Dissolved oxygen, temperature and salinity effects on the ecophysiology and survival of juvenile Atlantic sturgeon in estuarine waters: II. Model development and testing

Edwin J. Niklitschek [a,*], David H. Secor [b]

[a] Universidad Austral de Chile, Centro Trapananda, Portales 73, Coyhaique, CP 5950000, Region of Aysen, Chile
[b] University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, 1 Williams Street, P.O. Box 38, Solomons, MD 20688, USA

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ABSTRACT

Hypoxia–temperature interactions can have major effects upon fish physiology and energetics. In estuarine species, such effects can be also modified by natural salinity gradients leading to a three-way habitat contraction under extreme conditions. In this paper we use Fry's paradigm to propose an explanatory framework and to expand traditional mass balance bioenergetic models, incorporating dissolved oxygen and salinity effects. Water temperature was modeled as the controlling factor that establishes maximum potential rates and minimum oxygen demand; dissolved oxygen was considered to constrain physiological responses whenever oxygen demands exceed oxygen delivery rates; salinity was incorporated as a masking (loading) factor, demanding both energy and oxygen for osmoregulation processes. This general framework was expressed as a set of algorithms, with a total of 30 parameters, which were estimated using results from a large set of laboratory experiments conducted on young-of-the-year and yearling Atlantic sturgeons, as well as from other published studies. Compared to an empirical quadratic fit of these laboratory data, the model was more informative (lower AIC), suggesting that measured responses followed theoretical expectations. The model was tested in mesocosm trials, where strong correlations were observed between predicted and observed monthly and seasonal growth rates but modest to poor correlations were observed for predicted daily instantaneous growth rate. Sensitivity tests showed that uncertainty in activity cost and food consumption ratio parameters contributed most to model error.

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1. Introduction

Dissolved oxygen, temperature and salinity are key environmental factors affecting most physiological and many ecological responses in estuarine species. A relevant fraction of such effects can be generalized in the form of single bioenergetic responses or integrated bioenergetic models describing energy flow within individuals (Brett, 1979). Further, bioenergetics has been intimately linked with population dynamics and fitness by considering the ratio of instantaneous mortality over growth ($\mu\ G^{-1}$) as an integral that can relate habitat to cohort production (Werner et al., 1983; MacCall, 1989; Heath, 1996; Houde, 1997; Secor, 1999). As a result, bioenergetic models, largely based upon Winberg's (1956) energy balance equation, have been shown to be useful tools for testing ecological hypotheses (Kitchell and Breck, 1980; Stewart et al., 1981; Brandt, 1993; Hartman and Brandt, 1995b; Kitchell et al., 1997; Essington et al., 2002), indexing habitat quality (Brandt and Kirsch, 1993; Mason et al., 1995; Hondorp and Brandt, 1996) and fisheries management (Johnson et al., 1992; Hansen et al., 1993; Luo et al., 2001). In more recent years, bioenergetic approaches have also been used for

reconstructing and forecasting the effects of environmental stressors such as hypoxia and climate change on fishes (Niklitschek and Secor, 2005; Woodland et al., 2009).

Largely influenced by freshwater species investigations (Kitchell et al., 1974, 1977; Stewart et al., 1981) and available software (Hewett and Johnson, 1992; Hanson et al., 1997), most published bioenergetic models have focused on forage and temperature as key environmental factors (Bosclair and Sirois, 1993; Hansen et al., 1993; Hartman and Brandt, 1995a; Bevelhimer, 2002). Although other factors such as dissolved oxygen and salinity are well known to play key roles in the bioenergetics of estuarine species (Lankford and Targett, 1994; Neill et al., 1994; Luo et al., 2001; McKenzie et al., 2001; Wuenschel et al., 2004a,b; Stierhoff et al., 2006; Del Toro-Silva et al., 2008), limited advances have been made in extending such models to incorporate additional environmental factors. A noticeable exception is the Ecophys.Fish model, which contains a set of empirical relationships that incorporate temperature, salinity, dissolved oxygen (DO), pH and food effects into a mass balance model suitable for estuarine fishes (Neill et al., 2004). Parallel efforts made in this direction have included Niklitschek's (2001) and Wuenschel's (2002) dissertation work, both of which are unpublished thus far.

In the present work we provide model development and testing for a theory-based bioenergetic model developed by Niklitschek (2001),

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* Corresponding author. Tel.: +56 67 23127; fax: +56 67 233397.
E-mail address: eniklits@uach.cl (E.J. Niklitschek).

which was subsequently applied in studies of sturgeon nursery habitat suitability by Niklitschek and Secor (2005) and Woodland et al. (2009). Here, we specify an underlying theoretical basis for the inclusion of DO and salinity in bioenergetic models and develop predictive equations that may have general use for estuarine fishes, but focus in applying this model to juvenile Atlantic sturgeon *Acipenser oxyrinchus*. This species was chosen because of its known sensitivity to the interactions of DO, temperature and salinity, and because hypoxia has been identified as a principal factor limiting the recovery of this threatened species (Secor and Gunderson, 1998; Collins et al., 2000). Model parameters for juvenile Atlantic sturgeon were estimated using laboratory measured responses, reported in a companion paper (Niklitschek and Secor, 2009-this issue). We contrasted the goodness of fit in our model against a purely empirical fit using a multinomial regression model, and evaluated model sensitivity to uncertainty in parameter estimation. Finally, we conducted an independent test of the model against a new data set obtained from a 4-mo mesocosm study.

2. Methods

2.1. Model framework

Our overall modeling approach was based upon a balanced energy equation (Winberg, 1956; Kitchell et al., 1977), constrained by aerobic scope and described by the general form,

$$G = FC - (RM + SDA + ACT) - (EG + U) \qquad (1)$$

where, G = growth, FC = food consumption, RM = routine metabolism, ACT = activity cost, SDA = postprandial metabolism (classically named specific dynamic action), EG = egestion, and U = excretion. Dissolved oxygen, temperature and salinity effects upon bioenergetic components from Eq. (1) were modeled using the conceptual framework proposed by Fry (1971), which classifies environmental factors in five categories: controlling, limiting, masking, lethal and directive factors. Controlling factors (e.g., temperature, pH) set the potential rate of biochemical reactions. Limiting factors are resources (e.g., oxygen, ration) that, when insufficient, restrict such reaction rates. Masking factors (i.e., salinity) impose additional energy expenditures that increase standard metabolism. Lethal factors (e.g., severe hypoxia, toxins) induce short-term animal death. Finally, directive factors (e.g., photoperiod) guide fish behavior or induce physiological changes. Below we describe the theoretical framework of the bioenergetic model. Details of actual model construction are given in Appendix S1.

Following Fry's (1971) paradigm and traditional bioenergetic models (Hanson et al., 1997), we incorporated temperature as the main controlling factor, which determines the maximum rates for food consumption, routine metabolism and egestion. Through these direct effects upon predicted FC, RM and EG, temperature also affects activity cost, postprandial metabolism and excretion rates, which were modeled to be proportional to one or more of the first three components (FC, RM, EG). Temperature effects upon food consumption and routine metabolism reaction rates were modeled using Thornton and Lessem's (1978) algorithm, while its effects upon egestion rate were included into a modified version of Elliot's (1976) equation (see Appendix S1).

We included dissolved oxygen as a limiting factor that sets an upper limit for total metabolism under hypoxia. Although anaerobic responses to hypoxia are feasible as immediate short-term responses, such responses are not sustainable if total oxygen demand (OD) due to metabolic processes (RM, ACT and SDA) exceeds the maximum oxygen delivery rate (DO_{IN}). This assumption implies the inequality,

$$RM_{OD} + ACT_{OD} + SDA_{OD} \leq DO_{IN}. \qquad (2)$$

Given Eq. (2), we assumed that, under limited oxygen supply, basal metabolism required to sustain vital processes is prioritized over all remaining energy/oxygen expenditures. Thus, the aerobic scope (AS) available for activity and growth corresponds to the difference between potential (maximum) oxygen delivery rate (DO_{IN}) and basal metabolic oxygen demand, which can be approximated by routine metabolic oxygen demand (RM_{OD}) for practical purposes (Fig. 1). This concept of aerobic scope is closely related, although not fully equivalent, to the concept of metabolic scope, which is defined as the difference between maximum (active) metabolic and basal metabolic rates (Fry, 1971; see also Neill et al., 2004). When maximum metabolism becomes limited by oxygen delivery rate, both quantities (aerobic scope and metabolic scope) become directly proportional to each other.

