

Modeling the influence of hypoxia on the potential habitat of Atlantic sturgeon *Acipenser oxyrinchus*: a comparison of two methods

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ABSTRACT: Management of marine and estuarine fish and shellfish would benefit from a numerical approach that quantifies the impacts of climate variability and eutrophication. We present a proof-of-concept habitat volume model that incorporates predictions from a 3-dimensional biophysical model. Using temperature, salinity, and dissolved oxygen, habitat volumes were calculated based on threshold physiological tolerances (fixed criteria) and potential growth (bioenergetics) for Atlantic sturgeon *Acipenser oxyrinchus*. Simulations from a coupled oxygen and hydrodynamic model of the Chesapeake Bay, USA, were used to estimate habitat volumes of juvenile sturgeon and assess the sensitivity of habitat to environmental factors. In winter, salinity controlled the required (needed for survival) and optimal (needed for highest growth) habitat. Temperature and salinity defined spring and autumn optimal habitat, and a combination of salinity, temperature and dissolved oxygen influenced habitat volumes during summer. Although average summertime oxygen limitation reduced the volumes of juvenile habitat by 3.3–28.0%, the largest reductions in summertime habitat resulted from temperature limitation. The average difference in annual and seasonal volumes between fixed-criteria and bioenergetics methods was approximately 14%, with similar trends over the annual cycle for most life stages and habitat types. We conclude that fixed-criteria habitat volume models would be suitable when bioenergetics information is not available. Both habitat volume models can be used to assess the impacts of climate change and eutrophication on the habitat of fish and shellfish in regions where hydrodynamic models exist and for species for which physiological tolerances are known.

KEY WORDS: Habitat · Model · Biophysical · Hypoxia · Atlantic sturgeon · Physiological tolerance · Oxygen model

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INTRODUCTION

The synergistic impacts of climate change and multiple anthropogenic disturbances on marine and estuarine environments produce complex symptoms of ecosystem-scale degradation (Jackson et al. 2001).

A quantitative understanding is needed to separate the impact of climate variability and change on living resources from the impacts caused by nutrient enrichment for effective conservation and management. This requires accurate representations of both the physical system and the biological processes involved.

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Through the combination of 3-dimensional (3D) hydrodynamics and biogeochemistry, coupled biophysical models serve as useful tools to apply to this task (Stow et al. 2009, Hinrichsen et al. 2011). By accounting for the feedbacks and interactions taking place between the physical and biological components of a specific system, it is possible to predict the distributions of individual environmental factors (such as temperature, salinity, and dissolved oxygen) that define habitat conditions. Output from coupled biophysical models can then be directly incorporated into habitat modeling, which provides a numerical representation of a species' habitat preferences at high spatiotemporal resolution. We present a novel habitat model that calculates the volume of suitable habitat for a given species using predictions of temperature, salinity, and dissolved oxygen from a 3D coupled biophysical model. This habitat volume model quantifies the associations between an organism and environmental variables, hence providing the means to make inferences about a species' habitat and response to environmental change.

The development of high-resolution biophysical models that predict environmental variability, along with a habitat volume model that can assimilate and interpret this information, is integral to the future protection of marine and aquatic ecosystems. Many of the ecological disruptions created by anthropogenic nutrient loading are expected to worsen as a result of climate change (Justic et al. 1997, Conley et al. 2009, Najjar et al. 2010), as rising temperatures will promote bacterial respiration and reduce the amount of dissolved oxygen that can be saturated in water. Hypoxic ($\leq 2 \text{ mg O}_2 \text{ l}^{-1}$) and anoxic ($\leq 0.2 \text{ mg O}_2 \text{ l}^{-1}$) waters have the potential to significantly decrease species diversity by killing oxygen-dependent organisms that cannot escape the low oxygen and by reducing the potential habitat for those that survive (Ritter & Montagna 1999, Townsend & Edwards 2003). The destruction of benthic communities creates a domino effect, disrupting ecological interactions throughout the water column (Caddy 1993, Breitburg et al. 2003), which could potentially have negative effects on economically important fisheries. Quantifying the impacts of climate change and eutrophication on habitat is especially important in estuaries that provide essential habitat for a variety of ecologically important species (Lippson & Lippson 2006), and are subject to anthropogenic nutrient enrichment (Cloern 2001, Kemp et al. 2005, Breitburg et al. 2009) and systemic hypoxia (Officer et al. 1984, Diaz 2001).

Fixed-criteria and bioenergetics models are 2 habitat modeling approaches that can be applied in a habitat volume model framework. Fixed criteria, or habitat-affinity indices, are commonly used to define habitat in static habitat suitability models. These models utilize environmental variables such as temperature, salinity, and dissolved oxygen to define potential habitat based on a species' physiological tolerances. We refer to potential habitat as the possibility of occupying a location based on the environmental attributes of the site (Wintle et al. 2005). The main drawback of this method is the common assumption that physiological tolerances for each environmental factor do not interact with other environmental factors. It is, however, well known that interactions do exist; for example, an organism's physiological tolerance to dissolved oxygen can depend on the water temperature and salinity in the organism's immediate environment (McLeese 1956, Fry 1971, Claireaux & Lagardere 1999). Unfortunately, these 'physiological interactions' have been quantitatively defined for just a few species (e.g. Lankford & Targett 1994, Wuenschel et al. 2004) in a way that can be applied to habitat modeling. With the advancement of bioenergetics models (e.g. Hartman & Brandt 1995, Niklitschek & Secor 2005, Costantini et al. 2008), new tools are available to fill this information gap. The study of bioenergetics involves the partitioning of energy by living organisms through the application of thermodynamic principles to organisms and biological systems (Brett & Groves 1979). It provides a framework for the study of relationships between the feeding and growth rates of an organism that is subject to different environmental conditions (Enders & Scruton 2006). Bioenergetics approaches to habitat classification have been applied for different species and scaled up to include entire ecosystems (e.g. Luo et al. 2001, Neill et al. 2004, Costantini et al. 2008). Although bioenergetics modeling approaches have the potential for higher accuracy because they account for physiological interactions, they require a great deal of information to function properly (Enders & Scruton 2006). One of the primary objectives of our study was to compare the fixed-criteria and bioenergetics habitat modeling approaches to determine if fixed criteria could be used in cases where information concerning physiological interactions is difficult to obtain or does not exist.

We developed and applied fixed-criteria and bioenergetics habitat volume models for 2 life stages, young-of-the-year (YOY, age 0) and yearling juveniles (age 1), of the model organism Atlantic stur-

geon *Acipenser oxyrinchus*, with the Chesapeake Bay, USA, as the model study site. Atlantic sturgeon populations have not been subject to harvest in the Chesapeake Bay since they were severely overharvested prior to 1900, and Atlantic sturgeon were listed as an endangered species by the US National Marine Fisheries Service in 2012. Atlantic sturgeon have relatively sensitive physiological tolerances to environmental conditions compared with other estuarine species (Niklitschek & Secor 2009a), which makes them a useful species for assessing ecological change related to climate and anthropogenic perturbations. The Chesapeake Bay is a large, partially mixed estuary along the western North Atlantic US coast (Pritchard 1967) that is subject to persistent seasonal hypoxia (Officer et al. 1984). Predictions from a coupled biophysical model of the Chesapeake Bay were used as input for the habitat volume models, which calculated the volume of required and optimal habitat for Atlantic sturgeon based on either fixed-criteria or bioenergetics parameterizations. The models were applied to address the following objectives: (1) to assess the influence of temperature, salinity, and dissolved oxygen on habitat volume; (2) to quantify the effects of hypoxia on potential habitat; (3) to compare fixed-criteria and bioenergetics approaches for estimating potential habitat; and (4) to corroborate predicted habitat volume (bioenergetics model) against Atlantic sturgeon juvenile observations in the Chesapeake Bay. It was expected that habitat defined by bioenergetics would be more constrained than habitat defined by fixed criteria because the bioenergetics model includes physiological interactions between temperature, salinity, and dissolved oxygen, whereas the fixed-criteria model does not.

