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

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Abstract

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

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

The removal of migration barriers is a common technique used to restore migratory fish populations (Bednarek 2001; Anderson et al. 2014). However, it has the additional consequence of altering the dynamics of stream fish communities, providing an opportunity to measure the impact of novel interspecific interactions on resident fish populations (Kiffney et al. 2009, Pess et al. 2011, Naman et al. 2013, G. Temple, WDFW, unpublished data). The addition of salmonid species via recolonization may increase total salmonid biomass production in streams because of niche partitioning (Everest and Chapman 1972; McMichael and Pearsons 1988), or in the case of Pacific Salmon, through marine nutrient subsidies that benefit resident species (Schindler et al. 2003). However, niche overlap between species can result in competition for resources, leading.
to reduced abundance, growth, and survival, or altering the behavior or distribution of one or
both of the species (Hartman 1968, Glova 1984, Glova 1986, Harvey and Nakamoto 1996, Sabo
and Pauley 1997). Understanding the impacts of salmon recolonization on resident species is
important for resource managers weighing the benefits of restoring extirpated native species
against the potential impacts on extant native resident species (McMichael and Pearsons 1998,

In coastal watersheds of the Pacific Northwest the recolonization of Pacific salmon
creates the potential for strong interspecific interactions with trout because fall-spawning salmon
produce larger numbers of offspring that emerge earlier and at a larger size than those of spring–
spawning Coastal Cutthroat Oncorhynchus clarkii clarkii and Rainbow Trout O. mykiss (Quinn
2005). In particular, there is the potential for competition between Cutthroat Trout and Coho
Salmon O. kisutch, because Coho Salmon typically spend ~12 months in streams prior to
seaward migration (Quinn 2005) and use similar habitats to those occupied by juvenile Cutthroat
Trout (Bisson et al. 1988). Coho Salmon can competitively displace, or contribute to reduced
growth and survival of juvenile Cutthroat Trout (Glova 1984, 1986, Trotter 1989, Sabo and
Pauley 1997, Young 2004). Experiments at the habitat unit scale showed that Coho Salmon
were competitively dominant in pools and forced trout into higher velocity riffle habitats (Glova
1986) where they experience reduced growth rates due to higher metabolic costs (Rosenfeld and
Boss 2001). Accordingly, trout appear to prefer pools in the absence of salmon (Glova 1986).
Salmonids in Pacific Northwest streams may also partition their habitat use at larger spatial
scales; Coho Salmon dominate in low gradient reaches and lower in watersheds (Glova 1984,
Rosenfeld et al. 2000), whereas Cutthroat Trout often use headwater areas where they are
isolated from other species (e.g., Buehrens et al. 2013) and appear to benefit from such isolation (Connolly and Sauter 2008).

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

Although there is an extensive body of research on the roles of inter- and intraspecific competition in regulating stream salmonid communities in the Pacific Northwest, few studies have evaluated the effects of salmon reintroduction on extant trout populations. As the prevalence of salmon reintroduction projects grows (e.g., Anderson et al. 2014), a better understanding of effects on resident trout species is needed (McMichael and Pearsons 1998, Pearsons and Temple 2007, Brenkman et al. 2008). Construction of fish passage facilities at Landsburg Dam in 2003 provided access to upstream habitats for Pacific salmon in the Cedar River and Rock Creek, Washington, USA, where resident Coastal Cutthroat and Rainbow Trout had persisted above the dam in isolation from salmon for over 100 years. Recolonization of the upper Cedar River by Coho Salmon and Chinook Salmon *O. tshawytscha* occurred immediately following the installation of a fish ladder (Anderson and Quinn 2007) and the abundance and
spatial distributions of adults and juveniles of both species has continued to increase each year, increasing the opportunity for interactions with resident species (Anderson et al. 2008, Kiffney et al. 2009, Naman et al. 2013). Although restoring habitat connectivity appears to have benefited Coho and Chinook salmon populations, effects on resident trout are unknown. Therefore, the objective of this study was to determine the influence of juvenile Coho Salmon density, relative to other abiotic and biotic factors, on the growth, movement, and apparent survival of Cutthroat Trout in Rock Creek during a period of rapidly increasing Coho Salmon abundance (2005 – 2009).

