BIOENERGETICS MODELING AND ASSESSMENT OF SUITABLE HABITAT FOR JUVENILE ATLANTIC AND SHORTNOSE STURGEONS IN THE CHESAPEAKE BAY

By

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INTRODUCTION

Individual growth represents the final result of all energy processes occurring in a fish within a given time frame. Moreover, growth is a species-specific vital process, which not only assesses a fish's or population's well-being, but represents an integral of habitat-physiological interactions. Within pre-reproductive life-stages, somatic growth (g) by itself or in relation with mortality (u/g) can be used as a proxy for fitness and, therefore, as an useful index for habitat suitability (MacCall, 1989; Heath, 1996; Secor, 1999).

Since fish growth integrates the effects of environmental factors upon energy intake, assimilation, and allocation (bioenergetic processes), there is a clear opportunity to apply bioenergetics modeling approaches in quantitative and qualitative habitat evaluations (Brandt and Kirsch, 1993; Brandt, 1993; Hondorp and Brandt, 1996). Nonetheless, the development of such approaches during the last decade has been rather limited, particularly in terms of incorporating new environmental variables into a predictive framework.

Not only habitat applications but bioenergetics modeling per se have faced limited advancement in most recent years. Formally based upon Winberg's (1956) work, modern bioenergetics has been largely influenced by Kitchell et al.'s (1974, 1977) modeling work in freshwater systems. In addition, the widespread use of new computational tools and

the production and distribution of bioenergetic software by the University of Wisconsin (Hewett and Johnson, 1992; Hanson et al., 1997) led to an increased interest in bioenergetics modeling in the 1980s and 1990s. Most models used only temperature as the abiotic factor driving fish bioenergetics. Very limited advances have been made in extending those approaches to estuarine environments, where salinity can be a highly relevant factor affecting fish energetics and, ultimately, survival. A similar situation is observed in terms of dissolved oxygen. Because hypoxia is a widespread phenomenon in many estuarine and freshwater systems, there is a clear need to incorporate hypoxia effects on fish physiology into bioenergetic models (Miller et al., In press; Neill et al., 1994; van Dam and Pauly, 1995).

In this dissertation thesis, I used juvenile Atlantic and shortnose sturgeons as experimental subjects to evaluate the effects of temperature, salinity and dissolved oxygen on fish bioenergetics and propose a multivariable bioenergetic modeling approach, which incorporates the effects and interactions from all three environmental factors. Juvenile Atlantic and shortnose sturgeons use estuarine environments characterized by large seasonal and spatial variations in temperature, salinity, and dissolved oxygen in many of their natural nursery habitats (Secor and Gunderson, 1998; Collins et al., 2000).

Furthermore, there is a clear need to improve available knowledge on suitable spawning and nursery habitats and physiological tolerance of

juvenile Atlantic and shortnose sturgeons to environmental factors as recognized by recovery plans for shortnose (NMFS, 1998) and Atlantic sturgeons (ASMFC, 1998). These needs are especially relevant given the continued decline in most populations of these species, which played ecologically and economically important roles in the East Coast of the United States.

Atlantic sturgeon supported the largest caviar fishery in the United States yielding a maximum harvest of 3,200 metric tons in 1888 (Secor and Waldman, 1999). By 1901, landings had already dropped to 6% of 1888's harvest (Murawski and Pacheco, 1977). Shortnose sturgeon is a smaller species sympatric with Atlantic sturgeon. Although not frequently targeted, this species was probably taken as by-catch in the Atlantic sturgeon and shad fisheries (National Marine Fisheries Service, 1998; Waldman and Secor, 1999). While historical abundance of shortnose sturgeon is poorly documented, its decline to extremely low population sizes caused the species to be listed as endangered in 1967 (National Marine Fisheries Service, 1998).

Throughout the 20th century, Atlantic sturgeon remained at very low population levels. Evidence of reproductive failure was recently documented in the Hudson River (Peterson et al., 2000) and spawning populations of both sturgeon may be functionally extirpated from some estuarine systems (Speir and O'Connell, 1996; Grogan and Boreman, 1998; Collins et al. 2000). Shortnose sturgeon abundances have

remained at levels that are believed to risk population sustainability (National Marine Fisheries Service, 1998). The only documented recovery corresponds to the Hudson River shortnose sturgeon population (Bain, 1998). Today, shortnose sturgeon remains listed as an endangered species, over its entire geographical range in the U.S. A moratorium on all Atlantic sturgeon harvest was adopted in 1997 by the Atlantic States Marine Fisheries Commission, ASMFC (Colligan et al., 1988).

In synthesis, the main objectives of this dissertation were

(1) to evaluate the physiological responses of juvenile shortnose and Atlantic sturgeons to temperature, dissolved oxygen and salinity, within the ranges observed in the Chesapeake Bay during the last decade.

(2) to incorporate these responses in a multivariable habitat-based bioenergetic model able to predict spatial and seasonal availability of nursery habitats for these species.

(3) to apply this model to evaluate recent trends in suitability of nursery habitats for juvenile sturgeons in the Chesapeake Bay.

In Chapter I, I report the results from laboratory and mesocosm experiments and develop a bioenergetics model to predict consumption, growth and metabolic responses of juvenile shortnose and Atlantic sturgeon to temperature, dissolved oxygen, and salinity.

In Chapter II, I test 5 hypotheses related with the application of the

models generated in Chapter I to larger size classes and natural environments. Thus, I evaluate how changes in fish size, food type, and feeding frequency affect model predictions. I also test the ability of juvenile sturgeons to discriminate and select between optimal and sub-optimal water quality conditions and the effects of direct interactions between both species under limited food conditions.

Finally, In Chapter 3, I use the bioenergetic models developed in Chapter 1 to assess spatial and temporal availability and value of nursery habitats for juvenile Atlantic and shortnose sturgeons in the Chesapeake Bay .

CHAPTER I : BIOENERGETIC RESPONSES OF JUVENILE ATLANTIC AND SHORTNOSE STURGEONS TO TEMPERATURE, DISSOLVED OXYGEN AND SALINITY

INTRODUCTION

Shortnose and Atlantic sturgeons inhabit a wide geographical range along much of the Atlantic coast of North America. Shortnose sturgeon *Acipenser brevirostrum* populations have been reported between the St. John River in New Brusnick, Canada (Leim and Day, 1959) and the Indian River in Florida, USA (Evermann and Bean, 1898). Atlantic sturgeon *Acipenser oxyrinchus* range from the Gulf of St. Lawrence, Canada to the St. John River in Florida, USA (Vladykov and Greeley, 1963). Both species spawn in tidal freshwater environments, and most major estuaries within each species range support discrete populations. After supporting a large caviar fishery in the late 1800s and early 1900s Atlantic sturgeon populations collapsed (Secor and Waldman, 1999), but subsequently failed to show any recovery during the 1900s despite reduced fishing pressure and increasing protective measures. Shortnose populations also tended to decrease throughout most of their range during the last 100 years and the species has been fully protected as an endangered species since 1967 (National Marine Fisheries Service, 1998).

Spawning biomass, incidental fishing mortality, and suitability of spawning habitats and nursery habitats are key elements needed to be

addressed by restoration efforts (National Marine Fisheries Service, 1998; ASMFC, 1998; Colligan et al., 1998). Life table and elasticity analysis have shown that population recovery in sturgeons may be especially sensitive to changes in survival during the first years of life (Boreman, 1997, Gross et al., in press). At these early life-stages, decreased water quality (synergistic effects between hypoxia and high temperature) could represent a major factor limiting juvenile growth and survival in nursery areas (Secor and Gunderson, 1998; Collins et al., 2000). However, information on the physiological tolerance to environmental factors at different life-stages is limited in both species.

Nursery areas for young-of-the-year Atlantic and shortnose sturgeons partially overlap around the freshwater/brackish water interface in estuaries (Collins et al., 2000; Bain, 1997; Dadswell, 1979). Older juvenile shortnose sturgeon tend to remain in fresh and brackish waters, but Atlantic sturgeon initiate a predominantly marine life phase after 1-6 years of life in estuarine waters (Dovel and Berggren, 1983; Dadswell et al., 1984; Smith, 1985).

The present Chapter focuses on the evaluation of the effects of water quality on juvenile sturgeon growth and survival during their first year of life. Here, growth is understood as an integral of environmental effects upon fish physiological processes that affect energy intake, assimilation or allocation (bioenergetic processes). This approach, based upon Winberg's (1956) balanced equation allows a comprehensive

understanding of the physiological mechanism by which a given factor modifies fish growth and consumption; bioenergetics models also represent an analytical framework for forecasting fish growth or food consumption under different environmental scenarios.

Within the environmental factors that potentially affect juvenile sturgeon bioenergetics the most, I focused my research in measuring and modeling the effects of temperature, salinity and dissolved oxygen concentration. Temperature has been recognized as the most important factor controlling physiological processes in fishes (Fry, 1971), and is widely used as the only abiotic factor in predicting fish bioenergetic responses (Elliot, 1976; Kitchell et al., 1977; Thornton and Lessem, 1978; Stewart et al., 1983; Hanson et al., 1997). Significant effects of temperature on metabolism and food consumption have been reported for several sturgeons in Asia and North America (Winberg, 1956; Gershanovich, 1983; Cech et al., 1984; Khakimullin, 1984; Shelukhin et al., 1990; Hung et al., 1993). Nonetheless, no predictive models have been developed so far for any of sturgeon species.

Unlike the effects of temperature on fish bioenergetics, the magnitude and shape of salinity effects on estuarine fish energetics remain unclear and appear to be highly heterogeneous (Brett, 1979). Osmoregulation cost estimates range from 1 to 28% of routine metabolism in teleosts, depending upon species and assessment methodologies (Morgan and Iwama, 1991). Moreover, salinity affects fish

energetics beyond osmoregulation, including changes in relative costs of ion transportation (Mg, Ca) and collateral metabolic effects caused by hormonal responses to salinity stress (Morgan and Iwama, 1991; Kirschner, 1995). In juvenile Russian sturgeon, *Acipenser güldenstädtii*, salinity effects on routine metabolism depend upon temperature and fish size. In general, an asymmetrical U-shaped response indicated minimum regulatory cost occurs at c.a. 10 ppt (isotonic conditions), with metabolism increasing more rapidly during freshwater acclimation in comparison to marine water acclimation (Shelukhin et al., 1990).

Dissolved oxygen is a third major abiotic factor conditioning bioenergetic processes in fishes that inhabit highly productive stratified systems. An increasing magnitude of hypoxic events have affected the Chesapeake Bay since the 1930s, as a likely consequence of anthropogenic factors (Cooper and Brush, 1991b; Officer et al., 1984). Hypoxia has been suggested as a major cause of spawning and nursery habitat degradation, precluding natural recovery of Chesapeake Bay sturgeon populations (Secor and Gunderson, 1998). Sub-lethal hypoxia can impose strong limitations to most bioenergetic processes, reducing growth rates and, ultimately, survival (Fry, 1971; van Dam and Pauly, 1995). These effects seem to have especial relevance for sturgeons, which have been found to be particularly sensitive to hypoxia, especially under high temperature conditions (Klyashtorin, 1976; Secor and Gunderson, 1998).

In the present chapter, I evaluate and compare main effects and interactions between temperature, salinity and dissolved oxygen on growth, survival and energetics of juvenile Atlantic and shortnose sturgeons. I developed a theoretical model for the effect of these environmental variables on sturgeon bioenergetics and tested the suitability of this model to explain observations from laboratory experiments. Finally, I evaluated the performance of the bioenergetics 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 oriented to develop an energy-balanced equation for each species (Winberg, 1956), in which I assumed the basic bioenergetic processes (energy intake, metabolism and wastes) to be independently conditioned by environmental factors:

Growth (G)	=	Energy intake (C)	-	Metabolism (R_s + A_m + SDA)	-	Energy wastes (F + U)

where, G=Growth, C=Consumption, R_s=Routine metabolism, A_m=Activity cost, SDA=Specific Dynamic Action, F=Egestion, and U=Excretion. Since bioenergetics models are especially sensitive to growth, consumption and routine metabolism estimates (Bartell, 1986;

Hanson et al., 1997), I focused most of my experimental effort to the assessment of these components under laboratory controlled conditions.

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 (14 g ±10.7 SD). Shortnose juveniles were from Savannah River progeny, provided by the US Fish and Wildlife Service Bear's Bluff Laboratory (SC). Atlantic sturgeon juveniles were from Hudson River progeny, provided by the US Fish and Wildlife Service Northeast Fishery Center (Lamar, PA). Fish were individually tagged and acclimated to experimental conditions at transition rates no greater than 1 ppt, 1°C and/or 5% DO per day. Fish were measured and weighed 12 hours before and after each experiment. Unless otherwise stated, Biokyowa® pellets were used as feed, supplied *ad-libitum* 3 times a day. Non-consumed food was removed 30 minutes after each feeding. Average energy-density of pellets was estimated to be 21.9 $Kj*g^{-1}$ (see chapter 2).

Salinity was adjusted by mixing local well water with filtered ambient seawater (mouth of Patuxent River), adding artificial salt when necessary. Dissolved oxygen was kept within ±5% of targeted levels by mixing nitrogen with ambient air. Temperature was regulated using a combination of room-temperature control, water baths and individual heaters. Water quality parameters were checked and recorded at least 3 times a day.

Observed responses were analyzed using a three-step procedure. First, least-square multiple linear regression analysis was used to conduct standard diagnostics and preliminary selection of significant predictors. Second, a mixed model approach (MIXED Procedure; SAS Institute, 1997) was used to account for random effects and correlations within experiments. At this stage, final selection of explanatory variables was made. Finally, a non-linear mixed procedure (NLMIX macro, SAS Institute, 1997) was used to estimate parameters of theoretical non-linear functional responses to selected explanatory variables. When two or more alternative models were available for a given functional response, Akaike's Information Criteria was used to select the best fitting equation. Explanatory variables were standardized (mean=0, standard deviation=1) to avoid collinearity problems and to facilitate comparisons between variables. Values used to standardize variables are indicated in Table I-1. Unless otherwise stated, α=0.05 was used to define significance in all statistical analysis.

Table I-1: Average water quality conditions and fish-weight in growth/consumption and routine respirometry experiments for Atlantic and shortnose sturgeons.

Variable	Shortnose sturgeon		Atlantic sturgeon	
	Mean± SD	Range	Mean ± SD	Range
Temperature	18.9 ± 5.2	7.3 - 27.5	18.4±5.5	6.3 – 27.9
Salinity	10.0±4.8	1.5 – 22.1	8.9±5.9	1.1 – 28.7
Oxygen saturation	67.3±17.2	25.3 – 96.0	67.6 ±19.8	30.5 – 100.7
Ln(Weight in g)	2.3±0.5	1.6 – 3.8	2.8 ±0.5	1.5 – 4.2

Growth

Temperature, salinity and dissolved oxygen effects on growth and consumption 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% of saturation; and five levels of salinity: 1, 8, 15, 22 and 29 ppt (Figure I-1, Table I-1). This design allowed me to evaluate functional responses to main effects and first order interactions among temperature, salinity and dissolved oxygen.

Treatments were applied during 10-d growth-consumption experiments, conducted in 34-l glass aquarium with densities of 1 or 2 fish per tank. Number of fish per tank was adjusted upon individual fish weight to keep a similar biomass per tank as preliminary experiments showed no difference in growth or food consumption between fish reared

individually and in pairs. A total of 135 experimental trials were distributed in 7 sequential runs using a semi-random balanced procedure. Low survival was obtained below 40% DO_{sat} in both species and no survival was observed above 22°C in shortnose sturgeon at this oxygen range. Under considerations of harm to vertebrates, and preservation of sufficient experimental units, the number of replicates was reduced or eliminated for lethal treatments.

Daily instantaneous growth rate (G) was calculated for each individual following the relationship $W_t = W_0 e^{G(t-to)}$, where, W_t is final weight at time t; and W_0 is initial weight at time t_0. Energy-density in juvenile sturgeons was estimated from a sub-sample of the experimental fish (n=69). Both percent dry-wet and specific weight (Anderson and Neumann, 1996) were significant predictors of fish energy-density ($\alpha<0.0001$), with coefficients of determination of 0.78 and 0.59, respectively. No significant differences between species were detected regarding intercepts or slopes from both predictory equations. Although specific weight (W_s) had a lower coefficient of determination, it has the advantage of not requiring the sacrifice of experimental fish and was the default approximation used to transform gained weight into gained energy following the equation,

$$Ln(E) = 0.34 + 0.61*W_s + 0.195*lnW \qquad \text{(Eq.1)}$$

Where,

E = fish energy density in Kj g^{-1} wet weight

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

W_o = observed wet weight

W_e = expected wet weight from measured length and length-weight equations.

LnW= log-transformed weight.

Length-weight relationships were modeled for each species; 96 experimental fish were measured and weighed prior to experimental trials. Significantly different equations ($p<0.01$) were obtained for each species,

Atlantic sturgeon ($R^2=0.94$, $p<0.0001$),

$$\text{Ln}(W) = -6.0079 + 3.0579 * \ln(TL) \quad \text{(Eq. 2)}$$

Shortnose sturgeon ($R^2=0.98$, $p<0.0001$)

$$\text{Ln}(W) = -5.4173 + 2.8646 * \ln(TL) \quad \text{(Eq. 3)}$$

Survival

Survival was monitored in 21-d tests extended beyond growth/consumption experiments. Survivor analysis was conducted using Cox proportional hazard regression, (Allison, 1995; PHREG procedure, SAS-Institute, 1997). I assumed no-time dependence in the

effect of the covariates (i.e. temperature, dissolved oxygen level, and salinity) on survivorship and simplified the Cox survivor function to the expression,

$$S(t) = [S_0(t)]^{\exp(bX)} \qquad \text{(Eq. 4)}$$

Where,

$S(t)$ = the probability of surviving beyond time *t*.

$S_0(t)$ = baseline survivorship function when all covariates are zero.

β = vector of regression coefficients for standarized predictors (Table I-2)

X = matrix of covariates

I estimated the baseline survivorship function $S_0(t)$ across all treatments and experimental units using the nonparametric maximum likelihood method built into PROC PHREG (SAS-Institute, 1997). Thus, I adjusted observed survival by the statistical effect of the covariates and generated absolute survival estimates for each experiment, tank and day. These absolute estimates represented the theoretical survivorship if all covariates were set to zero. To transform absolute daily survival to constant instantaneous survival rate (suitable for forecasting survivorship), I used linear regression and the following exponential approximation (R^2=0.98, $p<0.01$),

$$Ln[S_0(t)] = (S_b\text{-}1) * Ln(J). \quad \text{(Eq. 5)}$$

Where,

$S_0(t)$ = predicted survival (Cox's survivorship function) at time *t*

S_b = Instantaneous survival rate at average conditions (10.2 ppt, 19.4°C, and 69.8% DO-saturation).

J = time (hours)

Table I-2: Average experimental conditions (± standard deviation) used in juvenile Atlantic and shortnose sturgeons survival experiments.

Variable	**Shortnose sturgeon**		**Atlantic sturgeon**	
	Mean± SD	Range	Mean ± SD	Range
Temperature	18.9 ± 5.3	7.22 - 27.9	19.7 ± 4.9	6.5 - 27.9
Salinity	10.3±5.1	1.1 – 30.1	10.1±6.4	1.1 – 30.02
Oxygen saturation	72.4 ± 16.2	25.3 – 96.0	67.7 ±16.1	33.0 – 97.4

Routine Metabolism

Respirometry experiments were done immediately before or after growth-consumption experiments, under the same 23 combinations of temperature, salinity and dissolved oxygen conditions (Figure I-1). Three to six replicates were obtained for each treatment, depending on fish density and survival in growth-consumption experiments.

Energy cost of routine metabolism was estimated from oxygen consumption rates, using an oxycalorific coefficient of 13.55 Kj $g\text{-}O_2^{-1}$

(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 were used for fish up to 8 g and the larger respirometers for fish>8 g. ANOVA indicated oxygen consumption results were not significantly affected by respirometer type once data was corrected by fish-weight ($p>0.2$). A time-lag correction (Niimi, 1978) was applied to results obtained from flow-through respirometers to account for bias derived from hydraulic residence time in the vessel.

In the flow-through respirometers, oxygen and temperature levels were maintained in the chambers through re-circulation from larger reservoirs (240-l) in which environmental variables were monitored and manipulated. In the static respirometers thermal conditions were regulated placing them in temperature-regulated baths; oxygen saturation was allowed to range within 110 to 90% of targeted values, excluding respiration readings above or beyond those limits.

Fish were acclimated to targeted water quality conditions for at least a week, and then placed in the respirometers for at least 12-h before each experiment began. Oxygen consumption rates were measured every 45 minutes for at least 4 hours or until 4 stable readings were obtained.

Energy cost of routine metabolism was modeled as a function of

fish weight, temperature, oxygen saturation and salinity using the equation,

$$RM = a_{RM} * W^{b_{RM}} * f(T)_{RM} * f(DO,T)_{RM} * f(Sal,W)_{RM} \qquad \text{(Eq.6)}$$

Where, a_{RM} and b_{RM} are the intercept and the exponent of the allometric function between weight (W) and routine metabolism at conditions yielding maximum routine metabolic rates (i.e. maximum temperature, dissolved oxygen and salinity); f(T), f(DO,T), f(S,W) are functional responses (scaled from 0 to 1) to temperature, dissolved oxygen-temperature and salinity-fish weight, respectively. The allometric exponent (b_{RM}) was not a highly significant covariate ($p=0.096$) for shortnose sturgeon, probably due to the reduced range of fish-sizes I used. As a surrogate I used an estimate of –0.196 obtained from Acipenseridae data compiled by Froese and Pauly (1997). This value is the same previously reported by Winberg (1956) for sturgeons and other fishes and close to the average value I observed in juvenile Atlantic sturgeon (b_{RM}=-0.189).

Functional responses of routine metabolism to temperature, salinity and dissolved oxygen were modeled using Fry (1971)'s analytical framework, were temperature is assumed to be a controlling factor, salinity a masking factor and dissolved oxygen a limiting one. Thus, the metabolic rate is basically driven by temperature-dependent physiological processes, which can be (1) increased by osmoregulatory and/or

endocrine mechanisms related with both hypo- and hyper-osmotic conditions; and/or (2) limited by an insufficient availability of oxygen to sustain oxidative processes.

Metabolic response to temperature, *f*(T), followed different patterns in both species and could not be properly represented by a common model. In Atlantic sturgeon, metabolic rate tended to reach an asymptote as temperature reached the maximum tested values. On the other hand, shortnose sturgeon metabolism tended to maintain an exponential rate of increase across the range of tested temperature.

