Body Size and Growth Rate Influence Emigration Timing of Oncorhynchus mykiss

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Published online: 02 Sep 2013.

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Abstract

Juvenile *Oncorhynchus mykiss* migrate extensively in freshwater during the fall. We used individual tagging to study the spatial origin, influences, and outcomes of fall migration on fish that emigrated from summer rearing tributaries during the fall (early emigrants) and those that did not (late emigrants) in the South Fork John Day River, Oregon. Fall migration amplified body size differences between early and late emigrants. There were more early emigrants from a lower-gradient stream than from a higher-gradient stream. Early emigration was positively related to individual summer growth rate and fall body size. *Oncorhynchus mykiss* dispersed downstream into higher-order streams during the fall. Early emigrants shifted to an alternative location and experienced significantly greater winter growth than did late emigrants that remained in tributaries. Early emigrants initiated smolt migration sooner the following spring than did late emigrants. Early and late emigration from the South Fork John Day River was associated with asynchronous emigrant-to-adult survival rates.

Stream fishes, including salmonids, can be highly mobile (Gowan et al. 1994; Kahler et al. 2001; Baxter 2002; Bramblett et al. 2002; Gowan and Fausch 2002; Roni et al. 2012). However, movement patterns are not uniform among streams nor among individuals (Northcote 1992). Patterns of movement vary among (Riddell and Leggett 1981) and within (Roni and Quinn 2001; Steingrímsson and Grant 2003; Roni et al. 2012) populations. Within a single population, there are both "movers" and "stayers" (Leider et al. 1986; Grant and Noakes 1987). This multiple behavior has been termed "partial migration" (Jonsson and Jonsson 1993).

Growth rate may influence which individuals become movers and which become stayers (McMillan et al. 2012). Movement can be a density-dependent response wherein smaller, less dominant individuals are forced to emigrate (Chapman 1962; Keeley 2001; Bujold et al. 2004; Imre et al. 2004; Griffiths et al. 2013). Conversely, dominant individuals may volitionally emigrate in search of higher levels of resources in alternative areas

(Armstrong et al. 1997; Roni and Quinn 2001; Gowan and Fausch 2002). In other instances, social hierarchies, growth rate, and condition factor may not appreciably influence which individuals emigrate (Riddell and Leggett 1981; Giannico and Healey 1998; Kahler et al. 2001). For instance, Riddell and Leggett (1981) observed different proportions of fall emigrants between two streams although growth rate and condition of Atlantic Salmon *Salmo salar* parr were similar between the streams. They theorized that higher fall emigration from one stream was an adaptive response to the higher gradient and cooler temperature in that stream. Similarly, Bjornn (1971) found fewer juvenile salmonids emigrated from experimental channels when large substrate was present, as opposed to small gravel substrate. Hence, the influence of abiotic factors may override biotic factors in some streams.

Anadromy complicates the study of local movement because anadromous salmonids will eventually smolt and migrate to the ocean. However, given this eventual migration, the timing and nature of individual migration in freshwater may still be influenced by biotic variables. For example, growth rate (Thorpe 1987a, 1987b; Thorpe and Metcalfe 1998; Cucherousset et al. 2005) and intraspecific competition (Chapman 1962; Huntingford et al. 1988) may influence seasonal migrations that occur prior to smoltification. The relative influence that biotic or environmental factors experienced during the summer have on later movement patterns, such as fall migration, remains unclear (Leider et al. 1986; Rodríguez 2002).

Fall migrations are a common seasonal behavior for anadromous salmonids (Bjornn 1971; Riddell and Leggett 1981; Roni et al. 2012). These migrations are often from low-order tributaries to higher-order streams. The locations selected for winter rearing influence growth and survival because higher-order streams are typically warmer, which may increase growth (Higgins 1985; Koskela et al. 1997; Morgan and Metcalfe 2001; Murphy et al. 2006) and decrease mortality (Smith and Griffith 1994). Additionally, the timing of smoltification may be advanced by an increased accumulation of degree-days (Zydlewski et al. 2005) in higher-order streams.

