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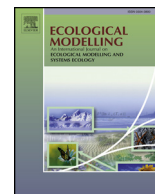
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## Applying a simplified energy-budget model to explore the effects of temperature and food availability on the life history of green sturgeon (*Acipenser medirostris*)



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### ABSTRACT

In highly regulated systems, like large dammed rivers, conservation legislation requires that systems are managed, in part, to avoid adverse impacts on endangered species. However, multiple endangered species can occur in the same system, and management actions that benefit one species may be detrimental to another species. The current water management strategies in the Sacramento River basin are an example of this conflict. Cold-water releases from Shasta Reservoir during the summer and fall months are aimed at protecting Sacramento River winter-run Chinook (SRWRC) salmon by providing suitable incubation temperatures for their eggs. However, the effects of these regulated water temperature releases on another threatened species, green sturgeon, are less well understood. In this study, we applied a simplified dynamic energy budget (DEB) model (aka DEBkiss) to explore the effect of food limitation and water temperature on the growth rates of green sturgeon. This model captures these effects and able to predict the growth of green sturgeon at different food levels and temperature conditions. We then linked the DEB model with a physically-based water temperature model. We applied the DEB - water temperature linked model for green sturgeon along with a temperature-dependent egg to fry survival model for SRWRC salmon to quantify the consequences of managing water temperatures to improve salmon eggs survival on the growth rate of green sturgeon. We found that mean temperature-dependent egg-to-fry survival of salmon increased across a modeled environmental gradient from critically dry to wet water year types, while the fractional growth rate of juvenile green sturgeon showed the opposite trend, and decreased as water years transitioned from dry to wet conditions. We also found a non-linear negative correlation between temperature-dependent mean growth rate of green sturgeon and mean temperature-dependent egg-to-fry survival of salmon, which indicated there is a river temperature related trade-off between early growth rate of green sturgeon and embryonic stage survival of salmon. However, the relatively small gains in the growth rate of green sturgeon achieved in years when temperature criteria for SRWRC salmon eggs were not met came at the cost of large reduction in temperature-dependent egg-to-fry survival of salmon. Thus, we concluded the current Sacramento River water-temperature management for the eggs of the endangered SRWRC salmon eggs have a relatively small impact on the growth rate of green sturgeon.

### 1. Introduction

Conservation laws, such as the Endangered Species Act (ESA, NMFS (2006)), are put in place to protect species at risk of extinction. However, in some cases multiple endangered species occur in the same system, and specific management actions that benefit one species may

be detrimental to another. For example, several anadromous fish populations spawn and rear in the Sacramento River, California and are impacted by environmental factors, such as altered water temperatures due to the operation of dams. Within the river basin, water operations and large-scale ecosystem restoration programs aim to recover and protect these fish populations (U.S. Department of the Interior Bureau

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of Reclamation Mid-Pacific Region, 2008). Water management operations include controlled water releases from Shasta Dam on the Sacramento River aimed at providing suitable temperatures downstream for the embryonic development of the endangered Sacramento River winter-run Chinook (SRWRC) salmon, *Oncorhynchus tshawytscha*. Significant efforts have been applied towards field work, laboratory experiments, and model development to predict how temperature affects salmon life history (Martin et al., 2017), however, much less is known about temperature impacts on other ESA-protected species, such as green sturgeon, *Acipenser medirostris*. While laboratory experiments have contributed some data on the growth of larval and juvenile green sturgeon (Mayfield and Chech, 2004; Allen et al., 2006; Poletto et al., 2018), analytical tools are needed to synthesize the results from these studies and to extrapolate these results to field conditions.

Green sturgeon spawn in three major river basins, supporting two populations, the Northern Distinct Population Segment (nDPS) and the Southern Distinct Population Segment (sDPS) (Adams et al., 2007). The nDPS is listed as a species of concern, and spawns in the Rogue River, in southern Oregon, and the Klamath River, in northern California. The sDPS spawns in the Sacramento River Basin and is listed as threatened under the federal ESA (Adams et al., 2007). After emergence from eggs, sDPS sturgeon spend up to two years of their early life history stages rearing in the Sacramento River (Heublein et al., 2017) before transitioning into brackish and saltwater environments.

Several factors have been suggested as causes for the decline of green sturgeon in the Sacramento River, including degradation of freshwater and estuarine habitats (Adams et al., 2007), blockage of historical habitats by impassable dams (Mora et al., 2009), and the effects of commercial fishing, including by-catch in bottom-trawl fisheries (Erickson and Hightower, 2007). One additional factor that may contribute to the decline of sDPS green sturgeon in the Sacramento River is that dam operations are aimed at maintaining cool temperatures to benefit endangered SRWRC eggs and may negatively affect the growth or survival of green sturgeon juveniles. Laboratory studies indicate that optimum green sturgeon growth rates occur between 16 and 19 °C (Mayfield and Chech, 2004). Water temperatures below 16 °C often occur in the Sacramento River, and it is possible that flow and temperature regulation in the Sacramento River may reduce the growth rates of green sturgeon, leaving them more vulnerable to size-dependent predation (Goto et al., 2015). Analytical tools are needed to predict green sturgeon growth under various water management conditions and to explore how structured water releases influence transitions through their early life history stages. Since food availability and temperature are known to strongly influence fish growth, the primary objective of this research was to develop a mechanistic model that can predict the combined effect of temperature and food density on the growth rate during early life history stages of green sturgeon.

In this study, we implemented the simplified Dynamic Energy Budget (DEB) model (aka DEBkiss, (Jager et al., 2013)) to explore the effects of food limitation and temperature on the early life history of green sturgeon. The model allows for a mechanistic interpretation of the effects of food limitation and temperature on sturgeon growth and reproduction. DEB theory is applicable to all organisms, but for individual species, parameter calibration requires precisely quantified rates of key physiological processes under different environmental conditions. Thus, to parameterize a DEB model, we compiled an extensive database of green sturgeon growth and reproduction studies over a wide range of environmental conditions. We then used the model to explore the effect of food limitation and temperature on sturgeon growth and reproduction. We then linked our DEB model with a physically-based water temperature model of the Sacramento River, River Assessment for Forecasting Temperature (RAFT) (Pike et al., 2013) to demonstrate the effects of temperature on the growth of juvenile green sturgeon. We used the coupled DEB-RAFT model to predict the effect of observed Sacramento River water temperatures on growth of larval and juvenile green sturgeon during their downstream migration, and to

