

## RESEARCH ARTICLE

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# A meta-analysis and model comparison of juvenile salmon growth across different habitat types

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## Abstract

The size of an organism is an important factor for a variety of physiological and ecological processes. For fishes, larger size can increase long-term survival and provide a population level benefit. Therefore, threatened and endangered species management often focuses on supporting high quality habitat that provides growth opportunities. There are numerous habitat characteristics that can affect growth, including food availability, temperature, and habitat complexity. Understanding how growth responds to habitat types of different quality is the first step in determining what could lead to increased growth and potentially increased individual survival. We use Bayesian techniques to determine which of the differing methods is best for modeling the effects of habitat type and temperature on growth. To apply this method, we gather data from previous studies of the growth benefits of differing habitats and temperature regimes on Chinook salmon on the Sacramento River, CA, USA. We find a consistent growth benefit of floodplain rearing across multiple studies and show that a Ratkowsky model is the best for modeling this growth data. This information can specifically help managers model and protect the endangered and threatened Chinook populations in this system and more generally understand fish growth across differing habitat types.

## KEYWORDS

Bayesian, floodplain, growth, habitat, modeling, Salmon

## 1 | INTRODUCTION

Size is a key physiological characteristic in ecology and is featured in several fundamental ecological theories (Bergmann, 1848; Mangel, 1994; Timofeev, 2001). In fish ecology, size can affect such things as behavior (Busch & Mehner, 2012; Keeley, 2000), physical performance (Wardle, 1975), thermal tolerance (Di Santo & Lobel, 2017), and survival (Bond, Hayes, Hanson, & MacFarlane, 2008; Duffy & Beauchamp, 2011; Osterback et al., 2014; Sogard, 1997; Zabel & Achord, 2004). The management

and recovery efforts of vulnerable freshwater fish species often rely on habitat restoration or river flow regulation in order to improve habitat quality and, as a result, individual fish sizes and growth rates (David et al., 2014; Weisberg & Burton, 1993). High quality habitat may include cover from predation, shelter from high flows, optimum temperatures, and abundant food resources. In addition to the direct increase in survival that fish might experience in high-quality habitats, survival benefits associated with increased growth could remain after fish leave these habitats. These size-based survival benefits, such as reduced predation (Osterback et al., 2014), can persist during

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migration to other regions or between high-quality habitats (Futamura, Morita, Kanno, & Kishida, 2022).

To gain a full understanding of how growth affects survival in a system, it is important to first understand how a system's available habitats affect growth. Numerous habitat characteristics can affect wild fish growth rates, such as different food density (Sommer, Nobriga, Harrell, Batham, & Kimmerer, 2001), capture or foraging success (Warfe & Barmuta, 2004), and feeding behavior (Kiefferl & Colgan, 1993). Transferring laboratory growth rates to wild systems can be misleading as they might not capture the complex influence of habitat on fish growth in the wild. For instance, maximum growth rates may be different (Forseth, Letcher, & Johansen, 2011), fish may not eat all available food (Metcalfe, Fraser, & Burns, 1998), and feeding with a non-constant food source can change intake rates (Bajer, Whitlege, Hayward, & Zweifel, 2003). Field studies conducted on the habitats of interest (with caged or free swimming tagged fish) may thus prove more informative for managers and scientists. While these studies still are not perfect models of natural conditions (e.g., cage effects, tag effects) (Kellison, Eggleston, Taylor, & Burke, 2003), they likely are a more realistic representation of the conditions wild fish experience compared to controlled laboratory experiments.

In California's Central Valley, Chinook salmon have faced a series of anthropogenic threats, including gold mining, industrial fishing, dam construction, and climate change (Munsch, Greene, Mantua, & Satterthwaite, 2022). These and other pressures have led to a decline in populations (Yoshiyama, Fisher, & Moyle, 1998) and caused the National Oceanic and Atmospheric Administration (NOAA) to list two of the four central valley populations of Chinook salmon as either endangered or threatened (NOAA, 2005). These listings help generate a great deal of work towards understanding, identifying, evaluating, and restoring habitat for rearing juvenile Chinook salmon. Much of the work focuses on restoring habitat or using flow management to encourage juvenile fish to move from the main stem of the river to better quality rearing habitat. This need has driven numerous field studies in the Central Valley to better understand the growth benefits in habitats such as floodplains (The Floodplain Forward Coalition, 2019), drained rice fields (Sommer et al., 2020), and low flow side channels. However, to understand how these habitats and associated management actions may affect fish growth, there is a need for a model that can predict growth over different habitat types and over a wide temperature range. Furthermore, such a model can be applied to lifecycle management models for evaluating the benefit of habitat restoration on long-term population dynamics (Holmes et al., 2021).

This study evaluated the differential growth benefit to juvenile Chinook salmon that experience different freshwater habitat types and temperature regimes and determined the best method for fitting juvenile Chinook growth data. We fitted growth study data from field studies in the Sacramento River (California, USA) to a Bayesian hierarchical framework. Specifically, we modeled the effects of floodplain vs. river habitat type on juvenile Chinook salmon growth with four different growth models. We then compared model fits with a variety of

metrics including the root mean squared (RMS) error between predicted and measured values, the slope of a line through the predicted vs. measured data, the deviance information criterion (DIC), and posterior predictive checks. These checks were to determine both the habitat-specific benefits and the best model for fitting these types of growth data. Explicitly including temperature and habitat type will make the model more robust to out of sample predictions compared to models which only consider one factor (temperature or habitat type in isolation). Further, we explicitly characterize uncertainty, enabling managers to better understand the state of our knowledge of the system and allowing other models which use these results as input to propagate that uncertainty.

