ABSTRACT

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A quantitative understanding is needed to identify the impacts of climate change and eutrophication on the habitat of living resources so that effective management can be applied. A systematic literature review was conducted to obtain the physiological tolerances to temperature, salinity, and dissolved oxygen for a suite of Chesapeake Bay species. Information obtained was used to define required and optimal habitat conditions for use in a habitat volume model. Quality matrices were developed in order to quantify the level of confidence for each parameter. Simulations from a coupled oxygen and hydrodynamic model of the Chesapeake Bay were used to estimate habitat volumes of juvenile sturgeon (*Acipenser oxyrinchus*) and to assess sensitivity of habitat to environmental factors. Temperature and salinity define spring and fall habitat and a combination of salinity, temperature and dissolved oxygen influence habitat in summer. Both fixed criteria and bioenergetics habitat volume models yielded similar results.

MODELING POTENTIAL HABITAT OF CHESAPEAKE BAY LIVING
RESOURCES

By

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Chapter 1. Background and Introduction

Estuaries comprise approximately 80% of the Eastern United States and Gulf coastlines along with 10% of the pacific coast (Alongi 1988). These areas, where saltwater from the ocean mixes with freshwater runoff from land (Pritchard 1967), provide essential habitat for a variety of ecologically important species (Lippson et al. 1979). Due to unique hydrologies and nutrient recycling dynamics, estuaries are characterized by high productivity with the potential to support large fish, crustacean, and mollusk populations (Lippson et al. 1979). Estuaries are ecological hot spots that not only give rise to significant species diversity and abundance, but also influence the stability of neighboring ecosystems (Witman 2004). However these biological traits, along with other characteristics such as shipping, transportation and desirable locations, have attracted considerable development with approximately 60% of the world's population living along estuaries (Wolanski 2007).

One of the major problems threatening estuaries is anthropogenic nutrient enrichment (Kemp et al. 2005). Nitrogen and phosphorus are introduced into estuarine systems through a variety of sources. Towns and cities produce high nitrogen wastewater effluent from industrial and municipal facilities that is often released directly into waterways. The phosphorus used in residential and industrial detergents is also released into estuaries. Of the 32 largest cities in the world, 22 are located on estuaries (Ross 1995). However, nonpoint sources may be the largest contributor of nutrient pollution (Boyton et al. 1995). Fertilizers used by most farming techniques tend to wash off into estuaries, thereby increasing nitrogen and phosphorus concentrations (Boyton ety al.

1995). Atmospheric deposition is also considered to be a significant nitrogen input to estuaries (Boyton et al. 1995). Because most estuaries already have high concentrations of naturally occurring nutrients along with efficient recycling capabilities, these large additions of anthropogenic nutrients can disrupt ecosystem structure and function.

This overabundance of nutrients, known as eutrophication, is a widespread problem facing estuaries all over the globe (Nixon 1995; Howarth et al. 2000, Cloern 2001, Kemp et al. 2005). Eutrophication results in massive plankton blooms, some of which can be harmful to humans (Kemp et al. 2005). The resulting plankton blooms noticeably reduces water quality, partially through increases in turbidity (Smayda 1990, Nielsen et al. 2002a). The blooms also create a high flux of organic material out of the water column to the bottom where it is degraded by bacterial communities. The process of microbial respiration, which causes the degradation of organic matter, requires a high demand for oxygen. With enough organic matter sinking to the bottom of estuaries, oxygen is quickly used up, creating areas of hypoxic or anoxic water (Officer et al. 1984). In some estuaries where anthropogenic nutrient input and subsequent eutrophication is a major problem, such as the Chesapeake Bay, large volumes of water can turn hypoxic (Officer et al. 1984). Anoxic and hypoxic waters, which herein refer to dissolved oxygen concentrations of <0.2 mg l^{-1} and <2.0 mg l^{-1} respectively (Hagy et al. 2004), have the potential to significantly decrease species diversity by killing oxygen dependent organisms that cannot escape in time and by reducing the potential habitat for those that survive (Ritter & Montagna 1999). The destruction of benthic communities creates a domino effect, disrupting ecological interactions throughout the water column (Breitburg

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et al. 2003), which could have the potential to negatively impact economically important fisheries, such as oysters, soft shell clam, blue crabs, and striped bass.

The ecological disruptions created by anthropogenic nutrient loading are mainly expected to grow worse as a result of climate change (Najjar et al. 2000, Justic et al. 1997). Rising temperatures will create more favorable conditions for bacterial respiration as well as make it possible for these warm conditions to persist for longer periods throughout the year. Higher temperatures will also reduce the amount of dissolved oxygen that can be saturated in water. Another potential consequence of climate change expected for the Chesapeake Bay region is a potential increase in precipitation rates (Najjar et al. 2000). These increases will lead to higher fertilizer runoff from the surrounding areas. The freshwater runoff will also create a more stratified water column throughout the bay, inhibiting dissolved oxygen from reaching bottom waters. However there may be positive effects associated with climate change as well, such as an increase in tidal mixing created by sea level rise, which could increase dissolved oxygen concentrations (Li et al. 2006). Although such a positive change may help to inhibit hypoxia, it may not be enough to stem the problem. If appropriate steps are not taken to mitigate anthropogenic nutrient loading, climate change may result in reduced water quality.

Eutrophication, hypoxia, and the ensuing decreases in water quality are problems that humans have been facing for decades (Kemp et al. 2005) and multiple efforts have been taken to increase our understanding of the mechanisms that create hypoxia and reduce their impacts. Conceptual modeling of the dynamics underlying the effects of anthropogenic nutrient loading have lead to more accurate water quality monitoring

programs and management policies (Cloern 2001). Yet in order for effective mitigation to take place, it is vital that predictive tools be created (Harding et al 2002). With the confounding influences of climate change and increasing human development, policy makers need a quantitative understanding so that appropriate and preventative efforts can be made.

The development and advancement of computer modeling has brought us closer to this quantitative understanding. Three dimensional circulation models allow for accurate assessment of water movement in estuarine systems (e.g., Li et al. 2005, Zhong and Li 2006). Biogeochemical models have also been built to better understand the flow of nutrients within an ecosystem (e.g., Kremer and Nixon 1978, Bierman et al. 1994, Cerco 1995, Peeters et al. 1995). These models provide insight into how the physics of a given system influence chemical processes and how that chemistry in turn influences biological dynamics. When these types of models are combined to create biophysical models, an enhanced understanding of anthropogenic nutrient loading can be achieved (Arhonditsis et al. 2002, Baretta et al. 1995, Arhonditsis and Brett 2004).

The development of high resolution biophysical, biogeochemical, and living resource models is integral to the future protection of marine and aquatic ecosystems. As stressors resulting from eutrophication and climate change grow worse, the ability to accurately model three-dimensional habitat distributions over a variety of spatial and temporal scales will become increasingly important. Coupled biophysical models can fulfill this role by directly incorporating output into habitat modeling, which provides a numerical representation of a species' habitat preferences (Secor 2010). Subsequent habitat estimates will allow managers to understand how nutrient loading and climate

change affect individual species and can be used to predict future habitat distributions under a variety of potential scenarios. This will provide information for management and conservation efforts so that resources can be efficiently and effectively allocated.

My thesis focuses upon 4D habitat volume model based on habitat suitability metrics and ecophysiological assessment models incorporating bioenergetics to predict habitat quantity, quality, and potential production of a suite of living resources. In order to run these models correctly, temperature, salinity, and dissolved oxygen physiological tolerances had to be obtained for a suite of Chesapeake Bay living resources. These tolerances were used to parameterize the habitat volume model. This required an in depth systematic literature review. Due to inconsistencies inherent in synthesizing a large number of individual studies, a quality matrix was developed to assign measures of confidence to each physiological tolerance. Points were attributed to each parameter which met a variety of quality measures. Parameters that did not meet a predetermined quality point threshold were deemed impractical for habitat volume modeling.

Once the appropriate physiological tolerance data was obtained, those that met the quality point cutoff were used to parameterize a habitat volume model developed by Smith et al. (in prep) for juvenile Atlantic sturgeon (*Acipenser oxyrinchus*). This habitat volume model was used to quantify changes in potential habitat resulting from climate variability and eutrophication. The model was designed to incorporate output from 3D hydrodynamic and water quality models to calculate the volume of water satisfying a given set of environmental parameters. Using temperature, salinity, and dissolved oxygen to constrain a potential habitat, the model calculates the respective habitat volume throughout the Chesapeake Bay and how it changes over time. The habitat volume model

was also combined with bioenergetic equations, to create 4D ecophysiological analyses that result in visual representations of potential growth in the Chesapeake Bay.

A simplified oxygen model developed by Li et al. (in prep) was used in order to obtain dissolved oxygen estimates. Although estimates from the simplified oxygen model capture yearly trends in oxygen cycling, there are differences in both magnitude and timing between the model and field observations. Despite these differences, the predictions are suitable to assess the capabilities of the habitat volume model as well as identify the major differences between potential habitat estimates using habitat suitability criteria (fixed criteria) and ecophysiological (bioenergetic) methodologies. This work serves as a proof-of-concept analysis of these models as a first and important step towards applying it to assess the impacts of climate change and nutrient management on a suite of living resources.

This research is part of the Coastal Hypoxia Research Project (CHRP), which is a large collaborative study with the goal of creating a robust predictive tool that can be applied to any coastal system. Using the multitude of data that has been compiled for the Chesapeake Bay and Delaware Bay, CHRP will create statistical models for quantitative interpretation of spatial-temporal changes in water quality with respect to nutrient loading and climate change as well as couple three dimensional models of physical circulation (Regional Ocean Model System, ROMS) and biogeochemistry (RCA). The systematic literature review and habitat volume model developed in my thesis will be used to extend the results of the coupled ROMS-RCA model to living resources as well as assess how changes in climate and nutrient management affect them.

In addition to this Introduction section, this thesis contains three sections. Chapter Two consists of the systematic literature review of physiological tolerances for Chesapeake Bay living resources. Chapter Three applies the habitat volume model to estimate potential habitat of juvenile sturgeon. The combined and individual influences of temperature, salinity, and dissolved oxygen on habitat volumes are quantitatively analyzed as well as the major differences and similarities between fixed criteria and bioenergetic habitat modeling approaches. Chapter Four contains an overall summary and conclusions of this research program.

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Chapter 1: Systematic literature review of the physiological tolerances of Chesapeake Bay living resources

Abstract

A systematic literature review was conducted in order to obtain physiological tolerances for a suite of Chesapeake Bay species for use in a habitat volume model. Extensive online and library searches were used to find documents containing information applicable to physiological tolerance parameters. All available studies for a particular species and lifestage were synthesized to provide the most accurate physiological range or threshold possible. Quality matrices were developed in order to assign measures of confidence to each physiological parameter. Dissolved oxygen was the parameter with the most missing information. Egg and larvae were the lifestages that lacked the most information. White perch, weakfish, menhaden, white flounder, soft shell clam, and striped bass were the species with the highest overall quality scores. A minimum quality score threshold was used to determine whether the information on a species and lifestage was suitable for inclusion in a habitat volume model.

Introduction

A major goal of this work is to quantify how the potential habitat of a variety of Chesapeake Bay species responds to nutrient loading and climate change. This requires knowledge of each species' physiological tolerance to temperature, salinity, and dissolved oxygen so that an accurate representation of habitat volume can be estimated. In order to compare the required and optimal habitat volumes between species, a detailed understanding of each species' response to environmental variables is required. Unfortunately acquiring such information is difficult because the source of information

can be inconsistent or contradictory, or simply not exist. In order to overcome the inherent uncertainty associated with synthesizing such a wide variety of research, a systematic literature review was conducted to gather physiological tolerance data on a suite of species and to standardize the quality of the data to develop confidence when comparing species and when applying the information in habitat models.

A systematic review refers to a formalized assessment and evaluation of current literature with a particular research question in mind (Cook et al 1997). The review follows a set of transparent guidelines that limit bias and random error so that the process can be repeated by outside parties. Systematic reviews generally include a comprehensive search of all available primary investigations, a method for assessing the quality of each study, and an organized synthesis of relevant information (Okoli and Schabram 2010). Although systematic review methodologies were primarily developed for use in clinical fields, their use in other applied disciplines is increasing. However, this conversion creates problems regarding the quality assessment of data. Most clinical studies can easily be divided into quality hierarchies. For example a higher degree of confidence can be placed in a double blind study with a completely randomized control when compared to uncontrolled or etiological relationship studies (Petticrew and Roberts 2006). Very rarely can this sort of quality organization be applied to ecological studies which may vary significantly in terms of spatial and temporal scales (Pullin and Stewart 2006). As a result, systematic reviews dealing with ecological applications require a unique set of guidelines designed to assess the quality of research so that uncertainty attributable to performance bias, detections bias, environmental variation, and methodological inconsistencies can be addressed.

This project applies a novel approach towards quantifying the quality of ecological studies so that direct measures of confidence can be placed in the physiological tolerances of organisms. Individual physiological tolerance values were given a certain amount of quality points directly related to the level of confidence that could be attributed to the studies supporting that value. Based on these quality points, a quality matrix was used to summarize the degrees of confidence in each physiological temperature, salinity, and dissolved oxygen parameter. A predetermined threshold in quality points was used to determine whether the information for a specific species and life stages had an acceptable degree of confidence.

The following systematic literature review synthesizes data from physiological tolerance studies related to a broad suite of Chesapeake Bay living resources. Through the use of quality points, a measure of confidence was derived for each physiological tolerance parameter. This information will be applied to future modeling efforts to ensure that only robust data is used to model the potential habitat of each species.

Methods

The purpose of this literature review was to obtain a set of required and optimal habitat physiological ranges based upon temperature, salinity, and dissolved oxygen for the egg, larvae, juvenile, and adult stages of blue crab (*Callinectes sapidus*), eastern oyster (*Crassostrea virginica*), bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), bay anchovy (*Anchoa mitchilli*), and Atlantic sturgeon (*Acipenser oxyrinchus*). Tolerances were also obtained for the juvenile stage of winter flounder (*Pseudopleuronectes americanus)*, Atlantic menhaden (*Brevoortia tyrannus)*, Atlantic

croaker (*Micropogonias undulates)*, weakfish (*Cynoscion regalis)*, soft shell clam (*Mya arenaria)*, and white perch (*Morone Americana)*.

Online searches were conducted using both 'Google Scholar' and 'Web of Science' for studies relating to the physiological tolerances of target species. A large variety of keywords and phrases were applied to the search engines so that as many relevant studies were found as possible. For any study deemed suitable for the synthesis, its literature cited section was analyzed for additional sources of information. The literature review methodologies and findings are presented for each individual species and lifestage. The results of this literature review are summarized in tables 1-12.

Potential habitat, in this study, was categorized into *required* and *optimal* habitat. Required habitat was defined as a range of environmental conditions outside of which mortality of a specific species will occur. Optimal habitat was defined as a range of environmental conditions outside of which physiological stress will occur, which may manifest through reductions in growth, movement, or other metabolic processes.

In order to maintain a high degree of objectivity throughout the systematic literature review, physiological tolerance ranges and thresholds were only defined when publications provided definitive numbers. In other words, 'educated guesses' based upon common ecological knowledge were not used to define fixed criteria parameters. For example, if it is known that a particular species spends a portion of the year in marine locations, an upper salinity tolerance reflecting marine salinities was not used to define the physiological salinity tolerance unless quantitative evidence from a published source was found.

With regard to Lethal Dose (LD_{50}) experiments dealing specifically with low oxygen stress, time-dependent relationships were converted into thresholds when necessary. The LD_{50} level of dissolved oxygen that resulted in 50% mortality within 6 hours was chosen as the physiological threshold for a species' required habitat. For some species, the value of one variable influences the tolerance of the organism to another variable, and this interdependency has been quantified in multivariate equations when there is enough information available. Whenever possible, multivariate equations were incorporated into the literature review instead of set ranges.

While analyzing field studies, required habitat was considered to be the entire range over which a specific species and lifestage was observed. Optimal habitat was considered to be the range over which the majority of a specific species and lifestage occurred. When laboratory, modeling studies, and presence and absence information could not be found, but a reasonable assumption could be applied then it was used (e.g., the dissolved oxygen tolerance of gravid female blue crabs was applied to the eggs they carry). This was only done if feasible and as a last resort.

All temperature and salinity tolerance ranges were rounded to the nearest integer. Dissolved oxygen tolerances were rounded to the nearest tenth of a mg l^{-1}. Original values taken from the literature are presented in the physiological tolerance descriptions for each respective species and lifestage.

Quality Matrix

Each paper used in the literature synthesis was assigned quality points, which are awarded for various measures of accuracy and consistency. Table 1 contains a summary

of the points awarded for each quality measure, which are described below. The major

difference between many publications depends on the methodology employed for a

particular study. Studies based upon laboratory experiments tend to be the most accurate

with regard to directly determining physiological tolerances and were awarded the most

points. More points were awarded to those studies with a larger number or wider variety

of replications. In some cases, results taken from laboratory studies do not include many

replicates throughout the entire range of physical conditions, are based on a limited

range, or could have been applied with other physiological information to model

physiological tolerances outside of the environmental conditions originally tested. These

modeling studies are used when laboratory data is unavailable. More points are awarded

for models derived from a laboratory experiments with a wide range or experimental

conditions and high resolution. There are also many papers that use field observations to

determine the physiological limitations of specific species. The presence and absence

information collected in these studies represent the spatial and temporal conditions

through which the field observations were recorded and usually do not represent the full

extent of potential habitat. Furthermore, it has been shown that avoidance behaviors of

specific environmental parameters tend to occur before conditions reach mortality

thresholds, resulting in more conservative physiological tolerance estimates for required

habitat (Brietburg et al. 2001). Although less confidence can be placed in field

observations as compared to laboratory or modeling studies, presence and absence data

provides a suitable alternative when more accurate information in not available. More

points are awarded to studies that cover a large spatial and temporal extent.

Additional quality points were awarded to physiological parameters based upon studies with higher levels of accuracy and relevancy to this literature review. Physiological tolerances change depending on the location of the population being researched. As a result, those studies that focus on Chesapeake Bay populations will produce information more applicable to this research project and receive more points. When there is enough information available, simple equations can also be used to quantify the influence of interacting factors on physiological tolerance. This provides an additional degree of realism when trying to model potential habitat.

There are a variety of sources used in this literature review in addition to peer reviewed publications. Many are technical reports, public contract statements, or published books. When compared to these alternative references, peer reviewed journals are subjected to a higher level of scrutiny and therefore can be considered more credible. The majority of publications cited in this review came from peer reviewed journals and are awarded more points to give them a higher weight than grey literature sources. Furthermore, there are many instances where studies agree with each other, such as field studies supporting the results of laboratory studies. In such cases, more confidence can be placed in physiological tolerances that are supported by additional sources.

A threshold of total quality points was used to determine if information for a species or lifestage did not meet the minimum confidence requirements. This threshold was developed by setting a quality point value cutoff for each individual physiological tolerance using the following criteria: the information must be derived from at least one peer reviewed field study and the study must also have at least one supporting study or focus on a Chesapeake Bay population. This results in a minimum quality point value of

12. For reliable confidence in the information for a species or life stage, its temperature, salinity, and dissolved oxygen physiological tolerances must have individual quality point scores of 12 and an overall score of 36. In addition, information for any species and lifestage that is missing a physiological tolerance parameter, despite having a higher total score than 36, will not be considered complete and viable for use in the habitat volume modeling.

<div align="center">Results</div>

The following sections are organized by species and individual lifestages (egg, larvae, juvenile, and adult). The results of the literature review for some species require additional explanations, which can be found at the beginning of the species review. A summary section is included at the end to synthesize the overall results of the literature review.

A. Blue Crab (*Callinectes sapidus*)

A summary of blue crab physiological tolerances can be found in Table 1.2 and quality scores in table 1.3.

Eggs

Required habitat. Required temperature and salinity ranges chosen for blue crab eggs are 17-30 ^{o}C and 9-33, respectively. Costlow and Bookhout (1959) observed that blue crab eggs hatched in salinities from 20 to 32, while Sandoz and Rogers (1944) found that hatching failure occurs outside of salinities between 9 and 33. Eggs failed to hatch outside temperatures between 17-30 ^{o}C (Sandoz and Rogers 1944). These salinity and temperature ranges (17-30 ^{o}C and 9-33) are similar to those summarized in a review of blue crab environmental physiology conducted by Tankersley and Forward (2007).

Optimal habitat. The optimal temperature and salinity ranges chosen for blue crab eggs are 19-29 ^{o}C and 23-28, respectively. Sandoz and Rogers (1944) determined that eggs hatched most successfully between salinities of 23-28. They also found that there was no variation in percent hatching within the temperature range of 19-29 ^{o}C.

No studies concerning the effect of low oxygen on blue crab egg survival and hatching success were found. Aguilar et al. (2005) showed that post copulatory females avoided deeper water from June through August, when hypoxia is most prevalent, and will also delay spawning migrations until the fall turnover of the water column when deleterious low oxygen conditions are reversed. Due to the lack of direct data, the optimal dissolved oxygen tolerance of adults was used as an estimate for the required and optimal ranges of blue crab eggs.

Larvae

Required range. Required temperature and salinity ranges chosen for blue crab larvae are 16-30 ^{o}C and 20-35, respectively. Costlow and Bookhout (1959) were able to rear larvae at up to 30 ^{o}C while Costlow (1967) observed a significant decline in survival below 16 ^{o}C. With regard to salinity, there seems to be uniform agreement that larval blue crabs do not develop at salinities lower than 20 throughout all larval stages (Sandoz and Rogers 1944, Costlow and Bookhout 1959, Tankersley and Forward 2007). In laboratory studies, mortality occurred at salinities of 32 (Costlow and Bookhout 1959). However, larvae have been collected in coastal waters of North Carolina in salinities up to 35 (Ogburn and Forward 2009). Therefore the required range for salinity was chosen to be 20-35 for the Chesapeake region. These ranges are within those summarized by Tankersley and Forward (2007).

The required oxygen range for blue crab larvae was chosen to be ≥0.9 mg l^{-1} and was based on LC$_{50}$ laboratory experiments conducted by Tankersley and Wieber (2000) on megalopae. Megalopae are more sensitive to hypoxia than earlier stages of blue crab larvae (Johnson and Welsh 1985) and will therefore be used to set the required dissolved oxygen range of blue crab larvae in general. Using results from Table 2 in Tankersley and Wieber (2000), a linear relationship was calculated to predict percent oxygen saturation (O) required for a given survival time (t):

$$O = (t + 4) / 0.8$$

Using the assigned threshold of 6 hours, oxygen saturation was calculated to be 12.5%. A polynomial equation dependent on water temperature and salinity (Truesdale et al. 1955) was then used to calculate the solubility of dissolved oxygen. The temperature and salinity values, set at 24.5 ^{o}C and 32 respectively, were taken from Tankersley and Wieber (2000). The resulting value was 0.85 mg l^{-1} and set the low oxygen tolerance threshold for the required habitat range.

Optimal range. The optimal temperature and salinity ranges chosen for blue crab larvae are 20-29 ^{o}C and 21-30, respectively. Highest movement and activity occurred at salinities >24 (Costlow and Bookhout 1959). Favorable conditions for growth occur at salinities of 21-28 (Sandoz and Rogers 1944) and larval survival is highest at 30 (Costlow and Bookhout 1959). The highest level of development and survivability occurred in the temperature range of 20-29 ^{o}C (Sandoz and Rogers 1944), which was used to set the optimal temperature range. These ranges are within those summarized by Tankersley and Forward (2007).

No studies were found regarding the optimal dissolved oxygen tolerance of blue crab larvae.

Juveniles and adults

Required. Because temperature tolerances are dependent on salinity (Tagatz 1969), a linear regression was used to specify the required temperature range for juveniles and adults. The required salinity range chosen for juvenile and adult blue crab is 3-50. Guerin and Stickle (1992) observed survival in salinities of 2.5-56. They also found that hypersaline-acclimated crabs can survive in salinities up to 66.5, but blue crabs in the Chesapeake Bay do not experience such high salinities. Crabs acclimated at a high salinity, 34, had a temperature tolerance range of 4.6-39 $^{\circ}$C, while crabs acclimated at a low salinity, 6.8, had a temperature tolerance range of 5.3-37 $^{\circ}$C (Tagatz 1969). However, Miller and Bauer (2010) found that blue crabs can survive temperatures as low as 3 $^{\circ}$C at high salinities. For the purposes of our model, two distinct linear relationships between salinity and temperature were created with information from Tagatz (1969) and Miller and Bauer (2010) for the upper and lower temperature ranges.

$$\text{Upper range: } T = 0.0735S + 36.5$$

$$\text{Lower range: } T = 0.0484S + 5.1548$$

where T represents temperature and S represents salinity.

In addition to being affected by salinity, thermal tolerance also changes with the time of exposures (Holland et al. 1971), consistency of exposures (Rome et al. 2005), and the overall size of the crab (Bauer and Miller 2010). Holland et al. (1971) showed that thermal tolerance is higher under shorter exposure times. Rome et al. (2005) observed

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that mortality increased significantly when blue crabs experienced periods of slightly colder temperatures (1 $^{\circ}$C for 30 d followed by 3 $^{\circ}$C for 30 d) compared to more consistent conditions (3 $^{\circ}$C for 60 d). Although time of exposure influences thermal tolerance, there was not enough information available to create a quantitative relationship for incorporation into the habitat model.

There were distinct differences between adults and juveniles with respect to required oxygen tolerance (Das and Stickle 1993, Tankersley and Wieber 2000). The required oxygen range for blue crab juveniles was chosen to be $\geq$1.22 mg l^{-1} and was based on LC$_{50}$ laboratory experiments conducted by Tankersley and Wieber (2000). Using results from their Table 2, a linear relationship was calculated to predict percent oxygen saturation (O) needed to produce a given survival time (t):

$$O = (t + 3) / 0.5$$

Using the 50% mortality threshold of 6 hours, oxygen saturation was calculated to be 18%. A polynomial equation dependent on water temperature and salinity (Truesdale et al. 1955) was then used to calculate the solubility of dissolved oxygen. The temperature and salinity was set at 24.5 $^{\circ}$C and 32 respectively (Tankersley and Wieber 2000). The resulting value was 1.2 mg l^{-1} and set the low oxygen tolerance threshold for the required habitat range.

Adult blue crab dissolved oxygen tolerance decreases over time of exposure (Stickle et al. 1989) with adults being able to withstand hypoxic conditions for 25 days (deFur et al. 1990) and anoxic conditions for up to 12 hours (Carpenter and Cargo 1957). As a result, their required habitat is not constrained by a 6 hour threshold. This time-

dependent survival is influenced by temperature as well (Carpenter and Cargo 1957). Crabs held at temperatures from 24-26 ^{o}C will live longer than crabs held at temperatures of 28-30 ^{o}C under the same oxygen concentrations. Yet in high water temperature experiments (temperatures between 28-30 ^{o}C and DO at 0.4 mg l^{-1}), the LC$_{50}$ was approximately 10 hours and so the 6 hour threshold still does not apply. Adult crabs are also relatively mobile with the ability to move to dry land as a last resort. Therefore, only the optimal dissolved oxygen tolerance will be used to constrain potential habitat in the model for adult blue crabs.

Optimal range. The optimal temperature range was less dependent on salinity levels (Cadman and Weinstein 1988) as compared to the required range, therefore a temperature and salinity linear relationship was not applied. The optimal temperature and salinity ranges chosen for blue crab juveniles and adults were 15-30 ^{o}C and 10-30, respectively. Cadman and Weinstein (1988) found that growth per day was greatest between 15-30 ^{o}C, but growth per ecdysis peaked at 23 ^{o}C. Therefore 15-30 ^{o}C was chosen as the optimal temperature range, which incorporates both measurements of growth. Salinity has a relatively minor impact on growth per day compared to temperature, with growth being relatively constant across salinity levels (Table 2 of Cadman and Weinstein 1988). Guerin and Stickle (1992) found that crabs showed positive growth in salinities between 2.5-56, but they had the highest scopes for growth between 10-25. Rosenburg and Costlow (1976) presented similar results showing that the fastest development times occurred between salinities of 10-30. Both of the chosen ranges are within those summarized by Tankersley and Forward (2007).

