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Mark L. Wildhaber
United States Geological Survey

Christopher K. Wikle
University of Missouri

Edward H. Moran
United States Geological Survey

Christopher J. Anderson
Iowa State University

Kristie J. Franz
Iowa State University, kfranz@iastate.edu

See next page for additional authors

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Abstract

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Disciplines

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Authors

Mark L. Wildhaber, Christopher K. Wikle, Edward H. Moran, Christopher J. Anderson, Kristie J. Franz, and Rima Dey

Hierarchical stochastic modelling of large river ecosystems and fish growth across spatio-temporal scales and climate models: the Missouri River endangered pallid sturgeon example

MARK L. WILDHABER^{1*}, CHRISTOPHER K. WIKLE², EDWARD H. MORAN¹,
CHRISTOPHER J. ANDERSON³, KRISTIE J. FRANZ⁴ & RIMA DEY²

¹*United States Geological Survey, Columbia Environmental Research Center,
4200 New Haven Road, Columbia, MO 65201-8709, USA*

²*Department of Statistics, University of Missouri, 146 Middlebush Hall,
Columbia, MO 65211-6100, USA*

³*Climate Science Initiative, Iowa State University, 2021 Agronomy Hall, Ames, IA 50011, USA*

⁴*Geological and Atmospheric Sciences, Iowa State University,
3023 Agronomy Hall, Ames, IA 50011, USA*

*Correspondence: mwildhaber@usgs.gov

Abstract: We present a hierarchical series of spatially decreasing and temporally increasing models to evaluate the uncertainty in the atmosphere – ocean global climate model (AOGCM) and the regional climate model (RCM) relative to the uncertainty in the somatic growth of the endangered pallid sturgeon (*Scaphirhynchus albus*). For effects on fish populations of riverine ecosystems, climate output simulated by coarse-resolution AOGCMs and RCMs must be downscaled to basins to river hydrology to population response. One needs to transfer the information from these climate simulations down to the individual scale in a way that minimizes extrapolation and can account for spatio-temporal variability in the intervening stages. The goal is a framework to determine whether, given uncertainties in the climate models and the biological response, meaningful inference can still be made. The non-linear downscaling of climate information to the river scale requires that one realistically account for spatial and temporal variability across scale. Our downscaling procedure includes the use of fixed/calibrated hydrological flow and temperature models coupled with a stochastically parameterized sturgeon bioenergetics model. We show that, although there is a large amount of uncertainty associated with both the climate model output and the fish growth process, one can establish significant differences in fish growth distributions between models, and between future and current climates for a given model.

Recent decades have brought substantive changes in land use and climate across the Earth, prompting a need to think of population and community ecology not as a static entity, but as a dynamic process (United States Climate Change Science Program: CCSP 2003). Increasingly, there is evidence of ecological changes due to climate change (e.g. Walther *et al.* 2005; Bergengren *et al.* 2011). Although much of this evidence comes from ground-truth observations of biogeographical data, there is increasing reliance on models that relate climate variables to biological systems (CCSP 2003). Such models are used to explore potential changes to population and community-level ecological systems in response to climate scenarios as obtained from atmosphere – ocean global climate models (AOGCMs) (Nakicenovic *et al.* 2000; CCSP 2003).

When modelling ecosystem response to climate, the resolution of AOGCMs is not typically sufficient to draw inferences at the scales of variability necessary for understanding ecological processes (e.g. Tabor & Williams 2010). Rather, the AOGCM physical variables must be ‘downscaled’ to local ecological/biological response scales that can be used in vulnerability and risk assessments of climate change (CCSP 2003). Traditionally, one either accomplishes the downscaling by linking the AOGCM to a smaller scale through the use of deterministic models (i.e. ‘dynamical downscaling’) or through the use of statistical models (e.g. Grotch & MacCracken 1991; Fowler *et al.* 2007). In the case of evaluating individual organism response to potential climate variability, one must project across multiple scales of spatial and temporal variability,

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and it is not likely that the 'transfer function' that converts large-scale climate simulation results to very small spatial and temporal scales can be represented well by a single statistical downscaling model, especially given the non-linear nature of the transfer of information across scale. Rather, a more realistic transfer function would attempt to accommodate the various scales of variability, such as through a series of deterministic process models.

Consideration of the 'cascade of uncertainty' that arises in the application of multiple models is a necessary step (e.g. Henderson-Sellers 1993; Jones 2000; Wilby & Harris 2006). Several studies exploring the potential hydrological impacts from climate change have shown substantial uncertainty associated with the large-scale hydrological model forcing derived from climate models (e.g. Stone *et al.* 2003; Jasper *et al.* 2004; Wood *et al.* 2004; Salathé 2005; Chen *et al.* 2006; Wilby & Harris 2006). Uncertainty in climate models results from the initial and boundary conditions, parameter uncertainty, and the structural uncertainty in the models themselves (Knutti *et al.* 2010). There are two primary approaches used to attempt to account for this uncertainty in climate change studies, the so-called 'multi-model ensemble' (MME) and 'perturbed physics ensemble' (PPE) methods. The MME approach considers a sample of opportunity consisting of output from multiple models of similar complexity, whereas the PPE method typically assumes a model with a common core but with ensembles chosen based on multiple parameter sets, often selected based on some climate sensitivity index. For a recent comparison between uncertainties associated with MME and PPE, see Collins *et al.* (2011). In the context of hydrological downscaling MME, Fowler *et al.* (2007) found that, in general, hydrological impacts are sensitive to spatial and temporal biases in precipitation and temperature, and are, thus, sensitive to the particular GCM considered. In general, as summarized by Knutti (2010) and Knutti *et al.* (2010), there are numerous fundamental issues that arise when considering such ensembles, including lack of model independence, unresolvable structural uncertainty, calibration and choice of evaluation metrics. Yet, until such time as fully stochastically parameterized GCMs are in common use, the MME and PPE frameworks provide the most viable approach for accounting for climate model uncertainty.

In addition to the uncertainty associated with the climate models, in ecological impact studies there is typically substantial uncertainty associated with our knowledge of the ecological phenomena of interest. It is possible that ecological model uncertainty could be greater than the uncertainty associated with the climate/physical/hydrological models and/or

greater than the variation that would occur under different climate scenarios, thereby limiting the ability to draw inference concerning potential impacts to the ecological system. This leads to the fundamental question that this paper seeks to address: when the uncertainty in the ecological process is taken into account through a stochastic parameter ensemble, are there still significant differences in the ecological response forced from various climate models in a MME framework? If the answer is yes, is the difference in ecological response associated with a future climate scenario and a current climate scenario also significant relative to the uncertainty associated with the ecological process? If the answer is no, then we must address in what ways the uncertainty associated with the ecological response can be reduced.

We address the questions above for the case of the Missouri River pallid sturgeon (*Scaphirhynchus albus*), which was Federally listed as endangered in 1990 and is rare in the Missouri River Basin (Dryer & Sandvol 1993). The conceptual life-history model for pallid sturgeon of Wildhaber *et al.* (2007, 2011a) provides the framework to illustrate how climate may interact with river management actions to affect species recovery. As Figure 1 illustrates, we add stochastic parameterization to a pallid sturgeon bioenergetics model developed by Chipps *et al.* (2008) to translate potential changes in water temperature and velocity associated with potential climate change into pallid sturgeon growth. We use data from multiple climate models to force fixed/calibrated hydrological flow and temperature models to obtain river discharge, velocity and temperature at the river reach scale. To quantify uncertainty, it is important that uncertainty associated with critical parameters be accounted for across these scales of variability.

As mentioned above, downscaling the hydrological processes from the climate scale to river reach scale could also be performed via statistical downscaling through the development of empirical relationships between basin runoff and air temperature, and mainstem flow and river temperature, respectively (Larson & Schwein 2004; Blevins 2006; Vrac *et al.* 2007). Although statistical downscaling methods have become quite sophisticated and useful in the study of climate impacts (e.g. Maraun *et al.* 2010), statistical approaches inherently imply extrapolation in the context of climate change studies and, more critically, would likely be unable to directly account for multivariate spatio-temporal variability for many important variables (e.g. evapotranspiration, snow melt, river management). Indeed, the development of multivariate non-linear spatio-temporal statistical models is beyond the current state of the art (e.g. see Cressie & Wikle 2011). Perhaps more importantly, since much of

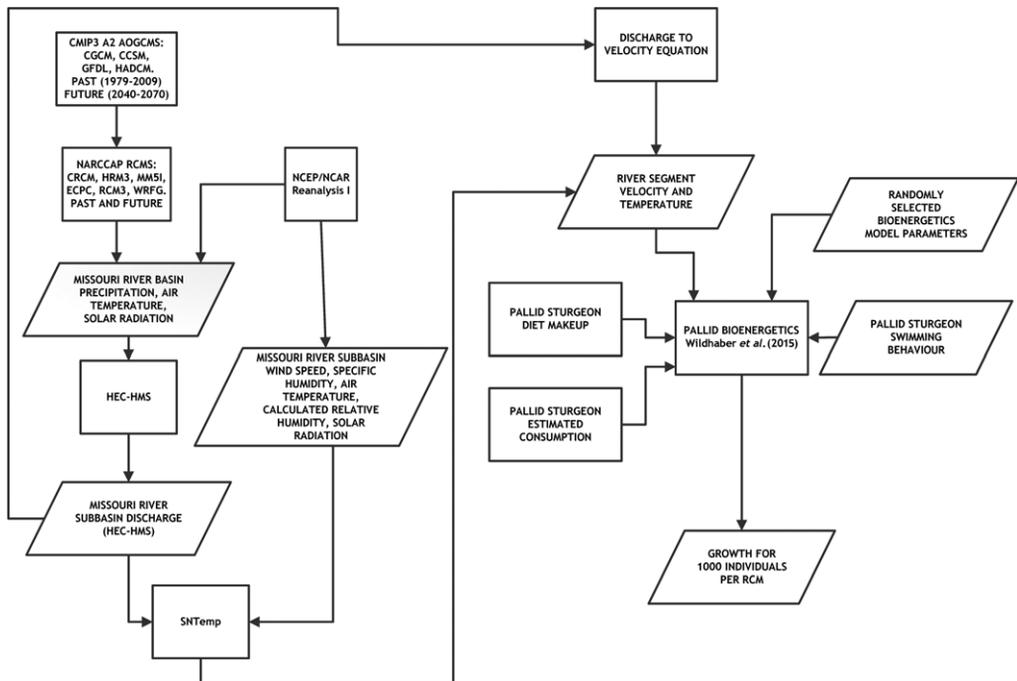


Fig. 1. Flowchart illustrating the linkages between models within and across temporal and spatial scales. NARCCAP datasets are used in the simulations. AOGCM simulations were taken from the WCRP’s CMIP3 multi-model dataset (Meehl *et al.* 2007) based on the A2 emissions scenario (representing less international co-operation to reduce greenhouses gases) that projects relatively high greenhouse gas concentration increases. Model data used include four AOGCMs: CGCM (Flato 2005), CCSM, GFDL and HADCM. Model data used include six Regional Climate Models (RCM) within the AOGCMs: CRCM, HRM3, MM5I, ECPC, RCM3 and WRFG. Measured/observed data: NCEP/NCAR Reanalysis 1 (Kalnay *et al.* 1996) (NCEP/NCAR) from Earth System Research Laboratory (www.esrl.noaa.gov). River discharge simulated using a lumped-parameter runoff model HEC-HMS (USACE 2010 – see Appendix A for more details). Water temperature is simulated using the physical-process SNTemp stream-temperature model (Theurer *et al.* 1984).

our interests are in evaluating the impacts of uncertainties across a wide range of spatial and temporal scales, a hybrid deterministic/statistical approach is more useful for the present study. Although these models still require calibration to define model parameters through fitting to observed data, the underlying structure is based on known physical properties and does not solely rely on empirical associations.

We present here one of many possible approaches to address the potential for meaningful inference associated with uncertainty in AOGCMs and regional climate models (RCMs), and hydrological models v. uncertainty in the ecological response through application of a set of physical and biological models that cover a hierarchy of scales. While a complete climate prediction may be intractable at this time – for instance, the climate projections may not incorporate land use and other physical changes into the system (e.g. geomorphology) or solar fluctuations into the boundary

conditions – our framework is flexible enough to adapt to advances in climate simulations.

