1   Body Size and Growth Rate Influence Emigration Timing of *Oncorhynchus mykiss*

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3   Ian A. Tattam[*1]

4   Oregon Cooperative Fishery Research Unit, Department of Fisheries and Wildlife, 104 Nash

5   Hall, Oregon State University, Corvallis, OR 97331

6   James R. Ruzycki

7   Oregon Department of Fish and Wildlife, 203 Badgley, EOU, One University Boulevard,

8   LaGrande, OR 97850

9   Hiram W. Li

10   Oregon Cooperative Fishery Research Unit, Oregon State University

11   Guillermo R. Giannico

12   Department of Fisheries and Wildlife, Oregon State University

13

14

15   [*]Corresponding Author: Ian.A.Tattam@state.or.us

16   [1]Present Address: Oregon Department of Fish & Wildlife, P.O. Box 9, John Day, OR 97845

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Abstract

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19   Juvenile *Oncorhynchus mykiss* migrate extensively in freshwater during fall. We used

20   individual tagging to study the spatial origin, influences, and outcomes of fall migration on fish

21   that emigrated from summer rearing tributaries during fall (early-emigrants) and those that did

22   not (late-emigrants) in the South Fork John Day River, Oregon. Fall migration amplified body

23   size differences between early and late-emigrants. There were more early-emigrants from a

24   lower gradient stream than from a higher gradient stream. Early-emigration was positively

25   related to individual summer growth rate and fall body size. *Oncorhynchus mykiss* dispersed

26   downstream into higher order streams during fall. Early-emigrants shifted to an alternative

27   location and experienced significantly greater winter growth compared to late-emigrants that

28   remained in tributaries. Early-emigrants initiated smolt migration sooner the following spring

29   than late-emigrants. Early and late-emigration from the South Fork John Day was associated

30   with asynchronous emigrant-to-adult survival rates.

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Introduction

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33   Stream fishes, including salmonids, can be highly mobile (Gowan et al. 1994; Kahler et

34   al. 2001; Baxter 2002; Bramblett et al. 2002; Gowan and Fausch 2002; Roni et al. 2012).

35   However, movement patterns are not uniform among streams nor individuals (Northcote 1992).

36   Patterns of movement vary among (Riddell and Leggett 1981) and within (Roni and Quinn 2001;

37   Steingrimmson and Grant 2003; Roni et al. 2012) populations. Within a single population, there

38   are both "movers" and "stayers" (Leider et al. 1986; Grant and Noakes 1987). This multiple

39   behavior has also been termed "partial migration" (Jonsson and Jonsson 1993).

40   Growth rate may influence which individuals become movers and which become stayers

41   (McMillan et al. 2012). Movement can be a density dependent response wherein smaller, less

42   dominant individuals are forced to emigrate (Chapman 1962; Keeley 2001; Bujold et al. 2004;

43   Imre et al. 2004; Griffiths et al. 2013). Conversely, dominant individuals may volitionally

44   emigrate in search of higher levels of resources in alternative areas (Armstrong et al. 1997; Roni

45   and Quinn 2001; Gowan and Fausch 2002). In other instances, social hierarchies, growth rate,

46   and condition factor may not appreciably influence which individuals emigrate (Riddell and

47   Leggett 1981; Giannico and Healey 1998; Kahler et al. 2001). For instance, Riddell and Leggett

48   (1981) observed different proportions of fall emigrants between two streams although growth

49   rate and condition of Atlantic salmon parr were similar between streams. They theorized that

50   higher fall emigration from one stream was an adaptive response to the higher gradient and

51   cooler temperature in that stream. Similarly, Bjornn (1971) found fewer juvenile salmonids

52   emigrated from experimental channels when large substrate was present, as opposed to small

53   gravel substrate. Hence, the influence of abiotic factors may override biotic factors in some

54   streams.

55   Anadromy complicates the study of local movement because anadromous salmonids will

56   eventually smolt and migrate to the ocean. However, given this eventual migration, the timing

57   and nature of individual migration in freshwater may still be influenced by biotic variables. For

58   example; growth rate (Thorpe 1987a, 1987b; Thorpe and Metcalfe 1998; Cucherousset et al.

59   2005) and intraspecific competition (Chapman 1962; Huntingford et al. 1988) may influence

60   seasonal migrations which occur prior to smoltification. The relative influence that biotic or

61   environmental factors experienced during summer have on later movement patterns, such as fall

62   migration, remains unclear (Leider et al. 1986; Rodriguez 2002).

63   Fall migrations are a common seasonal behavior for anadromous salmonids (Bjornn

64   1971; Riddell and Leggett 1981; Roni et al. 2012). These migrations are often from low-order

65   tributaries to higher-order streams. Locations selected for winter rearing influence growth and

66   survival because higher order streams are typically warmer, which may increase growth (Higgins

67   1985; Koskela et al. 1997; Morgan and Metcalfe 2001; Murphy et al. 2006) and decrease

68   mortality (Smith and Griffith 1994). Additionally, timing of smoltification may be advanced by

69   increased accumulation of degree-days (Zydlewski et al. 2005) in higher order streams.