From previous considerations, we forecast strong interactions between dissolved oxygen, temperature and salinity effects upon aerobic scope. While dissolved oxygen saturation limits potential oxygen delivery rate (DO_{IN}), temperature controls baseline oxygen demand (RM_{OD}), which is loaded by the extra cost of osmoregulation imposed by the corresponding salinity level. Under moderate hypoxia, aerobic scope decreases and TM_OD might exceed DO_IN (Fig. 1). Here, ACT and SDA are necessarily diminished, while RM might remain unaffected. Below critical DO levels, RM will also be reduced, first by lowering spontaneous activity (Crocker and Cech, 1997), and then by initiating anaerobic production of ATP to sustain vital processes such as ion equilibrium and membrane polarity, until acidosis reached lethal levels (Nilsson and Östlund-Nilsson, 2008).

To model hypoxia effects upon RM and FC reaction rates, we constructed a simple mathematical expression (Appendix S1, Fig. 2), defined by two biologically relevant points: the critical DO threshold (DOC) at which decreasing DO_{SAT} starts to affect RM or FC, and the reaction rate at the lowest tested DO_{SAT} level (KO1). Both points were modeled to be functions of metabolic oxygen demand, as detailed in Appendix S1. Postprandial metabolism (SDA) was modeled as a constant proportion of assimilated energy (and nutrients), which decreases under hypoxia due to both curtailed food consumption (FC) and increased egestion rates (EG) (Appendix S1). Such proportionality results from presumed feedback regulation mechanisms connecting aerobic scope, metabolism, stomach fullness, intestinal irrigation and food consumption (Jobling, 1981). Under hypoxia, a limiting aerobic scope would reduce anabolism and intestinal irrigation, therefore curtailing intestinal absorption and SDA, while increasing the egested fraction of consumed food. As a result, appetite, food intake and assimilation rates would be also reduced, maintaining
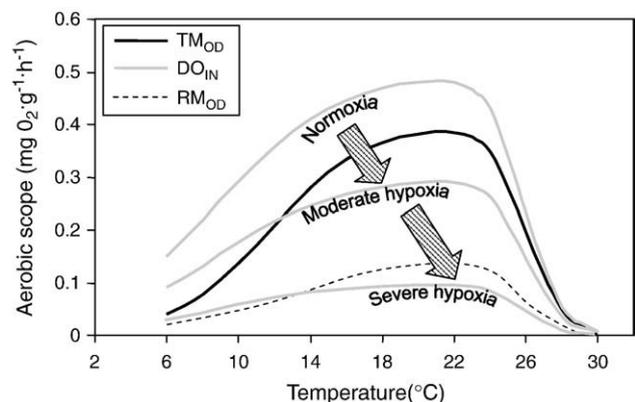

Fig. 1. Aerobic scope (mg O$_2$ g^{-1} h^{-1}) for growth and activity under three scenarios (long-term responses). Under normoxia, maximum oxygen delivery rate (DO_{IN}) exceeds total metabolism oxygen demand (TM_{OD}); thus total metabolism reaches its full potential in response to directive and masking factors. At moderate hypoxia, total metabolism becomes limited by DO_{IN}, and locomotory activity and/or growth rates are reduced, although routine metabolism oxygen demand (RM_{OD}) is still satisfied. Below critical DO level, routine metabolism is limited by hypoxia and vital functions cannot be sustained.
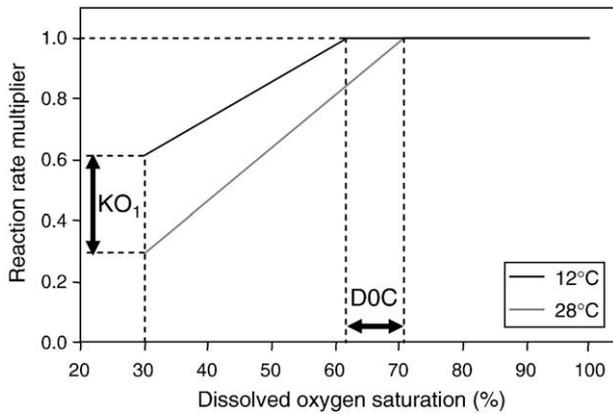
Fig. 2. Schematic representation of modeled routine metabolism and food consumption responses to dissolved oxygen saturation. KO_1 represents reaction rate at the minimum tested DO_{SAT} level, while DOC represents the lower DO_{SAT} threshold at which reaction rate becomes independent from DO_{SAT}. Although both KO_1 and DOC were modeled as functions of temperature and salinity, only temperature effects are represented in this diagram.

amino acid and free radical concentrations in the blood below toxic levels (Jobling, 1981; van Dam and Pauly, 1995).

As a second addition to traditional bioenergetic models we incorporated the effects of salinity (a masking factor) associated to the increased cost of osmoregulation (Fry, 1971). We modeled this as a "loading effect" (Neill et al., 2004) that increases routine metabolism at both hyper- and hypo-osmotic salinities (Fig. 3), causing a reduction both in aerobic scope and surplus energy available for activity and growth. As a result, SDA and therefore food consumption rates would decrease. Besides such interactions, there is strong evidence of direct salinity effects upon food consumption rates from several field and laboratory studies (Peters and Boyd, 1972; Lankford and Targett, 1994; Swanson, 1998; Boeuf and Payan, 2001; Imsland et al., 2001; Wuenschel et al., 2004a; Rubio et al., 2005; Niklitschek and Secor, 2009-this issue). Such an outcome might result from reduced intestinal irrigation to reduce ion-interchange or from endocrinous responses to salinity (cortisol, GH, prolactin), observed in salmonids and other species (Ron et al., 1995; Nakano et al., 1998; Kelly and Woo, 1999; Boeuf and Payan, 2001). Since food consumption
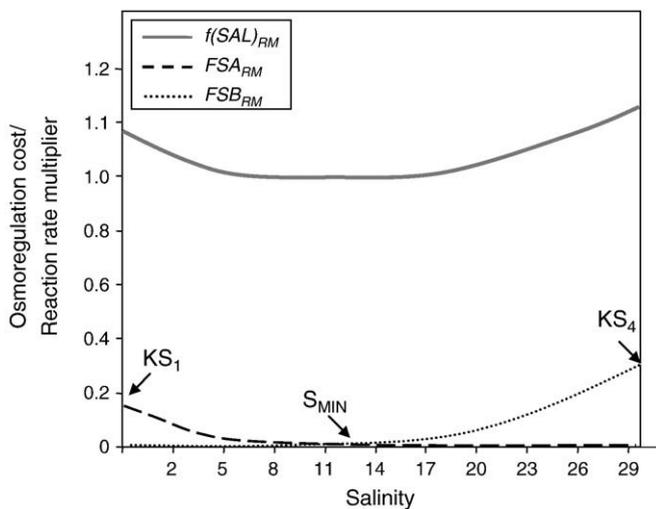
responses to salinity are highly variable between species (Imsland et al., 2001), we used again Thornton and Lessem's (1978) algorithm as a very flexible model, to incorporate these direct salinity effects into our food consumption sub-model (Appendix S1).

2.2. Model application

We applied the proposed model (Appendix S1) and estimated corresponding parameters from the raw data set of laboratory results for young-of-the-year (YOY) and age 1 (yearling) Atlantic sturgeon described by Niklitschek and Secor (2009-this issue). In that work, we measured temperature, dissolved oxygen and salinity effects upon all major bioenergetic components except excretion and activity. Conservative values were assumed for excretion losses, although scaled to our routine metabolism laboratory results. Activity cost proportionality coefficient was estimated using a balance equation approach and observed consumption-growth, as described in Appendix S2.

All parameters within each bioenergetic sub-model (Appendix S2) were simultaneously estimated by non-linear mixed regression (NLMIXED procedure) in SAS 9.1 (SAS Institute, 2004). This platform allowed us to implement a Gauss–Newton iterative method, within a maximum likelihood framework, where we accounted for correlation within experimental runs by including them as a random source of covariance in the mixed model (Littel et al., 1996). We used an information theory approach (Akaike's information criteria; AIC) for model comparison (Burnham and Anderson, 2002). Because some sub-models used predicted responses from other sub-models, the overall fitting procedure followed the required sequence: RM→FC→EG→SDA→U→ACT. Estimated model parameters are reported in Table S1, while a full and explicit formulation of the applied model is specified in Appendix S2, along with special considerations related to this particular application of the proposed model to juvenile Atlantic sturgeon.