Metabolic response to temperature in Atlantic sturgeon was best represented by sub-equation K_A of Thornton and Lessem's (1978)'s algorithm, defined as,

$$f(T)_{RM} = \left(\frac{RTK_1 e^{Y_{RM}(T - T_1)}}{1 + RTK_1 (e^{Y_{RM}(T - T_1)} - 1)} \right) \qquad \text{(Eq.7)}$$

Where,

T = water temperature

RTK_1 = reaction rate multiplier at the lowest tested temperature

Y_{RM} = coefficient of increase

T_1 = lowest tested temperature

Metabolic response to temperature in shortnose sturgeon was instead described using an exponential function, defined as,

$$f(T)_{RM} = \exp^{\{-Y_{RM}*(T_4-T)\}} \quad \text{(Eq.8)}$$

Where,

T_4 = highest tested temperature

Functional response to dissolved oxygen-temperature *f*(DO,T) was described using a segmented model, which allowed metabolism to be independent from dissolved oxygen saturation once a given threshold level (DO_{crit}) was exceeded (Figure I-2). This threshold level was, in turn, assumed to be a function of temperature.

$$f(DO,T)_{RM} = COK_{RM} + (1 - COK_{RM}) * \frac{KO_i}{KO_{\max}} \quad \text{(Eq. 9)}$$

$$f(DO,T)_{RM} = 1$$

Where,

$$KO_i = (DO - DO_1) * \exp^{(c_{RM}*(DO-DO_1)}$$

KO_{max}= KO_i at DO_{crit}

$$c_{RM} = \frac{g_{RM} * \ln(T_4)}{\ln(T)}$$

$$DO_{crit} = -\frac{1}{c_{RM}} + DO_1$$

$$COK_{RM} = \exp(-d_{rm} * T)$$

DO = dissolved oxygen saturation (%)

DO_1 = lowest tested dissolved oxygen saturation

c_{RM}, d_{RM}, = empirical parameters

T = temperature

T_4 = maximum tested temperatue

Functional response to salinity-temperature $f(S,T)$ was modeled as a U-shaped curve, resulting from a combination of two exponential curves (Figure I-3). One curve (KS_a) represented osmo-regulation cost (and metabolic effects) at hyper-osmotic conditions and increased as salinity increased. The other (KS_b) represented osmoregulatory costs (effects) at hypo-osmotic conditions and increased as salinity decreased. The model predicts minimum metabolic rates around iso-osmotic conditions (circa 10 ppt).

To model the effects of fish size (weight), I assumed that sensitivity to salinity decreases in direct proportion to the reduction in the ratio between total gill surface area and individual fish biomass. I used a slope of –0.158 for the latter relationship based upon the work conducted by (Burggren et al., 1979) on *Acipenser transmontanus*. To scale $f(Sal,W)$ to a range between 0 and 1, I set the maximum response (1.0) to the maximum salinity tested within each temperature. The salinity sub-model equation is described by,

$$f[Sal,W]_{RM} = \frac{K_{sa} + K_{sb}}{K_{Smx}} \qquad \text{(Eq. 10)}$$

Where,

$$K_{sa} = e^{[j1_{RM} * (S\max - Sal)]} * W^{b_{GSA}}$$

$$K_{sb} = e^{[j2_{RM} * (Sal - S\min)]} * W^{b_{GSA}}$$

$$K_{Smx} = 1 + e^{[j2_{RM} * (S\max - S\min)]} * W^{b_{GSA}}$$

$j1_{RM}$, $j2_{RM}$ = parameters

S_{max}, = maximum tested salinity

S_{min} = minimum tested salinity

Sal = salinity (ppt)

T = temperature (^{o}C).

W = fish weight (g)

b_{GSA} = -0.158 (exponent for gill surface area – fish weight relationship)

Post-Prandial Metabolism (SDA)

Temperature and dissolved oxygen effects on specific dynamic action were estimated through respirometry in a factorial design with three replicates at three temperatures: 12, 20 and 28^{o}C and two levels of oxygen saturation: 50 and 100%, for each species. Salinity was kept constant at 8 ppt across all experiments.

Oxygen consumption was measured in fasted fish (>48 hrs), transferred to the respirometers no less than 12 hours prior each experiment. Experiments were conducted in 14.5-l flow-through respirometers especially adapted to allow long-term experiments and retrieval of non-consumed food. Otherwise, general procedures were equivalent to those used for routine metabolism. After measuring routine metabolism ≥4 hr, flow was interrupted and a pre-weighed ration was added, allowing the fish to eat for 30 minutes. After that period, excess food was removed and flow restored to normality (1 liter/min).

Respiration was measured for 48-60 hours after the feeding, depending on the time required to return to previously observed routine metabolism levels. Measurements were taken every 1-2 hours during the first 16 hrs post-feeding, and every 2-4 hours thereafter. A noticeable peak in metabolism was commonly observed within 0.5-1 hr after feeding, which was interpreted as the result of feeding activity and/or manipulation costs. Consequently, data between 0 and 2 hrs post-feeding were discarded from the analyses.

Individual fish respiration rates were interpreted as a function of time (J) using the following modification of (Thornton and Lessem, 1978)'s algorithm,

$$SDA_{rate} = K_A * K_B \qquad \text{(Eq. 11)}$$

Where,

$$KA_{SDA} = \frac{KR_{SDA} * \exp^{y1_{SDA} * t}}{1 + KR_{SDA}\{e^{y1_{SDA} * t} - 1\}}$$

$$KB_{SDA} = \frac{KR_{SDA} e^{y2_{SDA} * (t_4 - t)}}{1 + KR_{SDA}\{e^{y2_{SDA} * (t_4 - t)} - 1\}}$$

$$y1_{SDA} = \frac{1}{t} \ln\left(\frac{0.98(1 - KR_{SDA})}{0.02 * KR_{SDA}}\right)$$

$$y2_{SDA} = \frac{1}{t_4 - t_3} \ln\left(\frac{0.98(1 - KR_{SDA})}{0.02 * KR_{SDA}}\right)$$

KR_{SDA} = ratio between routine metabolic rate and maximum post-prandial metabolic rate (SDA_{max}).

J_2 = lower limit of time period at which SDA ≥ 0.98 SDA_{max}

J_3 = upper limit of time period at which SDA ≥ 0.98 SDA_{max}

J_4 = time at which post-prandial metabolism has returned to pre-feeding (routine) level.

This equation provided an adequate fit to the data, facilitating the computation of total oxygen consumption and providing a framework to compare the shape of SDA responses between treatments based upon the parameters KR_{SDA}, J_2, J_3, and J_4.

Oxygen consumption rates during each experiment were corrected for hydraulic lag as indicated in the previous section (Niimi, 1978) and integrated to obtain the total post-prandial oxygen consumption. Total oxygen consumption (mg O_2) was then transformed into energy expenditure (Kj) using an oxycalorific coefficient of 13.55 Kj g-O_2^{-1} (Brett and Groves, 1979).

Activity cost

I did not conduct direct measurements of activity metabolism, which is a sensitive but poorly predicted parameter in bioenergetic models (Kitchell et al., 1977; Bartell, 1986; Hansen et al., 1993). Instead, I used results from laboratory and mesocosm experiments to estimate A_m indirectly from growth, as the value required to equilibrate the energy budget (Hartman, 1993). Multiple linear regression was used to model such residuals and to interpret them as indirect estimates for activity metabolism. To be explicit about this source of uncertainty, I modeled A_m as an additive term instead of the more traditional multiplicative approach (Kitchell et al., 1977; Thornton and Lessem, 1978; Stewart et al., 1983; Hanson et al., 1997)

Food Consumption

Food consumption measurements were obtained from growth-consumption experiments described above. Linear regression analysis indicated that food consumption rate was significantly affected, in both species, by main effects from log-transformed fish-weight, temperature, and interactions between dissolved oxygen and temperature, and between salinity and temperature (see Results). I modeled the effects of these parameters using the following equation,

$$C = C_{max} * f(T)_{FC} * f(DO,T,Sal)_{FC} * f(Sal,T)_{FC} \quad \text{(Eq.12)}$$

Where,

C_{max} = allometric effect of size on maximum consumption rate

$f(T)_{FC}$ = the main effect of temperature on food consumption, regardless of salinity and dissolved oxygen conditions;

$f(DO,T,Sal)_{FC}$ = the effect of dissolved oxygen, given a particular combination of temperature and salinity conditions.

$f(Sal,T)_{FC}$ = the effect of salinity at a given temperature level.

While maximum specific consumption rate, C_{max}, was expressed in absolute energy units (Kj d^{-1} g^{-1}), all the other components were expressed as reaction rate multipliers between 0 and 1. C_{max} was estimated using data from a larger set of 10 consumption experiments, which included fish between 6 and 320 g. To exclude confounding effects from water quality covariates, I only used data from fish reared at 20°C, 8 ppt and >70% of oxygen saturation. C_{max} equation was defined as,

$$C_{\max} = a_{FC} * W^{b_{FC}} \quad \text{(Eq. 13)}$$

Where, W is the individual fish weight in grams; a_{FC} and b_{FC} are empirical coefficients, obtained by linear regression conducted on log-transformed variables.

Functional responses to temperature $f(T)$ were modeled in both

species based upon Thornton and Lessem's (1978) algorithm. Differences in observed responses between species (see Results) indicated that the temperature effect in shortnose sturgeon was better described by an asymptotic curve. Hence, sub-equation KB_{FC} was set to 1 for this species.

$$f(T)_{FC} = KA_{FC} * KB_{FC} \qquad \text{(Eq. 14)}$$

Where,

$$KA_{FC} = \frac{CTK_1 e^{y1_{FC}(T-T_1)}}{1+CTK_1(e^{y1_{FC}(T-T_1)}-1)}$$

$$KB_{FC} = \frac{CTK_4 * \exp^{y2_{FC}(T_4-T)}}{1+CTK_4 * (\exp^{y2_{FC}(T_4-T)}-1)} \quad \text{, for Atlantic sturgeon}$$

$$KB_{FC} = 1 \quad \text{, for shortnose sturgeon}$$

$$y1_{FC} = \frac{1}{T_4 - T_1} \ln\left(\frac{0.98(1-CTK_1)}{0.02 * CTK_1}\right)$$

$$y2_{FC} = \frac{1}{T_4 - T_3} \ln\left(\frac{0.98(1-CTK_4)}{0.02 * CTK_4}\right)$$

T = water temperature

CTK_1 = reaction rate multiplier at the lowest tested temperature

T_1 = lowest tested temperature

T_4 = highest tested temperature

Dissolved oxygen effects upon food consumption were modeled

using a balanced oxygen budget approach (van Dam and Pauly, 1995). Oxygen delivery to the tissues (DO_s) was assumed to be limiting, and allocated among competing processes: growth, routine metabolism, spontaneous and feeding activity, digestion, and assimilation and growth (anabolism). Within this context, I assumed that standard metabolism, i.e. a proportion of routine metabolism (DO_{RM}), is prioritized over all remaining oxygen-consuming processes and would reduce oxygen available for feeding and growth processes. As a result, increased metabolism due to high temperature or extreme salinity would increase sensitivity of food consumption responses to low oxygen levels.

To represent these concepts I used a segmented equation which is defined by two basic parameters: COK_1, the reaction rate multiplier at the lowest tested DO level (DO_1); and DO_{max}, the threshold value above which food consumption is assumed to be independent of dissolved oxygen. Both COK_1 and DO_{max} were assumed to be functions of both routine metabolism (defined by temperature and salinity) and potential consumption rate (defined by temperature). Thus,

$$f(DO,T,Sal)_{FC} = COK + (1-COK) * \frac{KO_i}{KO_{\max}} \quad \text{, if} \quad DO < DO_{max} \quad \text{(Eq.15)}$$

$$f(DO,T,Sal)_{FC} = 1 \quad \text{, if} \quad DO \geq DO_{max}$$

where,

$$KO_i = (DO - DO_1) * \exp^{\{c_{FC} * (DO - DO_1)\}}$$

$$KO_{\max} = (DO_{\max} - DO_1) * \exp^{\{c_{FC} * (DO_{\max} - DO_1)\}}$$

$$DO_{\max} = -\frac{1}{c_{FC}} + DO_1$$

$$c_{FC} = -d_{FC} * \{2 - (KT + RM)\}$$

$$COK = 1 - g_{FC}(RM + f(T)_{FC})$$

DO = Dissolved oxygen saturation (%)

DO_1 = Minimum tested DO

KA_{FC} = Sub-equation KA_{FC} from equation 13

RM = $f(T_{RM})*f(SAL_{RM})$;

$f(T)_{RM}$ = Reaction rate multiplier for the effect of temperature on routine metabolism (equation 8)

$f(SAL,W)_{RM}$ = Reaction rate multiplier for the effect of salinity on routine metabolism (equation 10).

d_{FC} , g_{FC} = empirical parameters.

Following the balanced oxygen approach, the functional response of sturgeon food consumption to salinity was interpreted and modeled as an inverse proportion of the increase in routine metabolism caused by the interaction between temperature and salinity under either hypo- or hyper-osmotic salinity conditions. In other words, a salinity driven increase in metabolism is expected to cause a proportional reduction in oxygen available for food digestion/assimilation and anabolism (Figure I-4). Thus,

$$f(Sal,T)_{FC} = 1 - Sr_1 * \left(1 - \frac{Ks_{\min} * f(T_{RM})}{f(Sal_{RM}) * f(T_{RM})}\right) \qquad \text{(Eq.16)}$$

Where,

Sr_1 = empirical coefficient

$f(T)_{RM}$ = routine metabolism-temperature multiplier at normoxia (equation 8).

$f(Sal,W)_{RM}$ = routine metabolism-salinity multiplier at normoxia (equation 10).

KS_{min} = minimum value expected for routine metabolism-salinity multiplier.

Egestion

Egestion experiments were conducted under the same combination of dissolved oxygen and temperature indicated for the SDA experiments. In addition, 3 ration sizes were tested, corresponding to 10, 55 and 100% of the maximum consumption observed for each fish during the acclimation period. Before each experiment, each fish was fasted for 60 hours, weighed, rinsed and transferred to a clean 38-l tank with filtered 8 ppt water (5 µm) and left overnight. Fish were then fed three times at 2.5-h intervals until satiation. Non-consumed food was removed after 30 minutes and dry-weighed. Preliminary experiments indicated that feces evacuation began 8-9 hours in previously fasted juvenile sturgeons.

During the 60 hours trials, feces were pipetted into a container every 12 hours or less and frozen for further analysis. Water quality was monitored and adjusted three times a day to maintain nominal conditions. After the experiment was concluded, fish were rinsed, removed and weighed, and the water from each tank filtered through a 35 µm mesh. The filters were promptly rinsed into vessels suitable for desiccation.

Feces 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 weighed for energy content analysis through a colorimetric variant of Maciolek's (1965) technique. Here, closed reflux digested samples were analyzed using a standard spectrophotometer at 600 nm wave length, and compared with a standard potassium dichromate digestion solution (KHP), which has a theoretical chemical demand of oxygen of 1.176 mg O_2 mg^{-1}.

I checked for experimental bias in three complementary ways: (1) checking energy content in the 35-um filtrate from experimental tanks; (2) running control tanks without fish for 60 hrs and then measuring ~~its~~ energy content from sampled water; and (3) running control tanks with fasted fish for the same period. 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 (pseudo-feces) accounted for an average of 0.024 Kj ±0.0070

(SE) per gram of fish (wet weight), which was subtracted from feces energy content in experimental tanks.

Egestion results were modeled following 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}). A dome-shaped response observed for the effects of ration-size upon egestion (see Results) required a further modification of the original model. Thus,

$$F = C_i * a_{EG} * T^{b_{EG}} * \exp^{\left\{\left(d_{EG} * \frac{C_i}{C_{\max}}\right) + \left(g_{EG} * \frac{C_i}{C_{\max}}\right)^2 + h_{EG} * DO\right\}} \quad \text{(Eq.17)}$$

Where, a_{EG}, b_{EG}, d_{EG}, g_{EG}, and h_{EG} are empirical parameters; C_i is consumed food and C_{max} is maximum daily consumption (both expressed in Kj).

Excretion

Excretion rate is one of the least sensitive and less variable parameters in bioenergetics models (Bartell, 1986; Hanson et al., 1997). In fact, this components has been frequently modeled as a constant proportion of the energy intake or calculated by difference (Kitchell et al., 1977; Hartman, 1993; Hanson et al., 1997; Kitchell et al., 1997).

Despite the previous generalized approach, there are theoretical reasons to consider excretion rate as both a function of metabolic rate and ingestion rate. The first component, routine nitrogenous excretion

rate (RNE), corresponds to the rate at which metabolizable nitrogen is catabolized as part of routine/standard metabolism (Brett and Groves, 1979). In experimental terms, RNE corresponds to the energy lost in excretory products by starved fish. The second component, exogenous nitrogenous excretion (XNE), represents energy losses resulting from deamination of assimilated but non-metabolizable nitrogen intake. I combined both components in the general equation,

$$U = RNE + XNE \qquad \text{(Eq. 18)}$$

Where,

$$RNE = a_{EX} * W^{b_{EX}} * RM_{T,Sal,DO}$$

$XNE = c_{EX} * C_I$

a_{EX} = 0.056, for Atlantic sturgeon.

a_{EX} = 0.062 for shortnose sturgeon.

W = fish weight (g).

b_{EX} = 0.71;

RM = routine metabolism from equation 6.

c_{EX} = 0.039, average value from

Table I-3.

The intercepts a_{EX} for the RNE component were estimated with basis upon average excretion rates reported in the literature for juvenile

Acipenseridae (Tables 3 and 4), scaled to represent average fish of 14.4 g from each species, reared at 17.7°C, 0 ppt. and ~100% DO_{sat}. Exponential slope b_{EX} was obtained from Cui et al.'s (1996) results for *A. transmontanus*.

Table I-3: Routine nitrogenous excretion (RNE) as calculated from the literature and used to estimate parameters of excretion sub-model

Fish-weight (g)	Temperature (°C)	NH_4-N mg $g^{-1}d^{-1}$	Urea-N[1] mg $g^{-1}d^{-1}$	RNE J g^{-1} d^{-1}	Source
38	16.5	0.209	0.149	8.6	(Gershanovich and Pototskij, 1992)
11.1	20	0.254	0.125	9.2	(Gershanovich and Pototskij, 1995)
60-2000	17.2	0.042	0.091	1.2	(Salin and Williot, 1991)
0.09-0.3	17.0	0.288	0.059	8.5	(Dawrowski et al., 1987)
2.4-22.5	18.5	-	-	4.1	(Cui et al., 1996)

[1] When urea was not reported, it was assumed to represent a 17% of total nitrogenous excretion.

Table I-4: Exogenous nitrogenous excretion (XNE) as calculated from the literature and used to estimate parameters of excretion sub-model.

Fish-weight (g)	Temperature (^{o}C)	Ration J $g^{-1}d^{-1}$	Total Excretion J $g^{-1}d^{-1}$	XNE J g^{-1} d	Percent of total ration	Source
2.4	18.5	93.2	3.82	1.53	4.1	(Cui et al., 1996)
11.1	18.5	93.2	3.17	2.85	3.4	
22.5	18.5	93.2	3.54	3.41	3.8	
2.4	18.5	186.5	8.20	5.91	4.4	
11.1	18.5	186.5	5.97	5.65	3.2	
22.5	18.5	186.5	5.97	5.84	3.2	
2.4	18.5	279.7	12.31	10.01	4.4	
11.1	18.5	279.7	9.23	8.91	3.3	
22.5	18.5	279.7	8.95	8.82	3.2	
2.4	18.5	372.9	15.66	13.37	4.2	
11.1	18.5	372.9	12.68	12.36	3.4	
45.4	18	72.7	14.52	5.91	8.1	(Gershanovich and Pototskij, 1992)
44.6	17.5	145.4	15.44	6.84	4.7	
45.4	16	277.7	22.64	14.03	5.1	
47	18.5	314.0	21.17	12.56	4.0	
45.9	16.5	347.1	17.04	8.43	2.4	
0.339	17	377.0	14.68	9.04	2.4	(Dawrowski et al., 1987)
0.339	17	418.0	10.55	2.55	0.6	
0.339	17	1159.0	8.78	1.65	0.1	
0.339	17	1692.0	25.93	12.74	0.8	

Mesocosm validation

Two mesocosm experiments were conducted to validate bioenergetics models generated from the laboratory results under conditions more similar to the field. A mesocosm experiment for juvenile shortnose sturgeon was conducted between September 1998 and January 1999. A second one for Atlantic sturgeon occurred from March to June 1999. Both experiments were conducted in outdoor 3,200 liter tanks at CBL Outdoor Seawater Facility, located at the mouth of the Patuxent River (Chesapeake Bay).

Daily records of water quality conditions and weekly records of fish weight and length were used to compare observed responses with predictions made from laboratory-based models. Temperature, salinity and dissolved oxygen tended to vary according to natural river conditions. However, oxygen saturation reached extremely high levels at noon during the warmer months of each period (see Table I-5). Fish were fed *ad libitum*, three times a day, six days a week. In the Atlantic sturgeon experiment, I used the same Biokyowa® pellets used in laboratory experiments. On the other hand, for shortnose I used frozen Chironomidae larvae (San Francisco Bay Brand®). I obtained 8 crude estimations of consumption rates for each mesocosm experiment, using a combination of bottom feeding trays and active siphoning.

Table I-5: Average and range of water quality conditions in mesocosm experiments for Atlantic and shortnose sturgeons.

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	13.3-15.5
Temperature (°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

Error analysis

To evaluate the sensitivity of each bioenergetic model to experimental error and parameter uncertainty, I conducted a series of error analyses (Bartell, 1986) based upon a Monte Carlo simulation

approach. Thus, 300 values were randomly obtained for each parameter, assuming a normal distribution of the error around the log-transformed mean and a standard deviation equal to the observed standard error. I assumed independence between parameters for all sub-models, with the exception of the food consumption and routine metabolism sub-models, where correlation between some parameters exceeded r=0.7. For these two sub-models I used asymptotic covariance estimates provided by SAS-PROC MIXED (SAS-Institute, 1997), to generate a Cholesky matrix suitable to simulate adjusted individual variances.

Random perturbations of each parameter were used 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 main ranking criteria. $RPSS_{\%}$ correspond to the percent of the residual variance explained by a given parameter after the effects of all the other parameters have been statistically removed (Bartell, 1986).

I lacked reliable estimates for uncertainty in parameters corresponding to the excretion sub-model. Hence, standard deviation for each parameter was arbitrarily set at 20% of the parameter mean estimate.

To evaluate if the sensitivity of the model depended upon the particular set of predictors used for forecasting bioenergetic responses, I

repeated the described error analysis procedure under the 4 water quality scenarios defined in Table I-6.

Table I-6: Simulated water quality conditions used for error analysis of Atlantic and shortnose sturgeons bioenergetic models.

