ABSTRACT

Title of Dissertation:	ATLANTIC STURGEON ACIPENSER OXYRINCHUS GROWTH RESPONSES TO DUAL SEASONAL SPAWNING, LATITUDINAL THERMAL REGIMES, AND CHESAPEAKE BAY ENVIRONMENTAL STRESSORS
	Erin Lorraine Markin, Doctor of Philosophy, 2017
Dissertation directed by:	Professor, Dr. David Secor, University of Maryland Center for Environmental Science Chesapeake Biological Laboratory

Recovery of Atlantic sturgeon, *Acipenser oxyrinchus*, will depend on actions that improve assessment of habitat conditions, particularly during the first year of life. Here, evaluation of stressors included temperature, salinity, and nitrite effects on survival of age-0 Atlantic sturgeon. Performance of a principal Atlantic sturgeon bioenergetics models was evaluated first by describing trends in habitat suitability during a recent 20+ year span in the Chesapeake Bay, and then by testing model predictions against incidence data for an abbreviated period which included 1562 observations of Atlantic sturgeon. In common garden experiments, thermal performance of juveniles from two populations of Atlantic sturgeon was evaluated. Finally, a growing-degree-day (GDD) model was developed to evaluate the

phenology of spawning and early growth across latitudinally distributed Atlantic sturgeon populations, some of which exhibit dual seasonal spawning. Lethal levels of nitrite observed in the laboratory (24-hr LC50: 4.1 mg L^{-1} nitrite in 2 mg L^{-1} chloride) do not occur in the Chesapeake Bay, indicating that early juvenile Atlantic sturgeon are presently not at risk for nitrite toxicity. Application of bioenergetics models to long-term Chesapeake Bay data predicted consistently higher juvenile growth in spring and fall seasons. During summer months, Atlantic sturgeon were frequently captured in regions that the bioenergetics model predicted nil or negative growth, indicating that older Atlantic sturgeon may not be as sensitive to these environmental parameters than younger juveniles, which have been the focus of past research and bioenergetics models. Common garden experiments performed on Saint Lawrence and Altamaha strain Atlantic sturgeon juveniles showed no population effect on growth performance among thermal regions, allowing development of a predictive equation of juvenile length from GDDs. Predicted sizes of age 1.0 juveniles were within the size ranges reported in literature. Thus, the GDD model holds promise in future assessments of juvenile presence, recruitment, and recovery. Findings suggest that Chesapeake Bay Atlantic sturgeon are more resilient than previously believed. The Chesapeake Bay offers an environment conducive to recovery and where dual-spawning may be a successful strategy, thus improving resilience to climate change.

ATLANTIC STURGEON ACIPENSER OXRINCHUS GROWTH RESPONSES
TO DUAL SEASONAL SPAWNING, LATITUDINAL THERMAL REGIMES,
AND CHESAPEAKE BAY ENVIRONMENTAL STRESSORS

by

Erin Lorraine Markin

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2017

Advisory Committee:
  Dr. David H. Secor, Chair
  Dr. Jeffrey Cornwell
  Dr. Andrew Lazur
  Dr. Allen Place
  Dr. Curry Woods

Dedication

To my family, Chris and Isabel. Thank you for your support through what seemed like a never-ending process.

Acknowledgements

I began this journey nine long years ago when I thought to myself, "why not?". I had been a Faculty Research Assistant at Horn Point Laboratory (HPL) for five years at this point, after having finished my Master's degree at University of Arizona in 2003, and decided it would be good, professionally, to get a Ph.D. Without the support of family and friends, this dissertation would never have been possible.

I would like to express my gratitude to my husband, Chris, and my daughter, Isabel, for supporting me through this process that included late nights, weekends, and little time to take vacations. I would like to thank my parents, Dave and Valerie, and my sister, Jen, for their support as well. I would like to express my appreciation to my HPL family. Ralph Kimes and Gordy Dawson were there for me professionally and personally. Their jobs at HPL were to make sure the Aquaculture and Restoration Ecology Laboratory (AREL) at HPL ran smoothly and systems continued to work. However, they would go above and beyond to assist me in setting up for experiments, making sure I had the "flavor" of water I needed, and being on-call when systems would inevitably fail at 3 am. Their friendship extended beyond our professional lives and for that, I am grateful. I am also grateful for the rest of HPL maintenance department, Blaise Brown, Eric Doty, James "Bear" Kampmeyer, Chris Farnell, Richie Long, and Jeff Miley who helped me keep the other part of my work alive – shad. Without their willingness to help maintain numerous ponds for shad rearing, I would not have secured the funding I did for my duration at HPL.

Finally, I would like to express my thanks for the rest of my HPL family for their guidance and friendship.

In addition to my HPL family, I would like to express my appreciation to my DNR family: Chuck Stence, Brian Richardson, Matt Baldwin, Mark Bowermaster, Mark Matsche, and Kevin Rosemary. They were always willing to lend a hand whenever needed and provide some much-needed distractions by allowing me to tag along during their fieldwork. Not only was the funding I received from them much appreciated, it was their willingness to share their expertise and provide me with guidance and opportunities that rounded-out my professional experience while at HPL.

I would like to thank my committee for their guidance and support of these nine years. Without your knowledge, expertise, and guidance, I would not have been able to be where I am today. Thank you, Dave, Andy, Jeff, Curry, and Al.

Table of Contents

List of Tables

Chapter 2

Table 1: Water quality conditions (± standard deviation) experienced by Atlantic sturgeon juveniles during 24-hour study.

Table 2: ANCOVA results of chloride effect on juvenile mortality while controlling for nitrite.

Chapter 4

Table 1: Sub-adult and adult Atlantic sturgeon captures in the Chesapeake Bay (north-south orientation).

Table 2: Monthly occurrence of sub-adult and adult Atlantic sturgeon in the Mid-Bay, Lower Eastern Shore, and James River during years 1997, 1998, 2005, 2006 combined.

Table 3: Ranking of potential growth average (±SE) of juvenile Atlantic sturgeon growth by year.

Table 4: Juvenile Atlantic sturgeon growth in individual tributaries in the winter.

Table 5: Juvenile Atlantic sturgeon growth in individual tributaries in the spring.

Table 6: Juvenile Atlantic sturgeon growth in individual tributaries in the summer.

Table 7: Juvenile Atlantic sturgeon growth in individual tributaries in the fall.

Table 8: Wilcoxon-signed rank results of greater incidence than expected for sub-adult and adult Atlantic sturgeon for conditions of higher growth, higher dissolved oxygen, lower temperature and higher salinity.

Chapter 5

List of Figures

Figure 5: Mean (± std dev) juvenile Atlantic sturgeon lactate concentrations (µmol per g fish wt) after acclimation to three temperatures (13°C, 18°C, 26°) and four salinities (0, 1, 11, 21). Different letters denote significant differences (ANOVA, $p<0.05$).

Chapter 4

Chapter 5

Figure 1. Locations of National Estuarine Research Reserve Systems used in comparison of growth-degree-days along a latitudinal gradient. 1) Well, ME, 2) Great Bay, NH, 3) Hudson River, NY, 4) Chesapeake Bay, MD/VA, 5) North Carolina, 6) North Inlet-Winyah Bay, SC, and 7) Ashepoo-Combahee-Edisto Basin, SC.

Figure 2. Comparisons of fish lengths (mm) among thermal regimes and between strains within thermal regimes. Different letters denote significant differences according to ANOVA, Tukey's honest significant difference. Error bars represent standard error.

Figure 3. Comparisons of fish weights (g) among thermal regimes and between strains within thermal regimes. Different letters denote significant differences according to ANOVA, Tukey's honest significant difference. Error bars represent standard error.

Figure 4. Length at experimental day (a) and GDD (b) for the Saint John's River thermal regime comparing Canada-strain and Altamaha-strain Atlantic sturgeon.

Figure 5. Length at experimental day (a) and GDD (b) for the Choptank River thermal regime comparing Canada-strain and Altamaha-strain Atlantic sturgeon.

Figure 6. Length at experimental day (a) and GDD (b) for the Edisto River thermal regime comparing Canada-strain and Altamaha-strain Atlantic sturgeon.

Figure 7. Regression of Atlantic sturgeon length on GDD for thermal regimes and strains combined using von Bertalanffy equation.

Figure 17. Temperature profile and growth of Atlantic sturgeon in the Edisto River thermal regime.

Chapter 1: Introduction

Atlantic sturgeon were of great cultural and economic importance in the late 1800s and early 1900s (Secor 2002). Industrial-scale fisheries, driven by the production and export of caviar, were established on many of the large tributaries along the east coast in New York, Delaware, Virginia, South Carolina, and Georgia (Secor 2002). By the early 1900s, the Atlantic sturgeon industry crashed; and failure of the species to recover later led to a coast-moratorium in the mid-1990s. In 2012, Atlantic sturgeon, *Acipenser oxyrinchus*, were listed as Endangered under the Endangered Species Act (77 FR 5914, 77 FR 5880) prompting federal and state programs of recovery.

Although historically overfished; pollution, eutrophied waters, and hypoxia are viewed as extant threats curtailing recovery of this species in the Chesapeake Bay. Atlantic sturgeon populations had been considered non self-sustaining in the Chesapeake Bay (Secor et al. 2000). However, a reproducing population was recently discovered in the James and York Rivers, Virginia (Musick 2005; Balazik et al. 2013) and sexually mature Atlantic sturgeon have been found in freshwater portions of other tributaries of the Chesapeake Bay (Kahn et al. 2014). Although substantial uncertainty exists in what limits recovery of Chesapeake Bay Atlantic sturgeon, stressors operating during the first year of life play a dominant role. In general, early life stages of fish (embryos, larvae, early juveniles) are more sensitive than adults to stressors such as water pollutants, and temperature (Bonga 1997) and salinity changes (Potts and Rudy 1972; McEnroe and Cech 1985; Kynard and Horgan

2002; Singer and Ballantyne 2004). Synergies in stressors are likely. For instance, nitrite, known to cause mortality in fish in aquaculture systems particularly in concert with lower salinity (chloride), is typically found in low concentrations (μM) in natural aquatic habitats (Eddy, 1994). However, in eutrophic systems like the Chesapeake Bay, industrial and sewage effluents can contain high levels of nitrite, which are then concentrated in bottom layers of the water column during seasonal stratification or released into surface waters (Eddy, 1994). Another example is the well- known synergy between hypoxia and thermal conditions (Breitburg et al. 1997, Coutant 1987).

Under the premise that Atlantic sturgeon were extirpated in the Chesapeake Bay, approximately 3,300 juvenile Atlantic sturgeon were released into the Nanticoke River in July 1996 to determine whether juveniles could survive and grow in the Chesapeake Bay (Secor et al. 2000). The relatively high recapture rate and growth rates of released fish suggested that Maryland's portion of the Chesapeake Bay may provide suitable nursery habitat for juvenile Atlantic sturgeon. However, the summer of 1996 corresponded to the highest volume of total suitable habitat, predicted over a 10-year period (Niklitschek and Secor 2005). Thus, the high growth observed from 1996 fish may have been an anomaly. High inter-annual variation in suitable habitats is predicted to occur in the Chesapeake Bay particularly during summer months (Niklitschek and Secor 2005; Schlenger et al. 2013). Past research has emphasized water quality limitations through rearing experiments on age-0 and age-1 juveniles and through the development of bioenergetics models (Niklitschek and Secor 2009a,b; Schlenger et al. 2013).

In temperate systems, cessation of growth and lethal temperatures during winter months are thought to drive a latitudinal countergradient in juvenile growth, where juveniles of higher latitude populations grow faster during their first growth season (Conover 1990). Winter mortality is thought to select for this growth variation, where smaller or lower conditioned individuals are predicted to experience higher mortality rates owing to thermal stress, starvation, predation, disease, winter hypoxia, and physical disturbance (e.g. ice flows) (Hurst 2007). Atlantic sturgeon span a wide geographical range, yet no research has been conducted to determine if there is a difference between strains in their genetic capacity for growth as evident in other fish species (Conover 1990). With recent evidence for Atlantic sturgeon spawning during two seasons (spring and fall) in some regions (Balazik et al. 2013; Balazik and Musick 2015), one would expect very different sizes at the onset of winter and different sizes at age 1.0 years. Growth-degree-day models, (Neuheimer 2007) have been used to predict length-at-day or length-at-date and can act as a common currency among species and environments to evaluate questions related to growth performance and growth phenology (seasonality of growth).

Length-at-date predictions are also important for assessment of juvenile presence and abundance in nursery systems. Assignment of juveniles to age-0 and age-1 based on length has been uncertain owing to incomplete knowledge of how first year growth occurs across the broad latitudinal range (15 degrees) in which the species occurs (Satilla River, Florida to St. Lawrence River, Canada). Dual seasonal spawning in some portions of the species range would also confound these assignments.

Following this Introduction, I address nitrite toxicity in early juvenile Atlantic sturgeon, in Chapter 2. The objective of this study was to determine the lethality (LC50) of Atlantic sturgeon juveniles exposed to nitrite in concert with varying chloride levels. Mortality responses by age-0 Atlantic sturgeon to elevated nitrite concentrations in combination with mitigating chloride concentrations were evaluated in 24-hr LC50 trials. Chloride concentrations tested represented concentrations found in tidal freshwater tributaries of the Chesapeake Bay. Juveniles (4.8±0.8g) were exposed, in a full factorial experiment, to eight nitrite concentrations, 0 mg L^{-1}, 2 mg L^{-1}, 4 mg L^{-1}, 8 mg L^{-1}, 17 mg L^{-1} 34 mg L^{-1}, 66 mg L^{-1} and 132 mg L^{-1} and three chloride levels, 2 mg L^{-1}, 15 mg L^{-1}, and 60 mg L^{-1}. I found early juvenile Atlantic sturgeon are presently not at risk for nitrite toxicity in Chesapeake Bay tributaries considering nitrite concentration in these areas (<0.6 mg L^{-1}) is less than the 24-hr LC50 determined by this study (4.1 mg L^{-1}, 2 mg L^{-1} chloride).

In Chapter 3, I conducted 30-day laboratory trials to determine the lethal, growth, and physiological responses of age-0 juvenile Atlantic sturgeon to a range of temperatures and salinities, which they would encounter in natural nursery systems. In a balanced block design, four salinity levels (0, 1, 11 and 21 psu; 3 replicates/treatment; 10 fish per replicate) were crossed with three temperature treatments (13°C, 18°C, 26°C) for a total of 36 trials. Each fish was individually measured for length and whole body lactate concentration. Mortality in the high temperature and high salinity treatments were significant greater than in the lower temperature and salinity treatments. Significant interactive effects also occurred between temperature and salinity on mortality. Specific growth rates did not differ

among or between treatments, perhaps due to the short experimental duration and ranged from 1.3% day^{-1} to 1.9% day^{-1}. Lactate concentrations were significantly affected by temperature and salinity. Lactate decreased with increasing temperature and salinity. Overall, it seems as though age-0 Atlantic sturgeon tolerate acclimation from 0 to 11 psu at 13°C and 18°C since no mortality was observed in these treatments. Changes to higher temperatures and salinities resulted in significant mortality and decreases in lactate concentrations. Increases in temperature and salinity intrusion as predicted to occur due to climate change (Najjar 2010) may curtail habitat available and/or result in sub-lethal effects of age-0 Atlantic sturgeon.

In Chapter 4, I tested predictions of Chesapeake Bay Atlantic sturgeon habitat suitability obtained through a bioenergetics model against incidence data for the period 1990-2013. Application of bioenergetics models to long term Chesapeake Bay data predicted consistently higher juvenile (age-1) growth in spring and fall seasons and in Eastern Shore and Virginia segments of the Lower Chesapeake Bay. There were no long-term trends in juvenile habitat quality observed over the model period (1990-2013), but juvenile growth was inversely correlated with the Chesapeake Bay's summertime hypoxic volume. During summer months, juveniles, sub-adult, and adult Atlantic sturgeon (<500-1500 cm TL) were frequently captured in regions that the bioenergetics model predicted nil or negative growth (i.e., <40% dissolved oxygen saturation and > 27°C); sub-adult and adult Atlantic sturgeon may not be as sensitive to these environmental parameters than juveniles (< 500 mm) responses, which have been the focus of past research and bioenergetics models. Results of this study indicate that sub-adult and adult Atlantic sturgeon may not be as sensitive to

summertime conditions of high temperature and low dissolved oxygen as suggested

by past research and bioenergetics models. However, the duration spent by sub-adult

and adult Atlantic sturgeon in these sub-optimal habitats warrant further investigation

to fully understand the impact dissolved oxygen and temperature may impact

distribution and habitat utilization in the Chesapeake Bay.

In Chapter 5, I investigated latitudinal countergradient variation in growth

between populations of Atlantic sturgeon. I compared growth of Canada- and

Altamaha (Georgia, US) strain Atlantic sturgeon juveniles (age-0) in a common

garden experiment in which they were exposed to three thermal regimes, which were

representative of the species latitudinal range. Results indicated no effect of strain on

growth performance; Atlantic sturgeon length and weight were significantly

influenced by thermal regime treatment independent of strain. To evaluate possible

confounding influences of dual spawning on juvenile growth and size predictions, I

applied a growth-degree-day (GDD) model, using water temperature data from seven

NOAA National Estuarine Research Reserve System (NERRS) sites, over the

latitudinal range of Atlantic sturgeon. The annual accumulation of GDDs varied

significantly over a latitudinal gradient. The laboratory experiment supported a

general species response to thermal conditions during the first year of life, and

allowed a predictive equation of juvenile length from GDDs. Predicted sizes of age

1.0 juveniles were smaller north of the Chesapeake Bay than south of the Delaware

Bay and reflected differences in sub- and supra-optimal temperatures across the

species range. The number of days of surpra-optimal temperatures accumulated

resulted in annual bi-modal GDD distribution south of the Chesapeake Bay. The

GDD model may support predictions of growth performance related to future climate

change scenarios and thereby forecast climate impacts to Atlantic sturgeon

recruitment and recovery throughout the species range.

References

Balazik, M., G.C. Garman, J.P. Van Eenennaam, J. Mohler, and L.C. Woods III. 2013. Empirical evidence of fall spawning by Atlantic sturgeon in the James River, Virginia. Transactions of the American Fisheries Society 141(6): 1465-1471.

Balazik, M.T. and J.A. Musick. 2015. Dual annual spawning races in Atlantic sturgeon. PloS ONE 10(5): 1-16.

Bonga, S.E.W. 1997. The stress response of fish. Physiological Reviews 77(3): 591-625.

Breitburg, D.L., T. Loher, C.A. Pacy, and A. Gerstein. 1997. Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. Ecological Monographs 67(4): 489-507.

Conover, D. O. 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. Transactions of the American Fisheries Society 119(3): 416-430.

Coutant. C.C. 1987. Thermal preference: when does an asset become a liability? Environmental Biology of Fishes 18(3): 161-172.

Eddy, F. & Williams, E. (1994) Freshwater fish and nitrite. In: Water quality for freshwater fish (ed. by G. Howells), pp. 117–143. Gordon and Breach Science Publishers, Langhorne, PA.

Hager, C., J. Kahn, C. Watterson, J. Russo, and K. Hartman. 2014. Evidence of Atlantic Sturgeon Spawning in the York River System. Transactions of the American Fisheries Society 143(5): 1217-1219.

Hurst, T.P. and Conover, D.O. 2003. Seasonal and interannual variation in the allometry of energy allocation in juvenile striped bass. Ecology 84(12): 3360-3369.

Kahn, J.E., C. Hager, J.C. Watterson, J. Russo, K. Moore, and K. Hartman. 2014. Atlantic sturgeon annual spawning run estimate in the Pamunkey River, Virginia. Transactions of the American Fisheries Society 143(6): 1508-1514.

Kynard, B. and M. Horgan. 2002. Ontogenetic behavior and migration of Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus*, and shortnose sturgeon, *A. brevirostrum*, with notes on social behavior. Environmental Biology of Fishes 63: 137-150.

McEnroe, M. and J.J. Cech, Jr. 1985. Osmoregulation in juvenile and adult white sturgeon, *Acipenser transmontanus*. Environmental Biology of Fishes 14(1): 23-30.

Musick, J.A. 2005. Essential Fish Habitat of Atlantic Sturgeon *Acipenser oxyrinchus* in the Southern Chesapeake Bay. Final Report to NOAA/NMFS NA03NMF4050200 (AFC) 37.

Najjar, R.G., C.R. Pyke, M.B. Adams, D. Breitburg, C. Hershner, M.Kemp, R. Howarth, M.F. Mulholland, M. Paolisso, D. Secor, K. Sellner, D. Wardtop, and R. Wood. 2010. Potential climate-change impacts on the Chesapeake Bay. Estuarine, Coastal and Shelf Science 86: 1-20.

Neuheimer, A.B. 2007. Growth in fishes: size-at-age, temperature and food. Ph.D. Thesis, Department of Oceanography, Dalhousie University, Halifax, Canada.

Niklitschek, E. and D.H. Secor. 2005. Modeling spatial and temporal variation of suitable nursery habitats for Atlantic sturgeon in the Chesapeake Bay. Estuaries and Coastal Shelf Science 64: 135-148.

Niklitschek EJ, Secor DH (2009a) Dissolved oxygen, temperature and salinity effects on the ecophysiology and survival of juvenile Atlantic sturgeon in estuarine waters: I. Laboratory results. Journal of Experimental Marine Biology and Ecology 381(Suppl): S150−S160.

Niklitschek EJ, Secor DH (2009b) Dissolved oxygen, temperature and salinity effects on the ecophysiology and survival of juvenile Atlantic sturgeon in estuarine waters: II. Model development and testing. Journal of Experimental Marine Biology and Ecology 381(Suppl): S161−S172.

Potts, W.T.W., and P.P. Rudy. 1972. Aspects of osmotic and ionic regulation in the sturgeon. Journal of Experimental Biology 56: 701-715.

Schlenger, A.J., E.W. North, Z. Schlag, Y. Li, D.H. Secor, K.A. Smith, E.J. Niklitschek. 2013. Modeling the influence of hypoxia on the potential habitat of Atlantic sturgeon *Acipenser oxyrinchus*: a comparison of two methods. Marine Ecology Progress Series 483: 257-272.

Secor. D.H. 2002. Atlantic sturgeon fisheries and stock abundances during the late nineteenth century. American Fisheries Society Symposium 28: 89-98.

Secor, D.H., E. Niklitschek, J.T. Stevenson and T.E. Gunderson, S. Minkkinen, B Richardson, and B. Florence, M. Mangold and J Skjeveland, A. Henderson-Arzapalo.

2000. Dispersal and growth of yearling Atlantic sturgeon, Acipenser oxyrinchus, released into Chesapeake Bay. Fisheries Bulletin 98:800-810.

Singer, T.D. and J.S. Ballantyne. 2004. Sturgeon and Paddlefish Metabolism. Pages 167-194 *in* G.T.O. LeBreton, F.W.H. Beamish, R.S. McKinley, editors. Sturgeons and Paddlefish of North America. Kluwer Academic Publishers, Netherlands.

Smith, T.I.J. 1985. The fishery, biology, and management of Atlantic sturgeon, *Acipenser oxyrhynchus* in North America. Environmental Biology of Fishes 14(1): 61-72.

Smith, J.A., H.J. Flowers, and J.E. Hightower. 2015. Fall spawning of Atlantic sturgeon in the Roanoke River, North Carolina. Transactions of the American Fisheries Society 144: 48-54.

Chapter 2: Role of chloride mitigation in nitrite tolerance of age-0 Atlantic sturgeon *Acipenser oxyrinchus*

Abstract

Atlantic sturgeon (*Acipenser oxyrinchus*) spend the first several months of their early life in tidal freshwater where natural chloride levels are typically low and toxic levels of nitrite can accumulate due to pollution or natural processes. Toxic levels of nitrite can also occur in sturgeon aquaculture owing to high fish densities. Toxicity responses by age-0 Atlantic sturgeon to nitrite were tested in 24-hr LC50 exposures of nitrite in combination with mitigating chloride concentrations, which emulated ambient levels in tidal freshwater estuarine habitats. Atlantic sturgeon (4.8±0.77g; mean±S.D) were exposed to eight nitrite concentrations, 0 mg/L, 2 mg/L, 4 mg/L, 8 mg/L, 17 mg/L 34 mg/L, 66 mg/L and 132 mg/L with mitigating chloride concentrations of 2 mg/L, 15 mg/L, and 60 mg/L. Results indicated an increase in nitrite tolerance from 4.1 to 21.6 mg/L occurred with increasing chloride concentrations from 2 to 60 mg/L.

Introduction

Understanding the physiological tolerances of sturgeon to degraded habitats and water quality are important for recovery and artificial propagation of Atlantic sturgeon (*Acipenser oxyrinchus),* which is depleted throughout its range (ASSRT 2007). Presently the Chesapeake Bay designated population segment (DPS: a metapopulation unit) of Atlantic sturgeon is federally protected as *Endangered* under the Endangered Species Act (ESA). Although historically overfished, pollution,

eutrophied waters, and hypoxia are viewed as extant threats curtailing recovery of this species in the Chesapeake Bay.

Nitrite is an intermediate compound formed in natural nitrogen cycling processes (nitrification and denitrification) and is typically found in low concentrations (µM) in natural aquatic habitats (Eddy, 1994). However, in eutrophic systems like the Chesapeake Bay, industrial and sewage effluents can contain high levels of nitrite, which are then concentrated in bottom layers of the water column during seasonal stratification or released into surface waters (Eddy, 1994). In addition, nitrite may also be problematic in aquaculture and other facilities where fish are stocked at artificially high densities, particularly in closed systems where water is recirculated (Timmons, 2002). Nitrite toxicity in intensive aquaculture systems is relevant to sturgeon research and recovery programs (Mims et al. 2002).

Toxicity of nitrite in age-0 Atlantic sturgeon is not known. The limited data available indicates that sturgeon and other ancestral actinopterygii are sensitive to elevated nitrite (Boudreaux, 2007; Huertas, 2002; Fontenot, 1998), which can result in mortality and sublethal effects. Atlantic sturgeon spend the first couple months in tidal freshwater where natural chloride levels are typically low and nitrite may accumulate due to pollution or natural processes. Climate change (increased precipitation and runoff), coupled with eutrophication will result in increased nitrite loads in Chesapeake Bay tributaries (Najjar et al. 2010), exposure to which could lead to physiological stress or mortality of young sturgeons. In fishes, nitrite binds with hemoglobin to form methemoglobin, which has restricted affinity to oxygen, thereby affecting fish respiration, elevating stress chemistry and potentially leading to

11

suffocation (Lewis and Morris 1986; Huertas et al. 2002; Kroupova et al. 2008; Kroupova et al. 2010, Matsche et al. 2012).

The degree of nitrite sensitivity and toxicity in sturgeons and other fishes is related to the chloride concentration of water as chloride is known to compete with nitrite for absorption through the gills (Lewis and Morris 1986; Fontenot et al. 1998). In tidal freshwater tributaries of the Chesapeake Bay, chloride concentrations range from 5-250 mg/L chloride (Chesapeake Bay Water Quality Program, 2001-2005). Shortnose sturgeon (*A. brevirostrum*) juveniles (9.2 ± 3.4g; mean $\pm$ SD) have been shown to tolerate nitrite concentration, 11.3 mg/L during 96-hour LC 50 trials at <1.0 mg/L chloride (Fontenot et al., 1998). At high chloride concentration (130.5 mg/L), the median-lethal concentration of nitrite was ~10-fold higher (130 mg/L) for Siberian sturgeon (*A. baerii*) (yearlings; 172.0 ± 18 g; mean$\pm$S.D.) in a 72-hour experiment (Huertas et al. 2002). Still, this nitrite exposure resulted in extracellular hyperkalemia (high potassium), elevated chloride, and decreased sodium levels (Huertas et al. 2002).

The objective of this study was to determine the LC50 for Atlantic sturgeon juveniles when exposed to nitrite. Mortality responses by age-0 Atlantic sturgeon to elevated nitrite concentrations in combination with mitigating chloride concentrations were evaluated in 24-hr LC50 trials. Chloride concentrations tested represented concentrations found in tidal freshwater tributaries of the Chesapeake Bay.

Materials and Methods

Atlantic sturgeon fertilized eggs (Acadian Sturgeon and Caviar, Inc., New Brunswick, Canada) were hatched and larvae and juveniles reared in well water (17.8°C, 2 mg L^{-1} chloride, 0 mg L^{-1} nitrite, 8.4 pH) until 60-days old. At this age, juveniles (4.8±0.8g) were exposed, in a full factorial experiment, to eight nitrite concentrations, 0 mg L^{-1}, 2 mg L^{-1}, 4 mg L^{-1}, 8 mg L^{-1}, 17 mg L^{-1} 34 mg L^{-1}, 66 mg L^{-1} and 132 mg L^{-1} (sodium nitrite, EMD Chemicals, Gibbstown, NJ, USA) and three chloride levels, 2 mg L^{-1}, 15 mg L^{-1}, and 60 mg L^{-1} (sodium chloride, J.T. Baker, Phillipsburg, NJ, USA). Each nitrite and chloride combination was tested with 10 fish in triplicate for a total of 72 trials each in 8-L containers. Sodium nitrite was mixed in 72-L reservoir tanks with well water to obtain concentrations. Treatment containers received 6L from the nitrite reservoirs. Measured amounts of sodium chloride were added to each tank to obtain target chloride concentrations. Complete volume water exchanges were performed daily, refilling from the nitrite reservoirs and chloride as needed and temperatures were maintained via water bath (Table 1). Dissolved oxygen remained on average >7.8 mg L-1, temperatures were between 18.3-19.3°C, and pH averaged 8.52 (±0.13) for the first 24-hours of the study (Table 1). There was no significant difference in pH levels between nitrite concentrations (p>0.05). Sturgeon mortalities were recorded at 8 and 24 hours (Tables 2-4). Fish were not fed during the study following OECD (Organization for Economic Co-operation and Development) guidelines (1992). A trimmed Spearman-Karber (Hamilton et al. 1977) (10% trim) method was used to determine the LC50 occurring for each chloride treatment at 24-hrs post-exposure An analysis of covariance with

13

binomial data was conducted to determine statistically significant difference between chloride concentrations on Atlantic sturgeon juvenile mortality controlling for nitrite concentrations (R Core Team 2014; Crawley 2007).

Results

Results indicated an increase in nitrite tolerance with increasing chloride concentrations (Fig. 1). For the 2 mg L^{-1} chloride treatment, the 24-hr LC50 was 4.1 mg L^{-1} nitrite (3.4-4.8, 95% confidence limits). The 24-hr LC50 for nitrite increased to 8.9 mg L^{-1} (7.4-10.7, 95% confidence limits) for the 15 mg L^{-1} chloride treatment and 21.60 mg L^{-1} nitrite (18.3 – 25.5, 95% confidence limits) for the 60 mg L^{-1} chloride treatment. There was a clear linear relationship between chloride concentrations and 24hr LC50 nitrite concentration (Fig.2). There was a significant effect ($p<0.05$) of chloride concentrations on juvenile mortality after controlling for nitrite concentrations. The higher the chloride concentration is in the water, the lower the mortality rates are since chloride buffers the detrimental effects of nitrite uptake by fish. The ANCOVA model for mortality, nitrite, and chloride has significant differences for intercepts (Table 2) which indicates mortality was reduced as chloride concentrations increased. These results are as expected since chloride, not nitrite, is preferentially diffused across fish gills which decreases the amount of nitrite entering the blood, hence reducing mortality. In addition to significant difference in intercepts, slopes were also significantly different between 2mg L^{-1} chloride and 60 mg L^{-1} chloride treatments (Table 2). A decrease in slope for the 60 mg L^{-1} chloride treatments results in a decrease in mortality as nitrite concentrations increase.

14

Overall, chloride concentrations influence mortality rates when Atlantic sturgeon are exposed to varying nitrite concentrations.

Discussion

We used mortality as a marker of nitrite toxicity in this study. Since no mortality was observed in the control treatments (0 mg L^{-1} nitrite with mitigating concentrations of 0, 15, 60 mg L^{-1} chloride), we can assume all mortality observed was due to nitrite toxicity. Atlantic sturgeon juvenile were less tolerant (4.1 mg L^{-1} at 2 mg L^{-1} Cl) to nitrite concentrations than other sturgeon species, albeit fish were smaller (4.8±0.8g) than those used in other studies. LC50 ranged from 11.3 mg L^{-1} (<1 mg L^{-1} Cl; 96-hr LC50) to 130 mg L^{-1} nitrite (130.5 mg L^{-1} Cl; 72-hr LC50) for shortnose sturgeon (9.2 ± 3.4g) and Siberian sturgeon (172.0±18 g), respectively (Fontenot et al., 1998, Huertas et al. 2002). However, Matsche et al. (2012) found that larger Atlantic sturgeon juveniles (544±0.13 g; mean±SD) were physiologically affected (hemolytic anaemia, ion imbalances) to nitrite at concentrations as low as 1 mg/L (5 mg/L Cl) which may show a reduced tolerance to nitrite as Atlantic sturgeon grow.

Nitrite toxicity in freshwater fish is well documented and is influenced by water quality (i.e. pH, temperature, oxygen concentration), rate of nitrite uptake which differs between species, and other factors such as length of exposure, fish size, and fish activity; inactive fish have lower oxygen demand (Kroupova, 2005; Lewis, 1986; Jensen, 2003). Influx of environmental nitrite in freshwater fish occurs predominantly through the active chloride uptake mechanism in the gills, and interspecific differences in chloride uptake rates may explain differences in nitrite

sensitivity among fish (Tomasso Jr, 2005). Also, nitrite and chloride competitively inhibit each other in uptake across the gills (Williams, 1986). Therefore nitrite toxicity in fish typically decreases with increasing environmental chloride concentrations (Hilmy, 1987; Fontenot, 1999; Yanbo, 2006; Atwood, 2001).

In tidal freshwater environments in the Chesapeake Bay, nitrite concentration range from 0 mg L^{-1} to 0.6 mg L^{-1} (Chesapeake Bay Program Water Quality Program (2010-2014)). These nitrite concentrations are significantly lower than the LC 50 concentration (4.1 mg L^{-1}) detected for the low chloride (2 mg L^{-1}) level observed in our experiment. Natural chloride levels in these tidal reaches are typically higher than 2 mg L^{-1} so we would not expect acute toxicity to occur in tidal freshwater tributaries of the Chesapeake Bay. However, Matsche et al. (2012) did note sublethal effects of 1 mg L^{-1} nitrite (5 mg L^{-1} chloride) for juvenile Atlantic sturgeon. The likelihood of these conditions occurring in the Chesapeake Bay tidal freshwater tributaries is slight but possible. Chloride concentrations in these areas can be as low as 5 mg L-1 and nitrite concentrations of 0.6 mg L-1 have been measured in these systems. Also, decreased nitrite tolerance with age/size has been reported (Lewis and Morris 1986; Kroupova et al. 2005) so in the tidal freshwater areas of tributaries, it may be the spawning adult Atlantic sturgeon that are more at risk to experience sub-lethal effects than juvenile Atlantic sturgeon. It is possible that nitrite concentrations in the Chesapeake Bay will increase owing to (1) the long-term prediction of increased precipitation and runoff associated with climate change (Najjar et al. 2010) and (2) increased industrial and sewage effluents (Eddy, 1994).

In aquaculture systems, nitrite concentrations can reach 50mg L^{-1} or more in recirculating systems, which depend on biological filters, or when imbalances occur in managing nitrogenous wastes (Kroupova et al. 2005). Chloride concentration in water is considered one of the most important factors influencing nitrite toxicity and is easily manipulated in recirculating aquaculture systems. As shown in our studies, and as practiced in intensive aquaculture, additions of sodium chloride or calcium chloride should ameliorate the effect of nitrite toxicity in sturgeon (Fontenot et al.1999; Matsche et al. 2012) and other fish species (Bowser et al. 1983; Himly et al. 1987; Aggergaard and Jensen 2001; Atwood et al. 2001).

In conclusion, early juvenile Atlantic sturgeon are presently not at risk for nitrite toxicity in Chesapeake Bay tributaries considering nitrite concentration in these areas (<0.6 mg L^{-1}) is less than the 24-hr LC50 determined by this study (4.1 mg L^{-1}, 2 mg L^{-1} chloride). However, spawning adult Atlantic sturgeon may be more at risk to experience sub-lethal effects of nitrite toxicity in the freshwater environments. If future restoration efforts include aquaculture to supplement the population, these results are important in order to understand the water criteria needed for rearing Atlantic sturgeon in recirculating systems.

References

ASSRT (Atlantic Sturgeon Status Review Team). 2007: Status review of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*). Report to NMFS/NOAA. 174 pp.

Atwood, H., Fontenot, Q., Tomasso, J. and Isely J. 2001: Toxicity of nitrite to Nile tilapia: Effect of fish size and environmental chloride. N Am J Aquacut. 63**,** 49-51.

Boudreaux, P., Ferrara A. and Fontenot Q. 2007: Chloride inhibition of nitrite uptake for non-teleost Actinopterygiian fishes. Comp Biochem Phys A. 147**,** 420-423.

Crawley, M.J. 2007: "Chapter 16: Proportion Data." *The R Book*. West Sussex: John Wiley and Sons. pp. 569-592.

Eddy, F. & Williams, E. (1994) Freshwater fish and nitrite. In: Water quality for freshwater fish (ed. by G. Howells), pp. 117–143. Gordon and Breach Science Publishers, Langhorne, PA.

Fontenot, Q. C., J. J. Isely and J.R. Tomasso. 1998: Acute toxicity of ammonia and nitrite to Shortnose sturgeon fingerlings. Prog Fish Cult. 60,315-318.

Fontenot, Q. C., J. J. Isely and J.R. Tomasso. 1999: Characterization and inhibition of nitrite uptake in shortnose sturgeon fingerlings. J Aquat Anim Health. 11**,**76-80.

Hamilton, M.A., R.C Russo, and R.V. Thurston. 1977: Trimmed Spearman-Karber method for estimating median lethal concentrations in toxicity bioassays. Environ Sci Technol. 11(7), 714-719.

Hilmy, A., El-Domiaty N., and Wershana K. 1987: Effect of sodium chloride and calcium chloride on nitrite induced methemoglobinemia in *Clarias lazera*. Water Air Soil Pol. 33**,** 57-63.

Huertas M, Gisbert E, Rodrıguez A, Cardona L, Williot P, Castello´-Orvay F. 2002: Acute exposure of Siberian sturgeon (*Acipenser baeri*, Brandt) yearlings to nitrite: median-lethal concentration (LC50) determination, haematological changes and nitrite accumulation in selected tissues. Aquat Toxicol. 57, 257-266.

Jensen, F. 2003: Nitrite disrupts multiple physiological functions in aquatic animals. Comp Biochem Phys A. 135**,** 9-24.

Kroupova, H., Machova, J., Piackova, V. 2005: Nitrite influence on fish: a review. Veterinarni Medicina-Praha. 50**,** 461.

Kroupova H, Machova J, Piackova V, Blahova J, Dobsikova R, Novotny L, Svobodova Z. 2008: Effects of subchronic nitrite exposure on rainbow trout (*Oncorhynchus mykiss*). Ecotox Environ Safe. 71, 813-820.

Kroupova, H., M. Prokes, S. Macova, M. Penaz, V. Barus, L. Novotny and J. Machova. 2010: First International Workshop on Aquatic Toxicology and Biomonitoring: Effect of nitrite on the early-life stages of common carp (*Cyprinus carpio* L.). Environ Toxicol Chem. 29(3), 535–540.

Lewis W, Morris D. 1986: Toxicity of nitrite to fish: a review. T Am Fish Soc. 115, 183-195.

Matsche, M.A., E. Markin, E. Donaldson, A. Hengst and A. Lazur. 2012: Effect of chloride on nitrite-induced methaemoglobinemia in Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus* (Mitchill). J Fish Dis. 35, 873–885.

Mims, S.D., Lazur, A., Shelton, W.L., Gomelsky, B., and Chapman, F. 2002: Species Profile: Production of Sturgeon. Southern Regional Aquaculture Center. Publication no. 7200.

Najjar, R.G., C.R. Pyke, M.B. Adams, D. Breitburg, C. Hershner, M. Kemp, R. Howarth, M.R. Mulholland, M. Paolisso, D. Secor, D. Sellner, D. Wardrop, and R. Wood. 2010: Potential climate-change impacts on the Chesapeake Bay. Estuar Coast Shelf S. 86, 1-20.

NOAA. 2010: Endangered and Threatened Wildlife and Plants; Proposed Listings for Two Distinct Population Segments of Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the Southeast. Federal Register 75 (193): 61904-61929.

OECD. 1992: *Test No. 203: Fish, Acute Toxicity Test*, OECD Guidelines for the Testing of Chemicals, Section 2, OECD Publishing, Paris. DOI: http://dx.doi.org/10.1787/9789264069961-en

R Core Team. 2014: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Timmons, M., Ebeling J., Wheaton, F., Summerfelt, S. and Vinci, B. 2002: Recirculating aquaculture systems, Cayuga Aqua Ventures, Ithica, NY.

Tomasso Jr, J.R. & Grosell, M. 2005: Physiological basis for large differences in resistance to nitrite among freshwater and freshwater-acclimated euryhaline fishes. Environ. Sci. Technol, 39, 98-102.

Williams, E. & Eddy, F. 1986: Chloride uptake in freshwater teleosts and its relationship to nitrite uptake and toxicity. J Comp Physiol B. 156, 867-872.

Yanbo, W., Wenju, Z., Weifen, L. and Zirong, X. 2006: Acute toxicity of nitrite on tilapia (*Oreochromis niloticus*) at different external chloride concentrations. Fish Physiol Biochem. 32**,** 49-54.

Tables

Table 1
Water quality conditions (± standard deviation) experienced by
Atlantic sturgeon juveniles during 24-hour study

Treatment				
Chloride	Nitrite	DO (mg/L)	Temp (°C)	pH
2	0	8.3±0.2	18.9±0.1	8.28
2	2	8.4±0.1	18.8±0.2	8.30
2	4	8.3±0.4	18.8±0.3	8.24
2	8	8.6±0.2	18.8±0.3	8.24
2	17	8.5±0.1	19.3±0.5	8.50
2	34	8.5±0.1	19.3±0.5	8.44
2	64	8.3±0.3	18.8±0.0	8.41
2	132	8.5±0.1	19.0±0.1	8.50
15	0	8.3±0.3	18.4±0.0	8.44
15	2	8.4±0.1	18.3±0.0	8.56
15	4	8.4±0.2	18.3±0.1	8.57
15	8	8.4±0.2	18.3±0.1	8.60
15	17	8.7±0.1	18.5±0.4	8.64
15	34	8.7±0.1	18.3±0.0	8.61
15	66	8.5±0.1	18.4±0.1	8.62
15	132	8.6±0.0	18.5±0.1	8.61
60	0	7.8±1.4	18.4±0.1	8.65
60	2	8.0±0.4	18.4±0.0	8.62
60	4	8.2±0.4	18.4±0.1	8.62
60	8	8.2±0.2	18.5±0.0	8.59
60	17	8.3±0.2	19.2±0.4	8.64
60	34	8.4±0.3	19.1±0.5	8.66
60	66	8.6±0.2	19.2±0.5	8.63
60	132	8.5±0.1	19.3±0.5	8.58

Table 2. ANCOVA results of chloride effect on juvenile mortality while controlling for nitrite. * denotes significance at 0.05

	Estimate	Std. Error	Z value	Pr (>|z|)
Intercept	-1.7	0.3	-5.6	0.000*
Nitrite	0.3	0.1	5.7	0.000*
Chloride (15 mg L-1)	-3.2	0.5	-2.9	0.004*
Chloride (60 mg L-1)	-3.2	0.5	-3.1	0.002*
Nitrite:Chloride (15 mg L-1)	0.3	0.1	0.1	0.922
Nitrite:Chloride (60 mg L-1)	0.1	0.1	-3.1	0.002*

Figure 1. Mortality of Atlantic sturgeon juveniles after 24-hour period exposure to eight nitrite concentrations (mg L^{-1}) crossed with three chloride concentrations (mg L^{-1}).
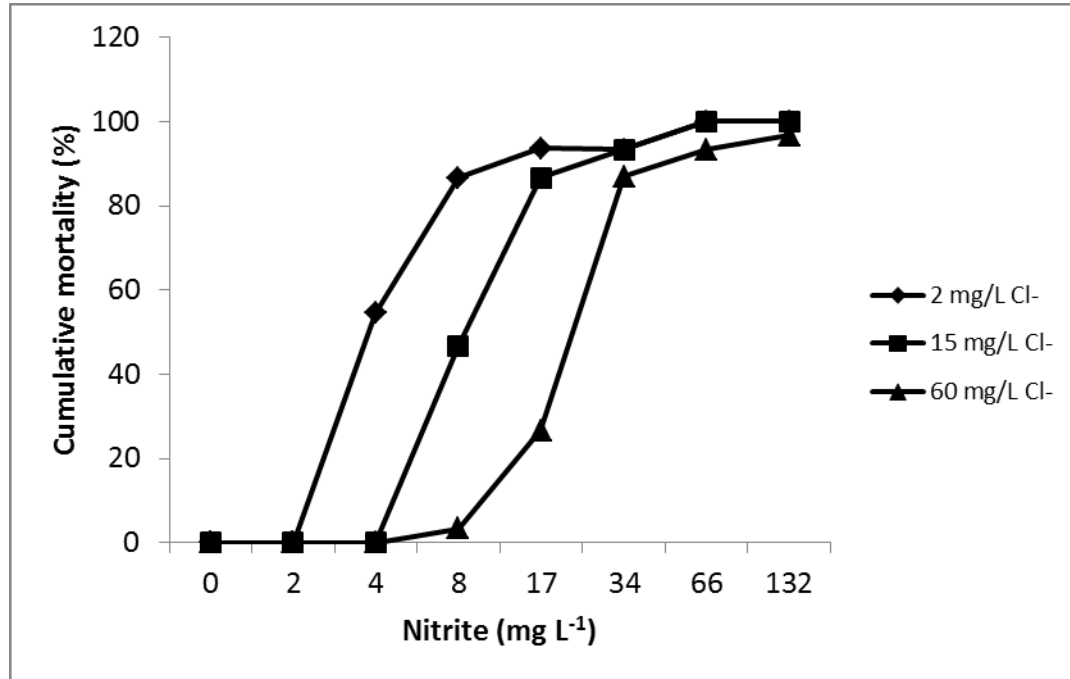
Fig. 2. Relationship between chloride concentrations (mg L^{-1}) and LC50 nitrite concentrations (mg L^{-1}).
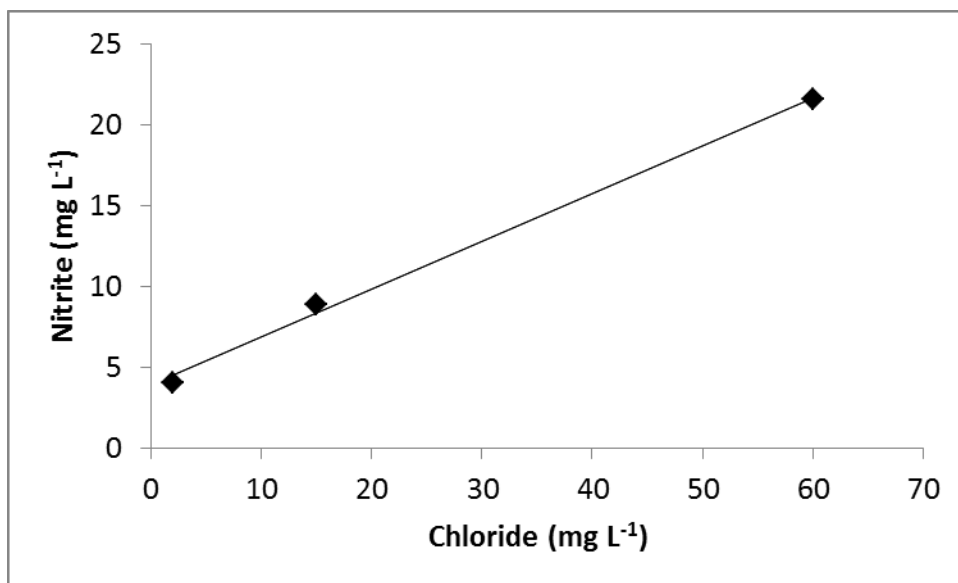
Chapter 3: The effects of acclimation to temperature and salinity on age-0 Atlantic sturgeon *Acipenser oxyrinchus* using lactate as an indicator

Abstract

Temperature and salinity are known stressors in aquatic environments and may determine habitat available to larval and juvenile euryhaline species. Atlantic sturgeon are anadromous so spawning occurs in freshwater portions of tidal tributaries. Embryos, larvae, and early juveniles are thought to be salinity intolerant but it is unknown at what salinity physiological stress occurs in this species. I acclimated 40dph Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) to three temperatures (13°C, 18°C, 20°C) and four salinities (0, 1, 11, 21) at 1°C day^{-1} and 1 psu day^{-1}. Whole body lactate, mortality, and specific growth rates were determined. Results indicate decreases in lactate concentrations with increasing temperature (3-5.10 µmol per gram fish weight) and salinity (2.58-5.16 µmol per gram fish weight). Higher mortality was observed in higher salinity treatments (0-27.8%). Specific growth rates (1.3-1.9 % day^{-1}) were comparable across treatments.

Introduction

Hematological values of fishes can be affected by environmental factors which include water quality parameters such as water temperature, salinity, oxygen, pH, etc. (Zarejabad et al. 2010). Environmental factors can act as the "stressor" or "stress factor" which is the stimulus that inflicts stress on the fish (Barton 2000). "Stress" or "stressed state" is the altered state of the fish and "stress response" are the

physiological or behavioral responses that can be measured to indicate the degree of stress experienced (Barton 2000). Stress in fishes can be described by three responses: primary, secondary, and tertiary (Bonga 1997; Barton 2000; Wedemeyer et al. 1990). The primary response (the endocrine system) is the initial neuroendocrine response and involves the activation of the brain center resulting in the release of catecholamines and corticosteroids (Wedemeyer et al. 1990; Bonga 1997; Barton 2000). The secondary response (blood and tissue alterations) includes changes in blood glucose and lactate, electrolytes and osmality, and hematological features that relate to physiological functions such as metabolism and hydromineral balance (Wedemeyer et al. 1990; Bonga 1997; Barton 2000). Secondary physiological changes can take minutes to hours to manifest in circulation and can remain altered for extended periods (Barton 2000). The tertiary response (individuals and populations) is a whole-animal response and is extended to the level of the organism and population (Wedemeyer et al. 1990; Bonga 1997; Barton 2000). Tertiary responses include changes in growth, resistance to disease, behavior, reproduction, and survival (Wedemeyer et al. 1990; Bonga 1997; Barton 2000). Cortisol is the primary stress response in fish (Bonga 1997; Tsui et al. 2012) and most likely the main stress steroid in Acipenseriformes (Singer and Ballantyne 2004) of which sturgeon are members (Bermis et al. 1997; Krayushkina et al. 1995). For the present study, I used lactate as an indicator in age-0 Atlantic sturgeon acclimated to various temperatures and salinities. Plasma glucose and lactate levels are indicators of a secondary stress response in fish (Tsui et al. 2012). When fish are stressed, energy reserves are mobilized and increases in plasma glucose and lactate occur (Barton

26

2000). Measuring these secondary responses in fish provides physiological

information assimilated at a higher biological level within the organism and may

characterize the severity of stress and the time needed for recovery (Wedemeyer et al.