Methods

Study site.—The Cedar River is a 487 km² watershed originating at the crest of the Cascade Mountains in Washington State and draining westward into Lake Washington (Figure 1). The upper Cedar River flows over a series of impassable waterfalls, continuing through 53 km of historical anadromous fish habitat. Landsburg Diversion Dam, built in 1901, blocked anadromous fish access to the upper 20 km of historical habitat until a fish ladder was constructed in 2003 to allow fish passage above the dam. Rock Creek enters the Cedar River 2 km above Landsburg Dam and has approximately 13 km of habitat accessible to anadromous fish. The 15 km² watershed has a rain-dominated hydrograph with peak flows in winter and low flows in summer. From 2003 through 2009 the abundance of adult Coho and Chinook salmon upstream of the dam increased from 47 to 679 and 79 to 138, respectively (though there were 397 Chinook Salmon in 2007: Burton et al. 2013). For both species the vast majority of spawning occurred in the Cedar River; Chinook Salmon spawning only occurred in Rock Creek in 2007 (six redds), and Coho Salmon spawners were not documented in Rock Creek until fall.
2009, meaning that salmon presence was limited primarily to juvenile colonists. Past timber
harvest has locally reduced large woody debris abundance but habitat conditions are otherwise
largely intact within the upper Cedar River watershed. Because the Cedar River is the source of
drinking water for the City of Seattle, the watershed is protected from any further disturbance or
development. In addition to colonizing Coho and Chinook salmon, the upper Cedar River
contains populations of Coastal Cutthroat Trout, Rainbow Trout, Speckled Dace Rheinichthys
osculus, Mountain Whitefish Prosopium williamsoni, sculpins Cottus spp., and lampreys
Entosphenus tridentatus and Lampetra spp. Chinook Salmon were rarely encountered and
Rainbow Trout were < 10% of the trout population in Rock Creek, however Rainbow Trout were
included in trout densities and both species were included in total salmonid densities and
modeled as covariates.

Fish collection and habitat surveys.—Fish and habitat sampling occurred in 14 mark and
recapture events, lasting three to seven days each, during late winter, mid-summer, and fall each
year from 2005 through 2009 (Table 1). Sampling occurred at reach and habitat unit scales to
account for the hierarchical organization of riverine ecological processes (Frissell et al. 1986).
Mark and recapture events occurred in 26-52 habitat units within three 200-500 m reaches
numbered 1-3 in ascending order moving upstream from the mouth of Rock Creek to rkm (river
kilometer) 2.5 (Figure 1). Only pools and pool-like habitat units were sampled for this study
because pools act as congregation points for several fish species during summer low flow periods
(Glova 1986). The number of habitat units sampled during each event varied over time because
in some events some reaches were not sampled, and because seasonal high flows occasionally
changed the stream’s configuration. However, in most cases all pools and pool-like habitat units
within a reach were sampled (Table 1).
All fish species were collected using three-pass electrofishing depletion (Carle and Strub 1978); captured individuals were held in buckets, anesthetized with MS-222 (80 mg/L), measured (fork length to the nearest mm), weighed to the nearest 0.1 g, and enumerated. Cutthroat Trout > 60 mm and 2 g, which were large enough to tag (Peterson et al. 1994) were identified to species and implanted with a 12 mm Passive Integrated Transponder (PIT) tag in their body cavity using a syringe sterilized in 70% ethanol. After tagging, all fish were allowed to recover and released in the habitat unit where they were captured.

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

During each tagging event, surveys were completed on all habitat units to quantify maximum and tail-out depths and surface areas, water velocity, and to characterize substrate composition and available cover types. Water temperature data were collected by a series of continuously deployed data loggers (Onset Co., Cape Cod, MA). Stream discharge data were not available for Rock Creek, so we used discharge data from the Raging River (USGS 12145500) near Fall City, WA. The Raging River is representative of the temporal pattern of discharge in Rock Creek and has similar hydrological characteristics, but has approximately three times the drainage area. Because we wished to distinguish potential effects of stream flow, which varies predictably at a seasonal timescale, from the effect of season, we used a measure of flow.
anomalies (mean percent of mean daily flow or each day). These anomalies were then averaged across each between-sampling interval for use as a covariate in growth and survival analysis.

Fish densities (fish/m²) and fish biomass densities (grams of fish/m²) were estimated for each habitat unit during each event based on the sum of individuals (numerical density) or weights (biomass density) divided by the surface area of each habitat unit. Yearly mean densities were calculated for summer as the mean of densities in all habitat units in reaches 1 and 3, which were sampled in all summers, whereas mean fall densities were calculated for reach 1 only since it was the only reach sampled in each fall (Table 1). Linear regression was used to determine whether there were significant increases or decreases in mean log transformed fish density for both summer and fall between 2005 and 2009.

