Assessing and modeling the energetic responses of sympatric sturgeons *Acipenser oxyrinchus* and *A. brevirostrum* to estuarine gradients in temperature, dissolved oxygen and salinity

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INTRODUCTION

Few models, conceptual or otherwise, are available to evaluate how estuarine fish production is related to environment. A rich literature exists relating the abundance and occurrence of juvenile stage coastal fishes to various estuarine environments, but few quantitative models exist to predict likely patterns of habitat use and production. Estuarine environments are well known for variability, and are structured spatially by strong gradients in physical and chemical factors. While salinity and temperature variability are inherent features of most estuaries worldwide, hypoxia in shallow estuaries is a seasonal phenomena, which has become more pervasive during the past century, the likely as consequence of anthropogenic enrichment of highly productive stratified systems (Officer et al. 1984, Cooper and Brush 1991). Although high physiological plasticity is expected in estuarine species, strong effects of temperature, salinity and dissolved oxygen have been reported for responses related to behavior, distribution, physiology, energetics, growth and survival (Peters and Boyd 1972, Brett 1979, Gershanovich 1983, Boubee et al. 1991, Brandt 1993, Johnson and Evans 1996, Crocker and Cech 1997, Boeuf and Payan 2001).

Most physiological and many behavioral responses to environmental factors can be generalized as bioenergetic responses, measured or modeled as energy flow within individuals (Brett 1979). Further, bioenergetics has been more intimately linked with population dynamics and fitness by considering the ratio of instantaneous mortality over growth (/G) , as an integral that can relate habitat to cohort production. (Werner et al. 1983, MacCall 1989, Heath 1996, Houde 1997, Secor 1999).

Bioenergetics modeling, based upon Winberg's (1956) balance equation equates individual metabolic and production rates to environmental factors. The widespread use of new computational tools and the availability of suitable bioenergetics software (Hewett and Johnson 1992, Hanson et al. 1997) led to an increased interest in bioenergetic modeling in the 1980s and 1990s. Largely influenced by research conducted on freshwater species (Kitchell et al. 1974, Kitchell et al. 1977), most bioenergetics modelers have used only forage and temperature as factors driving fish bioenergetics (Bosclair and Sirois 1993, Hansen et al. 1993, Hartman and Brandt 1995a). Very limited advances have been made in extending those approaches to estuarine environments where other environmental factors can play a key role (Neill et al. 1994, Luo et al. 2001).

In this research, we focus on modeling the major effects and interactions of temperature, dissolved oxygen and salinity on fish metabolism and production. As experimental subjects we used two sympatric Acipenserids, shortnose (*Acipenser brevirosrtum*) and Atlantic (*A. oxyrinchus*) sturgeons, which inhabit a wide geographic range along much of the Atlantic coast of North America (Evermann and Bean 1898, Leim and Day 1959, Vladykov and Greeley 1963). Juvenile Atlantic and shortnose sturgeons naturally occur in estuarine waters, where a wide range of temperature, salinity and dissolved oxygen conditions are observed.

Discrete and abundant populations of sturgeons occurred in most major North American estuaries until the end of the 19th century (Wirgin et al. 2000, Walsh et al.

2001). Currently, shortnose sturgeons are listed under the U.S. Endangered Species Act and fishing is banned in U.S., but not in Canada, for Atlantic sturgeon. For Atlantic sturgeon, a 19th Century industrial fishery resulted in rapid overharvesting and population crashes throughout its range (Secor and Waldman 1999). Despite nearly 100 years of reduced fishing effort and protective regulations, Atlantic sturgeon have failed to recover to historical levels, which has suggested to some investigators that habitat may be limiting recruitment of sturgeons. In particular, Secor and Gunderson (1998) and Collins et al. (2001) have hypothesized that juveniles production in many estuaries may be depressed due to synergistic effects of increased hypoxia and temperature in nursery areas impacted by anthropogenic activities (Secor and Gunderson 1998, Collins et al. 2000). To test this hypothesis, more detailed information on the physiological tolerance of sturgeons to environmental factors at different life-stages is required.

The two selected sturgeon species are partially sympatric but differ in important ways in their relative use of fresh-, brackish- and marine water habitats. Both species spawn in tidal freshwater environments, although specific spawning locations differ (Bain, 1997). Nursery areas for young-of-the-year Atlantic and shortnose sturgeons overlap only partially in the vicinity of the freshwater/brackish water interface; shortnose juveniles tend to predominate in freshwater habitats and Atlantic juveniles predominate in brackish regions of estuaries (Dadswell 1979, Dovel and Berggren 1983, Dovel et al. 1992, Bain 1997, Haley 1999, Collins et al. 2000). Older juvenile shortnose sturgeon tend to remain in fresh and oligohaline waters (<15 ppt), whereas Atlantic

sturgeon initiate a predominantly marine life phase after 1 to 6 y of life in estuarine waters (Dovel and Berggren, 1983; Dadswell et al., 1984; Smith, 1985). These life history differences lead to speculation that physiological differences could exist in species-specific responses to estuarine gradients, specially salinity and temperature. Shortnose might be better adapted to support more extreme and variable temperature and dissolved oxygen conditions expected in freshwater areas. Atlantic sturgeon, on the other hand, might exhibit higher tolerance to high salinities found in lower estuaries and coastal areas.

In the present work we quantify and compare the magnitude and describe the functional effects of temperature, dissolved oxygen, and salinity upon major bioenergetics processes and energy allocation in *A. oxyrinchus* and *A. brevirostrum*. We interpret such effects using a conceptual framework based upon Fry´s (1971) paradigm, and propose a multivariable bioenergetic model suitable to predicting functional responses to temperature, dissolved oxygen and salinity in estuarine fishes. Important in this model is our inclusion of dissolved oxygen rather than forage as the primary limiting factor (van Dam and Pauly 1995). Finally, we evaluate the performance of the proposed model to predict growth from observed environmental conditions, and to predict consumption from observed growth in independent mesocosm experiments.

MATERIALS AND METHODS

Experimental design, analysis and modeling were directed at developing a balance energy equation for each species (Winberg 1956), in which we assumed the

basic bioenergetic processes (energy intake, metabolism and wastes) were independently conditioned by environmental factors:

$$G = C - (RM + ACT + SDA) - (F + U) \quad \text{(Eq.1)}$$

where, G=Growth, C=Consumption, RM=Routine metabolism, ACT=Activity cost, SDA=Post-prandial metabolism, F=Egestion, and U=Excretion. Since bioenergetics models are especially sensitive to consumption and routine metabolism estimates (Bartell et al. 1986, Hanson et al. 1997), we focused most of our experimental effort on the assessment of these components.

Bioenergetic responses to salinity, temperature and dissolved oxygen saturation (DO_{sat}) were measured in microcosm studies conducted on young-of-the-year Atlantic and shortnose sturgeons (6-48 g). All experimental fish were made available from US Fish and Wildlife hatcheries, but were of limited supply and thus experimental design was accommodated to gain maximum use from several hundred individuals of each species. Juvenile shortnose sturgeon were from Savannah River progeny and juvenile Atlantic sturgeon were offspring from Hudson River parents. Fish were acclimated to experimental conditions at transition rates no greater than 1 ppt, 1°C and/or 5% Dissolved Oxygen saturation (DO_{sat}) per day. Salinity was maintained with ± 5% of targeted levels by mixing local well water with filtered ambient brackish water(3-18 ppt, Patuxent River, Chesapeake Bay). Artificial salt (Instant Ocean®) was added when necessary. Dissolved oxygen was kept within ±10% of targeted levels by mixing

nitrogen with ambient air. Temperature was regulated within ±8 % of targeted levels by using a combination of room-temperature control, water baths and individual heaters. Water quality parameters were checked at least 3 times each day unless otherwise stated.

Food consumption and growth

Temperature, salinity and dissolved oxygen effects on food consumption and growth rates were assessed through an incomplete factorial design. This design included twenty-three combinations of four levels of temperature: 6, 12, 20 and 28^{o}C; four levels of dissolved oxygen (DO_{sat}): 25, 45, 70 and 95% DO_{sat}; and five levels of salinity: 1, 8, 15, 22 and 29 ppt (Figure 1). This design allowed us to evaluate functional responses to main effects and first order interactions between temperature and salinity, and between temperature and dissolved oxygen. We planned to obtain six replicates for the treatment representing center conditions in each species (20^{o}C, 70% DO_{sat}, 8 ppt), and three replicates for all the remaining treatments. However, low survival was obtained at certain conditions, such as <40% DO_{sat} in both species, and > 22 ppt salinity in shortnose sturgeon. To minimize harm to individual fish and preserve sufficient experimental animals , lethal treatments were not replicated, causing some unequal replication. A total of 135 independent trials were successfully completed in seven sequential runs, where treatments and replicates were allocated using a semi-random balanced procedure.

All experiments lasted 10 d, and were conducted in 34-L glass aquaria with either one or two fish per tank. The number of fish per tank (1-3) was adjusted based

upon individual fish weight to maintain similar biomass among tanks. Preliminary experiments showed no difference in growth or food consumption between fish reared individually and in pairs (Niklitschek 2001). Fish were measured and weighed 12 h before and after each experiment. Fish were fed *ad-libitum* 3-mm Biokyowa® pellets thrice a day. Non-consumed food was removed 30-40 min after each feeding and dried to constant weight (≥48 h) at 60^{o}C. Average energy-density in Biokyowa pellets, estimated by wet digestion (Maciolek 1962), was equal to 21.9 KJ g^{-1}. Daily consumption rates were calculated for each tank by dividing total consumed food by the expected fish weight, which was back-calculated from observed growth. Median daily consumption rate for each tank was used in subsequent statistical tests and modeling.

The effect of fish weight on maximum daily consumption rate ($C_{max)}$ was estimated from a larger set of consumption experiments, which included 32 fish (17 Atlantic sturgeon, 16 shortnose sturgeon) between 6 and 320 g, all reared at 20^{o}C, 8 ppt and >70% DO_{sat}. Data were fit to a linearized version of the allometric C_{max} equation (Kitchell, 1978),

$$\log_e[C_{max}] = \log_e[a_{FC}] + b_{FC} \cdot \log_e W + \qquad \text{(Eq. 2)}$$

Where, W is fish weight (in grams); a_{FC} and b_{FC} are empirical coefficients, and is the experimental error ~$N(0,\sigma^2)$. Daily instantaneous growth rate (G) was calculated for each individual, and averaged within each tank, from the relationship

$W_t = W_0 \cdot \exp^{G(t-t_0)}$, where, W_t is final weight at time t; and W_0 is initial weight at time t_0. Gained weight was transformed into gained energy based upon relative weight (W_s), using an empirical equation ($r^2 = 0.74$, $p<0.001$) we derived for juvenile sturgeons (Appendix 1).

Respirometry

Energy costs of both routine metabolism and specific dynamic action (SDA) were estimated by respirometry. Thus, measured consumed oxygen was transformed into consumed energy using an oxycalorific coefficient of 13.55 KJ g-O_2^{-1} (Brett and Groves 1979). Oxygen consumption was measured for individual fish using either 2-L flow-through or 15.4-L static respirometers. The smaller flow-through units (0.35 L min^{-1}) were used for fish up to 8 g, and the larger respirometers for fish>8 g. Previous experiments indicated oxygen consumption results were not significantly affected by respirometer type (Niklitschek 2001). In each respirometry run 6 to 8 respirometers were run simultaneously, including 1 or 2 respirometers without fish. These units were used as blanks to correct final results for microbial oxygen consumption

Once acclimated to targeted water quality conditions, fish were placed in the respirometers for at least 12-h before each experiment began. During acclimation to the respirometers, salinity, oxygen and temperature levels were maintained within ±10% of targeted values by recirculating water from 240-L reservoirs (240-L) in which these variables were monitored and manipulated. In static respirometers, temperature was controlled by placing them in temperature-regulated baths, while dissolved oxygen

saturation was allowed to fall from 110 to 90% of targeted values. Respiration readings outside those limits were excluded. All temperature, dissolved oxygen and salinity measurements were made using YSI-85 meters, re-calibrated in saturated water every time a new sequence of readings at a given temperature was initiated. Apparent oxygen consumption in flow-through respirometers was corrected later for hydraulic residence time (Appendix 1).

Routine metabolism respirometry experiments were done immediately before or after growth-consumption experiments, for the same fish and under the same 23 combinations of temperature, salinity and dissolved oxygen conditions (Figure 1). Two to six replicates were obtained for each treatment, depending on fish availability from growth-consumption experiments. We tested a total of 244 fish, which were randomly allocated into 7 acclimation groups and 44 respirometry experiments. Each acclimation group corresponded to a growth-consumption run, where 27-40 fish were simultaneously acclimated to targeted conditions in a series of aquaria, each containing 1 to 3 individuals. Oxygen consumption rates were measured every 45 min for at least 4 h or until 4 stable readings were obtained.

SDA respirometry experiments were based upon a factorial design with three replicates at three temperatures: 12, 20 and 28^{o}C and two levels of oxygen saturation: 50 and 100%. Salinity was kept constant at 8 ppt across all experiments. All experiments were conducted in 14.5-L flow-through respirometers adapted for long-term experiments and retrieval of non-consumed food. To increase precision in

dissolved oxygen measurements, hermetic probe holders with magnetic stirring systems were connected to tank inflows and outflows.

After measuring routine oxygen consumption ≥4 h, flow was interrupted and fish were allowed to eat Biokyowa® pellets for 30 min. After that period, excess food was removed, flow restored (0.6 L min^{-1}) and oxygen consumption measured every 1-2 h during the first 16 h, and every 2-4 h thereafter (48-60 hr) until oxygen consumption was estimated to decline to the previously observed routine metabolism levels. A noticeable peak in metabolism, observed within 0.5-1 h after feeding, was interpreted as the result of feeding activity and/or manipulation stress. Consequently, data between 0 and 2 h post-feeding were excluded.

Individual fish post-prandial respiration rates (SDA) were interpreted as a function of time, after modeling and integrating the area under the curve from a modification of Thornton and Lessem's (1978) algorithm (Appendix 1). ,

Activity cost

We did not conduct direct measurements of activity metabolism, which is a sensitive but poorly predictable parameter in bioenergetic models (Kitchell et al. 1977, Bartell et al. 1986, Bosclair and Sirois 1993). We used results from laboratory and mesocosm experiments to estimate A_m indirectly from growth, as the value required to balance the energy budget equation (Hartman and Brandt 1995a). Multiple linear regression was used to model these equation residuals and to interpret them as indirect

estimates of activity metabolism. Although we modeled A_m as a proportion of other components (routine metabolism, food consumption), we kept it as a separate and additive component instead of a constant multiplier, more commonly used in bioenergetics modeling (Kitchell et al. 1977, Hartman 1993, Hanson et al. 1997).

Egestion

Egestion experiments were conducted with the same fish and under the same combination of dissolved oxygen and temperature used in SDA experiments. In addition to these abiotic variables, we tested 3 ration sizes: 10, 55 and 100% of maximum consumption observed during the acclimation period. Before each experiment, fish were fasted for 60 h, weighed, rinsed and transferred to a clean 38-L tank with filtered (5 m) 8 ppt water and left to recover overnight (12-14 h). Three tanks with one fish per tank were used for all treatments levels. Fish were then fed *ad libitum* three times at 2.5-h intervals.

Non-consumed food was removed after 30 min and dry-weighed. After the feeding period we monitored and adjusted water quality 3 times a day and pipetted observed feces . Feces were then frozen for further analysis. After 60 h the experiments were concluded, fish were rinsed, removed and weighed, and water from each tank filtered through a 35 m filter. Feces and filters were dried at 60^{o}C for 48 h or until weight was stable. After weighing the sample, 1-3 sub-samples of circa 10 mg each were measured for energy content analysis through a colorimetric variant of Maciolek's (1962) technique. Here, closed reflux digested samples were analyzed using a standard

spectrophotometer at 600 nm wave length, and compared with a standard potassium hydrogen phthalate solution, which had a theoretical chemical oxygen demand of 9,408 g O_2 ml^{-1}. Energy content in experimental filtrates and no-fish control tanks was below the sensitivity of the dichromate technique. On the other hand, organic matter in control tanks with fasting fish accounted for an average of 0.024 KJ ±0.0070 (SE) per gram of fish (wet weight), which was subtracted from estimated energy content in feces from experimental tanks.

