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Use of a mechanistic growth model in fish habitat restoration: juvenile Chinook salmon and steelhead as a test case

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Abstract. Few studies of in-stream habitat restoration effectiveness address whether traits that affect fitness of individuals (e.g., growth) are altered by restoring habitat. We used mark-recapture studies to measure growth of sub-yearling Chinook salmon and steelhead in restored and unrestored habitat in the Entiat River, Washington, USA. In each of five sampling years (2009, 2010, 2012, 2013, 2016), we compared growth rates between habitat types, using a mechanistic growth model which we fit to our data using Hamiltonian Monte Carlo (HMC) techniques. Modeling strategies differed for the two species: For Chinook, we compared growth patterns of individuals recaptured in restored habitat for 15-60 d with those not recaptured regardless of initial habitat at marking. For steelhead, we had enough recaptured fish in each habitat type to use the model to directly compare growth between habitats. Chinook juveniles remaining in restored habitat reached a larger size earlier in the season than transient individuals with all study years combined, but this pattern varied slightly among years. Steelhead showed more rapid growth in restored habitat in 2009 and 2010 only, but were of a larger size earlier in the season in unrestored habitat. We explain these patterns in the context of spatio-temporal partitioning habitat. Despite this, there was no case where fish performed better overall in unrestored habitat. Size-corrected raw growth rates for steelhead (mm $\cdot$ day^{-1}) supported the model in that growth rate was higher in restored habitat in the same years as the corresponding model parameter. Finally, we compared growth patterns with the relative density of these species in each habitat type and found that growth did not always correspond to observed density differences. Chinook abundance was higher in restored habitat in each study year, but no growth parameter differences were found in 2012 or 2016. Steelhead growth and density both favored restored habitat in 2009, whereas growth was higher in restored habitat in 2010 when there was no density difference between habitats. Thus, measurement of

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growth rate complements restoration efficacy studies because it can both prevent overconfidence in density data and detect benefits when density data are inconclusive.

Key words: growth, salmonids, habitat restoration, Monte-Carlo analysis

Running head: GROWTH MODELS AND FISH HABITAT RESTORATION

INTRODUCTION

In many species, differences in habitat quality have important implications for fitness (Street et al. 2015), driving heterogeneity in growth and development across individuals, and leading to life-history variation and trait evolution (LaRue et al. 2017). Variation in growth rates across habitats has therefore been documented in all vertebrate taxa, including mammals (Mosser et al. 2009), birds (Schekkerman et al. 2003), reptiles (Bjorndal et al. 2000), amphibians (Todd and Rothermel 2006) and fish (Polivka 2005, Höckendorff et al. 2017). In conservation biology, growth can provide a more robust indication of habitat quality than censuses of abundance or population density (Van Horne 1983, Mosser et al. 2009, Davies et al. 2016), especially given that growth is often correlated with survival and reproduction (Tarkan et al. 2016). Nevertheless, growth rates and other life-history traits are only rarely used to assess habitat restoration efforts in species conservation (Höckendorff et al. 2017).

These issues are particularly important in restoration of fish habitats in rivers, where one or more species can be the target of restoration (Roni et al. 2002 2008). In the Pacific Northwest, USA, in-stream habitat restoration is frequently used as a conservation strategy for threatened and endangered salmonids (Roni et al. 2002, Irwin et al. 2015, Sivakoff et al. 2016). Ambiguity in assessments of salmon restoration efforts is nevertheless often substantial (Smokorowski and Pratt 2007, Roni et al. 2008, Whiteway et al. 2010, Stranko et al. 2012) because of inadequate replication of treatments or insufficient observation frequency (Roni et al. 2010). In addition, distribution patterns of salmonids vary spatio-temporally, and differ between species (Beechie et al. 2005). Anadromous Chinook (*Oncorhynchus tschawytscha*) and Coho (*O. kisutch*) salmon of the "stream type" life history grow and develop in streams for 1 year before migrating to the marine environment, but juvenile steelhead trout (*O. mykiss*) grow and develop in streams for 1-3 years.

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A common stream restoration technique is the installation of engineered log jams (ELJs) in streams, which create pools that protect young of the year salmon and steelhead trout. In principle, log jams should improve growth and survival to the smolt stage, which is when juveniles migrate to sea. Indeed, growth and development are key features of salmonid life-cycle models, which are often able to accurately predict population trajectories (Scheuerell et al. 2006). Studies of restoration effectiveness, however, only occasionally quantify salmonid growth or survival, whether in the Pacific Northwest or in other parts of the world (Rosenfeld 2003, Roni et al. 2008, Sievers et al. 2017). The extent to which these life history traits are changed by restoration is of high importance in applying life cycle models to predict and confirm population-level responses (Honea et al. 2009).

Efforts to evaluate restoration efficacy often rely on observations of relative density in restored habitat and unrestored habitat, but such data often have high uncertainty (Taylor and Wade 2000) or show weak or no effects of restoration (Irwin et al. 2015, Sievers et al. 2017). Measurements of life history traits such as growth rates could therefore increase confidence in distribution and abundance studies. Moreover, mechanistic approaches to quantifying growth rates could augment raw growth rate data obtained from mark-recapture studies (Croak et al. 2013), expanding the conceptual basis of restoration ecology (Young et al. 2005).

Polivka et al. (2015) showed that, in a river sub-basin of the Interior Columbia River in the Pacific Northwest, pools created by ELJs and rock weirs increased occupancy by Chinook salmon and steelhead relative to unrestored habitat. Density patterns varied between species, across study years, and between the beginning and end of the growing season. Because growth at the fry and parr stages for these species is positively correlated with survival during downstream migration (Achord et al. 2007), studies of individual growth could usefully augment these and other habitat occupancy studies (Whiteway et al. 2010). More broadly, density increase alone does not mean that restoration is successful, because it is not clear in advance whether behavioral selection of restored habitats is associated with a growth benefit relative to unrestored habitats (Rosenfeld 2003).

Here we present a multi-year study of growth observations in a field setting. We collected data

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through the entire rearing season in each of five years to determine whether growth of young-of-the-year Chinook and steelhead is improved in restored habitat. In these species, individual growth data are typically collected via mark-recapture studies, but the high mobility of Chinook (Hillman et al. 1987) often limits their recapture rates in unrestored habitats (Polivka 2010).

To address this challenge, we combined two different types of data. The first type of data is mark-recapture data, which allowed us to directly estimate growth rates. The second type of data is measurements of size for recaptured individuals, and for individuals captured only once. Because these fish grow more or less continuously during the growing season, we were able to fit growth models to both types of data for both species of fish. We then attempted to compensate for the smaller sample sizes for Chinook recaptures by comparing our inferences based on recaptures to our inferences based on observations of size-over-time, and by comparing our inferences based on Chinook with our inferences based on steelhead.

Because salmonid growth rates are rarely constant, we allowed for the possibility that growth-rate parameters would change over time (Karkach 2006, Tjørve and Tjørve 2010). We used Bayesian model fitting techniques to estimate the parameters of our growth functions, and we compared growth rates between individuals with different habitat selection behaviors. Because steelhead recaptures were sufficient in both habitat types, we were able to use raw growth data to determine the extent to which the model accurately reproduces growth rates in the field. We then compared our estimates of growth rates with previous observations of occupancy (Polivka et al. 2015) to determine the frequency with which increased abundance in restored habitat is associated with increased growth rates.

