

Partial migration alters population ecology and food chain length: evidence from a salmonid fish

SUZANNE J. KELSON^{1,4,†} MARY E. POWER,² JACQUES C. FINLAY,³ AND STEPHANIE M. CARLSON¹

¹Department of Environmental Science, Policy and Management, University of California, Berkeley, 130 Mulford Hall, Berkeley, California 94720 USA

²Department of Integrative Biology, University of California, Berkeley, 23060 Valley Life Sciences Building #3140, Berkeley, California 94720 USA

³College of Biological Sciences, University of Minnesota, 1987 Upper Buford Circle, St. Paul, Minnesota 55108 USA

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Abstract. Many migratory species, from monarch butterflies to wildebeest, express partial migration, where only a subset of a population migrates. This intraspecific variation is likely to have large ecological consequences. We studied the ecological consequences of partial migration in a salmonid fish, *Oncorhynchus mykiss*, in coastal streams in California, USA. One ecotype, steelhead trout, migrates to the ocean, whereas the other, rainbow trout, completes its lifecycle in freshwater. Migration has a strong genetic basis in *O. mykiss*. In one stream, we found differences in the frequency of migration-linked genotypes below and above a waterfall barrier (migratory allele frequency of 60% below vs. 31% above). Below the waterfall, in the migratory-dominated region, the density of young fish (<1 yr old) was approximately twice that in the resident-dominated region above the waterfall (0.46 vs. 0.26 individuals/m², respectively), presumably reflecting the higher fecundity of migratory females. Additionally, there were half as many older fish (>1 yr old) in pools downstream of the waterfall (0.05 vs. 0.13 individuals/m²). In a second stream, between-year variation in the dominance of migratory vs. resident fish allowed us to explore differences in fish density and size structure through time, and we found a consistent pattern. In brief, when migratory genotypes dominated, we found higher densities of young fish and lower densities of older fish, resulting in a simpler size structure, compared to when resident genotypes dominated. Moreover, large resident trout had a slightly higher trophic position than young fish (3.92 vs. 3.42 in one creek and 3.77 vs. 3.17 in the other), quantified with stable isotope data. The difference in fish size structure did not generate trophic cascades. Partial migration is widespread among migratory populations, as is phenotypic divergence between resident and migratory forms, suggesting the potential for widespread ecological effects arising from this common form of intraspecific variation.

Key words: eco-evolutionary dynamics; extended phenotype; food chain length; intraspecific variation; life history; *Oncorhynchus mykiss*; size structure; steelhead/rainbow trout.

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⁴Present address: Biology Department, University of Nevada, Reno, Mail Stop #314, 1664 North Virginia Street, Reno, Nevada, 89557, USA

† E-mail: skelson@berkeley.edu

INTRODUCTION

There is growing appreciation that phenotypic variation among individuals of the same species

(i.e., intraspecific variation) can have strong ecological consequences for community structure (Bolnick et al. 2011) and ecosystem processes (Raffard et al. 2017). For example, divergence in

foraging traits of predatory alewife alters body size and species richness of their zooplankton prey (Palkovacs and Post 2009). In some systems, the magnitude of ecological effects of intraspecific variation can match or even exceed those due to species-level variation (Des Roches et al. 2018).

When genetic variation drives ecological change, such changes are considered an extended phenotype of a genotype (Whitham et al. 2003), and a concept has been studied extensively in plants (Whitham et al. 2012). This line of research has revealed, for example, that genetic variation determines the composition of root fungal communities in pine trees and, consequently, host drought tolerance (Gehring et al. 2017). Despite the attention paid to the ecological consequences of both genetic variation and intraspecific variation, research linking genetic variation, intraspecific trait variation, and ecology is lacking.

Here, we suggest that partial migration is a form of intraspecific variation likely to have large ecological consequences. Partial migration describes the phenomenon where a subset of individuals within a population migrates, while others do not. Partial migration is common across migratory taxa (Chapman et al. 2011), including ungulates (Ball et al. 2001, Cagnacci et al. 2011), fishes (Chapman et al. 2012), birds (Boyle 2008, Jahn et al. 2010, Sanz-Aguilar et al. 2012), and insects (Attisano et al. 2013, Odermatt et al. 2017). Past research on partially migratory animals has focused on trade-offs favoring this polymorphism (reviewed in Chapman et al. 2011) or the evolutionary stability of this polymorphism (Lundberg 2013, De Leenheer et al. 2017). Ecological implications of, rather than as a cause for, migration remain poorly understood, with fewer studies exploring this topic (Fryxell and Sinclair 1988, Palkovacs and Post 2009, Hansen et al. 2019).

Partial migration could have ecological implications whenever the two life history forms diverge in traits related to ecological function. For example, migratory and resident conspecifics often differ in body size (Chapman et al. 2011), with consequences for size-dependent thermal tolerance (Belthoff and Gauthreaux 1991), predation risk (Hansson and Hylander 2009), and diet specialization (Dobson 2009). Body size affects

fecundity (Blueweiss et al. 1978), feeding preferences (Werner and Gilliam 1984), per capita nutrient cycling (Torres and Vanni 2016), and numerous other traits related to ecological function (Peters 1983). Moreover, when resident individuals continuously occupy habitats, they will have markedly different impacts on food webs and ecosystems than will migratory individuals with pulsed, seasonal occupancy (Fryxell and Sinclair 1988, Brodersen et al. 2011). These phenotypic divergences could be considered to be part of the extended phenotype of life history type.

The genetic basis of migration is well established within the Salmonidae family (Dodson et al. 2013), in which partial migration is common (Jonsson and Jonsson 1993). In the case of *Oncorhynchus mykiss*, migration has been linked to a specific region of the genome (Pearse et al. 2014). Migratory and resident *O. mykiss* (steelhead and rainbow trout) commonly co-occur in coastal watersheds, including tributaries of the South Fork Eel River in northern California, where we investigated links between genotypes, intraspecific trait variation, and ecology. Overall, we predicted that the pattern of partial migration in this species, that is, the existence of two divergent ecotypes, has ecological effects at the population level (density and size structure) and at the community level (food chain length and distribution of trophic level biomass). We first characterized the spatial and temporal distribution of migratory alleles in *O. mykiss* in two streams. At the population level, we predicted that (1) pools and regions dominated by migratory genotypes would be characterized by a high density of juvenile (young of year) fish due to the high fecundity of large, migratory females and (2) pools and regions where resident genotypes dominate would be characterized by reduced density and more complex size structure due to the presence of remaining older, larger resident fish. At the community level, we predicted that large resident fish would add a trophic level due to some cannibalism, leading to a higher mean trophic level and longer food chain length in regions where they remain. Finally, we predicted that the biomass of benthic macroinvertebrates would be reduced in regions where small fish, who directly prey on invertebrates, dominate, and would be increased (released from predation by small fish)

in the regions where small fish are less dense. Similarly, we predicted that macroinvertebrates in the regions dominated by resident fish would be smaller due to the presence of this larger-gaped predator.

MATERIALS AND METHODS

Study system and location

Partially migratory populations of *O. mykiss* include both migratory steelhead trout and resident rainbow trout. Steelhead remain in freshwater for 1–3 yr, migrate to the ocean for feeding and rearing for another 1–3 yr, and then return to streams to breed, usually without feeding or lingering in freshwater. Resident trout remain in freshwater for their life history, often remaining near their natal site in streams. Juvenile migratory and resident trout rear together in the same streams. Migratory adult trout are much larger than resident trout, reaching >700 mm on average (Quinn 2005), while the largest resident trout we observed in our study streams was 265 mm. Consequently, migratory adults are much more fecund than resident adults (approximately 5000 eggs for migratory females (Quinn 2005) vs. <1000 eggs for resident females (Moyle 2002)).