Excretion

We did not conduct experiments aimed to obtain direct measurements of excretion rates in juvenile sturgeons. 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 1993, Hanson et al. 1997, Kitchell et al. 1997). We used excretion rates measured in other Acipenserids, scaled by our own routine metabolism results to model excretion in juvenile *A. oxyrinchus* and *A. brevirostrum* as a function of both metabolic and ingestion rates (Appendix 1).

Hypotheses testing

Bioenergetic responses of growth, food consumption, routine metabolism, SDA and egestion rates were analyzed using a two-step procedure. First, least-square multiple linear regression analysis was used to conduct standard diagnostics (residuals,

collinearity, influence). Second, a mixed model approach (MIXED Procedure; SAS Institute, 1997) was used to test null hypotheses after accounting for random effects and correlation within experiments. Environmental effects on activity cost were evaluated through multiple linear regression on the residuals between observed and predicted responses from bioenergetic sub-models (see below). We tested temperature and dissolved oxygen effects on A_m, since they were the only factors common to all the other bioenergetics sub-models.

Hypothesis testing was conducted for main linear and quadratic effects; first order interactions between environmental factors (temperature, dissolved oxygen and salinity); species effect (intercept and parallelism); and $\log_e$-transformed fish weight effect (intercept). Log-transformation of egestion observations was required to meet ANOVA assumptions regarding homogeneity of variances and normality. All other dependent variables were tested using originally scaled values for the response variables. Explanatory variables were centered ($_i$-) to avoid collinearity derived from polynomials and interactions. Unless otherwise stated, α=0.05 was used to define significance in all statistical analyses.

Bioenergetics model development

Multiple linear regressions were used to generate predictive equations for SDA, activity cost, egestion and excretion (see above). Here, we develop a novel model to predict food consumption and routine metabolism, the most sensitive components of

bioenergetics models, based upon non-linear and interactive effects of multiple environmental parameters.

Non-linear functions are most commonly used to model the effects of fish weight (Winberg 1956) and temperature (Kitchell et al. 1974, Elliot 1976, Thornton and Lessem 1978, Stewart et al. 1983) on fish respiration and food consumption. Nonetheless, few multivariable bioenergetic models are available to integrate other environmental factors, such as dissolved oxygen, and salinity. In order to model main bioenergetic effects and interactions between these factors (temperature, dissolved oxygen and salinity), we used the theoretical framework proposed by Fry (1971) to built a semi-balanced oxygen budget (Figure 2). Thus, physiological rates were assumed to be driven by temperature (controlling factor), but limited to the aerobic scope, i.e. the oxygen available in the tissues to sustain oxidative processes (van Dam and Pauly 1995). Aerobic scope for growth was expected, in turn, to be reduced by additional metabolic costs, specially those imposed by either hypo- or hyper-osmotic conditions (masking effects).

Our approach to model bioenergetic responses to environmental factors required of 4 major assumptions,

1. Oxygen delivery to the tissues has a maximum, which depends upon anatomical and physiological constrains, and upon dissolved oxygen saturation in the water.

2. If available oxygen become limiting, it is hierarchically allocated among competing processes in the following order: 1. standard (routine) metabolism, 2. osmoregulation, 3. activity, 4. assimilation and growth (anabolism).
3. The aerobic cost of growing is represented by SDA.
4. Under limited oxygen supply, food consumption and assimilation are reduced to avoid exceeding aerobic scope for anabolism (Figure 2).

Both food consumption and routine metabolism sub-models followed the general form,

$$Y = f[\mathrm{W}] \cdot f(\mathrm{T, DO, SAL}] \qquad \text{(Eq. 3)}$$

Where, Y represents either food consumption or routine metabolic rate, $f[\mathrm{W}]$ the maximum (fish weight dependent) expected rate, and $f(\mathrm{T, DO, SAL}]$ the combined effect of temperature, dissolved oxygen and salinity. While the maximum expected rates $f[\mathrm{W}]$ were expressed in absolute units of energy intake (KJ d^{-1} g^{-1}) or oxygen consumption (O_2 g^{-1} d^{-1}), the functions $f(\mathrm{T, DO, SAL}]$ was scaled as reaction rate multiplier ranging between 0 and 1. The latter function was, in turn, composed by 2 or more multiplicative sub-equations, each ranging between 0 and 1, and representing main effects and/or interactions among the three abiotic factors. Maximum expected rates $f[\mathrm{W}]$ were modeled as allometric functions of fish weight (Winberg, 1956), expressed by the general equation,

$$f[W] = a \cdot W^{b} \qquad \text{(Eq. 4)}$$

Where, W is the individual fish weight in grams, and *a* and *b* are empirical coefficients. The exponent *b* for the food consumption sub-model (b_{FC}) was independently obtained by linear regression analysis (Equation 2). All remaining parameters of functions f[W] and f(T, DO, SAL] were simultaneously estimated for each sub-model and species by non-linear regression. Non-linear parameter estimation was conducted using the non-linear mixed procedure (NLMIX macro for SAS 8.01) described by Littel et al. (1996). This procedure is based upon a Gauss-Newton iterative method and restricted maximum likelihood estimation of covariance matrices. Final model was coded in SAS 8.01 (SAS-Institute 1999).

We used Thornton and Lessem's (1978) algorithm as the default algorithm to model the directive effect of temperature f[T]. This algorithm, based upon two antagonistic logistic curves, has been widely used in bioenergetics (Stewart et al. 1983, Stewart and Binkowski 1986, Hartman and Brandt 1995b, Hanson et al. 1997) and allows relative independence between the increasing, decreasing and stationary sections of the response curve.

Several alternative algorithms were developed or modified to describe and predict functional responses to dissolved oxygen and salinity, which were compared through an iterative approach, based upon matching the following criteria,

a) Functional response represented theoretical expectations, fit the available data, and was consistent with results from multiple linear regression analysis.
b) All parameters within each alternative model were significant at =0.05 in both species.
c) Akaike's Information Criteria was the lowest among competing models meeting criteria a) and b).

Mesocosm validation

Two mesocosm experiments were conducted to validate bioenergetics models. The shortnose sturgeon mesocosm experiment was conducted in 3 replicates (tanks) with 22 fish per tank, between September 1998 and January 1999. The mesocosm experiment for Atlantic sturgeon was replicated using 4 tanks with 10 fish per tank, and lasted from March to June 1999. Both experiments were conducted in outdoor 3,200-L tanks at CBL Outdoor Seawater Facility, which received ambient brackish water from the the Patuxent River.

Water quality conditions were monitored 3 times a day between 7:00 AM and 20:00 PM. Temperature, salinity and dissolved oxygen varied according to natural river conditions. However, oxygen saturation reached supersaturation levels at noon during the warmer months of each period (Table 1). The fish were fed *ad libitum,* three times a day, six days a week. We used Biokyowa® pellets for Atlantic sturgeon, but Chironomidae larvae (San Francisco Bay Brand®) for shortnose sturgeon. Individual weight and total length were recorded once a week. Five fish from the initial stock and

3 fish from each tank were sacrificed at the beginning and at the end of each experiment, respectively. These fish were used to estimate energy content through the modified Maciolek's (1962) technique described above. Pearson´s correlation was used to evaluate parallelism between observed and predicted growth rates. T-test was used to evaluate if final weights were significantly different from model predictions for each tank.

Error analysis

To evaluate the sensitivity of bioenergetic models for each species to experimental error and parameter uncertainty, we conducted a series of error analyses (Bartell et al. 1986) based upon a Monte Carlo simulation approach. Thus, 5,000 values were randomly obtained for each parameter, under the assumption of normal or log-normal error distributions (depending upon each submodel formulation), and 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 and routine metabolism, where correlation between some parameters exceeded r=0.7. For each of these two sub-models we used restricted maximum likelihood covariance estimates (SAS-Institute 1997) to generate a Cholesky matrix suitable to simulate correlated parameter values (SAS-Institute 1999). Since the excretion sub-model was mostly based upon averaged data from other authors and species, we lacked reliable estimates for uncertainty in its parameters. Hence, standard deviation for each parameter of this sub-model was arbitrarily set at 20% of the

parameter mean estimate. This percent has been suggested as a conservative expectation for uncertainty in biological experiments (Bartell et al. 1986).

The random perturbations of each parameter were combined to generate equal number of daily growth predictions for each species. Growth predictions were 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 predictors used for forecasting bioenergetic responses, we repeated the described error analysis procedure under 3 water quality scenarios, representing hypoxia, high salinity and high temperature conditions (Table 2).

RESULTS

Food consumption:

Daily consumption tended to be higher in Atlantic sturgeon, but average rates were not significantly different between species ($p>0.05$), with a pooled mean of 0.52 KJ g^{-1} d^{-1} ± 0.056 SE. Linear regression analysis indicated that food consumption rate was significantly affected by main and quadratic effects due to dissolved oxygen, salinity and temperature, and by log-transformed fish-weight. Significant interactions between species, salinity and temperature and between species and temperature

suggested that the shape of food consumption responses to salinity and temperature differed between species ($p<0.05$).

Maximum likelihood estimates of regression parameters indicated dome-shaped responses to salinity and dissolved oxygen in both species. Food consumption response to temperature also followed a dome-shape pattern in Atlantic sturgeon, but a continuous increasing trend in shortnose sturgeon. The interaction we found between species, temperature and salinity suggests that maximum consumption in shortnose sturgeon is reached at lower salinity than in Atlantic sturgeon, given a fixed level of temperature. For instance, at 20ºC, maximum consumption would be reached at 9.1 ppt in shortnose sturgeon, but at 12.2 ppt in Atlantic sturgeon.

Submodel development

Following the general model from Equation 6 we have,

$$C = C_{max} \cdot f(T)_{FC} \cdot f(DO,Sal)_{FC} \quad \text{(Eq.5)}$$

Where,

C_{max} = $a_{FC} \cdot W^{b_{FC}}$, maximum food consumption rate (Eq.6)

a_{FC}, b_{FC} = empirical coefficients (Table 3).

W = individual fish weight in grams.

$f(T)_{FC}$ = controlling effect of temperature, regardless of salinity and dissolved oxygen conditions;

$f(\mathrm{DO,Sal})_{FC}$ = limiting effect of dissolved oxygen (given temperature and salinity conditions)

We observed that food consumption was inhibited by high temperature in Atlantic sturgeon, but it tended to a plateau in shortnose sturgeon. Therefore, Thornton and Lessem's (1978) sub-equation KB_{FC} was set to 1 for the latter species. Thus

$$f[T]_{FC} = KA_{FC} * KB_{FC} \qquad \text{(Eq. 7)}$$

Where,

$$KA_{FC} = \frac{CTK_1 e^{y2_{FC}(CT_{98}-T)}}{1+CTK_1(e^{y2_{FC}(CT_{98}-T)}-1)} \qquad \text{(Eq.8)}$$

$$KB_{FC} = \begin{cases} \dfrac{CTK_4 e^{y2_{FC}(T-CT_{98})}}{1+CTK_4(e^{y2_{FC}(T-CT_{98})}-1)} & \text{, for Atlantic sturgeon} \\ 1 & \text{, for shortnose sturgeon} \end{cases}$$

$$y1_{FC} = \frac{1}{CT_{98}-T_1}\log_e\left(\frac{0.98(1-CTK_1}{0.02\cdot CTK_1}\right) \qquad \text{(Eq.9)}$$

$$y2_{FC} = \frac{1}{T_4-CT_{98}}\log_e\left(\frac{0.98(1-CTK_4}{0.02\cdot CTK_4}\right) \qquad \text{(Eq.10)}$$

T = water temperature

CTK_1 = reaction rate multiplier at T_1 (Table 3)

CTK_4 = reaction rate multiplier at T_4 (Table 3)

T_1 = lowest tested temperature (6°C)

T_4 = highest tested temperature (28°C)

CT_{98} = estimated temperature at which 98% of maximum rate is reached (Table 3)

The limiting effect of hypoxia upon food consumption was represented by a segmented equation defined by two main parameters: COK_1, the reaction rate multiplier at the lowest tested DO level (DO_1); and CDO_{98}, a threshold value above which food consumption was no longer limited by dissolved oxygen. COK_1 and CDO_{98} were assumed to be functions of physiological processes competing for oxygen, such as routine metabolism (see below) and post-prandial metabolism, here surrogated by the KA_{FC} component from the food consumption model (Equation 8). The model predicts COK_1 to be minimum, when oxygen demand is maximum due to temperature and salinity effects upon spontaneous activity and/or osmoregulatory processes. CDO_{98} is predicted to be maximum, when potential post-prandial demand is maximum given temperature-controlling effects upon food consumption rate. Here negative effects of extremely low and high salinities upon food consumption, which were shown by linear regression analysis, were assumed to be well represented by salinity effects upon routine metabolism and, thus, food consumption. Thus, the sub-equationl we used followed the form,

$$f[\mathrm{DO}]_{\mathrm{FC}} = \begin{cases} COK_1 + \dfrac{(1-COK_1)COK_i}{COK_{max}} & \text{, if DO } \quad CDO_{98} \\ 1 & \text{, otherwise} \end{cases} \qquad \text{(Eq. 11)}$$

where,

$$COK_i = (DO_i - DO_1) \cdot e^{c_{FC} \cdot (DO_i - DO_1)} \quad \text{(Eq.12)}$$

$$COK_{max} = (CDO_{98} - DO_1) \cdot e^{c_{FC} \cdot (CDO_{98} - DO_1)} \quad \text{(Eq.13)}$$

$$CDO_{98} = 100 \cdot d_{FC} \cdot KA_{FC} \quad \text{(Eq.14)}$$

$$COK = 1 - g_{FC} \cdot f[T, Sal]_{RM} \quad \text{(Eq.15)}$$

$$f[T, Sal]_{RM} = f[T]_{RM} \cdot f[Sal]_{RM} \quad \text{(Eq.16)}$$

$$c_{FC} = -\frac{1}{CDO_{98} - DO_1} \quad \text{(Eq.17)}$$

DO_i = Dissolved oxygen saturation (%)

DO_1 = Minimum tested $DO_{\%}$ (25%)

KA_{FC} = Sub-equation KA_{FC} (from Equation 8)

$f(T)_{RM}$ = Reaction rate multiplier for the effect of temperature on routine metabolism (Equations 19 and 20, below)

$f[SAL]_{RM}$ = reaction rate multiplier for the effect of salinity on routine metabolism (Equation 25 below)

d_{FC}, g_{FC} = empirical parameters (Table 3)

Test of Consumption Submodel

The submodel explained a significant fraction of the observed variance (57 and 83%, in Atlantic and shortnose sturgeon, respectively) and showed a better fit than the linear regression model (lower AIC). All parameters were estimated to be significant ($p<0.05$). Consistent with linear regression results, the submodel predicted overall

consumption rates to be similar between sturgeon species along most of the tested conditions. Food consumption responses to temperature followed a very similar pattern in both species between 6 and 20ºC. On the other hand, as temperature reached the highest tested level (28ºC), consumption rates were sharply inhibited in juvenile Atlantic sturgeon, but remained maximal in shortnose sturgeon (Figure 3a).

In agreement with laboratory effects, the submodel predicted very strong effects of dissolved oxygen upon food consumption (Figure 3b). A strong interaction between oxygen and temperature displaced the CDO_{98} threshold to higher DO saturations as temperature increased. In Atlantic sturgeon, thresholds for oxygen-independence (CDO_{98}) were predicted at 45, 60 and 65% DO_{sat} for 12, 20 and 28ºC, respectively. In shortnose sturgeon, CDO_{98} thresholds were much higher, with predicted values at 73, 86 y 95% DO_{sat} for 12, 20 and 28ºC, respectively. Despite these differences, the slopes at the oxygen-dependent sections of the response curves were lower in shortnose than in Atlantic sturgeon, suggesting that shortnose sturgeon juveniles would sustain higher food consumption rates at sub-lethal hypoxia (Figure 3b).