2.3. Model assessment

2.3.1. Laboratory results

We compared the goodness of fit between proposed food consumption, routine metabolism and egestion sub-models against alternative, purely empirical, regression sub-models, which followed the general polynomial form,

$$Y = \beta_0 + \beta_1 \cdot T + \beta_2 \cdot T^2 + \beta_3 \cdot DO_{SAT} + \beta_4 \cdot DO_{SAT}^2 + \beta_5 \cdot SAL + \beta_6 \cdot SAL^2 + \beta_7 \cdot \log_e(W).$$

Goodness of fit comparison was based upon Akaike's information criteria, which penalizes overfitting (due to increased number of parameters) and has been shown to be theoretically sound and robust under a range of modeling situations, including maximum likelihood procedures to what it is naturally related (Burnham and Anderson, 2002).

To provide a more intuitive index for the quality of the fit, we also computed the proportion of the total variance observed in the laboratory data that was explained by each sub-model, according to the relationship,

$$EV_{\%} = 100 \cdot \left[1 - \frac{\sum \left(Y_i - \hat{Y}_i \right)^2}{\sum (Y_i - \bar{Y})^2} \right] \tag{3}$$

where,

$EV_{\%}$	explained variance (%)
Y_i	measured value at observation i
$\hat{Y}_i$	model predicted value for observation i.

Fig. 3. Schematic representation of modeled routine metabolism responses to salinity, $f(SAL)_{RM}$. Hyper-osmotic (FSA_{RM}) and hypo-osmotic (FSB_{RM}) osmoregulation costs are scaled to zero at iso-osmotic conditions (SAL_{MIN}), reaching maximum values of KS_4 and KS_1 at maximum and minimum tested salinities, respectively. $f(SAL)_{RM}$ represents the increment in routine metabolism relative to iso-osmotic conditions, where the function reaches a value of 1.

2.3.2. Error analysis

To evaluate the sensitivity of bioenergetic models to experimental error and parameter uncertainty, we conducted a series of error analyses (Bartell et al., 1986) based upon a Monte Carlo simulation approach. A total of 5000 samples were randomly obtained for each parameter probability distribution function, under the assumption of normal or log-normal error distributions (depending upon each sub-model formulation), using estimated standard errors as surrogates for actual standard deviations. We assumed independence between parameters for all sub-models, with the exception of food consumption, routine metabolism and egestion, where correlation between some parameters exceeded $r = 0.7$. For each of these three sub-models we used restricted maximum likelihood covariance estimates (Littel et al., 1996) to generate a Cholesky matrix suitable to simulate correlated parameter values. Since we lacked reliable estimates for uncertainty in excretion parameters, we arbitrarily set standard errors at 20% of the mean parameter estimates.

The random perturbations of each parameter were combined to generate equal number of daily growth predictions. Growth dependance upon model parameters was then analyzed through multiple linear regression, using relative partial sum of squares ($RPSS_{\%}$) as the main ranking criteria. We defined $RPSS_{\%}$ as the percent of the residual variance explained by a given parameter, after adjusting for the effects of all the other parameters in the model (Bartell et al., 1986). To evaluate whether the sensitivity of the model depended upon the particular set of environmental variables considered for forecasting bioenergetic responses, we repeated the described error analysis procedure under four water quality scenarios, representing optimal, hypoxia, high salinity and high temperature conditions (Table 1).

2.3.3. Mesocosm validation

A mesocosm validation experiment was conducted to test model predictions against a data set that was independent from the one used for estimating model parameters and represented a higher degree of realism. Four mesocosm trials were conducted in outdoor 3200-L tanks with 10 fish each; trials lasted 130 days between March and July 1999. Tanks received ambient brackish water from the Patuxent River, with temperature, salinity and dissolved oxygen varying according to natural river conditions and monitored at least three times a day. Oxygen saturation reached super-saturation levels at noon during March, probably due to enhanced primary production (Table 2). The fish were fed Biokyowa® pellets three times a day, a ration equivalent to 1.3 times the maximum daily consumption rate predicted by the bioenergetic model. Actual consumption was not assessed due to tank size and water turbidity.

Individual weight and total length were recorded once a week. Five fish from the initial stock and three fish from each tank were sacrificed at the beginning and at the end of each experiment and used to estimate energy content through a modified Maciolek's (1962) technique (Niklitschek, 2001). Spearman's correlation was used to evaluate parallelism between observed and predicted growth rates. A t-test (alpha = 0.05) was used to evaluate if final weights were significantly different from model predictions for each tank.

Table 1
Simulated water quality conditions used for error analysis of the Atlantic sturgeon bioenergetic model.

Scenario #	Temperature (°C)	Salinity	Dissolved oxygen (%)	Environmental conditions represented
1	23	9	100	Optimal
2	23	9	40	Hypoxia
3	28	9	100	High temperature
4	23	29	100	High salinity

Table 2
Average and range of water quality conditions in mesocosm experiments for Atlantic sturgeon.

Variable	Mean ± SD	Range
Salinity	13.2 ± 1.3	11.3–15.5
Temperature (°C)	18.3 ± 6.1	4.5–28.7
Oxygen saturation (%)	102.5 ± 9.2	78.4–127.5

3. Results

3.1. Application to laboratory results

The routine metabolism sub-model explained 78% of the variance observed in laboratory results (AIC = 76.5), outperforming the multiple linear regression model (AIC = 87.9). Predicted routine metabolism showed a sigmoid response to temperature, with a maximum rate predicted at 38 °C, beyond the highest tested temperature of 28 °C (Fig. 4). Predicted RM responses were clearly affected by the hypoxia-temperature interaction. For instance, at salinity 8, a temperature increase from 6 °C to 28 °C produced a rise in critical oxygen threshold (DOC) from 46 to 74% DO_{SAT}. Modeled routine metabolism increased towards low and high salinity conditions, with minimum values estimated at salinity 9 ± 2.9 (Fig. 4). These loading effects of salinity were equivalent to an increase of 5 and 29% in routine metabolism at salinities 1 and 29, respectively (100% DO_{SAT}).

The food consumption sub-model explained 66% of observed variance and was more informative (AIC = 52.7) than the alternative linear regression model (AIC = 132.1). Food consumption was predicted to increase with temperature, mostly from 6 to 20 °C (Fig. 5). As temperature exceeded 26 °C, predicted consumption rates were sharply reduced. In agreement with observed responses, the sub-model predicted very strong effects and interactions between dissolved oxygen and temperature upon food consumption (Fig. 5). The critical level (DOC) for food consumption increased with temperature, reaching values of 34 and 66% DO_{SAT} for 6 and 28 °C, respectively. Highest consumption rates were predicted to occur close to iso-osmotic conditions (salinity 9), with the lowest food consumption rates predicted at the highest tested salinity (29). These inhibiting effects of salinity were equivalent to 42% and 60% of maximum food consumption at salinities 1 and 29, respectively.

Although the egestion sub-model performed much better (AIC = 20.3) than its alternative multiple linear regression model (AIC = 92.5), it explained only 29% of observed variance in experimental results. Egestion ratio was predicted to increase by c. 50% between normoxia and hypoxia (40% DO_{SAT}, Fig. 6). As an example, at 20 °C and salinity 9, predicted egestion ratio for a 20-g fish increased from 6.3 to 12.4%, when DO_{SAT} was reduced from 100% to 40%. The SDA model explained 52% of observed variance and was more informative (AIC = 46.8) than either a constant proportion of ingested energy (AIC = 49.5) or a multiple linear regression model (AIC = 62.5). Limiting effects of hypoxia upon SDA increased with temperature, with a reduction of c. 50% between normoxia and 40% DO_{SAT} predicted at 28 °C (Fig. 6). Applying the excretion sub-model to laboratory data, a 20-g fish was predicted to exhibit excretion rates of 4.1 to 4.5% of consumed energy, depending upon temperature, DO and salinity conditions.