METHODS

Study Site

The restoration projects studied here were implemented in the Entiat River sub-basin ($49.6567°$ N, $120.2244°$ W), a tributary of the interior Columbia River, as part of a systematic program of restoration, combined with post-treatment monitoring (Bennett et al. 2016). Restoration efforts in

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the Entiat IMW spanned the years 2008-2016, and during this period, in-stream habitat structures were installed in multiple reaches of the river.

The river basin is composed of three geomorphically distinct valley segments (Godaire et al. 2009), and reaches were treated in all segments. We used two closely situated reaches in the lower valley segment: a restored reach that was 4.5-4.9 km from the confluence with the Columbia River, and an unrestored reach that was 0.3 km upstream of the restored reach (Fig. 1). Pools in the restored reach ("restored pools") were created in 2008 using either small engineered log jams (N = 6), or rock barbs (N = 5) that had been designed by the US Bureau of Reclamation. For purposes of comparison, unrestored pools (N = 11) that lacked major log and rock structures were identified on the stream margin in the unrestored reach. Unrestored pools were 20-40% smaller and shallower than restored pools, but Polivka et al. (2015) showed that the unrestored pools had a similar rate of increase in fish density with increasing area to the restored pools. We therefore concluded that the unrestored pools served as reasonable controls for the restored pools.

Fish Capture and Marking

We collected growth data using mark and recapture of young-of-the-year Chinook and steelhead in restored and unrestored pools during the growing seasons of 2009, 2010, 2012, 2013 and 2016. In each set of pools, capture and recapture were carried out every 10-14 days throughout the growing season, and recapture intervals therefore ranged from 15-65 days (Polivka 2010). We collected no growth data in 2011, 2014 or 2015 because periods of high water (2011) and post-fire sediment deposition (2014, 2015) severely restricted the time available for research (Polivka 2010, Polivka et al. 2015, Polivka and Claeson in review).

Fish were captured using a 3 m $\times$ 1.5 m $\times$ 3 mm mesh seine. The substrate and flow conditions made it impossible to pull the seine through the water, and so two field crew members instead stood at the downstream end of the pool and held the seine open as two other crew members, snorkeling in the water, used large hand nets to capture fish individually or to coerce fish into the seine. Visibility in the Entiat River is 4-5 m, so the two snorkelers could see the entire sampled area,

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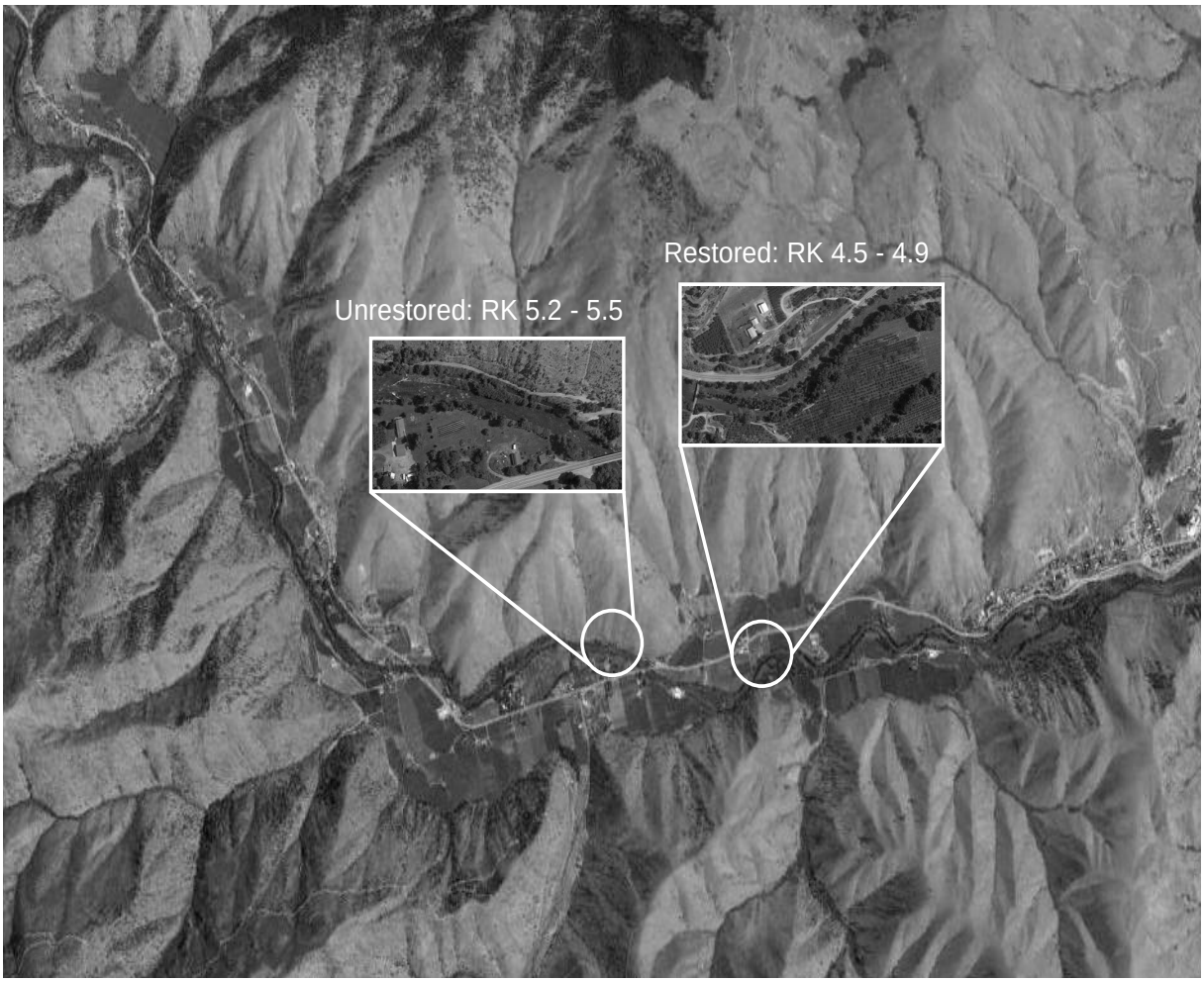
FIG. 1: Map of study area in the Entiat River showing the locations (river km relative to the confluence with the Columbia River) of the study reaches with restored pools and with unrestored pools



ensuring that few fish escaped capture. Captured fish were transferred to insulated, aerated buckets for enumeration, marking and recording of size data (standard length, SL, in mm and mass in g).

Mild anaesthetization using MS-222 (<0.1 g·l^{-1}) exposure for 2-3 minutes made it possible to measure, weigh and apply an identifying mark to each fish. We avoided PIT tagging because it would have caused too much handling stress (Tiffan et al. 2015) to allow for robust mark and recapture, especially given the small size ($<$ 50 mm SL) of some fish at the start of field sampling each year. We therefore marked fish with a subcutaneous injection of visual implant elastomer (VIE, Northwest Marine Inc.), a minimally invasive procedure. Individuals were identified by varying VIE color combinations and positions on the body. We marked $\sim$ 1000 fish each year,

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with fewer than 2-3 deaths per year from handling/marking procedures. Following handling, fish were held in an aerated bucket for at least 10 min, or until they displayed a full righting response and normal activity, and were then released into the pool in which they were captured.