70   We studied population-scale and individual-scale migration of *Oncorhynchus mykiss* in

71   the South Fork of the John Day River, Oregon. Our focus was on the movement patterns

72   expressed by *O. mykiss* during fall, as behavior during fall influences survival in the upcoming

73   winter stress period. We tested four hypotheses concerning "early-emigrant" (defined herein as

74   individuals which emigrated from summer habitat during October-December and migrated

75   downstream to higher-order streams for winter) and "late-emigrant" (defined herein as

76   individuals which did not emigrate from summer habitat until after December) individuals. Our

77   predictive hypotheses were that: *i*) the proportion of emigrants from a low-gradient creek differs

78   from a high-gradient creek; *ii*) growth rates during summer differ between individuals who

79   subsequently expressed early-emigrant or late-emigrant patterns; *iii*) winter growth rates differ

80   between early and late-emigrants; *iv*) smolt migration timing differs between early and late-

81   emigrants.

<div align="center">**Methods**</div>

83   *Study Location*

84   The South Fork John Day River basin (SFJD) is a fifth-order watershed in northeast

85   Oregon. Anadromy in the SFJD is limited by a waterfall at rkm 45. We studied two tributaries

86   downstream of this waterfall, Black Canyon and Murderers creeks, and the SFJD downstream

87   from the confluence with Murderers Creek (Figure 1). These streams support a population of

88   *Oncorhynchus mykiss* with both anadromous and non-anadromous life-history forms. Mature

89   non-anadromous *O. mykiss* are present and rarely exceed 200 mm fork length (FL, McMillan et

90   al. 2012). The anadromous form is commonly referred to as summer steelhead. Juvenile

91   summer steelhead commonly spend two years in the SFJD (range: 1–4), after which they

92   undergo a physiological transformation referred to as "smolting" which facilitates migration to

93   saltwater via the Columbia River. Migration through the Columbia River occurs from April

94   through June. Steelhead spend 1–2 winters in the Pacific Ocean, then re-enter the Columbia

95   River during July-September. Mature adult steelhead spend one winter in freshwater prior to

96   migrating back to the SFJD and spawning from March-May. The two life-history forms are

97   visually indistinguishable with the exception of adult steelhead (due to their FL of 500–800 mm).

98   Since all fish we captured and tagged were < 250 mm (Table 1) and may have been either form,

99   we refer to all tagged individuals as *O. mykiss*. Of the *O. mykiss* that we captured and marked

100   during our study, similar proportions of the individuals from Black Canyon and Murderers

101 creeks ultimately migrated to the ocean based on our estimates of survival to John Day Dam on

102 the Columbia River (Table 1; detection data from DART 2012; survival estimates following

103 Paulsen and Fisher 2001). Principal downstream migration periods for *O. mykiss* in the SFJD are

104 fall (October-December), and spring (April-May). During 2003–2004, 36% of the total annual

105 emigrants migrated during October-February, and 64% during February-June (Schultz et al.

106 2006).

107   The environments of Black Canyon Creek, Murderers Creek, and the SFJD differed.

108 Water temperatures in Black Canyon ranged from 20°C during summer to 1°C during winter,

109 with minimal ice formation. Water temperatures in Murderers Creek ranged from 26°C in

110 summer to 0°C in winter and surface ice $\leq$ 20 cm thickness intermittently covered pools and

111 glides. Stream temperatures in the SFJD were similar to Murderers Creek and ranged from 0°C

112 during winter to 26°C during summer. Ice formation occurred only in shaded canyon sections.

113 Stream flows in Black Canyon Creek ranged from 0.3–5.7 m³/s. Stream flows in Murderers

114 Creek ranged from 0.07 m³/s during summer to 14.2 m³/s during winter. Stream flows in the

115 SFJD ranged from 0.5–70.8 m³/s.

116 *Capture and Tagging*

117   Our sampling frame for Black Canyon and Murderers creeks was defined as the distance

118 of each creek that we could logistically access (Figure 1). Within this sampling frame we

119 identified three distinct geomorphic valley segments in each creek (Frissell et al. 1986; Gregory

120 et al. 1991). The Black Canyon valley segments had gradients of 3.2%, 4.8%, and 5.7%

121 (downstream to upstream). The Murderers Creek valley segments had gradients of 1.3%, 0.8%,

122 and 1.3% (downstream to upstream). During summer 2004 and summer 2005 we systematically

123 rotated sampling effort through each of these six valley segments. A starting channel unit within

124   each valley segment was randomly selected for each day's sampling. We sampled upstream

125   from the starting channel unit each day, and sampled habitat units without replacement on

126   subsequent visits to achieve the greatest spatial coverage possible in each valley segment. In

127   addition to our systematic summer capture and tagging, we randomly selected "sentinel reaches"

128   within each of the six geomorphic valley segments. Sentinel reaches encompassed at least five

129   pools, ranged in thalweg length from 99–363 m, and were sampled four times per year (June,

130   September, December/January, March/April). The three sentinel reaches in each stream were

131   labeled "one", "two", and "three" in ascending order proceeding upstream from the SFJD

132   (Figure 1). As *O. mykiss* from Black Canyon and Murderers creek emigrated into the SFJD

133   during fall and winter, we sampled the SFJD during December/January and March/April. We

134   captured *O. mykiss* at sites representative of available habitat to estimate winter growth rates in

135   the lower SFJD.

