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Abstract

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Disciplines

Aquaculture and Fisheries | Climate | Environmental Sciences | Statistical Models | Terrestrial and Aquatic Ecology

Comments

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A stochastic bioenergetics model-based approach to translating large river flow and temperature into fish population responses: the pallid sturgeon example

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Abstract: In managing fish populations, especially at-risk species, realistic mathematical models are needed to help predict population response to potential management actions in the context of environmental conditions and changing climate while effectively incorporating the stochastic nature of real world conditions. We provide a key component of such a model for the endangered pallid sturgeon (*Scaphirhynchus albus*) in the form of an individual-based bioenergetics model influenced not only by temperature but also by flow. This component is based on modification of a known individual-based bioenergetics model through incorporation of: the observed ontogenetic shift in pallid sturgeon diet from macroinvertebrates to fish; the energetic costs of swimming under flowing-water conditions; and stochasticity. We provide an assessment of how differences in environmental conditions could potentially alter pallid sturgeon growth estimates, using observed temperature and velocity from channelized portions of the Lower Missouri River mainstem. We do this using separate relationships between the proportion of maximum consumption and fork length and swimming cost standard error estimates for fish captured above and below the Kansas River in the Lower Missouri River. Critical to our matching observed growth in the field with predicted growth based on observed environmental conditions was a two-step shift in diet from macroinvertebrates to fish.

Bioenergetics models can be used in fish life-history models to help partition energy intake based on the laws of thermodynamics, where the energy consumed by a fish must balance the energy required by physiological processes and growth (Enders & Scruton 2006). A bioenergetics model provides an approach of estimating the consumed energy that is partitioned into three basic components: metabolism, waste loss and growth. This modelling framework accounts for the energy cost experienced by the fish and is used to solve for the level of consumption consistent with the observed growth, integrating the array of environmental conditions experienced by the fish (Moss 2001). Essentially, bioenergetics models are used to understand the relationship between growth and feeding rates under different environmental conditions. Over the last few decades, bioenergetics models have been used widely as a tool

in fisheries management and the agricultural industry to address issues related to management of sport fish populations (Chipps & Wahl 2008).

One well-known bioenergetics modelling approach used in fisheries is known as the Wisconsin model (Kitchell *et al.* 1977); its application has been reviewed by Hanson *et al.* (1997). The Wisconsin model refers to an approach that incorporates maximum feeding rates (C_{\max}) and P values (proportion of C_{\max}) as a way to explore consumption patterns. The P values are meant to put consumption estimates into context (i.e. a fish feeding at 40% or 95% of C_{\max}). As part of the Wisconsin approach, consumption is equated to the sum of metabolic cost, waste loss and net gain in weight, with metabolic cost being a function of temperature and body mass. Previous analyses have shown that the model output is sensitive to consumption and

respiration parameters (Bartell *et al.* 1986). In practice, estimates of bioenergetics model parameters are obtained through field studies and carefully designed laboratory experiments in which fish of various sizes are tested at different water temperatures and food-ration levels. However model parameters are often borrowed from related species or, due to difficulty in obtaining the parameter estimates for different sized fish, by extrapolating parameters to other size classes. This borrowing and/or extrapolation of parameter estimates consequently results in a source of uncertainty in the bioenergetics model. Therefore, it is of paramount importance to develop model parameter estimates in a way that accounts for such uncertainty and bias to increase the utility of the bioenergetics model.

Bioenergetics models have been developed for a wide variety of fish species and ontogenetic stages that include freshwater (e.g. mosquitofish (*Gambusia affinis*); Chipps & Wahl 2004) to salt water species (e.g. Pacific herring (*Clupea pallasii*); Megrey *et al.* 2007), larvae (walleye (*Sander vitreus*); Madon & Culver 1993), small species (e.g. minnows; Schindler *et al.* 1993) and large species (e.g. tunas; Boggs 1984). Although the bioenergetics literature is vast and dates back over 50 years, research on sturgeon *Acipenser* spp. populations began fairly recently for white sturgeon (*A. transmontanus*; Bevelhimer 2002), green sturgeon (*A. medirostris*; Mayfield & Cech 2004), Atlantic sturgeon (*A. oxyrinchus*; Niklitschek 2001; Niklitschek & Secor 2009), and gulf sturgeon (*A. oxyrinchus*; Flowers *et al.* 2010). However, a bioenergetics model for the endangered pallid sturgeon (Dryer & Sandvol 1993) has only recently been developed (Chipps *et al.* 2010).

Wildhaber *et al.* (2007, 2011) introduced a conceptual life-history model for pallid sturgeon (*Scaphirhynchus albus*). The pallid sturgeon is an endangered fish endemic to the turbid waters of the Missouri and Lower Mississippi rivers (Dryer & Sandvol 1993). The model was developed to delineate how *Scaphirhynchus* sturgeon ecology relates to river management. It provided the framework for expanding the Bajer & Wildhaber (2007) population forecasting model to include environmental variables for prediction of future population size and distribution of Missouri River pallid and shovelnose (*S. platyrhynchus*) sturgeon. Because sturgeon in large rivers may move long distances (DeLonay *et al.* 2007), a life-history model should incorporate various environmental conditions related to different parts of the river and tributary system. For greatest utility in assessing habitat effects on population processes, the life-history model should accommodate fine-scale, three-dimensional models of habitat use and availability, and fish behaviour nested within a broader geographic extent. One

way to incorporate spatial and temporal environmental and habitat conditions into such a life-history model for large river fishes is through the use of bioenergetics models.

Chipps *et al.* (2010) developed a bioenergetics model for juvenile pallid sturgeon using laboratory measurements of consumption and respiration and field-derived information for growth, diet and water temperature from the inter-reservoir sector of the Missouri River above Gavins Point Dam in South Dakota. Their model was developed on two size classes of juvenile pallid sturgeon: 200–400 mm fork length (FL) and 500–700 mm FL. The model estimates of food consumption agreed well with those from laboratory experiments over a wide range of water temperatures. Although uncertainty quantification was not incorporated in individual parameter estimates, uncertainty was accommodated in the model by developing a corrective equation that reduced mean error and hence increased reliability of the model output.

In applying bioenergetics models like that of Chipps *et al.* (2010) for pallid sturgeon, parameter estimates are assumed true, and held constant among individuals and across time and space. Without incorporating stochasticity into parameter estimates, the results of such models provide an unrealistic perception of certainty in their predictions. Furthermore, inclusion of parametric stochasticity in the bioenergetics model can be used to help account for differences in observed responses among individual fish. The deterministic bioenergetics model as developed by Chipps *et al.* (2010) produces a point estimate for the individual parameters that could potentially vary among individual fish due to physiological differences. The stochastic bioenergetics model we develop here includes not only point estimates of individual model parameters but also their associated distributions, and thus reflects current uncertainty about their true values.

This paper focuses on development of an individual-based bioenergetics model for pallid sturgeon that extends Chipps *et al.*'s (2010) pallid sturgeon bioenergetics model with swimming costs (Geist *et al.* 2005), diet shift (Grohs *et al.* 2009; Chipps *et al.* 2010), and parameter uncertainty as key components within a framework for informing management decisions. The goal is a model that comes closer to providing more realistic predictions of pallid sturgeon growth potential within the Lower Missouri River mainstem (the Missouri River mainstem below Gavins Point Dam to its confluence with the Mississippi River). To inform and validate the model we used on-going US Geological Survey (USGS) Comprehensive Sturgeon and Research Program work on migration, physiology, habitat choice and spawning success of pallid sturgeon (DeLonay *et al.* 2009) and US Army Corps

of Engineers (USACE) Pallid Sturgeon Population Assessment Program (PSPAP) (Drobish 2008) data. Temperature and discharge data obtained from the USGS (USGS 2011) for gauging stations at Nebraska City, Nebraska (USGS 06 807 000 Missouri River at Nebraska City, NE; referred to here as Nebraska) and Boonville, Missouri (USGS 06 909 000 Missouri River at Boonville, MO; referred to here as Missouri) (Fig. 1) were used for input into the pallid sturgeon bioenergetics model to produce simulated pallid sturgeon growth trajectories. Ultimately, this model provides the basis of a forecasting tool that could be used to quantify the relative importance of various environmental factors in the Lower Missouri River on individual growth and consumption of juvenile and adult pallid sturgeon.