The effects of salinity upon food consumption were predicted to be similar between both species (Figure 3c). Highest consumption rates were predicted close to expected iso-osmotic conditions (10 ppt) and lowest consumption rates at the highest tested salinity (29 ppt). In Atlantic sturgeon the inhibiting effect of salinity was relatively constant across temperature and the model predicted a reduction of circa 35% in the food consumption rate when salinity increased from 10 ppt to 29 ppt. In

shortnose sturgeon, however, salinity effects increased with temperature, and the model predicted food consumption rate reductions of 40, 45 and 49% when salinity was raised to 29 ppt at 12, 20 and 28ºC, respectively.

Routine metabolism

Routine oxygen consumption depended significantly upon temperature, dissolved oxygen, salinity, and $\log_e$-transformed weight in both sturgeons (ANOVA, $p<0.05$). Significant interactions were found between salinity and temperature, but not between dissolved oxygen and temperature. Although average oxygen consumption (0.18 mg O_2 g^{-1} h^{-1} ± 0.016 SE) was not significantly different between species, the effects of temperature upon routine metabolism were significantly different between sturgeons. These significant differences between species included both linear and quadratic components of temperature effects.

Multiple linear regression analysis indicated that respiration rates increased at a decreasing rate in Atlantic sturgeon, following a dome-shaped response with a maximum response at 26.3ºC. In shortnose sturgeon, on the other hand, the respiration rate tended to increase at an increasing rate along the tested temperature range. Routine metabolic responses to dissolved oxygen followed a dome-shaped responses in both species, with predicted maximum values circa 80% DO_{sat}. Responses to salinity, on the other hand, followed inverse dome-shaped response curves in both sturgeons, with minimum routine respiration rates expected circa 8 ppt in shortnose sturgeon, and 11 ppt in Atlantic sturgeon.

Submodel development

We built a predictive sub-model essentially analogous to the one used for predicting food consumption rate. Here we decomposed *f*[T,DO,Sal] in three independent multiplicative sub-equations,

$$RM = a_{RM} \cdot W^{b_{RM}} \cdot f[T]_{RM} \cdot f[DO]_{RM} \cdot f[Sal]_{RM} \qquad \text{(Eq.18)}$$

Although log-transformed fish weight was not a significant covariate in the regression analysis, it was kept in the model given the strong evidence supporting such effect in sturgeons and other fishes (Winberg 1956, Brett and Groves 1979, Hanson et al. 1997). Non-linear regression indicated the allometric exponent (b_{RM}) was a significant covariate in Atlantic, but not in shortnose sturgeon. For the latter species, we used a surrogate value of -0.196 obtained from Acipenseridae data compiled by Froese and Pauly (1997). This value was coincident with Winberg's (1956) estimate for sturgeons and close to the estimates we obtained for Atlantic sturgeon (b_{RM}=-0.189).

Since metabolic response to temperature followed very different patterns in both species (Figure 4a) we could not represent f[T] by a common submodel. Species-specific sub-models were defined as follows,

Atlantic sturgeon (Thortnon and Lessem's (1978) sub-equation K_A),

$$f[T]_{RM} = \left(\frac{RTK_1 \cdot e^{Y_{RM} \cdot (T - T_1)}}{1 + RTK_1 \cdot (e^{Y_{RM} \cdot (T - T_1)} - 1)} \right) \qquad \text{(Eq.19)}$$

Where,

T = water temperature (°C)

RTK_1 = reaction rate multiplier at the lowest tested temperature (29°C)

Y_{RM} = coefficient of increase (Table 3)

T_1 = lowest tested temperature (6°C)

Shortnose sturgeon (exponential model),

$$f[T]_{RM} = e^{[-Y_{RM}\cdot(T_4-T)]} \quad \text{(Eq.20)}$$

Where,

T_4 = highest tested temperature (29°C)

Y_{RM} = decreasing rate (Table 3)

Functional responses to dissolved oxygen f[DO] were described by segmented sub-models analogous to the ones used in food consumption sub-models. The critical $DO_{\%}$ level for routine metabolism (RDO_{98}) was, however, assumed to be only a function of temperature (i.e. independent from salinity), following the equations,

$$f[\mathrm{DO}] = \begin{cases} ROK_1 + \dfrac{(1-ROK_1)\cdot ROK_i}{ROK_{max}} & \text{, if DO} < \mathrm{RDO}_{98} \\ 1 & \text{, otherwise} \end{cases} \quad \text{(Eq. 21)}$$

Where,

$$ROK_i = (DO_i - DO_1)\cdot e^{(c_{RM}\cdot(DO_i-DO_1)} \quad \text{(Eq.22)}$$

ROK_{max} = ROK_i at RDO_{98}

$$ROK_1 = e^{(-d_{RM} \cdot T)} \quad \text{(Eq.23)}$$

$$RDO_{98} = -\frac{1}{c_{RM}} + DO_1 \quad \text{(Eq.24)}$$

$$c_{RM} = \frac{g_{RM} \cdot \log_e(T_4)}{\log_e(T)} \quad \text{(Eq.25)}$$

DO_i = dissolved oxygen saturation (%)

DO_1 = lowest tested $DO_{\%}$ (30%)

d_{RM}, g_{RM}, = empirical parameters (Table 3)

T = temperature

T_4 = maximum tested temperature (Table 3)

Functional response to salinity f[SAL] was modeled as a U-shaped curve, following the trends suggested by the linear regression analysis. This U-shaped response was obtained from a combination of two exponential curves. One curve (K_{sa}) represented osmo-regulation cost (and metabolic effects) at hyper-osmotic conditions, and increased as salinity increased. The other (K_{sb}) represented osmoregulatory costs (effects) at hypo-osmotic conditions and increased as salinity decreased. Interactions between salinity and temperature were expressed by the product $f[T] \cdot f[SAL]$

We assumed that the effects of salinity decreased with fish weight in proportion to the relative surface exposed to direct ionic interchange, i.e. gills and intestine (Brett 1979). Thus we scaled metabolic response to salinity by the specific gill surface area (cm^2 g^{-1}), which tends to decrease allometrically with fish size or weight (Pauly, 1981). An

allometric exponent of –0.158 was used with basis upon Burggren et al.'s (1979) work on *Acipenser transmontanus.* The resulting salinity sub-model is described by the equation,

$$f[Sal]_{RM} = \frac{K_{sa} + K_{sb}}{K_{smax}} \quad \text{(Eq. 26)}$$

Where,

$$K_{sa} = e^{[h1_{RM} \cdot (S_{max} - Sal)]} \cdot W^{b_{GSA}} \quad \text{(Eq.27)}$$

$$K_{sa} = e^{[h2_{RM} \cdot (Sal - S_{min})]} \cdot W^{b_{GSA}} \quad \text{(Eq.28)}$$

$$K_{smax} = 1 + e^{[h2_{RM} \cdot (Sal - S_{min})]} \cdot W^{b_{GSA}} \quad \text{(Eq.29)}$$

$h1_{RM}$, $h2_{RM}$ = parameters (Table 3)

S_{max}, = maximum tested salinity (29 ppt)

S_{min} = minimum tested salinity (1 ppt)

Sal = salinity (ppt)

T = temperature (^{o}C).

W = fish weight (g)

b_{GSA} = allometric exponent for gill surface area (-0.158)

Test of Routine Metabolism Submodel

Our submodel explained a significant proportion of the variance in both species (80 and 74 %, in Atlantic and shortnose sturgeons, respectively), and showed a better performance (lower AIC) than the linear regression model. All estimated parameters were significant ($p<0.05$). Overall, this submodel predicted higher sensitivity of routine metabolism to dissolved oxygen in Atlantic sturgeon, but higher sensitivity to

extreme salinity in shortnose sturgeon. Routine metabolism submodels indicated metabolic responses to temperature were similar in both species up to 20ºC. Above this level, Atlantic sturgeon metabolism was predicted to reach a plateau, while shortnose sturgeon metabolism maintained an exponentially increasing rate (Figure 4a). The limiting effects of hypoxia upon routine metabolism were evident in both species below 60-70% DO-saturation (Figure 4b).

Hypoxia limiting effects occurred at all tested temperatures, but were much more pronounced at high temperature conditions. As a result, critical oxygen levels (RDO_{98}) at the highest tested temperature were close (Atlantic sturgeon) or exceeded (shortnose sturgeon) 100% dissolved saturation. Routine metabolism tended to increase exponentially at both extremely low and high salinity conditions, with minimum values about 10 ppt in both species. These effects were more pronounced in shortnose sturgeon (Figure 4c). The effects of salinity upon routine metabolism were much more evident in fish < 8 g, and decreased sharply as fish-weight increased in both species.

Post-Prandial Metabolism (SDA)

Post-prandial metabolism ranged across experiments between 0.02 and 0.37 KJ g^{-1} with an average value of 0.24 KJ $g^{-1} \pm 0.031$ (SE). Total energy spent in post-prandial metabolism was significantly affected by species, and the linear components of total energy intake, temperature, dissolved oxygen saturation and $\log_e$-transformed fish weight. Nonetheless, after re-expressing SDA as a proportion of total energy intake ($SDA_{\%}$), $DO_{\%}$ continued to have a significant effect (Figure 5), but temperature,

species and fish weight no longer affected posprandial metabolism in a significant way. Although the proportion of energy spent as SDA tended to increase with temperature, this relationship was only significant at the 10% level. Average $SDA_{\%}$ was 13 % ± 1.3 (SE) of total energy intake for both species.

Post-prandial metabolism tended to be lower in magnitude but longer in duration under limited oxygen saturation conditions. The maximum post-prandial metabolic rate (KR_{SDA}), expressed as a proportion of the routine metabolism level, increased linearly with dissolved oxygen saturation and decreased with fish weight ($p<0.05$). Total duration of the post-prandial metabolic increase ($_4$) tended to be shorter at higher dissolved oxygen conditions, but this relationship was not significant at the specified level ($p=0.09$).

Submodel development

We modeled post-prandial metabolism as a proportion of total energy intake (FC), following evidence both from linear regression analysis and from other species (Hanson et al. 1997). We add, however, a coefficient (b_{SDA}) to adjust by dissolved oxygen saturation. From linear regression results, we conclude that a single model could be used for both sturgeon species. Thus,

$$SDA = (a_{SDA} + b_{SDA} \cdot DO_{\%}) \cdot FC \qquad \text{(Eq. 30)}$$

Where,

a_{SDA}, b_{SDA} = empirical parameters (Table 3)

$DO_{\%}$ = dissolved oxygen saturation (centered value over a mean of 79.6)

Activity cost (ACT)

Analysis of residuals between observed and predicted growth indicated that food consumption, routine metabolism and temperature explained significant fractions of activity cost variability. Best fit according to Akaike´s information criteria was obtained using food consumption as a single predictor of activity cost, without significant differences between species. Thus, activity cost was estimated to be 0.20 times food consumption ± 0.053 (SE), both in Atlantic and shortnose sturgeon. Given this modeling approach activity was predicted to remain maximum above 20ºC in shortnose sturgeon, but to decrease above 26ºC in Atlantic sturgeon. Qualitative observations on shortnose sturgeon indicated, however, that this species also tended to reduce activity when temperature approached 28ºC.

Submodel development

Given the uncertainty and lack of direct estimations for this component, we did not pursue a more complex alternative model, but used linear regression results from above,

$$A_m = a_{AC} \times FC \qquad \text{(Eq. 31)}$$

Where,

a_{AC} = empirical parameter (Table 3)

FC = Food consumption

Egestion

Egestion was significantly affected by temperature, dissolved oxygen and ration size in both species. There was a tendency for shortnose sturgeon to exhibit higher egestion rates, but means were not significantly different between species. Average egestion rate for both species (pooled data) was 10.0 % ± 0.21(SE) of total energy intake. Egestion rate was inversely related with temperature and dissolved oxygen saturation (Figure 6), but increased with ration size at an increasing rate. While some synergism between low oxygen and low temperature conditions was apparent, especially in shortnose sturgeon, no significant interactions were found between dissolved oxygen, temperature, and/or species.

Submodel development

A single egestion sub-model was fit for both species. This sub-model followed the general approach used by Elliot (1976) and Stewart et al. (1983), but included dissolved oxygen saturation ($DO_{\%}$) as an additional covariate to temperature (T) and ration size (C_i/C_{max}). The dome-shaped response observed in ration-size required a further modification of the original model. Thus,

$$F = C_i \cdot e^{a_{EG}} \cdot T^{b_{EG}} \cdot e^{\left\{ d_{EG} \cdot \frac{C_i}{C_{max}} + g_{EG} \cdot \left(\frac{C_i}{C_{max}} \right)^2 + h_{EG} \cdot DO_{\%} \right\}} \quad \text{(Eq.32)}$$

Where,

a_{EG}, b_{EG}, d_{EG}, g_{EG}, h_{EG} = empirical parameters (Table 3);

C_i = consumed food (KJ)

C_{max} = maximum daily consumption (KJ)

T = temperature

Excretion

We used an excretion sub-model based upon reported excretion rates for other Ascipenserid species (Appendix 1). Therefore, the only parameter computed from our own data was the scaling factor a_{EX}, calculated to be 0.56 and 0.62 for Atlantic and shortnose sturgeons, respectively. Given this input, excretion for an average 14.4 g juvenile sturgeon (both species) was estimated to range from 4.1 to 4.5% of consumed energy, depending upon temperature, dissolved oxygen and salinity conditions.

Growth

Regression analysis indicated that growth was significantly affected by temperature, salinity and dissolved oxygen, in both species. Significant linear and quadratic effects were found for all three main factors, and for interactions between temperature and dissolved oxygen. No significant interactions were observed, however, between temperature and salinity. Average instantaneous growth was similar in both sturgeons ($p>0.05$), and exhibited an average rate of 0.029 ± 0.0033 SE. Nonetheless, growth responses to temperature were significantly different between sturgeons and

some evidence for different responses to salinity was observed, although significant only at α=0.1.

Multiple linear regression analysis indicated dome-shaped growth responses to temperature, salinity and dissolved oxygen in both sturgeons, with maximum growth expected at 20^{o}C, 12 ppt and 86 % DO_{sat} in Atlantic sturgeon, and at 22^{o}C, 12 ppt and 91 % DO_{sat} in shortnose sturgeon. Predicted growth from bioenergetics modeling (Figure 7) showed more complex functional responses to environmental factors, but tended to agree in predicting environmental conditions required to maximize growth. Thus, somatic growth was expected to be maximum at 19^{o}C, 11 ppt and >70 % DO_{sat} in Atlantic sturgeon, and at 20^{o}C, 11 ppt and 100 % DO_{sat} in shortnose sturgeon.

Growth responses to temperature were predicted similar in both species (Figure 7), shortnose tended to growth faster than Atlantic sturgeon at temperatures greater than 15^{o}C, especially close to the highest tested temperature (28^{o}C). Temperature effects were predicted to be flatter in Atlantic sturgeon with a relatively large plateau between 18 and 21^{o}C (Figure 7a)

Dissolved oxygen effects upon growth showed greater differences between species than main temperature effects (Figures 7a and 7b). Atlantic sturgeon responses were predicted to be less affected by temperature, where growth was independent of dissolved oxygen saturation, above 70% DO_{sat} across most of the temperature range.

Shortnose sturgeon growth was much more sensitive to dissolved oxygen and temperature variations, and no clear plateau was predicted at any tested temperature.

Growth had a similar dome-shaped response to salinity in both species (Figure 7c), which was much more pronounced in shortnose than in Atlantic sturgeon. Reflecting observed responses, salinity was modeled to be highly dependent from temperature, especially in shortnose sturgeon. This dependence resulted from the modeled links between temperature, salinity, metabolism and food consumption in Equation 15. In this context, while salinity had almost no effect upon growth at very low temperatures (i.e. 6ºC), its masking effect would increase with temperature, exponentially in shortnose sturgeon and logistically in Atlantic sturgeon.