METHODS

We used a coupled hydrodynamic and oxygen model to predict water temperature, salinity, and dissolved oxygen in the Chesapeake Bay, and then applied fixed-criteria and bioenergetics habitat volume models to quantify the potential habitat of YOY and yearling Atlantic sturgeon. Physiological tolerances and bioenergetics equations were obtained from a series of laboratory experiments and modeling exercises (Niklitschek 2001, Niklitschek & Secor 2005, 2009a,b). Using information from the same set of experiments to parameterize the bioenergetics and fixed-criteria models facilitated model comparison.

Coupled hydrodynamic and oxygen models

The Regional Ocean Modeling System (ROMS) is a state-of-the-art coastal hydrodynamic model (Song & Haidvogel 1994, Shchepetkin & McWilliams 2005). It is based on free-surface, hydrostatic primitive equations with horizontal orthogonal curvilinear coordinates and stretched, terrain-following vertical coordinates. The system includes accurate and efficient numerical algorithms as well as advanced turbulent mixing parameterization schemes. The model is forced by open-ocean tides, freshwater inflows at river heads, and observed winds and heat exchange across the water surface. We configured the ROMS hydrodynamic model for the Chesapeake Bay and validated it using time series of sea level, temperature, salinity and currents at a number of monitoring stations, and data from 3D synoptic hydrographic surveys (Li et al. 2005, Zhong & Li 2006, Zhong et al. 2008, Li & Zhong 2009). The model shows considerable capability to reproduce estuarine dynamics at seasonal and interannual timescales (Li et al. 2005, Hilton et al. 2008, North et al. 2008, Li & Li 2011). It also captures the estuary's response to extreme weather events such as hurricanes and tropical storms (Li et al. 2006, 2007). The ROMS grid covers the major tributaries and main stem of the Chesapeake Bay from the Susquehanna River to the mouth of the bay with a resolution of ~1 km. Grid cells located outside the mouth of the bay were removed from the analysis.

A simplified oxygen model incorporating biogeochemical processing was used in conjunction with ROMS to predict oxygen concentrations throughout the Chesapeake Bay. The ROMS hydrodynamic model was coupled with an empirical dissolved oxygen model (Li 2012), in which major source (phytoplankton production) and sink (sediment oxygen demand and water column respiration) terms in the oxygen equation are parameterized via empirical formulas derived from the regression analysis of observational production and respiration data. From 1996 to 2005, the average volume of water during July with dissolved oxygen concentrations $<0.2 \text{ mg l}^{-1}$ in the model was approximately half of that estimated from observations by Murphy et al. (2011), while the volume with concentrations $<1 \text{ mg l}^{-1}$ and $<2 \text{ mg l}^{-1}$ were 1.2× and 1.6× greater than estimated from observations, respectively. Although there were both magnitude and timing differences in dissolved oxygen concentrations between the model and observations, the model reproduced the general seasonal cycle and provided consistent predictions with which to compare the fixed-criteria and bioenergetics habitat volume models.

Habitat volume model

The fixed-criteria and bioenergetics habitat volume models are based on an algorithm that calculates a geometric volume of suitable habitat given one or more constraints (Smith et al. 2009), such as temperature, salinity, and oxygen (fixed criteria), or potential growth (bioenergetics). The habitat volume model uses these constraints along with predictions from the coupled hydrodynamic and oxygen models to calculate the volume of suitable habitat in each model grid cell, which are identical to the ROMS model grid cells. For each grid cell, linear interpolation in the vertical direction was used to find the depth of the constraints (e.g. minimum dissolved oxygen required for survival) (Fig. 1a). Then the most constraining factors in each grid cell were used to define the volume of habitat in the cell that fulfills all requirements (Fig. 1b). This volume was then divided into 4 triangular 'prisms', created by joining the triangles formed by the vertices and midpoints of the top and bottom faces (Fig. 1c). The grid-cell habitat volume was then calculated as the sum of the volume of each prism. The volume of all model grid cells was summed (Fig. 1d) to derive the bay-wide total habitat volume in each time step (e.g. Fig. 2). As Atlantic sturgeon is a predominantly benthic species, the habitat volume model was adjusted so that only the bottom 2 m of the water column and associated environmental conditions were included in the volume calculations. The model, which we programmed in FORTRAN, is an open-source code (http://northweb.hpl.umces.edu/open_source_code/HabitatVolumeModel.htm) that reads the ROMS model output and allows the user to specify fixed-criteria or bioenergetics calculations.

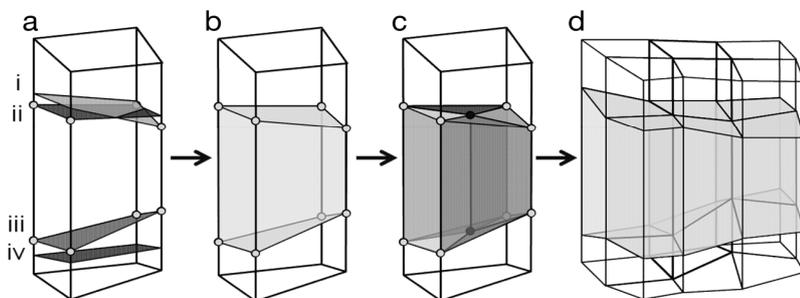


Fig. 1. Habitat volume calculation. (a) Upper bound for salinity (i), lower bound for dissolved oxygen (iii), and upper (ii) and lower (iv) bounds for temperature were found based on linear interpolation of properties in the vertical direction and the species' physiological tolerances. (b) The most limiting tolerance constraints (gray circles) define the habitat volume of the grid cell. (c) Volume is calculated by dividing the volume into 4 'prisms' and summing their volumes. (d) This process is repeated for all grid cells in the model, and the volumes are summed to find the bay-wide habitat volume

Fixed-criteria habitat volume model

The physiological tolerances of Atlantic sturgeon to temperature, salinity, and dissolved oxygen were taken primarily from Niklitschek (2001) and Niklitschek & Secor (2005, 2009a). Atlantic sturgeon juvenile stages were divided into YOY and yearlings because these 2 stages have different physiological tolerances (Niklitschek & Secor 2009a). These physiological tolerances (Table 1) were used to parameterize the fixed-criteria habitat volume model. The habitat predicted by this model was categorized into 'required' and 'optimal' habitat. Required habitat was defined as the domain (volume) of environmental conditions outside of which mortality would occur. Optimal habitat was defined as the domain of environmental conditions outside of which physiological stress would occur, leading to decreased growth, production, or impairments to other metabolic processes. The laboratory studies, on which many of the physiological tolerances were based, did not investigate the effects of acclimation on tolerance thresholds. Acclimation is a phenomenon that happens in the majority of estuarine species (e.g. Brady et al. 2009) and we would expect the same to be true with sturgeon. However, there is not enough evidence available to accurately account for this in the model.