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

$$SGR = \left[ \frac{\ln(w_f) - \ln(w_i)}{\Delta t} \right] \times 100$$

where \( w \) is weight, and \( t_i \) and \( t_f \) denote time periods in which the initial and the final measurements of weight were made. A comparison of growth rates among seasons was conducted to determine whether they could be pooled for subsequent analysis. Variance in growth among seasons was unequal (Levene’s test, \( P = 0.02 \)). Thus, a generalized linear model (GLM) assuming normal error structure with a linear link function, with observations weighted by the inverse variance of growth in each season, was used to compare growth among seasons. A series of candidate GLMs, assuming normal error structure with linear link functions, were constructed to correlate the growth of individual fish within each seasonal interval with combinations of explanatory variables. Maximum likelihood estimates were obtained for all GLM parameters. The explanatory variable list included covariates measured at multiple spatial locations.
scales which were thought to include many of the common factors affecting resident trout populations: movement history (variable indicating whether a fish was recaptured in the same habitat unit it was originally captured) was a covariate corresponding to individual fish; habitat quality and fish community densities (fish / m² and biomass—grams of fish / m²) were measured at the habitat unit scale; reach was a factor denoting the reach fish were tagged in; water temperature, discharge and time period were factors applied to all individuals tagged within an event (Table 2). Initial weight was also included in growth models as an independent variable to account for allometric scaling of growth with size. Our models were exploratory in nature and it was unknown what combinations of factors might explain Cutthroat Trout growth (n = 217 Cutthroat Trout parr and 68 fry growth rates). Consequently, all subsets of variables were considered during model selection (1942 per age class) but models were limited to a maximum of four explanatory variables (e.g., Pess et al. 2011).

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

Model selection.—Akaike’s Information Criterion for small sample sizes (AICc) was calculated to compare and rank the various growth and movement models including the null (intercept only) model. The lowest AICc value denoted the best model and models with ΔAICc
<2 were considered to have substantial support, those with values from 4 to 7 had little support, and those greater than 10 had no support (Burnham and Anderson 2002). We also calculated Akaike weight, $w_i$, a measure of the relative likelihood of the best fitting model compared to other models. The ratio of Akaike weights ($w_j/w_i$) indicates the plausibility of the best fitting model ($w_j$) compared to other models ($w_i$). All statistical analyses were performed in R (R Development Core Team 2011) unless otherwise noted.

**Survival analysis.**—Cutthroat Trout survival and covariates affecting it were modeled with Cormack-Jolly-Seber (CJS) open population models (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992) using program RMARK (Laake and Rexstad 2008) and MARK (White and Burnham 1999). CJS models incorporate a binary capture history for each fish (observed/not observed) and the length of this history corresponds to the number of capture occasions in a study. The model structure simultaneously estimates the probability of apparent survival (the proportion of animals remaining alive and within the study area) between occasions and the probability that surviving individuals are encountered on each occasion. Apparent survival is appropriate for open populations where individuals can leave the study area and it is not possible to differentiate between fish that died and fish that emigrated. The CJS model assumes 1) all marked animals present at time $i$ have an identical probability of being captured, $p_i$, during that period and of surviving, $\Phi_i$, between time $i$ and the following sampling event $i+1$; 2) that tags (marks) are not lost or undetected in captured individuals; 3) sampling occasions are instantaneous; 4) emigration of tagged individuals is permanent; 5) the probability of capture and survival is independent among individuals (Williams et al. 2002). Our study reasonably satisfied assumptions 3-5: The length of time of sampling events relative to the time between events was very small (3), we excluded known emigrants from our analyses (4), and there was no *a priori*
reason to suspect a lack of independence between sampling of individuals (5). Tag retention and
detection rates (2) have been high in comparable studies of Cutthroat Trout (Berger and
Gresswell 2009); although some tags were undoubtedly lost or not detected we did not correct
for this bias which would tend to underestimate survival (Knudsen et al. 2009). Identical capture
probability for all animals in each period (1) was the most difficult assumption to satisfy since
fish may move within the study area and certain locations may be more or less conducive to their
capture. Efforts were made to meet this assumption through accounting for sampling intensity
by constructing separate models for data subsets that included the same sampling frequency and
intensity.

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

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

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

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

The program RELEASE within MARK was used to assess the goodness of fit of full
models (separate estimate of survival (\( \Phi \)) for each time period) for both datasets and to generate
estimates of the variance inflation factor \( \hat{e} \), a measure of over-dispersion. Goodness of fit tests
suggested no significant overall lack of fit for either dataset; however, for the reach 1 dataset
where $c = 1.33$, this value was thus used to adjust model selection criteria (QAICc), standard
errors and confidence intervals, resulting in somewhat reduced statistical power. A value of $c = 1.0$
was used for the reach 1 and 3 dataset since the estimate generated by RELEASE was $< 1$.