## 2 | METHODS

### 2.1 | Data

We conducted searches on Web-of-Science for articles that matched the following term set for either the title or topic: (delta OR bay OR river OR floodplain) AND (Chinook) AND (feeding OR growth OR consumption OR size) AND (Sacramento OR California OR "Central Valley"). We then filtered the 253 resulting articles based on title and abstract and finally selected those which contained data on fish growth rates, temperature, and habitat type. We also flagged articles which did not present these data, but which indicated that researchers had collected data of those types. We contacted the authors of these articles requesting their data, and authors of other studies to find reports or unpublished data. This effort resulted in 10 studies with useable data (Cordoleani et al., 2020; Cordoleani, Holmes, Tilcock, Johnson, & Jeffres, 2021; Jeffres, 2017; Jeffres, Opperman, & Moyle, 2008; Katz et al., 2014, 2019; Sommer et al., 2001, 2020; Takata, Sommer, Louise Conrad, & Schreier, 2017). While most of the studies used caged fish, two included data from tagged free swimming fish (Sommer et al., 2001; Takata et al., 2017) and thus provided apparent growth rates. These studies covered two habitat types: lower velocity, higher temperature, more eutrophic floodplain habitat and faster velocity, lower temperature, more oligotrophic riverine habitat. As there were no data for very high or low temperatures (field data range 10.2–16.4°C), we used lab data for temperatures >23°C (Brett, Clarke, & Shelbourn, 1982; Yanke, 2006) and temperatures <6°C (Stauffer, 1973) to anchor the fits close to the minimum and maximum growth temperatures. Without these anchors, the models can predict positive growth in the floodplain habitat at temperatures above the known critical thermal maximum for Chinook. As feeding conditions in the floodplain are likely closer to the near satiation/satiation conditions of these lab studies, we only used the high temperature lab data to assist in the fitting of the floodplain data. In addition, the river data did not have the issue of predicting unrealistic growth conditions at high temperatures.

From each study, we extracted the start and end date of the experiment, the start mass or length, the end mass or length, the

growth rate, the habitat type (floodplain or riverine), and the mean temperature over the experimental window. We chose to use the mean temperature over the whole window because, in some reports, finer scale data were not available. This reduced the noisiness of the data, and allows management-models with course time resolutions to use our results. For studies which only reported mass, we converted mass to length ( $\text{length [cm]} = (\text{mass [g]}/0.0189)^{0.34}$ ). We chose to model length as it is often the metric used in management, measured in the field when processing a large number of captured fish, and used in management models. These parameters are based on averages from the literature (Chapman et al., 2013; Kimmerer et al., 2005; MacFarlane & Norton, 2002; Michel et al., 2013; Petrusso & Hayes, 2001). Table S1 presents the field data used in the models.

## 2.2 | Growth models

We used two different types of growth models; a von Bertalanffy growth (VBG) model (von Bertalanffy, 1938) and a Ratkowsky growth model (Ratkowsky, Lowry, McMeekin, Stokes, & Chandler, 1983). We fitted two versions of each type of model to the data, with each using different methods to model either the effect of habitat and/or temperature. To model the effect of habitat type, we allowed the growth rate parameter (or a parameter closely related to growth rate) and the optimum or maximum temperature values to change between habitats. This was because the optimum and maximum temperature for fish growth are often dependent on food availability (Lusardi, Hammock, Jeffres, Dahlgren, & Kiernan, 2020; Osterback, Kern, Kanawi, Perez, & Kiernan, 2018).

### 2.2.1 | Ratkowsky models

For the first Ratkowsky model, we cast the growth equation from (Perry, Plumb, Huntington, & C., 2015) in terms of length (the original formulation was in terms of mass). Changing from mass to length simply changes the values of two parameters, thus the model structure is still valid for length.

$$\begin{aligned} L_t &= \left( L_0^b + \frac{\Omega bt}{100} \right)^{1/b} \\ \Omega &= d(T - T_L) \left[ 1 - e^{g(T - T_U)} \right] \\ T_U &= T_M + \frac{\ln[1 + g(T_M - T_L)]}{g} \end{aligned} \quad (1)$$

Here,  $L_t$  is length at time  $t$ ;  $L_0$  is the starting length;  $b$  is the allometric growth exponent; the 100 factor is included because  $\Omega$ , the length standardized growth rate, is expressed in percent;  $T$  is the temperature;  $T_L$ ,  $T_U$ , and  $T_M$  are the lower, upper, and optimum temperature for growth, respectively; and  $d$  and  $g$  are shape parameters. Each habitat  $i$  had a unique  $d_i$ ,  $T_{U,i}$  for habitat  $i = (1,2)$ . We chose  $d$  based on a similar logic to Forseth, Hurley, Jensen, and Elliott (2001) which

mathematically relates maximum consumption to  $d$ . Going forward, we will call this model the ‘‘Perry model.’’

For the second Ratkowsky model, we explored the same model (Equation 1) except allowing  $g$  (not  $d$ ) to vary between habitats, following Manhard, Som, Perry, and Plumb (2018). That is, for habitat  $i$  the parameters were  $g_i$ , and  $T_{U,i}$  for  $i = (1,2)$ . Going forward, we will call this model the ‘‘Manhard model.’’

### 2.2.2 | von Bertalanffy models

For the von Bertalanffy (VBG) models, each model starts with a classic von Bertalanffy equation

$$L = L_\infty - (L_\infty - L_0)e^{-kt} \quad (2)$$

where  $L_0$  is length at hatch,  $L_\infty$  is ultimate (asymptotic) length,  $k$  is growth rate and  $t$  is time. For the first VBG model, the growth rate  $k$  is modeled as a function of temperature using Rosso's function (Kielbassa, Delignette-Muller, Pont, & Charles, 2010)

$$k = k_{opt} \frac{(T - T_{min})(T - T_{max})}{(T - T_{min})(T - T_{max}) - (T - T_{opt})^2} \quad (3)$$

where  $T_{min}$  is the minimum temperature for growth,  $T_{max}$  is the maximum temperature for growth,  $T_{opt}$  is the optimum temperature for growth, and  $k_{opt}$  is the optimum growth rate. There is a relationship between two of the main parameters ( $L_\infty$  and  $k$ ) and temperature in this formulation of the VBG model. Kielbassa et al. use an equation from a previous paper (Munro & Pauly, 1983) to capture this relationship.

$$\Phi = \log(k) + 2\log(L_\infty)$$

with

$$\Phi = \Phi_0 + \Phi_1 T \quad (4)$$

where  $\Phi_0$  and  $\Phi_1$  are constants. In this version, we allow  $k_{opt}$  (the optimum growth rate),  $T_{opt}$  (optimum temperature for growth), and  $T_{max}$  (maximum temperature for growth) to vary between habitats. Going forward, we will call this model the ‘‘Kielbassa model.’’