Bioenergetics habitat volume model

Bioenergetics equations for YOY and yearling Atlantic sturgeon were derived from Niklitschek & Secor (2009b). Potential growth (G) is estimated as

a YOY b Yearling

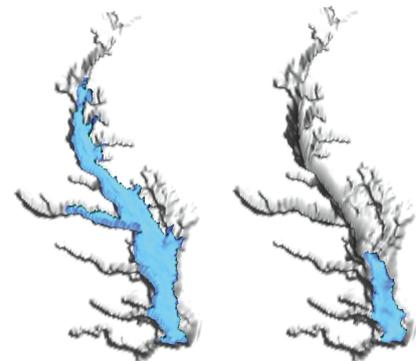


Fig. 2. Example of optimal habitat volume (blue) for (a) young-of-the-year (YOY) and (b) yearling Atlantic sturgeon *Acipenser oxyrinchus* on July 6, 1996. Optimal habitat requirements are listed in Table 1

Table 1. Required and optimal physiological tolerances used for fixed-criteria thresholds of young-of-the-year and yearling Atlantic sturgeon *Acipenser oxyrinchus*. Criteria were based on a literature review

Environmental variable	Physiological tolerance		Reference(s)
	Required	Optimal	
Young-of-the year			
Temperature (°C)	0–28	16–24	Niklitschek & Secor (2005, 2009a), Dovel & Berggren (1983)
Salinity	0–22	3.5–18.5	Niklitschek (2001), Niklitschek & Secor (2005, 2009a),
Dissolved oxygen (mg l ⁻¹)	3.3	5.0	Niklitschek & Secor (2009a)
Yearling			
Temperature (°C)	0–28	16–24	Niklitschek & Secor (2005, 2009a), Dovel & Berggren (1983)
Salinity	0–29	18.5–25.5	Niklitschek & Secor (2005, 2009a)
Dissolved oxygen (mg l ⁻¹)	3.3	5.0	Niklitschek & Secor (2009a)

$G = FC - (RM + SDA + ACT) - (EG + U)$, where FC = food consumption, RM = routine metabolism, ACT = activity cost, SDA = postprandial metabolism (classically named specific dynamic action), EG = egestion, and U = excretion. This model, validated against field, mesocosm and behavioral observations (Niklitschek & Secor 2005, 2009b, 2010), expands the classical temperature-based bioenergetics equations to incorporate direct dissolved oxygen saturation effects on FC, RM and SDA, and direct salinity effects on FC and RM. As SDA, EG, U and ACT are modeled to be proportional to FC, the whole model becomes sensitive to temperature, salinity and dissolved oxygen.

Required habitat in the bioenergetics habitat volume model was defined as the domain of all environmental conditions that resulted in positive growth. This parallels the definition of required habitat for fixed criteria in that prolonged exposure to conditions of negative growth would lead to death (also known as incipient lethality). Optimal habitat was defined as the domain of environmental conditions resulting in highest potential growth. Potential growth estimates falling in the 90th percentile were used to compute volumes of optimal habitat because this standard percentile was reflective of highest potential growth.

The bioenergetics equations were adjusted for incorporation into the habitat volume model. Consumption in these equations was set to a maximum, under the assumption that food availability was not limiting. Although this represents a departure from realism, the focus of this research was to assess the influence of physical conditions on potential habitat. Fish weight was set to 14 g in YOY model simulations and 200 g in yearling model simulations. In addition, slight adjustments were made to temperature and oxygen input values to maintain numerical stability (i.e. prevent division by zero) and to avoid extrapolation of the bioenergetics equations well beyond the

original experimental conditions used to parameterize them. When temperatures fell below 4°C, instantaneous growth was set to zero. A similar adjustment was made for dissolved oxygen so that the minimum value of percent saturation used in the bioenergetics equations was 25%. This value is consistent with hypoxic conditions and the adjustment did not influence the volume of habitat lost as a result of low dissolved oxygen.

Although the 2 modeling approaches relied on similar information about Atlantic sturgeon, these habitat volume models were fundamentally different. The fixed-criteria habitat volume was determined by calculating the intersecting volume of water meeting the individual physiological requirements of temperature, salinity, and dissolved oxygen for Atlantic sturgeon. Thus, each environmental parameter was separately represented in the habitat volume (Fig. 1). The bioenergetics habitat volume was based on a series of sophisticated equations that accounted for the interaction of temperature, salinity and dissolved oxygen on the physiology of Atlantic sturgeon. Here, rather than considering 3 separate environmental layers, the bioenergetics model integrated environmental parameters into a single habitat volume describing a level of potential growth rate.

Model simulations

Three sets of model simulations were conducted. First, simulations were run with the fixed-criteria habitat volume model to identify the interannual variability in volumes of habitat defined by temperature, salinity, and dissolved oxygen and to determine which parameter(s) have the greatest influence on required and optimal habitat of YOY and yearling sturgeon. The model was run for each life stage and

habitat type using the predictions from the coupled hydrodynamic and oxygen model, which spanned 1996 to 2005, with predictions stored every 12 h. The coupled hydrodynamic and oxygen model simulations were not run continuously, but were completed for each individual year and concatenated. Initial conditions for the hydrodynamic model were estimated using archived model output, which was forced by coarse wind fields. As a result, the distributions of temperature, salinity, and dissolved oxygen at the end of one year may not align completely with the initial conditions of the next, which can be seen during 1998–1999, 1999–2000, 2001–2002, and 2002–2003 (see Figs. 3 & 4).

Next, simulations were conducted to compare fixed-criteria and bioenergetics habitat volume models. Volumes of required and optimal habitat based on fixed criteria and bioenergetics criteria were calculated for each life stage and habitat type at 12 h time steps in each year. Daily means of bay-wide volumes were summed over the entire year to obtain annual indices of habitat volume. In addition, daily means of bay-wide volumes were summed over the period from May 1 to November 15 to obtain seasonal indices of habitat volume that correspond to the time range during which habitat reduction due to dissolved oxygen limitation occurs. Fixed-criteria and bioenergetics annual and seasonal indices were then compared using correlation and paired *t*-test analyses (SAS v. 9.2).

Finally, simulations were conducted with and without dissolved oxygen limitation so that an estimate of the loss in habitat due to hypoxia could be calculated. For the fixed-criteria model, this was accomplished by removing dissolved oxygen from the habitat volume calculation. For the bioenergetics model, dissolved oxygen concentrations across the entire model domain were set to saturation levels so that oxygen was not a limiting factor. For both models, the reduction in habitat resulting from dissolved oxygen limitation was the difference in habitat volumes from runs with and without oxygen limitation during the period from May 1 to November 15. This time frame was chosen because it captured the entire time range during which habitat reduction due to dissolved oxygen limitation was present for all years. The total volume of habitat reduction from May 1 to November 15 was calculated for each life stage and habitat type by summing the differences between models with and without oxygen over all time steps for each year and calculating the percent decrease in volume. In addition, the onset date of habitat reduction due to oxygen limitation and the duration of reduced habi-

tat were determined for each year, life stage, and habitat type.

Statistical analyses

Indices of annual volume, seasonal volume, the reduction of habitat volume due to dissolved oxygen, and the percent decrease in habitat volume due to dissolved oxygen were compared between fixed-criteria and bioenergetics models to determine if they have similar magnitude and trends. To evaluate whether modeling approaches showed similar temporal trends, Pearson's and Spearman's correlation coefficients (see Table 3) were calculated for annual volume index, seasonal volume index, volume reduction index and percent reduction using SAS (v. 9.2). P-values <0.05 were considered significant. Either paired *t*-tests or Wilcoxon signed rank tests for nonparametric distributions were also conducted to determine if means are different between the 2 modeling approaches within each simulation (see Table 2). To control for the number of tests, a Bonferonni correction was applied to control familywise error rates. The presence of statistically significant trends for individual annual indices over the 10 yr period was tested using a combination of linear regression and generalized least squares analyses (R v. 2.15.2). The presence of autocorrelation was identified using the Durbin-Watson test (Zeileis & Hothorn 2002). If no autocorrelation was detected, a linear regression was used to assess whether there was a significant trend. If autocorrelation was detected, a generalized least squares regression (Venables & Ripley 2002) was used to test the significance of the trend. Power analyses were conducted for all tests using the 'pwr' package in R (Champely 2012). Out of the 32 time series tested for trend, the majority of these tests had very low power, with only 2 showing statistically significant trends, therefore a table of these results is not shown.