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

<A>Results

<B>Fish tagging and habitat characteristics.—Between summer 2005 and fall 2009 we
captured 3047 Coho Salmon, 2553 sculpins, 1975 Cutthroat Trout, 1004 trout fry, 551 dace, 178
Rainbow Trout, 39 lampreys, 34 Chinook Salmon, and two Largemouth Bass Micropterus
salmoides, which comprised 32%, 27%, 21%, 11%, 6%, 2%, < 1%, <1%, and < 1% of the fish
population, respectively. We tagged 1851 Cutthroat Trout and trout fry (mean length = 113 mm,
range 60-280 mm) in Rock Creek. We recaptured 394 individuals with a total of 483 recaptures
events when including individuals recaptured multiple times (Table 3). Of these captures and
recaptures 325 occurred in consecutive events and 285 of the recaptures occurred in the fall,
primarily resulting from tagging earlier that summer. Abiotic and biotic conditions in Rock
Creek hypothesized to affect Cutthroat Trout growth and survival did not show a directional
change over time other than Coho Salmon density increasing in summer and fall in all reaches
and trout fry and parr densities increasing in each 1 in the fall (Table 2). In 2005 mean Coho
Salmon density started at 0.04 (summer) and 0.08 fish/m² (fall), which was below that of
combined trout parr and fry (mean = 0.22 and 0.18 fish/m² in summer—reaches 1 and 3, and
fall—reach 1 only, respectively). However, Coho Salmon density increased over the course of
our study in both summer and fall (ΔAICc = 0.01, and 7.08 respectively relative to a null
model) by approximately eightfold to 0.32 and 0.68 fish/m², in summer and fall 2009,
respectively, surpassing the combined trout density in both seasons (Figure 2). Trout fry (age 0),
tROUT parr (age 1 and older), and total trout densities (which were consistently comprised of
>90% Cutthroat Trout) did not show linear trends across years in summer (ΔAICc = 2.05, 0.96,
and 1.51, respectively relative to a null model). Fall densities of trout fry, trout parr, and total
tROUT in reach 1 increased (ΔAICc = 4.9, 5.4, and 12.74 respectively relative to a null model),
however these increases were smaller (0.35-0.95, 0.14-0.20, and 0.18-0.3 fish/m² for trout fry,
parr, and total trout, respectively) than changes in Coho Salmon density (Figure 2).

There were correlations (Pearson’s product-moment correlation coefficient r > 0.6)
between many of the independent variables used to model Cutthroat Trout growth, movement,
and survival. Multicollinear variable sets included negative correlations between temperature and
flow (r = -0.80) and positive correlations between maximum and residual habitat depth (r =
0.85), and the density and corresponding biomass density of each species or species group (r =
0.87, 0.81, and 0.67, for Coho Salmon, all trout, and all salmonids, respectively). Trout and
Coho Salmon densities were positively correlated with total salmonid density (r = 0.83 and 0.75,
respectively) and trout density was correlated with total salmonid biomass density ($r = 0.8$).

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

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

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

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

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

**Summer growth.**—GLM analysis suggested growth rates differed ($\Delta$AICc = 129.6 relative to null model of no age effect) between age classes (assigned based on length), so separate models were constructed for fry and parr to describe the effects of independent variables on specific growth rates (Table 4). Summer growth of both Cutthroat Trout parr and fry was negatively correlated with the density of conspecifics but positively correlated with total salmonid density, and was not related to Coho Salmon density (Table 4; Figure 4). Models of parr growth were not well differentiated by model selection criteria, and explained little of the variance ($R^2 = 0.12$ for
the best model). However, all models of summer parr growth with ΔAICc ≤ 3 included a positive correlation with flow and total salmonid density and a negative correlation with trout density. Reach, Coho Salmon density, and initial weight were each included in one of the best models but did not appreciably affect model selection criteria. The best model of Cutthroat Trout fry growth included negative correlations with initial body weight, year (fit as a continuous fixed effect), and trout biomass density, and a positive correlation with total salmonid biomass density (model $R^2 = 0.41$; Table 4). Models of Cutthroat Trout fry summer growth were better differentiated by model selection criteria than parr growth models and no additional variables were included in the top model set (ΔAICc < 3). Habitat characteristics including distance upstream from the mouth of Rock Creek, maximum and residual habitat depth, and habitat unit surface area were not strongly correlated with growth for either age class of Cutthroat Trout. Individual attributes including condition factor, and whether fish moved or not, also appeared to have little influence on summer growth of Cutthroat Trout parr or fry.

**Survival.**—No effect of Coho Salmon density on Cutthroat Trout survival was detected, however, all individual, abiotic, and biotic covariates had 95% confidence intervals that overlapped zero (Table A1), suggesting that survival was not explained by the variables measured. There was weak evidence that survival decreased with TSM (in both datasets) and differed among time periods (reaches 1 and 3 dataset only), but was similar among reaches. The best models of survival probabilities for the reach 1 dataset were the null model of constant survival over time and a model including a negative correlation with the time-since-marking (TSM) (model: phi ~ TSM), which together accounted for 87% of the model weight (Table B1). The best models of survival for the reaches 1 and 3 dataset included a negative correlation with TSM and an effect of time dependence meaning that monthly survival generally declined with
increasing TSM for all individuals and there was also significant time-dependence (independent survival within each time period) (Table B1). Season was not included in the best models of survival for either dataset.

