

Supporting Online Material for:

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APPENDIX S1: MODEL CONSRTRUCTION

This model is an expansion of classical, temperature-based, bioenergetics models (Hewett and Johnson, 1992; Hanson et al., 1997) to which we added direct and indirect effects of dissolved oxygen and salinity for all major bioenergetics components, following theory as described above.

Routine metabolism and food consumption

Food consumption and routine metabolism are frequently modeled as the product between a size-dependent maximum rate, $a \cdot W^b$, and a multiplicative function $f(T)$, which represents temperature controlling effect, scaled between 0 and 1 (Kitchell et al., 1977; Hanson et al., 1997). In our model, we added two multiplicative functions $f(DO)$ and $f(SAL)$, which accounted for the limiting effects of dissolved oxygen and the masking effects of salinity, respectively, yielding expanded equations with the form,

$$(Eq. 1) \quad FC \text{ or } RM = a \cdot W^b \cdot f(DO) \cdot f(SAL)$$

Where, W is individual fish weight (g), and a and b are empirical parameters.

We chose Thortnon and Lessem's (1978) algorithm to model $f(T)$ in both food consumption and routine metabolism sub-models. This widely used algorithm (Stewart et al., 1983; Stewart and Binkowski, 1986; Hartman and Brandt, 1995a; Hanson et al., 1997), corresponds to the product between point values from two antagonistic logistic curves: K_A and K_B . It allows for relative independence between increasing, decreasing and stationary sections of the response curve, according to the following set of general relationships, with unknown parameters K_1 , K_4 , LT_{98} and UT_{98} .

$$(Eq. 2) \quad f[T] = K_A \cdot K_B$$

$$(Eq. 3) \quad K_A = \frac{TK1 \cdot \exp[Y_A \cdot (T - T_1)]}{1 + \langle TK1 \cdot \exp[Y_A \cdot (T - T_1)] - 1 \rangle}$$

$$(Eq. 4) \quad K_B = \frac{TK4 \cdot \exp[Y_B \cdot (T_4 - T)]}{1 + \langle TK4 \cdot \exp[Y_B \cdot (T_4 - T)] - 1 \rangle}$$

$$(Eq. 5) \quad Y_A = \frac{1}{LT_{98} - T_1} \log_e \left[\frac{0.98 \cdot (1 - TK1)}{0.02 \cdot TK1} \right]$$

$$(Eq. 6) \quad Y_B = \frac{1}{T_4 - UT_{98}} \log_e \left(\frac{0.98 \cdot (1 - TK4)}{0.02 \cdot TK4} \right)$$

Where,

T = water temperature (°C)

T_1 = lowest tested temperature

T_4 = highest tested temperature

$TK1$ = estimated reaction rate multiplier at T_1

$TK4$ = estimated reaction rate multiplier at T_4

LT_{98} = estimated lower temperature threshold at which 98% of maximum rate is reached

UT_{98} = estimated upper temperature threshold at which reaction rate remains $\geq 98\%$ of maximum rate.

Functional responses to dissolved oxygen $f(DO)$ were described by a segmented sub-model composed by an increasing linear response predicted at the minimum tested DO_{SAT} (KO_1) to a threshold predicted at and above the critical DO level (DOC), whereafter routine metabolism or food consumption responses become independent to DO_{SAT} . KO_1 and DOC were modeled to be proportional functions of relative oxygen demand, scaled between 0 and 1. Here, an increased oxygen demand was expected to reduce KO_1 and increase DOC, i.e., to reduce physiological rates at the lower modeled DO_{SAT} and to increase the thresholds at which these rates become independent from DO_{SAT} . The general expression contains 3 empirical parameters; c , g and d , and becomes,

$$(Eq. 7) \quad f(DO) = \begin{cases} 1 - SL \cdot (DOC - DO)^c, & \text{if } DO < DOC \\ 1 & \text{if } DO \geq DOC \end{cases}$$

$$(Eq. 8) \quad SL = \frac{KO_1 - 1}{[0.01 \cdot (DOC - DO_1)]^c}$$

$$(Eq. 9) \quad KO_1 = 1 - d \cdot \exp(ROD - 1)$$

$$(Eq. 10) \quad DOC = 100 \cdot [1 - g \cdot \exp(-ROD)]$$

Where,

DO = dissolved oxygen saturation (%)