After 24 hrs field crews returned to the same pools as part of a separate short-term behavioral study (Polivka *unpublished data*) and captured all fish using the same methods. Recaptured fish were released to the pool and newly captured fish on that day were given marks as described above. The pools were sampled again 10-14 days later, with size data recorded on recaptured fish and marks applied to newly captured fish that had immigrated into the pool during the sampling interval.

Data Analysis

To analyze our data, we constructed mechanistic growth models that described fish growth over each growing season, and we fit these models to data on fish size. We then compared best-fit growth models in restored and unrestored habitats. Size data included observations both of individuals marked and recaptured, and of individuals that were marked but never recaptured. For Chinook, we had very few recaptures in unrestored pools and so comparison of changes in size between individual Chinook could have led to highly uncertain conclusions (Polivka 2010). Fitting growth models, in contrast, allowed us to make use of data for fish that were measured once but never recaptured.

Because we did not recapture many Chinook in unrestored habitats, we fit separate growth models to data for recaptured fish ("recaptures"), and non-recaptured fish ("others"), being careful to account for the repeated measurements on recaptured fish (see "Model Specification" below). We then compared growth rates for the two groups. For steelhead in contrast, we had a large number of recaptures in unrestored habitat (N = 179), and so we fit models to the data for recaptured fish and compared habitat types.

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Model Specification

We constructed our growth model to describe the growth of young-of-the-year Chinook salmon and steelhead in streams during the growing season. Size-over-time models in fisheries (e.g., Von Bertalanffy 1938) usually describe growth over the lifetime of the organism. One important consideration was that inspection of our data showed that there were inflection points; therefore, we used a generalized version of a logistic growth model (Richards 1959, Schnute and Richards 1990, Birch 1999). This model allows for accelerating growth in the early stages of the growing season, followed by an inflection point, after which growth decelerates,leading to a maximum size at the end of the first season. The use of a size asymptote is consistent with patterns evident in our data, and in size data reported from several years of downstream migration of smolts in the spring (Grote and Desgroseillier 2016). Our model is:

$$l_t = Y' + \frac{L_\infty - Y'}{1 + e^{\hat{\alpha} - at}}. \tag{1}$$

Here, l_t is the length at time t, Y' is the lower bound on size, effectively a minimum, and a is the rate of increase in the size curve. L_∞ is the maximum size that a fish can reach during the growing season, so that $Y' \leq l_t \leq L_\infty$ for all time t. The inflection point of the curve occurs at $\hat{t} = \frac{\hat{\alpha}}{a}$.

Importantly, both $\hat{\alpha}$ and a can have profound effects on the dynamics during the growing season, potentially resulting in substantial differences in l_t at any given time t (Fig. 2). As the value of $\hat{\alpha}$ decreases, with the other parameters held constant, fish reach larger sizes earlier in the season. The a parameter describes the steepness of of the curve at small sizes, so that increasing values of a result in more rapid increases in size over time.

To avoid confusion with other models such as the Von Bertalanffy model, we re-parameterized the model according to $Y_\infty = L_\infty - Y'$, so that Y_∞ is the total amount by which a fish increases in size during the growing season. The model is then:

$$l_t = Y' + \frac{Y_\infty}{1 + e^{\hat{\alpha} - at}}, \tag{2}$$

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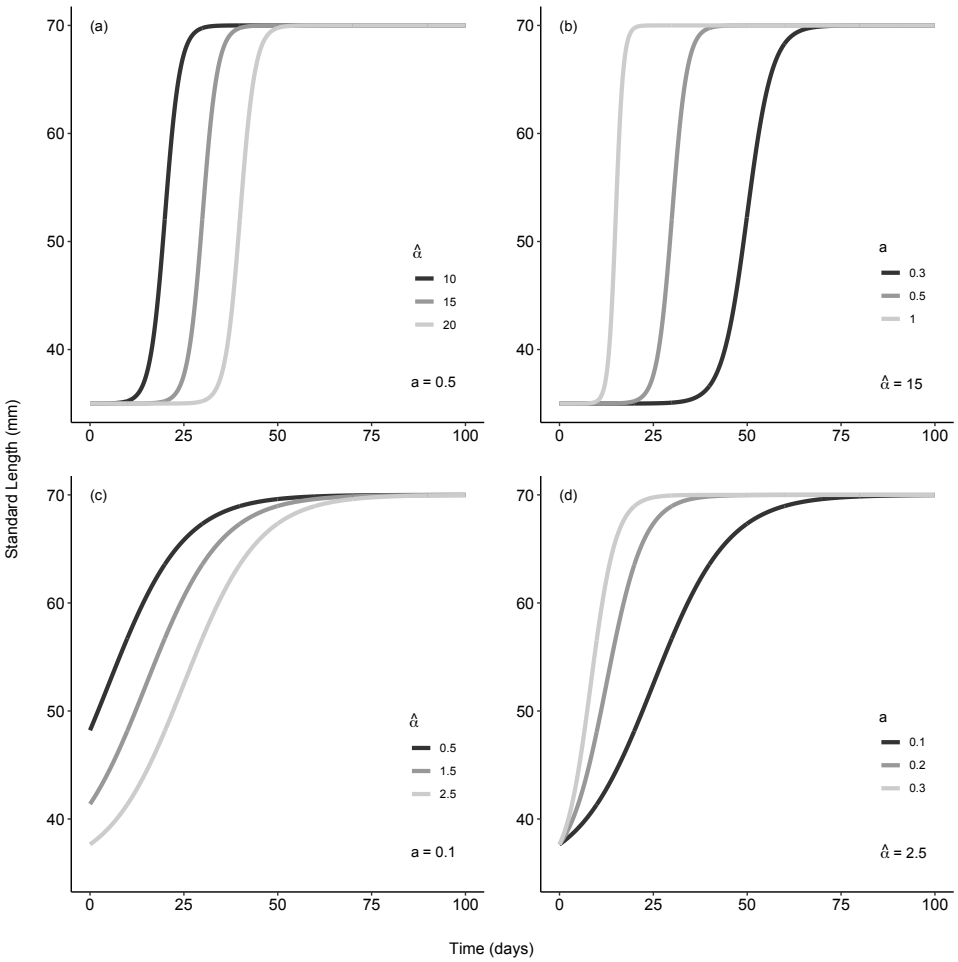
FIG. 2: Growth curves generated from Equation (2) over a 100 day growing period. Panel (a) shows that $\hat{\alpha}$ affects the timing of the inflection point, while panel (b) shows that a affects the slope of the growth curve. Panels (c) and (d) show growth curves for values of the two parameters that are closer to those estimated from our data. For the curves in panel (c) in particular, the inflection point occurs close to time $t = 0$, so that the intercepts vary between parameter values. In these cases, fish are close to the lower bound on the curve Y' when time is less than zero, which is to say, before sampling begins. In all panels $Y' = Y_\infty = 35$.



When non-linear models are fit to data, a standard approach is to transform the model into a linear form to accommodate linear least-squares fitting routines and their assumptions, such as normally distributed residuals. For our data, however, it turned out that the residuals are normal even without transformation of the model, and the variance in the residuals for the untransformed model was roughly constant. We therefore did not transform the model. Instead we simply added

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residual variation to the non-linear model, according to:

$$l_{it} = Y' + \frac{Y_\infty}{1 + e^{\hat{\alpha} - at}} + \epsilon_{it}, \tag{3}$$

Here i indicates individual fish i. We then assume that the residual ϵ_{it} for fish i at time t follows a normal distribution with mean zero, and variance $\sigma^2_{residual}$, which we estimated from the data. We thus have $\epsilon_{i,t} \sim N(0, \sigma^2_{residual})$, so that $\sigma^2_{residual}$ is the residual variation in length. Thus, Y' and Y_∞ describe growth bounds averaged over individuals in the population.