1990).

Acute stress caused by capture, handling, hypoxia, osmotic and temperature

shock, or exposure to water pollutants has been reported to result in the increase of

lactate in muscle and plasma of fish (Bonga 1997). In sturgeon species, glucose and

lactate have been used as stress indicators for experiments such as air exposure

(Lankford et al. 2003; Zuccarelli et al. 2008; Eslamloo and Falahatkar 2014),

handling/exercise (Kieffer et al. 2001; Singer and Ballantyne 2004; Webb et al.

2007), salinity (Potts and Rudy 1972; McEnroe and Cech 1985; Bain 1997;

McKenzie et al. 2001; Singer and Ballantyne 2004; Allen and Cech 2007) and

temperature (Lankford et al. 2003; Zhang and Kieffer 2014). Exhaustive exercise in

sturgeon can stimulate a reduced stress response (i.e. change in lactate) (Wokoma and

Johnston 1981; Baker et al. 2005), however, it is more likely that changes in lactate

are a result of energy stores not being restored under high metabolic costs (Allen and

Cech 2007; Haller et al. 2014). Lack of energy reserves and the ability of an animal

to recover from exhaustive exercise can limit performance during exercise (Kieffer

2000). Several biological constraints (i.e. body size and nutrition) as well as

environmental constraints (i.e. water temperature and salinity) can influence pre- and

post-exercise condition of fish (Kieffer 2000). In addition, the nutritional state can

influence a fish's ability to recover from energetic costs, that is fish with lower

energy stores display a lower anaerobic capacity (i.e. production of lactate) (Kieffer et

al. 2000). Temperature can also influence and change physiological processes in sturgeon (Zhang and Kieffer 2014). In white sturgeon (*Acipenser transmontanus*), high temperatures can increase mortality, decrease growth rate, and reduce swimming activity (Zhang and Kieffer 2014). In shortnose sturgeon, thermal stress was shown to increase lactate levels suggesting that increased metabolic rates could not be maintained with aerobic metabolism; therefore anaerobic metabolism was used to generate energy; a response to agitation and burst-swimming as their thermal maximum was approached (Zhang and Kieffer 2014).

In general, early life stages of fish (embryos, larvae, early juveniles) are more sensitive than adults to stressors such as water pollutants and temperature changes (Bonga 1997) and salinity changes (Potts and Rudy 1972; McEnroe and Cech 1985; Kynard and Horgan 2002; Singer and Ballantyne 2004). Sturgeons are described taxonomically as Acipenseriformes and they are similar to teleosts in main features of their osmoregulation (Potts and Rudy 1972; Krayushkina et al. 1995; Bermis et al. 1997; Singer and Ballantyne 2004) and stress response (Eslamloo and Falahatkar 2014). The ability of euryhaline fish to adapt to varying environmental salinities depends on activation of ion transport which impose energetic costs (Singer and Ballantyne 2004; Sinha et al. 2015). Compared to teleosts, sturgeon species are less capable of tolerating rapid seawater exposure and may require more time to adjust to salinity changes (Singer and Ballantyne 2004). Atlantic sturgeon are anadromous, with spawning occurring in freshwater tidal regions of estuaries, with some evidence of spawning in brackish water, and both juveniles and adults forage in the marine environment (Smith 1985; Bain 1997; Singer and Ballantyne 2004). Larvae and

young juveniles of anadromous sturgeon species are initially intolerant to higher

salinities but as they grow higher salinities are selected (Cataldi et al. 1999; Bain et

al. 2000; Kynard and Horgan 2002; Allen and Cech 2007; Ziegeweid et al. 2008;

Allen et al. 2009, 2011). Age-0 Atlantic sturgeon are vulnerable to salinities >20

(Niklitschek & Secor 2005). Thus salinity determines the area available to juveniles

as nursery grounds (Schlenger et al. 2013) and may explain why sturgeon are

typically confined to major river systems with large estuaries where abrupt salinity

changes are less likely to occur (Potts and Rudy 1972; Singer and Ballantyne 2004).

Atlantic sturgeon <3 months old may be less tolerant to environmental changes and

information is needed to fully understand how temperature and salinity interactions

can constrain habitat availability for this age group of Atlantic sturgeon. There is

limited data on how long Atlantic sturgeon juveniles remain in freshwater

environment or at what age/size they can tolerate higher salinities (Smith 1985; Bain

1997; Lazzari et al. 1986). Over the past 55+ years of the VIMS Trawl Survey (1955-

2011), forty-eight Atlantic sturgeon ranging in size from 85-997mm TL (avg.

433mm) have been captured; the smallest of which was captured in freshwater (0.1

salinity) (M. Fabrizio and T. Tuckey, VIMS, un-published data). Given the scarcity

and difficulty catching early juvenile Atlantic sturgeon, this research may shed new

light on habitat (i.e. temperature and salinity) utilized by early juvenile Atlantic

sturgeon and their physiological state (i.e. stress level, survival, growth) while

inhabiting these environments. I hypothesized that lactate concentrations can be used

as an indicator of thermal and salinity stress in Atlantic sturgeon resulting with

increased stress with increasing salinities and higher temperature.

29

Materials and Methods

Fish Source and Husbandry

Age-0 juveniles were obtained from US Fish and Wildlife Service, Bears Bluff/Orangeburg National Fish Hatchery Complex, Wadmalaw Island, South Carolina and were progeny of Atlantic sturgeon broodstock collected from the Altamaha River, GA between November 2008 – May 2009. At 27 days post-hatch (dph) fish were shipped to University of Maryland Center for Environmental Science Horn Point Laboratory (UMCES HPL) and reared in freshwater (18.7 ± 0.2°C, 7.8 ± 0.3 mg L^{-1} dissolved oxygen). Fish were fed brine shrimp (Brine Shrimp Direct, Ogden, UT) using a bellows metering pump (Gorman-Rupp Industries, Bellville, OH) set to feed every twelve minutes for 90 seconds from a reservoir of hatched brine shrimp in order to maintain a density of 1.5 nauplii per 10 mL in the tank (Mohler 2004).

Experimental Design

At 40 dph (39 ± 5.5mm TL; 3.5 ± 0.07g (average weight of 10 fish)) fish were stocked in 8-L containers. Juveniles were acclimated to treatment temperatures and salinities at a rate of 1°C and 1 psu day^{-1}. In a balanced block design, four salinity levels (0, 1, 11 and 21 psu; 3 replicates/treatment; 10 fish per replicate) were crossed with three temperature treatments (13°C, 18°C, 26°C) for a total of 36 trials. Reservoirs of well water were heated, chilled, or held at ambient temperature to be used for water exchanges that occurred daily. Instant Ocean® was used in salinity treatments and was added to each individual 8-L container to obtain targeted salinity.

Temperature, dissolved oxygen, and salinity were recorded daily. Mortality was recorded daily and cumulative mortality calculated for each treatment container. Fish were fed artemia nauplii by hand two to three times per day at a density of 1.5 nauplii per 10 mL. When treatments reached the desired temperature and salinity concentrations, survivors were euthanized (300 mg L-1 MS-222 buffered with sodium bicarbonate). Each fish was individually measured for length and stored in a -80 freezer until lactate analysis could be completed. Specific growth rates (SGR(% day^{-1})=(((ln(final length)-ln(initial length))/# days)*100) using length data were calculated for each treatment tank to determine if temperature and/or salinity affected growth rates.

Lactate and Statistical Analysis

Whole body lactate concentrations were measured for individual juvenile Atlantic sturgeon in the study. Following the protocol in Wokoma and Johnston (1981), individual fish were weighed (g) then homogenized in 5 mL of 0.6 mol L^{-1} perchloric acid. Homogenates were chilled on ice and centrifuged for ten minutes at 6000 revs min^{-1}. Supernatants were removed, neutralized with 2 M-K$_2$HCO$_3$, and lactate acid concentrations were determined colorimetrically (450nm) using a lactate analysis kit (Lactate Assay Kit II, Sigma-Aldrich, catalog number MAK065). Standard curves were run concurrently with samples. Each sample was run in duplicate. Lactate concentrations were converted to µmol g^{-1} fish weight for statistical analysis.

Two-way ANOVA (R Core Team 2014) was used to determine the effect of temperature and salinity on mortality, SGR, and lactate concentrations. Tukey's

31

honestly significant difference multiple comparison tests of means were used if the overall ANOVA was found to be significant.

Results

Mortality and Specific Growth Rates

A two-way ANOVA of temperature (13°C, 18°C, 26°C) and salinity (0, 1, 11, 21) on mortality (morts:total) and SGR (% day^{-1}) was conducted. A significant main effect of temperature on mortality was found, $F_{(2,24)}=15.90$, $p<0.05$. Mortality (%) was higher in the 26°C treatment (mean=27.5) than in the 13°C (mean=3.3) and 18°C (mean=5.8). There was no significant difference in mortality between 18°C and 13°C treatments. A significant main effect of salinity on mortality was found, $F_{(3,24)}=9.056$, $p<0.05$. Mortality was higher in the 21 salinity treatment (mean=27.8) compared to the 0, 1, and 11 salinity treatments (means=8.9, 0, 12.2, respectively). The temperature x salinity interaction was significant, $F_{(6,24)}=4.2$, $p<0.05$. Within the 26° treatment, significant differences in mortality occurred between salinities of 0 (mean=13.3) and 21 (mean=60), 1 (mean=0) and 21 (mean=60), and 1 (mean=0) and 11 (mean=36.7) with higher mortality occurring in the higher salinities (Fig.1). Additionally, significant interactions at 11 and 21 salinities occurred between 26°C and the other temperatures (13°C and 18°C) (Fig. 1). There were no additional significant interactions at other levels.

The main effect of temperature on SGR was not significant, $F_{(2,24)}=1.466$, $p=0.251$. The main effect of salinity on SGR was also not significant, $F_{(3,24)}=0.371$, $p=0.775$. Additionally, the temperature x salinity interaction was not significant,

F(6,24)=1.048, p=0.42. SGRs ranged from 1.3 % day^{-1} to 1.9 % day^{-1} across all treatments (Fig. 2).

Lactate

A two-way ANOVA of temperature (13°C, 18°C, 26°C) and salinity (0, 1, 11, 21) on lactate (μmol g^{-1} fish weight) was conducted. A significant main effect of temperature on lactate was found, F(2,258)=148.26, p<0.05. Lactate concentrations decreased as temperatures increased. The lactate concentrations in the 13°C treatment (mean=5.10) was significantly higher than the lactate concentrations in both the 18°C treatment (mean=3.27) and 26°C treatment (mean=3.02) (Fig. 3). A significant main effect of salinity on lactate was found, F(3,258)=107.57, p<0.05. Lactate concentrations decreased as salinity increased with mean lactate concentrations of 5.16, 4.32, 3.37, and 2.58 in salinity treatments 0, 1, 11, and 21, respectively. Lactate concentrations were significantly different across all salinities (Fig. 4). The temperature x salinity interaction was significant, F(6,258)=8.65, p<0.05. Within the 13°C all salinity levels were significantly different from one another (Fig. 5). Mean (± standard of deviation) lactate concentrations in the 13°C treatment were 6.84 (±0.9), 5.95 (±1.0), 4.54 (±0.8), and 2.98 (±0.7) for 0, 1, 11, and 21 salinity treatments, respectively. Within the 18°C treatment, significant differences were found between 0 salinity (4.48±0.9) and both 11 salinity (2.46±0.8) and 21 salinity (2.00±0.4) (Fig. 5). There was no significant difference between 0 salinity (4.48±0.9) and 1 salinity (3.69±0.6) at 18°C. Significant differences were also found between 1 salinity (3.69±0.6) and both 11 salinity (2.46±0.8) and 21 salinity (2.00±0.4) in the 18°C treatment. In the 26°C, 0 salinity (3.9±1.1) was

significantly higher than 1 (1.79±0.5), 11 (2.75±1.72), and 21 (2.27±0.72) salinities (Fig. 5). There were no significant differences between the other salinity treatments at this temperature.

Lactate concentrations decrease in 0 salinity treatments with increasing temperatures (Fig.5). Lactate concentrations are significantly higher in the 0 salinity at 13°C (6.84±0.9) compared to both the 18°C and 26°C 0 salinity groups (4.48±0.9, 3.9±1.1, respectively). Additionally, the 1 salinity treatment is significantly different among all temperature treatments with lactate concentration significantly decreasing as temperatures increase (5.95±1.0, 3.69±0.6, 1.79±0.5 for 13°C, 18°C, 26°C, respectively). For the 11 salinity treatment, the 13°C group had significantly higher lactate concentration (4.54±0.8) than both the 18°C and 26°C group (2.46±0.8, 2.75±1.72, respectively) but there was no difference at 11 salinity between the 18°C and 26°C groups. The highest salinity treatment, 21, also showed a decrease in lactate concentrations as temperatures increased. There was significant difference at 13°C (2.98±0.7) and 18°C (2.00±0.4) but no difference between 13°C and 26°C or 18°C and 26°C.

Discussion

Growth and Mortality

Sturgeon maintain plasma ion levels hypoosmotic to seawater and hyperosmotic to freshwater and studies suggest osmoregulatory costs are lowest in freshwater during juvenile development (Singer and Ballantyne 2004). Salinity-

related effects on growth have been studied for other sturgeon species (McKenzie et al. 1999, Altinok & Grizzle 2001; McKenzie et al. 2001b) but growth potential for sturgeon in various salinities may vary depending on life history and age/size (Allen & Cech 2007). In a study by Jarvis et al. (2001), juvenile shortnose sturgeon had higher weight gain in freshwater and lost weight at 20‰. Juvenile Gulf sturgeon (*A. oxyrinchus desotoi*) experienced higher specific growth rates in 3‰ and 9‰ than 0‰ and 1‰ (Altinok and Grizzle 2001). Adriatic sturgeon had lower specific growth rates at 20‰ than 0‰ (McKenzie et al. 1999). I did not see an effect of salinity or temperature on specific growth rates for 40dph Atlantic sturgeon. The growth rates observed were within the range of growth rates for other sturgeon species observed in other studies (Altinok and Grizzle 2001; Allen and Cech 2007; McKenzie et al. 1999) so acclimation of 1 psu day^{-1} and 1°C day^{-1} did not inhibit growth. However, a difference in mortality rates was observed with higher mortality occurring in the higher salinity treatments and also at the higher temperature. McEnroe and Cech (1985) showed white sturgeon ranging in weight from 0.4 g to 56 g survived abrupt transfer to 5 salinity but fish below 1.8g did not survive transfer to 10 salinity and those below 4.9 g did not survive transfer to 15 salinity. No juvenile fish survived transfer to salinities of 25 and above (McEnroe and Cech 1985). Ziegeweid et al. 2008 found 48hr salinity LC50 values increased with increasing size of shortnose sturgeon with 56mm TL fish having a LC50 value of 14.8 salinity. In this study, >50% mortality only occurred at 26°C in 21 salinity but it is possible if fish were exposed for a longer period to higher salinities, I may have seen higher mortality as observed in other studies. For shortnose sturgeon (68mm TL, 70dph), the 48hr LT50

was 28.2°C (Ziegeweid et al. 2008) so it is possible we were approaching the higher temperature tolerance of age-0 Atlantic sturgeon. It is also likely that that there is an interaction between temperature and salinity, as seen by Niklitschek and Secor (2005) and Schlenger et al. (2013).

Lactate

Results from this study indicate a clear effect of temperature and salinity on lactate concentration in age-0 Atlantic sturgeon. Studies on the effect of salinity on several sturgeon species has shown that salinity tolerance increases with body size/age (Cataldi et al, 1999; Allen and Cech 2007; Ziegeweid et al. 2008; Amiri et al. 2009; Allen et al. 2011). Age-0 Atlantic sturgeon were 40dph (39±5.5mm TL; 3.5±0.07g (average weight of 10 fish)) which is younger and smaller than sturgeon used in most previous studies. Allen and Cech (2007) looked at the effect of age and size of green sturgeon (*A. medirostris*) on osmoregulation and found that plasma lactate decreased in saltwater (33‰) treatments in the younger age groups tested (100 and 170dph) compared to both freshwater (<3‰) and brackish water (10‰) treatments. A decreased in lactate concentrations with increasing salinities was also observed in my study. A possible explanation for the decrease of lactate in the higher salinities is the reduction in food consumption due to stress which means energy stores were not replenished but osmoregulatory costs were high in the higher salinities as observed by Allen and Cech (2007). Haller et al. (2014) observed a trend toward lower lactate in feed-restricted groups of green sturgeon (214dph) across all salinity treatments (0, 8, 16, 32) and suggest that lactate was utilized for maintenance of glucose levels due to increased lactate use as a substrate for hepatic

36

gluconeogenesis. Food consumption was not observed but given the higher mortality

observed in the higher salinities, it is possible sturgeon in these treatments were not

feeding well although specific growth rates of survivors did not differ between

treatments. Additionally, Allen and Cech (2007) observed less swimming activity in

the higher salinity treatments where plasma lactate was also low. Reduced activity by

Siberian sturgeon (*A. baerii*) has also been observed following an acute stressor and

resulted in lower plasma lactate levels (Eslamloo and Falahatkar 2014) and reduced

swimming activity was also observed in Adriatic sturgeon following a salinity

challenge (McKenzie et al. 2001a). It has been shown that lactate increases with

"burst swimming" or periods of hypoxia will increase lactate concentrations (Kieffer

et al. 2001; Jarvis and Ballantyne 2003; Lankford et al. 2003; Baker et al. 2005).

Swimming activity was not noted but it is possible that the lower lactate levels

observed in the higher salinities and temperatures could be the result of less

swimming activity in stressed fish. In a study using 16-month old (274g) shortnose

sturgeon (*A. brevirostrum*), a small increase in plasma lactate was observed in the

high-salinity (20‰) group indicating an oxygen debt incurred which may have been

due to gill shrinkage due to the sturgeon being transferred from freshwater to

seawater (Jarvis and Ballantyne 2003). In my study using Atlantic sturgeon, I

observed the opposite response of sturgeon in higher salinity with regards to lactate.

It is possible in my study that the energy requirement for osmoregulation was greater

than the energy stores available since it is believed that the energy requirement of the

fish gill is maintained by the oxidation of glucose and lactate (Laiz-Carrion et al.

2002). Allen et al. (2009, 2011) stated that developmental growth and an ontogenetic

37

change in gills occurs between 3-6 months post-hatch in green sturgeon that may be necessary before fish can acclimate to saltwater and internal and external cues may stimulate osmoregulatory mechanisms. In my study, it is possible that 40 dph Atlantic sturgeon have not developed the osmoregulatory mechanisms needed to tolerate high salinities. Gills of sturgeon contain large numbers of chloride cells which are the primary site for salt secretion and Atlantic sturgeon adapted to brackish and salt water have large and higher numbers of chloride cells compared with freshwater fish (Singer and Ballantyne 2004). In future studies with age-0 Atlantic sturgeon it would be interesting to look at gill structure after exposure to various salinities to determine if the structures for osmoregulation are developed in fish this age or start to develop when exposed to salinity as proposed in other studies (Allen and Cech 2007; McEnroe and Cech 1985).

Temperature also had an effect on lactate levels. Higher lactate concentrations were observed in the 13°C treatment compared to the 18°C and 26°C treatments. It is possible that sturgeon in the 13°C treatment had lower feed needs and less metabolic/respiratory costs so energy stores could be used for osmoregulation resulting in increased lactate at this temperature because a deficit in energy stores would not occur. This deficit was observed in the study by Allen and Cech 2007 where low plasma glucose was found in younger age green sturgeon in saltwater due to energy stores being used up through tissue catabolism. The lower lactate levels observed in the 26°C of my study could also be explained by this since metabolic rates increase in warmer water (Zarejabad et al. 2010) and osmoregulatory costs would be greater in higher salinities. Zhang and Kieffer (2014) found that thermal

stress caused lactate levels to increase in shortnose sturgeon especially when the fish

were initially acclimated to lower temperatures (10°C and 15°) compared to 20°C,

however lactate levels decreased with increases in acclimation temperature so the

20°C treatment had the lowest lactate levels when the critical thermal maximum was

reached. In my study, sturgeon were reared in 18°C water and water temperatures

were either lowered to 13°C or raised to 26°C. Although Zhang and Kieffer (2014)

found an increase in lactate with thermal stress, my results are similar to what they

observed in that my fish were acclimated at 18°C at the start of the experiment and

lactate levels decreased in the treatment where water temperature was increased at a

rate of 1°C day^{-1}. The explanation made by Zhang and Kieffer (2014) for this

observation is increased hematocrit associated with thermal stress may negatively

impact hemoglobin-oxygen affinity resulting in higher dependency on anaerobic

pathways. I did not measure additional hematological parameters in my study so I

cannot make conclusions about hematocrit, but given the similarity in the results, it is

possible this occurred in the fish in the 26°C treatment.

In conclusion, specific growth rates did not vary much between treatments but

there was a significant effect of temperature and salinity on mortality and lactate

levels. I hypothesize that lactate levels decreased at as temperatures and salinities

increased due to energy stores being depleted for metabolism and osmoregulation.

Given the size of the fish I was using (39mm TL), I was unable to process multiple

indices to measure the effect of temperature and salinity since I used whole fish to

complete the lactate analysis. In future studies, it would be beneficial to also measure

glucose levels to better understand the effect on energy stores. In addition, gill

morphology may also be used to better predict and understand the effect salinity will have on age-0 Atlantic sturgeon since the number and size of chloride cells may determine their salinity tolerance (Singer and Ballantyne 2004; Allen et al. 2009, 2011). Overall, it seems as though age-0 Atlantic sturgeon tolerate acclimation to 11 salinity reasonably well at 13°C and 18°C since no mortality was observed in these treatments. Mortality did increase at this salinity in the 26°C treatment so an interaction of temperature and salinity may be occurring at these treatment levels. It may be age-0 Atlantic sturgeon are more tolerant of higher salinities than initially believed and survival in brackish water is possible, at least for short periods of time. It is also interesting that the sturgeon seemed to be less physiologically stressed (i.e. higher lactate levels, lower mortality, comparable SGR) in the 13°C across all salinities compared to the other two temperature treatments. This study may assist researchers in their attempt to find age-0 Atlantic sturgeon within salinity zones of their nursery habitats and understand potential costs of persisting in high salinity environments.

References

Allen, P.J., and J.J. Cech, Jr. 2007. Age/size of juvenile green sturgeon, *Acipenser medirostris*, oxygen consumption, growth, and osmoregulation in saline environments. Environmental Biology of Fishes 79: 211-229.

Allen, P.J., J.J. Cech Jr., D. Kültz. 2009. Mechanisms of seawater acclimation in a primitive, anadromous fish, the green sturgeon. Journal of Comparative Physiology B 179: 903-920.

Allen, P.J., M. McEnroe, T. Forostyan, S. Cole, M.M. Nicholl, B. Hodge, and J.J. Cech Jr. 2011. Ontogeny of salinity tolerance and evidence for seawater-entry preparation in juvenile green sturgeon, *Acipenser medirostris*. Journal of Comparative Physiology B 181: 1045-1062.

Altinok, I. and J.M. Grizzle. 2001. Effects of brackish water on growth, feed conversion and energy absorption efficiency by juvenile euryhaline and freshwater stenohaline fishes. Journal of Fish Biology 59: 1142-1152.

Amiri, B.M., D.W. Baker, J.D. Morgan, and C.J. Brauner. 2009. Size dependent early salinity tolerance in two sizes of juvenile white sturgeon, *Acipenser transmontanus*. Aquaculture 286: 121-126.

Baker, D.W., A.M. Wood, M.K. Litvak, and J.D. Kieffer. 2005. Haematology of juvenile *Acipenser oxyrinchus* and *Acipenser brevirostrum* at rest and following forced activity. Journal of Fish Biology 66: 208-221.

Bain, M.B. 1997. Atlantic and shortnose sturgeons of the Hudson River: common and divergent life history attributes. Environmental Biology of Fishes 48: 347-358.

Balazik, M., G.C. Garman, J.P. Van Eenennaam, J. Mohler, and L.C. Woods III. 2013. Empirical evidence of fall spawning by Atlantic sturgeon in the James River, Virginia. Transactions of the American Fisheries Society 141(6): 1465-1471.

Barton, B.A. 2000. Stress. Pages 892-898 *in* Robert R. Stickney, editor. Encyclopedia of Aquaculture. John Wiley and Sons, Inc. New York, New York.

Bemis, W.E., E.K. Findels, and L.Grande. 1997. An overview of Acipenseriformes. Environmental Biology of Fishes 48: 25-71.

Bonga, S.E.W. 1997. The stress response of fish. Physiological Reviews 77(3): 591-625.

Cataldi, E., C. Barzaghi, P. Di Marco, C. Boglione, D.J. McKenzie, P. Bronzi, and S. Cataudella. 1999. Some aspects of osmotic and ionic regulation in Adriatic sturgeon

Acipenser naccarii, I: Ontogenesis of salinity tolerance. Journal of Applied Ichthyology 15: 57-60.

Eslamloo, K. and B. Falahatkar. 2014. Variations of some physiological and immunological parameters in Siberian sturgeon (*Acipenser baerii*, Brandt, 1869) subjected to an acute stressor. Journal of Applied Animal Welfare Science 17: 29-42.

Haller, L., S.S.O. Hung, S. Lee, J.G. Fadel, J.H. Lee, M. McEnroe, N.A. Fangue. 2014. Effect of nutritional status on the osmoregulation of green sturgeon (*Acipenser medirostris*). Physiological and Biochemical Zoology 88(1): 22-42.

Jarvis, P.L., J. S. Ballantyne, and W.E. Hogans. 2001. The influence of salinity on the growth of juvenile shortnose sturgeon. North American Journal of Aquaculture 64(4): 272-276.

Jarvis, P.L., and J.S. Ballantyne. 2003. Metabolic responses to salinity acclimation in juvenile shortnose sturgeon *Acipenser brevirostrum*. Aquaculture 219: 891-909.

Kieffer, J.D., A.M. Wakefield, and M.K. Litvak. 2001. Juvenile sturgeon exhibit reduced physiological responses to exercise. The Journal of Experimental Biology 204: 4281-4289.

Kieffer, J.D., F.M, Penny, V. Papadopoulos. 2014. Temperature has a reduced effect on routine metabolism rates of juvenile shortnose sturgeon (*Acipenser brevirostrum*). Fish Physiology and Biochemistry 40: 551-559.

Krayushkina, L.S. 2006. Considerations on evolutionary mechanisms of osmotic and ionic regulation in Acipenseridae: an overview. Journal of Applied Ichthyology 22 (Suppl. 1): 70-76.

Kynard, B. and M. Horgan. 2002. Ontogenetic behavior and migration of Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus*, and shortnose sturgeon, *A. brevirostrum*, with notes on social behavior. Environmental Biology of Fishes 63: 137-150.

Laiz-Carrión, S. Sangiao-Alvarellos, J.M. Guzmán, M. P. Martín del Río, J. M. Míguez, J. L. Soengas, and J. M. Mancera. 2002. Energy metabolism in fish tissues related to osmoregulation and cortisol action. Fish Physiology and Biochemistry 27: 179-188.

Lankford, S.E., T.E. Adams, J.J. Cech, Jr. 2003. Time of day and water temperature modify the physiological stress response in green sturgeon, *Acipenser medirostris*. Comparative Biochemistry and Physiology Part A 135: 291-302.

Lazzari, M.A., J. C. O'Herron II, R.W. Hastings. 1986. Occurrence of juvenile Atlantic sturgeon *Acipenser oxyrhynchus*, in the Upper Tidal Delaware River. Estuaries 9(4B): 356-361.

McEnroe, M. and J.J. Cech, Jr. 1985. Osmoregulation in juvenile and adult white sturgeon, *Acipenser transmontanus*. Environmental Biology of Fishes 14(1): 23-30.

McKenzie, D.J., E. Cataldi, P. Di Marco, A. Mandich, P. Romano, S. Ansferri, P. Bronzi, and S. Cataudella. 1999. Some aspects of osmotic and ionic regulation in Adriatic sturgeon *Acipenser naccarii*. II: Morpho-physiological adjustments to hyperosmotic environments. Journal of Applied Ichthyology 15: 61-66.

McKenzie, D.J., E. Cataldi, P. Romano, E.W. Taylor, S. Cataudella, and P. Bronzi. 2001a. Effects of acclimation to brackish water on tolerance of salinity challenge by young-of-the-year Adriatic sturgeon (*Acipenser naccarii*). Canadian Journal of Fisheries and Aquatic Sciences 58: 1113-1121.

McKenzie, D.J., E. Cataldi, P. Romano, S.F.Owen, E.W. Taylor, and P Bronzi. 2001b. Effects of acclimation to brackish water on the growth, respiratory metabolism, and swimming performance of young-of-the-year Adriatic sturgeon (*Acipenser naccarii*). Canadian Journal of Fisheries and Aquatic Sciences 58: 1104-1112.

Mohler, J.W. 2004. Culture manual for the Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*. U.S. Fish and Wildlife Service, Hadley, Massachusetts. 70pp.

Niklitschek, E. and D.H. Secor. 2005. Modeling spatial and temporal variation of suitable nursery habitats for Atlantic sturgeon in the Chesapeake Bay. Estuaries and Coastal Shelf Science 64: 135-148.

Potts, W.T.W., and P.P. Rudy. 1972. Aspects of osmotic and ionic regulation in the sturgeon. Journal of Experimental Biology 56: 701-715.

R Core Team. 2014: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Schlenger, A.J., E.W. North, Z. Schlag, Y. Li, D.H. Secor, K.A. Smith, E.J. Niklitschek. 2013. Modeling the influence of hypoxia on the potential habitat of Atlantic sturgeon *Acipenser oxyrinchus*: a comparison of two methods. Marine Ecology Progress Series 483: 257-272.

Sinha, A.K., A. F. Dasan, R. Rasoloniriana, N. Pipralia, R. Blust, G. De Boeck. 2015. Hypo-osmotic stress-induced physiological and ion-osmoregulatory responses in European sea bass (*Dicentrarchus labrax*) are modulated differentially by nutritional status. Comparative Biochemistry and Physiology Part A 181: 87-99.

Smith, T.I.J. 1985. The fishery, biology, and management of Atlantic sturgeon, *Acipenser oxyrhynchus*, in North America. Environmental Biology of Fishes 14(1): 61-72.

Singer, T.D. and J.S. Ballantyne. 2004. Sturgeon and Paddlefish Metabolism. Pages 167-194 *in* G.T.O. LeBreton, F.W.H. Beamish, R.S. McKinley, editors. Sturgeons and Paddlefish of North America. Kluwer Academic Publishers, Netherlands.

Tsui, W.C., J.C. Chen, S.Y. Cheng. 2012. The effects of a sudden salinity change on cortisol, glucose, lactate, and osmolality levels in grouper *Epinephelus malabaricus*. Fish Physiology and Biochemistry 38: 1323-1329.

Webb, M.A.H., J.A. Allert, K.M. Kappenman, J. Marcos, G.W. Feist, C.B. Schreck, C.H. Shackleton. 2007. Identification of plasma glucocorticoids in pallid sturgeon in response to stress. General and Comparative Endocrinology 154: 98-104.

Wedemeyer, G.A., B.A. Barton, and D.J. McLeay. 1990 Stress and Acclimation. Pages 451-489 *in* C.B. Schreck and P.B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Wokoma, A. and I.A. Johnston. 1981. Lactate production at high sustainable cruising speeds in rainbow trout (*Salmo gairdneri* Richardson). Journal of Experimental Biology 90:361-364.

Zhang, Y. and J.D. Kieffer. 2014. Critical thermal maximum (CTmax) and hematology of shortnose sturgeon (*Acipenser brevirostrum*) acclimated to three temperatures. Canadian Journal of Zoology 92: 215-221.

Zarejabad, A. M., M. Sudagar, S. Pouralimotlagh, K.D. Bastami. 2010. Effects of rearing temperature on hematological and biochemical parameters of great sturgeon (*Huso huso* Linnaeus, 1758) juvenile. Comparative Clinical Pathology 19:367-371.

Ziegeweid, J.R., C.A. Jennings, D.L. Peterson, M.C. Black. 2008. Effects of salinity, temperature, and weight on the survival of young-of-year shortnose sturgeon. Transactions of the American Fisheries Society 137: 1490-1499.

Zuccarelli, M.D., M. Kusakabe, I. Nakamura, E.F. Prentice, G. Young, and R.L. Ingermann. 2008. Acute stress response of Kootenai River white sturgeon *Acipenser transmontanus* Richardson reflected in peritoneal fluid and blood plasma. Journal of Fish Biology 72: 1831-1840.

Figure 1. Mean (± std dev) juvenile Atlantic sturgeon mortality (%)
after acclimation to three different temperatures (13°C, 18°C, 26°) and
four different salinities (0, 1, 11, 21). Different letters indicate
significant differences (ANOVA, $p<0.05$).
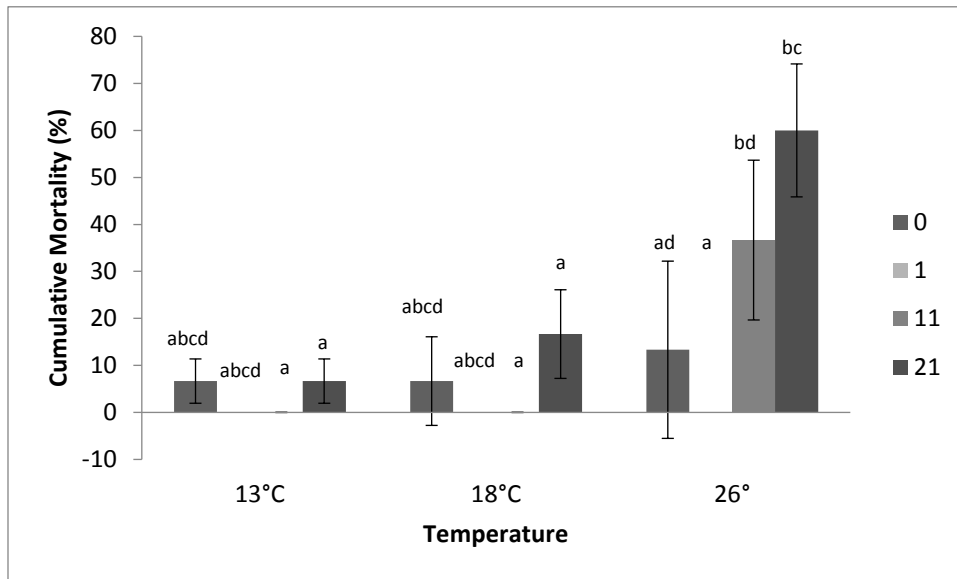
Figure 2. Mean (±std dev) juvenile Atlantic sturgeon SGR (% day-1) after acclimation to three different temperatures (13°C, 18°C, 26°) and four different salinities (0, 1, 11, 21).
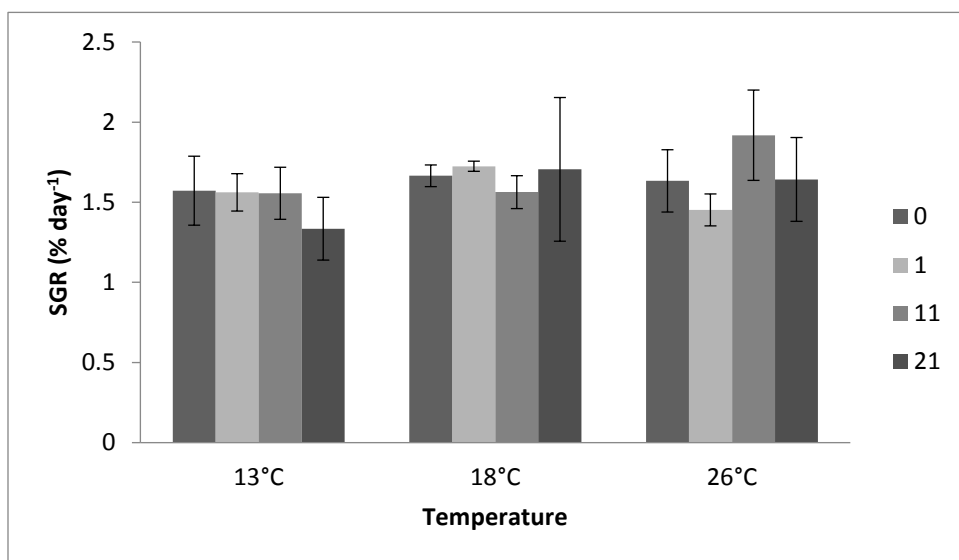
Figure 3. Mean (±std dev) juvenile Atlantic sturgeon lactate concentrations (µmol per g fish wt) after acclimation to three different temperatures (13°C, 18°C, 26°) regardless of salinity treatment. Different letters denote significant differences (ANOVA, $p<0.05$).
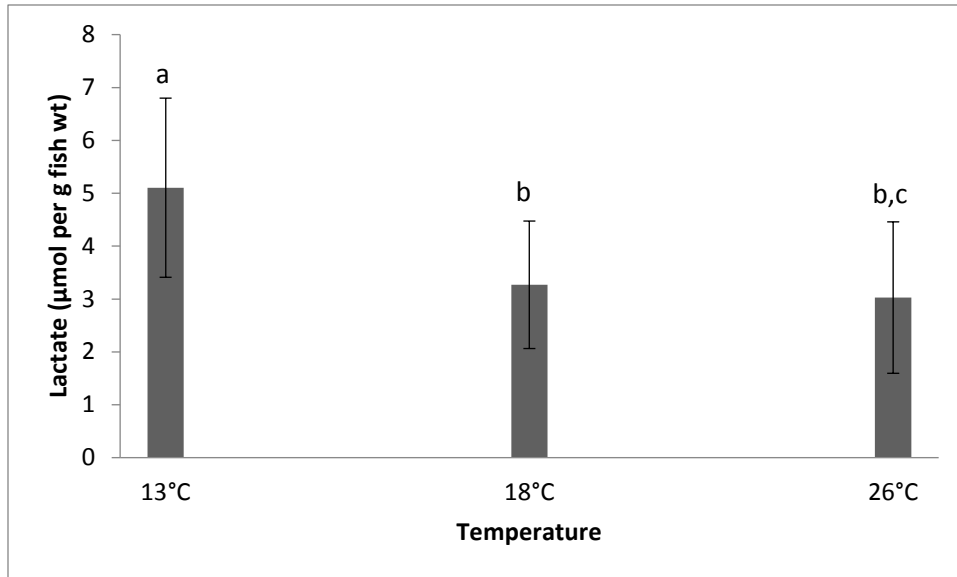
Figure 4. Mean (±std dev) juvenile Atlantic sturgeon lactate concentrations (µmol per g fish wt) after acclimation to four different salinities (0, 1, 11, 21) regardless of temperature treatment. Different letters denote significant differences (ANOVA, $p<0.05$).
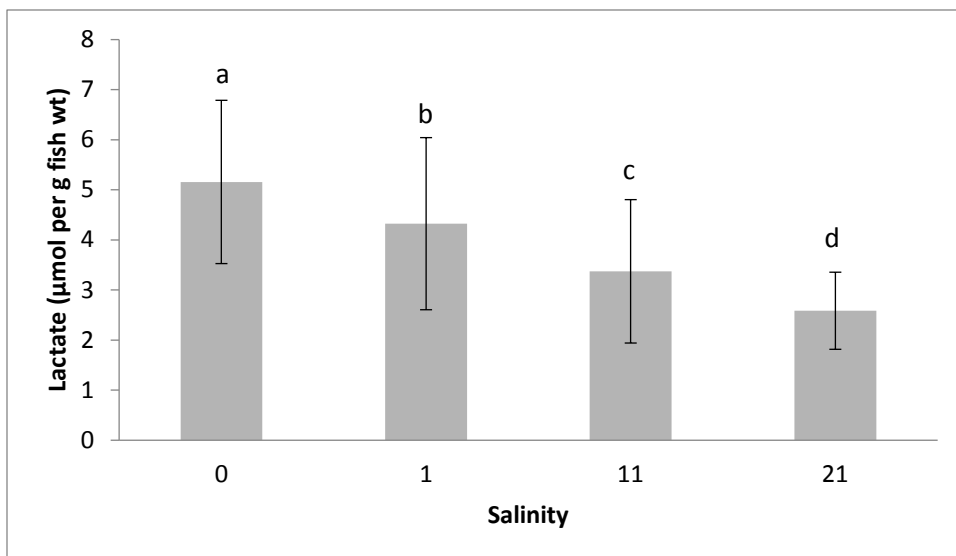
Figure 5. Mean (± std dev) juvenile Atlantic sturgeon lactate concentrations (µmol per g fish wt) after acclimation to three temperatures (13°C, 18°C, 26°) and four salinities (0, 1, 11, 21). Different letters denote significant differences (ANOVA, $p < 0.05$).
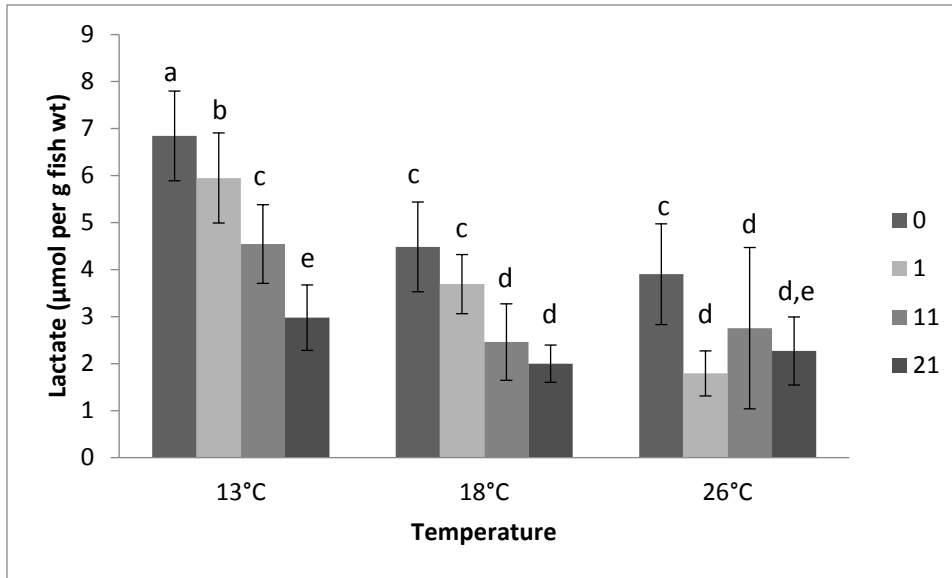
Chapter 4: Testing the sensitivity of Chesapeake Bay Atlantic sturgeon to hypoxia through comparison of modeled and observed habitat distribution

Abstract

The Environmental Protection Agency (EPA) in 2003 established a DO criterion of 60% (5 mg L^{-1}) at 25°C to protect sturgeon species in the Chesapeake Bay. To determine if these criteria are protective of sturgeon, this study tested predictions of Chesapeake Bay Atlantic sturgeon habitat suitability obtained through a bioenergetics model against incidence data for the period 1990-2013. Growth rate was modeled through bioenergetics responses to dissolved oxygen (DO), temperature, salinity, and their interactions. Bottom water data on DO (mg L^{-1}), temperature (°C), and salinity were used to develop values of potential growth rate using Chesapeake Bay Program water quality data (Chesapeake Bay Program 2012) from 1990 – 2013. To compare juvenile potential growth with occurrence data for sub-adult and adult Atlantic sturgeon, capture data from the USFWS reward program was used. Most of the time, sub-adult and adult Atlantic sturgeon were captured at sites predicated to have positive growth potential, however, Atlantic sturgeon captures occurred at DO levels <60% saturation during spring, summer, and fall for the Mid Bay segment and during summer in the Lower Eastern Shore segment. Fifty-four of the 163 captures occurred at DO levels <30% DO saturation. In the Lower Eastern Shore, mean DO levels of occurrence in the summer was higher (64 ± 9%) and ranged between 37% and 75%. During summer months in both these segments, there was a tendency for

captures to occur between 22 and 25°C, although captures were observed between 25 and 27° C during 1997 and 1998 in the Lower Eastern Shore segment and in 1997 in the James River and Mid Bay. Results of this study indicate that sub-adult and adult Atlantic sturgeon may not be as sensitive to these environmental parameters as suggested by past research and bioenergetics models.

Introduction

Geospatial models of habitat suitability represent a powerful means to predict current threats and future recovery of endangered species, for which an empirical basis for evaluation is curtailed by their rare incidence. Further, such models can provide a means to evaluate ecosystem management efforts against the species recovery. As an example, a habitat suitability model for satellite-tagged blue whales (*Balaenoptera musculus)*, an endangered species, identified areas of high use and provided management with relevant data regarding whale activity within shipping lanes and suggested changes to reduce vessel-whale interactions (Irvine et al. 2014; Hazen et al. 2016). As a management strategy to alleviate by-catch, geospatial modelling using satellite tags tracked critically endangered leatherback turtles (*Dermochelys coriacea*) to better understand the spatial and temporal overlap of turtle habitat use and the fishery (Roe et al. 2014; Howell et al. 2015). Modeling efforts for shortnose sturgeon (*Acipenser brevirostrum*) demonstrated that nursery habitat was historically sensitive to improvements in water quality contributing to its likely recovery in the Hudson River (Woodland et al. 2009). Habitat suitability modelling for deep-sea corals and sponges has been used to predict presence outside known areas, yet underscored the limitations of these models when used in data poor

areas where species occurrence data is missing (Anderson et al. 2016). A limitation of habitat suitability models is the lack of absence/presence data for rare species, which is needed to calibrate and validate these models.

Atlantic sturgeon are demersal fish, whose depleted status in many large US estuaries has been tied to ecosystem hypoxia (Secor and Niklitschek 2001; Collins et al. 2002; Niklitschek and Secor 2005). The Chesapeake Bay is subject to persistent hypoxia especially during summer months, and the extent and duration of the hypoxic zone varies annually (Hagy et al. 2004; Batiuk et al. 2009). From 1950-2001, summer hypoxic volume increased and expanded southward towards Virginia (Hagy et al. 2004; Murphy et al. 2011). During this period, Atlantic sturgeon fishery captures were a small fraction of historical levels seen in the late 19th century (Secor 2002). Further, Atlantic sturgeon juveniles and large adults had been absent from fishery independent surveys since 1996 (Grogan and Boreman 1998; Secor et al. 2000), with little evidence of spawning in the Chesapeake Bay for decades. Deterioration of water quality (e.g. dissolved oxygen (DO)) appears to degrade nursery function of systems, creating a recruitment bottleneck (Collins et al. 2000). In the southern range of sturgeon, mortalities related to effects of low DO and high summer temperature may be responsible for extirpations and severe population depressions (Collins et al. 2000). Virginia closed the fishery for sturgeon in 1976 and Maryland in 1996. Fisheries for Atlantic sturgeon in the U.S. were closed by the Atlantic States Marine Fisheries Commission in 1998.

Despite strong expectations for sturgeon extirpation in the Chesapeake Bay, a U.S. Fish and Wildlife Service (USFWS) reward program resulted in thousands of

sturgeon records from 1996-2010 (Welsh et al. 2002; Mangold et al. 2007). The reward program targeted commercial watermen reports of Atlantic sturgeon incidental catches, principally taken in gill nets and pound nets (Table 1). Quantifying the spatial habitat available within the Chesapeake Bay for Atlantic sturgeon is a conservation priority given its status as an endangered species under the U.S. Endangered Species Act (NOAA 2010), yet until recently incidence data was insufficient to develop an empirical basis for their habitat requirements.

The extensive water quality monitoring program within the Chesapeake Bay provided past scientists a unique opportunity to apply a bioenergetics model to advance the understanding of how water quality limits Atlantic sturgeon juvenile production. The Chesapeake Bay Program Water Quality Database contains data from 1984-present from fixed stations providing extensive spatial coverage of the Chesapeake Bay and its tributaries. Atlantic sturgeon are sensitive to environmental hypoxia (Secor and Gunderson 1998; Secor and Niklitschek 2001). Warm conditions in summer and fall can result in a "habitat squeeze" associated with hypoxia and elevated water temperatures (Niklitschek and Secor 2005; Schlenger et al. 2013), providing relevance to a model that can make spatial predictions of habitat suitability on the basis of the interaction of temperature, DO, and salinity. The bioenergetics model was developed through a series of laboratory experiments; and predicted growth rates corroborated through mesocosm trials and behavioral choice experiments (Niklitschek and Secor 2009a; Niklitschek and Secor 2010). Further, early analysis of sturgeon incidence data (1997-2001) suggested that Atlantic sturgeon were routinely captured in areas predicted to have high habitat suitability

(Niklitschek and Secor 2005; Schlenger et al. 2013). However, over the past two decades, Atlantic sturgeon have been captured in the mid-Bay during the summer, an area that routinely experiences below-pycnocline hypoxic conditions and negative production, which disagrees with previous model predictions.

The purpose of this study was to rigorously test predictions of Chesapeake Bay Atlantic sturgeon habitat suitability obtained through the bioenergetics model developed by Niklitschek (2001) against incidence data for the period 1990-2013. Modeled growth values are generated by levels of DO, temperature, salinity, and their interactions. During the summertime, growth values in the mid-Bay are likely driven by DO but in shallower tributaries it may be temperature and its interaction with DO that determines habitat suitability. Based on laboratory studies performed by Niklitschek (2001) and others, the Environmental Protection Agency (EPA) in 2003 established a DO criteria of 60% (5 mg L^{-1}) at 25°C to protect sturgeon species in the Chesapeake Bay (Batiuk et al. 2009). Further, at higher temperatures (<30° C), a more conservative DO concentration threshold of 3.2 mg L^{-1} was designated (Batiuk et al. 2009). However, the Chesapeake Bay routinely experiences DO of <60% saturation and temperatures >25°C yet Atlantic sturgeon have been captured throughout much of the Bay. This suggests that sturgeon may not be as sensitive to these environmental parameters as suggested by past research and bioenergetics models.