DO_1 = lowest tested DO_{SAT} (25%)

When modeling dissolved oxygen effects upon routine metabolism, i.e. $f(DO)_{RM}$, we considered relative oxygen demand (ROD_{RM}) to be proportional to the product between the temperature and salinity reaction rate functions. Thus,

$$(Eq. 11) \quad ROD_{RM} = f(T)_{RM} \cdot f(SAL)_{RM}$$

To compute ROD for the food consumption $f(DO)$ model, we assumed ROD to be proportional to all three routine metabolism multiplicative functions. Therefore,

$$(Eq. 0) \quad ROD_{FC} = f(T)_{RM} \cdot f(SAL)_{RM} \cdot f(DO)_{RM}$$

Salinity effects on routine metabolism $f(SAL)_{RM}$ were modeled as a U-shaped curve, following theoretical expectations about minimum osmoregulation costs circa iso-osmotic conditions (Morgan and Iwama, 1991), which were consistent with laboratory results in Atlantic and shortnose sturgeons (Niklitschek, 2001; Niklitschek and Secor, in review). This U-shaped response results from the product between two exponential curves: FSA_{RM} that represents the response to hyper-osmotic conditions and increases with salinity; and FSB_{RM} that represents the response to hypo-osmotic conditions and decreases with salinity.

Salinity effects are expected to decrease with fish size in proportion to the relative surface exposed to direct ionic interchange, i.e. gills and intestine (Brett, 1979; Pauly, 1981). In our salinity sub-model, we modeled the slopes of both osmoregulation curves (FSA_{RM} and FSB_{RM}) to decrease in proportion to the size-dependent reduction in specific gill surface area ($\text{cm}^2 \cdot \text{g}^{-1}$). The latter is an anatomical quantity that has been directly measured for several species (Pauly, 1981). The resulting salinity sub-model becomes,

$$(Eq. 13) \quad f(SAL)_{RM} = \frac{FSA_{RM} \cdot FSB_{RM}}{1.0201}$$

$$(Eq. 14) \quad FSA_{RM} = 1 + 0.01 \cdot \exp[h_{RM} \cdot W^{GSA} \cdot (S - S_{MIN})]$$

$$(Eq. 15) \quad FSB_{RM} = 1 + 0.01 \cdot \exp[i_{RM} \cdot W^{GSA} \cdot (S_{MIN} - S)]$$

Where,

h_{RM} , i_{RM} = empirical parameters to be estimated;

S_{MIN} = estimated salinity at which RM becomes minimal.

S = salinity

W = fish weight (g)

GSA = allometric exponent for gill surface area

At extreme salinities, osmoregulation costs reduce aerobic scope and, therefore it also reduces food consumption through $f(DO)_{FC}$. Besides this indirect effect, direct effects of salinity upon food consumption, $f(SAL)_{FC}$ have been reported for several species (Peters and Boyd, 1972; Boeuf and Payan, 2001; Wuenschel et al., 2004), including sturgeons (Allen and Cech, 2007; Niklitschek and Secor, in review). Such responses tend to follow dome-shaped curves, with maximum values expected around minimal routine metabolism (iso-osmotic conditions). For model consistency and flexibility of the algorithm we chose again Thorton and Lessem's (1978) algorithm (Eq. 5-Eq. 9), where parameters K_1 , K_4 , L_{98} and U_{98} became,

$$(Eq. 16) \quad K1 = SK1_{FC} = j_{FC} \cdot W^{GSA} = \text{size-dependent reaction rate at the lowest tested salinity}$$

$$(Eq. 17) \quad K4 = SK4_{FC} = k_{FC} \cdot W^{GSA} = \text{size-dependent reaction rate at the highest tested salinity}$$