We studied partially migratory *O. mykiss* in Elder Creek (16.8 km² drainage area) and Fox Creek (2.7 km²), both tributaries of the South Fork Eel River (123°39' W, 39°44' N; Fig. 1) within the UC Angelo Coast Range Reserve. *O. mykiss* represents >99% of the fish biomass in both creeks. Elder Creek has a 3 m high waterfall located 2.5 km upstream from the creek mouth (Fig. 1) that is impassible to adult steelhead under most stream flows (Trush 1989), and typically passable less than 40 d/yr (Kelson et al. 2020). This waterfall allows for ecological comparisons between the reach of stream that is easily accessible to migratory fish (below the waterfall) to reaches that are less accessible (above the waterfall). We also surveyed the fish-bearing tributaries to Elder Creek, Misery (1.9 km²) and Paralyze (4.9 km²) creeks, both located upstream of the waterfall (Fig. 1). Elder Creek is characterized by pool-riffle morphology in the lower reaches and step-pool morphology in the upper reaches, including in both tributaries. The transition from pool-riffle to step-pool morphology occurs near the confluence with

Misery Creek, 4.1 km upstream from the Elder Creek mouth. While ecological gradients occur upstream-to-downstream in rivers (Vannote et al. 1980), here there are no major environmental changes that would drive shifts in population and food web ecology within Elder Creek. Canopy cover is similarly high throughout (mean \pm standard deviation [SD] in canopy cover of 89.5% \pm 8.0% below the waterfall vs. 92.2% \pm 5.8% for all regions above the waterfall). While the surveyed pools were slightly longer and wider below the waterfall as drainage area increased (length of 7.5 \pm 2.8 m vs. 6.0 \pm 3.2 m and width of 3.9 \pm 1.0 m vs. 2.8 \pm 1.2 m below vs. above the waterfall, respectively), depths were similar across the reaches (mean depth of 0.2 \pm 0.1 m in both reaches). Furthermore, the entire drainage area of Elder Creek is contained within the reserve, so land use and human impacts are minimal throughout. In Fox Creek, the largest barrier is a step (knickpoint) at its confluence with the South Fork Eel River, rendering the entire creek inaccessible to migratory adults in years with less precipitation (Kelson et al. 2020). Fox Creek is also heavily shaded, with a canopy cover of 94.1% \pm 4.2%. The surveyed pools in Fox Creek tended to be smaller and shallower than Elder (4.0 \pm 1.6 m long, 2.0 \pm 0.9 m wide, and average of 0.1 \pm 0.1 m deep). Fox Creek morphology is also transitional, with mostly step-pool habitat and some pool-riffle habitat.

Fish sampling to estimate density and size structure

All pools, runs, and riffles in both streams were numbered and mapped. We then randomly selected study units using a spatially stratified design to represent the entire length of stream occupied by fish. We focused on slow-moving habitat units (pools and runs), because this habitat type is dominant and comparable throughout both watersheds. We excluded a few pools that were too deep for electrofishing (maximum depth >1 m). We estimated the surface area of each study pool by multiplying the length by average width, estimated from five evenly spaced width measurements.

To estimate fish density and size structure, we captured fish from study pools from late July to early August in 2014–2017. Across years, we

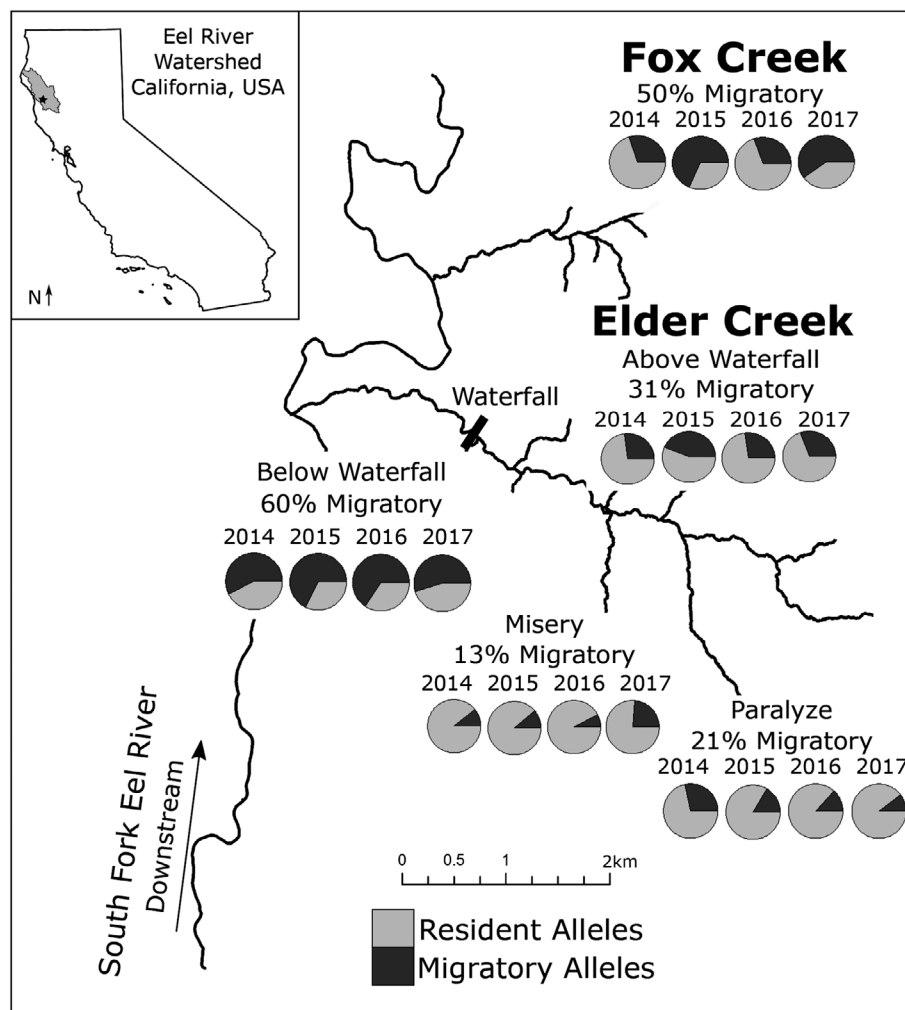


Fig. 1. The proportion of migratory alleles was higher below than above the waterfall in Elder Creek, including the reach immediately above the waterfall and in the tributaries, Misery and Paralyze, across all years of study. In contrast, the proportion of migratory alleles in Fox Creek varied among years and was highest in 2015 and 2017. The overall percent of migratory alleles for each stream/stream region (compiling fish from all age classes from all four years for each region) is written below each name.

sampled fish from 140 to 143 pools in Elder Creek and 55 to 57 pools in Fox Creek, returning to the same pools, with only a few exceptions due to variation in channel morphology among years. When a pool was no longer accessible or present due to winter sediment redistribution or tree falls, we sampled the next upstream pool. We captured fish using standard three-pass electrofishing, with block nets at the upstream and downstream ends of the pool. Fish were counted, measured for fork length (FL, mm), and weighed to the nearest 0.01 g. We removed a small

portion of the caudal fin from each fish for genetic and isotopic analyses.