The dissolved oxygen optimal range was chosen to be ≥ 2.8 mg l^{-1}. Juvenile and adult blue crabs can detect hypoxia, which manifests through alterations in their behavior (e.g. movement and antennule flick rates) and physiology (e.g. ventilation rates) when exposed to DO concentrations below 4 mg l^{-1} (Batterton & Cameron 1978, Das & Stickle 1994). However Bell et al. (2003) has shown that despite these detection rates, blue crab avoidance behavior does not significantly change in water with oxygen concentrations below 4 mg l^{-1}. Blue crabs frequently exposed to hypoxic water become more tolerant (Mangum 1994), which may explain why avoidance behavior was not observed when DO reaches 4 mg l^{-1}. In contrast, deFur et al. (1990) found that crabs became active when oxygen saturation dropped below 2.8 mg l^{-1} in an attempt to relocate. Therefore 2.8 mg l^{-1} was chosen as an acceptable optimum DO tolerance for blue crabs exposed to regular hypoxic events, such as those that occur in the Chesapeake Bay.

B. Eastern Oyster (*Crassostrea virginica*)

A summary of eastern oyster physiological tolerances can be found in Table 1.4 and quality scores in table 1.5.

Eggs

This section refers to fertilized eggs, which are known to have higher thermal tolerances than unfertilized eggs. This literature review has found that most studies focus on the period of development between fertilization and the blastula lifestage.

Required Habitat – The required temperature and salinity range chosen for eastern oyster eggs are 15-33 $^{\circ}$C and 8-39, respectively. Davis and Calabrese (1964) laboratory studies show that normal development of oyster eggs occurred in the temperature range of 17.5-32.5 $^{\circ}$C, although some experiments showed higher mortalities at the extremes of this range when compared to others. Clark (1935) experiments successfully raised fertilized eggs to the first swimming larval stage at temperatures ranging from 15 to 30 $^{\circ}$C. The chosen temperature range of 15-32.5 $^{\circ}$C is supported by additional laboratory studies (Loosanoff 1965, Roosenburg et al. 1970, Hidu et al. 1974, MacInnes and Calabrese 1979, Wright et al. 1983). The salinity tolerance of eastern oyster eggs and larvae is dependent upon the salinity at which the parent oysters were acclimated (Davis 1958, Davis and Calabrese 1964). Considering the habitat volume model does not take into account generational differences, the entire range over which all oyster eggs can survive is applied to the model so that oyster eggs produced by adults throughout the entire model domain can be accounted for. It has also been shown that the degree and rapidity of salinity change is likely more important than actual salinity (Davis 1958, Davis and Calabrese 1964). As a result, salinity tolerances were taken from studies that subjected oysters to extended periods of exposure. Davis and Calabrese (1964) show that normal larvae have the potential to develop from eggs in salinities from 7.5-27. The entire salinity range is given over which any appreciable percent survivorship occurred in order to reduce the influence of parental salinity acclimation. Clark (1935) showed that normal larvae developed from eggs at salinities of 14.5-39. Several other laboratory studies support these ranges (Amemiya 1929, Davis 1958, Loosanoff 1965) Although the

differences between studies were small, choosing the broadest range found will account for differences created by variable salinity adaptation in parent populations.

Optimal Habitat – The optimal temperature and salinity range chosen for eastern oyster eggs are 23-30 $^{\circ}$C and 10-30, respectively. Davis and Calabrese (1964) show the highest rates of normal egg development and survival occurred in the temperature range of 22.5-27.5 $^{\circ}$C. During Clark (1935)'s experiments, eggs developed to the first swimming larval stage the fastest at 30 $^{\circ}$C. With regard to salinity, Davis (1958) reports that the optimal salinity for the development of oyster eggs is between 10 and 22.5, depending on the parental salinity acclimation. During a similar laboratory study conducted by Amemiya (1929), 24.5-29.8 was determined as the optimal salinity range for egg development. These ranges are supported by additional laboratory studies (Davis and Calabrese 1964, Loosanoff 1965, Cake et al. 1983). Similarly, the broadest salinity range was chosen to account to parental salinity acclimation.

No studies could be found concerning the oxygen tolerance of eastern oyster eggs.

Larvae

The following values reflect data associated with early larval lifestages, which include gastrula, trocophore, and veliger developmental periods.

Required Habitat – The required temperature and salinity range chosen for eastern oyster larvae are 15-32 $^{\circ}$C and 8-39, respectively. Hidu et al. (1974) shows that eastern oyster ciliated gastrula larvae can survive temperatures up to 32 $^{\circ}$C for 16 hours while veliger larvae can survive 33 $^{\circ}$C. Wright et al. (1983) reports low mortality of trocophore larvae at extended exposures of temperatures up to 32.5 $^{\circ}$C as well as low mortality for straight-hinge larvae at temperatures up to 34 $^{\circ}$C. Davis and Calabrese

(1964) reported that no growth occurred at 15 $^\circ$C. Due to the lack of information regarding the lower lethal temperature limit for oyster larvae, 15 $^\circ$C was chosen. This temperature is close to the mean lower thermal limit as estimated by Lough (1975). The upper thermal limit was chosen to be 32 $^\circ$C because the ciliated gastrula phase is the most physiologically constrained larval phase. With regard to salinity, Davis (1958) experiments show that oyster larvae can develop normally throughout a salinity range of 7.5-35. In a similar study, Amemiya (1926) observed the occurrence of normal oyster larval development over the salinity range of 15-39. These ranges are further supported by laboratory and field studies (Carriker 1929, Davis and Calabrese 1964).

The required dissolved oxygen tolerance chosen for oyster larvae is $\geq$0.0 mg l^{-1}. Oyster larvae at early developmental stages can be tolerant of low dissolved oxygen, surviving anoxic conditions (0.02 mg l^{-1}) for up to 11 hours (Widdows et al. 1989, Baker and Mann 1992, 1994).

Optimal Habitat – The optimal temperature and salinity range chosen for eastern oyster larvae are 25-33 $^\circ$C and 13-33, respectively. Davis and Calabrese (1964) reported the highest rates of survival and growth occurred between 27.5 and 32.5 $^\circ$C. MacInnes and Calabrese (1979) provided evidence for 25 $^\circ$C as the optimal temperature for larval growth. Therefore 25 $^\circ$C was chosen as the lower optimal limit. With regard to salinity, Davis and Calabrese (1964) show the highest rates of growth at salinities of 12.5-27. Amemiya (1926) observed the highest rates of normal development and survival in the salinity range of 22-33. These ranges are supported by a similar laboratory study conducted by Davis (1958). Considering parental salinity acclimation still plays a role at this lifestage, a broad salinity range of 12.5-33 was chosen.

The optimal dissolved oxygen tolerance chosen for oyster larvae is ≥ 1.5 mg l^{-1}. Metamorphosis and growth suppression likely result when dissolved oxygen is at 1.5 mg l^{-1} for 3 days or more (Baker and Mann 1994).

Juveniles

Juveniles were not included in this literature review due to the lack of information available for that specific lifestage.

Adults

Required Habitat – The required temperature and salinity range chosen for adult oysters are -2-41 $^{\circ}$C and 5-44, respectively. Evidence shows that the rate of temperature change determines the absolute thermal tolerance for adult eastern oysters (Fingerman and Fairbanks 1957). The temperature limit at which oysters survived prolonged exposures was used in order to account for this effect. Oysters are found over a wide range of temperatures from -2 to 36 $^{\circ}$C (Butler 1954, Stanley et al 1986, Shumway 1996). Loosanoff (1965) also reported that oysters can tolerate the freezing of their tissues and revive as long as they are not disturbed. Fingerman and Fairbanks (1957) found that oysters exposed to increases of 0.74 $^{\circ}$C hr^{-1} suffered 50% mortality at 41 $^{\circ}$C while oyster exposed to increases of 13.2 $^{\circ}$C hr^{-1} experience 50% mortality at 47.5 $^{\circ}$C. These results suggest that the rate of temperature change plays a major role in thermal tolerance. Oyster living in more southern latitudes can be subjected to temperatures up to 46-49.5 $^{\circ}$C during exposure at low tides (Galtsoff 1964, Ingle et al. 1971), but these conditions do not exist in the Chesapeake Bay. The upper thermal tolerance of 41 $^{\circ}$C chosen for this

literature review was selected using laboratory results from Fingerman and Fairbanks (1957). 41 ^{o}C was used instead of 47.5 ^{o}C because the latter coincides with a temperature increase of 13.2 ^{o}C per hour, which also does not occur in the Chesapeake Bay. Several other studies report mortality temperatures above and below this chosen range (Henderson 1929, Nichy and Menzel 1960, Copeland and Hoese 1966, Tinsman and Maurer 1974), however they were not included due to potentialaly inaccurate mortality estimation techniques.

Adult oyster are also found in a wide range of salinities. Commercial production occurs in areas with salinity variation at some points in the tidal cycle between 0 and 43.5 (Menzel et al. 1966, Ingle and Dawson 1950, Copeland and Hoese 1966, Galtsoff 1964, Butler 1952, Gunter 1950). Wells (1961) determined the lower salinity death point for adult oysters to be 7 in a laboratory setting. In a similar experiment Loosanoff (1953) determined 5 as the minimum salinity for survival and these results were supported by Chanley (1958).

Sparks et al. (1957) shows that adult oysters can survive in water with less than 1.0 mg l^{-1} dissolved oxygen for up to 5 days. Galtsoff (1964) reports that oyster can survive anaerobically for up to 3 days. For the purpose of habitat modeling, any grid cell within a depth range of less than 10 meters in which anoxic conditions (0.00 mg l^{-1}) are present for more than 3 days will be considered unavailable habitat and will be removed from the total volume of potential habitat. The combined effects of temperature and salinity also influence the dissolved oxygen tolerance of adult oysters (Stickle et al. 1989). Yet, this influence has only been seen over the course of 28 days for adult oysters.

There are few areas in the bay where waters remain hypoxic for such an extended period of time and therefore this dependency should not significantly change model results.

Optimal Habitat – The optimal temperature and salinity range chosen for adult oysters are 20-32 ^{o}C and 8-30, respectively. Stanley et al. (1986) reported that the optimum temperature range for oysters is between 20 and 30 ^{o}C, while various other studies observed that adult oysters can grow in temperatures ranging from 6 to 32 ^{o}C (Galtsoff 1927, Collier 1951, Galtsoff 1964). In these studies, the optimum pumping capacity and pumping rate falls within the range of 20-30 ^{o}C, indicating that feeding is maximal in this range. Loosanoff (1958) also showed that the pumping rate declined above 32 ^{o}C and showed severe stress at 34 ^{o}C. With regard to salinity, Galtsoff (1964) stipulated that optimal oyster habitat can be found in areas with average salinities between 5 and 30. Loosanoff (1953) shows that oysters were able to grow in waters with a salinity of 7.5 or higher. These results are supported by Chanley (1958). Butler (1954) describes adult optimal salinity range of 10-20, which takes into account the detrimental influence of low salinities and the higher predation mortalities at higher salinities. However, his study focuses only on the physiological limitations of each organism with regard to potential habitat. Therefore the biological controls that manifest through ecosystem processes, such as predator prey interactions, are not included.

C. Striped Bass (*Morone saxatilis*)

A summary of striped bass physiological tolerances can be found in Table 1.6 and quality scores in Table 1.7.

Eggs

Required Habitat – Required temperature and salinity ranges chosen for striped

bass eggs are 12-27 ^{o}C and 0-18, respectively. Morgan and Rasin (1981) show that

striped bass eggs can hatch and develop normally at a temperature of 12 ^{o}C, but not at 11

^{o}C in a laboratory setting. Albrecht (1964), Barkuloo (1970), Morgan and Rasin (1973),

and Crance (1984) all came to similar conclusions during their laboratory studies. In a

field survey of the Chesapeake and Delaware estuaries, Dovel (1971) observed eggs in

water with temperatures as low as 11 ^{o}C. However, it is unknown whether these eggs

were able to hatch. Morgan and Rasin (1981) and Morgan and Rasin (1973) found that

striped bass eggs could develop normally in temperatures up to 27 ^{o}C in a laboratory

setting. With regard to salinity, Morgan and Rasin (1981) show that eggs can hatch and

develop normally in salinities between 0 and 10. Winger and Lasier (1994) provide

evidence for a larger salinity range of 0-18 during their laboratory study. The larger range

was chosen in order to capture all possible hatching conditions.

The required dissolved oxygen threshold chosen for striped bass eggs is ≥3.0 mg

l^{-1}. Turner and Farley (1971) observed normal development of striped bass eggs in water

with dissolved oxygen at 4 mg l^{-1}, but this study varied other environmental parameters

along with oxygen. Harrell and Bayless (1981) show that normal development can occur

in water with dissolved oxygen at 3 mg l^{-1}. Because Harrell and Bayless (1981) only

focused on variability in oxygen levels, their results were chosen for the required

dissolved oxygen range.

Optimal Habitat – Optimal temperature and salinity ranges chosen for striped

bass eggs are 14-22 ^{o}C and 1-10, respectively. Rogers and Westin (1978) describe

optimal rearing temperatures to be in the range of 16-20 ^{o}C in a hatchery setting. Morgan

and Rasin (1981) observed the largest percent hatch at temperatures between 14 and 22 ^{o}C. Morgan and Rasin (1981) experiments were conducted in a laboratory and were used to set the optimal temperature range. Several studies found that low salinities greater than zero enhance the survival of striped bass eggs (Albrecht 1964, Bonn et al. 1976, Geiger and Parker 1985). Bonn et al. (1976) and Geiger and Parker (1985) suggest that salinities >0.5 and 2-10 respectively result in optimal hatching and development for striped bass eggs. Dovel (1971) observed the highest numbers of eggs in salinities of 0-4 and North and Houde (2003) found >75% of striped bass eggs in salinities < 1, but presence and absence information cannot be relied upon as thoroughly as hatchery observations. Therefore, the optimal salinity range was chosen to be 0.5-10 in order to capture all potential optimal salinity conditions.

The optimal dissolved oxygen threshold chosen for striped bass eggs is ≥5.0 mg l^{-1}. O'Malley and Boone (1972) observed optimal hatching and development in water with dissolved oxygen concentrations greater than 5 mg l^{-1}.

Larvae

Required Habitat – Required temperature and salinity ranges chosen for striped bass larvae are 12-24 ^{o}C and 0-25, respectively. There are a variety of field observations, modeling studies, and laboratory experiments showing that striped bass larvae cannot develop normally in water less than 12 ^{o}C (Regan et al. 1968, Doroshev 1970, Dey 1981, Kernehan et al. 1981, Morgan and Rasin 1981, Boreman 1983, Logan 1985, Houde et al. 1988, Uphoff Jr. 1989, Rutherford and Houde 1995) Both Doroshev (1970) and Regan et al. (1968) provide evidence for larvae surviving temperatures up to 23 ^{o}C. However, Morgan and Rasin (1981) observed larval survival at a temperature of 24 ^{o}C. Therefore

12-24 ^{o}C was chosen as the required temperature range to capture all potential survival conditions. With regard to salinity, Albrecht et al. (1964) recorded normal development of striped bass larvae at salinities of 0-15 in a laboratory setting. In a similar laboratory experiment, Bayless (1972) observed normal development in salinities of 0 to a range somewhere between 21 and 28. Due to the lack of resolution in the upper salinity range for this study, the average of 21 and 28, 24.5, was selected as a general estimate to be used in the model.

The required dissolved oxygen threshold chosen for striped bass larvae is $\geq$4.0 mg l^{-1}. During the development of a set hatchery methodology for rearing striped bass larvae, Rogers et al. (1980) found that larvae cannot survive in water with dissolved oxygen levels at 2 mg l^{-1}. This threshold is further supported by Turner and Farley (1971) who observed significant mortality of striped bass larvae in water with dissolved oxygen concentrations less than 4 mg l^{-1}.

Optimal Habitat – Optimal temperature and salinity ranges chosen for striped bass larvae are 16-21 ^{o}C and 1-11, respectively. Several studies indicate that growth and survival are highest for striped bass larvae at temperatures between 16 and 18-21 ^{o}C (Doroshev 1970, Rogers et al. 1977, Morgan and Rasin 1981, Regan et al. 1986). With regard to salinity, Albrecht (1964) observed highest rates of survival at salinities of 3-7 in a laboratory setting. Barwick (1973) reported the optimal survival rates occurred at salinities of 1-3 for striped bass larvae grown in experimental ponds. Germann and Reeves (1974) observed the highest rates of growth and survival within the same salinity range of 1-3 during laboratory experiments. However, Bayless (1972) and Morgan and Rasin (1973) concluded that 10-10.5 as the optimal salinity range for the growth of

striped bass larvae as derived from their own laboratory studies. A salinity range of 1-11 was chosen to capture all potential optimum conditions.

The optimal dissolved oxygen threshold chosen for striped bass larvae is ≥ 5.0 mg l^{-1}. In a laboratory study, Turner and Farley (1971) show that abnormalities increase for striped bass larva in water with dissolved oxygen concentrations less than 5 mg l^{-1}.

Juveniles

Required Habitat – Required temperature and salinity ranges chosen for striped bass juveniles are 2-35 ^{o}C and 0-33, respectively. Cook et al. (2006) conducted a laboratory and modeling study to determine the upper and lower incipient lethal temperatures for striped bass juveniles. Their model suggests that juveniles can survive within a temperature range of 2.4-33.9 ^{o}C. The upper limits of this range are supported by field observations reported in Matthews et al. (1989). Cox and Coutant (1981) observed the survival of striped bass juveniles in temperatures up to 34.5 ^{o}C. The temperature range of 2.4-34.5 ^{o}C was chosen to capture all potential habitat conditions. With regard to salinity, Otwell and Merriner (1975) found that 1-4 month old striped bass juveniles can survive in salinities between 4 and 20 in a laboratory experiment, but salinities of 0-4 were not tested. Tagatz (1961) observed the survival of juvenile striped bass during abrupt transfers from fresh to high salinity water (33) and vice versa with various temperature differences. It is therefore assumed that survival can occur during transfers at all salinities within this range.

The required dissolved oxygen threshold chosen for striped bass juveniles is ≥ 1.4 mg l^{-1}. Field observations provide evidence that striped bass juveniles cannot inhabit water with dissolved oxygen concentrations lower than 2 mg l[-1](Coutant 1985). However,

Chittenden (1972) conducted laboratory experiments showing that loss of equilibrium occurs when oxygen concentrations reach 1.44 mg l^{-1}.

Optimal Habitat – Optimal temperature and salinity ranges chosen for striped bass juveniles are 24-27 °C and 1-15, respectively. A variety of laboratory studies report that optimal growth and survival conditions for juvenile striped bass occur within the temperature range of 24-27 °C (Meldrin and Gift 1971, Cox and Coutant 1981, Coutant et al. 1984). This temperature range is supported by field observations conducted in Matthews et al. (1989). Field observations also show the highest concentrations of juvenile striped bass in salinities between 0 and 16 (Dovel 1971, Rothschild 1990). Bonn et al. (1976) reported that an optimal salinity of 10 resulted in the highest growth and survival rates of juveniles in hatchery conditions and during handling. Laboratory experiments conducted in Secor et al. (2000) provide additional support for this range, showing that optimal salinities were within the range of 0.5-15.

The optimal dissolved oxygen threshold chosen for striped bass juveniles is ≥4.0 mg l^{-1}. During a laboratory study conducted by Brandt et al. (2009), reduced growth was observed in striped bass juveniles when DO dropped below 4 mg l^{-1}. Meldrim et al. (1974) observed avoidance behavior in striped bass juveniles to water with dissolved oxygen concentration at or below 3.8 mg l^{-1}. In a similar experiment, Chittenden (1972) reports restlessness when oxygen drops to 3.12 mg l^{-1}. Multiple field observations and laboratory studies, summarized in Countant (1985) provide evidence that striped bass juveniles avoid water with dissolved oxygen concentration below 3 mg l^{-1}. The study of Brandt et al. (2009) provides the most thorough information on the influence of dissolved oxygen conditions on growth, therefore 4 mg l^{-1} was chosen as the optimal threshold.

Adults

    Required Habitat – Required temperature and salinity ranges chosen for striped bass adults are 0-31 ^{o}C and 0-35, respectively. Kelly and Kohler (1999) found that striped bass adults can survive in water with temperatures as low as 0 ^{o}C in a laboratory setting. A variety of field studies observed adults in water with temperatures as high as 25-28 ^{o}C (Merriman 1941, Wooley and Crateau 1983, Coutant and Benson 1990, Nelson et al. 2010). Farquhar and Gutreuter (1989) used thermal tracking transmitters during a field study and found adults in water with temperatures as high as 31.1 ^{o}C. With regard to salinity, both Tagatz (1961) and Hardy (1978) report survival of adult striped bass within the salinity range of 0-35.

    The required dissolved oxygen threshold chosen for striped bass adults is ≥ 2.0 mg l^{-1}. Chittenden (1971a) provides evidence that adult striped bass mortality will begin to occur at 2 mg l^{-1}. This conclusion is supported by field observations (Coutant 1985).

    Optimal Habitat - Optimal temperature and salinity ranges chosen for striped bass adults are 14-25 ^{o}C and 0-35, respectively. Talbot (1966) shows that the optimal temperatures for growth and survival of striped bass adults are within the range of 13.5-25.2 ^{o}C. These results are supported by field studies that observe the majority of adult striped bass within water with temperatures between 20 and 24 ^{o}C (Coutant and Carroll 1980, Schaich and Coutant 1980). There is a lack of information concerning the optimal salinity range for striped bass adults. During a field study conducted in Rothschild (1990), the highest percentages of striped bass adults were found in salinities of 0-15. Additional studies have documented adult striped bass growth in full strength sea water

with salinities up to 35 (Chapoton and Sykes 1961, Diodati and Richards 1996, Walter et al. 2003).

The optimal dissolved oxygen threshold chosen for striped bass adults is ≥3.0 mg l^{-1}. Using laboratory data, Chittenden (1971a) concluded that striped bass adults require dissolved oxygen concentrations of at least 3 mg l^{-1} for normal growth and survival. This threshold is supported by field observations recorded in Cheek et al. (1985) and Coutant (1985) that show striped bass adults in water with dissolved oxygen concentrations as low as 4 mg l^{-1} and 3 mg l^{-1} respectively.

D. Bay Anchovy (*Anchoa mitchilli*)

A summary of bay anchovy physiological tolerances can be found in Table 1.8 and quality scores in Table 1.9.

Eggs

Required – The required temperature and salinity ranges chosen for bay anchovy eggs are 9-31 ^{o}C and 1-32, respectively. Although bay anchovy tend to spawn only when temperatures exceed 12 ^{o}C (Dovel 1981), both Dovel (1971) and Dalton (1987) found bay anchovy eggs in waters with a temperature range of 9-31 ^{o}C. Rilling and Houde (1999) and Peebles (2002) observed eggs in higher temperature ranges of 25.3-26.8 ^{o}C and 23-29.2 ^{o}C, respectively. With regard to salinity, there are several studies providing presence- absence information. Dovel (1971) recorded bay anchovy eggs in salinities ranging from 1 to 22 while Olney (1983) observed the presence of eggs in a slightly higher salinity range of 6.4-31.9. These ranges are supported by several field studies

(Dovel 1967, and Dovel 1981, Rilling and Houde 1999, Peebles 2002). Therefore the chosen required salinity range is 1-39.9.

The required dissolved oxygen tolerance chosen for bay anchovy eggs is ≥ 2.8 mg l^{-1}. Chesney and Houde (1989) conducted laboratory experiments to determine the dissolved oxygen tolerance of bay anchovy eggs. It was found that the LC_{50} for bay anchovy eggs was at 2.8 mg l^{-1}.

Optimal – The optimal temperature and salinity ranges chosen for bay anchovy eggs are 20-27 ^{o}C and 4-26, respectively. Dovel (1971) shows the highest concentrations of bay anchovy eggs were found in temperatures of 20-27 ^{o}C. This temperature range is also supported by Dalton (1987), Rilling and Houde (1999), and Peebles (2002). Regarding salinity, Dovel (1971) observed the highest densities of eggs in salinities of 4-19. In a similar field study, Rilling and Houde (1999) reported the increased concentrations of eggs in water with slightly higher salinities of 5.8- 26.2. These ranges are supported by additional field observations in Lippson et al. (1979), Olney (1983), Jung and Houde (2003, 2004), and North and Houde (2004).

The optimal dissolved oxygen tolerance chosen for bay anchovy eggs is ≥ 3.0 mg l^{-1}. The results of Chesney and Houde (1989) indicate that the percentage of unhatched alive eggs significantly increases at 3.0 mg l^{-1}. Post hatch survival also drops when eggs are exposed to dissolved oxygen concentrations below 3.0 mg l^{-1}.

Larvae

Required - The required temperature and salinity ranges chosen for bay anchovy larvae are 3-32 ^{o}C and 0-32, respectively. During a field study conducted by Olney (1983) in the lower Chesapeake Bay, bay anchovy larvae were found during the winter

when temperatures fell to 2.5 ^{o}C. The range of 2.5-32 ^{o}C is supported by field studies conducted in Dovel (1971), Dokken (1984), and Rilling and Houde (1999). Houde (1974) conducted laboratory experiments in which bay anchovy larvae were exposed to temperatures up to 32 ^{o}C and survived. A range of 0-32 ^{o}C was chosen in order to capture all of these results. Dovel (1971) found bay anchovy larvae throughout a salinity range of 0-23. Dokken (1984) observed larvae in salinities of 0-49, for a Gulf coast population. Olney (1983) and Rilling and Houde (1999) also collected larvae in salinities of 6.4-31.9 and 5.8-26.2, respectively. Therefore 0-49 was selected as the required salinity range to capture the entire range.

The required dissolved oxygen tolerance chosen for bay anchovy larvae is $\geq$1.6 mg l^{-1}. Breitburg (1994) found that bay anchovy larvae have a dissolved oxygen tolerance threshold somewhere between 1 and 2 mg l^{-1}. The threshold is further refined by Chesney and Houde (1989)'s laboratory experiments, which resulted in an LC$_{50}$ at 1.6 mg l^{-1}.

Optimal – The optimal temperature and salinity ranges chosen for bay anchovy larvae are 23-32 ^{o}C and 3-26, respectively. Dovel (1971) recorded 88% of bay anchovy larvae in the range of 23-27 ^{o}C. Houde (1974) tested the effects of temperature on feeding, growth, and survival of bay anchovy larvae and found that the fastest growth rates and the largest lengths occurred in an upper temperature range of 28-32 ^{o}C. With regard to salinity, Dovel (1971) observed over 70% of bay anchovy larvae in salinities of 3-7 in collections limited to upper Chesapeake Bay. In a similar field study conducted by Rilling and Houde (1999), the highest concentrations of larvae were found in salinities of 5.8-26.2. These ranges are supported in field studies conducted by Dovel (1981) and Jung and Houde (2003, 2004).

The optimal dissolved oxygen tolerance chosen for bay anchovy larvae is ≥2.0 mg l⁻¹. Both Keister et al. (2000) and North and Houde (2004) show that bay anchovy larvae concentrations significantly decrease when dissolved oxygen drops below 2.0 mg l⁻¹.