Modelling approach

The modelling framework developed (Fig. 1) uses data and modelling results from synergistic monitoring and modelling studies. We make use of: (1) extensive and long-term biotic and abiotic data (e.g. Drobish 2008; USFWS 2008; Wildhaber *et al.* 2011b, 2012); (2) simulations of climate variation in high-rate rainfall and streamflow (Mauget 2004; CCSP 2008); (3) on-going analysis and modelling of spatial and temporal patterns of the benthic fish community, and their relationship to physical and chemical factors (e.g. Arab *et al.* 2008, 2012; Wildhaber *et al.* 2011b, 2012); (4) sturgeon life-history models developed by Wildhaber *et al.* (2007, 2011a) based on what is seen in the Missouri River; (5) sturgeon population models developed by

Bajer & Wildhaber (2007) as a basis for initial population viability analysis for Lower Missouri River sturgeons; and (6) on-going research identifying factors affecting Lower Missouri River sturgeon spawning physiology, behaviour, habitat choice and success as part of a comprehensive research programme designed to identify life-history bottlenecks (e.g. Wildhaber *et al.* 2007; DeLonay *et al.* 2009; Holan *et al.* 2009; McElroy *et al.* 2012). Initial models for each scale were developed using data collected by the United States Fish and Wildlife Service (USFWS), the USGS, the United States Army Corps of Engineers (USACE), the National Oceanic and Atmospheric Administration (NOAA), the United States Department of Agriculture (USDA), and numerous other federal and state natural resource agencies. The data include land use, geological and geomorphic, hydrological, water quality, atmospheric, and pallid sturgeon (*Scaphirhynchus albus*) growth and movement. Along with climatological modelling by the North American Regional Climate Change Assessment Program (NARCCAP) (Mearns *et al.* 2009; see <http://www.narccap.ucar.edu/> for details) and established hydrological models (HEC-HMS: USACE 2000; SNT-emp: Theurer *et al.* 1984), we use juvenile pallid sturgeon bioenergetics models (Chipps *et al.* 2008) extrapolated beyond a fork length of 700 mm in concert with observed growth of adult pallid sturgeon in the Missouri River

Global to regional climate models

For this downscaling component (Fig. 1), we focus on NARCCAP results owing to their comprehensive nature in consideration of multiple climate models and the availability of data that have already been downscaled to the regional level. The NARCCAP simulations provide physically downscaled air temperature, precipitation, solar radiation, humidity, cloud cover and wind speed on 50 km grids that are used as input to Missouri River Basin hydrological and water-temperature models. The data are generated from RCM simulations driven by AOGCMs over a domain covering most of North America. The AOGCM simulations were taken from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset (Meehl *et al.* 2007). Simulations of AOGCM in CMIP3 spanned 1850–2100, using historical climate drivers (e.g. greenhouse gas concentration, solar radiation, volcanic eruptions) from 1850 through to 2000 and scenarios of climate drivers from 2000 through to 2100. The NARCCAP RCMs were provided data for two 30 year periods: 1971–2000 and 2041–70. Data for the mid-twenty-first century period came from the A2 emissions

scenario (representing less international co-operation to reduce greenhouse gases: Nakicenovic *et al.* 2000) that projects relatively high greenhouse gas concentration increases and is useful as an upper bound for studying realistic impacts and adaptation strategies for climate warming. The NARCCAP simulation results include various combinations of six RCMs (Canadian Regional Climate Model (CRCM); Hadley Regional Climate Model Version 3.0 (HRM3); Mesoscale Meteorological model Version 5.0 (MM5I); Experimental Climate Prediction Center Regional Spectral Model (ECPC); Regional Climate Model 3.0 (RCM3); and Weather Research and Forecast Model 3.0 (WRFG)) and four AOGCMs (Canadian Global Climate Model Version 3.1 (CGCM) (Flato 2005); Community Climate System Model Version 3.0 (CCSM); Geophysical Fluid Dynamics Laboratory Climate Model Version 2.1 (GFDL); and Hadley Centre Climate Model Version 2.0 (HADCM)) (see Mearns *et al.* 2009 and references therein for full model descriptions) (Fig. 1; Table 1).

Multi-model ensembles are critical to climate change impacts analysis because differences in model formulations can produce uncertainty in model output (Solomon *et al.* 2007). In such studies, it is also important to understand the biases of the RCMs. Model developers may have suggestions of how the biases relate to particular submodels, and that may inform their model development approach for the next generation, but it is impossible to infer from the current formulation that created these simulations what bias will occur. For this reason, each NARCCAP RCM simulated the observed climate for 1979–2004, given data from the National Center for Environmental Prediction (NCEP) – Department of Energy (DOE) Atmospheric Model Intercomparison Project (AMIP-II) Reanalysis (Kanamitsu *et al.* 2002). These data are an approximation for observations, and so the regional models are expected to replicate the climate for the 1979–2004 period associated with the NCEP data, subject to their internal variability. The deviations of retrospective RCM simulations from observations show the simulation bias.

For the purposes of this paper, we focus on three climate models (i.e. CCSM, CGCM and GFDL) with available regional models for each (i.e. CRCM and WRFG for CGCM and CCSM, HRM3 for GFDL, MM5I for GFDL, and RCM3 for CGCM and GFDL) and NCEP/NCAR Reanalysis 1 (Kalnay *et al.* 1996), which is used to develop the river hydrology and water-temperature models (described in the next subsection) – a total of 17 scenarios (Fig. 1; Table 1). The uncertainty considered here is that of the differences in model outputs which occur between AOGCM–RCM combinations.

Table 1. NARCCAP datasets used in the simulations

Regional model	Global model				Regional model type	NCEP/NCAR reference
	CGCM	CCSM	GFDL	HADCM		
CRCM	2° latitude, 2° longitude	1.5° latitude, 1.5° longitude	2° latitude, 2.5° longitude	2.5° latitude, 3.75° longitude	University of Quebec, the Ouranos Consortium (Caya & Laprise 1999)	2.5° latitude, 2.5° longitude
HRM3	2° latitude, 2° longitude	1.5° latitude, 1.5° longitude	2° latitude, 2.5° longitude	2.5° latitude, 3.75° longitude	Atmospheric only	2.5° latitude, 2.5° longitude
MM5I	2° latitude, 2° longitude	1.5° latitude, 1.5° longitude	2° latitude, 2.5° longitude	2.5° latitude, 3.75° longitude	Limited-area, non-hydrostatic, terrain-following sigma-coordinate	2.5° latitude, 2.5° longitude
ECPC	2° latitude, 2° longitude	1.5° latitude, 1.5° longitude	2° latitude, 2.5° longitude	2.5° latitude, 3.75° longitude	Limited-area atmospheric numerical	2.5° latitude, 2.5° longitude
RCM3	2° latitude, 2° longitude	1.5° latitude, 1.5° longitude	2° latitude, 2.5° longitude	2.5° latitude, 3.75° longitude	Based on MM5I, 3D, sigma-coordinate, primitive equation regional climate	2.5° latitude, 2.5° longitude
WRFG	2° latitude, 2° longitude	1.5° latitude, 1.5° longitude	2° latitude, 2.5° longitude	2.5° latitude, 3.75° longitude	Grell Convective Parameterization Scheme, atmospheric model with infrastructure (buildings, concrete, etc.), land use/landscape, biospheric components, etc.	2.5° latitude, 2.5° longitude

Model data used included four AOGCMs: Canadian Global Climate Model Version 3.1 (CGCM) (Flato 2005); Community Climate System Model Version 3.0 (CCSM); Geophysical Fluid Dynamics Laboratory Climate Model Version 2.1 (GFDL); and Hadley Centre Climate Model Version 2.0 (HADCM). Model data used include six RCMs within the AOGCMs: Canadian Regional Climate Model (CRCM); Hadley Regional Climate Model Version 3.0 (HRM3); Mesoscale Meteorological model Version 5.0 (MM5I); Experimental Climate Prediction Center Regional Spectral Model (ECPC); Regional Climate Model 3.0 (RCM3); and Weather Research and Forecast Model 3.0 (WRFG). Measured/observed data: NCEP/NCAR Reanalysis 1 (Kalnay *et al.* 1996) (NCEP/NCAR) from Earth System Research Laboratory (www.esrl.noaa.gov).

Regional- to river-level hydrological and temperature models

For this downscaling component, we focus on the Missouri River Basin (Fig. 2). This basin encompasses approximately 1370 000 km² (529 000 square miles) and is home to around 12 million people (USACE 2006). The basin traverses 10 states and part of Canada, and extends from the Rocky Mountains to its confluence with the Mississippi River. The Missouri River mainstem flows for about 3735 km (2321 miles). Nearly 1.9 million acres of floodplain surround the Missouri River downstream of Sioux City, Iowa. Of the 894 impoundments throughout the Missouri River Basin (National Atlas of the United States – NAUS 2006), there are six dams along the mainstem in Montana, Nebraska, North Dakota and South Dakota.

The uncertainty evaluation of AOGCM/RCM/hydrology v. fish bioenergetics uncertainty is performed at two locations on the Lower Missouri River that correspond to gauges: Station 06807000 Missouri River at Nebraska City, NE (draining

about 1 062 000 km² at RK 906, referenced as ‘Nebraska’); and Station USGS 06909000 Missouri River at Boonville, MO (draining about 1300 000 km² at RK 317 and at 172 m above NAVD88, referenced as ‘Missouri’) (USGS 2011). The Nebraska site represents the Lower Missouri River between the Gavins Point Dam and the Kansas River confluence with the Missouri River. The Missouri site represents the Lower Missouri River between the Kansas River confluence and the mouth of the Missouri River.

To translate gridded climate data from regional to river level, continuous river velocity and water temperature are simulated using a lumped-parameter precipitation runoff model HEC-HMS (USACE 2010) and the physical-process SNTemp stream-temperature model (Theurer *et al.* 1984), respectively (see Appendix A for more details).

The NCEP/NCAR Reanalysis 1 data (Kalnay *et al.* 1996) (NCEP/NCAR) (Table 1) is used as input for both models. The HEC-HMS is a surface and quasi-subsurface hydrological modelling system. Our HEC-HMS model implementation for

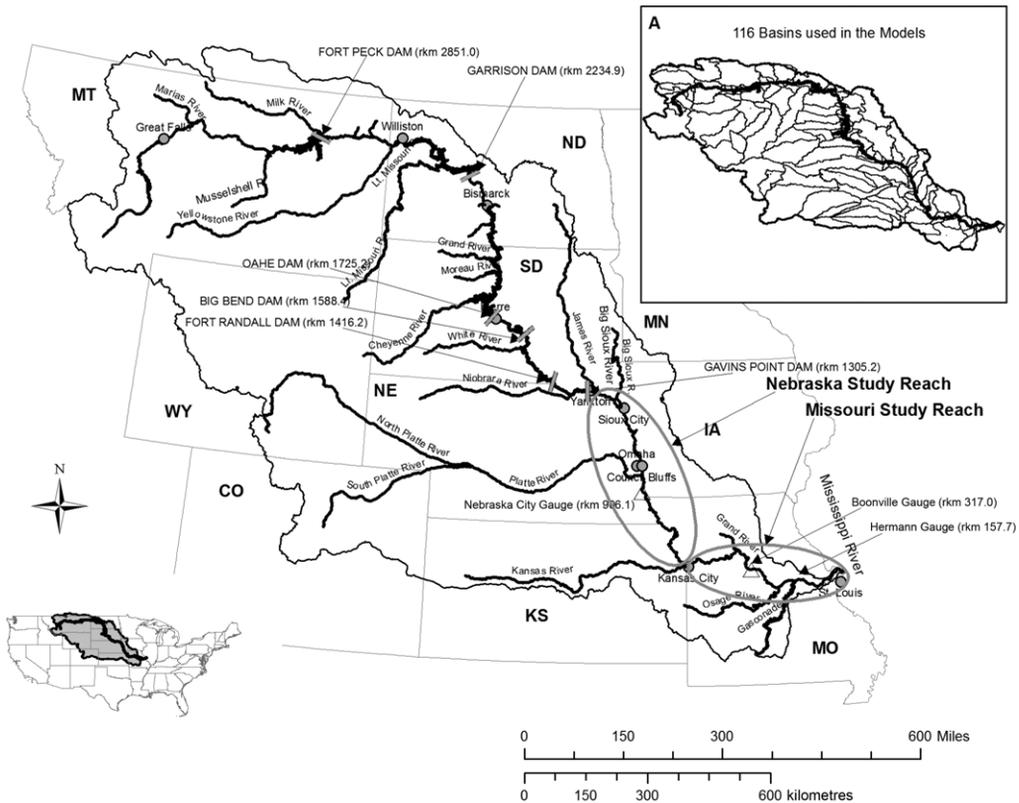


Fig. 2. Missouri River study area. The states included in the study area are: Missouri (MO), Kansas (KS), Iowa (IA), Nebraska (NE), Colorado (CO), Wyoming (WY), Minnesota (MN), South Dakota (SD), North Dakota (ND) and Montana (MT). rkm, river kilometre.

the Missouri River Basin includes 116 sub-basins and corresponding reaches. We use the Deficit and Constant Loss method for sub-basin runoff, the Priestley–Taylor potential evapotranspiration method for potential evapotranspiration, the Temperature Index method to simulate snow accumulation and melt, and the Kinematic-Wave Routing or Muskingum–Cunge methods for streamflow routing (USACE 2010) (see Appendix A for more detail). Inputs into the model are precipitation, air temperature and solar radiation data, as averaged over the defined sub-basins. The output from the HEC-HMS includes discharge at the sub-basin outlets and along the river reaches.

