\Delta AIC_c > 5$; Supplementary Materials Tables S1 and S4[1]). Among other covariates, density was included in all plausible models and had a negative relationship with $growth_{FL}$ and $growth_{WT}$ (Table 2 and Supplementary Materials Tables S2 and S5[1]). Evidence was weaker for an effect of water temperature, as models including temperature were plausible but received two to three times less support than the top model with only density (Table 2); temperature was negatively related to $growth_{FL}$ but positively related to $growth_{WT}$ (Supplementary Materials Tables S2 and S5[1]). There was an interaction between stream reach and cohort effects (Supplementary Materials Tables S3 and S6[1]), due to growth of some cohorts in main stem and upper Big Creek being higher (2015) or lower (2011 and 2013) than the population mean, while growth in Devils Creek was closer to the mean for all cohorts (Supplementary Material Fig. S2[1]). The large estimates of these random effects and residuals indicated high variability in growth among cohorts and individuals, respectively (Supplementary Materials Tables S2 and S5[1]). There was a roughly twofold difference in mean growth between the cohorts with lowest and highest growth, and within cohorts, there was a three- to fivefold difference in $growth_{FL}$ between the slowest and fastest growing individuals and six- to 18-fold difference in $growth_{WT}$.

Condition at age 0+ appeared to be influenced very little by any of the explanatory variables. The model with most support from the data was the simplest model that did not include sex, Omy05, density, or temperature as fixed effects (Table 3) or any random effect of cohort (Supplementary Material Table S9[1]). Models with sex or Omy05 were plausible but received about three times less support (Table 3); these models suggested that females had slightly higher $condition_{0+}$ than males and that $condition_{0+}$ increased slightly from AA to AR to RR genotypes (Supplementary Material Table S8[1]). Likewise, models with density or temperature were plausible but received less support than the simplest model and suggested a weak negative relationship between $condition_{0+}$ and density and a weak positive relationship with temperature (Supplementary Material Table S8[1]).

In contrast, at age 1+ there was strong evidence that condition differed with respect to Omy05 genotype and sex. Top models that included Omy05 alone or with additive or interactive effects with sex received very similar support from the data ($\Delta AIC \leq 0.6$; Table 4). Genotype effects were consistent across all plausible

Fig. 3. Predicted annual growth rate (with 95% confidence interval) from age 0+ to age 1+ for Omy05 genotypes of juvenile *O. mykiss* from the top linear mixed model that included Omy05 (M7). Growth is shown in terms of both length ($growth_{FL}$, left) and weight ($growth_{WT}$, right). Predicted values are at the population level of the random effects for the mean-sized fish (FL_{0+} = 80 mm) and averaged over the levels of stream reach.

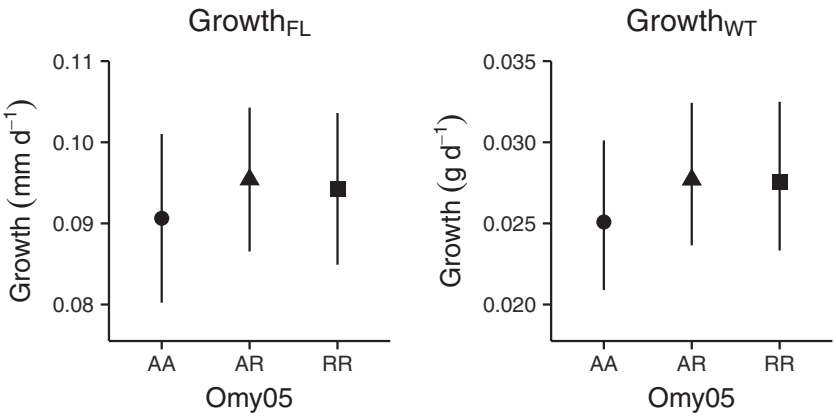


Table 3. Ranking of plausible ($\Delta AIC_c < 4$) linear models of juvenile *O. mykiss* condition at age 0+ ($condition_{0+}$) as a function of fixed effects variables.