Juveniles

Required – The required temperature and salinity ranges chosen for juvenile bay anchovy are 0-32 °C and 0-38, respectively. Dovel (1971) reported juvenile bay anchovy in waters with temperatures between 0°C and 31 °C. Chung and Strawn (1982) observed the survival of juvenile and adult bay anchovy within the discharge waters of a power plant and found that mortality began to occur when temperatures reached 33 °C. Kimura et al (2000) recorded juvenile bay anchovy within temperatures of 22.8-26.2 °C. During laboratory experiments, Terpin et al. (1976) found that heat shock occurs in bay anchovy juveniles when temperatures reach 32 °C. With regard to salinity, Dovel (1971) observed juveniles in waters with salinities of 0-23, while Kimura et al (2000) found juveniles in a salinity range of 5-28.8. Kilby (1995) also reported juvenile bay anchovy in salinities between 20 and 37.6.

The required dissolved oxygen tolerance chosen for bay anchovy juveniles is ≥1.0 mg l⁻¹. Taylor et al. (2007) observed the behavior of juvenile bay anchovy with respect to dissolved oxygen using stationary hydroacoustics. Individuals were observed in water with dissolved oxygen as low as 1 mg l⁻¹ when >70% of the water column was hypoxic.

Optimal – The optimal temperature and salinity ranges chosen for juvenile bay anchovy are 14-27 °C and 3-30, respectively. Terpin et al. (1976) found that the preferred temperature range for bay anchovy is 14-27.0 °C in laboratory studies. This temperature range is supported by a similar laboratory study conducted by Lou and Brandt (1993)

along with field observations reported by Dovel (1971) and Houde and Zastrow (1991). Dovel (1971) observed the highest concentrations of juvenile bay anchovy in a salinity range of 3-7. In a similar field study conducted by Houde and Zastrow (1991), the majority of juvenile bay anchovy were observed in a higher preferred salinity range of 9-30, which agrees with salinities recorded during field collections in Jung and Houde (2003). In order to capture the entire range of preferred salinities, 3-30 was used for the optimal salinity range.

The optimal dissolved oxygen tolerance chosen for bay anchovy juveniles is ≥ 3.0 mg l^{-1}. Ludsin et al. (2009) observed that juvenile and adult bay anchovy will avoid waters with dissolved oxygen levels below 3 mg l^{-1}. Taylor et al. (2007) came to a similar conclusion, reporting that individuals tend to avoid water with dissolved oxygen concentrations below 2.5 mg l^{-1}. The highest dissolved oxygen concentration resulting in avoidance behavior was selected as the threshold in order to identify the point closest to where optimal conditions most likely diverge.

Adults

Required - The required temperature and salinity ranges chosen for adult bay anchovy are 2-34 ^{o}C and 0-45, respectively. Roessler (1970) recorded adult bay anchovy in waters with a temperature range of 16-34 ^{o}C. Dovel (1981) collected bay anchovy in a range of 2.2-27.1 ^{o}C. Chung and Strawn (1982) observed the survival of juvenile and adult bay anchovy within the discharge waters of a power plant and found mortality when temperatures reached 33 ^{o}C. Gelwick et al. (2001) observed the presence of adult bay anchovy in temperatures between 18.8 ^{o}C and 32.4 ^{o}C. With regard to salinity, Dovel (1971) collected adults in a salinity range of 2-11. Massmann (1954) reported adult bay

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anchovies in fresh water with a salinity of 0. These observations are supported by Roessler (1970) and Gelwick et al. (2000) who made collections in salinities of 15.5-45.2 and 0.3-29.4 respectively.

The required dissolved oxygen tolerance chosen for bay anchovy adults is ≥ 1.0 mg l^{-1}. Gelwick et al. (2001) observed adult bay anchovy in waters with dissolved oxygen concentrations as low as 3.67 mg l^{-1}. But, Taylor et al. (2007) reported the presence of bay anchovy in waters with dissolved oxygen as low as 1 mg l^{-1}, and therefore was used to set the required threshold.

Optimal – The optimal temperature and salinity range chosen for adult bay anchovy are 5-30 ^{o}C and 9-30, respectively. Luo and Brandt (1993) estimated bay anchovy consumption and production using a series of laboratory experiments. They reported that the temperature of optimal consumption occurs at 27 ^{o}C while the temperature of optimal respiration occurs at 30 ^{o}C. This is supported by a field study conducted by Houde and Zastrow (1991) where the observed preferred temperature range for adult bay anchovy in the Chesapeake Bay was 5-30 ^{o}C and the preferred salinity range was 9-30.

The optimal dissolved oxygen tolerance chosen for bay anchovy adults is ≥ 3.0 mg l^{-1}. Ludsin et al. (2009) reported that adult bay anchovy will avoid waters where dissolved oxygen is 3.0 mg l^{-1}.

E. Bluefish (*Pomatomus saltatrix*)

A summary of bluefish physiological tolerances can be found in Table 1.10 and quality scores in Table 1.11.

Eggs

Required – The required temperature and salinity tolerances chosen for bluefish eggs are 8-26 ^{o}C and 27-38, respectively. Although no studies were found specifically testing the physical tolerances of bluefish eggs in a laboratory setting, there are a variety of sources reporting presence and absence information. According to Shepard and Packer (2006), eggs were collecting during NEFSC MARMAP surveys within temperatures of 8-26 ^{o}C. Norcross et al. (1974) observed slightly different distributions with eggs being present in temperatures of 18-26.3 ^{o}C. These ranges are further supported by a field study conducted in Smith et al. (1994). With regard to salinity, eggs were absent from waters with salinities less than 26.6 and greater than 34.9 (Norcross et al 1974), but spawning has been recorded in salinities up to 38 within the South Atlantic (Kendall and Walford 1979).

Optimal – The optimal temperature and salinity tolerances chosen for bluefish eggs are 13-26 ^{o}C and 30-32, respectively. Norcross et al. (1974) found that 93% of eggs were collected in surface temperatures of 22 ^{o}C or greater, and that 25.6 ^{o}C was the average temperature at which maximum spawning occurred. Shepard and Packer (2006) reported that the majority of eggs collected were within the temperature range of 13-26 ^{o}C with the highest concentrations at 22 ^{o}C. An optimal temperature range of 13-26 ^{o}C was chosen because it encompasses all observations during the highest spawning events. This range is supported by the field study of Smith et al. (1994). With regard to salinity, the greatest concentrations of eggs were observed in salinities between 30-32 in the Mid Atlantic Bight (Norcross et al.1974).

No information was found regarding bluefish egg dissolved oxygen tolerance in field or laboratory studies.

Larvae

Required – The required temperature and salinity tolerances chosen for bluefish larvae are 17-26 ^{o}C and 30-38, respectively. Surveys conducted by Kendall and Walford (1979) found bluefish larvae in two distinct temperature intervals. Larvae collected in the Mid Atlantic Bight region were taken from waters between 18 ^{o}C and 26 ^{o}C. Larvae collected in the South Atlantic were found in waters between 20 ^{o}C and 26 ^{o}C. Shepard and Packer (2006) observed similar distributions, finding bluefish larvae in waters between 17° and 26°C. Kendall and Walford (1979) also collected larvae in two distinct salinity regimes, ranging from 30 to 32 in the Mid Atlantic Bight region and from 35 to 38 in the South Atlantic. Therefore, 30-38 was chosen as the required salinity range.

Optimal – The optimal temperature and salinity tolerances chosen for bluefish larvae are 21-25°C and 30-32 respectively. Figure 39 in Shepard and Packer (2006) shows that peak collections of bluefish larvae varied from month to month in water temperatures between 17 ^{o}C and 26 ^{o}C, but were most consistent at temperatures of 21-25 ^{o}C. Kendall and Walford (1979) observed the highest larval concentrations within the same range during a similar field study. Deuel et al. (1966) reared bluefish larvae successfully in a laboratory setting in 20 ^{o}C water, but did not explore the affect of different temperatures on growth. With regard to salinity, although Kendall and Walford (1979) collected bluefish in salinities from 30-38, the Mid Atlantic Bight collections better characterize bluefish found in the Chesapeake Bay region. The majority of bluefish larvae found in this region were collected at a salinity of 31 with significantly less found

below 30 and above 32. To fully capture this range, optimal salinities were chosen to be between 30 and 32.

No information was found regarding dissolved oxygen tolerance within field or laboratory studies.

Juvenile

Required – The required temperature and salinity tolerance chosen for juvenile bluefish are 10-35 ^{o}C and 5-36 respectively. Lund (1971) has shown that juvenile bluefish are able to survive temporarily in water temperatures as low as 10 ^{o}C. While conducting laboratory experiments to observe the effect of high temperatures, Olla et al. (1975) found that juvenile bluefish lose equilibrium when water temperatures reach 34.5 ^{o}C. With regard to salinity, Buckel et al. (1995) reported survival of juvenile bluefish in water with salinities as low as 5 during a set of laboratory experiments. Field observations reported in Baird (1873) and Lippson and Lippson (2006) support this lower salinity tolerance. Shepard and Packer (2006) reported juvenile captures in salinities up to 36.

The required dissolved oxygen tolerance chosen for juvenile bluefish is ≥2.0 mg l^{-1} based on presence and absence information in relation to dissolved oxygen levels. Swanson and Sinderman (1979) reported that bluefish avoided areas of low dissolved oxygen, but did not give specific numbers. Shepard and Packer (2006) observed juvenile bluefish in water with dissolved oxygen concentrations as low as 5 mg l^{-1}. Brooks and Geer (2001) and Geer (2002) collected juvenile bluefish in waters with dissolved oxygen as low as 2 and 3 mg l^{-1}.

Optimal – The optimal temperature and salinity tolerance chosen for juvenile bluefish are 15-27 $^{\circ}$C and 18-31, respectively. During a laboratory study conducted by Olla et al. (1975) and Olla and Studholme (1975), a significant increase in swimming speed was observed when water temperatures fell below 15 $^{\circ}$C and when they reached 27 $^{\circ}$C, which is indicative of avoidance behavior. This temperature range is supported by a bioenergetics growth model developed by Hartman and Brandt (1995) as well as presence and absence information from a variety of field studies (Kendall and Walford 1979, Nyman and Conover 1988, Creaser and Perkins 1994, Farhey et al. 1999, Brooks and Gear 2001). With regard to salinity, Brooks and Gear (2001) collected juveniles in salinities between 3 and 31, but densities significantly increased above 16. Through a literature review conducted by Gear (2002), it was found that over 90% of juveniles were collected in salinities greater than 18 and up to 31.

The optimal dissolved oxygen tolerance chosen for juvenile bluefish is ≥4.0 mg l^{-1}. Shepard and Packer (2006) observed peak concentrations at 6 mg l^{-1}, while Brooks and Geer (2001) and Geer (2002) observed peak concentrations at 6-8 mg l^{-1}. While looking at the spawning behavior of silversides, Middaugh et al. (1981) saw that small predatory bluefish penetrated no farther than the 4 mg l^{-1} isopleth when oxygen concentrations decreased. Therefore 4 mg l^{-1} was selected as the value for optimal oxygen tolerance because it represents the minimum concentration that juvenile bluefish are willing to tolerate.

Adults

Required – The required temperature and salinity tolerance chosen for adult bluefish are 8-35 $^{\circ}$C and 5-36 respectively. Although there is no direct evidence for the

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upper thermal tolerance of adult bluefish, Olla et al. (1975) observed a loss of equilibrium for juvenile bluefish at 34.5 $^{\circ}$C. Considering that in many fish species, adults have a broader thermal tolerance range than juveniles, 34.5 $^{\circ}$C was used as a conservative estimate of the upper thermal tolerance for adults. Lund (1971) reported that adult bluefish can survive in water with a temperature down to at least 7.5 $^{\circ}$C. This temperature range is further supported by a field study conducted in Shepard and Packer (2006). With regard to salinity, Buckel et al. (1995) conducted a laboratory experiment testing the effects of salinity on growth and consumption. It was found the adult bluefish were able to survive in salinities as low as 5. Field observations reported in Lippson and Lippson (2006) support this lower salinity tolerance. Shepard and Packer (2006) captured adult bluefish in salinities ranging from 29-36.

The required dissolved oxygen tolerance chosen for adult bluefish is ≥ 5.1 mg l^{-1}. Similar to juveniles, there is a lack of data describing the effects of dissolved oxygen concentration. Swanson and Sinderman (1979) reported low oxygen concentration avoidance behavior, but provided no specific numbers. Grothues and Able (2007) observed adults in waters with dissolved oxygen concentrations as low as 5.05 mg l^{-1} during field observations.

Optimal – The optimal temperature and salinity tolerance chosen for adult bluefish are 14-30 $^{\circ}$C and 25-35. Olla and Studholme (1971) conducted experiments to determine the upper and lower temperatures that induce stress in adult bluefish. As temperatures were reduced to 14.3 $^{\circ}$C, fish significantly increased their swim speed. This increase in swim speed was accompanied by changes in color near the pectoral fins. As temperatures were increased to 29.8 $^{\circ}$C, there was another significant increase in swim

speed, increased opening of the mouth and opercula, and body color along the lateral line darkened. This temperature range is supported by similar laboratory studies conducted by Olla et al. (1975) and Olla and Studholme (1975) as well as a variety of field observations (Lund and Maltezos 1970, Farhey et al. 1999, Grothues and Able 2007). With regard to optimal salinity, Shepard and Packer (2006) collected the highest concentrations of adult bluefish in salinities between 31 and 35 while Grothues and Able (2007) observed adult bluefish in salinities between 25 and 31. In order to capture this potential range, 25-35 was chosen as the optimal salinity range.

The optimal dissolved oxygen tolerance chosen for adult bluefish is ≥ 8.0 mg l^{-1}. Grothues and Able (2007) found that the highest concentrations of adult bluefish could be seen in waters with dissolved oxygen concentrations around 8 mg l^{-1}. These observations were qualitatively consistent with Swanson and Sinderman (1979).

F. Atlantic Sturgeon (*Acipenser oxyrinchus*)

A summary of Atlantic sturgeon physiological tolerances can be found in Table 1.12 and quality scores in Table 1.13.

Eggs

Required – The required salinity tolerance chosen for Atlantic sturgeon eggs is ≥ 0. No information was found concerning required thermal tolerance. Van Eenanaam et al. (1996) observed Atlantic sturgeon eggs above the salt front in the Hudson River, suggesting that it was due to their tolerance of low salinity. Dovel (1978) and Borodin

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(1925) support this conclusion in similar field studies. However, no evidence was found suggesting an upper salinity threshold.

Optimal – The optimal temperature tolerance chosen for Atlantic sturgeon eggs is 18-24 °C. Smith et al. (1980) found that Atlantic sturgeon eggs optimally hatch at temperatures between 18 and 20 °C. Mohler et al. (2003) reports 18-24 °C as the optimal temperature range for incubation and that incubation times decrease with increasing temperature. Smith et al. (1981) incubated eggs in 132-140 hours at temperatures of 17.5-18 °C. These ranges are supported by two similar experiments conducted by Vladykov and Greeley (1963) and Dean (1984). No information was found concerning optimal salinity tolerance.

No information was found regarding the optimal dissolved oxygen tolerance.

Larvae

Required – The required temperature and salinity range chosen for Atlantic sturgeon larvae are 15-25 °C and 0-2, respectively. Bath et al. (1981) observed Atlantic sturgeon larvae in the Hudson River in water with temperatures ranging from 15 to 24.5 °C and in salinities ranging from 0 to 2.2.

No information was found regarding the required dissolved oxygen tolerance.

Optimal – The optimal temperature range chosen for larval Atlantic sturgeon is 15-21 °C. Hardy and Litvak (2004) report the fastest growth times for Atlantic sturgeon larvae between temperatures of 18 to 21 °C during laboratory experiments. Mohler et al. (2003) suggests that lower temperatures of 15-19 °C are optimal for the growth of sturgeon larvae in a hatchery setting. Kelly and Arnold (1999) observed largest growth

rates at 19 ^{o}C under high ration conditions. No information was found regarding optimal salinity tolerance.

No information was found regarding the optimal dissolved oxygen tolerance.

Juveniles

The physiological tolerances and preferences of juvenile Atlantic sturgeon significantly change as they grow larger. In order to account for the differences between younger and older juveniles, this section was split into young-of-the-year (YOY) and yearling tolerances.

YOY Required - The required temperature, salinity, and dissolved oxygen tolerances chosen for YOY Atlantic sturgeon are 0-28 ^{o}C, 0-22, and $\geq$3.3 mg l^{-1}, respectively. Niklitschek and Secor (2005) report decreased survivorship when temperatures exceeded 28 ^{o}C for YOY sturgeon. Field observations taken by Dovel and Breggren (1983) indicate that juvenile sturgeon over-winter in deep refuges in which temperatures can drop to 0 ^{o}C. This temperature range is consistent with additional field observations (Kieffer and Kynard 1993, Bain et al. 2000). Laboratory experiments in Niklitschek and Secor (2009) show that YOY sturgeon can survive in salinities as low as 0. The upper salinity mortality threshold of 22 is set by using a mortality equation derived from laboratory experiments conducted by Niklitschek (2001). This is calculated by solving for the salinity resulting in a 50% mortality rate over a six hour period under optimal temperature and dissolved oxygen conditions. The resulting upper threshold of 22 is supported by laboratory observations in Niklitschek and Secor (2009) and a variety of field observations (Brundage and Meadows 1982, Dovel and Berggren 1983, Smith

1985b, Haley et al. 1996, Bain et al. 2000). Niklitschek (2001) reports mortality under summer temperatures at dissolved oxygen levels ≤ 3.3 mg l^{-1}.

YOY Optimal - The optimal temperature, salinity, and dissolved oxygen tolerances chosen for YOY Atlantic sturgeon are 16-24 ^{o}C, 4-19, and ≥ 5.0 mg l^{-1}, respectively. Optimal temperature and salinity tolerances are derived from laboratory experiments in Niklitschek and Secor (2009). Ranges are chosen to include conditions resulting in peak rates of potential daily production. With regard to dissolved oxygen, Niklitschek (2001) reports reductions in the growth of juvenile Atlantic sturgeons exposed to water with oxygen concentrations less than 5.0 mg l^{-1}.

Yearling Required - The required temperature, salinity, and dissolved oxygen tolerances chosen for yearling Atlantic sturgeon are 0-28 ^{o}C, 0-29, and ≥ 3.3 mg l^{-1}, respectively. Laboratory experiments in Niklitschek and Secor (2005) show increased mortality when temperatures exceeded 28 ^{o}C and Dovel and Berggren (1983) provide evidence that juveniles survived in temperatures as low as 0 ^{o}C. Niklitschek and Secor (2005) report survival of yearling sturgeon in salinities of 0-29 and an increase in mortality when salinity exceeds this range. These results are consistent with field observation made in Secor et al. (2000). A dissolved oxygen tolerance of ≥ 3.3 mg l^{-1} is chosen based on the findings of Secor and Gunderson (1998) and Niklitschek and Secor (2009).

Yearling Optimal - The optimal temperature, salinity, and dissolved oxygen tolerances chosen for yearling Atlantic sturgeon are 16-24 ^{o}C, 19-26, and ≥ 5.0 mg l^{-1}, respectively. Temperature and salinity ranges for yearling sturgeon are chosen from Niklitschek and Secor (2009) to include peak rates of potential daily growth. Secor and

Gunderson (1998) report reductions in the growth of juveniles exposed to oxygen concentrations less than 4.3-4.7 mg l^{-1} at 22 $^{\circ}$C and ≤5.0 mg l^{-1} at 26 $^{\circ}$C. Because summer temperatures in the Chesapeake Bay commonly exceed 26 $^{\circ}$C, the higher dissolved oxygen threshold is selected. This threshold is also used by the US Environmental Protection Agency as being protective for sturgeon species in the Chesapeake Bay (Batiuk et al. 2009)

Adults

Required – The required temperature and salinity range chosen for adult Atlantic sturgeon is 9-28 $^{\circ}$C and 0-29, respectively. Brundage and Meadows (1982) made summertime observations of adult Atlantic sturgeon in waters with a temperature range of 8.6-28.1 $^{\circ}$C through the Delaware River estuary. They also observed adult sturgeons within the salinity range of 0-29. Kieffer and Kynard (1993) found adult Atlantic sturgeon in salinities of 0-27.5.

No information was found regarding the optimal dissolved oxygen tolerance.

G. Soft Shell Clam (*Mya arenaria*)

A summary of soft shell clam physiological tolerances can be found in Table 1.14 and quality scores in Table 1.15.

Juvenile

Required - The required temperature and salinity tolerances chosen for soft shell clam juveniles are -9-33 $^{\circ}$C and 3-35, respectively. Juvenile soft shell clams can survive a wide range of temperatures (Harrigan 1956, Kennedy and Mihursky 1971, Loi and

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Wilson 1979, Borget 1983). Borget (1983) determined -8.8 ^{o}C to be the lower median

lethal temperature for small juvenile soft shell clams (<1 cm) in a laboratory setting. This

lower temperature tolerance is supported through a field study conducted by Loi and

Wilson (1979) in the Chesapeake Bay during which soft shell clams were observed in

waters with temperatures as low as -5 ^{o}C. Juvenile soft shell clams are known to have a

higher upper temperature tolerance than adults (Kennedy and Mihursky 1971). In a

laboratory experiment conducted by Kennedy and Muhursky (1971), it was found that the

LC50 temperatures for juvenile soft shell clams (14-23 mm) acclimated to temperatures

of 1-30°C were 30.9-34.4 ^{o}C respectively. A midpoint of 32.65 ^{o}C was calculated for this

LC50 range so that a single upper thermal tolerance could be incorporated into the model.

Unlike the upper temperature tolerance, juvenile soft shell clams are less tolerate

to salinity than adults (Matthiessen 1960). Matthiesen (1960) found that soft shell clam

juveniles can survive exposure to water with salinities as low as 1, but mortality occurred

after 24 hours. During a series of laboratory experiments, Chanley (1958) found that soft

shell clams can survive salinities as low as 2.5 indefinitely with appropriate acclimation

periods. Experiments were conducted in salinities of 2.5-28 in which no morality

occurred. Several field studies have shown that soft shell clams can survive in salinities

up to 35 (Castagna and Chanley 1973, Lucy 1976, Brousseau 1978). No laboratory

studies were found concerning the upper salinity tolerance of soft shell clams.

The dissolved oxygen tolerance chosen for juvenile soft shell clams is ≥0.2 mg l^{-1}.

Theede et al. (1969) shows that the LC50 for juvenile soft shell clams in water with

dissolved oxygen concentrations of 0.15 mg l^{-1} was 504 hours or 21 days.

Optimal – The optimal temperature and salinity tolerances chosen for juvenile soft shell clams are 16-20 $^{\circ}$C and 15-32, respectively. In a laboratory study conducted by Harrigan (1956), it was observed that optimal pumping rates occur within the temperature range of 16-20 $^{\circ}$C. This range is supported by laboratory studies conducted by Kennedy and Mihursky (1972) and Anderson (1978) focusing on soft shell clam respiration and metabolic rate, respectively.

With regard to salinity, Matthiessen (1960) observed a significant decrease in pumping rate when salinities dropped below 15. It was also found that growth was higher with increasing salinities up to 32. Therefore 15 was chosen as the lower optimal salinity tolerance limit and 32 as the upper. This range is supported by a laboratory study conducted in Stewart and Bamford (1976).

The optimal dissolved oxygen tolerance chosen for soft shell clam juveniles is ≥ 1.5 mg l^{-1}. During a laboratory study conducted by Taylor and Eggleston (2000), soft shell clams showed a significant decrease in burial depth and a significant increase in siphon extension when dissolved oxygen dropped below 1.5 mg l^{-1}. These behaviors are response mechanisms to environmental variables and can be associated with physiological stress.

H. Winter Flounder (*Pseudopleuronectes americanus*)

A summary of winter flounder physiological tolerances can be found in Table 1.16 and quality scores in Table 1.17.

Juvenile

Required - The required temperature and salinity tolerances chosen for juvenile winter flounder are 0-29 $^{\circ}$C and 1-34, respectively. During a laboratory study conducted by Pearcy (1962), the minimum lethal temperature for juvenile winter flounder was between -1.5 $^{\circ}$C and 1 $^{\circ}$C. In order to determine a single value for incorporation into the habitat model, the midpoint of this range, -0.25 $^{\circ}$C, was chosen then rounded to 0. Through a similar set of laboratory experiments, Hoff and Westman (1966) reported an upper lethal temperature of 29 $^{\circ}$C. This required temperature range is supported by a laboratory study conducted by McCracken (1963) along with a variety of field observations (Pearcy 1962, Armstrong 1997, Lazzari 2008). With regard to salinity, Peacry (1962) observed a minimum salinity tolerance of 1 for juvenile winter flounder during a series of experiments. This minimum value is supported in field studies conducted by Armstrong (1997) and Howell et al. (1999). During a study to quantify the growth rate of juvenile winter flounder in field conditions, Meng et al. (2000) reported survival in salinities as high as 34. This upper limit is supported by additional field observations conducted by Lazzari (2008).

The required dissolved oxygen tolerance chosen for juvenile winter flounder is ≥ 1.5 mg l^{-1}. During a laboratory study, Ziskowski (1991) found that mortality for juvenile winter flounder occurred when dissolved oxygen concentrations fell between 1.1 and 1.5 mg l^{-1}. Bejda (1992) conducted a similar laboratory study where it was found that mortality occurred when dissolved oxygen reached 1.4 mg l^{-1}. For this literature review, the highest dissolved oxygen concentration at which mortality was observed will be used as the required tolerance threshold.

Optimal – The optimal temperature and salinity tolerances chosen for juvenile winter flounder are 8-21 $^{\circ}$C and 7-24, respectively. During a laboratory study testing the influence of oxygen and temperature on growth rates, it was found that growth significantly decreases when temperatures rose from 20 $^{\circ}$C to 25 $^{\circ}$C (Stierhoff et al. 2006). Manderson et al. (2002) came to similar conclusions during their growth experiments, showing that growth is reduced at temperatures above 21 $^{\circ}$C. Therefore the upper limit was chosen to be 21 $^{\circ}$C, which is also supported by presence and absence observations in several field studies (Olla et al. 1969, Armstrong 1997, Stoner et al. 2001). Casterlin and Reynolds (1982) conducted a habitat quality study in which juvenile winter flounder avoided water with temperatures below 8 $^{\circ}$C. This lower temperature is supported by growth data obtained from field experiments in Meng et al. (2000). With regard to salinity, Armstrong (1997) observed the majority of juvenile winter flounder in water with salinities between 6.5 and 23.9. However, laboratory studies conducted by Frame (1973) and Manderson et al. (2002) show that juvenile winter flounder experience higher respiration rates in salinities greater than 20 and that growth rates begin to decrease in salinities above 24. These laboratory studies do not explore the influence of low salinity on growth. The salinity range of 6.5-24 is supported by a field study conducted by Stoner et al. (2004).

The optimal dissolved oxygen tolerance chosen for juvenile winter flounder is ≥ 7.0 mg l^{-1}. Bejda et al. (1992) found that the growth rates of juvenile winter flounder in water with dissolved oxygen concentrations of 6.7 mg l^{-1} doubled when compared to water with concentrations of 2.5 mg l^{-1}. Stierhoff et al. (2006) conducted a similar study incorporating more oxygen treatments. It was observed that juvenile winter flounder

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growth rates were reduced when dissolved oxygen concentrations dropped below 7.0 mg l^{-1}.

I. Menhaden (*Brevoortia tyrannus*)

A summary of menhaden physiological tolerances can be found in Table 1.18 and quality scores in Table 1.19.

