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Title: Incorporating temporal heterogeneity in environmental conditions into a somatic growth model

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Abstract:

Evaluating environmental effects on fish growth can be challenging because environmental conditions may vary at relatively fine temporal scales compared to sampling occasions. Here we develop a Bayesian state-space growth model to evaluate effects of monthly environmental data on growth of fish that are observed less frequently (*e.g.*, from mark-recapture data where time between captures can range from months to years). We assess effects of temperature, turbidity, food availability, flow variability, and trout abundance on subadult humpback chub (*Gila cypha*) growth in two rivers, the Colorado River (CR) and the Little Colorado River (LCR), and we use out-of-sample prediction to rank competing models. Environmental covariates explained a high proportion of the variation in growth in both rivers; however, the best growth models were river-specific and included either positive temperature and turbidity duration effects (CR) or positive temperature and food availability effects (LCR). Our approach to analyzing environmental controls on growth should be applicable in other systems where environmental data vary over relatively short time scales compared to animal observations.

65 Introduction:

66 Statistical models are commonly used to describe relationships between fish growth and
67 environmental variables and inform management of species of concern. Accordingly, there is
68 extensive literature that relates somatic growth to environmental variables (Campana et al. 1995,
69 Kimura 2008, Sigourney et al. 2012), with various approaches differing in both assumption
70 requirements and model complexity. Nevertheless, relating growth to environmental covariates
71 is complicated by the fact that observations of fish frequently occur at intervals that may
72 encompass substantial variation in environmental conditions. Often, studies relate the mean
73 environmental covariate (*e.g.*, mean temperature) over the entire sampling interval to observed
74 growth (Letcher et al. 2014, Millar et al. 1999, Vøllestad and Olsen 2008), disregarding
75 variability in environmental conditions within each sampling interval (*i.e.*, an interval in which
76 temperatures were always 15° C would be treated the same as an interval in which temperatures
77 increased smoothly from 9° C to 21° C). An alternate approach to incorporate environmental
78 effects is to use fine-scale environmental measurements to estimate fish growth over longer time
79 intervals. For example, Mooij and van Tongeren (1990) predicted daily growth of juvenile roach
80 (*Rutilus rutilus*) from daily water temperature measurements, summed daily growth estimates to
81 obtain growth over time at large (*i.e.*, over time between initial capture and recapture), then
82 minimized sums of squares of predicted and observed growth to obtain growth parameter
83 estimates. While the current approach is in some ways similar to that of Mooij and van
84 Tongeren (1990), the current approach describes a method that can be used to incorporate
85 multiple sources of uncertainty into parameter estimates, as well as quantify how much
86 environmental covariates describe growth.

Here, we present an approach for relating somatic growth to environmental covariates, which has many advantages over other growth models. The model we present uses a state-space framework (Carlin et al. 1992) to differentiate process and observation errors, thereby minimizing bias in parameter estimates that results from ignoring sampling error (Carroll et al. 2006, Gould and Nichols 1998, Shenk et al. 1998), while providing a flexible model framework (Clark and Bjørnstad 2004). In addition to modeling the growth process at a finer temporal scale than intervals between observations, the current modeling approach also accommodates variability in the interval between captures (*i.e.*, fish can be at large from months to years). Moreover, the process model includes a month random effect to account for potential model misspecification (*e.g.*, if mean monthly growth strays from the specified log-linear relationships with environmental covariates, or if there is an important unmeasured covariate), and to account for the dependence of observations that are at large over the same monthly intervals. Inclusion of monthly random effects allows us to calculate multi-level R^2 values (Gelman and Pardoe 2006), which partitions out the variance explained by environmental covariates at the scale of months from the variance explained at the scale of individual fish observations by the overall process model.

We begin by introducing the general form of the model then apply it to growth of endangered subadult humpback chub (*Gila cypha*) in two very different river systems, the highly regulated Colorado River (CR) in the Grand Canyon, and one of its tributaries, the smaller, less regulated Little Colorado River (LCR). Past studies of humpback chub in this system have established large differences in average monthly growth rates between these two rivers (Yackulic et al. 2014) and have emphasized the role of temperature in controlling growth (Clarkson and Childs 2000, Coggins and Pine 2010, Petersen and Paukert 2005, Robinson and Childs 2001)

with more recent studies suggesting that other environmental factors may also be important (Dzul et al. 2014, Finch et al. 2013). None of these studies, however, addressed multiple competing hypotheses through formal statistical comparisons, or considered models in which multiple factors controlled growth. In particular, we assess the roles of temperature, food availability, turbidity, flow variability, and non-native rainbow trout (*Oncorhynchus mykiss*) abundance in determining the river-specific growth of humpback chub.

Methods

A state-space growth model with an underlying log-linear process model.

State-space models assume there is an underlying process (e.g., growth) model leading to changes in the “true” state (e.g., total length) of a fish and that the state is observed imperfectly (e.g., there are errors in measurements of total length). In theory, the underlying process model could have any temporal resolution; however, finer temporal resolutions require increased computational times. After initial consideration of scales of temporal variation in potential environmental covariates and preliminary model fitting to determine model speed, we chose to model the process at a monthly scale. For our application, models with environmental covariates measured on a monthly scale took between ~2-3 (LCR models) or ~8-12 (CR models) hours to run.