The SNTemp model is a physically based, steady-state one-dimensional (1D) heat transport model. The SNTemp calculates net-heat flux as the sum of heat from solar radiation, convection, conduction, evaporation, streamside shading, streambed fluid friction and the back radiation of water (Theurer *et al.* 1984). The model assumes homogeneous stream segments, where each is described by flow/discharge, length, width, slope, channel roughness or travel time. SNTemp requires continuous discharge and stream temperature values at all upstream points (upper-flow boundaries) on each modelled reach, although zero-flow headwaters are an exception and do not require actual water temperature values (Bartholow 2000). Riparian shading characteristics can be included but were not considered in this study. Model inputs are air temperature, relative humidity, wind speed, percent possible sunshine (inverse of cloud cover) and ground-level solar radiation, in addition to discharge simulations from the HEC-HMS. The model calculates within-segment streamflow accretions by mass balance, while including a component for contributing groundwater accretion flow and temperature. Simulated temperatures, however, represent the average value of all water within the dimensions of a specified channel location.

The SNTemp model has been used to investigate the effects of discharge timing, release temperature and/or release volume, riparian shading, thermal loading by power plants, and changes in channel morphology on downstream water temperatures (Bartholow 2000). When high-quality input data are used, the model simulates daily water temperatures quite accurately, typically to within less than 0.5°C of observed values, while requiring little or no calibration (Bartholow 1991). The core SNTemp model is designed to model only one meteorological station. To model the 116 sub-basins and river segments of the Missouri River Basin, each with their own set of meteorological datasets, SNTemp was programmed to cascade HEC-HMS discharge and SNTemp-generated water temperatures from upper to lower sub-basins/reaches.

Both the HEC-HMS and SNTemp models were calibrated through manual parameter adjustment to find values that minimized residuals between observed and simulated discharge and water temperature, respectively (see Appendix A for details). In addition, for the HEC-HMS, sub-basin characteristics such as hydraulic conductivity and actual water capacity of soils were extracted from the National Resource Conservation Service soils property database (NRCS 2011), and elevation, land-use class and impervious area were obtained from the USGS National Land Cover Database (Fry *et al.* 2011). The calibration period was selected as 1972–95, which corresponds to a period in which mainstem reservoir operations were stable, as measured in terms of flow at the Nebraska site (USGS at Gavin's Point Dam). The model was validated for the 1996–2009 period at locations with measured discharge.

The simulated discharge estimated using HEC-HMS, velocity (calculated based on the equation, $V = aD^b$ (Leopold & Maddock 1953), where V is velocity, D is discharge, and a and b are the empirical coefficients of the non-linear equation) and water temperature were evaluated using the Nash–Sutcliffe model efficiency coefficient (NS), the Pearson product – moment correlation coefficient (r), the percentage bias (PBIAS) and the ratio of the root mean square error to the standard deviation of measured data (RSR). The possible values for NS range from 1 (perfect fit) to negative infinity, where negative values suggest that the mean value of observed data is a better predictor than the simulated value (Moriassi *et al.* 2007). Values of RSR and PBIAS closer to 0 indicate reduced root-mean squared error or residual variability and percentage bias, respectively, thus suggesting better model performance (Moriassi *et al.* 2007). Based on a monthly time step, review of previous studies found that the 'rule of thumb' for satisfactory model calibration was $NS > 0.4$ (Engel *et al.* 2007) to $NS > 0.5$, $PBIAS \pm 25\%$ and $RSR \leq 0.7$; however, Moriassi *et al.* (2007) did acknowledge that $NS > 0.36$ has also been considered satisfactory.

To establish the initial model states, a 1 year spin-up period (starting in January) was used in HEC-HMS and discarded from any analyses. The calibrated HEC-HMS produced better than satisfactory results, as set forth by Engel *et al.* (2007) and Moriassi *et al.* (2007) for discharge and velocity simulations at Nebraska and Missouri (Table 2; Fig. 3); even better results were found for seasonal patterns (i.e. days of the year averaged for a 23 year period). In addition, using the model to extrapolate (i.e. validation time period) produced near or better than satisfactory results, thus demonstrating the validity of this model for use in future climate scenario modelling.

The calibrated SNTemp model showed a correlation coefficient of 0.94, with an NS of 0.87 and an RSR of 0.13 for stream temperature (Table 2; Fig. 3). In addition, results were near perfect for seasonal patterns (i.e. days of the year averaged for a 23 year period). Moreover, using the model produced near perfect results for the verification period at Nebraska and extremely good results for Missouri, where there were no data available for calibration.

River flow and temperature to a bioenergetics model

A substantial focus of this study was the development of a stochastic bioenergetics model for fish

growth. Specifically, to translate water velocity and temperature into fish growth, we implement a daily time step, individual-based, bioenergetics model for the endangered pallid sturgeon based on a basic pallid sturgeon bioenergetics model (Chippis *et al.* 2008), combined with swimming energetics described for other sturgeon species (Geist *et al.* 2005); a general description is given below (details of the model can be found in Wildhaber *et al.* 2015). The parameters of the bioenergetics model were estimated through field study of pallid and other sturgeon species, extrapolated across different size classes or kept constant throughout the population (Tetzlaff *et al.* 2011). A key source of pallid sturgeon swimming data was the on-going USGS Comprehensive Sturgeon and Research Program study of

Table 2. Statistical results for the HEC-HMS runoff discharge model, discharge-velocity calculation and SNTemp water-temperature model

Statistic	Discharge (m ³ s ⁻¹)		Velocity (m s ⁻¹)		Temperature (°C)	
	Calibration	Validation	Calibration	Validation	Calibration	Validation
<i>Nebraska City</i>						
Daily values						
Time period	1972–1995	1996–2009	1972–1995	1996–2009	1972–1995	2006–2009
NS	0.4	0.27	0.43	0.28	0.87	0.74
Correlation	0.63	0.53	0.66	0.56	0.94	0.92
PBIAS	1.94	-1.14	-0.21	-1.35	2.39	13.07
RSR	0.6	0.73	0.57	0.72	0.13	0.26
Count	8766	5114	8766	5114	2504	670
Seasonality						
Time period	1972–1995	1996–2009	1972–1995	1996–2009	1972–1977	
NS	0.9	0.88	0.95	0.89	0.97	
Correlation	0.95	0.97	0.96	0.97	0.98	
PBIAS	1.94	-4.44	-0.21	-2.24	1.57	
RSR	0.1	0.12	0.05	0.11	0.03	
<i>Boonville</i>						
Daily values						
Time period	1972–1995	1996–2009	1972–1995	1996–2009		2006–2009
NS	0.44	0.41	0.45	0.34		0.64
Correlation	0.66	0.67	0.68	0.65		0.9
PBIAS	1.46	-8.86	-1.2	-4.01		13.72
RSR	0.56	0.59	0.55	0.66		0.36
Count	8766	5114	8766	5114		896
Seasonality						
Time period	1972–1995	1996–2009	1972–1995	1996–2009		
NS	0.75	0.69	0.82	0.66		
Correlation	0.9	0.94	0.93	0.95		
PBIAS	1.45	-11.5	-1.2	-4.78		
RSR	0.25	0.31	0.18	0.34		

The results include the Nash–Sutcliffe model efficiency coefficient (NS), the Pearson product–moment correlation (*r*), the percentage bias (PBIAS) and the root mean square error to the standard deviation (RSR) for model calibration and validation periods. Intermittent observed/measured daily temperature data were available from 1972 to 2009 for Nebraska (i.e. Nebraska City gauge) and from 2006 to 2009 for Missouri (i.e. Boonville gauge); whereas continuous daily observed/measured discharge data were available for the 1972–1995 calibration period and 1996–2009 validation period for both locations. Daily statistics represent values for daily time steps. Seasonality (seasonal values) represent days of the years averaged over the identified period (i.e. 1972–95, 1996–2009 and 2006–09). Seasonal water temperature statistics could only be calculated for Nebraska from 1972 to 1977 owing to the lack of continuous observed/measured data.

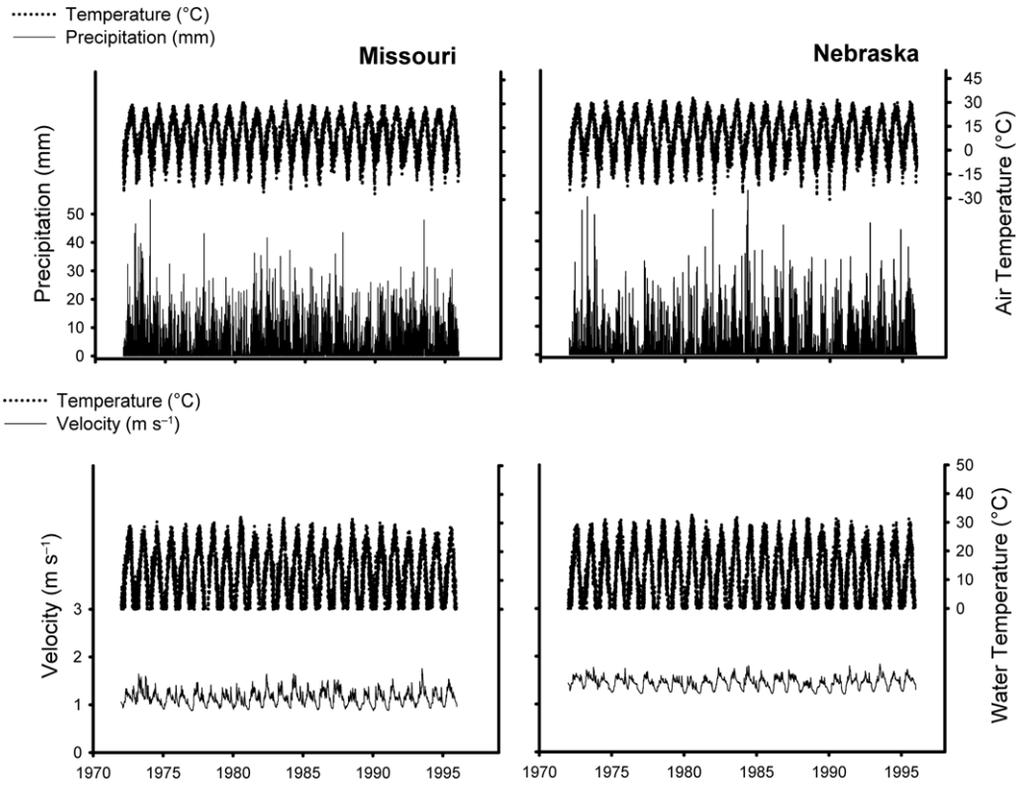


Fig. 3. Average daily precipitation, velocity, water temperature, and air temperature for Missouri (left-hand column) and Nebraska (right-hand column) for NCEP/NCAR Reanalysis I data. Ambient temperature and precipitation were daily averages. Velocity based on river discharge simulated using a lumped-parameter precipitation runoff model HEC-HMS (USACE 2010). Water temperature is simulated using the physical-process SNTemp stream-temperature model (Theurer *et al.* 1984) (see Appendix A for more details).

migration, physiology, habitat choice and spawning success of pallid sturgeon (DeLonay *et al.* 2009).