Juvenile

Required - The required temperature and salinity tolerances chosen for juvenile Atlantic menhaden are 5-33 ^{o}C and 18-35, respectively. During a laboratory study conducted in Burton et al. (1979), mortality was observed when temperatures dropped to 5 ^{o}C. In a similar study focusing on the upper thermal limit for juvenile Atlantic menhaden, Lewis and Hettler (1968) reported mortality when temperatures rose above 33 ^{o}C. This limit is also supported in a similar laboratory study conducted by Terpin et al. (1999) along with a field study described in Gibson and Young (1973). With regard to salinity, Gunter (1961) found Atlantic menhaden juveniles in water with salinities as low as 0.18. Engel et al. (1987) tested the effect of abrupt transfers of juvenile Atlantic menhaden between waters with salinities of 3.5 and 35. It was found that juveniles could survive immediate transfers in both directions. This upper salinity tolerance is supported by a similar laboratory study conducted in Hettler (1976). Gunter (1961) also reported juvenile Atlantic menhaden in water with salinities as high as 60. However, these observations were made for Gulf of Mexico populations exposed to hypersaline conditions, which do not occur in the Chesapeake Bay.

The required dissolved oxygen tolerance chosen for juvenile Atlantic menhaden is ≥ 1.1 mg l^{-1}. In a laboratory study, Burton et al. (1980) derived toxicity curves which they used to estimate the lethal threshold concentrations of oxygen for juvenile Atlantic menhaden to be 1.1 mg l^{-1}.

Optimal – The optimal temperature and salinity tolerances chosen for juvenile Atlantic menhaden are 14-30 ^{o}C and 5-10, respectively. Terpin et al. (1999) tested the preferred temperature range for juvenile Atlantic menhaden through a series of laboratory experiments. Juveniles that were acclimated over a range of temperatures preferred to stay in water with temperatures of 14-29 ^{o}C. During a modeling study to determine the potential growth of juvenile Atlantic menhaden in the Patuxent River, Brandt and Mason (2003) found that juveniles show high rates of consumption and growth over the temperature range of 21-30 ^{o}C. In order to synthesize these two papers, a range of 14-30 ^{o}C was chosen for optimal temperature. With regard to salinity, Hettler (1976) conducted laboratory studies to determine the influence of salinity on routine metabolic rate and growth. It was found the juvenile Atlantic menhaden have higher rates of consumption and growth in lower salinities, 5-10, when compared to higher salinities, >26. This range is supported by field observations of abundance (Friedland et al. 1996, Gunter 1961, Massman et al. 1954).

The optimal dissolved oxygen tolerance chosen for juvenile Atlantic menhaden is ≥ 3.0 mg l^{-1}. During a bioenergetic growth modeling study conducted by Brandt and Mason (2003), it was shown that consumption and growth are significantly reduced when dissolved oxygen concentrations drop below 3.0 mg l^{-1}.

<u>J. Atlantic Croaker (*Micropogonias undulates*)</u>

A summary of Atlantic croaker physiological tolerances can be found in Table 1.20 and quality scores in Table 1.21.

Juvenile

Required - The required temperature and salinity tolerances chosen for juvenile Atlantic croaker are 1-36 ^{o}C and 0-36, respectively. Studies have found that juvenile Atlantic croaker have a lower temperature tolerance than adult croaker (Schwartz 1964, Parker 1971). During a laboratory study conducted by Shwartz (1964), it was observed that mortality occurred for juveniles when water temperatures fell to 0.6 ^{o}C while mortality occurred for adults at 3.3 ^{o}C. In a similar laboratory study, Lankford and Targett (2001) came to the same conclusion. Although no laboratory studies determining an upper lethal temperature were found, field studies have shown that juvenile Atlantic croaker can be found in waters up to 35.5 ^{o}C. This temperature tolerance range is supported by several other field observations (Haven 1957, Bearden 1964, Parker 1971, Knudesen and Herke 1978, Miller et al. 2003). With regard to salinity, juvenile Atlantic croaker have been found in salinities ranging from completely fresh to full strength sea water with salinities as high as 35.5 (Haven 1957, Bearden 1964, Milagrese et al. 1982). They have also been found in super saline conditions of 70 (Simmons 1957), however these conditions were observed in the Gulf of Mexico and do not occur within the Chesapeake Bay.

There were no studies found determining the lethal dissolved oxygen threshold for juvenile Atlantic croaker.

Optimal – The optimal temperature and salinity tolerance chosen for juvenile Atlantic croaker are 13-28 °C and 5-20, respectively. According to a field study conducted in Parker (1971), Atlantic croaker can grow over a wide range of temperatures from 12.6 °C to 28.4 °C. An additional field study conducted by Milagrese et al. (1982) support this growth range with respect to temperature. With regard to salinity, Abud (1991) conducted a laboratory study focusing on the influence of salinity on routine metabolism. Although lower salinities were not tested, it was found that salinities above 20 result in a significant increase in oxygen consumption. Peterson (1999) reports highest growth at salinities of 5 during similar laboratory experiments. Therefore an optimal salinity range of 5-20 was chosen. This optimal salinity range is supported by a variety of additional laboratory and field studies that show growth and high concentrations in this range (Parker 1971, Milagrese et al. 1982, Moser and Gerry 1989, Miller et al. 2003).

The optimal dissolved oxygen tolerance of juvenile Atlantic croaker is ≥1.0 mg l^{-1}. Bell and Eggleston (2005) sampled near-shore habitats frequently enough to capture fish occupying hypoxic areas during short duration hypoxic upwelling events. They observed fish in water with dissolved oxygen concentrations as low as 1.0 mg l^{-1}. Several field studies have reported similar avoidance behavior for juvenile Atlantic croaker in the presence of dissolved oxygen concentrations less than 1 mg l^{-1} (Eby and Crowder 2000, Craig and Crowder 2002, Eby et al. 2005).

K. Weakfish (*Cynoscion regalis*)

A summary of weakfish physiological tolerances can be found in Table 1.22 and quality scores in Table 1.23.

Juvenile

Required - The required temperature and salinity tolerances chosen for juvenile weakfish are 3-31 ^{o}C and 5-32, respectively. During a laboratory study conducted by Shwartz (1964), mortality of juvenile weakfish was observed when water temperatures dropped to 3.3 ^{o}C. This lower temperature tolerance is supported by field observations made by Hildebrand and Cable (1934). No laboratory studies determining an upper lethal temperature tolerance were found, but field studies have reported the presence of juvenile weakfish in water with temperatures as high as 31 ^{o}C (Massmann et al. 1958, Richards and Castagna 1970, Thomas 1971). With regard to salinity, Lankford and Targett (1994) reported that mortality occurred after the transfer of juvenile weakfish to water with a salinity of 5. During a field study conducted by Richards and Castagna (1970), the presence of juvenile weakfish was reported in water with salinities as high as 31.7.

The required dissolved oxygen tolerance chosen for juvenile weakfish is ≥0.4 mg l^{-1}. According to a laboratory study conducted by Brady et al. (2009), mortality of juvenile weakfish occurred when exposed to water with dissolved oxygen concentrations of 0.4 mg l^{-1}.

Optimal – The optimal temperature and salinity tolerances chosen for juvenile weakfish are 10-29 ^{o}C and 12-19, respectively. Shwartz (1964) found that juvenile weakfish swimming speed drastically slowed when temperatures reached 10 ^{o}C. During another laboratory experiment conducted by Lankford and Targett (1994), an optimum growth temperature of 29 ^{o}C was determined. This optimal temperature tolerance range is supported by additional laboratory studies (Terpin et al. 1977, Wilk 1979) as well as a field study conducted by Massmann et al. (1958). Lankford and Targett (1994) also

observed that maximum growth conditions for juvenile weakfish occurred within the salinity range of 12-19 during the same set of experiments. High abundances of juvenile weakfish were found within this salinity range in a field study conducted by Massmann et al. (1958).

The optimal dissolved oxygen tolerance chosen for juvenile weakfish is ≥ 2.0 mg l^{-1}. Stierhoff et al. (2009) reports that juvenile weakfish have a high tolerance to hypoxic conditions and do not experience significant reductions in growth until dissolved oxygen concentrations drop to 2.0 mg l^{-1} during a series of laboratory experiments. Brady et al. (2009) also showed that juvenile weakfish will avoid water with dissolved oxygen concentrations lower than 2.0 mg l^{-1}, but have no preference when concentrations are greater than 2.0 mg l^{-1} in laboratory conditions. This threshold is supported by field observations made by Ebby and Crowder (2002) and Tyler and Targett (2007) which indicate that weakfish are not found in waters <2.1 and <2.0 mg l^{-1}, respectively.

L. White Perch (*Morone Americana*)

A summary of white perch physiological tolerances can be found in Table 1.24 and quality scores in Table 1.25.

Juvenile

Required - The required temperature and salinity tolerances chosen for juvenile white perch are 3-34 ^{o}C and 0-22, respectively. Laboratory experiments conducted by Johnson and Evans (1990) observed juvenile white perch mortality when water temperatures were 2.5 ^{o}C. This lower thermal limit is supported by field studies synthesized in Stanley (1983). In a laboratory study by Kellogg and Gift (1983),

mortality increased to over 50% when temperatures reached 34.7 ^{o}C. This upper lethal

thermal limit is supported by similar lab experiments conducted by Hall et al. (1978) and

Meldrim and Gift (1971). With regard to salinity, although it has been observed that

white perch juvenile populations did not inhabit waters with salinity greater than 16

(Stanley 1983, Kraus and Secor 2004, Kraus and Secor 2005, Hanks and Secor 2011)

individuals have been collected in salinities up to 21.6 (Nemerson and Able 2004).

Several field studies have found white perch juvenile populations in completely fresh

water (Stanley 1983, Kraus and Secor 2004, Nemerson and Able 2004, Kraus and Secor

2005).

The required dissolved oxygen tolerance chosen for juvenile white perch is ≥0.8

mg l^{-1}. Dorfman and Westman (1970) observed a significant increase in mortality when

exposed to dissolved oxygen concentrations of 0.5-1.0 mg l^{-1}. In order to determine a

single value for incorporation into the habitat model, the midpoint of this range, 0.75, was

chosen.

Optimal – The optimal temperature and salinity tolerances chosen for juvenile

white perch are 12-33 ^{o}C and 0-16, respectively. Laboratory studies conducted by Hanks

and Secor (2011) found that the lower limit of positive growth for juvenile white perch is

12 ^{o}C. Kellogg and Gift (1983) determined that juvenile white perch prefer to remain

within the temperature range of 24-33 ^{o}C. This higher optimal thermal limit is supported

by similar laboratory studies on preference (Terpin et al. 1977, Hall et al. 1978) as well as

a field study conducted in Stanley (1983). With regard to salinity, laboratory experiments

conducted by Hanks and Secor (2011) found that energy rate and consumption began to

decline when salinities reached 16, with little change between 0 and 16. This range is

supported in field abundance observations reported in Stanley (1983) and Kraus and Secor (2004, 2005).

The optimal dissolved oxygen tolerance chosen for juvenile white perch is ≥2.9 mg l^{-1}. During the laboratory study, Hanks and Secor (2011) found that a threshold effect level likely occurs between 20-40% oxygen saturation, with markedly decreasing growth and consumption rates below this range. In order to determine a single value for incorporation into the habitat model, the midpoint of this range, 30%, was chosen. This value was then converted into mg l^{-1} using standard temperature and pressure. The resulting value was 2.9 mg l^{-1}. Field observations made by AuClair (1954) and Stanley (1983) also show that white perch were not found in waters with oxygen concentrations below 2.8 and 3.0 mg l^{-1}, respectively.

Overall Quality Matrix

Information for each species varied significantly, resulting in a wide range of quality values for each species and lifestage (Fig 1.1, Fig 1.2, Fig 1.3). Out of the individual physiological tolerances, the most reliable information was for temperature tolerances followed by salinity (Fig 1.1, Fig 1.2). Information on dissolved oxygen tolerances was not available for many of the species and lifestages. In general, there were more instances of missing data with respect to optimal habitat tolerances than for required habitat tolerances (Fig 1.2). However when data was available, quality scores for optimal habitat tolerances tended to be higher compared to required habitat.

Overall, the majority of species had enough information available to exceed the quality threshold of 11, and hence was deemed suitable for inclusion into a habitat

volume model (Fig 1.3). Blue crab, eastern oyster, Atlantic sturgeon, and bluefish were species with the most instances of missing information, while eggs and larvae were the lifestages with the most missing information for each species. White perch, weakfish, menhaden, white flounder, soft shell clam, striped bass, eastern oyster, and blue crab were the species with the highest overall quality scores (Fig 1.3). The species and lifestages that did not have the necessary quality scores for incorporation into the model are listed in Table 1.26.

Discussion

This systematic literature review, along with the quality matrices, makes it possible to evaluate the current status of research with respect to the physiological tolerances of a suite of Chesapeake Bay living resources. The methods used in this study highlight areas in which there are a variety of high quality studies available and areas where there is a significant lack of information. Information incorporated into this review expands upon previous reviews (Lippson et al. 1980, Funderburk et al. 1991, Lippson and Lippson 2006) through the inclusion of more recent research. This review also places a higher focus upon physiological tolerances to environmental conditions in order to provide the information necessary for habitat modeling. Due to the importance of this data in not only habitat modeling, but management and conservation efforts in general, this literature review can be used to highlight potential gaps in information and to direct future research efforts.

Of all the species covered in this review, most showed an increase in physiological tolerances to environmental conditions as they develop. A few, such as

Atlantic sturgeon, also changed their habitat preferences as they grow. Many species appear to have similar mortality responses to dissolved oxygen, with required thresholds on average between 1 and 3 mg l^{-1}, excluding Atlantic sturgeon and bluefish. With respect to optimal dissolved oxygen tolerances, most species were within the range of 2-5 mg l^{-1}, with the exception of winter flounder, which had an optimal tolerance of 7 mg l^{-1}. The adult and juvenile stages of all species had a wide range of required temperature tolerance, as is expected for species subjected to strong seasonal variation in temperature. Optimal temperature tolerances were much more constrained and were on average between 15-30 °C. Juvenile striped bass had a notably narrow preferred range. Required salinity tolerances also generally covered a broad range, excluding species with larvae that develop in higher salinities, such as blue crab, eastern oyster, and bluefish. Preferred salinities varied between species as well. Blue crab, oysters, bluefish, juvenile and adult Atlantic sturgeon, and juvenile soft shell clam had high optimal salinity ranges, while all other species preferred fresh to brackish water.

If temperatures continue to rise due to future climate change as expected, many of these species should be able to survive a few degrees increase at the expense of reduced growth and metabolism. Because they are the most temperature sensitive, Atlantic sturgeon, striped bass, winter flounder, and the eggs and larvae of bluefish, may show increased mortality under global warming as seen in a variety of modeling studies (Stierhoff et al. 2006, Constantini et al. 2008, Niklitschek and Secor 2009). Further stress resulting from more frequent and severe hypoxia will most likely affect all species, excluding blue crab, eastern oyster, and juvenile soft shell clams due to their high dissolved oxygen tolerances. Hypoxia related changes in this respect have already been

documented (Townsend and Edwards 2003, Breitburg et al. 2003, 2009). Atlantic sturgeon and bluefish would be affected the most due to their markedly oxyphilic nature as has already been seen (Secor and Gunderson 1998).

Although the influence of future climate change and nutrient loading will affect the survival and growth of all these species, the magnitude of that influence will differ, even between lifestages of the same species (Drinkwater 2005). Atlantic sturgeon could suffer severe population decreases in the Chesapeake Bay due to temperature and dissolved oxygen constraints (Niklitschek and Secor 2005) while blue crab may display a higher degree of resilience based on their wide tolerance ranges. A major difficulty in making future climate-related predictions deals with understanding how important required and optimal habitats are to population growth and survival. Although the required tolerances of a species may allow it to survive as temperature increases, the reduction in optimal habitat may play a more dominant role in actual population growth and distribution. Furthermore, physiological limitations for specific lifestages of a given species may have a significantly higher influence on overall population structure. Using the habitat volume model, the physiological thresholds derived from this review will make it possible to quantify changes in optimal and required habitat as well as identify major lifestage-dependent sensitivities.

Blue crab, eastern oyster, Atlantic sturgeon, bluefish, and Atlantic croaker all have one or more lifestages that will not be used in the habitat volume model because they do not meet the quality point threshold. Past studies of these species focused on other aspects of their ecology, but very few set out to identify physiological tolerances. With the advancement of modeling techniques and bioenergetics, these measures of

required habitat conditions play a more important role in management decisions than they have in the past (Turner et al. 1995, Akcakaya, H.R. 2000, Niklitschek and Secor 2005). The use of these methodologies in future conservation necessitates the need for further research on these particular species with regard to physiological tolerances.

Although there are a few apparent contradictions to common knowledge, the strictly evidence-based methodology followed in this review was chosen to maintain a rigorous procedure and to reduce human induced error. By defining physiological parameters based upon quantitative data in the literature, only available evidence was used to define ranges and thresholds rather than assumptions, which can be vulnerable to subjective bias. However, this perspective works best for those species with an abundance of quantitative information. In cases where laboratory information does not exist, and only one or two available presence and absence studies provide evidence for a physiological tolerance, there is a good chance that those studies do not reflect the entire range that a particular species may be found. For example, bluefish adults most likely have an optimal dissolved oxygen threshold somewhere below 8 mg l^{-1}, but because that was the only quantitative piece of evidence to support an optimal threshold, it was used to set the physiological parameter. This preserves the systematic nature of the literature review, and clearly highlights areas in need of further research.

The fact that this review had a Chesapeake Bay centric focus also has important implications with respect to the physiological parameters used. Quantitative data obtained from Chesapeake Bay studies were preferentially used when compared to outside locations or populations. Due to the domain used in the habitat volume model, information pertaining to studies located outside the mouth of the bay was given less

weight. As a result, some physiological tolerance parameters, specifically salinity, may not encompass the maximum range in which a species is known to exist, but rather reflect known species distributions relevant to the Chesapeake Bay

The lack of information necessary for accurate habitat modeling is a widespread problem (Hirzel et al. 2001, Campomizzi et al. 2008, Barry and Elith 2006), but the use of a quality point threshold addresses this problem by creating a standard which supports informed use of the information. The purpose of this project is to use the habitat volume model to make informed decisions about habitat conditions for ecologically and commercially important species, and without accurate physiological tolerances, this cannot be accomplished. With the quality point minimum threshold, a single presence or absence study on a non-Chesapeake Bay population of a particular species and lifestage is not enough to produce reliable habitat volume estimates. The spatial and temporal variability inherent in field conditions makes it difficult for presence and absence studies to capture the complete picture and this is especially the case if conditions differ from those within the Bay. There are, however, some very thorough field studies that have taken place in the Chesapeake Bay and such studies represent the minimum requirements for incorporation of physiological tolerances into the model.

Although the quality point cutoff sets the bar for the use of specific physiological tolerances to estimate habitat volume, there is certainly room for progress. Overall habitat volumes calculated in the model can vary greatly with only a few degrees difference in temperature or a small change in salinity (see Chapter 3). Therefore, confidence placed in the physiological tolerances used to parameterize the model has a large influence on the reliability of the habitat model estimates. All the lifestages of bay anchovy, for example,

meet the minimum requirements for inclusion, but the quality scores are noticeably lower

than some of the more well studied species, such as striped bass. In addition, there are

dozens of other important species within the Chesapeake Bay for which almost no work

has been done, much less physiological tolerance research. With climate change and

nutrient loading significantly changing the structure and function of the Chesapeake Bay,

it is important to understand how these species will be affected. Advanced modeling

techniques provide the tools to do so, as long as the information to drive them is

available. Further research on physiological tolerances is needed for several important

Chesapeake Bay species (Table 1.26).

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Table 1.1: Quality measures and respective point values which are used to assign measures of accuracy and consistency to publications in this literature review.

Measure of Quality	Points
Laboratory Study	15-20
Modeling Study	10-15
Presence and Absence Study	5-10
Chesapeake Bay Populations	3
Multivariate Physiological Equations	5
Peer Reviewed Paper	1
Supporting Publications	1

Table 1.2: Blue crab (*Callinectes sapidus*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for eggs, larvae, juveniles, and adults. Cases in which no studies were found are denoted by N.D. T and S represent temperature and dissolved oxygen respectively. Derivation of the equations can be found in the Blue Crab Juvenile and Adult section.

	Temperature (^{o}C)		Salinity		DO (mg l^{-1})		References
	Req	Opt	Req	Opt	Req	Opt	
Eggs	17-30	19-29	9-33	23-28	≥2.8	N.D.	Sandoz and Rogers (1944), deFur et al. (1990), Aguilar et al. (2005)
Larvae	16-30	20-29	20-35	21-30	≥0.9	N.D.	Sandoz and Rogers (1944), Costlow and Bookhout (1959), Tankersley and Wieber (2000), Ogburn and Forward (2009),
Juvenile	Lower Limit T = 0.0484S + 5.1548 Upper Limit T = 0.0735S + 36.5	15-30	3-56	10-30	≥1.2	≥2.8	Tagatz (1969), Cadman and Weinstein (1988), deFur et al. (1990), Guerin and Stickle (1992), Das and Stickle (1993), Tankersley and Wieber (2000)
Adult	Lower Limit T = 0.0484S + 5.1548 Upper Limit T = 0.0735S + 36.5	15-30	3-56	10-30	≥0.0	≥2.8	Tagatz (1969), Cadman and Weinstein (1988), deFur et al. (1990), Guerin and Stickle (1992), Das and Stickle (1993), Tankersley and Wieber (2000)

Table 1.3: Blue crab (*Callinectes sapidus*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for eggs, larvae, juveniles, and adults. Cases in which no studies were found are denoted by N.D.

Lifestatge	Habitat	Temp	Sal	DO	Total
Egg	Rep	25	26	2	53
	Opt	25	25	N.A.	50
Larvae	Req	19.5	19.5	20	59
	Opt	25	22	N.A.	47
Juvenile	Req	26	22	20	68
	Opt	25	19.5	25	69.5
Adult	Req	26	22	27	75
	Opt	25	19.5	25	69.5

Table 1.4: Eastern oyster (*Crassostrea virginica*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for eggs, larvae, juveniles, and adults. Cases in which no studies were found are denoted by N.D.

	Temperature (^{o}C)		Salinity		DO (mg l^{-1})		References
	Req	Opt	Req	Opt	Req	Opt	
Eggs	15-33	23-30	8-39	10-30	N.D.	N.D.	Amemiya (1929), Clark (1935), Davis (1958), Davis and Calabrese (1964), Loosanoff (1965), Roosenburg et al. (1970), Hidu et al. (1974), MacInnes and Calabrese (1979), Cake et al. (1983), Wright et al. (1983)
Larvae	15-34	25-33	8-39	13-33	≥0.0	≥1.5	Amemiya (1926), Davis (1958), Davis and Calabrese (1964), Hidu et al. 1974, Lough (1975), MacInnes and Calabrese (1979), Wright et al. (1983), Widdows et al. (1989), Baker and Mann (1992) and (1994)
Adult	-2-41	20-32	5-44	10-30	0 for 3+days	N.D.	Federighi (1929), Collier (1951), Loosanoff (1953), Butler (1954), Fingerman and Fairbanks (1957), Sparks et al. (1957), Chanley (1958), Loosanoff (1958), Wells (1961), Galtsoff (1964), Loosanoff (1965), Ingle et al. (1971), Stanley et al (1986), Shumway (1996)

Table 1.5: Eastern oyster (*Crassostrea virginica*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for eggs, larvae, juveniles, and adults. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Egg	Rep	26.5	24.5	N.D.	51
	Opt	21.5	25	N.D.	46.5
Larvae	Req	23.5	24	26	73.5
	Opt	23.5	23	24	70.5
Juvenile	Req	26	20	22	68
	Opt	24.5	25.5	N.D.	50
Adult	Req	26	20	22	68
	Opt	24.5	25.5	N.D.	50

Table 1.6: Striped bass (*Morone saxatilis*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for eggs, larvae, juveniles, and adults. Cases in which no studies were found are denoted by N.D.

	Temperature (°C)		Salinity		DO (mg l⁻¹)		References
	Req	Opt	Req	Opt	Req	Opt	
Eggs	12-27	14-22	0-18	1-10	≥3.0	≥5.0	O'Malley and Boone (1972), Geiger and Bonn et al. (1976), Harrell and Bayless (1981), Morgan and Rasin (1981), Parker (1985), Winger and Lasier (1994)
Larvae	12-24	16-21	0-25	1-11	≥4.0	≥5.0	Albrecht et al. (1964), Turner and Farley (1971), Bayless (1972), Morgan and Rasin (1973), Germann and Reeves (1974), Rogers et al (1977), Morgan and Rasin (1981),
Juvenile	2-35	24-27	0-33	1-15	≥1.4	≥4.0	Tagatz (1961), Chittenden (1972), Cox and Coutant (1981), Coutant et al. (1984), Secor et al. (2000), Cook et al. (2006), Brandt et al. (2009)
Adult	0-31	14-25	0-35	0-35	≥2.0	≥3.0	Tagatz (1961), Talbot (1966), Chittenden (1971a), Coutant and Benson 1990, Rothschild (1990), Kelly and Kohler (1999), Brandt et al. (2009)

Table 1.7: Striped bass (*Morone saxatilis*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for eggs, larvae, juveniles, and adults. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Egg	Rep	28	22	22	72
	Opt	26	23	19	68
Larvae	Req	33	20	22	75
	Opt	25	22	21	68
Juvenile	Req	20	22	22	64
	Opt	24	27	27	78
Adult	Req	19	22	19	60
	Opt	25	15	21	61

Table 1.8: Bay anchovy (*Anchoa mitchilli*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for eggs, larvae, juveniles, and adults. Cases in which no studies were found are denoted by N.D.

	Temperature (^{o}C)		Salinity		DO (mg l^{-1})		References
	Req	Opt	Req	Opt	Req	Opt	
Eggs	9-31	20-27	1-32	4-26	≥2.8	≥3.0	Dovel (1971), Olney (1983), Chesney and Houde (1989), Rilling and Houde 1999
Larvae	3-32	23-32	0-32	3-26	≥1.6	≥2.0	Dovel (1971), Houde (1974), Olney (1983), Chesney and Houde (1989)
Juvenile	0-32	14-27	0-38	3-30	≥1.0	≥3.0	Dovel (1971), Terpin et al. (1976), Houde and Zastrow (1991), Kilby (1995), Taylor et al. (2007), Ludsin et al. (2009)
Adult	2-34	5-30	0-45	9-30	≥1.0	≥3.0	Massmann (1954), Roessler (1970), Dovel (1981), Houde and Zastrow (1991), Luo and Brandt (1993), Taylor et al. (2007), Ludsin et al. (2009)

Table 1.9: Bay anchovy (*Anchoa mitchilli*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for eggs, larvae, juveniles, and adults. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Egg	Rep	17	19	24	60
	Opt	17	18.5	24	59.5
Larvae	Req	22.5	17	25	64.5
	Opt	20	15	15	50
Juvenile	Req	21	14.5	11	46.5
	Opt	26	16	15	57
Adult	Req	13.5	15.5	12	41
	Opt	17	14	15	46

Table 1.10: Bluefish (*Pomatomus saltatrix*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for eggs, larvae, juveniles, and adults. Cases in which no studies were found are denoted by N.D.