Similar to previous studies (Fabens 1965, Francis 1988), the process model is a parameterization of the von Bertalanffy model that can be fit to capture-recapture data of tagged fish (Sigourney et al. 2012). Our log-linear process model describes growth as a function of environmental covariates, fish size (to account for the expectation that small fish grow faster than large fish), sample-level process error, and a monthly random effect. Note the log link only

allows positive growth (*i.e.*, fish cannot shrink). Specifically for individual j in month m growth, $\Delta L_{j,m}$, is modelled as:

$$(1) \quad L_{j,m} = L_{j,m-1} + \Delta T_{j,m} e^{(\beta_0 + \beta_L L_{j,m-1} + \beta \mathbf{X}_m + \omega_m + \tau_j)}$$

where $\Delta T_{m,j}$ is an offset that corresponds to the proportion of month m when individual j was at large, β_0 is an intercept representing growth under average environmental conditions, β_L is an effect on fish size on growth, $L_{j,m-1}$ is the length of individual j at the beginning of the month, β is a vector of estimated environmental coefficients, $\mathbf{X}_m$ is a vector of environmental conditions for month m , ω_m is the monthly random effect, and τ_j is sample-level process error for individual j . For each month m , the length estimate for each individual is updated by adding the current month's growth estimate ($\Delta L_{j,m}$) to the previous month's length estimate ($L_{j,m-1}$).

Our model included month-level process error, ω_m , in the form of monthly random effects to allow month-specific growth estimates to stray from deterministic predictions based on the environmental covariates (To be clear, this a random effect for each month of a study, not each month in a calendar year, so a 3 year study would include 36 random effects). In other words, the monthly random effect acts as a residual that groups observations by month and thereby describes how much mean growth for a particular month differs from the value predicted by environmental covariates (Barry et al. 2003). Accordingly, the monthly random effects accounts for un-modelled time-varying covariates (*e.g.*, fish density) or misspecification of functional form (*e.g.*, if effects of a particular covariate are not exactly log-linear). The monthly random effect was centered on zero with standard deviation δ :

$$(2) \quad \omega_m \sim N(0, \delta)$$

Monthly random effects are necessary for this application because fish observed over the same interval are not statistically independent replicates of the same environmental conditions. For instance, if an unmeasured time-varying covariate affects growth of all individuals in a month, then the residuals for these individuals are not independent. Similar to the monthly random effect, sample-level process error was also centered on zero but with standard deviation ρ . Note that, because sample-level process error is modelled on a monthly time scale, process error accumulates as time at large increases.

Whereas the process model operates over a monthly interval and estimates length even when fish are not observed, the observation model compares observed and predicted lengths when fish are captured. Accordingly, we use $t2_j$ in the observation model to depict the month of recapture for individual j . The observation model assumes that when individual j is captured in month $t2$, the observed length ($oL_{j,t2}$) is normally distributed with respect to the true length of the fish:

$$(3) \quad oL_{j,t2_j} \sim N(L_{j,t2_j}, \sigma)$$

where σ represents measurement error. Fish that are captured within the same sampling trip typically displayed 1-9 days between captures; these fish were used to improve estimation of σ (as growth will be near zero over these time periods). Thus, incorporating within-trip recaptures helped distinguish between process and measurement errors. We assumed measurement error occurred only when samples were recaptured (*i.e.*, no observation error when a fish was first captured). Although unrealistic, this assumption greatly decreased time to convergence and did not noticeably affect assessment of environmental covariates when compared to models in which observation error was included for the first capture.

Application of the model to assess environmental drivers of humpback chub growth in two rivers.

We evaluated growth of subadult humpback chub (80-200 mm total length), because this size class is less likely to move between the LCR and the CR compared to juveniles or adults (Yackulic et al. 2014). Specifically, 1-2% of subadults move from the LCR to the CR and 0.3-0.8% move from the CR to the LCR on a monthly basis (Yackulic et al. 2014). Data come from a long-term mark-recapture monitoring program designed to inform management of Glen Canyon Dam.

Study site: Environmental data from both the CR and LCR are briefly described in Table 1. For a more detailed description of environmental covariates, refer to Appendix A. All spatial locations referred to in this paper are reported in river kilometers (rkm). In the CR, rkm's refer to distance downstream of Glen Canyon Dam. All CR sampling occurred just below its confluence with the LCR because this location is associated with the largest aggregation of humpback chub in the Grand Canyon reach of the CR. The CR is a regulated river in which water temperature is determined by the temperature of releases from Glen Canyon Dam, as well as air temperatures, the lake level of Lake Powell, and discharge (Wright et al. 2009). CR turbidity is largely driven by tributary inputs (including from the LCR) and is relatively uncoupled from discharge. Mean monthly water temperatures in the CR near the LCR confluence can range from 8-15°C and daily temperature fluctuations are negligible (< 2°C).