Methods

Study area

Using a modified version of Chipps *et al.*'s (2010) bioenergetic model for pallid sturgeon, we

developed growth/consumption relationships for two locations along the mainstem of the Lower Missouri River (Fig. 1). These two locations lie along the Lower Missouri River: Above Kansas River (AKR) (Gavins Point Dam to Kansas River confluence) and Below Kansas River (BKR) (Kansas River confluence to Missouri River mouth), with the AKR segment tending to have higher velocities than the BKR segment (Galat *et al.* 2001).

Model development

The bioenergetics model developed here uses parameter estimates from Chipps *et al.* (2010) for pallid sturgeon and Geist *et al.* (2005) for white sturgeon with additional information on parameter distributions from various other sources (Table 1). This model, along with daily river velocity (calculated from discharge) and temperature data, were used to predict pallid sturgeon growth potential under different river conditions both in time (season – described later) and space (location – AKR and BKR).

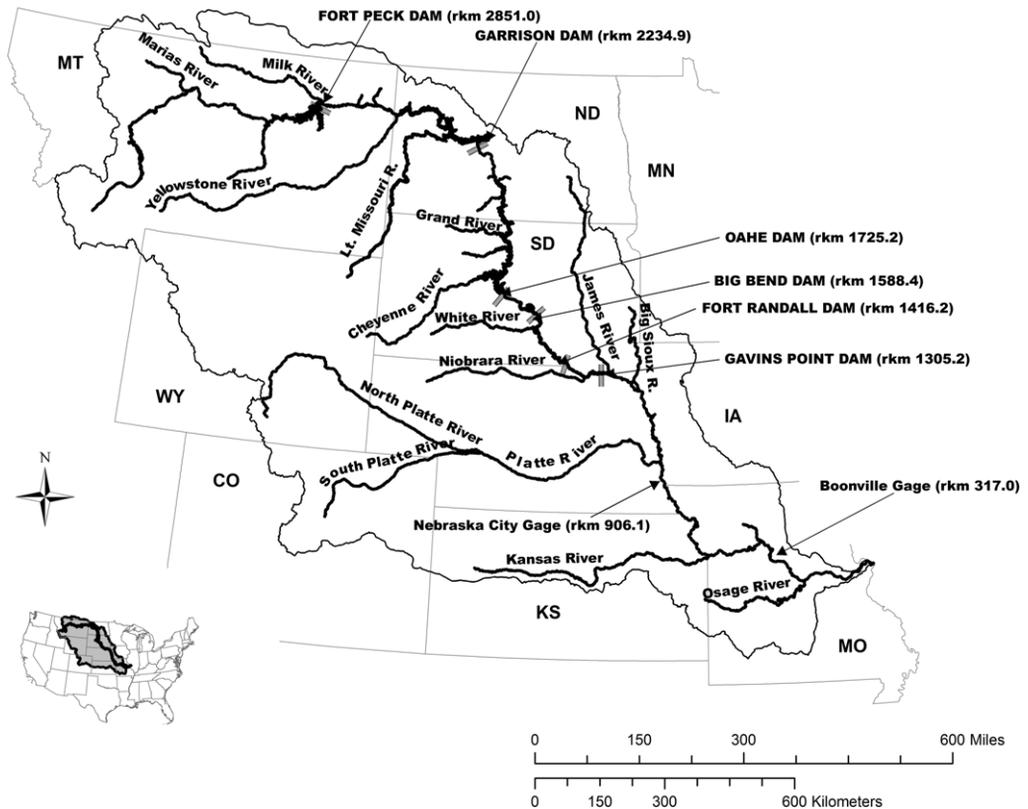


Fig. 1. Missouri River study area (rkm, river kilometre).

Table 1. Distributional assumptions of bioenergetics model parameters

Parameter	Description	Value	Distribution	Source
Consumption (g g ⁻¹ day ⁻¹)	$C = a_c W^{b_c} f(T) P$			
a_c	Intercept	0.553	exp(trunc-N(-2.6698, 0.135) + (ln(Q_C)/10)28), truncated 2 SE	Chipps <i>et al.</i> (2010).
b_c	Slope	-0.326	trunc-N(0.674, 0.0767) - 1, truncated 2 SE	Chipps <i>et al.</i> (2010)
Q_C	Q_{10} rate at low temperature	2.1	exp(10*trunc-N(0.074, 0.00286)), truncated 2 SE	Chipps <i>et al.</i> (2010), distribution Dowd <i>et al.</i> (2006b).
T_{o_c} (°C)	Optimum feeding temp.	28		Chipps <i>et al.</i> (2010)
T_{m_c} (°C)	Maximum feeding temp.	33		Chipps <i>et al.</i> (2010)
P	Proportion of maximum consumption for small fish		trunc-N(0.544, 0.028) AKR trunc-N(0.528, 0.024) BKR truncated 2 SE	Model fitting Pallid Sturgeon Population Assessment (PSPAP) data (Drobish 2008)
P	Proportion of maximum consumption for large fish		$= 1 - \exp[-(FL/\theta)]I[FL \geq x]$	
θ			trunc-N(764.98, 6.22), truncated 2 SE, Boonville trunc-N(697.43, 5.56), truncated 2 SE, Nebraska	Model fitting PSPAP data
Respiration (J g ⁻¹ day ⁻¹)	$R = 13562a_r W^{b_r} g(T) \exp(a_s$ $p_u(0.58V + S_u)$ $+ (1 - p_u)S_d$			
a_r	Intercept	0.017	exp(trunc-N(-6.041, 0.147) + (ln(Q_R)/10)30), truncated 2 SE	Chipps <i>et al.</i> (2010), distribution Dowd <i>et al.</i> (2006a)
b_r	Slope	-0.15	trunc-N(0.85255, 0.01198) - 1, truncated 2 SE	Chipps <i>et al.</i> (2010), distribution Dowd <i>et al.</i> (2006a)
Q_R	Q_{10} rate at low temp.	1.92	exp(10*trunc-N(0.06554, 0.00912)), truncated 2 SE	Chipps <i>et al.</i> (2010), distribution Dowd <i>et al.</i> (2006a)
T_{o_R} (°C)	Optimum temp. for respiration	30		Chipps <i>et al.</i> (2010).
T_{m_R} (°C)	Lethal water temp.	35		Chipps <i>et al.</i> (2010).
a_s	Coefficient of swimming speed	0.00914	trunc-N(0.00914, 0.008), truncated left, 0	Geist <i>et al.</i> (2005).