	Temperature (C)		Salinity (ppt)		DO (mg/L)		References
	Req	Opt	Req	Opt	Opt	Req	
Egg	8-26	13-26	27-38	30-32	N.D.	N.D.	Norcross et al (1974), Kendall and Walford (1979), Smith et al. (1994), Shepard and Packer (2006)
Larvae	17-26	21-25	30-38	30-32	N.D.	N.D.	Kendall and Walford (1979), Shepard and Packer (2006)
Juvenile	10-35	15-27	5-36	18-31	≥ 4.0	≥ 2.0	Lund (1971), Olla et al. (1975), Middaugh et al. (1981), Buckel et al. (1995), Gear (2002), Shepard and Packer (2006)
Adult	8-35	14-30	5-36	25-35	≥ 8.0	≥ 5.1	Lund (1971), Olla and Studholme (1971), Olla et al. (1975), Middaugh et al. (1981), Buckel et al. (1995), Gear (2002), Shepard and Packer (2006), Grothues and Able (2007)

Table 1.11: Bluefish (*Pomatomus saltatrix*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for eggs, larvae, juveniles, and adults. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Egg	Rep	15.5	15	N.D.	30.5
	Opt	16	14	N.D.	30
Larvae	Req	14.5	14	N.D.	28.5
	Opt	16	14	N.D.	30
Juvenile	Req	18.5	18	14	50.5
	Opt	29	14	14	57
Adult	Req	18	18	12	48
	Opt	29	14	12	55

Table 1.12: Atlantic sturgeon (*Acipenser oxyrinchus*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for eggs, larvae, young-of-the-year, yearling, and adults. Cases in which no studies were found are denoted by N.D.

	Temperature (^{o}C)		Salinity		DO (mg l^{-1})		References
	Req	Opt	Req	Opt	Req	Opt	
Eggs	N.D.	18-24	0-N.D.	N.D.	N.D.	N.D.	Smith et al. (1981), Van Eenanaam et al. (1996), Mohler et al. (2003)
Larvae	15-25	15-21	0-2.2	N.D.	N.D.	N.D.	Bath et al. (1981), Mohler et al. (2003), Hardy and Litvak (2004)
Juvenile YOY	0-28	16-24	0-22	3-19	≥3.3	≥5.0	Dovel and Berggren (1983), Niklitschek (2001), Niklitschek and Secor (2005), Niklitschek and Secor (2009)
Juvenile Yearling	0-28	16-24	0-29	19-26	≥3.3	≥5.0	Dovel and Berggren (1983), Secor and Gunderson (1998), Secor et al. (2000), Niklitschek and Secor (2005), Niklitschek and Secor (2009)
Adult	9-28	N.D.	0-29	N.D.	N.D.	N.D.	Brundage and Meadows (1982)

Table 1.13: Atlantic sturgeon (*Acipenser oxyrinchus*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for eggs, larvae, young-of-the-year, yearling, and adults. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Egg	Rep	N.D.	13	N.D.	13
	Opt	24.5	N.D.	N.D.	24.5
Larvae	Req	11	11	N.D.	22
	Opt	22.5	N.D.	N.D.	22.5
Juvenile YOY	Req	19	29.5	24	72.5
	Opt	24	24	24	72
Juvenile Yearling	Req	17.5	25	25	67.5
	Opt	24	24	25	73
Adult	Req	14	15	N.D.	29
	Opt	N.D.	N.D.	N.D.	0

Table 1.14: Soft shell clam (*Mya arenaria*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for juveniles. Cases in which no studies were found are denoted by N.D.

	Temperature (^{o}C)		Salinity		DO (mg l^{-1})		References
	Req	Opt	Req	Opt	Req	Opt	
Juvenile	-9-32	16-20	3-35	15-32	≥0.2	≥1.5	Van Dam (1935), Harrigan (1956), Chanley (1958), Matthiessen (1960), Ricketts and Calvin (1967), Kennedy and Muhursky (1971), Castagna and Chanley (1973), Borget (1983), Taylor and Eggleston (2000)

Table 1.15: Soft shell clam (*Mya arenaria*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for juveniles. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Juvenile	Req	24	22.5	23	69.5
	Opt	27	22	22	71

Table 1.16: Winter flounder (*Pseudopleuronectes americanus*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for juveniles. Cases in which no studies were found are denoted by N.D.

	Temperature (°C)		Salinity		DO (mg l^{-1})		References
	Req	Opt	Req	Opt	Req	Opt	
Juvenile	0-29	8-21	1-34	7-24	≥1.5	≥7.0	Pearcy (1962), Hoff and Westman (1966), Casterlin and Reynolds (1982), Ziskowski (1991), Armstrong (1997), Meng et al. (2000), Manderson et al. (2002), Stierhoff et al. (2006)

Table 1.17: Winter flounder (*Pseudopleuronectes americanus*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for juveniles. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Juvenile	Req	24.5	18.5	22	65
	Opt	26	17.5	25	68.5

Table 1.18: Atlantic menhaden (*Brevoortia tyrannus*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for juveniles. Cases in which no studies were found are denoted by N.D.

	Temperature (^{o}C)		Salinity		DO (mg l^{-1})		References
	Req	Opt	Req	Opt	Req	Opt	
Juvenile	5-33	14-30	0-35	5-10	≥1.1	≥3.0	Gunter (1961), Hettler (1976), Hettler (1968), Burton et al. (1979), Lewis and Burton et al. (1980), Engel et al. (1987), Terpin et al. (1999), Brandt and Mason (2011)

Table 1.19: Atlantic menhaden (*Brevoortia tyrannus*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for juveniles. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Juvenile	Req	23.5	18.5	24	66
	Opt	21	24	19	64

Table 1.20: Atlantic croaker (*Micropogonias undulates*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for juveniles. Cases in which no studies were found are denoted by N.D.

	Temperature (^{o}C)		Salinity		DO (mg l^{-1})		References
	Req	Opt	Req	Opt	Req	Opt	
Juvenile	1-36	13-28	0-36	5-20	N.D.	$\geq$1.0	Haven (1957), Bearden (1964), Shwartz (1964), Parker (1971), Peterson et al. (1999), Bell and Eggleston (2005)

Table 1.21: Atlantic croaker (*Micropogonias undulates*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for juveniles. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Juvenile	Req	20	15.5	N.D.	35.5
	Opt	12	26	14	52

Table 1.22: Weakfish (*Cynoscion regalis*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for juveniles. Cases in which no studies were found are denoted by N.D.

	Temperature (^{o}C)		Salinity		DO (mg l^{-1})		References
	Req	Opt	Req	Opt	Req	Opt	
Juvenile	3-31	10-29	5-32	12-19	≥ 0.4	≥ 2.0	Shwartz (1964), Richards and Castagna (1970), Lankford and Targett (1994), Brady et al. (2009), Stierhoff et al. (2009)

Table 1.23: Weakfish (*Cynoscion regalis*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for juveniles. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Juvenile	Req	20.5	19	24	63.5
	Opt	25	25	27	77

Table 1.24: White perch (*Morone Americana*) required (req) and optimal (opt) physiological tolerances with respect to temperature, salinity, and dissolved oxygen for juveniles. Cases in which no studies were found are denoted by N.D.

	Temperature (^{o}C)		Salinity		DO (mg l^{-1})		References
	Req	Opt	Req	Opt	Req	Opt	
Juvenile	3-34	12-33	0-22	0-16	≥0.8	≥2.9	Dorfman and Westin (1970), Kellogg and Gift (1983), Johnson and Evans (1990), Nemerson and Able (2004), Hanks and Secor (2011)

Table 1.25: White perch (*Morone Americana*) required (req) and optimal (opt) quality scores for individual temperature, salinity, and dissolved oxygen physiological tolerances and total scores for juveniles. Cases in which no studies were found are denoted by N.D.

Lifestage	Habitat	Temp	Sal	DO	Total
Juvenile	Req	23	19	20	62
	Opt	24	27	26	77

Table 1.26: Summary of species, lifestages, and habitat types that did not meet the minimum quality score requirement for inclusion in the habitat volume model

Species	Lifestage	Habitat Type
Blue crab	Egg	Required
Blue crab	Egg	Optimal
Blue crab	Larvae	Optimal
Eastern oyster	Egg	Required
Eastern oyster	Egg	Optimal
Eastern oyster	Juvenile	Optimal
Eastern oyster	Adult	Optimal
Atlantic sturgeon	Egg	Required
Atlantic sturgeon	Egg	Optimal
Atlantic sturgeon	Larvae	Required
Atlantic sturgeon	Larvae	Optimal
Atlantic sturgeon	Adult	Required
Atlantic sturgeon	Adult	Optimal
Bluefish	Egg	Required
Bluefish	Egg	Optimal
Bluefish	Larvae	Required
Bluefish	Larvae	Optimal
Atlantic croaker	Juvenile	Required
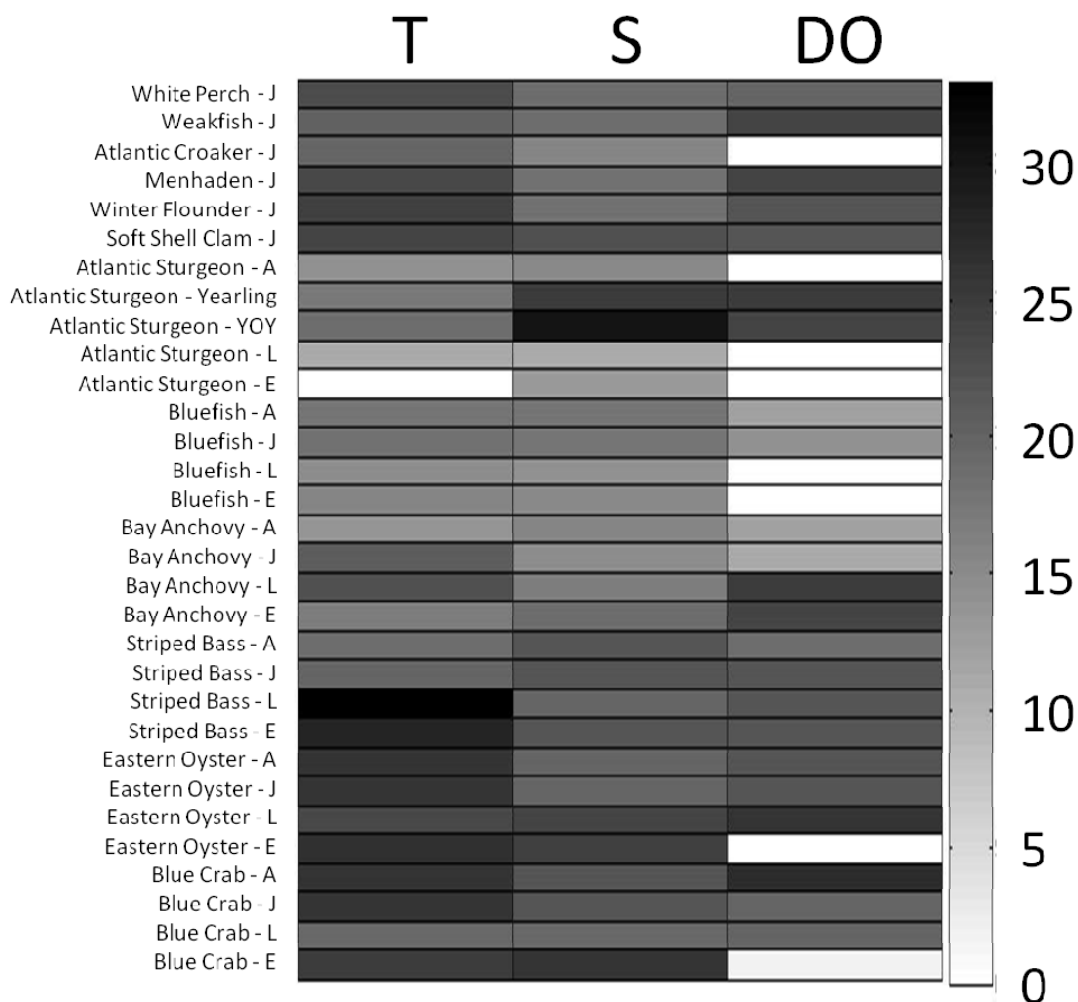
Figure 1.1: Quality score matrix for required habitat. Each species and life stage is shaded (gray-scale bar on left) according to the quality of information available on their required physiological tolerances to temperature (T), salinity (S), and dissolved oxygen (DO). The species include blue crab (*Callinectes sapidus*), eastern oyster (*Crassostrea virginica*), bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), bay anchovy (*Anchoa mitchilli*), and Atlantic sturgeon (*Acipenser oxyrinchus)* winter flounder (*Pseudopleuronectes americanus)*, Atlantic menhaden (*Brevoortia tyrannus)*, Atlantic croaker (*Micropogonias undulates)*, weakfish (*Cynoscion regalis)*, soft shell clam (*Mya arenaria)*, and white perch (*Morone americana).*The life stage of each species is denoted by a letter to the left of the color panel: egg (E), larvae (L), juvenile (J), young-of-the-year (YOY), yearling, and adult (A).

Figure 1.2: Quality score matrix for optimal habitat. Each species and life stage is shaded (gray-scale bar on left) according to the quality of information available on their required physiological tolerances to temperature (T), salinity (S), and dissolved oxygen (DO). The species include blue crab (*Callinectes sapidus*), eastern oyster (*Crassostrea virginica*), bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), bay anchovy (*Anchoa mitchilli*), and Atlantic sturgeon (*Acipenser oxyrinchus)* winter flounder (*Pseudopleuronectes americanus)*, Atlantic menhaden (*Brevoortia tyrannus)*, Atlantic croaker (*Micropogonias undulates)*, weakfish (*Cynoscion regalis)*, soft shell clam (*Mya arenaria)*, and white perch (*Morone americana).*The life stage of each species is denoted by a letter to the left of the color panel: egg (E), larvae (L), juvenile (J), young-of-the-year (YOY), yearling, and adult (A).

Figure 1.3: Quality score matrix for required and optimal habitat totals. Each species and life stage is shaded (gray-scale bar on left) according to the quality of information available on their required physiological tolerances to temperature (T), salinity (S), and dissolved oxygen (DO). The species include blue crab (*Callinectes sapidus*), eastern oyster (*Crassostrea virginica*), bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), bay anchovy (*Anchoa mitchilli*), and Atlantic sturgeon (*Acipenser oxyrinchus*) winter flounder (*Pseudopleuronectes americanus*), Atlantic menhaden (*Brevoortia tyrannus*), Atlantic croaker (*Micropogonias undulates*), weakfish (*Cynoscion regalis*), soft shell clam (*Mya arenaria*), and white perch (*Morone americana*).The life stage of each species is denoted by a letter to the left of the color panel: egg (E), larvae (L), juvenile (J), young-of-the-year (YOY), yearling, and adult (A).

Chapter 2: Modeling the potential habitat of Atlantic sturgeon (Acipenser oxyrinchus): a comparison of two methods

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. Through the combination of 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 (Secor 2010). We present a novel habitat model which 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 the habitat volume model which can assimilate and

interpret this information, are integral to the future protection of marine and aquatic ecosystems. Many of the ecological disruptions created by anthropogenic nutrient loading are expected to grow worse 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 (≤ 2 mg l^{-1} O_2) and anoxic (≤ 0.2 mg l^{-1} O_2) 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 and Montagna 1999, Townsend and Edwards 2003). The destruction of benthic communities creates a domino effect, disrupting ecological interactions throughout the water column (Caddy 2000, Breitburg et al. 2003), which could have the potential for negative effects on economically important fisheries. Quantifying the impacts of climate change and eutrophication on habitat is especially important in estuaries which provide essential habitat for a variety of ecologically important species (Lippson et al. 1979) and which can be threatened by anthropogenic nutrient enrichment (Howarth et al. 2000, Cloern 2001, Tett et al. 2003, Kemp et al. 2005, Wooldridge et al. 2006, Breitburg et al. 2009) and can be subject to systemic hypoxia (Officer et al. 1984, Diaz 2001).

Fixed criteria and bioenergetics models are two habitat modeling approaches which 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. In this study, potential habitat refers to 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 assumption that physiological tolerances for each environmental factor do not interact with other environmental factors. It is, however, well known that interactions 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 et al. 1956, Fry 1971, Claireaux and Lagardere 1999). Unfortunately these "physiological interactions" have been quantitatively defined for just a few species (e.g., Lankford and 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 and Brandt 1995, Niklitschek and Secor 2005, Constantini 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 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 and Scruton 2006). Bioenergetic 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, Wuenschel et al. 2004, Niklitschek and Secor 2005, Costantini et al. 2008). Although bioenergetic 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 and Scruton 2006). This study compares the fixed criteria and bioenergetics habitat modeling approaches in order to determine if fixed criteria could be used in cases where information concerning physiological interactions are difficult to obtain or do not exist.

For this research, fixed criteria and bioenergetics habitat volume models are developed and applied for two life stages, young-of-the-year (YOY, age-0) and yearling juveniles (age-1), of Atlantic sturgeon (*Acipenser oxyrinchus*) as the model organism and the Chesapeake Bay as the model study site. Atlantic sturgeon have relatively sensitive physiological tolerances to environmental conditions compared to other estuarine species (Niklitschek and Secor 2005), which makes them a useful species to assess ecological change related to climate and anthropogenic perturbations. The Chesapeake Bay is a large, partially-mixed estuary along the western North Atlantic Coast (Pritchard 1967) which is subject to persistent seasonal hypoxia (Officer et al. 1984). Predictions from a coupled biophysical model of the Chesapeake Bay are used as input to the habitat volume models which calculate the volume of required and optimal habitat for sturgeon based on either fixed criteria or bioenergetics parameterizations. The models are 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, and 3) to compare fixed criteria and bioenergetics approaches for estimating potential habitat. 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 did not.

Methods

We use a coupled hydrodynamic and oxygen model to predict water temperature, salinity, and dissolved oxygen in Chesapeake Bay and then apply fixed criteria and bioenergetic habitat volume models to quantify potential habitat of YOY and yearling

sturgeon. Physiological tolerances and bioenergetic equations are obtained from a series of laboratory experiments and modeling exercises (Niklitschek 2001, Niklitschek and Secor 2005, 2009). Using information from the same set of experiments to parameterize the bioenergetics and fixed criteria modelsfacilitates model comparison. Model simulations are conducted to determine the influence of temperature, salinity, and dissolved oxygen on habitat volume and to estimate the influence of oxygen limitation on potential habitat. In addition, results of the fixed criteria and bioenergetics modeling approaches are compared.

Coupled hydrodynamic and oxygen models. The Regional Ocean Modeling System (ROMS) is a state-of-the-art coastal hydrodynamic model (Song and Haidvogel 1994, Shchepetkin and 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. In this study, the ROMS hydrodynamic model is configured for Chesapeake Bay and validated using time series of sea level, temperature, salinity and currents at a number of monitoring stations, and data from three-dimensional synoptic hydrographic surveys (Li et al. 2005, Zhong and Li 2006, Zhong et al. 2008, Li and Zhong 2009, Li and Li 2011). The model is forced by open-ocean tides, freshwater inflows at river heads, and observed winds and heat exchange across the water surface. The ROMS grid covers the major tributaries and main stem of the Chesapeake Bay from the Susquehanna River to the mouth of the Bay. Grid cells located outside the mouth of the Bay are removed from the analysis.

A simplified oxygen model incorporating biogeochemical processing is used in conjunction with ROMS to predict oxygen concentrations throughout the Chesapeake Bay. The ROMS hydrodynamic model is coupled with an empirical dissolved oxygen model (Li et al. in prep), 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. For all ten years, the average volume of water during July with dissolved oxygen concentrations <0.2 mg l^{-1} in the model is approximately half of that estimated from observations by Murphy et al. (2011), while the volume with concentrations < 1 mg l^{-1} and <2 mg l^{-1} are 1.2 and 1.6 times greater than estimated from observations, respectively. Although there are both magnitude and timing differences in DO concentrations between the model and observations, the model reproduces the general seasonal cycle and provides 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 the volume of habitat given one or more constraints (Smith et al. 2009 ICES CM, Smith et al. *in prep*), such as temperature, salinity, and oxygen (fixed criteria), or potential growth (bioenergetics). The habitat volume model uses these constraints and predictions from the coupled hydrodynamic and oxygen models to calculate the volume of suitable habitat in each model grid cell. For each grid cell, linear interpolation in the vertical direction is used to find the depth of the constraints (e.g., minimum DO required for survival) (Fig. 2.1a). Then the most constraining factors in each grid cell are used to define the volume of habitat in the cell

that fulfills all requirements (Fig. 2.1b). This volume is then divided into four triangular "prisms" created by joining the triangles formed by the vertices and midpoints of the top and bottom faces (Fig. 2.1c). The grid cell habitat volume is then calculated as the sum of the volume of each prism.   The volume of all model grid cells is summed (Fig. 2.1d) to derive the Bay-wide total habitat volume in each time step (e.g., Fig. 2.2). Because Atlantic sturgeon are a predominantly benthic species, the habitat volume model was adjusted so that only the bottom two meters of the water column were included in the volume calculations.

   Fixed criteria habitat volume model. Physiological tolerances of Atlantic sturgeon (*Acipenser oxyrinchus*) to temperature, salinity, and dissolved oxygen are taken primarily from Niklitschek (2001) and Niklitschek and Secor (2005, 2009). Atlantic sturgeon juvenile stages are divided into YOY and yearlings because these two stages have different physiological tolerances (Niklitschek and Secor 2009a). These physiological tolerances (Table 2.1) are used to parameterize the fixed criteria habitat volume model and are summarized below. The habitat predicted by the fixed criteria habitat volume model is categorized into *required* and *optimal* habitat. Required habitat is defined as the domain (volume) of environmental conditions outside of which mortality would occur. Optimal habitat is 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 required temperature, salinity, and dissolved oxygen tolerances chosen for YOY Atlantic sturgeon are 0-28 $^{\circ}$C, 0-22, and ≥ 3.3 mg l^{-1}, respectively. Niklitschek and Secor (2005) report decreased survivorship when temperatures exceeded 28 $^{\circ}$C for YOY

sturgeon. Field observations taken by Dovel and Breggren (1983) indicate that juvenile

sturgeon over-winter in deep refuges in which temperatures can drop to 0 $^\circ$C. This

temperature range is consistent with additional field observations (Bain et al. 2000, Dovel

and Berggren 1983, Kieffer and Kynard 1993). Laboratory experiments in Niklitschek

and Secor (2009) show that YOY sturgeon can survive in salinities as low as 0. The

upper salinity mortality threshold of 22 is set by using a mortality equation derived from

laboratory experiments conducted by Niklitschek (2001). This is calculated by solving for

the salinity resulting in a 50% mortality rate over a six hour period under optimal

temperature and dissolved oxygen conditions. The resulting upper threshold is supported

by laboratory observations in Niklitschek and Secor (2009) and a variety of field

observations (Smith 1985b, Brundage and Meadows 1982, Bain et al. 2000, Haley et al.

1996, Dovel and Berggren 1983). Niklitschek (2001) reports mortality under summer

temperatures at dissolved oxygen levels $\leq$3.3 mg l^{-1}.

The optimal temperature, salinity, and dissolved oxygen tolerances chosen for

YOY Atlantic sturgeon are 16-24 $^\circ$C, 3.5-18.5, and $\geq$5.0 mg l^{-1}, respectively. Optimal

temperature and salinity tolerances are derived from laboratory experiments in

Niklitschek and Secor (2009). Ranges are chosen to include conditions resulting in peak

rates of potential daily production. With regard to dissolved oxygen, Niklitschek (2001)

reports reductions in the growth of juvenile Atlantic sturgeons exposed to water with

oxygen concentrations less than 5.0 mg l^{-1}.

The required temperature, salinity, and dissolved oxygen tolerances chosen for

yearling Atlantic sturgeon are 0-28 $^\circ$C, 0-29, and $\geq$3.3 mg l^{-1}, respectively. Laboratory

experiments in Niklitschek and Secor (2005) show increased mortality when

temperatures exceeded 28 $^{\circ}$C and Dovel and Berggren (1983) provide evidence that juveniles survived in temperatures as low as 0 $^{\circ}$C. Niklitschek and Secor (2005) report survival of yearling sturgeon in salinities of 0-29 and an increase in mortality when salinity exceeds this range. These results are consistent with field observation made in Secor et al. (2000). A dissolved oxygen tolerance of $\geq$3.3 mg l^{-1} is chosen based on similar findings in Secor and Gunderson (1998) and Niklitschek and Secor (2009).

The optimal temperature, salinity, and dissolved oxygen tolerances chosen for yearling Atlantic sturgeon are 16-24 $^{\circ}$C, 18.5-25.5, and $\geq$5.0 mg l^{-1}, respectively. Temperature and salinity ranges for yearling sturgeon are chosen from Niklitschek and Secor (2009) to include peak rates of potential daily growth. Secor and Gunderson (1998) report reductions in the growth of juveniles exposed to oxygen concentrations less than 4.3-4.7 mg l^{-1} at 22 $^{\circ}$C and $\leq$5.0 mg l^{-1} at 26 $^{\circ}$C. Because summer temperatures in the Chesapeake Bay commonly exceed 26 $^{\circ}$C, the higher dissolved oxygen threshold is selected. This threshold is also used by the US Environmental Protection Agency as being protective for sturgeon species in the Chesapeake Bay (Batiuk et al. 2009)

Bioenergetics habitat volume model. Bioenergetics equations for YOY and yearling Atlantic sturgeon are derived from Niklitschek and Secor (2009). These equations are used to estimate required and optimal habitat for each species. Required habitat in the bioenergetics habitat volume model is defined as the domain of all possible environmental conditions that result 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 (aka incipient lethality). Optimal habitat is defined as the domain of environmental conditions resulting in highest potential growth. Optimum

levels are defined at the 75th and 90th percentile values of potential growth. Only results of simulations with the 90th percentile values are presented here because they resulted in the greatest similarity between fixed criteria and bioenergetics approaches.

The bioenergetics equations have to be parameterized for incorporation into the habitat volume model. Consumption in these equations is set to a maximum, under the assumption that food availability is not limiting. Although this represents a departure from realism, the focus of this research is to assess the influence of physical conditions on potential habitat. Fish weight is set to 14 g in YOY model simulations and 200 g in yearling model simulations. In addition, slight adjustments are made to temperature and oxygen input values to maintain numerical stability. In the presence of zero or negative temperatures in the hydrodynamic model, temperature is set to a constant value of $0.1\ ^{o}C$ in the bioenergetics habitat volume model. A similar adjustment is made for dissolved oxygen so that values of zero percent saturation are fixed at 0.1 percent saturation.

Model simulations. Three sets of model simulations are conducted. First, simulations are run with the fixed criteria habitat volume model to identify the interannual variability in volumes of habitat defined by temperature, salinity, and dissolved oxygen. The fixed criteria habitat volume model is used to calculate these individual habitat volumes and to determine which parameter(s) have the greatest influence on required and optimal habitat of YOY and yearling sturgeon. The model is run for each lifestage and habitat type using the predictions from the coupled hydrodynamic and oxygen model, which spanned 1996 to 2005, with predictions stored every 12 hr. The coupled hydrodynamic and oxygen model simulations are not run continuously, but are completed for each individual year and concatenated. Initial

conditions for the hydrodynamic model are estimated using archived model output, which are 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 1998-99, 1999-00, 2001-02, and 2002-03 (Fig. 3 and Fig. 4).

Next, simulations are conducted to compare fixed criteria and bioenergetics habitat volume models. Volumes of required and optimal habitat based upon fixed criteria and bioenergetics criteria are calculated for each lifestage and habitat type at every time step in each year. Daily averages of Bay-wide volumes are summed over the entire year to obtain annual indices of habitat volume. In addition, daily averages of Bay-wide volumes are summed over the period from May 1st to November 15th to obtain seasonal indices of habitat volume that correspond to the time range during which habitat reduction due to low dissolved oxygen limitation occurs. Fixed criteria and bioenergetics annual and seasonal indices are then compared using correlation and paired t-test analyses.