Scenario #	Temperature (°C)	Salinity (ppt)	Dissolved Oxygen (%)	Notes
1	20	8	70	Average experimental conditions
2	20	8	40	Hypoxia
3	6	8	100	Winter conditions
4	29	29	40	Extreme summer conditions

RESULTS

Growth

Growth was significantly affected by temperature, salinity and dissolved oxygen in both species. Multiple regression analysis indicated significant linear and quadratic effects for all three variables. A combined analysis for both species suggested significant differences between sturgeons regarding interaction coefficients for salinity and temperature, dissolved oxygen and temperature, and salinity and log-transformed weight. Thus, to facilitate interpretation and analysis, separated regression analyses were conducted for each species leading to

the following predictive equations,

Atlantic sturgeon,

$$G = 0.043 - 0.00013*T + 0.005*Sal + 0.008*DO - 0.007*T^2 - 0.004*Sal^2 - 0.005*DO^2 - 0.007*\ln(W) + 0.007*\ln(W)*Sal^2 + 0.003*\ln(W)*T^2$$

Shortnose sturgeon,

$$G = 0.050 + 0.007*T - 0.0008*Sal + 0.008*DO - 0.007*T^2 - 0.0015*Sal^2 - 0.0036*DO^2 - 0.005*\ln(W) + 0.007*T*DO - 0.005*T*DO^2$$

Where, T, Sal, DO, ln(W) are standardized values (see Methods) for temperature, salinity, dissolved oxygen, and natural logarithm of individual fish weight, respectively.

Significant second order fits for both growth models predicted dome-shaped functional responses to temperature, salinity and dissolved oxygen in both sturgeons (Figures 5-7). According to these predictions maximum growth would be reached at 18.9^{o}C, 11.6 ppt and 84.9% DO_{sat} in Atlantic sturgeon and at 22.6^{o}C, 11,1 ppt and 82.2% DO_{sat} in shortnose sturgeon.

Although growth responses to temperature followed similar patterns in both species (Figure I-5), shortnose sturgeon tended to show higher growth rates at most tested condition with the exception of very low temperatures and highly saline conditions. In Atlantic sturgeon, there was a significant interaction ($p<0.003$) between log-transformed fish-weight and salinity (quadratic coefficient), which suggested a

decreasing effect of extreme salinities on fish growth at larger sizes. This trend was not significant (P=0.12) in shortnose sturgeon, at least within the size range used within the experiments.

I found significant interactions between temperature and both (linear and quadratic) components of dissolved oxygen only in shortnose sturgeon. Thus, more acute growth responses to changes in dissolved oxygen level would be expected as temperature increases (Figure I-6a).

Survival

All three environmental variables significantly affected survival in both species. Survival decreased at lower dissolved oxygen (Figure I-8) and higher salinity conditions (Figure I-9), especially at the highest tested temperature. Cox's survival analysis indicated that survival increased exponentially with DO-saturation, while decreased exponentially with increasing salinity and temperature conditions ($p<0.01$). Cox's analysis also suggested that temperature would have the strongest negative effect upon survival. I failed to detect significant interactions between explanatory variables, as well as significant differences in intercepts or slopes between species ($p=0.12$). The predictive equation ($p<0.001$) for mortality is given by

$$S(t|Sal,T,DO) = [\exp(-Z_b)]^{\exp(bs_1*Sal + bs_2*T + bs_3*DO)}$$

Where

Z_b = 0.010 ± 0.0080 (SE)

βs_1 = 0.4±0.11 (SE)

βs_2 = 0.8±0.15 (SE)

βs_3 = -0.3±0.13 (SE)

Sal, T, DO = standardized values (M=0, STD=1) for average salinity, temperature and dissolved oxygen saturation respectively according to Table I-2.

Routine metabolism

Metabolic responses to temperature were similar in both species up to 20°C. Above this level, Atlantic sturgeon metabolism tended to reach a plateau, while shortnose sturgeon metabolism tended to maintain an exponentially increasing rate (Figure I-10). Limiting effects of low dissolved oxygen levels upon routine metabolism where evident in both species below 60-70% DO-saturation, at almost all tested salinities and temperatures (Figures 11 and 12). Limiting effects of dissolved oxygen upon metabolism were much more pronounced at extreme temperature conditions. As a result, critical oxygen levels at high temperatures were very close (Atlantic sturgeon) or exceeded (shortnose sturgeon) 100% of dissolved saturation, and response curves tended to be steeper (Figure I-11).

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 I-12). 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.

Parameters obtained through non-linear fit of routine metabolism models for each species (Table I-7) suggest higher sensitivity to dissolved oxygen in Atlantic sturgeon, but higher sensitivity to extreme salinities in shortnose sturgeon.

Table I-7: Estimated and stipulated parameters used to model routine metabolic responses (Kj g^{-1} d^{-1}) in juvenile Atlantic and shortnose sturgeons.

Parameter	**Definition**	**Estimated value ± SE**	
		Atlantic Sturgeon	**Shortnose sturgeon**
Maximum specific growth rate C_{max} (Kj g^{-1} d^{-1})			
α	Allometric intercept	0.5±016	1.2±0.28
β	Allometric slope	-0.19±0.077	-0.196[1]
Functional response to temperature f(T)			
RK_1	Reaction rate multiplier at T_1	0.15±0.018	n.a.
γ_1	Exponential rate of increase	n.a.	0.084±0.0064
θ_1	Minimum tested temperature	6	6
Functional response to Dissolved Oxygen f(DO)			
c_{RM}	Proportionality constant for COK_1	0.034±0.090	0.026±0.0085
d_{RM}	Proportionally constant for DO_{max}	0.014±0.053	0.017±0.0085
DO_1	Minimum tested DO level (%)	25	25
Functional response to Salinity f(S)			
S_1	Hyposmotic coefficient	0.05±0.021	0.07±0.022
S_2	Hyperosmotic coefficient	0.06±0.027	0.09±0.025

Post-Prandial Metabolism (SDA)

The absolute amount of energy spent in post-prandial metabolism was directly proportional to energy intake and ranged across all experiments between 0.02 and 0.37 Kj g^{-1} with an average value of 0.17 Kj g^{-1} ±0.031 SE. As discussed below, energy intake was in turn, significantly conditioned by temperature, oxygen saturation and fish-weight ($p<0.05$).

The relative magnitude of post-prandial metabolism ($SDA_{\%}$) represented an average of 14.8% ± 1.1 SE of the individual energy intake. A linear increase in $SDA_{\%}$ was observed along the tested temperature (T) gradient (Figure I-13). This relationship ($p<0.03$) was described by the equation,

$$SDA_{\%} = a_{SDA} + b_{SDA} * T$$

Where, $a_{SDA} = 0.07 \pm 0.010$ SE

$b_{SDA} = 0.004 \pm 0.0018$ SE

I failed to detect significant differences between sturgeon species, as well as significant effects of dissolved oxygen or fish weight on $SDA_{\%}$. The maximum post-prandial metabolic rate (KR_{SDA}) expressed as the proportional increase in metabolism above the routine metabolic rate increased linearly with dissolved oxygen saturation and decreased with fish-weight, following the relationship ($p<0.03$),

$$KR_{SDA} = -2.24 + 0.05*D0 - 0.3 \ln W$$

The total duration of post-prandial metabolic increase (θ_4) tended to be shorter at higher dissolved oxygen conditions. Nevertheless, this relationship was significant only at the 10% level ($p=0.093$).

Activity cost

Analysis of the residuals from the balanced bioenergetics equation suggested that both species responded with different activity patterns to environmental variables. In Atlantic sturgeon, activity metabolism tended to be a fixed proportion of routine metabolism, which decreased with fish weight following the relationship ($p<0.0001$),

$$AM = A * RM$$

Where,

AM = Activity metabolism cost (Kj g^{-1} day^{-1})

A = 1.72 ± 0.083 (SE)

RM = Routine metabolism (Kj g^{-1} day^{-1})

In shortnose sturgeon, on the other hand, activity metabolism showed a dome-shaped response with maximum values at intermediate temperature conditions. This relationship was described by an increasing coefficient, proportional to routine metabolism, and a decreasing coefficient proportional to temperature. No significant ontogenetic decrease in activity cost was detected by the available data. Qualitative observations on the experimental fish are consistent with reduced activity at extreme temperature conditions. A predictive equation

for shortnose sturgeon was formulated as,

$$AMW = a_{AM} * RMW - b_{RM} * T$$

Where,

AMW = Activity metabolism cost (Kj g^{-1} day^{-1})

RM = Routine metabolism (Kj g^{-1} day^{-1})

$a_{AM} = 3.8 \pm 0.24$

$b_{RM} = 0.132 \pm 0.00923$

T = temperature

Food consumption

In both species, multiple linear regression analysis showed that food-consumption was significantly affected by temperature, dissolved oxygen, salinity and log-transformed fish weight. Observed responses to dissolved oxygen and temperature were described by quadratic equations with no significant interactions between variables ($p>0.1$). Nonetheless, significant differences were found between species regarding the quadratic components of consumption responses to temperature ($p<0.001$).

Food consumption response to temperature tended to reach maximum values at 20.8 and 25.8°C for Atlantic and shortnose sturgeons, respectively. Food consumption increased with oxygen saturation at a decreasing rate tending to a plateau close to $DO_{\%}=100$,

with no significant differences between species ($p>0.1$). Food consumption decreased with salinity in both species, but this inhibiting effect decreased as fish grew. Linear regression analysis revealed a significant interaction ($p<0.01$) between salinity and log-transformed fish-weight in both species.

Non-linear modelling led to a much better fit of the data (smaller AIC) than linear multiple regression and suggested additional differences between species (Figures 14–18). Overall consumption rates were lower in shortnose sturgeon, however the shape of temperature response followed a similar pattern across the tested range in both species. As temperature reached the highest tested level (28^{o}C) consumption rates were sharply inhibited in juvenile Atlantic sturgeon, but remained maximal in shortnose sturgeon (Figure I-14).

Dissolved oxygen had a very strong and similar effect on food consumption rates in both species (Figure I-15). Depending upon temperature, a threshold for oxygen-independence was predicted between 40 and 70% of oxygen saturation in Atlantic sturgeon and between 40 and 85% in shortnose sturgeon (Figure I-16). A clear interaction between oxygen and temperature displaced this threshold to higher dissolved oxygen saturation as temperature increased. Similar responses of food consumption to salinity were also observed between the two sturgeons, with highest consumption rates around iso-osmotic conditions and lowest consumption rates at the highest tested salinity

(Figure I-17).

Regarding the fish-weight effect, log-transformed weight was a significant predictor of maximum consumption ($p<0.001$). While slopes were not significantly different between species ($p=0.84$), shortnose sturgeon exhibited a significantly higher intercept, suggesting higher overall consumption rates (Table I-8).

Table I-8: Estimated or stipulated parameters for consumption rate sub-models for juvenile Atlantic and shortnose sturgeons.

Parameter	Definition	Estimated value ± SE	
		Atlantic sturgeon	Shortnose sturgeon
Maximum specific growth rate C_{max} (Kj g^{-1} d^{-1})			
α_1	Allometric intercept	1.3±0.11	1.2±0.12
β_1	Allometric slope	-0.20±0.069	-0.20±0.069
Functional response to temperature f(T)			
CK_1	Reaction rate multiplier at T_1	0.20±0.027	0.24±0.048
CK_4	Reaction rate multiplier at T_4	0.6±0.13	n.a.
T_{98}	Temperature at which reaction rate = 0.98	26.8±0.67	n.a.
T_1	Minimum tested temperature	6	6
T_4	Highest tested temperature	28	28
Functional response to Dissolved Oxygen f(DO)			
c_{RM}	Proportionality constant for COK	0.39±0.052	0.39±0.069
d_{RM}	Proportionality constant for DO_{max}	0.04±0.011	0.017±0.0055
DO_1	Minimum tested DO level (%)	30	30
Functional response to Salinity f(S)			
S_1	Linear component of salinity effect	1.8±0.47	1.093±0.38

Egestion

Egestion was significantly affected by temperature, dissolved oxygen and ration size in both species. There was a trend in shortnose sturgeon to show higher egestion rates, but mean values were not significantly different between species ($p>0.6$). Pooled average for both species was 10.0 % ± 0.21(SE) of total energy intake.

Egestion rate in both species decreased with temperature at a decreasing rate following a parabola. In turn, a significant increase in egestion rate (i.e. a decrease in assimilation rate) resulted when dissolved oxygen saturation was experimentally decreased from 100% to 50%. The latter effect seemed more pronounced at lower temperatures, especially in shortnose sturgeon (Figure I-18), however no significant interactions between dissolved oxygen, temperature, and/or species were found. Egestion rates in both species followed inverse dome-shaped responses to ration size, with minimum values (maximum food assimilation) about 50% of the maximum ration size (Figure I-19). Since I failed to detect differences between intercepts, main effects or interactions between both species, pooled responses were used in building a single predictive model for both sturgeons. Parameters for the linearized form of the predictive equation described elsewhere (see Methods, equation 16), are summarized in Table I-9.

Table I-9: Estimated parameters for the linearized version of the predictive sub-model for egestion rate in juvenile Atlantic and shortnose sturgeons.

Parameter	Definition	Estimated value ± SE
$Ln(a_{EG})$	Log-transformed intercept	-2.7±0.16
b_{EG}	Exponent for temperature	-0.17±0.059
d_{EF}	Exponent for linear component of ration size	-0.05±0.066
g_{EG}	Exponent for quadratic component of ration size	0.27±0.079
h_{EG}	Exponent for dissolved oxygen	-0.23±0.059

Mesocosm Validation

On average, bioenergetic models overestimated final fish weight in mesocosm tanks by 6% in Atlantic sturgeon, and underestimated it by 10.7% in shortnose sturgeon. In both species, bioenergetic models overestimated actual fish growth rates during the first 3-5 weeks of the mesocosm trials (Figure I-20). Such overestimation was especially noticeable in Atlantic sturgeon, where initially overestimated growth rates were propagated as higher than expected fish weights for most of the experimental period (Figure I-21).

Mesocosm results for Atlantic sturgeon where highly variable between weeks. Thus, predictions from bioenergetics model were the poorest for Atlantic sturgeon, where the coefficient of correlation between predicted and observed growth rates was only 0.45 ($p=0.042$), compared with shortnose sturgeon where the coefficient reached 0.79 ($p<0.0001$).

Error analysis

The shortnose sturgeon bioenergetic model tended to be less sensitive to parameter uncertainty with lower coefficients of variation and R^2-values for three out of four modeling scenarios. Highest model uncertainty was predicted at one of the most hypoxic scenarios (scenario 2) for Atlantic sturgeon and at the most stressful salinity-temperature scenario for shortnose sturgeon (Table I-10). The relative importance of parameters uncertainty also changed substantially between water quality scenarios. As a general result, the allometric exponent (b_{FC}) for the food consumption submodel was one of the 3 most sensitive parameters in all four scenarios for both species with $RPSS_{\%}$ between 24 and 93%. High sensitivity to the allometric intercept (a_{FC}) of the food consumption sub-model was also observed for all scenarios in both species, with the exception of scenario 4 in shortnose sturgeon (Table I-10).

Parameters from the activity metabolism sub-model corresponded to a second most sensitive group, especially in shortnose sturgeon and both low oxygen simulations for Atlantic sturgeon. Model sensitivity tended to be moderated or low regarding error in parameters from egestion and post-prandial metabolism sub-models. Variation in excretion sub-model parameters never exceeded 5% RPSS.

Table I-10: Relative partial sum of squares, %RPSS (rank order) in Monte Carlo simulations conducted under four water quality scenarios. Cells with dots correspond to individual parameters explaining <5% of residual variance.

Parameter	Atlantic sturgeon				Shortnose sturgeon			
	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Temp (°C)	20	20	6	29	20	20	6	29
Sal (ppt)	8	8	8	29	8	8	8	29
DO_{sat} (%)	100	40	100	40	100	40	100	40
Overall model error								
CV(%)	25.4	96.4	35.1	32.2	11.0	23.9	17.1	127.3
R^2	0.76	0.89	0.82	0.91	0.96	0.91	0.97	0.91
Food Consumption submodel								
a_{FC}	28.3 (2)	31.9 (3)	7.0 (3)	9.4 (6)	56.9 (2)	33.9 (7)	49.4 (7)	.
b_{FC}	63.1 (1)	66.7 (1)	24.4 (1)	40.5 (3)	92.8 (1)	85.9 (1)	90.0 (2)	48.6 (1)
CTK_1	.	.	14.0 (2)	6.4 (8)	.	.	71.1 (3)	.
d_{FC}	.	16.8 (6)	.		11.1 (11)	55.4 (2)	.	31.2 (5)
g_{FC}	.	29.5 (5)	.	5.6 (9)	26.4 (7)	8.9 (12)	.	.
CTK_4	.	57.1 (2)	.	51.3 (1)	n.a.	n.a.	n.a.	n.a.
T3	13.9 (3)		.	.	n.a.	n.a.	n.a.	n.a.
Sr1	.	.	.		.	.	.	26.5(6)
Routine metabolism submodel								
RTK_1	.	.	.	.				
Y_{RM}	n.a.	n.a.	n.a.	n.a.	.	.	5.8 (15)	
a_{RM}	.	.	.	.	.	11.8 (9)	6.7 (14)	26.0 (7)
b_{RM}	.	.	.	.	18.4 (9)	28.1 (8)	16.3 (11)	38.2 (4)
$J1_{RM}$	.	.	.	10.0 (4)	.	.	.	.
$J2_{RM}$	.	.	.	9.9 (5)	.	.	.	5.4 (10)
c_{RM}	.	12.4 (8)	.	8.5 (7)	.	5.6 (4)	.	6.3 (9)
d_{RM}	.	7.2 (9)	.	.	.	.	.	.
Activity metabolism sub-model								
a_{AM}	.	31.3 (4)	.	43.2 (2)	15.5 (10)	34.0 (6)	17.3 (10)	47.3 (2)
b_{AM}	.	.	.	.	51.7 (3)	38.7 (5)	53.9 (5)	5.1 (11)
Post-prandial metabolism sub-model								
a_{sda}	.	.	.	.	.	.	.	.
b_{sda}	7.9 (4)	15.3 (7)	.	.	40.6 (6)	39.7 (4)	.	8.8 (8)
c_{sda}	7.7 (5)	6.1 (10)	.	.	47.8 (5)	11.5 (10)	61.8 (4)	.

... Table 10 continued.

Egestion sub-model								
a_{EG}	.	.	.	.	22.4 (8)	10.9 (11)	37.8 (8)	.
d_{EG}	5.3 (6)	.	.	.	5.5 (12)	.	10.2 (13)	.
g_{EG}	.	.	.	.	.	.	24.1 (9)	.
b_{EG}	.	.	.	.	.	.	51.3 (6)	.
h_{EG}	.	.	.	.	.	5.7 (13)	12.4 (12)	.
Excretion sub-model								
a_{ex}	.	.	.	.	.	.	.	.
b_{ex}	.	.	.	.	.	.	.	.
c_{ex}	.	.	.	.	.	.	.	.

DISCUSSION

Comparing bioenergetics between juvenile Atlantic and shortnose sturgeons

Results indicate that besides temperature, dissolved oxygen and salinity are highly relevant parameters, which should not be ignored in modelling bioenergetic responses for estuarine species. Still temperature served a clear controlling function, which explained about 50% of the total variation in predicted growth rates for the range of tested conditions. Dissolved oxygen accounted for about 35%, and salinity accounted for 15% of total predicted variation.

Observed responses to environmental parameters suggest that rather small differences in the shape of bioenergetic responses occur between Atlantic and shortnose juveniles regarding survival and bioenergetic responses across most of the tested range of dissolved

oxygen, salinity and temperature conditions. Nonetheless, noteworthy differences were evident regarding the effects of temperature upon consumption and metabolism at the highest tested temperature (28°C). At this temperature level, shortnose sturgeon were able to maintain food consumption and a pattern of exponential increase in routine metabolism. Atlantic sturgeon, on the other hand, reduced food consumption and did not show further increases in metabolism. Juvenile shortnose sturgeon sustained higher growth and routine metabolic rates not only at higher temperatures, but also at low oxygen conditions. For instance, critical dissolved oxygen values both for food consumption and routine metabolic rates were consistently lower in shortnose sturgeon than in Atlantic sturgeon.

Although differences in temperature responses might be related to latitudinal differences between the progenies from which experimental groups were obtained, results are also consistent with observed distribution of sturgeon juveniles in natural environments. In the Hudson River, where both species still coexist in relatively high abundance, juvenile shortnose sturgeon tend to have a wider summer distribution than juvenile Atlantic sturgeon (Dovel et al., 1992; Bain, 1997; Haley, 1999). Hence, juvenile shortnose sturgeon use most of the freshwater and seasonally brackish water sections of the Hudson system, while juvenile Atlantic sturgeon are largely concentrated in the lower (cooler) sections of the estuary.

In contrast to their tolerance to higher temperature and/or lower oxygen conditions, juvenile shortnose sturgeon showed higher sensitivity (lower growth, higher metabolism) to high salinity. Nonetheless, my results indicate that species-specific differences would tend to decrease with size. This result is again consistent with observed patterns in nature where juvenile Atlantic sturgeon initiate a much earlier exploration of brackish and mesohaline waters than juvenile shortnose sturgeon (Dadswell et al., 1984; Dovel and Berggren, 1983; Dovel et al., 1992).

Indirect estimates obtained for active metabolism suggested that shortnose had a better ability to regulate (reduce) spontaneous activity under extreme temperature/low oxygen conditions. This ability might be associated with their higher capability to face such conditions through a larger allocation of available oxygen supply to sustain routine metabolism while keeping some (minimal) levels of feeding/digestion and growth.

Energy partitioning in juvenile sturgeon

Food consumption and routine metabolism rates estimated for Atlantic and shortnose sturgeon in this study were consistent with reported results for other acipenserids once size and temperature were properly adjusted to match reported conditions in those studies (Table I-14). Thus, under normoxia, both species were able to transform an average of 30% of consumed energy into fish biomass, which is

consistent with average values found across carnivorous teleosts (Brett and Groves, 1979). This ratio is also similar to the 35% conversion efficiency reported by (Cui et al., 1996) for white sturgeon, calculated based upon metabolizable energy.

As dissolved oxygen saturation decreased, energy allocation changes led to a noticeable reduction in the proportion allocated to growth, which falls to 20% of total energy intake in shortnose sturgeon and to 17% in Atlantic sturgeon at 50% DO-saturation (Figure I-22). A similar trend in reduced allocation of energy to growth below 70% DO saturation was observed by (Pedersen, 1987) in rainbow trout *Oncorynchus mykiss*. Nonetheless, the magnitude of the drop in the latter species was much more pronounced, where negative growth was observed at 40% DO saturation and 15^{o}C.