p_u	Proportion of time swimming upstream		trunc N(0.0097,0.031), with prob p_1 trunc N(0.471,0.178), with prop p_2 , Mar–Jun	Model fitting non-spawning pallid sturgeon tracking data (Delonay <i>et al.</i> 2009). Based on a combination of Dirichlet(1,2) for Mar–Jun and Dirichlet(3,5,2) for Nov–Feb and multinomial(1,1,p) with p based on appropriate Dirichlet distribution.
S_u (cm s ⁻¹)	Upstream swimming speed		trunc-N(0.4469, 0.255), Jul–Oct trunc N(0.0167,0.047), with prob p_1 trunc N(0.4275,0.149), with prop p_2 trunc N(0.97,0.064), with prob p_3 , Nov–Feb truncated at 0 and 1 exp(0.556), Mar–Jun exp(0.923), Jul–Oct exp(1.616), Nov–Feb	Model fitting Delonay <i>et al.</i> (2009) tracking data.
S_d (cm s ⁻¹)	Downstream swimming speed		exp(0.527), Mar–Jun exp(0.685), Jul–Oct exp(2.300), Nov–Feb	Model fitting Delonay <i>et al.</i> (2009) tracking data.
Fa	Proportion of energy egested	0.1	triangular(0.1, 0.05, 0.2)	Chipps <i>et al.</i> (2010), distribution Wetherbee & Gruber (1993)
Ua	Proportion of energy excreted	0.04	triangular(0.04, 0.02, 0.08)	Chipps <i>et al.</i> (2010), distribution Brett & Groves (1979), Duffy (1999)
D	Proportion of C adjusted for egestion (F), used to calculate specific dynamic action (SDA)	0.13	triangular(0.13, 0.065, 0.26)	Chipps <i>et al.</i> (2010), distribution DuPreez <i>et al.</i> (1988), Sims & Davies (1994), Duffy (1999), Ferry-Graham & Gibb (2001)
W (g)	Fish weight		trunc-N(603.647, 270.93), truncated left, 0	Model fitting PSPAP data
FL (mm)	Fish fork length = $a_w W^{b_w}$			
a_w	Intercept		trunc-N(82.339, 2.46), truncated 2 SE	Model fitting PSPAP data
b_w	Slope		trunc-N(0.301924, 0.005), truncated 2 SE	Model fitting PSPAP data
m_{11} (J g ⁻¹)	Prey (fish) energy density	4473.533		Hansen <i>et al.</i> (1993), Venturelli & William (2006), Grohs <i>et al.</i> (2009).
m_{12} (J g ⁻¹)	Prey (mayfly) energy density	3065.83		Sitaramaiah (1967).
m_2 (J g ⁻¹)	Predator energy density	2698	trunc-N(2698, 254), truncated 2 SE	Chipps <i>et al.</i> (2010).

Basic bioenergetics model

The bioenergetics model (starting with Chipps *et al.* 2010) was developed using a general mass balance equation:

$$C = (R + \text{SDA}) + (F + U) + G,$$

where C is food consumption, R is standard metabolism, SDA is specific dynamic action, F is egestion, U is excretion and G is gonadal or somatic growth.

The rate of feeding (C) is defined as a function of the maximum consumption rate (C_{\max}) achievable at the optimal temperature for consumption for an individual fish of a given size, as follows,

$$C = C_{\max} Pr_c, \quad (1)$$

where C is obtained by simply balancing the model as in the previous equation, and through an iterative process, a P value is fitted until $C_{\max} Pr_c$ is equal to C with r_c being a temperature dependent proportional adjustment of consumption rate that lies between 0 and 1 with

$$\begin{aligned} r_c &= (V_C^{X_C})(e^{X_C(1-V_C)}), \\ V_C &= \frac{T_{mc} - T}{T_{mc} - T_{oc}}, \\ X_C &= \frac{Z_C^2(1 + (1 + 40/Y_C)^{1/2})^2}{400}, \\ Z_C &= \ln(Q_C)(T_{mc} - T_{oc}), \\ Y_C &= \ln(Q_C)(T_{mc} - T_{oc} + 2). \end{aligned}$$

where T is ambient water temperature in degree Celsius, T_{oc} optimum feeding temperature = 28 °C, T_{mc} maximum feeding temperature = 33 °C, Q_C approximates a Q_{10} rate over the low range of temperatures = 2.1. The proportionality constant (P) is used to adjust the actual consumption as a proportion of maximum consumption in fitting the growth curve, having values in [0,1]. $C_{\max} = 0.553W^{-0.326}$ is the maximum specific feeding rate as estimated from feeding experiments conducted at the optimum temperature for the particular fish species, where W is fish weight (g) and 0.553 and -0.326 are the intercept and slope values for a 1-g fish, respectively.

The SDA value is estimated based on the metabolic cost of digestion, deposition and absorption of consumed energy and is assumed to be a proportion of the food consumption rate as follows (Kitchell *et al.* 1977):

$$\text{SDA} = D(C - F), \quad (2)$$

where D is a proportion. Waste losses, based on F and U , are modelled as constant proportions of

consumed energy and are given by Chipps *et al.* (2010) as

$$F = FaC, \quad (3)$$

$$U = Ua(C - F), \quad (4)$$

where Fa is the proportion of energy egested and Ua is the proportion of energy excreted.

Proportional consumption and length

The proportion of maximum consumption (P) is one of the key parameters in determining the growth of fish. In practice, the true P associated with a pallid sturgeon is unknown. Based on the fixed parameter model, we estimated P using observed beginning and ending weights over corresponding time periods for pallid sturgeon recorded in PSPAP data. Observed water temperature and velocity (computed from observed discharge) at the USGS gauging station central to the river location in which the fish were collected were used as input to the bioenergetics model. Preliminary analyses determined that a constant P across all size classes of pallid sturgeon could not account for observed growth in the field. We found that a function that related P to FL was necessary for the model to successfully mimic observed growths for fish larger than 500 mm FL. However, for smaller fish (FL less than 500 mm), there was no significant relationship between P and FL.

In order to correctly parameterize the P to FL relationship, we trained the bioenergetics model for the gauges at Boonville, MO and Nebraska City, NE separately as representative of BKR and AKR, respectively. By ‘training’ the model, we refer to developing a separate P to FL relationship for each of the two segments of the Missouri River based on their specific water velocities and temperatures. To accomplish this, we used mark-recapture data from the PSPAP; (Drobish 2008) and Pallid Sturgeon Stocking Program of the US Fish and Wildlife Service (USFWS 2008). Only beginning and ending weights for pallid sturgeon captured and recaptured in the same river location (i.e. AKR, BKR) were used to estimate growth and to develop a separate relationship between FL and P for each of these river segment. To develop these relationships, we ran the model keeping all physiological parameters of the bioenergetics model constant. To estimate P , we used observed water temperature and flow velocity from the corresponding river segment where the fish had been captured and recaptured for the period of time in which the fish growth occurred. Finally, given the initial and final weight of the fish, we solved for the proportion of maximum food necessary under the model to

attain the observed final weight at recapture. Based on our preliminary assessment mentioned above, once the P values were estimated, we fitted the non-linear regression model (Table 1) to a set of P values for fish having FL larger than 500 mm (referred to as large fish) and a truncated normal distribution to the set of P values estimated for fish 500 mm or smaller (referred to as small fish).

Diet

Diet composition plays an important role in determining growth of pallid sturgeon (Grohs *et al.* 2009). Grohs *et al.* (2009) found that mayflies (Ephemeroptera), particularly the family Isonychiidae, are an important component of the juvenile pallid sturgeon diet. In addition, the diet of pallid sturgeon changes from macroinvertebrates to fish as their body length increases, with fish between 350 and 500 mm FL consuming 57% fish by wet weight and those more than 500 mm FL consuming 90% fish by wet weight (Gerrity *et al.* 2006; Grohs *et al.* 2009). We used these size ranges and their associated percentages of fish and macroinvertebrates to determine the relationship between FL and P . Based on previous work (Sitaramaiah 1967; Hansen *et al.* 1993; Venturelli & William 2006; Grohs *et al.* 2009), the caloric densities used for prey fish and macroinvertebrates were 4473.5 J g^{-1} wet mass and 3065.8 J g^{-1} wet mass, respectively, with caloric density assumed to be constant over time. We used a mean caloric density of 2698 J g^{-1} wet mass for pallid sturgeon (Table 1).

