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Increasing juvenile Coho Salmon densities during early recolonization have not affected resident Coastal Cutthroat Trout growth, movement or survival

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1 **Increasing juvenile Coho Salmon densities during early recolonization have not affected**
2 **resident Coastal Cutthroat Trout growth, movement or survival**

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21 Running Head: Effects of salmon colonization on resident trout

22 Keywords: Cutthroat Trout, Coho Salmon, Competition, Growth, Movement, Survival, Dam
23 Removal

24 <A>Abstract

25 The process of salmon colonization in the upper Cedar River and Rock Creek, WA, USA,
26 following the installation of a fish ladder at Landsburg Diversion Dam in 2003, offered an
27 opportunity to measure the effects of interspecific interactions on the dynamics of resident fish
28 populations. Rapid recolonization by Coho Salmon *Oncorhynchus kisutch* provided a natural
29 experiment to determine the influence of Coho Salmon densities on resident Cutthroat Trout *O.*
30 *clarkii clarkii* growth, movement and survival relative to other abiotic and biotic factors such as
31 habitat quality, environmental conditions, and conspecific density. During 14 seasonal sampling
32 events from 2005 to 2009, we PIT tagged 1851 and recaptured 394 Cutthroat Trout in Rock
33 Creek, collected habitat data, enumerated fish populations, and monitored fish movements with
34 PIT tag antenna arrays. Trout growth varied significantly among seasons and was greatest
35 during spring and early summer. Mean juvenile Coho Salmon density in summer and fall
36 increased eightfold from 0.04-0.32 and 0.08-0.68 fish m², respectively, approaching levels seen
37 in established populations but did not explain variation in trout growth, movement, or survival.
38 Summer growth of trout parr and fry were both negatively correlated with the density of
39 conspecifics but were positively correlated with total salmonid density. Additionally, trout parr
40 growth was positively correlated with stream discharge, whereas trout fry growth was negatively
41 correlated with initial size and declined during the course of the study. However, abiotic and
42 biotic explanatory variables accounted for little of the variation in trout growth, movement and
43 survival, suggesting that a great deal of individual variation exists. Overall, trout were largely
44 unaffected by Coho Salmon colonists despite large increases in juvenile Coho Salmon density,
45 though this may change if salmon populations continue to grow.

46

47 <A>Introduction

48 Populations of stream-rearing salmonids are often regulated by inter- and intraspecific
49 density-dependent processes that influence survival and abundance through competition for
50 limited resources (Hearn 1987, Milner et al. 2003). In addition, density-independent
51 environmental factors such as stream size (Berger and Gresswell 2009, Ebersole et al. 2009),
52 discharge (Harvey et al. 2006, Berger and Gresswell 2009, Teichert et al. 2010), water
53 temperature (Bærum et al. 2013), food availability, and physical habitat, such as cover (Boss and
54 Richardson 2002), as well as unexplained temporal variation (Carlson et al. 2008, Berger and
55 Gresswell 2009) can affect the growth, movement and survival of stream-rearing salmonids. In
56 many cases it is a challenge to disentangle the relative importance of these factors but systematic
57 changes in species composition can provide an opportunity to identify key processes. Species
58 composition can be altered experimentally, or by stocking a species, but this change can also
59 occur more naturally when a migration barrier is removed and colonization of habitat brings two
60 species into (or back into) sympatry.

61 The removal of migration barriers is a common technique used to restore migratory fish
62 populations (Bednarek 2001; Anderson et al. 2014). However, it has the additional consequence
63 of altering the dynamics of stream fish communities, providing an opportunity to measure the
64 impact of novel interspecific interactions on resident fish populations (Kiffney et al. 2009, Pess
65 et al. 2011, Naman et al. 2013, G. Temple, WDFW, unpublished data). The addition of salmonid
66 species via recolonization may increase total salmonid biomass production in streams because of
67 niche partitioning (Everest and Chapman 1972; McMichael and Pearsons 1988), or in the case of
68 Pacific Salmon, through marine nutrient subsidies that benefit resident species (Schindler et al.
69 2003). However, niche overlap between species can result in competition for resources, leading

70 to reduced abundance, growth, and survival, or altering the behavior or distribution of one or
71 both of the species (Hartman 1968, Glova 1984, Glova 1986, Harvey and Nakamoto 1996, Sabo
72 and Pauley 1997). Understanding the impacts of salmon recolonization on resident species is
73 important for resource managers weighing the benefits of restoring extirpated native species
74 against the potential impacts on extant native resident species (McMichael and Pearsons 1998,
75 Ham and Pearsons 2001, Pearsons and Temple 2007, Brenkman et al. 2008).

76 In coastal watersheds of the Pacific Northwest the recolonization of Pacific salmon
77 creates the potential for strong interpecific interactions with trout because fall-spawning salmon
78 produce larger numbers of offspring that emerge earlier and at a larger size than those of spring-
79 spawning Coastal Cutthroat *Oncorhynchus clarkii clarkii* and Rainbow Trout *O. mykiss* (Quinn
80 2005). In particular, there is the potential for competition between Cutthroat Trout and Coho
81 Salmon *O. kisutch*, because Coho Salmon typically spend ~12 months in streams prior to
82 seaward migration (Quinn 2005) and use similar habitats to those occupied by juvenile Cutthroat
83 Trout (Bisson et al. 1988). Coho Salmon can competitively displace, or contribute to reduced
84 growth and survival of juvenile Cutthroat Trout (Glova 1984, 1986, Trotter 1989, Sabo and
85 Pauley 1997, Young 2004). Experiments at the habitat unit scale showed that Coho Salmon
86 were competitively dominant in pools and forced trout into higher velocity riffle habitats (Glova
87 1986) where they experience reduced growth rates due to higher metabolic costs (Rosenfeld and
88 Boss 2001). Accordingly, trout appear to prefer pools in the absence of salmon (Glova 1986).
89 Salmonids in Pacific Northwest streams may also partition their habitat use at larger spatial
90 scales; Coho Salmon dominate in low gradient reaches and lower in watersheds (Glova 1984,
91 Rosenfeld et al. 2000), whereas Cutthroat Trout often use headwater areas where they are

92 isolated from other species (e.g., Buehrens et al. 2013) and appear to benefit from such isolation
93 (Connolly and Sauter 2008).

94 Alternatively, intra- rather than interspecific interactions may exert stronger influence on
95 trout populations, therefore minimizing the impacts of salmon reintroduction on resident trout.
96 Indeed, intraspecific competition is more frequently documented in salmonid populations than
97 inter-specific competition, suggesting that species-specific differences in ecology and life history
98 can reduce competitive interactions (Milner et al. 2003). Density-dependent limitations of
99 movement (Gowan and Fausch 2002), growth, and survival due to intraspecific interactions are
100 well-documented in stream rearing salmonids (Keeley 2001, Imre et al. 2004, Harvey et al. 2005,
101 Imre et al. 2005). Furthermore, habitat type (e.g. pools vs. riffles), food availability, and size of
102 individuals can interact with fish density to influence growth and survival (Harvey and
103 Nakamoto 1997, Rosenfeld and Boss 2001, Rosenfeld et al. 2005).

104 Although there is an extensive body of research on the roles of inter- and intraspecific
105 competition in regulating stream salmonid communities in the Pacific Northwest, few studies
106 have evaluated the effects of salmon reintroduction on extant trout populations. As the
107 prevalence of salmon reintroduction projects grows (e.g., Anderson et al. 2014), a better
108 understanding of effects on resident trout species is needed (McMichael and Pearsons 1998,
109 Pearsons and Temple 2007, Brenkman et al. 2008). Construction of fish passage facilities at
110 Landsburg Dam in 2003 provided access to upstream habitats for Pacific salmon in the Cedar
111 River and Rock Creek, Washington, USA, where resident Coastal Cutthroat and Rainbow Trout
112 had persisted above the dam in isolation from salmon for over 100 years. Recolonization of the
113 upper Cedar River by Coho Salmon and Chinook Salmon *O. tshawytscha* occurred immediately
114 following the installation of a fish ladder (Anderson and Quinn 2007) and the abundance and

115 spatial distributions of adults and juveniles of both species has continued to increase each year,
116 increasing the opportunity for interactions with resident species (Anderson et al. 2008, Kiffney et
117 al. 2009, Naman et al. 2013). Although restoring habitat connectivity appears to have benefited
118 Coho and Chinook salmon populations, effects on resident trout are unknown. Therefore, the
119 objective of this study was to determine the influence of juvenile Coho Salmon density, relative
120 to other abiotic and biotic factors, on the growth, movement, and apparent survival of Cutthroat
121 Trout in Rock Creek during a period of rapidly increasing Coho Salmon abundance (2005 –
122 2009).