Mesocosm Validation

On average, bioenergetic models underestimated final fish weight in mesocosm tanks by 2 % in Atlantic sturgeon, and overestimated it by 8 % in shortnose sturgeon (Figure 8). The Atlantic sturgeon bioenergetics model tended to overestimate actual fish growth rates during the first 3 weeks of the mesocosm trials. Growth rates were then underestimated for this species during most of the remaining experimental period (Figure 8a). Model predictions for shortnose sturgeon closely followed observed growth rates (Figure 8b), which where also less variable between measuring events than in Atlantic sturgeon. Spearman´s correlation between observed and predicted growth rates (paired observations) reached 0.99 ($p<0.001$) in shortnose sturgeon, but only 0.50 ($p<0.05$) in Atlantic sturgeon.

Error analysis

Energy gain predictions from Atlantic and shortnose sturgeon bioenergetics models were highly sensitive to uncertainty in food consumption submodels, which explained >50% of total residual variance under all scenarios for both species (Table 4). Uncertainty in metabolism submodels (activity cost, routine metabolism and SDA) tended to have the second largest effects upon residual variance, while the error contribution from egestion and excretion submodels (egestion and excretion) tended to be the smallest one. Nonetheless, uncertainty in the egestion submodel had the second largest contribution to residual variance (10-17%) under the hypoxia scenario (Table 4).

The relative importance of uncertainty in individual parameters, as indexed by the relative partial sum of squares ($RPPS_{\%}$), followed the overall trends described above, but changed between species and water quality scenarios (Figure 9). Food consumption allometric parameters, b_{FC} and a_{FC}, and the activity cost proportionality constant a_{AC} had the largest individual effects upon predicted errors in the shortnose sturgeon model, regardless of the modeling scenario (Figure 9). In the Atlantic sturgeon model, on the other hand, uncertainty in a_{FC} had the largest overall effect upon predicted errors, but the relative importance of other parameters (mainly CT_{98}, b_{FC}, d_{FC} and a_{AC}) depended upon the modeling scenario. Other parameters showing strong effects upon errors in the Atlantic sturgeon model included CK_4, a_{RM} and a_{SDA} (Figure 9). The rank order for the six most sensitive parameters at reference conditions of

20ºC, 100% DO_{sat} and 12 ppt were $a_{FC} > CT_{98} > b_{FC} > a_{AC} > a_{SDA} > a_{RM}$ for Atlantic sturgeon; and $a_{FC} > b_{FC} > a_{AC} > a_{SDA} > d_{EG} > b_{SDA}$ for shortnose sturgeon.

When Atlantic and shortnose bionergetic models were used to predict growth in live-weight instead of energy units, very significant sources of error were added to these models. These sources of error corresponded to the three parameters used to estimate energy content in live fish from log-transformed specific weight and total length (Appendix 1, Equation 2). Uncertainty in parameters a_{EC} y d_{EC} from this equation represented >50% of the total error in both models.

DISCUSSION

Comparing bioenergetics between juvenile Atlantic and shortnose sturgeons

In estuaries, dissolved oxygen and salinity are highly relevant parameters, which should not be ignored in modeling bioenergetic responses. As expected, temperature had a strong controlling function, and explained most of the total variation in growth rates predicted for Atlantic (67%) and shortnose (50%) sturgeons under the tested conditions. Still, dissolved oxygen accounted for 25 and 29%, and salinity accounted for 8 and 21% of predicted growth variation in Atlantic and shortnose sturgeons, respectively

We observed similar bioenergetic responses between Atlantic and shortnose juveniles across most of the tested ranges of oxygen, salinity and temperature

conditions. Nonetheless, some noteworthy differences between species were evident in their consumption and metabolic rates as they approached the highest temperature and salinity tested levels (28°C and 29 ppt., respectively). Shortnose sturgeon were able to maintain food consumption and increase routine metabolism even when temperature approached 28°C. Atlantic sturgeon, on the other hand, reduced food consumption and did not show further increased metabolism above 24°C. At high salinity, juvenile shortnose sturgeon showed a larger increase in routine metabolism (osmoregulatory cost) and a much larger reduction in food consumption rates than Atlantic sturgeon .

Apparent differences in temperature and salinity responses between these two sturgeon species might be related to latitudinal and/or genetic differences between the progenies we used: Atlantic sturgeon were from the Hudson River population (NY) and shortnose sturgeon from the Savannah River population (SC). Nevertheless, our results are consistent with distribution patterns of sturgeon juveniles observed in natural environments. In the Hudson River, where both species still coexist at relatively high abundance (Bain 1997; Kynard 1997), juvenile shortnose sturgeon tend to have a wider summer distribution than juvenile Atlantic sturgeon, using most of the fresh and seasonally brackish water sections of the Hudson system. Juvenile Atlantic sturgeon are instead largely concentrated in the lower (cooler and saltier) sections of the estuary (Dovel et al. 1992, Bain 1997, Haley 1999). A lower tolerance to high salinity in juvenile shortnose sturgeon is also consistent with observed patterns in nature where juvenile Atlantic sturgeon initiate a much earlier exploration of brackish and mesohaline

waters than juvenile shortnose sturgeon (Dovel and Berggren 1983, Dadswell et al. 1984, Dovel et al. 1992).

Comparing bioenergetics between sturgeons and teleosts

Overall consistency was observed between our results and those reported for other acipenserids in the literature, once size and temperature were properly adjusted (Table 5). Routine metabolism estimates were within 30% of expected values in most cases, with the exception of Winberg´s (1956) and Gershanovich´ (1983) results, which were 1.5- and 2-fold higher than values expected for juvenile Atlantic and shortnose sturgeons. In terms of both food consumption and growth rates, our results lied in between those reported for *A. transmontanus* and *A. sinensis*, and Russian species (*A. nudiventris, A. guldenstadti, Huso huso).* The only other post-prandial metabolism estimates we obtained for sturgeons (Dawrowski et al. 1987) were about half our own ones. Such a difference could be related to quite distinct methodological approaches, being our estimates closer to typical values for other fishes (Hanson et al. 1997).

Given the methodological constrains existing to obtain direct estimates of activity cost, Winberg (1956) proposed that total metabolism (routine metabolism + SDA + activity cost) could be approximated by doubling the energy expenditure attributed to routine metabolism. Since then, fixed multipliers around 2 (1-4.4) have been used to transform routine metabolism into active metabolism (routine metabolism + activity cost), keeping SDA as a separate additive component (Kitchell et al. 1977, Hanson et al. 1997). We estimated active metabolism to be between 2.8 (Atlantic)-3.3

(shortnose) times routine metabolism. These relationships depended, however, upon water quality conditions, being the activity cost better predicted as a proportion of food consumption than of routine metabolism.

Although large activity multipliers (>2) have been observed in some other fishes, such us *Morone saxatilis* (Hartman and Brandt 1993) and walleye *Stizostedion vitreum* (Hanson et al. 1997), the values we calculated exceeded indirect activity cost estimates available for sturgeons. Khakimullin (1984) suggested an activity multiplier as low as 1.38 for *Acipenser baeri*, and Winberg (1956) gave a multiplier of 1.6-2.1 for *A. gueldenstaedtii*. Nonetheless, Winberg´s (1956) and Khakimullin´s (1984) estimates for routine metabolism in these species were 1.3-1.5 times higher than the values we observed in Atlantic and shortnose sturgeons. Therefore, differences in terms of total metabolism would tend to be much smaller than in terms of activity multipliers. Using a different approach, Levin (1982) observed 2.4 times diurnal variations in spontaneous swimming speed for juvenile *Acipenser gueldenstaedtii*, which is an indirect estimation of both the relative value and large variability of the activity cost in this species.

The average excretion and egestion rates we estimated (4 and 10% of the energy intake, respectively) were noticeably lower than rates reported for teleosts, which average 8 and 20%, respectively (Brett and Groves 1979). Although these results might be biased by the use of commercial food pellets, they were close to estimated rates for other Acipenserids fed natural food (Dawrowski et al. 1987, Gershanovich and Pototskij 1992, Cui et al. 1996). High assimilation efficiency (and low excretion rates)

might , in fact, be expected in sturgeons due to the high absorptive surface provided by the presence of the spiral valve in the intestine (Buddington and Christofferson 1985).

Sturgeons and hypoxia

The average sensitivity of Asian sturgeons to hypoxia has been suggested to exceed even oxyphylic species like rainbow trout Oncorynchus mykiss (Klyashtorin 1976). High sensitivity of Acipenserids to low oxygen has been also reported for *A. transmontanus* by Burggren and Randall (1978) who found critical values close to 100% of dissolved saturation at 18ºC. Nonnotte et al. (1993), however, found that *A. baeri* was able to maintain standard metabolism down to a dissolved oxygen saturation of 25% at 15ºC. The responsiveness of Atlantic and shortnose sturgeon observed in our study are intermediate: average critical dissolved oxygen saturations at 15ºC would be 83% and 72% DO_{sat} for juvenile Atlantic and shortnose sturgeons, respectively. The heightened sensitivity of metabolism to oxygen levels may be characteristic of sturgeons, and has been ascribed to an inefficiently functioning oxyregulatory system. Klyashtorin (1982) concluded that ancestral morphological and physiological traits caused sturgeons to be less efficient in respiration than other fishes. These traits include less efficient gill ventilation, low cardiac performance (Agnisola et al. 1999), and lower affinity of hemoglobin to oxygen.

This overall pattern of especially high sensitivity of sturgeons to hypoxia seems counterintuitive. Many sturgeon populations may have historically used shallow warm estuaries, where hypoxia occurred naturally in the deepest waters before recent

anthropogenic effects (Burggren and Randall 1978, Crocker and Cech 1997). At the same time, this limited ability to adapt to hypoxia could explain the lack of recovery observed for sturgeon populations inhabiting heavily eutrophied estuaries along the East Coast of the United States (Collins et al. 2000).

Energy partitioning in juvenile sturgeon

We estimated that, under optimal conditions (20ºC, 12 ppt and 100% DO_{sat}), Atlantic and shortnose sturgeons transformed an average of 41 and 43% of consumed energy into fish biomass, respectively. These efficiency levels were similar to the 43.5% reported by Winberg (1956) for 11-21 g *A. gueldenstaedtii*, but higher than the average value of 29% estimated for "well fed" carnivorous teleosts by Brett & Groves (1979), and the 35% net conversion efficiency calculated for white sturgeon (Cui et al. 1996). Conversion efficiency and energy allocation patterns departed, however, from this average values depending upon water quality.

We predicted the proportion of energy allocated to growth to decrease slightly under sublethal hypoxia (40% DO-saturation), being estimated as 39 and 38% of consumed energy in Atlantic and shortnose sturgeons, respectively (Figure 11). Nonetheless, model predictions indicate hypoxia would cause a severe reduction in absolute levels of growth, as large as 22% in Atlantic sturgeon, and 48% in shortnose sturgeon. Hypoxia-driven reductions in the amount of energy allocated to growth was also observed in rainbow trout *Oncorynchus mykiss* by Pedersen (1987), although the

magnitude of this drop was more pronounced, showing negative growth rates already at 40% DO_{sat} (15°C).

While a similar (Atlantic) or larger (shortnose) proportion of the energy budget was allocated to metabolism under hypoxia (Figure 11), the absolute amount of energy spent in metabolism showed a significant decrease. Routine metabolism decreased by 18-20%, and total metabolism by 15-25%, depending upon the species. Active metabolism was estimated to fall by an average of 19% in Atlantic and 33% in shortnose sturgeon under hypoxia. These were much less severe reductions than the 78% drop in relative activity reported for *A. transmontanus*, under 50% dissolved oxygen saturation conditions by Crocker & Cech (1997).

Egestion and post-prandial metabolism showed much larger changes under hypoxia than other bioenergetic parameters. In inverse proportions, egestion rose c. 2-fold and post-prandial metabolism decreased by half under hypoxia. This appears as a potential compensatory mechanism, complementary to the reduction in food consumption, which would help to avoid toxic concentrations of unstable amino acids in the blood when catabolism is limited by hypoxia (Pauly, 1981). Although it is not clear how sturgeon and other fishes reduce assimilation rates, it has been hypothesized that fish might increase egestion by reducing irrigation of absorptive intestinal tissues (Brett 1979, Jobling 1981).

Generically defined as “the cost of digestion and food processing”, SDA integrates different post-prandial energy losses, including intestinal work (Tandler and Beamish 1979), amino acid oxidation / urea synthesis (Dabrowski et al. 1987) and protein synthesis / growth (Jobling 1983). Although the relative contribution of these energy losses is still unclear, available experimental evidence supports the idea that SDA mostly represents the energy cost of protein synthesis, i.e. growth (Brett and Groves 1979, Jobling 1983, Brown and Cameron 1991, Brodeur et al. 2002). We observed, nonetheless, that hypoxia caused a much larger reduction in the amount of energy spent in SDA, than in growth. Thus, the relationship between SDA and growth appears not to be linear, which could be explained by non-linearities in the cost of protein synthesis itself, or by a higher than expected contribution from the post-prandial processes.

In summary, ours results support the idea that sturgeons reduce not only food consumption, but also assimilation rates to compensate for hypoxia-driven reductions in metabolic scope . This evidence is in agreement with theoretical expectations (Jobling 1981, Pauly 1981, van Dam and Pauly 1995), but in contrast with actual observations in *Oncorhynchus mykiss*, where food consumption, but not assimilation rate was reduced under hypoxia (Pedersen 1987).

Overall performance of developed bioenergetics model.

As indicated by mesocosm experiments, bioenergetic models fit separately to Atlantic and shortnose sturgeon juveniles were able to provide reasonably accurate

forecasts for growth rates within a 3-month timeframe. Within this period fish grew up to 120 and 200 g in shortnose and Atlantic sturgeons, respectively, which was well above the maximum size used in the laboratory to generate the models (48 g). Lower accuracy was observed in growth forecasts for Atlantic than for shortnose sturgeon, coinciding with larger fish at the end of the mesocosm experiment. Thus, it would be unadvisable to extend the age and size scopes of the bioenergetics models we developed beyond 120-200 g, which correspond to the end of the first year of life in shortnose (Dovel et al. 1992) and Atlantic sturgeons(Stevenson and Secor 1999), respectively (Hudson River populations).

Use of bioenergetic models to forecast weight-at-time has the limitation of intrinsic dependence form previous daily estimates, in such a way that errors tend to propagate quasi-exponentially with time. Less autocorrelated, predictions of daily growth rates were, instead, much more accurate (Figure 9). Moreover, our results showed that growth predictions are also affected by uncertainty in energy content estimates, which has been often assumed as a constant value through growth forecast applications of bioenergetic models (Hanson et al. 1997). Although we did not succeed verifying daily food consumption forecasts in the mesocosm, we did expect these predictions to be much more accurate than growth ones as observed by Bartell et al.´s (1986) work evaluating bioenergetic models developed for perch (Kitchell et al. 1977) and alewife (Stewart et al. 1981)..

In terms of uncertainty in the model, allometric parameters defining maximum food consumption rate were the most sensitive to experimental error, which is also consistent with Bartell et al.'s (1986) conclusions. Excretion rate was, in turn, the least sensitive to error as also reported for other fishes (Kitchell et al. 1977, Bartell et al. 1986, Hanson et al. 1997). Low sensitivity of this parameter may be related to its low share of total energy expenditure (circa 4%), as well as to the fact we used stipulated literature values and arbitrary uncertainty (CV=20%) in the derivation of the excretion parameters.