For fish growth, along with considering the uncertainty between results that occurs with AOGCM–RCM combinations, our uncertainty analysis critically depends on the incorporation of parameter stochasticity through random sampling from reported parameter distributions. Forcing uncertainties were accommodated through river temperature and flow distributions. We use output from HEC-HMS (USACE 2000) and SNTemp (Theurer *et al.* 1984) to produce Missouri River velocities (based on USGS historical channel morphology at the gauge modelled) and temperatures (see Appendix A for details). These water velocities and temperatures were used as input into the pallid sturgeon bioenergetics model to produce simulated growth trajectories. In addition, using the simulated temperature and velocity from two locations within the Lower Missouri River mainstem, we demonstrate the importance of incorporating spatial uncertainty.

Basic bioenergetics model

Our bioenergetics model (as originally described by Kitchell *et al.* 1977) (Wildhaber *et al.* 2015) is fundamentally based on the following simple relationship that conserves energy input and output:

$$C = (R + S) + (F + U) + G \quad (1)$$

where C is food consumption (g/g/day), R is standard metabolism (g/g/day), S is specific dynamic action (g/g/day), F is egestion (g/g/day), U is excretion (g/g/day) and G is gonadal or somatic growth (g/g/day). Consumption (C) is defined as a function of the maximum consumption rate ($C_{\max} = a_1 W^{b_1}$, where W is weight (g) and a_1 and b_1 are the empirical coefficients of the non-linear equation) achievable at the optimal temperature for consumption for an individual fish of a given size, as follows:

$$C = C_{\max} P r_c \quad (2)$$

where r_c is a temperature-dependent proportional adjustment of consumption rate, with P being the actual proportion of maximum consumption consumed. Both take values between 0 and 1.

Pallid sturgeon diet changes from macroinvertebrates to fish as the pallid sturgeon increases in size (Grohs *et al.* 2009). Gerrity *et al.* (2006) and Grohs *et al.* (2009) showed that pallid sturgeon between 350 and 500 mm in fork length consume 57% fish, and those with fork length more than 500 mm consume 90% fish. To incorporate this information into the bioenergetics model, we have pallid sturgeon shifting to a 57% diet of fish between 350 and 500 mm, and 90% fish >500 mm. These transitions from macroinvertebrates to fish were chosen randomly from a uniform distribution of size ranges (i.e. 250–350 and 500–600 mm, respectively) to incorporate the fact that the size at which the switch was observed to occur varied between individuals tested.

Respiration rate (R) is measured by oxygen consumption, which is dependent on water temperature, fish size and activity cost. Chipps *et al.* (2008) defined this as: $R = R_{\max} A r_R$, where $R_{\max} = a_2 W^{b_2}$, where W is weight (g) and a_2 and b_2 are the empirical coefficients of the non-linear equation, the maximum weight-specific standard respiration rate at the optimum temperature. Again, r_R is a temperature-dependent proportional adjustment of consumption rate between 0 and 1, and A is an activity parameter used to specify respiration rates.

The cost of swimming associated with varying water velocities was accounted for by replacing constant activity costs (A) in the standard model with a function that relates swimming speed to activity cost based on white sturgeon (Geist *et al.* 2005). Accuracy of swimming cost estimates was improved by including seasonality in swimming, based on observed swimming patterns of Lower Missouri River pallid sturgeon and their associated variability (DeLonay *et al.* 2009). We incorporated the cost of swimming upstream by assuming that swimming speed was equivalent to the observed upstream swimming speed plus the velocity of the water through which the fish swam. This water velocity was estimated from the water velocity of observed upstream paths travelled by pallid sturgeon in the Lower Missouri River, based on the observation by McElroy *et al.* (2012) that the chosen upstream path of pallid sturgeon was energetically less costly than the average possible based on a random sample of possible paths. The chosen path had an estimated energetic cost equivalent to an average velocity of 1.18 m s^{-1} ; the average possible path velocity was 2.03 m s^{-1} (B. McElroy pers. comm.). Therefore, a constant 58% (i.e. $1.18/2.03 \times 100$) of the estimated average velocity was used as the estimate of the velocity experienced

by the fish. Using a proportion is valid because when average velocity changes in a channel section, the relative distribution of high and low velocities does not (i.e. the flow is fastest in channel and slowest along edges). A proportional adjustment provides additional utility, thus making it possible to apply the model to both migrating and non-migrating pallid sturgeon if the assumption is that reproductive state does not change energetic cost choices. Here, this proportion was held constant since the actual swimming speed cost coefficient was the focus. This cost coefficient was randomly chosen on a daily basis.

Specific dynamic action (S) is a proportion of consumption (C), and is the metabolic cost of digestion, deposition and absorption of consumed energy (Kitchell *et al.* 1977). Waste losses due to egestion (F) and excretion (U) were modelled as a constant proportion of consumed energy, as given by Chipps *et al.* (2008).

We estimated P , actual proportion of maximum consumption consumed, using an empirically determined non-linear function for the relationship of fork length (FL) to P for fish >500 mm FL. To determine these functions of P to FL, we used mark-recapture data from the Pallid Sturgeon Population Assessment Program (PSPAP) (Drobish 2008) and the Pallid Sturgeon Stocking Program (PSSP) (USFWS 2008) for pallid sturgeon recaptured in the Missouri River between the Gavins Point Dam and the Kansas River confluence (i.e. Nebraska), and between the Kansas River confluence to the Missouri River mouth (i.e. Missouri) parts of the Lower Missouri River (Fig. 1). For Nebraska and Missouri separately, we estimated P using observed beginning and ending weights over corresponding time periods and location for pallid sturgeon using the fixed parameter bioenergetics model. We used those estimates to develop relationships between FL and P . The resulting functions were:

- Nebraska: $P = 1 - e^{(-\text{FL}/696.42)}$,
- Missouri: $P = 1 - e^{(-\text{FL}/764.98)}$.

For further details on the development, description and parameterization of the pallid sturgeon bioenergetics model, see Wildhaber *et al.* (2015).

Hydrological/water temperature model validation relative to bioenergetics

We tested the effectiveness and validity of our combined HEC-HMS–SNTemp modelling by using the resulting simulated temperature and velocity data in place of observed data in the previously described bioenergetics model. This is important because, as mentioned in the introduction, our downscaling here is effectively a means to transfer AOGCM–RCM multi-model uncertainty to fish growth. It is

critical that simulations relative to the current climate can be downscaled to produce similar fish growth response as when the bioenergetics model is forced with observations. Thus, the simulated data were used in our stochastically parameterized bioenergetics model for known periods of time in which we had observed pallid sturgeon growth in the Lower Missouri River (Fig. 3). For validation of our combined HEC-HMS-SNTemp model-simulated temperature and velocity data, we used basin-distributed NCEP data in place of individual meteorological-station observed data (NCDC 2010) in our bioenergetics model. Using these simulated water temperatures and velocities, and the bioenergetics models developed for Missouri and Nebraska separately, we demonstrate the effectiveness and validity of our physical models using Monte Carlo simulation of 1000 individual pallid sturgeon (somewhat less than half the number of wild pallid sturgeon estimated to be in the Lower Missouri River at the time of the listing of the species) (Fig. 4). For 14 pallid sturgeon in Nebraska and 18 in Missouri, when the observed initial weight was used in the bioenergetics model, the observed final weight was found within the bounds set by the lower 2.5 percentile and the upper 97.5 percentile of the distribution of the 1000 simulated fish with the same initial weight for all but one fish in Missouri (Fig. 4).

One reason for the effectiveness of the pallid sturgeon bioenergetics model is the nature of the velocity data. A common means to obtain velocity is by using the velocity power equation relationship developed by Leopold & Maddock (1953). The nature of the power-function relationship results in a flattening out of velocity at high and extreme discharge values. Even so, our results are more remarkable than might seem at first glance when one considers the limited information known and available about actual conditions to which these fish were exposed. All that was known about these fish and the conditions they might have experienced was their initial and final weights with limited or no record of the location in which the fish were growing in the river during the time period (i.e. some for nearly 2 years). The initial and final collection locations were used to identify a presumptive restriction to either the Nebraska or Missouri segments of the Lower Missouri River for a given fish.

Methods

Evaluation of multi-model uncertainty relative to the bioenergetics parameter uncertainty

To demonstrate whether one can draw a meaningful inference with climate simulations given

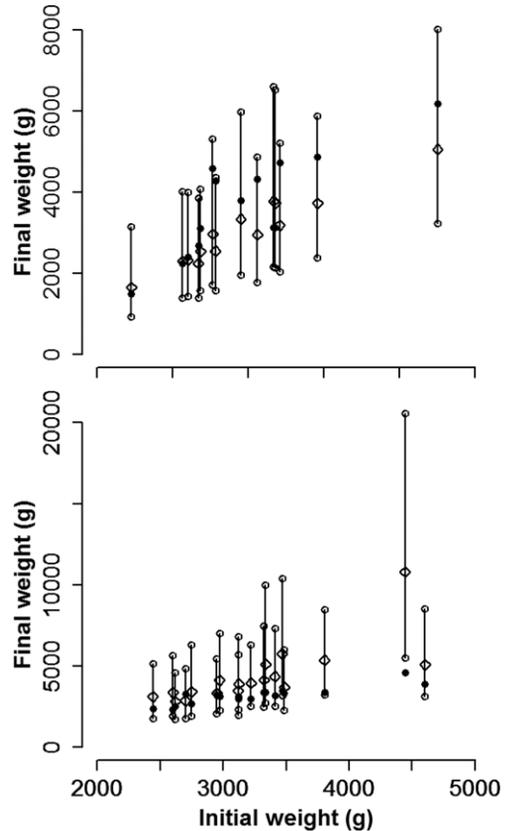


Fig. 4. Observed (filled circles) v. predicted (median, open diamond; upper and lower 95% percentiles, open circles) pallid sturgeon growth based on Missouri (bottom) and Nebraska (top) water velocity and temperature using the bioenergetics model developed by Wildhaber *et al.* (2015). Velocity is based on the river discharge simulated using a lumped-parameter precipitation runoff model HEC-HMS (USACE 2010). Water temperature is simulated using the physical-process SNTemp stream-temperature model (Theurer *et al.* 1984) (see Appendix A for more details).

multi-model uncertainty and ecological response parameter uncertainty, we present results from modelled sturgeon growth using fixed/calibrated system model outputs of water flow and temperature, and a stochastically parameterized bioenergetics model for fish growth that uses those outputs as inputs (Fig. 1). These results include recent-past and future simulated climate conditions under three climate models with available regional models for each (Table 1), with the NCEP/NCAR data considered as measured/observed data – a total of 17 datasets. The multi-model climate simulation uncertainty considered here is that of the differences in results that occurs between AOGCM-RCM combinations at two distinctively different points

along the Lower Missouri River: Nebraska and Missouri (Fig. 2). We used the climate data from each regional model run as input into HEC-HMS and SNTemp in order to simulate temperature and velocity data from both points over 25 years for past (i.e. 1970–94) and future (i.e. 2039–63) climate models, along with NCEP/NCAR (i.e. 1970–94) as input into the bioenergetics model. These two 25 year time frames were chosen for consistency and for the sake of comparison based on the length of the dataset with the shortest, maximum continuous record length (i.e. 25 years).

Although the focus of this study is on the fish growth response relative to uncertainty in the multi-model climate ensemble and the bioenergetics model uncertainty, the ability of the physical downscaling system of models to represent a plausible variability in the river condition relative to the climate simulations is also important. Thus, we do consider the downscaled physical model output relative to the climate simulations in our results to help gauge the variability in these quantities relative to the climate simulation uncertainty. In doing this, bias corrections were not applied to the RCM climate data when it was downscaled to the sub-basins. We use HEC-HMS and SNTemp results based on NCEP/NCAR as the reference response for current conditions. We then compare those results with the results for each AOGCM–RCM combination to provide an assessment of the effectiveness of each AOGCM–RCM association at simulating the observed conditions (see Appendix B).