For the second VBG model, we use the formulation described by Kim, Lim, Seo, and Sheen (2017) to model the growth rate  $k$  as a function of temperature in the following manner:

$$k = \begin{cases} k_{opt} e^{\left( \frac{\alpha}{T - T_{min}} - \frac{\beta}{T_{max} - T} \right)}, & T_{min} < T < T_{max} \\ 0, & \text{Otherwise} \end{cases} \quad (5)$$

Here we allow  $k_{opt}$  (the optimum growth rate) and  $T_{max}$  (maximum temperature for growth) to change between habitats. Going forward, we will call this model the ‘‘Kim model.’’

### 2.3 | Model fitting

We fitted the two Ratkowsky and two VBG models using a Bayesian hierarchical approach. This was modeled in Program R with rjags and other necessary packages (Plummer, 2003; R Core Team, 2015; RStudio Team, 2015; Wickham, 2016a, 2016b; Wickham, François, Henry, & Müller, 2018). The Perry model is as follows:

$$\begin{aligned}
 P &\sim \text{Lognormal}\left(\ln(L) - \frac{1}{2}\sigma^2, \frac{1}{\sigma^2}\right) \\
 \ln(L) &= \ln\left[\left(L_0^b + \frac{\Omega bt}{100}\right)^{\frac{1}{b}}\right] \\
 \Omega &= \max\left[d(T - T_{\min})\left(1 - e^{\left\{g\left[T - (T_{\text{diff}} + T_{\min}) + \frac{\ln(1+g+T_{\text{diff}})}{g}\right]\right\}}\right), 0\right] \\
 T_{\text{diff}} &= T_{\text{flood}}f_{\text{flood}} + T_{\text{river}} \\
 d &= d_{\text{flood}}f_{\text{flood}} + d_{\text{river}}
 \end{aligned} \tag{6}$$

Here,  $T_{\text{diff}}$  is the optimum temperature minus the minimum temperature,  $f_{\text{flood}}$  is a binary indicator if the data are from a floodplain or not,  $T_{\text{river}}$  is a baseline value for  $T$ , and  $T_{\text{flood}}$  represents the increase in  $T_{\text{diff}}$  from moving from a river to a floodplain habitat. We used a similar concept for the following three models where a parameter changes between floodplain and river. That is, we explicitly modeled the value for the river and then the difference between the river and floodplain.

The Manhard model is as follows:

$$\begin{aligned}
 P &\sim \text{Lognormal}\left(\ln(L) - \frac{1}{2}\sigma^2, \frac{1}{\sigma^2}\right) \\
 \ln(L) &= \ln\left[\left(L_0^b + \frac{\Omega bt}{100}\right)^{\frac{1}{b}}\right] \\
 \Omega &= \max\left[d(T - T_{\min})\left(1 - e^{\left\{g\left[T - (T_{\text{diff}} + T_{\min}) + \frac{\ln(1+g+T_{\text{diff}})}{g}\right]\right\}}\right), 0\right] \\
 T_{\text{diff}} &= T_{\text{flood}}f_{\text{flood}} + T_{\text{river}} \\
 g &= g_{\text{flood}}f_{\text{flood}} + g_{\text{river}}
 \end{aligned} \tag{7}$$

The Kielbassa Model is as follows:

$$\begin{aligned}
 P &\sim \text{Lognormal}\left(\ln(L) - \frac{1}{2}\sigma^2, \frac{1}{\sigma^2}\right) \\
 \ln(L) &= \ln\left[L_{\infty} - (L_{\infty} - L_0)e^{(-kt)}\right] \\
 k &= \max\left[\frac{k_{\text{opt}}(T - T_{\min})(T - T_{\max})}{(T - T_{\min})(T - T_{\max}) - (T - T_{\text{opt}})^2}, 1\right] \\
 &\quad \Phi = \Phi_0 + \Phi_1 T \\
 L_{\infty} &= \sqrt{\frac{10^{\Phi}}{k}} \\
 T_{\text{opt}} &= T_{\text{opt,flood}}f_{\text{flood}} + T_{\text{opt,river}} + T_{\min} \\
 T_{\text{max}} &= T_{\text{max,flood}}f_{\text{flood}} + T_{\text{max,river}} + T_{\text{opt}} \\
 k_{\text{opt}} &= k_{\text{opt,flood}}f_{\text{flood}} + k_{\text{opt,river}}
 \end{aligned} \tag{8}$$

Finally the Kim model is as follows:

$$\begin{aligned}
 P &\sim \text{Lognormal}\left(\ln(L) - \frac{1}{2}\sigma^2, \frac{1}{\sigma^2}\right) \\
 \ln(L) &= \ln\left[L_{\infty} - (L_{\infty} - L_0)e^{(-kt)}\right] \\
 k &= k_{\text{opt}}e^{\left(-\frac{\beta}{T - T_{\min}} - \frac{\beta}{T_{\max} - T}\right)} \\
 T_{\text{max}} &= T_{\text{max,flood}}f_{\text{flood}} + T_{\text{max,river}} + T_{\min} \\
 k_{\text{opt}} &= k_{\text{opt,flood}}f_{\text{flood}} + k_{\text{opt,river}}
 \end{aligned} \tag{9}$$

For each model, we ran three chains with 1,000 adaptation steps and 4,000 burn-in steps and saved 4,000 samples with 90% thinning. The starting parameter values for each chain were random values drawn from the prior distributions (see Table 1 for a list of all the priors for the four models). We checked that all models converged using the mcmcplots package (Curtis, 2018). We checked the performance of each model using the RMS error between predicted and measured values, the slope of a linear fit through the predicted versus measured data, the DIC, and posterior predictive checks. For the posterior predictive checks, we divided up the samples into river and floodplain habitats and among three different size categories (i.e., small, medium, or large fish). Dividing the data among these six categories allowed us to see exactly which portions of the data and predictions might have discrepancies. We then looked at the distributions of measured final lengths versus distributions of predicted final lengths to see if there were systematic differences between the two distributions. We also validated the models using Chinook growth data from experiments on floodplains on the Stanislaus River (Zeug, Wiesenfeld, Sellheim, Brodsky, & Merz, 2019). These experiments were caged growth experiments using fall-run Chinook from the Mokelumne River Fish Hatchery and took place from February to May of 2016. Temperature increased during the experimental window from ~15–25°C. There were six replicates in this experiment, and we tested our models' ability to predict the result of each replicate.