Predictive regressions constructed using either food consumption or routine metabolism as single explanatory variables explained significant fractions of variation attributed to active metabolism (Fig. 7). The most informative of these two models (AIC = 654.1) predicted ACT as a direct proportion (0.29 ± 0.036 SE) of predicted maximum food consumption rate. The alternative model based upon routine metabolism was much less informative (AIC = 1122.7) although still significant ($p < 0.05$). Here, activity cost was predicted to be 1.89 times ± 0.044 SE predicted routine metabolism rate, which corresponds to a Winberg's multiplier of 2.89.
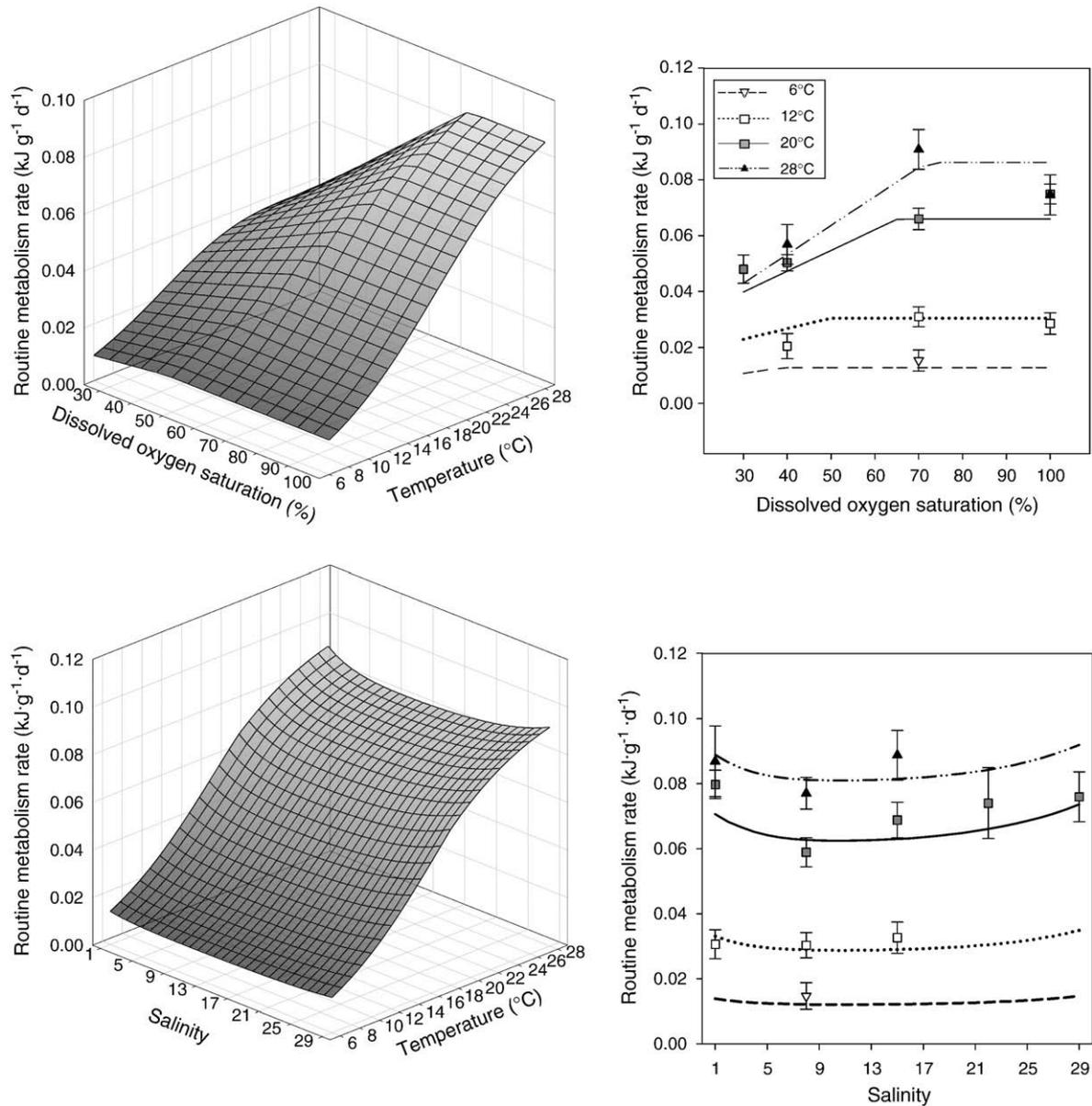
Fig. 4. Predicted (left panels) and mean observed ± SE (right panels) effects of temperature, dissolved oxygen saturation and salinity on routine metabolism rate in juvenile Atlantic sturgeon. Figures show variability caused by two factors at a time, holding the third at fixed conditions (salinity 9 for top panels, 100% DO_{SAT} for bottom panels). Predicted and observed values are weight-normalized to represent a 20-g fish.

The integrated bioenergetic model explained 60% of variance in observed growth from laboratory experiments, when used to predict growth from measured food consumption. When used to predict both growth and food consumption simultaneously, the integrated model explained 48% of variance in observed growth. In both applications, the model outperformed an alternative multiple linear regression model, which explained 43% of observed variance in growth. Due to several direct and indirect relationships among temperature, dissolved oxygen and salinity, predicted growth was characterized by strong three-way interactions between these environmental factors (Fig. 8).

At normoxia (100% DO_{SAT}) and iso-osmotic (salinity 9) conditions, maximum growth was predicted at 23 °C, with an instantaneous rate of 0.052 d^{-1} for a 20-g Atlantic sturgeon. This optimal temperature for growth decreased with dissolved oxygen saturation (Fig. 8) to 17 °C at 40% DO_{SAT} and to 16 °C at 30% DO_{SAT} (salinity 9, in both cases). Keeping the fish at normoxia, but manipulating salinity would also affect the predicted optimal temperature for growth, which would become 20 °C

at salinity 1, and 16 °C at salinity 29. A drop in dissolved oxygen to 40% saturation would produce a reduction of 52% in instantaneous growth rate, while an increase in salinity to 29 would reduce instantaneous growth rate by 88%, both compared to maximum growth conditions (23 °C, 100% DO_{SAT}, salinity 9).