Activity cost has been shown to be a very large and variable bioenergetic component (Bosclair and Legget 1989, Bosclair and Sirois 1993), affected by the inherently random nature of spontaneous activity, and amplified by short-term stress responses. Our estimations for activity cost were also high in magnitude and uncertainty, indicating that 20% ± 3.26 (SE) of the ingested energy was spent in activity, regardless of the sturgeon species. Nonetheless, it must be considered that we used and indirect approach, where it was assumed that activity cost was a constant proportion of food consumption. Despite uncertainty and potential bias in these activity estimates, we found a reasonable consistency between laboratory and mesocosm results, suggesting that similar activity cost values might be expected for non-migrating free-swimming sturgeons in nature.

Modeling Fry's paradigm in a bioenergetics framework

Laboratory and mesocosm results showed consistency with theoretical assumptions used in the model, which depended heavily upon assigning controlling, limiting and masking roles to temperature, dissolved oxygen and salinity, respectively (Fry 1971). Bionergetics sub-models, reformulated under the concept of a balanced oxygen equation (van Dam and Pauly 1995), allowed hierarchical and horizontal integration of limiting and masking effects, adding a second dimension to the bioenergetics models. This approach allowed the simultaneous analysis of potential maximum rates, controlled by temperature, and actual realized ones, limited by aerobic scope (Figure 11). Here, the concept of aerobic scope is closely related but not equivalent to Fry´s (1971) scope for activity, as interpreted by Mallekh and Lagardère (2002). Scope for activity, defined as the difference between maximum and resting metabolism (Fry 1971), is affected by biochemical power (within cells) and oxygen delivery constrains, following a dome-shaped curve along the temperature range of interest. Aerobic scope, instead, is explicitly referred to oxygen delivery constrains, and is defined as the difference between the maximum amount of oxygen deliverable to and demanded by the tissues to sustain resting (or routine) metabolism.

The masking role of salinity was modeled within the balanced oxygen equation rather than including masking factors as a third dimension. This general approach is also consistent with Fry's (1971) suggestion that osmoregulatory cost can be added to standard metabolism, reducing the aerobic scope for activity. This approach, however, does not account for potential indirect effects due to osmoregulatory hormones, which

might also affect both anabolism and catabolism (Morgan and Iwama 1991, Kirschner 1995).

Adding complexity to bioenergetic models

Our experimental results matched the expectations that oxygen and salinity strongly influenced bioenergetics in both sturgeons, thus confirming the theoretical and practical need to model individual and synergistic effects of temperature, dissolved oxygen and salinity on sturgeon metabolism, growth and production (Neill et al. 1994, van Dam and Pauly 1995)..

We do acknowledge that increasing complexity in bioenergetic models does not necessarily result in significant improvements regarding their predictive capabilities (Bartell et al. 1986). Improvement in more complex models is often limited by low sensitivity of the model to additional parameters, and/or by uncertainty in the additional information required to estimate them (Brandt and Hartman 1993, Hanson et al. 1997). Nonetheless, even under limited improvement in quantitative terms, explicit bioenergetic models represent a valuable framework to integrate and synthesize scientific understanding about key ecophysiological processes in fishes (Bartell et al. 1986).

The present work was designed to contribute to both explanatory and predictive frameworks. Thus, we incorporated formally and explicitly in the proposed models the observed effects of salinity and oxygen on different fish bioenergetic processes. At the

same time, we expected to increase forecasting capabilities on fish bioenergetics for species living in estuarine environments where salinity and regular (seasonal) hypoxia are very relevant ecophysiological factors. The availability of intense and regular monitoring programs, such us the Chesapeake Bay one, allow the use of these forecasting tools as an integrative way to project habitat suitability. Moreover, this approach might remain as the only option to evaluate habitat when observational data on fish abundance and distribution is scarce or missing, as it is the case of many sturgeon populations.

This modeling approach should be viewed as a first approximation, and future improvement is needed. Food consumption and metabolic responses to hypoxia below 40% DO_{sat} and salinity above 20 ppt, as well us the ontogenetic aspects of salinity tolerance need further investigation in both species. Modeling algorithms to describe food consumption and metabolic responses to salinity also deserve to be improved and enriched from both experimental data and theoretical contributions. Reducing uncertainty in sensitive parameters is also a major challenge, specially regarding the activity cost, which remains as one of lest accurate component of bioenergetics models.

ACKNOWLEDGMENTS

We thanks the Chilean Ministry for Planning and Cooperation, the Hudson River Foundation and the Nature Conservancy, who supported E. Niklitschek doctoral dissertation work; and the National Fish and Wildlife Service, who provided us with

experimental fish. We are grateful of intense laboratory help from S. Larsen, S. McGuire, J. Smith, K. Norman, T. Gunderson and B. Millsaps.

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Variable	Shortnose sturgeon		Atlantic sturgeon	
	Mean ± SD	Range	Mean ± SD	Range
Salinity (ppt)	17.1±0.7	15.2-18.2	13.2±1.3	11.3-15.5
Temperature (^{o}C)	12.2±5.0	3.2-21.4	18.3±6.1	4.5-28.7
Oxygen saturation (%)	91.3±6.9	74.0-107.7	102.5±9.2	78.4-127.5

Scenario #	Temperature (°C)	Salinity (ppt)	Dissolved Oxygen (%)	Environmental conditions represented
2	20	8	40	Hypoxia
3	28	20	100	High temperature
4	20	29	100	High salinity

Parameter	Definition	Estimated value ± SE	
		Atlantic sturgeon	Shortnose sturgeon
Food consumption			
a_{FC}	Scaling coefficient	1.0±0.16	1.2±0.15
b_{FC}	Allometric exponent	-0.20±0.042	-0.20±0.042
CK_1	Reaction rate multiplier at T1 (6ºC)	0.32±0.094	0.28±0.049
CK_4	Reaction rate multiplier at T4 (28ºC)	0.7±0.11	Set to 1
CT_{98}	Temperature at which rate = 0.98	21±4.3	Set to 28ºC
d_{FC}	Proportionality constant for COK_1	0.6±0.22	2.0±0.20
g_{FC}	Proportionality constant for CDO_{98}	0.8±0.31	1.1±0.15
Routine Metabolism			
a_{RM}	Allometric intercept	0.5±016	1.3±0.31
b_{RM}	Allometric slope	-0.19±0.077	-0.20±0.030[1]
RTK_1	Reaction rate multiplier at T_1	0.15±0.018	n.a.
Y_{RM}	Exponential rate of increase	n.a.	0.085±0.0070
d_{RM}	Proportionality constant for ROK_1	0.034±0.090	0.027±0.0085
g_{RM}	Proportionally constant for RDO_{98}	0.014±0.053	0.015±0.0077

[1] Standard error corresponds to linear regression analysis of Acipenserids routine metabolism data obtained from Froese and Pauly (1997)

$h1_{RM}$	Hypo-osmotic coefficient	0.05±0.021	0.09±0.018
$h2_{RM}$	Hyper-osmotic coefficient	0.06±0.027	0.11±0.022
Post-prandial metabolism (SDA)			
a_{SDA}	Intercept	0.12±0.019	0.12±0.019
b_{SDA}	DO-slope	0.010±0.0042	0.010±0.0042
Activity cost			
a_{AC}	FC proportionality coefficient	0.20±0.053	0.20±0.053
Egestion			
a_{EG}	Log_e-transformed intercept	-2.6±0.14	-2.6±0.14
b_{EG}	Exponent for temperature	-0.5±0.19	-0.5±0.19
d_{EG}	Ration size, linear effect	-0.3±0.19	-0.3±0.19
g_{EG}	Ration size, quadratic effect	2.6±0.14	2.6±0.14
h_{EG}	Dissolved oxygen effect exponent	-0.010±0.0028	-0.010±0.0028
Excretion (standard errors not available, see methods)			
a_{EX}	RNE, scaling factor	0.056	0.062
b_{EX}	RNE, exponent	0.71	0.71
d_{EX}	XNE, FC proportionality coefficient	3.9	3.9

Species	Bioenergetic component	Scenario (temperature/salinity/DO%)			
		20/12/100 (optimal)	20/12/40	20/29/100	28/12/100
Atlantic	C	66.5	68.7	61.2	51.2
	ACT	13.8	6.4	12.9	8.0
	RM	7.2	4.7	12.1	14.1
	SDA	8.8	9.2	10.0	6.6
	F	3.3	10.5	3.3	2.3
	U	0.4	0.5	0.5	0.6
Shortnose	C	54.1	41.8	50.9	51.3
	ACT	19.2	12.2	17.1	16.2
	RM	5.5	15	10.4	14.6
	SDA	13.7	13.2	13.5	12.5
	F	6.5	17.1	6.0	4.5
	U	1.1	0.7	1.0	0.9

Species	Average weight	Rearing conditions			Reported rate in literature	Predicted rate at similar conditions (this work)		Reference
		T	Sal	$DO_{\%}$	Rate	Atlantic	Shortnose	
Routine Metabolism (mg O_2 g^{-1} h^{-1})								
A. transmontanus	63.1	20	0	100	0.180	0.179	0.218	Crocker & Cech (1997)
A. transmontanus	63.1	20	0	53	0.150	0.158	0.199	Crocker & Cech (1997)
A. transmontanus	1900	18	0	100	0.094	0.09	0.104	(Ruer et al., 1987)
A. oxyrinchus	40.5	19	2.3	80	0.218	0.185	0.211	(Secor & Gunderson, 1998)
A. oxyrinchus	40.5	26	2.3	78	0.276	0.21	0.361	(Secor & Gunderson, 1998)
A. baeri	5	20	0	100	0.354	0.27	0.315	(Khakimullin, 1989)
A. baeri	0.339	17	0	100	0.373	0.337	0.336	Dabrowski et al. (1987)
Huso huso	4.245	24	0	100	0.336	0.305	0.452	Gershanovich (1983)
A. nudiventris	3.67	24	0	100	0.278	0.312	0.461	Gershanovich (1983)
Acipenserids (pooled data)	14.4	20	0	100	0.337	0.228	0.245	Winberg (1959)

Food consumption (KJ g^{-1} day^{-1})								
A. transmontanus	12.7	18.5	0	100	0.429	0.577	0.628	Cui et al. (1996)
A. transmontanus	50	20	0	100	0.623	0.439	0.494	Cui & Hung (1995), optimum FR
Huso huso	7.2	24	0	100	0.418	0.625	0.781	Gershanovich (1983)
A. nudiventris	6.6	24	0	100	0.327	0.637	0.795	Gershanovich (1983)
Egestion (proportion of food consumption)								
A. transmontanus	11.1	18.5	0	100	0.089	0.092	0.084	Cui et al. (1996)
Instantaneous Growth Rate								
A. transmontanus	50	20	0	100	0.025	0.051	0.058	Cui & Hung (1995),
A. transmontanus	1.6	20	0	100	0.055	0.13	0.148	Cech et al (1984)
Huso huso	7.2	24	0	100	0.119	0.127	0.122	Gershanovich (1983)
A. nudiventris	6.6	24	0	100	0.079	0.08	0.097	Gershanovich (1983)
A. sinensis	24.3	15.6	0	100	0.044	0.082	0.099	Xiao et al (1999)
A. guldenstadti	26	19.6	0	100	0.109	0.06	0.062	Winberg (1959)
SDA (proportion of food consumption)								
A. baeri	0.339	17	0	100	0.070	0.142	0.142	Dabrowski et al. (1987)

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Figure 6: Effects of temperature and dissolved oxygen saturation on egestion rates of a) juvenile Atlantic sturgeon; and b) juvenile shortnose sturgeon. Data represent only fish fed *ad-libitum* to exclude ration size effect. Error bars indicate ±1 standard errors.

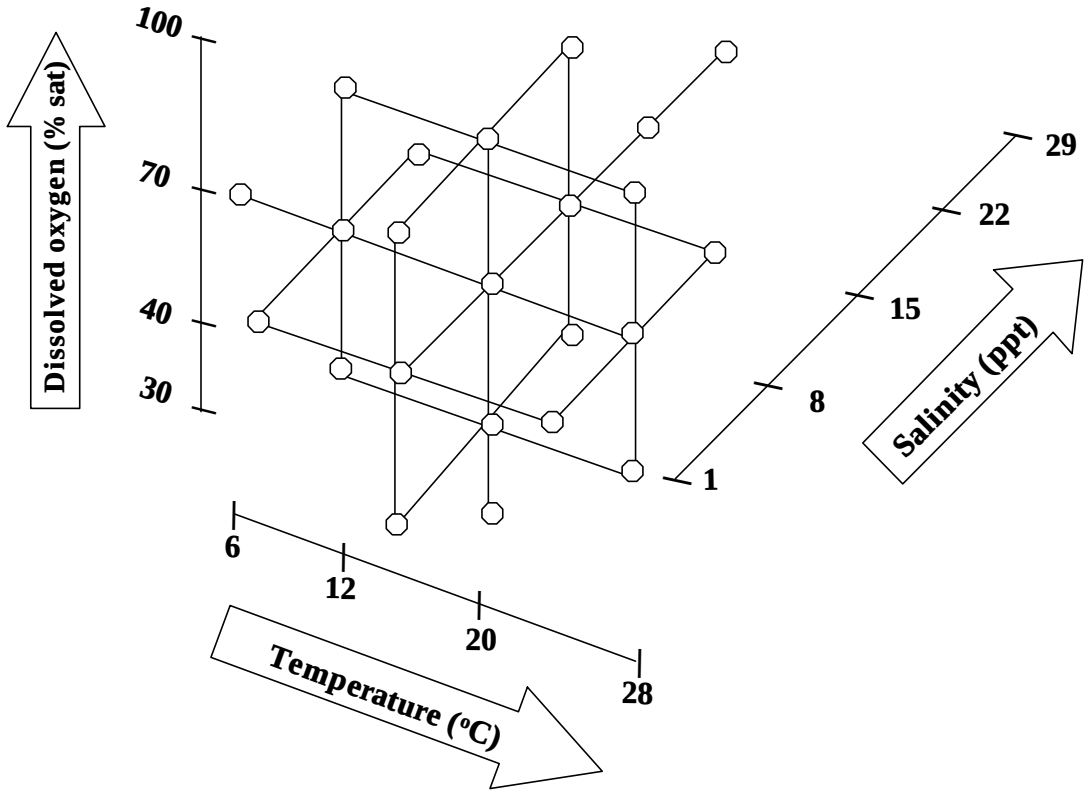
Figure 7: Effects of temperature (A), dissolved oxygen saturation (B) and salinity (C) on growth rates of juvenile Atlantic and shortnose sturgeons. Figures show variability caused by a single factor, while the others are kept at fixed conditions (20ºC, >100% DO_{sat} and/or 8 ppt). Bioenergetics model predictions (lines) and observed values (symbols) are weight-normalized to represent a 14.4-g fish.