We studied population-scale and individual-scale migration of *Oncorhynchus mykiss* in the South Fork of the John Day River, Oregon. Our focus was on the movement patterns expressed by *O. mykiss* during the fall, as behavior during the fall influences survival in the upcoming winter stress period. We tested four hypotheses concerning "early emigrants" (defined herein as individuals that emigrated from summer habitat during October–December and migrated downstream to higher-order streams for winter) and "late emigrants" (defined herein as individuals that did not emigrate from summer habitat until after December). Our predictive hypotheses were that (1) the proportion of emigrants from a low-gradient creek differs from that of a high-gradient creek, (2) the growth rates during summer differ between individuals who subsequently expressed early-emigrant or late-emigrant patterns, (3) the winter growth rates differ between early and late emigrants, and

(4) the smolt migration timing differs between early and late emigrants.

METHODS

Study location.—The South Fork John Day River (SFJD) basin is a fifth-order watershed in northeast Oregon. Anadromy in the SFJD is limited by a waterfall at river kilometer (rkm; measured as distance above the river mouth) 45. We studied two tributaries downstream of this waterfall, Black Canyon and Murderers creeks, and the SFJD downstream from the confluence with Murderers Creek (Figure 1). These streams support a population of *Oncorhynchus mykiss* with both anadromous and nonanadromous life history forms. Mature nonanadromous *O. mykiss*, commonly referred to as Rainbow Trout, are present and rarely exceed 200 mm FL (McMillan et al. 2012). The anadromous form is commonly referred to as summer steelhead. Juvenile summer steelhead commonly spend 2 years in the SFJD (range: 1–4 years). Principal downstream migration periods for *O. mykiss* within the SFJD are fall (October–December) and spring (April–May). During 2003–2004, 36% of the total annual emigrants migrated during October–February and 64% migrated during February–June (Schultz et al. 2006). During late winter to early spring, juvenile summer steelhead undergo a physiological transformation referred to as "smolting," which facilitates migration to saltwater via the Columbia River. Migration through the Columbia River occurs from April through June. Steelhead spend one to two winters in the Pacific Ocean,
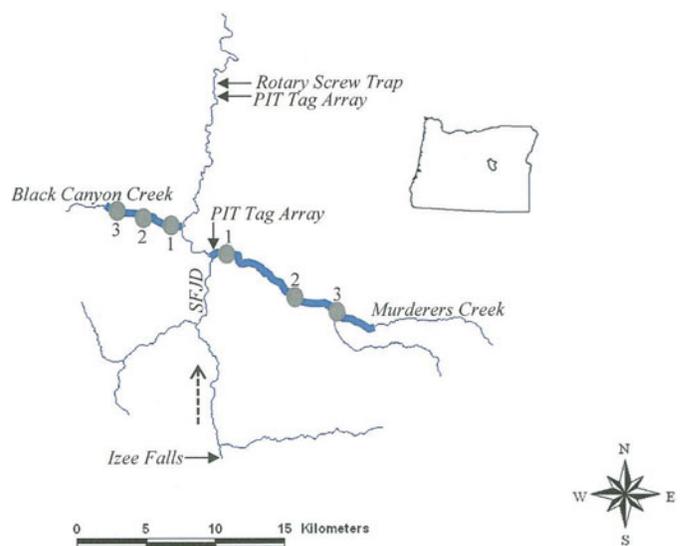
FIGURE 1. Map of the South Fork John Day River (SFJD) basin showing the location of the PIT tag arrays, rotary screw trap, and tributary sampling universe. Inset shows the location of the SFJD basin in Oregon. Dashed arrow denotes streamflow direction. *Oncorhynchus mykiss* were PIT-tagged throughout the sampling universe (highlighted portions) of Black Canyon and Murderers creeks during summer 2004 and 2005. Numbered circles denote sentinel reaches where capture–recapture of *O. mykiss* occurred during all seasons. [Figure available in color online.]

TABLE 1. Summary of *O. mykiss* tagged with PIT tags in Murderers and Black Canyon creeks during summer 2004 and summer 2005. Estimated survival (95% confidence interval in parentheses) to John Day Dam (JDD) represents the component of each tagging cohort which survived and initiated anadromous migration.