We present fish density as the total catch divided by the pool surface area (fish/m²). We present count data rather than estimates from population depletion methods because many study pools did not meet the assumptions of depletion models (Kelson and Carlson 2019). We used the length data to characterize size/age structure of fish by visually examining the length-frequency histogram and determining the size where the two primary size peaks intersect

(Hall et al. 2016). We classified fish <85 mm FL at capture in July as young of the year (hereafter “young” fish) and fish ≥85 mm as age-1 and older fish (hereafter “older” fish).

Summarizing variation in migratory vs. resident allele frequencies

We extracted DNA from tissue samples (total $n = 3149$ individuals) and genotyped individuals as described in Kelson et al. (2019). In short, we conducted restriction site-associated DNA (RAD) capture (Ali et al. 2016) and sequenced libraries using HiSeq (Illumina, San Diego, California, USA). We randomly sampled one read at each single nucleotide polymorphism (SNP) per individual. We then conducted a discriminant analysis on the principle components from 415 SNPs on the migration-linked region of the genome (Pearse et al. 2014), which allowed us to group individuals into clusters of migratory, heterozygous, or resident genotypes (Kelson et al. 2019).

We summarized life history genotype data in three ways. At the pool level, we calculated the proportion of migratory alleles, which is a quantitative metric (from 0 to 1) that incorporates information about heterozygotes in addition to homozygotes. In detail, we summed the number of migratory alleles (2 per migratory genotype fish and 1 per heterozygote genotype fish) and then divided by the total number of alleles (2 per fish) for each pool. Also at the pool level, we summed the number of homozygous migratory genotype fish per pool, which facilitates direct comparisons with total fish density. Finally, to provide an overall pattern of allele frequencies across space and time at the regional level, we summarized the migratory allele frequency across pools for Fox Creek and each stream reach within Elder Creek (below waterfall, above waterfall, and the two tributaries, Misery and Paralyze).

Data analyses to understand relationships between genotype, density, and size structure

We explored the relationship between migratory allele frequency and population ecology, and evaluated by two metrics, density of young fish and density of older fish. We predicted that the density of young fish would increase with the proportion of migratory alleles per pool,

while the density of older fish would decrease. We used linear mixed-effects models in order to account for non-independence of data (Millar and Anderson 2004), specifically the non-independence of pools that were sampled within the same stream and stream region, by including sample location and year as random effects. In detail, for both response variables (density of young and old fish), we conducted a linear mixed-effects model, with the proportion of migratory alleles per pool as a fixed effect, and random effects of sample year and location (Fox Creek, and each of the four regions within Elder Creek). We also explicitly tested if density of young and old fish differed among locations within Elder Creek, using an ANOVA that included a random effect of year, to account for repeated samples. In Fox Creek, we used a one-way ANOVA to test whether the density of young and old fish differed among years. All linear mixed models were fit by maximum likelihood using the R package lme4 (Bates et al. 2015), and parameter significance was assessed using the Satterthwaite approximations to degrees of freedom implemented in the R package lmerTest (Kuznetsova et al. 2016).

Trophic position and food web sampling

We used stable isotope analyses to describe the bottom-up trophic position of young vs. older *O. mykiss* (more vs. less common in migratory genotype stream reaches, see *Results*, included fish from all streams), and the food chain length in stream reaches dominated by each. We used $\delta^{15}\text{N}$, which is enriched up the food web (Minagawa and Wada 1984), to estimate trophic position for *O. mykiss* in each size class. We conducted isotope analyses primarily on samples from fish of two size classes, young fish, certainly under 1 yr of age (40–70 mm FL), and older fish, likely over 2 yr of age (>150 mm FL). Fish from these size classes were sampled from Fox and Elder Creeks in 2015–2017. For young fish, we combined tissue samples from 1 to 3 fish in order to meet the minimum weight requirements for stable isotope analysis. For older fish, we used tissue from individual fish. Caudal fin clips were desiccated in glass vials for 24 h at 60°C, weighed to the nearest 0.001 mg, and wrapped in tin capsules. Samples were analyzed at the UC Berkeley

Center for Stable Isotope Biogeochemistry, with continuous flow dual isotope analysis on a CHNOS elemental analyzer interfaced to an IsoPrime100 mass spectrometer (Isoprime, Cheadle, UK). We tested that older fish were more enriched for $\delta^{15}\text{N}$ enrichment than young fish using a two-sided t test.

In order to compare mean trophic position and food chain length across pools and regions of each stream, we used our isotope data to estimate the trophic position of every fish sampled in the longitudinal density surveys. We predicted the $\delta^{15}\text{N}$ value for every fish that we captured from its body length. To do so, we used previously published data (Finlay et al. 1999, 2002), which encompassed a broader distribution of fish sizes (including fish from 70 to 150 mm FL), in addition to the data collected in 2015–2017 (Methods, Trophic position and food web sampling), to run a linear regression between FL and $\delta^{15}\text{N}$ enrichment. We found a strong linear relationship between fish length and $\delta^{15}\text{N}$ enrichment ($r^2 = 0.57$, P -value < 0.01 , Appendix 1: Fig. S1). We used the linear regression to predict $\delta^{15}\text{N}$ enrichment for all fish that were captured in our longitudinal surveys.

In order to estimate trophic position and food chain length, we characterized the $\delta^{15}\text{N}$ baseline of food webs in these streams. We used data from Finlay et al. (1999, 2002), Finlay (2001), and Sabo et al. (2010), as well as unpublished data collected using the same methods, to characterize baseline isotopic signatures. The samples were collected in 1997–1999 in Fox and Elder Creek. Primary consumers (herbivores) that were sampled consisted of Ephemeroptera (primarily *Heptageniidae* spp.) and Trichoptera (primarily *Dicosmoecus gilvipes*, *Glossosoma* spp., *Neophylax* spp., and *Psychoglypha* sp.). Invertebrate predators were also sampled, including Odonate spp., Megaloptera spp., and Perlidae spp. Although basal consumers were sampled in different years than fish predators, the isotopic signature was consistent across sample years (no difference between the three years that were sampled, $P > 0.1$ in an ANOVA), and there have been no changes to the watershed or study streams that would change $\delta^{15}\text{N}$ enrichment in salmonid prey.

We estimated bottom-up trophic position using the equation:

$$\text{TrophicPosition}_{\text{consumer}} = [\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}] / \Delta + 2 \quad (1)$$

where $\delta^{15}\text{N}_{\text{consumer}}$ is the $\delta^{15}\text{N}$ value for the consumer, $\delta^{15}\text{N}_{\text{baseline}}$ is the value of a primary consumer, Δ is the trophic fractionation factor between food web levels, assumed to be 3.4‰ (Post 2002, McCutchan et al. 2003), and 2 is added to compensate for using a primary consumer rather than a primary producer or detritus (Anderson and Cabana 2007). Here, we used mean values for Ephemeroptera herbivores as our primary consumer. The values of primary consumers differed in Fox and Elder Creek ($P < 0.01$ in a t test; Appendix S1: Fig. S2), so we estimated food chain length separately for each stream. We used the same formula to estimate food chain length, which is equivalent to the trophic position of the top predator, or the maximum trophic position in a study pool.