We then extended the model to allow for fixed treatment effects, and random year and individual effects. First, to include habitat treatment effects, restored vs. unrestored, we allowed the four model parameters (Y', Y_∞, $\hat{\alpha}$, and a) to vary by habitat type, as fixed effects. Second, to account for the statistical properties of our sampling design, we included random effects of year, to allow for annual variability in the parameters. Third, in the case of individuals that were recaptured during a season, we accounted for repeated measurements by including random effects of individual. Given these considerations, the model becomes:

$$l_{ihyt} = (Y'_h + \epsilon^1_{hy}) + \frac{(Y_{\infty h} + \epsilon^2_{hy})}{1 + e^{\left[(\hat{\alpha_h} + \epsilon^3_{hy}) - (a_h + \epsilon^4_{hy})t\right]}} + \epsilon^5_{ih} + \epsilon^6_{iht} \tag{4}$$

Here i is again the individual, h is the habitat type, restored or unrestored, y is the sampling year, and t is time within a growing season. The ϵ's represent the different types of random effects, as follows.

The random effects of year on each of the four model parameters, $\epsilon^{1\ldots4}_{hy}$, vary between the two habitats, such that, for example, $\epsilon^1_{hy} \sim N(0, \sigma^2_{Y'})$, where $\sigma^2_{Y'}$ is the random variation in initial size Y' measured across habitats h and years y. For the random effect of recaptured individuals, $\epsilon^5_{ih} \sim N(0, \sigma^2_{individual_h})$, where $\sigma^2_{individual_h}$ is the variance in fish length among recaptured individuals from a given habitat type. This random effect of individual affects only the overall length, rather than the rate of growth. Among other things, this means that we can account for the possibility of observing fish that start off larger than average being more likely to continue being larger than

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average throughout the growth period (Pfister and Stevens 2002). To be conservative, we began by assuming that no Chinook in the unrestored pools were recaptured, and so the random effects of individual Chinook are only relevant for recaptures in the restored habitats.

Finally, the residual variation is allowed to differ between the two habitats, where $\epsilon^6_{ht} \sim N(0, \sigma^2_{residual_h})$. This is particularly important for the Chinook data set, because some of the variation among the recaptured individuals in restored habitats can be explained by the random individual effects. In the unrestored habitats in contrast, no individuals were recaptured, and therefore more variation was left unexplained. Because of this, it turned out to be the case that $\sigma^2_{residual_{unrestored}} > \sigma^2_{residual_{restored}}$.

Model fitting

We fit our models using Hamiltonian Monte Carlo (HMC) with the open-source software, *Stan* (Stan Development Team 2017*b*) and **R** (R Core Team 2017), utilizing the package *rstan* (Stan Development Team 2017*a*). The HMC algorithm provides an efficient method of fitting nonlinear models, and the software platforms ensure that our methods are open and reproducible. All of our data and model-fitting code are available in an open-source repository: `https://bitbucket.org/jrmihalj/mechanistic_growth_salmon`

In general, we used vague priors for our parameters, but to aid HMC performance, we centered the prior distributions of Y' and Y_∞ on realistic values, based on previous work with these two species. Also, we constrained $\hat{\alpha}$ and a to fall within realistic ranges, namely 0-10 and 0-1, respectively, again based on previous work. Sensitivity analysis showed that these priors did not strongly influence our posterior inferences, and that the posterior was clearly dominated by the likelihood, rather than by the prior distributions. For each model, we ran three HMC chains for 9000 iterations, using the first 2000 iterations as a warm up. We then thinned by 7 iterations to produce a total of 1000 samples per chain. We evaluated HMC chain convergence based on Gelman and Rubin's potential scale reduction factor, $\hat{R}$ (Gelman et al. 2014). We visually inspected chain mixing using traceplots, running mean plots, and marginal posterior density plots (Gelman et al.

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2014), and we saw no evidence of pathological MCMC behavior. Although we thinned our chains to avoid auto-correlation, our effective sample size was close to the total number of iterations, and thinning was likely unnecessary (Link and Eaton 2012).

To compare parameter estimates between the restored and unrestored habitats, we calculated differences between paired parameter values for the restored and unrestored habitats for each sample in the model's joint posterior. For example, to calculate differences in the shape parameter between restored habitats r and unrestored habitats u, we calculated $\hat{\alpha}_r - \hat{\alpha}_u$ for each of the 3000 samples in the posterior (our 3 Markov chains each produced 1000 samples). We then calculated the 95% credible interval (CI) of that set of differences. This approach allowed for the possibility of correlations in parameters across the samples in the posterior, and is therefore a more robust method than calculating parameter differences by making independent draws of each parameter from the posterior (Kruschke 2013).

Note that, in the case of Chinook, the u group consisted of all uncategorized fish, meaning transient individuals that were not recaptured, regardless of habitat of original capture. Accordingly, when we tested for interactions between habitat and year for Chinook, we took into account the random year effects. For example, in testing for differences in the shape parameter between years for Chinook, we calculated $(\hat{\alpha}_r + \epsilon^1_{r,y}) - (\hat{\alpha}_u + \epsilon^1_{u,y})$ for each posterior draw, where $\epsilon^1_{r,y}$ and $\epsilon^1_{u,y}$ are the random year effects in year y.

We considered the parameter estimates for the two habitats to be meaningfully different if the 95% CIs of their differences did not overlap zero. For most parameters, however, the fraction of differences that was above or below zero was reasonably consistent across years, even if the 95% CI overlapped zero. Because this consistency provides at least modest additional support for some of our arguments, we report the fraction of differences that were above or below zero in each case.

Our best-fit models suggested that fish almost always exceeded the minimum size Y' before sampling began. To estimate fish size at the beginning of sampling, we therefore used the best-fit models to back calculate median fish length at time $t = 0$ when observations began. This also allowed us to confirm that there were no differences in fish size among habitat types at the

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start of the season. Such initial differences can lead to growth advantages that are independent of environmental factors such as habitat quality (Pfister and Stevens 2002).

Model Comparison With Direct Measurement of Growth in Steelhead

Because we recaptured steelhead in both restored and unrestored pools, we were able to directly compare observed growth rates for steelhead between habitat types, in addition to our estimates of growth that came from fitting models to the data. In carrying out these calculations, a key consideration is that, in many organisms, individual growth rates are strongly size dependent (Elliott 1975, Beckman et al. 1998, Pfister and Stevens 2002). Because we encountered a wide range of initial sizes (40-75 mm SL), it was important to allow for the possibility of size-dependent growth when comparing steelhead growth rates between habitats.

We generated a predicted growth vs. size regression for steelhead for each year, by carrying out a log-linear regression of change in size (mm $\cdot$ day^{-1} = $\frac{SL_{recaptured} - SL_{marked}}{days}$) on initial standard length, for each recaptured individual. To compare growth in restored vs. unrestored habitat in these regressions, we kept track of the habitat in which each individual was recaptured. We then used the residual for each point as an indicator of growth rate relative to the population average for that size, where the average for the size was calculated from the regression line of growth on size. A positive residual indicates that an individual has a higher than average growth rate, adjusted for size, whereas a negative residual indicates that an individual has a lower than average growth rate, again adjusted for size (Fig. 3). In comparing size-dependent growth rates between habitats, we compared the mean residual from restored habitat to the mean residual from unrestored habitat for each year of the study, using two-sample *t*-tests. Because growth rate in mm $\cdot$ day^{-1} corresponds to the a term in Equations 1-4, we compared differences among habitats in mean residuals with differences among habitats in the a parameter.