Model	Sex	Omy05	Density	Temp.	*K*	AIC_c	ΔAIC_c	AIC_c wt
20					5	−1345.77	0	0.23
18			+		6	−1344.79	0.98	0.14
19				+	6	−1344.31	1.46	0.11
16	+				6	−1343.74	2.03	0.08
12		+			7	−1343.62	2.15	0.08
17			+	+	7	−1343.54	2.23	0.07
14	+		+		7	−1342.74	3.03	0.05
10		+	+		8	−1342.40	3.37	0.04
15	+			+	7	−1342.28	3.49	0.04
11		+		+	8	−1342.03	3.74	0.03

Note: Condition was modeled as weight as a linear function of length on log_e-transformed data. All models also included $lnFL_{0+}$ and stream reach as fixed effects. Plus (+) symbols indicate that a variable is included in a particular model. *K* is the number of parameters in the model, and AIC_c wt is model selection weight. None of the plausible models included Omy05 × Sex. Full model selection results for all candidate models are shown in Supplementary Material Table S7.[1]

models, where $condition_{1+}$ was about 3%–5% greater for RR than AA genotypes and intermediate for AR genotypes (Supplementary Material Table S11[1]). The nature of the sex effects was more ambiguous, with similar support for additive and interactive effects (Table 4). The models with additive Omy05 and sex effects suggested that the genotype differences occurred in both sexes and that, in addition, $condition_{1+}$ was about 1% higher in males than in females (Fig. 4). However, the models with an Omy05 × sex interaction suggested that the genotype differences occurred only in males (Fig. 4). With respect to other covariates, density and water temperature were included in the top models (Table 4), having negative and positive relationships with $condition_{1+}$, respectively (Supplementary Material Table S11[1]), and $condition_{1+}$ also varied among cohorts (Supplementary Material Table S12[1]).

Discussion

We found phenotypic differences related to sex and migration-linked genotype in juvenile *O. mykiss* in a natural population 1–2 years prior to anadromous migration or freshwater maturation. The differences in growth and condition that we observed were small (≤10%), and it is somewhat surprising that they were detectable in these wild fish so far in advance of expression of migratory life history and despite the very high variability among individuals and cohorts. Nonetheless, our results appear to be robust given that they are based on eight cohorts and reflect a wide range of environmental conditions in our study system such as temperature, stream flow, and fish density. Our study provides additional evidence of the association among sex, Omy05 genotype, and individual phenotype in California *O. mykiss* populations (Kelson et al. 2019, 2020*a*; Pearse et al. 2019). Furthermore, to our knowledge, ours is the first study to demonstrate sex-specific genotype–phenotype differences during juvenile development in *O. mykiss* or any salmonid.

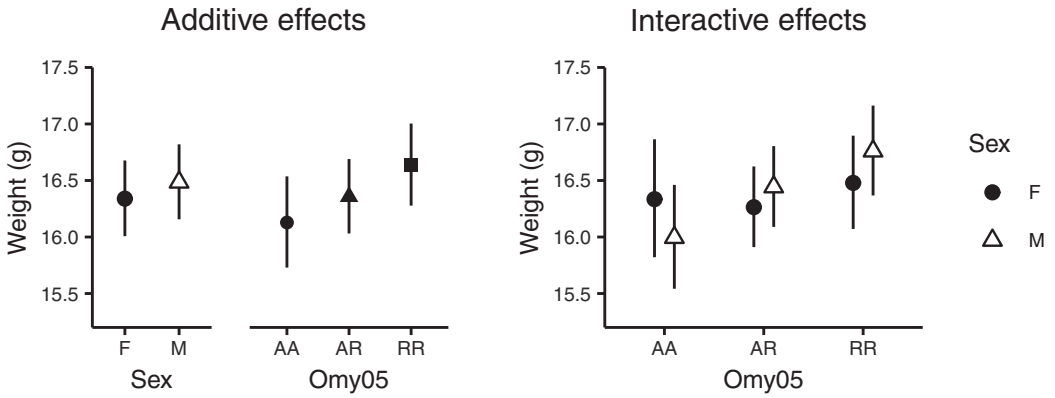
The fact that we found differences in juvenile growth and condition related to sex and life history-associated genotype is consistent with studies that have shown that differences in gene expression between sexes and life-history types begin as early as hatching and continuing during the first 1–2 years of development in *O. mykiss* (McKinney et al. 2015; Hale et al. 2018). Those differences in gene expression involved genes related to growth, development, and migration, included genes located on Omy05 (McKinney et al. 2015; Hale et al. 2018). McKinney et al. (2015) found that the greatest number of differentially expressed genes between life-history types occurred in males at 8 months of age, and our results show a parallel pattern in which pronounced differences in condition were not evident until the second fall (when fish were older than 8 months) and occurred in males. Our

Table 4. Ranking of plausible ($\Delta AIC_c < 4$) linear mixed models of juvenile *O. mykiss* condition at age 1+ ($condition_{1+}$) as a function of fixed effects variables.