To test Chesapeake Bay Atlantic sturgeon sensitivity to summer-fall conditions of hypoxia, I used capture data to assess seasonal habitat being utilized by Atlantic sturgeon, with the assumption that Atlantic sturgeon will be captured in areas

of high growth potential and within physiological boundaries. The USFWS program yielded a rich database on fish size, location (latitude/longitude) and date of capture. Most of the captures comprised sub-adults (500-1500mm TL; average 2.0-7.7 kg) and adults (>1500mm TL; average 26.0 kg) and occurred in mid-Bay, lower Eastern Shore, and James River (Fig, 1). These systems encompass a wide range of water quality conditions and predicted habitat suitabilities. Although I apply a juvenile bioenergetics model to sub-adult and adult Atlantic sturgeon, the DO criteria are protective of all stages of sturgeons so I investigated whether sub-adults and adults are similarly sensitive to DO as previously determined for juveniles. Niklitschek and Secor (2009b) found that larger juveniles (70-300g) conformed to predictions of the model supporting tests of more general application to sub-adult stages. I made predictions of annual and seasonal growth potential both Bay-wide and across tributaries over a 24-year period (1990-2013) and tested these predictions along with interpolated water quality data against sturgeon capture data. Patterns of habitat selectivity based on DO, temperature, and predicted growth levels were tested through quotient analysis (Overholtz et al. 2011). Specific hypotheses included 1) on an annual basis predicted growth will vary inversely with the spatial extent of the hypoxia; 2) predicted growth will be lowest in summer and fall, corresponding to periods with the greatest level of hypoxia; 3) predicted growth will be higher in Virginia and Eastern Shore tributaries than elsewhere in the Chesapeake Bay as suggested by increased observations of sub-adults and adults in these systems; and 4) Atlantic sturgeon will be captured in areas of positive predicted growth within the Chesapeake Bay and avoid areas of low DO (60%) and high temperatures (>25°C).

Methods

Water Quality

Water quality (DO (mg L^{-1}), temperature (°C), and salinity) from the Chesapeake Bay Program's (Chesapeake Bay Program 2012) monitoring stations was interpolated on a seasonal basis from 1990 – 2013 (Fig. 2). Dissolved oxygen was converted using the temperature and salinity associated with DO (mg/L) (see Appendix 1 for formula) to percent saturation for analysis and presentation of results. Water quality parameters sampled at sites below the pycnocline and bottom layers at stations located in polyhaline to tidal freshwater areas were used in the interpolation. At stations where a below-pycnocline sample was recorded, only the bottom layer was used in the analysis. Interpolations were conducted using a distance matrix and kriging (see below) to predict values over the spatial extent of the Chesapeake Bay (Fig. 3) (Appendix 1). This was accomplished using a shapefile of the Chesapeake Bay (Chesapeake Bay Program Monitoring Segments) (Fig. 1). For all interpolation and spatial analyses, the Chesapeake Bay was gridded into 1x1 km^2 cells. As a first step, data available for each water quality variable, temperature, salinity, and DO were aggregated to produce median values per each season and sampled cell. Water quality medians corresponding to non-sampled cells were obtained by interpolation through simple linear kriging, considering the effective distance among sampled and non-sampled cells, and Matern's model of geostatistical covariance (Diggle & Ribeiro 2007). Effective distances among cells "as the water flows" were calculated to avoid interpolations across land by using a transition spatial matrix where conductance was defined as 0.01 for land cells and 0.99 for water cells, and a

minimum cost distance function (Dijkstra 1959) as implemented in the R package

"gdistance" (Van Etten 2012). Matern's model parameters were obtained by fitting

variograms for each water quality variable using maximum likelihood and the R

package "SpatialTools" (French 2014). Seasonal averages for each station was

computed annually for each environmental factor; winter (December – February),

spring (March – May), summer (June – August), fall (September – November).

Resolution for interpolations was 2 km^2. Moving sturgeon captured within a 2 km^2

area may not fully experience the assigned water quality medians. To evaluate this

further, I examined whether a larger grid resolution, 10km^2, would produce similar

results. At 1 body length s^{-1}, a 500-1000 mm TL sturgeon would traverse 10 km^2 in

2.7-5.4 hours (Peake 2008). No substantial differences occurred between 10 km^2 and

2 km^2 grids. Still, an important assumption that I could not test was that predicted

water quality represented a 1-month period, while sturgeon captures represented a

much more abbreviated period of time (<1 d). A 2 km^2 spatial resolution was used

for all analyses in order to keep a fine spatial resolution of all parameters.

Bioenergetics Model

After environmental interpolations were conducted, instantaneous potential

growth of a 14 g Atlantic sturgeon juvenile was modeled using the bioenergetics

model developed by Niklitschek (2001) (Appendix 2). The components of the

bioenergetics model developed by Niklitschek (2001) is G = FC – (RM + SDA +

ACT) – (EG + U); G = growth, FC = food consumption, RM = routine metabolism,

ACT = activity cost, SDA = postprandial metabolism, EG = egestion, and U =

excretion. Temperature, salinity, and DO were found to influence FC, RM, ACT, and

U while SDA and EG depended only on temperature and DO (Niklitschek and Secor 2005). Growth was modeled under maximum consumption (100%) and mortality was minimal since it was only dependent upon abiotic factors (Niklitschek and Secor 2005). Potential growth, defined as the instantaneous amount of biomass per day, was obtained by supplying the bioenergetics model with interpolated environmental values hence potential growth was modeled seasonally for the period of 1990 – 2013.

To compare juvenile potential growth with occurrence data for sub-adult and adult Atlantic sturgeon, capture data from the USFWS reward program was used (Table 1). Here, as opposed to the analysis of long term potential growth, which focused on smaller juvenile production, I modeled predicted growth on the basis of a 300 g sub-adult. Incidences of sub-adult and adult Atlantic sturgeon in the Chesapeake Bay occur in the Chesapeake Bay and the majority of these captures have occurred in the Lower Eastern Shore, Mid Bay, and James River. Atlantic sturgeon captures (n=1562) were recorded with latitude and longitude coordinates from 1997-1998, 2005-2006, representing over half of the captures that occurred in the Chesapeake Bay from 1993- 2010 (Table 1), affording me the opportunity to use the results of the juvenile bioenergetics model to understand habitat utilized by sub-adult and adult Atlantic sturgeon. Gillnets and pound nets were the most common gear type associated with captures in the Lower Eastern Shore and Mid Bay. In the Mid Bay there was an even distribution of captures between the gear types. In the Lower Eastern Shore, pound nets accounted for approximately two times the gillnet captures. In the James River, gillnets were responsible for all captures used in these analyses.

Chesapeake Bay and Tributary Production

Annual and seasonal changes in potential growth of juvenile Atlantic sturgeon in the Chesapeake Bay were analyzed for normality (Shapiro-Wilk test). Data was normally distributed so was further analyzed using two-way analysis of variance in R (R Core Team 2014). Summer and fall growth predictions were evaluated for the influence of summertime and fall hypoxic volume (km^3) (Murphy et al. 2011) through regression analysis. I also compared tributaries across years and seasons using two-way analysis of variance. Tukey Honest Significant Difference (HSD) was used for post-hoc comparisons of main effects and interactions.

Sub-adult and adult Atlantic sturgeon habitat utilization

To better understand habitat utilized by sub-adult and adult Atlantic sturgeon, I matched dates and coordinates of captured sturgeon with monthly growth estimates and interpolated environmental values for each individual capture. My goals were to determine if 1) sub-adult and adult Atlantic sturgeon were captured in habitats supporting higher potential growth than that which was available to them; 2) sub-adult and adult sturgeon were captured within environments falling within the Environmental Protection Agency's (EPA) DO criteria of 60% at 25°C; and 3) sub-adult and adult sturgeon were preferentially selecting specific habitats associated with DO, temperature, salinity, and potential growth. For the first goal, I used a Wilcoxon's signed-rank test to compare median potential growth, DO, temperature, and salinity between sites of capture and available habitat. This analysis was completed seasonally, combining months in which captures occurred, for the Mid Bay, Lower Eastern Shore, and James River for years 1997, 1998, 2005 and 2006;

59

these years comprised the highest number of captures. Segments were separately

analyzed since these systems environments are inherently different. To address EPA

DO thresholds, I first plotted captures by their associated temperature (°C) and DO

(%) data creating a bivariate convex hull which encompassed all available

combinations of these variables. I then overlaid temperature x DO coordinates where

sturgeon were captured. I evaluated whether these incidences of capture occurred

above the 60% DO saturation threshold and below the 25°C threshold.

To quantify habitat selection in the Mid Bay and Lower Eastern Shore, I used

a quotient analysis (Overholtz et al. 2011) to determine preferential selection of

habitat variables seasonally, again combining monthly data for years 1997, 1998,

2005, and 2006. Frequency was computed for intervals of each environmental

parameter. Environmental parameters were divided into intervals based on what

sturgeon may be able to detect in the environment (Niklitschek and Secor 2010).

Dissolved oxygen (%) values were broken into 5% intervals, and salinity and

temperature (°C) were divided into intervals of 2 salinity or °C. In general potential

growth ranged between 0.01 to 0.05 g day^{-1}, so I used an interval of 0.01. Still in

some cases, the range of potential growth was too narrow to divide into 0.01

intervals, and was not analyzed further. Quotient analysis calculated the proportion

(p) of stations (station = 2 km^2 grid) in each environmental interval (pS$_E$) by dividing

the number of stations within each interval by the total number of stations. I then

calculated the proportion of stations positive for Atlantic sturgeon (M) in each

environmental interval (pM$_E$) by dividing the number of stations in the environmental

interval with Atlantic sturgeon by the total number of stations with Atlantic sturgeon.

The quotient value (Q_E) is calculated as pM_E / pS_E with quotient values greater than 1 indicating positive selection. Using the protocol described by Bernal et al. (2007), a resampling procedure (R package "boot") (Davison and Hinkley 1997; Canty and Ripley 2014) was used to compile confidence intervals against which to test for the significance of single quotient estimates. The number of incidences of Atlantic sturgeon in each interval (with original explanatory variables unchanged – DO saturation, temperature, salinity, and potential growth) was randomly selected from a vector of original sturgeon incidences, with replacement. A new pseudo-survey was created and the quotient value for each bin of the explanatory variable retained. I repeated this 999 times and the 0.025 and 0.975 percentiles of the observed quotient values within each interval were used as the confidence intervals for that bin. Quotient values greater than one and above the 0.975 confidence interval were assigned to be areas that Atlantic sturgeon positively selected. Quotient values less than one and below the 0.025 confidence interval were assigned to be areas that Atlantic sturgeon would avoid.

Results

Inter-annual and seasonal variation within Chesapeake Bay potential growth

Mean potential growth rates ranged between 0.026 - 0.034 g day^{-1}, and showed no discernable trend over the 24 years (Fig. 4; Table 3). Highest estimated production occurred in 2012, which was ~30% higher than the lowest production in 2003. Some apparent oscillation in potential growth rates occurred with lower growth periods during 1993-1996 and 2007-2011 and higher growth periods during

1991-1992 and 1997-2000; peak years occurred in 2006 and 2012 (ANOVA; p<0.05; see posthoc contrasts in Figure 4). Multiple regression analysis showed significant effects of water temperature (p<0.01) but not DO (p>0.05) effect on annual growth rate (Appendix 3).

Potential growth rates predicted for juvenile Atlantic sturgeon in the Chesapeake Bay showed strong seasonality ordered as fall > spring > summer > winter (Fig. 5). This held true for all years except in 1992 when summer growth was greater than spring growth (Fig. 6). There was a significant interaction (ANOVA; p<0.05) between year*season. Within all years, winter was lower than spring, summer, and fall growth; and fall growth was significantly different than spring and summer growth. Spring growth was typically higher than summer growth but not significantly so in years 1992, 1996, and 2007 (Fig. 6). Among years, predicted growth rates were more variable in winter (coefficient of variation CV=0.57) and summer (CV=0.70) than for spring (CV=0.34) and fall (CV=0.32) (Fig. 7 a-d).

A separate analysis investigated seasons of greatest hypoxic extent: summer and fall. The hypoxic volume (km^3) in the summer ranged approximately 4.5-11 km^3 from 1990 to 2013. The highest hypoxic volume (~11 km^3) occurred in 2003 and the lowest hypoxic volume (4.5 km^3) occurred in 2012 (Fig. 8). Summer hypoxic volume was significantly and negatively correlated to summer potential growth (n=24; p=<0.05; R^2=0.35) (Fig. 9). Predicted daily production rates declined from 0.028 g day^{-1} at 4.5 km^3 hypoxic volume to 0.023 g day^{-1} at 11 km^3 hypoxic volume. Fall hypoxic volumes were substantially reduced in comparison to summer and ranged

approximately 0-4.2 km^3 (Fig. 10). Estimated fall potential growth of juveniles was not significantly correlated with hypoxic volume (p=0.33).

Tributary Potential Growth

Juvenile Atlantic sturgeon potential growth varied significantly between tributaries (ANOVA; p<0.05) (Fig. 11). I hypothesized that Virginia tributaries and the Lower Eastern Shore would have higher potential growth compared to other Chesapeake Bay segments and indeed, highest estimated potential growth occurred in the York River, Lower Eastern Shore, and James River. Lowest predicted growth occurred in the Mid Bay, Potomac River, and Lower Bay. Tributaries were differently ranked between years (ANOVA; interaction term; p<0.05).

The ranking of tributary potential growth also varied seasonally (ANOVA; interaction term; p<0.05) (Fig. 12). In the winter, Elizabeth River had the highest potential growth rates (mean=0.14 g day^{-1}), likely driven by warmer temperatures there, and was significantly different than all other tributaries except the James River and York River (Table 4). In the spring, York River had the highest potential growth rates (mean=0.043 g day^{-1}) and was significantly different than all tributaries except Elizabeth River (Table 5). In the summer, Lower Eastern Shore had the highest potential growth rates (mean=0.044 g day^{-1}) and was significantly higher than all other tributaries (Table 6). The Patuxent River had the highest fall growth rates (mean=0.058 g day^{-1}) while the Lower Bay had the lowest fall growth rates (mean=0.034 g day^{-1}) and was significantly lower than all tributaries (Table 7).

Sub-adult and adult Atlantic sturgeon habitat utilization

Sub-adult and adult Atlantic sturgeon were captured at sites predicated to have positive growth potential, except for two captures that occurred in the James River in the summertime (Fig. 13). In the Wilcoxon's signed-rank tests of growth potential (Table 8), statistical significance references those seasons and segments where sturgeon were captured in areas of higher/lower growth potential compared to the overall Chesapeake segment in which they were captured (Fig. 14 a-c). Within the Mid Bay segment, Atlantic sturgeon were captured in areas of higher growth compared to the median growth value of the Mid Bay segment during winter, spring and summer. Within the Lower Eastern Shore, Atlantic sturgeon were captured in areas of higher growth in the spring and summer compared to the median growth value of the entire Lower Eastern Shore. In the James River, winter and fall resulted in captures occurring in areas of higher growth compared to the James River growth potential. Individual environmental parameters (DO, temp, and salinity) were also tested between captures sites and segments. No consistent patterns were observed for selection of DO or salinity. However, when significant differences in temperature occurred between capture sites and the segment, temperature at capture sites were significantly lower in the summertime (Fig. 15 a-c).

Bivariate depictions of the temperature and DO levels where sturgeon were captured showed that occurrences at DO levels <60% saturation were observed during spring, summer, and fall for the Mid Bay segment (Fig. 16 a, b) and during summer in the Lower Eastern Shore segment (Fig. 17 a, b). The James River had very few captures in the summer months, limiting inference within that system (Fig.

18). Captured Mid Bay sturgeon in the summer occurred between 23% and 63% DO

saturation (mean: $38 \pm 8\%$) (Fig. 16 b). Fifty-four of the 163 captures occurred at DO

levels <30% DO saturation. In the Lower Eastern Shore, mean DO levels of

occurrence in the summer was higher ($64 \pm 9\%$) and ranged between 37% and 75%

(Fig. 17 b). During summer months in both these segments, there was a tendency for

captures to occur between 22 and 25°C, although captures were observed between 25

and 27 C during 1997 and 1998 in the Lower Eastern Shore segment and in 1997 in

the James River and Mid Bay.

The quotient analysis (Q_e) using summer captures in the Mid Bay segment

showed no evidence for preferential selection of habitats but contrary to expectations,

there was significant avoidance of the highest growth interval (0.015-0.025 g day^{-1};

(Fig. 19 a)). For environmental parameters, significant positive deviations in

expected captures occurred at 24.9-34.9% and 44.9-49.9% DO, 16.1-18.1°C, and

10.5-12.5 salinity (Fig. 19 b-d). The Lower Eastern Shore summer captures were

preferentially caught at sites predicted to yield high growth rates (0.013-0.023 g day^{-1};

(Fig. 20 a)). Significant positive deviations in expected captures occurred at 66.5-

76.5% DO, 19.1-21.1 and 23.1-25.1°C and 10-16 salinity (Fig. 20 b-d). Winter

captures resulted in selection for higher temperatures in the Mid Bay segment (5.9-

7.9°C) and James River (6.7-8.7°C) but no apparent selection for higher temperatures

in the Lower Eastern Shore segment (Fig. 21 a-c). Winter captures, however, did not

select for the highest available temperatures (7.9-9.9 °C) (Fig. 21a).

Discussion

The bioenergetics model's predictions for juvenile growth supported past literature indicating that seasonal and regional habitat suitability rankings were ordered by the severity of hypoxia (Collins et al. 2002; Niklitschek and Secor 2005; Schlenger et al. 2013). Summertime hypoxia in particular caused predicted growth to decline to low levels in certain years and in certain regions, especially the Mid Bay and Upper Eastern Shore segments, as well as the Choptank River. But this prediction of growth sensitivity to hypoxia during warm summer months did not conform well to sub-adult and adult incidence data. Although these stages avoided temperatures predicted to be super-optimal, they frequently occurred in hypoxic conditions (<60% saturation) during summer months. Habitat electivity analysis indicated that during summer, Atlantic sturgeon tended to occupy sub-optimal habitat, even though higher predicted quality habitats were available to them. Although I could only compare juvenile (age-2) production predictions against sub-adult and adult incidence data, my results indicate that Atlantic sturgeon may be more tolerant to summertime hypoxia than laboratory-derived bioenergetics responses would predict.

Chesapeake Bay hypoxia

The extent of hypoxia in the Chesapeake Bay can cause significant ecological harm (Breitburg 1990; Hagy et al. 2004; Davidson et al. 2016) and encompasses an additional constraint on available habitat for estuarine species (Breitburg et al. 2009; Tyler et al. 2009; Schlenger et al. 2013). The seasonal cycle of bottom hypoxia is initiated with increasing thermal stratification and algal blooms in the spring, which

intensify in the summer and dissipate with reduced stratification in the fall and winter (Breitburg et al. 1997; Keister et al. 2000; Testa and Kemp 2014). Seasonally persistent hypoxia occurs in below-pycnocline water, which encompasses 25% of the total volume of the Chesapeake Bay and may last hours to weeks (Keister et al. 2000; Hagy et al. 2004). Maximum hypoxic volume typically occurs in July and August (Murphy et al. 2011; Testa and Kemp 2014). From 1950 – 2001, summer hypoxia (DO <2.0 mg L^{-1}) in the Chesapeake Bay increased significantly from 3.4 x10^9 m^3 to 9.2 x 10^9 m^3; a 2.7-fold increase (Hagy et al. 2004). Most of this increase occurred in the in the mesohaline and is coincident with an expansion southward to polyhaline portions in Virginia (Hagy et al. 2004; Testa and Kemp 2014).

The spatial and temporal extent of hypoxic zones in the Chesapeake Bay is dependent on factors such as season, water column depth, wind conditions, and proximity to freshwater inflows and the influence of the Atlantic Ocean (Breitburg et al. 1997). The Eastern Shore and Virginia tributaries consistently exhibited higher DO levels and potential growth rates compared to other tributaries and segments when ranked annually. In the Mid Bay, seasonal hypoxia occurs most frequently from mid-May to mid-September and newly affected areas include the high-mesohaline and polyhaline regions of the Chesapeake Bay (Hagy et al. 2004; Murphy et al. 2011). Lower predicted growth rates in the Lower Bay where hypoxia was less prevalent relates to super-optimal salinities, which occur there. Niklitschek and Secor (2009) found that juvenile Atlantic sturgeon maximum growth rates shift from salinity 15 to 22 between age-0 and age-1. Although temperatures were warmer in the Lower Bay, they were not super-optimal. Salinity conditions masked the

otherwise acceptable conditions, i.e. adequate DO concentrations and temperatures, for age-0 Atlantic sturgeon growth. In contrast in portions of the Eastern Shore and Virginia tributaries, temperatures may become super-optimal in freshwater reaches but down-tributary brackish bottom waters can be moderately hypoxic (Niklitschek and Secor 2009). Still, these joint temperature-DO conditions are better than most other segments within the Chesapeake Bay where DO can be less than 30%. On the other hand, even in these low DO conditions, Atlantic sturgeon were captured.

Sturgeon responses to hypoxia

Low DO conditions occur at greater frequency in demersal habitats particularly during summer and fall, when sturgeons and other fishes are abundant in the Chesapeake Bay (Table 2; Jung and Houde 2003; Buchheister et al. 2013). These conditions have been associated with lower fish abundance (Tyler and Targett 2007; Stierhoff et al. 2009), spatial distribution (Breitburg 2009; Altenritter et al. 2013), and behavioral changes (Breitburg 1992; Sullivan et al. 2003; Brady et al. 2009; Brady and Targett 2010). Examples include, (1) a positive correlation between DO and the number of juvenile weakfish (*Cynoscion regalis*) collected in Pepper Creek, Delaware, with no collections at DO levels <2 mg L^{-1} (Tyler and Targett 2007); (2) in the Patuxent River, Maryland, densities of bay anchovy (*Anchoa mitchilli*) eggs and larvae, *Chrysaora quinquecirrha* (jellyfish), and zooplankton was lower in bottom water DO <2 mg L^{-1} in comparison to >2 mg L^{-1} (Keister et al. 2000); and (3) low DO has also been shown to cause evacuation behaviors from affected oyster reefs by naked gobies *Gobiosoma bosc* (Breitburg 1992), and summer and winter flounder (Stierhoff et al. 2006; Davidson et al. 2016).

The lack of observed avoidance of hypoxic habitat by sub-adult and adult

Atlantic sturgeon in the Chesapeake Bay was inconsistent with past research showing

lower growth and survival by sturgeons in general (Jenkins et al. 1993; Secor and

Niklitschek 2001; Cech and Doroschov 2004; Niklitschek and Secor, 2009;

Niklitschek and Secor 2010). Field work also provided some support for avoidance

behaviors by sturgeons. Electronically-tagged white sturgeon (*A. transmontanus*) in

the Snake River moved laterally when they encountered low DO levels (<6 mg L^{-1})

(Sullivan et al. 2003). Seasonal distribution of juvenile lake sturgeon (*A fulvescens*)

in Muskegon Lake, Michigan and shortnose sturgeon (*A. brevirostrum*) in Savannah

River, Georgia-South Carolina, were affected by periodic hypoxia in these systems

(Collins et al. 2002; Altenritter et al. 2013). In an earlier analysis of juvenile sturgeon

captured during the 1997-2001 USFWS reward program, Niklitschek and Secor

(2005) observed that these fish avoided persistently hypoxic channel waters. Further,

behavioral responses by juvenile (21-30cm) observed in the laboratory, showed

avoidance of hypoxia (40% DO) (Niklitschek and Secor 2010).

Sturgeon are an ancient family (Bemis et al. 1997) and their ancestral

morphological and physiological traits (less efficient gill ventilation, low cardiac

performance, lower affinity of hemoglobin to oxygen) cause them to be less efficient

in respiration than other fish species (Klyashtorin 1982; Secor and Niklitschek 2001).

Oxyregulation in sturgeons exposed to hypoxia can result in increased ventilation and

routine metabolism, aquatic surface respiration (movement to the upper water

column; Breitburg 1992), and decreased swimming (Secor and Gunderson 1998).

Critical DO concentrations (i.e. the point of inflection of a metabolic response curve

where below that point metabolism and other functions will be constrained) for some

Eurasian sturgeon species ranged between 25-60% saturation but these values

increased as temperature increased (Secor and Niklitschek 2001).

Despite existing laboratory and field evidence for sturgeon sensitivity to

hypoxia, I found that sub-adult and adult Atlantic sturgeon were routinely captured in

DO concentrations <<60%. Indeed, in many instances normoxic bottom habitats were

within several hours travel (c. 10km). Field studies suggest that sub-adult and adult

sturgeon do not exclusively select habitats on the basis of DO conditions. Sub-adult

and adult green sturgeon (*A. medirostris*) in the San Francisco Bay estuary,

California, experienced mean DO concentrations (range 6.5 -8.75 mg L^{-1}) lower than

the mean value of the environment in which they inhabited (Kelly et al. 2007),

indicating, in this case, that sturgeon did not select for the highest DO levels. Lake

sturgeon during the summer in Manistee Lake, Michigan, were observed in areas with

widely ranging DO levels, 1.1 – 13.3 mg L^{-1}, and in some cases were observed in

areas of lower DO even though higher DO levels occurred in adjacent habitats

(Damstra and Galarowicz 2013).

Limiting assumptions of the bioenergetics model

Bioenergetics models provide a framework to determine habitat suitability for

rare species and draw broad inferences on the spatial and temporal distributions of

potential habitats. Still, these models can show biases in their parameterization owing

to experimental design limits, including the size of study organisms, the manner in

which fish are experimentally exposed to water quality conditions, and the measured

responses. Principal limiting assumptions in my analysis include (1) extrapolation of

the bioenergetics model to large sub-adults and adults, (2) exclusive demersal behavior, (3) long-term (weeks) stationarity to assessed water quality conditions measured in Bay segments, and (4) lack of consideration of other physiological or ecological endpoints beyond growth. Still, it should be noted that the bioenergetics model developed by Niklitschek and Secor (2009a) was tested against growth rates observed in microcosms (Niklitschek and Secor 2009b) and the field (Niklitschek and Secor 2005) and in behavioral trials (Niklitschek and Secor (2010).

As sturgeon grow larger and older their tolerance to low DO conditions increase. Jenkins et al. (1995) found age-specific mortality young juvenile shortnose sturgeon: mortality at 2.5 mg L^{-1} was 100%, 96%, and 86% for ages 25, 32, and 64 days post-hatch. At ages 104 and 310 days, mortality was only 12%. Campbell and Goodman (2004) had similar results of Jenkins (1995) where shortnose sturgeon aged (77-134 day-old) showed increased tolerance to low DO conditions as they aged with a LC50 of 2.7mg L^{-1} for 77 day-old sturgeon compared to 2.2 mg L^{-1} for 104 and 134 day-old sturgeon. White sturgeon showed a trend of reduced metabolic response with hypoxia as sturgeon grew larger (0.2g – 63.1g) (Crocker and Cech 1997). Higher susceptibility by small juveniles in comparison to larger juveniles and adults have been observed in other estuarine species (bay anchovy, MacGregor and Houde 1996; Rilling and Houde 1999; largemouth bass, Spoor 1977; striped bass, Brandt et al. 2009) and supports more stringent water quality criteria for nursery habitats than other habitat types (Batuik et al. 2009). In adult fish, exposure to hypoxia results in an initial response to counteract the effects of hypoxia (i.e. increase blood flow) and later responses commence counteractive measure to encourage mechanisms to reduce

71

oxygen update (i.e. reduce activity) (Hughes 1973). One mechanism fish use when exposed to hypoxia is anaerobic ATP production for survival and in this instance larger fish have advantage over smaller fish since their energy stores are greater (Nilsson and Östlund-Nilsson 2008). The bioenergetics model was calibrated using several sizes of juvenile sturgeon in a series of laboratory studies (Niklitschek 2009b). The largest juvenile sturgeon group was 300g whereas the recaptured sturgeon in my sample ranged 2.0-26kg. Niklitschek and Secor (2009b) found that larger juveniles (70-300g) conformed to predictions of the model. Our assumption was this model could also be applied more generally to sub-adult and adult stages. However, the application of the model for sub-adult and adult habitat utilization does not seem be appropriate. The sub-adult and adult sturgeon did not avoid areas of hypoxia within the Chesapeake Bay as observed in laboratory behavior responses and field observations conducted by Niklitschek and Secor (2005; 2010), most likely due to the fact that hypoxia tolerance increases with age in sturgeon and behavioral adaptations.

I further assumed that sturgeon as a demersal fish would spend the majority of the time at the bottom of the water column (Brown and Murphy 2010) and within the segments where water quality measures were taken. Thus, bottom water quality conditions used in the bioenergetics model may not fully represent sturgeon incidence data. It is possible, especially for sturgeon captured in gill nets, that they were captured higher in the water column, possibly above the hypoxic zone. It has been shown that juvenile sturgeon exhibit increased surfacing under hypoxic conditions (Secor and Gunderson 1998). In freshwater environments, Gulf sturgeon are believed

to jump as a form of communication that maintains group structure on summer holding grounds (Sulak et al. 2002). Other research has shown that when sturgeon are making directed movements, they do so farther up in the water column (Balazik et al. 2012). Still, their dependence on benthic substrates and bottom water for spawning, feeding, migration, and refuge from stressful environments (Secor and Niklitschek 2001), makes it plausible that these sturgeon were captured in hypoxic environments within the Chesapeake Bay. At 1 body length s^{-1}, a 500-1000 mm TL sturgeon would traverse 10 km^2 in 2.7-5.4 hours (Peake 2008). The mid-Bay segment is approximately 128 km north to south. A 1000 mm TL sturgeon traversing this segment if entering from the lower Bay would take approximately 35 hours to reach the upper Bay. Hence, Atlantic sturgeon captured within this segment are very likely to have been exposed to sub-optimal conditions when captured, yet Atlantic sturgeon were routinely captured in the mid-Bay during all seasons, including the summer when hypoxia was present throughout this segment. Behavioral adaptations, such as surficial respiration, may be displayed when sturgeon encounter hypoxic areas.

The sturgeon occurrence data I used to determine habitat utilization of sturgeon in the Chesapeake Bay did not include the depth at which individual sturgeon were captured. Depth information is a missing component of this study and would provide valuable insight in the behavior of sturgeon when hypoxic areas are encountered. In addition to depth information for sturgeon, water quality data collected at a finer temporal and spatial scale, corresponding to the resolution of capture data would have reduced uncertainty in my inferences. Kraus et al. 2015 demonstrated that striped bass avoided areas of hypoxia but inhabited areas of super-

optimal temperatures when these were the only areas where normoxia occurred. Sufficient tracking or observation data is also necessary to fully utilize models predicting habitat utilization (Hazen et al. 2016). However, even when large data sets are used, ongoing validation of the models are necessary, especially if climate changes beyond the scope of the study (Hazen et al. 2016), which may change species distribution, both spatially and temporally.

The bioenergetics model was based on an ecophysiological construct on the limiting (curtailing) effect of DO on growth, but controlling influences of temperature, particularly super-optimal thermal habitats could over-ride avoidance of hypoxic habitats. Atlantic sturgeon in the Chesapeake Bay were occasionally captured in temperatures >25°, however most summertime captures occurred between 22-25°C and temperature at capture sites was significantly lower than the average water temperature within those areas. However, avoidance of higher temperatures by Atlantic sturgeon in the Chesapeake Bay may have caused them to occur in habitats with sub-optimal DO. This was evident in the Mid Bay where sturgeon showed significant positive deviations in expected captures at 24.9-34.9% and 44.9-49.9% DO. In choice studies, Niklitschek and Secor (2010) showed juvenile Atlantic sturgeon (21-30cm) avoided 28°C and displayed a preference for 12°C and 20°C. Fish in general have an upper and lower avoidance temperature where within these extremes is their preferred temperature (Coutant 1977). Preferred temperatures as determined in a laboratory setting can be offset by several factors such as food availability, competition, and DO requirements (Coutant 1987). While the distribution of Acipenseriformes in North America extends over an area with

temperature variation of up to 30°C, this taxonomic order prefers and performs optimally at temperatures <25°C (Cech and Doroshov 2004), typically between 16-24°C for Atlantic sturgeon (Schlenger et al. 2013). Many studies focus on early (Cech et al. 1984; Zhang and Kieffer 2014) and juvenile (Hung et al. 1993; Lankford et al. 2003; Kieffer et al. 2014) life stages of sturgeon to determine temperature preference and tolerance. Using incidence data for sub-adult and adult sturgeon is one method to understand habitat preferences of these life stages but it is difficult to determine all the factors that may be influencing their presence in temperature ranges. In this study, captures denote a specific period in time when sturgeon were utilizing the area. Interpolating data on a larger temporal and spatial scale can do not capture daily changes in water quality (i.e. DO, temperature, salinity) and inaccurately portray sturgeon as being captured under sub-optimal DO or temperature conditions. Additionally, bioenergetics models account for physiological effects from specific water quality criteria but these models do not account for behavioral adaptations that sturgeon may possess for foraging, spawning, and migration.

Rather than responding immediately to stressful dissolved and oxygen conditions, adult Atlantic sturgeon may be enduring such conditions to accommodate a fall spawning behavior. Adults may be tolerating sub-optimal DO and super-optimal temperatures to time the production of their progeny when environmental parameters are in a suitable range to increase survival and growth of their young (Bonga 1997). Fall spawning may be the dominant spawning behavior in Chesapeake Bay and South Atlantic Bight spawning tributaries (Balazik et al. 2012; Balazik and Musick 2015; Smith et al. 2015; Ingram and Peterson 2016). In the James River, fish were routinely

captured in temperature >25°C in the lower portion of the James River where Atlantic sturgeon were staging during summer months prior to spawning between August and early October (Balazik and Musick 2015). Pacific salmon life cycle depends on appropriately timing spawning events so mismatch between the needs of the progeny does not occur but this may put adults in less than favorable conditions (i.e., higher energetic costs, higher predation risk, thermal stress) (Crozier et al. 2008). Northern populations of American shad (*Alosa sapidissima*) spawn in environments that have harsher temperatures and more environmental variability compared to those populations that spawn in their southern geographic range and as a result have different life history strategies (Leggett and Carscadden 1978). Fish time their spawning to take place when conditions would be favorable for their offspring (Cushing 1990).

Offspring survival and growth potential may not be the only reason Atlantic sturgeon are present in sub-optimal habitats; optimal foraging opportunities may occur in these areas. I modelled growth of Atlantic sturgeon under the assumption that prey was not limited, however benthic prey densities would vary seasonally (Long and Seitz 2008; Diaz and Rosenberg 2008). In the Chesapeake Bay, changes in predator-prey interactions may depend on the DO tolerance of both the predator (i.e. swimming and feeding behavior) and prey (i.e. escape behavior), influencing prey-predator relationships (Breitburg et al. 1997; Keister et al. 2000). Sufficient prey abundance and density may compensate for the negative effects DO and temperature have on growth (Costantini et al. 2008; Thompson and Rice 2013; Kraus 2015). Benthic invertebrates may respond to hypoxia by moving up in the sediment

column creating an opportunity for predators to increase foraging opportunities (Pihl et al. 1992; Baustian et al. 2009; Craig 2012). Baird and Ulanowicz (1989) found predators of macrobenthos remove 40% of the summer and 45% of the fall production of their prey, corresponding to peak benthic production in the Chesapeake Bay. The closer proximity of prey to the surface would reduce search time need for predators and may result in a shift where predation rates are higher during periods of episodic hypoxia (Seitz et al. 2003; Long and Seitz 2008). However, there may be a narrow range of hypoxic conditions where predators can take advantage of prey as their tolerance to low dissolved oxygen is usually less than that of benthic organisms (Diaz and Rosenberg 2008). Yet, areas affected by hypoxia typically recover afterwards and increases in benthic populations are related to recruitment events timed to increase in input of organic matter (i.e. spring and fall blooms) (Diaz and Rosenberg 2008). Sturgeon growth was highest in the spring and fall due to optimal water quality parameters associated with these seasons. The addition of increased foraging opportunities may increase growth potential of Atlantic sturgeon. In addition, sturgeon are demersal fish and may take advantage of increased foraging opportunities by accessing hypoxic habitats. Future studies should evaluate prey availability against Atlantic sturgeon occurrence to better understand sub-optimal habitat utilization by Atlantic sturgeon in the Chesapeake Bay.

Sturgeon recovery implications

The EPA established an instantaneous minimum of 5 mg L^{-1} DO to be protective of survival and growth of juveniles and spawning adults of fish species inhabiting the Chesapeake Bay, including shortnose and Atlantic sturgeon (Batuik et

al. 2009). At temperatures >25°C this translates to DO levels > 60%. Results from this study show Atlantic sturgeon are routinely captured in Bay segments, which do not meet these thresholds. Although various studies have shown that juvenile Atlantic sturgeon are sensitive to low DO in terms of survival, growth and avoidance; this study shows sub-adult and adult Atlantic sturgeon are capable of utilizing these environments. One piece of critical information is missing – duration of time spent in these conditions. The capture information used in this study provided a snapshot of habitat utilized by Atlantic sturgeon and assumed long-term (days-weeks) stationarity in assessed habitats. Telemetry, especially mobile telemetry data, would provide a more complete picture of the habitat utilized by Atlantic sturgeon, especially if multiple sizes/age classes could be tagged within the Chesapeake Bay. Small juvenile growth and survival is more sensitive to hypoxia than sub-adult and adult responses, which was the focus of my study. Unfortunately, because only a handful of age-0 juveniles have ever been captured in the Chesapeake Bay, I was unable to test bioenergetics predictions for this critical life history stage. Thus, it may be precautionary to retain current water quality standards, which are specific to the nursery function of juveniles, until we can evaluate juvenile growth responses in the field.

Specific to juvenile production, improvements to water quality through limits to nutrient inputs could have benefits to sturgeon recovery. During the time period I studied (1990-2013), I found summer hypoxic volume (km^3) was negatively correlated to modelled age-0 juvenile Atlantic sturgeon growth rates. This suggests that increases in overall DO levels could increase habitats to Atlantic sturgeon. The

severity of late summer hypoxic volume has been decreasing when compared to previous decades (Murphy et al. 2011). If these conditions dissipate early, the Chesapeake Bay may higher starting point for DO concentrations in the fall creating a longer time period for Atlantic sturgeon growth before the onset of winter. Similar assumptions could be made for summer hypoxic volume; higher initial concentrations of DO at the beginning of June could decrease summer hypoxic volume (Murphy et al. 2011) creating more Atlantic sturgeon habitat.

Summary and future studies

In conclusion, the bioenergetics model predicted key seasonal and regional patterns of sub-adult and adult distribution data: incidences were higher in spring and fall than in summer and winter when hypoxia and temperatures were predicted to limit growth rates; and captures were greater in regions with less severe summertime hypoxia (Lower Eastern Shore and the James River) than those with higher bottom hypoxia (Mid-Bay). On the other hand, sturgeon in summer and fall months frequently occurred in hypoxic warm conditions where poor juvenile growth was predicted. This mismatch has significant management implications as current water quality criteria in the Chesapeake Bay and elsewhere have been enacted at DO and temperature levels, which are intended to be protective of sturgeon but may be overly conservative for sub-adult and adult stage Atlantic sturgeon. Still, there remain key uncertainties in principal assumptions related to how laboratory studies and the bioenergetics model have been applied. In this study, I applied the bioenergetics model, calibrated for juvenile Atlantic sturgeon (<300mm TL) to incidences of sub-adult and adult sturgeon (>500mm TL). Future research should focus on applying the

results of the bioenergetics model to incidences of juvenile Atlantic sturgeon in the Chesapeake Bay. Additionally, I made the assumption that Atlantic sturgeon were captured below-pycnocline in these hypoxic areas and remained in assessed regions for days to weeks. Future telemetry studies should utilize depth-transponding tags to determine what parts of the water column are utilized by Atlantic sturgeon within the Chesapeake Bay, especially during the summer season when much of the mainstem of the Chesapeake Bay contains unsuitable habitat. Telemetry data can also provide behavioral patterns associated with these sub-optimal habitats such as time spent in sub-optimal conditions, movement within the water column, and avoidance of specific areas. This information would provide valuable information to management to determine if the water quality criteria established for the Chesapeake Bay to be protective of sturgeon species is protective of these critical life stages or if the criteria overly conservative. The moderately high incidence of larger sturgeon during summer months suggests compensating factors for their occurrence. New discoveries on their broad summer distribution and fall spawning behaviors emphasize the need to understand if reproductive staging and feeding are offsetting direct physiological responses to DO, temperature, and salinity that drive incidences of sub-adult and adult Atlantic sturgeon in presumed sub-optimal environments.

References

Altenritter, M.E.L., A.C. Wieten, C.R. Ruetz III, K.M. Smith. 2013. Seasonal spatial distribution of juvenile lake sturgeon in Muskegon Lake, Michigan, USA. Ecology of Freshwater Fish 22: 467-478.

Anderson, O.F., J.M. Guinotte, A.A. Rowden, M.R. Clark, S. Mormede, A.J. Davies, and D.A. Bowden. 2016. Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: Implications for the use of broad-scale models in fisheries management. Ocean and Coastal Management 120: 110-126.

Baird, D. and R.E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecological Monographs 59(4): 329-364.

Balazik, M.T., K.J. Reine, A.J. Spells, C.A. Fredickson, M.L. Fine, G.C. Garman and S.P. McIninch. 2012. The potential for vessel interactions with adult Atlantic sturgeon in the James River, Virginia. North American Journal of Fisheries Management 32(6): 1062-1069.

Balazik, M.T. and J.A. Musick. 2015. Dual annual spawning races in Atlantic sturgeon. PLOS One 10(5). E0128234. Doi: 10.1371/journal.pone.0128234

Batiuk, R.A., D.L. Breitburg, R.J. Diaz, T.M. Cronin, D.H. Secor, and G. Thursby. 2009. Derivation of habitat-specific dissolved oxygen criteria for Chesapeake Bay and its tidal tributaries. Journal of Experimental Marine Biology and Ecology 381:S204-S215.

Baustian, M.M., J.K. Craig, N.N. Rabalais. 2009. Effects of summer 2003 hypoxia on macrobenthos and Atlantic croaker foraging selectivity in the northern Gulf of Mexico. Journal of Experimental Marine Biology and Ecology 381:S31-S37.

Bemis, W.E., E.K. Findeis, and L. Grande. 1997. An overview of Acipenseriformes. Environmental Biology 48:25-71.

Bernal. M., Y. Stratoudaki, S. Coombs, M.M. Angelico, A. Lago de Lanzós, C. Porteiro, Y. Sagarminaga, M. Santos, A. Uriarte, E. Cunha, L. Valdés, and D. Borchers. 2007. Sardine spawning off the European Atlantic coast: Characterization of and spatio-temporal variability in spawning habitat. Progress in Oceanography 74: 210-227.

Bonga, S.E.W. 1997. The stress response of fish. Physiological Reviews 77(3): 591-625.

Brady, D.C. and T.E. Targett. 2010. Characterizing the escape response of juvenile summer flounder *Paralichthys dentatus* to diel-cycling hypoxia. Journal of Biology 77: 137-152.

Brady, D.C., T.E. Targett, and D.M. Tuzzolino. 2009. Behavioral responses of juvenile weakfish (*Cynoscion regalis*) to diel-cycling hypoxia: swimming speed, angular correlation, expected displacement, and effects of hypoxia acclimation. Canadian Journal of Fisheries and Aquatic Sciences 66: 415-424.

Brandt, S.B., M. Gerken, K.J. Hartman, E. Demers. 2009. Effects of hypoxia on food consumption and growth of juvenile striped bass (*Morone saxatilis*). Journal of Experimental Marine Biology and Ecology 381: S143-S149.

Breitburg, D.L. 1990. Near-shore hypoxia in the Chesapeake Bay: patterns and relationships among physical factors. Estuarine, Coastal, and Shelf Science 30: 593-609.

Breitburg, D.L. 1992. Episodic hypoxia in Chesapeake Bay: Interacting effects of recruitment, behavior, and physical disturbance. Ecological Monographs 62(4): 525-546.

Breitburg, D.L., T. Loher, C.A. Pacy, and A. Gerstein. 1997. Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. Ecological Monographs 67(4): 489-507.

Breitburg, D.L., D.W. Hondorp, L.A. Davias, and R.J. Diaz. 2009. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. Annual Review of Marine Science 1: 329-349.

Brown, J.J. and G.W. Murphy. 2010. Atlantic sturgeon vessel-strike mortalities in the Delaware estuary. Fisheries 35(2): 72-83.

Buchheister, A., C.F. Bonzek, J. Gartland, R.J. Latour. 2013. Patterns and drivers of the demersal fish community of Chesapeake Bay. Marine Ecology Progress Series 482:161-180.

Campbell, J.G. and L.R. Goodman. 2004. Acute sensitivity of juvenile shortnose sturgeon to low dissolved oxygen concentrations. Transactions of the American Fisheries Society 133:727-776.

Canty, A. and B. Ripley. 2014. Boot: Bootstrap R (S-Plus) Functions. R package version 1.3-13.

Cech Jr., J.J., S.J. Mitchell, R.E. Wragg. 1984. Comparative growth of juvenile white sturgeon and striped bass: Effects of temperature and hypoxia. Estuaries 7(1):12-18.

Collins, M.R., S. G. Rogers, T.I.J. Smith, and M.L. Moser. 2000. Primary factors affecting sturgeon populations in the southeastern United States: Fishing mortality and degradation of essential habitats. Bulletin of Marine Science 66(3): 917-928.

Collins, M.R., W.C. Post, D.C. Russ, and T.I.J. Smith. 2002. Habitat use and movements of juvenile Shortnose sturgeon in the Savannah River, Georgia-South Carolina. Transactions of the American Fisheries Society 131: 975-979.

Constantini, M., S.A. Ludsin, D.M. Mason, X.S. Zhang, W.C. Boicourt, and S.B. Brandt. 2008. Effect of hypoxia on habitat quality of striped bass (*Morone saxatilis*) in Chesapeake Bay. Canadian Journal of Fisheries and Aquatic Sciences 65(5): 989-1002.

Coutant, C.C. 1977. Compilation of temperature preference data. Journal of the Fisheries Research Board of Canada 34: 739-745.

Coutant. C.C. 1987. Thermal preference: when does an asset become a liability? Environmental Biology of Fishes 18(3): 161-172.

Craig, J.K. 2012. Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. Marine Ecology Progress Series 445: 75-95.

Crocker, C.E. and J.J.Cech, Jr. 1997. Effects of environmental hypoxia on oxygen consumption rate and swimming activity in juvenile white sturgeon, *Acipenser transmontanus*, in relation to temperature and life intervals. Environmental Biology of Fishes 50: 383-389.

Crozier, L.G., A.P. Hendry, P.W. Lawson, T.P. Quinn, N.J. Mantua, J. Battin, R.G. Shaw, and R.B. Huey. 2008. Evolutionary Applications 252-270.

Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 26: 249-293.

Damstra, R.A. and T.L. Galarowicz. 2013. Summer habitat use by Lake sturgeon in Manistee Lake, Michigan. Transactions of the American Fisheries Society 142: 931-941.

Davidson, M.I., T.E. Targett, and P.A. Grecay. 2016. Evaluating the effects of diel-cycling hypoxia and pH on growth and survival of juvenile summer flounder *Paralichthys dentatus*. Marine Ecology Progress Series 556: 223-235.

Davison, A.C. and Hinkley, D.V. 1997. Bootstrap methods and their applications. Cambridge University Press, Cambridge.

Diaz, R.J. and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. Science, New Series 321(5891): 926-929.

Diggle, P. and P.J. Ribeiro. 2007. Model-based geostatistics. Springer.

Dijkstra, E.W. 1959. A note on two problems in connexion graphs. Numerische mathematic, 1: 269-271.

Environmental Protection Agency. 2003. Ambient Water Quality Criteria for Dissolved Oxygen, Water Clarity and Chlorophyll a for the Chesapeake Bay and Its Tidal Tributaries.

French, J. 2014. SpatialTools: Tools for spatial data analysis. R package version 0.5.8. https://CRAN-R-project.org/package=SpatialTools

Grogan, C. S., and J. Boreman. 1998. Estimating the probability that historical populations of fish species are extirpated. North American Journal of Fisheries Management 18(3): 522-529.

Chesapeake Bay Program. 2012. "Guide to using Chesapeake Bay Program water quality monitoring data," Chesapeake Bay Program. EPA 903-R-12-001 (1 February 2012), p. 1-155.

Hagy, J.D., W.R. Boyton, C.W. Keefe, and K.V. Wood. 2004. Hypoxia in Chesapeake Bay, 1950-2001: long-term change in relation to nutrient loading and river flow. Estuaries 27(4): 634-658.

Hanks, D.M. and D.H. Secor. 2011. Bioenergetic responses of Chesapeake Bay white perch (*Morone americana*) to nursery conditions of temperature, dissolved oxygen, and salinity. Marine Biology 158: 805-815.

Hazen, E.L., D.M. Palcios, K.A. Forney, E.A. Howell, E. Becker, A.L. Hoover, L. Irvine, M. DeAngelis, S.J. Bograd, B.R. Mate, and H. Bailey. 2016. WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. Journal of Applied Ecology doi:10.1111/1365-2664.12820

Howell, E.A., A. Hoover, S.R. Benson, H. Bailey, J.J. Polovina, J.A. Seminoff and P.H. Dutton. 2015. Enhancing the TurtleWatch product for leatherback sea turtles, a

dynamic habitat model for ecosystem-based management. Fisheries Oceanography 24(1): 57-68.

Hughes, G.M. 1973. Respiratory responses to hypoxia in fish. American Zoologist 13(2): 475-489.

Hung, S.S.O., P.B. Lutes, A.A Shqueir, and F.S. Conte. 1993. Effect of feeding rate and water temperature on growth of juvenile white sturgeon (*Acipenser transmontanus*). Aquaculture 115: 197-303.