Finally, simulations are conducted with and without dissolved oxygen limitation so that an estimate of the loss in habitat due to hypoxia can be calculated. For the fixed criteria model, this is accomplished by removing dissolved oxygen from the habitat volume calculation. For the bioenergetics model, dissolved oxygen concentrations across the entire model domain are set to be above saturation levels so that oxygen is not a limiting factor. For both models, the reduction in habitat resulting from dissolved oxygen limitation is determined by subtracting habitat volumes from runs with and without oxygen limitation during the period from May 1st to November 15th. This time frame is

chosen because it captures the entire time range during which habitat reduction due to dissolved oxygen limitation is present for all years. The total volume of habitat reduction from May 1st to November 15th is calculated by summing the differences between models with and without oxygen over all time steps for each lifestage and habitat type for each year. The percent decrease in habitat volume is also calculated. The onset date of habitat reduction due to oxygen limitation and the duration of reduced habitat are determined for each year, lifestage, and habitat type as well. These indices are compared between fixed criteria and bioenergetics models with correlation and paired t-test analyses.

Results

Results of model simulations are analyzed to 1) identify the interannual variability in volumes of habitat defined by each environmental parameter, 2) compare habitat volumes predicted by fixed criteria and bioenergetics habitat volume models, and 3) quantify the influence of dissolved oxygen limitation during periods of seasonal hypoxia.

Interannual variability in habitat volume. Required habitat volumes based upon individual (temperature, salinity, dissolved oxygen) and combined constraints show strong seasonal trends and differ between years (Fig. 2.3). Salinity was the most constraining factor determining the magnitude of required habitat volume during the winter for both life stages, while temperature and dissolved oxygen contribute to summertime decreases in required habitat. The volume of water corresponding to the required salinity range for YOY sturgeon, 0-22, shows the expected pattern of decrease in volume during summer related to low freshwater flow in the Chesapeake region at this time, and wintertime volumes are higher near the beginning and end of the time series. In

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contrast, yearling required habitat volume defined by salinities of 0 to 29 shows little seasonal or annual variability. The volume of water meeting the required dissolved oxygen tolerance of each life history stage, ≥ 3.3 mg l^{-1}, remains high until the summer during which volumes sharply decrease. This pattern varies between years, but shows no trend over the time series. Temperature-based volumes for each lifestage show a similar pattern to dissolved oxygen. However, decreases in volume during the summer due to temperature are much sharper and occur over a smaller time period. In 2005, water temperatures during this particularly warm summer drive the largest reduction in habitat volume in the time series.

Volumes of optimal habitat for YOY and yearlings exhibit complex modal and bimodal seasonal patterns (Fig. 2.4). Temperature is the main factor controlling the presence of optimal habitat during spring and fall for both life stages, with a secondary influence of dissolved oxygen seen in the late spring and early fall. Although the seasonal occurrence of habitat is controlled by temperature and dissolved oxygen, the magnitude of optimal habitat is predominantly limited by salinity for each life stage. Volumes of YOY optimal habitat are consistently larger than those of yearlings, suggesting the presence of larger volumes of lower salinity water optimal for YOY (3.5-18.5) compared to higher salinities optimal for yearlings (18.5-25.5) throughout much of the Bay (e.g., Fig. 2.2). Between 1999 and 2003, yearling optimal habitat volumes and corresponding salinity volumes are high. During this same time period, optimal habitat volumes of YOY and corresponding salinity volumes are low, suggesting a reciprocal relationship between YOY and yearling optimal habitat based on changes in salinity.

Volumes for optimal temperature and dissolved oxygen for both life stages show little interannual variation.

Comparison of model approaches. The seasonal patterns in habitat volume are similar between fixed criteria and bioenergetics modeling approaches, but the magnitudes differ depending upon lifestage and type of habitat (Fig. 2.5). For both modeling approaches, required habitat remains high during the winter and then decreases from spring into summer before rising again in the fall. In addition, optimal habitat is bimodal with peaks in spring and fall for both modeling approaches. Although these seasonal patterns are similar, optimal habitat based on fixed criteria drops to zero or near zero during summer due to temperature thresholds whereas optimal habitat based on bioenergetics does not approach zero for extended periods of time during summer. The timing and appearance of optimal habitat is similar between model approaches, but ends slightly later in fixed criteria model runs. Both modeling approaches predict interannual variability in the amount of required habitat present during summer, with markedly reduced volumes in 1999, 2002, and 2005. These reductions coincide with temperature limitation predicted by the fixed criteria model (Fig. 2.3). Although seasonal trends are similar, the magnitude of volumes calculated with the two approaches differ, with higher volumes predicted by the bioenergetics model compared to the fixed criteria model for required habitat of the two life stages and for optimal habitat of yearlings.

The annual volume indices (the sum of average daily volumes) are similar between fixed criteria and bioenergetics approaches for the required habitat of both life stages and for the optimal habitat of YOY (Fig. 2.6). For the required habitat of YOY and yearlings, the volumes estimated through fixed criteria are on average 15.9% and 4.2%

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less than volumes based upon bioenergetics, respectively. For YOY optimal habitat, the fixed criteria predictions are on average 17% greater than those defined by bioenergetics. In addition, yearling required habitat and YOY optimal habitat show statistically similar patterns in variation between modeling approaches (Table 2.2). Only the annual yearling optimal habitat volumes differ markedly between the bioenergetics and fixed criteria approaches, with bioenergetics estimates on average twice as large as fixed criteria volume estimates.

The total volumes of habitat during the time period of seasonal hypoxia (May 1st and November 15th) show similar patterns of interannual variability between life stages and habitat type, except for yearling optimal habitat (Fig. 2.7). 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, do not exceed 18.2% and are significantly correlated (Table 2.2). Model predictions of volumes of optimal habitat for yearlings do not agree in trend or magnitude, with volumes calculated through bioenergetics being 101.2% higher than volumes calculated with the fixed criteria model.

Influence of hypoxia on habitat volumes. The volumes of required habitat for YOY (Fig. 2.8) and yearlings (Fig. 2.9) show the largest differences between model runs with and without oxygen during the summer, while the largest difference in volume of optimal habitat occurred in late spring and early fall. For optimal habitat, the bioenergetics model shows a larger seasonal decrease in available habitat than the fixed criteria model due in part to the loss of potential habitat volume during mid-summer due to low oxygen, which is already absent in the fixed criteria model predictions due to temperature limitations.

The start dates of habitat reduction due to oxygen limitation range from May 5th to June 18th (Fig. 2.10). The start date of oxygen limitation on optimal habitat occurs on average 9 days earlier in the year than the onset of reduction in required habitat. The bioenergetics modeling approach for required habitat results in a start date 17 and 18 days earlier on average than the start date calculated with the fixed criteria model for both YOY and yearlings, respectively. Despite the offset, the models respond similarly to interannual variability as seen by significant correlation coefficients of 0.87 and 0.89, respectively (Table 2.2). For optimal habitat, there is an average difference of 2 days between modeling approaches which is not significantly different (Table 2.3) and no consistent offset is present.

The duration of oxygen limitation on available habitat ranges from 139 to 187 days (Fig. 2.10). Although the durations of seasonal oxygen limitation on optimal habitat is on average 14 days longer than those estimated for required habitat, there is little difference between life stages and modeling approaches in terms of both magnitude and interannual variability. The average difference in the duration of seasonal oxygen limitation between fixed criteria and bioenergetics models is 1 day (Fig. 2.10) and is not statistically different for YOY required habitat, yearling required, and yearling optimal habitat (Table 2.3). In addition, the durations of limitation of required habitat between modeling approaches are significantly correlated (Table 2.2).

The total volumes of required and optimal habitat that are reduced by low dissolved oxygen during the time period of seasonal hypoxia vary considerably between years and have similar magnitudes between modeling approaches and life stages, except for yearling optimal habitat defined by fixed criteria, which is markedly lower than the

rest (Fig. 2.11). No significant trends in the time series are present. The smallest

reductions in required and optimal habitat due to oxygen limitation occur in 1999 and

2005, which are years when habitat limitation is predominantly influenced by

temperature (Fig. 2.3). In contrast, largest reductions due to oxygen limitation occur in

1998 and 2004 when volumes of low salinity water are relatively large. For the required

habitat of both life stages, reductions estimated by fixed criteria are on average 21.0%

(YOY) and 16.7% (yearling) larger than reductions calculated through bioenergetics. In

addition, the time series of reductions in habitat are significantly correlated between

modeling approaches (Table 2.2). For YOY optimal habitat, the average reduction in

habitat volume defined by fixed criteria is 65.5% smaller than that defined by

bioenergetics (Fig. 2.11A). Despite the difference in magnitude, there is a strong

correlation between methods (Table 2.2). For yearling optimal habitat, the average

reduction in habitat volume predicted by the fixed criteria model is 1.5 times smaller

than, and is negatively correlated with, that predicted by the bioenergetics model (Fig.

2.11B, Table 2.2). The negative correlation likely results from salinity limitation on

yearling optimal habitat in the fixed criteria model which confines potential habitat to the

lower portion of the Chesapeake Bay (Fig. 2.2) where hypoxia does not occur (Hagy et

al. 2004).

The percent reduction in habitat volume during the time period of seasonal

hypoxia (May 1st and November 15th) is similar between YOY and yearling sturgeon

(Fig. 2.12). Reductions varied between 9% and 32% with optimal habitat having higher

proportional decreases than required habitat for both life stages. Differences between

fixed criteria and bioenergetics models for the required habitat of YOY and yearlings are

on average 3.8% and 2.2%, respectively. For optimal habitat, the average difference in percent reduction between methods is 14.6% for YOY and 17% for yearlings.

Discussion

Results of this exercise suggest that using a habitat volume model with a coupled biophysical model to estimate potential habitat is an effective new means of habitat modeling. The high spatial and temporal resolution of this approach allows for evaluation of a species' responses to environmental stressors like hypoxia as well as climate variability and change. Although the concept of relating habitat volume to growth and survival is not new (e.g., Secor et al. 1996, Niklitschek and Secor 2005), the calculation of habitat volume as the intersection of multiple water masses within a three-dimensional 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 three dimensional changes in habitat volume. Neuenfeldt et al. (2002) estimate volumes of hypoxic water and respective predator-prey overlap in the Bornholm Basin using a time series of oxygen observations. Kimmerer et al. (2009) use a hydrodynamic model and resource selection functions to calculate an index of total habitat based on salinity. Our research builds upon 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 change that can be applied to understand the influence of past and future environmental variability on species' habitat.

Interannual variability in environmental conditions has long been known to have a strong influence over the potential habitat available to estuarine species. Model results suggest a complex interaction between temperature, salinity, and dissolved oxygen in determining potential habitat volume. Changes in fresh water flow lead to varying distributions of salinity throughout an estuary, which in turn affects the habitat distributions of salinity-dependent fish species (Dovel 1971, Garcia et al. 2003, Lippson and Lippson 2006). Salinity dependent patterns are observed for each lifestage of Atlantic sturgeon during this study (Fig 2.2 and 2.3). The volume of required and optimal habitat for YOY and yearling sturgeon vary closely with their respective salinity tolerances for most of the year, excluding the summer. Interannual salinity variability is particularly important considering abrupt changes in salinity can lead to mass mortalities of fish at various life stages (e.g., *Morone saxatilis*: Houde et al. 1988, *Clarias gariepinus*: Bennett 2010). Secor et al. (2000) found a change in salinity preference between YOY and yearling juveniles, with older juveniles favoring higher salinity waters. This difference in salinity preference can be seen in the differences between optimal habitat volumes (Fig 2.4), with YOY and yearling habitat showing opposite trends with respect to low (3.5-18.5) and high (18.5-25.5) salinity volumes. The influence of salinity is even more pronounced due to the fact that juvenile sturgeon spend the majority of their time in the bottom 2 meters of water (Bain et al. 2000). As a result, changes in freshwater flow and stratification, which in turn affect the degree of salt intrusion in the bottom waters of the estuary, have a direct impact on sturgeon habitat, with the degree of that impact varying for YOY and yearling individuals. This model is able to quantify interannual variation in

salinity distributions and habitat volumes, making it a useful tool in age-specific sturgeon research.

Temperature also plays a major role in dictating potential habitat availability (Attrill and Power 2004) (Fig 2.3 and 2.4), at times responsible for the largest summertime reductions in habitat out of the three physiological variables used in this study. For required habitat, increased temperatures significantly reduce habitat volumes, with almost no available habitat present during the summer of 2005 for either lifestage. Optimal habitat is limited throughout most of the year by temperature, with the formation of potential habitat in the spring and fall. Similarly, potential growth of striped bass (*M. saxatilis*) based on prey sizes, prey densities, and water temperature was highest in spring and fall and near zero in summer in Chesapeake Bay (Brandt and Kirsh 1993). Variability in temperature regimes can also lead to mass mortalities at both very high and low temperatures (e.g., *M. saxatilis*: Hurst and Conover 1998, *Hippocampus capensis*, *Rhabdosargus globiceps*, and *Lithognathus lithognathus*: Russell 2010), and therefore it is important to understand how temperature changes from year to year when estimating potential habitat. Atlantic sturgeon are temperature sensitive in comparison to many other estuarine species, especially regarding higher temperature ranges (Bain et al. 2000, Niklitschek and Secor 2005). This limits available habitat volumes during the winter and summer months. Consumption rates have also been shown to have a direct relation to temperature, with decreasing rates at lower temperatures (Mohler 2004). Temperature-dependent changes in available habitat can be seen in the seasonal variations of habitat volume using both model approaches (Fig. 2.3 and Fig. 2.4). Quantitative predictions of temperature volumes produced by this model make it possible to estimate the impact of

temperature limitation on available habitat with high spatial and temporal resolution and have direct application for assessing potential impact of climate change on 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 (Breitberg 2002), reductions of available habitat, which can lead to density dependent reductions in growth rate (Eby et al. 2005), and decreases in reproductive potential (Diaz and Rosenberg 2008). Changes in the structure of the water column resulting from hypoxic water can also influence abundance distributions (Tomkiewicz et al. 1997) 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 and 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. 2011). These percentages are similar to the percent reductions in seasonal habitat estimated for YOY and yearling sturgeon in this 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 to many estuarine species (Niklitschek 2001). Overfishing in the Chesapeake Bay led to a population collapse in the early 1900's and the persistence of seasonal

hypoxia likely has hindered the ability of spawning stocks to make a recovery (Secor and 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 and Niklitschek 2002, Baker et al. 2005). Niklitschek and Secor (2005) used bioenergetic equations and survival rates to calculate instantaneous potential production in the Chesapeake Bay during 1993-2002. They estimated that habitat reduction derived from hypoxia occurred over 35% of Chesapeake Bay's seabed. This estimate agrees with the upper end of the percent reduction ranges calculated for optimal habitat in this study. Despite the influence of hypoxia on potential habitat, the magnitude of subsequent summertime reductions can be markedly smaller than habitat limitation resulting from temperature (e.g. 2005). This is an important distinction because it implies that nutrient enrichment and hypoxia may not be the most significant threats to Atlantic sturgeon habitat when compared to temperature increases linked to climate change. Indeed, in a simulation of increased temperature everywhere in the Chesapeake Bay by 1 ^{o}C during July, overall habitat was reduced by 37% to 100% during the 1993-2002 period (Niklitschek and Secor 2005).

Overall findings in this study indicate that the volume of habitat calculated using fixed criteria and bioenergetic 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. In addition, excluding yearling optimal habitat, all lifestage and habitat combinations show closely related responses to changes in environmental conditions, as seen from the significant correlations between indices (Table 2.2). This indicates that volumes of habitat calculated with fixed criteria and

bioenergetic approaches respond to changing conditions in a similar fashion, even though the magnitudes can differ. 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 bioenergetic 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 be able to capture it, leading to smaller habitat volume estimates.

For yearling optimal habitat, the volumes of habitat defined by fixed criteria differ in magnitude and trends from those predicted by bioenergetics models. This lack of consistency is a consequence of the narrow optimal salinity range used in the fixed criteria model. The chosen salinity range limits optimal habitat to the lower end of the Chesapeake Bay (Fig. 2.2), while dissolved oxygen limitation on habitat due to hypoxia predominantly occurs in the upper region of the Bay. Therefore, yearling optimal habitat generally does not intersect with volumes of water influenced by dissolved oxygen limitation, resulting 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 a. 2009), which may have led to this narrow salinity range, and it is known that yearlings can survive and grow in freshwater (Mohler 2004, Niklitschek et al. 2009). A broader optimal salinity range could result in a better relationship between fixed criteria and bioenergetics models.

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One of the main factors influencing the volume of optimal habitat is the definition of habitat which is used. In the case of required 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. Because there is no universal definition for optimal habitat, determining optimal ranges is a more complex and subjective process. The reliability of this habitat volume modeling approach depends on the accuracy of literature-derived values and consistent definitions of optimal habitat. Results of this study suggest that additional laboratory studies on growth and physiological tolerances are needed for yearling sturgeon, and that future laboratory, modeling, and field studies should be designed to better describe optimal habitat based on both environmental conditions and growth indices.

Both the fixed criteria and bioenergetics methods incorporate only physical constraints on habitat volume, excluding trophic interactions and food distributions. Although the inclusion of trophic interactions to assess the realized niche of juvenile sturgeon would improve the model, fish predator and prey distributions are not a standard part of three dimensional biophysical models (although see, for example, Rose et al. 2007) . Temperature, salinity, and dissolved oxygen effectively capture variability linked to precipitation, 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. In systems where eutrophication may not be a major problem, this method of modeling can serve as a useful tool to predict changes in habitat resulting from future climate trends. 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 like Ecopath with Ecosim (Christensen and Walters 2004).

The overall results of this study suggest that using a habitat volume modeling approach can effectively estimate potential habitat, and that the fixed criteria habitat volume model produces estimates similar to the bioenergetics habitat volume model for most life stages and habitat types. Habitat volume estimates using fixed criteria tend to be lower than volumes estimated using bioenergetics, but these differences were small. This is a meaningful distinction due to the effort involved in parameterizing each model. Despite increased accuracy resulting from bioenergetic equations, they require a considerable amount of laboratory experimentation in order to determine the necessary coefficients. Although there are a variety of bioenergetic models available (e.g., *Anchoa mitchilli*: Luo and Brandt 1993, *Gadus morhua*: Horne and Schneider 1994, *M. saxatilis* and *Pomatomus saltatrix*: Hartman and Brandt 1995, *A oxyrinchus*: Niklitschek and Secor 2005, *Morone americana*: Hanks and Secor 2011, *Sardinops melanostictus*: Okunishi et al. 2011) they do not fully incorporate all of the important species that play a vital role in ecosystem structure and function. Furthermore, some of the experiments used to define bioenergetics relationships do not cover a wide range of environmental conditions, making them impractical for habitat modeling studies. Fixed criteria habitat volume models are more readily parameterized due to the availability of published

laboratory and field studies, providing the ability to model habitat for many species for

which bioenergetics information is not yet available. Bioenergetic models have more

physiological realism and can incorporate prey abundance into the calculation of habitat.

Both 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 functional hydrodynamic and biogeochemical model allows these approaches

to be implemented across a broad range of systems and ecological applications.

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Stage	Physiological Tolerance	Value		Reference
		Required	Optimal	
Young-of-the year	Temperature(^{o}C)	0-28	16-24	Niklitschek and Secor (2005,2009), Dovel and Berggren 1983
	Salinity	0-22	3.5-18.5	Niklitschek (2001), Niklitschek and Secor (2005,2009),
	Dissolved Oxygen (mg l^{-1})	3.3	5.0	Niklitschek and Secor (2009)
Yearling	Temperature (^{o}C)	0-28	16-24	Niklitschek and Secor (2005,2009), Dovel and Berggren 1983
	Salinity	0-29	18.5-25.5	Niklitschek and Secor (2005,2009)
	Dissolved Oxygen (mg l^{-1})	3.3	5.0	Niklitschek and Secor (2009)

Table 1: Required and optimal physiological tolerances of young-of-the-year and yearling Atlantic sturgeon based on a literature review.

Table 2: Correlation coefficients based on the comparison of fixed criteria and

	Annual	Seasonal	Start Date	Duration	Reduction
YOY- Required	N.S.	0.74**	0.87***	0.68*	N.S.
YOY- Optimal	0.81**	0.81**	N.S.	N.S.	0.87***
Yearling- Required	0.98***	0.95***	0.79**	0.65*	0.65*
Yearling- Optimal	N.S.	N.S.	N.S.	N.S.	-0.67*

bioenergetics habitat modeling approaches for five metrics of each life stage and habitat type. 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 1st to November 15th). Start date refers to the date of hypoxia onset. Duration refers to the duration of seasonal hypoxia. Reduction refers to the volume of habitat that was reduced by hypoxia (daily differences in volume between models with and without dissolved oxygen limitation summed from May 1st to November 15th).

Footnote:
Significant correlation coefficient values derived from Pearson's correlation analysis between predictions calculated with fixed criteria and bioenergetics habitat volume models for combinations of lifestage and habitat type. * = P<0.05, **=P<0.01, ***=P<0.001. N.S. = not significant.

	Annual	Seasonal	Start Date	Duration	Reduction
YOY- Required	<0.0001	<0.0001	<0.0001	N.S.	0.0012
YOY- Optimal	0.0005	0.0006	N.S.	0.0031	0.0008
Yearling- Required	<0.0001	<0.0001	<0.0001	N.S.	0.0025
Yearling- Optimal	<0.0001	<0.0001	N.S.	N.S.	<0.0001

Table 3: Significant P-values derived from paired t-tests of metrics estimated using fixed criteria and bioenergetics habitat modeling approaches for each life stage and habitat type. 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 1st to November 15th). Start date refers to the date of hypoxia onset. Duration refers to the duration of seasonal hypoxia. Reduction refers to the volume of habitat that was reduced by hypoxia (daily differences in volume between models with and without dissolved oxygen limitation summed from May 1st to November 15th). N.S. = not significant.
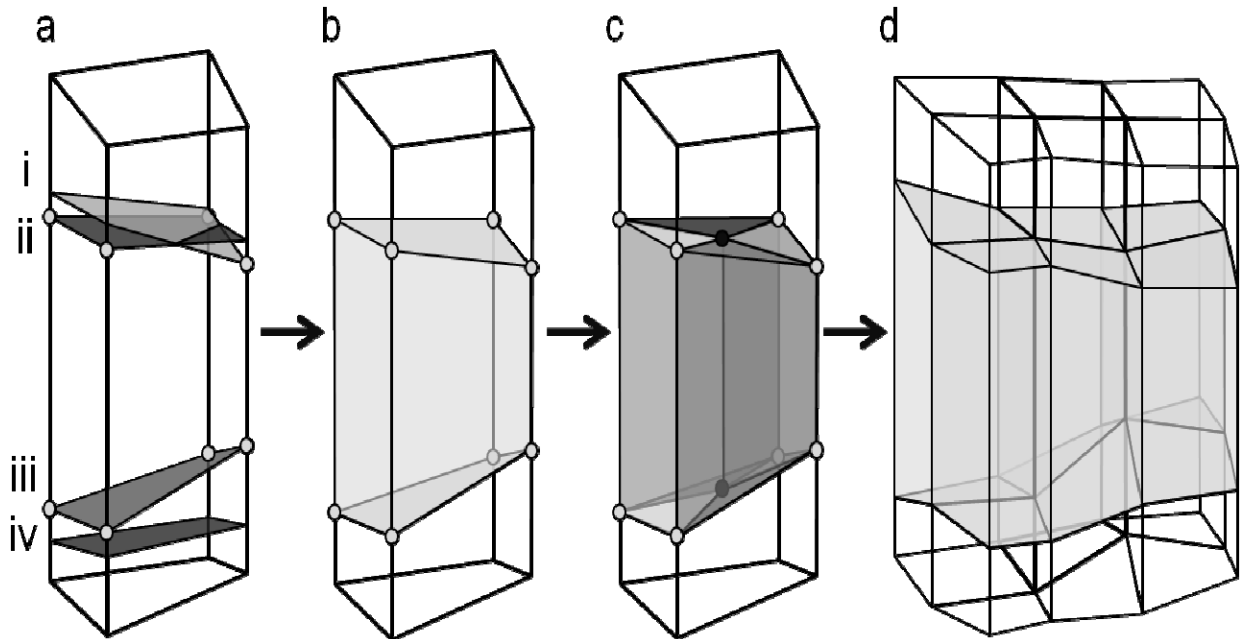
Figure 2.1: Diagram of habitat volume calculation. (a) Upper bound for salinity (i), lower bound for dissolved oxygen (iii), and upper (ii) and lower (iv) bounds for temperature are found based on linear interpolation of properties in the vertical direction and the species' physiological tolerances. (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 four "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.