We calculated food chain length with young fish as the top predator vs. with older fish as the top predator, the two scenarios representing food web structure in the migratory vs. resident stream reaches (see *Results*). Next, we used Eq. 1 to estimate the trophic position for every fish that was captured in our longitudinal surveys, given the estimated $\delta^{15}\text{N}$ value for each fish. We then estimated the mean trophic position and the food chain length (highest trophic position) for every sample pool in Fox and Elder Creek in each year. We conducted a nested ANOVA to compare the mean trophic position and food chain length among regions in Elder Creek, nested within year to account for repeated measures across 4 yr. We also conducted one-way ANOVAs to compare mean trophic position and food chain length among years in Fox Creek.

Next, we tested for a top-down trophic cascade driven by fish predators. We tested this separately because trophic position, indexed by the number of energy transfers from the basal source of fixed carbon and as described by isotopic fractionation, does not necessarily imply that predators deplete the population of their primary food source (Power et al. 1996). We predicted that in the migratory genotype region where young fish were found in higher densities and not suppressed by older fish (see *Results*), fish would exert stronger top-down effects on benthic

macroinvertebrates, resulting in lower biomass of macroinvertebrates. Even though trout are often considered drift-feeders, we predicted a top-down trophic effect because drifting invertebrates eventually settle and contribute to the benthos (Rosenfeld et al. 2014), and we observed that juveniles feed directly on the benthos in these streams (Finlay et al. 2002), which has been previously noted elsewhere (Harvey and Railsback 2014). To test whether fish density and size structure influenced macroinvertebrate abundance and size in a trophic cascade, we sampled benthic macroinvertebrates above and below the waterfall in Elder Creek in June–August of 2015. We sampled over a short length of the stream to reduce variation in environmental conditions, sampling in three pools downstream and three pools upstream of the waterfall, the point where there was a sharp change in fish density and size structure (see *Results*). These pools did not differ in light availability as measured by canopy cover (mean \pm SD of $85\% \pm 8\%$ below the waterfall vs. $89\% \pm 2\%$ above the waterfall). In the invertebrate sample pools, the mean density of young fish below the waterfalls was twice as high as the mean density above the waterfall (0.34 ± 0.14 fish/m² below vs. 0.17 ± 0.05 fish/m² above the waterfall). To collect benthic macroinvertebrates, we removed invertebrates from 4 to 6 cobbles within each study pool. We rolled individual cobbles into a 1-mm mesh dip net and collected all invertebrates in the net and on the cobble. We sampled benthic invertebrates on cobbles to focus on the invertebrates that are most available to trout, following methods of Meissner and Muotka (2006). To standardize samples by surface area, we estimated the surface area of each cobble by wrapping it in foil and then weighing the foil (Bergey and Getty 2006). We identified all collected aquatic invertebrates to the family level and to genus/species when possible. Biomass of invertebrates was estimated by weight–length regressions (Benke et al. 1999, Sabo et al. 2002). Invertebrates were then classified into one of the two categories, armored or unarmored. We separated these because unarmored prey, who are more vulnerable, are more likely to be reduced in biomass and size due to predation, than armored prey. Armored taxa include Coleoptera adults, Gastropoda, cased Trichoptera, and Hemiptera (*Gerridae* spp.), cased

Diptera (i.e., *Rheotanytarsus*). Unarmored taxa include Ephemeroptera, Plecoptera, uncased Trichoptera, Acari, Collembola, unarmored Diptera, Coleoptera larva, Nematoda, Megaloptera, Odonata, and Oligochaeta.

We conducted two nested ANOVAs with macroinvertebrate biomass (armored and unarmored) as the response variable and location (above vs. below the waterfall) as a fixed effect, and included study pool as a random (nested) effect to account for repeated measures (multiple cobble samples) in each pool. Additionally, we predicted that benthic macroinvertebrates would be smaller in the resident region, as larger fish prey on larger macroinvertebrates (Keeley and Grant 1997). We conducted a similar pair of nested ANOVAs as described above, with invertebrate (armored vs. unarmored) length as the response variable and location (above vs. below waterfall) as the predictor variable, including study pool as a random (nested) effect.

RESULTS

Distribution of migratory alleles

The region of Elder Creek below the waterfall was dominated by fish with migratory genotypes (60% migratory alleles), while regions above the waterfall were dominated by resident genotypes (69% resident alleles in Elder Creek above the waterfall, 87% in Misery, 79% in Paralyze). This pattern was consistent across years in Elder Creek (Fig. 1; Appendix S1: Table S1). In Fox Creek, genotype frequencies varied among years rather than stream reaches (Fig. 1; Appendix S1: Table S1) and were dominated by resident alleles in two years (70% resident in 2014 and 2016) and by migratory alleles in two years (68% migratory in 2015, 60% in 2017).

The proportion of migratory alleles correlates with density and size structure of fish

The proportion of migratory alleles within a study pool was correlated with fish density and size structure. For young fish, density increased with the proportion of migratory alleles per pool ($F_{1, 258} = 8.8$, $P < 0.01$, slope \pm standard error (SE) = 0.20 ± 0.07 ; Fig. 2). Pools that were dominated by migratory alleles (>50% migratory alleles) were characterized by nearly twice as many young fish on average as pools dominated by

resident alleles (mean \pm SD: 0.52 ± 0.41 fish/m² vs. 0.28 ± 0.28 fish/m², respectively). In contrast, the density of older fish decreased with the proportion of migratory alleles per pool ($F_{1, 242} = 20.6$, $P < 0.01$, slope \pm SE = -0.11 ± 0.02 ; Fig. 2). The number of older fish was nearly three times as high in pools dominated by resident alleles compared to pools dominated by migratory alleles (mean \pm SD: 0.14 ± 0.13 fish/m² vs. 0.05 ± 0.07 fish/m², respectively).

Local spatial patterns in the proportion of migratory alleles scaled up to larger, reach-scale spatial patterns in density and size structure of trout in Elder Creek (Fig. 3a–d). Young fish were twice as dense in the region below the waterfall, where migratory genotypes were common, than in the upstream resident-dominated regions (mean \pm SD: 0.46 ± 0.31 fish/m² below the waterfall vs. 0.20 ± 0.22 fish/m² above the waterfall, 0.21 ± 0.23 fish/m² in Misery, and 0.27 ± 0.26 fish/m² in Paralyze). The drop in the density of young of year fish occurred immediately above the waterfall (Fig. 3c), suggesting that the waterfall is the cause of this shift rather than longitudinal changes in environmental

factors. In contrast, older fish were less dense in the migratory-dominated region than in the resident-dominated region (Fig. 3d, mean \pm SD: 0.05 ± 0.06 fish/m² below the waterfall vs. 0.09 ± 0.08 fish/m² above the waterfall, 0.16 ± 0.16 fish/m² in Misery, and 0.14 ± 0.13 fish/m² in Paralyze). Location was significant in an ANOVA for densities of both young fish ($F_{3, 337} = 23.2$, $P < 0.01$) and old fish ($F_{3, 337} = 12.4$, $P < 0.01$). In summary, when fish with migratory genotypes were abundant, size structure was simple and characterized by many small fish (unimodal length-frequency histogram, Fig. 4, gray-colored histograms), whereas in the resident-dominated regions, fish size structure was more complex and included more large fish, leading to a bimodal length-frequency histogram (Fig. 4, black-colored histograms).