Model	Sex	Omy05	Omy05 × Sex	Density	Temp.	*K*	AIC_c	ΔAIC_c	AIC_c wt
9		+		+	+	10	−1341.50	0	0.12
5	+	+		+	+	11	−1341.41	0.10	0.11
11		+			+	9	−1341.29	0.21	0.11
6	+	+			+	10	−1341.11	0.39	0.10
1	+	+	+	+	+	13	−1340.92	0.58	0.09
3	+	+	+		+	12	−1340.71	0.79	0.08
8	+	+				9	−1340.49	1.01	0.07
12		+				8	−1340.40	1.10	0.07
4	+	+	+			11	−1340.26	1.24	0.06
7	+	+		+		10	−1340.04	1.46	0.06
10		+		+		9	−1339.83	1.67	0.05
2	+	+	+	+		12	−1339.74	1.76	0.05

Note: Condition was modeled as weight as a linear function of length on log_e-transformed data. All models also included $lnFL_{1+}$ and stream reach as fixed effects and (1|Cohort) as a random effect. Plus (+) symbols indicate that a variable is included in a particular model. *K* is the number of parameters in the model, and AIC_c wt is model selection weight. Full model selection results for all candidate models are shown in Supplementary Table S10.[1]

Fig. 4. Predicted weight (with 95% confidence interval) for age 1+ *O. mykiss* by sex and Omy05 genotype from the top linear mixed models for $condition_{1+}$ that included additive (M5, left) or interactive (M1, right) effects of these factors; models with additive or interactive effects received similar support from the data. Condition was modeled as weight as a linear function of length on log_e-transformed data. Predicted values are at the population level of the random effects for the mean-sized fish (FL_{1+} = 114 mm) and averaged over the levels of stream reach.



finding of higher growth in fish with RR and AR Omy05 genotypes than in fish with AA genotypes also is in agreement with previous results from laboratory crosses of *O. mykiss* where the Omy05 R haplotype was associated with more rapid embryonic development (Miller et al. 2012) and with results from a population in northern California where age 0+ *O. mykiss* with the RR genotype were larger in late summer than those with the AA genotype, suggesting higher growth rate (Kelson et al. 2020*a*).

Sex and Omy05 genotype appeared to have additive effects on annual growth of juvenile *O. mykiss* (from ~6 to 18 months old) in Big Creek, with males growing more than females and individuals with RR and AR genotypes growing more than fish with AA genotypes. The sex and genotype differences were similar in size; however, there was less support from the data for the genotype effects, suggesting that differences among genotypes were less consistent than between sexes. This is somewhat in contrast with laboratory studies on *O. mykiss* with a 2-year juvenile stage. In those, growth did not differ between sexes from 12 to 15 months of age (Nichols et al. 2008; Hecht et al. 2012); but higher growth in future residents than in future smolts was found at this age in one study (Hecht et al. 2012). In addition, unlike patterns previously observed for overall migratory life-history expression in this population (Pearse et al. 2019), there was no evidence in our study that growth at this stage in development involved an interaction between sex and genotype. It is possible that such sex-specific differences in growth between genotypes may emerge later in development, as Hale et al. (2018) found that the vast majority of sex bias in gene expression occurred during the second year of development.

Condition at age 0+ appeared to be influenced very little by sex or Omy05 genotype, but at age 1+ (~18 months old) there was strong evidence that condition differed with respect to Omy05 and sex. Differences among Omy05 genotypes were consistent across all plausible models and indicated that $condition_{1+}$ increased with the number of copies of the R haplotype (AA < AR < RR). However, the relationship between genotype and sex with respect to $condition_{1+}$ was unclear, as the data provided similar support for models with additive or interactive effects between these factors. The models with additive effects suggested that the genotype differences occurred in both sexes and that, additionally, $condition_{1+}$ was slightly higher in males than in females. Alternatively, the models with interactive effects suggested that the genotype differences occurred only in males. Notwithstanding this uncertainty in the exact differences, our results are generally consistent with previous laboratory studies that found that condition was higher in future residents than in future smolts and also higher in males than in females at 15 months old but not earlier (Hecht et al. 2012) and with studies that found higher lipid content in maturing versus smolting or nonmaturing fish (McMillan et al. 2012; Sloat and Reeves 2014). In contrast, Kelson et al. (2020*a*)

found that condition of age 0+ *O. mykiss* in late summer was slightly lower for individuals with the RR Omy05 genotype than for individuals with the AA genotype in a population in northern California. However, condition of age 1+ fish in their study population was higher for individuals with the RR than with the AA genotype (S. Kelson, personal communication), similar to our results, further indicating that differences in growth and condition with respect to future migratory life history may vary at different stages during juvenile development.