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

Discussion

There were no detectable effects of initial Coho Salmon colonization on Cutthroat Trout growth, movement patterns, or survival, even though salmon densities increased in each year of our study and were almost an order of magnitude greater in the last year. Coho Salmon density not only varied over the years but also varied greatly among habitat units in each year but no within-year effects were detected either. The role of interspecific competition on stream salmonids is not well resolved; evolved niche segregation may minimize competitive interactions between co-occurring species but, alternatively, realized niches of co-occurring species may be reduced by competition relative to their abiotic niches (Hutchinson 1957, Milner et al. 2003).

Our study suggests that for Coastal Cutthroat Trout and Coho Salmon, which evolved in sympatry, sufficient options may have existed in Rock Creek to minimize negative interspecific interactions during the early stages of colonization by salmon. Alternatively, Coho Salmon impacts may have been undetectable, owing to our lack of study design controls, limited data, or
small effect size (Ham and Pearsons 2000, 2001). In this case the effects may become evident in
the future, particularly if Coho Salmon densities continue to increase, thus increasing the
potential effect size (e.g., Pearsons and Temple 2010).

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

Alternatively, the intraspecific and interspecific density thresholds for growth effects may
differ. There were negative correlations between trout density and both Cutthroat Trout fry and
parr growth, suggesting negative intraspecific density dependence. Conspecific density
dependence has long been recognized to regulate stream salmonid populations (Milner et al.
2003), and may manifest in reduced growth (Spalding et al. 1995, Keeley 2001, Harvey et al. 2005, Teichert et al. 2010). Interestingly, both fry and parr growth were positively associated with total salmonid density; this result is difficult to interpret, but suggests that high growth rates may occur in habitat units that contain good conditions for all salmonid species. Trout fry summer growth also declined across years of the study, and although the reason is unknown, the only factors known to have undergone directional change over the course of the study were the abundance and density of Coho Salmon and the density of trout fry in reach 1 during the fall. The lack of negative effects of Coho Salmon on Cutthroat Trout growth in our study may be a result of habitat partitioning; Coho Salmon prefer slower, deeper areas and are primarily surface feeders, whereas Cutthroat Trout have less association with depth and prefer microhabitats with good conditions for foraging on invertebrate drift (Bisson et al. 1988).

Indeed, micro-habitat measurements in Rock Creek reveal partial segregation of the species by water depth and velocity (Quinn, unpublished data). It is possible, however, that Coho Salmon populations have simply not reached a threshold density where they begin to affect Cutthroat Trout, or that potential effects will not manifest in a relationship with density at the habitat unit scale. For example, after seven years of data collection, Pearsons and Temple (2010) detected negative impacts of introduced stream-type spring Chinook Salmon juveniles resulting from a supplementation program, that they were unable to detect after five years of the program (Pearsons and Temple 2007).

Cutthroat Trout growth was also related to abiotic factors including season, with the highest growth rates occurring from spring to midsummer. Spring was reported as the period of highest growth rates in steelhead (Sogard et al. 2009) and Atlantic Salmon (Bacon et al. 2005), and may provide an optimal balance of temperature, food availability, and stream discharge.
Warmer temperatures in Rock Creek during spring reduce physiological constraints that may limit growth during winter without exceeding thresholds that often result in lower growth during summer months (e.g. McCarthy et al. 2009, Davidson et al. 2010). Discharge in Rock Creek remained relatively high in the spring, and this can enhance growth (Teichert et al. 2010), perhaps related to increased invertebrate drift (Harvey et al. 2006), or usable habitat area. Support for this hypothesis was provided by models of Cutthroat Trout parr summer growth, which indicated a positive effect of stream discharge. Reduced growth during late summer and early fall may result from low flows concentrating fish in the few remaining areas with suitable depth (Glova 1986), food limitation owing to reduced invertebrate drift biomass (Harvey et al. 2006), increased energetic demands from elevated temperatures, or some combination of these factors.

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

The limited movement distances we observed between capture events was consistent with many previous studies of resident trout movement involving physical recaptures (Kahler et al. 2001, Roni et al. 2012), and was likely due in part to the bias imposed by our inability to detect movements to areas outside of our sampled reaches (Gowan et al. 1994). Moreover, most
recaptures occurred at the end of the summer, when fixed antenna detections indicated that
movement was least common. Accordingly, antenna detections revealed that many fish moved
further than was documented by physical recaptures. Evidence of length-dependent emigration
in our study suggests that as they grew, fish increasingly tended to move downstream out of the
study reaches, perhaps as part of an ontogenetic niche shift as their resource needs were no
longer met in small tributary habitat like Rock Creek (Jonsson and Jonsson 1993). In fact there
appeared to be a threshold of ~150 mm length at tagging, above which all individuals that were
detected emigrating did so within the first year after tagging. This size corresponds to the size of
typical smolts in Cutthroat Trout populations and was also the size at which piscivory became
more common in Cutthroat Trout in the Cedar River basin (P. Kiffney, unpublished data), which
may indicate changing energetic demands and associated habitat requirements.