While density and size structure of *O. mykiss* varied spatially in Elder Creek, this was not the case in Fox Creek, where the largest barrier is a steep cascade at the creek mouth, precluding access for migratory fish in some years. In Fox Creek, we saw the same patterns emerge in time

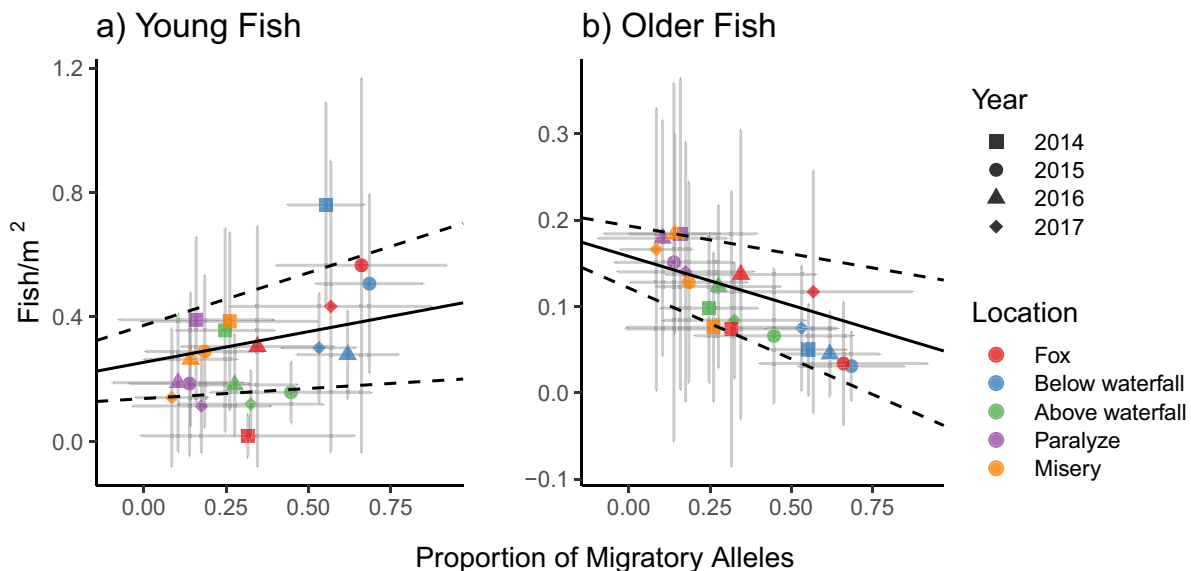


Fig. 2. (a) Density of young fish was positively correlated to the proportion of migratory alleles per pool, whereas (b) the density of older fish was negatively correlated to the proportion of migratory alleles per pool. Points represent the mean value for each stream region and year, gray bars are standard deviation. Black lines are the slope and intercept of the linear mixed-effects model, and dashed lines are 95% confidence intervals. See Fig. 1 for map of locations.

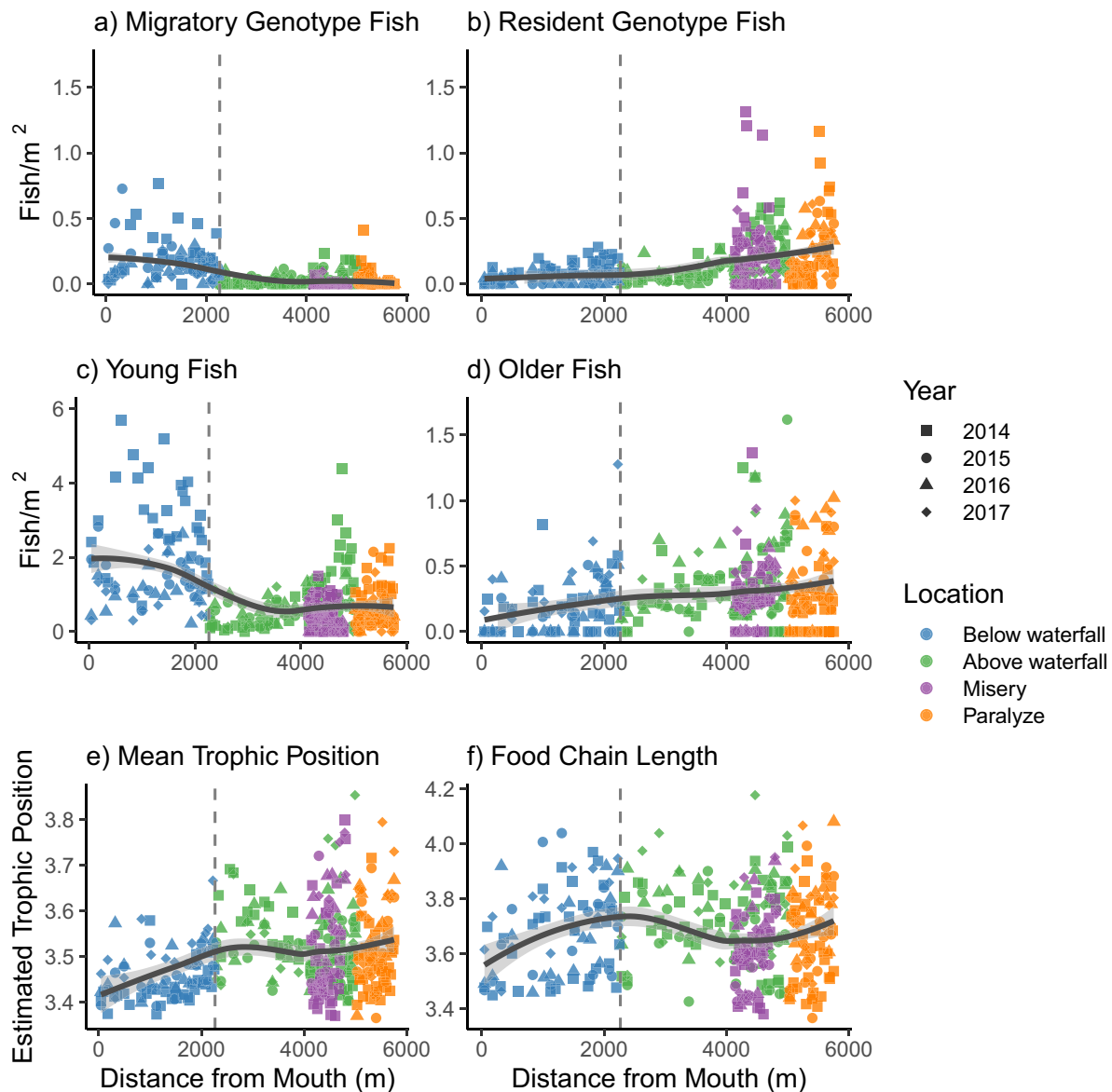


Fig. 3. Within Elder Creek, (a) fish with migratory genotypes were more abundant in pools below the barrier waterfall (gray line), while (b) fish with resident genotypes were more abundant in pools above the waterfall. Similarly, (c) density of young fish was relatively higher in pools below the waterfall, while the (d) density of older fish was higher in pools above the waterfall. Differences in size structure of fish led to differences in (e) mean trophic position of fish and (f) food chain length (maximum trophic position of fish) in each study pool. Trends are visualized with a loess smoothing curve (gray line) with standard error (gray bands).

rather than space. Specifically, among year variation in migratory allele frequency was correlated with among year variation in fish density and size structure. In years when densities of migratory genotypes were low (2014 and 2016), densities of young fish were also low (mean \pm SD:

0.02 ± 0.07 and 0.30 ± 0.39 fish/m² in 2014 and 2016 vs. 0.57 ± 0.60 and 0.43 ± 0.47 fish/m² in 2015 and 2017; Fig. 5a, c). The density of migratory and resident genotypes differed among years ($F_{3,94} = 6.0$ and $F_{3,94} = 5.7$, $P < 0.01$ for both comparisons, Fig. 5a, b), as did the density