136   Capture methods varied by season. During June and September, *O. mykiss* were captured

137   via seining or electrofishing. During December/January and March/April we night snorkeled

138   with handheld dive lights and dip-netted *O. mykiss*. Captured fish were anesthetized, scanned for

139   the presence of a Passive Integrated Transponder (PIT) tag, and if not already tagged, a full-

140   duplex PIT tag (12 · 2.02 mm, 134.2 kHz ISO; Digital Angel Corp., St. Paul, MN) was injected

141   into the peritoneal cavity (e.g., Prentice et al. 1990, PTSC 1999). We recorded FL (nearest mm)

142   and location of capture (to the channel unit scale, i.e., pool or riffle specific). Fish were

143   recovered and released into their channel unit of capture.

144   *Recapture and Redetection*

145   We used recaptures at sentinel reaches of Murderers and Black Canyon creeks to estimate

146   seasonal growth rates for each valley segment. When *O. mykiss* migrated past rkm 10 of the

147   SFJD, we used a 1.52 m diameter rotary screw trap (RST, E.G. Solutions Inc., Corvallis, OR,

148   Figure 1) to capture them. We concurrently operated a PIT antenna array 80 m upstream of the

149   RST to detect previously PIT tagged individuals (Figure 1).

150   During fall 2005 (September 27 to December 27), we used an array of two PIT tag

151   antennas separated by >100 m to detect *O. mykiss* emigrating from Murderers Creek. The array

152   was located 0.9 km upstream of the SFJD (Figure 1). The Murderers Creek PIT array allowed us

153   to estimate the proportion of early-emigrants from Murderers Creek independently of migration

154   to the RST. The inclusion of two parallel arrays allowed us to determine the direction of

155   movement. The detection efficiency of the Murderers Creek PIT array was estimated to be 82%.

156   Logistical constraints precluded us from operating a PIT array on Black Canyon Creek. To

157   avoid bias, we did not use data from the Murderers Creek PIT array and only used data from the

158   RST and PIT array at rkm 10 of the SFJD (Figure 1) to compare the proportion of early-

159   emigrants between Murderers and Black Canyon creeks.

160   As *O. mykiss* migrated through the Columbia River, they had a probability of detection at

161   fixed PIT arrays in John Day Dam (Columbia River km 347, 4 km downstream of the John Day

162   River confluence, DART 2012), and mobile PIT arrays in the Columbia River estuary (Columbia

163   River km 75; Ledgerwood et al. 2004, DART 2012). These detections provided migration

164   timing for early-emigrant and late-emigrant individuals. We assumed detection probability did

165   not differ between groups (early-emigrant and late-emigrant) within a year.

166   *Statistical Analyses*

167   We used z-tests to compare the proportions of *O. mykiss* migrating past the RST which

168   had previously been PIT tagged anywhere in the sampling frame of Murderers or Black Canyon

169   creeks (Table 1 summarizes the tagged individuals used for these comparisons). Since the RST

170   sub-sampled the total migrant population, we estimated capture efficiency of the RST via

171   upstream release and recapture of marked *O. mykiss* (Tattam et al. 2013). We used these capture

172   efficiencies to estimate abundance of PIT tagged *O. mykiss* passing the RST site. During periods

173   when the RST was not operated, we used the PIT arrays (efficiency of the arrays was calibrated

174   with captures at the RST during simultaneous operation) to estimate abundance of PIT tagged *O.*

175   *mykiss* passing the RST site.

176   We used logistic regression to analyze fall emigration from sentinel reaches in Murderers

177   Creek during 2005. We only included individuals that were captured in both June and

178   September (n = 54). Each PIT-tagged individual had a binary response of either: early-emigrant

179   (migrated past the Murderers Creek PIT array during fall), or late-emigrant (not detected at the

180   array during fall). This response was modeled as a function of FL (measured in September),

181   specific growth rate during summer (specific growth rates were calculated as: mm·mm^{-1}·d^{-1}, and

182   we hereafter refer to specific growth rate as "growth"), substrate index, pool depth, and stream

183   geomorphic reach. Since the availability of winter concealment habitat may influence

184   emigration rates (Bjornn 1971) in addition to FL and summer growth, we quantified concealment

185   habitat of the closest downstream pool to each individual's location in September using

186   maximum depth and substrate size. We visually estimated substrate size (sand/silt, gravel,