Survival.—Temporal, seasonal, spatial, and individual covariates including Coho Salmon
density did not explain variability in Coastal Cutthroat Trout survival. It is possible that this was
due to our limited ability to differentiate apparent survival, which includes emigration, from
actual survival. Although our model attempted to remove individuals leaving the study area,
upstream emigrants would not have been detected by our antenna arrays, and fish moving to
riffles and other un-sampled habitat units within our study reaches could have complicated our
ability to differentiate survival from emigration. Regardless, we had expected that environmental
conditions such as discharge and temperature, which are seasonally variable in streams, and
influence important aspects of salmonid ecology including growth rates and life history
transitions (Thorpe et al. 1998, Milner et al. 2003), would result in seasonal survival patterns.
Indeed, survival of Coastal Cutthroat in small Oregon streams was lower during late summer-fall
periods, coinciding with the period of lowest discharge (Berger and Gresswell 2009).
Contrasting effects of season on survival for various age classes of stream salmonids, such as those observed in Brown Trout (Carlson et al. 2008), may have limited our ability to detect an effect of seasonality since exact fish ages were not available. Additionally, survival bottlenecks related to density may operate over relatively short intervals of time (Milner et al. 2003) with fish moving to mitigate competitive interactions during such bottlenecks (Keeley 2001, Gowan and Fausch 2002). This competition-mediated movement may have alleviated any density effects on individuals through more efficient use of variable resources over a spatial scale greater than the habitat unit. However, the lack of an observable effect of Coho Salmon density on Cutthroat Trout survival, despite substantial increases in salmon density, suggests that other factors may have been more important in explaining variation in Cutthroat Trout survival in Rock Creek.

Alternative explanations for the absence of Coho Salmon effects.—Although we did not detect effects of increasing juvenile densities of Coho Salmon on Cutthroat Trout growth, movement, or survival, it is possible that effects occurred but were not detected due to low power, or that they will occur in the future (Ham and Pearsons 2000, Ham and Pearsons 2001; Pearsons and Temple 2010). Specifically, negative effects from existing Coho Salmon densities may also simply take time to emerge as a result of the lag time required for the Cutthroat Trout population to achieve equilibrium with current fish community conditions. In this case it is conceivable that effects will become apparent as older cohorts of Cutthroat Trout, which experienced low Coho Salmon densities early in life die off, and future cohorts are less successful. This is particularly likely if Coho Salmon spawners increase their use Rock Creek because Cutthroat Trout would face more continuous exposure to high juvenile Coho Salmon
densities than they have with Coho spawning limited to the Cedar River. Future negative impacts would also be likely if Coho Salmon populations continue to grow, increasing the disparity in relative densities (Harvey and Nakamoto 1996), or as a result of changing environmental conditions which intensify interspecific interactions. Alternatively, if Coho Salmon populations grow, they may increasingly provide benefits to Cutthroat Trout directly through their eggs and flesh and indirectly though marine nutrient subsidies to the food web (Schindler et al. 2003; Romine et al. 2013).

Conclusions.—Despite an eightfold increase in juvenile Coho Salmon density over four years, we observed no adverse effects on the resident Cutthroat Trout population. However, seasonal and within-season variation in stream discharge, and conspecific density affected growth and movement of trout. Our results suggest that abiotic factors and intraspecific competition may have had stronger influence on Cutthroat Trout populations than interspecific competition with Coho Salmon. It is possible that we were simply unable to detect effects of colonizing salmon, or that impacts on trout will emerge in the future corresponding to continued expansion of the spatial distribution and abundance of Coho Salmon populations. However, during our study juvenile Coho Salmon densities were already comparable to those found in similar streams in the U. S. Pacific Northwest. Effective resource partitioning between the species resulting from a legacy of co-evolutionary history may explain the lack of detectable impacts thus far. Our results suggest that restoration of native anadromous salmon populations may not measurably impact resident salmonid species relative to other sources of variability over short time periods. However, care should be taken to identify acceptable impact limits, and to design studies with sufficient power and duration to detect those effects.
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Table 1. Timing of electrofishing and habitat survey events and the number of habitat units sampled in three reaches of Rock Creek from 2005 through 2009. Efforts were made to sample all pools and pool-like habitats within each reach; in some events some habitat units, typically at the bottom or top of a reach were not sampled and the number of these are listed in parentheses.