## 3 | RESULTS

Both the data and the fits show two groupings, one for floodplain and another for riverine habitats (mean parameter values obtained from model fitting can be found in the Appendix; Table S2). All four models show a higher maximum growth rate and higher maximum and/or optimum temperature for floodplain habitat (Figure 1). Each model formulation shows a slightly different curve shape when fitting the data, and all four models predict different benefits from rearing in floodplain versus riverine habitat. The Kim model noticeably has a broader peak for the floodplain data owing to it having only two parameters governing the shape of the curve while the other models have three parameters. It also shows a higher growth rate benefit from the floodplain than the others, owing to it having a flatter and broader curve (Figure 1).

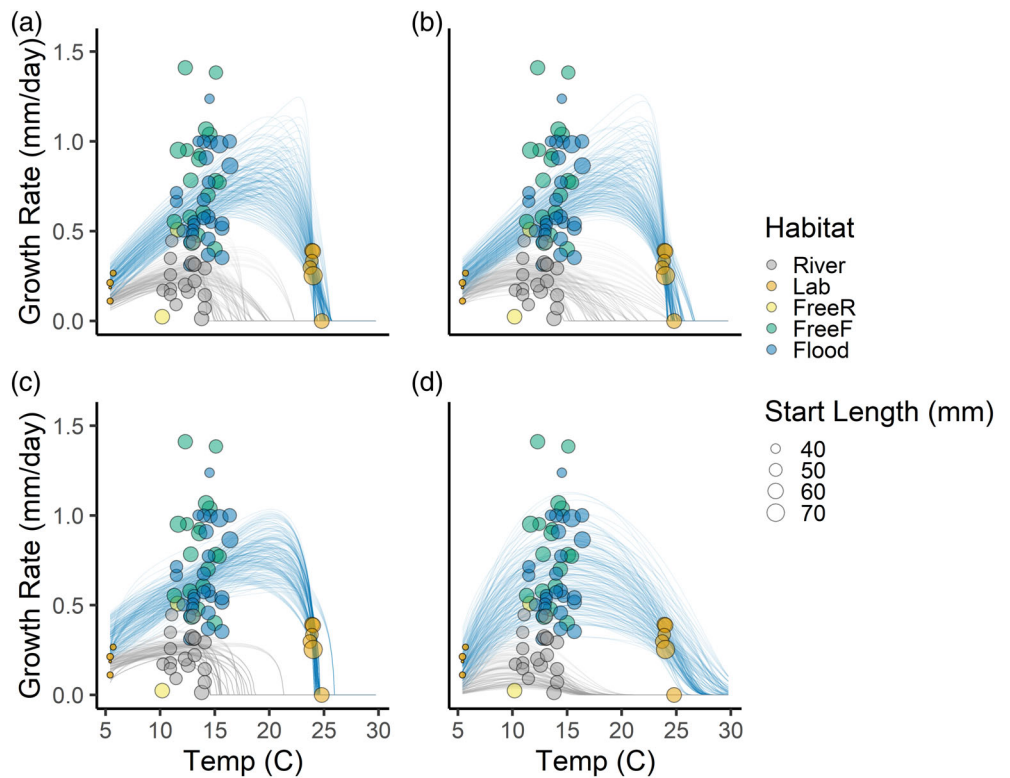
The median difference in the optimum temperature (or maximum temperature) between floodplain and riverine habitats ranged from below 5 to over 10°C (Figure 2), but were all distributed away from 0 indicating a benefit from rearing in the floodplain. Taking the median values for starting length (39 mm) and experiment duration (14.9 days) and using a middle temperature (15.1°C), the bulk of the growth rate difference values between floodplain and riverine habitats from just above 0.5 to just above 1.0 mm/day (Figure 2).

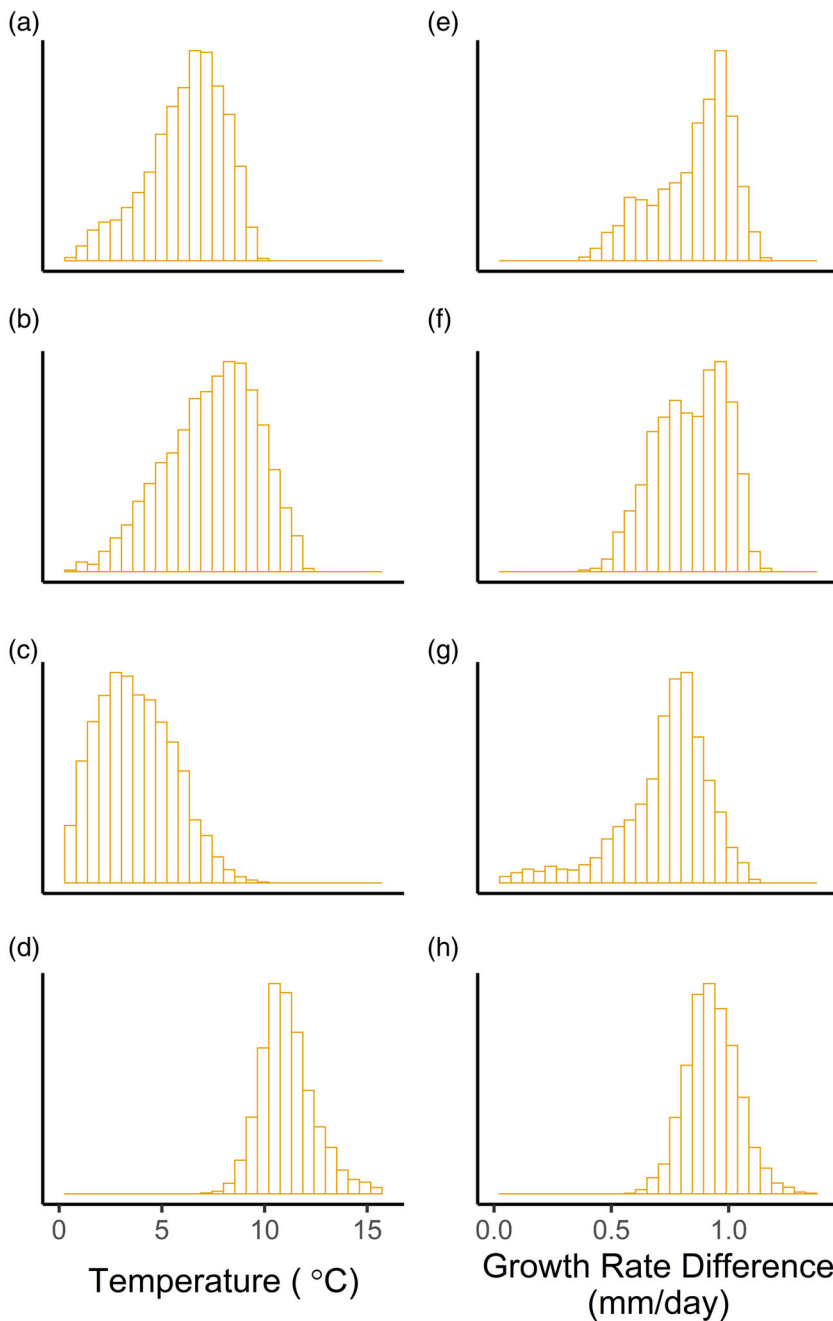
The RMS error metric for the four models showed all four models performing similarly (Figure 3). All four models had slopes for the linear models fit to the data of less than 1, showing a tendency to