Ingram, E.C. and D.L. Peterson. 2016. Annual spawning migrations of adult Atlantic sturgeon in the Altamaha River, Georgia. Marine and Coastal Fisheries 8(1): 595-606.

Irvine L.M., Mate B.R., Winsor M.H., Palacios D.M., Bograd S.J., D.P. Costa, H. Bailey. 2014. Spatial and temporal occurrence of blue whales off the U.S. West Coast, with implications for management. PLoS ONE 9(7): e102959.

Jenkins, W.E., T.I.J Smith, L.D Heyward, and D.M. Knott. 1995. Tolerance of shortnose sturgeon, *Acipenser brevirostrum*, juveniles to different salinity and dissolved oxygen concentrations. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 47: 476-484.

Jung, S., and E. D. Houde. 2003. Spatial and temporal variabilities of pelagic fish community structure and distribution in Chesapeake Bay, USA. Estuarine, Coastal and Shelf Science 58:335-351.

Kieffer, J.D., F.M, Penny, V. Papadopoulos. 2014. Temperature has a reduced effect on routine metabolism rates of juvenile shortnose sturgeon (*Acipenser brevirostrum*). Fish Physiology and Biochemistry 40: 551-559.

Keister, J., E.D. Houde, D.L. Breitburg. 2000. Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. Marine Ecology Progress Series 205: 43-59.

Kelly, J.T., A.P. Klimley, and C.E. Crocker. 2007. Movements of green sturgeon, *Acipenser medirostris*, in the San Francisco Bay estuary, California. Environmental Biology of Fishes 79: 281-295.

Kraus, R.T., D.H. Secor, and R.L. Wingate. 2015. Testing the thermal-niche oxygen-squeeze hypothesis for estuarine striped bass. Environmental Biology of Fishes 98: 2083-2092.

Lankford, S.E., T.E. Adams, J.J. Cech, Jr. 2003. Time of day and water temperature modify the physiological stress response in green sturgeon, *Acipenser medirostris*. Comparative Biochemistry and Physiology Part A 135: 291-302.

Leggett, W.C. and J.E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. Journal of the Fisheries Research Board of Canada 35: 1469-1478.

Long, W.C. and R.D. Seitz. 2008. Trophic interactions under stress: hypoxia enhances foraging in an estuarine food web. Marine Ecology Progress Series 362: 59-68.

Mangold. M., S. Eyler, S. Minkkinen, and B. Richardson. 2007. Atlantic sturgeon reward program for Maryland waters of the Chesapeake Bay and tributaries 1996-2006. U.S. Fish and Wildlife Service, Maryland Fishery Resources Office.

Moser, M.L. and S.W. Ross. 1995. Habitat use and movements of Shortnose and Atlantic sturgeons in the Lower Cape Fear River, North Carolina. Transactions of the American Fisheries Society. 124: 225-234.

Murphy, R.R., W.M. Kemp, W.P. Ball. 2011. Long-term trends in Chesapeake Bay seasonal hypoxia, stratification, and nutrient loading. Estuaries and Coasts 34: 1293-1309.

Niklitschek, E.J. 2001. Bioenergetics modeling and assessment of suitable habitat for juvenile Atlantic and shortnose sturgeons (*Acipenser oxyrinchus* and *A. brevirostrum*) in the Chesapeake Bay. Doctoral dissertation. University of Maryland at College Park, College Park.

Niklitschek, E.J. and D.H. Secor. 2005. Modeling spatial and temporal variation of suitable nursery habitats for Atlantic sturgeon in the Chesapeake Bay. Estuarine, Coastal and Shelf Science 64: 135-148.

Niklitschek, E.J. and D.H. Secor. 2009a. Dissolved oxygen, temperature and salinity effects on the ecophysiology and survival of juvenile Atlantic sturgeon in estuarine waters: II. Model development and testing. Journal of Experimental Marine Biology and Ecology 381: S161-S172.

Niklitschek, E.J. and D.H. Secor. 2009b. Dissolved oxygen, temperature and salinity effects on the ecophysiology and survival of juvenile Atlantic sturgeon in estuarine waters: I. Laboratory results. Journal of Experimental Marine Biology and Ecology 381: S150-S160.

Niklitschek, E.J. and D.H. Secor. 2010. Experimental and field evidence of behavioral habitat selection by juvenile Atlantic *Acipenser oxyrinchus oxyrinchus* and shortnose *Acipenser brevirostrum* sturgeons. Journal of Fish Biology 77: 1293-1308.

Nilsson, G.E. and S. Östlund-Nilsson. 2008. Does size matter for hypoxia tolerance in fish? Biological Reviews 83: 173-189.

NOAA. 2010. Endangered and Threatened Wildlife and Plants; Proposed Listings for Two Distinct Population Segments of Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the Southeast. Federal Register 75 (193): 61904-61929.

Overholtz, W.J., J.A. Hare and C.M. Keith. 2011. Impacts of interannual environmental forcing and climate change on the distribution of Atlantic mackerel on the U.S. Northeast Continental Shelf. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 3(1): 219-232.

Peake, S.J. 2008. Swimming performance and behavior of fish species endemic to Newfoundland and Labrador: A literature review for the purpose of establishing design and water velocity criteria for fishways and culverts. Canadian Manuscript Report of Fisheries and Aquatic Sciences, No. 2843.

Pihl, L., S.P. Baden, R.J. Diaz, and L.C. Schaffner. 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea. Marine Biology 112: 349-361.

R Core Team. 2014: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Roe, J.H., S.J Morreale, F.V. Paladino, G.L. Shillinger, S.R. Benson, S.A. Eckert, H. Bailey, P.S. Tomillo, S.J. Bograd, T. Eguchi, P.H. Dutton, J.A. Seminoff, B.A. Block, and J.R. Spotila. 2014. Predicting bycatch hotspots for endangered leatherback turtles on longlines in the Pacific Ocean. Proceedings of the Royal Society B 281: 20132559.

Schlenger, A.J., E.W. North, Z. Schlag, Y. Li, D.H. Secor, K.A. Smith and E.J. Niklitschek. 2013. Modeling the influence of hypoxia on the potential habitat of Atlantic sturgeon *Acipenser oxyrinchus*: a comparison of two methods. Marine Ecology Progress Series 483: 257-272.

Secor, D.H. 2002. Atlantic sturgeon fisheries and stock abundances during the late 19th century. American Fisheries Society Symposium 28: 89-98.

Secor, D.H. and T.E. Gunderson. 1998. Effects of hypoxia and temperature on survival, growth, and respiration of juvenile Atlantic sturgeon, *Acipenser oxyrinchus*. Fishery Bulletin 96(3): 603-613.

Secor, D.H., E.J. Niklitschek, J.T. Stevenson, T.E. Gunderson, S.P. Minkkinen, B. Richardson, B. Florence, M. Mangold, J. Skjeveland, A. Henderson-Arzapalo. 2000. Dispersal and growth of yearling Atlantic sturgeon, *Acipenser oxyrinchus*, released into Chesapeake Bay. Fisheries Bulletin 98: 800-810.

Secor, D.H. and E.J. Niklitschek. 2001. Sensitivity of sturgeons to environmental hypoxia: a review of physiological and ecological evidence. Pp. 61-78 *In*: Thurston, R.V. (Ed.), Fish Physiology, Toxicology, and Water Quality. Proceeding of the Sixth International Symposium, La Paz, Mexico, 22-26 Jan. 2001.

Seitz, R.D., L.S. Marshall, A.H. Hines, and K.L. Clark. 2003. Effects of hypoxia on predator-prey dynamics of the blue crab *Callinectes sapidus* and the Baltic clam *Macoma balthica* in Chesapeake Bay. Marine Ecology Progress Series 257: 179-188.

Smith, J.A., H.J. Flowers, and J.E. Hightower. 2015. Fall spawning of Atlantic sturgeon in the Roanoke River, North Carolina. Transactions of the American Fisheries Society 144(1): 48-54.

Spoor, W.A. 1977. Oxygen requirements of embryos and larvae of the largemouth bass, *Micropterus salmoides* (Lacépède). Journal of Fish Biology 11(2): 77-86.

Stierhoff, K.L., T.E. Targett, K. Miller. 2006. Ecophysiological responses of juvenile summer and winter flounder to hypoxia: experimental and modeling analyses of effects on estuarine nursery quality. Marine Ecology Progress Series 325: 255-266.

Stierhoff, K.L., R.M. Tyler, T.E. Targett. 2009. Hypoxia tolerance of juvenile weakfish (*Cynoscio regalis*): laboratory assessment of growth and behavioral avoidance reponses. Journal of Experimental Marine Biology and Ecology 381: S173-S179.

Sullivan, A.B., H.I. Jager, and R. Myers. 2003. Modeling white sturgeon movement in a reservoir: the effect of water quality and sturgeon density. Ecological Modelling 167: 97-114.

Testa, J.M. and W.M. Kemp. 2014. Spatial and temporal patterns of winter-spring oxygen depletion in Chesapeake Bay bottom water. Estuaries and Coasts 37: 1432-1448.

Thompson, J.S. and J.A. Rice. 2013. The relative influence of thermal experience and forage availability on growth of age 1-5 striped bass in two southeastern reservoirs. American Fisheries Society Symposium 80: 93-120.

Tyler. R.M. and T.M. Targett. 2007. Juvenile weakfish *Cynoscion regalis* distribution in relation to diel-cycling dissolved oxygen in an estuarine tributary. Marine Ecology Progress Series 333: 257-269.

Tyler, R.M., D.C. Brady, T.E. Targett. 2009. Temporal and spatial dynamics of diel-cycling hypoxia in estuarine tributaries. Estuaries and Coasts 32: 123-145.

Van Etten, J. 2012. gdistance: Distances and routes on geographical grids. http://CRAN.R-project.org/package=gdistance. R package version, 1-1.

Welsh, S.A., S.M. Eyler, M.F. Mangold, and A.J. Spells. 2002. Capture locations and growth rates of Atlantic sturgeon in the Chesapeake Bay. American Fisheries Society Symposium 28: 183-194.

Woodland, R.J., D.H. Secor, and E.J. Niklitschek. 2009. Past and future habitat suitability for the Hudson River population of shortnose sturgeon: A bioenergetics approach to modeling habitat suitability for an endangered species. American Fisheries Society Symposium 69: 589-604.

Zhang, Y. and J.D. Kieffer. 2014. Critical thermal maximum (CTmax) and hematology of shortnose sturgeon (*Acipenser brevirostrum*) acclimated to three temperatures. Canadian Journal of Zoology 92: 215-221.

Tables

Table 1. Sub-adult and adult Atlantic sturgeon captures in the Chesapeake Bay (north-south orientation)

Year	Upper Bay	Upper Western Shore	Upper Eastern Shore	Patapsco and Back	Lower Western Shore	Choptank	Patuxent	Potomac	Lower Eastern Shore	Mid Bay	Rappahannock	York	James	Elizabeth	Lower Bay	Total
1993	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
1994	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
1995	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1996	2	0	0	0	1	1	0	1	6	7	0	0	0	0	0	18
1997	19	0	6	6	3	1	1	14	66	138	26	1	196	0	12	489
1998	30	0	2	1	1	7	0	6	36	397	0	0	72	0	0	552
1999	13	0	0	0	0	0	0	1	37	131	0	0	1	0	2	185
2000	3	0	0	0	0	0	0	2	8	29	0	0	0	0	0	42
2001	4	0	0	0	1	4	0	18	9	47	0	0	0	0	0	83
2002	1	0	0	0	1	1	0	1	4	15	0	0	0	0	0	23
2003	0	0	0	0	0	0	0	12	2	7	0	0	0	0	0	21
2004	2	0	0	1	1	0	0	13	4	28	0	0	0	0	0	49
2005	6	0	1	0	0	3	0	12	22	200	0	0	1	0	1	246
2006	6	0	3	0	0	5	0	23	132	290	0	0	37	0	0	496
2007	4	0	2	0	0	3	0	34	5	61	0	0	4	0	1	114
2008	10	0	1	0	0	0	0	24	9	74	0	0	0	0	0	118
2009	1	1	0	0	0	0	0	5	1	6	0	0	0	0	0	14
2010	1	0	0	0	0	0	0	1	0	2	0	0	0	0	0	4
Total	102	1	15	8	8	25	1	167	341	1435	26	1	311	0	16	2457

Table 2. Monthly occurrence of sub-adult
and adult Atlantic sturgeon in the Mid Bay,
Lower Eastern Shore, and James River
during years 1997, 1998, 2005, 2006
combined.

	James River	Lower Eastern Shore	Mid Bay
January	5	5	144
February	82	7	90
March	17	4	7
April	32	50	161
May	19	124	281
June	2	40	150
July	1	4	12
August	2	3	1
September	4	0	0
October	91	10	15
November	51	6	28
December	0	1	113

Table 3. Ranking of potential growth average (±SE) of juvenile Atlantic sturgeon growth by year.

Year	Growth	Rank
1990	0.02922(±0.00019)	9
1991	0.03020(±0.00016)	4
1992	0.02923(±0.00017)	8
1993	0.02714(±0.00017)	17
1994	0.02713(±0.00017)	18
1995	0.02701(±0.00016)	20
1996	0.02687(±0.00019)	22
1997	0.02921(±0.00016)	10
1998	0.03013(±0.00017)	5
1999	0.02920(±0.00016)	11
2000	0.02923(±0.00017)	6
2001	0.02706(±0.00018)	19
2002	0.02850(±0.00016)	13
2003	0.02600(±0.00018)	24
2004	0.03072(±0.00018)	3
2005	0.02696(±0.00017)	21
2006	0.03308(±0.00018)	2
2007	0.02751(±0.00015)	16
2008	0.02913(±0.00016)	12
2009	0.02814(±0.00018)	14
2010	0.02644(±0.00017)	23
2011	0.02756(±0.00020)	15
2012	0.03363(±0.00016)	1
2013	0.02964(±0.00016)	7

Table 4. Juvenile Atlantic sturgeon growth in individual tributaires in the winter. ANOVA and pairwise contrasts using Tukey's honest signficant difference pairwise contrasts between tributaries are shown as S=significant, NS=not significant. Average growth for each tributary is reported. North-south orientation.

Tributary	Tributary	Upper Bay	Upper Western Shore	Upper Eastern Shore	Patapsco and Back Rivers	Lower Western Shore (MD)	Choptank River	Patuxent River	Potomac River	Lower Eastern Shore (Tangier)	Mid Bay	Rappahannock River	York River	James River	Elizabeth River	Lower Bay
Tributary	Average	0.00846	0.00609	0.00789	0.00961	0.00983	0.00898	0.01050	0.00882	0.00922	0.01065	0.01020	0.01253	0.01211	0.01405	0.00768
Upper Bay	0.00846	■	S	NS	NS	NS	NS	S	NS	NS	S	S	S	S	S	S
Upper Western Shore	0.00609	S	■	NS	S	S	S	S	S	S	S	S	S	S	S	NS
Upper Eastern Shore	0.00789	NS	NS	■	NS	NS	NS	S	NS	S	S	S	S	S	S	NS
Patapsco and Back Rivers	0.00961	NS	S	NS	■	NS	NS	NS	NS	NS	NS	NS	S	S	S	S
Lower Western Shore (MD)	0.00983	NS	S	NS	NS	■	NS	NS	NS	NS	NS	NS	S	S	S	S
Choptank River	0.00898	NS	S	NS	NS	NS	■	NS	NS	NS	S	NS	S	S	S	S
Patuxent River	0.01050	S	S	S	NS	NS	NS	■	S	NS	NS	NS	S	NS	S	S
Potomac River	0.00882	NS	S	NS	NS	NS	NS	S	■	NS	S	S	S	S	S	S
Lower Eastern Shore (Tangier)	0.00922	NS	S	S	NS	NS	NS	NS	NS	■	S	NS	S	S	S	S
Mid Bay	0.01065	S	S	S	NS	NS	S	NS	S	S	■	NS	S	S	S	S
Rappahannock River	0.01020	S	S	S	NS	NS	NS	NS	S	NS	NS	■	S	S	S	S
York River	0.01253	S	S	S	S	S	S	S	S	S	S	S	■	NS	NS	S
James River	0.01211	S	S	S	S	S	S	NS	S	S	S	S	NS	■	NS	S
Elizabeth River	0.01405	S	S	S	S	S	S	S	S	S	S	S	NS	NS	■	S
Lower Bay	0.00768	S	NS	NS	S	S	S	S	S	S	S	S	S	S	S	■

Table 6. Juvenile Atlantic sturgeon growth in individual tributaries in the summer. ANOVA and pairwise contrasts using Tukey's honest signficant difference pairwise contrasts between tributaries are shown as S=significant, NS=not significant. Average growth for each tributary is reported. North-south orientation.

	Tributary	Upper Bay	Upper Western Shore	Upper Eastern Shore	Patapsco and Back Rivers	Lower Western Shore (MD)	Choptank River	Patuxent River	Potomac River	Lower Eastern Shore (Tangier)	Mid Bay	Rappahannock River	York River	James River	Elizabeth River	Lower Bay
Tributary	Average	0.02563	0.03577	0.02074	0.01954	0.01117	0.02330	0.01873	0.01555	0.04386	0.01281	0.02608	0.04179	0.03966	0.03969	0.02586
Upper Bay	0.02563	■	S	S	S	S	S	S	S	S	S	NS	S	S	S	NS
Upper Western Shore	0.03577	S	■	S	S	S	S	S	S	S	S	S	S	S	S	S
Upper Eastern Shore	0.02074	S	S	■	NS	S	S	S	S	S	S	S	S	S	S	S
Patapsco and Back Rivers	0.01954	S	S	NS	■	S	S	NS	S	S	S	S	S	S	S	S
Lower Western Shore (MD)	0.01117	S	S	S	S	■	S	S	S	S	NS	S	S	S	S	S
Choptank River	0.02330	S	S	S	S	S	■	S	S	S	S	S	S	S	S	S
Patuxent River	0.01873	S	S	S	NS	S	S	■	S	S	S	S	S	S	S	S
Potomac River	0.01555	S	S	S	S	S	S	S	■	S	S	S	S	S	S	S
Lower Eastern Shore (Tangier)	0.04386	S	S	S	S	S	S	S	S	■	S	S	S	S	S	S
Mid Bay	0.01281	S	S	S	S	NS	S	S	S	S	■	S	S	S	S	S
Rappahannock River	0.02608	NS	S	S	S	S	S	S	S	S	S	■	S	S	S	NS
York River	0.04179	S	S	S	S	S	S	S	S	S	S	S	■	S	NS	S
James River	0.03966	S	S	S	S	S	S	S	S	S	S	S	S	■	NS	S
Elizabeth River	0.03969	S	S	S	S	S	S	S	S	S	S	S	NS	NS	■	S
Lower Bay	0.02586	NS	S	S	S	S	S	S	S	S	S	NS	S	S	S	■

Table 7. Juvenile Atlantic sturgeon growth in individual tributaries in the fall. ANOVA and pairwise contrasts using Tukey's honest signficant difference pairwise contrasts between tributaries are shown as S=significant, NS=not significant. Average growth for each tributary is reported. North-south orientation.

Tributary	Tributary	Upper Bay	Upper Western Shore	Upper Eastern Shore	Patapsco and Back Rivers	Lower Western Shore (MD)	Choptank River	Patuxent River	Potomac River	Lower Eastern Shore (Tangier)	Mid Bay	Rappahannock River	York River	James River	Elizabeth River	Lower Bay
Tributary	Average	0.05313	0.05144	0.05315	0.05554	0.05699	0.05711	0.05842	0.05012	0.05239	0.05193	0.04949	0.05273	0.04962	0.04515	0.03383
Upper Bay	0.05313	■	NS	NS	S	S	S	S	S	NS	S	S	NS	S	S	S
Upper Western Shore	0.05144	NS	■	NS	S	S	S	S	NS	NS	NS	NS	NS	NS	S	S
Upper Eastern Shore	0.05315	NS	NS	■	S	S	S	S	S	NS	S	S	NS	S	S	S
Patapsco and Back Rivers	0.05554	S	S	S	■	NS	NS	S	S	S	S	S	S	S	S	S
Lower Western Shore (MD)	0.05699	S	S	S	NS	■	NS	NS	S	S	S	S	NS	S	S	S
Choptank River	0.05711	S	S	S	NS	NS	■	NS	S	S	S	S	S	S	S	S
Patuxent River	0.05842	S	S	S	S	NS	NS	■	S	S	S	S	S	S	S	S
Potomac River	0.05012	S	NS	S	S	S	S	S	■	S	S	NS	S	NS	S	S
Lower Eastern Shore (Tangier)	0.05239	NS	NS	NS	S	S	S	S	S	■	NS	S	NS	S	S	S
Mid Bay	0.05193	S	NS	S	S	S	S	S	S	NS	■	S	NS	S	S	S
Rappahannock River	0.04949	S	NS	S	S	S	S	NS	S	S	■	S	NS	S	S
York River	0.05273	NS	NS	NS	S	NS	S	S	S	NS	NS	S	■	S	S	S
James River	0.04962	S	NS	S	S	S	S	S	NS	S	S	NS	S	■	S	S
Elizabeth River	0.04515	S	S	S	S	S	S	S	S	S	S	S	S	S	■	S
Lower Bay	0.03383	S	S	S	S	S	S	S	S	S	S	S	S	S	S	■

95

Table 8. Wilcoxon-signed rank results of greater incidence than expected for sub-adult and adult Atlantic sturgeon for conditions of higher growth, higher dissolved oxygen, lower temperature and higher salinity. Years (1997, 1998, 2005, 2006) have been combined for analysis. S=significant, NS=not significant.

Segment	Season	n=	Production (g day-1)	Dissolved Oxygen (%)	Temperature (°C)	Salinity
James River	Winter	87	S	S	S	S
	Spring	68	NS	S	NS	S
	Summer	5	NS	NS	NS	NS
	Fall	146	S	NS	S	NS
Lower Eastern Shore	Winter	13	NS	NS	S	S
	Spring	178	S	S	S	S
	Summer	47	S	NS	S	S
	Fall	16	NS	NS	NS	NS
Mid Bay	Winter	347	S	S	S	S
	Spring	449	S	S	S	S
	Summer	163	S	NS	S	S
	Fall	43	NS	S	NS	NS

Figure 1. Map of the Chesapeake Bay with Program Monitoring Segments, labeled according to region. 1. Choptank River, 2. Elizabeth River, 3.James River, 4. Lower Bay, 5. Lower Eastern Shore (LES), 6. Lower Western Shore, 7. Mid Bay, 8. Patapsco and Back Rivers, 9. Patuxent River, 10. Potomac River, 11. Rappahannock River, 12. Upper Bay, 13. Upper Eastern Shore, 14. Upper Western Shore, 15. York River.
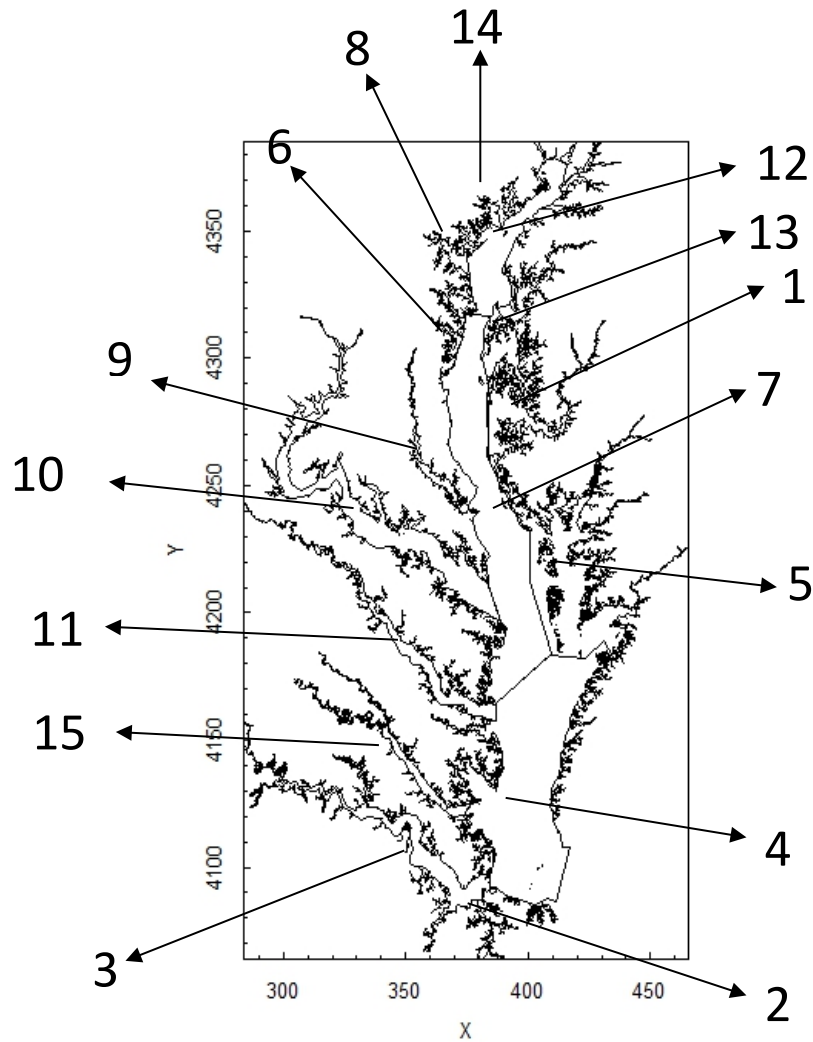
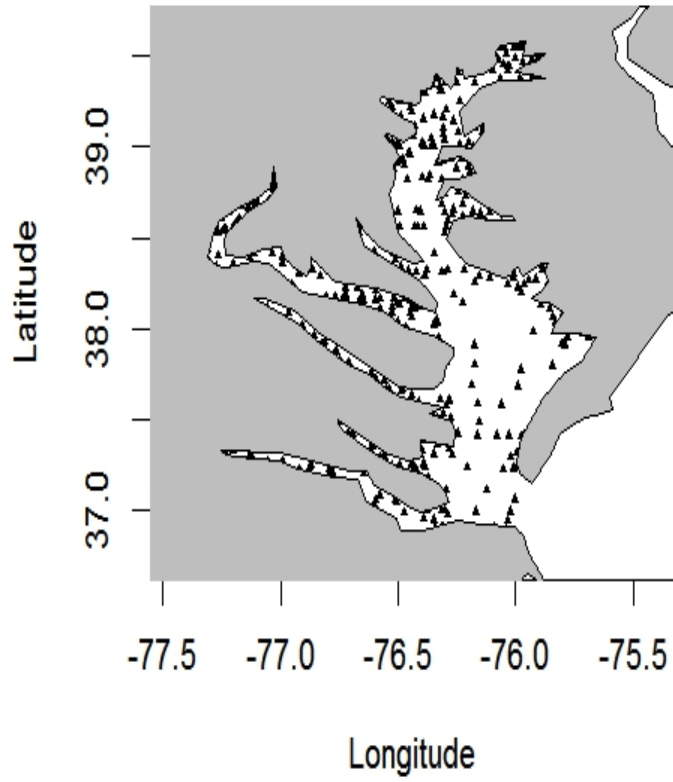Figure 2. Locations of fixed stations in the Chesapeake Bay

Figure 3. Interpolated spatial maps of water quality and predicted Atlantic sturgeon growth in the Chesapeake Bay. Examples are from summer 1998: a) dissolved oxygen (% saturation); b) temperature (°C); c) salinity and d) growth (g day^{-1}).

a

Chesapeake Bay Summer 1998 Dissolved

b

Chesapeake Bay Summer 1998 Temperature
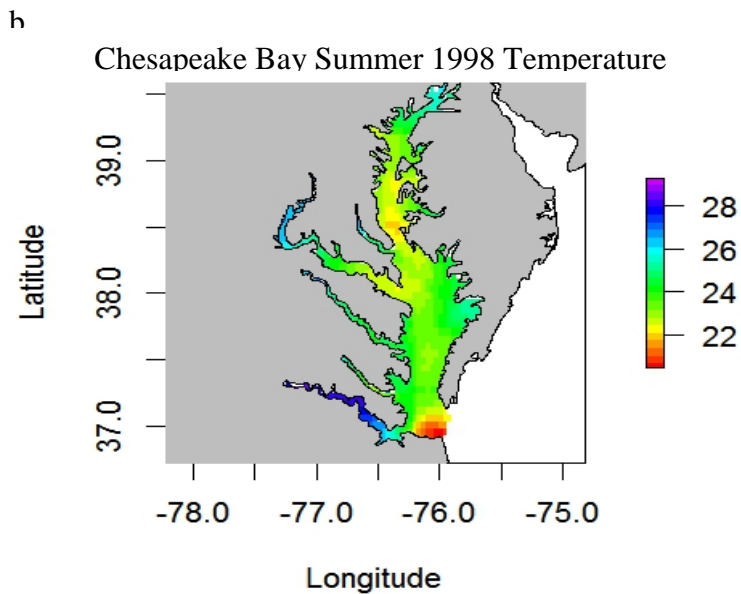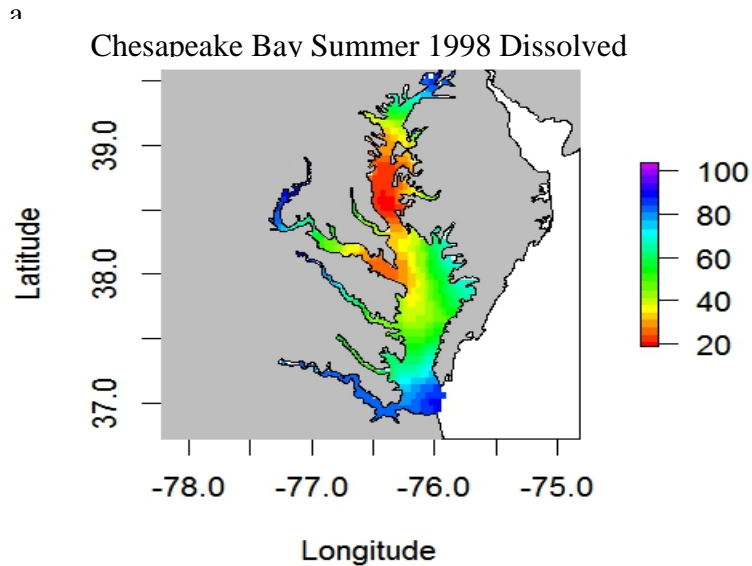
c. Chesapeake Bay Summer 1998
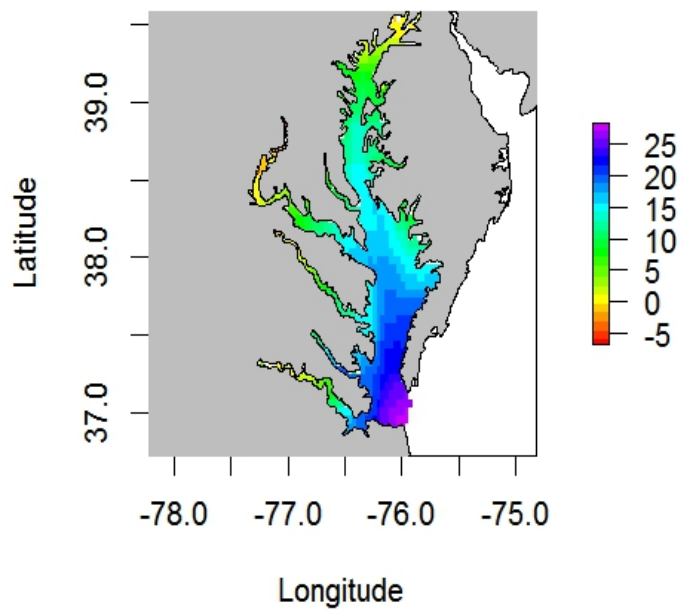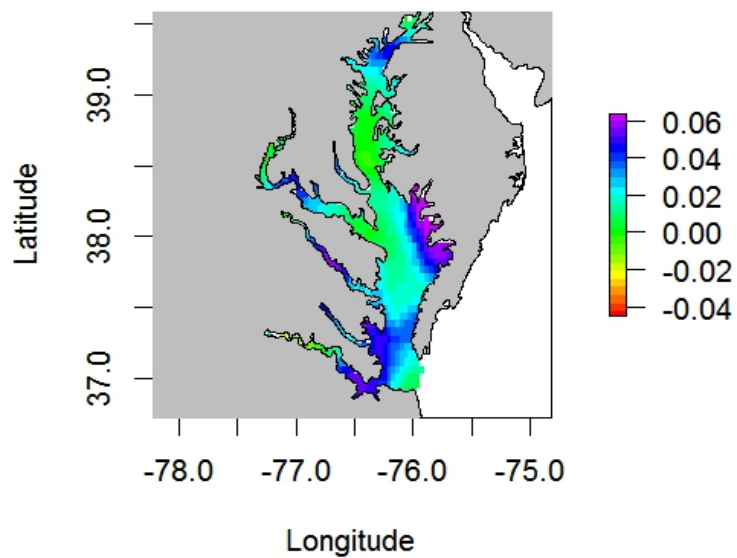

d. Chesapeake Bay Summer 1998 Potential

Figure 4. Predicted mean annual growth for juvenile Atlantic sturgeon in the Chesapeake Bay. Error bars are standard error. Different letters denote significant differences (ANOVA, Tukey honest significant difference; p<0.05).

Figure 5. Predicted mean seasonal growth for juvenile Atlantic sturgeon in the Chesapeake Bay. Different letters denote significant differences (ANOVA, Tukey honest significant difference; $p<0.05$).
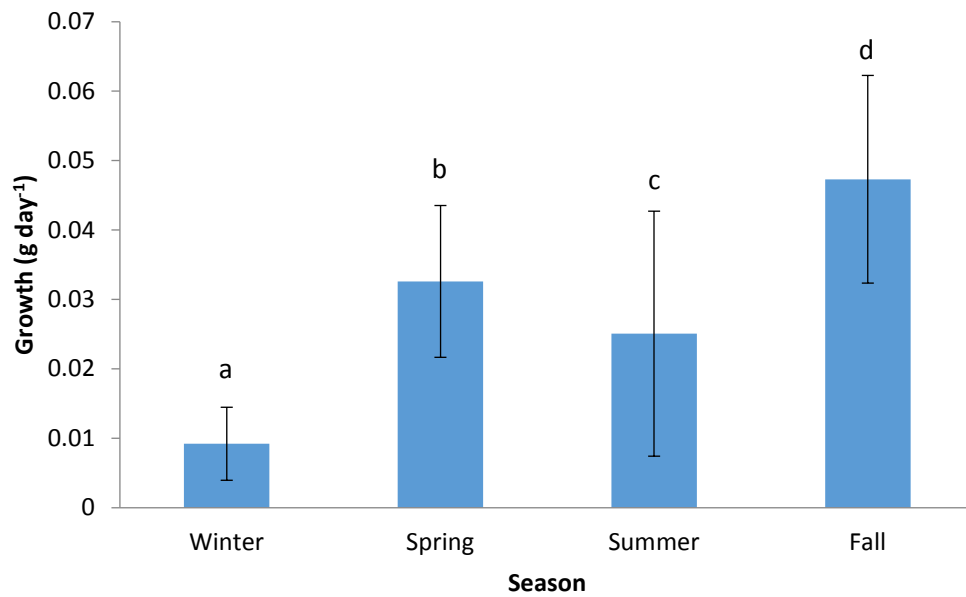
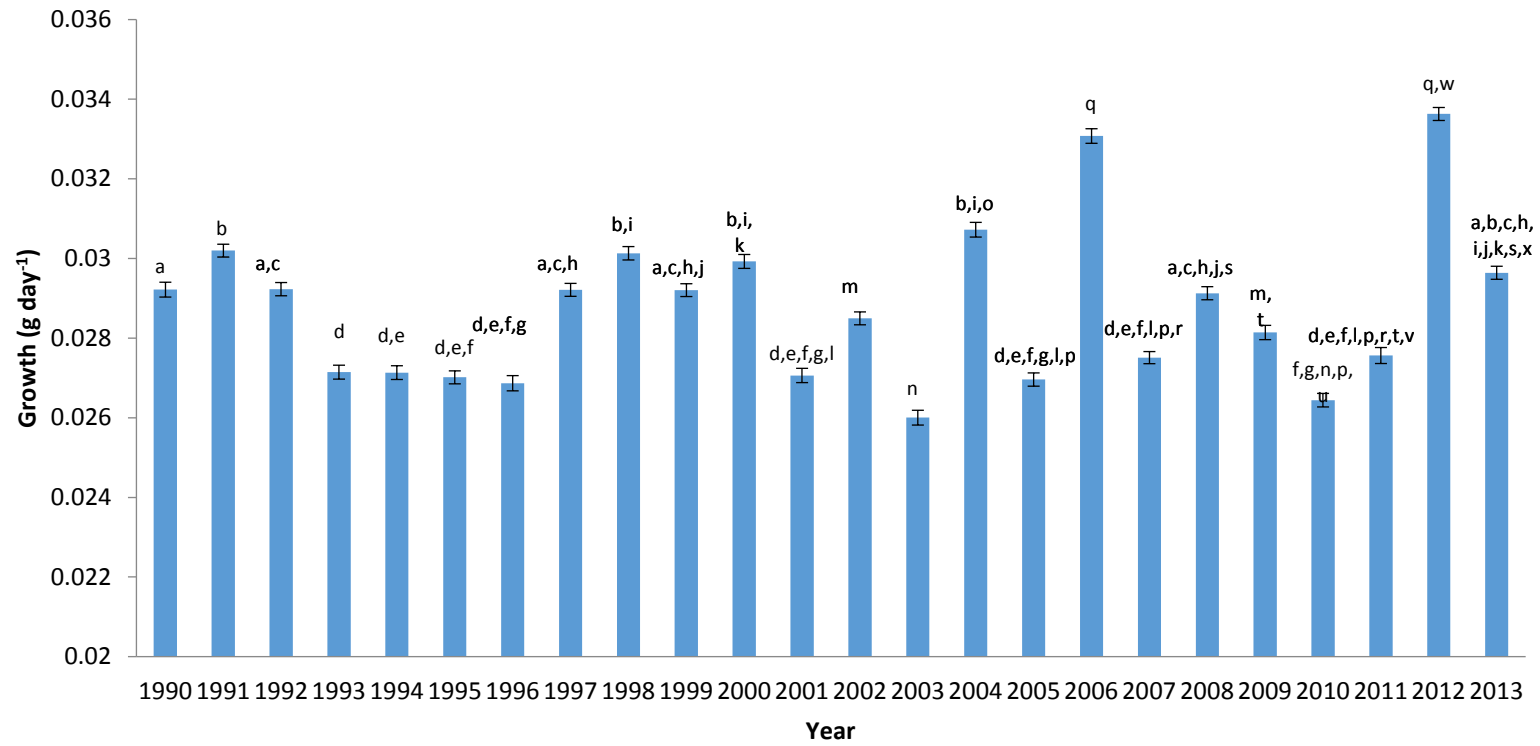Figure 6. Predicted mean seasonal growth by year for juvenile Atlantic sturgeon in the Chesapeake Bay.
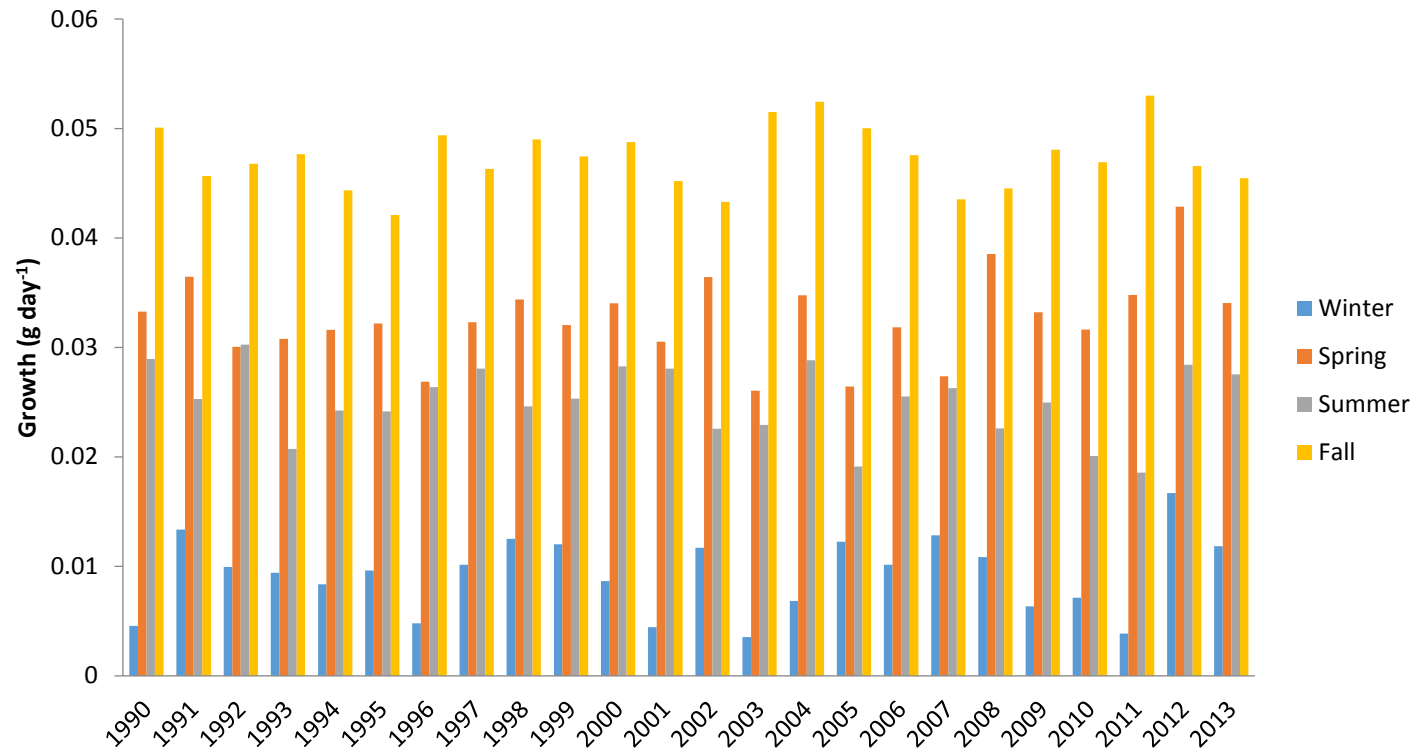
Figure 7. Predicted mean seasonal growth by year for juvenile Atlantic sturgeon in the Chesapeake Bay. a. winter, b. spring, c. summer, d. fall
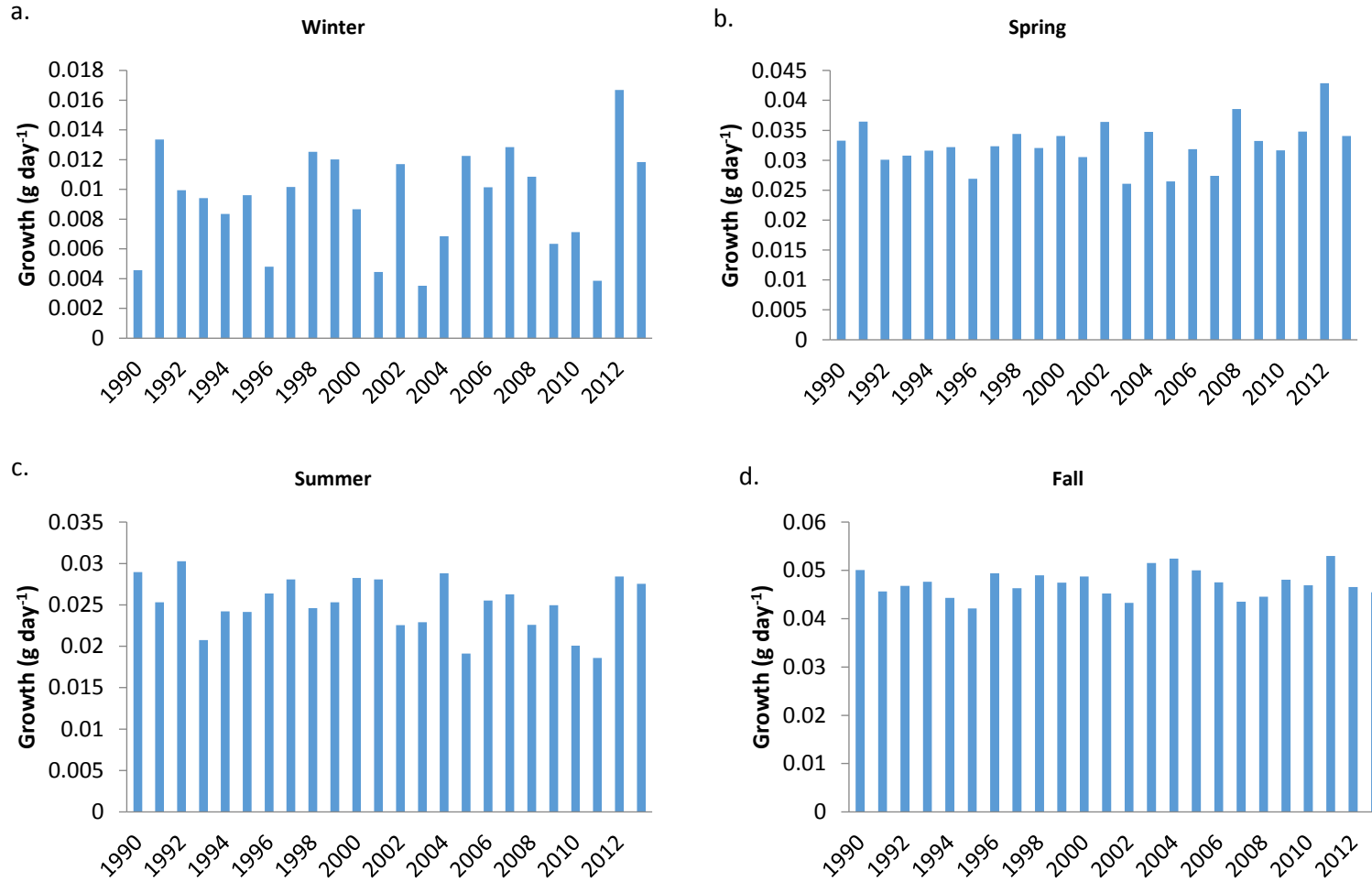
Figure 8. Comparison of predicted mean summertime growth (bars) for juvenile Atlantic sturgeon and summertime hypoxic volume (km^3) (line) (1990-2013) for entire Chesapeake Bay.
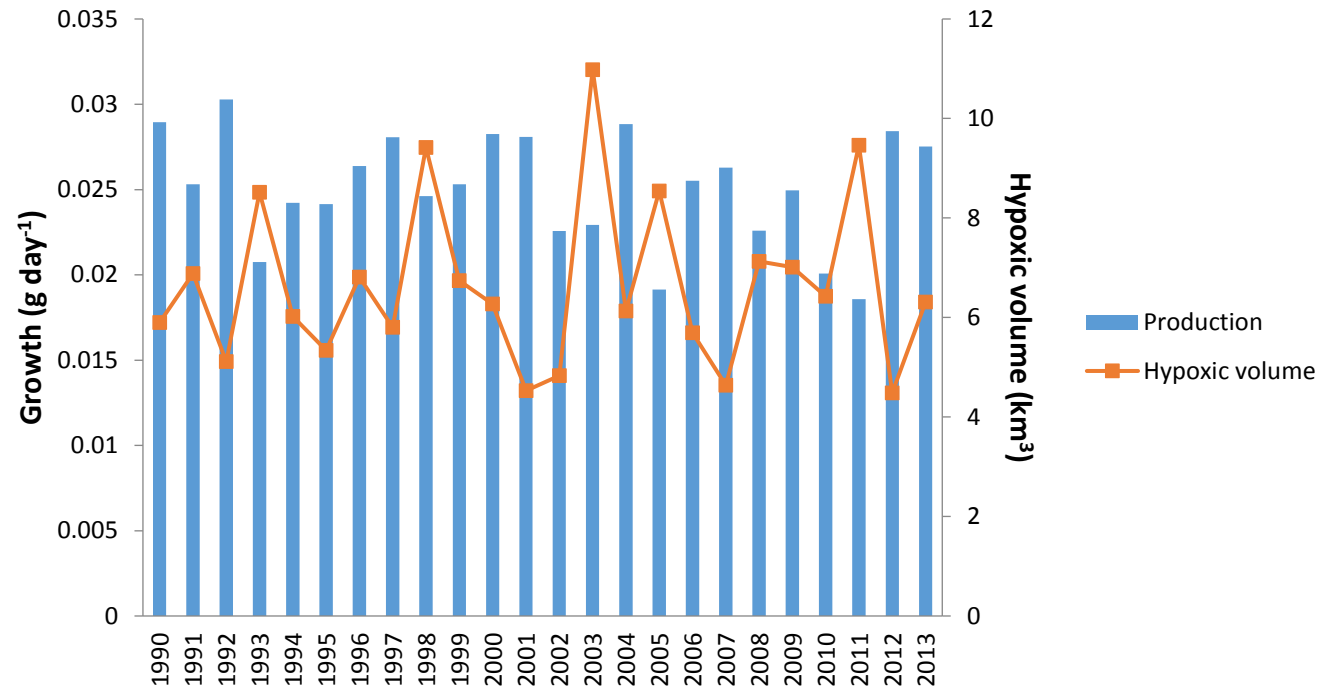
Figure 9. Regression of predicted mean summertime growth for juvenile Atlantic sturgeon and summertime hypoxic volume (km^3) (1990-2013) for the entire Chesapeake Bay.
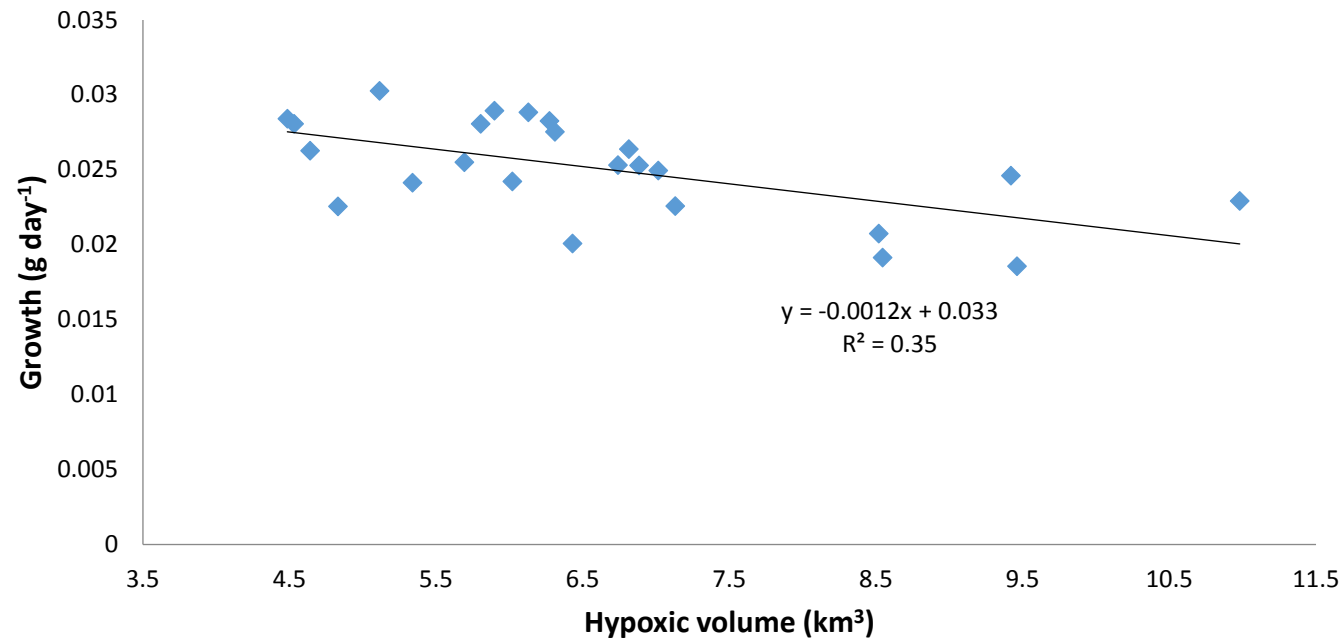
Figure 10. Comparison of predicted mean fall growth (bars) for juvenile Atlantic sturgeon and fall hypoxic volumes (km^3)(lines) (1990-2013) for the entire Chesapeake Bay.
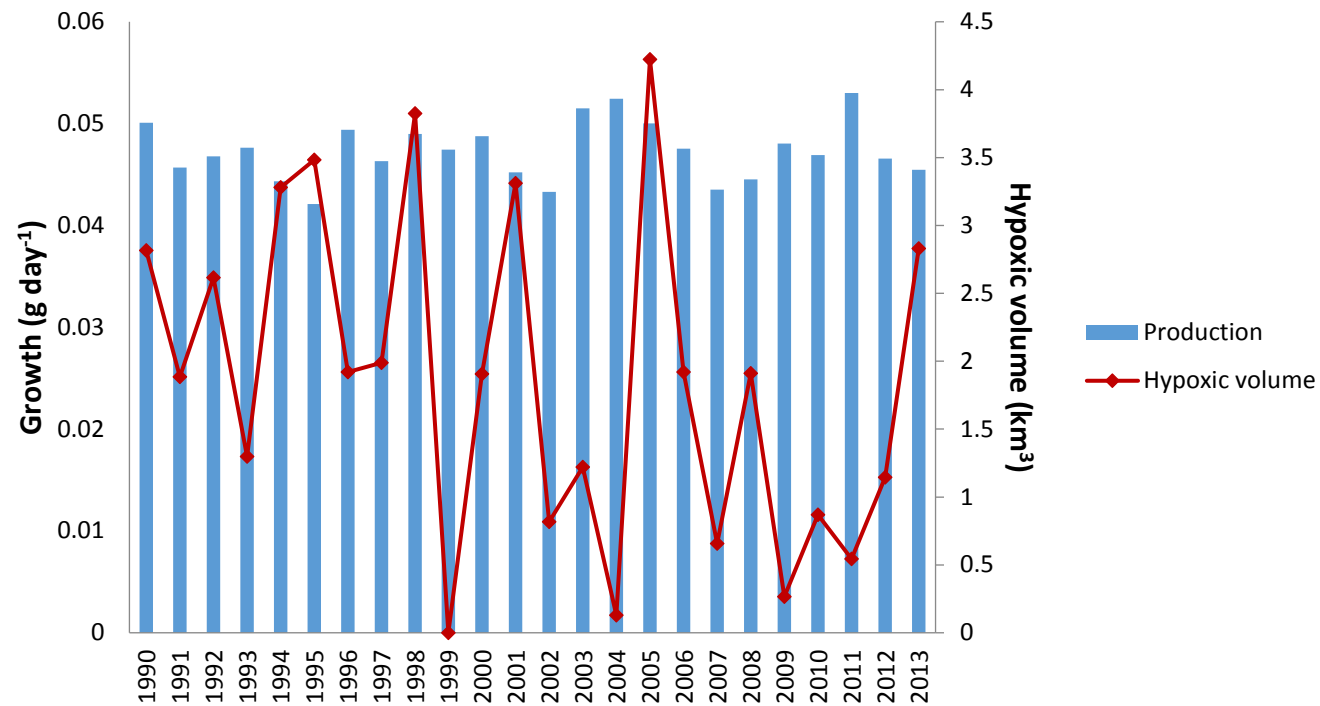
Figure 11. Predicted mean growth among tributaries and bay regions for juvenile Atlantic sturgeon (1990-2013). Different letters denote significant differences (ANOVA, Tukey honest significant difference; $p<0.05$).
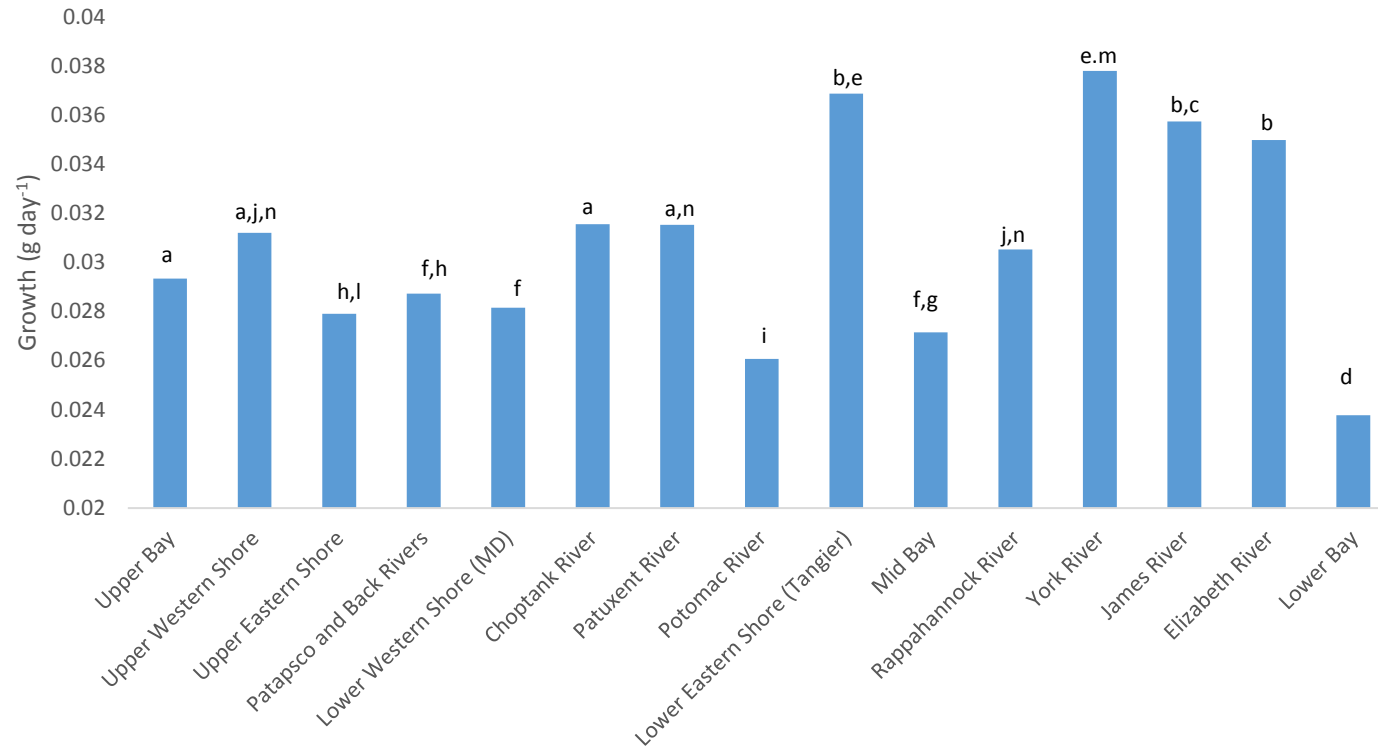
Figure 12. Predicted mean growth among tributaries and bay regions by season for juvenile Atlantic sturgeon (1990-2013).