Comparison of model predictions with locations of Atlantic sturgeon captures

A validation analysis was conducted to determine if the bioenergetics habitat volume model predicted suitable habitat where Atlantic sturgeon have been captured. The expectation was that sturgeon would predominately occur in suitable habitat areas predicted by the bioenergetics habitat vol-

ume model. The locations of Atlantic sturgeon captured through a government tagging program were used rather than the number of sturgeon captured to reduce bias resulting from locations with higher fishing effort from fishermen who were more willing to record their captures. Locations of captured sturgeon weighing 600 g or less were used so that the influence of age-specific differences in habitat preferences was limited. Capture locations recorded during the period of seasonal hypoxia (May 1 to November 15) were taken from 1997 and 1998—the time period when most captures occurred ($n = 1047$). For each model time step during these periods, the presence or absence of suitable habitat was determined for each grid cell in the model domain. Grid cells with occurrences of suitable habitat in the 75th percentile or higher were used to create boundaries of suitable habitat for required and optimal habitat in each year. The percentage of capture locations falling within the boundaries of suitable habitat predicted by the bioenergetics model for 1997 and 1998 were determined and compared.

RESULTS

Results of model simulations are presented that (1) identify the interannual variability in volumes of habitat defined by fixed criteria associated with each environmental parameter; (2) compare habitat volumes predicted by fixed-criteria and bioenergetics habitat volume models; (3) quantify the influence of dissolved oxygen limitation during periods of seasonal hypoxia; and (4) compare model predictions with observations of sturgeon captures.

Interannual variability in habitat volume

Required habitat volumes based on fixed individual (temperature, salinity, dissolved oxygen) and combined criteria showed strong seasonal effects and differed between years (Fig. 3). For instance, temperature had a very strong role in limiting summertime habitat volumes in 1999 and 2005. Salinity was the most constraining (i.e. limiting) environmental factor during the winter for both life stages, while

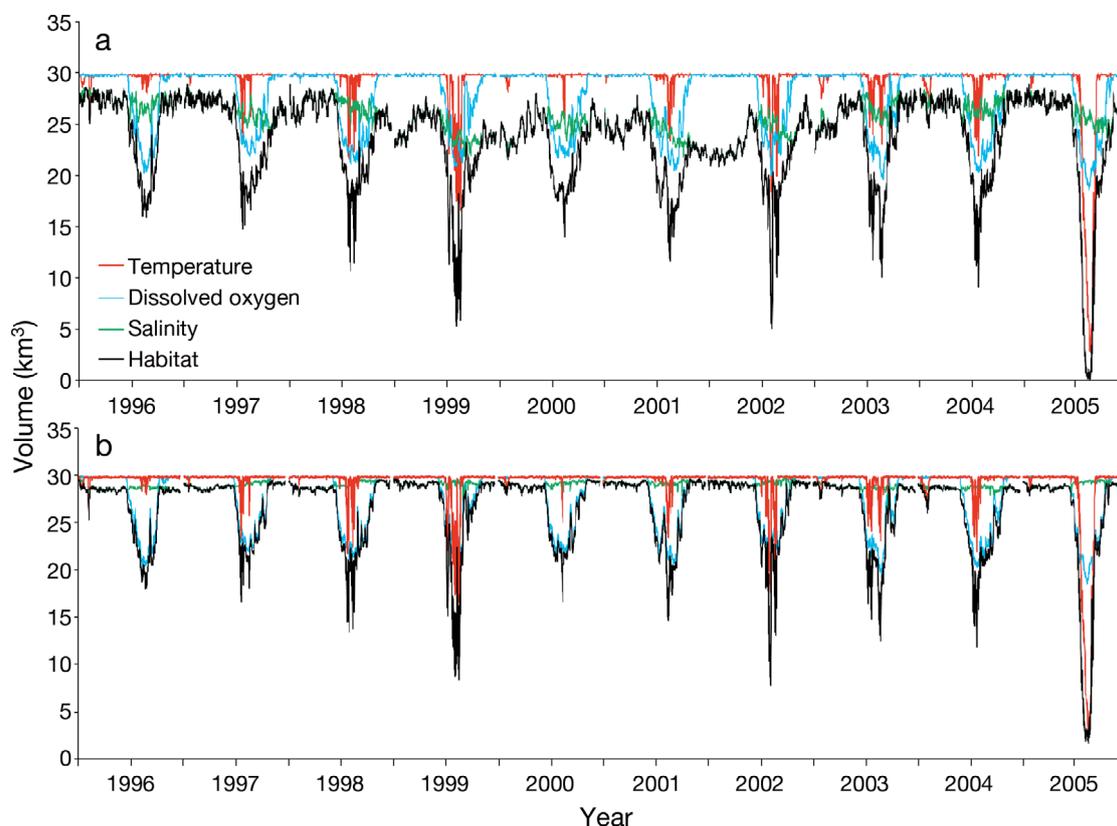


Fig. 3. Annual volume index of water meeting fixed-criteria required temperature (red), salinity (green), and dissolved oxygen (blue) constraints as well as overall required habitat (black) for (a) young-of-the-year (YOY) and (b) yearling Atlantic sturgeon *Acipenser oxyrinchus*. Constraints for required habitat for YOY and yearlings are listed in Table 1. Axis tick marks above each year are centered on June

temperature and dissolved oxygen were the primary factors that contributed to summertime decreases in required habitat. The volume of water corresponding to the required salinity range for YOY sturgeon (salinity 0–22) showed the expected pattern of decrease in volume during summer related to low freshwater flow in the Chesapeake region during this time. In contrast, salinity-based required habitat volume for yearlings (salinity 0–29) showed little seasonal or annual variability. The volumes of water meeting required dissolved oxygen conditions, $\geq 3.3 \text{ mg l}^{-1}$ for both life stages, remained high until the summer, during which these volumes sharply decreased. Temperature-based volumes for each life stage showed a similar pattern to dissolved oxygen. However, decreases in volume during the summer due to temperature were much sharper and occurred over a smaller time period. In 2005, water temperatures during a particularly warm summer drove the largest reduction in habitat volume in the time series.

Volumes of optimal habitat associated with fixed criteria (Table 1) for YOY and yearlings exhibited complex modal and bimodal seasonal patterns (Fig. 4). Temperature was the main factor controlling the seasonal timing of optimal habitat during spring and autumn for both life stages, with a secondary influence of dissolved oxygen seen during these seasons. Although the seasonal presence of habitat was controlled by temperature and dissolved oxygen, the magnitude of optimal habitat was predominantly limited by salinity for each life stage. Volumes of

YOY optimal habitat were consistently larger than those for yearlings, suggesting the presence of larger volumes of lower salinity water for YOY (3.5–18.5) compared with higher salinity water for yearlings (18.5–25.5) throughout much of the bay (e.g. Fig. 2). Between 1999 and 2003, yearling optimal habitat volumes and corresponding salinity-based habitat volumes were high. During this same time period, optimal habitat volumes of YOY and corresponding salinity-based habitat volumes were low, suggesting a reciprocal relationship between YOY and yearling optimal habitat based on changes in salinity. Optimal temperature-based and dissolved oxygen-based habitat volumes for both life stages showed little interannual variation. For the most part, no significant trends in required or optimal habitat volume from 1996 to 2005 were detected (results not shown).