For the bioenergetics model, we demonstrate the potential effect of uncertainty associated with model parameterization. We do this by assigning distributions to each of the empirically derived parameters using their observed variation. Distributions of the parameters are based on literature, statistical analysis and pilot studies. Most of the parameters are normally (left truncated) distributed (Bevelhimer *et al.* 1985). Waste losses and specific dynamic action are assumed to follow a triangular distribution (Dowd *et al.* 2006). The swimming speed distribution was based on pallid sturgeon movement data (DeLonay *et al.* 2009). For full details of and the parameter values used in the bioenergetics model, see Wildhaber *et al.* (2015).

Simulations

We considered an initial distribution of 1000 pallid sturgeon from a truncated normal distribution with mean weight of 571.21 g (SD = 317.35 g) for the Lower Missouri River. The distribution used is based on a best fit to observed data collected by PSPAP. Once the initial population was determined, the bioenergetics model was run on a daily time step using the velocities and temperatures from a

given hydrological/climate model or dataset. All bioenergetics model parameters were sampled from their respective distributions at the beginning of each day. No births or deaths were allowed. It is important to note that this was not meant to serve as a real-world population study, but rather as a comparison of the sensitivity of the bioenergetics of the fish across climate model scenarios.

Statistical analyses

To evaluate climate and hydrological variables (i.e. air and water temperature, precipitation, and velocity), we used the annual average (i.e. the sum of daily values for a year divided by the number of days in a year, either 365 or, for leap years, 366) so that seasonal variation did not mask any long-term trends. For fish growth, we used the final weights of the 1000 simulated fish. The statistical tests performed to assess differences in response between climate models were non-parametric owing to a lack of constancy of variance for climate and hydrological data, and non-normality of final fish weights. Our goal was to test differences between distributions. Therefore, we chose a combination of tests to assess differences in overall distributions and variances. To do this, the Kruskal–Wallis non-parametric one-way analysis of variance (ANOVA) and the Conover squared rank test of variances were used to test between climate scenarios at each gauge (i.e. Nebraska and Missouri). Kruskal–Wallis was used to test overall differences between distributions, while Conover was used to test differences in variances. There were three groups of tests carried out for each parameter at each of the gauges. In addition to the ANOVA tests, we considered pairwise tests within each group (note that the Kruskal–Wallis test is simply a Mann–Whitney test of two samples in this case, but requires Type I error adjustment to account for the multiplicity). In particular, the three groups of tests considered were: (1) differences between AOGCM–RCM scenarios and NCEP/NCAR for the recent past (Bonferroni-adjusted Type I errors for effective significance levels of $0.05/36 = 0.0014$); (2) differences between model scenarios for future climates (Bonferroni-adjusted Type I errors for an effective significance of $0.05/28 = 0.0018$); and (3) differences between the recent past and the future within each AOGCM/RCM scenario (Bonferroni-adjusted Type I error significance levels of $0.05/8 = 0.0063$).

Results

For all climate, hydrology and growth variables, the Kruskal–Wallis one-way ANOVA models revealed

Table 3. *Kruskal–Wallis non-parametric one-way ANOVA to test the overall differences between distributions and the Conover squared rank test of variance results*

Parameter	Gauge	Kruskal–Wallis		Conover	
		χ^2 statistic	<i>p</i> value	χ^2 statistic	<i>p</i> value
<i>Recent past</i>					
Ambient temperature (°C)					
	Nebraska City, NE	165.70	<0.0001	15.74	0.0463
	Boonville, MO	155.67	<0.0001	14.01	0.0815
Water temperature (°C)					
	Nebraska City, NE	174.16	<0.0001	17.00	0.0301
	Boonville, MO	159.90	<0.0001	16.01	0.0423
Velocity (m s ⁻¹)					
	Nebraska City, NE	194.79	<0.0001	23.93	0.0024
	Boonville, MO	179.04	<0.0001	35.50	<0.0001
Precipitation (cm)					
	Nebraska City, NE	139.92	<0.0001	43.29	<0.0001
	Boonville, MO	114.10	<0.0001	31.81	0.0001
Fish growth (g g ⁻¹) in their respective models					
	Nebraska City, NE	4300.19	<0.0001	3098.56	<0.0001
	Boonville, MO	5544.67	<0.0001	6665.33	<0.0001
Fish growth (g g ⁻¹) in their reverse models					
	Nebraska City, NE	4034.32	<0.0001	343.38	<0.0001
	Boonville, MO	3424.81	<0.0001	7152.55	<0.0001
<i>Future</i>					
Ambient temperature (°C)					
	Nebraska City, NE	139.77	<0.0001	4.89	0.6731
	Boonville, MO	137.99	<0.0001	6.66	0.4652
Water temperature (°C)					
	Nebraska City, NE	150.79	<0.0001	3.50	0.8355
	Boonville, MO	148.85	<0.0001	3.46	0.8389
Velocity (m s ⁻¹)					
	Nebraska City, NE	172.44	<0.0001	11.86	0.1053
	Boonville, MO	163.37	<0.0001	14.47	0.0434
Precipitation (cm)					
	Nebraska City, NE	131.74	<0.0001	24.41	0.001
	Boonville, MO	112.42	<0.0001	11.09	0.1348
Fish growth (g g ⁻¹) in their respective models					
	Nebraska City, NE	3397.91	<0.0001	1097.91	<0.0001
	Boonville, MO	4254.99	<0.0001	2878.73	<0.0001
Fish growth (g g ⁻¹) in their reverse models					
	Nebraska City, NE	3018.58	<0.0001	446.53	<0.0001
	Boonville, MO	4434.87	<0.0001	6201.45	<0.0001

Annual mean of climate scenario data is used as input into the hydrological model, and outputs from that model along with bioenergetics growth model outputs were individually analysed for each river gauge. The Nebraska City, NE gauge corresponds to ‘Nebraska’ and the Boonville, MO gauge corresponds to ‘Missouri’. There were nine climate models for the recent past and eight for future tests. *p*, probability.

highly significant differences (Table 3). Air and water temperature, precipitation, water velocity, and fish growth produced a significant difference in the Conover squared rank of the variances for the recent past, but only for precipitation, velocity and fish growth for the future. For the pairwise Kruskal–Wallis test, the great majority of the Bonferroni-adjusted pairwise comparisons were significant (Table 4; Appendix B). For precipitation,

>50%, around 65% and 0% of the comparisons were significant between climate models for the recent past, between climate models for the future, and between the recent past and the future within a climate model, respectively. For air temperature, >70%, >75% and 100% of the comparisons were significant with respect to the recent past, the future, and between the recent past and the future, respectively. For velocity, >75%, >75% and >37%

Table 4. Probabilities from the pairwise climate scenario non-parametric Kruskal–Wallis tests conducted for fish growth (*g*) at each gauge ($n = 36$)

		G																GF			
		CC	CC	CC	CC	CC	CC	CC	CG	GF	GF	GF	GF								
Model	R	CR	CR	MM	MM	WR	WR	CR	CR	RC	RC	WR	WR	HR	HR	RC	RC				
Site	G	R	Period	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F		
B	NC		P	+		+		-		-		+		-		+		+			
N	NC		P	NO		+		-		-		+		-		+		+			
B	CC	CR	P		+	+		-		-		+		-		+		+			
N	CC	CR	P		+	+		-		-		+		-		+		+			
B	CC	CR	F				MA		-		-		+		-		+		+		
N	CC	CR	F				UN		-		-		+		-		+		+		
B	CC	MM	P			+	+		-		-		+		+		+		+		
N	CC	MM	P				+	+		-		-		+		+		+			
B	CC	MM	F						-		-		+		-		+		+		
N	CC	MM	F						-		-		+		-		+		+		
B	CC	WR	P						+	+		+		NO		+		+			
N	CC	WR	P						+	UN		+		-		+		+			
B	CC	WR	F								+		+		-		+		+		
N	CC	WR	F								+		+		-		+		+		
B	CG	CR	P								+	+		-		+		+			
N	CG	CR	P								+	+		-		+		+			
B	CG	CR	F									+		+		-		+			
N	CG	CR	F									+		+		-		+			
B	CG	RC	P									+	-		-		NO		+		
N	CG	RC	P									+	-		-		+		+		
B	CG	RC	F											-		NO		-	MA		
N	CG	RC	F											-		-		+	MA		
B	CG	WR	P											+	+		+				
N	CG	WR	P											+	+		+				
B	CG	WR	F													+		+			
N	CG	WR	F													+		+			
B	GF	HR	P													+		+			
N	GF	HR	P													+		+			
B	GF	HR	F																-		
N	GF	HR	F																+		
B	GF	RC	P																+		
N	GF	RC	P																+		
B	GF	RC	F																+		
N	GF	RC	F																+		

There were three groups of tests performed for each parameter at each of the gauges: (1) differences between climate models and NCEP/NCAR for the recent past (Bonferroni-adjusted alpha for significance of $0.05/36 = 0.0014$); (2) differences between climate models for the future (Bonferroni-adjusted alpha for significance of $0.05/28 = 0.0018$); and (3) differences between the recent past and the future within each climate model ($0.05/8 = 0.0063$). Missouri (i.e. Boonville gauge) designated as 'B' and Nebraska (Nebraska City gauge) as 'N'. Global climate models (G): NC, NCEP/NCAR; CC, CCSM; CG, CGCM; GF, GFDL. Regional climate models (R): CR, CRCM; MM, MM5I; RC, RCM3; WR, WRFG; HR, HRM3; P, recent past; F, future; - or +, significantly less or greater, respectively, row model than column model at Bonferroni alpha; UN, *p* value between Bonferroni alpha and 0.05; MA, *p* value between 0.05 and 0.1; NO, *p* value above 0.1 (*p*, probability).

of the pairwise comparisons were significant, respectively. For water temperature, around 78%, >75% and 100% of the tests were significant, respectively. For fish growth, around 94%, around 93% and 100% of the comparisons were significant, respectively.

Despite the variation in response observed within and between climate models for the environmental parameters (Appendix B), resulting

differences in fish weight were much more consistent, with more than half of the 34 climate model combinations (past and future combined) significantly different from all other climate models, with the rest being similar to only one other climate model (Table 4). For Missouri, all non-significant comparisons for the recent past were between the same RCMs from different AOGCMs. For Missouri future and Nebraska recent past and future, two of