123

124 <A>Methods

125 *Study site.*—The Cedar River is a 487 km² watershed originating at the crest of the Cascade
126 Mountains in Washington State and draining westward into Lake Washington (Figure 1). The
127 upper Cedar River flows over a series of impassable waterfalls, continuing through 53 km of
128 historical anadromous fish habitat. Landsburg Diversion Dam, built in 1901, blocked
129 anadromous fish access to the upper 20 km of historical habitat until a fish ladder was
130 constructed in 2003 to allow fish passage above the dam. Rock Creek enters the Cedar River 2
131 km above Landsburg Dam and has approximately 13 km of habitat accessible to anadromous
132 fish. The 15 km² watershed has a rain-dominated hydrograph with peak flows in winter and low
133 flows in summer. From 2003 through 2009 the abundance of adult Coho and Chinook salmon
134 upstream of the dam increased from 47 to 679 and 79 to 138, respectively (though there were
135 397 Chinook Salmon in 2007; Burton et al. 2013). For both species the vast majority of
136 spawning occurred in the Cedar River; Chinook Salmon spawning only occurred in Rock Creek
137 in 2007 (six redds), and Coho Salmon spawners were not documented in Rock Creek until fall

138 2009, meaning that salmon presence was limited primarily to juvenile colonists. Past timber
139 harvest has locally reduced large woody debris abundance but habitat conditions are otherwise
140 largely intact within the upper Cedar River watershed. Because the Cedar River is the source of
141 drinking water for the City of Seattle, the watershed is protected from any further disturbance or
142 development. In addition to colonizing Coho and Chinook salmon, the upper Cedar River
143 contains populations of Coastal Cutthroat Trout, Rainbow Trout, Speckled Dace *Rhinichthys*
144 *osculus*, Mountain Whitefish *Prosopium williamsoni*, sculpins *Cottus* spp., and lampreys
145 *Entosphenus tridentatus* and *Lampetra* spp. Chinook Salmon were rarely encountered and
146 Rainbow Trout were < 10% of the trout population in Rock Creek, however Rainbow Trout were
147 included in trout densities and both species were included in total salmonid densities and
148 modeled as covariates.

149 **Fish collection and habitat surveys.**—Fish and habitat sampling occurred in 14 mark and
150 recapture events, lasting three to seven days each, during late winter, mid-summer, and fall each
151 year from 2005 through 2009 (Table 1). Sampling occurred at reach and habitat unit scales to
152 account for the hierarchical organization of riverine ecological processes (Frissell et al. 1986).
153 Mark and recapture events occurred in 26-52 habitat units within three 200-500 m reaches
154 numbered 1-3 in ascending order moving upstream from the mouth of Rock Creek to rkm (river
155 kilometer) 2.5 (Figure 1). Only pools and pool-like habitat units were sampled for this study
156 because pools act as congregation points for several fish species during summer low flow periods
157 (Glova 1986). The number of habitat units sampled during each event varied over time because
158 in some events some reaches were not sampled, and because seasonal high flows occasionally
159 changed the stream's configuration. However, in most cases all pools and pool-like habitat units
160 within a reach were sampled (Table 1).

161 All fish species were collected using three-pass electrofishing depletion (Carle and Strub
162 1978); captured individuals were held in buckets, anesthetized with MS-222 (80 mg/L),
163 measured (fork length to the nearest mm), weighed to the nearest 0.1 g, and enumerated.
164 Cutthroat Trout > 60 mm and 2 g, which were large enough to tag (Peterson et al. 1994) were
165 identified to species and implanted with a 12 mm Passive Integrated Transponder (PIT) tag in
166 their body cavity using a syringe sterilized in 70% ethanol. After tagging, all fish were allowed
167 to recover and released in the habitat unit where they were captured.

168 PIT tags contain a unique code that allowed us to quantify growth, movement and
169 survival of individuals (Prentice et al. 1990) during subsequent recapture events. In addition to
170 capturing tagged fish, three rows of stream-spanning stationary PIT tag antenna arrays at the
171 mouth of Rock Creek were continuously operated starting in September 2005 allowing the
172 detection of fish immigrating to and emigrating from Rock Creek. These antennas also allowed
173 us to quantify detection efficiency and determine the direction of movement for most fish (e.g.,
174 Connolly et al. 2008).

175 During each tagging event, surveys were completed on all habitat units to quantify
176 maximum and tail-out depths and surface areas, water velocity, and to characterize substrate
177 composition and available cover types. Water temperature data were collected by a series of
178 continuously deployed data loggers (Onset Co., Cape Cod, MA). Stream discharge data were not
179 available for Rock Creek, so we used discharge data from the Raging River (USGS 12145500)
180 near Fall City, WA. The Raging River is representative of the temporal pattern of discharge in
181 Rock Creek and has similar hydrological characteristics, but has approximately three times the
182 drainage area. Because we wished to distinguish potential effects of stream flow, which varies
183 predictably at a seasonal timescale, from the effect of season, we used a measure of flow

184 anomalies (mean percent of mean daily flow for each day). These anomalies were then averaged
185 across each between-sampling interval for use as a covariate in growth and survival analysis.
186 Fish densities (fish / m²) and fish biomass densities (grams of fish / m²) were estimated for each
187 habitat unit during each event based on the sum of individuals (numerical density) or weights
188 (biomass density) divided by the surface area of each habitat unit. Yearly mean densities were
189 calculated for summer as the mean of densities in all habitat units in reaches 1 and 3, which were
190 sampled in all summers, whereas mean fall densities were calculated for reach 1 only since it
191 was the only reach sampled in each fall (Table 1). Linear regression was used to determine
192 whether there were significant increases or decreases in mean log transformed fish density for
193 both summer and fall between 2005 and 2009.

194 *Growth and movement analysis.*—Growth of individual fish over seasonal intervals was
195 measured as specific growth rate (SGR) (Ricker 1975):

$$196 \quad \text{SGR} = \left[\frac{\ln(w_t) - \ln(w_0)}{\Delta t} \right] \times 100$$

197 where w is weight, and 0 and t denote time periods in which the initial and the final
198 measurements of weight were made. A comparison of growth rates among seasons was
199 conducted to determine whether they could be pooled for subsequent analysis. Variance in
200 growth among seasons was unequal (Levene's test, $P = 0.02$). Thus, a generalized linear model
201 (GLM) assuming normal error structure with a linear link function, with observations weighted
202 by the inverse variance of growth in each season, was used to compare growth among seasons.
203 A series of candidate GLMs, assuming normal error structure with linear link functions, were
204 constructed to correlate the growth of individual fish within each seasonal interval with
205 combinations of explanatory variables. Maximum likelihood estimates were obtained for all
206 GLM parameters. The explanatory variable list included covariates measured at multiple spatial

207 scales which were thought to include many of the common factors affecting resident trout
208 populations: movement history (variable indicating whether a fish was recaptured in the same
209 habitat unit it was originally captured) was a covariate corresponding to individual fish; habitat
210 quality and fish community densities (fish / m² and biomass—grams of fish / m²) were measured
211 at the habitat unit scale; reach was a factor denoting the reach fish were tagged in; water
212 temperature, discharge and time period were factors applied to all individuals tagged within an
213 event (Table 2). Initial weight was also included in growth models as an independent variable to
214 account for allometric scaling of growth with size. Our models were exploratory in nature and it
215 was unknown what combinations of factors might explain Cutthroat Trout growth (n = 217
216 Cutthroat Trout parr and 68 fry growth rates). Consequently, all subsets of variables were
217 considered during model selection (1942 per age class) but models were limited to a maximum
218 of four explanatory variables (e.g., Pess et al. 2011).

219 Two movement response variables were used to assess movements of Cutthroat Trout: 1)
220 we compared the locations of recaptured fish with their original tagging locations, and 2) we
221 detected movement of individuals at fixed instream PIT antenna arrays located at the mouth of
222 Rock Creek. A series of GLM models assuming binomial error with a logit link function were
223 used to determine what factors affected whether fish moved between capture events. Models
224 included the same candidate independent variable set (Table 2) as our growth analyses. Linear
225 regression was used to relate fish length at tagging with log-normalized time before first
226 emigration from Rock Creek.