Predicted mean growth among tributaries and bay regions by season (1990-2013)
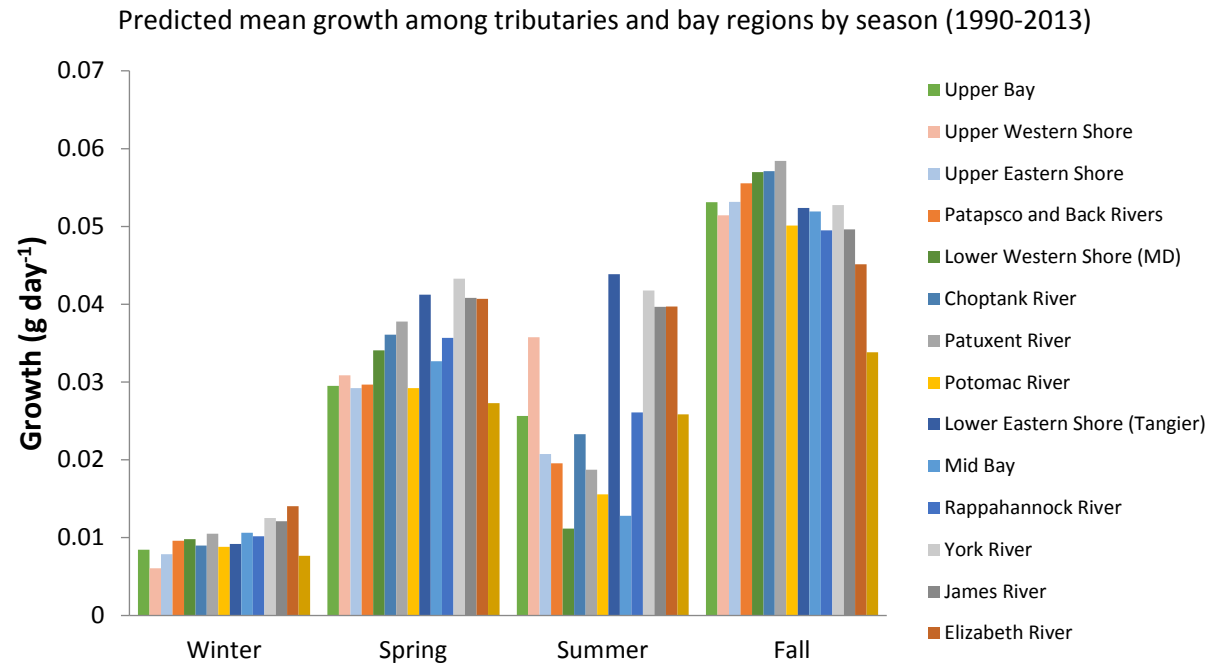
Figure 13. Frequency distribution of predicted growth rates for sub-adult and adult Atlantic sturgeon capture locations in the Mid Bay, Lower Eastern Shore, and James River in 1997, 1998, 2005, and 2006. n=1562.

Captures from Mid Bay, Lower Eastern Shore, and James River
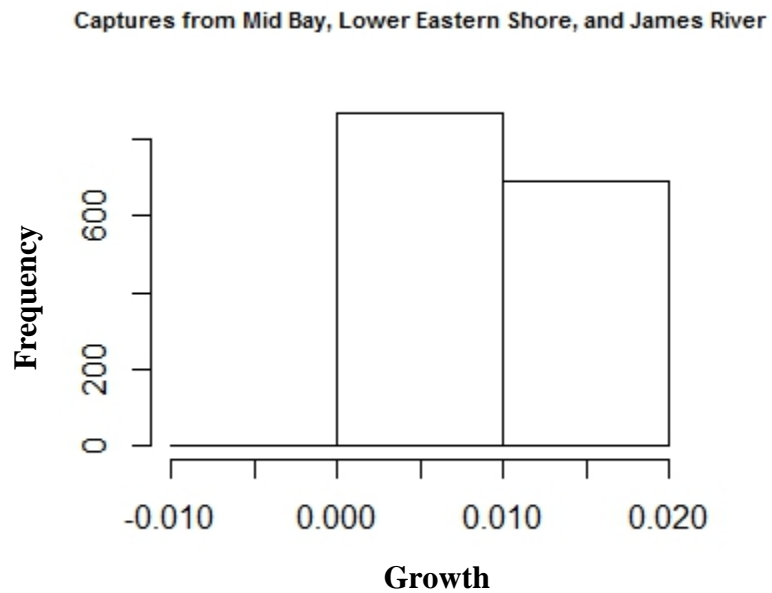
Figure 14. Box-whisker plots of predicted mean growth for sub-adults and adults captured in: a. Mid Bay, b. Lower Eastern Shore, and c. James River. *significant difference within a season between segment and capture environment (p<0.05) according to Wilcoxon's signed-rank test.
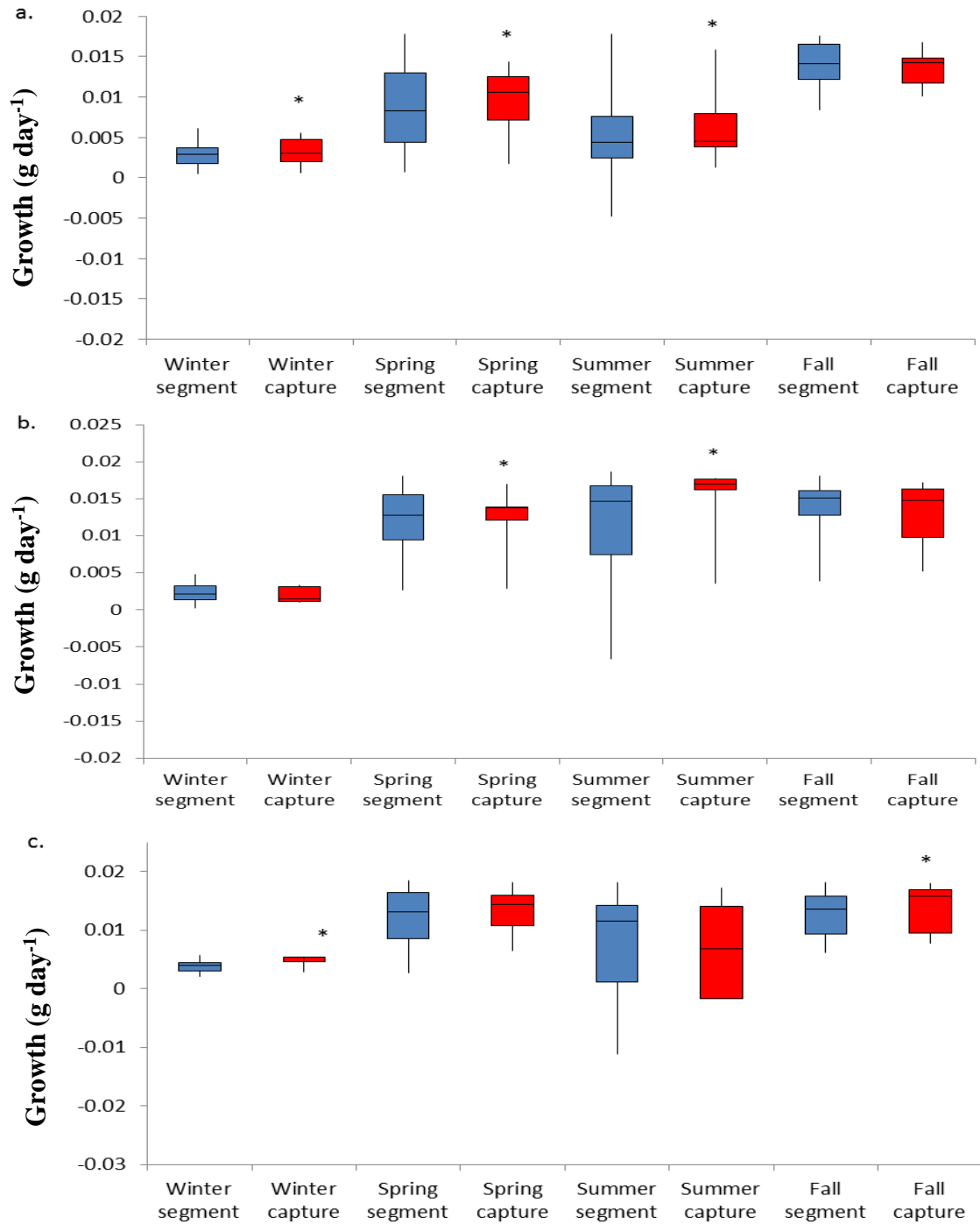
Figure 15. Box-whisker plots of mean temperature (°C) for sub-adults and adults captured in: a. Mid Bay, b. Lower Eastern Shore, and c. James River. *significant difference within a season between segment and capture environment (p<0.05) according to Wilcoxon's signed-rank test.
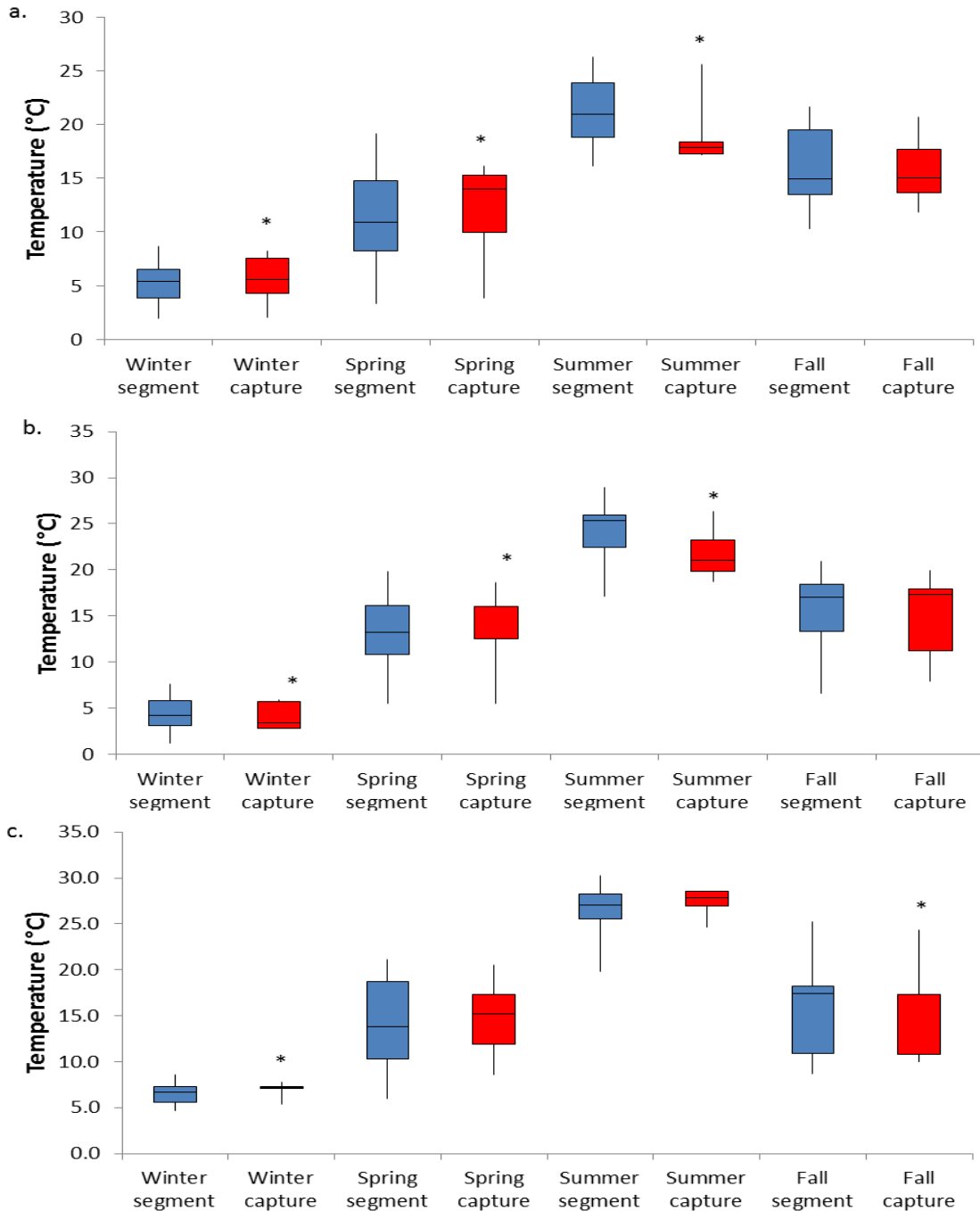
Figure 16. Bivariate convex hull plot of Atlantic sturgeon captures occurring in the Mid Bay (1997, 1998, 2005, 2006) as they relate to DO and temperature conditions. Confidence ellipses (dashed lines) represent 90% and 50% inclusion of environmental variables. Black vertical and horizontal lines represent DO saturation and temperature levels for EPA dissolved oxygen criteria. a. seasonal captures, and b. summer captures.
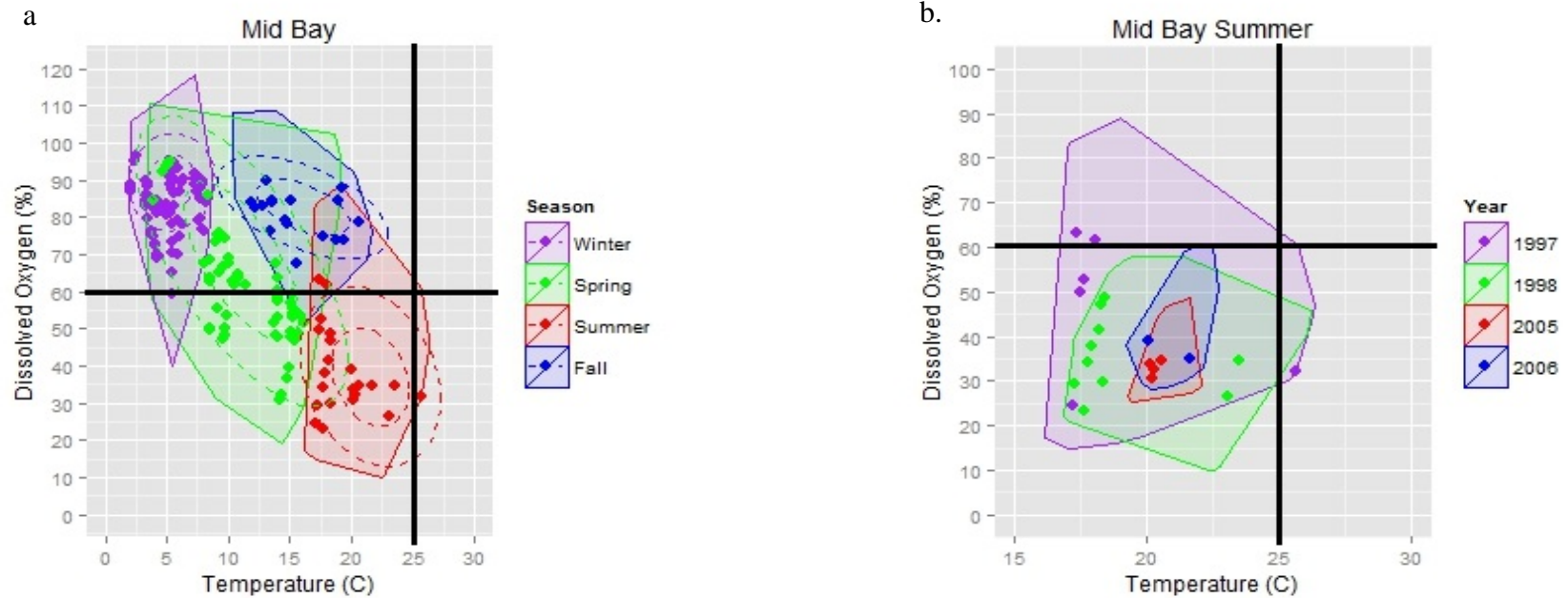
Figure 17. Bivariate convex hull plot of Atlantic sturgeon captures occurring in the Lower Eastern Shore (1997, 1998, 2005, 2006) as they relate to DO and temperature conditions. Confidence ellipses (dashed lines) represent 90% and 50% inclusion of environmental variables. Black vertical and horizontal lines represent DO saturation and temperature levels for EPA dissolved oxygen criteria. a. seasonal captures, and b. summer captures.
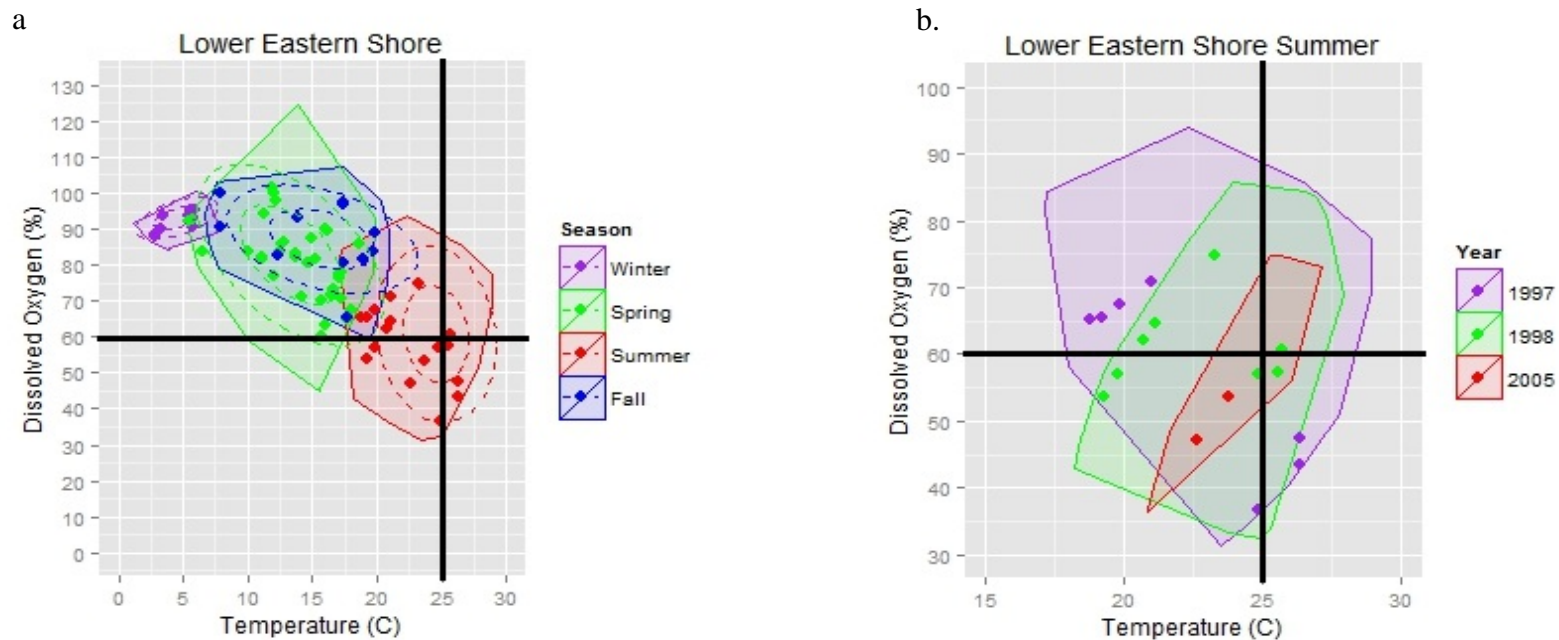
Figure 18. Bivariate convex hull plot of Atlantic sturgeon captures in the James River (1997, 1998, 2005, 2006) as they relate to DO and temperature conditions. Confidence ellipses (dashed lines) represent 90% and 50% inclusion of environmental variables. Black vertical and horizontal lines represent DO saturation and temperature parameters for EPA dissolved oxygen criteria.
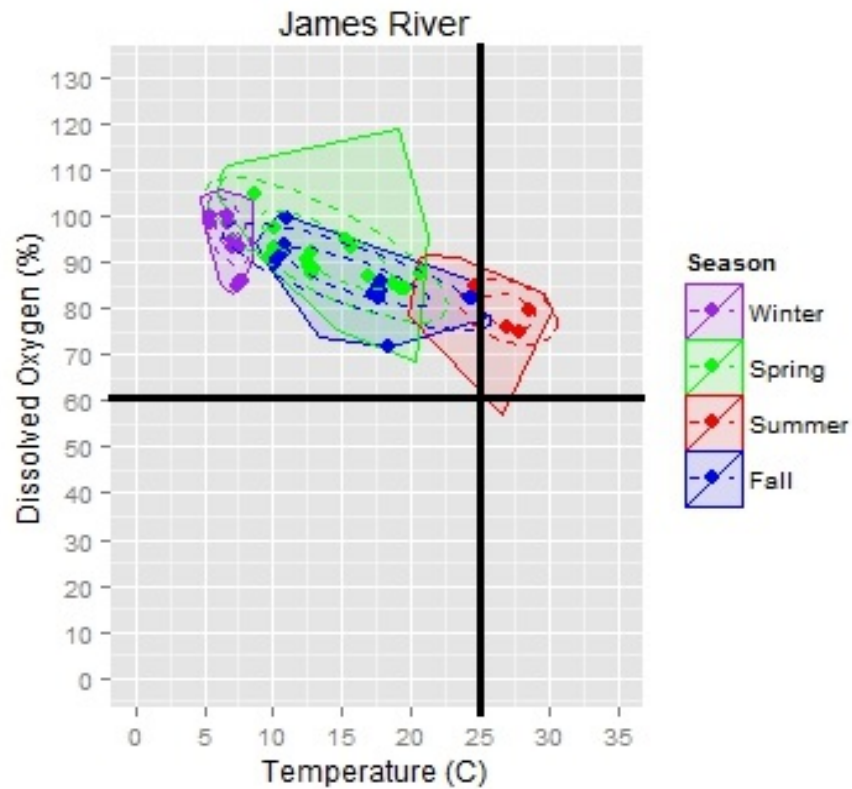
Figure 19. Quotient analysis for Atlantic sturgeon captures that occurred in the summer in the Mid Bay segment. Red line represents quotient value. Gray dashed lines represent 0.975 and 0.025 confidence intervals. a. modeled growth, b. dissolved oxygen, c. temperature, d. salinity.
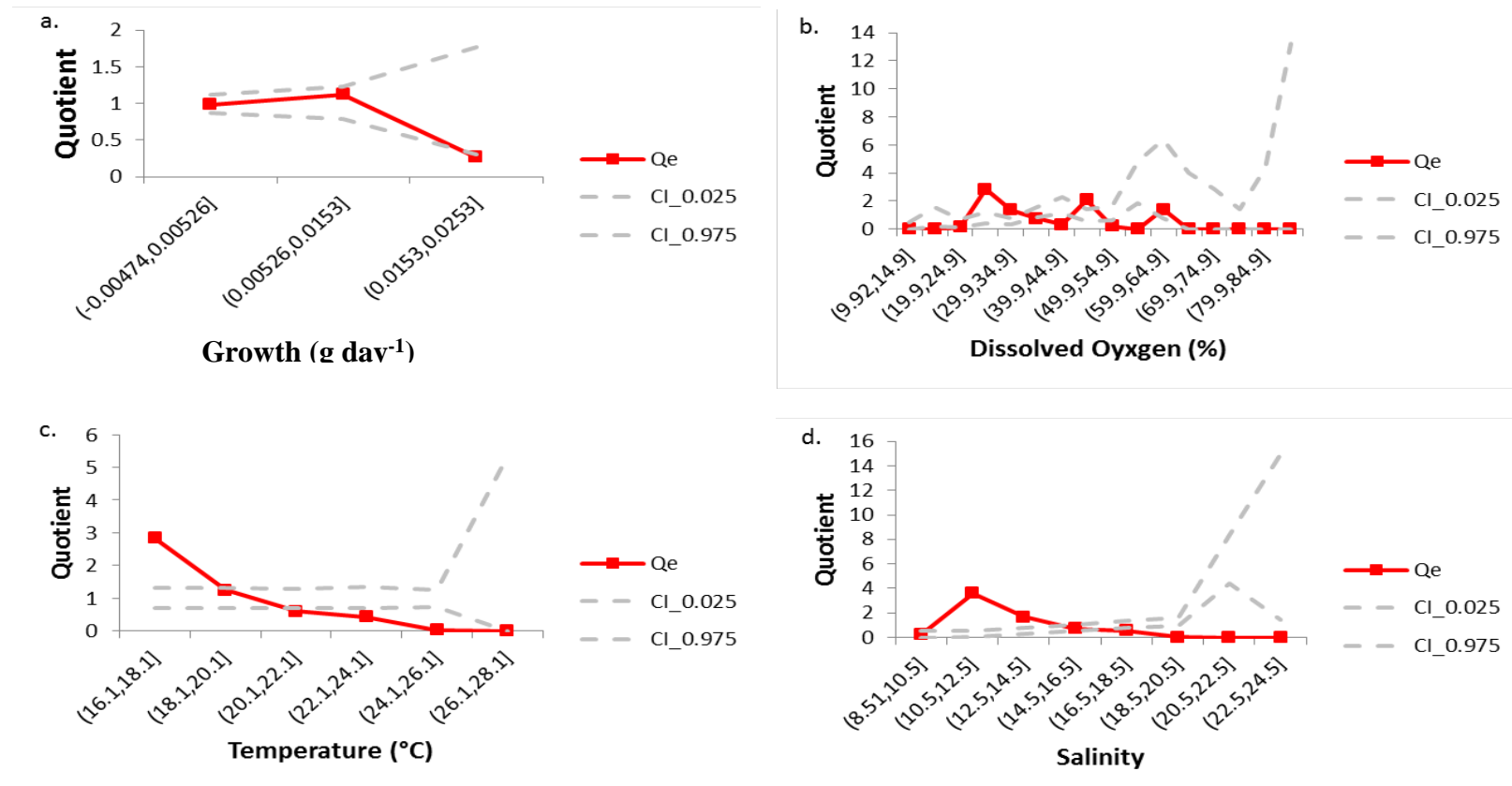
Figure 20. Quotient analysis for Atlantic sturgeon captures that occurred in the summer in the Lower Eastern Shore segment. Red line represents quotient value. Gray dashed lines represent 0.975 and 0.025 confidence intervals. a. modeled growth, b. dissolved oxygen, c. temperature, d. salinity.
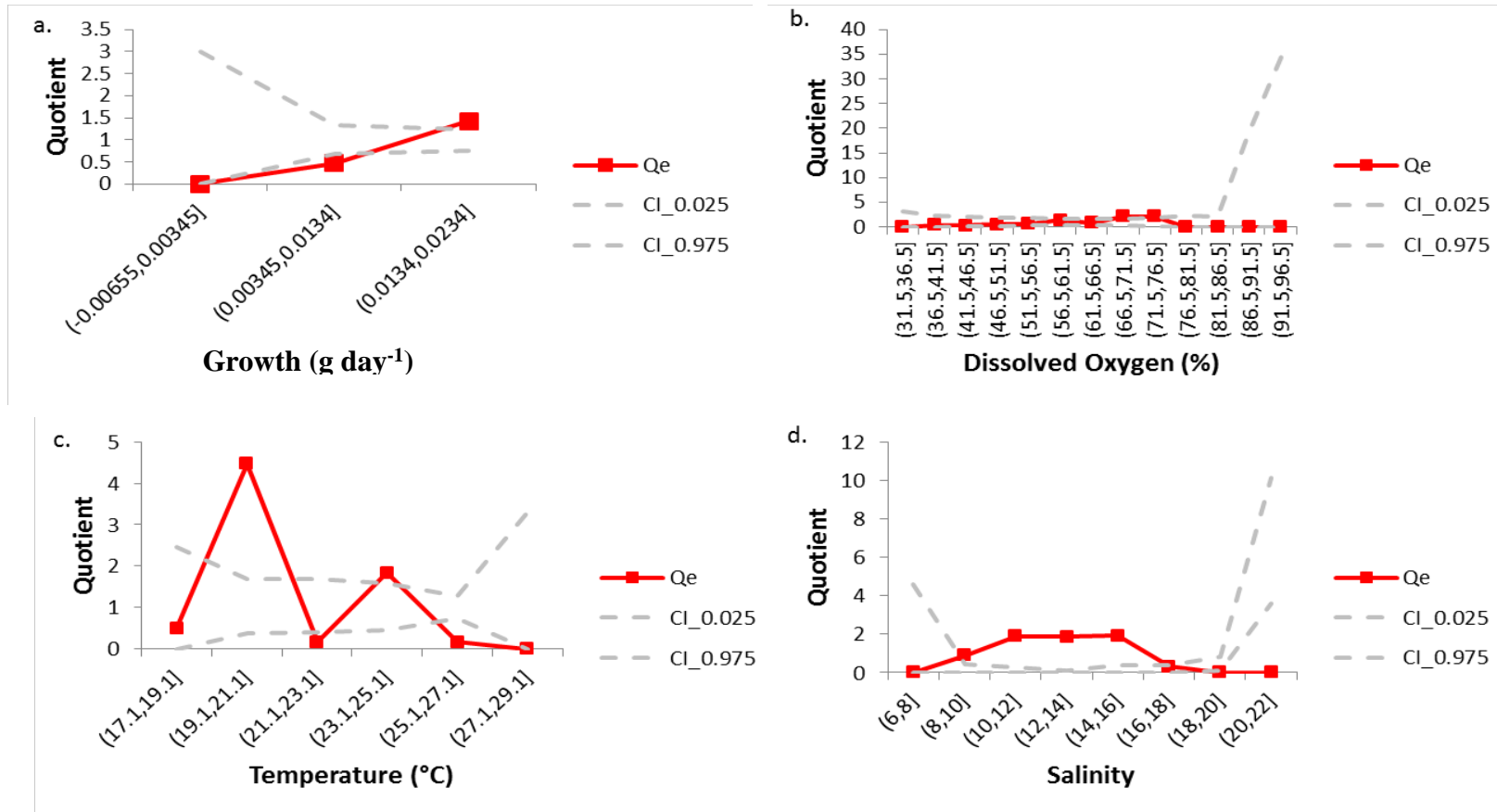
Figure 21. Quotient analysis of temperature for Atlantic sturgeon captures that occurred in the winter. Red line represents quotient value. Gray dashed lines represent 0.975 and 0.025 confidence intervals. a. Mid Bay, b. Lower Eastern Shore, c. James River.
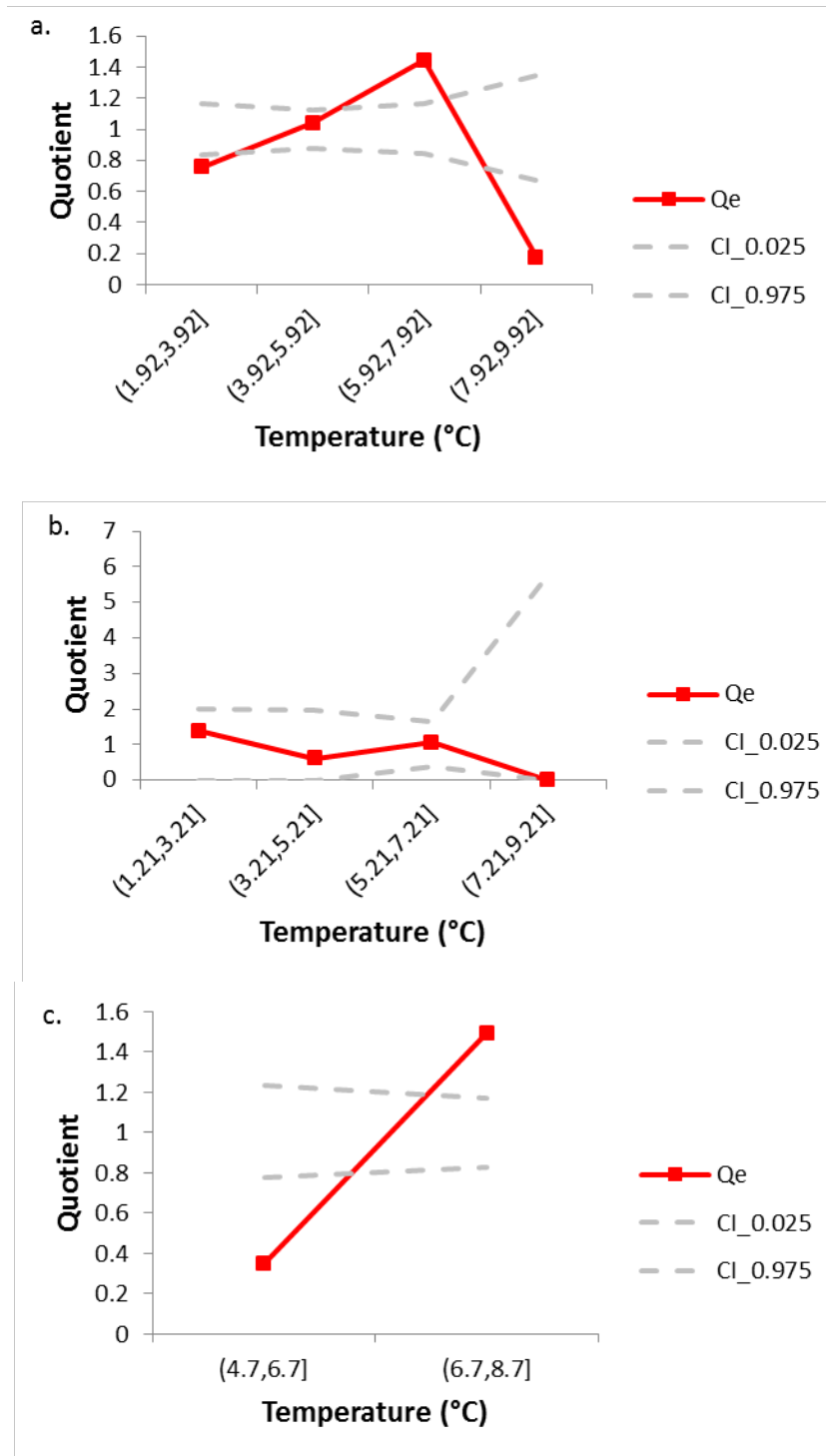
Appendices

Appendix 1.
require(Hmisc)
require(PBSmapping)
require(geoR)
require(maptools)
library(SpatialTools);
library(raster);
library(gdistance)

```
#---start script 1----
setwd ("folder path")
```

#1. Read shapefile
chesapeake.km<-importShapefile("reporting_regions_new.shp", proj="utm",
zone=18)
#chesapeake.km<-
importShapefile("shapefiles/reporting_regions_simplified/reporting_regions_new.shp
",
                  #proj="utm",zone=18)
# Transform units to kilometres instead of meters
chesapeake<-cbind(chesapeake.km[,1:3],chesapeake.km[,4:5]/1000)
x11();plotMap(chesapeake)
#2. Define resolution and create matrices
res<-2 #horizontal resolution (km)
resumen<-data.frame(); vcov.st<-data.frame()

#---1990-----
#create dataframe
CBPWQ<-read.csv ("water quality file.csv")
CBPWQ$dosat<-with(CBPWQ,DO/((exp(-
173.4292+249.6339*(100/(TEMP+273))+143.3483*log((TEMP+273)/100)
                  -21.8492*((TEMP+273)/100)+SALINITY*(-
0.033096+0.014259*((TEMP+273)/100)
                  -0.0017*((TEMP+273)/100)^2)))*1.428)*100)
data1<-
with(CBPWQ,data.frame(lat=LATITUDE,lon=LONGITUDE,temp=TEMP,DO=dosa
t,SALINITY=SALINITY))
summary(data1)
#--
Create distance matrix
#--
#add utm coordinates
ll.ini<-data.frame(EID=c(1:dim(data1)[1]),X=data1$lon,Y=data1$lat)

119

```
aux1<-convUL(as.EventData(ll.ini,projection="LL"),km=TRUE)
data1<-cbind(data1[,1:5],aux1[,2:3])
names(data1)[6:7]<-c("easting","northing")

# Average data within resolution
data1$reasting<-res*round(data1$easting/res,0)
data1$rnorthing<-res*round(data1$northing/res,0)

# Create analysis grid
grd0<-
with(data1,expand.grid(seq(min(reasting,na.rm=T),max(reasting,na.rm=T),res),
                    seq(min(rnorthing,na.rm=T),max(rnorthing,na.rm=T),res)))
grd0$EID<-c(1:dim(grd0)[1])
names(grd0)<-c("X","Y","EID")
# Identify which points are located within the bay (needed to build distance matrix)
test<-as.data.frame(findPolys(grd0,chesapeake))
test<-aggregate(PID~EID,data=test,FUN=min)
grd1<-merge(grd0,test,by="EID",all.x=T)
attr(grd1,"projection")<-"UTM"; attr(grd1,"zone")<-18

# Calculate effective distances (as the fish swim)
# Define a differential "conductance" for land and water cells
grd1$cond<-0.01+!is.na(grd1$PID)*0.99
# First we create a global raster
grd2<-
SpatialPixelsDataFrame(points=grd1[,c("X","Y")],data=data.frame(grd1$cond),
                    tolerance=0.99,proj4string=CRS("+proj=utm +datum=WGS84
+zone=18"))
# create a RasterLayer with the extent of GPRED
rd<- raster(grd2,layer=1)
plot(rd)

# and create a global transition matrix that represets the pairwise product of
# cells conductance
prod<-function(x){x[1]*x[2]}
trd <- transition(rd,prod,8)
trd<-geoCorrection(trd)

# get median responses by cell for all responses
data.med<-
aggregate(cbind(temp,DO,SALINITY)~reasting+rnorthing,data=data1,FUN=median,
na.rm=T)
# Finally we use the transition matrix to calculate corrected distances (as the fish
swim)
xy<- as.matrix(data.med[,1:2])
d0<-costDistance(trd,xy)
```

```
d<-as.matrix(as.dist(d0,diag = TRUE, upper = TRUE))


#----------------------------------------------
# Interpolate
#----------------------------------------------
# Prediction grid
gr.pred<-grd1[!is.na(grd1$PID),]

# Prediction distances
pred.xy<- as.matrix(gr.pred[,2:3]) #define zona
# Use again the transition matrix to calculate corrected distances (as the fish swim)
pred.d0<-costDistance(trd,pred.xy)
pred.d<-as.matrix(as.dist(pred.d0,diag = TRUE, upper = TRUE))

# Calculate distances between observaded a predicted values
op.d0<-costDistance(trd,xy,pred.xy)
op.d<-as.matrix(op.d0,diag = TRUE, upper = TRUE)
Xp <- as.matrix(cbind(1, gr.pred[,c(2,3)]))

#ciclo for looping along the three variables
for (v in c("temp","DO","SALINITY"))
{
 # Fit geostatistical model for the temp data
 geo.med<-as.geodata(cbind(data.med[,c("reasting","rnorthing",v)]), data.col=v)
 vg<-variog(geo.med, max.dist=600,dists.mat=d)
 # Eyefit
 # x11();eyefit(vg)
 # ML fit
 X <- as.matrix(cbind(1, data.med[,c(1,2)]))
 vpar<-maxlik.cov.sp(X, as.matrix(data.med[,v]) , coords =
as.matrix(data.med[,c(1,2)]),
               sp.type = "matern", range.par = 600, error.ratio = 0.5,D=d,
               reml = TRUE)
 # Define spatial structure of prediction matrix from fited spatial model
 V0<-cov.sp(coords = as.matrix(data.med[,c(1,2)]), sp.type = "matern",
        sp.par = vpar$sp.par,error.var = vpar$error.var,
        smoothness = vpar$smoothness, finescale.var = 0,
        pcoords = as.matrix(gr.pred[,c(2,3)]),
        D = d, Dp = pred.d, Dop = op.d)
 # Apply spatial structure nd model to predict values
 krige <- krige.uk(as.vector(data.med[,v]),
            V = V0$V, Vop=V0$Vop, Vp=V0$Vp,
            X = X, Xp = Xp, nsim = 0)
 gr.pred[[v]]<-krige$pred
 gr.pred[[paste(v,"se",sep=".")]]<-krige$mspe
}
```

```
pred.utm<-as.EventData(gr.pred[,1:3])
attr(pred.utm,"projection")="UTM";attr(pred.utm,"zone")<-18
pred.ll<-convUL(pred.utm)
names(pred.ll)[2:3]<-c("Lon","Lat")
pred<-cbind(gr.pred,pred.ll[,2:3])
head(pred)

write.csv(pred,"Title")
```

Appendix 2.

```
#        ATLANTIC STURGEON MODEL
#        REFERENCE: Niklitschek E.J. & Secor D.H. 2009. Dissolved oxygen,
temperature and salinity effects on the ecophysiology and survival
#                   of juvenile Atlantic sturgeon in estuarine waters: II. Model
development and testing. Journal of Experimental Marine Biology
#                   and Ecology 381: S161-S172.
#        SCRIPT : 20110803
#        LAST UPDATE: 20140702
#   Programmer: Edwin Niklitschek; edwin.niklitschek@ulagos.cl

#*** READING DATA ***;
# REPLACE data1 BY YOUR OWN ENVIRONMENTAL DATA SET;
#data1<-expand.grid(SAL=1:29,DO=25:100,TEMP=6:29)

#DEFINING FISH WEIGHT AND OBSERVED CONSUMPTION;
GR=14; #REPLACE THIS BY YOUR ACTUAL FISH WEIGHT IF NEEDED;
TL=NA; #REPLACE THIS BY TOUR ACTUAL FISH TOTAL LENGTH OR
LEAVE IT AS NA IF YOU DO NOT HAVE IT;
CJ_OBS=0; #IF YOU DECLARE THIS VARIABLE EQUAL TO 0, THE MODEL
ASSUMES MAXIMUM CONSUMPTION RATE (CMAX);
RATION=1; #IF YOU DECLARE THIS VARIABLE EQUAL TO 1, THE MODEL
ASSUMES p-value=1;
#----------------------------------------------------------------------
#BIOENERGETICS PARAMETERS
#----------------------------------------------------------------------
## ROUTINE METABOLISM;
arm = 0.522;
brm = -0.17;
tk1rm = 0.141;
tk4rm = 0.796;
crm = 1.0;
drm = 1.048;
grm = 0.748;
hrm = 0.268;
irm = 0.352;
smin = 9.166;
b1=-.158;
## FOOD CONSUMPTION;
afc = 1.028;
bfc = -0.197;
tk1fc = 0.195;
tk4fc = 0.556;
tl98fc = 26.09;
cfc=1;
```

```
dfc = 2.516;
gfc = 0.733;
jfc = 0.359;
kfc = 0.247;

## EGESTION;
aeg = 0.335;
ceg = -0.75;
deg = -0.62;
geg=0;

## EXCRETION;
aex=0.055703;
bex=-0.29;
cex=0.0392;

## SDA;
asda=0.1657;

## AM;
aact=0.29;

## Constants
S4=29; S1=1; do1=25;
#---------------------------------------------------------------------
# MODELING
#---------------------------------------------------------------------

attach(data1)
#---------------------------------------------------------------------
# RM MODEL;
#---------------------------------------------------------------------
## RM Model Constants;
ox=13.55; rt1=6; rt4=28;

## FT;
      y1=(1/(rt4-rt1))*log(tk4rm*(1-tk1rm)/(tk1rm*(1-tk4rm)));
      ey1=exp(y1*(TEMP-rt1));
 FTrm=tk1rm*ey1/(1+tk1rm*(ey1-1));
## FS;
      FSArm=1+0.01*exp(hrm*GR**b1*(SAL-smin));
      FSBrm=1+0.01*exp(irm*GR**b1*(smin-SAL));
      FSrm=FSArm*FSBrm/(1.0201);
## FO;
      DOCrm=100*(1-crm*exp(-FTrm*FSrm));
      KO1rm=1-drm*exp(FTrm*FSrm-1);
```

```
        dorel=(DOCrm-DO)/100;
        SLrm=(.98-KO1rm)/((.02*(DOCrm-do1))**crm);
        FOrm=ifelse(dorel>0,(0.98-SLrm*dorel**crm)/0.98,1)

        KRM=FOrm*FSrm*FTrm;
        RM=GR*(arm*GR**brm)*KRM*24*ox/1000;
#------------------------------------------------------------------------
# FC MODEL;
#------------------------------------------------------------------------
## FC model constants;
        ct1=6; ct4=28;
## FT;
        cy1=(1/(tl98fc-ct1))*log(0.98*(1-tk1fc)/(tk1fc*0.02));
        ecy1=exp(cy1*(TEMP-ct1));
  cka=tk1fc*ecy1/(1+tk1fc*(ecy1-1));

        cy2=(1/(ct4-tl98fc))*log(0.98*(1-tk4fc)/(tk4fc*0.02));
        ecy2=exp(cy2*(ct4-TEMP));
        ckb=tk4fc*ecy2/(1+tk4fc*(ecy2-1));

        FTfc=cka*ckb;
## FS;
        CKS1=jfc*GR**-b1;
        CKS4=kfc*GR**-b1;

        YA=(1/(smin-S1))*log(0.98*(1-CKS1)/(CKS1*0.02));
        EYA=exp(YA*(SAL-S1));
  KSA=CKS1*EYA/(1+CKS1*(EYA-1));

        YB=(1/(S4-smin))*log(0.98*(1-CKS4)/(CKS4*0.02));
        EYB=exp(YB*(S4-SAL));
  KSB=CKS4*EYB/(1+CKS4*(EYB-1));
        FSfc=(KSA*KSB)/(1);

## FO;
        DOCfc=100*(1-gfc*exp(-KRM));
        KO1fc=1-dfc*exp(KRM-1);
        dorel=(DOCfc-DO)/100;
        SLfc=(.98-KO1fc)/((.02*(DOCfc-do1))**cfc);
        FOfc=ifelse(dorel>0,(0.98-SLfc*dorel**cfc)/0.98,1)

        CJG_MAX=(afc*GR**bfc)*FTfc*FSfc*FOfc;
        CJ_MAX=GR*CJG_MAX;
        CJG_PRED=RATION*CJG_MAX;
        CJ_PRED=CJG_PRED*GR;
```

```
        if (CJ_OBS==0) CJ=CJ_PRED else CJ=CJ_OBS;
#----------------------------------------------------------------------
# EGESTION MODEL
#----------------------------------------------------------------------
        E=aeg*(TEMP/6)**ceg*(DO/DOCrm)**deg*RATION**geg;
        EG=E*CJ;
#----------------------------------------------------------------------
# EXCRETION MODEL;
#----------------------------------------------------------------------
        EX=aex*GR**bex*RM+cex*CJ;
#----------------------------------------------------------------------
# SDA MODEL;
#----------------------------------------------------------------------
        SDA=(CJ-EG)*asda;
#----------------------------------------------------------------------
# ACTIVE METABOLISM ;
#----------------------------------------------------------------------
        AM=CJ_MAX*aact;
#----------------------------------------------------------------------
# ENERGY CONTENT;
#----------------------------------------------------------------------
        TL=ifelse(is.na(TL),exp((log(GR)+6.1488)/3.113),TL);
        LNL=log(TL);
        WS=TL/exp((log(GR)+6.1488)/3.113);
        ENEC=exp(-1.0065+1.0336*log(WS)+0.6807*LNL);
#----------------------------------------------------------------------
# GROWTH
#----------------------------------------------------------------------
        GKJ_PRED=CJ-RM-EG-SDA-EX-AM;
        G_PRED=log((GR+GKJ_PRED/ENEC)/GR);
```

Appendix 3: Results from generalized linear model regression of production versus DO and temperature.