Comparison of model approaches

The seasonal patterns in habitat volume were similar between fixed-criteria and bioenergetics modeling approaches, but the magnitudes differed across most life stages and type of habitat (Fig. 5, Table 2). For both modeling approaches, required habitat remained high during the winter and then decreased from spring into summer before rising again in the autumn. In addition, optimal habitat was bimodal with peaks in spring and autumn for both modeling approaches. Although these seasonal patterns were

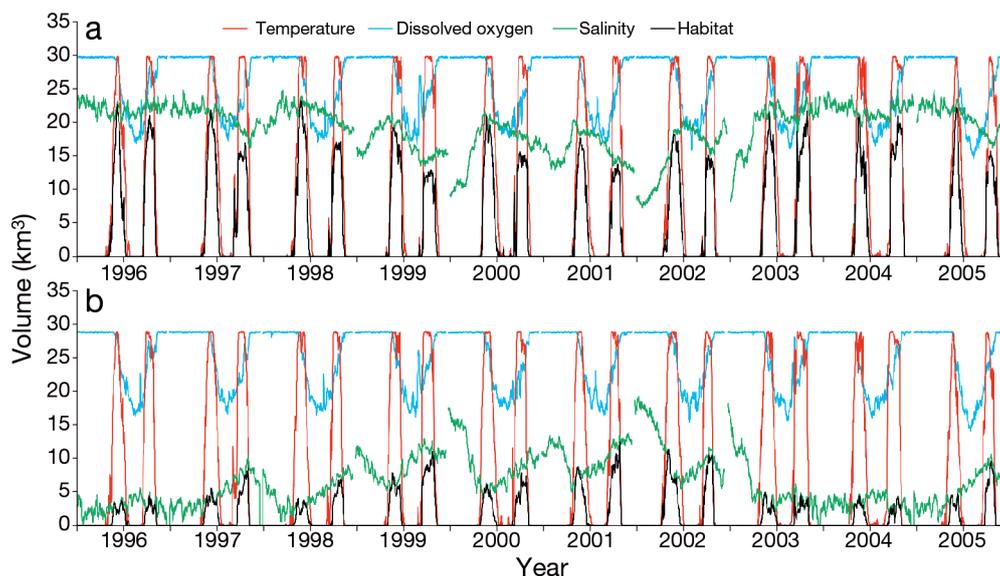


Fig. 4. Annual volume index of water meeting fixed-criteria optimal temperature (red), salinity (green), and dissolved oxygen (blue) constraints as well as overall optimal habitat (black) for (a) young-of-the-year (YOY) and (b) yearling Atlantic sturgeon *Acipenser oxyrinchus*. Constraints for optimal habitat for YOY and yearlings are listed in Table 1. Axis tick marks above each year are centered on June

Table 2. Results of paired *t*-test and Wilcoxon signed rank tests used to compare means of habitat indices between fixed-criteria and bioenergetics over a 10 yr period for 3 metrics of each Atlantic sturgeon *Acipenser oxyrinchus* life stage (young-of-the-year [YOY] and yearling) and habitat type (required and optimal). Annual refers to the comparison between annual volume indices (daily volumes summed up over entire year). Seasonal refers to the seasonal volume indices (daily volumes summed from May 1 to November 15). Reduction refers to the decrease in the volume of habitat due to hypoxia (daily differences in volume between models with and without dissolved oxygen limitation summed from May 1 to November 15). * denotes a Wilcoxon signed rank test

Life stage and habitat type	Annual		Seasonal		Reduction	
	p	Power	p	Power	p	Power
YOY, required	0.0020*	0.67	0.0020*	0.27	<0.0001	>0.99
YOY, optimal	0.0940	0.39	0.1100	0.36	0.0005	0.99
Yearling, required	0.0020*	0.12	0.0020*	0.29	<0.0001	>0.99
Yearling, optimal	<0.0001	>0.99	<0.0001	>0.99	<0.0001	>0.99

similar, optimal habitat based on fixed criteria dropped to zero or near zero during summer due to temperature thresholds, whereas optimal habitat based on bioenergetics did not approach zero for extended periods of time during summer. The timing and appearance of optimal habitat was similar between model approaches, but ended slightly later in fixed-criteria model runs. Both modeling approaches predicted large interannual variability in the required habitat volume present during summer, with markedly reduced volumes in 1999, 2002, and 2005. These reductions coincided with the temperature limitation predicted by the fixed-criteria model (Fig. 3). Although seasonal trends were similar, the magnitude of volumes calculated with the 2 approaches were statistically different (Table 2), with higher volumes predicted by the bioenergetics model compared with the fixed-criteria model for required habitat of the 2 life stages and for optimal habitat of yearlings.

The annual volume indices (the sum of average daily volumes) were consistent between fixed-criteria and bioenergetics approaches for the required habitat of both life stages and for the optimal habitat of YOY (Fig. 6). For the required habitat of YOY and yearlings, the volumes estimated through fixed criteria were on average 20.2% and 8.6% less than volumes based on bioenergetics, respectively. For YOY optimal habitat, the fixed-criteria predictions were on average 8.3% greater than those defined by bioenergetics. In addition, YOY required and optimal habitat showed statistically similar patterns in variation

between modeling approaches (Table 3). Large differences between modeling approaches occurred for annual yearling optimal habitat volumes, with bioenergetics estimates on average twice as large as fixed-criteria volume estimates (Fig. 6).

The total volumes of habitat during the time period of seasonal hypoxia (May 1 and November 15) showed similar patterns of interannual variability between the 2 modeling approaches, except for yearling optimal habitat (Fig. 7). Differences in the total seasonal volumes of required habitat defined by fixed-criteria and bioenergetics for both life stages, as well as the optimal habitat for YOY, ranged from 8.0 to 25.4% and were significantly correlated (Table 3). Model predictions of optimal habitat volumes for yearlings differed significantly in both trend and magnitude, with volumes calculated through bioenergetics being 108.3% higher than volumes calculated with the fixed-criteria model.

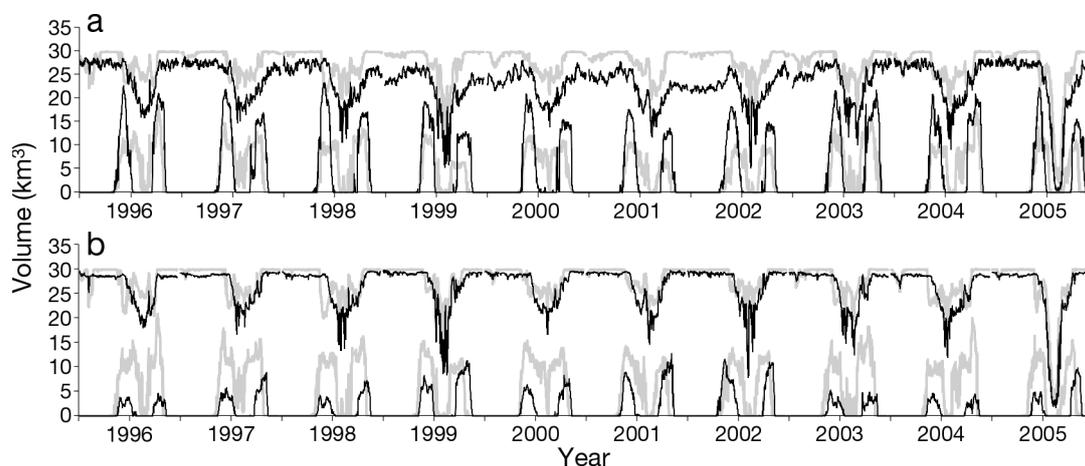


Fig. 5. Bay-wide volume of required (upper lines) and optimal (lower lines) habitat over the course of each year predicted by fixed-criteria (black lines) and bioenergetics (gray lines) models for (a) young-of-the-year and (b) yearling Atlantic sturgeon *Acipenser oxyrinchus*. Axis tick marks above each year are centered on June