The differences in growth and condition that we detected between sexes may correspond to the higher rate of freshwater maturation in males that is commonly seen in partially migratory *O. mykiss* populations (Ohms et al. 2014; Kendall et al. 2015), including Big Creek (Rundio et al. 2012; Pearse et al. 2019). McKinney et al. (2015) suggested that the high level of differential gene expression between resident and anadromous males at 8 months of age might be due to a higher degree of maturation at age 2 in males compared with females. In a wild *O. mykiss* population in Oregon, nearly 40% of males but only 1% of females were beginning to mature at age 1+, and maturing males showed higher growth and lipid content 6–12 months prior to spawning (McMillan et al. 2012). There is some evidence that resident males mature earlier than females in Big Creek. In a small number of sexually mature resident fish that we captured during surveys in late spring from 2006 to 2019, the minimum size of males was smaller than that for females (135 versus 179 mm), although only two mature males were <150 mm and mean sizes of mature males (n = 50) and females (n = 4) were similar (198 and 196 mm, respectively). In general, however, maturation or anadromous migration in this population appears to occur after 2 or 3 years of juvenile rearing in both sexes when a size of 150 mm or greater has been reached (Hanson 2008; Rundio et al. 2012; Pearse et al. 2019). Therefore, based on the mean size at age 1+ in the fall (114 mm) and growth rates that we observed in the current study, it appears that most fish probably had more than a year of additional rearing before maturing or migrating. For example, the only fish from this study that was eventually recaptured as a mature resident was a male that was 121 mm at age 1+ in the fall and recaptured about 1.5 years later in spring when it was 175 mm and expressing milt. Nevertheless, a small number (1%) of fish in this study, both males and females, reached 150 mm at age 1+, so it is possible that some males may have been maturing already or that some males or females may have smolted during the following spring.

In addition to the differences related to sex and Omy05 genotype, growth and condition$_{1+}$ were influenced by *O. mykiss* density and water temperature and exhibited high variation among individuals and cohorts. Density was negatively related to growth$_{FL}$, growth$_{WT}$, and condition$_{1+}$ (Supplementary Materials Tables S2, S5, and S11[1]). Reduced growth with increasing density has been widely demonstrated in salmonids, including *O. mykiss* (e.g., Keeley 2001; Grant and Imre 2005; Elliott 2015). Water temperature appeared to have a weaker influence on growth than density, with a negative relationship with growth$_{FL}$ but positive relationship with growth$_{WT}$ and hence also a positive relationship with condition$_{1+}$. This result suggests that fish were differentially allocating energy to somatic growth in length versus body condition or energy storage depending on temperature. However, this conflicts with previous results for juvenile *O. mykiss* in which growth in length increased with temperature in both field (McMillan et al. 2012) and laboratory (Beakes et al. 2010; Doctor et al. 2014) studies under relatively similar temperature ranges to Big Creek. Furthermore, Sloat and Reeves (2014) found higher growth in weight under warmer conditions despite reduced lipid content, and McMillan et al. (2012) similarly found higher growth in length but lower lipid content in warmer streams. Bioenergetics and energy allocation are complex processes in stream-dwelling salmonids and involve interactions in temperature, food supply, metabolic rate, and habitat conditions (Elliott 1994; Jobling 1994), as well as sex and life history (McMillan et al. 2012; Sloat and Reeves 2014), and it is unclear what might be driving the apparent different effect of temperature on growth in Big Creek compared with other studies.

There was very high variation in growth and condition$_{1+}$ among individuals within cohorts and among cohorts in Big Creek. Within cohorts, there was a three- to fivefold difference in growth$_{FL}$ between the slowest and fastest growing individuals and six- to 18-fold difference in growth$_{WT}$. High individual-level heterogeneity in growth is consistent with previous studies of *O. mykiss* (Shelton et al. 2013) and other salmonids (Jenkins et al. 1999; Lobón-Cerviá 2010; Elliott 2015). There also was high variation in growth across the eight cohorts, with a roughly twofold difference in mean growth across years and a range in mean fork length at age 1+ of 104 to 124 mm across years. Although this result seems expected considering the high environmental variability in water temperature, stream flow, and *O. mykiss* density (Table 1; Supplementary Material Fig. S1[1]), it contrasts with the results of Kelson and Carlson (2019), who detected no difference in summer growth or condition of juvenile *O. mykiss* among three years (2015–2017) encompassing drought to wet conditions in two headwater tributaries in northern California. They attributed the lack of difference to high habitat quality due to unimpaired, groundwater-fed flows and undisturbed forests. However, similar conditions occur in Big Creek, and temperatures and *O. mykiss* densities appeared similar between our study and theirs. The most likely explanation for the different results between our studies seems to be that they focused on summer growth, which, as they discussed, was very low in their populations and also in other coastal *O. mykiss* populations in California (Harvey et al. 2005; Hayes et al. 2008; Sogard et al. 2009), whereas we analyzed annual growth that integrated over periods of low and high growth during the year. In addition, growth differences among cohorts varied among the three study reaches in Big Creek, indicating that *O. mykiss* growth may vary at fine spatial scales in relation to local conditions even within a basin with high habitat quality. Thus, while we agree with Kelson and Carlson's (2019) conclusion that unimpaired, high-quality habitat is important for the persistence of *O. mykiss* populations and should be prioritized for conservation, our results demonstrate that even in systems with high-quality, intact habitat, there still may be high interannual and site-specific variation in growth and condition.