**TABLE 1** The prior values used in the Bayesian model fitting. All priors follow a gamma distribution

	Perry		Manhard		Kielbassa		Kim		Rate units
	Shape	Rate	Shape	Rate	Shape	Rate	Shape	Rate	
$\sigma$	1.0	0.2	1.0	0.2	1.0	1.0	1.0	1.0	Mm
$T_{\min}$	2.0	1.0	2.0	1.0	2.0	1.0	2.0	1.0	$^{\circ}\text{C}^{-1}$
$T_{\text{river}}$	2.0	0.2	2.0	0.2	-	-	-	-	$^{\circ}\text{C}^{-1}$
$T_{\text{opt,river}}$	-	-	-	-	2.0	0.2	-	-	$^{\circ}\text{C}^{-1}$
$T_{\text{max,river}}$	-	-	-	-	2.0	0.2	2.0	0.2	$^{\circ}\text{C}^{-1}$
$T_{\text{flood}}$	2.0	0.2	2.0	0.2	-	-	-	-	$^{\circ}\text{C}^{-1}$
$T_{\text{opt,flood}}$	-	-	-	-	2.0	0.2	-	-	$^{\circ}\text{C}^{-1}$
$T_{\text{max,flood}}$	-	-	-	-	2.0	0.2	2.0	0.2	$^{\circ}\text{C}^{-1}$
$b$	2.0	0.2	2.0	0.2	-	-	-	-	-
$d$	-	-	6.0	0.1	-	-	-	-	$^{\circ}\text{C}/\text{mm}$
$d_{\text{river}}$	4.0	0.1	-	-	-	-	-	-	$^{\circ}\text{C}/\text{mm}$
$d_{\text{flood}}$	2.0	0.1	-	-	-	-	-	-	$^{\circ}\text{C}/\text{mm}$
$g$	1.0	0.5	-	-	-	-	-	-	$^{\circ}\text{C}$
$g_{\text{river}}$	-	-	1.0	1.0	-	-	-	-	$^{\circ}\text{C}$
$g_{\text{flood}}$	-	-	1.0	1.0	-	-	-	-	$^{\circ}\text{C}$
$k_{\text{opt,river}}$	-	-	-	-	1.0	0.1	2.0	0.2	Years
$k_{\text{opt,flood}}$	-	-	-	-	1.0	1.0	2.0	0.2	Years
$\Phi_0$	-	-	-	-	1.0	0.1	-	-	-
$\Phi_1$	-	-	-	-	1.0	10.0	-	-	$^{\circ}\text{C}$
$L_{\infty}$	-	-	-	-	-	-	-	-	1/mm
$\alpha$	-	-	-	-	-	-	2.0	0.2	$^{\circ}\text{C}$
$\beta$	-	-	-	-	-	-	2.0	0.2	$^{\circ}\text{C}$

**FIGURE 1** Plots of sampled posterior fits and the data points. Data points show fish reared in cages placed in a river habitat (“River”), in a lab setting (“Lab”), freely in a floodplain habitat (“Free”), and in cages placed in a floodplain habitat (“Flood”). Starting length and experiment time for each fit line are selected from the mid-value of either the top, middle, or bottom third of the range of starting length and experimental time values in the data set. The point size represents the fish length at the start of the experiment. Growth rates modeled with the Perry model (a), the Manhard model (b), the Kielbassa model (c), and the Kim model (d). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]





**FIGURE 2** Histograms of the difference in the optimum (or maximum for the Kim model) temperature parameters (floodplain temperature minus riverine temperature) (left column) and the difference in growth rates (floodplain growth rate minus riverine growth rate) (right column). (a,e) is the Perry model, (b,f) is the Manhard model, (c,g) is the Kielbassa model, and (d,h) is the Kim model. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/tra.4078)]

underestimate higher growth rates. The DIC states that the Kim model has the most support, the two Ratkowsky models receiving less support, and the Kielbassa model has the least support.