227 *Model selection.*—Akaike's Information Criterion for small sample sizes (AICc) was
228 calculated to compare and rank the various growth and movement models including the null
229 (intercept only) model. The lowest AICc value denoted the best model and models with ΔAICc

230 < 2 were considered to have substantial support, those with values from 4 to 7 had little support,
231 and those greater than 10 had no support (Burnham and Anderson 2002). We also calculated
232 Akaike weight, w_i , a measure of the relative likelihood of the best fitting model compared to
233 other models. The ratio of Akaike weights (w_j/w_i) indicates the plausibility of the best fitting
234 model (w_j) compared to other models (w_i). All statistical analyses were performed in R (R
235 Development Core Team 2011) unless otherwise noted.

236 *Survival analysis.*—Cutthroat Trout survival and covariates affecting it were modeled with
237 Cormack-Jolly-Seber (CJS) open population models (Cormack 1964, Jolly 1965, Seber 1965,
238 Lebreton et al. 1992) using program RMARK (Laake and Rexstad 2008) and MARK (White and
239 Burnham 1999). CJS models incorporate a binary capture history for each fish (observed/not
240 observed) and the length of this history corresponds to the number of capture occasions in a
241 study. The model structure simultaneously estimates the probability of apparent survival (the
242 proportion of animals remaining alive and within the study area) between occasions and the
243 probability that surviving individuals are encountered on each occasion. Apparent survival is
244 appropriate for open populations where individuals can leave the study area and it is not possible
245 to differentiate between fish that died and fish that emigrated. The CJS model assumes 1) all
246 marked animals present at time i have an identical probability of being captured, p_i , during that
247 period and of surviving, Φ_i , between time i and the following sampling event $i+1$; 2) that tags
248 (marks) are not lost or undetected in captured individuals; 3) sampling occasions are
249 instantaneous; 4) emigration of tagged individuals is permanent; 5) the probability of capture and
250 survival is independent among individuals (Williams et al. 2002). Our study reasonably satisfied
251 assumptions 3-5: The length of time of sampling events relative to the time between events was
252 very small (3), we excluded known emigrants from our analyses (4), and there was no *a priori*

253 reason to suspect a lack of independence between sampling of individuals (5). Tag retention and
254 detection rates (2) have been high in comparable studies of Cutthroat Trout (Berger and
255 Gresswell 2009); although some tags were undoubtedly lost or not detected we did not correct
256 for this bias which would tend to underestimate survival (Knudsen et al. 2009). Identical capture
257 probability for all animals in each period (1) was the most difficult assumption to satisfy since
258 fish may move within the study area and certain locations may be more or less conducive to their
259 capture. Efforts were made to meet this assumption through accounting for sampling intensity
260 by constructing separate models for data subsets that included the same sampling frequency and
261 intensity.

262 Survival modeling followed the stepwise process recommended by Lebreton et al.
263 (1992), where 1) the fully time-dependent model was assessed for goodness of fit, 2) the best
264 model of capture probabilities was established while holding survival constant, and 3) the best
265 model of survival was established while using the best model of capture probabilities. In order
266 to determine which temporal, spatial or tagging event strata could be pooled we evaluated
267 models of survival and capture probability that included main effects and one and two way
268 interactions of the following variable set: reach, time period or season (but not both), and time
269 since marking (TSM) (See Tables B1 and B2 for a complete list of models tested). Akaike's
270 Information Criterion for small sample sizes (AICc) was calculated to compare and rank the
271 various models that included temporal or spatial structure. The lowest AICc value denoted the
272 best model, which was used for covariate analyses.

273 Because CJS models estimate apparent survival of animals alive and remaining in the
274 study reach, estimates of apparent survival will increasingly diverge from "true" survival with
275 increasing emigration. To improve the precision of our estimates of apparent survival (referred

276 to hereafter simply as survival) and capture probabilities, we applied the methods of Horton and
277 Letcher (2008) in which the capture history of individuals known to have emigrated (i.e.,
278 detected at the mouth of Rock Creek) was modified to include a 1 for the most recent sampling
279 event (because the animal was alive and subsequently emigrated) and the frequency associated
280 with that capture history was changed to -1, which results in the individual's capture history
281 being excluded from the model likelihood following its last capture. Although some fish
282 undoubtedly emigrated without detection, consistently high antenna detection efficiency (~92 %)
283 minimized this problem (Pess et al. 2011).

284 Additional modifications to survival modeling, in which separate models were
285 constructed for subsets of encounter histories, were necessitated by inconsistent surveying of
286 study reaches. Reaches 2 and 3 were not sampled during all events, which would have violated
287 CJS assumptions (#1 above—identical capture probabilities), had those data been included with
288 reach 1 data from all periods, so two separate datasets were used to model Cutthroat Trout
289 survival. One survival analysis included data only from reach 1 (612 fish) and spanned sampling
290 events 2-14 corresponding to fall 2005 through fall 2009, for which downstream antenna
291 detection data were available to censor capture histories of known emigrants. The second
292 survival analysis included pooled data from reaches 1 and 3 for sampling events 7-14
293 corresponding to summer 2007 through fall 2009 (678 fish). For both analyses, time intervals
294 were set to the number of months between sampling events to account for varying amounts of
295 elapsed time between events.

296 The program RELEASE within MARK was used to assess the goodness of fit of full
297 models (separate estimate of survival (Φ) for each time period) for both datasets and to generate
298 estimates of the variance inflation factor \hat{c} , a measure of over-dispersion. Goodness of fit tests

299 suggested no significant overall lack of fit for either dataset; however, for the reach 1 dataset
300 where $\hat{c} = 1.33$, this value was thus used to adjust model selection criteria (QAICc), standard
301 errors and confidence intervals, resulting in somewhat reduced statistical power. A value of $\hat{c} =$
302 1.0 was used for the reach 1 and 3 dataset since the estimate generated by RELEASE was < 1 .

303 A series of covariate models were constructed to explain variability in survival using
304 various environmental and biological variables (Table 2) which were each tested individually
305 (see Table A1 for complete model list). Due to the long duration of the study and the attendant
306 difficulty of interpreting the effect of initial conditions on subsequent survival far in the future,
307 as well as the unavailability of covariate data for each individual within all tagging periods, the
308 effect of covariates was restricted to the survival interval immediately following tagging for all
309 individuals. The 95% confidence intervals (CI) of coefficients were used to evaluate
310 significance, and those not overlapping zero were interpreted to signify biologically meaningful
311 relationships.

312

313 <A>Results

314 *Fish tagging and habitat characteristics.*—Between summer 2005 and fall 2009 we
315 captured 3047 Coho Salmon, 2553 sculpins, 1975 Cutthroat Trout, 1004 trout fry, 551 dace, 178
316 Rainbow Trout, 39 lampreys, 34 Chinook Salmon, and two Largemouth Bass *Micropterus*
317 *salmoides*, which comprised 32%, 27%, 21%, 11%, 6%, 2%, $< 1\%$, $< 1\%$, and $< 1\%$ of the fish
318 population, respectively. We tagged 1851 Cutthroat Trout and trout fry (mean length = 113 mm,
319 range 60-280 mm) in Rock Creek. We recaptured 394 individuals with a total of 483 recaptures
320 events when including individuals recaptured multiple times (Table 3). Of these captures and
321 recaptures 325 occurred in consecutive events and 285 of the recaptures occurred in the fall,

322 primarily resulting from tagging earlier that summer. Abiotic and biotic conditions in Rock
323 Creek hypothesized to affect Cutthroat Trout growth and survival did not show a directional
324 change over time other than Coho Salmon density increasing in summer and fall in all reaches
325 and trout fry and parr densities increasing in reach 1 in the fall (Table 2). In 2005 mean Coho
326 Salmon density started at 0.04 (summer) and 0.08 fish/m² (fall), which was below that of
327 combined trout parr and fry (mean = 0.22 and 0.18 fish/m² in summer—reaches 1 and 3, and
328 fall—reach 1 only, respectively). However, Coho Salmon density increased over the course of
329 our study in both summer and fall ($\Delta\text{AICc} = 10.01$, and 7.08 respectively relative to a null
330 model) by approximately eightfold to 0.32 and 0.68 fish/m², in summer and fall 2009,
331 respectively, surpassing the combined trout density in both seasons (Figure 2). Trout fry (age 0),
332 trout parr (age 1 and older), and total trout densities (which were consistently comprised of
333 >90% Cutthroat Trout) did not show linear trends across years in summer ($\Delta\text{AICc} = 2.05$, 0.96,
334 and 1.51, respectively relative to a null model). Fall densities of trout fry, trout parr, and total
335 trout in reach 1 increased ($\Delta\text{AICc} = 4.9$, 5.4, and 12.74 respectively relative to a null model),
336 however these increases were smaller (0.35-0.95, 0.14-0.20, and 0.18-0.3 fish/m² for trout fry,
337 parr, and total trout, respectively) than changes in Coho Salmon density (Figure 2).