Where,

J_{FC} , k_{FC} = estimated parameters

$L_{98FC} = U_{98FC} = S_{MIN}$

Egestion

We used Elliot's (1976) equation as a base model, to which we added a term that accounted for hypoxia effects showed to increase egestion rates (Niklitschek and Secor, in review). Here, the aerobic scope was represented by the quotient between DO_{SAT} and routine metabolism critical DO_{SAT} (Eq. 12). Due to practical convergence issues, we standardized temperature by the minimum tested temperature level (6°C). Thus, the modified model became,

$$(Eq. 18) \quad EG = FC_i \cdot \left[a_{EG} \cdot \left(\frac{T}{T_1} \right)^{c_{EG}} \cdot \left(\frac{DO}{DOC_{RM}} \right)^{d_{EG}} \cdot \left(\frac{FC_i}{FC_{max}} \right)^{g_{EG}} \right]$$

Where,

a_{EG} , c_{EG} , d_{EG} , g_{EG} = empirical parameters

FC_i = consumption rate

FC_{MAX} = maximum consumption rate predicted at a given combination of T, DO_{SAT} and SAL-

T	= temperature (°C)
T ₁	= minimum tested temperature (6°C)

Post-prandial metabolism

Postprandial metabolism (SDA) includes energy costs related to food digestion, absorption, transportation and, in a probably larger proportion, to protein synthesis and growth (Vahl, 1984; van Dam and Pauly, 1995; Secor, 2009). Although SDA has been sometimes computed as a proportion of food consumption, its close relationship to the energy cost of growth (Vahl, 1984) makes reasonable to think it would be better expressed as a proportion of assimilated energy (Hewett and Johnson, 1992; Hanson et al., 1997), following the equation,

$$(Eq. 19) \quad SDA = a_{SDA} \cdot (FC - EG)$$

Where a_{SDA} is the single estimated parameter, which represents the proportion of assimilated energy expended in post-prandial metabolism.

Temperature, dissolved oxygen and salinity effects are implicitly incorporated in Eq. 18 through their effects upon both FC and EG. Thus, fish would respond to limiting aerobic conditions by reducing SDA oxygen demand in the same proportion that assimilated energy is reduced due to the combined effect of lower food consumption and higher egestion rates. This mechanism is consistent with our modeling framework and laboratory observations in Atlantic sturgeon that showed SDA to be inversely related to egestion, particularly, under hypoxia (Niklitschek and Secor, in review).

Excretion

Excretion is one of the least sensitive and least variable parameters in bioenergetics models, which has been frequently modeled as a constant proportion of energy intake or calculated by difference (Kitchell et al., 1977; Hartman and Brandt, 1995b; Hanson et al., 1997). From theoretical considerations, we divided excretion into two major components: routine nitrogenous excretion rate (RNE) and exogenous nitrogenous excretion (XNE). While RNE corresponds to the total energy lost in nitrogenous sub-products (ammonia and urea) by starved fish, XNE represents energy losses from deamination of assimilated but non-metabolizable nitrogen. Thus, RNE is expected to be proportional to routine metabolism and XNE to food consumption. Assuming both components are additive, excretion rate (U) can be defined by the following equations,

$$(Eq. 20) \quad U = RNE + XNE$$

$$(Eq. 21) \quad RNE = a_{EX} \cdot RM^{b_{EX}} \quad (KJ \cdot g^{-1} \cdot d^{-1})$$

$$(Eq. 22) \quad XNE = c_{EX} \cdot FC \quad (KJ \cdot g^{-1} \cdot d^{-1})$$

Where

a_{EX} , b_{EX} = allometric parameters

RM = routine metabolism ($KJ \cdot g^{-1} \cdot d^{-1}$)

c_{EX} = excreted proportion of total energy intake

Activity cost

Bioenergetics theory addressing dissolved oxygen, temperature and salinity interactive effects upon activity cost are limited, although there is a consistent view that at a limited aerobic scope either food consumption, activity or both must be reduced to match oxygen availability (Jobling, 1981). Available models for activity cost can be classified into two main groups (Hanson et al., 1997): those based upon swimming speed (Rice et al., 1983; Stewart et al., 1983) and those that treat activity as a fixed proportion of standard/routine metabolism (Winberg, 1956; Kitchell et al., 1977).