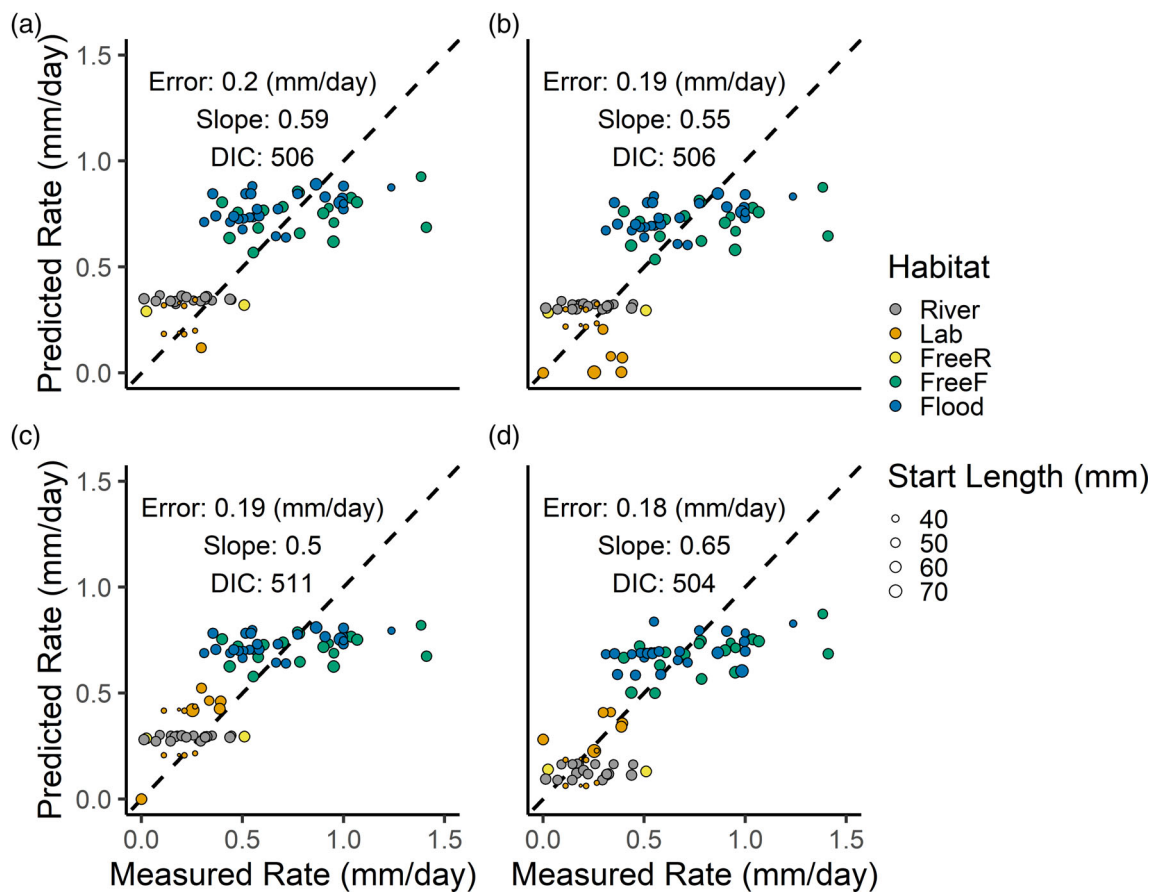
The posterior predictive checks generally show good agreement between the predicted and measured distributions of final lengths. The measured values in the floodplain do show a broader distribution than the posterior distribution from the models (Figure 4).

For the six-out-of sample validation data points, no model was able to make predictions in which all six points were within the 90% prediction intervals (i.e., predictions between the fifth and 95th percentiles; Figure 5). In both Ratkowsky models (i.e., Perry and Manhard models) validation points 1 and 6 were outside of the 90% prediction intervals. In the Kielbassa model, validation point 6 was outside the

interval, whereas under the Kim model, validation points 2,3,4, and 5 were outside the interval.

## 4 | DISCUSSION

In this work, we evaluated the differential growth benefits from different habitat types and a range of temperatures and determined the best model for fitting field experiment growth data. We did this using a hierarchical Bayesian approach on a data set gathered from available, relevant literature. Using the aggregated data from multiple studies on our system, all four models consistently reflected the benefit of floodplain rearing found in some of the empirical studies that supplied

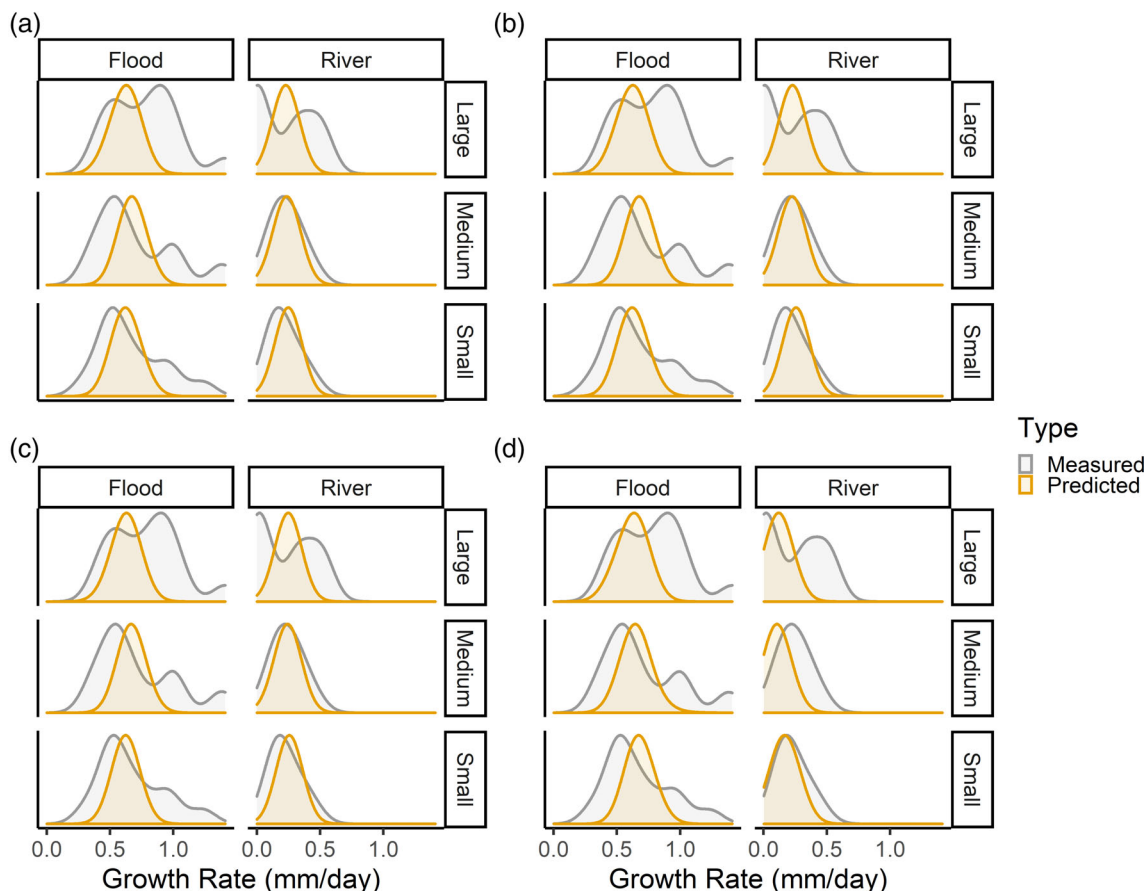


**FIGURE 3** Plots of predicted versus observed growth rates for the four models. Data points show fish reared in cages placed in a river habitat (“River”), in a lab setting (“Lab”), freely in a floodplain habitat (“Free”), and in cages placed in a floodplain habitat (“Flood”). The dashed line is a 1:1 line. Error is the RMS value, with a lower value meaning a better fit. Point size represents the fish length at the start of the experiment. (a) is the Perry model, (b) is the Manhard model, (c) is the Kielbassa model, and (d) is the Kim model. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