338 There were correlations (Pearson's product-moment correlation coefficient $r > 0.6$)
339 between many of the independent variables used to model Cutthroat Trout growth, movement,
340 and survival. Multicollinear variable sets included negative correlations between temperature and
341 flow ($r = -0.80$) and positive correlations between maximum and residual habitat depth ($r =$
342 0.85), and the density and corresponding biomass density of each species or species group ($r =$
343 0.87, 0.81, and 0.67, for Coho Salmon, all trout, and all salmonids, respectively). Trout and
344 Coho Salmon densities were positively correlated with total salmonid density ($r = 0.83$ and 0.75,

345 respectively) and trout density was correlated with total salmonid biomass density ($r = 0.8$).
346 Trout and Coho Salmon biomass densities were also positively correlated with total salmonid
347 density ($r = 0.67$ and 0.65 , respectively) and trout biomass density was correlated with total
348 salmonid biomass density ($r = 0.96$), but trout and Coho Salmon densities, and biomass densities
349 were not correlated with each other ($r = 0.34$ and 0.17 , respectively).

350 *Fish movements.*—Movements of Cutthroat Trout varied by season, age, and size, but were
351 not correlated with Coho Salmon density. Due to prohibitively small sample sizes for other
352 seasons and substantial support for a movement model including season relative to the intercept
353 only model ($\Delta AICc = 8.58$), our analysis of recapture movements was limited to summer ($n =$
354 285 summer-fall recaptures). The best logistic GLM model set ($\Delta AICc < 3$) of Cutthroat Trout
355 movement in summer indicated that the probability of moving between capture events was
356 positively correlated with initial weight within age-groups, the amount of elapsed time between
357 tagging and recapture, and was greater for parr than fry. Individual models in this set also
358 included either a positive correlation with trout density or total salmonid density, or a negative
359 correlation with the surface area of the habitat unit where a fish was captured but none of these
360 variables had strong effects on model selection criteria. Of these recaptures, 70% were in the
361 same habitat unit where they were initially captured, and those that moved between captures did
362 not move far; the mean distance was only 110 m or 54 m after excluding five fish that moved
363 between reaches.

364 Although fish that were physically recaptured did not move far from their tagging
365 locations, detections of Cutthroat Trout at stationary antennas as they left Rock Creek revealed
366 that some individuals moved considerable distances. In each year 8-23% of the Cutthroat Trout
367 tagged in reach 3 and 42-53% of those tagged in reach 1 were detected leaving Rock Creek

368 (Table 3), which required traveling at least 2223 m from reach 3 and 0-430 m from reach 1. The
369 proportion of Cutthroat Trout leaving Rock Creek was relatively constant among years and
370 movements of parr and fry appeared to be more related to the time of year; greater than 50% of
371 annual detections of unique individuals moving in both directions occurred in the fall between
372 October and December, whereas no more than 10% of annual movements were detected in other
373 months. Additionally, there was a negative correlation (Pearson's product-moment correlation
374 coefficient $r = -0.26$, $\Delta\text{AICc} = 38.7$ relative to the null model) between initial length and the
375 amount of time following tagging before Cutthroat Trout left Rock Creek ($n = 523$), indicating
376 that larger fish tended to move sooner after tagging than smaller fish, and there was no evidence
377 this pattern was related to Coho Salmon density (Figure 3).

378 *Seasonal growth.*—Fewer trout were tagged or recaptured during spring than summer or
379 fall, resulting in limited sample sizes for fall to spring ($n = 10$) and spring to summer ($n = 10$)
380 growth rates relative to summer to fall ($n = 285$). Nevertheless, there was strong support for an
381 effect of season on growth rate relative to an intercept only model ($\Delta\text{AICc} = 59.8$). Growth was
382 highest in spring (mean SGR = 0.53 ± 0.04) and was greater in summer (mean SGR = $0.20 \pm$
383 0.02) than in fall (mean SGR = 0.11 ± 0.02).

384 *Summer growth.*—GLM analysis suggested growth rates differed ($\Delta\text{AICc} = 129.6$ relative to
385 null model of no age effect) between age classes (assigned based on length), so separate models
386 were constructed for fry and parr to describe the effects of independent variables on specific
387 growth rates (Table 4). Summer growth of both Cutthroat Trout parr and fry was negatively
388 correlated with the density of conspecifics but positively correlated with total salmonid density,
389 and was not related to Coho Salmon density (Table 4; Figure 4). Models of parr growth were not
390 well differentiated by model selection criteria, and explained little of the variance ($R^2 = 0.12$ for

391 the best model). However, all models of summer parr growth with $\Delta\text{AICc} \leq 3$ included a
392 positive correlation with flow and total salmonid density and a negative correlation with trout
393 density. Reach, Coho Salmon density, and initial weight were each included in one of the best
394 models but did not appreciably affect model selection criteria. The best model of Cutthroat Trout
395 fry growth included negative correlations with initial body weight, year (fit as a continuous fixed
396 effect), and trout biomass density, and a positive correlation with total salmonid biomass density
397 (model $R^2 = 0.41$; Table 4). Models of Cutthroat Trout fry summer growth were better
398 differentiated by model selection criteria than parr growth models and no additional variables
399 were included in the top model set ($\Delta\text{AICc} < 3$). Habitat characteristics including distance
400 upstream from the mouth of Rock Creek, maximum and residual habitat depth, and habitat unit
401 surface area were not strongly correlated with growth for either age class of Cutthroat Trout.
402 Individual attributes including condition factor, and whether fish moved or not, also appeared to
403 have little influence on summer growth of Cutthroat Trout parr or fry.

404 **Survival.**—No effect of Coho Salmon density on Cutthroat Trout survival was detected,
405 however, all individual, abiotic, and biotic covariates had 95% confidence intervals that
406 overlapped zero (Table A1), suggesting that survival was not explained by the variables
407 measured. There was weak evidence that survival decreased with TSM (in both datasets) and
408 differed among time periods (reaches 1 and 3 dataset only), but was similar among reaches. The
409 best models of survival probabilities for the reach 1 dataset were the null model of constant
410 survival over time and a model including a negative correlation with the time-since-marking
411 (TSM) (model: $\phi \sim \text{TSM}$), which together accounted for 87% of the model weight (Table B1).
412 The best models of survival for the reaches 1 and 3 dataset included a negative correlation with
413 TSM and an effect of time dependence meaning that monthly survival generally declined with

414 increasing TSM for all individuals and there was also significant time-dependence (independent
415 survival within each time period) (Table B1). Season was not included in the best models of
416 survival for either dataset.

417 However, there was more evidence for both spatial and temporal variability in the
418 probability of capturing Cutthroat Trout (Table C1). The best model predicting capture
419 probabilities for the reach 1 analysis of fall 2005-fall 2009 data included a negative correlation
420 with TSM plus an additive effect of time-dependence (model: $p \sim \text{TSM} + \text{time}$) while the best
421 model of capture probabilities for the combined reaches 1 and 3 dataset from summer 2007- fall
422 2009 included an interaction between reach and time dependence (model: $p \sim \text{reach} : \text{time}$).

423

424 <A>Discussion

425 There were no detectable effects of initial Coho Salmon colonization on Cutthroat Trout
426 growth, movement patterns, or survival, even though salmon densities increased in each year of
427 our study and were almost an order of magnitude greater in the last year. Coho Salmon density
428 not only varied over the years but also varied greatly among habitat units in each year but no
429 within-year effects were detected either. The role of interspecific competition on stream
430 salmonids is not well resolved; evolved niche segregation may minimize competitive interactions
431 between co-occurring species but, alternatively, realized niches of co-occurring species may be
432 reduced by competition relative to their abiotic niches (Hutchinson 1957, Milner et al. 2003).
433 Our study suggests that for Coastal Cutthroat Trout and Coho Salmon, which evolved in
434 sympatry, sufficient options may have existed in Rock Creek to minimize negative interspecific
435 interactions during the early stages of colonization by salmon. Alternatively, Coho Salmon
436 impacts may have been undetectable, owing to our lack of study design controls, limited data, or

437 small effect size (Ham and Pearsons 2000, 2001). In this case the effects may become evident in
438 the future, particularly if Coho Salmon densities continue to increase, thus increasing the
439 potential effect size (e.g., Pearsons and Temple 2010).