Formula: production ~ Temp + DO, data= production				
	Sum Sq	Mean Sq	F value	Pr(>F)
Temp	3.93E-05	3.93E-05	18.104	0.0003532
DO	2.68E-06	2.68E-06	1.231	0.279752

Chapter 5: Latitudinal Countergradient Variation in the Growth of Juvenile Atlantic sturgeon

Abstract

Atlantic sturgeon populations occur over a very broad latitudinal range (Satilla River, Florida to St. Lawrence River, Canada; 15 degrees), such that size-dependent winter mortality of juveniles could select for countergradient latitudinal variation in juvenile growth rate. Any latitudinal trend in juvenile growth rate could be confounded by dual spring and fall spawning, which has been recently documented for several populations. To investigate latitudinal countergradient variation in growth between populations, growth of Canada- and Altamaha (GA) strain Atlantic sturgeon was compared in a common garden experiment in which they were exposed to three thermal regimes, which were representative of the species latitudinal range. Results indicated no effect of strain on growth performance; Atlantic sturgeon length and weight were significantly influenced by thermal regime treatment independent of strain. To evaluate possible confounding influences of dual spawning on juvenile growth and size predictions, I applied a growth-degree-day (GDD) model, using water temperature data from seven NOAA National Estuarine Research Reserve System (NERRS) sites, over the latitudinal range of Atlantic sturgeon to predict growth performance across systems and seasonal spring and fall cohorts. The annual accumulation of GDDs varied significantly over a latitudinal gradient. For the spring cohort, which occurs throughout the species range, accumulation of GDDS diminished rapidly north of the Chesapeake Bay. Interestingly, there was no significant difference for GDDS between fall and spring cohorts throughout the

species range, indicating equivalent annual growth performance in those systems where both spring and fall spawning occurs. Using a regression of length versus GDD estimated from laboratory experiments, total length of age-1.0 fish was estimated across a latitudinal gradient using the accumulated GDD for each system (2008-2012). Predicted lengths of age-1.0 sturgeon (241.8-346.0 mm north of Chesapeake Bay; 354.1-416.0 mm south of the Hudson River) generally fell within the range of age-1 Atlantic sturgeon reported in literature. The GDD model of predicted size should hold promise in assessing recruitment and related recovery in Atlantic sturgeon and evaluating scenarios of warming and dual spawning across throughout the range of the species.

Introduction

Conservation of threatened and endangered sturgeon is most sensitive to factors that influence first year survival (Gross et al. 2002). Age-0 and older juveniles (<100 cm total length) of the federally protected Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus* are encountered in spawning tributaries but assignment of juveniles to age-0 and age-1 based on length has been uncertain owing to incomplete knowledge of how first year growth occurs across the broad latitudinal range (15 degrees) in which the species occurs (Satilla River, Florida to St. Lawrence River, Canada). Confounding the identification of age-0,1 juveniles further is that in some portions of their range, Atlantic sturgeon spawn in both the spring and the fall (Smith et al. 1985; Balazik et al. 2013; Smith et al. 2015; Hager et al. 2014; Balazik and Musick 2015), which could result in two size modes associated with age-0,1 juveniles in any given season.

Species for which populations occur over broad latitudinal ranges may experience countergradient juvenile growth, where growth rates are higher at higher latitudes (Conover 1992). Higher latitude areas are distinguished by shorter growing season, earlier onset of winter, and severity of winter (Yamahira and Conover 2002) as well as wintertime scarcity of prey items (Shuter et al. 2012). In North America, the latitudinal gradient of shorter summers and longer winters can result in systematic changes in population characteristics such as spawning time, somatic growth, size and age at reproduction, and lifespan (Shuter et al. 2012). Atlantic silversides (*Menidia menidia*) occur over a similar latitudinal range as Atlantic sturgeon, and juveniles grow faster at higher latitudes; at the end of the first summer growing season size is independent of latitude even though the growing season declines by a factor of 2.5 with increasing latitude (Conover and Present 1990). Cod (*Gadus morhua*) from higher latitudes also tended to have greater intrinsic rates of growth (Wijekoon et al. 2009) yet Purchase and Brown (2001) found that growth rates were not due to higher genetic capacities for growth but related to how all tested populations responded to similar thermal regimes. Lake sturgeon (*Acipenser fulvescens*) demonstrated a relationship between length-at-age and thermal opportunity for growth whereby sturgeon in the northern part of the range were smaller-at-age, but grew at a higher rate, when growth was adjusted for expected thermal conditions (Power and McKinley 1997). There are several theories that relate latitudinal countergradient variation to evolutionary fitness, the main one involving over-winter mortality (Conover 1992; Schultz et al. 1996; Power and McKinley1997).

In temperate system, cessation of growth and lethal temperatures during winter months are thought to drive latitudinal countergradient trends in juvenile growth. Winter mortality may occur due to thermal stress, starvation, predation, disease, winter hypoxia, and physical disturbance (e.g. ice flows) (Hurst 2007). However, it is thermal stress (e.g., inability to maintain homeostasis) and starvation (e.g., allotment of energy stores) that have been assumed to be the principal culprits for winter mortality of fish (Hurst 2007). At higher latitudes, smaller body size and associated energy stores may increase overwinter mortality (Yamahira and Conover 2002; Garvey and Marschall 2003; Crossman et al. 2009; Pörtner and Peck 2010; Shuter et al. 2012). Brown trout (*Salmo trutta*) along a thirteen-degree latitudinal gradient exhibited increased lipid stores in higher latitudes (30% increase) but growth was approximately 20% lower for higher latitudes indicating a selective allocation of energy stores associated with overwintering (Berg et al. 2011). Regardless of ration allocation, smaller largemouth bass (*Micropterus salmoides*) from higher latitudes selectively allocated consumed energy into growth rather than reproduction in order to increase fat storage capacity before the onset of winter to increase survival (Garvey and Marschall 2003). Striped bass (*Morone saxatilis*) in the Hudson River displayed a shift from increasing length early in the growing season to increasing energy reserves towards the end of the growing season, presumably to reduce overwinter mortality risk (Hurst and Conover 2003). Atlantic silversides in northern latitudes accumulated energy stores faster than their southern counterparts, providing evidence that risk of winter starvation resulted in selection to accumulate energy during the first growing season (Schultz and Conover 1997). There has been minimal research

131

on winter mortality of sturgeon species except when evaluating hatchery restoration efforts (Crossman et al. 2009; Falahatker et al. 2013). Crossman et al. 2009 observed only 40% of stocked lake sturgeon (*Acipenser fulvescens*) survived their first winter, indicating that overwinter mortality could be an important agent of natural selection. They observed no relationship between size and winter survival.

Differences in growth rates across a latitudinal gradient is heritable in some fish species. Mummichogs (*Fundulus heteroclitus*) showed a difference in their genetic capacity for growth when fish from northern latitudes were reared in a common garden experiment with fish from southern latitudes; northern latitude strains had a higher capacity for growth (Schultz et al. 1996). This has also be observed in juvenile Atlantic silversides (Conover and Present 1990) and larval (Conover et al. 1997) and juvenile (Secor et al. 2000a) striped bass where fish from high latitudes grew faster than those from lower latitudes in common garden experiments. Many species that exhibit countergradient variation in growth between high and low latitude have large geographic ranges. Atlantic sturgeon span a large geographical range, yet no research has been conducted to determine if there is a difference between strains in their genetic capacity for growth.

Given the latitudinal range of Atlantic sturgeon and evidence of dual-spawning, I investigated countergradient growth variation of Atlantic sturgeon along a latitudinal range. Seasonal changes in temperature that juveniles encounter during their first year of life, referenced here as thermal phenology, plays an integral role in determining their growth and size. To evaluate thermal phenology, a valuable tool is the growth-degree-day (GDD) model, which integrates temperatures that a fish

experiences together with thermal tolerance thresholds. The GDD method allows for growth to be scaled to expected thermal performance throughout the first year's growing season (Neuheimer and Taggart 2007; Humphrey et al. 2014). This thermal concept should be applicable to most fish species and when GDD is unable to explain the seasonal and variations in length, it is an indication that other factors may be contributing to the size-at-age variation (e.g., food availability, genetics) (Neuheimer and Taggart 2007). The GDD method also allows individual growth calendars to be tracked for differing hatch dates, regions, and years making this method ideal for comparing the thermal phenology of Atlantic sturgeon growth along their latitudinal gradient. Although fish weight can be used as the principal growth variable explained by GDD, length of the fish is preferred since it has either nil or positive changes on a seasonal basis (i.e. fish will not shrink in length) (Neuheimer and Taggart 2007; Humphrey et al. 2014).

Growth rates of Atlantic sturgeon and the better-studied sympatric shortnose sturgeon (*A. brevirostrum*) tend to be higher in the southern portion of their range (Murawski and Pacheco 1977; Dadwell et al. 1984; Smith 1985). Shortnose sturgeon attain lengths of 140-300 mm by the end of the first growing season (age-0 juveniles), depending on latitude (Dadswell et al. 1984). In the Saint John River, shortnose sturgeon range from 155-190 mm during their second growing season (age-1 juveniles) but in the Hudson River, shortnose sturgeon may reach 250 mm by the end of their first growing season (Pekovitch 1979). Growth information for Atlantic sturgeon after the first growing season is less well documented. In the Altamaha River, age-1 Atlantic sturgeon, confirmed using ageing techniques, reached a

133

maximum 600 mm total length (Schuller and Peterson 2010) and in the Hudson

River, age-1 Atlantic sturgeon were <550 mm total length (Peterson et al. 2000); both

systems were sampled during the summer. Under hatchery conditions in South

Carolina, Atlantic sturgeon grew to 177 mm by day 204 (Gilbert 1989) and in a PA

hatcher grew to 360 mm at age-1 (Secor et al. 2000b).

To test if northern and southern populations of Atlantic sturgeon express

countergradient variation in growth, I used juveniles, representing populations from

the Altamaha River, GA and the Saint John River, Canada in a common garden

experiment in which they were exposed to three thermal regimes, which were

representative of the species latitudinal range. In addition to this laboratory

experiment, I applied a GDD model over the latitudinal range of Atlantic sturgeon to

determine: 1) the number of GDD accumulated during the first year of life and 2)

predicted size of Atlantic sturgeon at the first year of life (age=1.0). Specific

hypotheses included: 1) differences in growth between genetic strains will occur

when exposed to thermal regimes that represent the range of the species occurrence;

2) the number of GDD accumulated over the first year of life will be inversely related

to latitude (i.e. higher latitudes will have less accumulation of GDD); 3) accumulated

GDD for age-1 Atlantic sturgeon will be less for northern populations than southern

populations; and 4) the accumulated GDD for age-1 Atlantic sturgeon will be similar

for spring-spawned and fall-spawned Atlantic sturgeon.

Methods

Laboratory experiment

A comparison of juvenile growth between Saint John River, New Brunswick, Canada ("Canada") and Altamaha River, GA ("Altamaha") strain Atlantic sturgeon was conducted in the laboratory to (1) provide insight into genetic growth differences between strains exposed to the same thermal regimes, which were representative of the species latitudinal range and (2) determine the effect of thermal regime on growth of juvenile Atlantic sturgeon over their first year of life. Canada-strain Atlantic sturgeon were acquired from Dr. Cornel Ceapa (Acadian Sturgeon and Caviar, Inc., Saint John, New Brunswick, Canada) in July 2013 (hatch date: July 21, 2013). Altamaha-strain Atlantic sturgeon were acquired from U.S. Fish and Wildlife Bears Bluff National Fish Hatchery (Warm Springs, Georgia) in August 2013 (hatch date: August 9, 2013). All fish were initially reared in freshwater (~17.8°C) and fed *Artemia* nauplii before being weaned to commercial diet and acclimated to ambient Choptank River (Maryland, Chesapeake Bay) water until the start of the experiment.

Thermal regimes for the study included those simulating the mean monthly temperatures, using 2013 water quality data for the Edisto River, South Carolina and Saint John River, New Brunswick, Canada (Table 1). Treatments included Saint John River strain juveniles reared in an Edisto River temperature profile and Altamaha River strain reared in a Saint John River temperature profile as well as controls where each strain was reared in its natal thermal regime. Seven fish were stocked in each tank (148-L) prior to the start of the experiment and acclimated to the target

135

temperature ($\Delta 1°C$ day^{-1}). Six replicates were used for each strain for both the Saint

John River and Edisto River temperature treatments (total = 24 tanks). Additionally,

both strains were reared in ambient Choptank River as an intermediate latitudinal

temperature profile. Due to the limitation in the number of 148-L tanks available,

larger tanks were used for the Choptank River treatment (~1600-L). The experiment

was conducted December 2013 – June 2014 for the Choptank River and Edisto River

thermal treatments. Unfortunately, due to a mechanical failure, the Saint John River

thermal treatment was terminated early during March 2014. Fish were fed 5% body

weight day^{-1} (commercial pellets; Zeigler Bros, Inc., Gardner, PA) during the course

of the experiment. Saint John and Edisto thermal regimes were regulated using heat

exchangers in a partially recirculating aquaculture system using filtered ($2\mu m$)

Choptank River water. Salinity was ambient Choptank River water and ranged 8-12

psu. Weights (g) and lengths (mm total length (TL)) were measured for all

experimental fish, and recorded within a couple days of the end of each 4-week

interval before temperatures was stepped up or down ($1°C$ day^{-1}) for the next

corresponding temperature in the Saint John River and Edisto River system profiles.

Due to the small initial size of the fish (Altamaha River strain: mean = 178 mm ±8.1

SD; Saint John River strain: mean = 180 mm ±9.2 SD, individual fish were not

marked so lengths and weights for each tank were summed for statistical

comparisons. There was no statistical difference in the initial lengths of stocked fish

among treatment levels (ANOVA: between strains, n= 30; p=0.48; between thermal

regimes, n=30; p=0.76). There was also no statistical difference in the initial weights

of stocked fish among treatment levels (ANOVA: between strains, n=30; p=0.06); between thermal regimes, n=30; p=0.84).

Growth-degree-days (GDD) were calculated for each temperature profile during this period to provide a standardized response of growth among thermal regimes. Using the minimum temperature threshold, I used the following equation:

$$GDD = \Sigma \ (T_i - T_{th})*\Delta d;$$

where T_i is the mean daily water temperature, T_{th} is the minimum (4°C) or maximum (28 °C) thermal threshold of the species, and Δd is the number of days between sampling. When calculating GDD at thermal maximum, T_{th} and T_i were switched in the GDD equation. Note, I assumed that fish cannot lose length, therefore GDD was assigned a value of 0 if temperatures were outside the species tolerance limits. Little information was available related to lower temperature thresholds for Atlantic sturgeon. Niklitschek and Secor (2009) found at 6°C (70% dissolved oxygen), Atlantic sturgeon had minimal food consumption (< 0.1 kJ g^{-1} d^{-1}) and oxygen consumption (<0.05 mg h^{-1}). In a hatchery setting, Mohler (2004) similarly observed very low food consumption rates at 6.8 °C and reported weight losses by juveniles at <5 °C. Juvenile Atlantic sturgeon exposed to ambient Patuxent River water temperatures stopped feeding and experienced lost equilibrium at <4°C (Dr. David Secor, personal communication, 2017). Thus for a low temperature threshold I chose 4°C. For the thermal maximum, I chose 28°C based on laboratory experiments of thermal tolerance in Atlantic sturgeon (Dovel and Berggren 1983; Niklitschek and Secor 2005; Niklitschek and Secor 2009).

Repeated measures ANOVA (R Core Team 2016) was used to compare the

effects of thermal regime and strain on the repeated tank measurements of mean

length, weight, and specific growth rate. Four models were compared to determine

the best covariance structure among repeated measures: (1) a baseline model

assuming independence (Model 1), (2) a model with dependence between tanks but

no correlation between days (Model 2), (3) a model with dependence between tanks

and AR1 correlation (an autoregressive lag 1 covariance structure) between days

(Model 3), and (4) a model with dependence between tanks and AMRA(1,1)

correlation (autoregressive moving average model) between days (Model 4). The

best model was determined using the lowest AIC (Akaike Information Criterion)

value after which the final model structure was determined using restricted maximum

likelihood. Post-hoc comparisons using Tukey's honest significant difference were

used to determine which comparisons were significant. In addition, regressions were

used to determine the extent GDD could explain overall SGR and length-at-day

(LaD).

Comparison of GDD along a latitudinal gradient

Water quality data (2008-2013) for estuarine systems from Maine to South

Carolina were obtained from the National Oceanic and Atmospheric Administration

National Estuarine Research Reserve System (NERRS). Seven NERRS sites were

selected to represent the latitudinal distribution of Atlantic sturgeon along the east

coast of the United States: (1) Wells, Maine, (2) Great Bay, New Hampshire, (3)

Hudson River, New York, (4) Chesapeake Bay, Maryland, (5) North Carolina, (6)

North Inlet-Winyah Bay, South Carolina (hereafter "South Carolina"), and (7)

138

Ashepoo-Combahee-Edisto Basin (ACE Basin), South Carolina (Fig. 1). Within each

NERRS, one station was selected to represent the estuarine system for calculating

GDD. Selected stations were tidal freshwater areas within the estuary, or the station

with the lowest salinity. Water temperature data was averaged on a daily basis for all

systems, allowing for daily calculations of GDD. The GDDs for each representative

station were calculated using the same formula as described previously. After daily

GDD was calculated, GDDs were summed for each month. For stations where winter

water temperature data was not recorded, I assumed zero growth occurred during

these months since water temperature data recorded before or after the missing period

was at or below the temperature threshold for Atlantic sturgeon.

Using an ANOVA, I compared NERRS sites and years to determine if there

was a statistical difference in GDD estimates between NERRS sites (i.e., over a

latitudinal gradient) and years. Additionally, cumulative GDD was calculated for the

first year of life (age 1.0) for each NERRS site for spring-spawned sturgeon and fall-

spawned sturgeon, where appropriate, to determine if the number of GDDs

experienced by sturgeon were different depending on the season in which they were

spawned. I used an ANOVA to make statistical comparisons between NERRS and

years. Post-hoc comparisons for all comparisons were completed using Tukey's

honest significant difference.

Length at age-1.0 was predicted from combined experimental data using a von

Bertalanffy growth model: $l_{GDD}=L_\infty(1-e^{-K(GDD-GDD_0')})$; where the age term t is

substituted for GDDs. The model was fitted using an iterative fitting procedure

within Excel (Solver ©). In the prediction for all GDDs from hatch to age 1.0,

experimental period GDDs were summed with an estimate of GDDs occurring from hatch to the start of the experiment (122 days 18°C~1708 GDDs).

Results

Laboratory experiment

Owing to the early termination of the Saint John's River thermal regime experiment, I did initial thermal regime comparisons for the abbreviated period December 2013 - March 2014. Based on AIC criteria, ANOVA tests of average sturgeon length and weight responses utilized a within-tank autoregressive moving average between days (Table 2). There was no effect of strain on average fish length (p=0.82) or weight (p=0.88). Nor was there a significant interaction between thermal regime and strain on length (p=0.80) or weight (p=0.78), so these factors were dropped in the development of the final model. Both sturgeon length and weight were significantly influenced by thermal regime treatment (p<0.05) (Table 3). Thus regardless of strain, juveniles exposed to the Edisto River thermal regime were significantly larger (mean = 232.0 mm TL; 57.0 g) than from the Saint John's River thermal regime (mean = 180.6 mm TL; 23.6 g; p<0.001) and the Choptank River thermal regime (mean = 192.8 mm TL; 30.7 g; p<0.03) (Figs 2, 3). Although higher growth was observed for the Choptank River thermal regime, no significant difference was detected in the lengths of fish between the Saint John's River and the Choptank River thermal regimes (p>0.8) (Figs 2, 3).

Using AIC criteria, predictions of size were compared on the basis of experimental days versus GDDs for single and combined strains (Table 4). In the Saint John River thermal regime, predictions of length was improved for the number of experimental days in comparison to GDDs for individual and combined strains yet AIC criteria were close for the Altamaha-strain and combined strains (Table 4; Figures 4, 6). In the Edisto and Choptank River thermal regimes, predictions of length for individual and combined strains were improved for the number of GDDs in comparison to experimental days, except for Canada-strain in the Edisto River thermal regime which was better predicted by experimental days (Table 4; Figure 5). AIC differences were larger in the Choptank River thermal regime than those for the St. John's and Edisto thermal regimes, so that for combined regimes, GDD was also selected as providing the best prediction of length (Table 4; Figure 7). Combining strains resulted in a saturation curve. The von-Bertalanffy growth equation was used to develop a non-linear equation to best represent length across GDD. The resulting regressions equation, length = 803.93*(1-exp(-0.000167*(GDD-(110.3)))), was used to estimate age-1.0 sturgeon along a latitudinal gradient, as discussed in subsequent sections. For the predictive equation, I had to account for GDDs that accumulated before the start of the experiment so 1708 GDDs were added to the calculated experimental GDDs.

Comparison of GDD along a latitudinal gradient

The annual accumulation of GDDs varied significantly over a latitudinal gradient (Table 5; Fig. 8). Annually, Maine accumulated significantly less GDDs than all systems south of New Hampshire (p<0.001). New Hampshire accumulated

141

significantly less GDDs than all systems south of New York (p<0.001). New York

accumulated less GDDs annually compared to southern systems but was only

significantly different from the Chesapeake Bay and South Carolina (p<0.05).

Chesapeake Bay, North Carolina, South Carolina, and ACE Basin were not

significantly different from the systems located south of them. Interestingly, systems

south of the Chesapeake Bay accumulated less GDDs on an annual basis than the

Chesapeake Bay, where the maximum accumulation of GDDs occurred (Fig. 8, Table

6). The Chesapeake Bay also has the least number of days with sub-optimal

temperatures (<4°C) compared to systems to the north and the least number of days

of supra-optimal temperatures (>28°C) compared to systems to the south (Table 6).

Systems from the Chesapeake Bay north to Maine have peak accumulation of GDDs

in July (Fig. 12 a-d). However, systems south of the Chesapeake Bay have two peaks

annually, one in May and one in September or October (Fig. 9 e-g). The decrease of

GDDs during the summer months in these systems is due to supra-optimal

temperatures.

Accumulation of GDD across a latitudinal gradient for age 1.0 sturgeon

There was a significant difference in the accumulation of GDDs for spring-

spawn sturgeon over a latitudinal gradient (n=35, p<0.05) (Fig. 10). Age-1.0

sturgeon in the three most northern systems (Maine, New Hampshire, and New York)

accumulated significantly less GDD over the first year of life than the southern

latitude systems. Age-1.0 sturgeon in the Chesapeake Bay region, accumulated the

most GDDs (mean=4295±149) compared to all other systems, particularly those to its

north. GDDs were fairly similar between the Chesapeake and systems to its south.

142

There was no significant difference in the accumulation of GDDs for fall-spawn sturgeon over a latitudinal gradient (n=20; p>0.05) (Fig. 11). Within systems that experience both a spring- and fall-spawn event, there was no significant differences in the accumulation of GDDs between the seasons or systems in which sturgeon spawn after one year of life (n=20; p>0.05) (Fig. 12). Sturgeon in systems where both spring- and fall-spawning are believed to occur accumulate more GDDs during their first year of life than in systems where only spring-spawning occurs (Fig. 13). Under a hypothetical scenario where fall-spawning occurs in all systems, the same pattern holds; there isn't a significant difference between spring- and fall-spawn accumulation of GDD (n=35; p>0.05) (Fig. 14) and there may be a threshold around 4000 GDD for fall spawning to occur in systems.

Length of age-1.0 sturgeon over a latitudinal gradient

Using the model of length versus GDD estimated for my laboratory experiments (Fig. 10), I estimated the total length of age-1.0 fish across a latitudinal gradient using the accumulated GDD for each system (2008-2012) (Figure 15). Spring-spawn age-1.0 Atlantic sturgeon attained the smallest size in Maine (253.2±8.6 mm; range=241.8-267.6 mm) whereas the Chesapeake Bay produced the largest size Atlantic sturgeon (404.2±10.0 mm, range = 386.9-416.0 mm). Age-1.0 Atlantic sturgeon in New Hampshire were estimated to be 307.0 mm (±5.7; range=300.8-315.4 mm) while in New York, age-1.0 sturgeon were estimated to be 335.7 mm (±8.7; range=321.5-346.0 mm). South of the Chesapeake Bay, age-1.0 sturgeon sizes were comparable. In North Carolina, spring-spawned age-1.0 sturgeon were estimated to reach a length of 381.9 mm (±16.1; range=367.1-406.8 mm).

143

Within the two sites in South Carolina, sizes were estimated to be 382.5 mm (±16.3; range=354.1-403.9 mm) and 374.1 mm (±24.1; range=340.9-409.2 mm). Fall-spawned sturgeon were of comparable size as their spring-spawned counterparts.

Discussion

Results from the phenology laboratory experiment showed no strain effect on growth of Atlantic sturgeon reared in a common-garden environment, therefore latitudinal countergradient growth variation does not appear to occur in Atlantic sturgeon. Although countergradient growth variation has been highlighted in other ectotherms exhibiting wide latitudinal ranges (Conover et al. 2009), there are species that do not exhibit this behavior. The California grunion, *Leuresthes tenuis*, does not experience countergradient growth, which may be due to their oceanic life history (Brown et al. 2012). Atlantic cod (*Gadus morhua*) populations responded similarly to a warm thermal regime indicating that observed higher growth rates of southern populations were not due to higher genetic capacities for growth (Purchase and Brown 2001). Species from the salmonid family have also shown a lack of strain effect in their capacity for growth. Atlantic salmon (*Salmo salar*) from five Norwegian rivers reared in common thermal conditions showed no association between their river of origin and maximal or threshold growth rates (Jonsson et al. 2001). Atlantic salmon from British populations also exhibited similar growth performance (Elliot and Hurley 1997). Arctic charr, *Savelinus alpinus*, from waters between 54 and 70°N showed no geographical trend in growth performance (Larsson et al. 2005). In this study, Atlantic sturgeon had higher growth in warmer temperatures, which is expected for ectotherms, but Canada-strain Atlantic sturgeon did not compensate for a

shorter growing season with a greater capacity for growth. If strain does not influence growth then thermal growth performance should be generalizable across latitudes and spawning periods and permit predictions of juvenile sizes across the species range.

Experimental results shown here for Atlantic sturgeon and those for lake sturgeon (Power and McKinley 1997) indicate that GDDs represent a common currency for growth performance and length predictions. Because fish are ectotherms, the thermal integral concept, or GDD, should be applicable to most fish species and in instances when GDD cannot explain variation in size-at-age, other factors such as food availability may be contributing to the variation (Neuheimer and Taggart 2007). Sub-adult and adult lake sturgeon total length was well explained by GDDs, 76% and 86%, respectively (Power and McKinley 1997). Like Atlantic sturgeon, lake sturgeon span a large geographical range, spanning approximately 24° of latitude and like Atlantic sturgeon in my study, individuals with the lowest thermal opportunity for growth were shorter and weighed less (Power and McKinley 1997). Similar to Atlantic sturgeon, as lake sturgeon age the rate of increase in length decreases, yet the significance of GDD as an explanation of length at age for lake sturgeon persisted (Power and McKinley 1997). Variation in length of other species is well explained by GDDs. The GDD metric has been used to explain 98% and 93% of the variation in length-at-day for larval Atlantic herring (*Clupea harengus*) and age 2-4 Atlantic cod, respectively (Neuheimer and Taggart 2007). In the Chesapeake Bay, the GDD model explained 80% of the variability in length for age-0 Atlantic menhaden (*Brevoortia tyrannus*) (Humprey et al. 2014). For age-0 walleye (*Sander*

vitreus), a model using GDD described 65% of the variability in annual mean length (Uphoff et al. 2013). In this study, GDD was explained 86% of the variation in length of Atlantic sturgeon, which is within the range of the reviewed literature. This GDD model allows practical estimates of age 1.0 lengths throughout the species range, but also permits exploration of the dual spawning behavior by Atlantic sturgeon, which apparently occurs in only the southern part of its range (Balazik and Musik 2015).

Based on the seasonal observations of adult and early life stages in Atlantic sturgeon spawning tributaries, dual-spawning events have been proposed for populations in Maryland, Virginia, North Carolina, and South Carolina (Smith et al. 1984; Balazik et al. 2013; Smith et al. 2015; Hager et al. 2014; Balazik and Musick 2015), and in the Altamaha River, Georgia, Atlantic sturgeon spawning may only occur in the fall (Ingram and Peterson 2016). Results from the GDD model indicated that thermal conditions experienced by northern populations (Maine to New York), may be inadequate to support fall spawning. Although GDDs for both fall and spring spawning components were similar for Northern populations, predicted sizes at winter onset would be substantially different between the two seasonal cohorts. For instance, Hudson River spring and fall age-0 juveniles would be expected to be 318±9.0 mm and 102.3±4.3 mm on 1 January. In comparison Chesapeake Bay spring and fall age-0 juveniles would be 351.5±8.7 mm and 148.6±7.4 mm on 1 January. Smaller sizes at the onset of winter would be expected to result in increased mortality owing to thermal stress (e.g., inability to maintain homeostasis) and starvation (e.g., allotment of energy stores) (Hurst 2007). Spring-spawned juveniles from northern

146

populations, albeit smaller in size than their southern population counterparts, may be sufficiently large at winter onset to weather the longer and more intense winters encountered at higher latitudes. Interestingly, there is a strong threshold difference in days < 4 C between the Hudson River (119.2±13.8 days) and the Chesapeake Bay (4.2±6.0 days) (Table 6) associated with the apparent shift from spring spawning in the north to dual spawning in the south. A supra-optimal thermal threshold may also curtail the incidence of dual spawning. In areas where fall-spawning may exclusively occur, as proposed in the Altamaha River, GA (Ingram and Peterson 2016), supra-optimal temperatures (>28°C) may curtail successful spring-spawning events or at least reduce growth and possibly survival of juveniles. Atlantic sturgeon experienced a sharp increase in the number of supra-optimal days between the Chesapeake Bay (0 days) and North Carolina (58.7±20 days) (Table 5). With regional warming in the Mid- and South-Atlantic (Kennedy et al. 2002; Najjar et al. 2010), increased supra-optimal days experienced could negatively affecting spring-spawned sturgeon. If this results in a reduction of recruitment of spring-spawn individuals, then population stability may become dependent on successful fall-spawning events.

My GDD model predicts that the dual spawning strategy should be most successful in the middle latitudinal range of Atlantic sturgeon. Here the number of sub-optimal and supra-optimal days may not limit juvenile sturgeon growth enough to affect size-dependent survival, allowing recruitment to occur regardless of the season of spawning. A remarkable model outcome is that where dual spawning occurs, fall and spring spawning cohort attain equivalent sizes at age 1.0 regardless of thermal regime. This suggests that over generations, selection for either behavior could lead

to equivalent reproductive success. There is some evidence in systems where spring- and fall-spawn sturgeon are genetically distinct (Balazik and Musick 2015; Hilton et al. 2016; Farrae et al. 2017). Although mixing of juveniles would occur in the nursery before migrating seaward, there is some evidence that fall- and spring-run adults do not mix on the spawning grounds (Balazik and Musick 2015). Atlantic herring from autumn- and winter-spawned fish mix extensively yet spawning aggregations consisted almost exclusively of autumn-spawned fish which suggests the season and location of spawning is imprinted on larvae and not due to genetic differences (Brophy et al. 2006). Similarly, Pacific salmon returning to the same tributaries exhibit genetically discrete seasonal spawning runs (Burgner 1991; Dittman and Quinn 1996). Further work to determine if Atlantic sturgeon that undergo dual spawning is related to genetic differentiation and/or if larval and juvenile sturgeon are able to imprint on specific systems during particular seasons merits additional study.

The cryptic behavior of dual spawning may have conferred resilience to Atlantic sturgeon populations. Historically, Atlantic sturgeon adults were harvested mainly during the spring months, either as a targeted fishery (Brundage and Meadows 1982; Smith et al. 1984; Secor and Waldman 1999; Armstrong and Hightower 2002; Secor 2002) or by-catch (Armstrong and Hightower 2002). The moratorium established in the mid-1990s to protect Atlantic sturgeon from commercial and recreational fishing may have provided the opportunity for sturgeon to mature and the population to have overlapping age classes, allowing for recent stabilization of populations along the east coast. Spawning-condition Atlantic sturgeon have recently

been discovered in smaller tributaries of the Chesapeake Bay in the Nanticoke River, York, Rappahannock Rivers (Musick 2005; Hager et al. 2014). It is unknown if this is a new occurrence or if Atlantic sturgeon historically spawned in these systems. However, if historical spawning occurred in these smaller tributaries, it may have protected sturgeon populations from overfishing that occurred in the early 1900s.

Atlantic sturgeon are long-lived fish that mature late in life and typically spawn every 2-5 years. This strategy may foster Atlantic sturgeon population growth (or at least maintain populations) in times when the environment is not conducive to successful spawns or survival of early life stages and juveniles. After Atlantic sturgeon population plummeted due to overfishing in the early 1900s, the storage effect concept (Secor 2007) may explain how Atlantic sturgeon populations were able to be maintained even with such low biomass in systems. The reproductive potential was "stored" in the many adult year classes. The historical cryptic nature of Atlantic sturgeon is becoming apparent as evidence of large adults and small juveniles has recently occurred in systems where it has not been noted in decades such as the Connecticut River (Savoy et al. 2017) and James River (Hilton et al. 2016).

Thermal performance predictions related laboratory and modeling results are curtailed by important experimental constraints and model assumptions. Two strains of Atlantic sturgeon were acquired for the laboratory growth study – Altamaha River, GA and Saint John River, Canada. Although they represent northern and southern strains of spawning populations, the addition of other strains would have strengthened inferences by providing a continuum of expected growth rates (had strain been a significant factor). The small size of the Atlantic sturgeon at the start of the

149

experiment was not conducive to marking individual fish hence, length and weight data were pooled for tanks. Individual growth rates can vary substantially within populations investigation into the variability of growth among different population is warranted. Finally, using progeny from one spawning event in a hatchery may not well represent the genetic variability in wild populations. However, hatchery-reared Atlantic sturgeon provide a reliable source for experimental research with known genetic parentage and utilization of these hatchery-reared sturgeon do not impact the wild populations.

Important GDD model assumptions included: 1) the lower and upper threshold temperatures for Atlantic sturgeon are 4 and 28°C; and 2) the exact timing of spawning associated with spring and fall periods, which likely vary with latitude. Thermal tolerances of Atlantic sturgeon have seen limited investigation, primarily focused on the Hudson River population (Mohler 2004; Niklischek and Secor 2009). It is conceivable that populations could vary in these thresholds, which would influence inferences made related to juvenile size predictions. Still, laboratory experiments indicated that both strains experienced nil growth rates for the Saint John's River at <4°C. In the Edisto River, fish were exposed only briefly to temperatures of 28°C, but this period coincided with a marked decline in growth rate (Figure 16 and 17). Under extreme thermal conditions growth curves saturated indicating nil to very low growth rates. Early termination of the Saint John's River treatment constrained analysis on growth under this temperature regime, however, results did indicate that the Canada-strain did not perform better than the Altamaha-strain, supporting my results that the strains do not appear to have different capacities

for growth. Still, measurements of growth over an entire year's thermal regime would improve the model used in determining size at age 1.0. However, age 1.0 sizes across a latitudinal range were well predicted using the model generated from the laboratory study.

The predicted lengths of age-1.0 sturgeon generally fell within the range of age-1 Atlantic sturgeon reported in literature (Table 6). The age-1.0 length predicted for Maine (241.8-267.6 mm) and New Hampshire (300.8-315.4 mm) were larger than the range of reported age-1 Atlantic sturgeon lengths for Saint John River (217 mm) to the north and less variable than those reported for the Connecticut River (225-640 mm) to the south. The predicted length for age-1.0 in New York (321.5-346.0 mm), which would hypothetically be sampled in April, fell below the range of age-1 Atlantic sturgeon (425-525 mm) sampled in the Hudson River between March-July but were approximately the size of those sampled October-May (323 mm). The length of predicted age 1.0 Atlantic sturgeon in the Chesapeake Bay (386.9-416.0 mm) is within the size range of juveniles captured during summer in the James River (406-431 mm). Predicted lengths of fall-collected juvenile Atlantic sturgeon in North Carolina (367.1-406.8 mm) did not have observed samples from North Carolina systems with which to compare, but the upper range was the same for the lower range in the James River but similar in range to those reported for rivers in Georgia (310-550 mm). The predicted lengths of age-1.0 Atlantic sturgeon in South Carolina (340.9-409.2 mm) are smaller than the length of age-1 Atlantic sturgeon reported for coastal rivers in South Carolina (reported mean=550 mm; sampling period unknown). Thus, in a coarse manner, the predictive model developed in this study was

151

corroborated by observed juvenile lengths. However, a major limitation to such comparisons was lack of knowledge on whether age 1 juveniles were in fact <1.0 or >1.0 owing to time of observation and spawning period. Here, the GDD model – if credible - can be used to evaluate what observed juveniles represent in terms of age and time of spawning.

If researchers have reasonable knowledge of when fish spawn in a system and have access to water temperature data to calculate GDDs, observed Atlantic sturgeon lengths can compared to predicted lengths using the regression equation to predict the age of the fish when sampled. This information provides researchers and managers a way to designate age-1 fish to other attributes such as habitat, abundance, and stresses over a geographical range that does not require use of traditional ageing techniques. Since Atlantic sturgeon do not reach the same length after the first year of growth across a latitudinal gradient (i.e. they do not exhibit countergradient variation in growth), a way to determine the length of an age-1 Atlantic sturgeon within systems is imperative to determine if recruitment is occurring within systems and how long juveniles may spend in their natal estuaries. In addition to gleaning more insight into juvenile life histories, being able to predict length of sturgeon during their first year of growth will help managers and researchers determine: 1) if the sampled sturgeon are < age-1, and thereby provide evidence of successful spawning in a given tributary and 2) the likelihood of juvenile fish sampled in systems are from a spring- or fall-spawn event.

More information on lengths of Atlantic sturgeon between age-1 and age-2, particularly using validated ageing techniques would further validate and refine the

model. Additional research to determine the lower temperature threshold of Atlantic sturgeon would further fine-tune the model. Additionally, fine scale water temperature data within systems in which Atlantic sturgeon spawn could be used to better predict length of age-1 sturgeon on a local scale . The coarse resolution of water quality parameters in many systems, or complete lack of monitoring, currently limits predictions of age-1.0 Atlantic sturgeon in most east-coast systems. The Chesapeake Bay Program as well as Maryland Department of Natural Resources Eye on the Bay contains decades worth of water quality data on a fairly fine scale considering the spatial range of the Chesapeake Bay and its tributaries. However, within-tributary data is still lacking making predictions of age-1.0 sizes between tributaries of the Chesapeake Bay difficult. Data from NERRS sites, as used in this study to calculate GDDs, is also a great source for water temperature data but monitoring sites are intermittently placed within the reserves. Down-scaled climate predictions use regional climate models to better predict climate patterns at a regional scale (Maurer et al. 2007; Tabor and Williams 2010). These finer-scale models may fill in data gaps for systems where monitoring does not occur, however, in-system monitoring would generate more accurate predictive sizes of age-1.0 Atlantic sturgeon.

In conclusion, Atlantic sturgeon strains (Saint John's River and Altamaha River) did not differ in their capacity for growth in thermal regimes that represented the species latitudinal range. This allowed construction of a general predictive model to determine length of age-1.0 sturgeon based on a common species thermal performance. Using water quality data from NERRS sites, GDDs accumulated

153

during the first growing season were calculated and used to predict length of Atlantic

sturgeon across a latitudinal gradient. These predicted lengths are comparable to

lengths reported in literature from the same or nearby systems demonstrating the

validity of the model. In addition, comparisons of GDDs among systems validates

the theory of dual-spawning in systems from the Chesapeake Bay to South Carolina

as well as provides rationale why this behavior may not occur in the more northern

and extreme southern systems of their range. I have shown that the number of days

of sub-optimal and supra-optimal temperatures may be the constraining factors in

systems that have not shown evidence of dual-spawning. In addition, accumulated

GDDs can be calculated under different climate change scenarios and predicted

length of age-1.0 sturgeon across a latitudinal range can determine the effect of

climate change on the size of Atlantic sturgeon in systems, which may alter predation

risks, overwinter survival, tolerance to water quality parameters (i.e. dissolved

oxygen, temperature and salinity), affecting survival of Atlantic sturgeon juveniles

and recruitment in systems.

References

Armstrong, J.L. and J.E. Hightower. 2002. Potential for restoration of the Roanoke River population of Atlantic sturgeon. Journal of Applied Ichthyology 18: 475-480.

Balazik, M., G.C. Garman, J.P. Van Eenennaam, J. Mohler, and L.C. Woods III. 2013. Empirical evidence of fall spawning by Atlantic sturgeon in the James River, Virginia. Transactions of the American Fisheries Society 141(6): 1465-1471.

Balazik M.T. and J.A. Musick. 2015. Dual annual spawning races in Atlantic sturgeon. PLoS ONE 10(5): e0128234. doi:10.1371/journal.pone.0128234.

Berg, O.K., G. Rød, Ø. Solem, and A.G. Finstad. 2011. Pre-winter lipid stores in brown trout *Salmo trutta* along altitudinal and latitudinal gradients. Journal of Fish Biology 79: 1156-1166.

Brophy, D. B.S. Danilowicz, and P.A. King. 2006. Spawning season fidelity in sympatric populations of Atlantic herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences 63: 607-616.

Brundage, H.M. and R.E. Meadows. 1982. The Atlantic sturgeon, *Acipenser oxyrhynchus*, in the Delaware River Estuary. Fishery Bulletin 80(2): 1982.

Burgner, R. L. 1991. Life History of Sockeye Salmon (*Oncorhynchus nerka*), pp 3-117 In C. Groot and L. Margolis (ed.s) Pacific Salmon Life Histories. UBC Press. Vancouver.

Conover, D.O. and T.M.C. Present. 1990. Countergradient variation in growth rate: Compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia 83(3): 316-324.

Conover, D.O., J.J. Brown, and A. Ehtisham. 1997. Countergradient variation in growth of young striped bass (*Morone saxatilis*) from difference latitudes. Canadian Journal of Fisheries and Aquatic Sciences 54: 2401-2409.

Conover. D.O., T.A. Duffy, and L.A. Hice. 2009. The covariance between genetic and environmental influences across ecological gradients. The Year in Evolutionary Biology 1168: 100-129.

Crossman, J.A., P.S. Forsythe, E.A. Baker, and K.T. Scribner. 2009. Overwinter survival of stocked age-0 lake sturgeon. Journal of Applied Ichthyology 25: 516-521.

Dadswell, M.J. 1976. Biology of the shortnose sturgeon (*Acipenser brevirostrum*) in the Saint John River estuary, New Brunswick, Canada. Transactions of the Atlantic Chapter of Canadian Society of Environmental Biology Annual Meeting, pp. 20-72.

Dovel, W.L. 1979. The biology and management of shortnose and Atlantic sturgeon of the Hudson River. Final Report. Project No. AFS9-R.

Dovel, W.L. and T.J. Bergrren. 1983. Atlantic sturgeon of the Hudson Estuary, New York. New York Fish and Game Journal 30(2): 140-172.

Elliott, J.M. and M.A. Hurley. 1997. A functional model for maximum growth of Atlantic salmon parr, *Salmo salar*, from two populations in Northwest England. Functional Ecology 11: 592-603.

Falahatkar, B. S.R. Akhavan, I. Efatpanah, and B. Mcknatkhah. 2013. Effect of winter feeding and starvation on the growth performance of young-of-year (YOY) great sturgeon, *Huso huso*. Journal of Applied Ichthyology 29: 26-30.

Farrae, D., P.M. Schueller, and D.L. Peterson. 2009. Abundance of juvenile Atlantic sturgeon in the Ogeechee River, Georgia. Proceedings on the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 172-176.

Farrae, D.J., W.C. Post, and T.L. Darden. 2017. Genetic characterization of Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus*, in the Edisto River, South Carolina and identification of genetically discrete fall and spring spawning. Conservation Genetics (doi:10.1007/s10592-017-0929-7).

Fritts, M.W., C. Grunwald, I. Wirgin, T.L. King, and D.L. Peterson. 2016. Status and genetic character of Atlantic sturgeon in the Satilla River, Georgia. Transactions of the American Fisheries Society 145(1): 69-82.

Garvey, J.E. and E.A. Marschall. 2009. Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation. Canadian Journal of Fisheries and Aquatic Sciences 60: 938-948.

Gilbert, C.R. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic Bight)—Atlantic and shortnose sturgeons. U.S. Fish and Wildlife Service Biological Report 82 (11.122). U.S. Army Corps of Engineers TR EL-82-3. 28pp.

Hager, C., J. Kahn, C. Watterson, J. Russo, and K. Hartman. 2014. Evidence of Atlantic Sturgeon Spawning in the York River System. Transactions of the American Fisheries Society 143(5): 1217-1219.