While the absolute amount of energy spent for routine metabolism decreased at low oxygen conditions, its relative proportion remained circa 10% of the total energy intake between 50 and 100% DO_{sat}. This trend supports the hypothesis that under limited oxygen supply, catabolism is prioritized over anabolism. A reduction in food assimilation (increased egestion rate) was also observed under low oxygen conditions. This response may have been achieved by reducing irrigation of absorptive intestinal tissues, as a complementary response to expected reductions in food consumption (Brett, 1979). Thus, fish avoid an excessive and potentially deleterious intake of aminoacids beyond the aerobic capacity

of the fish to transform them into stable compounds (Pauly, 1981). As a complementary response to hypoxia, sturgeons have been also reported to reduce spontaneous swimming activity as observed in *A. transmontanus* by Crocker and Cech (1997). This behavior would maintain aerobic balance and delay further reductions in oxidative processes associated with basal metabolism.

Post-prandial metabolism (SDA) has been shown to represent the energetic cost of protein synthesis and, therefore, growth (Brown and Cameron, 1991; Jobling, 1983). As a result, the capability of removing amminoacids from the blood would be directly proportional to $SDA_{\%}$ and any reduction in $SDA_{\%}$ would need to be mirrored by a similar decrease in assimilation rate, as seems to be the case in sturgeons. Such relationship was not evident, however, in Pedersen's (1987) work on rainbow trout (*Oncorhynchus mykiss*).

Assumed excretion and observed egestion rates (circa 4 and 10% of energy intake, respectively) were noticeable lower than reported values for other fishes, which averaged 8 and 20% of total energy intake, respectively (Brett and Groves, 1979). Although this result might be linked to the use of commercial pellets in my laboratory experiments, they are consistent with previous estimations for Acipenserids, in which low egestion and/or excretion rates were obtained using natural food (Dawrowski et al., 1987; Cui et al., 1996; Gershanovich and Pototskij, 1992). High assimilation efficiency could be related to the high absorptive

surface provided by the spiral valve in sturgeons (Buddington and Christofferson, 1985). This anatomical feature might also explain in part the dome-shaped relationship observed between egestion rate and ration size.

Sensitivity of sturgeon metabolism to reductions in dissolved oxygen has been suggested to exceed even oxyphylic species like rainbow trout species name (Klyashtorin, 1976). Critical oxygen saturations[2] estimated in the present work for Atlantic and shortnose sturgeons are higher than those reported for rainbow trout, but similar to other sturgeon species (Figure I-23). Critical levels reported by Klyashtorin (1976) for Asian sturgeons are about 50% and 40% lower than levels I obtained for Atlantic and shortnose sturgeons, respectively. However, this difference is consistent with our use of routine metabolism rather than standard metabolism in estimating critical oxygen saturation. Routine metabolism under laboratory conditions should be about 1.35 times standard metabolism (Khakimullin, 1989).

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 18°C. Nonnotte et al., (1993), however, found that *A. baeri* was able to maintain standard metabolism up to a dissolved oxygen saturation of 25% at 15°C.

[2] Critical oxygen saturation here is defined as the level below which any further reduction in oxygen content in the water causes a related reduction in the corresponding metabolic rate.

The present results are intermediate and estimate average critical dissolved oxygen saturations (15°C) of 83 and 72% for juvenile Atlantic and shortnose sturgeons, respectively. An overall pattern of especially high sensitivity of sturgeons to hypoxia seems counterintuitive. Many sturgeon populations may have historically used shallow warm estuaries, where hypoxia have naturally occurred before recent anthropogenic effects (Burggren and Randall, 1978; Crocker and Cech, 1997). At the same time, this limited adaptation 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).

Table I-11: Average routine metabolism estimates in Acipenserids at normoxia. Parameters a and b correspond to the intercept and slope of the allometric relationship between metabolism and fish weight. When these parameter were not available, the overall mean (?) is reported.

Species (weight range)	Metabolism type	Environmental conditions	Parameters	Source
A. transmontanus (2 – 23 g)	Routine	18.5°C, 0 ppt, normoxia	a = 0.285 b =-0.073	(Cui et al., 1996)
A. transmontanus (820-1,060 g)	Standard	15°C,0 ppt, normoxia	?=0.081	(Burggren and Randall, 1978)
A. transmontanus (1,940 g)		18°C,	?=0.094	(Ruer et al., 1987)
A. oxyrinchus (12-69 g)	Routine	19°C, 2.25 ppt 80% DO_{sat}	? = 0.218	(Secor and Gunderson, 1998)
A. oxyrinchus (12-69 g)	Routine	26°C, 2.25 ppt 78% DO_{sat}	? = 0.276	(Secor and Gunderson, 1998)
A. oxyrinchus (6-64 g)	Routine	6-28°C, 1-29 ppt, 30-100% DO_{sat}	a=0.5182 b=-0.188	This study
A. brevirostrum (8-69 g)	Routine	6-28°C, 1-22 ppt, 30-100% DO_{sat}	a=1.1623 b=-0.196	This study
A. baeri (0.01-0.4 g)	Standard	20°C, 0 ppt, normoxia	a=0.426 b=-0.132	(Khakimullin, 1984)
A. baeri (3-7)	Routine	20°C, 0 ppt, normoxia	a=0.463 b=-0.167	(Khakimullin, 1989)
A. baeri (1,800 g)	Standard	15°C, 0 ppt normoxia	? = 0.056	(Nonnotte et al., 1993)

Overall performance of developed bioenergetics model.

As indicated by mesocosm experiments, both bioenergetic models were able to provide reasonable forecast for growth rates within a 3 month timeframe. Bioenergetic models have been shown to have lower forecasting performance for expected growth than for expected consumption rates (Bartell, 1986). Forecasting errors for growth tend to increase with time in bioenergetic models as it would for longer mesocosm experiments.

In terms of parameter uncertainty, allometric relationships for food consumption rate were the most sensitive to experimental error, which is consistent with Bartell's (1986) results evaluating perch (Kitchell et al., 1977) and alewife (Stewart et al., 1981) bioenergetic models. Excretion rate was, in turn, the least sensitive to error component. Low sensitivity for this parameter may be related to its low share of total energy expenditure (circa 4%) but also due to stipulated literature values used in the derivation of excretion parameters. Nonetheless, low expected sensitivity to excretion rates has been frequently reported in sensitive and error analyses for other species (Kitchell et al., 1977; Bartell, 1986; Hanson et al., 1997).

Activity metabolism, indirectly measured from model residuals, was estimated to represent between 30 and 43% of the total energy expenditure and was the second most sensitive component of both models. Activity metabolism involves an inherently random component of

spontaneous activity, which may be amplified by short-term stress responses.

The relative consistency between mesocosm and laboratory results suggest that energy expenditure in activity was not severely limited by tank size and that it could be representative of non-migrating juvenile activity in nature. Winberg (1956) suggested that activity metabolism would be equivalent to twice standard metabolic rate, and a fixed multiplier around 2 has been used as the default to estimate total metabolism in many bioenergetic models (Hanson et al., 1997). My results suggest that activity may not be a constant fraction of energy expenditure, especially when metabolism is limited by insufficient oxygen delivery, i.e. under low oxygen-high temperature conditions. Moreover, my average estimates for sturgeon activity represent a cost closer to thrice routine (standard) metabolic rate. The latter coefficient is closer to estimates obtained using optimal cruising speed theory, which suggests optimal swimming is reached when swimming cost is equal to half the total metabolic cost (Ware, 1978; Weihs, 1973). Activity levels that optimize swimming energetics might be expected in sturgeons given their roving and grazing feeding behavior, characterized by constant searching for rather small prey items.

Although my results seem to exceed those expected from Winberg's (1956) generalization, activity multipliers close to 3 have been reported in some other species like YOY weakfish (Hartman, 1993) and juvenile

walleye pollock (Hanson et al., 1997). Although these two species are pelagic they are also expected to be much more efficient swimmers than sturgeons. On the other hand, Khakimullin (1984) suggested an activity multiplier as low as 1.38 for *Acipenser baeri*. This work was based upon swimming respirometry studies and average swimming speeds observed in aquaculture ponds. However nominal swimming speed in ponds was assumed based upon linear trajectories, laminar flow and no circadian activity cycles. In fact, Levin (1982) observed average spontaneous swimming speed in juvenile *Acipenser gueldenstaedti* (0.52 bl s^{-1}), to rise 2.4 times at night.

In conclusion, activity metabolism remains as a very relevant uncertainty in the proposed bioenergetic models for juvenile sturgeons. Further research would be needed to test the hypothesis that activity in sturgeons refflects optimal swimming speeds, which would be constrained by oxygen delivery rate at extreme temperature and/or hypoxic conditions.

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). This approach was combined with the use of a balanced oxygen equation (van Dam and

Pauly, 1995), allowing hierarchical and horizontal integration of limiting and masking effects. Moreover, the oxygen balanced approach adds a second dimension to the bioenergetic models, which allows simultaneous analysis of maximum potential rates (controlled by temperature), as well as actual realized rates (limited by dissolved oxygen delivery rate).

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 up to the point it exceeds the limits of the oxygen supply system. However, this approach, does not account for potential effects due to osmoregulatory hormones, which might also affect anabolic and metabolic rates (Morgan and Iwama, 1991; Kirschner, 1995).

Adding complexity to bioenergetic models

Dissolved oxygen and salinity fluctuations are subjects to enormous seasonal and daily fluctuations in many estuarine systems, and these two factors strongly influenced most bioenergetic processes in both sturgeons. Hence, there is a theoretical and practical need for modeling the synergistic effects of temperature, dissolved oxygen and salinity on sturgeon metabolism and production. Modern bioenergetics modeling has been largely based upon work in freshwater systems (Kitchell et al., 1977; Kitchell et al., 1974). Most of these approaches

have used temperature as the only abiotic factor driving fish bioenergetics and very limited advances have been made in extending those approaches to estuarine environments, where salinity can be a highly relevant factor affecting fish metabolism and, ultimately, survival. A similar situation is observed in terms of dissolved oxygen, where few efforts have been made to formally incorporate expected fish responses to hypoxia into bioenergetic models (Neill et al., 1994; van Dam and Pauly, 1995, Miller et al., In press).

Increasing complexity in bioenergetics model may not necessarily result in significant improvements regarding their predictive capabilities (Bartell, 1986). Limited improvement in more complex models seems often related with low sensitivity of the modified component or limited quality and high uncertainty of the information required to derive model parameters (Brandt and Hartman, 1993; Hanson et al., 1997). Nonetheless, explicit bioenergetic models represent a valuable framework to integrate and synthesize scientific understanding about key ecophysiological processes in fish, the value of which goes beyond forecasting capabilities (Bartell, 1986).

The present work was aimed to contribute to both both explanatory and predictive frameworks. Thus, the proposed models are expected to increase forecasting capabilities in estuarine environments where hypoxia is a regular (seasonal) phenomenon. In order to achieve that goal, I incorporated formally and explicitly the observed effects of

salinity and oxygen on different fish bioenergetic processes. This modeling approach should be viewd as a first approximation, and future improvement is guaranteed regarding better understanding of responses to extreme conditions, improvement of mathematical representation of theoretical responses, and reduction in the uncertainty of sensitive parameters.

CHAPTER II : SCALING UP LABORATORY BASED BIOENERGETIC MODELS TO EVALUATE HABITAT FOR ATLANTIC AND SHORTNOSE STURGEONS

INTRODUCTION

The development of spatially-explicit bioenergetic models (Brandt and Kirsch, 1993) has provided both a synoptic and quantitative framework within which evaluate habitat quality (Mason et al., 1995). Extending Brandt and Kirsch's (1993) approach, bioenergetic models could also be used to make spatial predictions of potential fish distribution, growth and trophic interactions, under different scenarios of population abundance and habitat restoration. Bioenergetics approaches may be especially useful in those cases where the population of interest is heavily jeopardized and, thus, observational data is unavailable or limited. The latter situation occurs for several Atlantic and shortnose sturgeon populations, which are rare or extirpated from their original habitats (National Marine Fisheries Service, 1998; Colligan et al., 1998).

Bioenergetic models based upon key environmental factors – temperature, dissolved oxygen saturation (DO_{sat}) and salinity - have been developed for juvenile (young-of-the-year) Atlantic and shortnose sturgeons (see Chapter 1). These models, based upon laboratory experiments, allow forecasting growth and food consumption rates based upon fish-weight and important abiotic parameters. My goal is to apply

these models at the ecosystem level (Chapter 3). But before doing so, several scaling and experimental assumptions need further examination for both juvenile Atlantic and shortnose sturgeons.

A first assumption is that individual fish are capable of discriminating between optimal, sub-optimal and deleterious water quality conditions. Strong temperature selectivity has been reported for several fishes (Jobling, 1981; Coutant, 1987; Richardson et al., 1994), where preferred temperatures tend to match levels at which growth is maximized (Jobling, 1981). Moreover, a laboratory study on *Rutilus rutilus* suggested that temperature in some instances was more influential in habitat selection than foraging opportunities (Krause et al., 1998). Although the ability by fish to recognize hypoxia per se remains unclear (Kramer, 1987), avoidance of low oxygen conditions has been shown in laboratory experiments for sturgeons (Khakimullin, 1987) and several other species (Stott and Buckley, 1979; Stott and Cross, 1973; Matthews and Hill, 1979; Ogilvie, 1982). Salinity is well known to covary with patterns of life-cycle migration. There are few experimental demonstrations, however, that fish are able to actively select between salinity levels. What experimental evidence exists tends to match expected behaviors in both migratory and non-migratory estuarine species (Girsa et al., 1980).

A second area of concern in applying bioenergetic models is their relative sensitivity to ontogenetic changes in physiological responses. Pre-

adaptations to marine life (smoltification) occur in most anadromous species and may include increased metabolic rates (Maxime et al., 1989), morphological and functional adaptations of kidney, intestine and gills (Boeuf, 1993), increased gill enzymatic activity (Boeuf et al., 1978), and strong alterations in endocrine balance (Hoar, 1988). Size thresholds are well documented for smoltification and salinity tolerance in salmonids, where a combination of size, photoperiod and temperature would trigger the egress to marine environments during discrete periods of the year (Hoar, 1988). Aerobic scopes for activity and growth are also expected to be affected by fish size (Pauly, 1981; Hughes and Al-Kadhomiy, 1988). Differences in the rates of decrease between both gill surface area and basal metabolism may lead to ontogenetic changes in scope for activity as suggested by Hughes (1984), and Hughes and Al-Kadhomiy (1988).

Differences in food quality or digestibility, and in feeding frequency corresponded to other sources of bias I investigated in this Chapter. Commercial pellets were the only feed used in building bioenergetic models for juvenile Atlantic and shortnose sturgeons (Chapter 1). Differences in food digestibility are expected in fishes and explicitly included in some bioenergetic models (Stewart et al., 1983), although ignored in many others (Hanson et al., 1997). In fact, Xiao et al. (1999) found no differences in growth rates of Chinese sturgeon *A. sinensis* between fish fed live tubificid worm and fish fed a practical semi-moist diet. Feeding frequency is another potential source of error found to

affect growth rates in white sturgeon *A. transmontanus*. (Cui et al., 1997). Feeding frequency in my experiments was fixed to three meals per day, while in nature it would be randomly distributed in time and magnitude.

In addition to the previous sources of biass, I was interested in evaluating the effects of direct competition between both sturgeons upon predicted responses. Laboratory data and proposed bioenergetic models (Chapter 1) suggest high potential for species overlap and competition between sturgeon species, within estuarine systems. Under limited food supply, bioenergetics models predict that more efficient species (higher food consumption rate and/or growth conversion efficiency) should out-compete the less efficient species. However, behavioral factors could overwhelm bioenergetics disadvantages and affect competition results.

In summary the present chapter evaluates four potential sources of error associated with applying bioenergetic models to natural ecosystems:

(1) sturgeons' ability to select and discriminate between abiotic conditions that are optimal or suboptimal according to bioenergetic model predictions.

(2) Potential error caused by extending bioenergetic predictions to larger sizes and ages than those tested in the laboratory.

(3) Magnitude of errors produced by differences in food quality and feeding frequency between laboratory experiments and nature.

(4) Potential interactions between the two sturgeons assuming simpatry and limited availability of food.

MATERIALS AND METHODS

Experimental fish for all experiments corresponded to 0-1 years old Shortnose sturgeon (Savannah River progeny), provided by the US Fish and Wildlife Service Bear's Bluff Laboratory (SC), and 0-2 years old Atlantic sturgeon juveniles (Hudson River progeny) provided by the US Fish and Wildlife Service Northeast Fishery Center (Lamar, PA). Experimental stock was hold in flow-through circular tanks at 8 ppt of salinity, 20^{o}C and >80% DO_{sat}. Fish handling followed vertebrate animal care protocol approved by the University of Maryland Center for Environmental Science No. S-CBL-99-01.

Behavior experiments

Nine binary combinations of salinity, temperature and dissolved oxygen (Table II-1) were tested on 3-7 young of the year Atlantic (n=57) and shortnose sturgeons (n=49), with mean weight 25.1 g ± 3.12 SD. All nine combinations were tested for each fish, following a random sequence of treatments within experimental subjects. All fish were allowed to recover in holding tanks for at least 48-h between subsequent tests. Fish were divided and acclimated into three temperature groups

(12, 20 and 28°C); two oxygen saturation groups (50 and 100% DO_{sat}); and three salinity groups: 1, 8 and 15 ppt.

Experiments were conducted in a choice chamber composed of two converging raceways or arms (Figure II-1). Each raceway head was supplied with a constant water flow of 3.8 l min^{-1} from two head-tanks where temperature, dissolved oxygen and salinity were controlled to meet experiment specifications (Table II-1). The experimental chamber kept a strong gradient between arms, which declined towards the holding cell. Qualitative evaluations using commercial dye indicated a laminar flow for most binary combinations. Nevertheless, 3 air-lifts had to be set in each chamber arm to avoid thermal stratification in experiments involving temperature choices. Water depth was kept between 5 and 8 cm.

During each experiment, individual fish were transferred from their acclimation tank to the choice chamber and left for ≥30 minutes in the holding cell. The fish was then allowed to swim freely along the choice chamber, after which the fish's relative position (chamber section as indicated by roman numbers in Figure II-1) was recorded every 60 seconds. After 30-45 minutes fish tended to become sedentary, remaining in a given chamber section. Experiments were terminated when the fish remained in the same section for > 5 min. and the section was recorded as "selected". The fish was then removed and water quality measured along all chamber sections. If selection was not observed within 60 minutes "no-selection" was recorded. Data was analyzed using

an extension of Fisher's exact test, which tests independence in observed responses based upon a three-way table (SAS-Institute, 1997), which included the effects of species, acclimation conditions, and treatment (binary choice).

Table II-1: Experimental conditions and choices provided to individual YOY Atlantic and shortnose sturgeons in behavioral experiments. T=temperature, Sal=salinity.

Experiment	Experimental conditions for non-tested factors	Choice 1	Choice 2
Salinity 1	T = 20°C DO_{sat} > 95%	Sal = 1 ppt	Sal = 8 ppt
Salinity 2	T = 20°C DO_{sat} > 95%	Sal = 1 ppt	Sal = 15 ppt
Salinity 3	T = 20°C DO_{sat} > 95%	Sal = 1 ppt	Sal = 15 ppt
Temperature 1	Sal = 8 ppt DO_{sat} > 95%	T = 12°C	T = 20°C
Temperature 2	Sal = 8 ppt DO_{sat} > 95%	T = 12°C	T = 28°C
Temperature 3	Sal = 8 ppt DO_{sat} > 95%	T = 20°C	T = 28°C
Oxygen1	Sal = 8 ppt T = 20°C	DO_{sat} = 40%	DO_{sat} = 100%
Oxygen1	Sal = 8 ppt T = 20°C	DO_{sat} = 40%	DO_{sat} = 70%
Oxygen1	Sal = 8 ppt T = 20°C	DO_{sat} = 70%	DO_{sat} = 100%

Ontogenetic change in growth and food consumption rates

Ontogenetic changes in food consumption and routine metabolic rates of juvenile Atlantic sturgeon were evaluated in 10-d growth-consumption experiments, following the general procedures

indicated in Chapter 1. Three size-classes where compared: Class I (6-64 g); Class II (100-250 g); and Class III (300-700 g). These three size-classes correspond coarsely with young-of-the-year, yearlings and 2-5 years old sturgeons (Dovel and Berggren, 1983; Dovel et al., 1992). While size-class I data was obtained from food consumption experiments described in Chapter 1, new experiments were conducted to estimate food consumption and growth rates in classes II and III.

Class II estimates were obtained using an incomplete factorial design based upon 15 combinations of three levels of temperature: 12, 20 and 28^{o}C and dissolved oxygen: 45, 70 and 95 % DO_{sat}, and four levels of salinity: 1, 15, 22 and 29 ppt (Figure II-2). Three complete blocks were sequentially run to obtain equal number of replicates. Fish were reared individually in 70-l tanks and fed commercial pellets (Biokyowa ®).

Due to limited number of experimental animals available for Class III experiments, only temperature effects on growth and food consumption were tested for this group. I tested 5 levels of temperature (12, 16, 20, 24 and 28^{o}C), at constant salinity (8 ppt) and oxygen saturated water (> 95% DO_{sat}), with 4 replicates per treatment.

Statistical analysis followed a three steps procedure: first, mean differences between observed (from current experiments) and predicted values (from bioenergetics model, Chapter 1) were tested under the null hypothesis of difference=0. Second, ANOVA was used to test the

hypothesis of difference=0 for each one of the tested treatments (tested set of temperature, salinity and dissolved oxygen levels). Finally, a lack of fit test was conducted using the log-likelihood ratio between a full model - where each treatment was considered as an independent explanatory variable - and a simplified alternative model - where predicted values were used as the only explanatory variable.

Ontogenetic change in routine metabolic rates

Routine metabolism (oxygen consumption) rates were measured in Class III (300-700 g) Atlantic sturgeon at 8, 12, 16, 20, 24 and 28^{o}C. All experiments were conducted at a nominal salinity of 8 ppt and >70% dissolved oxygen saturation. Three or more replicates were obtained for each temperature. However, the limited availability of large fish forced the repeated use individual fish among several temperature levels. Such fish were allowed to acclimate to the next experimental temperature at a rate $\leq$ 0.5^{o}C d^{-1}. Metabolic measurements were obtained using 600-l closed respirometers, where individual fish were placed at least 24 h before initiating each experiment. A total of 5 respirometers were available for simultaneous runs, all of them provided with a thermal control systems that maintained temperature within $\pm$0.5^{o}C of targeted value.

Statistical analysis was analogous to that used to evaluate ontogenetic change in food consumption and growth rates (see above). A

mixed model approach (Littel et al., 1996) was utilized to account for correlation within fish and respirometry runs.