Location	Year	*n* tagged	FL at tagging (mm)			Survival to JDD
			Mean	Median	Range	
Murderers	2004	1,125	120	117	65–232	19% (16–21%)
Black Canyon	2004	1,203	113	109	63–224	16% (14–18%)
Murderers	2005	1,521	128	125	65–248	16% (15–18%)
Black Canyon	2005	1,449	113	109	62–229	13% (11–15%)

then reenter the Columbia River during July–September. Mature adult steelhead spend one winter in freshwater prior to migrating back to the SFJD and spawning from March–May. The two life history forms are visually indistinguishable with the exception of adult steelhead (FL of 500–800 mm), which are larger than the nonanadromous form. Since all fish we captured and tagged were <250 mm (Table 1) and may have been either form, we refer to all tagged individuals as *O. mykiss*. Of the *O. mykiss* that we captured and marked during our study, similar proportions of the individuals from Black Canyon and Murderers creeks ultimately migrated to the ocean based on our estimates of survival to John Day Dam on the Columbia River (Table 1; detection data from CBR 2012; survival estimates following Paulsen and Fisher 2001).

The environments of Black Canyon Creek, Murderers Creek, and the SFJD differed. Water temperatures in Black Canyon Creek ranged from 20°C during summer to 1°C during winter, with minimal ice formation. Water temperatures in Murderers Creek ranged from 26°C in summer to 0°C in winter, and surface ice (<20 cm thick) intermittently covered pools and glides. Stream temperatures in the SFJD were similar to Murderers Creek and ranged from 0°C during winter to 26°C during summer. Ice formation occurred only in shaded canyon sections. Stream flows in Black Canyon Creek ranged from 0.3 to 5.7 m³/s. Stream flows in Murderers Creek ranged from 0.07 m³/s during summer to 14.2 m³/s during winter. Stream flows in the SFJD ranged from 0.5 to 70.8 m³/s.

Capture and tagging.—Our sampling frame for Black Canyon and Murderers creeks was defined as the distance of each creek that we could logistically access (Figure 1). Within this sampling frame, we identified three distinct geomorphic valley segments in each creek (Frissell et al. 1986; Gregory et al. 1991). The Black Canyon Creek valley segments had gradients of 3.2, 4.8, and 5.7% (downstream to upstream). The Murderers Creek valley segments had gradients of 1.3, 0.8, and 1.3% (downstream to upstream). During summer 2004 and summer 2005, we systematically rotated sampling effort through each of these six valley segments. A starting channel unit within each valley segment was randomly selected for each day's sampling. We sampled upstream from the starting channel unit each day, and we sampled habitat units without replacement on subsequent visits to achieve the greatest spatial coverage possible

in each valley segment. In addition to our systematic summer capture and tagging, we randomly selected "sentinel reaches" within each of the six geomorphic valley segments. Sentinel reaches encompassed at least five pools and ranged in thalweg length from 99 to 363 m. They were sampled four times per year (June, September, December–January, March–April). The three sentinel reaches in each stream were labeled 1, 2, and 3 in ascending order proceeding upstream from the SFJD (Figure 1). As *O. mykiss* from Black Canyon and Murderers creeks emigrated into the SFJD during fall and winter, we sampled the SFJD during December–January and March–April. We captured *O. mykiss* at sites representative of available habitat to estimate winter growth rates in the lower SFJD.

Capture methods varied by season. During June and September, *O. mykiss* were captured via seining or electrofishing. During December–January and March–April we night snorkeled with handheld dive lights and dipnetted *O. mykiss*. Captured fish were anesthetized and scanned for the presence of a passive integrated transponder (PIT) tag. If they were not already tagged, a full-duplex PIT tag (12 × 2.02 mm, 134.2 kHz ISO; Digital Angel Corp., St. Paul, Minnesota) was injected into the peritoneal cavity (e.g., Prentice et al. 1990; PTSC 1999). We recorded FL (nearest mm) and location of capture (to the channel unit scale, i.e., pool- or riffle-specific). Fish were recovered and released into their channel unit of capture.

Recapture and redetection.—We used recaptures at sentinel reaches of Murderers and Black Canyon creeks to estimate seasonal growth rates for each valley segment. When *O. mykiss* migrated past rkm 10 of the SFJD, we used a 1.52-m-diameter rotary screw trap (RST; E.G. Solutions, Corvallis, Oregon; Figure 1) to capture them. We concurrently operated a PIT antenna array 80 m upstream of the RST to detect previously PIT-tagged individuals (Figure 1).