In the LCR, rkm's refer to distance upstream of the LCR-CR confluence. The LCR is ephemeral in its mid-reaches, but the lower 21 kilometers are perennial and fed by Blue Spring, a ground-water spring of constant water temperature (20.5°C). As water moves downstream from

Blue Spring in the LCR, diel and seasonal variability in water temperature increases. Specifically, water temperatures at rkm=1.0 fluctuate ~2-6°C daily and average monthly temperatures range from ~12-24°C seasonally (Figure 1). Furthermore, the lower ~450 kilometers of the LCR are un-dammed, and thus its hydrograph is influenced by seasonal precipitation patterns in northern Arizona. The LCR hydrograph typically peaks between January-April (due to snowmelt) and July-September (due to midsummer monsoons), though the timing and intensity of floods varies from year to year. Compared to current conditions in the CR, the LCR is much less regulated (however impoundments do occur within its watershed) and its thermal and hydrologic regimes of the LCR more closely resemble that of the predam CR (Robinson and Childs 2001), though the predam CR experienced much colder winter water temperatures than the LCR.

Field methods:

Data from humpback chub captured in the CR were collected by biologists as part of the Near Shore Ecology project (NSE; 2009-2011) or as part of the Juvenile Chub Monitoring project (JCM; 2012-2014). Both the NSE and JCM trips sampled the CR near its confluence with the LCR; however, NSE trips sampled fish from rkm 126-130, whereas the JCM trips only sampled rkm 126-129. Moreover, sampling during NSE trips lasted 12 days and occurred in July, August, September, October whereas sampling for JCM trips lasted 10 days and occurred in January, April, July, and September. Both NSE and JCM trips used two gear types: 47-90 un-baited hoop nets (6mm nylon mesh, 50-60 cm diameter, 1 m long, single 10-cm throat), and night-time slow-speed boat electrofishing (pulsed DC current, 15-20 amps, 200-300 volts). Hoop nets were checked once every 24 hours, and electrofishing occurred either every 24 hours

(JCM trips) or once every 24-72 hours (NSE trips). NSE sampling methods are described by Finch et al. (2013) and JCM sampling methods are described by Korman et al. (2015).

Data from the LCR were collected twice in late spring (typically once in April and May but in 2010-11 sampling occurred in May and June) and twice in autumn (September and October) by the U.S. Fish and Wildlife Service. In addition, we included data from two U.S. Geological Survey trips to the LCR in July 2013 and July 2014. Humpback chub in the LCR were sampled using hoop nets (same type as described for CR sampling). All humpback chub from the LCR that were used in this analysis were sampled between rkm 2-7. For more details about sampling methods in the LCR, refer to Van Haverbeke et al. (2013).

All humpback chub captured in either the CR or LCR were measured for total length, scanned for a 134.2 kHz passive integrated transponder (PIT) tag, and given a PIT tag if they were previously unmarked and above 99 mm. Additionally, beginning in 2013, USFWS started using PIT tags to mark chub as small as 80 mm. Most fish used in the study were captured twice (*i.e.*, only had one interval over which growth could be estimated). For fish captured more than twice, we randomly selected one growth interval per individual to include in our dataset. The small loss of data was necessary because growth models without individual effects are subject to bias if they include multiple observations of the same individuals (Sainsbury 1980). Data used to fit the growth model included 936 samples from the CR and 649 samples from the LCR.

Model fitting and model selection.

All Bayesian analyses were conducted with Stan (Stan Development Team 2013) using the package rstan in R (R Core Development Team 2012). We include STAN code for the growth model with temperature effects in Appendix B. Each model was run with 3 chains of

Hamiltonian Monte Carlo (HMC) simulations with no U-turn extensions (NUTS) until chains converged ($\hat{R} < 1.1$; Gelman et al. 2014a). We discarded the first 1 000 posterior draws (burn-in), thinned by every 5th posterior draw, and saved 333 posterior draws from each chain to generate posterior parameter distributions for model selection. All environmental covariates were standardized and initial length was centered prior to running the model. Priors on all β parameters were normal (mean = 0, standard deviation = 10) with the exception of β_L which was given a uniform prior between -0.1 and 0.1. Uniform priors were used for observation error ($\sigma_m \sim U(0, 10)$), process error ($\sigma_p \sim U(0, 1)$), and month standard deviation ($\omega \sim U(0, 5)$).

We fit models separately to both CR and LCR growth data. The most complex (full) CR model we considered included five covariates: food availability (fo), temperature (te), turbidity (tu), flow variability (fv), and trout abundance (tr). The full LCR model included temperature, turbidity, and food availability, but not flow variability or trout abundance. Specifically, flow variability in the LCR was highly correlated with turbidity ($R > 0.7$), so flow variability was not assessed for the LCR. Also, the LCR model does not include a trout effect because trout rarely enter hoop nets (the only sampling gear used in the LCR) and thus it is difficult to approximate their abundance. In addition to the full model for each river, we also included all models that were nested within the full model.