Table 3. Pearson's and Spearman's correlation coefficients based on the comparison of fixed-criteria and bioenergetics habitat modeling approaches for 3 metrics of each Atlantic sturgeon *Acipenser oxyrinchus* life stage (young-of-the-year [YOY] and yearling) and habitat type (required and optimal). Annual refers to the comparison between annual volume indices (daily volumes summed up over entire year). Seasonal refers to the seasonal volume indices (daily volumes summed from May 1 to November 15). Percent reduction refers to the percent decrease in the volume of habitat due to hypoxia (daily differences in volume between models with and without dissolved oxygen limitation summed from May 1 to November 15). Significant correlation coefficient values derived from Pearson's and Spearman's correlation analyses are *p < 0.05, **p < 0.01, ***p < 0.001

Life stage and habitat type	Annual	Seasonal	Percent reduction
YOY, required	0.84**	0.82**	-0.25
YOY, optimal	0.77**	0.77**	0.88***
Yearling, required	0.47	0.67*	-0.29
Yearling, optimal	-0.70*	-0.70*	-0.63

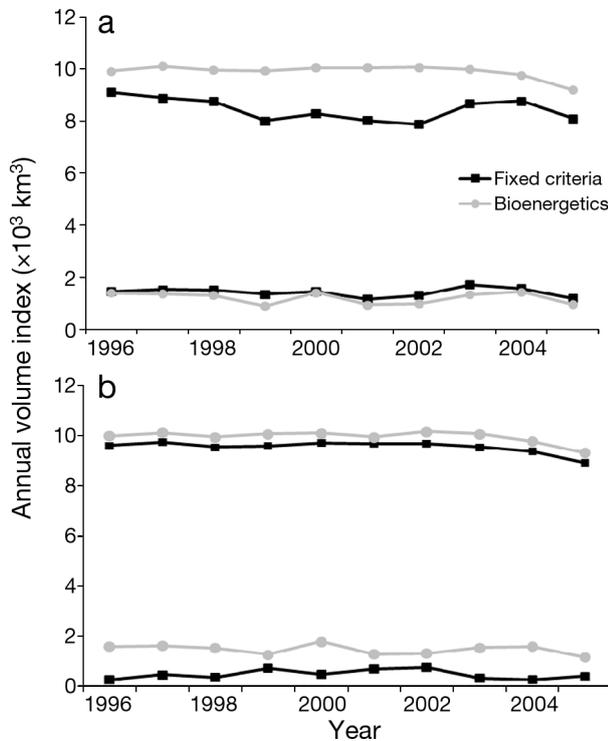


Fig. 6. Annual volume index of required (upper lines) and optimal habitat (lower lines) defined by fixed-criteria (black) and bioenergetics (gray) for (a) young-of-the-year and (b) yearling Atlantic sturgeon *Acipenser oxyrinchus* between 1996 and 2005. Annual volumes were calculated by summing daily average model predictions of habitat volume for each year

Influence of seasonal hypoxia on habitat volumes

Volumes of habitat reduced by hypoxia had modal (required) and bimodal (optimal) seasonal patterns for both fixed-criteria and bioenergetics models (Fig. 8). For required habitat, the fixed-criteria model predicted greater reductions in habitat due to hypoxia than the bioenergetics model, potentially because the fixed-criteria model did not include interactions between environmental variables. For optimal habitat, the bioenergetics model showed a larger seasonal decrease in habitat volume than the fixed-criteria model. This was partly caused by the fact that fixed-criteria model predictions were constrained by temperature in summer, so reductions in oxygen had no effect.

Reductions in habitat volume due to hypoxia differed in magnitude between model types but had similar trends, except for yearling optimal habitat. For the required habitat of both life stages, reductions estimated by fixed criteria were on average 2 times larger than seasonal reductions calculated through bioenergetics. For YOY optimal habitat, the average seasonal reduction in habitat volume defined

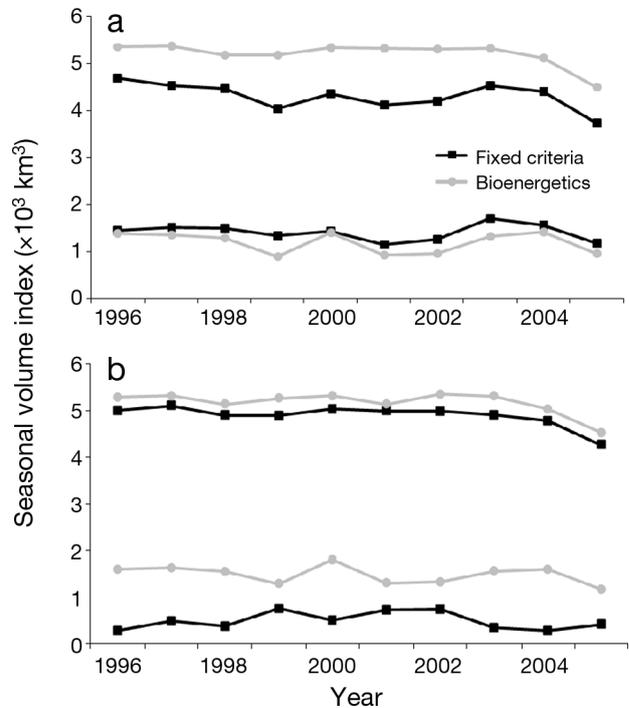


Fig. 7. Seasonal volume index of required (upper lines) and optimal habitat (lower lines) defined by fixed criteria (black) and bioenergetics (gray) for (a) young-of-the-year and (b) yearling Atlantic sturgeon *Acipenser oxyrinchus* between 1996 and 2005. Seasonal volumes were calculated by summing daily average model predictions of habitat volume during the time period of seasonal hypoxia (May 1 and November 15)

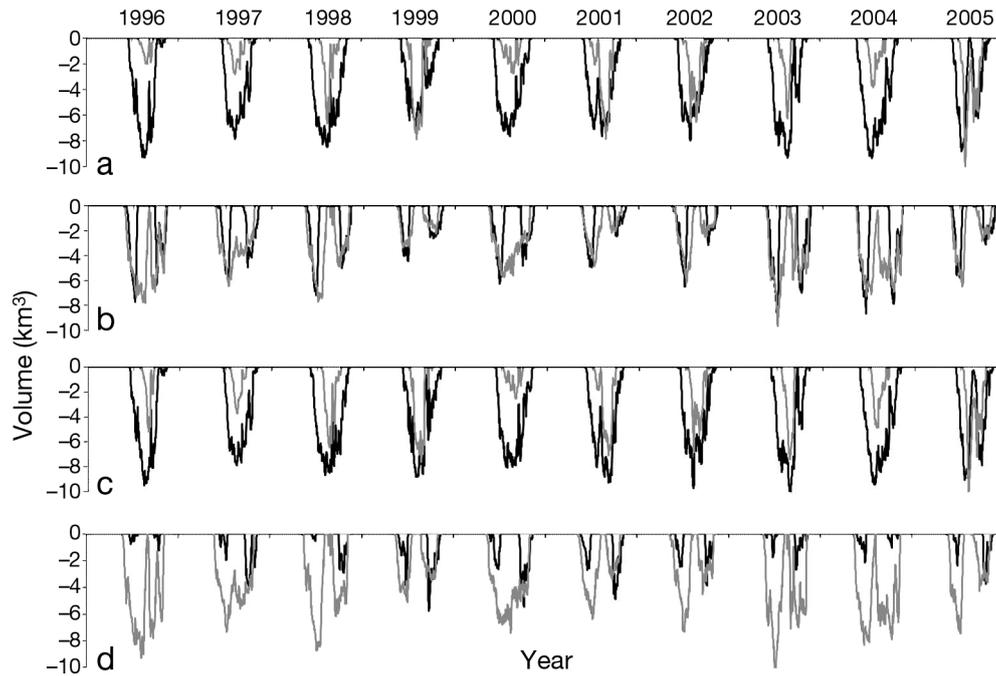


Fig. 8. Reduction in Atlantic sturgeon *Acipenser oxyrinchus* habitat volume resulting from dissolved oxygen limitation for (a) young-of-the-year required habitat, (b) young-of-the-year optimal habitat, (c) yearling required habitat, and (d) yearling optimal habitat, during 1996–2005. Estimates were calculated using fixed-criteria (black) and bioenergetics (gray) habitat volume models

by fixed criteria was 53.8% smaller than that defined by bioenergetics. Despite the differences in magnitude, there was a strong correlation between methods (Table 3). For yearling optimal habitat, the average seasonal reduction in habitat volume predicted by the fixed-criteria model was two-thirds the value predicted by the bioenergetics model, and was negatively (but not significantly) correlated with that predicted by the bioenergetics model (Table 3).