Food type experiments

Three food types were compared regarding their effects on growth, food consumption, egestion and post-prandial metabolic rates in both species. These were commercial dry pellets (Biokyowa®), live blackworms *Lumbriculus variegatus*, and live/ frozen lake amphipods *Gammarus lacustris*. Wet digestion (Maciolek, 1962) was used to estimate energy density for each food type. Mean energy densities (dry weight basis) correspondend to 21.9 Kj g^{-1} ± 0.56 (SE), 20.3 ±1.24 (SE) and 15.6 Kj g^{-1} ± 2.40 (SE), for pellets, blackworms and amphipods, respectively.

10-d growth consumption experiments were conducted in 34-l aquaria using fish with overall mean weight 30 g ± 12.7 SD. Growth/consumption experiments were followed by egestion and post-prandial metabolism measurements, all conducted under the same protocols described in Chapter 1.

In growth/consumption and post-prandial respirometry experiments, I tested interactions between food type and 3 levels of temperature (12, 20 and 28^{O}C) in both Atlantic and shortnose sturgeons. Thus, a total of 9 treatments per species, with 3 replicates each, were semi-randomly distributed among 3 sequentially balanced runs. Salinity was held at a constant value of 8 ppt for all experiments.

In egestion experiments, four ration sizes (0, 10, 55 and 100% maximum consumption) were tested within each of the 9 combinations of food type and temperature used in growth/ consumption experiments. Experimental design corresponded to a split-plot design where 4 ration sizes were tested within the same fish, following a randomly scheduled sequence, with 3-d feeding periods between experiments.

Feeding frequency experiments

The effect of feeding frequency upon food consumption and growth rates was evaluated in juvenile shortnose sturgeon (mean weight: 4.5 g ±3 SD) fed chironomidae larvae *ad-libitum*. Three feeding frequencies: 2, 4 and 6 times per day where tested at a single level of temperature (22^{o}C), salinity (1 ppt) and dissolved oxygen (>85% DO_{sat}). Feeding began at 6:00 AM every day and feedings were evenly spaced in treatments involving 2 and 4 meals per day. In the third treatment, the six daily meals were scheduled every 3 hours between 6:00 AM and 24:00 PM. Rearing (38-l tanks) and feeding protocols followed protocols described in Chapter 1.

Competition experiments

Competition between juvenile Atlantic and shortnose sturgeons was experimentally evaluated in 14-d growth experiments conducted in 3,200-l outdoor mesocosm tanks. Three tagged, similarly sized individuals (45-250 g) from each species were placed into “competition”

tanks. Control tanks also contained six individuals but all of them from the same species. I tested competition under two salinity conditions: 1 ppt and 16 ppt, obtained by mixing well water with untreated brackish water from the Patuxent River (Maryland, USA). Thus a total of 18 experimental units (3 treatments, 2 salinities, 3 replicates) were distributed in 5 sequential runs, each one composed of 3 or 4 tanks. Oxygen saturation in the water was kept above 85% by artificial aeration. Water temperature, however, changed between runs following the natural cycle of the Patuxent River. Average conditions for each trial are reported in Table II-2.

Fish were fed blackworms *Lumbriculus variegatus* three times a day, at 35% of maximum expected daily consumption rate, which was calculated based upon initial weight and water quality conditions. Fish were weighed 12 hours before and after the first and last meal, respectively. Instantaneous growth rate (Winberg, 1971) was used to compare competition effects between single species and two-species tanks.

Table II-2: Mean water quality conditions (± standard deviation) in mesocosm tanks during competition trials for juvenile Atlantic and shortnose sturgeons.

Trial	Temperature (°C)	Low Salinity (ppt)	High Salinity (ppt)	Dissolved Oxygen (DO_{sat})
1	20.6±1.3	-	16.7±0.2	96.1±10.4
2	18.7±1.0	-	16.4±0.3	98.5±14.0
3	14.0±2.5	0.9±0.2	16.1±0.3	94.3±8.3
4	11.8±3.5	1.0±0.1	15.8±0.3	92.5±9.1
5	16.1±2.1	0.9±0.2	-	78.0±12.1

RESULTS

Behavioral responses to water quality conditions

A majority of fish (65.5%, $p<0.01$) was able to discriminate and choose the highest provided oxygen level (Table II-3) regardless of sturgeon species, acclimation-DO_{sat}, water temperature, or treatment (binary choices between oxygen levels). There was, however, a minor trend in both species to be more sensitive to binary choices involving 40% DO_{sat} instead of 70% DO_{sat} as the lowest provided choice (Figure II-3).

In comparison to $DO_{sat,}$ behavioral responses to temperature were significantly different between species ($p<0.01$). While, 75.4% of tested Atlantic sturgeon chose the lowest provided temperature option, 55.1% of shortnose sturgeon chose the highest temperature alternative (**Error! Reference source not found.**). Temperature selection in Atlantic

sturgeon was independent from treatment and acclimation temperature (Figure II-4). In shortnose sturgeon, there was a very heterogeneous response to different binary choices, suggesting a potential effect due to the temperature of acclimation ($p=0.08$). Thus, the highest provided temperature option was selected by 47% of the fish acclimated to 12°C, 57% of the fish acclimated to 20°C, and 88% of the fish acclimated to 28°C (Figure II-4).

Table II-3: Summary of responses to binary choices in juvenile Atlantic and shortnose sturgeons, in percent of individuals selecting the highest or lowest available choice (see methods). Pooled data for all treatments and acclimation groups. Probability for pooled data corresponds to a one-way test, under the null hypothesis of equal distribution of preferences between choices.

Tested Factor	Species	Lowest choice (% preferences)	Highest choice (% preferences)	Pr ≤ P
Dissolved Oxygen	Atlantic	34	66	1.00
	Shortnose	35	65	
	Pooled	35	65	<0.01
Temperature	Atlantic	75	25	<0.01
	Shortnose	45	55	
	Pooled	61	39	<0.01
Salinity	Atlantic	59	41	0.52
	Shortnose	45	55	
	Pooled	51	49	1.00

Overall, no significant differences were found between sturgeon species regarding behavioral selection of water salinity (Table II-3). However, acclimation salinity had a significant effect on juvenile Atlantic

sturgeon. Fish acclimated to 15 ppt showed a higher preference for the highest salinity option ($p=0.03$). This response was not observed in juvenile shortnose sturgeon (Figure II-5).

Ontogenetic change in growth and food consumption rates

Overall the bioenergetics model tended to overestimate food consumption (Figure II-6) and underestimate growth rates (Figure II-7) in size-classes II and III Atlantic sturgeon. Food consumption was overestimated by an average of 0.05 Kj $g^{-1}d^{-1} \pm 0.017$ (SE) - i.e. 18.5% of the overall mean- with no significant differences between size-classes. A log-likelihood ratio test showed lack of fit for food consumption rates in both size-classes ($p<0.001$), indicating that the variance attributed to the treatments significantly exceeded the variance explained by the bioenergetic model. ANOVA analysis by treatment indicated food consumption was significantly overestimated in two experimental groups from size-class II (1 ppt/70% DO_{sat} and 15 ppt/100% DO_{sat}, both at 20°C), and in all class III treatments, with the exception of the lowest temperature (12°C), where food consumption was significantly underestimated.

Average difference between predicted and observed growth was not significantly different from zero in either size class. Nevertheless there was a certain trend to underestimate growth in both size classes (Figure II-7). A log-likelihood ratio test indicated lack of fit for growth rate in

Class III ($p<0.005$) but not in class II ($p>0.5$). ANOVA analysis by treatment revealed that growth was significantly underestimated in only one group from Class II (20°C/ 22 ppt/ 70% DO_{sat}). In contrast, growth predictions for class III were significantly different from observed values in all treatments. Thus, the model led to significant growth underestimation in experimental groups reared at 12 and 16°C, and significantly growth overestimation in fish reared at 20, 24 and 28°C (Figure II-7).

Ontogenetic change in routine metabolism

Average difference between observed and predicted values was not significantly different from zero and the log-likelihood ratio test indicated no lack of fit for the predictive model. Nevertheless, there was a trend to overestimate routine metabolism at higher temperatures (Figure II-8). This trend was reflected in ANOVA results by temperature treatment, which indicated a significant overestimation ($p<0.01$) of routine metabolic rate in about 18% of the observed value for the highest temperature treatment (28°C).

Food type experiments

Food type had a significant effect on growth, food consumption, and egestion rates, but not on post-prandial metabolism. Food consumption was significantly lower than the control (commercial pellets) in fish fed amphipods but similar for fish fed blackworms (Figure II-9).

No significant differences between species or interactions between food type and species were found. Nevertheless, shortnose sturgeon tended to exhibit higher consumption rates of amphipods than Atlantic sturgeons ($p=0.2$).

The effects of food type on growth rates were also evident (Figure II-10). Growth rates in fish fed amphipods were significantly lower than for fish fed blackworms and for the control. Additionally, fish fed blackworms grew significantly more than fish fed commercial pellets. Non-significant significant differences were found between sturgeon species except for the groups fed amphipods, where growth rate in juvenile shortnose sturgeon was almost twice the rate exhibited by juvenile Atlantic sturgeon

Egestion rate was significantly affected by food type (Figure II-11). Fish fed amphipods exhibited average egestion rates (fraction of total energy intake) of 0.17 ± 0.021 (SE), while fish fed either blackworms or commercial pellets had a pooled mean egestion rate of 0.10 ± 0.015 (SE). I failed to detect significant interactions between food type and sturgeon species, as well as between food type and either the temperature or ration-size components of the egestion sub-model described in Chapter I.

The fraction of energy intake spent in post-prandial metabolism (SDA_{rel}) was not significantly affected by food type ($p>0.4$). Average SDA_{rel} was 0.13 ± 0.012 (SE), with a noticeable but still non-significant trend

(p=0.12) for higher values in fish fed blackworms (Figure II-12). There was also a minor trend towards higher SDA values at 20°C, but I did not find temperature main effects or any of its interactions to be significant. I also failed to detect significant interactions between food type and sturgeon species for SDA responses.

Feeding frequency

Feeding frequency had a significant effect on food consumption rate in juvenile shortnose sturgeon (p=0.012). Fish fed six times per day showed circa 20% higher consumption rates than fish fed either 2 or 4 times per day (Figure II-13). I failed to detect significant differences in average food consumption between fish fed twice a day and those fed 4 times a day. Although similar trends were observed regarding growth rates (Figure II-13), these were only significant at the 10% level. Thus, fish fed 6 times a day grew an average 44% faster than fish fed either 2 of 4 times a day, but there were not significant differences between these two lower feeding frequencies (p=0.88).

Competition experiments

Atlantic sturgeon exhibited a significantly faster growth rate than shortnose sturgeon under mesocosm conditions when reared in single-species (control) tanks. The opposite was true in all treatment tanks containing both species simultaneously, in which case shortnose sturgeon showed consistently higher average growth rates, exceeding

those of Atlantic sturgeon by an average 24% (Figure II-14). Observed differences in growth rates tended to be smaller at 15 than at 1 ppt. Nevertheless, no significant interactions were found between salinity and competition treatment level (single species vs. combined species tank). Temperature along the experimental period declined from 22.1 to 10.8^{o}C and was included as a significant covariate in the ANOVA used to compare growth rates between treatments. A test of parallelism indicated that temperature changed the absolute magnitude of growth, but not the shape of the competition treatments effects, suggesting a consistent competition pattern between both species.

DISCUSSION

Behavioral responses to water quality conditions

The application of spatially-explicit bioenergetics models (Brandt and Kirsch, 1993) to predict or evaluate habitat suitability requires information about how fish distribute along environmental gradients. One could assume a random distribution (null model), while the alternative would be an energetically optimal distribution, where the fish distribute themselves according to the best available conditions for growth. In the first case, habitat selection does not depend upon energetics, and average population growth rate will be diminished because more productive habitats will not be preferentially utilized. In the second case, fish are assumed to have the capability to discriminate

and select between optimal and sub-optimal conditions. Thus, fish will tend to concentrate in productive habitats, and thereby increase average growth rates in the population.

Empirical results from current experiments indicate that both Atlantic and shortnose sturgeons are able to identify and select between those water quality conditions that significantly affects growth and metabolism. Observed behaviors tended to match bioenergetics optima as observed in several other species (Jobling, 1981). Similar sensitivity was observed regarding oxygen and temperature gradient responses, with both species showing relative independence from acclimation conditions and fish size. On the other hand, behavioral responses to salinity depended more clearly upon acclimation conditions, particularly for Atlantic sturgeon.

Provided temperature and salinity choices corresponded to circa 40, 70 and 100% of the maximum values these fish could face under natural conditions in the mid-Atlantic region. Salinity choices, instead corresponded to 3, 25 and 43% of maximum values fish could face in the same area. Atlantic and shortnose were able to discriminate and select between rather discrete choices in water quality levels. Nonetheless, it remains unclear what is the smallest resolution in water quality levels to which the sturgeons would respond. This issue is relevant given the continuous nature of water quality conditions in the wild. On the other hand, water quality conditions in the choice chamber tended to mix in

the experimental raceway portions most adjacent to the holding cell (Figure II-1), where the fish initiated each experiment. Thus, by their movements out of the holding cell, it is apparent that experimental fish were actually able to discriminate between smaller increments in water quality conditions than those represented by each experiment.

Results here are similar to those of Krause et al. (1998) for *Rutilus rutilus*, which also showed strong discriminatory behaviors driven by temperature. Further, the work on *R. rutilis* suggested that temperature had a more dominant role in habitat selection than foraging opportunities. Still, for sturgeon it would be expected that not only water quality, but also food availability, bottom substrate, depth and other factors would influence habitat selection (Haley, 1999; Kynard et al., 2000). Thus, the present work supplies only a fraction of what would be eventually required to build more realistic habitat selection models for the two species.

Observed behavioral differences between species match field (Dadswell, 1979; Dovel and Berggren, 1983; Dovel et al., 1992) and laboratory observations (see Chapter 1), which indicate a higher tolerance to high temperatures and a more freshwater oriented life-cycle in shortnose sturgeon. Hence, shortnose sturgeons did not consistently avoid the maximum temperature choice (28^{o}C), which is consistent with the less pronounced decrease in growth rate at maximum temperatures in this species compared to Atlantic sturgeon (Chapter 1). Shortnose

sturgeon, failed to show a behavioral pattern of acclimation to higher salinity as was suggested from Atlantic sturgeon results. Thus, salinity serves a more directive role in Atlantic sturgeon behavior, where a consistent pattern of progressive displacement to brackish waters is observed after the first year of life (Dovel et al., 1992; Colligan et al., 1998; Bain, 1997). Moreover, a quick and directional adaptation to increasing salinity was also observed in hatchery-produced Atlantic sturgeon yearlings released into the Chesapeake Bay (Secor et al., 2000).

Behavioral responses to dissolved oxygen matched expectations in terms of avoidance of deleterious conditions, which would reduce growth and survival in both species. This result also agrees with observations in Siberian sturgeon *A. baeri,* where juveniles >1.8 g were able to discriminate and select higher oxygen concentrations from an experimental gradient between 30 and 100% DO_{sat} (Khakimullin, 1987).

Ontogenetic change in food consumption and growth rates

Growth, consumption, and metabolism of large size classes (100 – 600 g) were poorly predicted based upon the bioenergetic model derived from young-of-the-year (6-70 g) responses to tested environmental variables. Prediction of responses was lowest for the largest size-class (300-600 g), where both the magnitude and shape of temperature response varied substantially from model predictions. For the smaller size class (100-250 g), significant lack of fit occurred for food

consumption rate, but not for predicted growth. Moreover, lack of fit in food consumption predictions for Class II seemed to depend more heavily upon the magnitude rather than the shape of temperature responses (see Figure II-6).

Bioenergetic models (Chapter I) predicted salinity effects to decrease continuously with size. Growth and consumption rates observed in class II at 22 and 29 ppt matched or exceeded predicted rates, indicating ontogenetic pre-adaptation to salinity may happen even earlier than expected (Secor et al., 2000). Temperature, salinity and photoperiod were kept constant within each experiment, as well as for the experimental stock between experiments. As a result, no environmental clues were provided to trigger salinity adaptation, indicating that the observed enhancement in tolerance to higher salinity should be mostly related to fish size (age). MacEnroe and Cech (1985) also found increased tolerance with size in juvenile white sturgeon (*A. transmontanus*), although no evidence was found for a discrete size threshold required to initiate coastal migrations, Shelukhin et al. (1990) speculated that seasonal cooling during the fall could trigger pre-migratory adaptations in *A. guldenstadtii*.

The absence of significant differences between predicted and observed values for all three oxygen level treatments also suggest a consistent response in growth between size-classes I and II. However, none of the bioenergetic sub-models included a component accounting

for size-related reductions in oxygen delivery rate and aerobic scope (Pauly, 1981; Hughes and Al-Kadhomiy, 1988). Gill surface area per unit of biomass (GSAW) has been reported to decrease in *A. transmontanus* as fish weight increases, following the relationship $GSAW = W^{-0.158}$ (Burggren et al., 1979). Thus, aerobic scope, and therefore routine metabolism and/or growth rates would be expected to decrease with size in sturgeons.

There are also physiological and life-history arguments to expect higher tolerance to extreme temperatures in younger sturgeons. They have a higher oxygen delivery capability in relation with body biomass (Pauly, 1981), and they are, in nature, restricted to upstream, usually shallower, estuarine sections. On the other hand, larger biomass in larger fish may provide thermo-regulatory benefits. Studies on walleye *Stizostedion vitreum* (Clapp et al., 1997) indicated that larvae were much more vulnerable than YOY juveniles to high temperatures. Shekk et al. (1990) found that YOY *Liza aurata* had a decreased tolerance to low temperatures compared with yearlings of the same species. On the other hand, Elliot (1991) failed to detect size differences in temperature effects on consumption and survival between YOY and yearling Atlantic salmon. A similar pattern was reported by Smale and Rabeni (1995), who failed to detect size-dependence in either temperature or dissolved oxygen effects upon survival for 35 Mississippi-drainage stream fishes .

Food type

Oligochaets and amphipods are two of the most regular diet components of Atlantic and shortnose sturgeons [Haley, 1998 #137; Dadswell, 1984 #88; Johnson, 1997 #29; Carlson, 1987 #182; Secor et al. 2000). Growth, food consumption and egestion rates were clearly affected by food type in both sturgeons. Data indicated that sturgeon increased total consumption rate (g) in order to compensate for the lower caloric content of blackworms (on a fresh-weight basis). They failed, however, to fully compensate for the lower digestibility and energy density of the amphipods. As a result growth rate was similar (shortnose sturgeon) or higher (Atlantic sturgeon) in fish fed blackworms than those fed commercial pellets. Sturgeon fed amphipods, instead, grew at a rate 50-75% lower than fish fed either blackworms or commercial pellets.

In addition, there was a different growth response between sturgeons to the lowest quality food (amphipods). Juvenile shortnose sturgeon tended to consume more and egest a lower fraction of the energy intake. These two trends lead to growth rates significantly higher than observed in juvenile Atlantic sturgeon fed the same food. A higher capability to digest and utilize energy from crustaceans may give shortnose sturgeon competitive advantages by expanding their feeding niche breadth.

As a result of food type differences in bioenergetic response, field applications of juvenile sturgeon bioenergetic models to obtain absolute

estimates of consumption from observed growth or vice-versa would require previous calibration for actual diet composition. Calibration could be achieved by adjusting food consumption and egestion rates, which seemed to adequately explain observed differences in sturgeon growth rates. Moreover, post-prandial metabolism was not significantly affected by food type and was properly represented as a constant fraction of the total energy intake.

On the other hand, the use of available bioenergetic models to index habitat quality, as well as for other applications based upon maximum potential growth, could be considered independent from food type. In this cases, maximum potential growth is used as a relative measure of physiological well-being rather than an absolute measure of energetic performance. Moreover, the results obtained with the best performing natural food (blackworms) were virtually identical to those obtained with the pellets used to generate the models. Therefore, similar responses would be expected under optimal conditions of food availability and water quality.

Feeding Frequency

Observed responses to feeding frequency tend to agree with those obtained by (Cui et al., 1997) showing beneficial effects of multiple daily feedings on fish growth. It should be noted that the only significance that could be assigned was due to continuous feeding (Cui et al., 1997) or

under a feeding frequency of 6 times per day (this study). The probabilities of such high feeding frequencies in nature are unknown for the two tested sturgeon species. Available reports indicate 60 to 98 % of stomachs were empty in juvenile Atlantic or shortnose sturgeons (Carlson and Simpson, 1987; Dadswell, 1979; Haley, 1998; Secor et al. 2001), which might indicate rather high feeding frequencies under natural conditions. On the other hand, most optimal feeding frequencies reported for other fishes range between 2 and 6 times per day, depending upon species, diets, rearing conditions and fish size (Cui et al., 1997). Nevertheless, most of these species were predators, in which feeding energetics and prey availability could be very different from the situation in sturgeons, which exhibit a roving and grazing behavior in search of small benthic invertebrates.

Inter-specific competition between sturgeons

Mesocosm results indicated a consistent ability of juvenile shortnose sturgeon to outcompete similarly-sized juvenile Atlantic sturgeon. Under the environmental conditions of the test, Atlantic sturgeon reared separately form shortnose sturgeon tended to growth faster than the last species. Bioenergetic models from laboratory experiments predicted slightly higher consumption rates in Atlantic sturgeon for observed mesocosm conditions. Thus, neither specific differences in consumption nor in growth explained the lower growth

rates exhibited for Atlantic sturgeons facing direct competition with shortnose. Qualitative observations on the mesocosm experiments suggested shortnose sturgeon were able to consume and deplete the provided meal at a much faster rate than Atlantic sturgeon. This observation could be explained in part by Dadswell et al.'s (1984) observation of a much wider mouth in shortnose sturgeon (63-81% of the inter-orbital width) than in Atlantic sturgeon (43-66% of the interorbital width).

Overall results from my research suggest that shortnose sturgeon exhibit higher tolerance to high temperature, higher capability to use alternative prey items (crustaceans) and a behavioral ability to interfere with Atlantic foraging under limited prey availability. How juveniles from these two species can co-exist in many estuaries of North America remains unclear. Salinity remains as the main factor producing some distinctive effects on energetics and behavior in Atlantic sturgeon. Moreover, salinity has been regularly regarded as the main cause of spatial segregation between both sturgeons (Dadswell, 1979; Dovel et al., 1992; Kieffer and Kynard, 1993). , however, has questioned this view claiming that significant overlap between juvenile Atlantic and shortnose sturgeons occurs in the Hudson River, which includes salinity, depth and diet. Interestingly enough, the Hudson River sturgeon populations have recently exhibited inverse trends in abundance. While the shortnose population has increased their number 4-5 fold in the last 20 years

(Bain, 1998), the Atlantic sturgeon population has faced extremely low abundance and potential recruitment failures in the last 5 years (Peterson et al., 2000).