the data. Studies both with caged and free fish had higher growth rates in the floodplain and were broadly in agreement. The two highest growth rates for floodplain fish did come from freely swimming fish (Takata et al., 2017), which may indicate a bias from size selective mortality. This work also quantified the extent of the benefit, showed how the effect interacts with temperature, and demonstrated a method for modeling these interactions. All four models showed the extent of the benefit of floodplain rearing in the form of higher growth rates and a greater optimum growth temperature. While the upper thermal tolerance of the floodplain fish was set using lab data, the field data independently indicated that the floodplain thermal tolerance is higher than that of fish in a river environment. The increased temperature tolerance on the floodplain was likely a direct effect of more available food (Lusardi et al., 2020; Osterback et al., 2018), while the increased growth rate likely stemmed from a variety of factors including food availability.

All four models performed well, however, we think the Perry model is best suited for modeling Chinook growth in the Sacramento River system. There was considerable variability in the maximum temperature for river rearing fish in each model. The Manhard model had the highest river maximum temperature while Kim had the lowest. All

four models had low RMS errors and slopes close to a half, with the Kim model having the slope closest to one. The slopes indicated that these models may underpredict growth, however, two high growth rate data points were mostly responsible for pulling the slope away from one. The posterior predictive checks also showed similar performance among the four models. The Kim model, a noticeable outlier in its shape owing to the use of only two temperatures, performed worse than the other three models on the out of sample validation test. The Kim model did have the lowest DIC, which is likely owing it to its comparative simplicity. The performance of the three other models on this validation test showed the applicability of these models to the growth of Chinook. Considering all the test results, the Ratkowsky models are best for modeling these data. The two different methods of allowing the Ratkowsky model to account for differing habitat types performed similarly. However, the Manhard model allowed the maximum growth temperature for river fish to be higher than the floodplain fish. Given how lower rations have a negative effect on maximum growth temperature (Brett et al., 1982), we think it is unlikely that the maximum growth temperature would be higher on the river than the floodplain. The Perry model prevents the river fish from having higher thermal maximums than the floodplain model



**FIGURE 4** Posterior predictive checks for the four models. The checks are divided into river and floodplain habitat types, and into large, medium, and small fish based on starting length (top, middle, and bottom third of lengths). The orange density plot is the curve for the distribution of the predicted growth rate, and the gray is for the actual growth rate. (a) is the Perry model, (b) is the Manhard model, (c) is the Kielbassa model, and (d) is the Kim model. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/rta.4078)]

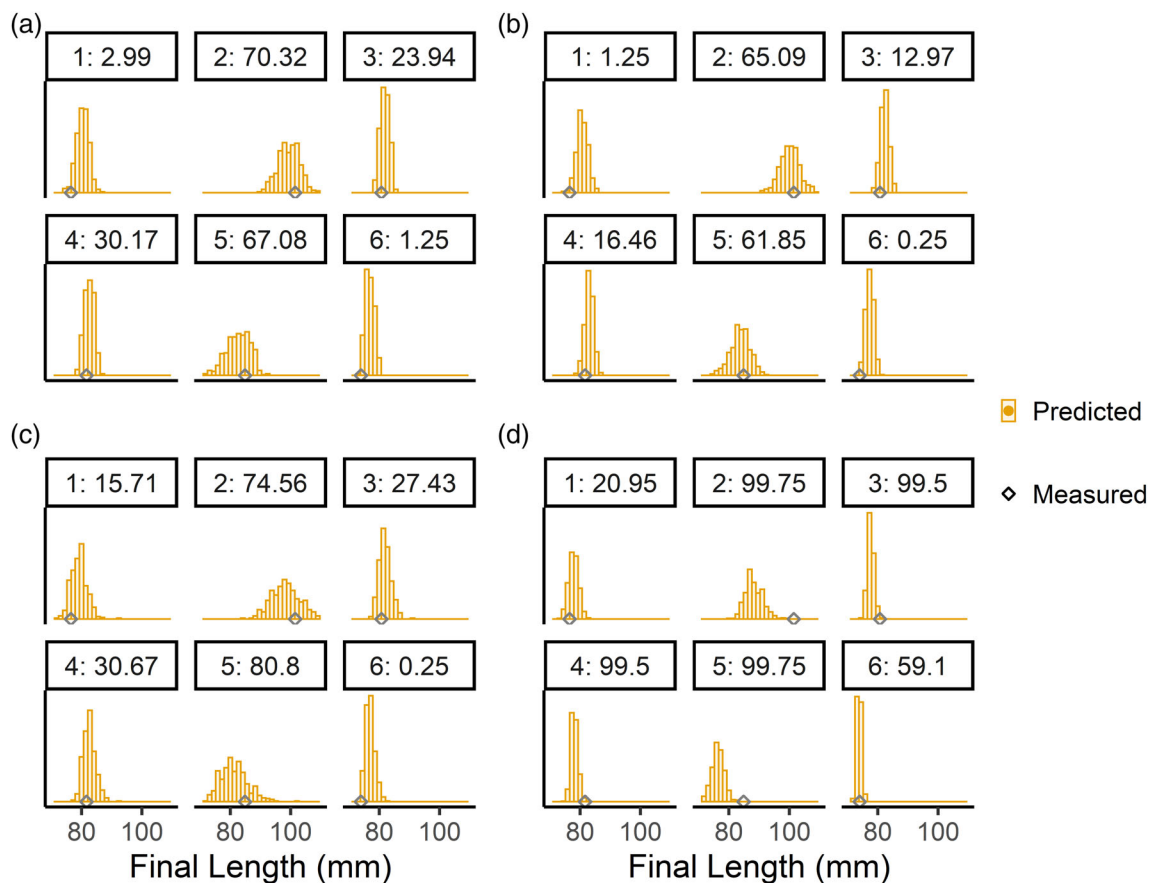
by not changing the shape of the curve (i.e., changing the  $g$  parameter) between habitats. While this constraint may seem like a detriment to the Perry model, it is a useful constraint to impose on our system given the paucity of high temperature data. Therefore, we think the Perry model is best suited for modeling larger riverine systems with connected floodplain habitat. This meta-analysis provides a more comprehensive view of the rearing benefit of floodplains than individual studies in isolation and will allow for better modeling of the growth benefit of floodplain rearing.