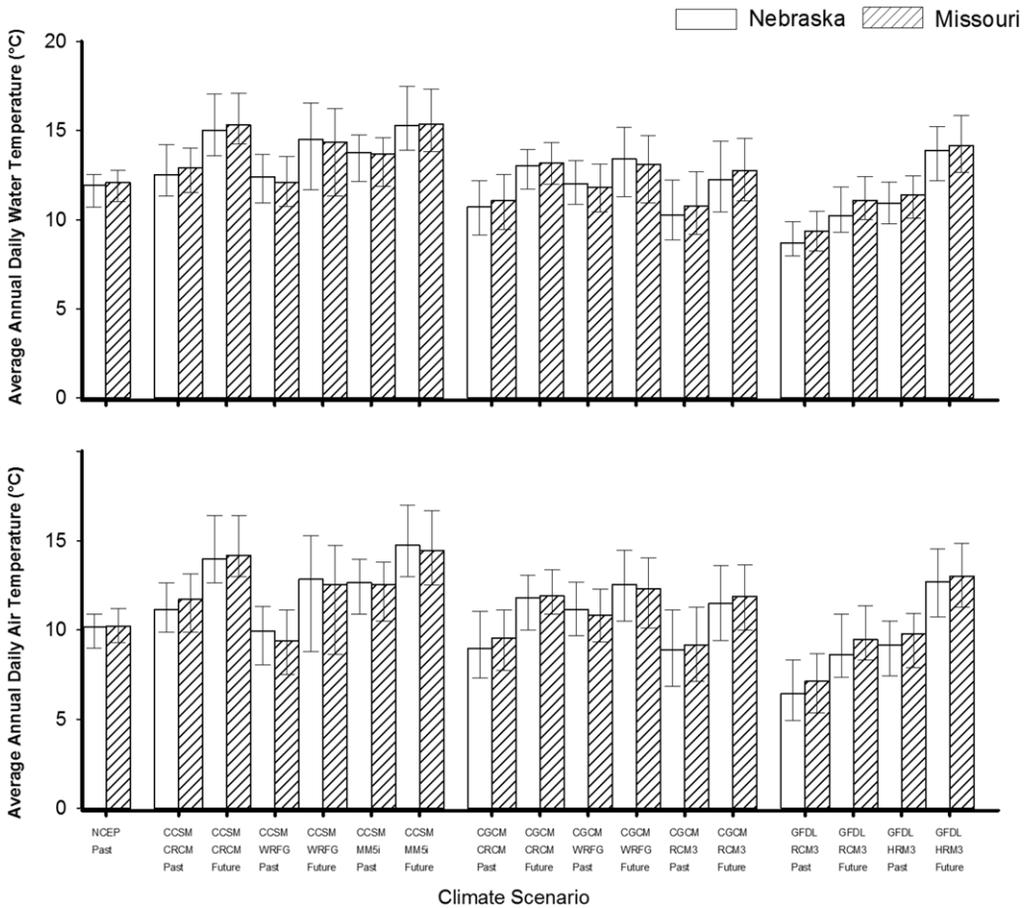


Fig. 5. Regional climate model (RCM) median, annual air temperature (lower panel) and median, annual, simulated water temperature (upper panel) for each climate scenario. Water temperature is simulated using the physical-process SNTemp stream-temperature model (Theurer *et al.* 1984) (see Appendix A for details). Bars represent minimum and maximum. North American NARCCAP datasets used in simulations. AOGCM simulations were taken from the WCRP’s CMIP3 multi-model dataset (Meehl *et al.* 2007) based on the A2 emissions scenario (representing less international co-operation to reduce greenhouse gases) that projects relatively high greenhouse gas concentration increases. Model data used included four AOGCMs: CGCM (Flato 2005), CCSM, GFDL and HADCM. Model data used include six RCMs within the AOGCMs: CRCM, HRM3, MM5I, ECPC, RCM3 and WRF-G. Measured/observed data: NCEP/NCAR Reanalysis 1 (Kalnay *et al.* 1996) (NCEP/NCAR) from Earth System Research Laboratory (www.esrl.noaa.gov).

the four non-significant comparisons showed the same pattern. Again, despite the inconsistency in response for the environmental variables between climate models and the fact that actual weights differed between climate models (Figs 5–7), all recent past weights were significantly greater than all future weights (Fig. 7); this was consistent with temperature differences (Fig. 5). In addition, median fish weight increased over the 25 year simulation period under all climate models except for GFDL/RCM3 and CGCM/RCM3 for the recent past and future, and for GFDL/HRM3 for the future for Nebraska (Fig. 7). The top five greatest fish weights

occurred for the CGCM/WRF-G recent past and future and the CGCM/CRCM recent past, the CCSM/WRF-G recent past, and the NCEP/NCAR recent past at Missouri. Although gauge differences were not directly tested, in all cases the increase in weight was greater for Missouri compared to Nebraska (Fig. 7).

Discussion

We found differences in all but a few of the comparisons between climate models for the recent past and the future, and for all comparisons within climate

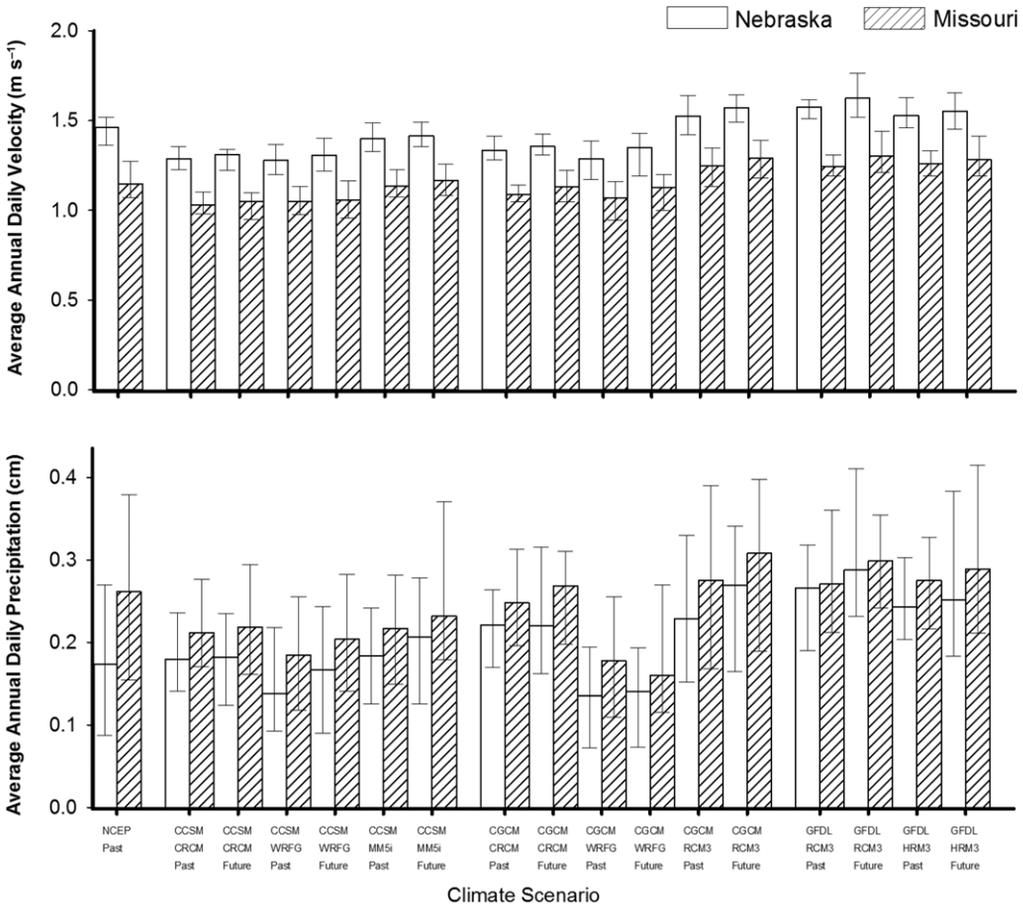


Fig. 6. Regional climate model (RCM) median, annual precipitation (lower panel) and median, annual, simulated velocity (upper panel) for each climate scenario. Velocity based on river discharge simulated using a lumped-parameter precipitation runoff model HEC-HMS (USACE 2010 – see Appendix A for more details). Bars represent minimum and maximum values. NARCCAP datasets were used in simulations. AOGCM simulations were taken from the WCRP’s CMIP3 multi-model dataset (Meehl *et al.* 2007) based on the A2 emissions scenario (representing less international co-operation to reduce greenhouses gases) that projects relatively high greenhouse gas concentration increases. Model data used included four AOGCMs: CGCM (Flato 2005), CCSM, GFDL and HADCM. Model data used include six RCMs within the AOGCMs: CRCM, HRM3, MM5I, ECPC, RCM3 and WRF-G. Measured/observed data: NCEP/NCAR Reanalysis 1 (Kalnay *et al.* 1996) (NCEP/NCAR) from Earth System Research Laboratory (www.esrl.noaa.gov).

models between the recent past and the future for growth rates of pallid sturgeon (Table 4). Actual predicted pallid sturgeon growth was dependent on the climate model considered (Fig. 7). However, despite the variation in responses seen between and within climate models for the various environmental parameters (Appendix B; Figs 5 & 6), the primary differences of greater growth for the recent past compared to the future, and for Missouri compared to Nebraska (Table 3; Fig. 7) held for all comparisons. Simultaneously, the model was able to capture, through predicted growth, the general

pattern of GFDL compared to the CCSM and CGCM, with greater differences occurring between the AOGMs than between the recent past and future conditions within an AOGCM (Fig. 7), and the opposite pattern seen when comparing the CCSM and CGCM. For GFDL, increased velocities resulted in increased energetic costs and slowest growth rate (Fig. 7). As a result of the narrower, channelized river in the Nebraska reach compared to the Missouri reach, water velocities tended to be higher for Nebraska (Appendix B; Fig. 6), while water temperatures were similar (Appendix

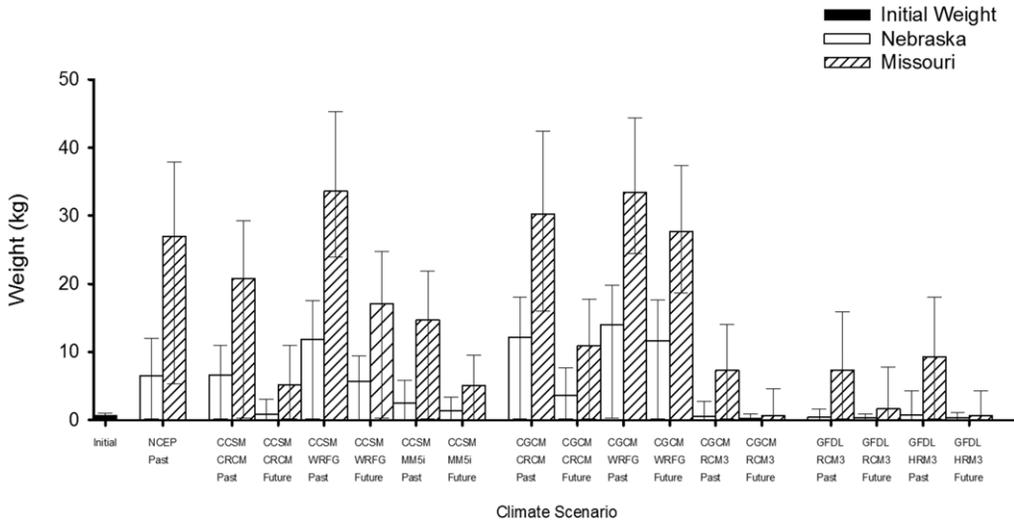


Fig. 7. Predicted, median final weight of pallid sturgeon based on Missouri and Nebraska water velocity and temperature using the bioenergetics model developed by Wildhaber *et al.* 2015). Velocity based on river discharge simulated using a lumped-parameter precipitation runoff model HEC-HMS (USACE 2010 – see Appendix A for more details). Water temperature is simulated using the physical-process SNTemp stream-temperature model (Theurer *et al.* 1984 – see Appendix A for more details). Bars represent minimum and maximum. NARCCAP datasets used in simulations. AOGCM simulations were taken from the WCRP’s CMIP3 multi-model dataset (Meehl *et al.* 2007) based on the A2 emissions scenario (representing less international co-operation to reduce greenhouses gases) that projects relatively high greenhouse gas concentration increases. Model data used included four AOGCMs: CGCM (Flato 2005), CCSM, GFDL and HADCM. Model data used include six RCMs within the AOGCMs: CRCM, HRM3, MMSi, ECPC, RCM3 and WRFG. Measured/observed data: NCEP/NCAR Reanalysis 1 (Kalnay *et al.* 1996) (NCEP/NCAR) from Earth System Research Laboratory (www.esrl.noaa.gov).

B; Fig. 5). These higher velocities translated into higher energetic costs and, thus, a need for different consumption-to-length relationships between locations, not one representing pallid sturgeon growth for the entire Lower Missouri River.

In conclusion, relative to the analysis goal of considering inference on potential fish growth in the context of simulated climate data given the uncertainty associated with fish bioenergetics and the necessity for multi-model ensembles of climate simulations, it is apparent that, in the three situations considered here (i.e. recent past, future, and past v. future), uncertainty associated with the bioenergetics model does not preclude our ability to find significant differences in fish growth. Indeed, although our uncertainty in the bioenergetics model parameters is quite large, and it does lead to a fairly large ‘spread’ in the results, this spread is not so large as to swamp the variability in the climate model simulators. In addition, the associated differences, or lack thereof, in the physically downscaled weather and river condition variables between climate models (or within climate model when considering the past/future comparisons) suggest that the physical differences in the variables that feed into the bioenergetics model are responsible for these

large differences in growth. This implies that it is possible to make inferential statements while capturing uncertainty in the climate model simulations and the ecological response. It also suggests that it is reasonable then to start considering the uncertainties associated with the intermediate scales as a next step.