CONCLUSIONS

The present work tested assumptions required to scale up bioenergetics models from laboratory results to field applications. Assumptions were supported related to the behavioral ability of both sturgeon species to discriminate and select water quality conditions where growth would be optimized. However, assumptions regarding diet composition and feeding frequency could have large effects on model predictions regarding absolute magnitudes of growth, consumption, and other metabolic responses. Relative growth and consumption responses would be, however, unaffected by diet composition and feeding frequency.

Models built for YOY Atlantic sturgeon (Chapter 1) can be extended to estimate growth from water quality conditions in yearling sturgeons up to 250 g (size-class II), but would unadvisable for larger fish. Still, in the former instance model extension would require a correction factor for consumption estimates that were systematically overestimated in class II sturgeons.

Competition interference for limited food resources was shown to occur between juvenile Atlantic and shortnose sturgeons. Mesocosm results indicate shortnose sturgeon might out-compete Atlantic sturgeon in the wild, which are sympatric in several systems.

CHAPTER III : AVAILABILITY AND RELATIVE VALUE OF NURSERY HABITATS FOR ATLANTIC AND SHORTNOSE STURGEONS IN THE CHESAPEAKE BAY.

INTRODUCTION

Mid-Atlantic populations of shortnose and Atlantic sturgeons dramatically collapsed during the 20th century, when annual landings dropped from 3 million metric tons in the early 1900s to 10 metric tons in the mid 1920s (Hildebrand and Schroeder, 1927). Following that period, some short term recoveries of Atlantic sturgeon stimulated minor fisheries in both SC (Smith, 1985) and NY (Stevenson and Secor, 1999), but only one case of significant recovery has been documented: that of the Hudson River population of shortnose sturgeon (Bain, 1998). Overall, all sturgeon populations in the East Coast of the United States are considered depleted, requiring immediate recovery measures (ASMFC, 1998; National Marine Fisheries Service, 1998). Atlantic sturgeon fishing is now banned in the U.S. and shortnose sturgeon is protected under the Endangered Species Act.

Overfishing seems to be the most likely cause of decline for mid-Atlantic populations of Atlantic sturgeon, which at the turn of the 19th Century experienced extreme rates of exploitation (Secor and Waldman, 1999; Hildebrand and Schroeder, 1927). Up until then, abundances were high (Secor and Waldman 1999), indicated that habitats remained

sufficiently productive to support large viable populations during the 19th Century. The historical situation is less certain for shortnose sturgeon where there is very little documentation of spawning over the past 150 years of records (J. Musick, VIMS, pers. comm.). In some systems shortnose sturgeon have persisted but at levels that are thought to represent levels near or below replacement. Shortnose sturgeon was not the target of intensive exploitation as were Atlantic sturgeon. These factors taken together could suggest that estuarine habitat change could have had more deleterious effects on shortnose sturgeon than Atlantic sturgeon.

For both species, a prominent anthropogenic change in habitat in the Chesapeake Bay - increased frequency of hypoxia (Cooper and Brush, 1991a; Officer et al., 1984) - could have played a critical role in reducing populations or slowing the pace population recovery (Secor and Gunderson, 1998; see Chapter 1).

Increasing concern on the conservation of both species during the past decade has led to development of Federal and Interstate recovery programs for Atlantic and shortnose sturgeon. A final version of a recovery plan for shortnose sturgeon was issued on December 1998 (NMFS, 1998), and an earlier fishery management plan (ASMFC 1990) for Atlantic sturgeon was revised to emphasize conservation aims (ASMFC,1998). Stocking trials to evaluate the potential of hatchery based restoration programs have been conducted with shortnose

sturgeon in the Savannah River, South Carolina (Smith et al., 1991) and with Atlantic sturgeon in the Hudson River, New York (Peterson et al., 2000) and the Nanticoke River, Maryland (Secor et al., 2000).

A critical issue identified in the Magnuson-Stevens Fisheries Conservation Act (16 U.S.C. 1801) is the identification of criteria to identify and categorize essential fish habitat. This concept is legally defined as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity". Nursery areas are viewed as particularly important essential habitats, which should be evaluated in terms of their potential to support growth and survival of larval and pre-migratory juvenile stages. Nursery habitats may be especially important in regulating sturgeon populations. Boreman (1997), for instance, showed that Atlantic sturgeon net reproduction rates were much more sensitive to changes in first year survival, than earlier maturing species such as striped bass and winter flounder.

A variety of habitat evaluation procedures (HEP) are currently used in the United States to identify and assess suitable habitat for managed species (Wang et al., 1998). Most of these procedures develop correlations between fish distribution and environmental parameters based upon literature review of biological responses to water quality, habitat occurrence data, and professional judgment (Wang et al., 1998). Detailed statistical testing is available for very few of these procedures (Rankin, 1995). A large number of such indexes are mainly qualitative, focused on

physical effects on entire biotic assemblages. A minority of methods includes more quantitative approaches and species-specific frameworks. An example of the latter kind is the habitat suitability index (HSI) proposed by the U.S. Fish and Wildlife Service (Terrel et al., 1982). This index is the product of individual scores (0 to 1) assigned to observed levels of a given environmental parameter, according to its expected effect on the species of interest (being 0 = not suitable; 1=optimum).

Although the concept of suitability has been widely used in habitat evaluation procedures, it is not well defined. McCall (1989) proposed an operational definition of habitat suitability as the instantaneous per capita growth rate as a proxy for reproductive value. Scaling down from the population level to a non-reproductive life-stage, reproductive value can be approximated by the ratio between somatic growth and mortality (Houde, 1997; Secor, 1999; Werner and Gilliam, 1984).

Following the same rationale, spatially explicit bioenergetic models could provide an alternative approach to evaluate fish habitat, as done for striped bass by Brandt and Kirsch (1993). This approach can serve to complement presence/absence based models. It uses available information on fish physiology to rank areas of expected fish presence, according to their relative capability to support fish growth. Thus, it is possible to generate indexes of habitat availability (fish presence, survival) as well as habitat value (potential growth). In addition, if a species is rare or extirpated from a given ecosystem, occurrence data are

usually scarce, biased, or absent. In such cases, bioenergetic models may be among the few available tools for predicting potential fish distribution, growth and trophic interactions under different restoration scenarios.

In this Chapter, I assess spatial and seasonal availability of nursery habitats for juvenile shortnose and Atlantic sturgeon in the Chesapeake Bay by developing and applying habitat-based energetic models for each species. I analyze expected growth, survival and potential production responses to water quality (temperature, dissolved oxygen, salinity) as a means to index habitat value for juvenile sturgeons.

In particular, I evaluated the magnitude of seasonal changes in suitable habitat expected from the enormous seasonal variations in temperature, dissolved oxygen and salinity conditions occurring in the Bay. Special effort was devoted to analyze recent trends (1990-1999) in habitat suitability during the summer, where severe habitat reduction and fragmentation was predicted for both species. I also compare suitable habitat between sturgeon species in order to test the hypothesis of physiological segregation along the salinity or thermal structures of the Bay (see Chapters I and II).

MATERIAL AND METHODS

Bioenergetic models developed in Chapter 1 were supplied with available bottom water quality data (<1 m from bottom; 1990-1999)

obtained from EPA's Chesapeake Bay Monitoring Program (Figure III-1). January, April, July and October were chosen as representative months for each season. Monthly averages by year, as well as for the 10-yr period were obtained and compared in search of potential trends, maximums or minimums.

These water quality data were used to generate spatially and temporally explicit predictions of potential growth, survival and production for each species in the Chesapeake Bay. Potential production rate was defined as the instantaneous amount of biomass generated per unit of cohort biomass per day, considering both growth and the mortality rates. Instantaneous potential production was calculated by subtracting the mortality rate from the growth rate according to the following derivation:

$$PP = (W_0 * eGt * N_0 * e\text{-}Zt)/(W_0 * N_0)$$

$$PP = \exp^{(G-Z)t} = \exp^{\varphi * t}$$

$$\varphi = G-Z$$

Where PP is potential production per unit of cohort biomass; φ is the instantaneous potential production rate, W_0 is average individual weight at time 0; N_0 is cohort abundance at time 0; G is the instantaneous growth rate; and Z is the instantaneous mortality rate.

Potential production was estimated for each sampling station, season and year and then interpolated between stations based upon a

300 by 300 grid, generated using point kriging (Cressie, 1991) in Surfer 7.0© software. Total suitable habitat (TSH) was then defined as the total area of the system supporting positive instantaneous potential production rates ($\varphi>0$).

Spatial estimations of relative habitat value (φ) and total suitable habitat were used to evaluate the following three hypothesis,

1. Hypoxia is a persistent feature (1990-1999) that reduces habitat suitability during the summer in the Chesapeake Bay.
2. Temperature regime of the Bay causes seasonal habitat contraction in summer and winter and a bimodal growth pattern in juvenile sturgeons, with optimal growth rates in spring and summer.
3. Suitable habitats for juveniles from both sturgeon species fully overlap with the exception of extreme summer conditions, where lower temperature tolerance in juvenile Atlantic sturgeon would concentrate this species in much more discrete thermal refuges.

RESULTS

During the studied period (1990-1999) average Bay temperature at the bottom layer ranged from 25.4°C in summer to 4.4°C in winter, and average dissolved oxygen between 69 and 94% of saturation in summer and winter, respectively (Table III-1). Moreover, average dissolved oxygen fail to represent the simultaneous presence of both supersaturated and anoxic waters during the summer in large fractions of the Bay. The salinity gradient tended to be more pronounced in spatial than in temporal dimensions, representing a key factor structuring the Chesapeake Bay environment. This factor was also the least predictable in terms of seasonal variations with noticeable inter-annual stochasticity.

Table III-1: Monthly averages and standard deviations of dissolved oxygen (mg/l), salinity (ppt) and temperature (°C) in the bottom waters (Lim) of Chesapeake Bay (1990-1999).

MONTH	Dissolved Oxygen		Salinity		Temperature	
	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.
January	11.6	1.9	8.3	9.4	4.4	2.5
February	11.6	2.0	7.9	9.2	4.4	2.4
March	10.8	2.0	7.7	8.8	7.4	3.0
April	9.0	2.1	7.2	8.6	12.4	3.2
May	7.3	2.5	7.4	8.7	17.3	3.4
June	6.0	2.5	7.9	9.0	22.4	3.9
July	5.4	2.6	8.6	9.4	25.5	3.8
August	5.8	2.4	9.0	9.6	24.9	3.5
September	6.4	2.2	9.2	9.5	22.2	3.7
October	7.8	2.0	9.3	9.7	16.7	3.7
November	9.3	2.1	8.8	9.6	10.6	3.2
December	10.2	2.0	8.9	9.7	7.6	2.8

Potential production rates for 14-g Atlantic and shortnose sturgeons in the Chesapeake Bay during 1990-1999 reflected the strong seasonal cycle in environmental conditions (Figures III-3 to III-6). Spring (Figure III-4) and fall (Figure III-6) months offered the best overall conditions for both species, particularly in tributaries and shallow areas. Discrete areas where negative or null production are predicted to occur mostly at the bay mouth area, where high salinity caused relatively high mortality that masked optimal conditions of temperature and dissolved oxygen.

Growth as well as mortality rates decreased to levels very close to zero during the winter. Thus potential production also approximated zero and a period of growth stasis was predicted under average January conditions (Figure III-3). Summer, in turn, represented the most critical season for both species in which hypoxia and high temperature conditions caused severe habitat fragmentation for both species, restricting suitable habitat to a small fraction of the Bay (Figure III-5). Negative potential production areas closely mirrored hypoxic areas occurring in the middle mainstem, as well as the lower Patuxent, Potomac and Rappahannock rivers (Figure III-7). Negative production areas were also predicted near the Bay mouth where very high salinities masked possitive conditions of dissolved oxygen and temperature. As a result, suitable habitat (null or positive production) would be restricted to very limited areas, which coincide only in part between sturgeon

species.

For Atlantic sturgeon, summer refuges for an average year would be restricted to the upper Bay between the Magothy River and the Susquehanna Flats. Slightly negative areas would be expected around Fishing Bay-Nanticoke River, between the Severn and Choptank rivers and in the upper Potomac River. For shortnose sturgeon, most suitable habitat in the mainstem would be restricted to the Bay head above Sassafras River. Additional positive production would occur in upper sections of the Potomac and James rivers, as well as in most of the Nanticoke River.

The total area supporting positive production (suitable habitat) under average July conditions corresponded to 1,586 and 1,076 km^2, for Atlantic and shortnose sturgeons, respectively. These areas represent 8.5% and 5.8% of the total surface area of the mainstem and tidal sections of Chesapeake Bay tributaries. According to model predictions, there was tremendous inter-annual variation in suitable habitat for juvenile sturgeons during the studied period (Figure III-8). Coefficients of variance of suitable habitat over the decade were 132.1 and 53.6% for shortnose sturgeon and Atlantic sturgeon, respectively. The best summer conditions for both sturgeons were predicted for 1996, where suitable habitat reached circa 4,200 km^2 for Atlantic sturgeon and 2,050 km^2 for shortnose sturgeon. The worst conditions for Atlantic sturgeon were observed in July 1999, where suitable habitat was close to 1 km^2

(Figure III-9). For shortnose sturgeon, the smallest summer habitat area was 165 km^2 corresponded to July 1993.

Inter-annual fluctuations in water quality conditions for July (Figure III-10) show that fluctuations in suitable habitat tended to be more closely related to fluctuations in temperature and salinity than with changes in dissolved oxygen. For instance, 1996, the year exhibiting the highest suitable habitat area for both species was a year where average temperature and salinity were the second lowest in the studied period, while average dissolved oxygen conditions were above the average. This year also exhibited the highest July freshwater inflow of the studied period. The year 1993, in turn, corresponded to the warmest year of the series, leading to a severe temperature-driven reduction in suitable habitat for both species. Finally, the year 1999 showed the highest overall salinity (and the lowest freshwater inflow) of the time series. This higher than usual salinity reduced the habitat value of the upper Bay section, which is typically the most productive section of the Chesapeake Bay (Figure III-11).

There was a significantly negative correlation between estimated suitable habitat area and average Bay temperature, within the period of study, for both species ($p<0.01$, Table III-3). Some level of correlation ($p<0.1$) was also suggested between salinity and suitable habitat for Atlantic sturgeon, and between river flow and suitable habitat for both species. No significant correlation was observed between dissolved

oxygen level and suitable habitat area for either species. Dissolved oxygen saturation showed no significant trend along the 10-yr period and a low coefficient of variation (4.1 % for July 1990-1999) compared with temperature (CV=4.9%) and salinity (8.9%).

Table III-2: Correlations between average water quality conditions and suitable habitat area for juvenile sturgeons in the Chesapeake Bay (1990-1999). Freshwater inflow estimate corresponds to the Susquehanna River.

Environmental Factor	Atlantic sturgeon		Shortnose sturgeon	
	Correlation coefficient	p>|r|	Correlation coefficient	p>|r|
Salinity	-0.57	0.088	-0.38	0.280
Temperature	**-0.73**	**0.016**	**-0.89**	**<0.001**
Freshwater inflow	0.58	0.080	0.63	0.052
DO_{sat}	-0.16	0.659	-0.41	0.240

DISCUSSION

Suitable habitat for juvenile sturgeons in the Chesapeake Bay

The present approach to evaluate sturgeon nursery habitat in the Chesapeake Bay indicates that the Bay may still serve nursery habitat functions for juvenile Atlantic and shortnose sturgeons. There was, however a tremendous inter-annual variation in available habitat during the last 10-yr. Due to the severe reduction in suitable habitat predicted under summer conditions. In fact, suitable habitats were predicted to be

nearly absent for Atlantic sturgeon under the most extreme scenario (year 1999). Such a scenario would theoretically produce massive or total cohort mortality. In general, suitable habitat availability was available on a more consistent basis across seasons and years for shortnose sturgeon than Atlantic sturgeon. This prediction is consistent with recent reports of wild juvenile shortnose sturgeon in the Upper Bay that, although spawned elsewhere (Delaware Bay), may be using foraging areas of the Bay on a regular basis (Welsh et al., 1999).

The ability of the Chesapeake Bay to support nursery functions for sturgeon was also confirmed by empirical evidence from a 1996 stocking experiment, where Atlantic sturgeon yearlings were able to survive, grow and disperse at rates, which were consistent with expectations from other systems (Secor et al., 2000). It is interesting to note that the year 1996 corresponds to the year where the largest suitable area was predicted within the 10-yr period of study.

High fragmentation and inter-annual fluctuations in value of summertime habitat indicate that juvenile sturgeons could be especially sensitive to climatic oscillations, as well as to anthropogenic intervention in terms of freshwater inflow, temperature and dissolved oxygen depletion. It should be emphasized that the lack of correlation between dissolved oxygen and suitable habitat was more related to the persistently loe level of DO and hence its low variability, rather than to low sensitivity of juvenile sturgeons to hypoxia. According to the present

results, at least 4 summer refuge areas were identified that may deserve special consideration in restoration efforts for these species: the upper Bay (above the mouth of the Chester River), the whole Nanticoke River, and the meso-oligohaline sections of the Potomac and James River.

The comparatively high inter-annual variability observed in Atlantic sturgeon is explained by a higher sensitivity to temperature variations and overall lower growth rate in comparison to shortnose sturgeon. In turn, these lower growth rates make potential production in this species more sensitive to all sub-optimal conditions and habitat loss. Higher variability in potential production during early life stages in Atlantic sturgeon could be compensated at least in part by a more periodic life-history strategy, which include attributes of delayed maturity and larger adult size (Winemiller and Rose, 1992). Shortnose sturgeon, albeit also a periodic strategist, show earlier maturation, smaller adult size and larger eggs, all of which suggest a more stable environment (Winemiller and Rose, 1992) or a lower sensitivity to environmental fluctuations for this matter.

Potential overlap between juvenile Atlantic and shortnose sturgeons

Consistent with outcomes from laboratory experiments (Chapter 1), similar growth, mortality and potential production were predicted between the two species for the observed range of Chesapeake Bay conditions. Consequently, significant spatial overlap, exploitation

competition for food resources and pre-emptive competition for scarce summer refuges could be expected between early juveniles of the two species. Salinity has been suggested as the main factor driving sturgeon species segregation and contributing to habitat partitioning in several estuarine systems (Dadswell, 1979; Dovel and Berggren, 1983; Dovel et al., 1992; Moser and Ross, 1995; Hall et al., 1991) . My modeling results give partial support to this hypothesis, at least for summer conditions. Alternatively, different depth preferences and subtle diet differences have been suggested as potential habitat partitioning mechanisms between Atlantic and shortnose sturgeons (Haley, 1999; National Marine Fisheries Service, 1998). Differences in average depth and diet between juvenile Atlantic and shortnose sturgeon were, in fact, reported recently for the Hudson River sturgeon populations (Haley, 1999). Although is unclear if these differences were the cause or consequence of observed differences in horizontal distribution between species, some level of diet differences has been suggested by other studies. Shortnose sturgeon consume more diverse prey, which includes annelids, small crustaceans (isopods, amphipods), and bivalves and gastropods (Dadswell, 1979; Carlson and Simpson, 1987). Only annelids and crustaceans typically occur in the diet of young Atlantic sturgeon (Vladykov and Greeley, 1963; Secor et al., 2000; Johnson et al., 1997).

Since niche overlap is expected to be a function of species abundance (Hurlbert, 1978; Petraitis, 1979), maximum segregation is

predicted at minimum population levels. Thus, competition between sturgeons under initial restoration stages would expected to be low as individuals would concentrate around relatively discrete optimal conditions that yield the highest growth rates (MacCall's Basin Model, 1989;. Natural or induced increases in population density might lower the maximum growth rate, expanding optimal growth habitats to neighboring zones and, thus, increasing niche overlap and competition between species.

Shortnose sturgeon spawn between February and May, and Atlantic sturgeon between April and June depending upon latitude (Dadswell et al., 1984; Colligan et al., 1998). Thus, juvenile sturgeon would face Chesapeake summer conditions at very small size (< 1 g), prior to development of tolerance to high salinity conditions. Bioenergetics modeling suggests that in comparison to Atlantic sturgeon, shortnose sturgeon have lower salinity tolerance but higher temperature tolerance during their early juvenile stage. This combined effect would probably restrict them to the upper reaches of those tributaries where temperature does not exceed lethal levels. Such prediction is consistent with field observations, which indicate freshwater residence for shortnose sturgeon during their first year of life (Carlson and Simpson, 1987; Dovel et al., 1992). Model predictions are, however, not consistent with (Dadswell, 1979)'s observations in the St. John's River (Canada), where juvenile shortnose sturgeon remain in freshwater for several years. This

pattern implies that other factors like forage supply, inter- or intra-specific competition preclude this population of taking advantage of brackish areas where higher temperatures would support higher growth rates for juveniles. On the other hand, if salinity tolerance is size dependent, a later movement to brackish water would be expected based upon relatively slow growth rates in the St. John's River population.

Using potential production to index habitat suitability

The present approach to evaluate potential habitat for fishes, used here for juvenile sturgeons differs from Mason et al. (1995) and Brandt and Kirsch (1993)'s approaches in two main aspects. First, I have used potential production instead of potential growth, thus incorporating survival, which is not always coupled with predicted growth, as a second dimension of habitat value. Hence, while most predictions would be similar between both methods, the potential growth index would fail to account for low survival rates in high salinity areas supporting positive predicted growth.

The present approach also differs from habitat suitability index (Terrel et al., 1982) in terms of emphasizing the functional responses to a reduced set of environmental parameters and their interactions, rather than a more general response obtained from much larger set of predictors. Integration of both approaches in a common framework would be possible given the flexibility of the habitat suitability index.

However, it would require subjective assignment of weight to each predictor.

Overall, inferences on habitat quality obtained from the present study are expected to be also applicable to other species. Sturgeons have been shown to be especially sensitive to hypoxia (Klyashtorin, 1976) and general predictions obtained from sturgeon species should serve as a lower limit reference to estimate habitat quality for other species.

Conclusions

Potential production of juvenile Atlantic and shortnose sturgeons in the Chesapeake Bay are substantially influenced by spatial and seasonal variations in temperature, salinity and dissolved oxygen. Severe hypoxia in bottom waters causes tremendous reduction in suitable nursery habitat for both species during the summer. Low overall habitat suitability was predicted in winter but with little evidence of habitat fragmentation or contraction. No improving trend in oxygen or suitable habitat for sturgeons was observed during the 10-yr period analyzed in the present research.