3.2. Error analysis

Growth predictions were highly sensitive to uncertainty in the food consumption sub-model (Fig. 9), which explained 20–67% of residual variance, and was the main source of errors in scenarios 3 (high salinity) and 4 (high temperature); Table 3. Uncertainty in activity cost showed the second largest effect on total model errors, explaining 12–63% of residual variance, and was the most sensitive bioenergetic component under scenarios 1 (optimal) and 2 (hypoxia). Model sensitivity to uncertainty in routine metabolism parameters ranked third among all components, explaining between 5 and 43% of total residual variance. Error contributions from egestion, SDA and
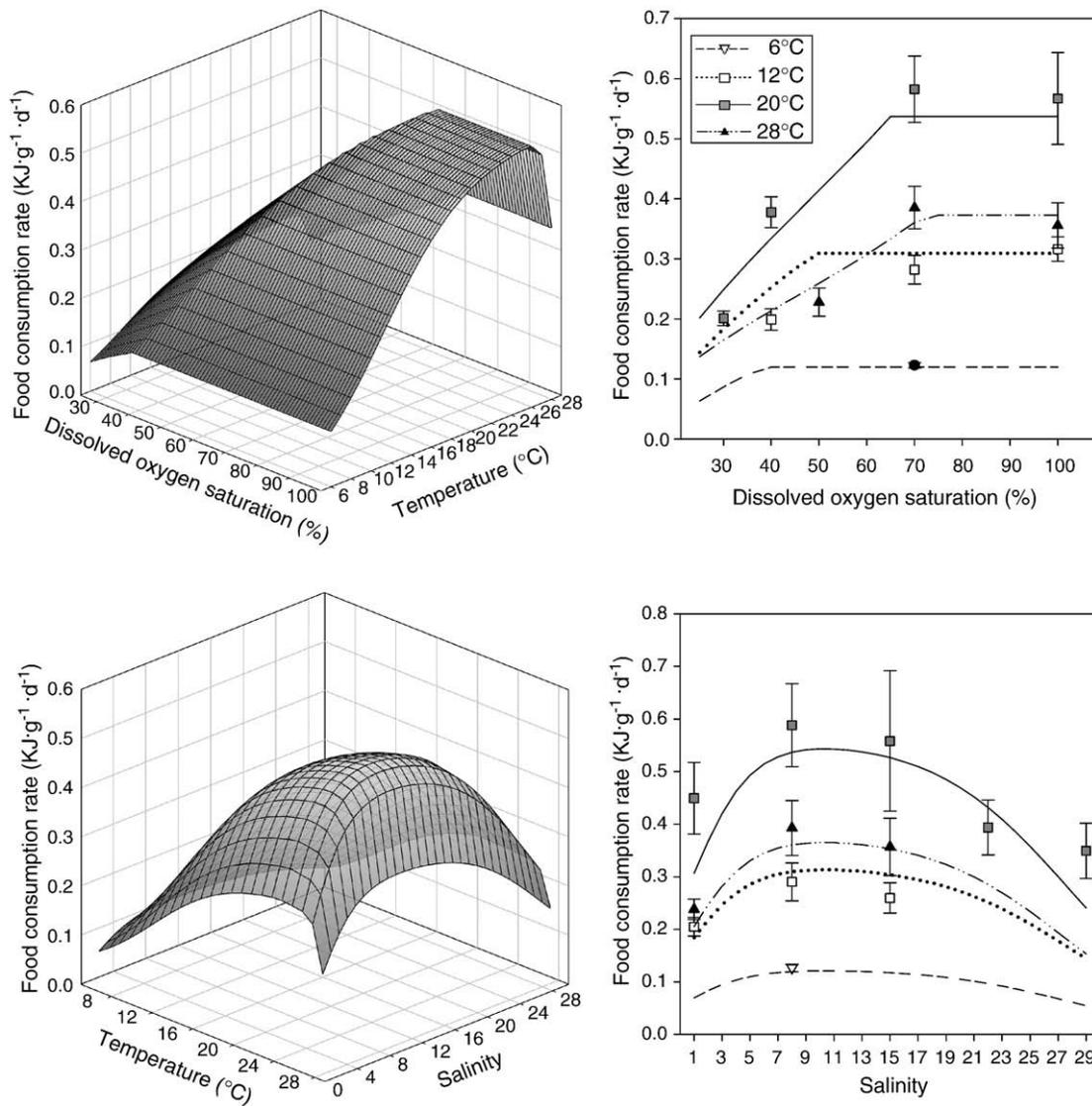
Fig. 5. Predicted (left panels) and mean observed ± SE (right panels) effects of temperature, dissolved oxygen saturation and salinity on food consumption rate in juvenile Atlantic sturgeon. Figures show variability caused by two factors at a time, holding the third at fixed conditions (salinity 9 for top panels, 100% DO_{SAT} for bottom panels). Predicted and observed values are weight-normalized to represent a 20-g fish.

excretion sub-models were the lowest, always below 6% of total residual variance (Table 3).

In terms of individual parameters (see Table S1 for definitions), uncertainty in a_{ACT}, the proportionality coefficient for activity cost, had the largest overall effect upon predicted errors (Fig. 9), being the dominant error contributor under scenarios 1 (optimal) and 2 (hypoxia). Under scenario 3 (high temperature), the largest source of model errors was the parameter $TK4_{FC}$, which corresponds to the food consumption reaction rate at the highest tested temperature level. Analogously, under scenario 4 (high salinity), the largest impact upon model uncertainty was related to parameter k_{FC}, that defines food consumption reaction rate at the highest tested salinity.

3.3. Mesocosm validation

Our bioenergetic model tended to overestimate both final weight and instantaneous growth rates observed in mesocosm experiments (Fig. 10). Thus, observed mean fish weight at the end of the experiments (180 g ± 15 SE) was significantly lower than the predictive value of 220 g ± 15 (SE). Significant differences were also found between predicted and observed growth rates, with overall means of

0.023 d^{-1} ± 0.0014 (SE) and 0.021 d^{-1} ± 0.0014 (SE), respectively. A weekly-based analysis of instantaneous growth rates showed a low, but still significant correlation between observed and predicted growth rates (Spearman's $r = 0.28$; <0.05). When computed on a monthly basis, correlation between predicted and observed growth rates increased to $r = 0.6$ ($p < 0.05$). Poor correlation was particularly evident at the beginning of the experiments, when there was a noticeable trend to overestimate observed growth rates. Improved agreement between predicted and observed values occurred during the second and third months of the experimental period (Fig. 10).

4. Discussion

4.1. Expanding bioenergetic model into a multi-variable framework

In the present work we have proposed a multi-variable bioenergetic model, which incorporates formally and explicitly the expected effects of hypoxia and salinity on different fish bioenergetic processes. The application of this model to a comprehensive set of laboratory and mesocosm results for juvenile Atlantic sturgeon showed reasonable model performance and gave support to the theoretical basis and
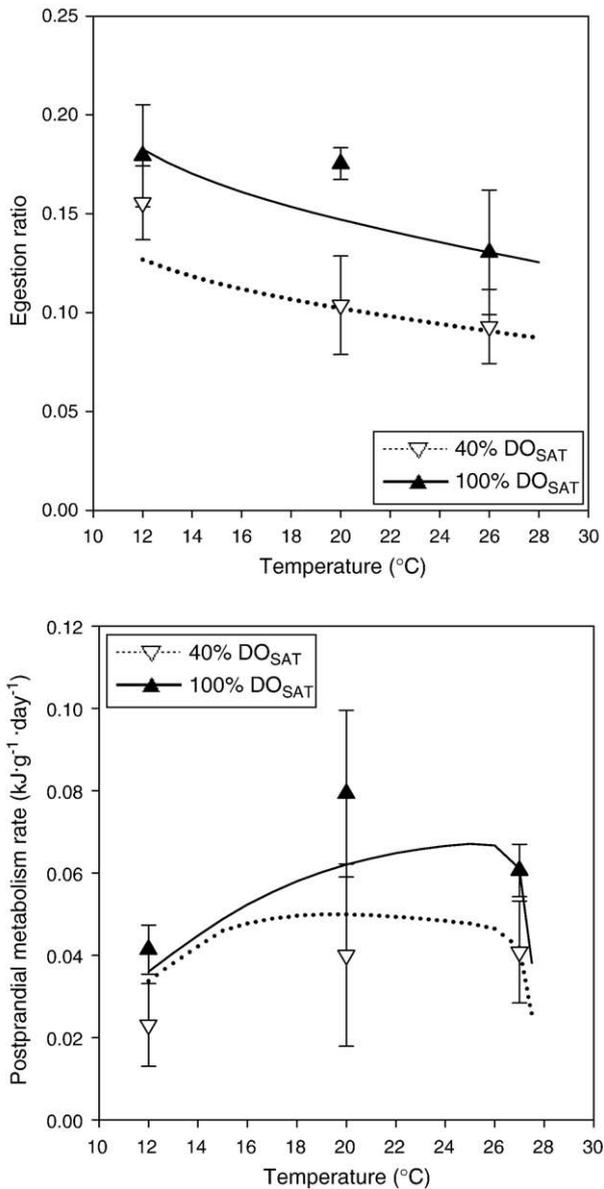
Fig. 6. Mean observed ± SE (triangles) and predicted (lines) effects of temperature and dissolved oxygen upon egestion (upper panel) and postprandial metabolism (lower panel) rates in YOY Atlantic sturgeon at salinity 9.

Fig. 7. Apparent activity cost computed by difference between food consumption and realized growth rate. Calculated values (circles) are plotted against food consumption rate (upper panel) and routine metabolism rate (lower panel) corresponding to each observation. Predicting lines correspond to constant proportions of either *x*-axis.

assumptions used to build the model. Such basis and assumptions were strongly related to Fry's (1971) concept of controlling, limiting and masking factors, as well as to Winberg's (1956) energy balance and van Dam and Pauly's (1995) metabolic oxygen balance concepts. The vertical and horizontal integrations of controlling, limiting and masking effects in the model allowed for simultaneous analysis of potential maximum rates, controlled by temperature, and realized ones, as limited by aerobic scope or modified by osmoregulation costs.