Areas for improvement

As described in the methods, our bioenergetics model had to be built using a combination of results directly taken from pallid sturgeon juveniles and other sturgeon species. We had to assume that the model that described juvenile pallid sturgeon bioenergetics also described the bioenergetics of adults, which is often an incorrect assumption (Hansen *et al.* 1993). We also had to assume that the swimming energetics of other sturgeon species represented the swimming energetics of pallid sturgeon. These assumptions identified important areas of research still needed on pallid sturgeon basic and swimming energetics.

Some of the next steps for this modelling effort would be to address the existing obvious sources of error and uncertainty: land use, geological and

geomorphic, hydrological, temperature, velocity and energetics models, and to add additional hydrology models to the analysis to better address the issue of error propagation across scales. For example, improved capabilities for simulation of snowmelt and base flow components, as well as more detailed accounting of anthropogenic effects, could reduce some uncertainty related to the hydrological response of the Missouri River Basin to changing climate. The framework we present works very well for the mainstem of the Missouri River where hydrological conditions are the result of aggregations of large areas and physical processes, but more detailed modelling (i.e. finer spatial discretization and more data) may be required to address locations on the Missouri River Basin other than the mainstem (e.g. headwaters and lower flow segments). Along with these additions is the need for the inclusion of more model-based analysis of the distributional results that can accommodate biases, interactions and uncertainties. As demonstrated by the place-based results we presented, there is a need to add spatial linkages and, most importantly, the need to fully develop an effective method for uncertainty propagation across scales (Wikle 2003; Clark 2007; Cressie *et al.* 2009; Cressie & Wikle 2011).

Critically, as we move into a modelling framework that seeks to evaluate probabilistic outputs, the standard simple statistical comparisons presented here will give way to more complicated assessments of distributional variability. The Bayesian paradigm is increasingly being used to address the issues associated with probabilistic impact studies (e.g. Tebaldi *et al.* 2004, 2005; Greene *et al.* 2006; Furrer *et al.* 2007; Rougier 2007; Berliner & Kim 2008; Rougier *et al.* 2009; Tebaldi & Sansó 2009; Sain *et al.* 2011). In particular, issues related to model weighting, information content and the role of expert opinion should be considered (e.g. Knutti *et al.* 2010; Knutti 2010). Such large-scale probabilistic impact studies are starting to be considered (e.g. Murphy *et al.* 2007; Rougier *et al.* 2009; Sankarasubramanian *et al.* 2009; Sokolov *et al.* 2009; Harris *et al.* 2010; Semenov & Stratonovitch 2010), but are still in their infancy when it comes to the consideration of individual scale ecological impacts.

Linking with pallid sturgeon recovery management

The life expectancy of pallid sturgeon is at least 40 years (USFWS 1993). This means individuals living under current management practices of the Pallid Sturgeon Recovery Plan will probably live to experience climate change. The most recent USFWS 5 year review of pallid sturgeon recovery

efforts urges an update of the Pallid Sturgeon Recovery Plan to include the most recent information regarding genetics, distribution, life history, abundance and trends, threats, and conservation measures (USFWS 2007). Climate change should be added to this list, and it should be recognized that understanding the sensitivity of pallid sturgeon to climate change means continuing to learn a great deal about the sensitivity of its habitat to climate variability and about conservation measures.

The capability to directly link projections of climate change with current and hypothetical management practices for pallid sturgeon is a critically important aspect of a flexible hierarchical approach to quantifying uncertainty. Although we illustrate integrating multi-model climate uncertainty and parameter-uncertainty species models using a bioenergetics growth model, the mathematical framework could also be applied to models for habitat (Jacobson *et al.* 2009), migratory constraints (Jacobson *et al.* 2009) and prey availability (Spindler *et al.* 2012). In addition, the hierarchical structure can use, as either parameter distributions or structural models, the knowledge gained from sampling programmes that have speculated on preferred habitats for spawning (Koch *et al.* 2012), migratory channels (DeLonay *et al.* 2009; Jacobson *et al.* 2009; McElroy *et al.* 2012) and habitats altered by sediment transport (DeLonay *et al.* 2009).

Since the Pallid Sturgeon Recovery Plan identifies as an immediate threat the present or threatened destruction, modification or curtailment of its habitat or range, a logical next step, then, should be to link climate projections not only to bioenergetics models but also to habitat models. However, the results of this preliminary study indicate that a primary change to the pallid sturgeon environment expected of climate warming is a tendency towards increased water temperature and velocity. Temperature change could alter the timing of spawning cues, and this suggests the possibility of a decoupling between the seasonality of flow pulses and water temperature appropriate for embryo development. Simultaneously, increased velocities could decrease growth, and, therefore, survival and reproductive potential.

Ultimately, any modelling approach used to help guide pallid sturgeon recovery efforts needs to be ecosystem based, such as that of the marine ecosystem modelling approach of Ecopath with Ecosim developed at the University of British Columbia (<http://www.ecopath.org/>). Without key ecosystem components (e.g. prey) incorporated into the modelling approach, important non-linear feedbacks are ignored. Therefore, these additional components need to be included as submodels that have a feedback loop with the primary model. For fish species fed on by adult pallid sturgeon, a separate

set of bioenergetics models is needed for each species to estimate their mass at any given time point. That mass then becomes the estimate of available food for adult pallid sturgeon. As a feedback, this prey mass is then affected by the predation rate of pallid sturgeon, and so on.

Conclusions

In climate impact studies, there is uncertainty in our models and observations at each scale from the global to the individual. Attempting to account for these uncertainties is critical in trying to evaluate potential effects of climate change since lakes and streams have been identified as sentinels of environmental change (Williamson *et al.* 2008). Through this work, we have advanced efforts to understand and accommodate model uncertainty based on stochastic individual model parameterization and multi-model climate simulation. In particular, we allow information from the multi-model climate simulators to propagate to the individual scale in a deterministic manner that accounts for multiple variables with realistic spatial and temporal variability. Ultimately, this allows us to examine whether there is a meaningful variation evident across climate model and scenario relative to the uncertainty associated with our knowledge of fish bioenergetics relative to the Missouri River sturgeon population dynamics. In support of the need for such an approach, we show how we have combined available data from numerous agencies (e.g. the USGS, the NOAA, the USACE, the USDA and the USFWS) and models (e.g. the North American Climate Change Assessment Program (NARCCAP), and sturgeon population, movement and bioenergetics models) across a variety of scales to try to develop initial simulations of potential pallid sturgeon population change.

Although not considered in this study, the ultimate goal is a framework for describing the potential consequences of regional and global climate changes on large riverine ecosystems and the related influence on fish growth using the uncertainty associated with various climate model scenario data sources. This work is the basis for such an approach that provides a tool for understanding the potential consequences of regional to global change and the resulting changes for large river ecological systems, and the options for sustaining and improving ecological systems and related goods and services, given projected regional to global changes – both questions identified in the USGS Strategic Science Plan (USGS 2007). The expectation is a framework for identifying potential consequences of climate change on large riverine ecosystems (key ecosystems), such as the Missouri

River, to alert decision-makers to the most likely consequences to such ecosystems. In addition, it should provide the basis for the development of a new suite of indicators of large riverine ecosystem change and health.

The Missouri River is a highly regulated river as a result of a series of mainstem reservoirs put in place for flood control and hydropower that influence water flow and temperature (Wright *et al.* 1999; Galat & Lipkin 2000). The result is natural flow regimes that are influenced by this reservoir network. Therefore, how releases/abstractions are managed today and in the future is/will be important. The framework presented here provides the basis for development of a model that allows comparisons of the effectiveness of such management practices and others (e.g. habitat changes, propagation), especially in the presence of climate change. Any future work should be designed to specifically address these management questions.

The Missouri Department of Conservation (V. Travnichek pers. comm.), the USFWS (C. Scott pers. comm.) and researchers (Quist *et al.* 2004; Bergman *et al.* 2008; Doyle *et al.* 2011) have indicated the need for this work for the very reasons just described. This might be achieved through the development of a predictive model to evaluate management options (e.g. reservoir management) for coping with global change effects and by providing a powerful tool for assessing the associated uncertainty. This model could be used to help assess sensitivity and adaptability of the Missouri River, document methods that could be applied to other large river ecosystems, and assess the potential effectiveness of adaptation and mitigation methodologies at minimizing the effects of directional and non-linear climate change on the Missouri River ecosystem and resident fishes. The ultimate model would refine, apply and interpret basin and ecosystem process models to assist natural resource managers.

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Appendix A

HEC-HMS and SNTemp model parameterization

To model the hydrological components (i.e. river velocity and water temperature) needed for the bioenergetics model, the Missouri River Basin was divided into 116 sub-basins and corresponding reaches delineated using the ArcGIS Geo-HEC program from the HYDRO1K hydrologically corrected dataset (last accessed 8 December 2011, http://eros.usgs.gov/#Find_Data/Products_and_Data_Available/gtopo30/hydro/america). The 116 sub-basins were based on 84 USGS stream gauges, with 32 additional self-generated based on topography and determined using ArcGIS Geo-HMS. Sub-basin size ranged from 82.9 to 60 780 km² (32 to 23 469 square miles), with stream length varying from 6.4 to 493.7 km (3.98–306.75 miles). Sub-basin boundaries were used to determine stream segmentation (Fig. 1) using a 10 000 km² threshold. Approximately 13 820 km (8584 miles) of stream channels were simulated, including 3460 km (2150 miles) of the Missouri River mainstem. All meteorological data were distributed or downscaled across each basin using the Thiessen Polygon technique (USACE 2000), giving 116 individual meteorological data points – a source of uncertainty not accounted for here but would be if other sources of uncertainty were considered.

For hydrological modelling using HEC-HMS, to account for initial soil moisture and soil-water loss rate (hydraulic conductivity), we used the Deficit and Constant Loss precipitation-runoff method with constant hydraulic conductivity available in the model. This method adequately allows for long-term simulation for use with potential evapotranspiration processes (USACE 2010) and requires the least number of unknown parameters when unsaturated/saturated aquifer interactions are not quantified. While the model might not predict losses well within a specific storm event due to the assumption of a constant loss rate, total loss is well simulated, and the model 'has been implemented successfully in many research projects conducted throughout the United States' (USACE 2001). Evapotranspiration was simulated through the Priestley–Taylor method, which is the only method

included in HEC-HMS at this time (USACE 2010). Snow accumulation and melt were simulated using the Temperature Index method (USACE 2010), a simpler method when assuming that solar radiation dominates the snowmelt process (Debele *et al.* 2010). Sub-basin outflows were computed using the Clark unit hydrograph (UH) (Clark 1945), a mathematical approach that relates direct runoff to one unit of uniformly distributed excess precipitation occurring over a specific duration. The Clark UH requires two parameters calculated from land use/class and soil class: the time of concentration of channel water from the sub-basin and a sub-basin storage coefficient, which accounts for the temporary storage of precipitation excess. Stream baseflow was computed using the HEC-HMS Recession method combined with the Ratio to Peak Threshold option (a constant determining when baseflow is reset on the falling limb of the hydrograph). This method best represents baseflow quantity when ground and surface water interactions are not quantified; HEC-HMS does not simulate groundwater conditions. However, the Monthly Baseflow HEC-HMS option was modified by using averaged daily baseflow from 1972 to 1995 (calibration period) for all headwater basins, as baseflow in HEC-HMS is computed only from simulated flow and does not automatically add additional channel water contributed directly from groundwater input. Baseflow volume was computed using baseflow separation techniques provided by the Web-based Hydrograph Analysis Tool (WHAT) (Lim *et al.* 2005).

In HEC-HMS, one of two channel routing methods was used, which represents the lag and attenuation of a flood wave as it moves downstream. Our preferred method was the Kinematic-Wave Routing method, a mathematical method relating streamflow dynamics to the shape, channel roughness (channel Manning's *n*) (Arcement & Schneider 1989) and slope of the channel (USACE 1993). If, however, the channel flow computation did not converge while using the Kinematic-Wave method, the Muskingum–Cunge Routing method was applied. The Muskingum–Cunge method is based on the conservation of mass equation and the diffusive form of the momentum equation (USACE 2001) and uses a transformed Kinematic-Wave diffusion equation that numerically attenuates an imperfectly centred finite-difference solution (USACE 1991). These methods allow for the use of more physical channel characteristics, such as channel shape, than other methods provided in HEC-HMS. All Missouri River mainstem reservoirs were simulated using HEC-HMS Reservoir Elements while applying Outflow Curve and Storage Discharge methods. The Storage Discharge function in HEC-HMS is a mathematical expression used to represent reservoir management. Following the HEC-HMS manual, the parameters that define this function were estimated using observed discharge and reservoir storage values, and calibrated on 1972–95 data.