In the Chesapeake Bay, all three factors here discussed - temperature, dissolved oxygen, and salinity- have been probably displaced from their natural levels by anthropogenic controls on freshwater flow, organic pollution and climatic change. Temperature has probably served an historical role as the most important habitat

structuring force (Coutant, 1987) and summer habitat reduction to discrete thermal refuges has probably always occurred. These refuges probably included deeper areas in the mainstem, which are now unavailable because hypoxia or increased salinity. The Bay mouth remains as a well oxygenated, temperature-moderated refuge, which only becomes available for larger pre-adapted fish. Available information from Chapters I and II suggests that this pre-adaptation would occur earlier in life for Atlantic than for shortnose sturgeon.

Sturgeon restoration in the Chesapeake Bay requires further improvement in water quality conditions and special protection of areas identified as potential summer refuges. Significant spatial overlap and high inter-specific competition are anticipated between early stages of Atlantic and shortnose sturgeons. As a result, recovery rates of Atlantic and shortnose sturgeons can be interdependent, and may be sensitive to direct manipulation of species abundance as done in aquaculture-based stock enhancement.

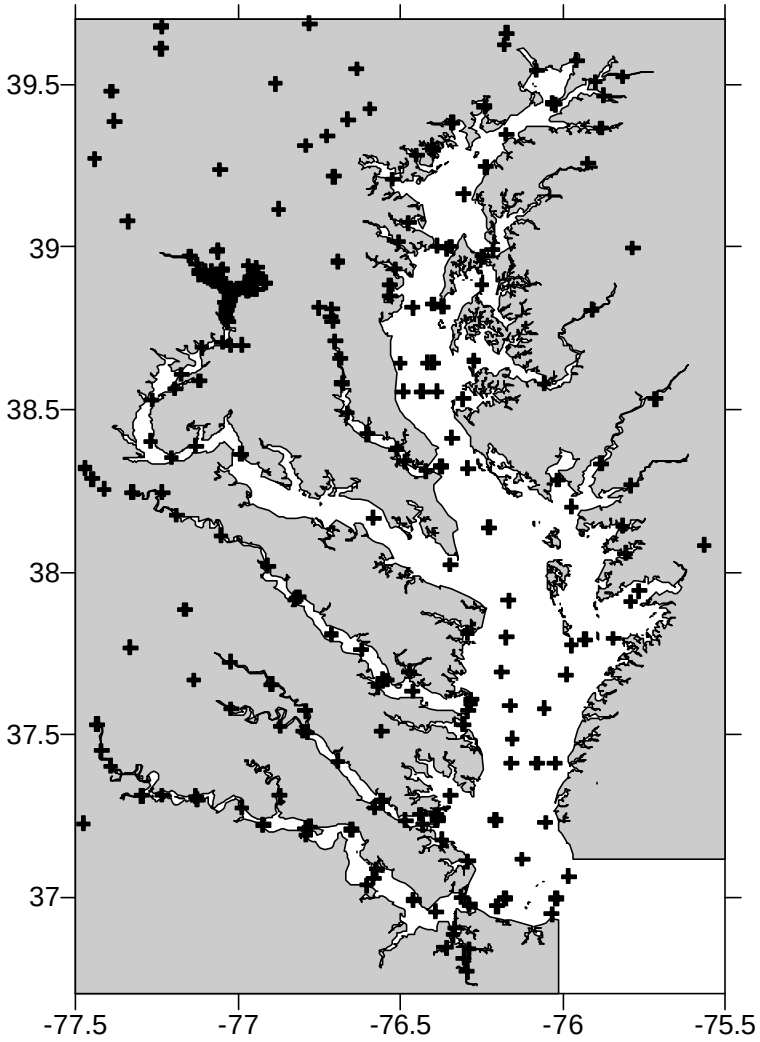


Figure III-1: EPA-Chesapeake Bay Program fixed stations for water quality monitoring program.

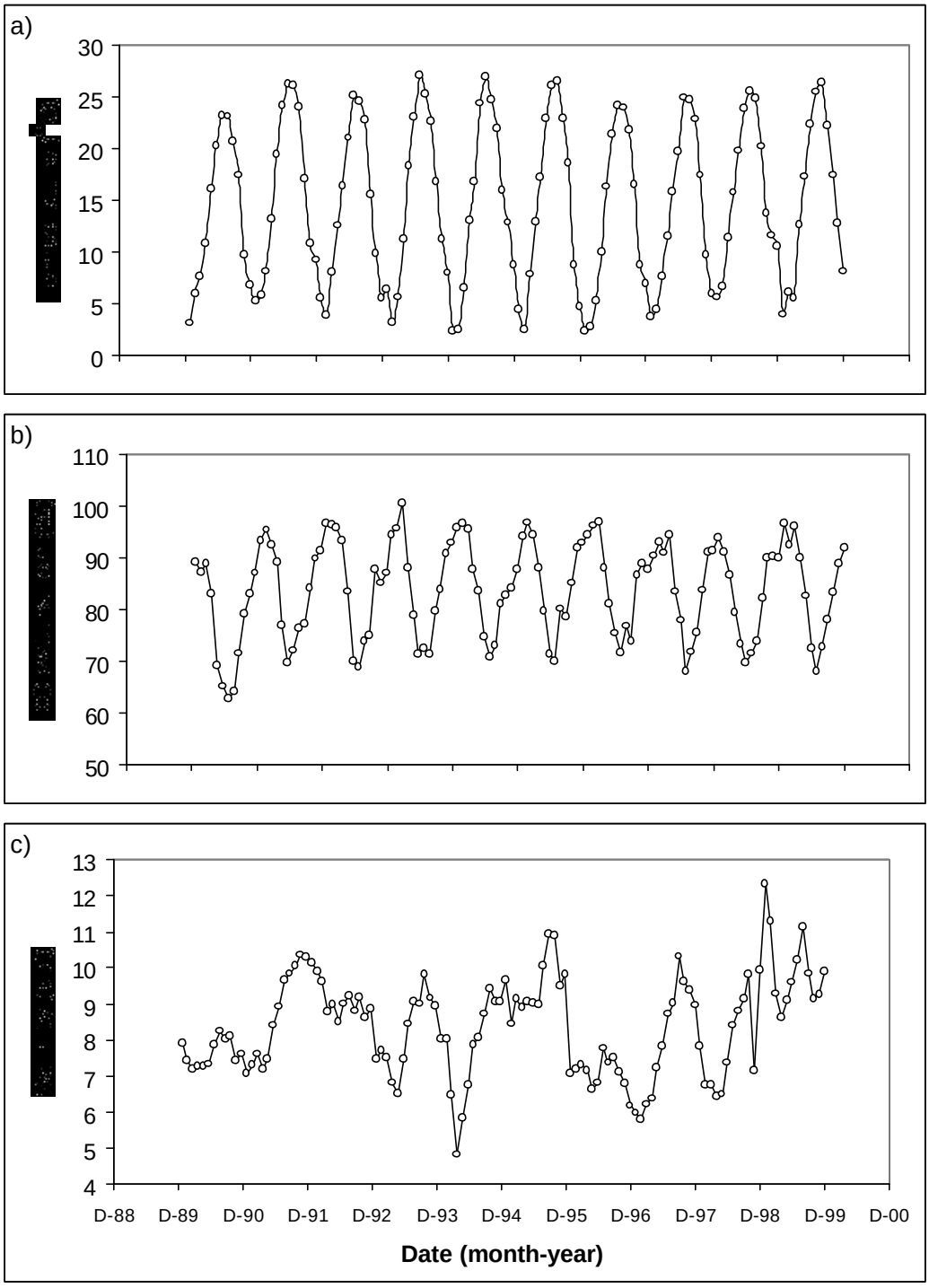
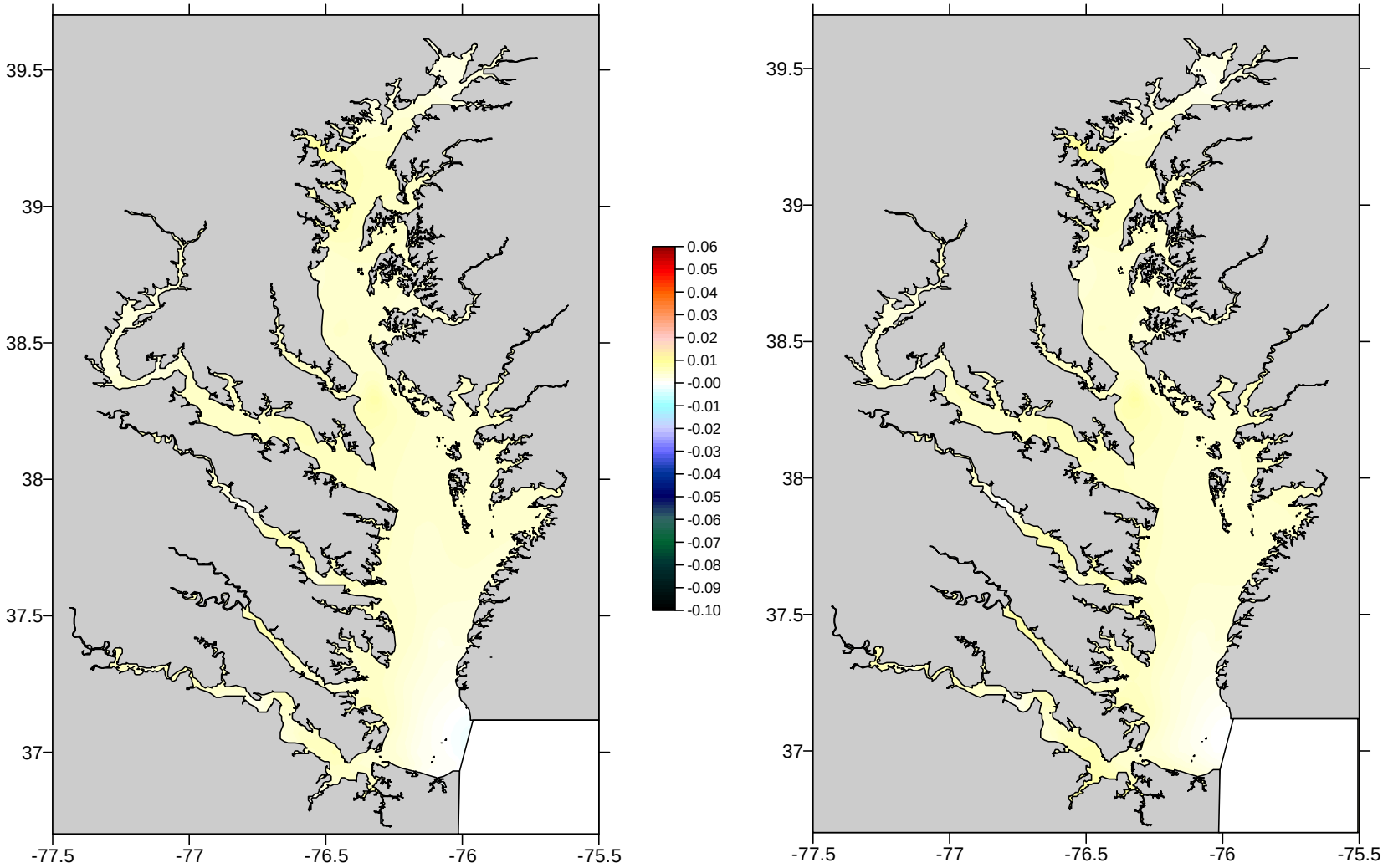


Figure III-2: Seasonal and interanual fluctuations in monthly averaged water quality conditions in the Chesapeake bay. **a)** Temperature (^{O}C); **b)** dissolved oxygen (DO_{sat}); **c)** salinity (ppt).

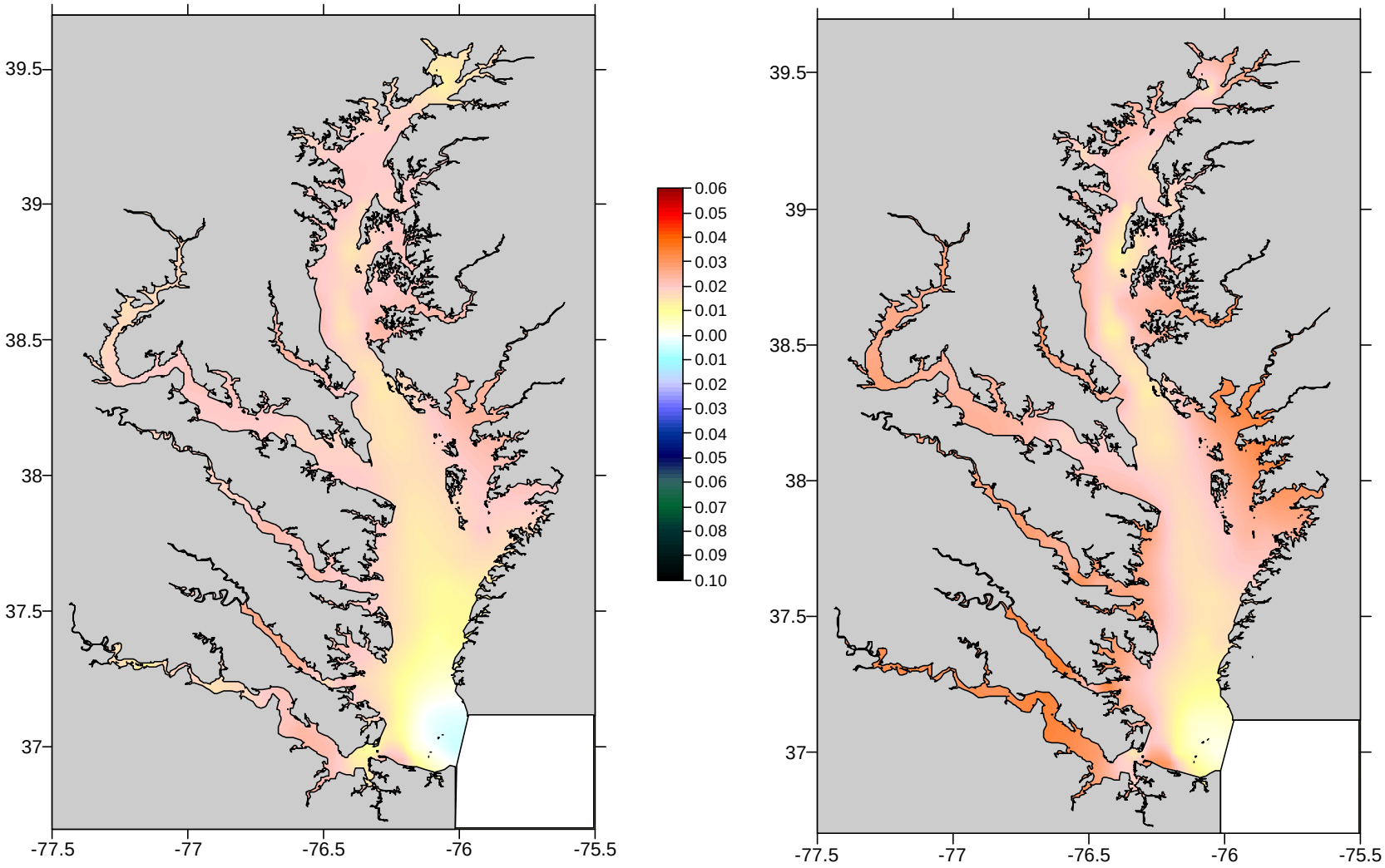
Figure III-3: Instantaneous potential production rate in Chesapeake Bay. Average conditions in January 1990-1999. **a)** Atlantic sturgeon; **b)** shortnose sturgeon.



a) Atlantic sturgeon

b) Shortnose sturgeon

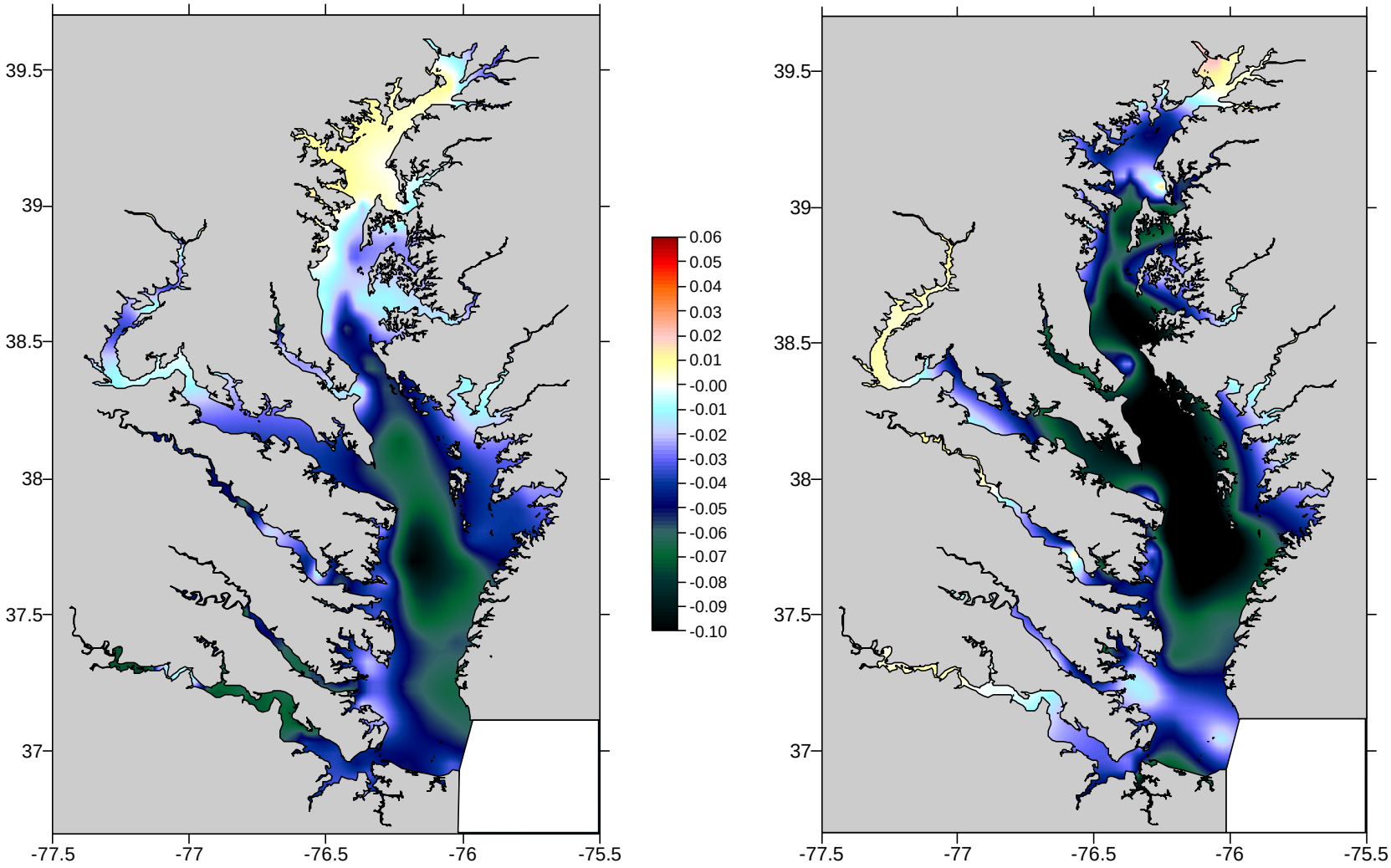
Figure III-4: Instantaneous potential production rate in Chesapeake Bay. Average conditions in April 1990-1999. **a)** Atlantic sturgeon; **b)** shortnose sturgeon.



a) Atlantic sturgeon

b) Shortnose sturgeon

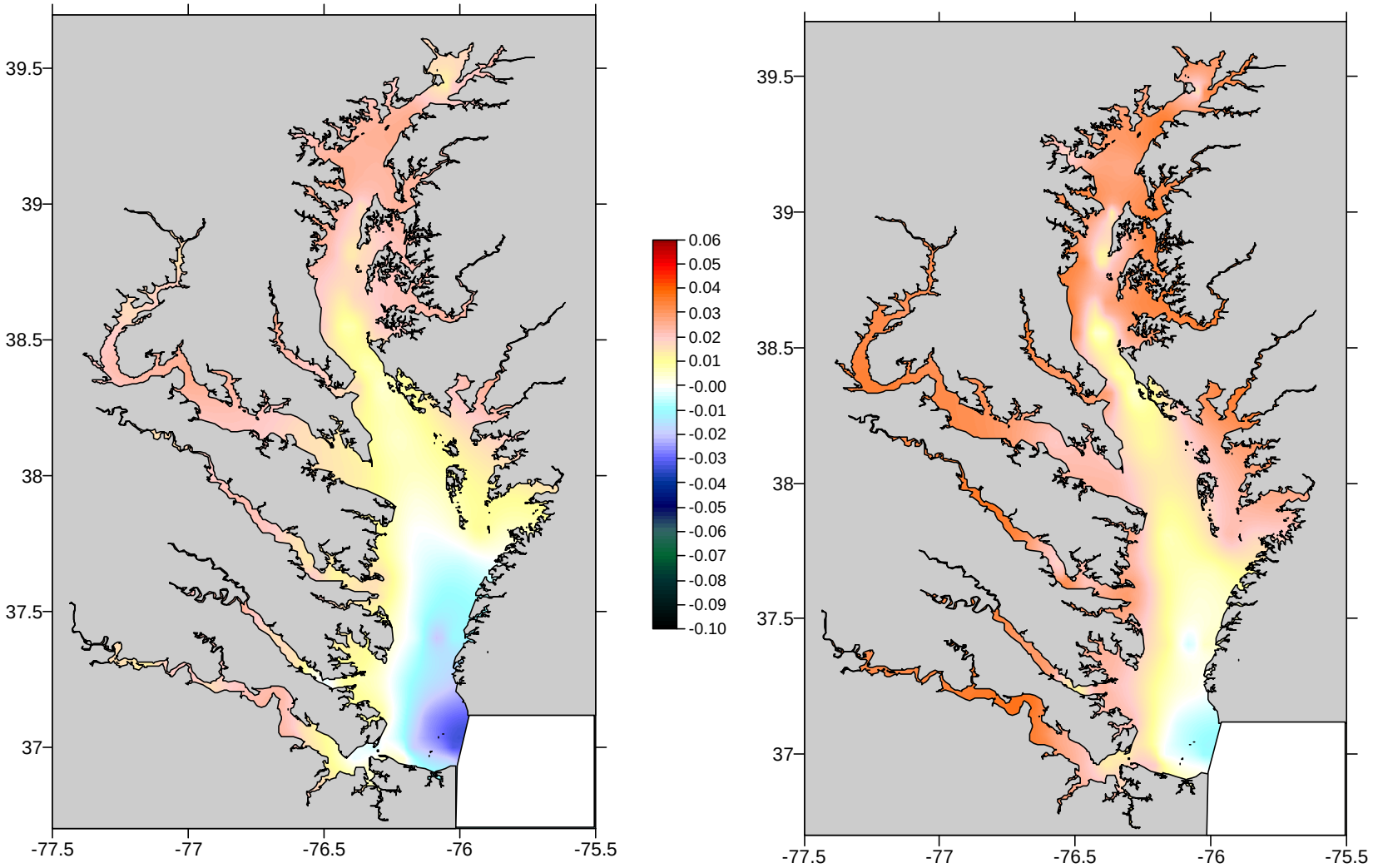
Figure III-5: Instantaneous potential production rate in Chesapeake Bay. Average conditions in July 1990-1999. **a)** Atlantic sturgeon; **b)** shortnose sturgeon.



a) Atlantic sturgeon

b) Shortnose sturgeon

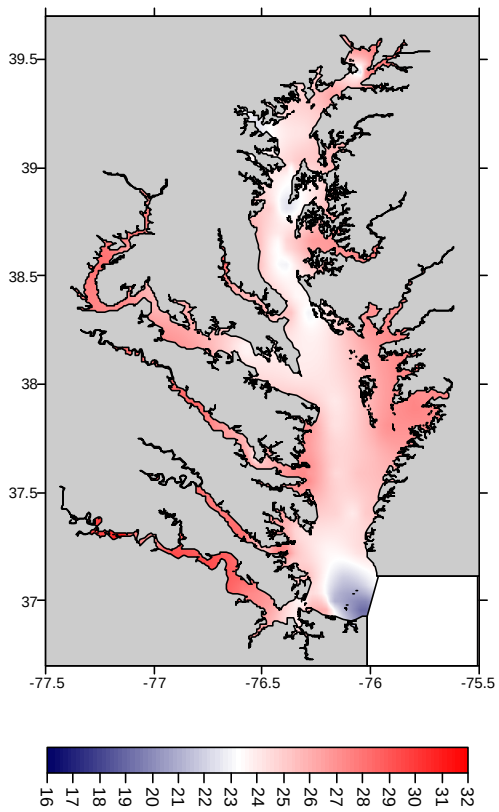
Figure III-6: Instantaneous potential production rate in Chesapeake Bay. Average conditions in October 1990-1999. **a)** Atlantic sturgeon; **b)** shortnose sturgeon.