<table>
<thead>
<tr>
<th>Event</th>
<th>Start Date</th>
<th>Season</th>
<th>Number of Habitat Units Sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Reach 1</td>
</tr>
<tr>
<td>1</td>
<td>8/9/2005</td>
<td>Summer 2005</td>
<td>23</td>
</tr>
<tr>
<td>2</td>
<td>10/20/2005</td>
<td>Fall 2005</td>
<td>23</td>
</tr>
<tr>
<td>3</td>
<td>2/21/2006</td>
<td>Winter 2006</td>
<td>19(3)</td>
</tr>
<tr>
<td>4</td>
<td>7/10/2006</td>
<td>Summer 2006</td>
<td>23</td>
</tr>
<tr>
<td>5</td>
<td>9/25/2006</td>
<td>Fall 2006</td>
<td>23</td>
</tr>
<tr>
<td>7</td>
<td>7/24/2007</td>
<td>Summer 2007</td>
<td>18(1)</td>
</tr>
<tr>
<td>8</td>
<td>9/25/2007</td>
<td>Fall 2007</td>
<td>17(2)</td>
</tr>
<tr>
<td>9</td>
<td>4/3/2008</td>
<td>Spring 2008</td>
<td>19</td>
</tr>
<tr>
<td>10</td>
<td>7/28/2008</td>
<td>Summer 2008</td>
<td>18</td>
</tr>
<tr>
<td>11</td>
<td>9/30/2008</td>
<td>Fall 2008</td>
<td>18</td>
</tr>
<tr>
<td>12</td>
<td>3/24/2009</td>
<td>Spring 2009</td>
<td>16(1)</td>
</tr>
<tr>
<td>13</td>
<td>8/17/2009</td>
<td>Summer 2009</td>
<td>15(1)</td>
</tr>
<tr>
<td>14</td>
<td>9/23/2009</td>
<td>Fall 2009</td>
<td>16</td>
</tr>
</tbody>
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Table 2. Descriptive statistics for variables used in growth and survival analyses from 2005-2009 in Rock Creek.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Abbreviation</th>
<th>Mean</th>
<th>Min</th>
<th>Max</th>
<th>CV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Individual Variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cutthroat Trout Length (mm)</td>
<td>Lgth</td>
<td>113</td>
<td>60</td>
<td>280</td>
<td>11</td>
</tr>
<tr>
<td>Cutthroat Trout Weight (g)</td>
<td>Wt</td>
<td>17.8</td>
<td>1.8</td>
<td>229.4</td>
<td>8</td>
</tr>
<tr>
<td>Movement Distance Between Captures (m)</td>
<td>Mov.dist</td>
<td>0.1</td>
<td>0</td>
<td>163</td>
<td>177</td>
</tr>
<tr>
<td>Movement Between Captures (Yes/No)</td>
<td>Mov.cat</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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<td><strong>Environmental and Temporal Variables</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Daily Discharge (m/s³)</td>
<td>Flow</td>
<td>3.59</td>
<td>0.26</td>
<td>72.21</td>
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<td>Mean Daily Water Temperature (°C)</td>
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<td>0.20</td>
<td>18.07</td>
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<td>Yr</td>
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<td>NA</td>
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<td>Event</td>
<td>Evt</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><strong>Habitat Variables</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat Unit Area (m²)</td>
<td>Area</td>
<td>48.08</td>
<td>3.64</td>
<td>189.42</td>
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</tr>
<tr>
<td>Habitat Unit Width (m)</td>
<td>Width</td>
<td>4.60</td>
<td>0.82</td>
<td>15.80</td>
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<tr>
<td>Habitat Unit Max. Depth (m)</td>
<td>Depth</td>
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<td>0.04</td>
<td>1.40</td>
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<tr>
<td>Habitat Unit Residual Depth (m)</td>
<td>RHD</td>
<td>0.36</td>
<td>0.00</td>
<td>1.15</td>
<td>17</td>
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<td>Reach (1, 2, 3)</td>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><strong>Biological Variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coho Biomass Density (g/m³)</td>
<td>Co.bm.den</td>
<td>0.74</td>
<td>0.00</td>
<td>22.37</td>
<td>255</td>
</tr>
<tr>
<td>Trout Biomass Density (g/m²)</td>
<td>Trt.bm.den</td>
<td>2.11</td>
<td>0.00</td>
<td>26.76</td>
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<tr>
<td></td>
<td>Sal.bm.den</td>
<td>Co.den</td>
<td>Trt.den</td>
<td>Sal.den</td>
<td></td>
</tr>
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<td>----------------</td>
<td>------------</td>
<td>--------</td>
<td>---------</td>
<td>---------</td>
<td></td>
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<tr>
<td>Salmonid Biomass Density (g/m²)</td>
<td>2.86</td>
<td>0.00</td>
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<td>Coho Density (#/m²)</td>
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<td>Trout Density (#/m²)</td>
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<td>1.35</td>
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<tr>
<td>Salmonid Density (#/m²)</td>
<td>0.31</td>
<td>0.00</td>
<td>5.18</td>
<td>141</td>
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</tr>
</tbody>
</table>