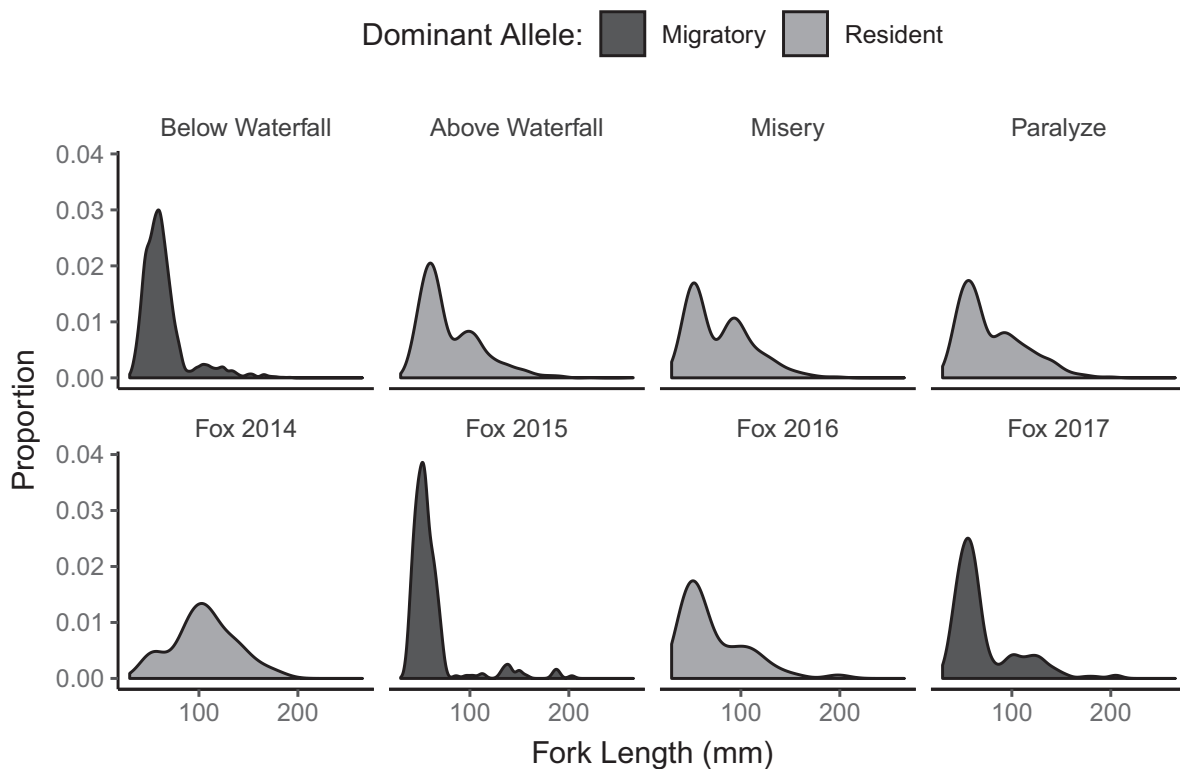


Fig. 4. In Elder Creek (top row), density plots reveal simple size structure (fork length, in mm) in the migratory-dominated region below the barrier waterfall vs. more complex size structure in the resident-dominated regions (above the waterfall, Misery, and Paralyze) using data from all four years combined (2014–2017). In Fox Creek (bottom row), size structure was simple in years when migratory genotypes dominated (2015 and 2017) and more complex in years when resident genotypes dominated (2014 and 2016).

of young fish ($F_{3,94} = 6.4$, $P < 0.01$, Fig. 5c). The density of old fish was not significantly different among years ($F_{3,94} = 2.4$, $P = 0.08$, Fig. 5d), but was highest in 2015, the year following the year when migratory juveniles were excluded from the creek.

Trophic position of large vs. small fish and food web effects

Older *O. mykiss* were more enriched for $\delta^{15}\text{N}$ than young fish (i.e., size/age class was statistically significant in a t test, $t_{153} = 15.0$, $P < 0.01$; Fig. 6). The average isotopic difference was 1.8‰ , less than the predicted 3.4‰ had the two groups fed at distinctly different trophic levels (mean \pm SD $\delta^{15}\text{N}$ was $6.1\text{‰} \pm 0.6\text{‰}$ for young fish vs. $7.9\text{‰} \pm 0.8\text{‰}$ for older fish). This pattern also held when only resident-genotype older fish were included, suggesting that age/size rather

than genotype controls trophic $\delta^{15}\text{N}$ enrichment. Similarly, older trout had a higher trophic position in both Elder and Fox Creeks, estimated at 3.92 for older trout vs. 3.42 for young trout in Elder, and 3.77 for older trout vs. 3.17 for young trout in Fox Creek. The trophic position of fish predators relative to other trophic levels in the stream is visualized in Fig. 6. Differences in the trophic position of young vs. older trout, in combination with differences in the regional differences in density and size structure of fish, led to regional differences in the estimated mean trophic position and food chain length in Elder Creek. In particular, mean trophic position at the pool level increased moving upstream in Elder Creek, especially in the tributaries, Misery and Paralyze, as did the food chain length (Fig. 3e, f). These pool-level trends led to reach-level trends, and the regions differed in mean trophic level