187   cobble, boulder) and relative composition (dominant or subdominant). We assigned numeric

188   values, increasing with particle size (1 for sand/silt to 4 for boulder), then a weighted sum ((1.25

189   · dominant) + (0.75 · subdominant)) was calculated for each pool. Higher scores indicated larger

190   substrate and presumably better overwintering habitat. Prior to developing logistic regression

191   models, we tested for correlation among explanatory variables. FL and growth were not

192   correlated (r = 0.06, P = 0.67). There was evidence of a negative correlation between pool depth

193   and substrate size (r = -0.59, P = 0.02). However, this relationship was dominated by one outlier,

194   and when removed, there was no significant correlation (r = -0.41, P = 0.15). There were also no

195   significant correlations between biotic (FL, growth) and abiotic (depth, substrate size) variables

196   (r < 0.25, P ≥ 0.07).

197   We jointly analyzed all three sentinel reaches in Murderers Creek. Significant serial

198   autocorrelation was present among model residuals. We grouped individuals by channel unit and

199   then by length and progressively increased each length grouping until no significant

200   autocorrelation was present among residuals. Final FL categories were ≤ 130, 131–159, and

201   ≥160 mm. This binomial logistic regression modeled the number of emigrants as a function of

202   the number released in each group, as influenced by group means of each explanatory variable.

203   We used small-sample corrected Akaike Information Criterion (AICc) to select a model which

204   explained the greatest amount of variation with the fewest parameters.

205   We compared growth for the December/January-March/April period among reaches. We

206   compared the Black Canyon and Murderers creeks sentinel reaches and one reach in the SFJD

207   with one-way ANOVA. We used Benjamini and Hochberg false discovery rate control with α =

208   0.05 to control type-1 errors during multiple comparisons (Verhoeven et al. 2005).

209   Finally, we compared detection date at John Day Dam of early-emigrant and late-

210   emigrant *O. mykiss* from Murderers Creek. We used two-way ANOVA to test for differences in

211   mean detection date between groups and between years. We used Pearson correlation to

212   evaluate the relationship between detection date at John Day Dam and detection date in the

213   Columbia River estuary for *O. mykiss* from all tagging locations in the SFJD.

214   **Results**

215   *Prevalence of Early-Emigration*

216   We estimated that 13.2% and 11.5% of *O. mykiss* PIT tagged in Murderers Creek

217   migrated past rkm 10 of the SFJD during fall 2004 and fall 2005, respectively. An estimated

218   3.1% and 3.2% of individuals PIT tagged in Black Canyon Creek were early-emigrants during

219   2004 and 2005 (Figure 2). The percentage of *O. mykiss* emigrating from Murderers Creek was

220   significantly greater than the percentage emigrating from Black Canyon Creek during both fall

221   2004 ($z = 9.0$, $P < 0.01$) and fall 2005 ($z = 8.6$, $P < 0.01$). The percentage emigrating during fall

222   did not differ significantly between years within either Black Canyon ($z = 0.2$, $P = 0.42$) or

223   Murderers creeks ($z = 1.3$, $P = 0.09$). Given the low percentage of early-emigrants from Black

224   Canyon Creek, we focused solely on Murderers Creek when examining potential correlates of

225   fall emigration.

226   *Correlates of Early-Emigration*

227   In Murderers Creek, our AICc selection identified three competing models (Table 2). All

228   three competing models included FL and reach as explanatory variables. Two of the competing

229   models included growth, in additions to FL and reach (Table 2). Inclusion of these three

230   explanatory variables in at least one of the competing models indicated their significant

231   association with early-emigration. Explanatory variables describing physical habitat

232   characteristics of Murderers Creek (pool depth and streambed particle size) were deemed not

233   significant as they were not included in any of our competing models (Table 2).   Interaction

234   terms for FL·reach, and growth·reach were included in two of our competing models. The

235   presence of these interaction terms in our competing models indicated that the influence of FL

236   and growth on early-emigration was spatially dependent in Murderers Creek. Larger individuals

237   were less likely to become early-emigrants from upstream reaches than from downstream

238   reaches.

239   *Outcome of Early-Emigration*

240   Early-emigrant and late-emigrant fish had differences in growth rate during winter. We

241   were unable to recapture PIT-tagged *O. mykiss* in reach 2 of Black Canyon Creek. Growth rates

242   were significantly different among the remaining five reaches in Black Canyon Creek, Murderers

243   Creek, and the SFJD ($F_{5,41} = 26.7$, $P < 0.001$). Mean growth in the SFJD was significantly higher

244   than mean growth in all other reaches, excepting reach two in Murderers Creek (Figure 3).