During fall 2005 (September 27 to December 27), we used an array of two PIT tag antennas separated by more than 100 m to detect *O. mykiss* emigrating from Murderers Creek. The array was located 0.9 km upstream of the SFJD (Figure 1). The Murderers Creek PIT array allowed us to determine the direction of movement and hence estimate the proportion of early emigrants from Murderers Creek independently of migration to the RST. The detection efficiency of the Murderers Creek PIT array was estimated to be 82%. Logistical constraints precluded us from

operating a PIT array on Black Canyon Creek. To avoid bias, we did not use data from the Murderers Creek PIT array and only used data from the RST and PIT array at rkm 10 of the SFJD (Figure 1) to compare the proportion of early emigrants between Murderers and Black Canyon creeks.

As *O. mykiss* migrated through the Columbia River, they had a probability of detection at fixed PIT arrays in John Day Dam (Columbia River rkm 347, 4 km downstream of the John Day River confluence; CBR 2012) and mobile PIT arrays in the Columbia River estuary (Columbia River rkm 75; Ledgerwood et al. 2004; CBR 2012). These detections provided migration timing for early-emigrant and late-emigrant individuals. We assumed detection probability did not differ between groups (early emigrant and late emigrant) within a year.

Statistical analyses.—We used z-tests to compare the proportions of *O. mykiss* migrating past the RST that had previously been PIT-tagged anywhere in the sampling frame of Murderers or Black Canyon creeks (Table 1 summarizes the tagged individuals used for these comparisons). Since the RST sub-sampled the total migrant population, we estimated capture efficiency of the RST via upstream release and recapture of marked *O. mykiss* (Tattam et al. 2013). We used these capture efficiencies to estimate the abundance of PIT-tagged *O. mykiss* passing the RST site. During periods when the RST was not operated, we used the PIT arrays (efficiency of the arrays was calibrated with captures at the RST during simultaneous operation) to estimate the abundance of PIT-tagged *O. mykiss* passing the RST site. After this calibration, which accounted for the influence of environmental variables on detection probability, we assumed equal detection probability at this site for PIT-tagged individuals emigrating from our two study streams.

We used logistic regression to analyze fall emigration from sentinel reaches in Murderers Creek during 2005. We only included individuals that were captured in both June and September ($n = 54$). Each PIT-tagged individual had a binary response of either early emigrant (migrated past the Murderers Creek PIT array during fall) or late emigrant (not detected at the array during fall). This response was modeled as a function of FL (measured in September), specific growth rate during summer (specific growth rates were calculated as mm·mm^{-1}·d^{-1}, and we hereafter refer to specific growth rate as "growth"), substrate index, pool depth, and stream geomorphic reach. Since the availability of winter concealment habitat may influence emigration rates (Bjornn 1971) in addition to FL and summer growth, we quantified concealment habitat of the closest downstream pool to each individual's location in September using maximum depth and substrate size. We visually estimated substrate size (sand–silt, gravel, cobble, boulder) and relative composition (dominant or subdominant). We assigned numeric values, increasing with particle size (1 for sand–silt to 4 for boulder), then a weighted sum $[(1.25 \cdot \text{dominant}) + (0.75 \cdot \text{subdominant})]$ was calculated for each pool. Higher scores indicated larger substrate and presumably better overwintering habitat. Prior to developing logistic regression models, we tested for correlation among explanatory variables. Fork length and growth were not correlated ($r = 0.06$, $P = 0.67$). There was evidence of a negative correlation between pool depth and substrate size ($r = -0.59$, $P = 0.02$). However, this relationship was dominated by one outlier and, when removed, there was no significant correlation ($r = -0.41$, $P = 0.15$). There were also no significant correlations between biotic (FL, growth) and abiotic (depth, substrate size) variables ($r < 0.25$, $P \geq 0.07$).

We jointly analyzed all three sentinel reaches in Murderers Creek. Significant serial autocorrelation was present among model residuals. We grouped individuals by channel unit and then by length and progressively increased each length grouping until no significant autocorrelation was present among residuals. Final FL categories were <130, 131–159, and >160 mm. This binomial logistic regression modeled the number of emigrants as a function of the number released in each group, as influenced by group means of each explanatory variable. We used Akaike information criterion (AICc) corrected for small sample size to identify models which best explained the data with the fewest parameters.

We compared growth for the period of December–January to March–April among reaches. We compared the Black Canyon and Murderers creeks sentinel reaches and one reach in the SFJD with one-way analysis of variance (ANOVA). We used Benjamini and Hochberg false discovery rate control with $\alpha = 0.05$ to control type-1 errors during multiple comparisons (Verhoeven et al. 2005).