Hatin, D., J. Munro, F. Caron, and R.D Simons. 2007. Movements, home range size, and habitat use selection of early juvenile Atlantic sturgeon in the St. Lawrence Estuarine Transition Zone. American Fisheries Society Symposium 56: 129-155.

Hilton, E.J., B. Kynard, M.T. Balazik, A.Z. Horodysky, and C.B. Dillman. 2016. Review of the biology, fisheries, and conservation status of the Atlantic sturgeon, (*Acipenser oxyrinchus oxyrinchus* Mitchill, 1815). Journal of Applied Ichthyology 32(S1): 30-66.

Humphrey, J., M.J. Wilberg, E.D. Houde, and M.C. Fabrizio. 2014. Effects of temperature on age-0 Atlantic menhaden growth in Chesapeake Bay. Transactions of the American Fisheries Society 143: 1255-1265.

Hurst, T.P. 2007. Review Paper: Causes and consequences of winter mortality in fishes. Journal of Fish Biology 71: 315-345.

Hurst, T.P. and Conover, D.O. 2003. Seasonal and interannual variation in the allometry of energy allocation in juvenile striped bass. Ecology 84(12): 3360-3369.

Ingram, E.C. and D.L. Peterson. 2016. Annual spawning migrations of adult Atlantic sturgeon in the Altamaha River, Georgia. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 8: 595-606.

Jonsson, G., R. Forseth, A.J. Jensen, and R.F. Naesje. 2001. Thermal performance in juvenile Atlantic salmon, *Salmo salar* L. Functional Ecology 15: 701-711.

Kenney, V.S., R.R. Twilley, J.A. Kleypas, J.H. Cowan Jr., and S.R. Hare. 2002. Coastal and marine ecosystems and global climate change: potential effects on U.S. Resources. Pew Center on Global Climate Change, Arlington, VA, 52pp.

Larsson, S. R. Forseth, I. Berglund, A.J. Jensen, I. Näslund, J.M. Elliot, and B. Jonsson. 2005. Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. Freshwater Biology 50: 353-368.

Maurer, E.P. L. Brekke, T. Pruitt, and P.B. Duffy. 2007. Fine-resolution climate projections enhance regional climate change impact studies. EOS 88(47): 504.

Mohler, J.W. 2004. Culture manual for the Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*. U.S. Fish and Wildlife Service, Hadley, Massachusetts. 70pp.

Murawski, S.A. and A.L. Pacheco. 1977. Biological and fisheries data on Atlantic sturgeon, Acipenser oxyrynchus (Mitchill). Sandy Hook Lab Tch. Ser. Rep. 10. National Marine Fisheries Service, Highlands, NJ. 69p.

Musick, J.A. 2005. Essential fish habitat of Atlantic sturgeon *Acipenser oxyrinchus* in the Southern Chesapeake Bay. Final report to NOAA/NMFS. VIMS Special Scientific Report #145.

Najjar, R.G., C.R. Pyke, M.B. Adams, D. Breitburg, C. Hershner, M.Kemp, R. Howarth, M.F. Mulholland, M. Paolisso, D. Secor, K. Sellner, D. Wardtop, and R. Wood. 2010. Potential climate-change impacts on the Chesapeake Bay. Estuarine, Coastal and Shelf Science 86: 1-20.

Neuheimer, A.B. and C.T. Taggart. 2007. The growing degree-day and fish size-at-age: the overlooked metric. Canadian Journal of Fisheries and Aquatic Sciences 64: 375-385.

Niklitschek, E.J. and D.H. Secor. 2005. Modeling spatial and temporal variation of suitable nursery habitats for Atlantic sturgeon in the Chesapeake Bay. Estuarine, Coastal and Shelf Science 64: 135-148.

Niklitschek, E.J. and D.H. Secor. 2009. Dissolved oxygen, temperature and salinity effects on the ecophysiology and survival of juvenile Atlantic sturgeon in estuarine waters: I. Laboratory results. Journal of Marine Biology and Ecology 381(Suppl): S150-S160.

Pekovitch, A.W. 1979. Distribution and some life history aspects of the shortnose sturgeon (*Acipenser brevirostrum*) in the upper Hudson River estuary. Hazleton Environmental Science Corporation, Illinois. 23pp.

Peterson, D.L., M.B. Bain, and N. Haley. 2000. Evidence of declining recruitment of Atlantic sturgeon in the Hudson River. North American Journal of Fisheries Management 20: 231-238.

Pörtner, H.O. and M.A. Peck. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. Journal of Fish Biology 77: 1745-1779.

Power, M. and R.S. McKinley. 1997. Latitudinal variation in lake sturgeon size as related to the thermal opportunity for growth. Transactions of the American Fisheries Society 126(4): 549-558.

Purchase, C.F. and J.A. Brown. 2001. Stock-specific changes in growth rates, food conversion efficiencies, and energy allocation in response to temperature change in juvenile Atlantic cod. Journal of Fish Biology 58: 36-52.

R Core Team. 2016. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Schlenger, A.J., E.W. North, Z. Schlag, Y. Li, D.H. Secor, K.A. Smith, and E.J. Niklitschek. 2013. Modeling the influence of hypoxia on the potential habitat of Atlantic sturgeon *Acipenser oxyrinchus*: a comparison of two methods.

Schueller, P. and D.L. Peterson. 2010. Abundance and Recruitment of juvenile Atlantic sturgeon in the Altamaha River, Georgia. Transactions of the American Fisheries Society 139: 1526-1535.

Schultz, E.T. and D.O. Conover. 1997. Latitudinal differences in somatic energy storage: Adaptive responses to seasonality in an estuarine fish (Atherinidae: Menidia menidia). Oecologia 109(4): 516-529.

Schultz, E.T., K.E. Reynolds, and D.O. Conover. 1996. Countergradient variation in growth among newly hatched *Fundulus heteroclitus*: Geographic differences revealed by common-environment experiments. Functional Ecology 10(3): 366-374.

Secor, D.H. and J.R. Waldman. 1999. Historical abundance of Delaware Bay Atlantic sturgeon and potential rate of recovery. American Fisheries Society Symposium 23: 203-216.

Secor, D.H., T.E. Gunderson, and K. Karlsson. 2000a. Effect of temperature and salinity on growth performance in anadromous (Chesapeake Bay) and nonanadromous (Santee-Cooper) strains of striped bass *Morone saxatilis*. Copeia 2000(1): 291-296.

Secor, D.H., E.J. Niklitschek, J.R. Stevenson, T.E. Gunderson, S.P. Minkkinen, B. Richardson, B. Florence, M. Mangold, J. Skjeveland, A. Henderson-Arzapalo. 2000b. Dispersal and growth of yearling Atlantic sturgeon, *Acipenser oxyrinchus*, released into Chesapeake Bay. Fisheries Bulletin 98: 800-810.

Secor, D.H. 2002. Atlantic sturgeon fisheries and stock abundances during the late nineteenth century. American Fisheries Society Symposium 28: 89-98.

Secor. D.H. 2007. The year-class phenomenon and the storage effect in marine fishes. Journal of Sea Research 57: 91-103.

Shuter, B.J., A.G. Finstad, I.P. Helland, I. Zweimüller, and F. Hölker. 2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. Aquatic Sciences 74: 637-657.

Smith, T.I.J., D.E. Marchette, and G.D. Ulrich. 1984. The Atlantic sturgeon fishery in South Carolina. North American Journal of Fisheries Management 4: 164-176.

Smith, T.I.J. 1985. The fishery, biology, and management of Atlantic sturgeon, *Acipenser oxyrhynchus* in North America. Environmental Biology of Fishes 14(1): 61-72.

Smith, J.A., H.J. Flowers, and J.E. Hightower. 2015. Fall spawning of Atlantic sturgeon in the Roanoke River, North Carolina. Transactions of the American Fisheries Society 144: 48-54.

Stewart, N.D., M.J. Dadswell, P. Leblanc, R.G. Bradford, C. Ceapa, M.J.W. Stokesbury. 2015. Age and growth of Atlantic sturgeon from the Saint John River, New Brunswick, Canada. North American Journal of Fisheries Management 35: 364-371.

Tabor, K. and J.W. Williams. 2010. Globally downscaled climate projections for assessing the conservation impacts of climate change. Ecological Applications 20(2): 554-565.

Uphoff, C.S., C.W. Schoenebeck, W.W. Hoback, K.D. Koupal, and K.L. Pope. 2013. Degree-day accumulation influences annual variability in growth of age-0 walleye. Fisheries Research 147: 394-398.

Wijekoon, M.P., V. Puvanendran, D.W. Ings, and J.A. Brown. 2009. Possible countergradient variation in growth of juvenile cod *Gadus morhua* from the northwest Atlantic. Marine Ecology Progress Series 375: 229-238.

Yamahira, K. and D.O. Conover. 2002. Intra- vs. Interspecific latitudinal variation in growth: Adaptation to temperature of seasonality? Ecology 83(5): 1252-1262.

Tables

Table 1. Experimental temperature schedules for Atlantic sturgeon juvenile growth studies.

Date	Treatment Temp
Saint John River, Canada (2013)	
December 2013	0C
January 2014	0C
February 2014	5C
March 2014	5C
Edisto River, SC (2013)	
December 2013	10C
January 2014	10C
February 2014	15C
March 2014	20C
April 2014	23C
May 2014	27C
June 2014	28C

Table 2. Comparison of covariance models for repeated measures analysis of length and weight between thermal regimes. Model 1: no covariance; Model 2: dependence between tanks only; Model 3: autoregressive lag 1 covariance structure; Model 4: autoregressive moving average model.

Model Structure	Model	AIC	ΔAIC	Random
Length~Thermal regime	1	1136.9	59.1	~1|Tank
	2	1128.2	50.4	~1|Tank
	3	1109.4	31.6	~1|Tank
	4	1077.8	0	~1|Tank
Weight~Thermal regime	1	1051.8	34.9	~1|Tank
	2	1022.3	5.4	~1|Tank
	3	1035.4	18.5	~1|Tank
	4	1016.9	0	~1|Tank

Table 3. ANOVA and Tukey honest significant difference pairwise comparisons between thermal regime and Atlantic sturgeon length.

Model Structure	Treatment	lsmean	SE	df	contrasts	p-value
Length~Thermal regime	Saint John	180.3	10.2	27	Choptank-Saint John	0.860
	Choptank	189.6	10.2	27	Choptank-Edisto	0.025
	Edisto	239	14.4	27	Edisto-Saint John	0.001
Weight~Thermal regime	Saint John	23.7	6	27	Choptank-Saint John	0.820
	Choptank	30.1	8.6	27	Choptank-Edisto	0.009
	Edisto	63.9	6	27	Edisto-Saint John	0.000

Table 4. Comparison of experimental days v. GDD in prediction of length for combinations of thermal regime and strain using regressions.

Model	Thermal Regime	Strain	Intercept	Slope	Adjusted R^2	AIC	ΔAIC
ln(Length~days)	Saint John's River	Canada	179.5	0.00127	0.94	-43.5	
ln(Length~GDD)	Saint John's River	Canada	180.2	0.00148	0.68	-37.1	6.4
ln(Length~days)	Saint John's River	Altamaha	176.9	0.00636	0.9	-28.9	
ln(Length~GDD)	Saint John's River	Altamaha	177.3	0.00826	0.92	-29.6	0.7
ln(Length~days)	Saint John's River	Combined	178.5	0.00382	0.58	-55.3	
ln(Length~GDD)	Saint John's River	Combined	178.7	0.00400	0.56	-55	0.3
Length~days	Choptank River	Canada	162.3	0.74000	0.72	62.3	
Length~GDD	Choptank River	Canada	187.9	0.12700	0.99	40.3	22
Length~days	Choptank River	Altamaha	144.7	0.93700	0.72	65.3	
Length~GDD	Choptank River	Altamaha	178.2	0.16200	0.99	45.4	19.9
Length~days	Choptank River	Combined	153.5	0.83800	0.74	122.6	
Length~GDD	Choptank River	Combined	182.7	0.14400	0.98	94.2	28.4
ln(Length)~days	Edisto River	Canada	177.5	0.00394	0.97	-15	
ln(Length)~GDD	Edisto River	Canada	195.4	0.00027	0.87	-6.4	8.6
ln(Length)~days	Edisto River	Altamaha	189.5	0.00389	0.95	-5.3	
ln(Length~GDD)	Edisto River	Altamaha	132.2	0.12205	0.84	-11.8	6.5
ln(Length)~days	Edisto River	Combined	183.4	0.00391	0.95	-14.7	
ln(Length)~GDD	Edisto River	Combined	169.1	0.00026	0.84	-28.5	13.8

	Maine	New Hampshire	New York	Chesapeake Bay	North Carolina	South Carolina	ACE Basin
Table 5. Statistical test significance (ANOVA; p=value) in pairwise comparisons of annual GDD between NERRS sites for years 2008-2013.							
Maine		0.1253	<0.001	<0.001	<0.001	<0.001	<0.001
New Hampshire	0.1253		0.3991	<0.01	<0.01	<0.01	<0.05
New York	<0.001	0.3991		<0.05	0.0644	<0.05	0.1024
Chesapeake Bay	<0.001	<0.01	<0.05		0.5912	0.7683	0.4611
North Carolina	<0.001	<0.01	0.0644	0.5912		0.8084	0.8384
South Carolina	<0.001	<0.01	<0.05	0.7683	0.8084		0.6565
ACE Basin	<0.001	<0.05	0.1024	0.4611	0.8384	0.6565	

Table 6. Annual GDDs and the number of days of sub-optimal and supra-optimal temperatures for NERRS systems for years 2008-2013.

NERRS	Average Annual GDD (±std)	Average # days with sub-optimal temperatures (±std)	Average # days with supra-optimal temperatures (±std)
Well, ME	197.3 (±9.8)	123.8 (±10.9)	0 (±0.0)
Great Bay, NH	249.2 (±9.7)	123.7 (±9.6)	0 (±0.0)
Hudson River, NY	277.7 (±14.8)	119.2 (±13.8)	0.7 (±1.1)
Chesapeake Bay, MD	358.4 (±14.5)	4.2 (±6.0)	0 (±0.0)
North Carolina	340.3 (±28.2)	3.5 (±4.8)	58.7 (±20.0)
North Inlet-Winyah Bay, SC	348.5 (±49.9)	2 (±4.0)	62 (±21.8)
Ashepoo-Combahee-Edisto Basin, SC	333.4 (±50.2)	1.2 (±2.6)	78 (±22.5)

Table 6. Reported and predicted lengths of age-0+ to age 2 Atlantic sturgeon from Canada to Georgia.

Location	Observed size (mm)	Age (yrs)	Predicted size (mm)	Age (yrs)	Reported sampling date	Hypothetical sampling date	Reference
St. Lawrence	448[+]	2			July		Hatin et al. 2007
Saint John River	217	1			May-October		Stewart et al. 2015
Maine			241.8-267.6[+++]	1.0		June[++++]	--
New Hampshire			300.8-315.4[+++]	1.0		May[++++]	--
Connecticut River	225-640	1			May-October 2014		Savoy et al. 2017
New York			321.5-346.0[+++]	1.0		April[++++]	--
Hudson River, NY	323[+]	0+			October-May 1975, 1976, 1978		Dovel 1979
Hudson River, NY	502[+]	1			October-May 1975-1978		Dovel 1979; Dovel and Berggren 1983
Hudson River, NY	425-525	1			March-July		Peterson et al. 2000
Hudson River, NY	450-550	1			August		Peterson et al. 2000
Hudson River, NY	525-600	1			September		Peterson et al. 2000
Hudson River, NY	575-625	1			October-December		Peterson et al. 2000
Chesapeake Bay			386.9-416.0[+++]	1.0		April[++++]	--
James River, VA	406-431[++]	?			November		unpublished
North Carolina			367.1-406.8[+++]	1.0		March[++++]	--

Location	Observed size (mm)	Age (yrs)	Predicted size (mm)	Age (yrs)	Reported sampling date	Hypothetical sampling date	Reference
South Carolina coastal rivers	550	1			Unk		McCord et al. 2007 as reported in Schueller and Peterson 2010
South Carolina			340.9-409.2[+++]	1.0		March[++++]	--
Savannah River, SC/GA	410[+]	0-1			various		Peterson et al. 2008
Ogeechee River, GA	310[+]	0-1			May-December		Peterson et al. 2008
Ogeechee River, GA	242-361	1			June-August 2007		Farrae et al. 2009
Altamaha River, GA	379[+]	0-1			June-August 2005		Peterson et al. 2008
Altamaha River, GA	350-550	1			various		Schueller and Peterson 2010
Satilla River, GA	340-540	1			September-July		Fritts et al. 2016

[+]mean lengths reported

[++]reported 16-17"

[+++]predicted using regression from this study

[++++]hypothetical sampling month

Figures

Figure 1. Locations of National Estuarine Research Reserve Systems used in comparison of growth-degree-days along a latitudinal gradient. 1) Well, ME, 2) Great Bay, NH, 3) Hudson River, NY, 4) Chesapeake Bay, MD/VA, 5) North Carolina, 6) North Inlet-Winyah Bay, SC, and 7) Ashepoo-Combahee-Edisto Basin, SC.

Figure 2. Comparisons of fish lengths (mm) among thermal regimes and between strains within thermal regimes. Different letters denote significant differenc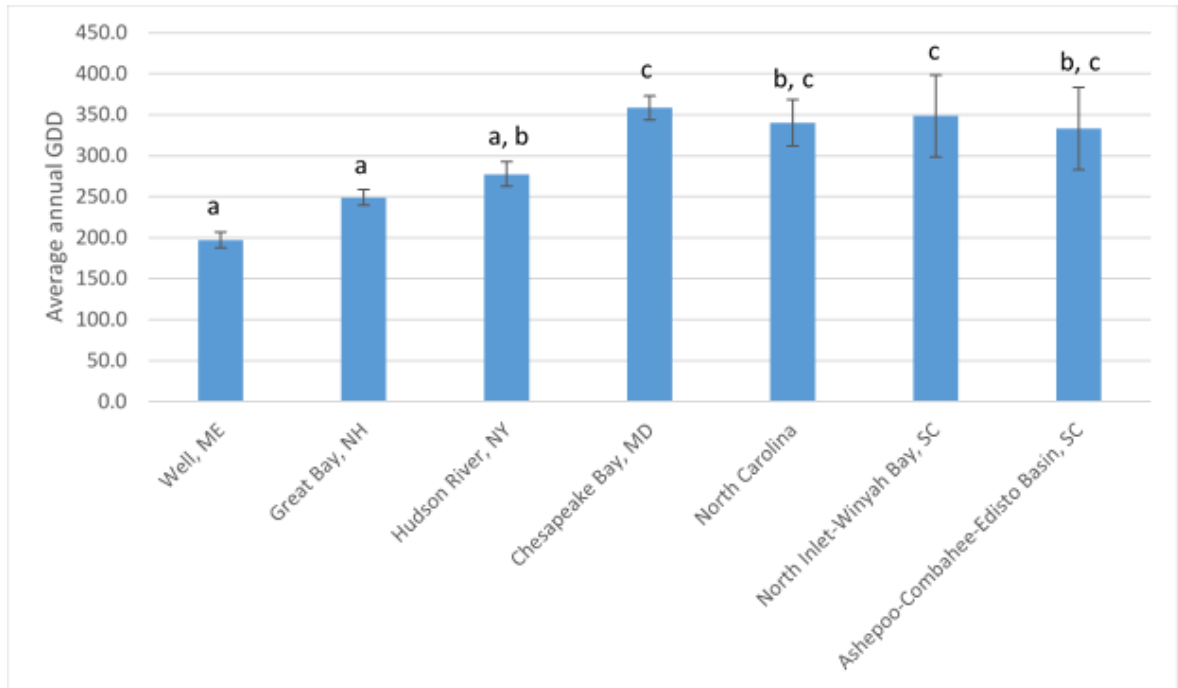es according to ANOVA, Tukey's honest significant difference (a,b represents treatment differences; x,y represent strain differences). Error bars represent standard error.

Figure 3. Comparisons of fish weights (g) among thermal regimes and between strains within thermal regimes. Different letters denote significant differenc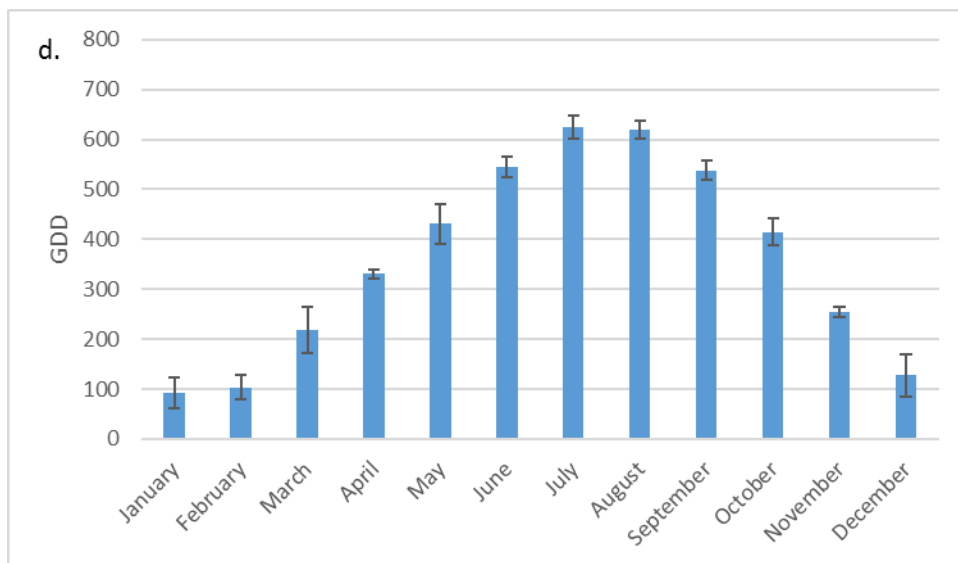es according to ANOVA, Tukey's honest significant difference (a,b represents treatment differences; x,y represent strain differences). Error bars represent standard error.

Figure 4. Length at experimental day (a) and GDD (b) for the Saint John's River thermal regime comparing Canada-strain and Altamaha-strain Atlantic sturgeon.

Figure 5. Length at experimental day (a) and GDD (b) for the Choptank River thermal regime comparing Canada-strain and Altamaha-strain Atlantic sturgeon.

Figure 6. Length at experimental day (a) and GDD (b) for the Edisto River thermal regime comparing Canada-strain and Altamaha-strain Atlantic sturgeon.

Figure 7. Regression of Atlantic sturgeon length on GDD for thermal regimes and strains combined using von Bertalanffy equation.

Figure 8. Comparison of annual GDD between NERRS sites (2008-2013). Error bars represent standard of deviation. Different letters denote significant differences according to ANOVA, Tukey's honest significant difference.

Figure 9. Monthly GDD averages (2008-2013) for a). Maine, b) New Hampshire, c) New York, d) Chesapeake Bay, e) North Carolina, f) South Carolina, g) ACE Basin.

d.

e.

178
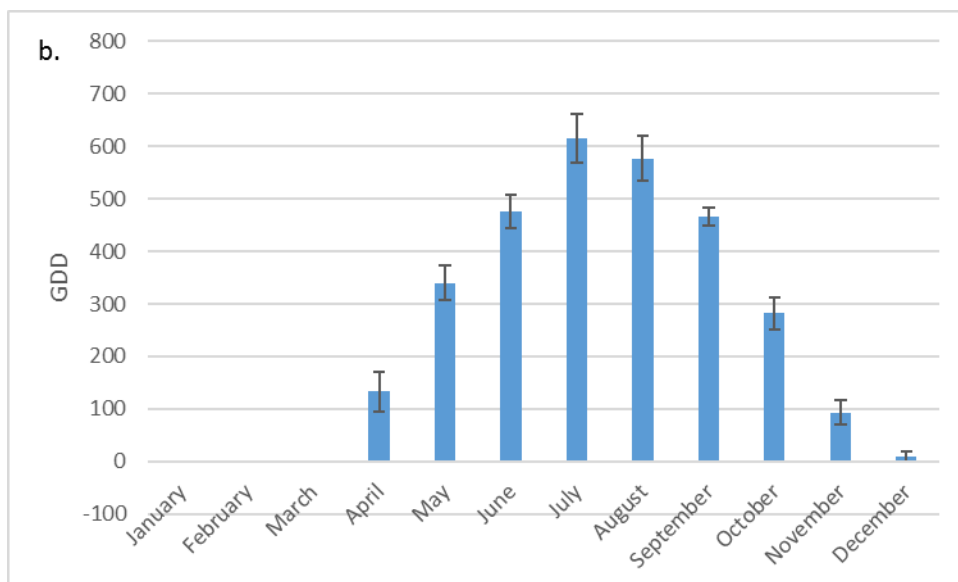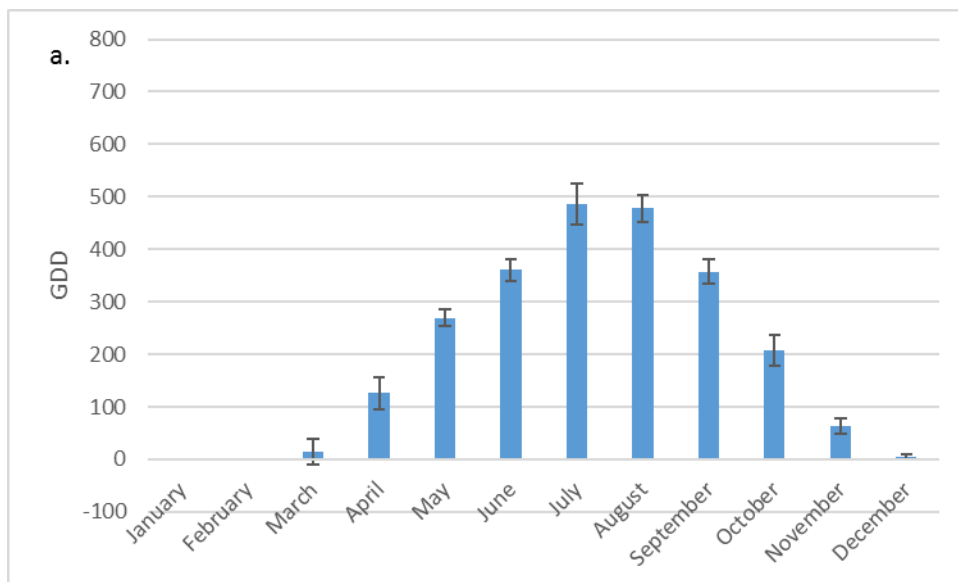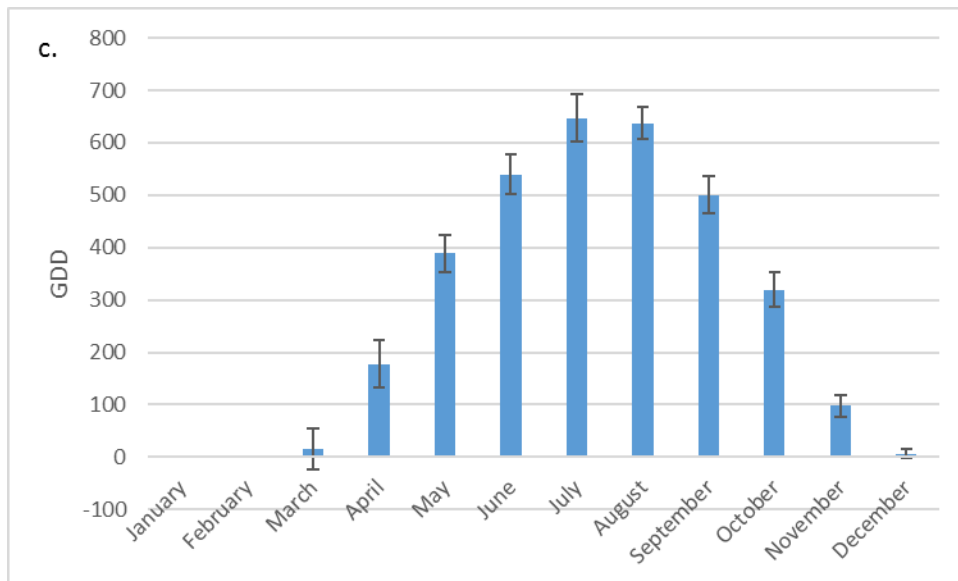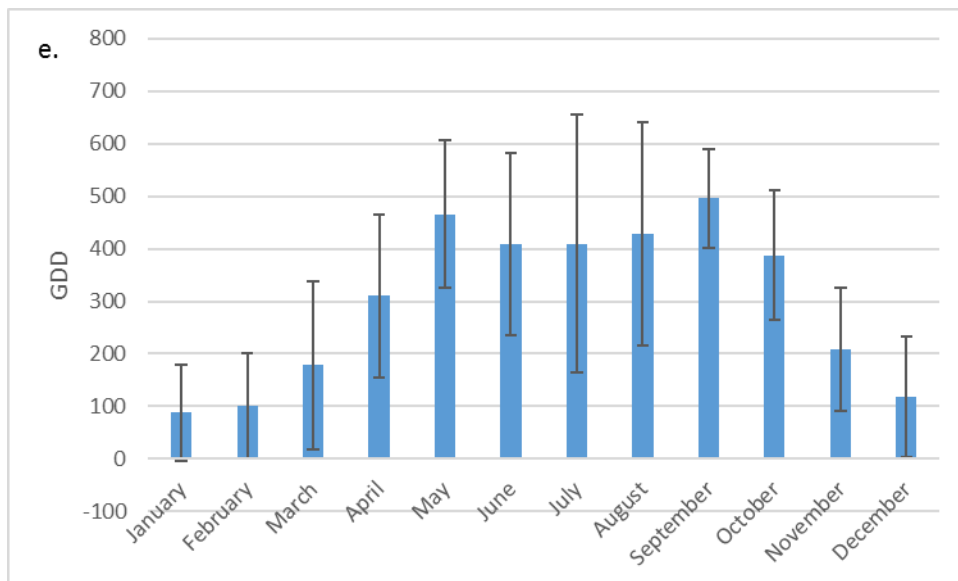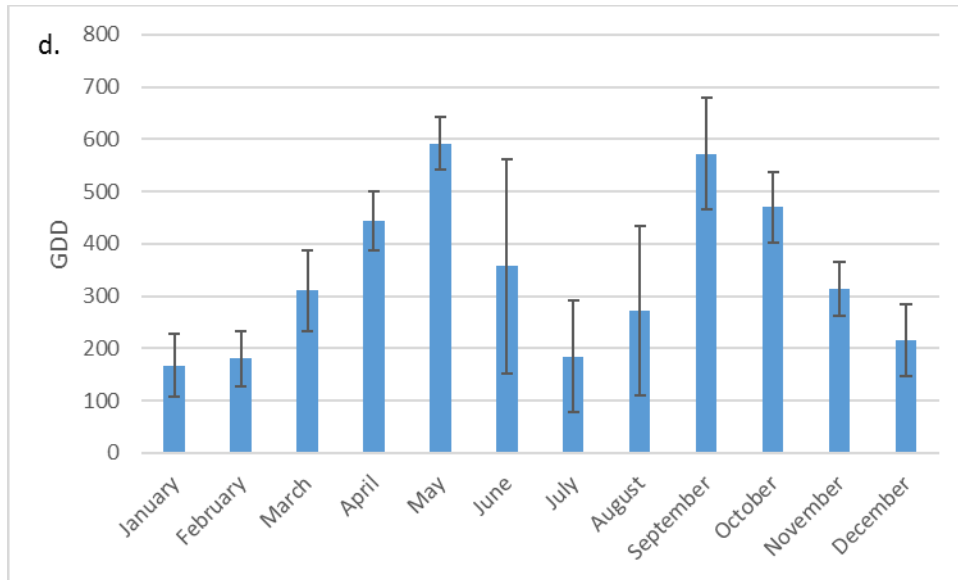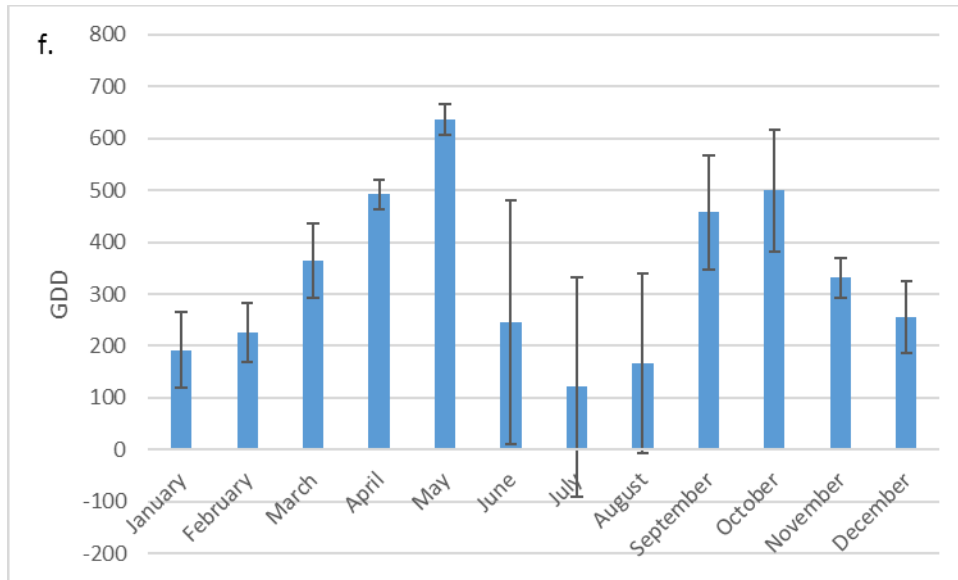
Figure 10. Accumulation of GDD for spring-spawn sturgeon after one year of life. Different letters denote significant difference (p<0.05) according to ANOVA, Tukey's honest significant difference. Error bars represent standard deviation.
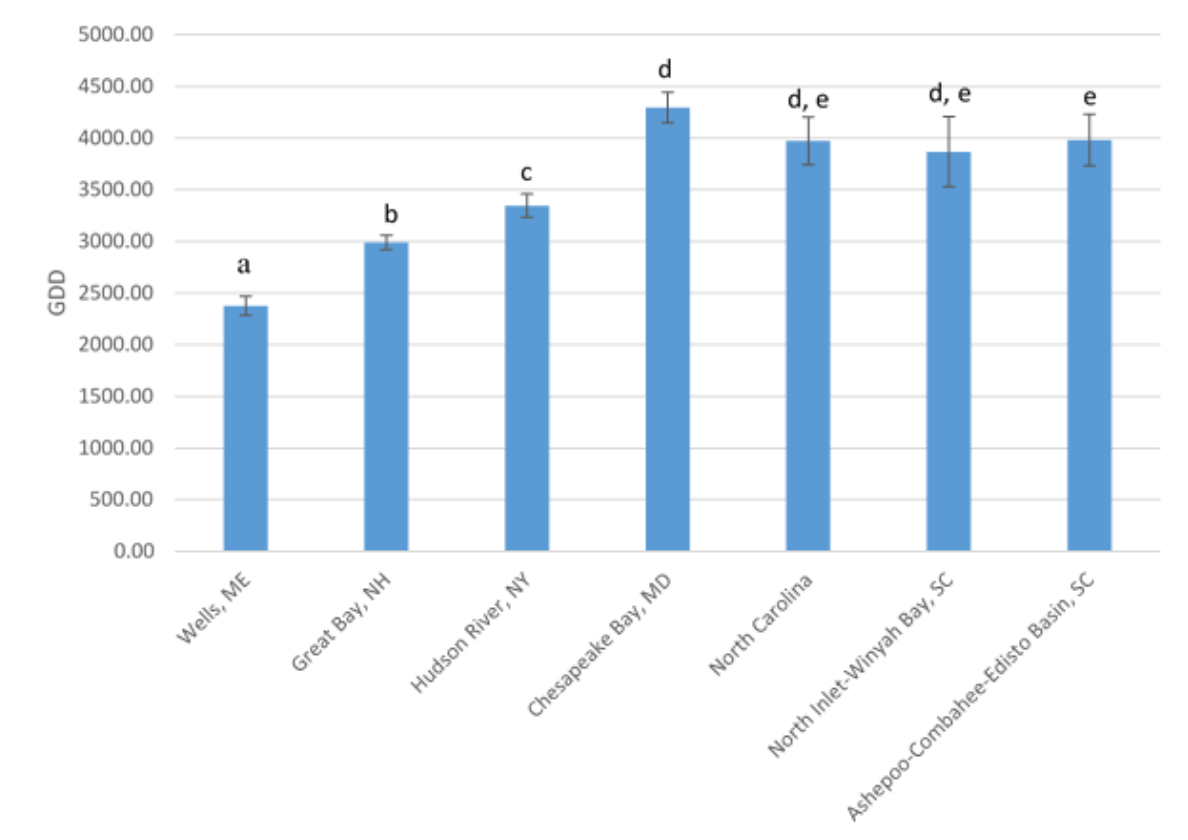
Figure 11. Accumulation of GDD for fall-spawn sturgeon after one year of life. Error bars represent standard deviation.
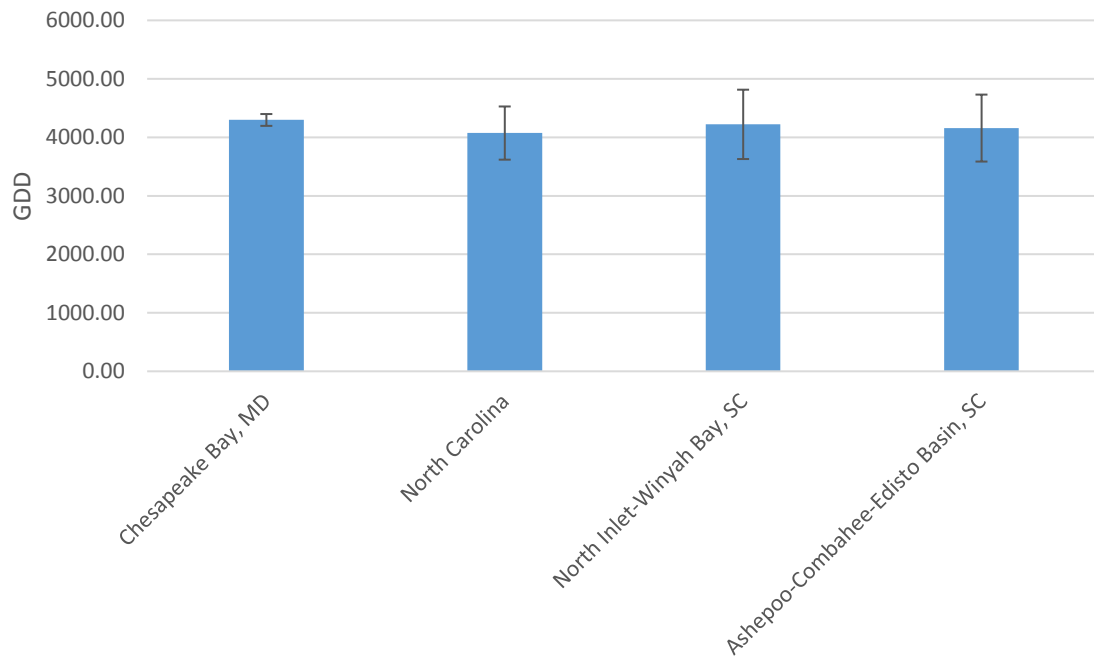
Figure 12. Comparison of the accumulation of GDD for spring- and fall-spawn sturgeon after one year of life. Error bars represent standard deviation.
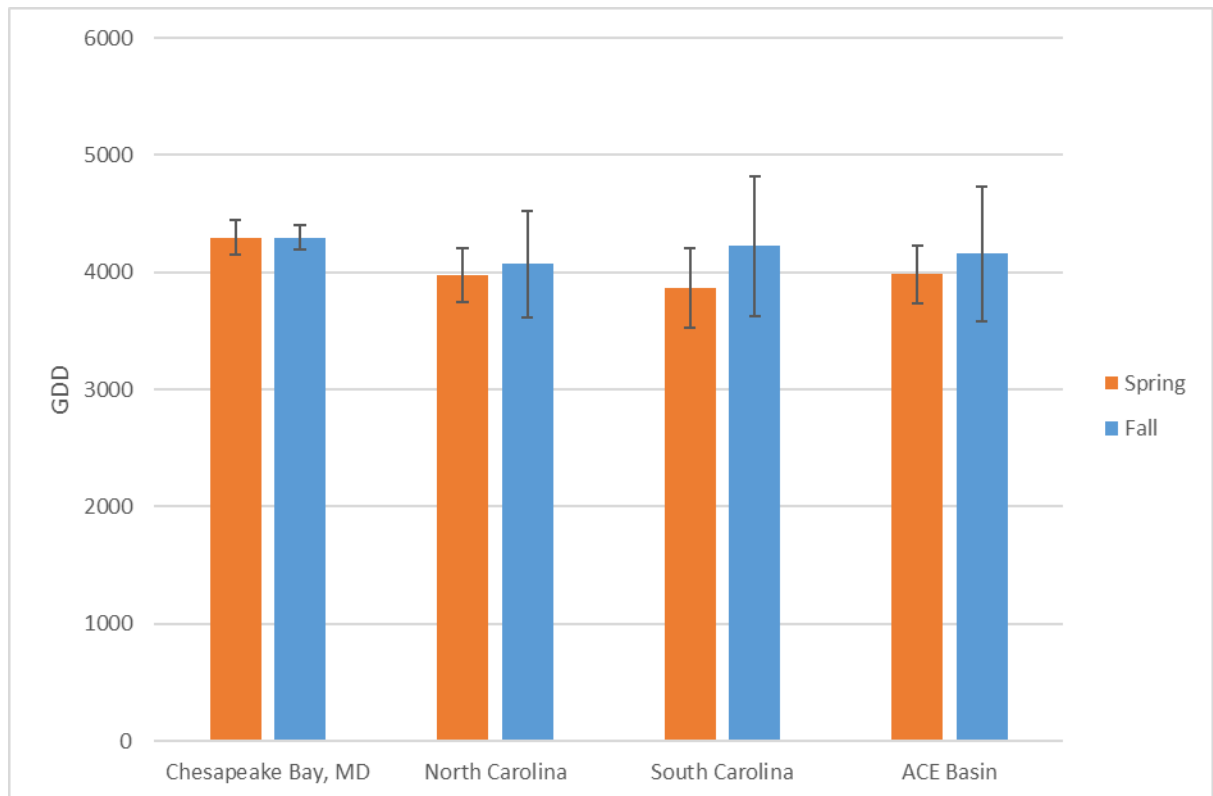
Figure 13. Accumulation of GDD in relation to time of spawning across NERRS sites. Error bars represent standard of deviation. Error bars represent standard deviation.
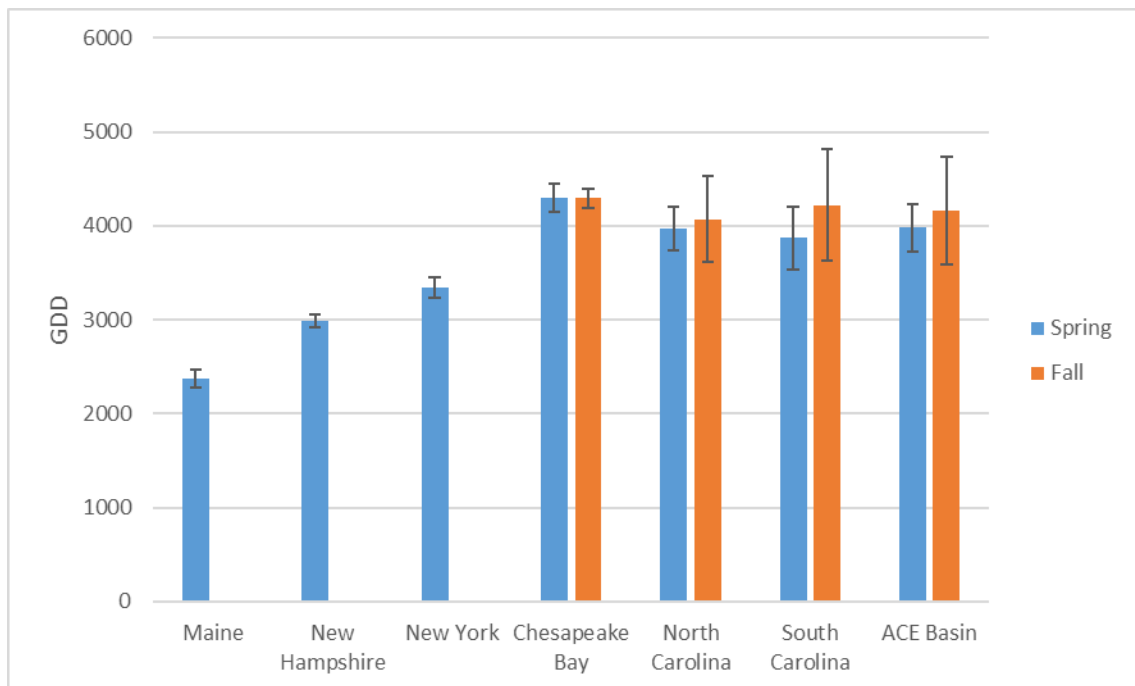
Figure 14. Comparison of the accumulation of GDD for spring- and fall-spawn sturgeon after one year of life, with inclusion of hypothetical fall spawn. Error bars represent standard deviation.
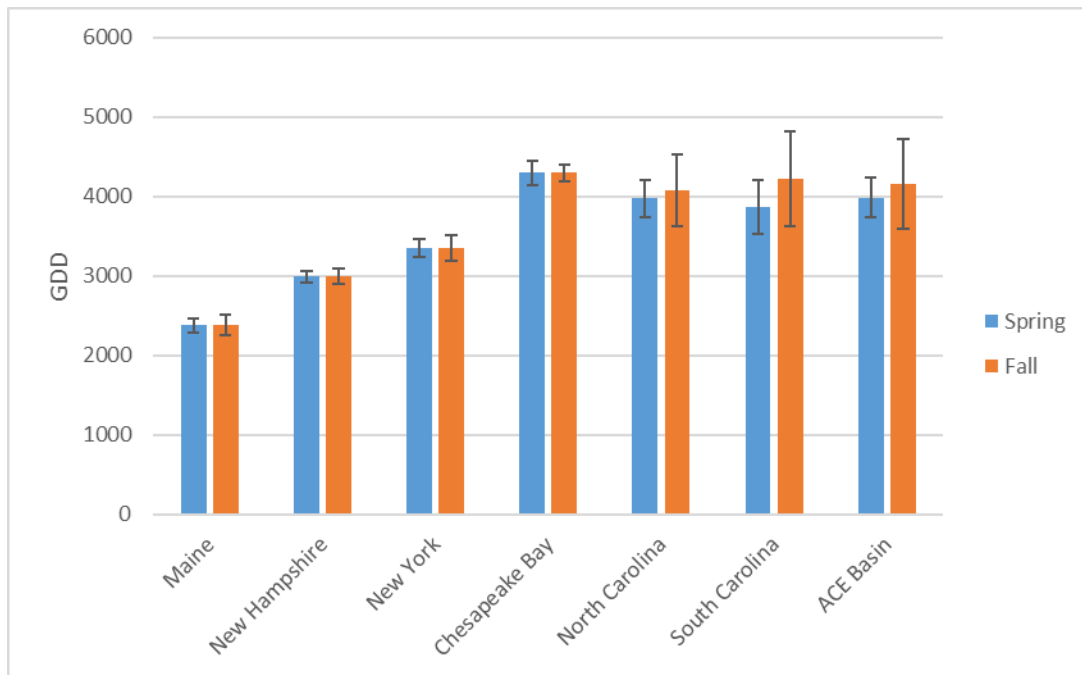
Figure 15. Length of age 1.0 Atlantic sturgeon across a latitudinal gradient. Error bars represent standard deviation.
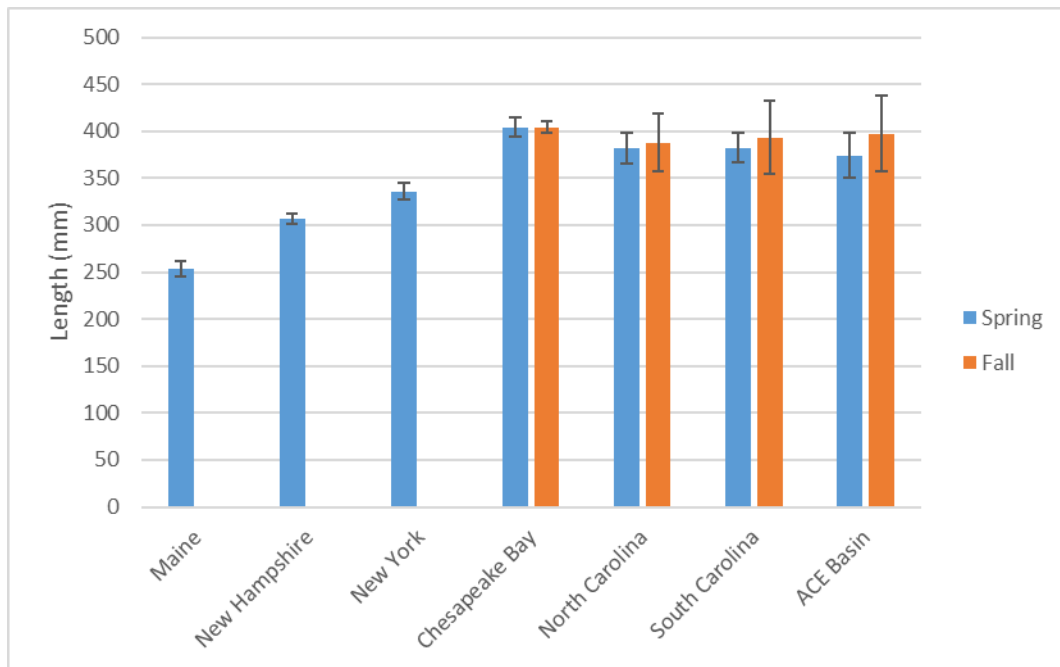
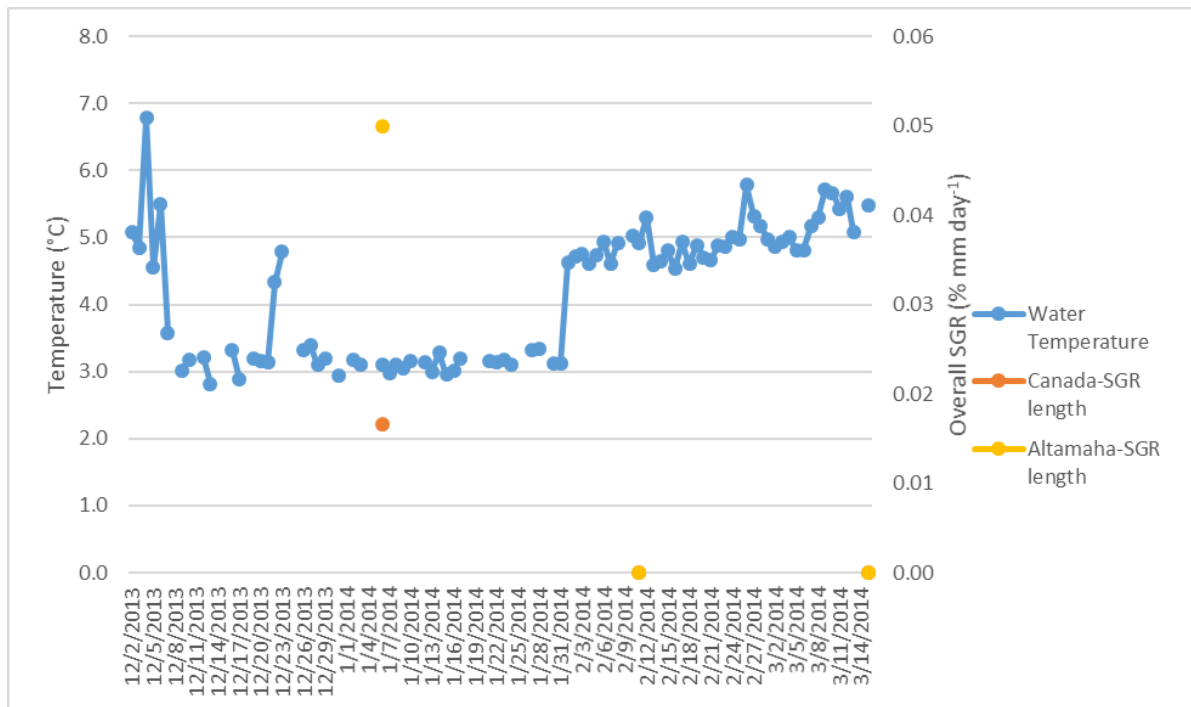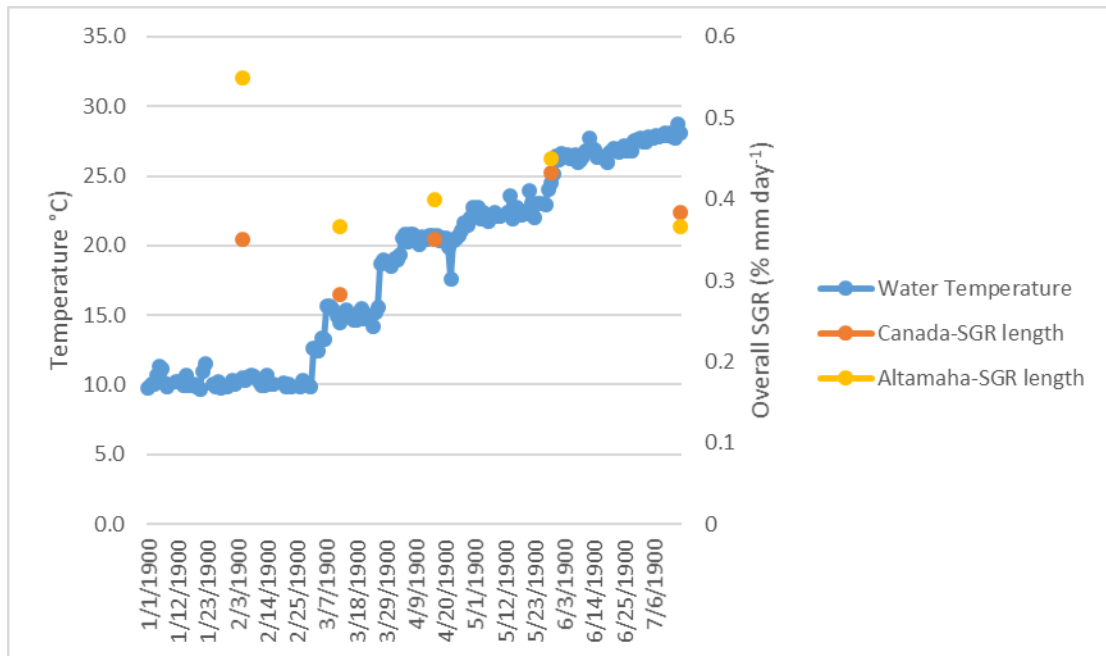Figure 16. Temperature profile and growth of Atlantic sturgeon in the Saint John's River thermal regime.