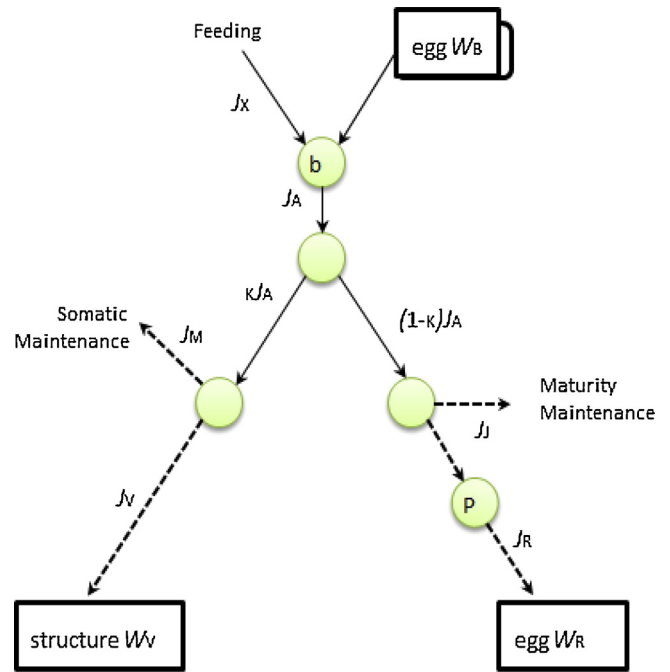


Fig. 1. The Schematic description of DEBkiss model. Arrows indicate energy fluxes ( $\rightarrow$  assimilated and mobilized energies,  $\dashrightarrow$  allocated energy) that drive the dynamics of the state variables, depicted in boxes (Structure,  $W_V$  and Reproductive Buffer,  $W_R$ ). Energy enters the animal as food,  $J_x$ , and then assimilated at a rate  $J_A$ . The assimilated food will be mobilized in proportion of  $k$  to somatic maintenance and structure) and  $1 - k$  to maturity and reproduction. The  $kJ_A$  proportion of mobilized flux will be allocated to somatic maintenance,  $J_M$  and growth  $J_V$ . The  $(1-k)J_A$  flux divided as maturity maintenance flux  $J_J$  and reproduction flux,  $J_R$ .

evaluate how spawning location and timing impacts juvenile growth rates. Finally, we used our green sturgeon DEB model along with a model of temperature-dependent embryonic survival developed for endangered SRWRC (Martin et al., 2017) to evaluate the extent to which managing water for SRWRC eggs negatively impacts larval and juvenile green sturgeon growth rates and quantitatively estimate the effect.

## 2. Methods

### 2.1. Model definition

DEBkiss is a mass-balance model founded on simple mechanistic descriptions of how individual organisms take up and use energy and materials, which is represented using state variables and energy/material flows (Fig. 1). Jager et al. (2013) present a detailed model description, including assumptions, of DEBkiss, which is summarized in the Supplementary material. The most important difference from the standard DEB model (Sousa et al., 2010) is that DEBkiss does not include a reserve compartment, and lacks a state variable for maturity (investment in reproduction starts at a fixed body size).

In our DEBkiss model we quantify one state variable, body mass ( $W_V$ , mg), and the model involves four mass fluxes: assimilation ( $J_A$ ), structural growth ( $J_V$ ), flux into the reproduction buffer ( $J_R$ ), and maturity maintenance ( $J_M$ ).

DEBkiss makes the assumption that assimilation rate,  $J_A$  scales with mass,  $W_V$ , to the  $2/3$  power and maintenance costs are proportional to mass. Thus, the four fluxes in DEBkiss, i.e., assimilation,  $J_A$ , maintenance,  $J_M$ , growth,  $J_V$  and reproduction,  $J_R$  are mathematically expressed as:

$$J_A = f J_{Am}^a W_V^{2/3} \tag{1}$$

$$J_M = J_M^v W_V \tag{2}$$

$$\frac{dW_V}{dt} = J_V = y_{VA}(\kappa J_A - J_M) \tag{3}$$

$$J_R = \begin{cases} (1 - \kappa) J_A - J_J & \text{if } W_V \geq W_{VP} \\ 0 & \text{if } W_V < W_{VP} \end{cases} \tag{4}$$

Where:  $f$  is the scaled functional response, which is the observed ingestion rate divided by the maximum ingestion rate for a fish of that size (the value of  $f$  is between 1: ad libitum food supply and 0: complete starvation).  $J_{Am}^a$  is maximum area-specific assimilation rate,  $y_{VA}$  is the conversion efficiency at which assimilated energy is synthesized into biomass,  $J_M^v$  is mass-specific maintenance cost,  $\kappa$  is the allocation fraction to growth and maintenance, and  $W_{VP}$  is body mass at puberty, defined as the onset of allocation to reproduction (a detailed mathematical description of the model can be found in the Supplementary material).

### 2.2. Modelling the effect of environmental factors

The effect of environmental factors can be included in the model by altering one or more model parameters, and we only considered food availability and water temperature. The effect of food availability can be included directly by altering the scaled function response,  $f$  as a function of food density.

The effect of temperature is included by scaling the rate parameters, i.e., the maximum area-specific assimilation rate ( $J_{Am}^a$ ) and the mass-specific maintenance costs ( $J_M^v$ ), as a function of temperature. Many studies have demonstrated an exponential relationship between biological rate constants and temperature (Hardiman and Mesa, 2014). Thus, the mass-specific maintenance costs at any temperature,  $T$  ( $J_{M,T}^v$ ) is given by:

$$J_{M,T}^v = J_{M,0}^v \cdot e^{a_1 T} \tag{5}$$

where  $J_{M,0}^v$  is the intercept of mass-specific maintenance rate at 0 °C, and  $a_1$  is a parameter that is the exponential rate of increase of maintenance costs with temperature,  $T$  (°C).

Similarly, the maximum area-specific assimilation rate at a given temperature,  $T$  ( $J_{Am,T}^a$ ) is given by:

$$J_{Am,T}^a = J_{Am,0}^a \cdot e^{b_1 T} \tag{6}$$

### 2.3. Parameter estimation

We obtained data from different sources (Table 1) and estimated the

parameters using maximum likelihood optimization (Table 2). Because the growth data sets included in our analysis reported body size in dry weight, wet weight, and length, we required conversions between these variables. We assumed a dry to wet weight ratio of 0.15 which was estimated from green sturgeon body composition analysis (Zheng et al., 2015). Zheng et al. (2015) reported that juvenile green sturgeon body mass is 82.1–86.0% water content. The relationship between wet weight and length is assumed to be:

$$W_V = (\delta_M L)^3 \tag{7}$$

Where  $L$  is length (cm) and  $\delta_M$  is a correction factor that accounts for the shape of the fish. Eq. (7) implicitly assumes a specific density of tissue of 1 g cm<sup>-3</sup> to relate the volume of a fish to its mass. The correction factor ( $\delta_M$ ) was estimated from previously measured length and weight allometric relationships (Gisbert and Doroshov, 2006; Zheng et al., 2015).

Reproduction is expressed as mass flux,  $J_R$  (Eq. (4)); however, in our analysis reproduction is expressed as number of eggs per individual green sturgeon per day. Assuming  $t_S$  is the mean time between spawning events, female green sturgeon produce a clutch size of  $F$  eggs. We translated DEB predictions for the reproduction flux  $J_R$ , to predictions of fecundity,  $F$  as follows:

$$F = \frac{y_{BA} \cdot J_R}{W_{B0}} t_S \tag{8}$$

Where  $y_{BA}$  is conversion efficiency of converting assimilated energy into eggs, and  $W_{B0}$  is the mass of a single freshly laid sturgeon egg. We assumed an average spawning interval of three years, which falls within the estimated range (2–5 years) for green sturgeon (Borin et al., 2017). We estimated  $W_{B0}$  from estimates of green sturgeon egg size. Egg diameter (Van Eenennaam et al., 2005, 2006; Brown, 2007) was used to estimate egg volume (by assuming the egg is a perfect sphere). This volume was converted to dry weight to yield the egg weight  $W_{B0}$ .