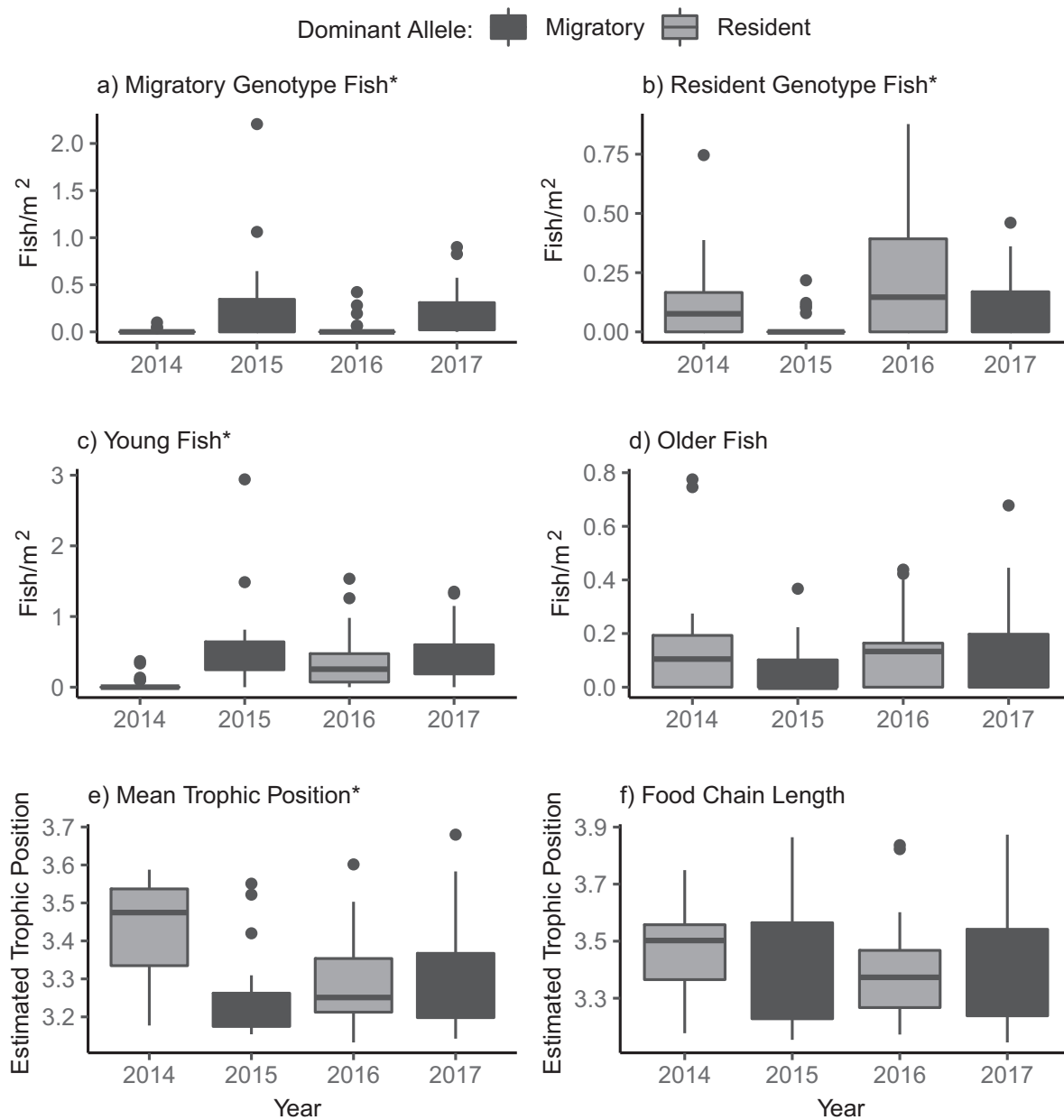


Fig. 5. In years when the density of migratory genotype fish was low (2014 and 2016) (a), the density of young fish was lower in Fox Creek (c). Similarly, in years when the density of resident-genotype fish was high (2014 and 2016) (b), the density of older fish was also higher (d). Mean trophic position (e) and food chain length (f) were highest in 2014, when young fish and migratory genotypes were less abundant. Significantly different comparisons are noted with an asterisk.

and food chain length in nested ANOVAs (nested within each sample year, $F_{3, 337} = 12.4$ for mean trophic position, $F_{3, 337} = 7.0$ for food chain length, and $P < 0.01$ for both statistical

models). In Fox Creek, mean trophic position differed by year ($P < 0.01$ in an ANOVA, $F_{3,88} = 7.5$, Fig. 5e), and in years when migratory genotypes and young fish were common, mean

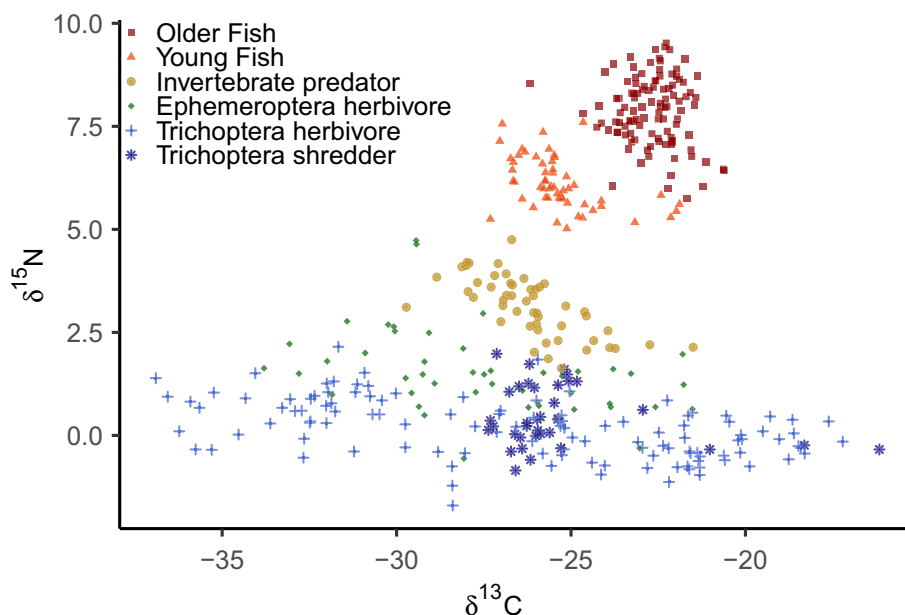


Fig. 6. A carbon–nitrogen bi-plot demonstrates that older fish are at a slightly higher trophic position than young fish, relative to baseline food sources (Ephemeroptera herbivores) and other invertebrates, leading to a longer food chain length where they are present in streams. Invertebrate predators include Odonates, Megaloptera, and Plecoptera. This plot includes data from both Fox and Elder Creek. Fish were sampled in 2014–2015. Invertebrates were sampled extensively in 1997–1999 to characterize seasonal variability in algal $\delta^{13}\text{C}$. The wide range of $\delta^{13}\text{C}$ for herbivores reflects season and spatial variation in algal $\delta^{13}\text{C}$ and variable reliance on algal and other food sources.

trophic position was lower. The trend of decreased food chain length in years when migratory genotypes dominated was the same, but not significant, for food chain length (Fig. 5f).

We predicted that low density of juvenile fish in resident regions would release aquatic macroinvertebrates, increasing their abundance. We did not find differences in the biomass nor the size of armored or unarmored benthic invertebrates below vs. above the waterfall in Elder Creek ($P > 0.05$ for all tests; Appendix S1: Fig. S3), despite differences in fish density and size structure between these regions.

DISCUSSION

Partial migration is a common form of intraspecific variation in nature. Previously explored migratory syndromes suggest that migration is linked with a suite of individual traits (Dingle and Drake 2007). We expand on

this body of work to highlight ecological implications of partial migration. We found that partial migration can have ecological effects at the population level (density and size structure of fish) and, to a lesser extent, community level (food chain length). In Elder Creek, in pools where migratory genotype fish dominated, juvenile densities were high and size structure was simple (many young fish). In contrast, in pools dominated by resident-genotype fish, densities of juvenile fish were lower and size structure was complex (both young and older fish). Because pools dominated by migratory genotypes were concentrated downstream of a waterfall, the pool-specific patterns in density and size structure resulted in reach-scale differences in density of young fish (twice as high below the waterfall than above) and size structure (simple, unimodal below the waterfall vs. complex, bimodal above). Mean trophic position of fish and food chain length, as indicated by increased $\delta^{15}\text{N}$ signatures, was slightly elevated in pools above the

waterfall, which were dominated by resident genotypes, but not enough to indicate the addition of a distinct new trophic level. In Fox Creek, fish with migratory genotypes dominated in two years, when passage at the mouth of the creek was possible, and fish with resident genotypes dominated in two other years. We found the same pattern that was manifest over space in Elder Creek was manifest over time in Fox Creek, such that, when migratory genotype fish dominated, juvenile densities were high, size structure was simple, and bottom-up trophic position of trout was lower.

Density in partially migratory populations

The spatial–temporal distributions of migratory vs. resident animals in partially migratory populations seem likely to generate variation in ecological dynamics. In our system, we found that high density of young fish was associated with migratory fish, a pattern that has been detected in other partially migratory populations of *O. mykiss* (McMillan et al. 2015) and salmonid fishes (e.g., *Salmo trutta*, Bohlin et al. 2001). Many aspects of salmonid population ecology are density-dependent; higher juvenile density reduces growth rates (Jenkins et al. 1999) but increases body size variation (Jacobson et al. 2015). In other species, seasonal differences in density associated with migratory individuals (pulsed, seasonal increase in densities) vs. resident individuals (year-round presence) can influence ecological dynamics. In grasslands, the continual presence of resident ungulates had a top-down effect on the regeneration rates and standing crop of forage vegetation, due to their continual, intense grazing pressure (Fryxell and Sinclair 1988). In lake ecosystems, the number of zooplanktivorous fish that migrate determines whether the lake enters a clear-water (phytoplankton-poor) vs. turbid-water (phytoplankton-dense) state (Brodersen et al. 2008).