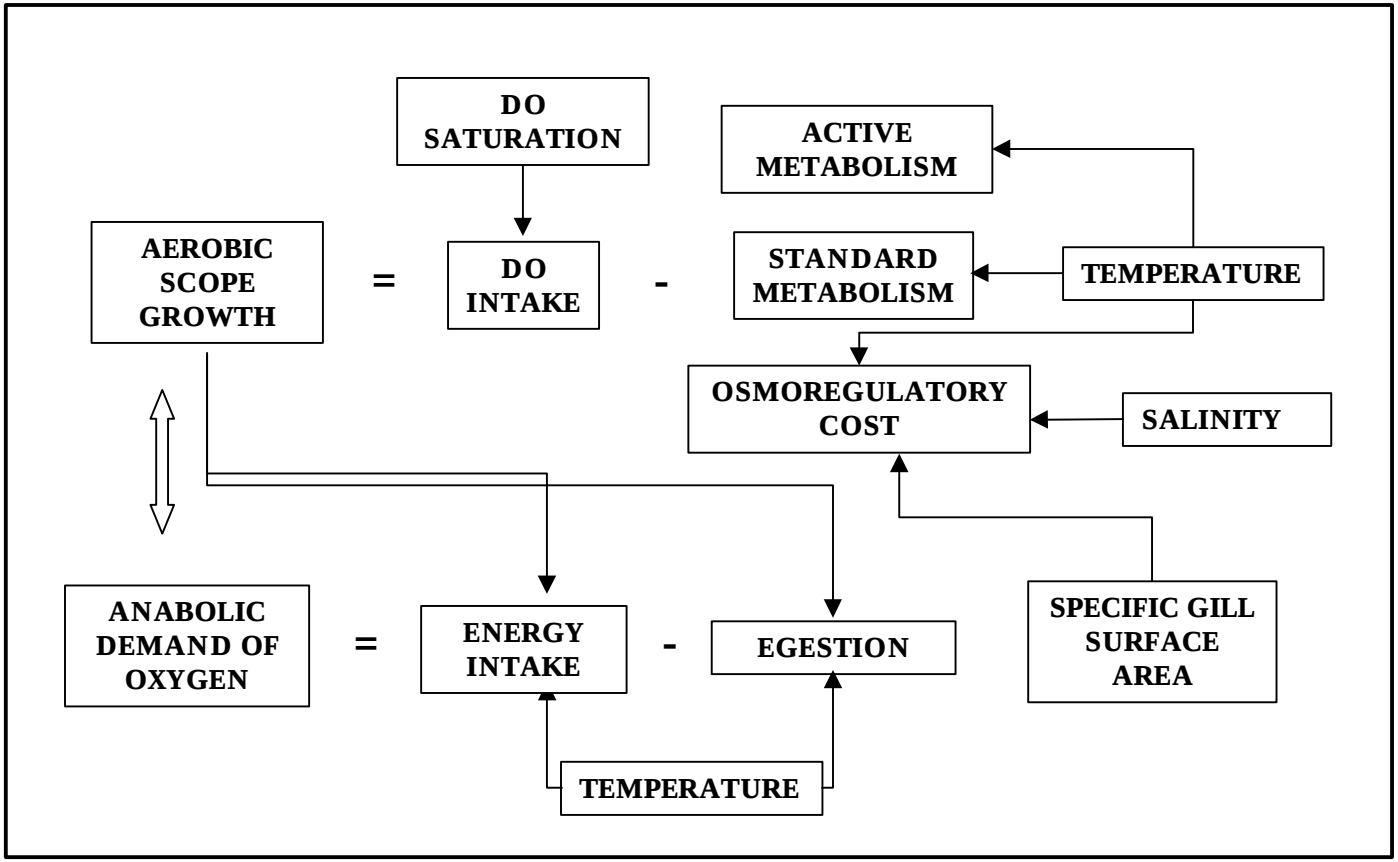
Figure 8: Predicted (lines) and observed (circles) weight and growth rates in Atlantic (a) and shortnose (b) sturgeons during 3-month mesocosm validation experiments. Error bars correspond to standard errors.

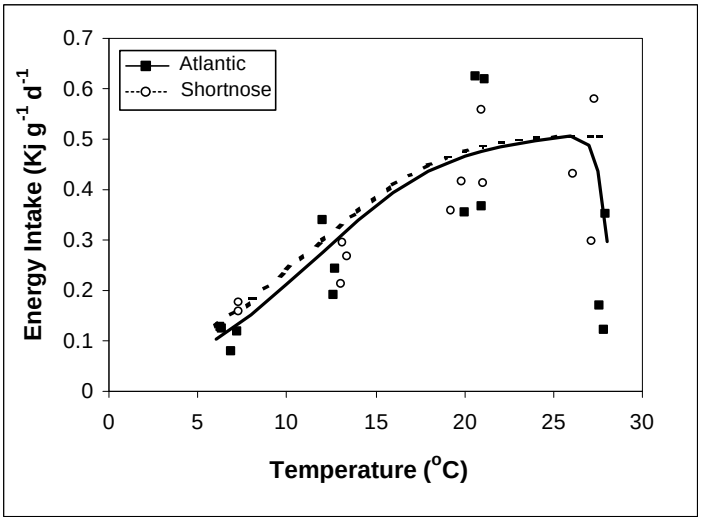
Figure 9: Percent of residual variance (% PRSS) explained by uncertainty in individual parameters from Atlantic (white bars) and shortnose (black bars) sturgeons bioenergetic models under 3 simulation scenarios. Scenario 1: U=excretion; SDA=post-prandial metabolism; RM=routine metabolism; F=egestion; C=food consumption; ACT=activity cost.

Figure 10: Energy partitioning among main bioenergetic components, under hypoxia (50% DO_{sat}) and normoxia (100% DO_{sat}), at constant temperature and salinity conditions (20ºC, 8 ppt), in juvenile Atlantic (a) and shortnose sturgeons (b).

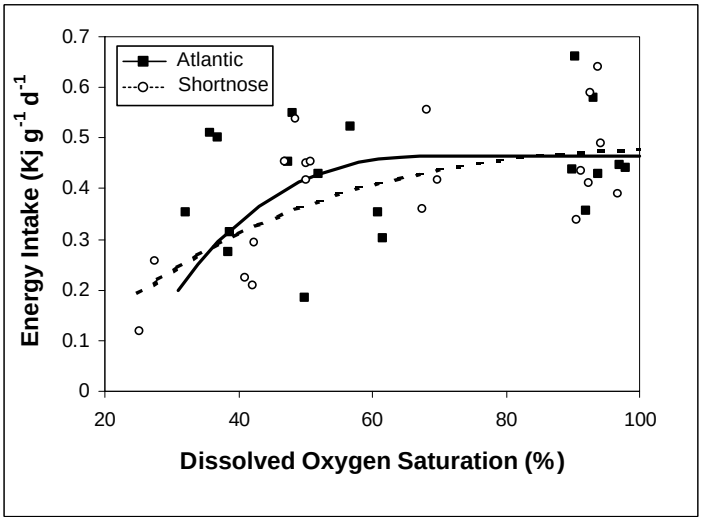
Figure 11: Diagram illustrating the relationship between anabolic and catabolic oxygen demands and aerobic scope in fishes.


Dissolved oxygen (% sat)
100
70
40
30
6
12
20
28
Temperature (°C)
1
8
15
22
29
Salinity (ppt)

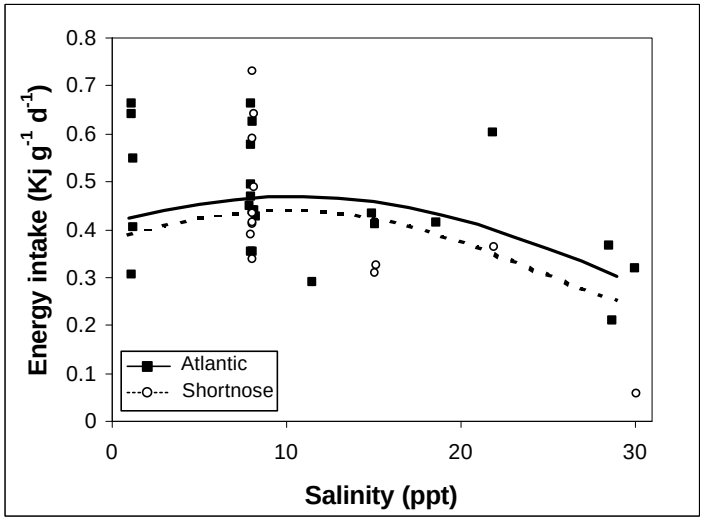

DO SATURATION
ACTIVE METABOLISM
AEROBIC SCOPE GROWTH
=
DO INTAKE
-
STANDARD METABOLISM
TEMPERATURE
OSMOREGULATORY COST
SALINITY
ANABOLIC DEMAND OF OXYGEN
=
ENERGY INTAKE
-
EGESTION
SPECIFIC GILL SURFACE AREA
TEMPERATURE


Atlantic
Shortnose
Energy Intake (Kj g-1 d-1
Temperature (oC)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0
5
10
15
20
25
30

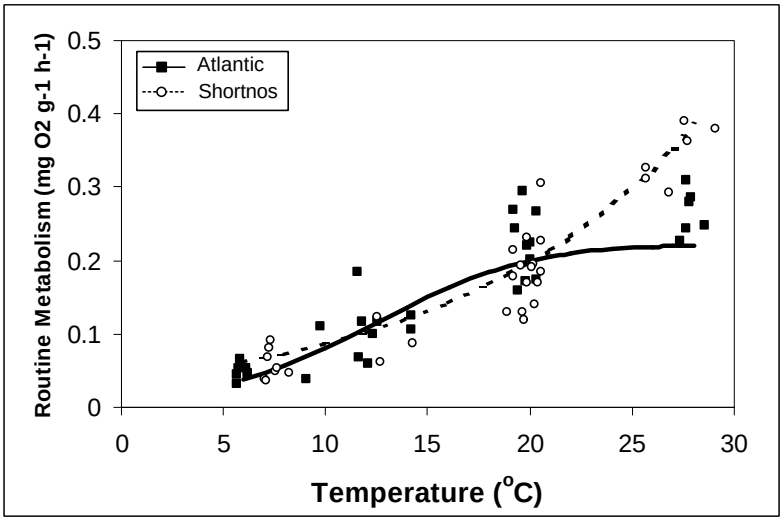
a)


Atlantic
Shortnose
Energy Intake (Kj g-1 d-1
Dissolved Oxygen Saturation (%)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
20
40
60
80
100

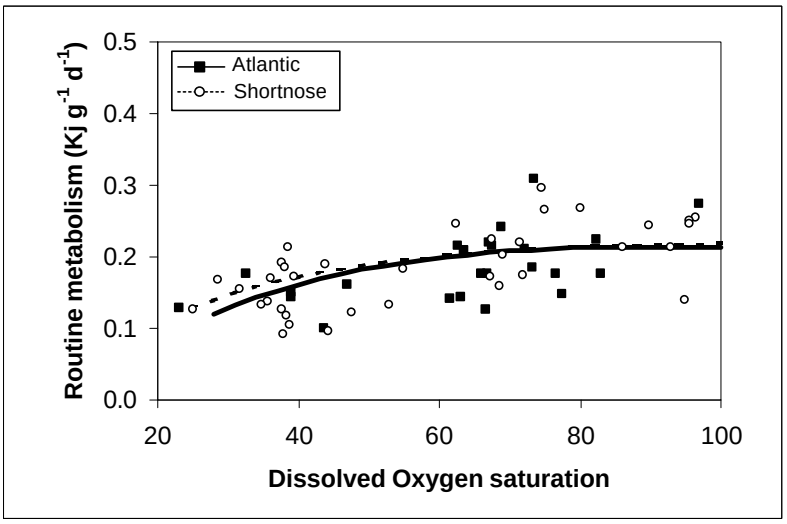
b)


Atlantic
Shortnose
Energy intake (Kj g-1 d-1)
Salinity (ppt)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0
10
20
30

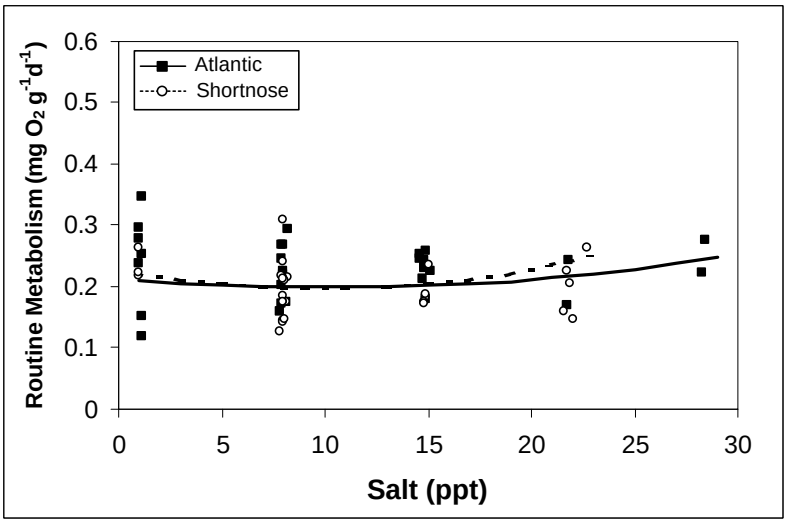
c)


Routine Metabolism (mg O2 g-1 h-1)
0.5
0.4
0.3
0.2
0.1
0
Atlantic
Shortnos
0
5
10
15
20
25
30
Temperature (°C)

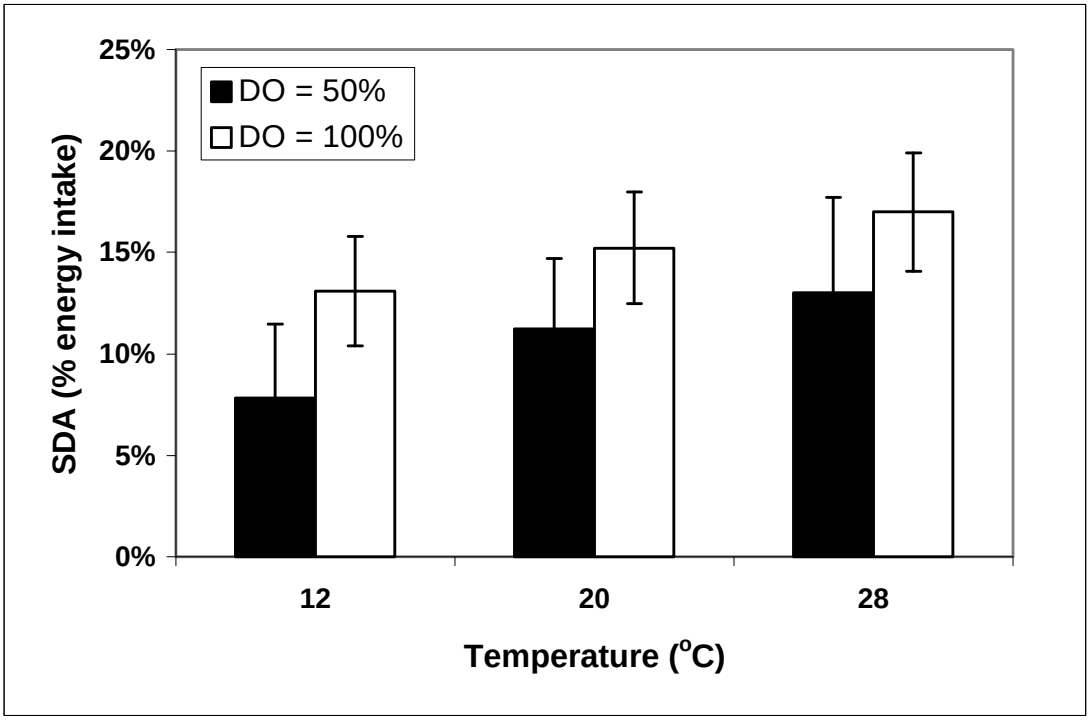
a)

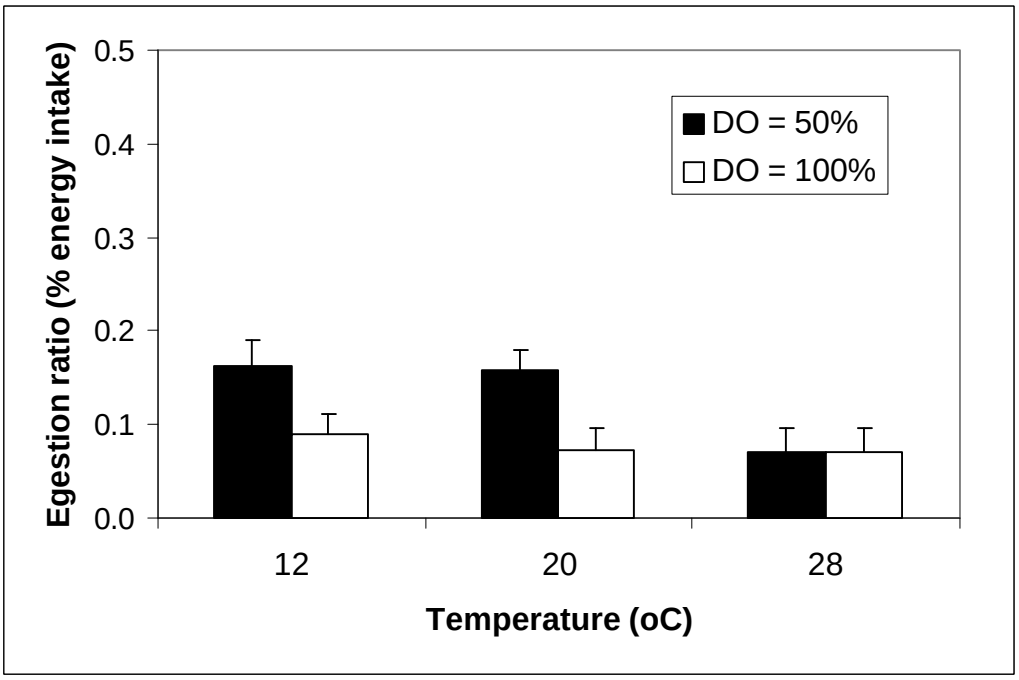

Routine metabolism (Kj g-1 d-1)
0.5
0.4
0.3
0.2
0.1
0.0
Atlantic
Shortnose
20
40
60
80
100
Dissolved Oxygen saturation

b)