440

441 *Growth.*—There was no evidence that Coho Salmon density affected Cutthroat Trout growth
442 during our study of initial Coho Salmon recolonization. This finding was consistent with studies
443 showing no effect of increasing Coho Salmon and stream-rearing spring Chinook Salmon
444 densities on growth, abundance, and condition of Rainbow Trout in the Yakima River, WA as a
445 result of salmon reintroduction and supplementation programs (McMichael and Pearsons 1998,
446 Pearsons and Temple 2007, Pearsons and Temple 2010, G. Temple, WDFW, unpublished data).
447 Similarly, a companion study found that increasing Coho Salmon densities have not reduced
448 sculpin abundance or body condition in Rock Creek (Naman et al. 2013). Conversely, Harvey et
449 al. (1996) found a negative effect of steelhead density on Coho Salmon growth. However, in
450 their study steelhead densities were six-fold higher than Coho Salmon, suggesting that relative
451 densities may be important in governing density dependent interactions. Additionally, habitat
452 saturation can affect whether density dependent growth occurs since growth is thought to be
453 more impacted by changes in density when densities are low (Grant and Imre 2005). Densities of
454 Cutthroat Trout may have been sufficiently high in our study to preclude interspecific density
455 dependent growth.

456 Alternatively, the intraspecific and interspecific density thresholds for growth effects may
457 differ. There were negative correlations between trout density and both Cutthroat Trout fry and
458 parr growth, suggesting negative intraspecific density dependence. Conspecific density
459 dependence has long been recognized to regulate stream salmonid populations (Milner et al.

460 2003), and may manifest in reduced growth (Spalding et al. 1995, Keeley 2001, Harvey et al.
461 2005, Teichert et al. 2010). Interestingly, both fry and parr growth were positively associated
462 with total salmonid density; this result is difficult to interpret, but suggests that high growth rates
463 may occur in habitat units that contain good conditions for all salmonid species. Trout fry
464 summer growth also declined across years of the study, and although the reason is unknown, the
465 only factors known to have undergone directional change over the course of the study were the
466 abundance and density of Coho Salmon and the density of trout fry in reach 1 during the fall.

467 The lack of negative effects of Coho Salmon on Cutthroat Trout growth in our study may
468 be a result of habitat partitioning; Coho Salmon prefer slower, deeper areas and are primarily
469 surface feeders, whereas Cutthroat Trout have less association with depth and prefer
470 microhabitats with good conditions for foraging on invertebrate drift (Bisson et al. 1988).
471 Indeed, micro-habitat measurements in Rock Creek reveal partial segregation of the species by
472 water depth and velocity (Quinn, unpublished data). It is possible, however, that Coho Salmon
473 populations have simply not reached a threshold density where they begin to affect Cutthroat
474 Trout, or that potential effects will not manifest in a relationship with density at the habitat unit
475 scale. For example, after seven years of data collection, Pearsons and Temple (2010) detected
476 negative impacts of introduced stream-type spring Chinook Salmon juveniles resulting from a
477 supplementation program, that they were unable to detect after five years of the program
478 (Pearsons and Temple 2007).

479 Cutthroat Trout growth was also related to abiotic factors including season, with the
480 highest growth rates occurring from spring to midsummer. Spring was reported as the period of
481 highest growth rates in steelhead (Sogard et al. 2009) and Atlantic Salmon (Bacon et al. 2005),
482 and may provide an optimal balance of temperature, food availability, and stream discharge.

483 Warmer temperatures in Rock Creek during spring reduce physiological constraints that may
484 limit growth during winter without exceeding thresholds that often result in lower growth during
485 summer months (e.g. McCarthy et al. 2009, Davidson et al. 2010). Discharge in Rock Creek
486 remained relatively high in the spring, and this can enhance growth (Teichert et al. 2010),
487 perhaps related to increased invertebrate drift (Harvey et al. 2006), or usable habitat area.
488 Support for this hypothesis was provided by models of Cutthroat Trout parr summer growth,
489 which indicated a positive effect of stream discharge. Reduced growth during late summer and
490 early fall may result from low flows concentrating fish in the few remaining areas with suitable
491 depth (Glova 1986), food limitation owing to reduced invertebrate drift biomass (Harvey et al.
492 2006), increased energetic demands from elevated temperatures, or some combination of these
493 factors.

494

495 **Movement.**—Movements of Cutthroat Trout inferred by recaptures and antenna detections
496 were not correlated with Coho Salmon density, and the proportions of Cutthroat Trout detected
497 moving were similar among years, inconsistent with an influence of Coho Salmon colonists on
498 trout movements. However, models based on recaptures did not identify factors correlated with
499 movement other than initial size and the amount of time between capture events. Our models
500 only explained a small proportion of the variability affecting which individuals moved between
501 captures, but the proportion of fish moving varied little among years.

502 The limited movement distances we observed between capture events was consistent with
503 many previous studies of resident trout movement involving physical recaptures (Kahler et al.
504 2001, Roni et al. 2012), and was likely due in part to the bias imposed by our inability to detect
505 movements to areas outside of our sampled reaches (Gowan et al. 1994). Moreover, most

506 recaptures occurred at the end of the summer, when fixed antenna detections indicated that
507 movement was least common. Accordingly, antenna detections revealed that many fish moved
508 further than was documented by physical recaptures. Evidence of length-dependent emigration
509 in our study suggests that as they grew, fish increasingly tended to move downstream out of the
510 study reaches, perhaps as part of an ontogenetic niche shift as their resource needs were no
511 longer met in small tributary habitat like Rock Creek (Jonsson and Jonsson 1993). In fact there
512 appeared to be a threshold of ~150 mm length at tagging, above which all individuals that were
513 detected emigrating did so within the first year after tagging. This size corresponds to the size of
514 typical smolts in Cutthroat Trout populations and was also the size at which piscivory became
515 more common in Cutthroat Trout in the Cedar River basin (P. Kiffney, unpublished data), which
516 may indicate changing energetic demands and associated habitat requirements.

517

518 *Survival.*—Temporal, seasonal, spatial, and individual covariates including Coho Salmon
519 density did not explain variability in Coastal Cutthroat Trout survival. It is possible that this was
520 due to our limited ability to differentiate apparent survival, which includes emigration, from
521 actual survival. Although our model attempted to remove individuals leaving the study area,
522 upstream emigrants would not have been detected by our antenna arrays, and fish moving to
523 riffles and other un-sampled habitat units within our study reaches could have complicated our
524 ability to differentiate survival from emigration. Regardless, we had expected that environmental
525 conditions such as discharge and temperature, which are seasonally variable in streams, and
526 influence important aspects of salmonid ecology including growth rates and life history
527 transitions (Thorpe et al. 1998, Milner et al. 2003), would result in seasonal survival patterns.
528 Indeed, survival of Coastal Cutthroat in small Oregon streams was lower during late summer-fall

529 periods, coinciding with the period of lowest discharge (Berger and Gresswell 2009).
530 Contrasting effects of season on survival for various age classes of stream salmonids, such as
531 those observed in Brown Trout (Carlson et al. 2008), may have limited our ability to detect an
532 effect of seasonality since exact fish ages were not available. Additionally, survival bottlenecks
533 related to density may operate over relatively short intervals of time (Milner et al. 2003) with
534 fish moving to mitigate competitive interactions during such bottlenecks (Keeley 2001, Gowan
535 and Fausch 2002). This competition-mediated movement may have alleviated any density effects
536 on individuals through more efficient use of variable resources over a spatial scale greater than
537 the habitat unit. However, the lack of an observable effect of Coho Salmon density on Cutthroat
538 Trout survival, despite substantial increases in salmon density, suggests that other factors may
539 have been more important in explaining variation in Cutthroat Trout survival in Rock Creek.

540
541 *****Alternative explanations for the absence of Coho Salmon effects.*—Although we did not
542 detect effects of increasing juvenile densities of Coho Salmon on Cutthroat Trout growth,
543 movement, or survival, it is possible that effects occurred but were not detected due to low
544 power, or that they will occur in the future (Ham and Pearsons 2000, Ham and Pearsons 2001;
545 Pearsons and Temple 2010). Specifically, negative effects from existing Coho Salmon densities
546 may also simply take time to emerge as a result of the lag time required for the Cutthroat Trout
547 population to achieve equilibrium with current fish community conditions. In this case it is
548 conceivable that effects will become apparent as older cohorts of Cutthroat Trout, which
549 experienced low Coho Salmon densities early in life die off, and future cohorts are less
550 successful. This is particularly likely if Coho Salmon spawners increase their use Rock Creek
551 because Cutthroat Trout would face more continuous exposure to high juvenile Coho Salmon

552 densities than they have with Coho spawning limited to the Cedar River. Future negative
553 impacts would also be likely if Coho Salmon populations continue to grow, increasing the
554 disparity in relative densities (Harvey and Nakamoto 1996), or as a result of changing
555 environmental conditions which intensify interspecific interactions. Alternatively, if Coho
556 Salmon populations grow, they may increasingly provide benefits to Cutthroat Trout directly
557 through their eggs and flesh and indirectly through marine nutrient subsidies to the food web
558 (Schindler et al. 2003; Romine et al. 2013).