245   Within Murderers Creek, reaches one and two were both significantly different from reach three

246   (Figure 3). There were no significant differences in growth among reaches one and two in Black

247   Canyon Creek, and reach three in Murderers Creek (Figure 3).

248   Early-emigration from Murderers Creek was associated with differences in smolt

249   migration timing at John Day Dam. Smolt timing was dependent on whether smolts were early-

250   emigrants or late-emigrants, where early-emigrants arrived significantly sooner at John Day Dam

251   ($F_{1,132} = 17.3$, $P < 0.001$). Migration timing of each group did not differ between years ($F_{1,132} =$

252   0.6, $P = 0.44$) and there was no interaction between life history and year ($F_{1,132} = 0.4$, $P = 0.54$).

253   In the spring of 2005, mean detection date at John Day Dam for early-emigrants (May 3) was

254   significantly earlier ($F_{1,132} = 3.9$, $P = 0.05$, Figure 4) than for late-emigrants (May 10). During

255   spring 2006, mean detection dates also differed significantly ($F_{1,132} = 27.4$, $P < 0.001$) between

256   early-emigrants (April 30) and late-emigrants (May 10; Figure 4). Detection date in the

257   Columbia River estuary was significantly correlated with detection date at John Day Dam during

258   2005 ($r = 0.92$, $P < 0.001$, $n = 13$) and 2006 ($r = 0.99$, $P < 0.001$, $n = 12$).

259   **Discussion**

260   The percentage of *O. mykiss* adopting an early-emigrant strategy differed between our

261   two study streams. The odds of early-emigration were associated with fish size and growth

262 during the preceding summer. Fewer individuals in Black Canyon Creek became early-

263 emigrants than in Murderers Creek. The parentage of tagged individuals may have influenced

264 our results. We did not determine the parentage (resident or anadromous) of the *O. mykiss* that

265 we tagged. Otolith sampling in these two streams has since observed that *O. mykiss* were

266 predominantly of anadromous maternal origin (Mills et al. 2012), but mature resident males were

267 also present (McMillan et al. 2012). Although our data cannot distinguish residency from

268 mortality, our life-time tracking of tagged individuals (Table 1) suggests an approximately equal

269 percentage of the individuals in each creek ultimately expressed anadromy. Our results

270 demonstrated that, in two streams which had a comparable percentage of anadromous

271 individuals, fish size and growth rates influenced short-term migration patterns.

272 Our observation of lower emigration rates from higher gradient reaches differs from that

273 of Riddell and Leggett (1981). Differences in stream temperature and growth potential may

274 explain why a higher proportion of PIT tagged fish emigrated from low gradient versus high

275 gradient reaches. Our lower gradient stream (Murderers Creek) had the coldest winter stream

276 temperatures, which was the inverse of what Riddell and Leggett (1981) observed. They also

277 observed comparable growth rates between streams of differing gradient, however, we found

278 individual summer growth rate was significantly greater in low-gradient Murderers Creek

279 reaches than in high-gradient Black Canyon Creek (I. Tattam, unpublished data). Lower growth

280 rates in Black Canyon possibly allowed fewer individuals to reach length or growth thresholds

281 (Metcalfe et al. 1988; Metcalfe 1998) needed to increase their odds of early-emigration

282 (Cucherousset et al. 2005). Additionally, McMillan et al. (2012) observed that *O. mykiss* in

283 Black Canyon Creek had higher lipid levels than those in Murderer Creek. Individuals in

284 Murderers Creek appear to be investing in length growth rather than lipid storage (McMillan et

285   al. 2012). Greater fish size and growth in Murderers Creek likely contributed to a higher

286   proportion of individuals becoming early-emigrants. Alternatively, our lower gradient valley

287   segments in Murderers Creek may have had higher sedimentation rates which reduced interstitial

288   concealment habitat (Cunjak 1996) and hence increased early-emigration (Bjornn 1971).

289   However, our regression modeling suggests that FL and growth had greater influence on early-

290   emigration than the habitat metrics that we measured. We suggest that individual growth rate,

291   and not stream gradient, was the principal driver of higher early-emigration from Murderers

292   Creek than Black Canyon Creek.

293   Higher growth rates are typically associated with individuals that are more "dominant" in

294   the social hierarchy (Metcalfe et al. 1992). The notion that dominant individuals emigrated from

295   Murderers Creek instead of sub-dominant individuals seemingly contradicts typical experimental

296   results (Chapman 1962; Keeley 2001; Bujold et al. 2004; Imre et al. 2004). When viewed in the

297   context of partial migration, however, our results become more coherent. Variation in growth

298   rates influences life history (Metcalfe 1998), and in Atlantic salmon populations this is

299   manifested in "upper modal" and "lower modal" groups. Upper modal individuals are prompted

300   to begin smolting in late summer or early fall, whereas lower modal individuals may not be

301   prompted to smolt until the following spring (Huntingford et al. 1988; Whitesel 1993; Jonsson et

302   al. 1998). Similarly, individual brown trout (Cucherousset et al. 2005) and brook trout

303   (Morinville and Rasmussen 2003) with a higher metabolic demand that could not be sustained in

304   small streams emigrated to larger rivers. Chapman et al. (2011) proposed a "fasting endurance

305   hypothesis" to explain why larger individuals with higher energy requirements undertake

306   seasonal migrations. The faster growing (as measured by FL) individuals in Murderers Creek

307   likely had a greater metabolic demand during fall as a result of having invested their energy into

308 length growth rather than lipid storage. During the fall-winter transition, we suggest that the

309 faster growing individuals did not have sufficient fasting endurance (Chapman et al. 2011) to

310 remain in Murderers Creek through winter and hence adopted an early-emigrant strategy.