The percent reduction in habitat volume due to seasonal hypoxia (May 1 and November 15) was similar between YOY and yearling sturgeon (Fig. 9). Average reductions varied between 3.3 and 28.1% with optimal habitat having higher proportional decreases than required habitat for both life stages. The difference between fixed-criteria and bioenergetics models for the required habitat of YOY and yearlings was on average 9.6% and 8.8%, respectively. For optimal habitat, the average difference in percent reduction between methods was 10.4% for YOY and 12.1% for yearlings.

Comparison of model predictions with locations of Atlantic sturgeon captures

The data on incidental captures of sturgeon during 1997 and 1998 indicates a wide distribution through-

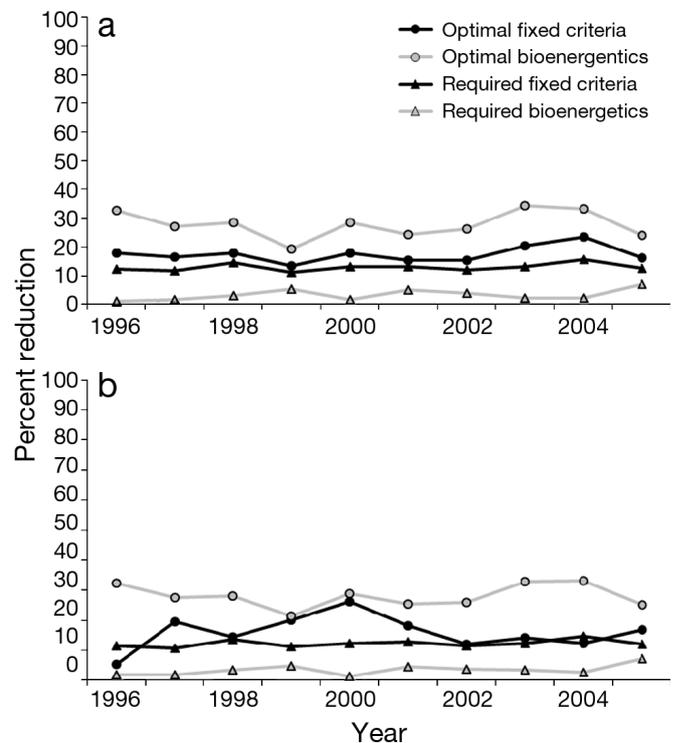


Fig. 9. Percent decrease of required and optimal habitat due to hypoxia calculated by fixed-criteria and bioenergetics models for (a) young-of-the-year and (b) yearling Atlantic sturgeon *Acipenser oxyrinchus* during the time period of seasonal hypoxia (May 1 and November 15) between 1996 and 2005

out the Chesapeake Bay, despite low recent abundances compared with historical levels. The validation analysis showed close agreement between summertime required habitat distributions and sturgeon capture locations. In 1997, 100% (N = 48) of the capture locations fell within the boundaries of the predicted bioenergetics required habitat. In 1998, 94% (N = 34) of the capture locations were found in the predicted bioenergetics required habitat. With respect to optimal habitat, 60% of the capture locations in 1997 and 53% of the capture locations in 1998 fell within predicted suitable habitat distributions.

DISCUSSION

This study represents a new approach to habitat modeling: (1) starting with a coupled biophysical model to predict volumes of available temperature, salinity and dissolved oxygen; (2) then defining habitat suitability using 2 different types of models; and (3) summing volumes that support required and optimal conditions for young Atlantic sturgeon. The high spatial and temporal resolution of this habitat volume approach allows for evaluation of a species' responses to environmental stressors such as hypoxia, as well as climate variability and change. Although the concept of relating habitat volume to growth and survival is not new (e.g. Brandt et al. 1992, Niklitschek & Secor 2005), the calculation of habitat volume at the intersection of multiple water masses within a 3D biophysical model is novel. Many habitat modeling methods estimate potential habitat based on static distributions of species in relation to environmental variables (Planque et al. 2011), but few estimate 3D changes in habitat volume. Neuenfeldt (2002) estimated volumes of hypoxic water and respective predator-prey overlap in the Bornholm Basin using a time series of oxygen observations. Kimmerer et al. (2009) used a hydrodynamic model and resource selection functions to calculate an index of total habitat based on salinity. Our research builds on this approach by including dissolved oxygen and temperature as well as the ability to calculate the volume of individual water masses and the volume of their intersection. This results in a quantitative means of tracking habitat changes at high temporal resolution that can be applied to understand the influence of past and future environmental variability on species' habitat.

Model results suggest a complex interaction between temperature, salinity, and dissolved oxygen

in determining potential habitat volume. Salinity-dependent patterns were observed for each life stage of Atlantic sturgeon (Figs. 2 & 3). The volume of required and optimal habitat for YOY and yearling sturgeon co-varied closely according to their respective salinity tolerances for most of the year, excluding the summer. Changes in freshwater flow and stratification, which in turn affect the degree of salt intrusion in the bottom waters of the estuary, had a direct impact on sturgeon habitat, with its influence negatively co-varying between YOY and yearling individuals. For instance, drought years would be predicted to compress YOY habitats centered in the upper Chesapeake Bay, but expand yearling habitats in the lower Chesapeake Bay. This model thus simulated realistic distribution patterns documented for this species (Dovel 1971, Niklitschek & Secor 2005).

As expected for estuarine fauna, temperature plays a major role in dictating potential habitat availability for young Atlantic sturgeon (Attrill & Power 2004), and was at times responsible for the largest summertime reductions in habitat (Figs. 3 & 4). For required habitat, increased temperatures significantly reduced habitat volumes, with almost no available habitat present during a portion of the summer in 2005 for either life stage. Optimal habitat was limited throughout most of the year by temperature, which in particular drives the seasonal availability of optimal habitat in the spring and autumn. The ability to make quantitative predictions of the influence of temperature on habitat volume at high spatial and temporal resolution indicates that this modeling approach will be useful for assessing climate change impacts to sturgeon habitat.

The presence of hypoxia encompasses an additional constraint on available habitat for estuarine species (Breitburg et al. 2003). Large hypoxic events can potentially result in mass mortalities (Breitburg 2002) and reductions of available habitat, which can lead to density-dependent reductions in growth rate (Eby et al. 2005) and decreases in reproductive potential (Diaz & Rosenberg 2008). Changes in the structure of the water column resulting from hypoxic water can also influence abundance distributions (Tomkiewicz et al. 1998) as well as trophic interactions, by changing the overlap of predator and prey distributions, as in the case of Baltic cod and herring (Neuenfeldt 2002). It can be particularly detrimental for benthic species that have no or limited access to oxic surface waters (Ritter & Montagna 1999). For demersal blue crabs, potential habitat in the Neuse Estuary decreased by 7–27% during the summers of 1997 and 1998 due to hypoxia (Selberg et al. 2001). These percentages are similar to the percent reduc-

tions in seasonal habitat estimated for YOY and yearling sturgeon in the present study (required 9.1–12.9%, optimal 15.9–32.9%). Similarly, Arend et al. (2011) found that average percent reductions in habitat due to hypoxia ranged from 8.5 to 35% for multiple life stages of rainbow smelt, emerald shiner, yellow perch, and round goby in Lake Erie.