We used out-of-sample prediction for model selection (Gelman et al. 2014b). When using out-of-sample prediction to assess models, some data are withheld from model fitting and instead used to assess model predictive performance (*i.e.*, out-of-sample data). Models are ranked by their ability to predict out-of-sample data. In the current study, models were fit to growth data from either April 2009-May 2013 (LCR) or July 2009-September 2013 (CR). Out-of-sample data were from the last year of the study (*i.e.*, August 2013-July 2014 for the LCR and

October 2013- September 2014 for the CR) and included 76 observations from the CR and observations from the LCR. Mean squared prediction error (Hooten and Hobbs 2014) was used to evaluate the predictive abilities of each model, and models with the lowest mean squared prediction error were considered the best models:

$$(4) \quad MSPE = \sum_{i=1}^n \frac{(y_i - \hat{y}_i)^2}{n}$$

Where y_i and $\hat{y}_i$ are the observed and median predicted out-of-sample data, respectively, and n is the sample size of out-of-sample data. Importantly, some fish included in the out-of-sample data were initially captured before the last year of the study and therefore they are not completely statistically independent of the fitted model. In other words, although these out-of-sample data were not used in fitting, the time at large of out-of-sample data sometimes overlapped the period in which fitting occurred. We reran the best model for each river with 5 000 total posterior draws to obtain better estimates of parameter posterior distributions. Similar to previous model runs, we ran 3 chains, discarded the first 1 000 samples (burn-in), and thinned by every 5th iteration. Furthermore, because state-space models can sometimes have identifiability issues, we used simulations to evaluate bias of this modeling method (see Appendix C).

Additionally, to further assess how well environmental covariates predicted growth, we used multi-level R^2 (Gelman and Pardoe 2006) to estimate the proportion of variance explained by the best model for each river. The variance explained, R^2 , at any level of a model can be generally defined as one minus a quantity defined as the variance in residuals divided by the total variance in the linear predictors and the residuals at that level (see equation 6 and 7 in Gelman and Pardoe 2006), which is equivalent to determining the proportion of the variation at a particular level that is accounted for by the linear predictors. In our example, the higher level of the hierarchy is the covariate-level R^2 value, which estimates the proportion of variability in

mean monthly growth rates that is explained by environmental covariates (where the monthly random effects act as the residuals). The lower level corresponds to the sample-level R^2 value, which describes the proportion of variability in observed growth at the sample level that is explained by monthly random effects, environmental covariates, and the size effect. At this level predictions from the model without sample-level process error were compared to the actual individual observations to calculate the residuals.

Results:

Simulation results suggest that coefficients associated with environmental covariates had a consistent, but minor ($<6\%$) positive bias (Appendix C). In addition, intercept values were negatively biased and month error terms were positively biased in models of both rivers. These two parameters were negatively correlated, suggesting a tradeoff that results from the use of log-link. Specifically, this is analogous to the joint role that the position and scale of a log-normal distribution play in determining the arithmetic mean. Importantly, the negative bias in the intercept and the positive bias in month error terms offset each other and did not noticeably affect estimation of environmental coefficients.

Environmental covariates used in the growth model were not strongly correlated ($R < 0.4$). The best CR growth model included temperature and turbidity duration (Table 2). Both temperature and turbidity duration were predicted to have a positive effect on growth (Figure 2; Table 4). Environmental covariates were fairly strong predictors of population scale CR growth as illustrated by the covariate-level R^2 value ($R^2 = 0.65$). Plots of log (observed) growth and log (predicted) growth indicated the CR growth model exhibited good fit (Appendix D), and the sample-level R^2 value ($R^2 = 0.80$) indicates that individual variation in growth is slight in

comparison to monthly variation in growth. Growth in the CR remained very low from November to May (typically months when temperature and turbidity were low) and increased substantially from July to October (Figure 3). Measurement error was estimated to be 2.34 mm, and monthly process error was 0.36 mm (Table 3).

The results of the growth model for the LCR indicate that growth was influenced by temperature and food availability (Table 2). The covariate-level R^2 value for the best LCR model was also high (0.72), indicating that environmental covariates explained most of the variation in the LCR growth model (Figure 4). Residual plots of predicted and observed growth showed that the LCR model exhibited reasonable fit. The sample-level R^2 value was high (0.84). Growth in the LCR was fastest from April to June, typically months when food availability was high and temperature was moderate, and in general LCR growth was much faster than CR growth. Measurement error was comparable to that of the CR (2.35 compared to 2.34), while LCR process error was lower (0.27 compared to 0.36; Table 3).

Discussion:

Incongruent time scales for environmental data and animal observations may be relatively common in ecological studies. For example, data loggers can record environmental data over short time intervals (*e.g.*, every hour or every day) that are unrealistic for mark-recapture studies (*i.e.*, animals often cannot be observed hourly or daily). Despite the temporal mismatch of these two different types of measurements, coupling fine-scale variability in environmental data with sporadic animal observations may be advantageous because ignoring fine-scale temporal variability in explanatory variables can lead to biased results in nonlinear models (Ruel and Ayres 1999). Specifically, nonlinear relationships between environmental

variables and species responses are common in ecological studies (Burkett et al. 2005, Hsieh et al. 2005, Schlenker and Roberts 2009), and accordingly including finer-scale temporal resolution of explanatory variables may be beneficial.