For ad libitum food conditions, we set  $f = 1$ , while for the food-limited experiments and field data we estimated  $f$ . For the conversion efficiency coefficients ( $y_{BA}$ ,  $y_{VA}$ ), we used the defaults as suggested in Jager et al. (2013).

We estimated other model parameters by simultaneously fitting the model to all 38 data sets described in Table 1. For the parameterization, we used maximum likelihood optimization, and derived the confidence intervals by profiling the likelihood (Jager and Zimmer, 2012). We used MATLAB (9.2.0.538062 (R2017a)) to develop the code. The basic scripts of the code can be found on <http://www.debttox.info/byom.php>.

**Table 1**

Data used for DEBkiss parameter estimation. More information on the individual dataset can be found in given references.

Data Type	Description	Source
<ul style="list-style-type: none"> <li>Growth of exogenous feeding larvae and juvenile at 5 different temperatures and 2 feeding conditions</li> </ul>	<ul style="list-style-type: none"> <li>Body weight measurement at 19, 16, 13 and 11 °C and 2 feeding conditions:                             <ul style="list-style-type: none"> <li>○ 9 weeks observation of body weight at 100% optimum feeding condition</li> <li>○ 12 weeks observation of body weight at 100% optimum feeding condition</li> <li>○ 12 weeks observation of body weight at 40% optimum feeding condition</li> </ul> </li> <li>Body weight measurement at 18 °C and 100% optimum feeding conditions:                             <ul style="list-style-type: none"> <li>● Observation of body weight for 9 weeks</li> <li>● Observation of body weight for 12 weeks</li> </ul> </li> </ul>	UC Davis lab, (Poletto et al., 2018)
<ul style="list-style-type: none"> <li>Growth as function of age at 2 feeding conditions</li> </ul>	Body weight measurement at 18 °C food deprivation experiment on exogenous feeding larvae	(Gisbert and Doroshov, 2006)
<ul style="list-style-type: none"> <li>Growth as function of age at 3 different temperatures</li> </ul>	<ul style="list-style-type: none"> <li>Wet weight and total length measurement for post-yolk-sac larval to early juvenile green sturgeon at a variable temperature, i.e., 19 – 24 °C and 2 constant temperature conditions, i.e., 19 °C and 24 °C.</li> </ul>	(Allen et al., 2006)
<ul style="list-style-type: none"> <li>Growth as function of age at 18 °C and at 6 feeding conditions</li> </ul>	<ul style="list-style-type: none"> <li>Wet weight measurement for green sturgeon fry to determine the effect of feeding rate on their growth performance</li> </ul>	(Zheng et al., 2015)
<ul style="list-style-type: none"> <li>Field Reproduction data for Klamath River Green Sturgeon</li> <li>Field growth data for Klamath and Oregon Rivers Green Sturgeon</li> </ul>	<ul style="list-style-type: none"> <li>Wet weight and fork length observations for Juvenile and matured adults</li> <li>Fecundity matured adults</li> </ul>	<ul style="list-style-type: none"> <li>(Van Eenennaam et al., 2006)</li> <li>Personal communication with Joel P. Van Eenennaam</li> </ul>

**Table 2**

Model parameters and estimated values; parameter estimation used maximum likelihood optimization from the feeding and temperature dependent data sets. Confidence intervals were derived using likelihood profiles.

Parameter	Unit	Value (95% CI)	Description
$J_{Am}^a$	mg/(mm <sup>2</sup> d)	0.01176 (0.008953 - 0.01449)	Specific assimilation rate
$J_M^a$	mg/(mm <sup>3</sup> d)	0.00012 (0.000073 - 0.00024)	Specific maintenance costs
$W_{VP}$	G	26830 (23,000 - 31,400)	Wet weight at puberty
$\kappa$	-	0.651 (0.5734 - 0.6926)	Allocation fraction to soma
$f_{40}$	-	0.55247 (0.4814 - 0.6448)	Scaled food level for the 40% of optimum feeding experiment at UC Davis
$a_1$	-	0.16524 (0.06924 - 0.231)	Temperature correction factor for maintenance
$b_1$	-	0.14775 (0.1343 - 0.1623)	Temperature correction factor for feeding and assimilation
$f_{Oregon}$	-	0.85427 (0.7524 - 0.916)	Scaled food level for Oregon Rivers
$f_{Klamath}$	-	0.963 (0.8666 - 1)	Scaled food level for Klamath Rivers
$W_{B0}$	g	0.09 (-)	Initial dry weight of a single egg
$y_{BA}$	-	0.95 (-)	Yield of egg buffer on assimilates
$y_{VA}$	-	0.8 (-)	Yield of structure on assimilates (growth)
$\delta_M$	-	0.2216 (-)	Shape correction factor
$dV$	-	0.15 (-)	Dry weight density
$T_C$	°C	20.52 (19.04 -)	Critical temperature

**2.4. Deviation of growth at higher temperatures**

The exponential relationship between feeding rate and temperature in Eq. (7) substantially overestimated the growth of green sturgeon at temperatures higher than 19 °C (see Fig. S2 of the Supplementary material). While physiological rates of ectotherms are often well described by an exponential relationship at low to intermediate temperatures, the relationship can break down towards the higher end of the temperature range, where feeding rate plateaus or even declines (Borin et al., 2017; Hung et al., 1993; Mizanur et al., 2014; Handeland et al., 2008; Lee et al., 2016). We hypothesized this mismatch in observed and predicted growth rates was due to leveling off of feeding rates at high temperatures. Thus, to avoid the overestimate, we assumed there is a critical temperature for the maximum area-specific assimilation rate, such that above a critical temperature,  $T_C$ , feeding rate no longer increases with temperature:

$$J_{Am,T}^a = \begin{cases} J_{Am,0}^a \cdot e^{a_1 T} & \text{if } T \leq T_C \\ J_{Am,0}^a \cdot e^{a_1 T_C} & \text{if } T > T_C \end{cases} \quad (9)$$

We estimated the critical temperature  $T_C$  based on the modified temperature correction factor presented in Eq. (9) and using the growth data reported in Allen et al. (2006).

**2.5. Model simulations**

We developed a simulation model that tracks the daily mean temperature exposure profiles of juvenile green sturgeon in the Sacramento River, based on their movement and migration behaviors. Our assumptions of how juvenile green sturgeon migrated downstream in our simulations were based on ontogenetic patterns of activity levels observed by Kynard et al. (2005), and the age, and size of saltwater tolerance observed by Allen et al. (2011).