Model structure and results from its application to juvenile Atlantic sturgeon matched the expectations that oxygen and salinity play major roles shaping bioenergetic responses in juvenile sturgeon and should not be ignored in bioenergetic models for estuarine species (Niklitschek and Secor, 2005; Breitburg et al., 2009). Overall, we consider this as a case where increasing model complexity has resulted in significant improvements in its predictive capabilities. Further, we wished to advance a bioenergetic framework that better integrated and synthesized scientific understanding about key eco-physiological processes than those that focus on temperature and forage or rely on statistical description alone (Bartell et al., 1986). A
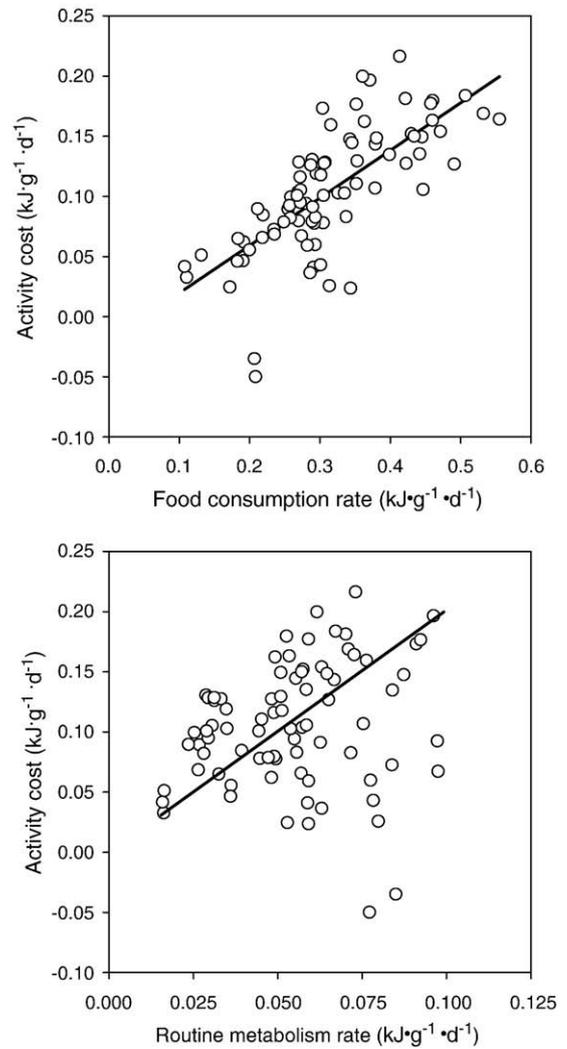
reasonable balance is needed between desired realism, parsimony, and experimental efforts needed to estimate model parameters. Hence, a detailed scrutiny of model sensitivity and uncertainty in the required data (Brandt and Hartman, 1993; Hanson et al., 1997) might allow for a reduction in the number of model parameters, which currently reach a total of 30 parameters in our proposed model.

Developed as parallel efforts, there is a noteworthy convergence between our model and Neill et al.'s (2004) Ecophys.Fish model. For instance, both frameworks use Fry's (1971) paradigm to guide model construction and use routine (standard) metabolism to canalize the bulk of masking and limiting effects. Our concept of aerobic scope is closely related, although not identical, to Neill et al.'s (2004) concept of marginal metabolic scope. Although algorithms used to forecast bioenergetic responses are different, overall consistency exists also in the shape of responses predicted by both models. Unlike Neill et al. (2004), we ignored pH controlling effects, but included hypoxia limiting effects upon SDA, egestion and excretion rate.

In our view, efforts to construct more elaborate and refined multi-variate bioenergetic models are justified by increased scientific and public agendas to manage for habitat suitability in estuaries where strong salinity gradients and regular (seasonal) hypoxia are highly relevant ecophysiological factors (Diaz, 2001; Breitburg et al., 2009). The increasing availability of spatially-explicit time series of data from
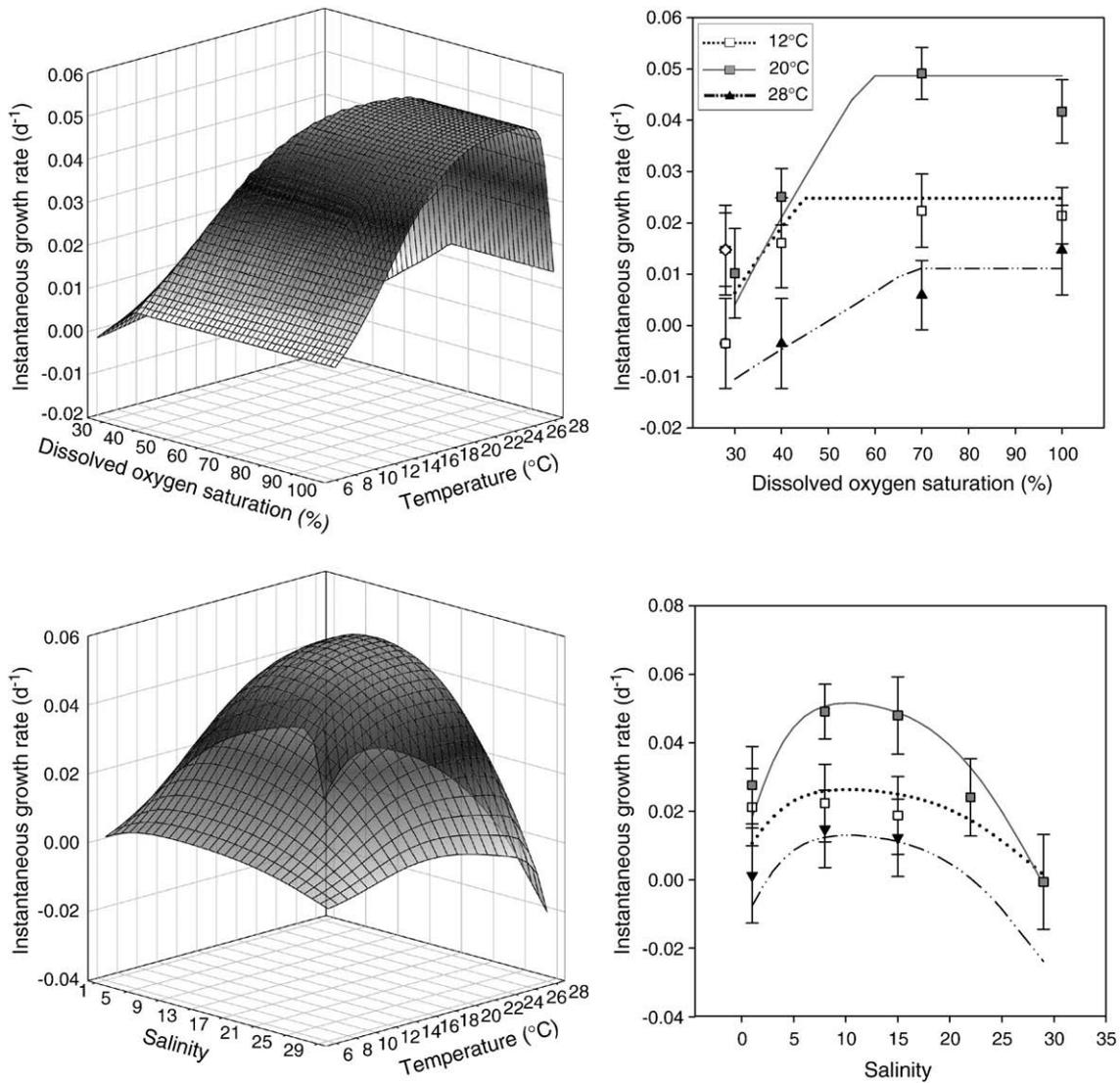
Fig. 8. Predicted (left panels) and mean observed ± SE (right panels) effects of temperature, dissolved oxygen saturation and salinity on instantaneous growth rate in juvenile Atlantic sturgeon. Figures show variability caused by two factors at a time, holding the third at fixed conditions (salinity 9 for top panels, 100% DO$_{SAT}$ for bottom panels). Predicted values are weight-normalized to represent a 20-g fish.

intense and regular monitoring programs, such as the Chesapeake Bay Program, transform such models into integrative tools suitable for evaluating or forecasting trophic interactions (Hartman and Brandt, 1995b) and habitat value (Niklitschek and Secor, 2005; Woodland et al., 2009) for estuarine species, among other applications. Moreover, model approaches of this nature might exist as the only option to identify essential habitats when observational data on fish abundance and

distribution are scarce or missing, as in the case of many sturgeon populations (Secor and Niklitschek, 2002).