Given limited availability of both theoretical basis and independent estimates for swimming activity we did not attempt any modeling approach based upon predicted swimming speed. We compared, instead, the relative adequacy of the traditional routine metabolism multiplier against an alternative model where activity cost was expressed as a fixed proportion of maximum food consumption rate. In the later case we considered that proportionality between routine and active metabolism might not be sustained under hypoxia, while both maximum (potential) food consumption and activity rates should be similarly affected by a reduced aerobic scope. Thus, activity cost, expressed as an additive quantity in the balance energy equation (Hartman and Brandt, 1995b), was approximated by the following alternative models

$$(Eq. 23) \quad ACT = a_{ACT} \cdot RM$$

or

$$(Eq. 24) \quad ACT = a_{ACT} \cdot FC_{MAX}$$

Where a_{ACT} corresponds to the estimated proportionality coefficient between activity cost and either routine metabolism or maximum food consumption (full ration size) predicted at a given combination of T, DO_{SAT} , and SAL.

APPENDIX S2: JUVENILE ATLANTIC STURGEON BIOENERGETICS MODEL

Special considerations regarding the general model proposed in Appendix S1.

1. Within the tested range, no inhibitory effects of high temperature upon routine metabolism were observed. Thus, we set $KB_{RM}=1$, making $f(T)_{RM}=KA_{RM} \cdot 1$, which required of estimating two parameters: $TK1_{RM}$ and $LT98_{RM}$.
2. A constant value of -0.158 was used for specific gill surface area (GSA) after Burggren et al.'s (1979) work on *Acipenser transmontanus*.
3. No plateau was evident in food consumption at high temperature, and the model failed to estimate feasible values for $UT98_{RM}$, which was set equal to $LT98_{RM}$. Therefore, applied algorithm had only 3 parameters: $TK1_{RM}$, $LT98_{RM}$ and $TK4_{RM}$.
4. We failed to produce a significant estimate for the ration size effect parameter (g_{EG}) in the egestion sub-model. Therefore, ration effects were ignored by setting $g_{EG}=0$.
5. Parameters a_{EX} and c_{EX} , belonging to equations 22 and 23, respectively, were obtained from published work in other Acipenserids (Dawrowski et al., 1987; Salin and Williot, 1991; Gershanovich and Pototskij, 1992; 1995; Cui et al., 1996). a_{EX} was scaled to our own routine metabolism results following the relationship,

$$(Eq. 25) \quad a_{EX} = \frac{1}{n} \sum_{i=1}^n \frac{RNE_i}{RM_i}$$

Where,

RNE_i = routine nitrogenous excretion in datum i from sturgeon literature.

RM_i = predicted routine metabolism (this work) at similar conditions.

6. Activity cost was estimated indirectly from growth-consumption experiments, as the value required to balance fish energy budget (Bosclair and Legget, 1989; Hartman and Brandt, 1995b; Guénard et al., 2008). This apparent activity cost involved all spontaneous or induced fish movements not accounted for as routine metabolism. For this purpose, we used equations 4 to 23 for estimating routine metabolism, SDA, egestion and excretion for each growth-consumption pair of observations, i , and then compute ACT following the equation,

$$(Eq. 26) \quad AM_i = g_i - [FC_i - \hat{R}\hat{M}_i + \hat{S}\hat{D}A_i + \hat{E}_i + \hat{U}_i]$$

7. Energy content (E , kJ g^{-1}) was either measured or computed using an empirical relationship (Niklitschek, 2001) based upon observed fish weight (W_o), expected fish weight (W_E , as predicted from a verified length weight relationship) and total length (TL). Thus,

$$(Eq. 27) \quad \log_e(E) = 0.1 + 0.6 \cdot W_r + 0.25 \cdot \log_e(W_o)$$

where,

$$W_r = \frac{W_o}{W_E}$$

$$W_E = 0.00205 \cdot TL^{3.12}$$

Full model specification (parameter estimates and definitions in Table S1)