Downstream migration of green sturgeon juveniles is facilitated by the transitional onset of saltwater tolerance (Heublein et al., 2017). Thus, there is a period after hatching where juvenile fish migrate to rearing habitats to wait until the size-dependent onset of the physiological processes that mediate salt water tolerance (Allen et al., 2011). Heublein et al. (2017) synthesized sources that suggest individuals smaller than 200 mm fork length (FL) are absent from downstream estuarine habitats. Green sturgeon juveniles show a period of limited movement after hatching, lasting about 10 days, then initiate a rapid nocturnal downstream migration until ~21 days post hatch (Kynard et al., 2005). After this early migration period, it is thought that juveniles settle into upriver rearing habitats until they reach the minimum salt water tolerant body size of 200 mm (Kynard et al., 2005).

Accordingly, we assumed that for days 0–10 larvae remain where

they were spawned. Then on days 10–21, green sturgeon migrate at 6.5 km/day (Kynard et al., 2005). After 21 days, they move both upstream and downstream with very little net downstream movement (0.1 km/day) until they reach 200 mm in length. These combined movement patterns determine the distance an individual juvenile migrates downstream, and consequently their location in the river.

We then determined the daily mean temperature exposure profile of the fish using RAFT, which provides predicted mean daily temperatures in the Sacramento River at a spatial resolution of 1 km (Pike et al., 2013). Then, using the DEBKiss model we were able to calculate the daily growth increment at that temperature to update the length of the individual. Finally, we used the DEBKiss-RAFT to evaluate tradeoffs of water temperature management between the growth rate of juvenile green sturgeon and the survival of endangered SRWRC salmon eggs.

Due to limited information on the food distribution in the river, however, we assumed juvenile green sturgeon experience a constant food supply. For the purpose of this simulation, we assumed a constant functional response value of  $f = 0.8$ , based on the values we estimated for Klamath and Oregon Rivers (Table 2).

**2.5.1. Effect of spawning location and spawning periods on early growth**

We first implemented the DEBKiss-RAFT simulation model to explore the effect of spawning location and timing on the early growth of green sturgeon offspring and to predict the number of days juvenile green sturgeon require before reaching the estuary; i.e., grow to minimum salt water tolerant body size of 200 mm. We assumed four spawning and hatching locations (Poytress et al., 2015) 426 river km (rkm), 391 rkm at Red Bluff Diversion Dam (RBDD), 366 rkm, upstream of Glenn-Colusa Irrigation District (GCID) and, 332.5 rkm at GCID which are located at 60 km, 95 km, 120 km and 153.5 km downstream of Keswick Dam respectively (Fig. 2). Surveys of spawning events on the Sacramento River indicate that the green sturgeon spawning window extends from early April until mid-July (Poytress et al., 2015). Accordingly, we considered two extreme spawning periods, early spawning (early April) and late spawning (late June). Based on the simulation results we explored the effects of the water temperature during these periods on juvenile growth, which resulted from the spatial-temporal differences in spawning and rearing conditions. We further evaluated the degree of influence of spatial and temporal variation of spawning sites using absolute growth and specific growth rates. In this simulation analysis, we considered the mean daily temperature over a 22 year (1990–2012) operation period of the Shasta Dam.

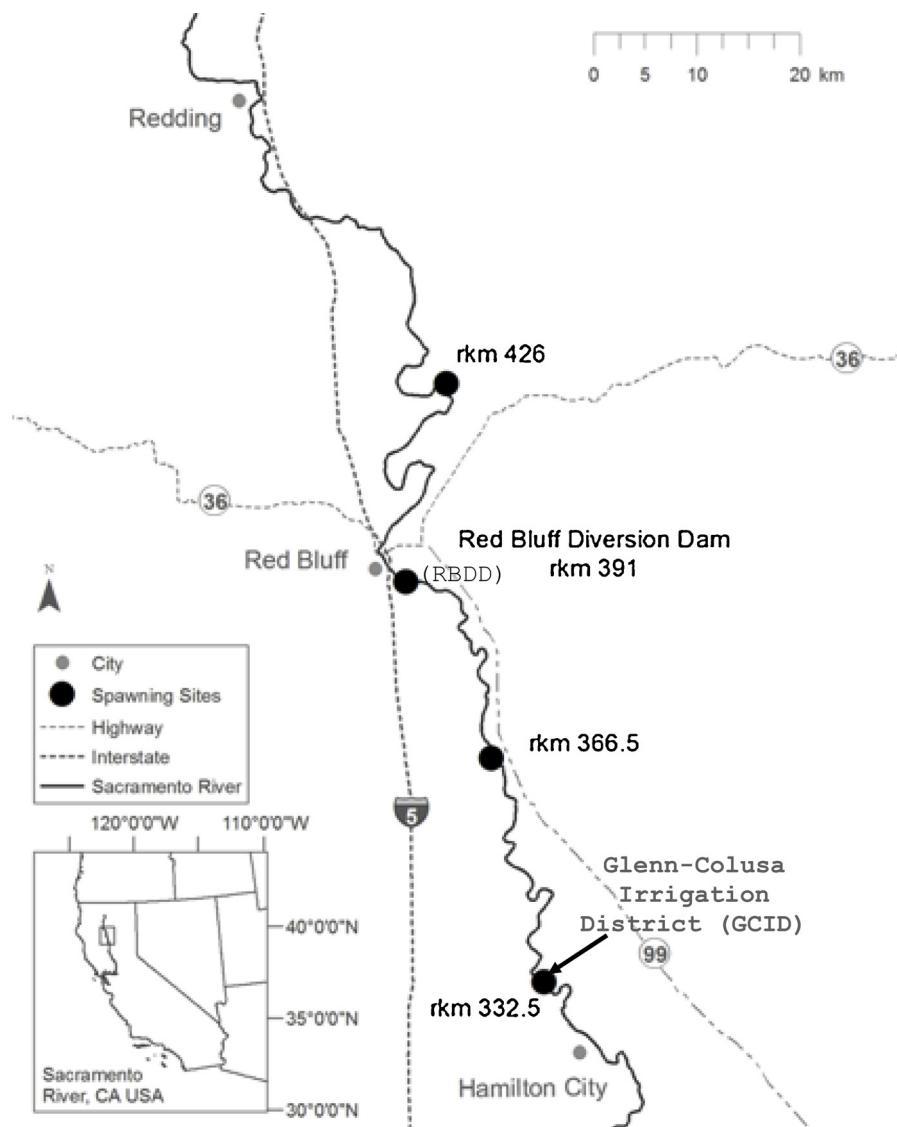


Fig. 2. Location map of the area considered in the simulation model (Table 3). The four known spawning and hatching locations of the green sturgeon are shown as black circles.

2.6. Evaluating temperature management tradeoffs for green sturgeon growth vs. Chinook salmon eggs survival

We compared our model’s predictions for the effects of river temperature on green sturgeon growth with the predicted effects on winter-run Chinook egg to fry survival using the model from Martin et al. (2017). For this, we explored the temperature effects of five historical water-year types- critical, dry, above normal, below normal, and wet (Fig. 7(a))- on the early growth rate of juvenile green sturgeon. Furthermore, we compared the mean SRWRC salmon egg-to-fry survival to the mean growth rate of green sturgeon for the time period of 1990 – 2015. We estimated the growth of green sturgeon in their first five months (i.e., from May 1<sup>st</sup> to September 31<sup>st</sup>) and assumed they hatched at RBDD, 391 rkm (i.e., 95 km downstream from the Keswick Dam).