Respiration and swimming speed

Respiration rate (R) as given in Chipps *et al.* (2010) is measured by oxygen consumption, which is dependent on water temperature, fish mass and activity cost:

$$R = R_{\max} r_R A, \quad (5)$$

where $R_{\max} = a_r W^{b_r}$, R_{\max} is the maximum weight-specific standard respiration rate at the optimum temperature, a_r and b_r are the intercept and slope for a 1-g fish, respectively, in the relationship between R_{\max} and W , and A is an activity parameter to specify respiration rates. Furthermore, r_R is a temperature dependent proportional adjustment of respiration rate that lies between 0 and 1 with

$$r_R = (V_R^{X_R}) e^{X_R(1-V_R)}$$

$$V_R = \frac{T_{m_R} - T}{T_{m_R} - T_{o_R}},$$

$$X_R = \frac{Z_R^2(1 + (1 + 40/Y_R)^{1/2})^2}{400},$$

$$Z_R = \ln(Q_R)(T_{m_R} - T_{o_R}),$$

$$Y_R = \ln(Q_R)(T_{m_R} - T_{o_R} + 2),$$

where T is ambient temperature in degree Celsius ($^{\circ}\text{C}$), T_{o_R} optimum temperature for respiration = 30°C , T_{m_R} maximum (lethal) water temperature = 35°C , and Q_R approximates a Q_{10} rate over the low range of temperatures = 1.92.

The costs associated with swimming under varying water velocity conditions were incorporated into the model by replacing the constant value most often used for activity costs with a function relating costs to swimming speed. The swimming speed function was taken from work done on white sturgeon (Geist *et al.* 2005). To increase the accuracy of swimming cost estimates, seasonality in swimming was introduced into the model based on observed swimming patterns, and associated variability, from tracking data on pallid sturgeon in the Lower Missouri River (DeLonay *et al.* 2009). Using tracking data for non-reproductive pallid sturgeon, we estimated the average upstream and downstream swimming speeds and the proportion of time the fish moved in either direction during spawning season or spring (March through June), summer/fall (July through October), and winter (November through February) (Fig. 2). Fish expend more energy moving upstream than downstream as a result of swimming against the flow. We incorporated this additional cost by assuming that a fish's swimming speed would be equivalent to the observed upstream swimming speed plus the water velocity through which the fish was swimming. This upstream estimate of swimming speed was further modified based on work by McElroy *et al.* (2012) on pallid sturgeon upstream migration paths. In an initial attempt to estimate energetic costs of swimming from observed telemetered fish, McElroy *et al.* (2012) observed that the chosen paths of upstream travel of pallid sturgeon were energetically less costly than the average possible path. The actual path chosen had an estimated energetic equivalent of an average velocity of 1.18 m s^{-1} compared to the average available estimated energetic equivalent of a random set of paths (i.e. velocity of 2.03 m s^{-1}) (B. McElroy, pers. comm., 2013). It is important to realize that this value is provisional and may change as more fish are evaluated. Based on McElroy *et al.* (2012), we used 58% (i.e. $(1.18/2.03) \times 100$) of the estimated average velocity found in a cross section of the Lower Missouri River as the estimate of the velocity experienced by

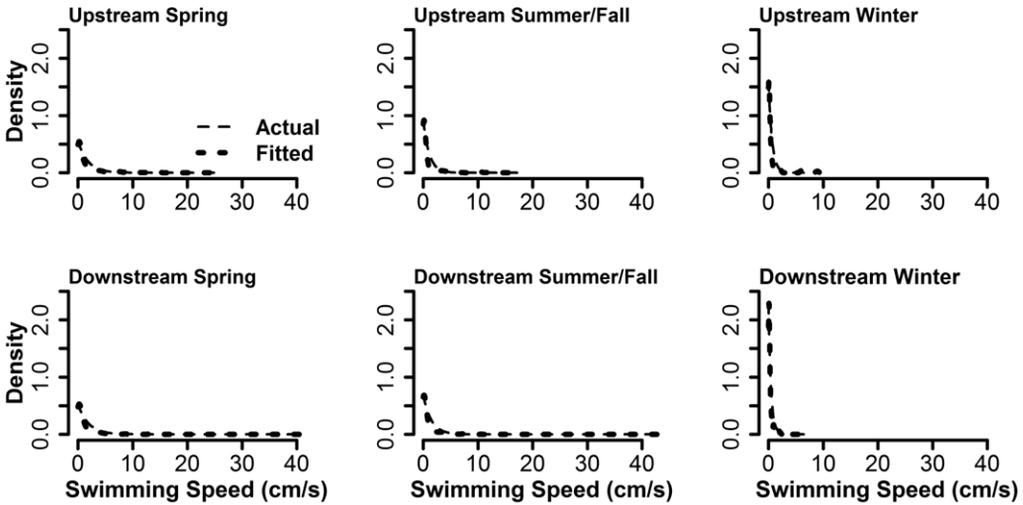


Fig. 2. Actual (dashed) and fitted (dotted) exponential distribution of upstream (upper row) and downstream (lower row) swimming speed of fish based on tracking data and separated on the basis of three seasons (from left to right columns: spring, summer/fall, and winter).

the fish. The logic of using a proportion is that when the average velocity changes in a channel section the relative distribution of high and low velocities does not (i.e. fastest in channel and slowest along the edges). Using a proportion also provides the ability to apply the model to both migrating and non-migrating pallid sturgeon through the use of actual, observed differences in swimming speeds (see below). Therefore, upstream swimming speed based on velocity was adjusted using a factor of 0.58 (see equation for S below).

The resulting model for daily oxygen consumption (M in $\text{g O}_2/\text{day}$) based on the above described modifications becomes:

$$\log(M_1) = -6.041 + 0.852 \log W + 0.065 T + 0.00914 S,$$

where

$$S = p_u(0.58V + S_u) + (1 - p_u)S_d.$$

Here, S is relative swimming speed (cm sec^{-1}), V is the flow velocity (cm s^{-1}), p_u is proportion of time the fish swims upstream, S_u is upstream swimming speed relative to a stationary point (cm s^{-1}) and S_d downstream swimming speed relative to a stationary point (cm s^{-1}).

We rewrite the above equations as follows:

$$M_1 = e^{-6.041+0.065(T)+0.00914(S)} W^{0.852}.$$

At $T = 30^\circ\text{C}$ (optimum temperature for respiration) maximum specific respiration rate in turn, is

estimated as

$$R_{\max} = \frac{M_1}{W} = 0.017 W^{-0.15} e^{0.00914(S)}.$$

Intermittent data collected in the field and reported for each gauging station by the USGS (USGS 2011) were used to calculate velocity based on methods discussed by Leopold & Maddock (1953). Discharge and velocity are related by the equation,

$$V = aD^b,$$

where V is the velocity (cm s^{-1}) and D is the discharge ($\text{m}^3 \text{s}^{-1}$).

In this case, a and b are the empirical coefficients of the non-linear equation. The estimated a and b for AKR (Nebraska) were 0.173 and 0.302, and for BKR (Missouri), 0.117 and 0.303, respectively. Knowing that these relationships change with changes in channel form, we used the longest sequence of field measured data available, between 1950 and 2009, to get long-term-average estimates for these relationships. Once estimated, these parameter values were used to convert daily discharge data as reported at each station to daily velocity data. It must be noted that using mean cross-sectional velocities at gauging stations is a simplification since gauging stations are preferentially located to measure in straight, uniform reaches and tend to have higher velocities compared to adjacent reaches. The computed velocity data were rounded to 0.5 dm s^{-1} (5 cm s^{-1}) to account for the

precision of the reported discharge data owing to the number of significant digits (USGS 2002, 2012).

Model parameter distribution

Distributions of the physiological parameters are based on literature, statistical analysis and pilot studies (Table 1). Most of the parameters, as found in previous literature (Bevelhimer *et al.* 1985), were given a truncated normal distribution. Parameters involved in waste losses and SDA were assumed to follow a triangular distribution (Dowd *et al.* 2006a). A truncated normal distribution was found from model fitting to be the best fit for computed P of small fish. For large fish, the distribution of the parameters of the non-linear regression model fitted between the P value and the FL was determined based on the Normality test (Shapiro-Wilk's test). The distributions for upstream and downstream swimming speeds were determined by model fitting of tracking data for non-spawning fish. All truncated normal distributions were truncated at \pm two standard errors (SE) to maintain the nature of the relationships (i.e. preserve the sign associated with each parameter) and control for unrealistically extreme relationships.