Not only does the above-described modeling approach aid researchers attempting to describe environmental effects on ecological processes, it also includes a realistic error structure where error is partitioned among different sources: month-level process error, sample-level process error, and sample-level measurement error. Because this error structure is fairly complex, and because state-space models can experience difficulties with convergence and parameter identifiability (Dennis et al. 2006, Hostetler and Chandler 2015), we include some suggestions for applying the above-described model to growth data. First, we recommend including within-trip recaptures into the model's structure to help differentiate sample-level observation and process errors. Second, we recommend that the study occur over a fairly long time span (*i.e.*, at least 3 years if environmental data are collected on a monthly scale) and that the study include some short-term recaptures (*e.g.*, where the interval between captures is 1-3 months) to differentiate month random effects from environmental covariates. Lastly, we emphasize the importance of including monthly random effects because previous studies have illustrated that environmental models without temporal random effects underestimate error and overestimate the magnitude of environmental coefficients (Barry et al. 2003). Nonetheless, our simulations suggested there was a small degree of bias in our applied example (Appendix C) and we recommend the further use of simulations to explore potential biases associated with different study designs, effect sizes, and amounts of data. A logical extension of this modeling approach would be to add an error term associated with individual, as previous growth studies have illustrated the importance of accounting for individual variability in growth modeling (Eveson et

al. 2007, Sainsbury 1980). Similarly, the current model does not account for size selectivity of sampling gear nor cohort-level growth variability, modifications which may further improve the accuracy of this modeling approach (Stawitz et al. 2015).

While this model could be formulated using maximum likelihood, estimating parameter distributions of model parameters would be analytically demanding due to the model having multiple levels of random effects. Thus, other studies have opted for Bayesian methods because obtaining posterior distributions of model parameters is relatively easy compared to classical methods (Zhang et al. 2009). Accordingly, Bayesian models present a relatively user-friendly method for ecologists to build more complex models that incorporate multiple sources of uncertainty (Gelman et al. 2014a). Sigourney et al. (2012) also describe a Bayesian state-space method for evaluating environmental influences on growth; however, their method differs from the current method by their use of Gaussian process (GP) model. One benefit of the GP method is that the growth model is nonparametric and environmental data can be used as an informative prior for growth covariates. However, formulating a GP model is fairly technical and interpretation of how environmental variables affect growth is less straight-forward than in the current study.

Results from the multi-level R^2 analysis illustrate that environmental covariates were good predictors of growth in both the CR and the LCR. The positive temperature effect identified by both CR and LCR models reinforces past findings that temperature influences humpback chub growth (Coggins and Pine 2010, Petersen and Paukert 2005). Unlike temperature, the positive effect of turbidity on humpback chub growth in the CR has not been previously examined in a study. We hypothesize that the positive effect of turbidity duration on CR humpback chub growth could be caused by behavioral changes and/or competitive release.

Specifically, CR humpback chub may change their behavior to become more active as turbidity increases. This hypothesis is based on the observation that humpback chub >180 mm display negative phototaxis (Stone and Gorman 2006), and that behavioral changes and increased risk-taking behaviors have been documented for numerous fishes under turbid conditions (Abrahams and Kattenfeld 1997, Gregory 1993, Miner and Stein 1996). An alternate, but not mutually exclusive, explanation of why turbidity positively affected CR growth is that turbid conditions may shift the competitive advantage from the visual sight-feeding, non-native rainbow trout to humpback chub. Rainbow trout are abundant in the CR (Yard et al. 2011) but less common in the LCR (Kaeding and Zimmerman 1983) due to its physico-chemical environment. Moreover, humpback chub diet overlaps with that of rainbow trout (Cross et al. 2013, Spurgeon et al. 2014), and rainbow trout are highly dependent on sight for foraging (Barrett et al. 1992). Consequently, rainbow trout growth typically declines when turbidity is high (Shaw and Richardson 2001), and high turbidity could perhaps decrease competition between rainbow trout and humpback chub.

While the best CR model included temperature and turbidity duration effects, it did not include effects of food availability, trout, and flow variability on subadult humpback chub growth. Importantly, our food availability metric did not include allochthonous inputs, which are an important source of food during flood events (Sabo et al. *In Review*). Furthermore, although neither trout nor food effects were included in the top CR model, the second best model ($te + tu + fo + tr$) included a negative trout effect and a positive food effect, lending some support to the hypothesis that trout compete with humpback chub. Trout abundance may affect food availability and thus exert indirect, long-term effects on chub growth that are difficult to detect. Flow variability, on the other hand, was not included in the top three CR models thus indicating

that hydropeaking may not have substantial effects on subadult humpback chub growth or that finer-scale temporal resolution is required when modeling flow variability effects.

In the LCR, growth was highest when food availability was high but temperatures were moderate (~18°C). Similar to the results of the LCR growth model, wild Atlantic salmon (*Salmo salar*) parr in northeast Scotland exhibited their highest growth in spring, when food availability was high but water temperatures were well below the optimal growth temperature for the species (Bacon et al. 2005). Our sparse food availability data suggest a synchronous timing of high invertebrate emergence and high humpback chub growth rates; however, more data are needed about year to year variability in food availability to more accurately determine its effect on humpback chub growth. Furthermore, because the food availability metric did not include food items such as fish, larvae, or eggs, it may underestimate food availability in April and May when egg and larval production are at their peak. Unlike Dzul et al. (2014), our model failed to detect an effect of turbidity duration on LCR humpback chub growth. However, comparing the current study to Dzul et al. (2014) is tenuous because of differences in the time scales and spatial extents of the two studies. In addition, it is difficult to disentangle turbidity and temperature effects during winter and spring months because increases in discharge associated with snowmelt often affect both temperature and turbidity in the LCR.