3. Results

3.1. Parameter estimates, and model fit

We estimated values for all parameters used in our model (Table 2), and fit the model to selected datasets (Figs. 3 and 4, S2–S6). In general, the model captured the trend of most of the laboratory and the field

growth (R-squared of 97.2%) and reproduction data (R-squared of 89.9%) (Figs. 3 and 4). Both temperature and food availability influence the growth of green sturgeon (Fig. 3), which increases monotonically for the temperature range of 11–19 °C. The exponential correction factor assumption, Eq. (7), captured the growth trend as a function of temperature in this range, but over predicted growth above 19 °C (Fig. S2 of the Supplementary material). After inclusion of an asymptotic temperature correction factor, Eq. (8), the model predicted growth at temperatures ranging from 19 to 24 °C (Fig. 5), and estimated  $T_C$  to be 20.5 °C, with the lower 95% CI of 19.0 °C. Due to limited data at higher temperatures, we were unable to get a precise upper 95% CI. Our estimates for the temperature exponents for maintenance ( $a_1$  is 0.165; 95% CI = 0.069–0.231) and feeding ( $b_1$  is 0.147 95% CI = 0.134–0.162) corresponded to  $Q_{10}$  values of 5.2 and 4.3 respectively. Based on this information, we estimated the  $Q_{10}$  for growth of green sturgeon (e.g., between 12 and 20 °C,  $Q_{10}$  = 4.1345 for a 10 g green sturgeon).

3.2. Model simulations

3.2.1. Effect of spawning location and spawning period on early growth

Model simulations indicate that green sturgeon growth is influenced

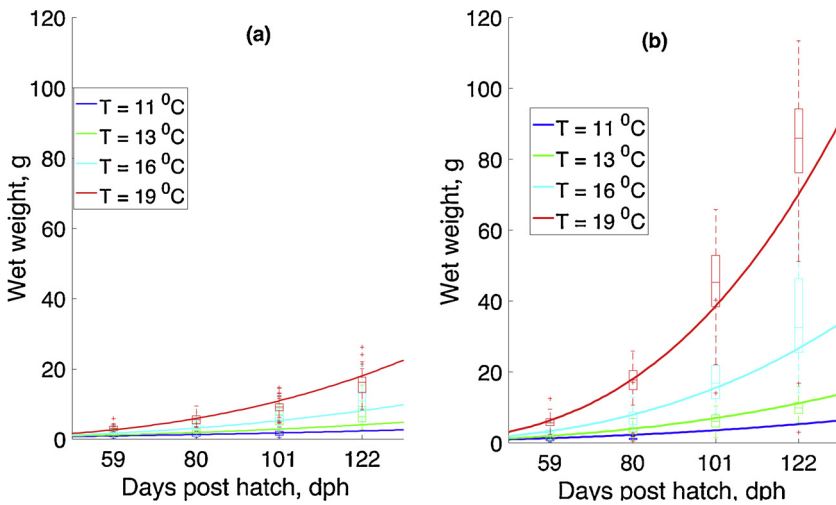


Fig. 3. The model fitted to experimental data sets obtained from UC Davis (Poletto et al., 2018). Growth pattern for larval to juvenile green sturgeon reared at four different temperatures (i.e., T = 11, 13, 16 and 19 °C) and two feeding conditions left: low feeding condition, 40% of optimal feed rate and right: high feeding condition, 100% of optimal feed rate). Detail description of the datasets and on the experimental design can be found in Poletto et al. (2018).

by both spawning location and timing (Fig. 6 and Table 3). There was a positive relationship between sturgeon growth and hatch distance downstream of the Keswick Dam in both body size and time to reach the minimum critical salt tolerance body size of 200 mm. There was a six-month difference in the time required to grow to the 200 mm threshold (1 year for upstream and six months for downstream, Fig. 6). However, the spatial effect was lessened for fish that hatched later in the season, where downstream fish required approximately 290 days to reach 200 mm. Regardless of hatching time, those hatched upstream near the dam reached the minimum critical salt tolerance body size after approximately the same amount of time. Depending on the spawning location and spawning period, our model predicted that a one-year old green sturgeon can reach a body weight of 108 g (hatched in mid of April, 60 km downstream of Keswick Dam) to 260 g (hatched in end of June, 154 km downstream of Keswick Dam) (Table 3). From these results, it is apparent that the mechanism driving the faster growth further downstream and later in the season is warmer temperature.

3.2.2. Evaluating temperature management tradeoffs for green sturgeon growth vs. Chinook salmon eggs survival

We examined the impact of five water year types (Critical, Dry, Below Normal, Above Normal, and Wet) on the specific growth rate of green sturgeon and temperature-dependent egg-to-fry survival of SRWRC salmon. Green sturgeon specific growth rate and egg-to-SRWRC salmon egg-to-fry survival both varied in space and time (Fig. 8). Temperature-dependent egg-to-fry survival of SRWRC salmon was highest closer to the dam and earlier in the spawn season (Fig. 8 lower panel), while specific growth rate of green sturgeon showed the opposite trend, with higher growth rates further down the river and later in the season (Fig. 8 upper panel). Temperature-dependent egg-to-fry

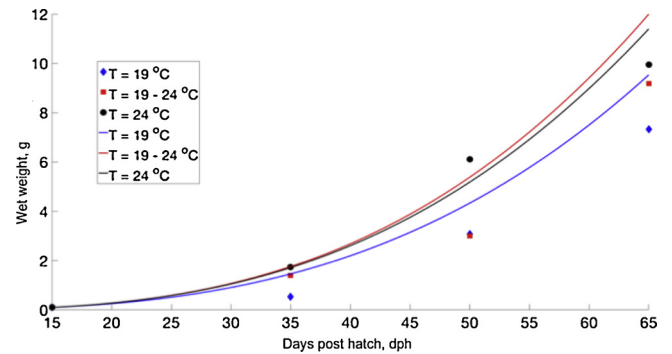


Fig. 5. The model refitted to experimental data sets obtained from (Allen et al., 2006) by assuming an asymptotic temperature scaling factors of Eq. (10). The asymptotic temperature correction factor improved the initial fit, (Fig. S2 of the Supplementary material), at a two higher temperatures (i.e., 19–24 °C and 24 °C).

survival of SRWRC salmon varied greatly across water year types, especially in the upper 20 km below the dam where most SRWRC salmon spawn. In some locations and during some spawn times, temperature-dependent egg-to-fry survival of SRWRC salmon was near 100% in wet years but near 0% in critical years. On the other hand, variation in specific growth rate of green sturgeon was relatively low across water year types compared to variation within a year due to differences in spawning location and spawning period. There was a negative correlation between temperature-dependent egg-to-fry survival of SRWRC salmon using observed redd distributions and specific growth rate of green sturgeon during their first five months of growth