4.2. Overall performance of model application to juvenile Atlantic sturgeon

The application of proposed sub-models to juvenile Atlantic sturgeon laboratory results showed better fits (lower AIC's) than multinomial linear regression models for all studied bioenergetic responses, although in many cases they demanded a larger set of parameters or depended upon parameters from other sub-models. Growth predictions from our model outperformed a purely empirical (polynomial) fitting and explained 48% of the variance in laboratory growth responses to a range of environmental conditions, representative of what juvenile Atlantic sturgeon would face during their first 2–3 years of life in North American estuaries. Neglecting the modeled effects of temperature, dissolved oxygen or salinity reduced explained variance from 48% in the full model to values of 18, 24 and 38%, respectively. Thus, temperature was the most influential factor, followed by dissolved oxygen and salinity. Still, a single-variable model based only on temperature explained no more than 17% of observed variance in laboratory results.

Table 3
Relative partial sum of squares (% RPSS) attributed to each major bioenergetic component of Atlantic sturgeon model under optimal water quality conditions and 3 alternative modeling scenarios (see Table 1 for scenarios).

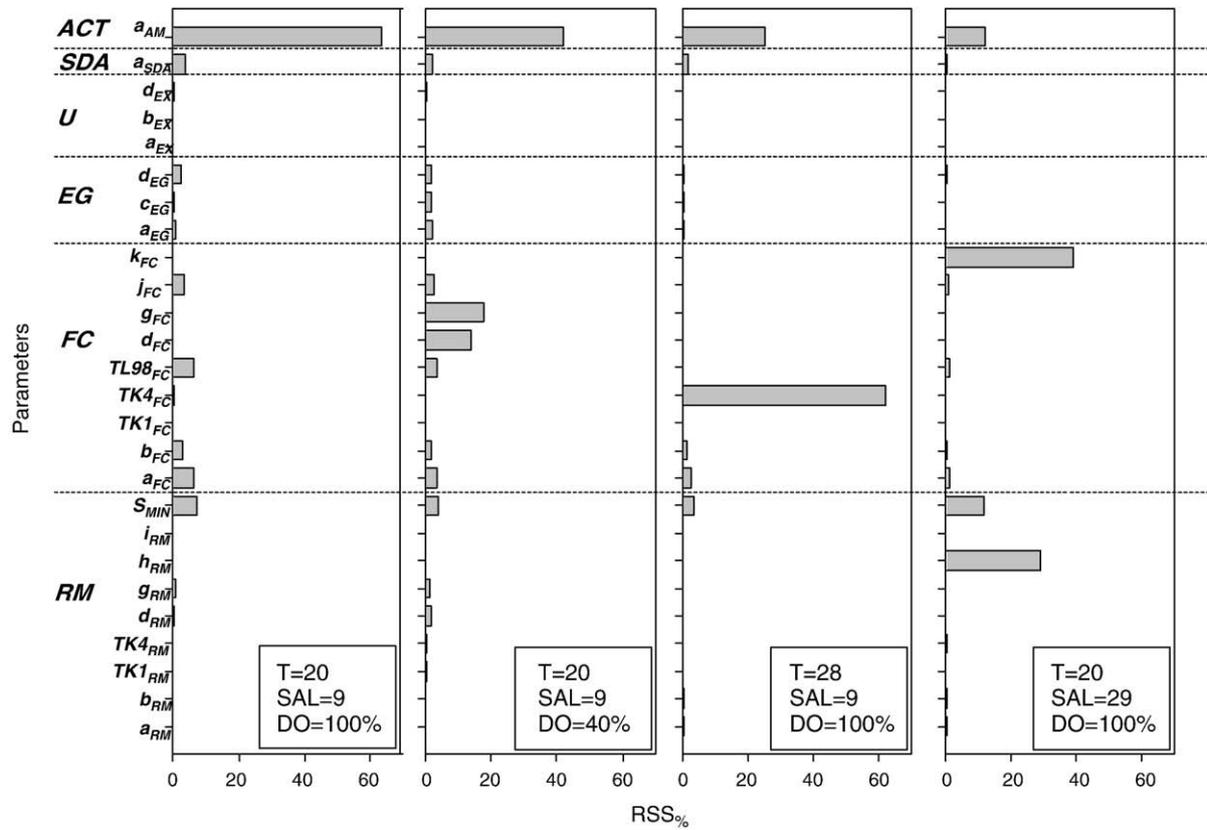| Bioenergetic component	Scenario (temperature/salinity/DO$_{\%}$)			
	23/9/100 (optimal)	23/9/40 (hypoxia)	23/29/100 (high salinity)	28/9/100 (high temp.)
AM	63.4	42.1	12.3	25.2
FC	20.1	42.6	43.5	66.5
EG	3.3	5.1	0.5	1.1
RM	8.6	7.6	42.8	5.0
SDA	3.8	2.0	0.8	2.0
U	0.8	0.6	0.3	0.2

Fig. 9. Percent of residual variance (RSS$_\%$) explained by uncertainty in individual parameters estimated for the Atlantic sturgeon bioenergetic model, under 4 simulation scenarios of temperature (*T*), salinity (*S*) and dissolved oxygen saturation (DO). See Table S1 for variable definitions. ACT = activity cost; SDA = postprandial metabolism; EG = egestion; U = excretion; RM = routine metabolism; FC = food consumption.

While model predictions overestimated observed growth in meso-cosm experiments by 20%, a least square estimation of the realized proportion of maximum consumption, *p*-value (Hanson et al., 1997), indicated a cumulated difference of just 4% between maximum and actual consumption rates. Although we fed the fish 1.3 times their predicted ration, tank size relative to the fish might have delayed feeding and increased nutrients leaching into the water. Since larger discrepancies between predicted and observed growth rates were concentrated in the first weeks of the mesocosm experiment (early fall, temperature range 6–11 °C), an alternative, or maybe complementary, explanation is model overestimation of growth rates at low temperature. While a limited number of experimental units was allocated by Niklitschek and Secor's (2009-this issue) experimental design to 6 °C treatments, other authors have found a severe drop in food consumption, growth and/or survival at c. 5 °C in partially sympatric species like Atlantic croaker *Micropogonias undulatus* (Lankford and Targett, 1994) and striped bass *Morone saxatilis* (Hurst and Conover, 2001).

As expected, the model exhibited much higher errors predicting growth rates on a weekly basis than on over a monthly period. This is consistent with Rice and Cochran's (1984) verification study, that concluded that finer (daily) resolution dynamics of metabolic processes were not well captured by the applied bioenergetic model. By the end of our mesocosm experiments, fish grew to c. 180 g. Although this weight was close to the maximum weight of 200 g recorded from yearlings used in routine metabolism and food consumption experiments, the most comprehensive set of laboratory data we used to estimate model parameters belonged to YOY fish with a maximum size of 60 g. Thus, we suggest a primary application of model parameters reported in this paper to YOY, which are expected to reach c. 120 g at the end of their first year in the wild (Stevenson and Secor, 1999). Only a cautious extension of the model to older/larger fish would be advisable before new validations were conducted.

In terms of model uncertainty, the activity cost proportionality coefficient (a_{ACT}) was the single parameter having the largest impact on total model error under optimal and normoxia scenarios. Activity cost has been shown to be a very sensitive and highly variable parameter in bioenergetic models (Kitchell et al., 1977; Bartell et al., 1986; Bosclair and Sirois, 1993; Hansen et al., 1993; Ney, 1993; Guénard et al., 2008), even under semi-controlled experimental conditions (Bosclair and Sirois, 1993; Guénard et al., 2008). Moreover, accurate measurement of activity levels in the field faces methodological constraints recognized since Winberg (1956), related to the inherently random nature of spontaneous activity and short-term responses to environmental stimuli. Even the most modern approaches remain expensive in time and resources, and can lead to highly variable results, which continue to confound the accurate inclusion of active metabolism in bioenergetic models (Guénard et al., 2008).