Evaluating species responses to environmental drivers can help biologists indirectly learn about species' life histories (Adolph and Porter 1993, Shuter et al. 1998). In the current study, the modeling approach allowed us to identify a positive turbidity duration effect on humpback chub growth, thus providing useful insight into the behavioral ecology of the species. Additionally, models that assess environmental influences on ecological processes can improve prediction compared to models that evaluate only temporal patterns (Keyl and Wolff 2008,

437 Planque et al. 2003, Rodhouse et al. 2014). In the case of humpback chub, a better
438 understanding of how environmental covariates affect growth in the CR and LCR may improve
439 the predictive capability of population models if the future climate in the southwestern U.S.
440 warms and becomes more arid (Seager et al. 2007) and can help inform management decisions
441 made by the Glen Canyon Adaptive Management Program. More generally, evaluating
442 environmental influences on ecological processes can lead to more informed decision-making
443 about conservation and management of species of concern (Brander 2003, Clark et al. 2001).

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Table 1. Description of environmental covariates used to fit a growth model to subadult humpback chub (*Gila cypha*) growth in the Colorado and Little Colorado Rivers (CR and LCR, resp.).

<i>Name</i>	<i>Site</i>	<i>Description</i>	<i>Data source</i>
Temperature	CR	Mean monthly temperature	USGS gage 09383100
Temperature	LCR	Mean monthly temperature	USGS gage 09402300
Turbidity duration	CR	Number of days per month with turbidity was ≥ 50 Formazin Turbidity Units	USGS gage 09402500
Turbidity duration	LCR	Number of days per month with flow $\geq 7.08 \text{ m}^3 \text{ s}^{-1}$ (i.e., 250 cfs)	USGS gage 09402300
Food availability	CR	Biomass of drift of aquatic macroinvertebrates (mg m^{-3})	Field sampling; T. Kennedy
Food availability	LCR	Biomass of emergence of adult invertebrates with aquatic larval stages (mg)	Field sampling; J. Muehlbauer
Flow variability	CR	Monthly standard deviation of mean daily flow	USGS gage 09402500
Trout abundance	CR	Number of rainbow trout captured using electrofishing	Field sampling; B.Pine, J. Korman, and M. Yard

Table 2. Mean squared prediction error (MSPE) for models fit to out of sample growth data of humpback chub in the Colorado River (CR) and Little Colorado River (LCR). Candidate models included temperature (te), turbidity duration (tu), food availability (fo), flow variability (fv; CR only), and trout catch (tr; CR only) effects. All combinations of additive models were included in model selection; however, only the top five models are listed for each river. Models were initially fit to growth data from April 2009-May 2013 (LCR) or July 2009-September 2013 (CR). Subsequently, MSPE was calculated for out-of-sample data from June 2013-July 2014 (LCR) or October 2013-September 2014 (LCR).

<i>Colorado River</i>		<i>Little Colorado River</i>	
<i>Model</i>	<i>MSPE</i>	<i>Model</i>	<i>MSPE</i>
te + tu	1.00	te + fo	0.26
te + tu + fo + tr	1.08	te + tu + fo	0.34
te + tu + tr	1.10	te	0.52
te + tu + fo	1.29	te + tu	0.59
te + fo	1.47	fo	0.61

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Table 3. Mean, standard deviation (SD), and 95% credible intervals (CI) of posterior draws from full growth models describing growth of subadult humpback chub in the Colorado River and Little Colorado River.

<i>Colorado River</i>				
<i>Parameter</i>	<i>Description</i>	<i>Mean</i>	<i>SD</i>	<i>95% CI</i>
σ	Measurement error	2.34	0.06	2.22 to 2.46
ρ	Process error	0.36	0.01	0.34 to 0.39
β_0	Intercept	-0.11	0.19	-0.56 to 0.19
β_{te}	Temperature effect	0.79	0.21	0.38 to 1.24
β_{tu}	Turbidity duration effect	0.6	0.2	0.25 to 1.01
δ	Month error	0.8	0.21	0.48 to 1.29
β_L	Initial length effect	<-0.01	<0.01	-0.003 to -0.00004
<i>Little Colorado River</i>				
<i>Parameter</i>	<i>Description</i>	<i>Mean</i>	<i>SD</i>	<i>95% CI</i>
σ	Measurement error	2.35	0.07	2.22 to 2.48
ρ	Process error	0.27	0.01	0.25 to 0.29
β_0	Intercept	1.37	0.12	1.08 to 1.57
β_{te}	Temperature effect	0.58	0.11	0.37 to 0.82
β_{fo}	Food availability effect	0.52	0.09	0.34 to 0.70
δ	Month error	0.42	0.14	0.20 to 0.75
β_L	Initial length effect	-0.008	<0.001	-0.009 to -0.007

Fig. 1. Monthly estimates of environmental covariates included in a model describing growth of subadult humpback chub (*Gila cypha*) in the Colorado River (CR; black dots) and Little Colorado River (LCR; white dots). Plots describe: a) mean monthly water temperature, b) number of days per month with turbidity greater than 50 FTU (CR) or flow greater than 7.08 m³ s⁻¹ (LCR), c) standardized drift of aquatic insects (mg m⁻³; CR) or standardized biomass of terrestrial insects per sticky trap (mg; LCR), d) mean daily standard deviation of flow, and e) catch of rainbow trout from the CR (rkm 126-129).