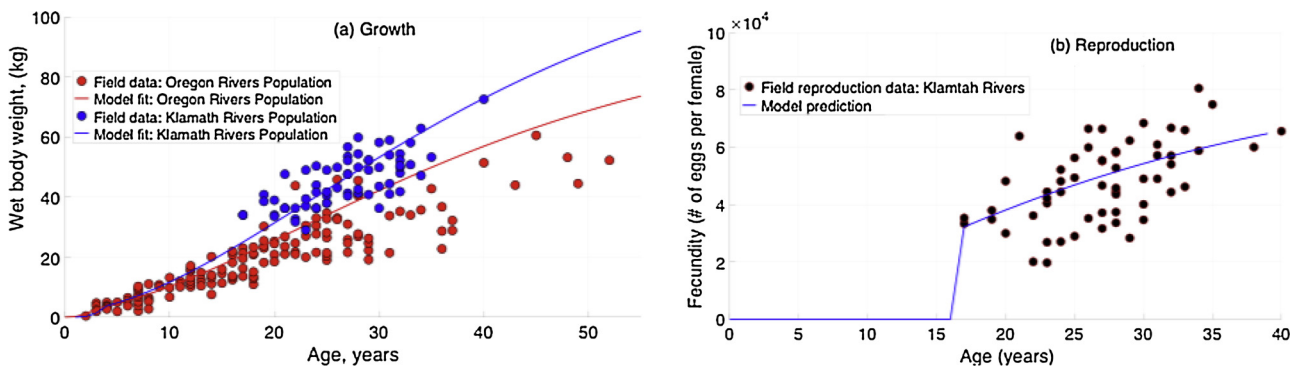


Fig. 4. The model fitted to field growth and reproduction data (unpublished). Growth data from Oregon Rivers population (nDPS) and Klamath Rivers (a) and Reproduction data from Klamath Rivers (b).

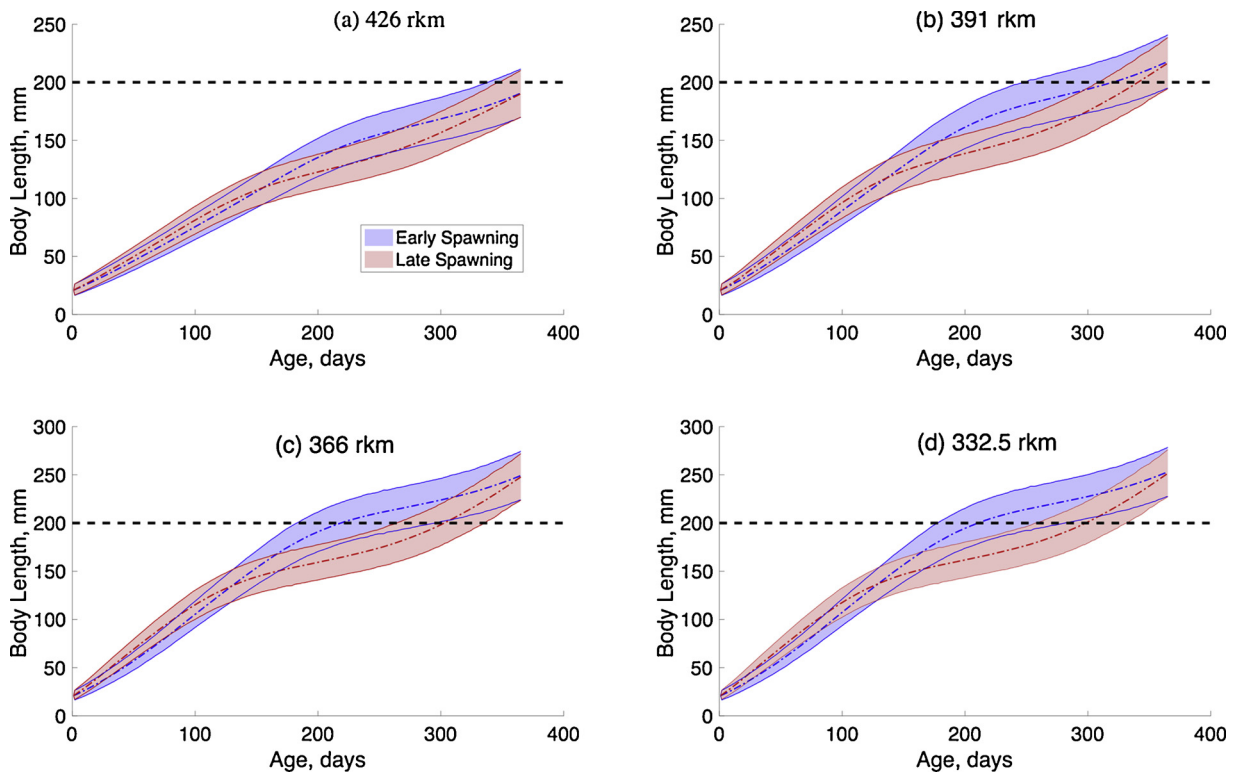


Fig. 6. Effect of spawning location and time to reach the minimum fork length of green sturgeon before entering the estuary. Each figure represents the different spawning location considered in the simulation analysis: (a) Paynes, 426 rkm, (b) RBDD, 391 rkm, (c) upstream of GCID, 366 rkm and (d) GCID, 332.5 rkm. 95% CI of body size predictions for early (blue shading) and late (red shading) spawning periods. The minimum saltwater tolerance length is 200 mm (dashed black line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

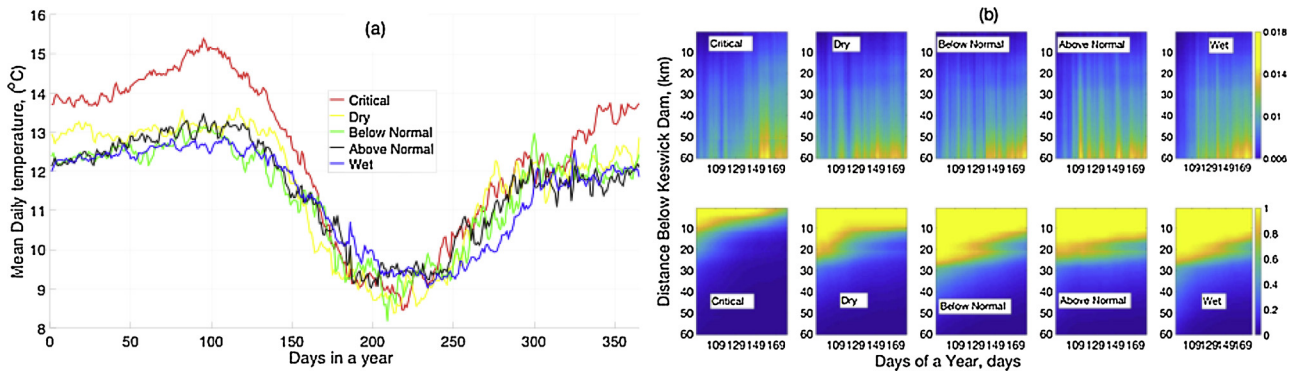


Fig. 7. Historical five years mean water temperature (i.e., Critical, Dry, Below Normal, Above Normal, and Wet) at the discharge of Keswick dam (a). The five heat maps in Fig. 7(b) represent the corresponding early growth rate of green sturgeon (upper panel) and temperature dependent egg-to-fry survival of SRWRC salmon (lower panel) for the five-historical water-years for the first 60 km down stream of Keswick dam (indicated on the y-axis) and for the period of Early April to end of June (indicated in the axis as day of year: 1 on January 1<sup>st</sup> to 365 on December 31<sup>st</sup>).