559

560 **Conclusions.**—Despite an eightfold increase in juvenile Coho Salmon density over four
561 years, we observed no adverse effects on the resident Cutthroat Trout population. However,
562 seasonal and within-season variation in stream discharge, and conspecific density affected
563 growth and movement of trout. Our results suggest that abiotic factors and intraspecific
564 competition may have had stronger influence on Cutthroat Trout populations than interspecific
565 competition with Coho Salmon. It is possible that we were simply unable to detect effects of
566 colonizing salmon, or that impacts on trout will emerge in the future corresponding to continued
567 expansion of the spatial distribution and abundance of Coho Salmon populations. However,
568 during our study juvenile Coho Salmon densities were already comparable to those found in
569 similar streams in the U. S. Pacific Northwest. Effective resource partitioning between the
570 species resulting from a legacy of co-evolutionary history may explain the lack of detectable
571 impacts thus far. Our results suggest that restoration of native anadromous salmon populations
572 may not measurably impact resident salmonid species relative to other sources of variability over
573 short time periods. However, care should be taken to identify acceptable impact limits, and to
574 design studies with sufficient power and duration to detect those effects.

575

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586

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843

844 <A>Tables

845 **Table 1.** Timing of electrofishing and habitat survey events and the number habitat units
 846 sampled in three reaches of Rock Creek from 2005 through 2009. Efforts were made to sample
 847 all pools and pool-like habitats within each reach; in some events some habitat units, typically at
 848 the bottom or top of a reach were not sampled and the number of these are listed in parentheses.

Event	Start Date	Season	Number of Habitat Units Sampled			
			Reach 1	Reach 2	Reach 3	Total
1	8/9/2005	Summer 2005	23	16	11	50
2	10/20/2005	Fall 2005	23	13(4)		36
3	2/21/2006	Winter 2006	19(3)	13(4)		32
4	7/10/2006	Summer 2006	23	17	11	51
5	9/25/2006	Fall 2006	23	18	11	52
6	3/8/2007	Winter 2007	20			20
7	7/24/2007	Summer 2007	18(1)	13	12	43
8	9/25/2007	Fall 2007	17(2)	13	9(2)	39
9	4/3/2008	Spring 2008	19		11	30
10	7/28/2008	Summer 2008	18		11	29
11	9/30/2008	Fall 2008	18		11	29
12	3/24/2009	Spring 2009	16(1)		12	28
13	8/17/2009	Summer 2009	15(1)		11	26
14	9/23/2009	Fall 2009	16		11	27

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851 **Table 2.** Descriptive statistics for variables used in growth and survival analyses from 2005-
852 2009 in Rock Creek.

Variable	Abbreviation	Mean	Min	Max	CV (%)
<i>Individual Variables</i>					
Cutthroat Trout Length (mm)	Lgth	113	60	280	11
Cutthroat Trout Weight (g)	Wt	17.8	1.8	229.4	8
Movement Distance Between Captures (m)	Mov.dist	0.1	0	163	177
Movement Between Captures (Yes/No)	Mov.cat	NA	NA	NA	NA
<i>Environmental and Temporal Variables</i>					
Mean Daily Discharge (m/s ³)	Flow	3.59	0.26	72.21	152
Mean Daily Water Temperature (°C)	Temp	9.21	0.20	18.07	42
Season	Ssn	NA	NA	NA	NA
Year	Yr	NA	NA	NA	NA
Event	Evt	NA	NA	NA	NA
<i>Habitat Variables</i>					
Habitat Unit Area (m ²)	Area	48.08	3.64	189.42	16
Habitat Unit Width (m)	Width	4.60	0.82	15.80	11
Habitat Unit Max. Depth (m)	Depth	0.56	0.04	1.40	14
Habitat Unit Residual Depth (m)	RHD	0.36	0.00	1.15	17
Reach (1, 2, 3)	Reach	NA	NA	NA	NA
<i>Biological Variables</i>					
Coho Biomass Density (g/m ²)	Co.bm.den	0.74	0.00	22.37	255
Trout Biomass Density (g/m ²)	Trt.bm.den	2.11	0.00	26.76	134

¹ Salmonid Biomass Density (g/m ²)	Sal.bm.den	2.86	0.00	29.35	134
Coho Density (#/m ²)	Co.den	0.14	0.00	4.86	252
Trout Density (#/m ²)	Trt.den	0.17	0.00	1.35	106
¹ Salmonid Density (#/m ²)	Sal.den	0.31	0.00	5.18	141

853 ¹Salmonid biomass and numerical densities were primarily comprised of Cutthroat Trout and
854 Coho Salmon but also included Chinook Salmon and Rainbow Trout, which were infrequently
855 encountered.

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872 **Table 3.** The number of Cutthroat Trout tagged (T) each year from 2005-2009 in reaches 1 and 3
 873 of Rock Creek and the percent of those were subsequently detected (D) by stationary antennas at
 874 the mouth of Rock Creek or physically recaptured (R) through the fall of 2010.¹

Year	Reach 1			Reach 3			Totals		
	T	D (%)	R (%)	T	D (%)	R (%)	T	D (%)	R (%)
2005	182	46	30	99	17	14	281	36	25
2006	118	49	42	153	24	31	271	35	35
2007	120	53	48	103	23	56	223	39	52
2008	204	53	39	81	11	40	285	41	39
2009	195	42	34	219	8	27	414	24	30
Total	819	48	38	655	16	32	1474	34	35

875 ¹Reach 2 is omitted because sampling did not continue beyond fall 2007.

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888 **Table 4.** Best candidate GLMs including covariates explaining variability in Cutthroat Trout parr
 889 and fry growth. Symbols (+,-) denote the trend of the slope for each covariate and are displayed
 890 for univariate models only. Models are listed from most plausible ($\Delta AIC_c=0$) to least plausible.
 891 The Akaike weight w_i indicates the relative likelihood of the best fitting model compared to other
 892 models. The ratio of Akaike weights (w_i/w_1) indicates the plausibility of the best fitting model
 893 (w_1) compared to other models (w_i). The five best models and the intercept only (.) model are
 894 shown.

Growth Model	ΔAIC_c	w_i	R^2	w_i/w_1
Cutthroat Parr				
Flow (+), Trt.den (-), Sal.den (+), Reach	0.00	0.17	0.12	1.00
Flow (+), Trt.den (-), Sal.den (+), Co.den (-)	0.91	0.11	0.11	1.58
Flow (+), Trt.den (-), Sal.den (+), Wt (-)	1.29	0.09	0.10	1.91
Flow (+), Trt.den (-), Sal.bm.den (+), Wt(-)	2.07	0.06	0.10	2.81
Flow (+), Trt.den (-), Sal.den (+)	3.86	0.03	0.09	6.89
(.)	16.92	0.00	0.00	4721.13
Cutthroat Fry				
Wt (-), Yr (-), Trt.bm.den (-), Sal.bm.den (+)	0.00	0.16	0.42	1.00
Wt (-), Yr (-), Trt.bm.den (-), Sal.den (+)	2.62	0.04	0.39	3.67
Wt (-), Yr (-)	3.36	0.03	0.34	5.27
Wt (-), Yr (-), Trt.bm.den (-)	4.19	0.02	0.36	8.32
Wt (-), Yr (-), Move.cat	4.29	0.02	0.36	8.32
(.)	27.28	0.00	0.00	919345.96

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896 <A> Figure Captions

897 **Figure 1.** Map of the Cedar River, WA and tributaries above Landsburg Diversion Dam. The
898 midpoints of three study reaches are shown as solid lines perpendicular to the creek. A stream-
899 spanning 6-antenna PIT tag detection array was located at the downstream boundary of reach 1
900 at the mouth of Rock Creek. Stream reaches accessible to upstream migrating fishes are solid
901 lines; dashed lines are stream reaches above natural migration barriers.

902

903 **Figure 2.** Summer (a) and Fall (b) mean + 1 SE fish density in pools of Rock Creek from 2005-
904 2009. Summer and fall data are from reaches 1 and 3, and reach 1, respectively, which were
905 sampled years in those seasons. Colors represent various species and age classes; age 0 trout fry
906 (black), age 1+ trout parr (dark gray), all trout (light gray), and Coho Salmon (white).