Finally, we compared the detection date at John Day Dam of early-emigrant and late-emigrant *O. mykiss* from Murderers Creek. We used two-way ANOVA to test for differences in mean detection date between groups and between years. We used Pearson's correlation to evaluate the relationship between the detection date at John Day Dam and the detection date in the Columbia River estuary for *O. mykiss* from all tagging locations in the SFJD.

RESULTS

Prevalence of Early Emigration

We estimated that 13.2% and 11.5% of *O. mykiss* PIT-tagged in Murderers Creek migrated past rkm 10 of the SFJD during fall 2004 and fall 2005, respectively. An estimated 3.1% and 3.2% of individuals PIT-tagged in Black Canyon Creek were early emigrants during 2004 and 2005 (Figure 2). The percentage of *O. mykiss* emigrating from Murderers Creek was significantly greater than the percentage emigrating from Black Canyon Creek during both fall 2004 ($z = 9.0$, $P < 0.01$) and fall 2005 ($z = 8.6$, $P < 0.01$). The percentage emigrating during fall did not differ significantly between years within either Black Canyon ($z = 0.2$, $P = 0.42$) or Murderers creeks ($z = 1.3$, $P = 0.09$). Given the low percentage of early emigrants from Black Canyon Creek, we focused solely on Murderers Creek when examining potential correlates of fall emigration.
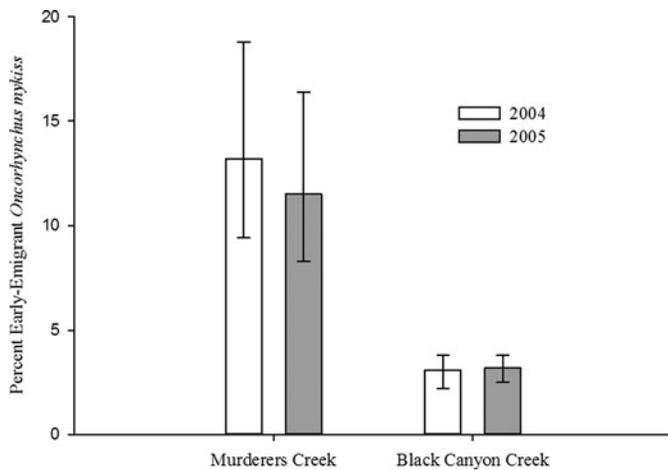
FIGURE 2. Percentage of early-emigrant *Oncorhynchus mykiss* from Black Canyon and Murderers creeks during 2004 and 2005. The abundance of early emigrants was estimated at a rotary screw trap in the South Fork John Day River (rkm 10). Error bars indicate 95% confidence intervals.

Correlates of Early Emigration

In Murderers Creek, our AICc selection identified three competing models (Table 2). All three competing models included FL and reach as explanatory variables. Two of the competing models included growth, in addition to FL and reach (Table 2). Inclusion of these three explanatory variables in at least one of the competing models indicated their significant association with early emigration. Explanatory variables describing physical habitat characteristics of Murderers Creek (pool depth and streambed particle size) were deemed not significant as they

TABLE 2. Model selection results for AICc analysis of early emigration from Murderers Creek. Explanatory variables evaluated were as follows: average FL, mean specific growth rate during summer (Growth), sentinel reach where tagged (Reach), pool depth, and streambed particle size. Models with a delta AICc of less than 5 and the null model are presented. The null model has no explanatory variables and serves as a check on the power of the explanatory variables. Multiplication signs indicate first order interactions.

Model	AICc	Delta AICc	Model weight
(FL) + (Growth) + (Reach) + (FL × Reach) + (Growth × Reach)	132.1	0.0	0.29
(FL) + (Growth) + (Reach) + (FL × Reach)	132.4	0.3	0.25
(FL) + (Reach) + (FL × Reach)	134.0	1.9	0.11
(FL) + (Growth) + (Reach)	134.7	2.6	0.08
(Growth) + (Reach) + (Growth × Reach)	135.0	2.9	0.07
(Growth) + (Reach)	135.1	3.0	0.07
(FL) + (Reach)	136.2	4.1	0.04
(Null)	165.1	33.0	0.00

were not included in any of our competing models (Table 2). Interaction terms for FL × reach and growth × reach were included in two of our competing models. The presence of these interaction terms in our competing models indicated that the influence of FL and growth on early emigration was spatially dependent in Murderers Creek. Larger individuals were less likely to become early emigrants from upstream reaches than from downstream reaches.