(Fig. 8). In the years with the coolest water temperatures (e.g. 1999, 2002, 2006, 2010, 2011), temperature-dependent egg-to-fry survival of SRWRC salmon was ~100%, and specific growth rate of green sturgeon was between 3.6 and 3.8% d<sup>-1</sup>. On the other hand, in the warmest years such as 2014 and 2015 (where due to the drought water temperature criteria were not met for SRWRC salmon eggs), temperature-dependent egg-to-fry survival of SRWRC salmon was only ~20%, and specific growth rate of green sturgeon was ~4.2% d<sup>-1</sup>. Furthermore, the relationship was non-linear. Moving from years that had 100% temperature-dependent egg-to-fry survival of SRWRC salmon to those that had ~80% improved specific growth rate of green sturgeon by 0.25% d<sup>-1</sup>. However, to improve specific growth rate of green sturgeon by an additional 0.25% d<sup>-1</sup> required dropping temperature-dependent egg-to-fry survival of SRWRC salmon from 80% to ~20% (Fig. 8).

## 4. Discussion

### 4.1. General

Our aim was to assess the impact of variation in water temperature, in part due to managing cool temperatures to benefit the eggs of the endangered SRWRC salmon, on the growth of green sturgeon juveniles during ontogeny through their outmigration to saltwater. By simultaneously fitting our model to an extensive database of green sturgeon growth studies under various temperature and food availability conditions, we were able to establish a relationship between temperature and growth rate from a much broader range of temperatures than evaluated in any one particular study. Furthermore, by integrating information across a wide range of studies, we expect our estimate of temperature-



**Table 3**  
Effect of spawning location and time on the growth performance of green sturgeon.

Spawning location	Spawning time					
	Early spawning: Mid April			Late Spawning: End of June		
	AGR <sup>a</sup> (gm/day)	SGR (%) <sup>b</sup>	Weight (gm) <sup>c</sup>	AGR (gm/day)	SGR (%)	Weight (gm) <sup>c</sup>
Paynes	0.2954	1.913	107.8	0.417	2.008	152.2
RBDD	0.3903	1.980	142.5	0.515	2.066	188.0
Upstream	0.577	2.097	210.6	0.690	2.146	251.9
GCID	0.601	2.108	219.4	0.713	2.155	260.3

$w_t$  and  $w_i$  indicates the final and initial weights respectively and  $t$  is the time period considered in the analyses (in days). In our case  $w_t$  is the weight of one year old green sturgeon, while  $w_i$  is the weight of freshly hatched green sturgeon larvae. The time  $t$  is 365 days.

<sup>a</sup> The absolute growth rate (AGR) is given by,  $AGR = \frac{w_t - w_i}{t}$ .

<sup>b</sup> The specific growth rate (SGR) is given by,  $SGR = \frac{\log(w_t) - \log(w_i)}{t} \cdot 100\%$ .

<sup>c</sup> Predicted weight of a one year old juvenile green sturgeon.

dependent growth to be more robust than would be obtained by any single study. Because the model explained most of the variation in growth trajectories suggests these studies are largely in agreement about the effects of temperature on green sturgeon growth. Our analysis suggests a strong temperature-dependence for growth with an exponential relationship indicating that green sturgeon growth is sensitive to temperature between the range of 11 and 20 °C. We also conclude that green sturgeon was sensitive to temperature management in the Sacramento River; however, our simulations suggest that managing temperatures for the eggs of the endangered SRWRC salmon has a relatively small impact on the growth rate of green sturgeon. The relatively small gains in the growth rate of green sturgeon achieved in years when temperature criteria for SRWRC salmon eggs was not met (e.g., years 2014–2015 in Fig. 8) came at the cost of large reduction in a temperature-dependent egg to fry survival of SRWC salmon. Another important finding of this study is the effect of spatial-temporal distribution of spawning habitats on the growth rate of green sturgeon. Individuals hatched downstream and later in the spawning season (i.e.,

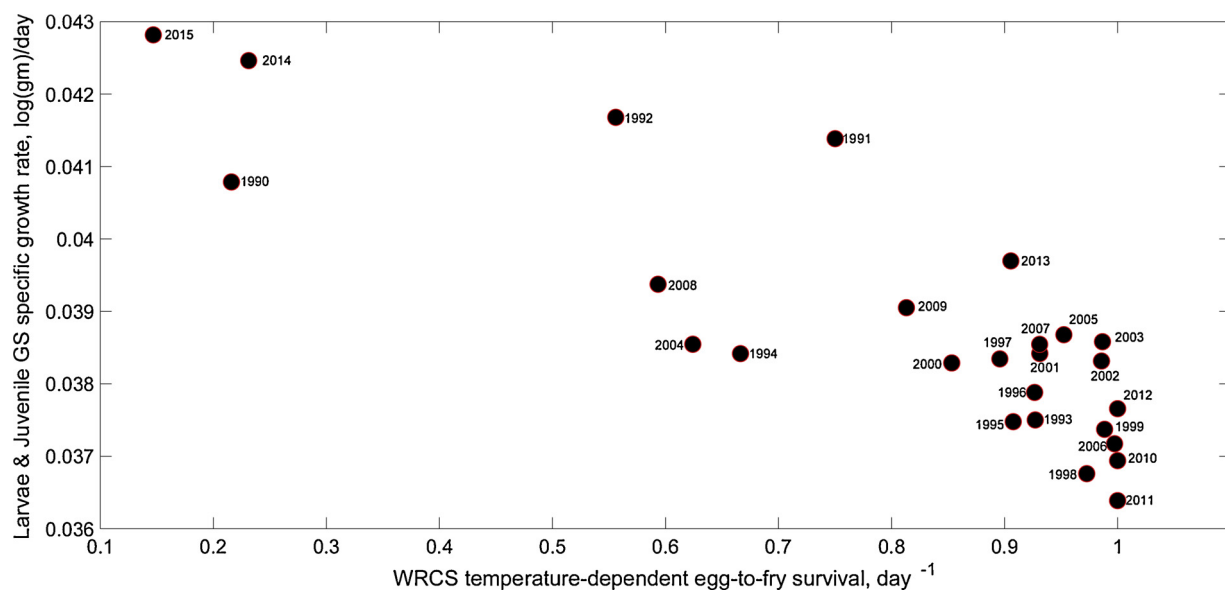
June) showed faster growth than those spawned near the Keswick Dam, and growth influences the timing of the outmigration of juvenile green sturgeon. Larval green sturgeon hatched further downstream from the dam experience higher water temperatures, which facilitates increased growth rates and the initiation of size-dependent processes at younger ages.