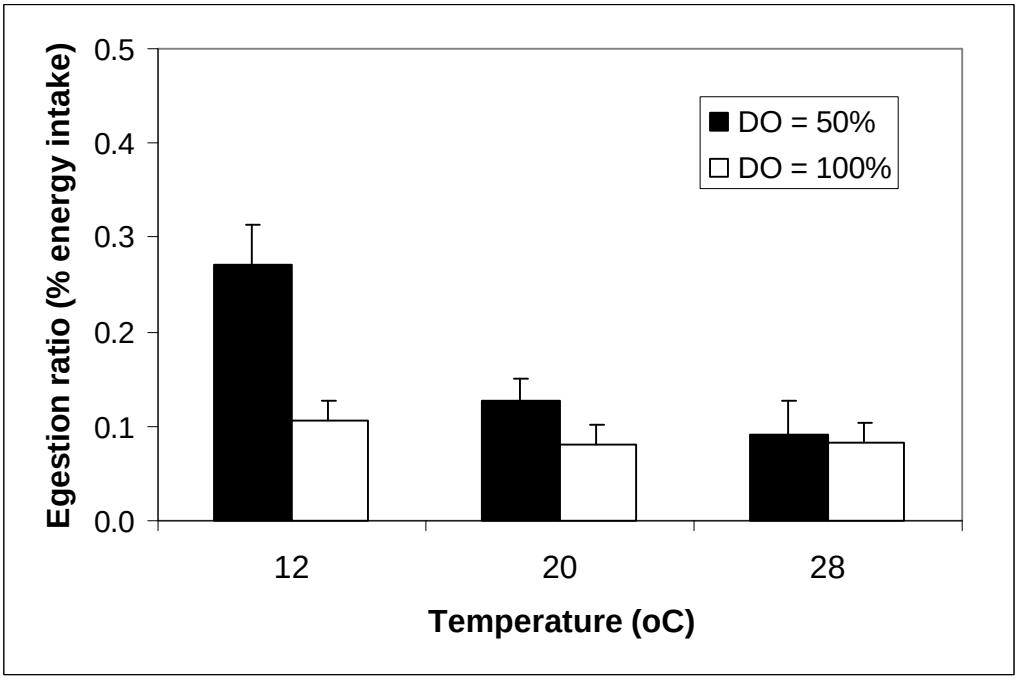

Routine Metabolism (mg O2 g-1d-1)
0.6
0.5
0.4
0.3
0.2
0.1
0
Atlantic
Shortnose
0
5
10
15
20
25
30
Salt (ppt)

c)

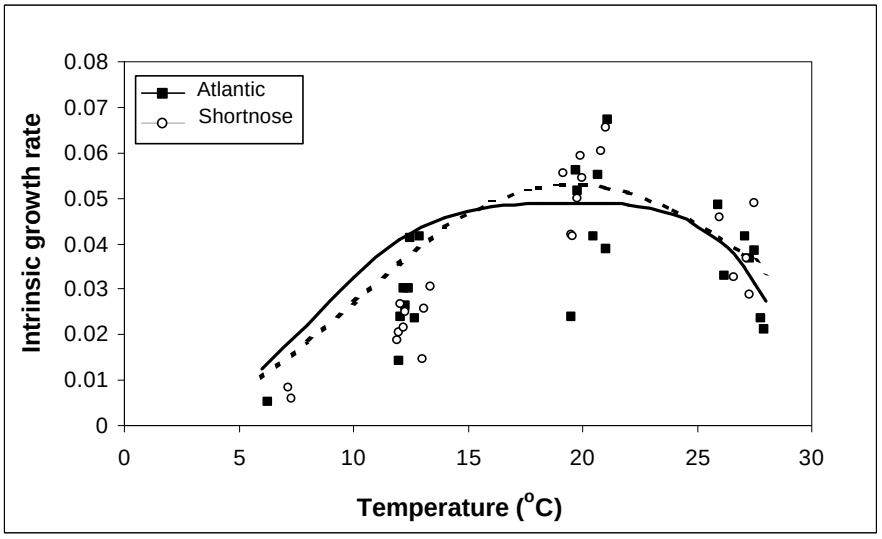

25%
20%
15%
10%
5%
0%
SDA (% energy intake)
DO = 50%
DO = 100%
12
20
28
Temperature (°C)



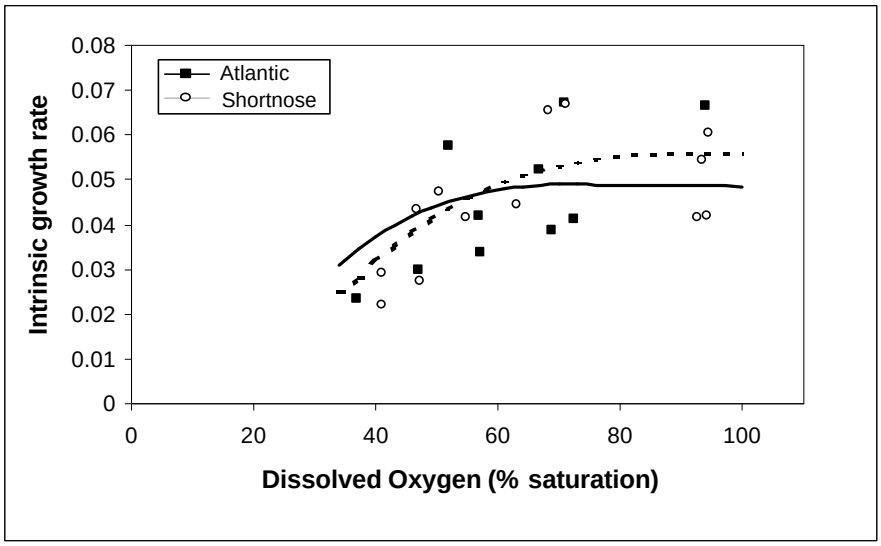
a) Atlantic sturgeon



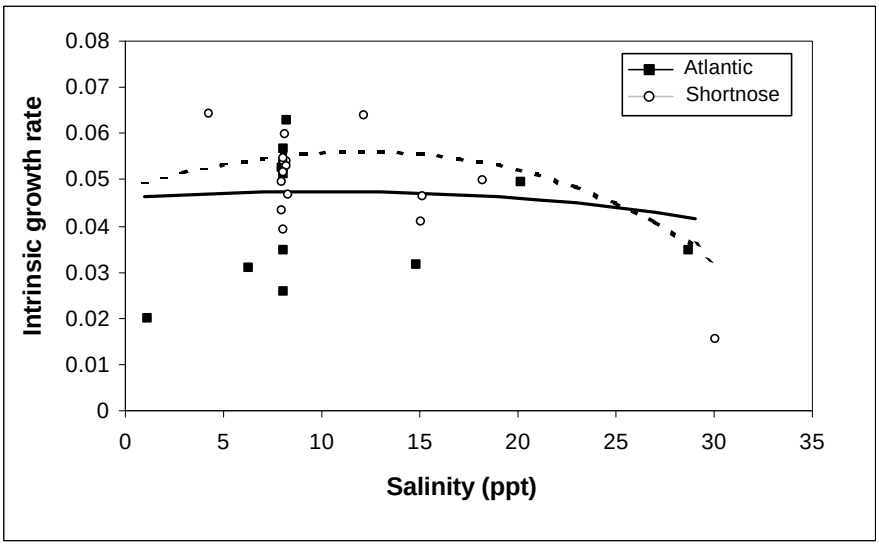
b) Shortnose sturgeon


Atlantic
Shortnose
Intrinsic growth rate
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
0
5
10
15
20
25
30
Temperature (°C)

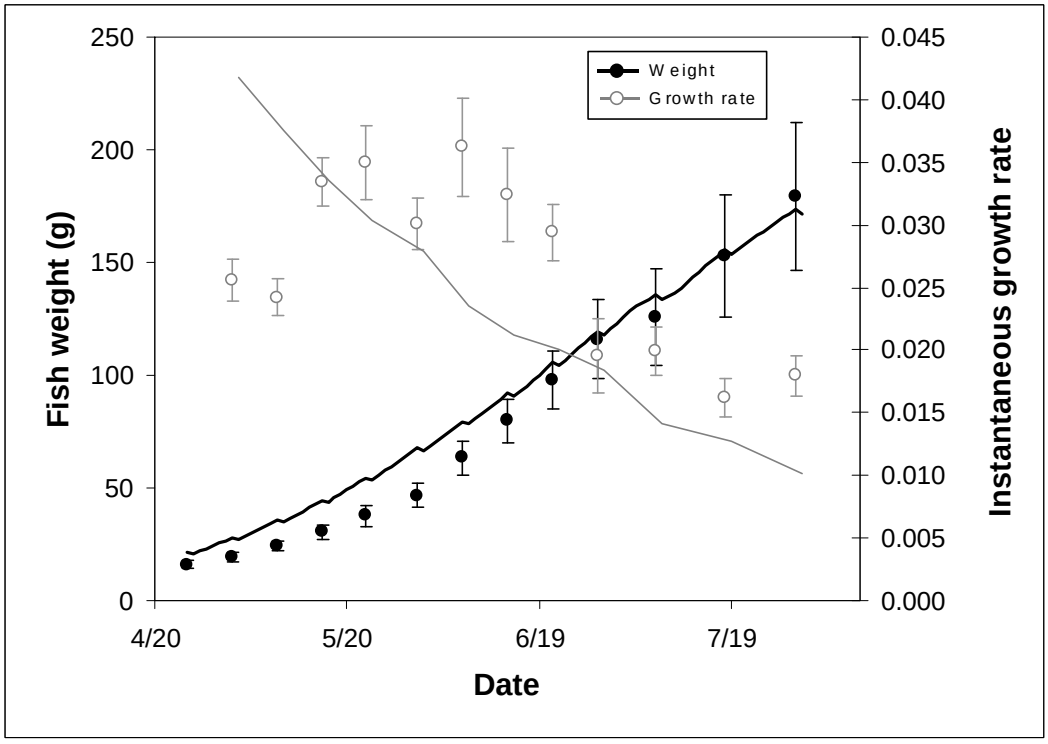
a)


Atlantic
Shortnose
Intrinsic growth rate
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
0
20
40
60
80
100
Dissolved Oxygen (% saturation)

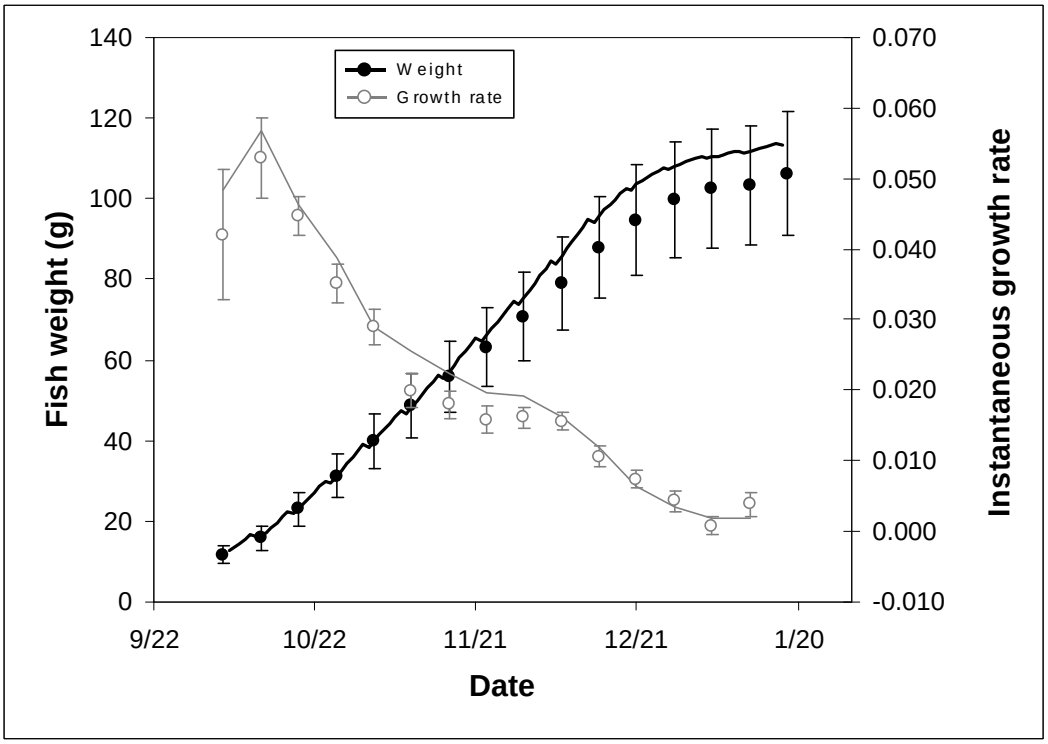
b)


Atlantic
Shortnose
Intrinsic growth rate
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
0
5
10
15
20
25
30
35
Salinity (ppt)

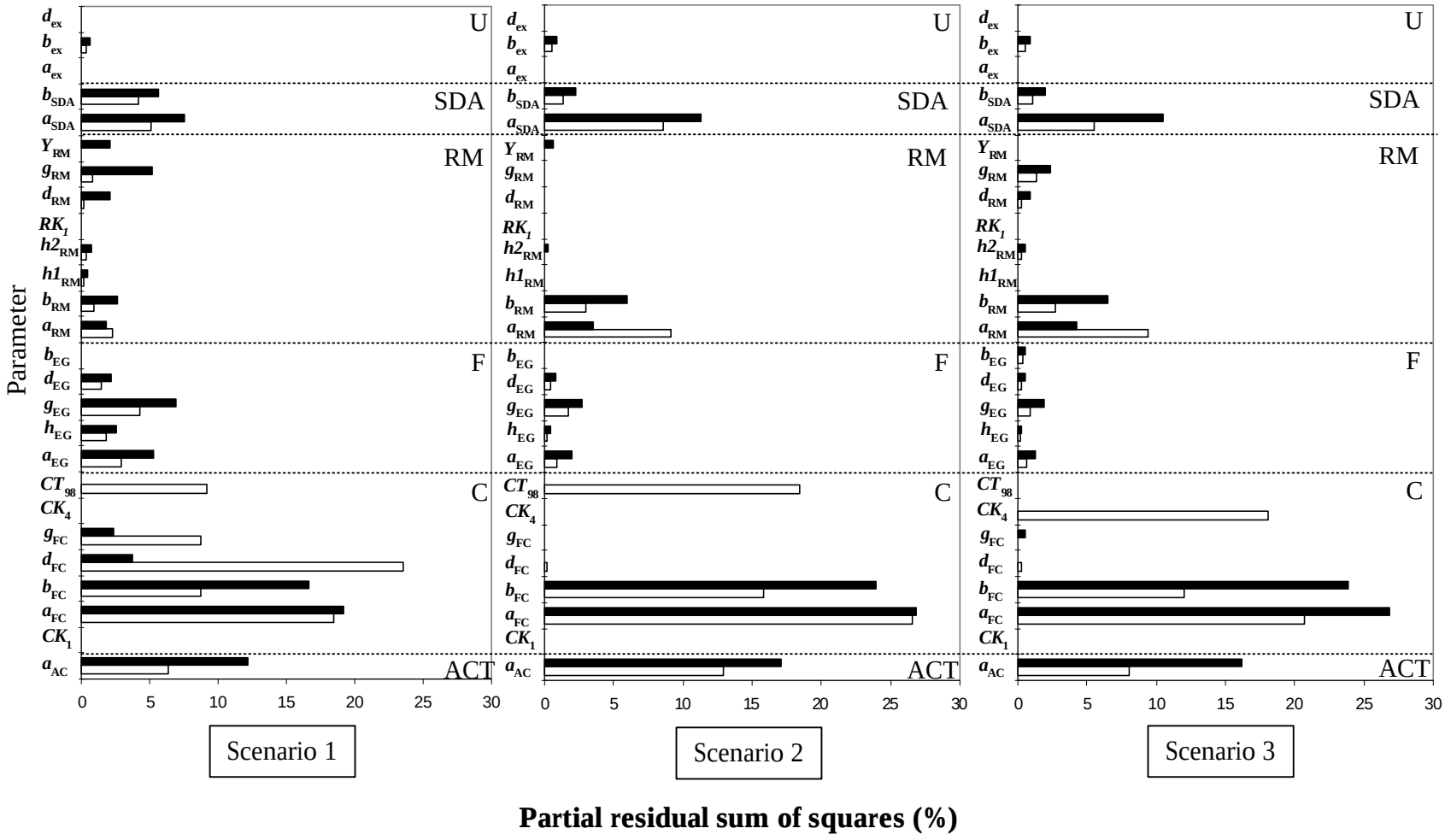
c)