Routine Metabolism Model

$$RM = a_{RM} \cdot W^{b_{RM}} \cdot f(T)_{RM} \cdot f(DO)_{RM} \cdot f(SAL)_{RM}$$

$$f(T)_{RM} = \frac{TK1_{RM} \cdot \exp[Y_A \cdot (T - T_1)]}{1 + TK1_{RM} \cdot [\exp(Y_A \cdot (T - T_1)) - 1]}$$

$$Y_A = \frac{1}{LT98_{RM} - T_1} \log_e \left(\frac{0.98 \cdot (1 - TK1_{RM})}{0.02 \cdot TK1_{RM}} \right)$$

$$f(DO)_{RM} = \begin{cases} 1 - SL_{RM} \cdot (DOC_{RM} - DO)^c, & \text{if } DO < DOC_{RM} \\ 1, & \text{if } DO \geq DOC_{RM} \end{cases}$$

$$SL_{RM} = \frac{KO1_{RM} - 1}{[0.01 \cdot (DOC_{RM} - DO_1)]^c}$$

$$DOC_{RM} = 100 \cdot [1 - g_{RM} \cdot \exp(-f(T)_{RM} \cdot f(SAL)_{RM})]$$

$$KO1_{RM} = 1 - d_{RM} \cdot \exp[f(T)_{RM} \cdot f(SAL)_{RM} - 1]$$

$$f(SAL)_{RM} = \frac{FSA_{RM} \cdot FSB_{RM}}{1.0201}$$

$$FSA_{RM} = 1 + 0.01 \cdot \exp[h_{RM} \cdot W^{GSA} \cdot (S - S_{MIN})]$$

$$FSB_{RM} = 1 + 0.01 \cdot \exp[i_{RM} \cdot W^{GSA} \cdot (S_{MIN} - S)]$$

Food Consumption Model

$$FC = a_{FC} \cdot W^{b_{FC}} \cdot f(T)_{FC} \cdot f(DO)_{FC} \cdot f(SAL)_{FC}$$

$$f[T]_{FC} = K_A \cdot K_B$$

$$K_A = \frac{TK1_{RM} \cdot \exp[Y_A \cdot (T - T_1)]}{1 + \langle TK1_{RM} \cdot \exp[Y_A \cdot (T - T_1)] - 1 \rangle}$$

$$Y_A = \frac{1}{LT98_{RM} - T_1} \log_e \left[\frac{0.98 \cdot (1 - TK1_{RM})}{0.02 \cdot TK1_{RM}} \right]$$

$$K_B = \frac{TK4_{RM} \cdot \exp[Y_B \cdot (T_4 - T)]}{1 + \langle TK4_{RM} \cdot \exp[Y_B \cdot (T_4 - T)] - 1 \rangle}$$

$$Y_B = \frac{1}{T_4 - UT98} \log_e \left(\frac{0.98 \cdot (1 - TK4)}{0.02 \cdot TK4} \right)$$

$$KS_A = \frac{SK1_{RM} \cdot \exp[Y_A \cdot (Sal - S_1)]}{1 + \langle SK1_{RM} \cdot \exp[Y_A \cdot (Sal - TS_1)] - 1 \rangle}$$

$$Y_A = \frac{1}{S_{MIN} - S_1} \log_e \left[\frac{0.98 \cdot (1 - SK1_{RM})}{0.02 \cdot SK1_{RM}} \right]$$

$$KS_B = \frac{SK4_{RM} \cdot \exp[Y_B \cdot (S_4 - S)]}{1 + \langle SK4_{RM} \cdot \exp[Y_B \cdot (S_4 - S)] - 1 \rangle}$$

$$Y_B = \frac{1}{S_4 - S_{MIN}} \log_e \left(\frac{0.98 \cdot (1 - SK4)}{0.02 \cdot SK4} \right)$$

Egestion Model

$$EG = FC_i \cdot \left[a_{EG} \cdot \left(\frac{T}{T_1} \right)^{c_{EG}} \cdot \left(\frac{DO}{DOC_{RM}} \right)^{d_{EG}} \cdot \left(\frac{FC_i}{FC_{max}} \right)^{g_{EG}} \right]$$