Velocity was calculated from observed and HEC-HMS simulated discharge based on the equation, $V = aD^b$ (Leopold & Maddock 1953), where V is velocity, D is

discharge, and a and b are the empirical coefficients of the non-linear equation, which are held constant. The estimated constants a and b for Nebraska were 0.173 and 0.302, and for Missouri 0.117 and 0.303, respectively. These relationships vary with changes in channel form and do not account for the 15% measurement error known to be present in the observed discharge data (Moriassi *et al.* 2007). Therefore, we used the longest available record of field measured data (i.e. 1950–2009) to produce long-term average estimates; additional sources of uncertainty that could be incorporated if known. Using these fixed, estimated parameter values, we used the discharge to velocity equation to convert daily discharge to daily velocity data. Computed velocity data were rounded to 0.5 dm s^{-1} to account for reporting precision (USGS 2002, 2012).

In SNTemp, required groundwater (baseflow) and ground temperatures are generally assumed to be at average annual ambient temperatures (Freeze & Cherry 1979; Bartholow 2000). However, we do acknowledge that groundwater temperatures do vary and, therefore, this study used a 365 day-centred moving average of ambient air temperatures for daily groundwater temperatures for each sub-basin/reach. This option is allowable in SNTemp and greatly influences stream water temperatures. Ground temperature (restricted by SNTemp to one value for each sub-basin for the entire simulation period) was estimated using average air temperatures for the entire period. Accounting for varying groundwater temperatures using the 365 day moving average method, however, accounts for much of the influence that changing soils temperatures have on surface water temperatures.

SNTemp was calibrated to water temperature data collected at the Nebraska USGS gauging station location, which is an upper point on the Lower Missouri River mainstem. The Nebraska location had the longest observed stream temperature record of all USGS gauging stations used in this study. To maintain model simplicity, the only SNTemp parameter calibrated in this study was the Bowen ratio, as this was considered the most uncertain value and results were most sensitive to this parameter. Bowen ratios range between 0.1 for

open water (specifically, ocean surfaces), 0.2 for mixed forests and wetlands, 2.0 for deserts and up to 10 for arid – shrubland regions (USEPA 2008). Bowen ratios can be negative, but such values are not allowed in SNTemp. A Bowen ratio of 0.05, appropriate for land-based surface-water bodies, was used for all reaches. This value was determined through trial and error calibration for river reaches in Nebraska where the only usable long-term temperature was available for the Lower Missouri River.

Appendix B

Precipitation, air temperature, water velocity and water temperature

Except for GFDL/RCM3 recent past and future, and CCSM/MM5I recent past air temperature, all climate models (recent past and future combined) were not significantly different from that of one to four other climate models for Nebraska and Missouri, and one–three climate models for water temperature; for all climate models, however, air and water temperatures were significantly different between the recent past and the future (Table B1). Except for NCEP/NCAR recent past, CCSM MM5I recent past and future, and CGCM/CRCM recent past and GFDL/RCM future for Nebraska, velocity for all climate models was not significantly different to that from one to three other climate models (Table B2). Velocity was only different between the recent past and the future for CGCM/CRCM, CGCM/WRF and GFDL/RCM for Nebraska and Missouri, and CCSM/MM5I for Nebraska. For precipitation, in comparisons between climate models for the recent past and the future, all climate models were not significantly different from at least one other climate model, while no comparison between the recent past and future within a climate model was significant. Although gauge differences were not directly tested, air and water temperature tended to be similar between Missouri and Nebraska, while precipitation tended to be less for Nebraska than Missouri, and velocity tended to be less for Missouri than Nebraska (Table 4).

Table B1. Probabilities from the pairwise climate scenario non-parametric Kruskal-Wallis tests conducted for air temperature (above diagonal) and water temperature (below diagonal) at each gauge (n = 36)

Model		G	NC	CC	CC	CC	CC	CC	CC	CG	CG	CG	CG	CG	CG	GF	GF	GF	GF	
		R	CR	CR	MM	MM	WR	WR	CR	CR	RC	RC	WR	WR	HR	HR	RC	RC		
Site	G	R	Period	P	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F
B	NC		P		-		-		+		+		+		UN		UN		+	
N	NC		P		-		-		NO		+		+		-		+		+	
B	CC	CR	P	+		-	UN		+		+		+		UN		+		+	
N	CC	CR	P	-		-	-		+		+		+		NO		+		+	
B	CC	CR	F		+			NO		+		+		+		+		+		+
N	CC	CR	F		UN			MA		+		+		+		+		+		+
B	CC	MM	P	+	+	-		-	+		+		+		-		+		+	
N	CC	MM	P	+	+	-		-	+		+		+		-		+		+	
B	CC	MM	F			NO	+			+		+		+		+		+		+
N	CC	MM	F			NO	+			+		+		+		+		+		+
B	CC	WR	P	NO	-		-		-	NO	UN		NO	UN		NO	UN		+	
N	CC	WR	P	UN	-		-		-	UN			NO	UN		NO	UN		+	
B	CC	WR	F			-	-		+		NO	UN		MA		-		UN		+
N	CC	WR	F		+	UN	-		+		UN		NO	UN		+		NO		+
B	CG	CR	P	-	-		-		-		-		NO	UN		NO	UN		+	
N	CG	CR	P	-	-		-		-		-		NO	UN		NO	UN		+	
B	CG	CR	F			-	-		-		-		+		NO	UN		-		+
N	CG	CR	F			-	-		-		-		+		NO	UN		-		+
B	CG	RC	P	-	-		-		-		NO	UN		MA		+		NO		+
N	CG	RC	P	-	-		-		-		NO	UN		MA		+		NO		+
B	CG	RC	F			-	-		-		-		+		+		NO		UN	
N	CG	RC	F			-	-		-		-		+		+		NO		UN	
B	CG	WR	P	NO	-		-		NO	NO			-		+		+		+	
N	CG	WR	P	NO	UN		-		NO	NO			-		+		+		+	
B	CG	WR	F			-	-		-		-		NO	UN		NO	UN		+	
N	CG	WR	F			-	-		-		-		NO	UN		NO	UN		+	
B	GF	HR	P	-	-		-		-		NO	NO		UN	UN		+		UN	
N	GF	HR	P	-	-		-		-		NO	NO		UN	UN		+		UN	
B	GF	HR	F			-	-		-		-		+		+		+		+	
N	GF	HR	F			-	-		-		-		+		+		+		+	
B	GF	RC	P	-	-		-		-		-		-		-		-		-	
N	GF	RC	P	-	-		-		-		-		-		-		-		-	
B	GF	RC	F			-	-		-		-		-		-		-		-	
N	GF	RC	F			-	-		-		-		-		-		-		-	

There were three groups of tests performed for each parameter at each of the gauges: (1) differences between climate models and NCEP/NCAR for recent past (Bonferroni-adjusted alpha for significance of $0.05/36 = 0.0014$); (2) differences between climate models for future (Bonferroni-adjusted alpha for significance of $0.05/28 = 0.0018$); and (3) differences between the recent past and the future within each climate model (alpha: $0.05/8 = 0.0063$). Missouri (i.e. Boonville gauge) designated as 'B' and Nebraska (Nebraska City gauge) as 'N'. Ambient temperature is the daily averages. Water temperature is the daily value simulated using SNTemp. Global climate models (G): NC, NCEP/NCAR; CC, CCSM; CG, CGCM; GF, GFDL. Regional climate models (R): CR, CRCM; MM, MM5I; RC, RCM3; WR, WRF; HR, HRM3; P, recent past; F, future; - or +, significantly less or greater, respectively, row model than column model at the Bonferroni alpha; UN, p value between the Bonferroni alpha and 0.05; MA, p value between 0.05 and 0.1; NO, p value above 0.1 (p , probability).

Table B2. Probabilities from the pairwise climate scenario non-parametric Kruskal–Wallis tests conducted for precipitation (above diagonal) and velocity (below diagonal) at each gauge (n = 36)

		G	NC	CC	CC	CC	CC	CC	CC	CG	CG	CG	CG	CG	CG	GF	GF	GF	GF
Model		R	CR	CR	MM	MM	WR	WR	CR	CR	RC	RC	WR	WR	HR	HR	RC	RC	
Site	G	R	Period	P	P	F	P	F	P	F	P	F	P	F	P	F	P	F	
B	NC		P		UN		UN		+		NO		NO		+		NO		NO
N	NC		P		NO		NO		UN		UN		-		UN		-		-
B	CC	CR	P	-		NO	NO		+		-		+		-		-		-
N	CC	CR	P	-		NO	NO		+		-		+		-		-		-
B	CC	CR	F		NO			MA		+		-			NO		-		-
N	CC	CR	F		NO			MA		+		-			MA		-		-
B	CC	MM	P	NO	+			NO		+	UN				+		-		-
N	CC	MM	P	-	+			MA		+					+		-		-
B	CC	MM	F			+	UN			+		UN	NO			UN		-	-
N	CC	MM	F			+				+		NO				UN		-	-
B	CC	WR	P	-	+		+			NO		-			NO		-		-
N	CC	WR	P	-	-		+			NO		-			NO		-		-
B	CC	WR	F			NO		-	NO		-				NO		-		-
N	CC	WR	F			NO		-	MA		-				NO		-		-
B	CG	CR	P	-	+				UN		NO	MA			+		UN		UN
N	CG	CR	P	-	+				+		NO	MA			+		-		UN
B	CG	CR	F			+		UN		+					+		UN		-
N	CG	CR	F			+				+					UN		UN		-
B	CG	RC	P	+	+		+		+		+				NO		NO		NO
N	CG	RC	P	+	+		+		+		+				NO		NO		NO
B	CG	RC	F			+		+		+		+	UN		+		NO		NO
N	CG	RC	F			+		+		+		+			+		NO		NO
B	CG	WR	P	-	NO		-		NO		UN				+		UN		UN
N	CG	WR	P	-	NO		-		NO		-				+		UN		UN
B	CG	WR	F			UN		-		NO	NO				+		-		-
N	CG	WR	F			UN		-		NO	NO				+		-		-
B	GF	HR	P	+	+		+		+		+			NO		NO		NO	NO
N	GF	HR	P	+	+		+		+		+			NO		NO		NO	NO
B	GF	HR	F			+		+		+		+		NO		UN			NO
N	GF	HR	F			+		+		+		+		NO		MA			UN
B	GF	RC	P	+	+		+		+		+			NO		NO			UN
N	GF	RC	P	+	+		+		+		+			UN		+			UN
B	GF	RC	F			+		+		+		+			NO		MA		+
N	GF	RC	F			+		+		+		+		*		+		+	+

There were three groups of tests done for each parameter at each of the gauges: (1) differences between climate models and NCEP/NCAR for the recent past (Bonferroni-adjusted alpha for significance of 0.05/36 = 0.0014); (2) differences between climate models for the future (Bonferroni-adjusted alpha for significance of 0.05/28 = 0.0018); and (3) differences between the recent past and the future within each climate model (0.05/8 = 0.0063). Missouri (i.e. Boonville gauge) designated as 'B' and Nebraska (Nebraska City gauge) as 'N'. Ambient temperature is the daily averages. Water temperature is the daily value simulated using SNTemp. Global climate models (G): NC, NCEP/NCAR; CC, CCSM; CG, CGCM; GF, GFDL. Regional climate models (R): CR, CRCM; MM, MM5I; RC, RCM3; WR, WRFG; HR, HRM3; P, recent past; F, future; - or +, significantly less or greater, respectively, row model than column model at the Bonferroni alpha; UN, *p* value between the Bonferroni alpha and 0.05; MA, *p* value between 0.05 and 0.1; NO, *p* value above 0.1 (*p*, probability).

Correction notice: The original version was incorrect. This was due to an error in the caption for Figure 1.

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