907

908 **Figure 3.** The relationship between fork length at tagging and the amount of time before
909 Cutthroat Trout were first detected emigrating from Rock Creek (n = 523). Points are colored
910 according coho density (split into four quartiles by number of observations) in habitat units at the
911 time fish were tagged. Dashed horizontal lines represent one and two years after tagging.

912

913 **Figure 4.** Relationships between habitat unit Coho Salmon density and whether or not Cutthroat
914 Trout moved from their tagging locations and were recaptured in a different habitat unit (a), and
915 relationships between habitat unit Coho Salmon density and Cutthroat Trout growth rate (b)
916 between summer and fall from 2005-2009 (n = 285). Movement data are frequency histograms
917 of the number of movers (grey) and non-movers (black). Data include both age-0 and age-1 and
918 older cutthroat trout. Note different scales on y-axis.

919

920 <A>Appendices

921 **Appendix A**

922 **Table A1.** Relative support¹ for covariates describing the effect of abiotic and biotic factors on
 923 survival probabilities for Coastal Cutthroat trout in the first period after marking in reach 1 of
 924 Rock Creek from fall 2005 through fall 2009. Variables were fit as continuous predictors (slope
 925 and intercept); the null model is (.). Models are listed from most plausible ($\Delta QAIC_c$ or $\Delta AIC_c =$
 926 0)¹ to least plausible. The Akaike weight w_i indicates the relative likelihood of the best fitting
 927 model compared to other models. DS denotes the dataset for corresponding models.

Survival Model	$\Delta(Q)AIC_c$	w_i	K	Slope	SE	2.5%CI	97.5%CI
<i>Reach 1 dataset</i>							
(.)	0.00	0.27	14	-	-	-	-
Residual Pool Depth	1.35	0.14	16	1.71	1.03	-0.31	3.72
Distance Upstream	1.62	0.12	16	0.00	0.00	-0.01	0.00
Maximum Pool Depth	1.86	0.11	16	1.58	1.00	-0.37	3.53
ln (Coho Biomass Density)	3.46	0.05	16	0.40	0.45	-0.47	1.28
ln (Coho Density)	3.56	0.05	16	0.15	0.17	-0.18	0.49
Condition Factor	3.62	0.04	16	1.77	2.19	-2.53	6.07
ln (Weight)	3.62	0.04	16	-0.19	0.23	-0.64	0.25
ln (Salmonid Density)	3.83	0.04	16	0.15	0.21	-0.26	0.56
Pool Area	4.02	0.04	16	0.00	0.01	-0.01	0.02
ln (Trout Density)	4.17	0.03	16	0.07	0.28	-0.47	0.61
ln (Salmonid Biomass Density)	4.19	0.03	16	0.04	0.20	-0.35	0.43
ln (Trout Biomass Density)	4.21	0.03	16	-0.02	0.20	-0.41	0.38

Reaches 1 & 3 dataset

(.)	0.00	0.26	14	-	-	-	-
ln (Trout Density)	1.95	0.10	16	0.30	0.21	-0.11	0.72
ln (Weight)	2.12	0.09	16	-0.26	0.20	-0.65	0.14
ln (Coho Density)	2.17	0.09	16	0.20	0.15	-0.10	0.50
ln (Salmonid Density)	2.42	0.08	16	0.22	0.18	-0.12	0.57
ln (Salmonid Biomass Density)	2.87	0.06	16	0.20	0.19	-0.18	0.58
ln (Trout Biomass Density)	3.10	0.06	16	0.17	0.18	-0.18	0.52
Distance Upstream	3.26	0.05	16	0.00	0.00	0.00	0.00
Condition Factor	3.38	0.05	16	1.11	1.52	-1.87	4.09
Pool Area	3.53	0.05	16	0.00	0.01	-0.02	0.01
Residual Pool Depth	3.83	0.04	16	0.27	0.83	-1.35	1.90
Maximum Depth	3.86	0.04	16	0.24	0.82	-1.36	1.84
ln (Coho Biomass Density)	3.91	0.04	16	0.05	0.31	-0.55	0.65

928 ¹QAIC_c for reach 1 dataset, AIC_c for reaches 1 and 3 dataset; see methods.

929

930 **Appendix B**

931 **Table B1.** Model structure and relative support¹ for temporal models of survival of Coastal
 932 Cutthroat Trout in Rock Creek. Capitalized model variables were fit as continuous variables and
 933 lower-case variables were fit as factors. Additive linear models are denoted by +, and
 934 multiplicative models (interaction) by :, and combined additive and multiplicative by *
 935 (interaction + additive effect). The null model is (.). TSM is the time-since-marking, time is the
 936 capture event and season is fall, spring, or summer. Models are listed from most plausible

937 ($\Delta Q A I C c$ or $\Delta A I C c = 0$)¹ to least plausible. The Akaike weight w_i indicates the relative
 938 likelihood of the best fitting model compared to other models. The number of parameter is
 939 denoted by K .

Survival Model	$\Delta(Q)AIC_c$	w_i	K
<i>Reach 1 dataset</i>			
(.)	0.00	0.44	14
TSM	0.05	0.43	15
season	3.86	0.06	16
TSM : season	4.28	0.05	17
TSM * season	8.21	0.01	19
TSM : time	8.41	0.01	21
time	10.46	0.00	22
TSM + time	13.26	0.00	24
TSM * time	30.60	0.00	33
<i>Reaches 1 & 3 dataset</i>			
TSM + time	0.00	0.23	18
TSM * time	1.16	0.13	22
TSM : time	1.88	0.09	19
(.)	2.21	0.08	14
season	2.55	0.06	16
TSM	2.84	0.06	15
reach	3.28	0.04	15
TSM * season	3.37	0.04	19

TSM : season	3.58	0.04	17
TSM : reach	3.65	0.04	16
reach + season	4.08	0.03	17
TSM + time + reach	4.09	0.03	20
TSM + reach	4.33	0.03	16
TSM + season	4.86	0.02	18
TSM * reach	5.67	0.01	17
reach : time	5.72	0.01	23
time	5.97	0.01	20
reach : season	6.55	0.01	19
TSM + season + reach	6.67	0.01	19
reach + time	7.80	0.00	21
TSM : season : reach	8.76	0.00	20
TSM : time : reach	9.40	0.00	23
TSM * season : reach	9.68	0.00	24
TSM * time : reach	13.05	0.00	32

940 ¹QAIC_c for reach 1 dataset, AIC_c for reaches 1 and 3 dataset; see methods.

941

942 **Appendix C**

943 **Table C1.** Model structure and relative support¹ for models of recapture probabilities for Coastal
 944 Cutthroat Trout in Rock Creek from fall 2005 through fall 2009. Capitalized model variables
 945 were fit as continuous variables and non-capitalized variables were fit as factors. Additive linear
 946 models are denoted by +, and multiplicative models (interaction) by :, and combined additive and

947 multiplicative by * (interaction + additive effect). The null model is (.). TSM is the time-since-
 948 marking, time is the capture event and season is fall, spring, or summer. Models are listed from
 949 most plausible ($\Delta QAIC_c$ or $\Delta AIC_c=0$)¹ to least plausible. The Akaike weight w_i indicates the
 950 relative likelihood of the best fitting model compared to other models. The number of parameter
 951 is denoted by K .

Recapture Model	$\Delta(Q)AIC_c$	w_i	K
<i>Reach 1 dataset</i>			
TSM + time	0.00	0.68	14
time	2.20	0.22	13
TSM * time	3.84	0.10	23
season	15.48	0.00	4
TSM + season	16.27	0.00	5
TSM * season	20.02	0.00	7
TSM	73.93	0.00	3
(.)	82.68	0.00	2
<i>Reaches 1 & 3 dataset</i>			
reach : time	0.00	0.88	14
time	5.63	0.05	8
reach + time	6.70	0.03	9
TSM + time	7.50	0.02	9
TSM + time + reach	8.51	0.01	10
TSM * time : reach	10.04	0.01	25
TSM * time	15.50	0.00	14

reach + season	29.96	0.00	5
TSM + season + reach	30.75	0.00	6
season	33.19	0.00	4
reach : season	33.47	0.00	7
TSM + season	33.56	0.00	5
TSM * season	37.53	0.00	7
TSM * season : reach	41.03	0.00	13
reach + TSM	118.33	0.00	4
reach * TSM	120.33	0.00	5
TSM	121.72	0.00	3
reach	127.82	0.00	3
(.)	131.41	0.00	2

952 ¹QAIC_c for reach 1 dataset, AIC_c for reaches 1 and 3 dataset; see methods.