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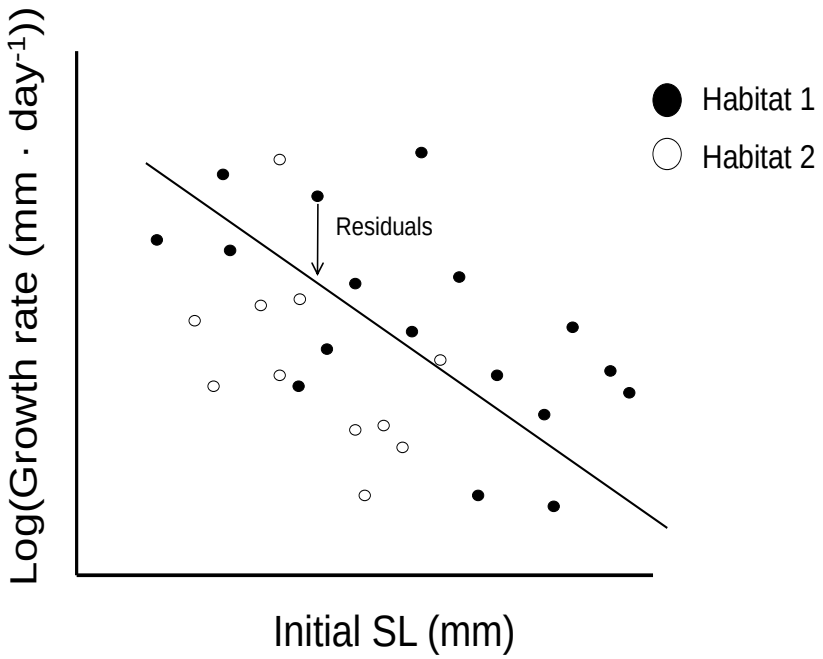
FIG. 3: Use of residual values from a size vs. growth rate regression to compare growth in different habitats. The arrow shows the distance from the points to the line. Mean residual values $\bar{R}$ are calculated for all individuals in each habitat, and if $\bar{R}_r > \bar{R}_u$, then we conclude that growth is higher in restored habitats.



Concordance of Growth and Habitat Occupancy Patterns

From a management perspective, our goal was to determine whether increased relative density in restored habitats was associated with increased relative growth rates. We therefore compared our model output first to the fish density data from Polivka et al. (2015) for study years 2009, 2010, 2012, and 2013, and second to fish the density data available from the current study in 2016.

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RESULTS

Chinook Salmon

Across the five sampling years (2009, 2010, 2012, 2013, and 2016), we collected 3,568 length records from Chinook. In the restored habitats, we recaptured 238 Chinook, for a total of 481 length records, with five fish that were recaptured more than once. The best-fit growth curves in Fig. 4 show that Chinook recaptured in restored habitats were generally larger early in the season compared to unrecaptured fish. This visual impression is confirmed by a lower value of $\hat{\alpha}$ for individuals recaptured in restored habitats compared to $\hat{\alpha}$ values for unrecaptured fish (Fig. 5). Because $\hat{\alpha}$ is an inverse measure of size early in the season, the difference in $\hat{\alpha}$ values means that the recaptured fish were larger than unrecaptured fish early in the season. Negative values of the difference in $\hat{\alpha}$ values occurred in 98.5% of sample differences for all years combined, and in 98.3%-100% of samples for 2009, 2010, and 2013 (Fig. 5). In 2012 and 2016, the 95% CIs overlapped zero, but negative values occurred in $>$ 90% of samples, consistent with the differences for the other years and with the differences for all years together.

In 2009 and 2010, however, values of the growth rate a were larger for unrecaptured fish than for recaptured fish. This observation, in combination with the larger $\hat{\alpha}$ values for unrecaptured fish describing small early-season size, indicates that unrecaptured fish experienced a rapid increase in size later in the season (Fig. 4) that compensated for the early season disadvantage. The difference in those two years was indicated in $>$99% of differences in sample values drawn from the posterior distributions of a (Fig. 5). Although the 95% CI for the differences in a for all years together overlapped zero, they were below zero in 91.1% of the draws, consistent with the trend observed in 2009 and 2010.

All else equal, smaller $\hat{\alpha}$ values lead to earlier inflection points $\hat{\alpha}/a$. To test whether the smaller values of $\hat{\alpha}$ for Chinook recaptured in restored habitat in all years combined, and in 2009, 2010, and 2013, led to earlier inflection points for those fish, we drew pairs of values of the shape parameter $\hat{\alpha}$ and the growth parameter a for recaptured and unrecaptured Chinook. We then calculated

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FIG. 4: Growth curves based on estimated model parameters (mean of the posterior) for Chinook salmon recaptured in treated habitat ("recaps," solid lines) vs. those captured in either habitat type, but not recaptured ("others," dashed lines). The left panel shows the data and the habitat-specific models for all years combined. The small panels to the right show the data and the habitat-specific models for individual years. Parameter differences (see Fig. 5) are shown in the upper left corner of each panel

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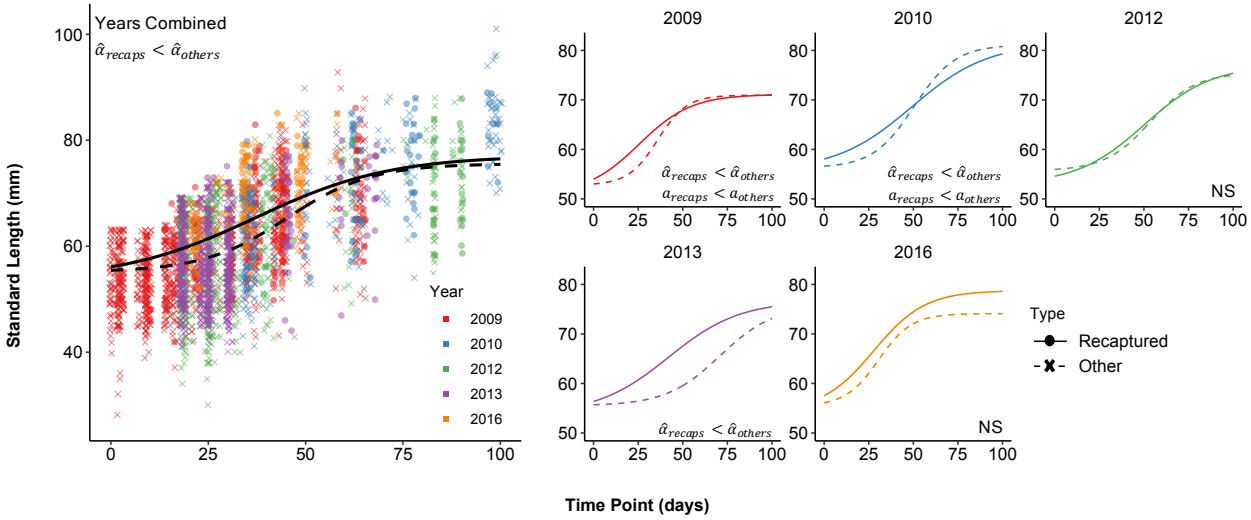

differences in inflection points $\hat{\alpha}/a$ for recaptured and unrecaptured fish in each year and for all years combined, as we did for the other parameters.