Outcome of Early Emigration

Early-emigrant and late-emigrant fish had differences in their growth rate during winter. We were unable to recapture PIT-tagged *O. mykiss* in reach 2 of Black Canyon Creek. Growth rates were significantly different among the remaining five reaches in Black Canyon Creek, Murderers Creek, and the SFJD ($F_{5, 41} = 26.7$, $P < 0.001$). Mean growth in the SFJD was significantly higher than mean growth in all other reaches, excepting reach 2 in Murderers Creek (Figure 3). Within Murderers Creek, reaches 1 and 2 were both significantly different from reach 3 (Figure 3). There were no significant differences in growth among reaches 1 and 3 in Black Canyon Creek and reach 3 in Murderers Creek (Figure 3).

Early emigration from Murderers Creek was associated with differences in smolt migration timing at John Day Dam. Smolt timing was dependent on whether smolts were early emigrants or late emigrants, where early emigrants arrived significantly sooner at John Day Dam ($F_{1, 132} = 17.3$, $P < 0.001$). Migration timing of each group did not differ between years ($F_{1, 132} = 0.6$, $P = 0.44$) and there was no interaction between life history and year ($F_{1, 132} = 0.4$, $P = 0.54$). In the spring of 2005, mean detection date at John Day Dam for early emigrants (May 3) was significantly earlier ($F_{1, 132} = 3.9$, $P = 0.05$; Figure 4)
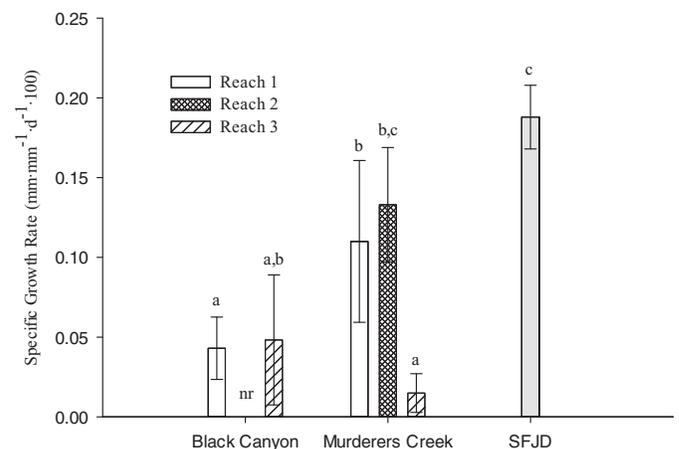

FIGURE 3. Comparison of mean specific growth rates during winter 2005 among five reaches in Murderers and Black Canyon creeks and one reach in the South Fork John Day River (SFJD). *Oncorhynchus mykiss* were individually marked in December 2004 and recaptured in late March 2005. Letters shared among bars indicate reaches that were not significantly different. Error bars indicate 95% confidence intervals and "nr" indicates that no recoveries of individually marked fish occurred in this reach.
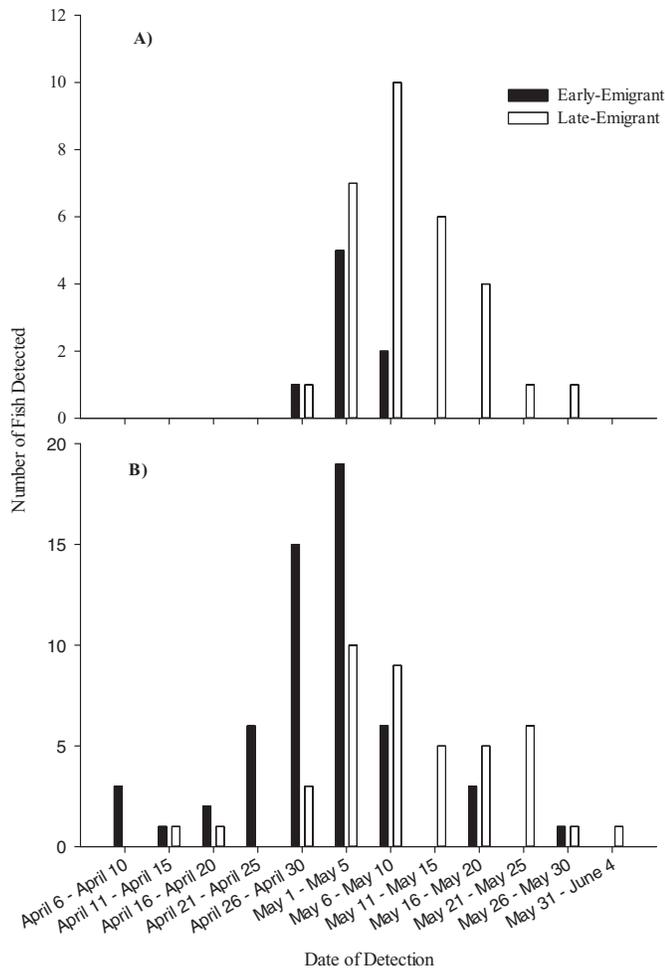
FIGURE 4. Frequency of detection of early-emigrant and late-emigrant *Oncorhynchus mykiss* at John Day Dam on the Columbia River (rkm 347) detected out-migrating during (**A**) spring 2005 and (**B**) spring 2006. Date of detection intervals are shared between panels.