Postprandial Metabolism Model

$$SDA = a_{SDA} \cdot (FC - EG)$$

Excretion Model

$$U = RNE + XNE$$

$$RNE = a_{EX} \cdot RM^{b_{EX}} \text{ (KJ} \cdot \text{g}^{-1} \cdot \text{d}^{-1}\text{)}$$

$$XNE = c_{EX} \cdot FC \text{ (KJ} \cdot \text{g}^{-1} \cdot \text{d}^{-1}\text{)}$$

Active Metabolism Model

$$ACT = a_{ACT} \cdot FC_{MAX}$$

Table S1: Atlantic sturgeon bioenergetics model parameters estimated from Niklitschek & Secor's (in review) and Niklitschek's (2001) experimental results. See Appendix S2 for bioenergetic sub-models equations. Excretion parameters were averaged and adapted from other authors (no standard errors provided). Other parameters lacking standard errors have been set to nominal values as detailed in model application section.

Parameter	Definition	Estimated value \pm SE
<u>Routine metabolism (RM)</u>		
a_{RM}	Allometric intercept (scaling coefficient)	0.52 \pm 0.092
b_{RM}	Allometric slope	-0.17 \pm 0.022
TK1 _{RM}	Reaction rate multiplier at the lowest tested temperature (6°C)	0.14 \pm 0.017
LT98 _{RM}	Lower temperature threshold where $f(T)_{RM} \geq 0.98$	0.38 \pm 0.094
c_{RM}	Dissolved oxygen response shape parameter	1 \pm 0.26
d_{RM}	Proportionally constant for reaction rate at lowest DO _{SAT}	0.75 \pm 0.097
g_{RM}	Proportionally constant for DOC _{RM}	0.27 \pm 0.051
h_{RM}	Hiperosmotic response coefficient	0.4 \pm 0.14
i_{RM}	Hiposmotic response coefficient	9 \pm 3.2
SAL _{MIN}	Salinity at which minimum osmoregulation cost is predicted	0.52 \pm 0.092
GSA	Specific gill surface area	-0.17 \pm 0.022
<u>Food consumption (FC)</u>		
a_{FC}	Allometric intercept (scaling coefficient)	1 \pm 0.1
b_{FC}	Allometric exponent	-0.2 \pm 0.019
TK1 _{FC}	Reaction rate multiplier at the highest tested temperature (6°C)	0.2 \pm 0.035
TK4 _{FC}	Reaction rate multiplier at the lowest tested temperature (28°C)	0.6 \pm 0.12
LT98 _{FC}	Lower temperature threshold where $f(T)_{FC} \geq 0.98$	2.61 \pm 0.088
c_{FC}	Dissolved oxygen response shape parameter	1
d_{FC}	Proportionally constant for reaction rate at lowest DO _{SAT}	2.5 \pm 0.46
g_{FC}	Proportionally constant for DOC _{RM}	0.73 \pm 0.072
j_{FC}	Size-dependent intercept for reaction rate at the lowest salinity	7
k_{FC}	Size-dependent intercept for reaction rate at the highest salinity	0.25 \pm 0.045
<u>Post-prandial metabolism (SDA)</u>		
a_{SDA}	Proportionality constant (to assimilated energy)	0.157 \pm 0.0093
<u>Active metabolism (ACT)</u>		
a_{ACT}	Proportionality constant to food consumption	0.29 \pm 0.041
<u>Egestion (EG)</u>		
a_{EG}	Scale parameter for egestion	0.3 \pm 0.12

Parameter	Definition	Estimated value \pm SE
c_{EG}	Dissolved oxygen effect exponent	-0.8 \pm 0.27
d_{EG}	Temperature effect exponent	-0.6 \pm 0.24
g_{EG}	Ration size effect exponent	0
<u>Excretion (U)</u>		
a_{EX}	RNE, scaling factor	0.0557
b_{EX}	RNE, exponent	-0.29
d_{EX}	XNE, FC proportionality coefficient	0.0392

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