311 Early-emigration compounded the phenotypic differences which existed between early-

312 emigrant and late-emigrant *O. mykiss* at the beginning of fall. The initially larger and faster

313 growing early-emigrants subsequently experienced higher growth during winter. Thus, size

314 differences between groups likely further diverged following emigration. Some of the early-

315 emigrants from Murderers Creek migrated downstream of our RST. We tracked the migration

316 and winter holding locations of some of these individuals with surgically-implanted radio

317 transmitters. Most individuals migrated < 20 km downstream of the RST to winter rearing areas

318 (I. Tattam, unpublished data). We were not able to recapture and measure these early-emigrants

319 immediately prior to smoltification for comparison with late-emigrants. Nonetheless, our data

320 suggest that early-emigrants attained a larger size at smoltification, which may facilitate greater

321 marine survival (Bilton et al. 1982; Ward et al. 1989; Tipping 1997). Future fish tagging should

322 focus on following the potential effect of increased length on smolt-to-adult survival by

323 recapturing tagged individuals at sampling facilities in Columbia River hydropower dams.

324 Differential smolt arrival timing at the Columbia River estuary could be traced back to

325 expression of either early-emigrant or late-emigrant behavior 5–8 months earlier. Physical

326 conditions and biotic communities in the estuary vary on a daily basis (Weitkamp et al 2012).

327 Likewise, ocean conditions can vary at short time scales and peak marine survival rates can

328 occur at different ocean-entry times in different years (Lundqvist et al. 1994). We hypothesize

329 that fall migration patterns ultimately manifest in different smolt-to-adult survival rates between

330 early-emigrant and late-emigrant groups. This may create differential parr to adult recruitment

331   between tributaries based on the prevalence of fall emigration. In the case of our study streams,

332   Murderers Creek will have a greater proportion of smolts with early ocean-entry than Black

333   Canyon Creek. Early ocean-entry may be disadvantageous during some years (Muir et al. 2006).

334   However, early-emigrants (and hence early ocean-entry smolts) from the SFJD had higher

335   survival (measured from the SFJD to adult return past Bonneville Dam) during 2005 ocean-

336   entry, but lower survival during 2006 ocean-entry (Wilson et al. 2008).

337   *Conclusions*

338   Fall emigration does not appear to be a fixed strategy, but rather a facultative tactic in

339   response to the constraints of the rearing environment. Although early-emigrants grow faster,

340   and presumably reach a larger size at smoltification, this life-history strategy is not exclusively

341   expressed in the population. Inter-annual variation in marine survival, associated with ocean-

342   entry timing differences between early-emigrant and late-emigrant individuals, likely creates

343   asynchronous productivity between these life-histories (Hilborn et al. 2003), and prevents any

344   single life-history from establishing population level dominance. Thus, the presence of both

345   early and late-emigrants increases the resilience of the population to changing environmental

346   conditions. Monitoring should estimate the abundance of both life-histories, with their relative

347   contribution to the population as a whole being an important indicator of viability. Identification

348   and protection of all habitats (both summer and winter rearing habitat) utilized by both life

349   histories will also be an important management action.

350

Acknowledgments

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541

542 TABLE 1.—Summary of *O. mykiss* tagged with Passive Integrated Transponders in Murderers

543 and Black Canyon creeks during summer 2004 and summer 2005. Estimated survival (95%

544 Confidence Interval in parentheses) to John Day Dam (JDD) represents the anadromous

545 component of each tagging cohort.

546

Location	Year	n Tagged	Fork Length 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%)

547
548

549   TABLE 2.—Model selection results for AICc analysis of fall emigration from Murderers Creek.

550   Explanatory variables include: average fork length (FL), mean specific growth rate during

551   summer (Growth), maximum depth of the nearest pool (Depth), and an index of streambed

552   particle size in the nearest pool (Substrate). Models with a Delta AICc of less than 5 and the null

553   model are presented. The null model has no explanatory variables and serves as a check on the

554   power of the explanatory variables. Product dots (·) 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

555

556

557   FIGURE 1.—Map of the South Fork John Day River (SFJD) basin showing location of PIT tag

558   arrays, rotary screw trap, and tributary sampling universe. Inset shows the location of the SFJD

559   basin in Oregon. Dashed arrow denotes streamflow direction. *Oncorhynchus mykiss* were PIT

560   tagged throughout the sampling universe (highlighted portions) of Black Canyon and Murderers

561   creeks during summer 2004 and 2005. Numbered circles denote sentinel reaches where capture-

562   recapture of *O. mykiss* occurred during all seasons.