Atlantic sturgeon have higher sensitivities to dissolved oxygen concentrations compared with many estuarine species (Niklitschek 2009a, Secor & Gunderson 1998). The combination of high summer temperatures and low dissolved oxygen interact in a way that severely inhibit growth and increase mortality rates in Atlantic sturgeon (Secor & Niklitschek 2002, Baker et al. 2005). Niklitschek & Secor (2005) used bioenergetics equations and survival rates to calculate instantaneous potential production in the Chesapeake Bay during 1993–2002. They estimated habitat reductions during summer of 65–100% due to the combined influence of salinity, hypoxia, and elevated temperature. Here we predicted that peak habitat reductions during summer were 62.5–100%, and that hypoxia by itself resulted in a 28.1% reduction in optimal habitat during summer. Still, the influence of hypoxia by itself can be markedly smaller than summertime habitat limitation resulting from temperature (see Fig. 3, e.g. 2005). This is an important distinction because it implies that hypoxia may not be the most significant threat to Atlantic sturgeon habitat when compared with temperature increases linked to climate change. Indeed, in a simulation of increased temperature everywhere in the Chesapeake Bay by 1°C during July, overall habitat was reduced by 37–100% during the 1993–2002 period (Niklitschek & Secor 2005).

To corroborate their bioenergetics predictions, Niklitschek & Secor (2005) examined records of Atlantic sturgeon captures within the Chesapeake Bay. When looking at capture locations, 76.6% of the locations they used were found in suitable habitat (defined as potential growth >0). Our analysis found 100% and 94% of the capture locations in required habitat for 1997 and 1998, respectively. The discrepancy may stem from the physical data used to make the model predictions. Niklitschek & Secor (2005) used interpolated observations of salinity, temperature and dissolved oxygen taken at 1–3 wk intervals. In the present study, these water-quality values were modeled at high resolution rather than being observed at lower resolution.

Overall our findings indicate that the volume of habitat calculated using fixed-criteria and bioenergetics models have similar patterns and magnitudes

for most required and optimal habitat types of YOY and yearling sturgeon, with the exception of the optimal habitat of yearlings. This similarity suggests that fixed criteria are a suitable substitute when bioenergetics information is not available. In addition, excluding yearling optimal habitat, all life stage and habitat combinations showed closely related responses to annual and seasonal changes in environmental conditions (Table 3). However, there was a lack of correlation between percent reduction in habitat due to hypoxia for the required habitat of each life stage. This was most likely due to the fact that there is little mortality data available to establish the required dissolved oxygen thresholds used for fixed criteria. In contrast, the percent reductions of YOY optimal habitat had very strong correlations between methods, and in this case there was more evidence to support the fixed-criteria approach.

The initial assumption was that habitat modeling using bioenergetics would result in more constrained habitat volume estimates due to the inclusion of physiological interactions. However, this was not the case. One potential reason is that bioenergetics equations explicitly contain compensations between physiological constraints. For example, unfavorable salinities may be tolerable in the presence of optimal temperature and dissolved oxygen conditions. If some form of metabolic compensation does occur, fixed criteria will not capture it, leading to smaller habitat volume estimates.

For yearling optimal habitat, the volumes of habitat defined by fixed criteria differed in magnitude and trends from those predicted by bioenergetics models. This lack of consistency was a consequence of the narrow optimal salinity range used in the fixed-criteria model. The chosen salinity range limited optimal habitat to the lower end of the Chesapeake Bay (Fig. 2), while dissolved oxygen limitation on habitat due to hypoxia predominantly occurred in the upper region of the bay. Therefore, yearling optimal habitat generally did not intersect with volumes of water influenced by dissolved oxygen limitation, which resulted in moderate reductions in habitat due to hypoxia and a unique interannual trend in reduction. There is only one study available to parameterize optimal physiological thresholds for yearling sturgeon (Niklitschek et al. 2009a), which may have led to this narrow salinity range, whereas it is known that yearlings can survive and grow in very low salinity and fresh water (Mohler 2004, Niklitschek et al. 2009a,b). A broader optimal salinity range could result in a better relationship between fixed-criteria and bioenergetics models.

Required habitat, representing regions where sturgeon survived, provided more consistent model results than did optimal habitat. Measuring the mortality of a given species with respect to environmental conditions is a relatively straightforward process and confidence can be placed in the range of physiological tolerances resulting in mortality. Consistent with this level of confidence, observed Atlantic sturgeon capture locations agreed closely with required habitat predictions. Because there is no universal definition for optimal habitat, determining optimal ranges is a more complex and subjective process. Adoption of consistent and standard definitions of optimum habitat is needed. In the context of this study, additional laboratory studies on growth and physiological tolerances are needed for yearling sturgeon based on the inconsistency of current model predictions and the observed distribution of >1 yr old Atlantic sturgeon in the Chesapeake Bay.

Both the fixed-criteria and bioenergetics methods incorporated only physical constraints on habitat volume, excluding trophic interactions and food distributions. Inclusion of trophic interactions to assess the realized niche of juvenile sturgeon would improve the model, but demersal prey data are not available at sufficient resolution to model on a bay-wide scale so accurate predictions are not available. Temperature, salinity, and dissolved oxygen effectively capture variability linked to precipitation, freshwater inflow regulation, sea-level rise, and eutrophication, making them invaluable indicators of a species' sensitivity to nutrient reduction and climate change. By determining the influence of hypoxia on potential habitat, future predictions of available habitat can be made under a variety of eutrophication and climate change scenarios. This will provide managers with the scenario-specific information with which to evaluate the consequences of management actions. The annual indices of habitat volume derived with this approach also may be used to improve stock-recruitment relationships and serve as habitat mediation functions in models such as Ecopath with Ecosim, which explicitly incorporate trophic dependencies (Christensen & Walters 2004; see also Rose et al. 2007).

Our overall results suggest that using the habitat volume modeling approach, beginning with a biophysical model and ending with volumes of habitat, provides a useful predictive framework, largely independent of whether habitat suitability is defined by a fixed-criteria or bioenergetics model. This is a meaningful distinction due to the effort involved in parameterizing each model. Despite increased accuracy

resulting from bioenergetics equations, they require a considerable amount of laboratory experimentation to determine the necessary coefficients. Although there are a variety of bioenergetics models available (e.g. for *Anchoa mitchilli*: Luo & Brandt 1993; *Gadus morhua*: Horne & Schneider 1994; *Morone saxatilis* and *Pomatomus saltatrix*: Hartman & Brandt 1995; *Acipenser oxyrinchus*: Niklitschek & Secor 2009b; *Morone americana*: Hanks & Secor 2011; *Sardinops melanostictus*: Okunishi et al. 2012), they are not available for many species that play a vital role in the structure and function of several ecosystems. Furthermore, some of the experiments used to define bioenergetics relationships do not cover a wide range of environmental conditions and life stages, making them impractical for many habitat modeling studies. Both fixed-criteria and bioenergetics habitat volume modeling approaches are able to quantify the influence of environmental variability, with strengths of physiological realism (bioenergetics) or broad application (fixed criteria). The ability to apply this methodology to any system that has a realistic hydrodynamic and biogeochemical model allows these approaches to be implemented across a broad range of systems and ecological applications.

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