We found that inferred activity cost in YOY Atlantic sturgeon experiments was more closely related to maximum food consumption rate than to routine metabolism. This finding matched theoretical expectations that both activity and food consumption would be limited under hypoxia (Jobling, 1981), and was also consistent with the general expectation that foraging (as well as predator avoidance) represents a major component in total fish activity at the wild (Rennie et al., 2005). A close correlation between consumption and activity finds support in empirical evidence from several authors (Madon and Culver, 1993; Swanson, 1998; Rennie et al., 2005), although it has not been the case in other studies (Sirois and Boisclair, 1995; Qian et al., 2001).

Under extreme temperature and salinity scenarios, the proposed model was highly sensitive to food consumption parameters that defined reaction rates at the highest tested temperature ($TK4_{FC}$) and salinity (k_{FC}) conditions. This was the combined result of higher
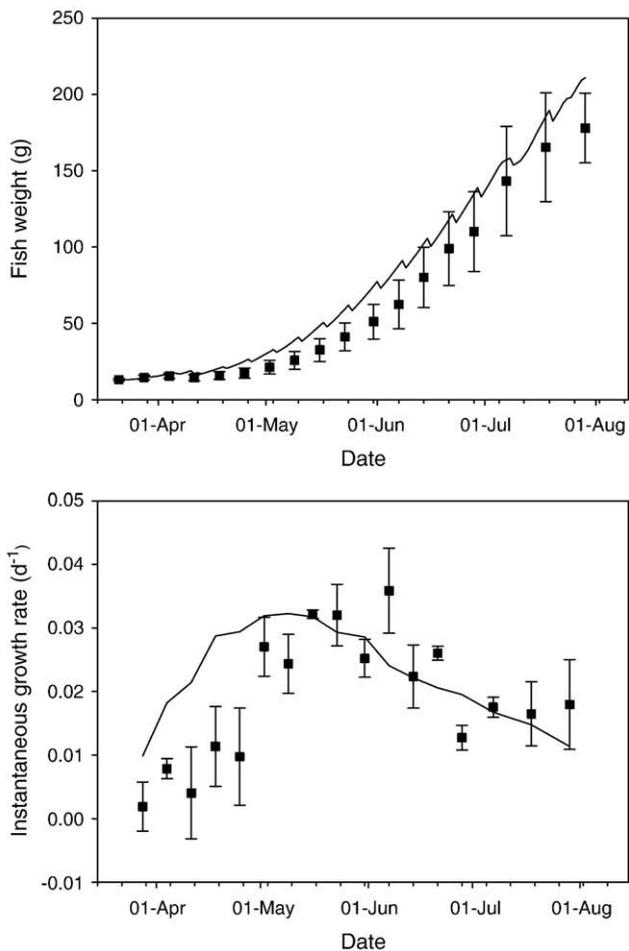
Fig. 11. Energy partitioning among main bioenergetic components in juvenile Atlantic sturgeon under hypoxia (40% DO_{SAT}) and normoxia (100% DO_{SAT}), at constant temperature and salinity conditions (20 °C, salinity 9). Percent labels are in reference to predicted consumption rates (FC) at each DO_{SAT} condition.

Fig. 10. Weight (upper panel) and growth rates (lower panel) in juvenile Atlantic sturgeon during a 4-month mesocosm validation experiment. Squares represent observed values, while lines represent predictions from the bioenergetic model. Error bars correspond to standard errors from 4 replicates (tanks).

variability in actual responses and comparatively low replication due to both the experimental design and higher mortality rates. Complementary experiments focused on testing activity cost and feeding rate responses at extreme conditions should be conducted to reduce such uncertainty in future applications.

4.3. Energy partitioning in juvenile Atlantic sturgeon

We estimated that, under optimal conditions (23 °C, salinity = 9 and 100% DO_{SAT}), YOY Atlantic sturgeon transformed an average of 31% of consumed energy into fish biomass (Fig. 11). This efficiency was slightly higher than the average 29% estimated for "well fed" carnivorous teleosts by Brett and Groves (1979), but lower than the 43.5% reported by Winberg (1956) for 11–21 g *A. gueldenstaedtii*, and the 35% net conversion efficiency calculated for 2–23 g white sturgeon by Cui et al. (1996). Conversion efficiency and energy allocation patterns departed, however, from this optimal value depending upon environmental conditions (Fig. 11). We predicted that the proportion of consumed energy allocated to growth would decrease to 24% under sub-lethal hypoxia (40% DO_{SAT}) at 20 °C (salinity 9), and to null values at 28 °C. Similar hypoxia-driven reductions in the amount of energy allocated to growth were observed in rainbow trout *Oncorynchus mykiss* by Pedersen (1987), although the magnitude of this drop was more pronounced, exhibiting negative growth rates at 40% DO_{SAT} and only 15 °C.

The proportion of the energy budget allocated to routine metabolism and activity under hypoxia (Fig. 11) increased from 39 to 41%,
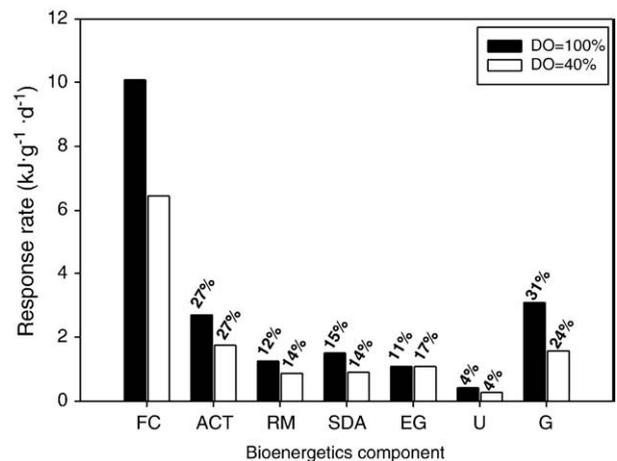
with minor changes in the proportions corresponding to excretion and postprandial metabolism. Egestion showed the largest relative change under hypoxia, increasing c. 60% relative to normoxic conditions. This change reflects our findings, which indicate that besides lowering their feeding rates, sturgeons reduce assimilation rates under hypoxia, shunting energy and oxygen supply from SDA towards respiration (Niklitschek and Secor, 2009, this issue).

Osmoregulation cost at extreme salinities was higher at hyper-osmotic than at hypo-osmotic conditions in agreement with results from Allen and Cech (2007). Instead of the compensatory increase in food consumption described in other species (Wuenschel et al., 2004a) we found (Niklitschek and Secor, 2009, this issue) and modeled a decrease in food consumption toward extreme salinities. Hence, consequences of extreme salinities upon juvenile sturgeon growth largely exceeded the direct effects upon osmoregulation cost. While the predicted cost of osmoregulation for a 20-g fish increased from 0 to 11% of consumed energy between salinities 9 and 29, food consumption was reduced by 60% between the same salinities. As a result, an 88% drop in growth rate was predicted between salinities 9 and 29. This reduction in food consumption might be a direct response aimed to reduce ion exchange at the intestine, or a more indirect result from other physiological effects of salinity upon hormonal balance, tissue permeability and/or ventilatory performance (Swanson, 1998; Boeuf and Payan, 2001). Relative effects of salinity upon predicted consumption and growth were modeled to decrease with size, in agreement with previous studies showing an ontogenetic increase in salinity tolerance, observed in several species, included sturgeons (Altinok et al., 1998; Allen and Cech, 2007).

4.4. Model implementation and future development

There are currently two main bioenergetic packages available for the fish ecology scientific community. The "Wisconsin" Bioenergetics 3.0© model (Hanson et al., 1997), which is a closed-code copyrighted self-contained software and the Ecophys.Fish model (Neill et al., 2004), which is a non-licensed freely available script that runs on the copyrighted general package Stella©. While Bioenergetics 3.0 is the most widely used package, it has the limitations inherent to self-contained software, which make it harder or plainly impossible to add new explanatory variables or other custom needs, such as spatially explicit factors. The Ecophys.Fish model has the advantage of great flexibility, which might facilitate an integration with models already written for Stella© (Bevelhimer, 2002) or with other models, like ours, written in general graphic languages such as R or SAS©. Currently, our

model is written as a SAS© script and is freely available for non-commercial purposes upon request.

Beyond software implementation, comparing our results to published ones for other species suggests relative consistency within sturgeons, but low transferability of salinity and hypoxia responses regarding other fish taxa. Therefore, anticipating eventual applications of our model to other species, we strongly recommend prioritizing species-specific laboratory work aimed at sensitive parameters

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jembe.2009.07.019.

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