Figure 17. Temperature profile and growth of Atlantic sturgeon in the Edisto River thermal regime.

References

Allen, P.J., and J.J. Cech, Jr. 2007. Age/size of juvenile green sturgeon, Acipenser medirostris, oxygen consumption, growth, and osmoregulation in saline environments. Environmental Biology of Fishes 79: 211-229.

Allen, P.J., J.J. Cech Jr., D. Kültz. 2009. Mechanisms of seawater acclimation in a primitive, anadromous fish, the green sturgeon. Journal of Comparative Physiology B 179: 903-920.

Allen, P.J., M. McEnroe, T. Forostyan, S. Cole, M.M. Nicholl, B. Hodge, and J.J. Cech Jr. 2011. Ontogeny of salinity tolerance and evidence for seawater-entry preparation in juvenile green sturgeon, Acipenser medirostris. Journal of Comparative Physiology B 181: 1045-1062.

Altenritter, M.E.L., A.C. Wieten, C.R. Ruetz III, K.M. Smith. 2013. Seasonal spatial distribution of juvenile lake sturgeon in Muskegon Lake, Michigan, USA. Ecology of Freshwater Fish 22: 467-478.

Altinok, I. and J.M. Grizzle. 2001. Effects of brackish water on growth, feed conversion and energy absorption efficiency by juvenile euryhaline and freshwater stenohaline fishes. Journal of Fish Biology 59: 1142-1152.

Amiri, B.M., D.W. Baker, J.D. Morgan, and C.J. Brauner. 2009. Size dependent early salinity tolerance in two sizes of juvenile white sturgeon, Acipenser transmontanus. Aquaculture 286: 121-126.

Anderson, O.F., J.M. Guinotte, A.A. Rowden, M.R. Clark, S. Mormede, A.J. Davies, and D.A. Bowden. 2016. Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: Implications for the use of broad-scale models in fisheries management. Ocean and Coastal Management 120: 110-126.

Armstrong, J.L. and J.E. Hightower. 2002. Potential for restoration of the Roanoke River population of Atlantic sturgeon. Journal of Applied Ichthyology 18: 475-480.

ASSRT (Atlantic Sturgeon Status Review Team). 2007: Status review of Atlantic sturgeon (Acipenser oxyrinchus oxyrinchus). Report to NMFS/NOAA. 174 pp.

Atwood, H., Fontenot, Q., Tomasso, J. and Isely J. 2001: Toxicity of nitrite to Nile tilapia: Effect of fish size and environmental chloride. N Am J Aquacut. 63, 49-51.

Bain, M.B. 1997. Atlantic and shortnose sturgeons of the Hudson River: common and divergent life history attributes. Environmental Biology of Fishes 48: 347-358.

Baird, D. and R.E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecological Monographs 59(4): 329-364.

Baker, D.W., A.M. Wood, M.K. Litvak, and J.D. Kieffer. 2005. Haematology of juvenile Acipenser oxyrinchus and Acipenser brevirostrum at rest and following forced activity. Journal of Fish Biology 66: 208-221.

Balazik M.T. and J.A. Musick. 2015. Dual annual spawning races in Atlantic sturgeon. PLoS ONE 10(5): e0128234. doi:10.1371/journal.pone.0128234.

Balazik, M., G.C. Garman, J.P. Van Eenennaam, J. Mohler, and L.C. Woods III. 2013. Empirical evidence of fall spawning by Atlantic sturgeon in the James River, Virginia. Transactions of the American Fisheries Society 141(6): 1465-1471.

Balazik, M.T. and J.A. Musick. 2015. Dual annual spawning races in Atlantic sturgeon. PLOS One 10(5). E0128234. Doi: 10.1371/journal.pone.0128234

Balazik, M.T., K.J. Reine, A.J. Spells, C.A. Fredickson, M.L. Fine, G.C. Garman and S.P. McIninch. 2012. The potential for vessel interactions with adult Atlantic sturgeon in the James River, Virginia. North American Journal of Fisheries Management 32(6): 1062-1069.

Barton, B.A. 2000. Stress. Pages 892-898 in Robert R. Stickney, editor. Encyclopedia of Aquaculture. John Wiley and Sons, Inc. New York, New York.

Batiuk, R.A., D.L. Breitburg, R.J. Diaz, T.M. Cronin, D.H. Secor, and G. Thursby. 2009. Derivation of habitat-specific dissolved oxygen criteria for Chesapeake Bay and its tidal tributaries. Journal of Experimental Marine Biology and Ecology 381:S204-S215.

Baustian, M.M., J.K. Craig, N.N. Rabalais. 2009. Effects of summer 2003 hypoxia on macrobenthos and Atlantic croaker foraging selectivity in the northern Gulf of Mexico. Journal of Experimental Marine Biology and Ecology 381:S31-S37.

Bemis, W.E., E.K. Findels, and L.Grande. 1997. An overview of Acipenseriformes. Environmental Biology of Fishes 48: 25-71.

Berg, O.K., G. Rød, Ø. Solem, and A.G. Finstad. 2011. Pre-winter lipid stores in brown trout Salmo trutta along altitudinal and latitudinal gradients. Journal of Fish Biology 79: 1156-1166.

Bernal. M., Y. Stratoudaki, S. Coombs, M.M. Angelico, A. Lago de Lanzós, C. Porteiro, Y. Sagarminaga, M. Santos, A. Uriarte, E. Cunha, L. Valdés, and D. Borchers. 2007. Sardine spawning off the European Atlantic coast: Characterization of and spatio-temporal variability in spawning habitat. Progress in Oceanography 74: 210-227.

Bonga, S.E.W. 1997. The stress response of fish. Physiological Reviews 77(3): 591-625.

Boudreaux, P., Ferrara A. and Fontenot Q. 2007: Chloride inhibition of nitrite uptake for non-teleost Actinopterygiian fishes. Comp Biochem Phys A. 147, 420-423.

Brady, D.C. and T.E. Targett. 2010. Characterizing the escape response of juvenile summer flounder Paralichthys dentatus to diel-cycling hypoxia. Journal of Biology 77: 137-152.

Brady, D.C., T.E. Targett, and D.M. Tuzzolino. 2009. Behavioral responses of juvenile weakfish (Cynoscion regalis) to diel-cycling hypoxia: swimming speed, angular correlation, expected displacement, and effects of hypoxia acclimation. Canadian Journal of Fisheries and Aquatic Sciences 66: 415-424.

Brandt, S.B., M. Gerken, K.J. Hartman, E. Demers. 2009. Effects of hypoxia on food consumption and growth of juvenile striped bass (Morone saxatilis). Journal of Experimental Marine Biology and Ecology 381: S143-S149.

Breitburg, D.L. 1990. Near-shore hypoxia in the Chesapeake Bay: patterns and relationships among physical factors. Estuarine, Coastal, and Shelf Science 30: 593-609.

Breitburg, D.L. 1992. Episodic hypoxia in Chesapeake Bay: Interacting effects of recruitment, behavior, and physical disturbance. Ecological Monographs 62(4): 525-546.

Breitburg, D.L., D.W. Hondorp, L.A. Davias, and R.J. Diaz. 2009. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. Annual Review of Marine Science 1: 329-349.

Breitburg, D.L., T. Loher, C.A. Pacy, and A. Gerstein. 1997. Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. Ecological Monographs 67(4): 489-507.

Brophy, D. B.S. Danilowicz, and P.A. King. 2006. Spawning season fidelity in sympatric populations of Atlantic herring (Clupea harengus). Canadian Journal of Fisheries and Aquatic Sciences 63: 607-616.

Brown, J.J. and G.W. Murphy. 2010. Atlantic sturgeon vessel-strike mortalities in the Delaware estuary. Fisheries 35(2): 72-83.

Brundage, H.M. and R.E. Meadows. 1982. The Atlantic sturgeon, Acipenser oxyrhynchus, in the Delaware River Estuary. Fishery Bulletin 80(2): 1982.

Buchheister, A., C.F. Bonzek, J. Gartland, R.J. Latour. 2013. Patterns and drivers of the demersal fish community of Chesapeake Bay. Marine Ecology Progress Series 482:161-180.

Burgner, R. L. 1991. Life History of Sockeye Salmon (Oncorhynchus nerka), pp 3-117 In C. Groot and L. Margolis (ed.s) Pacific Salmon Life Histories. UBC Press. Vancouver.

Campbell, J.G. and L.R. Goodman. 2004. Acute sensitivity of juvenile shortnose sturgeon to low dissolved oxygen concentrations. Transactions of the American Fisheries Society 133:727-776.

Canty, A. and B. Ripley. 2014. Boot: Bootstrap R (S-Plus) Functions. R package version 1.3-13.

Cataldi, E., C. Barzaghi, P. Di Marco, C. Boglione, D.J. McKenzie, P. Bronzi, and S. Cataudella. 1999. Some aspects of osmotic and ionic regulation in Adriatic sturgeon Acipenser naccarii, I: Ontogenesis of salinity tolerance. Journal of Applied Ichthyology 15: 57-60.

Cech Jr., J.J., S.J. Mitchell, R.E. Wragg. 1984. Comparative growth of juvenile white sturgeon and striped bass: Effects of temperature and hypoxia. Estuaries 7(1):12-18.

Chesapeake Bay Program. 2012. "Guide to using Chesapeake Bay Program water quality monitoring data," Chesapeake Bay Program. EPA 903-R-12-001 (1 February 2012), p. 1-155.

Collins, M.R., S. G. Rogers, T.I.J. Smith, and M.L. Moser. 2000. Primary factors affecting sturgeon populations in the southeastern United States: Fishing mortality and degradation of essential habitats. Bulletin of Marine Science 66(3): 917-928.

Collins, M.R., W.C. Post, D.C. Russ, and T.I.J. Smith. 2002. Habitat use and movements of juvenile Shortnose sturgeon in the Savannah River, Georgia-South Carolina. Transactions of the American Fisheries Society 131: 975-979.

Conover, D. O. 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. Transactions of the American Fisheries Society 119(3): 416-430.

Conover, D.O. and T.M.C. Present. 1990. Countergradient variation in growth rate: Compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia 83(3): 316-324.

Conover, D.O., J.J. Brown, and A. Ehtisham. 1997. Countergradient variation in growth of young striped bass (Morone saxatilis) from difference latitudes. Canadian Journal of Fisheries and Aquatic Sciences 54: 2401-2409.

Conover. D.O., T.A. Duffy, and L.A. Hice. 2009. The covariance between genetic and environmental influences across ecological gradients. The Year in Evolutionary Biology 1168: 100-129.

Constantini, M., S.A. Ludsin, D.M. Mason, X.S. Zhang, W.C. Boicourt, and S.B. Brandt. 2008. Effect of hypoxia on habitat quality of striped bass (Morone saxatilis) in Chesapeake Bay. Canadian Journal of Fisheries and Aquatic Sciences 65(5): 989-1002.

Coutant, C.C. 1977. Compilation of temperature preference data. Journal of the Fisheries Research Board of Canada 34: 739-745.

Coutant. C.C. 1987. Thermal preference: when does an asset become a liability? Environmental Biology of Fishes 18(3): 161-172.

Craig, J.K. 2012. Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. Marine Ecology Progress Series 445: 75-95.

Crawley, M.J. 2007: "Chapter 16: Proportion Data." The R Book. West Sussex: John Wiley and Sons. pp. 569-592.
Crocker, C.E. and J.J.Cech, Jr. 1997. Effects of environmental hypoxia on oxygen consumption rate and swimming activity in juvenile white sturgeon, Acipenser transmontanus, in relation to temperature and life intervals. Environmental Biology of Fishes 50: 383-389.

Crossman, J.A., P.S. Forsythe, E.A. Baker, and K.T. Scribner. 2009. Overwinter survival of stocked age-0 lake sturgeon. Journal of Applied Ichthyology 25: 516-521.

Crozier, L.G., A.P. Hendry, P.W. Lawson, T.P. Quinn, N.J. Mantua, J. Battin, R.G. Shaw, and R.B. Huey. 2008. Evolutionary Applications 252-270.

Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 26: 249-293.

Dadswell, M.J. 1976. Biology of the shortnose sturgeon (Acipenser brevirostrum) in the Saint John River estuary, New Brunswick, Canada. Transactions of the Atlantic Chapter of Canadian Society of Environmental Biology Annual Meeting, pp. 20-72.

Damstra, R.A. and T.L. Galarowicz. 2013. Summer habitat use by Lake sturgeon in Manistee Lake, Michigan. Transactions of the American Fisheries Society 142: 931-941.

Davidson, M.I., T.E. Targett, and P.A. Grecay. 2016. Evaluating the effects of diel-cycling hypoxia and pH on growth and survival of juvenile summer flounder Paralichthys dentatus. Marine Ecology Progress Series 556: 223-235.

Davison, A.C. and Hinkley, D.V. 1997. Bootstrap methods and their applications. Cambridge University Press, Cambridge.

Diaz, R.J. and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. Science, New Series 321(5891): 926-929.

Diggle, P. and P.J. Ribeiro. 2007. Model-based geostatistics. Springer.

Dijkstra, E.W. 1959. A note on two problems in connexion graphs. Numerische mathematic, 1: 269-271.

Dovel, W.L. 1979. The biology and management of shortnose and Atlantic sturgeon of the Hudson River. Final Report. Project No. AFS9-R.

Dovel, W.L. and T.J. Bergrren. 1983. Atlantic sturgeon of the Hudson Estuary, New York. New York Fish and Game Journal 30(2): 140-172.

Eddy, F. & Williams, E. (1994) Freshwater fish and nitrite. In: Water quality for freshwater fish (ed. by G. Howells), pp. 117–143. Gordon and Breach Science Publishers, Langhorne, PA.

Elliott, J.M. and M.A. Hurley. 1997. A functional model for maximum growth of Atlantic salmon parr, Salmo salar, from two populations in Northwest England. Functional Ecology 11: 592-603.

Environmental Protection Agency. 2003. Ambient Water Quality Criteria for Dissolved Oxygen, Water Clarity and Chlorophyll a for the Chesapeake Bay and Its Tidal Tributaries.

Eslamloo, K. and B. Falahatkar. 2014. Variations of some physiological and immunological parameters in Siberian sturgeon (Acipenser baerii, Brandt, 1869) subjected to an acute stressor. Journal of Applied Animal Welfare Science 17: 29-42.

Falahatkar, B. S.R. Akhavan, I. Efatpanah, and B. Mcknatkhah. 2013. Effect of winter feeding and starvation on the growth performance of young-of-year (YOY) great sturgeon, Huso huso. Journal of Applied Ichthyology 29: 26-30.

Farrae, D., P.M. Schueller, and D.L. Peterson. 2009. Abundance of juvenile Atlantic sturgeon in the Ogeechee River, Georgia. Proceedings on the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 172-176.

Farrae, D.J., W.C. Post, and T.L. Darden. 2017. Genetic characterization of Atlantic sturgeon, Acipenser oxyrinchus oxyrinchus, in the Edisto River, South Carolina and identification of genetically discrete fall and spring spawning. Conservation Genetics (doi:10.1007/s10592-017-0929-7).

Fontenot, Q. C., J. J. Isely and J.R. Tomasso. 1998: Acute toxicity of ammonia and nitrite to Shortnose sturgeon fingerlings. Prog Fish Cult. 60,315-318.

Fontenot, Q. C., J. J. Isely and J.R. Tomasso. 1999: Characterization and inhibition of nitrite uptake in shortnose sturgeon fingerlings. J Aquat Anim Health. 11,76-80.

French, J. 2014. SpatialTools: Tools for spatial data analysis. R package version 0.5.8. https://CRAN-R-project.org/package=SpatialTools

Fritts, M.W., C. Grunwald, I. Wirgin, T.L. King, and D.L. Peterson. 2016. Status and genetic character of Atlantic sturgeon in the Satilla River, Georgia. Transactions of the American Fisheries Society 145(1): 69-82.

Garvey, J.E. and E.A. Marschall. 2009. Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation. Canadian Journal of Fisheries and Aquatic Sciences 60: 938-948.

Gilbert, C.R. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic Bight)—Atlantic and shortnose sturgeons. U.S. Fish and Wildlife Service Biological Report 82 (11.122). U.S. Army Corps of Engineers TR EL-82-3. 28pp.

Grogan, C. S., and J. Boreman. 1998. Estimating the probability that historical populations of fish species are extirpated. North American Journal of Fisheries Management 18(3): 522-529.

Hager, C., J. Kahn, C. Watterson, J. Russo, and K. Hartman. 2014. Evidence of Atlantic Sturgeon Spawning in the York River System. Transactions of the American Fisheries Society 143(5): 1217-1219.

Hagy, J.D., W.R. Boyton, C.W. Keefe, and K.V. Wood. 2004. Hypoxia in Chesapeake Bay, 1950-2001: long-term change in relation to nutrient loading and river flow. Estuaries 27(4): 634-658.

Haller, L., S.S.O. Hung, S. Lee, J.G. Fadel, J.H. Lee, M. McEnroe, N.A. Fangue. 2014. Effect of nutritional status on the osmoregulation of green sturgeon (Acipenser medirostris). Physiological and Biochemical Zoology 88(1): 22-42.

Hamilton, M.A., R.C Russo, and R.V. Thurston. 1977. Trimmed Spearman-Karber method for estimating median lethal concentrations in toxicity bioassays. Environ Sci Technol. 11(7), 714-719.

Hanks, D.M. and D.H. Secor. 2011. Bioenergetic responses of Chesapeake Bay white perch (Morone americana) to nursery conditions of temperature, dissolved oxygen, and salinity. Marine Biology 158: 805-815.

Hatin, D., J. Munro, F. Caron, and R.D Simons. 2007. Movements, home range size, and habitat use selection of early juvenile Atlantic sturgeon in the St. Lawrence Estuarine Transition Zone. American Fisheries Society Symposium 56: 129-155.

Hazen, E.L., D.M. Palcios, K.A. Forney, E.A. Howell, E. Becker, A.L. Hoover, L. Irvine, M. DeAngelis, S.J. Bograd, B.R. Mate, and H. Bailey. 2016. WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. Journal of Applied Ecology doi:10.1111/1365-2664.12820

Hilmy, A., El-Domiaty N., and Wershana K. 1987: Effect of sodium chloride and calcium chloride on nitrite induced methemoglobinemia in Clarias lazera. Water Air Soil Pol. 33, 57-63.

Hilton, E.J., B. Kynard, M.T. Balazik, A.Z. Horodysky, and C.B. Dillman. 2016. Review of the biology, fisheries, and conservation status of the Atlantic sturgeon, (Acipenser oxyrinchus oxyrinchus Mitchill, 1815). Journal of Applied Ichthyology 32(S1): 30-66.

Howell, E.A., A. Hoover, S.R. Benson, H. Bailey, J.J. Polovina, J.A. Seminoff and P.H. Dutton. 2015. Enhancing the TurtleWatch product for leatherback sea turtles, a dynamic habitat model for ecosystem-based management. Fisheries Oceanography 24(1): 57-68.

Huertas M, Gisbert E, Rodrıguez A, Cardona L, Williot P, Castello´-Orvay F. 2002: Acute exposure of Siberian sturgeon (Acipenser baeri, Brandt) yearlings to nitrite: median-lethal concentration (LC50) determination, haematological changes and nitrite accumulation in selected tissues. Aquat Toxicol. 57, 257-266.

Hughes, G.M. 1973. Respiratory responses to hypoxia in fish. American Zoologist 13(2): 475-489.

Humphrey, J., M.J. Wilberg, E.D. Houde, and M.C. Fabrizio. 2014. Effects of temperature on age-0 Atlantic menhaden growth in Chesapeake Bay. Transactions of the American Fisheries Society 143: 1255-1265.

Hung, S.S.O., P.B. Lutes, A.A Shqueir, and F.S. Conte. 1993. Effect of feeding rate and water temperature on growth of juvenile white sturgeon (Acipenser transmontanus). Aquaculture 115: 197-303.

Hurst, T.P. 2007. Review Paper: Causes and consequences of winter mortality in fishes. Journal of Fish Biology 71: 315-345.

Hurst, T.P. and Conover, D.O. 2003. Seasonal and interannual variation in the allometry of energy allocation in juvenile striped bass. Ecology 84(12): 3360-3369.

Ingram, E.C. and D.L. Peterson. 2016. Annual spawning migrations of adult Atlantic sturgeon in the Altamaha River, Georgia. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 8: 595-606.

Irvine L.M., Mate B.R., Winsor M.H., Palacios D.M., Bograd S.J., D.P. Costa, H. Bailey. 2014. Spatial and temporal occurrence of blue whales off the U.S. West Coast, with implications for management. PLoS ONE 9(7): e102959.

Jarvis, P.L., and J.S. Ballantyne. 2003. Metabolic responses to salinity acclimation in juvenile shortnose sturgeon Acipenser brevirostrum. Aquaculture 219: 891-909.

Jarvis, P.L., J. S. Ballantyne, and W.E. Hogans. 2001. The influence of salinity on the growth of juvenile shortnose sturgeon. North American Journal of Aquaculture 64(4): 272-276.

Jenkins, W.E., T.I.J Smith, L.D Heyward, and D.M. Knott. 1995. Tolerance of shortnose sturgeon, Acipenser brevirostrum, juveniles to different salinity and dissolved oxygen concentrations. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 47: 476-484.

Jensen, F. 2003: Nitrite disrupts multiple physiological functions in aquatic animals. Comp Biochem Phys A. 135, 9-24.

Jonsson, G., R. Forseth, A.J. Jensen, and R.F. Naesje. 2001. Thermal performance in juvenile Atlantic salmon, Salmo salar L. Functional Ecology 15: 701-711.

Jung, S., and E. D. Houde. 2003. Spatial and temporal variabilities of pelagic fish community structure and distribution in Chesapeake Bay, USA. Estuarine, Coastal and Shelf Science 58:335-351.

Kahn, J.E., C. Hager, J.C. Watterson, J. Russo, K. Moore, and K. Hartman. 2014. Atlantic sturgeon annual spawning run estimate in the Pamunkey River, Virginia. Transactions of the American Fisheries Society 143(6): 1508-1514.

Keister, J., E.D. Houde, D.L. Breitburg. 2000. Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. Marine Ecology Progress Series 205: 43-59.

Kelly, J.T., A.P. Klimley, and C.E. Crocker. 2007. Movements of green sturgeon, Acipenser medirostris, in the San Francisco Bay estuary, California. Environmental Biology of Fishes 79: 281-295.

Kenney, V.S., R.R. Twilley, J.A. Kleypas, J.H. Cowan Jr., and S.R. Hare. 2002. Coastal and marine ecosystems and global climate change: potential effects on U.S. Resources. Pew Center on Global Climate Change, Arlington, VA, 52pp.

Kieffer, J.D., A.M. Wakefield, and M.K. Litvak. 2001. Juvenile sturgeon exhibit reduced physiological responses to exercise. The Journal of Experimental Biology 204: 4281-4289.

Kieffer, J.D., F.M, Penny, V. Papadopoulos. 2014. Temperature has a reduced effect on routine metabolism rates of juvenile shortnose sturgeon (Acipenser brevirostrum). Fish Physiology and Biochemistry 40: 551-559.

Kraus, R.T., D.H. Secor, and R.L. Wingate. 2015. Testing the thermal-niche oxygen-squeeze hypothesis for estuarine striped bass. Environmental Biology of Fishes 98: 2083-2092.

Krayushkina, L.S. 2006. Considerations on evolutionary mechanisms of osmotic and ionic regulation in Acipenseridae: an overview. Journal of Applied Ichthyology 22 (Suppl. 1): 70-76.

Kroupova H, Machova J, Piackova V, Blahova J, Dobsikova R, Novotny L, Svobodova Z. 2008: Effects of subchronic nitrite exposure on rainbow trout (Oncorhynchus mykiss). Ecotox Environ Safe. 71, 813-820.

Kroupova, H., M. Prokes, S. Macova, M. Penaz, V. Barus, L. Novotny and J. Machova. 2010: First International Workshop on Aquatic Toxicology and Biomonitoring: Effect of nitrite on the early-life stages of common carp (Cyprinus carpio L.). Environ Toxicol Chem. 29(3), 535–540.

Kroupova, H., Machova, J., Piackova, V. 2005: Nitrite influence on fish: a review. Veterinarni Medicina-Praha. 50, 461.

Kynard, B. and M. Horgan. 2002. Ontogenetic behavior and migration of Atlantic sturgeon, Acipenser oxyrinchus oxyrinchus, and shortnose sturgeon, A. brevirostrum, with notes on social behavior. Environmental Biology of Fishes 63: 137-150.

Laiz-Carrión, S. Sangiao-Alvarellos, J.M. Guzmán, M. P. Martín del Río, J. M. Míguez, J. L. Soengas, and J. M. Mancera. 2002. Energy metabolism in fish tissues related to osmoregulation and cortisol action. Fish Physiology and Biochemistry 27: 179-188.

Lankford, S.E., T.E. Adams, J.J. Cech, Jr. 2003. Time of day and water temperature modify the physiological stress response in green sturgeon, Acipenser medirostris. Comparative Biochemistry and Physiology Part A 135: 291-302.

Larsson, S. R. Forseth, I. Berglund, A.J. Jensen, I. Näslund, J.M. Elliot, and B. Jonsson. 2005. Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. Freshwater Biology 50: 353-368.

Lazzari, M.A., J. C. O'Herron II, R.W. Hastings. 1986. Occurrence of juvenile Atlantic sturgeon Acipenser oxyrhynchus, in the Upper Tidal Delaware River. Estuaries 9(4B): 356-361.

Leggett, W.C. and J.E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American shad (Alosa sapidissima): evidence for population specific life history strategies in fish. Journal of the Fisheries Research Board of Canada 35: 1469-1478.

Lewis W, Morris D. 1986: Toxicity of nitrite to fish: a review. T Am Fish Soc. 115, 183-195.

Long, W.C. and R.D. Seitz. 2008. Trophic interactions under stress: hypoxia enhances foraging in an estuarine food web. Marine Ecology Progress Series 362: 59-68.

Mangold. M., S. Eyler, S. Minkkinen, and B. Richardson. 2007. Atlantic sturgeon reward program for Maryland waters of the Chesapeake Bay and tributaries 1996-2006. U.S. Fish and Wildlife Service, Maryland Fishery Resources Office.

Matsche, M.A., E. Markin, E. Donaldson, A. Hengst and A. Lazur. 2012: Effect of chloride on nitrite-induced methaemoglobinemia in Atlantic sturgeon, Acipenser oxyrinchus oxyrinchus (Mitchill). J Fish Dis. 35, 873–885.

Maurer, E.P. L. Brekke, T. Pruitt, and P.B. Duffy. 2007. Fine-resolution climate projections enhance regional climate change impact studies. EOS 88(47): 504.

McEnroe, M. and J.J. Cech, Jr. 1985. Osmoregulation in juvenile and adult white sturgeon, Acipenser transmontanus. Environmental Biology of Fishes 14(1): 23-30.

McKenzie, D.J., E. Cataldi, P. Di Marco, A. Mandich, P. Romano, S. Ansferri, P. Bronzi, and S. Cataudella. 1999. Some aspects of osmotic and ionic regulation in Adriatic sturgeon Acipenser naccarii. II: Morpho-physiological adjustments to hyperosmotic environments. Journal of Applied Ichthyology 15: 61-66.
McKenzie, D.J., E. Cataldi, P. Romano, E.W. Taylor, S. Cataudella, and P. Bronzi. 2001a. Effects of acclimation to brackish water on tolerance of salinity challenge by young-of-the-year Adriatic sturgeon (Acipenser naccarii). Canadian Journal of Fisheries and Aquatic Sciences 58: 1113-1121.

McKenzie, D.J., E. Cataldi, P. Romano, S.F.Owen, E.W. Taylor, and P Bronzi. 2001b. Effects of acclimation to brackish water on the growth, respiratory

metabolism, and swimming performance of young-of-the-year Adriatic sturgeon (Acipenser naccarii). Canadian Journal of Fisheries and Aquatic Sciences 58: 1104-1112.

Mims, S.D., Lazur, A., Shelton, W.L., Gomelsky, B., and Chapman, F. 2002: Species Profile: Production of Sturgeon. Southern Regional Aquaculture Center. Publication no. 7200.

Mohler, J.W. 2004. Culture manual for the Atlantic sturgeon Acipenser oxyrinchus oxyrinchus. U.S. Fish and Wildlife Service, Hadley, Massachusetts. 70pp.

Mohler, J.W. 2004. Culture manual for the Atlantic sturgeon Acipenser oxyrinchus oxyrinchus. U.S. Fish and Wildlife Service, Hadley, Massachusetts. 70pp.

Moser, M.L. and S.W. Ross. 1995. Habitat use and movements of Shortnose and Atlantic sturgeons in the Lower Cape Fear River, North Carolina. Transactions of the American Fisheries Society. 124: 225-234.

Murawski, S.A. and A.L. Pacheco. 1977. Biological and fisheries data on Atlantic sturgeon, Acipenser oxyrynchus (Mitchill). Sandy Hook Lab Tch. Ser. Rep. 10. National Marine Fisheries Service, Highlands, NJ. 69p.

Murphy, R.R., W.M. Kemp, W.P. Ball. 2011. Long-term trends in Chesapeake Bay seasonal hypoxia, stratification, and nutrient loading. Estuaries and Coasts 34: 1293-1309.

Musick, J.A. 2005. Essential fish habitat of Atlantic sturgeon Acipenser oxyrinchus in the Southern Chesapeake Bay. Final report to NOAA/NMFS. VIMS Special Scientific Report #145.

Najjar, R.G., C.R. Pyke, M.B. Adams, D. Breitburg, C. Hershner, M.Kemp, R. Howarth, M.F. Mulholland, M. Paolisso, D. Secor, K. Sellner, D. Wardtop, and R. Wood. 2010. Potential climate-change impacts on the Chesapeake Bay. Estuarine, Coastal and Shelf Science 86: 1-20.

Neuheimer, A.B. 2007. Growth in fishes: size-at-age, temperature and food. Ph.D. Thesis, Department of Oceanography, Dalhousie University, Halifax, Canada.

Neuheimer, A.B. and C.T. Taggart. 2007. The growing degree-day and fish size-at-age: the overlooked metric. Canadian Journal of Fisheries and Aquatic Sciences 64: 375-385.

Niklitschek, E. and D.H. Secor. 2005. Modeling spatial and temporal variation of suitable nursery habitats for Atlantic sturgeon in the Chesapeake Bay. Estuaries and Coastal Shelf Science 64: 135-148.

Niklitschek, E.J. 2001. Bioenergetics modeling and assessment of suitable habitat for juvenile Atlantic and shortnose sturgeons (Acipenser oxyrinchus and A. brevirostrum) in the Chesapeake Bay. Doctoral dissertation. University of Maryland at College Park, College Park.

Niklitschek, E.J. and D.H. Secor. 2009. Dissolved oxygen, temperature and salinity effects on the ecophysiology and survival of juvenile Atlantic sturgeon in estuarine waters: I. Laboratory results. Journal of Marine Biology and Ecology 381(Suppl): S150-S160.

Niklitschek, E.J. and D.H. Secor. 2009. Dissolved oxygen, temperature and salinity effects on the ecophysiology and survival of juvenile Atlantic sturgeon in estuarine waters: II. Model development and testing. Journal of Experimental Marine Biology and Ecology 381: S161-S172.

Niklitschek, E.J. and D.H. Secor. 2010. Experimental and field evidence of behavioral habitat selection by juvenile Atlantic Acipenser oxyrinchus oxyrinchus and shortnose Acipenser brevirostrum sturgeons. Journal of Fish Biology 77: 1293-1308.

Nilsson, G.E. and S. Östlund-Nilsson. 2008. Does size matter for hypoxia tolerance in fish? Biological Reviews 83: 173-189.

NOAA. 2010. Endangered and Threatened Wildlife and Plants; Proposed Listings for Two Distinct Population Segments of Atlantic Sturgeon (Acipenser oxyrinchus oxyrinchus) in the Southeast. Federal Register 75 (193): 61904-61929.

OECD. 1992: Test No. 203: Fish, Acute Toxicity Test, OECD Guidelines for the Testing of Chemicals, Section 2, OECD Publishing, Paris.DOI: http://dx.doi.org/10.1787/9789264069961-en

Overholtz, W.J., J.A. Hare and C.M. Keith. 2011. Impacts of interannual environmental forcing and climate change on the distribution of Atlantic mackerel on the U.S. Northeast Continental Shelf. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 3(1): 219-232.

Peake, S.J. 2008. Swimming performance and behavior of fish species endemic to Newfoundland and Labrador: A literature review for the purpose of establishing design and water velocity criteria for fishways and culverts. Canadian Manuscript Report of Fisheries and Aquatic Sciences, No. 2843.

Pekovitch, A.W. 1979. Distribution and some life history aspects of the shortnose sturgeon (Acipenser brevirostrum) in the upper Hudson River estuary. Hazleton Environmental Science Corporation, Illinois. 23pp.

Peterson, D.L., M.B. Bain, and N. Haley. 2000. Evidence of declining recruitment of Atlantic sturgeon in the Hudson River. North American Journal of Fisheries Management 20: 231-238.

Pihl, L., S.P. Baden, R.J. Diaz, and L.C. Schaffner. 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea. Marine Biology 112: 349-361.

Potts, W.T.W., and P.P. Rudy. 1972. Aspects of osmotic and ionic regulation in the sturgeon. Journal of Experimental Biology 56: 701-715.

Power, M. and R.S. McKinley. 1997. Latitudinal variation in lake sturgeon size as related to the thermal opportunity for growth. Transactions of the American Fisheries Society 126(4): 549-558.

Purchase, C.F. and J.A. Brown. 2001. Stock-specific changes in growth rates, food conversion efficiencies, and energy allocation in response to temperature change in juvenile Atlantic cod. Journal of Fish Biology 58: 36-52.

Pörtner, H.O. and M.A. Peck. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. Journal of Fish Biology 77: 1745-1779.

R Core Team. 2016. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

R Core Team. 2014: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Roe, J.H., S.J Morreale, F.V. Paladino, G.L. Shillinger, S.R. Benson, S.A. Eckert, H. Bailey, P.S. Tomillo, S.J. Bograd, T. Eguchi, P.H. Dutton, J.A. Seminoff, B.A. Block, and J.R. Spotila. 2014. Predicting bycatch hotspots for endangered leatherback turtles on longlines in the Pacific Ocean. Proceedings of the Royal Society B 281: 20132559.

Schlenger, A.J., E.W. North, Z. Schlag, Y. Li, D.H. Secor, K.A. Smith and E.J. Niklitschek. 2013. Modeling the influence of hypoxia on the potential habitat of Atlantic sturgeon Acipenser oxyrinchus: a comparison of two methods. Marine Ecology Progress Series 483: 257-272.

Schlenger, A.J., E.W. North, Z. Schlag, Y. Li, D.H. Secor, K.A. Smith, and E.J. Niklitschek. 2013. Modeling the influence of hypoxia on the potential habitat of Atlantic sturgeon Acipenser oxyrinchus: a comparison of two methods.

Schueller, P. and D.L. Peterson. 2010. Abundance and Recruitment of juvenile Atlantic sturgeon in the Altamaha River, Georgia. Transactions of the American Fisheries Society 139: 1526-1535.

Schultz, E.T. and D.O. Conover. 1997. Latitudinal differences in somatic energy storage: Adaptive responses to seasonality in an estuarine fish (Atherinidae: Menidia menidia). Oecologia 109(4): 516-529.

Schultz, E.T., K.E. Reynolds, and D.O. Conover. 1996. Countergradient variation in growth among newly hatched Fundulus heteroclitus: Geographic differences revealed by common-environment experiments. Functional Ecology 10(3): 366-374.

Secor, D.H. 2002. Atlantic sturgeon fisheries and stock abundances during the late 19th century. American Fisheries Society Symposium 28: 89-98.

Secor, D.H. and E.J. Niklitschek. 2001. Sensitivity of sturgeons to environmental hypoxia: a review of physiological and ecological evidence. Pp. 61-78 In: Thurston, R.V. (Ed.), Fish Physiology, Toxicology, and Water Quality. Proceeding of the Sixth International Symposium, La Paz, Mexico, 22-26 Jan. 2001.

Secor, D.H. and J.R. Waldman. 1999. Historical abundance of Delaware Bay Atlantic sturgeon and potential rate of recovery. American Fisheries Society Symposium 23: 203-216.

Secor, D.H. and T.E. Gunderson. 1998. Effects of hypoxia and temperature on survival, growth, and respiration of juvenile Atlantic sturgeon, Acipenser oxyrinchus. Fishery Bulletin 96(3): 603-613.

Secor, D.H., E. Niklitschek, J.T. Stevenson and T.E. Gunderson, S. Minkkinen, B Richardson, and B. Florence, M. Mangold and J Skjeveland, A. Henderson-Arzapalo. 2000. Dispersal and growth of yearling Atlantic sturgeon, Acipenser oxyrinchus, released into Chesapeake Bay. Fisheries Bulletin 98:800-810.

Secor, D.H., T.E. Gunderson, and K. Karlsson. 2000. Effect of temperature and salinity on growth performance in anadromous (Chesapeake Bay) and nonanadromous (Santee-Cooper) strains of striped bass Morone saxatilis. Copeia 2000(1): 291-296.

Secor. D.H. 2002. Atlantic sturgeon fisheries and stock abundances during the late nineteenth century. American Fisheries Society Symposium 28: 89-98.

Secor. D.H. 2007. The year-class phenomenon and the storage effect in marine fishes. Journal of Sea Research 57: 91-103.

Seitz, R.D., L.S. Marshall, A.H. Hines, and K.L. Clark. 2003. Effects of hypoxia on predator-prey dynamics of the blue crab Callinectes sapidus and the Baltic clam Macoma balthica in Chesapeake Bay. Marine Ecology Progress Series 257: 179-188.

Shuter, B.J., A.G. Finstad, I.P. Helland, I. Zweimüller, and F. Hölker. 2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. Aquatic Sciences 74: 637-657.

Singer, T.D. and J.S. Ballantyne. 2004. Sturgeon and Paddlefish Metabolism. Pages 167-194 in G.T.O. LeBreton, F.W.H. Beamish, R.S. McKinley, editors. Sturgeons and Paddlefish of North America. Kluwer Academic Publishers, Netherlands. Singer, T.D. and J.S. Ballantyne. 2004. Sturgeon and Paddlefish Metabolism. Pages 167-194 in G.T.O. LeBreton, F.W.H. Beamish, R.S. McKinley, editors. Sturgeons and Paddlefish of North America. Kluwer Academic Publishers, Netherlands.

Sinha, A.K., A. F. Dasan, R. Rasoloniriana, N. Pipralia, R. Blust, G. De Boeck. 2015. Hypo-osmotic stress-induced physiological and ion-osmoregulatory responses in European sea bass (Dicentrarchus labrax) are modulated differentially by nutritional status. Comparative Biochemistry and Physiology Part A 181: 87-99.

Smith, J.A., H.J. Flowers, and J.E. Hightower. 2015. Fall spawning of Atlantic sturgeon in the Roanoke River, North Carolina. Transactions of the American Fisheries Society 144(1): 48-54.

Smith, T.I.J. 1985. The fishery, biology, and management of Atlantic sturgeon, Acipenser oxyrhynchus in North America. Environmental Biology of Fishes 14(1): 61-72.

Smith, T.I.J., D.E. Marchette, and G.D. Ulrich. 1984. The Atlantic sturgeon fishery in South Carolina. North American Journal of Fisheries Management 4: 164-176.

Spoor, W.A. 1977. Oxygen requirements of embryos and larvae of the largemouth bass, Micropterus salmoides (Lacépède). Journal of Fish Biology 11(2): 77-86.

Stewart, N.D., M.J. Dadswell, P. Leblanc, R.G. Bradford, C. Ceapa, M.J.W. Stokesbury. 2015. Age and growth of Atlantic sturgeon from the Saint John River, New Brunswick, Canada. North American Journal of Fisheries Management 35: 364-371.

Stierhoff, K.L., R.M. Tyler, T.E. Targett. 2009. Hypoxia tolerance of juvenile weakfish (Cynoscio regalis): laboratory assessment of growth and behavioral avoidance reponses. Journal of Experimental Marine Biology and Ecology 381: S173-S179.

Stierhoff, K.L., T.E. Targett, K. Miller. 2006. Ecophysiological responses of juvenile summer and winter flounder to hypoxia: experimental and modeling analyses of effects on estuarine nursery quality. Marine Ecology Progress Series 325: 255-266.

Sullivan, A.B., H.I. Jager, and R. Myers. 2003. Modeling white sturgeon movement in a reservoir: the effect of water quality and sturgeon density. Ecological Modelling 167: 97-114.

Tabor, K. and J.W. Williams. 2010. Globally downscaled climate projections for assessing the conservation impacts of climate change. Ecological Applications 20(2): 554-565.

Testa, J.M. and W.M. Kemp. 2014. Spatial and temporal patterns of winter-spring oxygen depletion in Chesapeake Bay bottom water. Estuaries and Coasts 37: 1432-1448.

Thompson, J.S. and J.A. Rice. 2013. The relative influence of thermal experience and forage availability on growth of age 1-5 striped bass in two southeastern reservoirs. American Fisheries Society Symposium 80: 93-120.

Timmons, M., Ebeling J., Wheaton, F., Summerfelt, S. and Vinci, B. 2002: Recirculating aquaculture systems, Cayuga Aqua Ventures, Ithica, NY.

Tomasso Jr, J.R. & Grosell, M. 2005: Physiological basis for large differences in resistance to nitrite among freshwater and freshwater-acclimated euryhaline fishes. Environ. Sci. Technol, 39, 98-102.

Tsui, W.C., J.C. Chen, S.Y. Cheng. 2012. The effects of a sudden salinity change on cortisol, glucose, lactate, and osmolality levels in grouper Epinephelus malabaricus. Fish Physiology and Biochemistry 38: 1323-1329.

Tyler, R.M., D.C. Brady, T.E. Targett. 2009. Temporal and spatial dynamics of diel-cycling hypoxia in estuarine tributaries. Estuaries and Coasts 32: 123-145.

Tyler. R.M. and T.M. Targett. 2007. Juvenile weakfish Cynoscion regalis distribution in relation to diel-cycling dissolved oxygen in an estuarine tributary. Marine Ecology Progress Series 333: 257-269.

Uphoff, C.S., C.W. Schoenebeck, W.W. Hoback, K.D. Koupal, and K.L. Pope. 2013. Degree-day accumulation influences annual variability in growth of age-0 walleye. Fisheries Research 147: 394-398.

Van Etten, J. 2012. gdistance: Distances and routes on geographical grids. http://CRAN.R-project.org/package=gdistance. R package version, 1-1.

Webb, M.A.H., J.A. Allert, K.M. Kappenman, J. Marcos, G.W. Feist, C.B. Schreck, C.H. Shackleton. 2007. Identification of plasma glucocorticoids in pallid sturgeon in response to stress. General and Comparative Endocrinology 154: 98-104.

Wedemeyer, G.A., B.A. Barton, and D.J. McLeay. 1990 Stress and Acclimation. Pages 451-489 in C.B. Schreck and P.B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Welsh, S.A., S.M. Eyler, M.F. Mangold, and A.J. Spells. 2002. Capture locations and growth rates of Atlantic sturgeon in the Chesapeake Bay. American Fisheries Society Symposium 28: 183-194.

Wijekoon, M.P., V. Puvanendran, D.W. Ings, and J.A. Brown. 2009. Possible countergradient variation in growth of juvenile cod Gadus morhua from the northwest Atlantic. Marine Ecology Progress Series 375: 229-238.

Williams, E. & Eddy, F. 1986: Chloride uptake in freshwater teleosts and its relationship to nitrite uptake and toxicity. J Comp Physiol B. 156, 867-872.

Wokoma, A. and I.A. Johnston. 1981. Lactate production at high sustainable cruising speeds in rainbow trout (Salmo gairdneri Richardson). Journal of Experimental Biology 90:361-364.

Woodland, R.J., D.H. Secor, and E.J. Niklitschek. 2009. Past and future habitat suitability for the Hudson River population of shortnose sturgeon: A bioenergetics approach to modeling habitat suitability for an endangered species. American Fisheries Society Symposium 69: 589-604.

Yamahira, K. and D.O. Conover. 2002. Intra- vs. Interspecific latitudinal variation in growth: Adaptation to temperature of seasonality? Ecology 83(5): 1252-1262.

Yanbo, W., Wenju, Z., Weifen, L. and Zirong, X. 2006: Acute toxicity of nitrite on tilapia (Oreochromis niloticus) at different external chloride concentrations. Fish Physiol Biochem. 32, 49-54.

Zarejabad, A. M., M. Sudagar, S. Pouralimotlagh, K.D. Bastami. 2010. Effects of rearing temperature on hematological and biochemical parameters of great sturgeon (Huso huso Linnaeus, 1758) juvenile. Comparative Clinical Pathology 19:367-371.

Zhang, Y. and J.D. Kieffer. 2014. Critical thermal maximum (CTmax) and hematology of shortnose sturgeon (Acipenser brevirostrum) acclimated to three temperatures. Canadian Journal of Zoology 92: 215-221.

Ziegeweid, J.R., C.A. Jennings, D.L. Peterson, M.C. Black. 2008. Effects of salinity, temperature, and weight on the survival of young-of-year shortnose sturgeon. Transactions of the American Fisheries Society 137: 1490-1499.

Zuccarelli, M.D., M. Kusakabe, I. Nakamura, E.F. Prentice, G. Young, and R.L. Ingermann. 2008. Acute stress response of Kootenai River white sturgeon Acipenser transmontanus Richardson reflected in peritoneal fluid and blood plasma. Journal of Fish Biology 72: 1831-1840.