Our analysis also suggests that above 20 °C, feeding rate no longer increases with temperature, and as a result, growth rates decline. Additional studies at these higher temperatures would allow for a more robust model of growth performance above 20 °C.

#### 4.2. The DEBkiss model, assumptions, parameter estimation and results

In spite of the simplified structure, the DEBkiss model was able capture most of the variation in growth and field reproduction data (Figs. 3 and 4, and Supplementary material). The main simplifications of the DEBkiss model are the elimination of reserve dynamics and maturity as state variables. An energy reserve compartment would lead to a different shape of growth curve at fluctuating food levels (Kooijman et al., 2008), however, at constant food density, the standard DEB growth model collapses into von Bertalanffy growth curve. Fig. 3, show the consistency of our model with the standard DEB without including reserve dynamics and the results validate the first assumption of the DEBkiss model. Another simplification of the DEBkiss model is constant size at first reproduction. Due to lack of information on the size at first reproduction, we were unable to validate this assumption. However, different studies indicate that green sturgeon outmigration is triggered by transitional onset of saltwater tolerance (Heublein et al., 2017) and this physiological switch is size-dependent rather than age-dependent (Allen et al., 2011). This combination of findings provides some support for the conceptual premise that maturity does not need to be followed explicitly as a state variable.

The other important model assumption is the asymptotic temperature correction factor, Eq. (9), we applied for correcting the maximum area-specific assimilation rate,  $J_{Am}^a$ . We included the effect of temperature in the DEBkiss model by scaling the maximum area-specific assimilation rate ( $J_{Am}^a$ ) and the volume-specific maintenance costs ( $J_M^v$ ), exponentially, Eqs. (5) and (6). However, our initial fit indicated that the model strongly over-predicted the growth of juvenile green sturgeon at temperatures higher than 19 °C. The model captured the trend



**Fig. 8.** Specific growth rates of green sturgeon (g per day) vs. mean temperature-dependent egg-to-fry survival (per day) of SRWRC salmon for the year 1990 - 2015. The specific growth rate of GS is calculated for their first five months (i.e., from May 1<sup>st</sup> to September 31<sup>st</sup>) and assuming hatching of green sturgeon occurred at RBDD, 391 rkm (i.e., 95 km downstream from the Keswick Dam).

of the growth data for most of the studies we considered, however, there is a clear discrepancy between the model prediction and growth observations at higher temperatures (Fig. S2). Assuming feeding rate levels off above a critical temperature improved this fit (Fig. 5). Considering growth as net result of assimilation and maintenance, i.e., Eq. (2), the critical temperature of  $T_C = 20.52^\circ\text{C}$  is near the optimum temperature that maximizes growth. This finding suggests the optimal temperature for growth may be slightly higher than estimates from (Mayfield and Chech, 2004), who suggested that the optimum was between  $15^\circ\text{C}$  to  $19^\circ\text{C}$ . Mayfield and Chech (2004) reported that food consumption, growth, and food conversion efficiency generally increased with temperature between  $11^\circ\text{C}$  and  $15^\circ\text{C}$  but stayed constant between  $15^\circ\text{C}$  and  $19^\circ\text{C}$ . However, a recent laboratory experiment (Poletto et al., 2018) found that green sturgeon reared at  $19^\circ\text{C}$  grew at faster rates than those reared at  $16^\circ\text{C}$ . In a recent simulation study, Borin et al. (2017) reported that the mass-specific growth rate of a 20-year old adult green sturgeon increased with temperature until  $19^\circ\text{C}$  and declined above this temperature. In this study, the authors applied the Wisconsin bioenergetics model (Hanson et al., 1997) to investigate the effects of different environmental factors, including temperature, on the consumption and growth potential of green sturgeon inhabiting Willapa Bay, Washington. Key bioenergetics variables in this study were derived from the bioenergetics model parameters estimated for white sturgeon (Bevelhimer, 2002). However, studies have revealed that green sturgeon and white sturgeon have physiological and behavioral differences that might affect their bioenergetics directly and indirectly (Poletto et al., 2014), (Mayfield and Chech, 2004), (Verhille et al., 2014). For instance, Mayfield and Chech (2004) found that green sturgeon exhibited high metabolic rates relative to other sturgeon species. Thus, we speculate that green sturgeon and white sturgeon might have different energy allocation strategies, and these two species might have different optimal physiological performance temperatures. Our parameter estimation results also indicated that the  $Q_{10}$  value of green sturgeon,  $\sim 4.13$ , is higher than  $Q_{10}$  value reported to most biological systems (i.e.,  $Q_{10} = 2\text{--}3$ ); which makes green sturgeon sensitive for temperature changes.

#### 4.3. Limitations and directions for future improvements

The ultimate goal of this study was to provide a mechanistic modelling framework that can support the management and conservation of the endangered sDPS of green sturgeon. To this end, we demonstrated the applicability of the model based on two case studies presented. Despite this promising outcome, the practical implementation of the model as management tool requires more work.

One limitation of the model is that it does not account for indirect effects of temperature on food availability or predation. Goto et al. (2015) incorporated a sized-based predation component acting on juvenile shovelnose sturgeon (*Scaphirhynchus platorynchus*) to a model evaluating recruitment dynamics of a target population. As juvenile salmon survival during their outmigration is strongly influenced by predation within this same migration corridor (Johnson et al., 2017), it is likely that size-based predation and the influence of temperature on growth rate would produce survival/biomass/abundance metrics that also vary by spawning location or time. It is also possible juvenile green sturgeon can encounter additional natural and anthropogenic stressors, like environmental contaminants. Further research to investigate the combined effects of potential environmental stressors will improve the applicability of the model and help to develop a reliable analytical tool. Research on the effects of temperature on the survival of green sturgeon eggs, larvae, and juveniles will help to more clearly show the effects of the current water management practice on the population dynamics.

The other limitation worth to mention here is lack of feedback between feeding and food availability in the model. In laboratory, we can easily quantify the relationship between feeding rate and food availability and also the effect of temperature on the maximum feeding rate.

However, it is difficult to quantify this relationship for the field population, hence food availability is a function of different factors, including the effect of temperature on the searching/foraging abilities of green sturgeon. Presumably, in rivers sturgeon have to work much harder to find food than in the experiments.

The assumed downstream migration behavior of juvenile green sturgeon is an additional element of the model that needs further research. Currently little is known about factors affecting downstream migration of green sturgeon in the Sacramento River. We estimated the typical downstream migration behavior of a juvenile green sturgeon based on published laboratory experiments (Kynard et al., 2005), and our movement sub-model uses a simplistic assumption about age/size-dependent movement. Generally, our movement behavior sub-model is tied explicitly to body size, as individuals do not embark upon a downstream migration until they have reached 200 mm. Conversely, results of juvenile green sturgeon out-migrant studies suggest that their downstream migration is concurrent with high flow events (Poytress, personal communication). In reality, this environmental cue might apply to all individuals regardless of age or size. Thus, incorporating flow-based migration cues into our model would likely amplify the seasonal and spatial differences in size and growth rates resulting in even larger differences between seasonal or spatial differences in spawning/hatching/emergence locations and dates.

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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ecolmodel.2019.01.005>.

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