The distribution of swimming speed was obtained from the tracking data of pallid sturgeon captured between 7 April 2006 and 5 May 2011 in the Lower Missouri River between 0 and 1303.5 rkm (0 and 810 river miles). Swimming speed was computed based on 109 unique non-reproductive pallid sturgeon individuals with average swimming for an individual based on 1 to 101 relocation points, discarding three non-spawning fish from the analysis since they had been recaptured and taken to the hatchery for potential broodstock. As previously mentioned, swimming speed was divided into spring, summer/fall and winter and, based on direction of travel, upstream and downstream. We found that an exponential distribution fitted seasonal upstream and downstream swimming speeds (Fig. 2). We fitted a mixture of truncated normal distributions to the different seasonal proportions of upstream swimming times.

As mentioned in 'Proportional consumption and length', we estimated the proportion of maximum consumption or P based on the PSPAP data (Drobish 2008) available for AKR and BKR. A total of 353 fish of unknown sex or reproductive stage were captured between November 2002 and October 2010 in various parts of the Lower Missouri River. We discarded those fish that were recaptured in less than 4 months to assure the fish had grown for one full season. A total of 265 fish (i.e. 181 for Nebraska, 84 for Missouri) were used to inform the model for initial and final weight and FL. For fish captured at a river kilometre less than

593.8 km (369 miles) or BKR, the Missouri (i.e. Boonville) gauge was used as the representative gauge with P computed using temperature and flow velocity from November 2002 to May 2010 when, essentially, a complete record was available. Consistent with the selection process applied for BKR, for fish captured at river kilometres above 593.8–1303.6 (369–810 miles) or AKR, the Nebraska (i.e. Nebraska City) gauge was used as the representative gauge with temperature and flow velocity data from March 2005 to May 2010. The recorded temperature for Nebraska had numerous missing data points, some of which were supplemented by the temperature recorded at Omaha (DeLonay *et al.* 2009). Missing values in the observed temperature data for AKR from 22 April to 18 November 2008 and 10 March to 7 December 2010 were linearly interpolated. For each fish, the analysis period for the temperature and flow velocity data overlapped with the time period between consecutive capture and recapture events to assure that the calculation of P was based on environmental conditions present during the time fish growth was measured. A regression model was fitted to the relationship between P and FL for big fish as a result of the clear indication of two separate relationships corresponding to the diet shift from macroinvertebrates to fish *c.* 500 mm FL (described in 'Results'). To incorporate stochasticity into the diet shift, we assumed that the pallid sturgeon diet starts to contain 57% fish between 250 and 350 mm FL, whereas fish comprise up to 90% of fish diet at 500–600 mm FL (Gerrity *et al.* 2006; Grohs *et al.* 2009). These shifts were incorporated into the model by assuming a uniform distribution for the two diet shifts over the ranges 250–350 mm and 500–600 mm, respectively.

For the swimming speed energetic cost coefficient (S), an SE was not available from the literature. Hence, to set SE for S , we used a separate, iterative procedure for AKR and BKR. In this procedure, all parameters of the model and associated SEs, except S , were set. To determine the SE for S , we set the SE and then simulated 1000 fish (see 'Model evaluation' below) for each of the observed PSPAP fish initial weights. We compared the median of the 1000 fish with the observed final weight. We increased or decreased SE and reran the simulations until an equal number of final-weight medians of the simulated fish ended up above and below the observed final fish weights.

Model evaluation

To assess the effectiveness of the model at forecasting pallid sturgeon growth, we applied it to a new set of 18 non-reproductive pallid sturgeon

captured and subsequently recaptured in BKR between January 2008 and October 2011 for the BKR growth/consumption relationship, and 14 non-reproductive fish initially captured and later recaptured in AKR between May 2006 and April 2011 for the AKR growth/consumption relationship. Extensive movement and infrequent relocations of these fish precluded identification of actual movement pathways and locations within the river between consecutive recaptures.

To demonstrate the importance of location on the growth/consumption relationship, we applied both the AKR and BKR modelled relationships to water temperature and flow velocity from Nebraska from 1 January 1972 to 31 December 1977. This location and the time period were chosen for the length and completeness of the record of water temperature that occurred after Missouri River mainstem reservoirs were filled and regulation began. These water temperature and flow velocity data were used as input in the model. For this location comparison, we used the relationship of P and FL obtained using inputs from Nebraska.

For each simulation, all parameters and variables of the bioenergetics model were sampled from their respective distributions daily. The model was run on a daily timeframe with no birth and mortality in the population. We started with a 1000-fish cohort of pallid sturgeon sampled from a truncated normal distribution with mean weight 571.21 g (SD = 317.36 g, truncated from left at 0) based on PSPAP data (1 February 2010 to 22 October 2010).

Results

On average we found that non-reproductive, tracked pallid sturgeon in the Lower Missouri River swam upstream 36% of the time during spring, 45% during summer/fall, and 39% during winter. Also, these pallid sturgeon travelled an average of 1.85 cm sec⁻¹ (SD = 3.9 cm sec⁻¹) in spring, 1.27 cm sec⁻¹ (SD = 3.27 cm sec⁻¹) in summer/fall, and 0.52 cm sec⁻¹ (SD = 1.27 cm sec⁻¹) in winter (combining upstream and downstream movements) (Fig. 2). Average upstream movement of these pallid sturgeon in spring was 1.80 cm sec⁻¹ (SD = 3.20 cm sec⁻¹), in summer/fall 1.08 cm sec⁻¹ (SD = 2.18 cm sec⁻¹) and in winter 0.62 cm sec⁻¹ (SD = 1.54 cm sec⁻¹), whereas that of downstream movement was 1.90 cm sec⁻¹ (SD = 4.47 cm sec⁻¹), 1.46 cm sec⁻¹ (SD = 4.09 cm sec⁻¹), and 0.43 cm sec⁻¹ (SD = 1.00 cm sec⁻¹), respectively. Overall upstream and downstream average swimming speeds were 1.34 cm sec⁻¹ (SD = 2.64 cm sec⁻¹) and 1.52 cm sec⁻¹ (SD = 4.04 cm sec⁻¹), respectively.

As previously described, we separated PSPAP collected pallid sturgeon from the Lower Missouri River based on whether they were captured BKR or AKR. There were 126 big (≥ 500 mm FL) and 55 small (< 500 mm FL) fish for AKR and 72 big and 12 small fish for BKR available for training the model. For AKR, we had to discard 6 fish since their capture dates fell outside the range of dates when temperature data were available in Nebraska. It was evident from the plot of P to FL (Fig. 3) that for big fish P increases as FL increases in a non-linear fashion.

The P for small fish captured BKR, having average FL 430.8 mm (SD = 59.2 mm) and computed based on the water temperatures and velocities in Missouri, ranged from 0.48 to 0.57 (Fig. 4), whereas big fish, having average FL 638.4 mm (SD = 88.3 mm), ranged from 0.49 to 0.70. For small fish captured AKR, with FL 426.8 mm (SD = 38.2 mm), P ranged from 0.49 to 0.94 (Fig. 4), whereas, for big fish with FL 671.7 mm (SD = 140.7 mm), P ranged from 0.48 to 0.80.

The slope of the non-linear regression fit for large fish for both AKR and BKR are similar (Fig. 3; Table 1). The difference in the two relationships lies in the intercept of the corresponding regression fit, suggesting that P increases with FL in a similar fashion irrespective of location. The reason behind the higher value of intercept of the regression fit for AKR can be attributed to the higher swimming speeds as estimated by recorded velocities (Fig. 7) from that location that translated into higher energy costs.