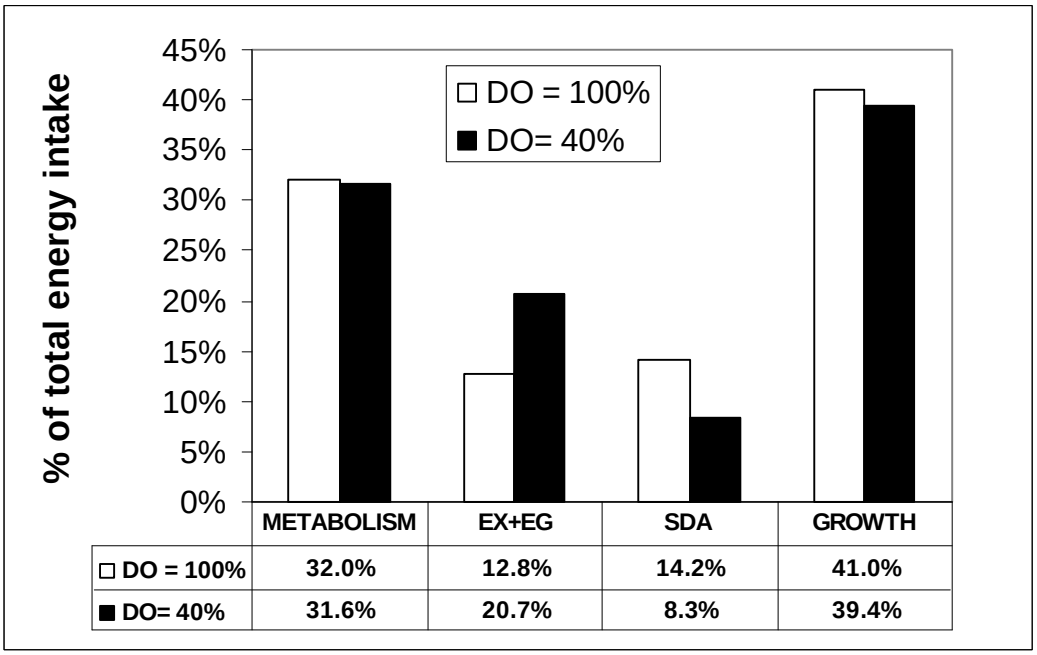


a) Atlantic sturgeon



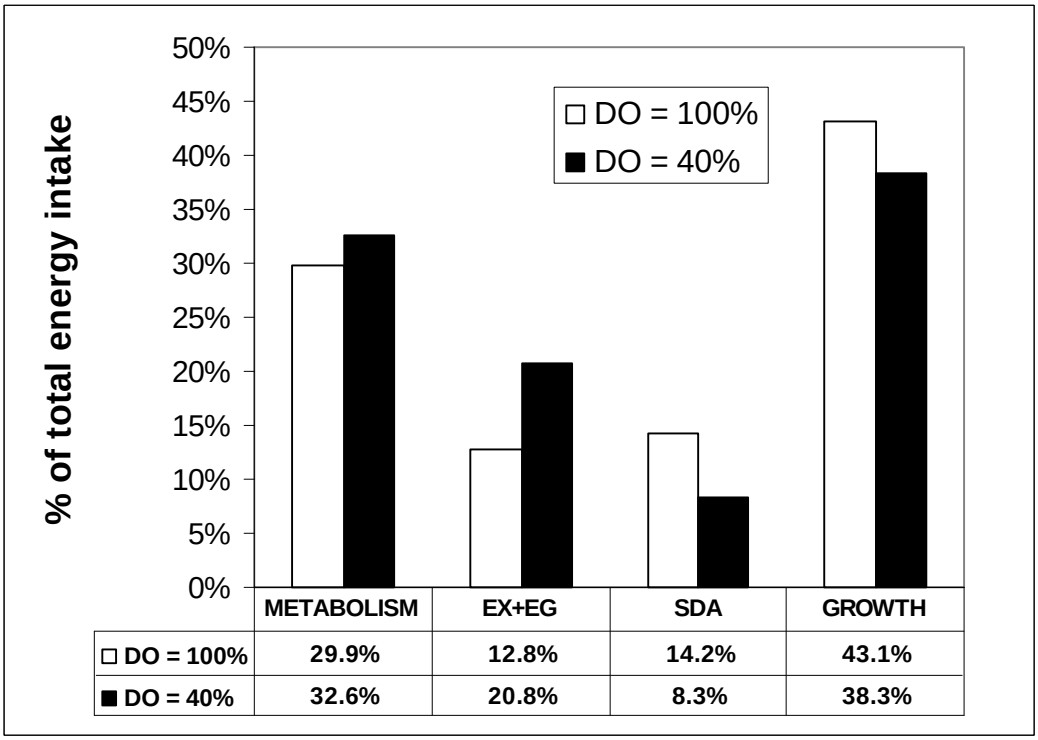
b) Shortnose sturgeon


Parameter
U
SDA
RM
F
C
ACT
d_{ex}
b_{ex}
a_{ex}
b_{SDA}
a_{SDA}
Y_{RM}
g_{RM}
d_{RM}
RK_1
$h2_{RM}$
$h1_{RM}$
b_{RM}
a_{RM}
b_{EG}
d_{EG}
g_{EG}
h_{EG}
a_{EG}
CT_{98}
CK_4
g_{FC}
d_{FC}
b_{FC}
a_{FC}
CK_1
a_{AC}
0 5 10 15 20 25 30
Scenario 1
Scenario 2
Scenario 3
Partial residual sum of squares (%)



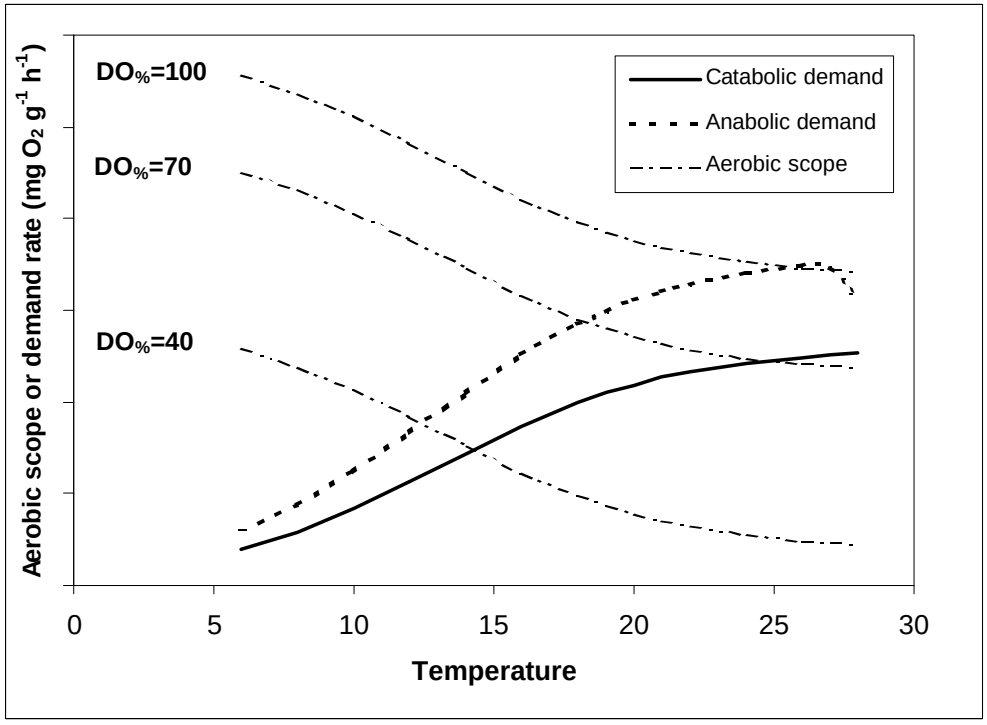
	METABOLISM	EX+EG	SDA	GROWTH
DO = 100%	32.0%	12.8%	14.2%	41.0%
DO= 40%	31.6%	20.7%	8.3%	39.4%

a) Atlantic sturgeon



	METABOLISM	EX+EG	SDA	GROWTH
DO = 100%	29.9%	12.8%	14.2%	43.1%
DO = 40%	32.6%	20.8%	8.3%	38.3%

b) Shortnose sturgeon


Aerobic scope or demand rate (mg O2 g-1 h-1)
DO%=100
DO%=70
DO%=40
Catabolic demand
Anabolic demand
Aerobic scope
0
5
10
15
20
25
30
Temperature

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Appendix 1: Models used to parameterize metabolic component of bioenergetics model.

A single relationship between $\log_e$-transformed weight (*ln*W) and $\log_e$-transformed total length (*ln*TL) was established for both species (Niklitschek 2001), and defined by the equation (r^2=0.99,p<0.0001),

$$lnW = -6.19 + 3.12 * lnTL \quad \text{(Eq. 33)}$$

Energy density was calculated (Niklitschek 2001) as

$$\text{Log}_e(E) = a_{EC} + b_{EC} \cdot ln(W_S) + d_{EC} \cdot lnW \quad \text{(Eq. 34)}$$

Where,

E = fish energy density (KJ g^{-1} dry weight)

$a_{EC} = 2.3 \pm 0.26$

$b_{EC} = 0.6 \pm 0.14$

$d_{EC} = 0.16 \pm 0.080$

W = fish weight (g)

$W_s = ln(W_o) / ln(W_e)$

W_o = observed wet weight (g)

W_e = expected wet weight from measured length and length-weight equations (g)

ln = natural logarithm

Estimates of consumed oxygen (MO) were all adjusted to account for hydraulic residence time in experimental tanks (Niklitschek 2001):

$$MO = 13.55\left[\frac{F}{V}\left(DOin_0 + \Delta DOin - DOout_t + \frac{\Delta DOin - DOout_0 - DOout_t}{e^{\frac{F}{V}\Delta t} - 1}\right) - \frac{\Delta DOin}{\Delta t}\right]$$

(Eq.35)

where,

F = Flow (L/h)

V = Respirometer volume (L)

$DOin_0$ = Dissolved oxygen in the inflow at time 0 (mg/L)

$D0in_t$ = Dissolved oxygen in the inflow at time t (mg/L)

DOin = $DOin_t - DOin_0$

$DOout_0$ = Dissolved oxygen in the inflow at time 0 (mg/L)

$DOout_t$ = Dissolved oxygen in the inflow at time t (mg/L)

Post-prandial respiration rates (SDA) was estimated

$$SDA = SDA_{max} \cdot KA_{SDA} \cdot KB_{SDA} \quad \text{(Eq. 36)}$$

Where,

$$KA_{SDA} = \frac{KR_{SDA} \cdot e^{y1_{SDA} \cdot t}}{1 + KR_{SDA}(e^{y1_{SDA} \cdot t} - 1)} \quad \text{(Eq. 37)}$$

$$KB_{SDA} = \frac{KR_{SDA} \cdot e^{y2_{SDA}(t_4 - t)}}{1 + KR_{SDA}(e^{y2_{SDA}(t_4 - t)} - 1)} \quad \text{(Eq. 38)}$$

$$y1_{SDA} = \frac{1}{t_2} \log_e \left(\frac{0.98(1 - KR_{SDA})}{0.02 \cdot KR_{SDA}} \right) \quad \text{(Eq. 39)}$$

$$y2_{SDA} = \frac{1}{t_4 - t_3} \log_e \left(\frac{0.98(1 - KR_{SDA})}{0.02 \cdot KR_{SDA}} \right) \quad \text{(Eq. 40)}$$

$$KR_{SDA} = \frac{SDA}{SDA_{max}} \quad \text{(Eq. 41)}$$

SDA_{max} = Maximum observed SDA (KJ h^{-1} g^{-1})

τ_2 = lower limit of time period at which SDA ≥ 0.98 SDA_{max} (min)

τ_3 = upper limit of time period at which SDA ≥ 0.98 SDA_{max} (min)

τ_4 = time at which SDA metabolism has returned to pre-feeding level (min)

From theoretical considerations, we divided excretion in two components: routine nitrogenous excretion rate (RNE) and exogenous nitrogenous excretion (XNE). RNE was defined as the total energy lost in nitrogenous sub-products (ammonia and urea) by starved fish. XNE represents, in turn, energy losses from deamination of assimilated but non-metabolizable nitrogen. Thus, while RNE depends upon routine metabolism, XNE depends upon food consumption rate. Assuming both components are additive, excretion rate (U) can be defined by the equation,

$$U = RNE + XNE \quad \text{(Eq. 42)}$$

Where,

$$RNE = a_{EX} \cdot W^{b_{EX}} \cdot RM_{TSO} \text{ (KJ g}^{-1}\text{ d}^{-1}\text{)} \quad \text{(Eq. 43)}$$

$$XNE = \frac{d_{EX} \cdot FC}{100} \text{ (KJ g}^{-1}\text{ d}^{-1}\text{)} \quad \text{(Eq. 44)}$$

W = fish weight (g)

a_{EX} = scaling parameter, see below.

b_{EX} = 0.71; from Cui et al. (1996)´s results for *A. transmontanus*

RM_{TSO} = routine metabolism (KJ g^{-1} d^{-1})

d_{EX} = 3.9, excreted percent of total energy intake (average value obtained using data from Dabrowski et al (1987) and Gershanovich & Pototskij (1992) in *A. Baeri*, and Cui et al. (1996) in *A. transmontanus.*

The parameter a_{EX} was estimated for each species by scaling the routine metabolic rates observed in this work for *A. oxyrinchus* and *A. brevirostrum* to the routine nitrogenous excretion rates reported under similar conditions for other sturgeons in the literature (Dawrowski et al. 1987, Salin & Williot 1991, Gershanovich & Pototskij 1992, Gershanovich & Pototskij 1995, Cui et al. 1996). Thus,

$$a_{EX} = \left[\sum_{1}^{i} \frac{RNE_i}{W^{b_{EX}} \cdot RM_{TSO}} \right]^{-i} \quad \text{(Eq. 45)}$$

Where,

RNE_i = Routine Nitrogenous Excretion data from sturgeon literature

RM_{TSO} = observed routine metabolism (this work) at similar water quality conditions.