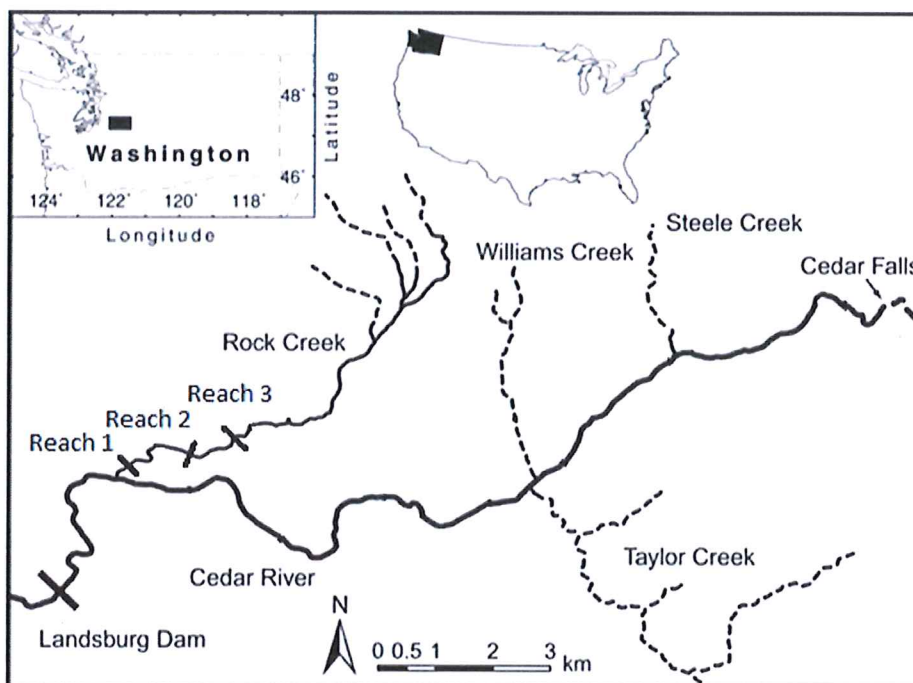


Figure 1. Map of the Cedar River, WA and tributaries above Landsburg Diversion Dam. The midpoints of three study reaches are shown as solid lines perpendicular to the creek. A stream-spanning 6-antenna PIT tag detection array was located at the downstream boundary of reach 1 at the mouth of Rock Creek. Stream reaches accessible to upstream migrating fishes are solid lines; dashed lines are stream reaches above natural migration barriers.

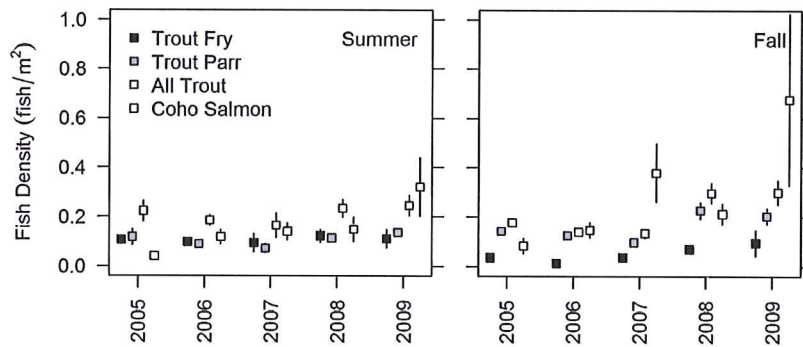


Figure 2. Summer (a) and Fall (b) mean + 1 SE fish density in pools of Rock Creek from 2005-2009. Summer and fall data are from reaches 1 and 3, and reach 1, respectively, which were sampled years in those seasons. Colors represent various species and age classes; age 0 trout fry (black), age 1+ trout parr (dark gray), all trout (light gray), and Coho Salmon (white).
165x88mm (300 x 300 DPI)

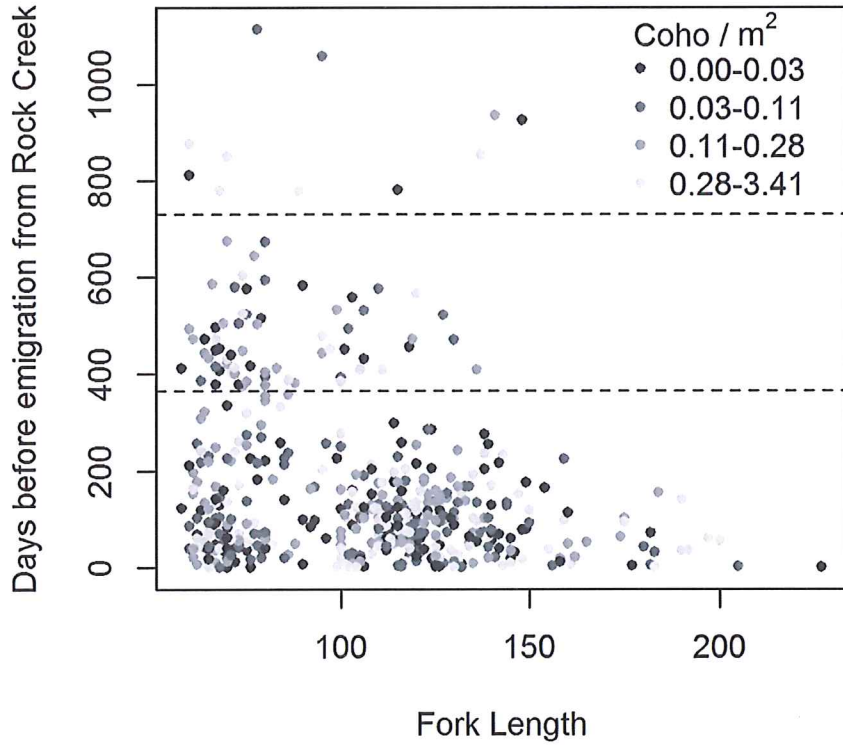


Figure 3. The relationship between fork length at tagging and the amount of time before Cutthroat Trout were first detected emigrating from Rock Creek (n = 523). Points are colored according coho density (split into four quartiles by number of observations) in habitat units at the time fish were tagged. Dashed horizontal lines represent one and two years after tagging.

101x101mm (300 x 300 DPI)

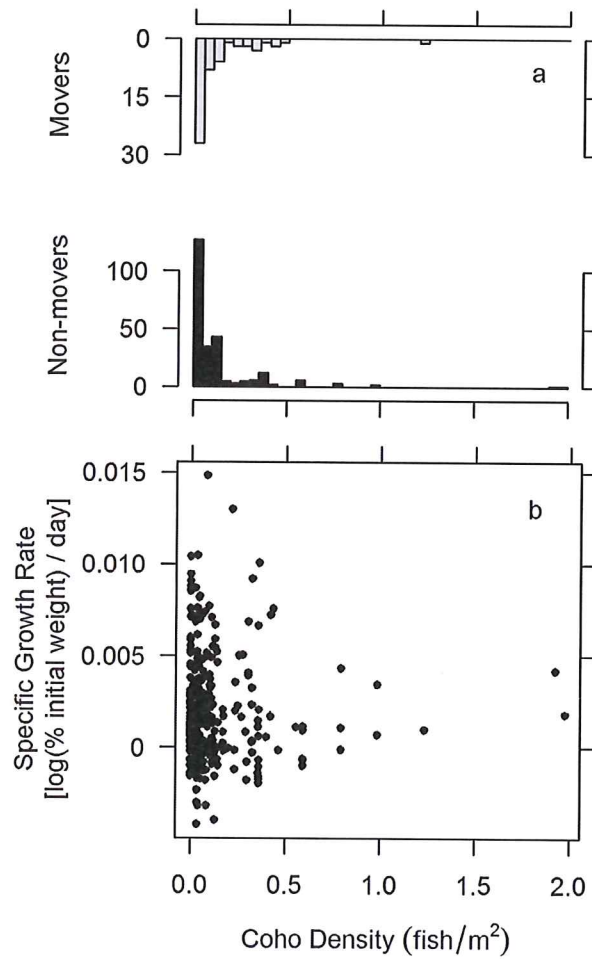


Figure 4. Relationships between habitat unit Coho Salmon density and whether or not Cutthroat Trout moved from their tagging locations and were recaptured in a different habitat unit (a), and relationships between habitat unit Coho Salmon density and Cutthroat Trout growth rate (b) between summer and fall from 2005-2009 (n = 285). Movement data are frequency histograms of the number of movers (grey) and non-movers (black). Data include both age-0 and age-1 and older cutthroat trout. Note different scales on y-axis.

88x152mm (300 x 300 DPI)