A) YOY   B) Yearling
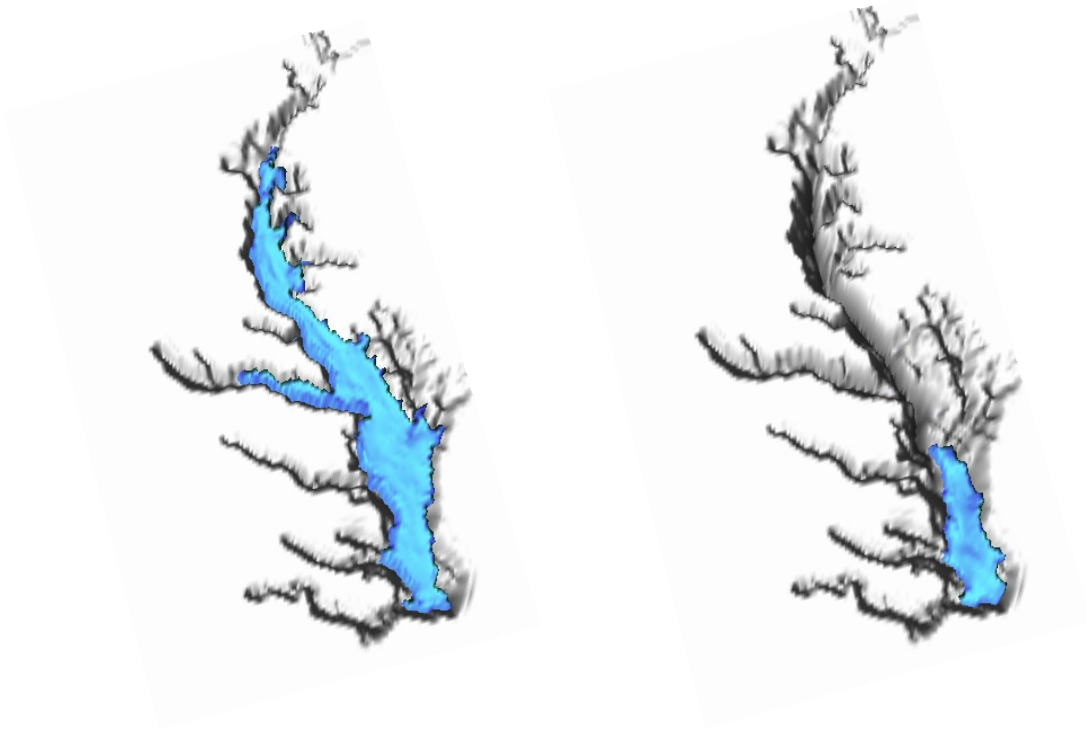
Figure 2.2: 3D habitat volume model output. Example of optimal habitat volume (blue) for young-of-the-year (YOY) (A) and yearling (B) Atlantic sturgeon on July 6, 1996. Optimal habitat requirements for YOY are as follows: temperature (16-24 $^{\circ}$C), salinity (3.5-18.5), and dissolved oxygen ($\geq$5.0 mg l^{-1}). Optimal habitat requirements for yearlings are as follows: temperature (16-24 $^{\circ}$C), salinity (18.5-25.5), and dissolved oxygen ($\geq$5.0 mg l^{-1}).
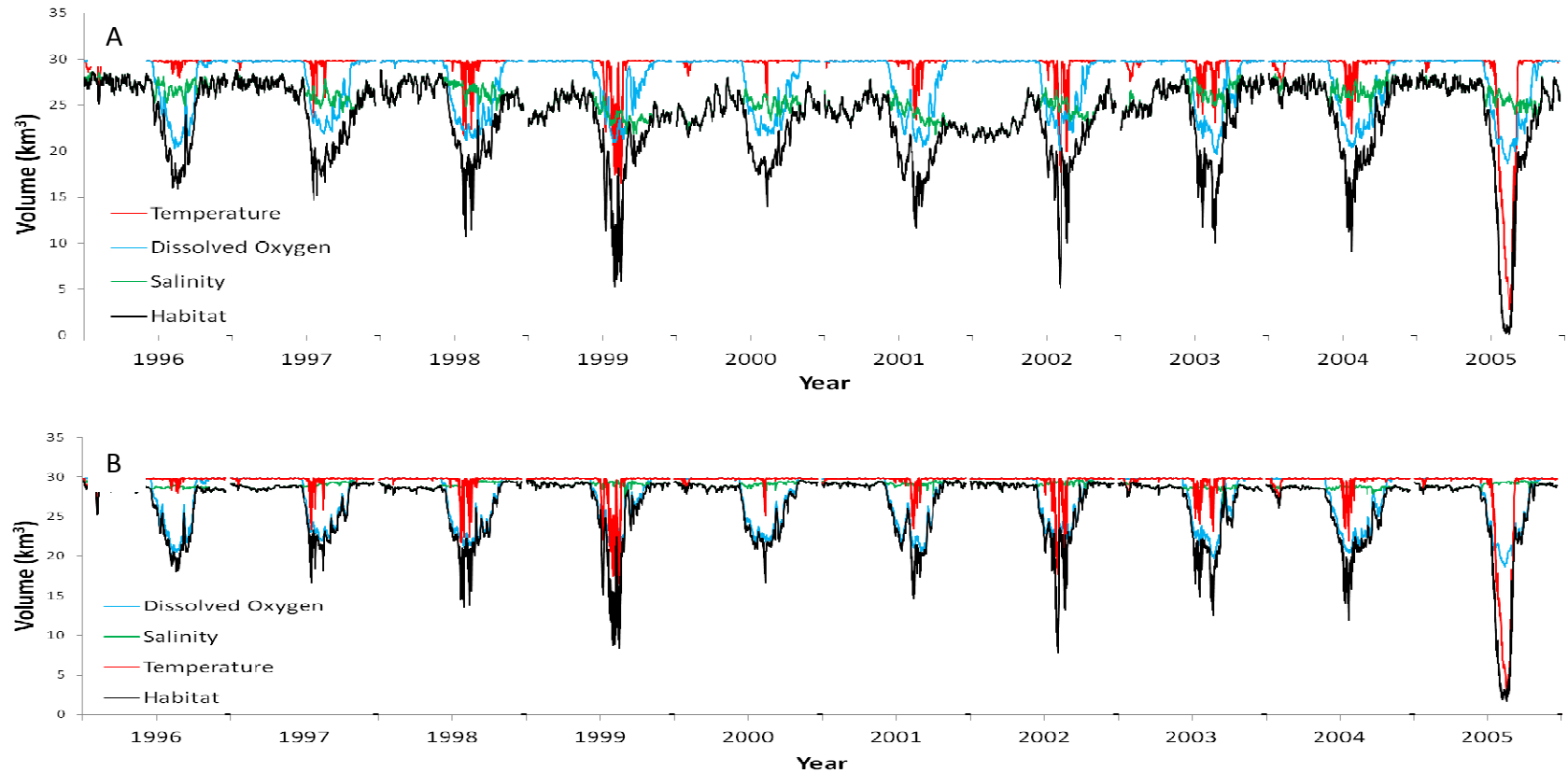
Figure 2.3: Time series of Bay-wide required habitat volumes. Lines indicate the daily volume index of water meeting specified temperature (red), salinity (green), and dissolved oxygen (blue) constraints as well as overall required habitat (black) for (A) young-of-the-year (YOY) and (B) yearling Atlantic sturgeon. Constraints for required habitat for YOY are 0-28 $^{\circ}$C for temperature, 0-22 for salinity, and $\geq$3.3 mg l^{-1} for dissolved oxygen. Constraints for yearling are 0-28 $^{\circ}$C for temperature, 0-29 for salinity, and $\geq$3.3 mg l^{-1} for dissolved oxygen.

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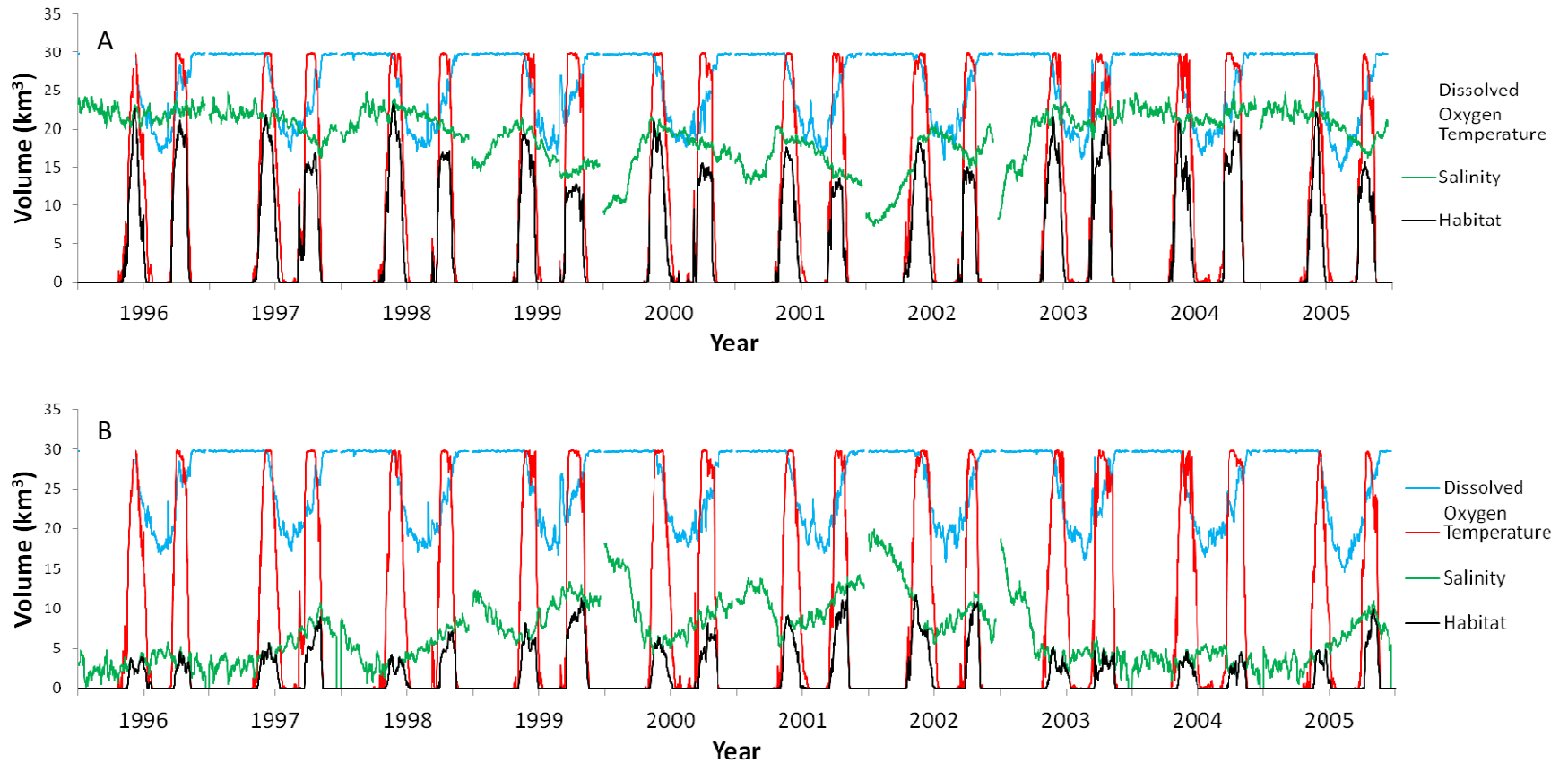
Figure 2.4: Time series of Bay-wide optimal habitat volumes. Lines indicate the daily volume index of water meeting specified temperature (red), salinity (green), and dissolved oxygen (blue) constraints as well as overall optimal habitat (black) for (A) young-of-the-year (YOY) and (B) yearling Atlantic sturgeon. Constraints for optimal habitat for YOY are 16-24 °C for temperature, 3.5-18.5 for salinity, and ≥5.0 mg l^{-1} for dissolved oxygen. Constraints for yearling are 16-24 °C for temperature, 18.5-25.5 for salinity, and ≥5.0 mg l^{-1} for dissolved oxygen.

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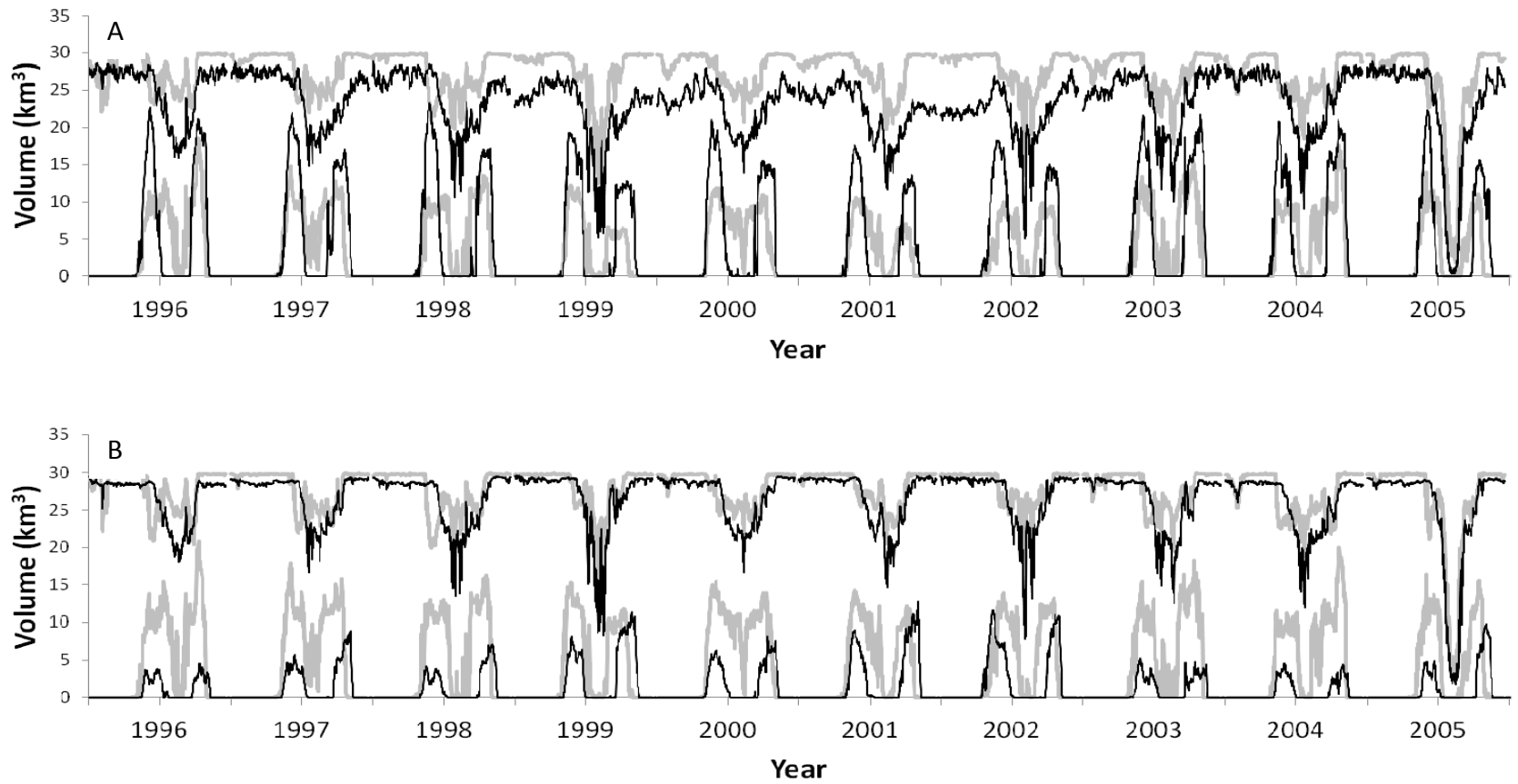
Figure 2.5: Comparison of fixed criteria and bioenergetics model output. Bay-wide volume of required (upper lines) and optimal (lower lines) habitat over the course of each year predicted by fixed criteria (black lines) and bioenergetics (grey lines) models for (A) young-of-the-year and (B) yearling Atlantic sturgeon.
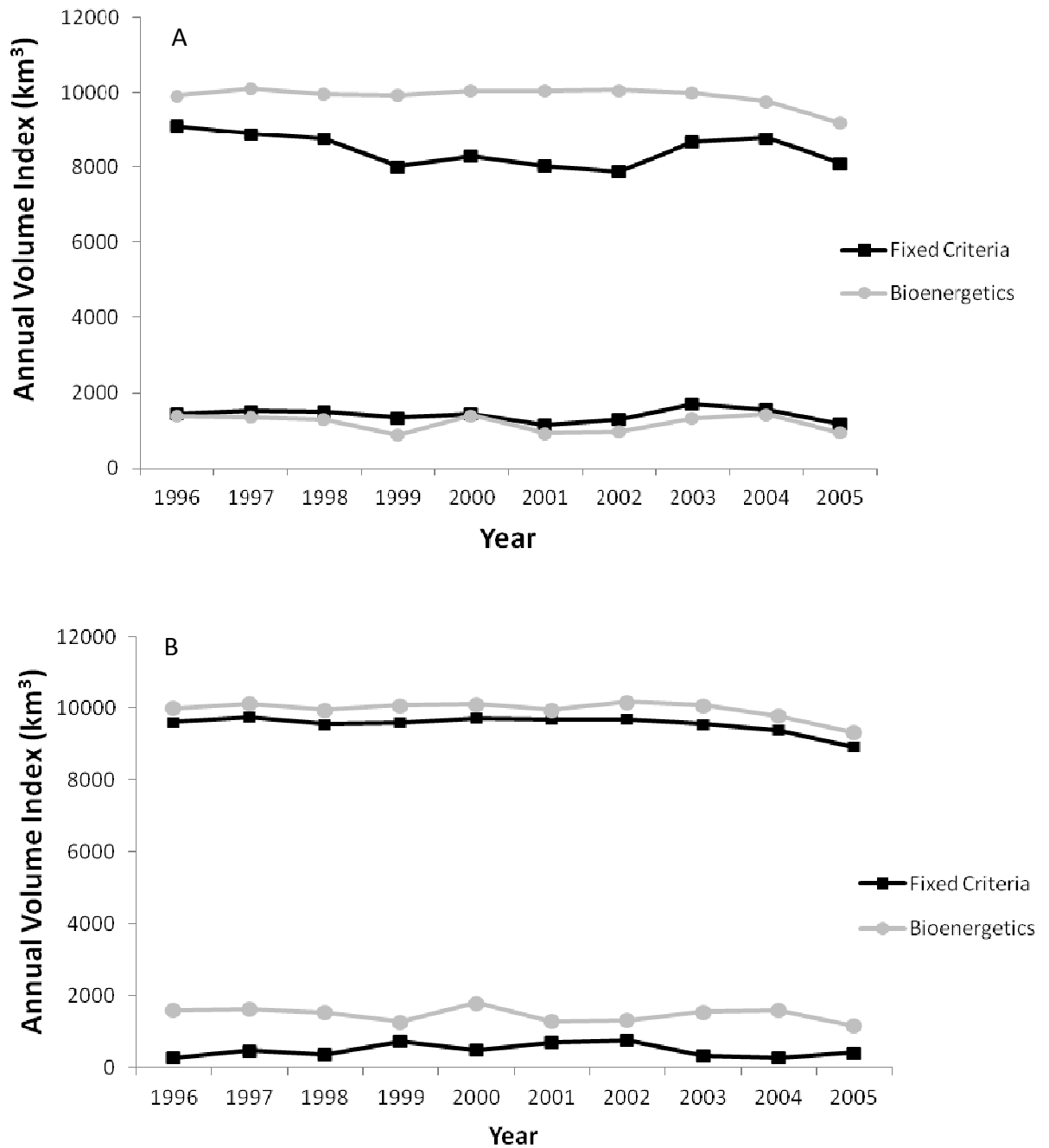
Figure 2.6: Time series of annual habitat volumes. Annual volume index of required (upper lines) and optimal habitat (lower lines) defined by fixed criteria and bioenergetics for (A) young-of-the-year and (B) yearling Atlantic sturgeon between 1996 and 2005. Annual volumes were calculated by summing model predictions of habitat volume for each year.
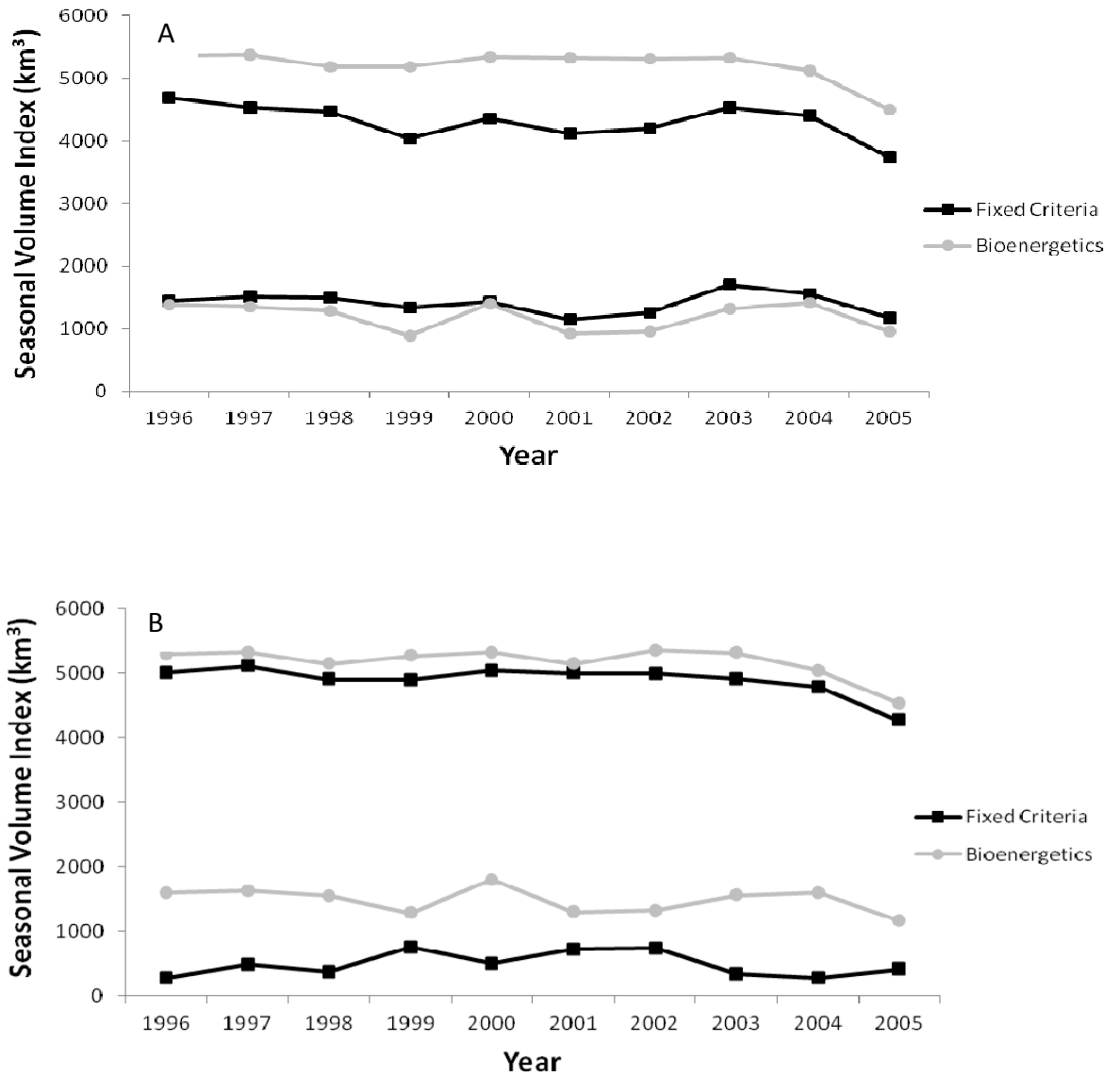
Figure 2.7: Time series of total habitat volumes between May 1st and November 15th. Seasonal volume index of required (upper lines) and optimal habitat (lower lines) defined by fixed criteria and bioenergetics for (A) young-of-the-year and (B) yearling Atlantic sturgeon between 1996 and 2005. Seasonal volumes were calculated by summing daily model predictions of habitat volume during the time period of seasonal hypoxia (May 1st and November 15th).
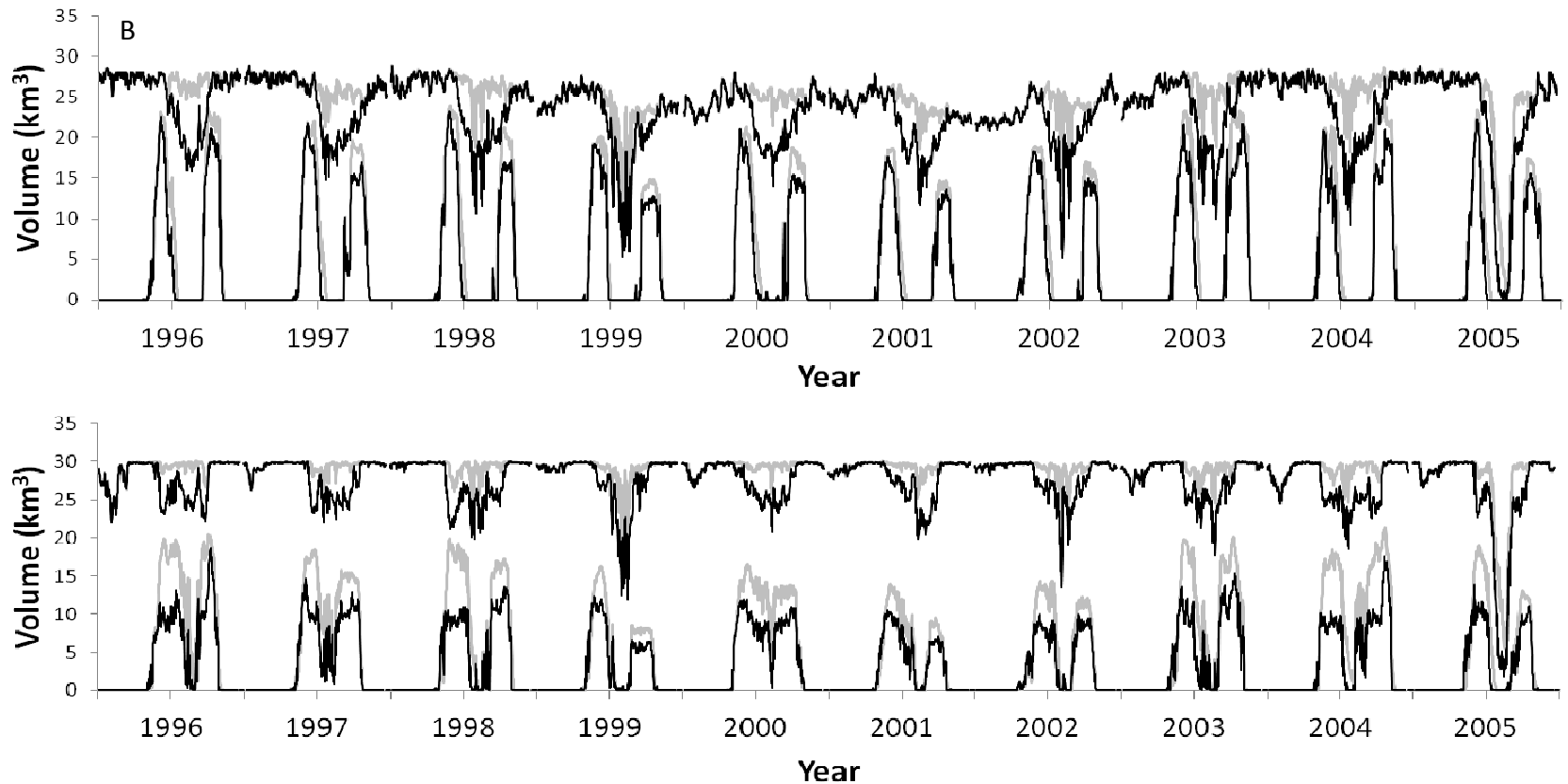
Figure 2.8: Time series of Bay-wide habitat volume with and without dissolved oxygen limitation for young-of-the-year Atlantic sturgeon. Predicted daily volume of required (upper lines) and optimal (lower lines) habitat in the presence of dissolved oxygen limitations (black lines) and without dissolved oxygen limitation (gray lines) during 1996-2005. Estimates were calculated with the (A) fixed criteria and (B) bioenergetics habitat volume models.
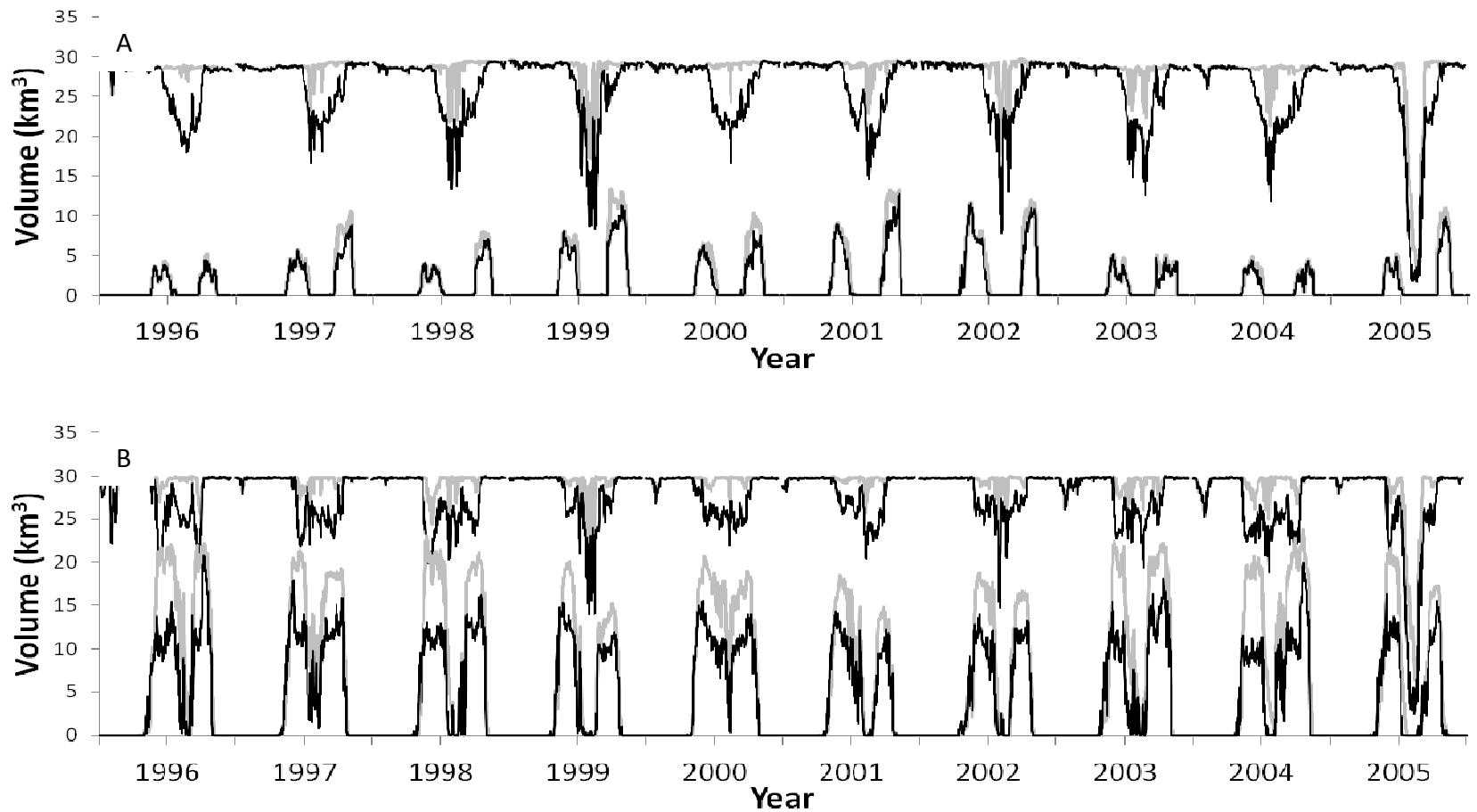
Figure 2.9: Time series of Bay-wide habitat volume with and without dissolved oxygen limitation for yearling Atlantic sturgeon. Predicted daily volume ofrequired (upper lines) and optimal (lower lines) habitat in the presence of dissolved oxygen limitations (black lines) and without dissolved oxygen limitation (gray lines) during 1996-2005. Estimates were calculated with the (A) fixed criteria and (B) bioenergetics habitat volume models.
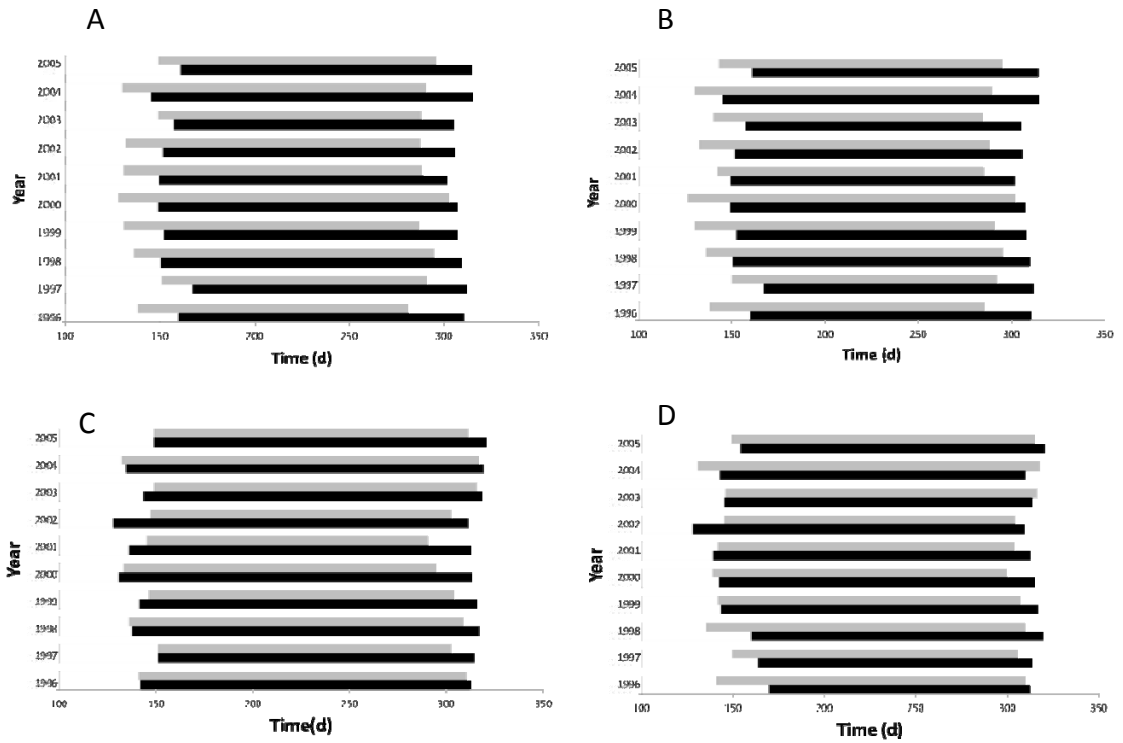
Figure 2.10: Duration of low dissolved oxygen limitation of required (A, B) and optimal (C, D) habitat for (A, C) young-of-the-year and (B, D) yearling Atlantic sturgeon defined by fixed criteria (black bars) and bioenergetics (gray bars) models.
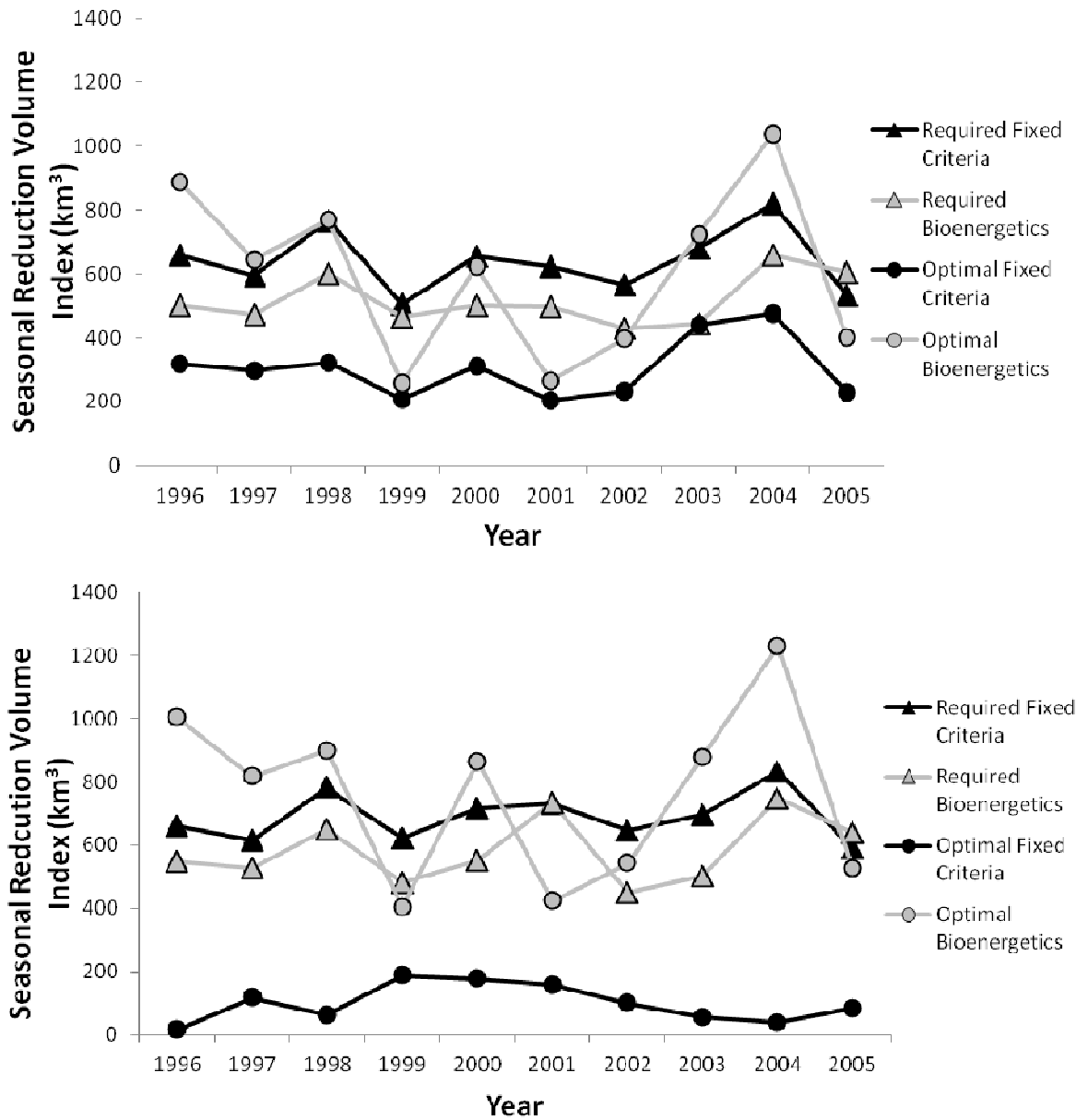
Figure 2.11: Reduction in habitat volume due to low dissolved oxygen from May 1st and November 15th. Seasonal volume reduction index of required and optimal habitat due to hypoxia defined by fixed criteria and bioenergetics for (A) young-of-the-year and (B) yearling Atlantic sturgeon between 1996 and 2005. Seasonal volume reductions were calculated by summing daily differences in model predictions of habitat volume with and without dissolved oxygen limitations during the time period of seasonal hypoxia (May 1st and November 15th).
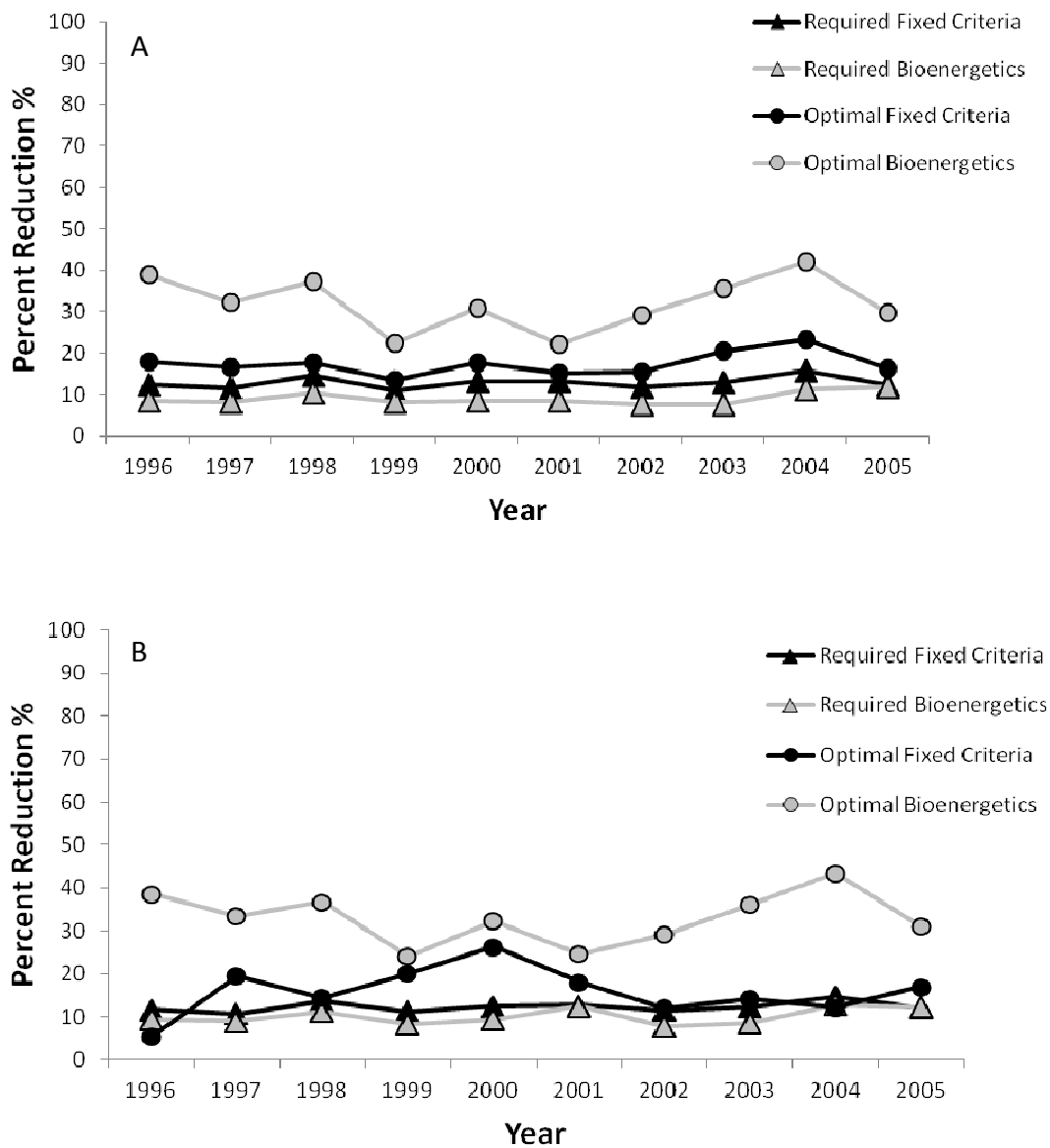
Figure 2.12: Percent decrease of required and optimal habitat due to hypoxia calculated by fixed criteria and bioenergetics models for (A) young-of-the-year and (B) yearling Atlantic sturgeon during the time period of seasonal hypoxia (May 1st and November 15th) between 1996 and 2005.