Validation of the model using independent fish showed that the model for BKR performed well; all of the observed weights of the 18 fish fall in the 95% quantile interval (Fig. 5). The model for AKR was less effective than the BKR model; however, it still correctly predicted 8 of the 14 final weights while underestimating or overestimating the final weights of the other 6.

Simulation results for Nebraska indicate that the 1000 fish started with an initial average weight of 597.15 g (SD = 285.70 g) and ended up with mean weight of 2164.78 g (SD = 2183.95 g) at the end of the 5-year simulation period, which is evidenced by the shift in fish weights to the right (Fig. 6). The final distribution of fish weight was wider (i.e. it had higher variance) than was the distribution for initial weights. Simulation results using the growth/consumption relationship for Missouri based on Nebraska temperatures and velocities predicted much less fish growth than that predicted using the Missouri temperatures and velocities. When conditioned on the Missouri growth/consumption relationship, a mean weight of 336.18 g (SD = 240.65 g) resulted (Fig. 6).

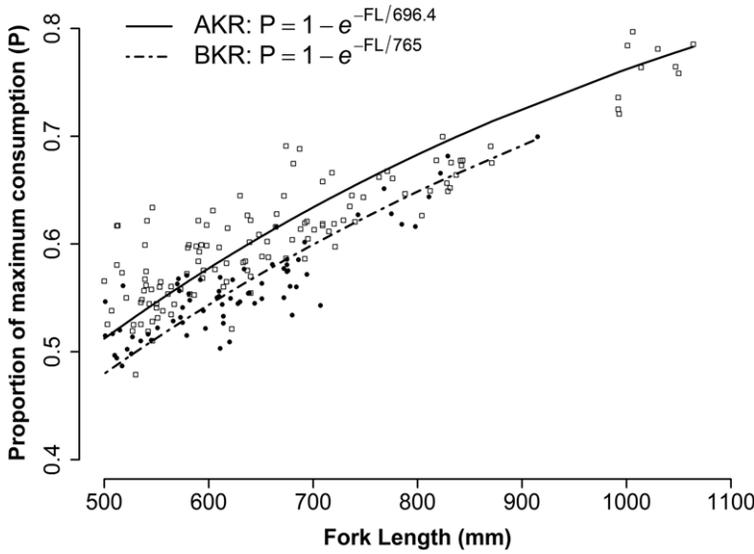


Fig. 3. Proportion of maximum consumption (P) v. fork length (FL) computed based on fish captured AKR trained on Nebraska City, Nebraska and BKR trained on Boonville, Missouri. Non-linear regression models were fitted on big fish having FL greater than 500 mm. The rectangles correspond to the fish captured AKR and circles to BKR. There was not a significant relationship between P and FL for fish less than 500 mm FL.

Discussion

Here we developed an individual-based, stochastic bioenergetics model for pallid sturgeon. The results indicate that pallid sturgeon growth estimates are dependent on the environmental conditions of the location where the model is trained. Assuming the observed velocities are representative of average velocities experienced by fish in the river, observed velocity of the narrower channelized river AKR tends to be higher resulting in higher estimated metabolic costs associated with swimming, and thus slower estimated growth rates. The varying

flow velocity of the river and its effect on growth played an important role in determining consumption-length relationships for fish in different parts of the Lower Missouri River.

Fish growth rate is affected by genetic, environmental and nutritional factors (Very & Sheridan 2002). Studies by Harvey *et al.* (2006) on salmonids suggest that changes in streamflow with only small changes in other aspects of physical habitat can result in substantial changes in individual growth. These authors demonstrated that fish allocate energy to growth only after meeting maintenance costs; they also showed that relatively modest differences

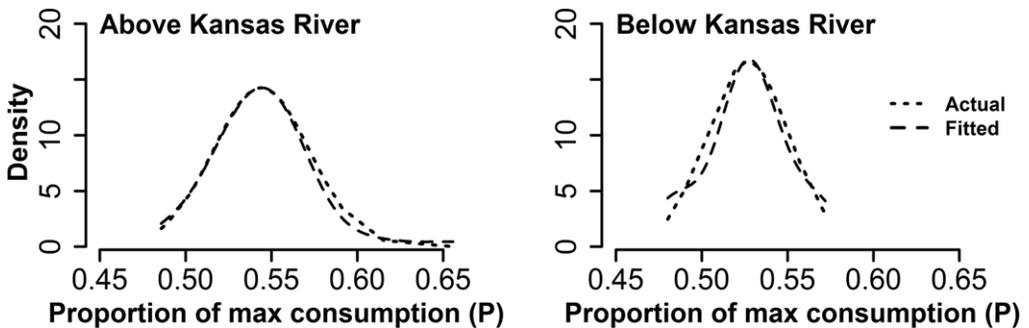


Fig. 4. Actual (dashed) and fitted (dotted) density plot of proportion of maximum consumption (P) for fish with FL less than 500 mm computed on fish captured in two different segments of the Lower Missouri River and trained using associated USGS gauge data. Left panel, AKR trained using Nebraska City, Nebraska data; right panel, BKR trained using Boonville, Missouri data.

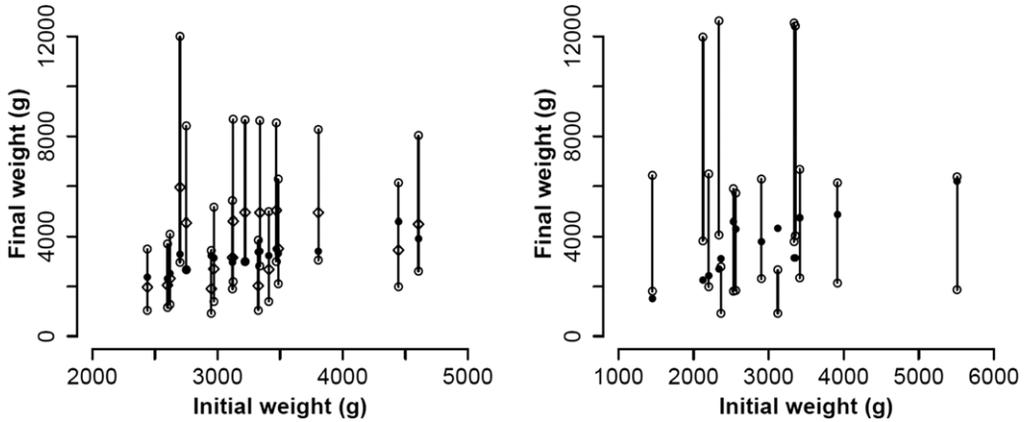


Fig. 5. Predicted 95% quantile interval and observed final fish weight. The left figure exhibits 18 fish captured BKR between January 2008 and October 2011. The right figure displays 14 fish captured AKR between May 2006 and April 2011. The *x* and *y*-axes indicate the observed initial and final weights respectively. The open diamonds indicate the median, circles indicate the 97.5 percent quantile, and the 2.5 percent quantile. The filled circles indicate the observed final weight of the corresponding fish. The 95% quantile intervals in both the plots are based on the data simulated from the bioenergetics model trained for BKR and AKR, respectively.