Fig. 2. The effect of temperature on monthly growth rates of subadult humpback chub *Gila cypha* in two different rivers: the Colorado River (CR) and the Little Colorado River (LCR). Note temperature ranges differ for these two rivers because the CR is typically much colder than the LCR. Growth estimates reflect growth of a 130mm humpback chub. In the CR, growth is much higher when turbidity duration is high (*i.e.*, when turbidity levels exceed 50 Formazin Turbidity Units (or FTU) for all 30 days in a month) than when turbidity duration is low (*i.e.*, when water never exceeds 50 FTU during the month). In contrast, food and temperature interact in the LCR to affect growth, and thus LCR growth is highest when both food availability and temperature are high.

Fig. 3. Comparison of growth model predictions describing the relationship between environmental covariates and growth of subadult humpback chub in the Colorado River. Growth predictions come from the best model with temperature and turbidity duration influences on growth. Predictions with month random effects (RE) include both environmental covariates and month random effects, whereas predictions without month random effects include only environmental covariates. Error bars represent 95% credible intervals in growth predictions.

Fig. 4. Comparison of growth model predictions describing the relationship between environmental covariates and growth of subadult humpback chub in the Little Colorado River. Growth predictions come from the best model that included a temperature effect and a food availability effect. Predictions with month random effects (RE) include both environmental covariates and monthly random effects, whereas predictions without monthly random effects include only environmental covariates. Error bars represent 95% credible intervals in growth predictions.

List of symbols

<i>Symbol</i>	<i>Description</i>
β_0	Intercept
β_L	Initial length effect
β_{te}	Temperature effect
β_{tu}	Turbidity effect
β_{fo}	Food effect
β_{fv}	Flow variability effect
β	Vector of environmental coefficients
ω	Monthly random effects
δ	Standard deviation of monthly random effects
σ	Measurement error
ρ	Process error

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Appendix A. *Environmental covariates.*

We use two different stream gages for the Colorado River (CR) calculating environmental covariates. Temperature data from the CR were logged at 15-minute intervals and obtained from U.S. Geological Survey (USGS) gage 09383100 at river kilometer (rkm) 123. This gage is in close proximity to the CR sampling site, but it is upstream of the Little Colorado River (LCR) and therefore it does not measure turbidity or discharge inputs from the LCR. Therefore, turbidity data from the CR were obtained from a gage located downstream of the LCR confluence (USGS gage 09402500 located at rkm 170). The turbidity effect in the CR was the number of days per month when turbidity exceeded 50 Formazin Turbidity Units (FTU). We chose 50 FTU because laboratory experiments evaluating rainbow trout predation rates on juvenile humpback chub have shown this concentration to be an important threshold that decreases predation (Ward et al. 2016). CR drift data were collected in January, April, July, and September (hereafter ‘sampled months’) of 2012-2014. CR food availability was estimated as milligrams per meter³ of all macroinvertebrates (excluding New Zealand mudsnails (*Potamopyrgus antipodarum*)) present in drift samples. We estimated food availability in sampled months as the average across years 2012-2014 (*i.e.*, food availability was used only to assess within-year and not across-year patterns in growth). We then used linear interpolation to estimate food availability in unsampled months. Flow variability was included in the model as the monthly mean of daily standard deviation in discharge. Lastly, we used number of rainbow trout captured using electrofishing in the CR (rkm 126-129) as an index for trout abundance.

In the LCR, temperature and discharge data were logged every 15 minutes from USGS gage 09402300 (rkm 1). Because continuous turbidity measurements were unavailable for the LCR, the LCR process model contained only terms for mean monthly water temperature and

flood duration (number of days above $7.08 \text{ m}^3 \text{ s}^{-1}$). Baseflow in the LCR is $6.57 \text{ m}^3 \text{ s}^{-1}$ and small increases in discharge cause the water color in the LCR to change from blue to brown (Stone 2010). Consequently, turbidity and discharge in the LCR are strongly correlated. Therefore, we used flood duration in the LCR as a proxy for turbidity duration and refer to flood duration in the LCR as a turbidity effect.

No drift data are available for the LCR, so we used biomass estimates of terrestrial adult stages of two abundant invertebrate taxa (Chironomidae and Simuliidae) to represent food availability in the LCR. Counts of invertebrates were collected at each rkm (from rkm 0-21) in April, May, June, September, and October of 2014 using sticky traps (Smith et al. 2014). Counts from rkms 3-7 were averaged to obtain an estimate of food availability for humpback chub in this section of the LCR, and count values were subsequently converted to biomass using a length-weight regression (Benke et al. 1999). Food availability values from 2014 were assumed to be representative of all other years, and linear interpolation was used to obtain food availability estimates for July and August. Because sampling in March 2015 suggested that emergence is very low in March, we fixed biomass from November thru March to be equivalent to October biomass.