1Salmonid biomass and numerical densities were primarily comprised of Cutthroat Trout and Coho Salmon but also included Chinook Salmon and Rainbow Trout, which were infrequently encountered.
**Table 3.** The number of Cutthroat Trout tagged (T) each year from 2005-2009 in reaches 1 and 3 of Rock Creek and the percent of those were subsequently detected (D) by stationary antennas at the mouth of Rock Creek or physically recaptured (R) through the fall of 2010.\(^1\)

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

\(^1\)Reach 2 is omitted because sampling did not continue beyond fall 2007.
Table 4. Best candidate GLMs including covariates explaining variability in Cutthroat Trout parr and fry growth. Symbols (+,-) denote the trend of the slope for each covariate and are displayed for univariate models only. Models are listed from most plausible ($\Delta$AICc=0) to least plausible.

The Akaike weight $w_i$ indicates the relative likelihood of the best fitting model compared to other models. The ratio of Akaike weights ($w_j/w_i$) indicates the plausibility of the best fitting model ($w_i$) compared to other models ($w_j$). The five best models and the intercept only (.) model are shown.

<table>
<thead>
<tr>
<th>Growth Model</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>$R^2$</th>
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<td><strong>Cutthroat Parr</strong></td>
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<tr>
<td>Flow (+), Trt.den (-), Sal.den (+), Reach</td>
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<td>0.17</td>
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<td>0.11</td>
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<td>Wt (-), Yr (-)</td>
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<td>Wt (-), Yr (-), Move.cat</td>
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<td>0.02</td>
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<td>0.00</td>
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</table>
<A> Figure Captions

**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).

**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.

**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.
Appendix A

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

<table>
<thead>
<tr>
<th>Survival Model</th>
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<th>( w_i )</th>
<th>( K )</th>
<th>Slope</th>
<th>SE</th>
<th>2.5%CI</th>
<th>97.5%CI</th>
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<td>14</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>16</td>
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<td>0.00</td>
<td>-0.01</td>
<td>0.00</td>
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<tr>
<td>Maximum Pool Depth</td>
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<td>0.11</td>
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<td>1.58</td>
<td>1.00</td>
<td>-0.37</td>
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<tr>
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<tr>
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<td>0.23</td>
<td>-0.64</td>
<td>0.25</td>
</tr>
<tr>
<td>ln (Salmonid Density)</td>
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<td>0.21</td>
<td>-0.26</td>
<td>0.56</td>
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<tr>
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<td>ln (Trout Density)</td>
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</table>
Reaches 1 & 3 dataset

<p>| | | | | | |</p>
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<tr>
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<td>14</td>
<td>-</td>
<td>-</td>
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<td>0.09</td>
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<td>0.15</td>
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<td>0.18</td>
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<tr>
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\(^1\) QAIC_c for reach 1 dataset, AIC_c for reaches 1 and 3 dataset; see methods.

Appendix B

Table B1. Model structure and relative support\(^1\) for temporal models of survival of Coastal Cutthroat Trout in Rock Creek. Capitalized model variables were fit as continuous variables and lower-case variables were fit as factors. Additive linear models are denoted by +, and multiplicative models (interaction) by ∗, and combined additive and multiplicative by ∗\(^2\). The null model is (.), TSM is the time-since-marking, time is the capture event and season is fall, spring, or summer. Models are listed from most plausible...
(ΔQAICc or ΔAICc−0) to least plausible. The Akaike weight $w_i$ indicates the relative likelihood of the best fitting model compared to other models. The number of parameter is denoted by $K$.

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<th>$K$</th>
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<tr>
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<tr>
<td>TSM * time</td>
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\(^1\)QAIC_c for reach 1 dataset, AIC_c for reaches 1 and 3 dataset; see methods.

**Appendix C**

**Table C1.** Model structure and relative support\(^1\) for models of recapture probabilities for Coastal Cutthroat Trout in Rock Creek from fall 2005 through fall 2009. Capitalized model variables were fit as continuous variables and non-capitalized variables were fit as factors. Additive linear models are denoted by +, and multiplicative models (interaction) by ;, and combined additive and
multiplicative by * (interaction + additive effect). The null model is (.). TSM is the time-since-marking, time is the capture event and season is fall, spring, or summer. Models are listed from most plausible ($\Delta$QAICc or $\Delta$AICc=0)\(^1\) to least plausible. The Akaike weight $w_1$ indicates the relative likelihood of the best fitting model compared to other models. The number of parameter is denoted by $K$.

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<td>0.00</td>
<td>3</td>
</tr>
<tr>
<td>reach</td>
<td>127.82</td>
<td>0.00</td>
<td>3</td>
</tr>
<tr>
<td>()</td>
<td>131.41</td>
<td>0.00</td>
<td>2</td>
</tr>
</tbody>
</table>

1AIC_c for reach 1 dataset, QAIC_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)