563

564   FIGURE 2.—Percentage of early-emigrant *Oncorhynchus mykiss* from Black Canyon and

565   Murderers creeks during 2004 and 2005. The abundance of early-emigrants was estimated at a

566   rotary screw trap in the South Fork John Day River (rkm 10). Error bars indicate 95%

567   confidence intervals.

568

569   FIGURE 3.—Comparison of mean specific growth rates during winter 2005 among five reaches in

570   Murderers and Black Canyon creeks and one reach in the South Fork John Day River (SFJD).

571   *Oncorhynchus mykiss* were individually marked in December 2004, and recaptured in late-March

572   2005. Letters shared among bars indicate reaches that were not significantly different. NR = no

573   recoveries of individually marked fish occurred in this reach. Error bars indicate 95%

574   confidence intervals.

575

576   FIGURE 4.—Frequency of detection of early-emigrant and late-emigrant *Oncorhynchus mykiss* at

577   John Day Dam on the Columbia River (rkm 347). Panel a shows *O. mykiss* detected out-

578   migrating during spring 2005 and panel b shows *O. mykiss* detected out-migrating during spring

579   2006. Date of detection intervals are shared between both panels.
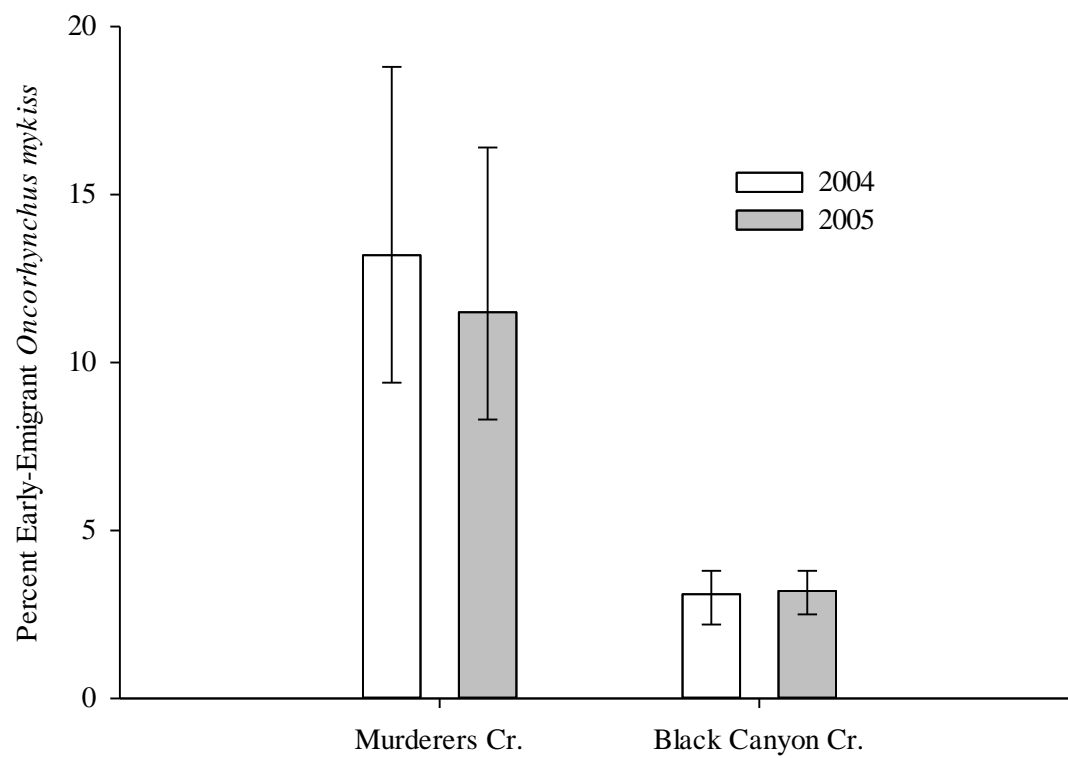
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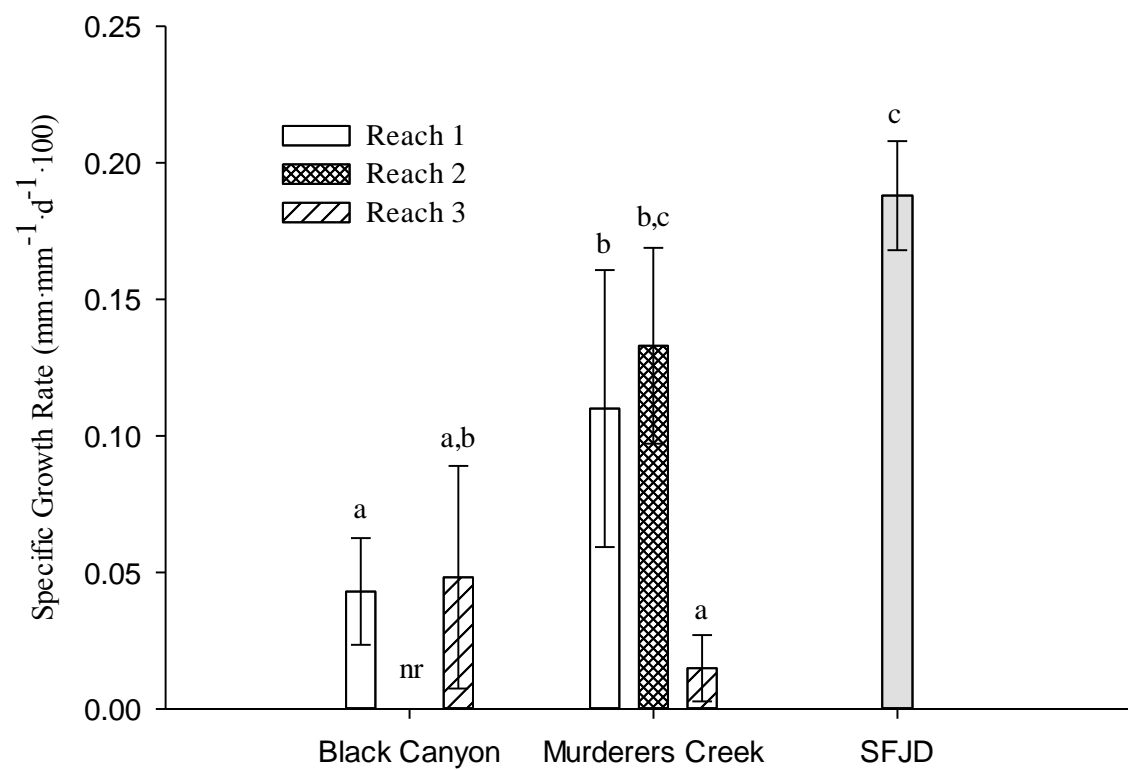581   Tattam et al. Figure 1.
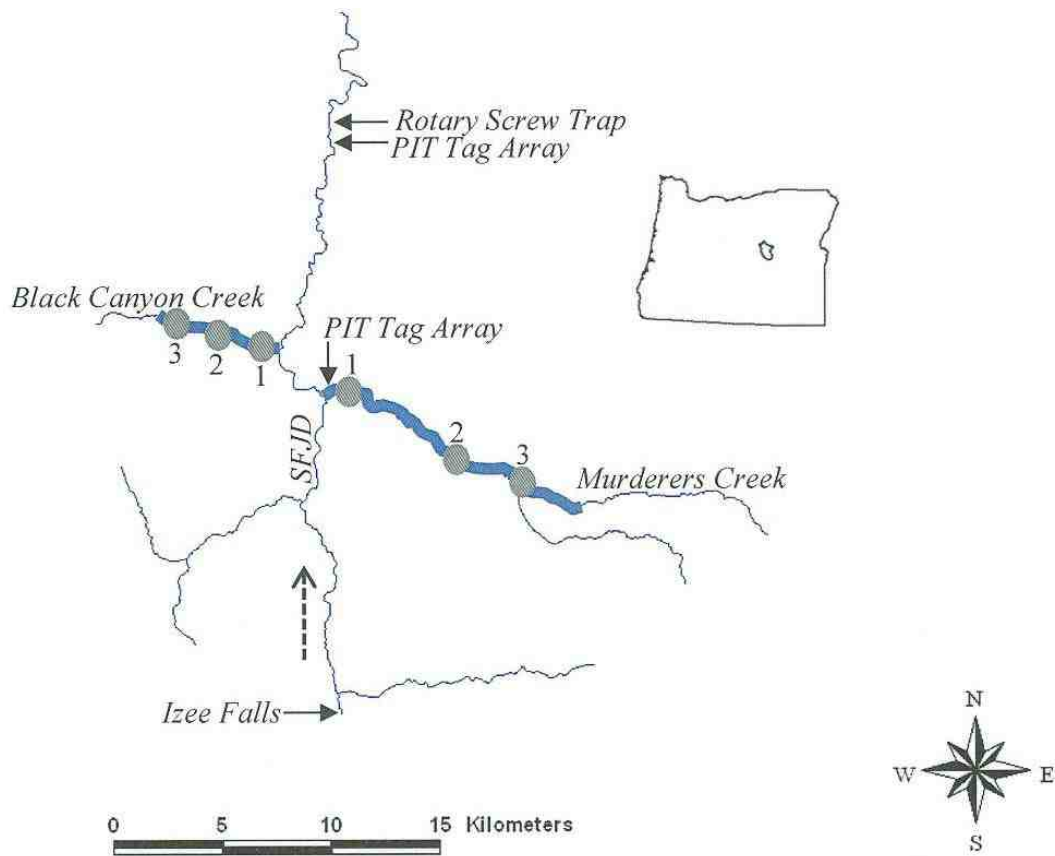
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587   Tattam et al. Figure 4.