Appendix B. Example of STAN growth model code for a model that includes effects of mean monthly temperature on growth:

```

data{
  int nobs; // number of observations
  int nt; // number of months
  vector[nt] temp; // vector of mean monthly temperature
  vector[nobs] L1_obs; // observed length at first capture
  vector[nobs] L2; // observed length at second capture
  int t1[nobs]; //vector of month of first capture for each observation
  int t2[nobs]; // vector of month of recapture for each observation
  matrix [nobs,nt] dT; // the proportion of the month that fish were at large
  int n_wtrip_caps; // number of within-trip captures
  vector[n_wtrip_caps] wtrip_caps; //difference between length measurements for within-
                                     //trip captures
}

parameters {
  real b_temp; //temperature coefficient
  real<lower=-0.1, upper=0.1> b_L; // initial length coefficient
  real b0; // intercept
  vector[nt] m; // monthly random effect
  real<lower=0, upper=5> mon_sig; // month error
  real<lower=0,upper=10> L_obs_err; // measurement error
  real<lower=0,upper=1> pe_sig; // process error
  vector[nobs] pe; // vector of individual process errors
}

model{

  matrix[nobs,nt] dL; //growth matrix
  matrix[nobs,nt] L; // length matrix
  b_temp ~ normal(0,10);
  b0~ normal(0,10);
  pe~normal(0,pe_sig);
  wtrip_caps~normal(0,L_obs_err);
  for(i in 1:nt) {m[i]~normal(0,mon_sig);}

  for(i in 1:nobs) {
    dL [i,t1[i]]<- dT[i,t1[i]]*(exp(b0+ b_L*L1[i]+b_temp*temp[t1[i]]+m[t1[i]]+pe[i]));
    L[i,t1[i]]<-L1_obs[i]+dL[i,t1[i]];
  }
}

```

```
for(j in (t1[i]+1):t2[i]) {  
  dL[i,j]<- dT[i,j]*(exp(b0+ b_L*L[i,j-1]+b_temp*temp[j]+ m[j]+pe[i]));  
  L[i,j]<-L[i,j-1]+dL[i,j];}  
L2[i]~normal(L[i,t2[i]],L_obs_err);}  
}
```

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Appendix C. Simulation and evaluation of model bias

To evaluate our modeling method, we simulated 100 data sets based on estimates from the best-fit models from both the Colorado and Little Colorado River. Data were simulated using the same values for environmental covariates as in the current study, the same initial lengths, and the same time for recapture (i.e., the same time at large). Observation error, process error, and monthly random effects were all simulated from normal distributions with standard deviations equal to estimates of σ , ρ , and δ , respectively for each river. All priors were identical to those used in model selection, as were the number of chains (3), burn-in (1000), posterior draws (333 per chain), and thin rate (5). We calculated the estimated value of a parameter for each simulation across all posterior draws, then we calculated bias by subtracting the true parameter values from fitted mean parameter estimates. We also report coverage as the proportion of simulations where the true parameter value was included in the 95% credible interval.

Simulations from both rivers illustrate that while the environmental coefficients displayed negligible positive bias (i.e., $< 6\%$), the model did have difficulty distinguishing the intercept from month error in both rivers (Fig. A1, A2). Specifically, month error and intercept terms were correlated, and accordingly the month error terms were positively biased while the intercepts were negatively biased. Despite the above-mentioned biases in mean parameters, coverage was high for all parameters in both rivers (Table A1).

Table C1. Coverage of simulations from the best-fit models describing growth of subadult humpback chub (*Gila cypha*) in the Colorado River (CR) and Little Colorado River (LCR), AZ. Coverage is defined as the proportion of 100 simulations where the true parameter value is included in the 95% credible interval for that parameter. Parameters evaluated include the temperature effect (β_{te}), turbidity effect (β_{tu}), food availability effect (β_{fo}), intercept term (β_0), initial length effect (β_{Li}), standard deviation of monthly random effects (δ), process error (ρ), and measurement error (σ).

<i>Parameter</i>	<i>River</i>	<i>Coverage</i>
β_{te}	CR	0.98
β_{tu}	CR	0.98
β_L	CR	0.96
β_0	CR	0.95
δ	CR	0.96
ρ	CR	0.96
σ	CR	0.98
β_{te}	LCR	0.96
β_{fo}	LCR	0.98
β_L	LCR	0.98
β_0	LCR	0.95
δ	LCR	0.94
ρ	LCR	0.98
σ	LCR	0.95

Fig. C1. Bias (estimated value – true value) from 100 simulations of a model describing growth of subadult humpback chub (*Gila cypha*) in the Colorado River, AZ. Parameters evaluated include the temperature effect (β_{te}), turbidity effect (β_{tu}), intercept term (β_0), initial length effect (β_{Li}), standard deviation of monthly random effects (δ), process error (ρ), and measurement error (σ).

Fig. C2. Bias (estimated value – true value) from 100 simulations of a model describing growth of subadult humpback chub (*Gila cypha*) in the Little Colorado River, AZ. Parameters evaluated include the temperature effect (β_{te}), food availability effect (β_{fo}), intercept term (β_0), initial length effect (β_{Li}), standard deviation of monthly random effects (δ), process error (ρ), and measurement error (σ).

Appendix D. Log of observed growth versus log of predicted growth for models describing the effects of environmental covariates on growth of subadult humpback chub *Gila cypha* inhabiting the lower Colorado River (CR) and Little Colorado River (LCR), AZ. Black dots represent residuals of fitted data, whereas grey triangles represent residuals of out of sample predictions.

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