This procedure showed that inflection points for recaptured fish did indeed occur earlier than for recaptured fish in 2009, with 99.8% of sampled differences being less than zero. In 2013, there was a similar trend, with 94.6% of sampled differences less than zero. Differences in the other years, and for the combined data, were not meaningful, likely because independent variation in the two parameters obscured differences in the inflection points. We therefore conclude that there is at least modest evidence that restoration is associated with larger Chinook size earlier in the season as indicated by the shape parameter $\hat{\alpha}$, but that variation in the two parameters prevents a consistently earlier inflection point.

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FIG. 5: The difference (Δ; recaptures $-$ others) in estimates of all model parameters $\pm$ the 95% credible interval between the two capture types of young-of-the-year Chinook salmon (recaptures in restored habitat; others = fish marked and not recaptured, regardless of capture origin). Year-specific estimates incorporate the random effect of year, and combined differences are based on the average parameter values among years. The fraction in the parentheses represents the fraction of posterior draws for which the difference was above or below zero, as appropriate. Δ Length at time = 0 was substituted for model parameter Y'

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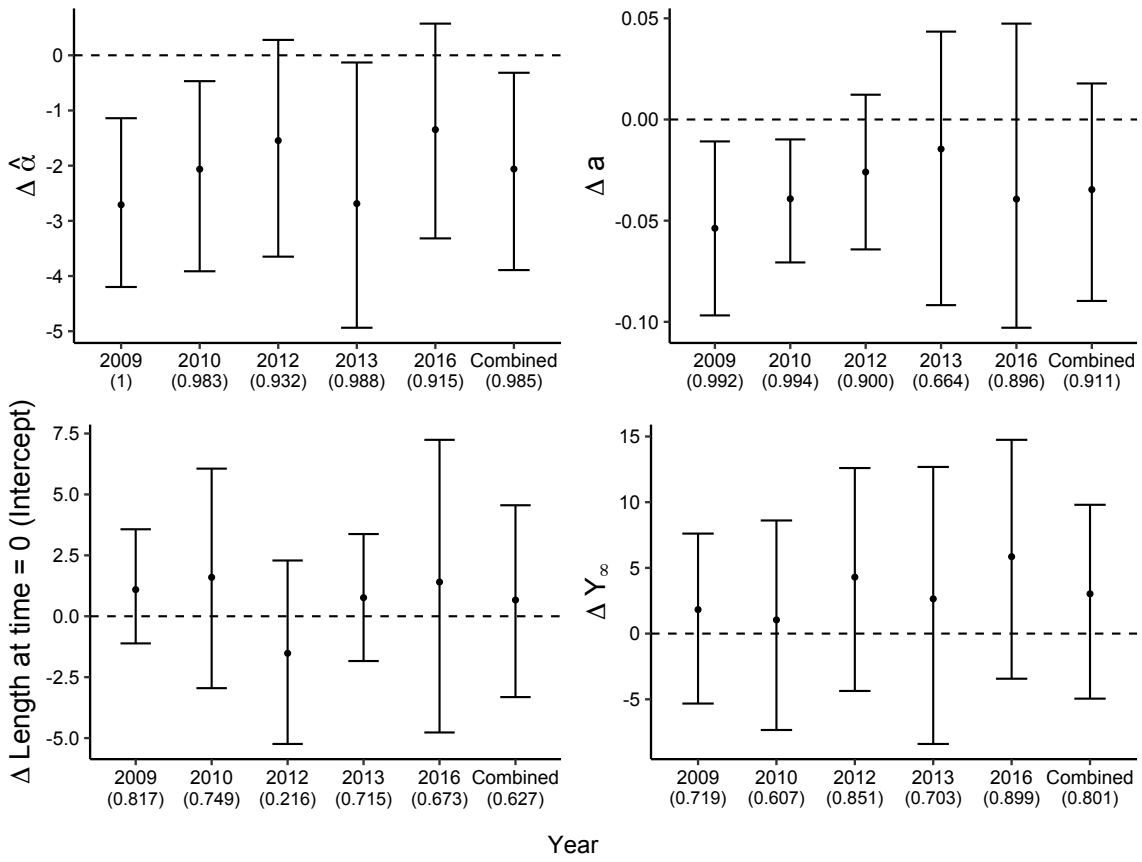

Steelhead

We recorded the lengths of 2,871 steelhead across the five sampling years. In the restored habitats, we recaptured 306 individuals for a total of 689 observations, whereas in the unrestored habitats, we recaptured 179 individuals for a total of 413 observations. The number of steelhead recaptured from unrestored habitats was thus sufficient to fit the model directly to recaptured individuals in each habitat type, in contrast with Chinook. In 2013, however, there were no recaptures of steelhead in unrestored habitat for recapture intervals of longer than 24h. We therefore excluded

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the 2013 data from our analyses.

For all years combined, there were no differences in growth parameters in steelhead recaptured in restored versus unrestored habitats (Fig. 6), but there were differences in some parameters in 2009 and 2010 (Fig. 7). In those two years, both the shape parameter $\hat{\alpha}$ and the growth rate parameter a were higher for fish in restored habitat in 99-100% of samples from the posterior distributions. Over all years, almost 90% of differences in $\hat{\alpha}$ were above zero, and almost 93% of differences in a were above zero, supporting the meaningful differences seen in 2009 and 2010.

The higher values of a for fish in restored habitat mean that growth rates were higher for steelhead in those two years, but the higher values of $\hat{\alpha}$ mean that fish in restored habitat reached larger size later in the season and caught up to the fish in unrestored habitats that were larger earlier. The lack of differences in total growth Y_∞ supports this conclusion. The inflection point was later for steelhead in restored habitats in 2010 only (99.3% of sampled differences above zero), again suggesting that the inflection point is not a specific indicator of growth differences among habitats. Nevertheless, mid-season occupancy of restored pools is associated with rapid growth.

FIG. 6: Growth curves based on estimated model parameters (mean of the posterior) for steelhead recaptured in restored habitat (solid lines) vs. those recaptured in unrestored habitat (dashed lines). Left panel shows data and fitted curves for all years combined; additional figures show individual years. Parameter differences (see Fig. 7) are indicated in the lower right corner of each panel. The analysis omits 2013 owing to lack of long-term steelhead recaptures in unrestored habitats.