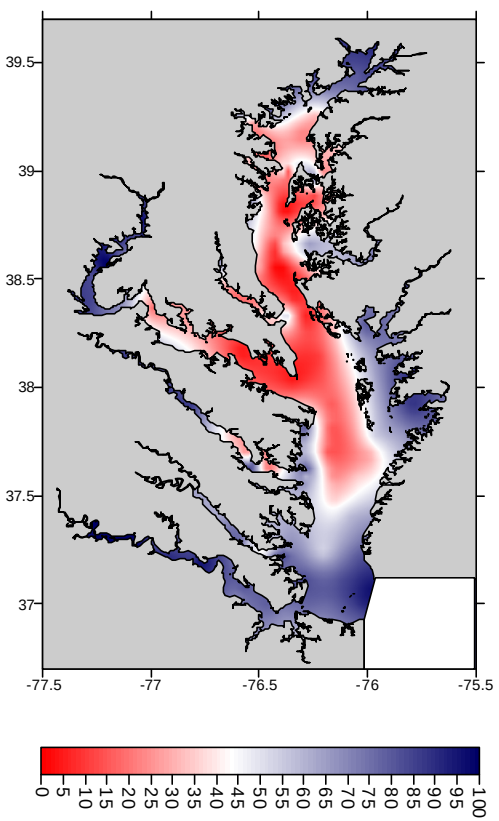
a) Atlantic sturgeon

b) Shortnose sturgeon

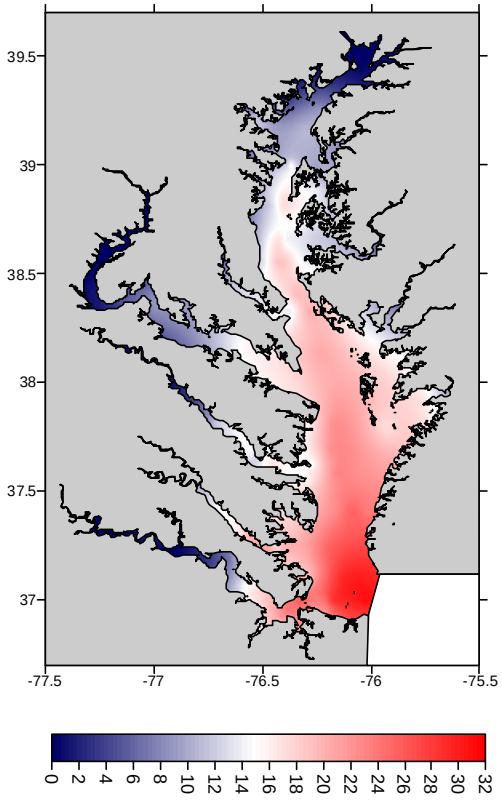
Figure III-7: Average water quality conditions in the Chesapeake Bay in July 1990-1999. **a)** Temperature (^{O}C); **b)** dissolved oxygen (DO_{sat}); **c)** salinity (ppt).



a) Temperature



b) Dissolved oxygen



c) salinity

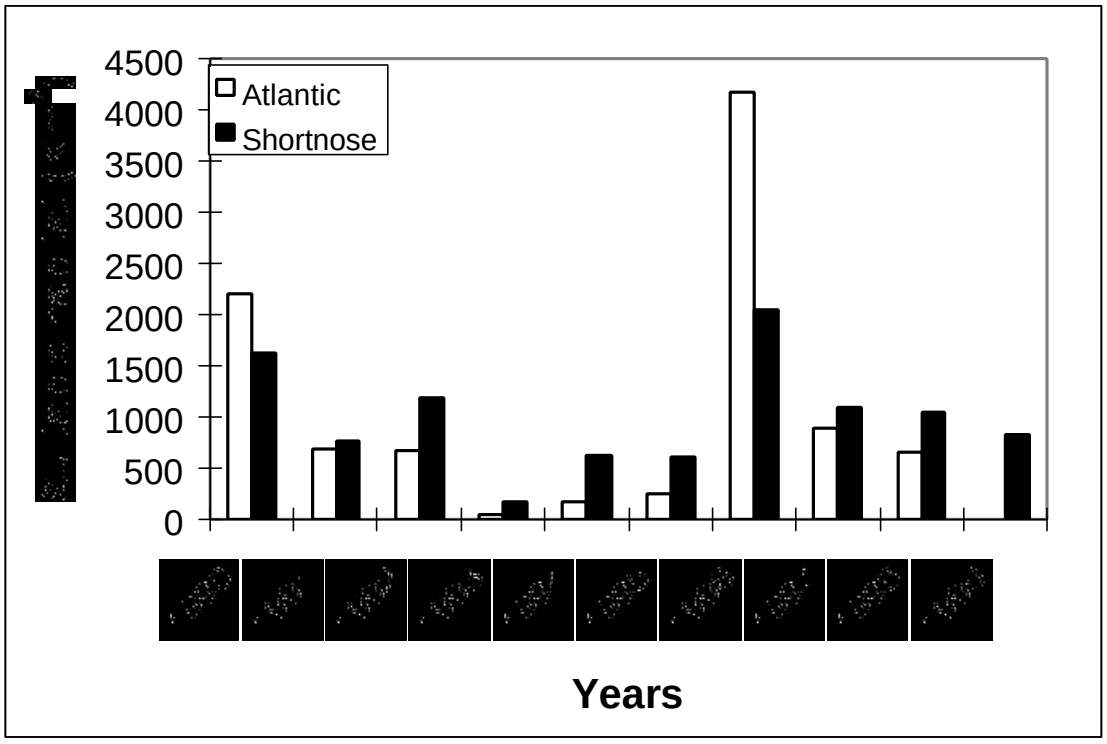
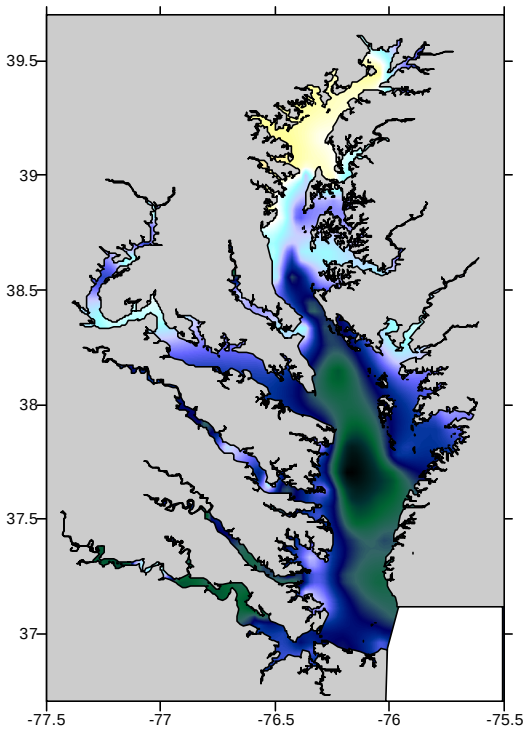
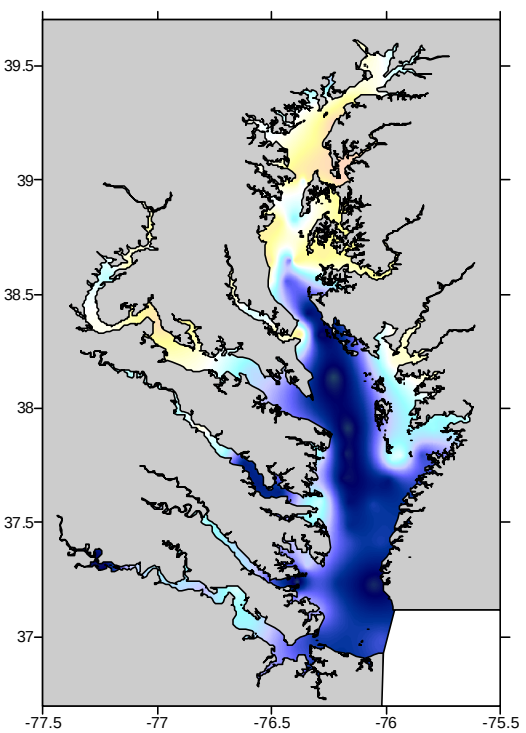


Figure III-8: Estimated suitable summer habitat for Atlantic and shortnose sturgeons in the Chesapeake Bay 1990-1999.

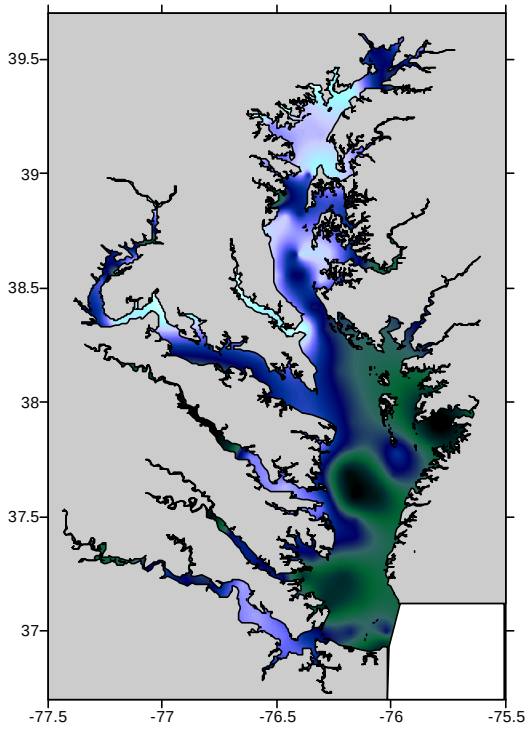
Figure III-9: Interannual variation in summer habitat quality (instantaneous potential production) for juvenile Atlantic sturgeon. **a)** average conditions July 1990-1999; **b)** July 1996; **c)** July 1999.



a) Average year (1990-1999)

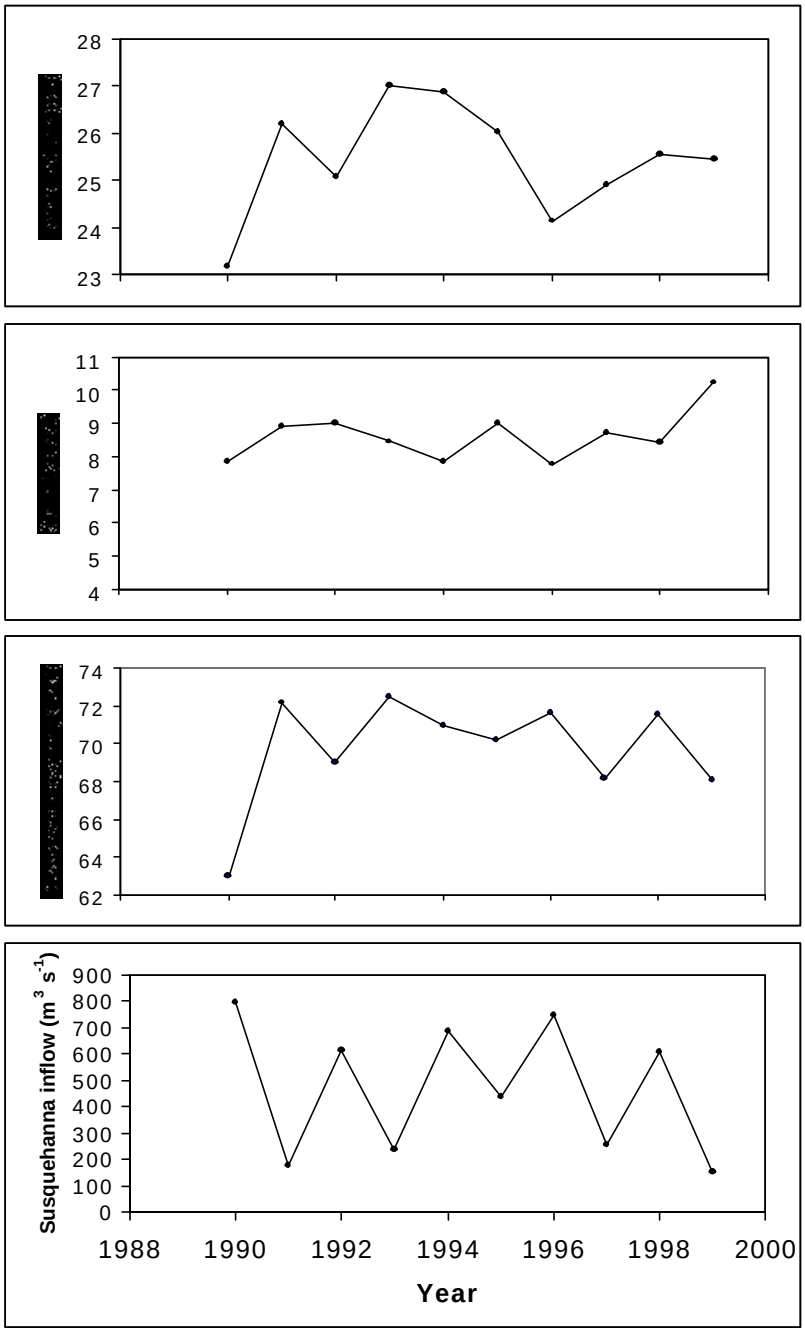


b) 1996



c) 1999

Figure III-10: Interannual variation in monthly averaged water quality conditions for July between 1990 and 1999. **a)** Temperature (^{O}C); **b)** dissolved oxygen (DO_{sat}); **c)** salinity (ppt).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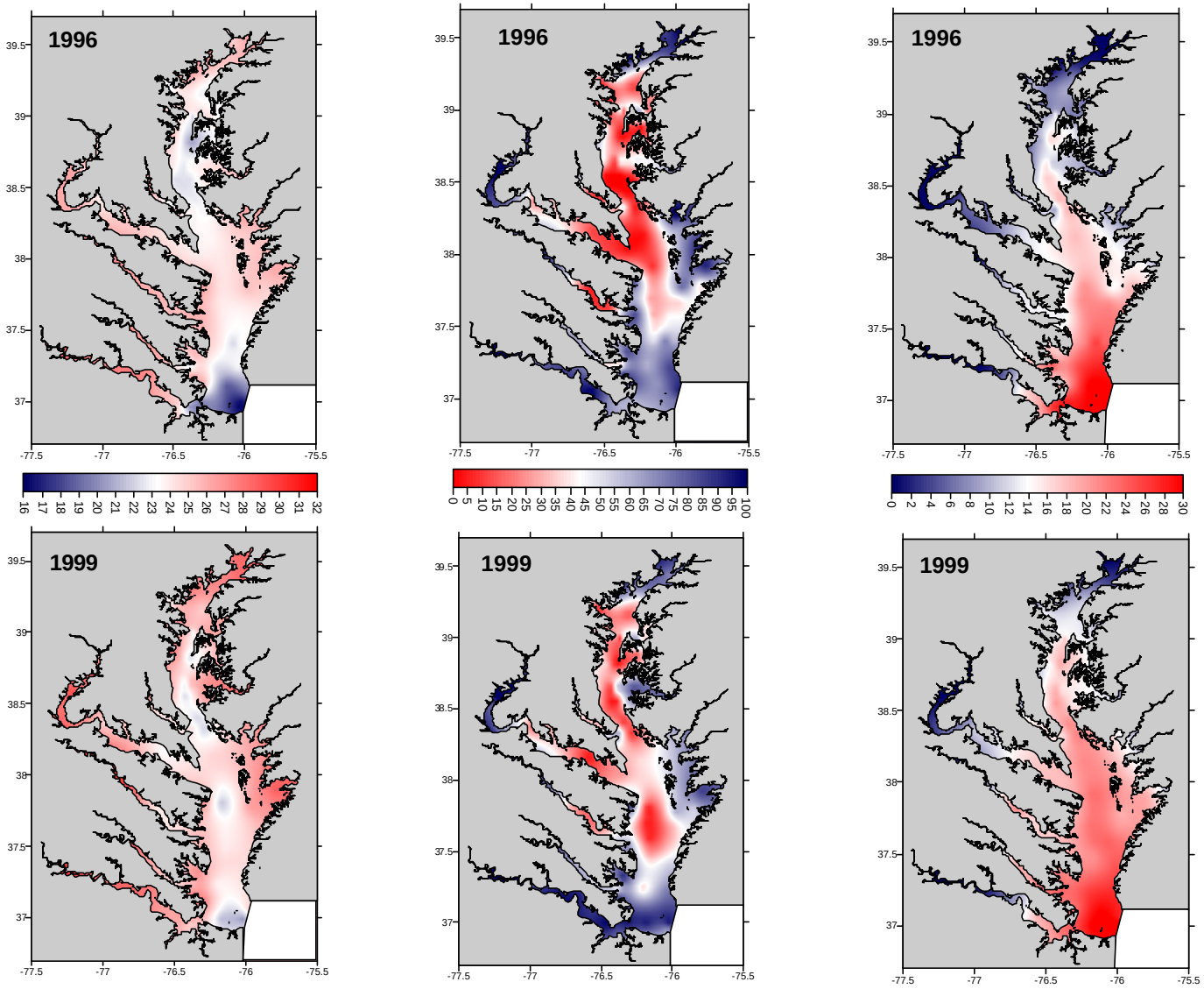
64
62
900
800
700
600
500
400
300
200
100
0
Susquehanna inflow (m3 s-1)
1988
1990
1992
1994
1996
1998
2000
Year

Figure III-11: Average water quality conditions in the Chesapeake Bay during July 1996 (upper pannel) and July 1999 (lower pannel).



a) Temperature **b) Dissolved oxygen** **c) salinity**

CONCLUSIONS

I evaluated and modeled the physiological responses of juvenile shortnose and Atlantic sturgeons to temperature, dissolved oxygen and salinity, within the ranges observed in the Chesapeake Bay during the last decade. These responses were incorporated into a multivariable habitat-based bioenergetic model and used to predict recent trends (1990-1999) in suitability of nursery habitats for juvenile sturgeons in the Chesapeake Bay. Investigation results can be summarized in the following conclusions:

1. All three factors significantly affect physiological energetics, growth and survival in juvenile Atlantic and shortnose sturgeons. Relative magnitude of observed responses indicated the highest effects were attributable to temperature and the lowest to salinity.

2. Overall responses to environmental factors were similar between juvenile Atlantic and shortnose sturgeons. Ecologically relevant differences were, however, identified at the highest tested temperature (28^{o}C) and salinity (29 ppt). Still, high potential overlap between juvenile sturgeons in the wild was evident, while mesocosm experiments suggested interference competition for limited food would favor juvenile shortnose sturgeon.

3. Ontogenetic changes in growth and metabolic responses due to size were evident in my results but not fully investigated in this dissertation. Bioenergetic models developed for young of the year Atlantic sturgeons (6 to 70-g) could be cautiously extrapolated to yearlings (100-250 g), but would need further investigation and re-parameterization if applied to older and larger sturgeons.

4. Behavioral responses to environmental factors were consistent with expectation from physiological energetics and survival results. Both species tended to identify and select optimal conditions. Differences in temperature and salinity preferences between species also tended to match expectations from energetics and life cycles in the wild.

5. Enormous inter-annual fluctuations in suitable summer habitat for juvenile sturgeons were estimated during the last 10-yr in the Chesapeake Bay. Persistent hypoxia in deeper areas consistently precluded access to thermal refuges, magnifying the effects of climatic oscillations. Thus, extremely dry years (e.g. 1999) may result in almost no suitable habitat for juvenile sturgeons, especially Atlantic sturgeon.

Further investigation would be required to expand available knowledge about functional responses, especially under extreme conditions, and to reduce uncertainty in bioenergetics parameters. Ontogenetic changes in metabolic responses are another area where further research is needed to facilitate the integration of all estuarine-dependent year classes into a common analytical framework.

While results were consistent with conceptual frameworks used for modeling responses, formal hypothesis testing would be required to demonstrate actual cause-effect associations. The formal mathematical expressions developed here were based upon Fry's classification scheme and necessarily incorporated assumptions for which little empirical verification have occurred. As understanding of basic Acipenseriform physiology improves, I expect that these expressions will need to be revisited. In addition, the basic design of my study dispersed degrees of freedom among many treatment levels. More intensive study of a reduced set of treatments should significantly reduce parameter uncertainty and possibly improve precision in future bioenergetic models.

This investigation indicates that sturgeon restoration efforts in the Chesapeake Bay should give special attention to nursery habitat suitability. Protection of current thermal refuges and alleviation of hypoxia to expand suitable areas are evident needs if survival in early life stages is to be enhanced. If sturgeons are an especially sensitive species

to habitat degradation, then these results probably represent a useful approximation to better understand habitat quality needs for many other estuarine or anadromous species in the Bay. Thus, protecting or improving sturgeon-habitat would benefit the overall health of the whole ecosystem.

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