than for late emigrants (May 10). During spring 2006, mean detection dates also differed significantly ($F_{1, 132} = 27.4$, $P < 0.001$) between early emigrants (April 30) and late emigrants (May 10; Figure 4). The detection date in the Columbia River estuary was significantly correlated with the detection date at John Day Dam during 2005 ($r = 0.92$, $P < 0.001$, $n = 13$) and 2006 ($r = 0.99$, $P < 0.001$, $n = 12$).

DISCUSSION

The percentage of *O. mykiss* adopting an early-emigrant strategy differed between our two study streams. The odds of early emigration were associated with fish size and growth during the preceding summer. Fewer individuals in Black Canyon Creek became early emigrants than in Murderers Creek. The parentage of tagged individuals may have influenced our results. We did not determine the parentage (resident or anadromous) of the *O. mykiss* that we tagged. Otolith sampling within our study

reaches in these two streams has since indicated that *O. mykiss* were predominantly of anadromous maternal origin (Mills et al. 2012). Maturity sampling in these same reaches indicated that mature resident males were present (McMillan et al. 2012). Although our data cannot distinguish residency from mortality, our lifetime tracking of tagged individuals (Table 1) suggests that an approximately equal percentage of the individuals in each creek ultimately expressed anadromy. Our results demonstrated that, in two streams which had a comparable percentage of anadromous individuals, fish size and growth rates influenced short-term migration patterns.

Our observation of lower emigration rates from higher-gradient reaches differs from that of Riddell and Leggett (1981). Differences in stream temperature and growth potential may explain why a higher proportion of PIT-tagged fish emigrated from low-gradient than high-gradient reaches. Our lower-gradient stream (Murderers Creek) had the coldest winter stream temperatures, which was the inverse of what Riddell and Leggett (1981) observed. They also observed comparable growth rates between streams of differing gradient. However, we found individual summer growth rate was significantly greater in low-gradient Murderers Creek reaches than in high-gradient Black Canyon Creek (I. A. Tattam, unpublished data). Lower growth rates in Black Canyon Creek possibly allowed fewer individuals to reach length or growth thresholds (Metcalfe et al. 1988; Metcalfe 1998) needed to increase their odds of early emigration (Cucherousset et al. 2005). Additionally, McMillan et al. (2012) observed that *O. mykiss* in Black Canyon Creek had higher lipid levels than those in Murderers Creek. Individuals in Murderers Creek appear to be investing in length growth rather than lipid storage (McMillan et al. 2012). Greater fish size and growth in Murderers Creek likely contributed to a higher proportion of individuals becoming early emigrants. Alternatively, our lower-gradient valley segments in Murderers Creek may have had higher sedimentation rates, which reduced interstitial concealment habitat (Cunjak 1996) and hence increased early emigration (Bjornn 1971). However, our regression modeling suggests that FL and growth had greater influence on early emigration than the habitat metrics that we measured. We suggest that individual growth rate, and not stream gradient, was the principal driver of higher early emigration from Murderers Creek than Black Canyon Creek.