Although we believe that our results are robust because they are based on eight cohorts that represented a wide range of environmental conditions in our study system, there are several potential limitations or qualifications of our study to keep in mind. First, we were not able to PIT-tag fish < 65 mm FL, so our sample excluded the smallest YOY that had not reached this size by their first fall. The proportion of YOY too small to tag was low (0.03–0.14) in 4 years (including 2010, which had the largest sample) but higher (0.26–0.37) in the other 4 years. However, sex ratios and proportions of Omy05 genotypes did not differ between years with low or high rates of YOY too small to tag (χ^2 tests, $P > 0.10$), so this did not appear to bias our sample with respect to the factors of interest. Second, there was a slight sex bias in our sample, which was 46% female overall, which could suggest that early-migrating females were disproportionately excluded from the study. However, sex ratio was not significantly different than 1:1 in any of the eight cohorts or overall (binomial tests, $P > 0.05$). Further, the skew was not consistent across cohorts, as sex ratio was slightly female-biased in two of the eight cohorts, including 2010, which had the largest sample (Table 1). As discussed above with respect to freshwater maturation, anadromous migration in this population generally occurs after 2–3 years of rearing. Sex ratios are stable around 1:1 in fish up to 150 mm but then become sharply male-skewed above that (Rundio et al. 2012; Pearse et al. 2019). In addition, emigration rates were similar between males and females with AA and AR Omy05 genotypes when fish were ~100 mm (Pearse et al. 2019). Therefore, the majority of evidence

indicates that emigration does not differ between sexes until after age 1+, and we suspect that the slight sex ratio bias in our study more likely reflects variability in small samples rather than differential emigration that would confound our estimates of growth and condition by sex and Omy05 genotype. Finally, the differences we found with respect to sex and Omy05 genotype during the first to second fall as juveniles (~ 6 to 18 months of age) may change, or additional differences may emerge, during the second year of development as fish get closer to expression of life-history type, as Hecht et al. (2012) observed temporal changes in the differences between sexes and smolts and nonsmolts.

In conclusion, expression of migration versus freshwater maturation in partially migratory salmonids is a complex process involving sex-specific interactions among an individual's genotype, condition, and environment (Dodson et al. 2013; Sloat et al. 2014; Phillis et al. 2016; Ferguson et al. 2019). Genotype–phenotype relationships appear to be context-dependent and may vary with environmental conditions across a species' range (Arostegui et al. 2019; Pearse et al. 2019; Weinstein et al. 2019). Advances in genotyping, tagging, and tracking wild fish are now permitting investigation of these relationships in natural populations, and *O. mykiss* has emerged as a model species for the study of partial migration because the genetic basis of migration is better understood than in other salmonids and because migration in southern populations is strongly associated with a single genomic region, facilitating analysis of genotype–phenotype relationships (Kelson et al. 2019, 2020*a*; Pearse et al. 2019). In this study, we have now shown that sex-specific genotype–phenotype differences in wild fish occur relatively early in juvenile development and well in advance of anadromous migration or freshwater maturation in a southern population of *O. mykiss*. Candidate genes potentially associated with migration have been identified in other salmonids (e.g., brown trout, Lemopoulos et al. 2018, 2019; sockeye salmon (*Oncorhynchus nerka*), Veale and Russello 2017), and laboratory experiments have indicated a genetic basis of juvenile growth that was associated with migration probability in Atlantic salmon (Debes et al. 2020). Continued research on the genetic architecture of migration and application of genomic markers with tagging-based field studies has potential to yield insights on the complex, sex- and context-dependent genotype–phenotype relationships underlying partial migration. This may provide a basis for understanding the observed variability and inconsistent patterns between juvenile growth or condition and migratory life history in *O. mykiss* and other salmonids (Kendall et al. 2015; Ferguson et al. 2019).

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