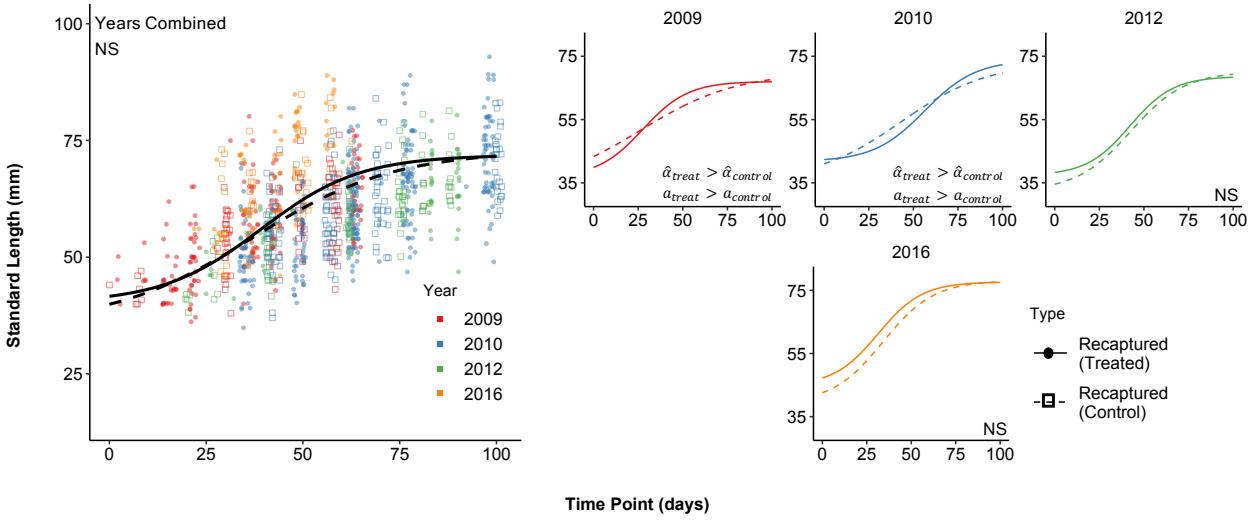

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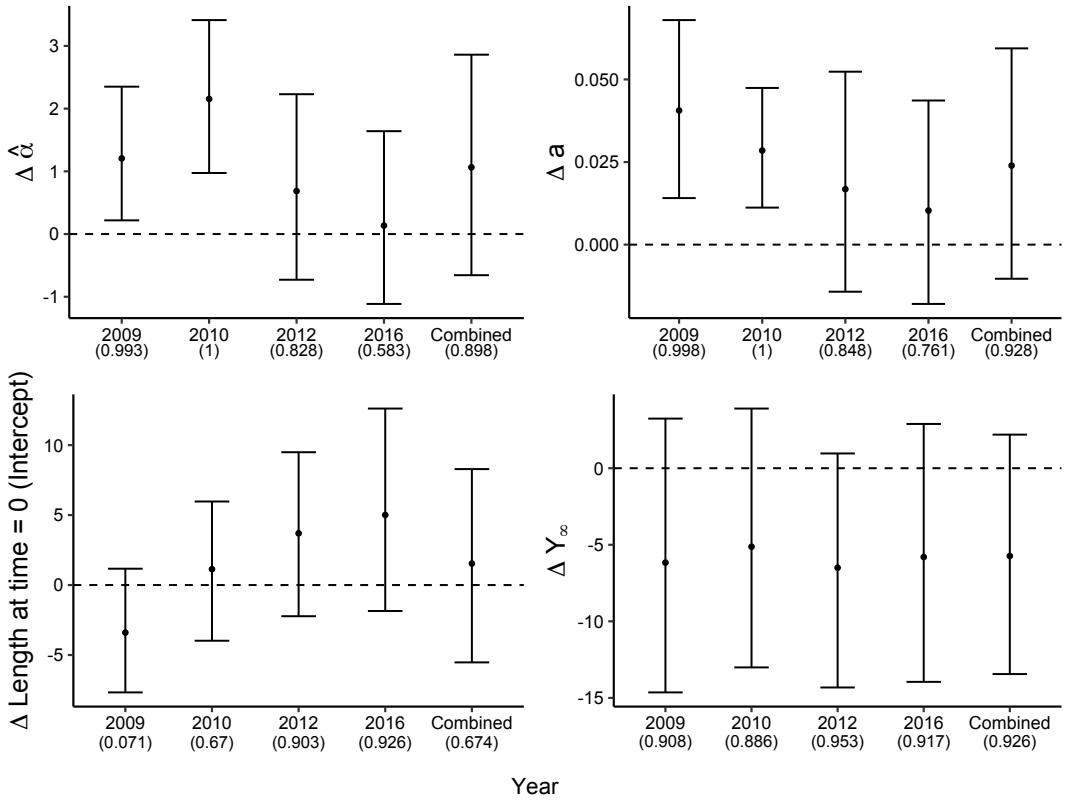
FIG. 7: The difference in estimates of all model parameters ± the 95% credible interval between the two capture types of young-of-the-year steelhead (recaptures in restored habitat - recaptures in unrestored habitat). Year-specific estimates incorporate the random effect of year, and combined differences are based on the average parameter values among years. The fraction in the parentheses represents the fraction of posterior draws for which the difference was above or below zero, depending on trend of the data. For all panels except the lower right, this represents the fraction of posterior draws above zero. Δ Length at time = 0 was substituted for model parameter Y'. The analysis omits 2013 owing to lack of long-term steelhead recaptures in unrestored habitats.



Direct Observations of Growth in Steelhead

Residuals from the log-linear regression of growth (mm · day^{-1}) on initial size were more positive, on average, for individuals marked and recaptured in restored habitat than in unrestored habitat, indicating higher growth in unrestored habitat. This trend, however, held for 2009 and 2010 but not 2012 or 2016 (Fig. 8). Inspection of the regression plots for 2009 and 2010 indicated that the largest differences in residuals between habitats in those two years were among individuals 55-60 mm in length. Separate residual analyses on individuals $<$ 60 mm, and individuals $>$ 60mm, produced significant differences in residuals only in individuals $<$ 60 mm (not shown).

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FIG. 8: Mean residuals from a log-linear regression of growth rate versus size, in restored vs. unrestored habitat, for each study year. The analysis omits 2013 owing to lack of long-term steelhead recaptures in unrestored habitats.

Concordance of growth and occupancy

In each year of our study, Chinook salmon were more abundant in restored habitat than in unrestored habitat whereas parameters from the growth model only showed a growth benefit in three of the five years (2009, 2010 and 2013; Table 1). For all years combined, however, abundance and growth were concordant for Chinook. For steelhead, 2009 was the only year in which there was concordance between observed fish abundance and growth patterns. In 2010, when there was no significant difference in habitat occupancy, there was nevertheless more rapid growth in restored pools, as indicated above by the a term in the model and by the positive mean residuals from the

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growth vs. size curve (Fig. 8 and Table 1).

TABLE 1: Concordance of occupancy differences and growth-parameter differences. Recall that large $\hat{\alpha}$ means that the inflection point comes later in the season, indicating less favorable growth conditions (NS = No difference/not significant.

Year	Occupancy higher in . . .	Growth more favorable in. . .	Parameters
a) Chinook Salmon			
2009	Restored	Restored	$\hat{\alpha}_{\text{restored}} < \hat{\alpha}_{\text{unrestored}}$
			$a_{\text{restored}} < a_{\text{unrestored}}$
2010	Restored	Restored	$\hat{\alpha}_{\text{restored}} < \hat{\alpha}_{\text{unrestored}}$
			$a_{\text{restored}} < a_{\text{unrestored}}$
2012	Restored	NS	
2013	Restored	Restored	$\hat{\alpha}_{\text{restored}} < \hat{\alpha}_{\text{unrestored}}$
2016	Restored	NS	
Years Combined	Restored	Restored	$\hat{\alpha}_{\text{restored}} < \hat{\alpha}_{\text{unrestored}}$
b) Steelhead			
2009	Restored	Restored	$a_{\text{restored}} > a_{\text{unrestored}}$
2010	NS	Restored	$a_{\text{restored}} > a_{\text{unrestored}}$
2012	Restored	NS	
2013	NS	NS	
2016	NS	NS	
Years Combined	Restored	NS	

DISCUSSION

Our estimates of growth parameters for Chinook salmon and steelhead show that habitat restoration can make growth conditions more favorable. In Chinook, differences in the model parameter $\hat{\alpha}$ indicated that fish reached large size earlier in three of the five study years, and across all years combined. This result provides compelling evidence that Chinook benefit from restoration. Given the high level of variability across years, the relatively long duration of our study was crucial. An important caveat, however, is growth patterns did not always match observations of abundance differences between restored and unrestored habitat (Polivka 2010, Polivka et al. 2015, Table 1). There were differences in abundance each year, but there were differences in the growth rate parameter (a) only in 2009 and 2010. The difference in a in those two years favored growth in fish

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that were not recaptured and that reached larger size later in the season (as indicated by $\hat{\alpha}$). This pattern is generally explainable by established spatio-temporal patterns of life history and habitat use in these two species (Everest and Chapman 1972, Hillman et al. 1987).