The observed differences in optimum growth temperature and growth rates across habitats are broadly consistent with other findings. Numerous different habitat types beyond floodplains, such as estuaries and lagoons, can also provide growth benefits when compared to rivers and headwaters (Davis et al., 2019; Hayes et al., 2008; Satterthwaite et al., 2012). Studies have also documented that artificially supplementing riverine habitat with food may impart a growth benefit (Boughton, Gibson, Yedor, & Kelley, 2007). As differential growth across habitats is relatively common in fish in a broad range of environments, our methods are broadly applicable and could be applied to numerous systems to investigate the differential growth between habitats, including river/ocean life histories for steelhead/rainbow trout (Eschenroeder et al., 2022), time remaining on spawning

grounds post spawning for sturgeon (Moser et al., 2016), warm water habitat for cold water river fish (Armstrong et al., 2021), mangrove habitats (Laegdsgaard & Johnson, 2001), lake bottom sediment type (Bowen, 1984), and so forth.

While the methods of this analysis are broadly applicable across many aquatic systems, these particular growth results are likely specific to this system and care should be taken when applying these findings to other floodplain and river systems or to other habitat types (Davis et al., 2019). Small changes in growth conditions, habitat, food availability and so forth, can change fish growth rates, and system specific effects even arise in controlled lab studies (Elliott & Hurley, 2003). Detailed analysis of growth in different habitats shows multiple covariates, including chlorophyll-a, temperature, and prey base composition (Cordoleani, Holmes, Bell-Tilcock, Johnson, & Jeffres, 2022). Many things may change between habitats such as foraging efficiency (Caldwell, Rossi, Henery, & Chandra, 2018), or different predator fields causing behavior shifts (Dill & Fraser, 1984; Steel, Hansen, Cocherell, & Fanguie, 2019) and different species may change their behavior in different habitats to a greater or lesser extent (Abrahams & Healey, 1993). Thus, specific context is important when assessing the growth benefits from differing habitats and selecting growth models, and no one general model fit is likely to be accurate





**FIGURE 5** Validation checks for the four models. There is one check for each of the six floodplain experiments. The orange histogram represents the distribution of predicted final lengths from the posterior parameter sets. The gray diamonds represent the mean value of final length from the experiment. The labels are the ID of the experiment (1–6) and the percent of the predicted final lengths in the histogram which are below the actual mean length. (a) is the Perry model, (b) is the Manhard model, (c) is the Kielbassa model, and (d) is the Kim model. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

across all systems. In addition, our use of mean temperature may require that researchers fit these models differently when using shorter time scales. Using mean temperature versus integrated temperature in an environment where temperature is changing may result in biases in calculating variables with nonlinear responses such as growth (Holsman & Danner, 2016). However, if future implementations of these models use similar time scales to this work, then use of mean temperature as an input should not pose an issue.

There have been other efforts to look at differing growth models on a single system. Briere and Pracros (1998) compared five equations for moth growth, and each provided reasonable fits, similar to our findings. Other approaches have also been used on this system to model growth in different habitats, including using hybrid approaches of calibrated growth rates on riverine habitats and mechanistic growth models on floodplain habitats (Bellido-Leiva, Lusardi, & Lund, 2021). While not directly comparable to our work, we mention it here as it is an option for researchers to explore, especially when there is a substantial difference between the data available from each habitat. Going beyond simple comparison, others have used similar data with differing methods to understand the interactions of growth and

habitat, which could be a future direction of this research. Studies have used observed growth rates in different habitats and used these to estimate consumption rates across habitats (Weber, Bouwes, & Jordan, 2014). When count data are available, it is possible to build more sophisticated Bayesian model frameworks and use these count data to examine the growth benefits of different habitats (Lecomte & Laplanche, 2012).

In the future, we intend to investigate additional habitat types such as side channels and plan to separate the floodplain into more specific sections, such as inlet zones or toe drains. This data set could also benefit from more data between 15–22°C, data closer to the estuary environments, and data in different sections of the river. Due to daily fluctuations in temperatures, it is unlikely that the higher temperature gap will be able to be filled with field experiments, as maximum temperatures in areas with mean temperatures in the sought-after range may exceed the thermal maximums of the fish. In addition, fish that experience high average temperatures may, during the hottest portions of the day, be under considerable thermal stress, which will reduce their growth. The data used from the lab experiment has constant temperatures and so it may be overestimating the

growth potential of these fish when compared to fish experiencing these mean temperatures but with fluctuations in temperature. Depending on the quality of the data, we may be able to incorporate additional variables, such as prey availability, in the future.

Through a meta-analysis, we produced modeled fits for Chinook growth in a riverine and floodplain environment. While all models performed well, the Ratkowsky type models performed best with the Perry model being the superior model. All models had a consistent benefit of floodplain rearing and were consistent in how the influence of temperature varies depending on habitat type. This finding reinforces the importance of reconnecting river habitat to its floodplain and restoring connected but degraded floodplain habitat. It also shows the importance of considering the interaction between food availability and temperature effects when performing management actions for Chinook salmon. This work will provide managers and modelers with a better understanding of the degree to which different habitats and temperature affect growth. Furthermore, these growth models can be integrated within lifecycle models to test hypotheses of how different size-specific survival rates (Hassrick, Ammann, Perry, John, & Daniels, 2022; Perry et al., 2018) could affect long-term population dynamics, ultimately informing efforts to recover threatened and endangered populations of Chinook salmon.

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://datadryad.org>, reference number <https://doi.org/10.7291/D1S68V>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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