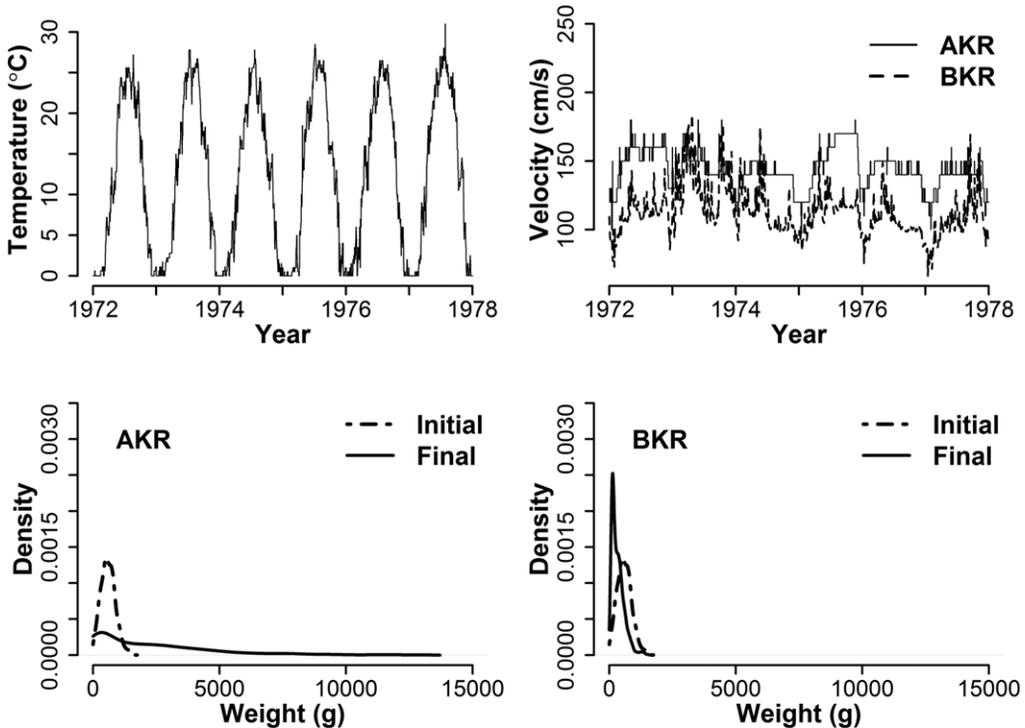


Fig. 6. Water temperature at Nebraska City, Nebraska (upper left, AKR); water velocity at Nebraska City, Nebraska and Boonville, Missouri (upper right, BKR); and simulated weight density plots for model trained AKR (lower left) and BKR (lower right) using the temperature and flow velocity of AKR from 1 January 1972 to 31 December 1977.

in total energy expenditure could potentially result in large differences in individual growth. As with salmonids, our observations from modelling pallid sturgeon growth suggest that water velocity may play an important role in their growth, and hence on population dynamics.

We found that shifting the diet of pallid sturgeon in the model was key to correctly estimating growth. Smaller fish diets are made up almost exclusively of macroinvertebrates that have lower energy densities compared to fish prey. Without shifting the diet to fish (higher energy density) as pallid sturgeon become larger, pallid sturgeon growth rate estimates were lower than the rates necessary to obtain the sizes observed in the field. Consistent with observed life-history attributes, as pallid sturgeon developed from juvenile to adult life stages, our modelling efforts indicated that a shift from aquatic invertebrates to piscine prey was necessary to attain growth rates observed in the field. It is important to note, however, that all things being equal, if a fish switches to a higher energy density food source, then its consumption rate (i.e. P value) should decrease because it would require less consumption per unit body weight to grow by the same amount. Hence, our model predictions, displaying increased P values in larger pallid sturgeon for growth estimates to approximate observed growths, were surprising. We hypothesize that once pallid sturgeon switch to fish, they become more efficient foragers. We did not have any measure of available prey. Though a shift in prey was necessary in our model, the hypothesis that a shift in prey is necessary for pallid sturgeon in the field requires further testing.

A primary controlling factor of fish growth is diet during different life stages; this is true for pallid sturgeon (Wildhaber *et al.* 2007, 2011). Grohs *et al.* (2009) found that the Isonychiidae family was an important component of juvenile pallid sturgeon diet. Duffy *et al.* (2010) found that the growth and survival of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) during the marine stage of their life depended on the quality and quantity of prey consumed. These authors found that variation in diet composition and quality of prey could translate into strong annual growth patterns for this marine stage of life. Daly *et al.* (2009) suggested that a successful shift to a more piscivorous diet could be an important factor in the growth and survival of juvenile coho salmon (*O. kisutch*) and Chinook salmon. Piscivorous fishes that consume other fishes early in development generally experience a dramatic increase in growth after the ontogenetic diet shift to piscine prey (Juanes *et al.* 1994).

To improve the accuracy of metabolic cost estimates, seasonality in swimming speed was included in the model along with its associated variability.

The inclusion of seasonality in the observed swimming pattern was important as high swimming speed translates into higher metabolic cost and consequently slower rate of growth. As evidenced from Figure 2, the observed swimming speed of pallid sturgeon when swimming upstream is highest in summer/fall and lowest in winter suggesting the need to account for seasonal variability in the model. We found that accurately reflecting the actual swimming costs to fish required inclusion of seasonal variation in swimming behaviour. Most previous work on swimming behaviour and associated energetics costs were conducted using laboratory acclimated fish without any consideration of season. Adams & Parsons (1998) found that swimming performance of field acclimated smallmouth buffalo (*Ictiobus bubalus*) varied significantly among seasons suggesting the need to account for seasonal variation. Examination of environmental change effects on seasonally acclimated white crappie (*Poximus annularis*) critical swimming speed revealed that both size and swimming speed were instrumental in determining swimming ability (Parsons & Smiley 2003). Similar to our observations, Parsons & Smiley (2003) found that performance of a fish was lowest during winter and highest in summer/fall. Similarly, we found that the mean swimming speed of pallid sturgeon was highest in summer and decreased with temperature. This seasonal effect on fish swimming speed was also seen by Facey & Grossman (1990).

Any bioenergetics model must be evaluated to ensure the accuracy of model predictions and to identify potential sources of error (Ney 1993). Here we evaluated our model by comparing our predicted growth of pallid sturgeon to the observed growth of an independent set of pallid sturgeon collected from the Lower Missouri River. The effectiveness of the model to predict pallid sturgeon growth was demonstrated by final observed fish weights occurring within the predicted distribution of final weights for fish captured BKR and 8 of the 14 fish captured AKR with a combination of underestimation and overestimation for the other 6. For whitefish (*Coregonus clupeaformis*), Madenjian *et al.* (2006) found that their model on average initially underestimated growth by 16%. Their model provided much more accurate predictions of growth after adjusting the estimated cost of respiration. These results are similar to ours in that respiration seemed to drive overestimation and underestimation through a limited certainty of the estimate of work in the form of swimming.

In general, estimated P for fish captured in Nebraska tended to be higher than those captured in Missouri as evidenced by the shift in the intercept of the regression lines (Fig. 3). This outcome reflects flow velocity being greater in Nebraska than in

Missouri (Fig. 7), forcing modelled fish to consume more food as a consequence of higher metabolic cost associated with swimming. Swimming speed and P played important roles in estimating fish growth. Small P and high flow velocity, as an estimate of swimming speed, can result in an estimated weight loss, thus the need to separate fish in the Lower Missouri River based on their river kilometres. The model, trained using temperature and velocity data obtained from Missouri but run with temperature and velocity inputs from Nebraska (Fig. 6), indicates the potential impact of using an inaccurate consumption rate to estimate fish growth. The change in the population growth response is linked to P and estimated swimming speed based on flow velocities in Missouri that are less than those in Nebraska; hence, the importance of training the model using the environmental conditions to which the fish was exposed.

There are several possible reasons for the tendency of the AKR model to underestimate or overestimate the growth. First, several model parameters were borrowed from different species. For example, the activity parameters were borrowed

from the white sturgeon (Geist *et al.* 2005). The high metabolic cost of swimming, as estimated based on water velocity, was very influential on the estimates of fish growth. It may be that swimming costs for white sturgeon are different from those of pallid sturgeon. This would result in overestimation or underestimation of growth, depending on whether the cost was higher or lower, respectively, of actual metabolic cost allocated by our model to swimming for pallid sturgeon when exposed to the same water velocities. Though not possible from current data, more intensive tracking with location-specific velocities and temperatures could be used to compare swimming speeds at different velocities. Additionally, Geist *et al.* (2005) found no relationship between slopes for swimming speed and fish weight, but they used a very narrow range of fish in their lab studies (600–800 mm). It may be possible that if the size range of the fish studied included a larger sized fish (as our study did), such a relationship might have occurred and yielded different regression outcomes.