Phenology is likely the most important driving mechanism for habitat-related growth patterns in the two species. Chinook fry emerge earlier in the season ($\sim$ April-May) than steelhead, and begin migrating downstream to overwintering habitat by late August/early September (Everest and Chapman 1972, Hillman et al. 1987). Steelhead, on the other hand, emerge in summer (June) and may or may not migrate out of streams after their first year (Everest and Chapman 1972). It is therefore not surprising that the apparent benefit of restored habitat for Chinook occurred earlier in the season, even though Chinook and steelhead overlap in restored pools (Polivka 2010, Polivka et al. 2015, Polivka and Claeson in review).

The start of downstream migration of Chinook in August opens up restored habitat for transient individuals and for steelhead. This is important because, as Chinook migrate downstream, slower growing and/or later hatching Chinook can immigrate into the pools being vacated by earlier occupants. This can lead to compensatory growth because of the release of from competition (Nicieza and Metcalfe 1997). Immigrating Chinook that were at a growth disadvantage in the presence of superior competitors may therefore increase their growth once their competitors leave, and may ultimately grow faster than their competitors once did (Ali et al. 2003). This effect could explain the observed difference in growth rate a between habitats for Chinook in 2009 and 2010 ($a_{\text{others}} > a_{\text{recaptures}}$; Fig. 5). Increases in habitat complexity as a result of restoration could thus mediate competitive interactions via effects on growth (Höjesjö et al. 2004).

These phenological differences can be even more important when restored pools are heavily occupied. The largest differences in density between restored and unrestored habitat for Chinook in this study system occurred in 2009 and 2010. The largest difference in density between habitats for steelhead occurred in 2009, but there was no difference in 2010 (Polivka et al. 2015). For Chinook, the large difference in abundance between habitats in 2009 and 2010 implies that the non-recaptured individuals were more likely to have been originally captured in restored pools.

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Because they could have occupied a pool up to 10-14 days (the typical interval between sampling events) prior to capture, mid-season immigrants into restored pools have the opportunity for rapid growth as downstream migration of Chinook originally in those pools increases. Downstream migration could provide the competitive release in more transient individuals. The smaller size of transient individuals earlier in the season indicated by the $\hat{\alpha}$ term, followed by a rapid increase in size later in the season, as indicated by the a term, is consistent with a pattern of compensatory growth in Chinook. The extent to which this pattern is associated with restored habitat, however, must be assumed from the fish density difference between restored and unrestored habitat in those years.

Competitive release could also be a parsimonious explanation for observed habitat differences in steelhead growth in 2009 and 2010. Steelhead overlap with Chinook in restored pools, but are less abundant in this study system (Polivka et al. 2015, Polivka and Claeson in review). When more abundant species limit pool use by steelhead, steelhead respond by adopting a more generalist habitat use pattern (Young 2004). This suggests that steelhead are at a phenological disadvantage because their later hatching (Hillman et al. 1987) leads to interspecific competition with Chinook. This competition, in turn, can slow early season growth by steelhead in restored pools and increase their residency time in unrestored pools. Indeed, steelhead recapture rates observed in those habitats support this conclusion. Steelhead at low density in unrestored habitat might achieve greater size earlier in the season compared with steelhead in restored pools that compete with Chinook. Downstream migration of Chinook could again result in competitive release for steelhead mid-season and growth compensation. In the two years with the greatest density of Chinook, the a term for steelhead showed rapid growth in restored habitats during mid-season at the time Chinook begin downtream migration. This pattern indicates that the growth benefit found in restored habitat may be very nuanced and species specific.

Direct measurements showed that there was more rapid steelhead growth in restored habitat, consistent with our estimates of high values of the growth parameter a in restored habitat in 2009 and 2010. Because temperature are current velocity are related to energetic expenditure and food

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delivery, we attempted to predict the growth data with a multiple regression that included those predictors. However, these exploratory analyses yielded no discernible pattern (Polivka 2010, and unpublished data), nor are they likely to be tractable when there are different intervals between mark and recapture for individual fish. Because our model-fitting approach uses size-over-time to compare recaptured and non-recaptured individuals, it integrates over the effects of environmental variables across the whole rearing season. Model fitting thus has important advantages over snapshots of growth. In addition, model-fitting allowed us to compare the effects habitat quality on Chinook, even though the Chinoook recapture rate in unrestored habitat type was nearly zero, as has been consistently observed in this study system (Polivka 2010). Furthermore, our technique identified that subtle differences in growth exist in early- and mid-season for both species.

A broader implication of our work relates to efforts to use life cycle models to predict population-level responses of salmonids to restoration (Scheuerell et al. 2006, Bartz et al. 2006). Our finding of improved growth in restored habitat suggests that young-of-the-year Chinook and steelhead benefit from increased habitat capacity as a result of restoration. Change in habitat capacity is a potential response to restoration in the life cycle models (Scheuerell et al. 2006), but has not yet been detected in nearby sub-basins (Honea et al. 2009). Positive growth in restored habitat is evidence of capacity increase, but whether this is important for the entire life cycle remains unclear. Salmonid growth at one life stage is sometimes (Achord et al. 2007), but not always a strong predictor of growth at a subsequent stage (Marco-Rius et al. 2012). It may also be problematic to infer that an observed capacity increase at only one or a few sites would apply at the scale of an entire sub-basin or population.

Surveys of relative abundance may overlook the processes that determine ecological differences between habitat types (Van Horne 1983, Rosenzweig 1991, Polivka 2005). In previous work with colleagues, the first author showed that it is possible to use density observations to distinguish redistribution of fish among good and poor habitats from true increases in fish abundance (Polivka et al. 2015, Polivka and Claeson in review). By comparing growth between restored and unrestored habitat, here we have shown that restoration enhances growth rather than simply redistributing

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fish. Compared to observations of abundance, fitting mechanistic growth models to data can thus provide stronger evidence in favor of restoration.

Our observation that, in Chinook, differences in growth between habitats were generally concordant with differences in relative density between habitats nevertheless emphasizes that observations of increased abundance in restored habitat in this study system can indeed indicate that a restoration effort has been successful. At the same time, however, it is worth noting that the model showed that two individual years did not show improved growth. Additionally, steelhead had higher growth in restored habitat in 2010, even when there was no abundance difference. Thus the model can both uncover evidence of restoration efficacy that is not apparent from abundance data and prevent overconfidence in abundance data. Growth studies are often less practical because of the time and labor needed to carry out mark-recapture, especially at the whole watershed scale. Fitting models to time series of fish sizes may thus provide a useful general tool for assessing the efficacy of habitat restoration.

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