Higher growth rates are typically associated with individuals that are more "dominant" in the social hierarchy (Metcalfe et al. 1992). The notion that dominant individuals emigrated from Murderers Creek instead of subdominant individuals seemingly contradicts typical experimental results (Chapman 1962; Keeley 2001; Bujold et al. 2004; Imre et al. 2004). When viewed in the context of partial migration, however, our results become more coherent. Variation in growth rates influences life history (Metcalfe 1998) and in Atlantic Salmon populations this is manifested in "upper-modal" and "lower-modal" groups. Upper-modal individuals are prompted to begin smolting in late summer or early fall, whereas lower-modal individuals may not be

prompted to smolt until the following spring (Huntingford et al. 1988; Whitesel 1993; Jonsson et al. 1998). Similarly, individual Brown Trout *Salmo trutta* (Cucherousset et al. 2005) and Brook Trout *Salvelinus fontinalis* (Morinville and Rasmussen 2003) with a higher metabolic demand that could not be sustained in small streams emigrated to larger rivers. Chapman et al. (2011) proposed a "fasting endurance hypothesis" to explain why larger individuals with higher energy requirements undertake seasonal migrations. The faster-growing (as measured by FL) individuals in Murderers Creek likely had a greater metabolic demand during fall as a result of having invested their energy into length growth rather than lipid storage. During the fall–winter transition, we suggest that the faster-growing individuals did not have sufficient fasting endurance (Chapman et al. 2011) to remain in Murderers Creek through winter and hence adopted an early-emigrant strategy.

Early emigration compounded the phenotypic differences that existed between early-emigrant and late-emigrant *O. mykiss* at the beginning of fall. The initially larger and faster-growing early emigrants subsequently experienced higher growth during winter. Thus, size differences between groups likely further diverged following emigration. Some of the early emigrants from Murderers Creek migrated downstream of our RST. We tracked the migration and winter holding locations of some of these individuals with surgically implanted radio transmitters. Most individuals migrated less than 20 km downstream of the RST to winter rearing areas (Tattam, unpublished data). We were not able to recapture and measure these early emigrants immediately prior to smoltification for comparison with late emigrants. Nonetheless, our data suggest that early emigrants attained a larger size at smoltification, which may facilitate greater marine survival (Bilton et al. 1982; Ward et al. 1989; Tipping 1997). Future fish tagging should focus on following the potential effect of increased length on smolt-to-adult survival by recapturing tagged individuals at sampling facilities in Columbia River hydropower dams.

Differential smolt arrival timing at the Columbia River estuary could be traced back to expression of either early-emigrant or late-emigrant behavior 5–8 months earlier. Physical conditions and biotic communities in the estuary vary on a daily basis (Weitkamp et al. 2012). Likewise, ocean conditions can vary at short time scales and peak marine survival rates can occur at different ocean entry times in different years (Lundqvist et al. 1994). We hypothesize that fall migration patterns ultimately manifest in different smolt-to-adult survival rates between early-emigrant and late-emigrant groups. This may create differential parr-to-adult recruitment between tributaries based on the prevalence of fall emigration. In the case of our study streams, Murderers Creek will have a greater proportion of smolts with early ocean entry than Black Canyon Creek. Early ocean entry may be advantageous during some years and disadvantageous during other years (Muir et al. 2006). Early emigrants (and hence early ocean entry smolts) from the SFJD had higher survival (measured from the SFJD to adult detection at Bonneville Dam) during 2005 ocean entry but lower survival during 2006 ocean entry (Wilson et al. 2008).

Conclusions

Fall emigration does not appear to be a fixed strategy but rather a facultative tactic in response to the constraints of the rearing environment. Although early emigrants grow faster, and presumably reach a larger size at smoltification, this life history strategy is not exclusively expressed in the population. Interannual variation in marine survival, associated with ocean entry timing differences between early-emigrant and late-emigrant individuals, likely creates asynchronous productivity between these life histories (Hilborn et al. 2003) and prevents any single life history from establishing population-level dominance. Thus, although emigration choice operates at the individual level, the presence of both early and late emigrants increases the resilience of the population to changing environmental conditions. Monitoring should estimate the abundance of both life histories, with their relative contribution to the population as a whole being an important indicator of viability. Identification and protection of all habitats (both summer and winter rearing habitat) utilized by both life histories will also be an important management action.

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