Second, the model assumed the upstream pathway taken by a pallid sturgeon required that the

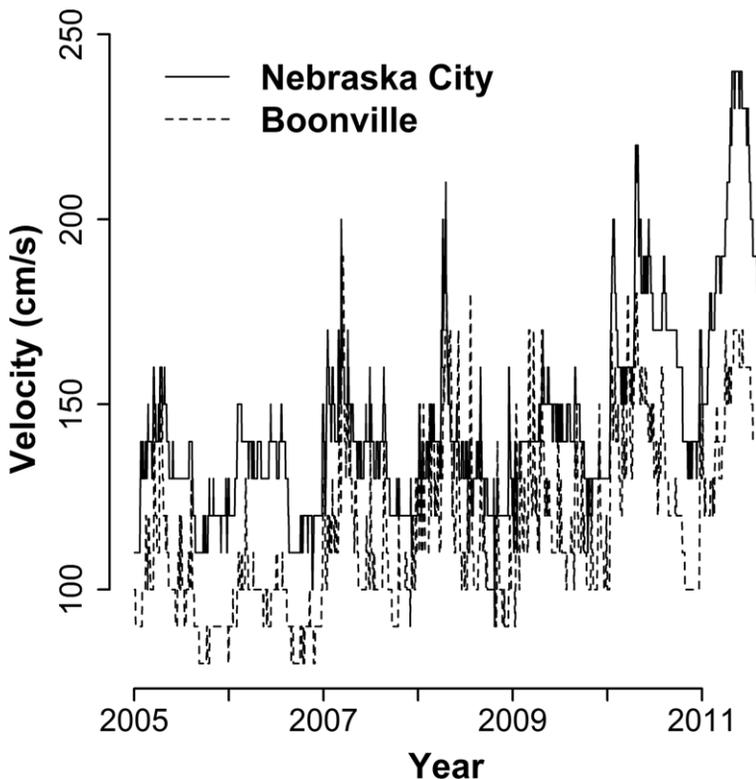


Fig. 7. Daily water velocity of Lower Missouri River at Nebraska City, Nebraska (solid line) and Boonville, Missouri (dashed line) from March 2005 to September 2011.

fish experiences 58% of the average flow velocity found in the segment of the river through which it is travelling (McElroy *et al.* 2012). Yet, the pathway taken by pallid sturgeon may expose them to lower or higher flow velocities.

Lastly, we were not able to model growth of the individual pallid sturgeon using the actual river conditions they experienced during their observed growth due to very sparse location data. We had to use velocities and temperatures from an available USGS gauge found in the portion of the river the fish was assumed to inhabit during its growing period based on first and last locations as representative of the conditions experienced by the fish. Using mean cross-sectional velocities at gauging stations is a simplification since gauging stations are preferentially located to measure in straight, uniform reaches and tend to have higher velocities compared to adjacent reaches. Further, empirical data from adjacent gauging stations can differ because discharge–velocity relationships depend on local hydraulics; hence, model outputs dependent on these values will be variously affected spatiotemporally. These field conditions and related observations suggest that more work is needed to further develop a precise model for pallid sturgeon, in particular: direct estimation of metabolic costs associated with swimming; finer scale estimation of actual swimming done in the field; and additional model validation using simultaneous measurements of water temperature and velocity actually experienced to estimate growth for individuals.

Even with inclusion of stochasticity, there are limitations to our model. First, the bioenergetics model, as originally developed by Chipps *et al.* (2010), is based on juvenile pallid sturgeon. Parametric values derived in Chipps *et al.* (2010) are all based on either larvae or juveniles (0.03–617.3 g), which were much smaller in weight than the upper range of weights used in this study. Because parameter estimates for large pallid sturgeon are not available in the existing literature, we extrapolated the model to adult life stages; hence, parameters used in our bioenergetics model are based on experimental study using juvenile pallid sturgeon and may not represent comparable values in adults.

Second, all parameter estimates come from laboratory studies whereas we implemented the model for pallid sturgeon in the wild. Fish behaviour and performance in the laboratory may be artificial and not truly representative of fish in the wild (Hansen *et al.* 1993; Ney 1993).

Third, the distributional assumptions obtained for the physiological parameters are based on literature found on other species, which may poorly represent pallid sturgeon physiology. Species-borrowing is common in scientific literature, yet a

recent study found that a model based on Pacific salmon species was unable to accurately predict the metabolic cost for another Pacific salmon species (Trudel *et al.* 2004), suggesting the need to avoid the practice of species-borrowing whenever possible. In our case, we borrowed parameter estimates for metabolic cost from the white sturgeon, but our model validation test based on a new set of fish indicated that the metabolic costs of swimming for white sturgeon and/or the estimated work done by pallid sturgeon based on path analyses failed to fully represent the metabolic costs due to swimming for pallid sturgeon. The current model, trained for Nebraska, either overestimated or underestimated metabolic cost due to swimming in just under half the fish. Despite limitations linked to species-borrowing, the stochastic bioenergetics model we developed is capable of capturing the embedded uncertainty of the parameters and emerges as a promising mechanism to predict the observed growth of pallid sturgeon. Indeed, as a starting point in bioenergetics research, initial developments in model building inevitably identify shortcomings associated with existing data derived from different species. However, these initial efforts point us toward species-specific studies to garner empirical values that offset these downsides to data extracted from existing literature.

The purpose of this work was to develop an individual-based bioenergetics model for the endangered pallid sturgeon to serve as the basis of a tool for predicting fish growth under changing environmental conditions. This model is being used as part of a larger effort to develop a tool that could be used to provide a better understanding of the effects of climate change on the Missouri River ecosystem (Wildhaber *et al.*, this volume, in prep). Such a tool would help managers identify strategies for mitigating potential negative impacts of climate change on endangered sturgeon populations. In doing this, the model we developed provides a methodological framework for development of a management tool that would have the ability to integrate various environmental factors along with accommodating their uncertainties. Ultimately, such a tool may serve as a means to assess the growth dynamics of the pallid sturgeon under changing environmental conditions. It could potentially be applied to help predict the response of pallid sturgeon populations to changes in environmental conditions as a result of management actions and/or changes in climate, thus providing information that could be used to guide recovery efforts.

Future research should be done to help develop a better understanding of the various components of the model and how their stochasticity affects model outcomes. For example, model components could be grouped as physiological parameters (e.g.

respiration), ecological parameters (e.g. diet shift), and environmental inputs (e.g. river flow and velocity, and temperature) to assess the relative influence of stochasticity of each of these groups, with the other two groups held constant, on model outcomes. The physiological (bioenergetics) parameters would seem to be conceptually different from the other two groups. For instance, these bioenergetics values have some 'correct' value, but we may not be sure of that value. Therefore, they may be (approximately) constant, but the value is uncertain. However, ecological and environmental values are 'inherently' stochastic, varying daily.

The model could be further improved in several ways. First, caloric density of fish and invertebrate prey and prey items consumed could be made stochastic. We did not include these components of stochasticity because, essentially, no information on energy density distributions of potential invertebrate and fish prey of pallid sturgeon were available. Here such stochasticity was implicitly incorporated to some degree through the daily variation in pallid sturgeon caloric density. Second, with the addition of stochasticity to prey energy density and makeup, a different form of stochasticity, such as Brownian motion where today's value is dependent on yesterday's value plus some change, could be used to model pallid sturgeon caloric density. Third, estimates of caloric density of adult pallid sturgeon should be obtained to ensure the representativeness of juvenile pallid sturgeon caloric density for all pallid sturgeon. If differences do exist, they could impact the estimates of P and the energy balance of the model.

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Correction notice: The previous version was incorrect. This was due to an error in Table 1.

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