Density-mediated ecological changes may be especially common in partially migratory populations where one life history form is associated with higher fecundity or reproductive success than the other. For some animals, migration leads to higher reproductive success (e.g., the giant tortoise, Swingland and Lessells 1979), and likewise an increase in the number of juveniles (e.g., white perch, Kerr et al. 2009). In

other systems, the resident form has higher reproductive success (e.g., red-spotted newts, Grayson et al. 2011). Another example comes from the American dipper (*Cinclus mexicanus*) where resident birds are more likely to have larger brood sizes or double brood than migrants (Gillis et al. 2008). Importantly, the relative reproductive success of migratory vs. resident individuals may change over time. For example, resident elk have higher rates of recruitment than migratory elk in Yellowstone National Park, USA, but the reproductive success of migratory elk may have recently declined due to changes in predation and habitat quality (Middleton et al. 2013).

Theoretical studies often cite density dependence as a cause, rather than a consequence, of migration (Kaitala et al. 1993, Taylor and Norris 2007, De Leenheer et al. 2017). This competitive release hypothesis, in which individuals migrate from high-density habitats to escape competition (Chapman et al. 2011), has considerable empirical support from birds (Nilsson et al. 2006), ungulates (Mysterud et al. 2011), and fishes (Olsson et al. 2006). In *O. mykiss* and other species, the two may be linked in a feedback loop such that migratory juveniles are present in a higher densities due to the increased fecundity of migratory adults, which then leads to higher competition and lower growth rates for juveniles (Grant and Imre 2005), encouraging migration via density dependence (Olsson et al. 2006). This possibility has yet to be explored, but density-dependent feedbacks on ecological dynamics have been shown in other contexts. For example, in the guppy *Poecilia reticulata*, guppies in low-predation environments differ in a suite of life history traits than those in high-predation environments, including higher densities (Reznick et al. 2001). Moreover, guppy density influences prey communities, standing stock of algal biomass, and decomposition rates in tropical streams (Bassar et al. 2010). The trophic effect of guppies then feeds back to influence the phenotype of guppies, such that the low predation phenotype is favored in high-density environments where food availability is low (Travis et al. 2014).

Body size in partially migratory populations

Most prior research on body size in partially migratory populations has focused on the effect

of body size on the decision to migrate or not (Chapman et al. 2011), including for our study subject, *O. mykiss* (Kendall et al. 2014). In some fish systems, larger individuals are more likely to migrate (e.g., bull trout, Monnot et al. 2008, and pelagic coregonids, Mehner and Kasprzak 2011). In birds, the body size-dependent migration is often linked to thermal tolerance hypothesis (Chapman et al. 2011), where smaller individuals migrate to avoid cold winters (Belthoff and Gauthreaux 1991), and larger individuals migrate to avoid hot summers (Alonso et al. 2009). However, size-biased migration has implications beyond the decision to migrate; it also influences the size structure of the remaining, resident population, which may then influence species interactions and community structure (Werner and Gilliam 1984). For example, the size structure differed above and below barriers to migration in white-spotted charr in Japan (Morita et al. 2009). Furthermore, migratory animals may be more subject to size selection along their movement pathway; for example, fish ladders can select for brown trout of intermediate body size (Haugen et al. 2008), and this may alter the size structure and reproductive potential of animals above and below these points. We did not measure the body size of migratory adults above and below the waterfall in our system, but this may have contributed to the change in densities that we observed, and could be a further topic of research.

Within anadromous fishes, including salmonids, migratory adults are larger at reproduction, but the resident form remains in freshwater and can become the largest consumer during freshwater rearing periods. In our system, these large resident fish become top predators. The mean difference in isotopic enrichment for large fish was less than the difference in trophic fractionation (3.4‰) expected if older fish were a full trophic level higher than young fish (Post 2002), suggesting that the diet of largest individuals overlapped with young fish in freshwater streams, but included more secondary consumers and young fish. Stable isotopes from fin tissue integrate diet information over <2 weeks for *O. mykiss* (Heady and Moore 2013), and so there may be a short time window, when fish are first emerging from the nest and are very vulnerable to predation, when there is an ephemeral

4-level food web. Diet changes throughout ontogeny of an organism are ubiquitous (Werner and Gilliam 1984, Post 2003), suggesting that body size-mediated diet changes in partially migratory populations may have at least transient effects on food web ecology.

Food web effects of partial migration

The $\delta^{15}\text{N}$ signatures suggested that large resident individuals fed higher in the food web, although by somewhat less than a full trophic level. This fractional change in food chain length (Higashi et al. 1989) did not drive a trophic cascade in our study streams. Top-down effects of juvenile *O. mykiss* have driven trophic cascades in sunny, mainstem pools of the South Fork Eel River nearby (Power 1990, Power et al. 2008), but environmentally contrasting with the shaded tributary streams we studied here (Elder and Fox creeks). In the tributaries, benthic macroinvertebrate abundance may be limited by primary productivity rather than predation, which is supported by the observation that algal blooms developed in Elder Creek following the removal of algivorous armored caddisflies (McNeely et al. 2007). Furthermore, steelhead in the tributaries may feed more heavily on terrestrial invertebrates, as suggested by isotopic data, particularly from reaches draining <10 km² (Finlay 2001, Tsui et al. 2014), and would therefore have less of an effect on the benthos than juvenile steelhead in the mainstem. Keeley and Grant (1997) found that larger salmonids include even the smallest items in their diet, which would reduce the strength of size selection on benthic macroinvertebrates by large fish, particularly in food limited, unproductive tributaries. In summary, trophic cascades are context dependent (Shurin et al. 2002), and it is unknown when partially migratory animals are most likely to drive top-down trophic cascades. Furthermore, partially migratory prey items may also drive bottom-up food web effects. For example, partial migration of prey fish can alter predator foraging behavior and food sources (Hansen et al. 2019). Future research could investigate when and where intraspecific variation of partial migration drives food web change, given that both prey and predators can be partially migratory.

CONCLUSIONS

Partial migration is a common form of intraspecific variation within migratory populations. Observations that resident and migratory individuals often differ in functional traits such as body size suggest that partial migration has implications for ecology. Our work demonstrates the consequences of partial migration for population and community ecology in a salmonid fish. Animal migration is on the decline globally (Wilcove and Wikelski 2008) as migrants are excluded from many habitats where they were historically present (Januchowski-Hartley et al. 2013, Beyer et al. 2016). This may tip the balance toward resident life histories in partially migratory populations (White et al. 2007), with many likely secondary effects for the ecology of these systems. Loss or restoration of migration in partially migratory populations may have ramifying ecological consequences well beyond the impacts on life history diversity of the focal population.

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DATA AVAILABILITY

Surveys for density of *O. mykiss*, macroinvertebrate samples, and isotopic data are available on Dryad Digital Repository: <https://doi.org/10.6078/d18t2s>. Genetic data and habitat data are available on the Dryad Digital Repository: <https://doi.org/10.6078/d1dm6g>. Raw sequence data are available at NCBI, SRA accession: PRJNA599015.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3044/full>