Chapter 4. Conclusions

This thesis project represents the first step towards an extensive quantitative assessment of habitat volumes for a suite of Chesapeake Bay living resources and how those volumes might change under future climate and nutrient loading scenarios. The systematic literature review and proof-of-concept model results provide a foundation for subsequent progress in the habitat modeling. With the inclusion of a more realistic biogeochemical model, the accuracy of habitat volume estimates using the habitat volume model will significantly increase. That increase in accuracy will provide policy makers with the information and confidence necessary to make appropriate management decisions. The information that these models provide could also be used for additional research opportunities. For example, habitat volume could potential be used as a metric to predict stock recruitment; something that has proven notoriously difficult to forecast. The implications of this work are also far reaching in that the habitat volume model can be applied to any system with a functional hydrodynamic model.

Results of the systematic literature review illuminate the need for more extensive research of physiological tolerances for species living within the Chesapeake Bay. Although such studies and data may not have been a historically critical component of ecological research, their use in modern modeling techniques makes them invaluable. Numerical modeling has resulted in a wide variety of high impact solutions to a number of ecologically relevant problems and future advancements will only increase their versatility (Elith 2002, Najjar et al. 2010, Hinrichsen et al. 2011). However, the power of these methodologies can only be fully realized if the information used to drive them is accurate and complete. In terms of modeling potential habitat for Chesapeake Bay living

resources, this literature review has exposed prominent gaps, inconsistencies, and inaccuracies in the current field of available research. The results of this review combined with the proof-of-concept habitat modeling emphasize the importance of this information for management and conservation and demonstrate the need for the continued study of these species.

Through the use of Atlantic sturgeon juveniles as a test species, this research has shown that the habitat volume model can make high spatial and temporal resolution estimates of potential habitat. What sets this methodology apart from general bioclimatic envelope modeling (Pearson and Dawson 2003, Araujo et al. 2005) is that habitat distributions are derived from physiological relationships rather than statistical correlations. Instead of estimating habitat based upon correlations to specific environmental factors, the habitat volume model incorporates the functional mechanisms underlying those relationships because it is based on physiological tolerances. In addition, the ability to quantify the volume of individual water masses along with the volume of their intersection makes this model unique when compared to previous habitat modeling efforts (Neuenfeldt et al. 2002, Kimmerer et al. 2009). The influences of temperature, salinity, and dissolved oxygen on habitat can be independently assessed or looked at in combination. The influence of each physiological constraint on habitat can be effectively quantified and converted into metrics to assess the living conditions available to a particular species as well as the effect of seasonal and spatial dynamics of hypoxia on them. This research has also demonstrated the habitat volume model's capability of incorporating various methods of defining habitat such as fixed criteria and

bioenergetics approaches. The proof-of-concept study presented in this thesis highlights the capabilities of this model and paves the way for future applications.

As numerical modeling techniques advance, with respect to biogeochemistry and hydrodynamics, the applicability of this model towards ecological problem solving will increase along with them. The versatility of the habitat volume model will also allow the inclusion of additional ecosystem characteristics when the respective data and quantitative relationships become available, such as predator and prey interactions or competition. Future research efforts will expand upon the species covered in this study, hopefully filling in essential gaps highlighted by the systematic literature review. The incorporation of these potential improvements will result in a robust tool, enabling the scientific community to gain insight into how future climate change and nutrient loading will affect the living resources of coastal systems and hopefully provide the quantitative information necessary to support effective policy decisions.

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Appendix A: Quality Point Assignments

The following are the quality point scoring explanations for each species and lifestage covered in the systematic literature review (Chapter 2). Each species is broken down into individual lifestages. Lifestages are further categorized into specific temperature, salinity, and dissolved oxygen parameters for both required and optimal habitats. Ratings are given to each relevant paper by summing points for various measures of accuracy and consistency (see Chapter 2, Methods, for a complete description). The quality matrix score for some parameters may be a combination of the average of ratings of more than one paper for the upper and lower boundaries of the given range. References for citations can be found in Chapter 2.

A. Blue Crab (*Callinectes sapidus*)
Egg
Required temperature: quality score = 25
 Sandoz and Rogers (1944) set entire range.
- Lab study, a numerous replications = 20
- Peer Reviewed = 1
- Supported by Tankersley and Forward (2007) = 1

- Chesapeake Bay population = 3

Optimal temperature: quality score = 25
Sandoz and Rogers (1944) set entire range
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Tankersley and Forward (2007) = 1
- Chesapeake Bay population = 3

Required salinity: quality score = 26
Sandoz and Rogers (1944) set entire range
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Tankersley and Forward (2007) and Costlow and Bookhout (1959) = 2
- Chesapeake Bay population = 3

Optimal salinity: quality score = 25
Sandoz and Rogers (1944) set entire range
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Tankersley and Forward (2007) = 1
- Chesapeake Bay population = 3

Required dissolved oxygen: quality score = 2
Aguilar et al. (2005) set threshold.
- Biological assumption = 2

Optimal dissolved oxygen: quality score = N.D.

Larvae
Required temperature: average of quality scores for lower and upper limit (17+22)/2 = 19.5
Costlow (1967) set lower limit
- Lab study, numerous replications = 20
- Peer Reviewed = 1
- Supported by Tankersley and Forward (2007) = 1
Costlow and Bookhout (1959) set upper limit
- Lab study, focused mainly on development and not many temperature replications = 15
- Peer Reviewed = 1
- Supported by Tankersley and Forward (2007) = 1

Optimal temperature: quality score = 25
Sandoz and Rogers (1944) set entire range
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Tankersley and Forward (2007) = 1
- Chesapeake Bay population = 3

Required salinity: average of quality scores for lower and upper limit (26+13)/2 = 19.5
Sandoz and Rogers (1944) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Costlow and Bookhout (1959) and Tankersley and Forward (2007)= 2
- Chesapeake Bay population = 3
Ogburn and Forward (2009) set the upper limit
- Field study, good spatial and temporal resolution = 10
- Peer reviewed = 1
- Supported by Costlow and Bookhout (1959) and Tankersley and Forward (2007) = 2

Optimal salinity: average of quality scores for lower and upper limit = (26+18)/2 = 22
Sandoz and Rogers (1944) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Costlow and Bookhout (1959) and Tankersley and Forward (2007)= 2
- Chesapeake Bay population = 3
Costlow and Bookhout (1959) set upper limit
- Lab study, focused mainly on development and not many temp replications = 15
- Peer Reviewed = 1
- Supported by Sandoz and Rogers (1944) and Tankersley and Forward (2007) = 2

Required dissolved oxygen: quality score = 20
Tankersley and Wieber (2000) set threshold
- Lab study, numerous replications, linear relationship applied to existing data for specific 6 hour LC50 = 18
- Peer Reviewed = 1
- Supported by Tankersley and Forward (2007) = 1

Optimal dissolved oxygen: quality score = N.A.

Juvenile/Adult
Required temperature: quality score = 26
Tagatz 1969 set entire range
- Lab study, numerous replications = 20
- Peer Reviewed = 1
- Supported by Miller and Bauer (2010) and Tankersley and Forward (2007) = 2
- Quantitative Relationship, only two points = 3

Optimal temperature: quality score = 25
Cadman and Weinstein (1988) set entire range
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Tankersley and Forward (2007) = 1

Required salinity: quality score = 22
Guerin and Stickle (1992) set entire range
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Tankersley and Forward (2007) = 1

Optimal salinity: average of quality scores for lower and upper limit = (22+17)/2 = 19.5
Guerin and Stickle (1992) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Tankersley and Forward (2007) = 1

Rosenburg and Costlow (1976) set upper limit = 17
- Lab study, also testing influence of cadmium = 15
- Peer reviewed =1
- Supported by Tankersley and Forward (2007) = 1

Adult Required dissolved oxygen: quality score = 27
Carpenter and Cargo (1957) set threshold
Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Stickle et al. (1989), deFur et al. (1990), Tankersley and Forward (2007) = 3

-

Juvenile Required dissolved oxygen: quality score = 20
Tankersley and Wieber (2000) set threshold

- Lab study, numerous replications, linear relationship applied to existing data for specific 6 hour LC50 = 18
- Peer Reviewed = 1
- Supported by Tankersley and Forward (2007) = 1

Optimal dissolved oxygen: quality score = 25
deFur et al. (1990) set threshold

- Lab study, numerous replications = 20
- Peer Reviewed = 1
- Chesapeake Population = 3
- Supported by Tankersley and Forward (2007) = 1

B. Eastern Oyster (*Crassostrea virginica*)
Eggs
Required temperature: average of quality scores for lower and upper limit = (23+30)/2 = 26.5
Clark (1935) set lower limit

- Lab study, numerous replications = 20
- Supported by Davis and Calabrese (1964), Loosanoff (1965), MacInnes and Calabrese (1979) = 3

Wright et al. (1983) set upper limit

- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Davis and Calabrese (1964), Roosenburg et al. (1970), Loosanoff (1965), (Hidu et al. 1974), Clark (1935), MacInnes and Calabrese (1979) = 6

Optimal temperature: average of quality scores for lower and upper limit = (22+21)/2 = 21.5
 Davis and Calabrese (1964) set lower limit

- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Clark (1935) = 1

Clark (1935) set upper limit

- Lab study, numerous replications = 20
- Supported by Davis and Calabrese (1964) = 1

Required salinity: average of quality scores for lower and upper limit = (25+24)/2 = 24.5

Davis and Calabrese (1964) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Clark (1935), Loosanoff (1965), Davis (1958), Amemiya (1929) = 4

Clark (1935) set upper limit
- Lab study, numerous replications = 20
- Supported by Davis and Calabrese (1964), Amemiya (1929), Loosanoff (1965), Davis (1958) = 4

Optimal salinity: average of quality scores for lower and upper limit = (25+25)/2 = 25
Davis (1958) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Loosanoff (1965), Cake et al. 1983, Davis and Calabrese (1964), Amemiya (1929) = 4

Amemiya (1929) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Loosanoff (1965), Cake et al. 1983, Davis and Calabrese (1964), Davis (1958) = 4

Required dissolved oxygen: quality score = N.A.

Optimal dissolved oxygen: quality score = N.A.

Larvae
Required temperature: average of quality scores for lower and upper limit = (22+25)/2 = 23.5
Davis and Calabrese (1964) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Lough (1975) = 1

Hidu et al. (1974) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Population = 3
- Supported by Wright et al. (1983) = 1

Optimal temperature: average of quality scores for lower and upper limit = (25+22)/2 = 23.5
MacInnes and Calabrese (1979) set lower limit
- Lab study, numerous replications = 20

- Peer reviewed = 1
- Chesapeake population = 3
- Supported by Davis and Calabrese (1964) = 1

Davis and Calabrese (1964) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by MacInnes and Calabrese (1979) = 1

Required salinity: average of quality scores for lower and upper limit = (24+24)/2 = 24

Davis (1958) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Davis and Calabrese (1964), Amemiya (1926), Carriker (1929) = 3

Amemiya (1926) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Davis and Calabrese (1964), Davis (1958), Carriker (1929) = 3

Optimal salinity: average of quality scores for lower and upper limit = (23+23)/2 = 23

Davis and Calabrese (1964) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Davis (1958), Amemiya (1926) = 2

Amemiya (1926) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Davis and Calabrese (1964), Davis (1958) = 2

Required dissolved oxygen: quality score = 26

Baker and Mann (1994) set threshold
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Population = 3
- Supported by Baker and Mann 1992, Widdows et al. (1989) = 2

Optimal dissolved oxygen: quality score = 24

Baker and Mann (1994) set threshold
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Population = 3

Juvenile/Adult

Required temperature: average of quality scores for lower and upper limit = (24+28)/2 = 26

Stanley et al (1986) set lower limit
- Lit review, in depth lab studies = 20
- Chesapeake Bay populations = 3
- Supported by Shumway (1996), Loosanoff (1965), Butler 1954 = 1

Fingerman and Fairbanks (1957) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Henderson (1929), Ingle et al. (1971), Galtsoff (1964), Copeland and Hoese (1966), Nichy and Menzel (1960), Tinsman and Maurer (1974), Loosanoff (1965) = 7

Optimal temperature: average of quality scores for lower and upper limit = (24+25)/2 = 24.5

Stanley et al. (1986) set lower limit
- Lit review, in depth lab studies = 20
- Chesapeake Bay populations = 3
- Supported by Galtsoff (1964), Collier (1951), Galtsoff (1927) = 1

Loosanoff (1958) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Stanley et al. (1986), Galtsoff (1964), Collier (1951), Galtsoff (1927) = 4

Required salinity: average of quality scores for lower and upper limit = (24+16)/2 = 20

Loosanoff (1953) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Wells (1961), Chanley (1958), Galtsoff (1964) = 3

Copeland and Hoese (1966) set upper limit
- Field Study = 10
- Peer reviewed = 1
- Supported by Menzel et al. (1966), Ingle and Dawson (1950), Galtsoff (1964), Butler (1952), Gunter (1950) = 5

Optimal salinity: average of quality scores for lower and upper limit = (24+27)/2 = 25.5

Loosanoff (1953)
- Lab study, numerous replications = 20

-   Peer reviewed = 1
-   Supported by Chanley (1958), Galtsoff 1964, Butler (1954) = 3

Galtsoff (1964)
-   Lit synthesis, in depth lab studies = 20
-   Peer reviewed = 1
-   Chesapeake Bay population = 3
-   Supported by Chanley (1958), Loosanoff (1953), Butler (1954) = 3

Required dissolved oxygen: quality score = 22
Sparks et al. (1957) set threshold
-   Lab study, numerous replications = 20
-   Peer reviewed = 1
-   Supported by Galtsoff (1964) = 1

Optimal dissolved oxygen: quality score = N.A.

C. Striped Bass (*Morone saxatilis*)
Egg
Required temperature: quality score = 28
Morgan and Rasin (1981) set entire range
-   Lab study, numerous replications = 20
-   Peer reviewed = 1
-   Chesapeake population = 3
-   Supported by Morgan and Rasin (1973), Crance (1984), Barkuloo (1970), and Albrecht (1964) = 4

Optimal temperature: quality score = 26
Morgan and Rasin (1981) set entire range
-   Lab study, numerous replications = 20
-   Peer reviewed = 1
-   Chesapeake population = 3
-   Supported by Morgan and Rasin (1973) and Rogers and Westin (1978) = 2

Required salinity: quality score = 22
Winger and Lasier (1994) set entire range
-   Lab study, numerous replications = 20
-   Peer reviewed = 1
-   Supported by Morgan and Rasin (1981) = 1

Optimal salinity: average of quality scores for lower and upper limit = (23+23)/2 = 23
Geiger and Parker (1985) set lower limit
-   Analysis of hatchery survey = 18

- Peer reviewed = 1
- Supported by Bonn et al. (1976), Albrecht (1964), Dovel (1971), North and Houde (2003) = 4

Bonn et al. 1976 set upper limit
- Lab study, numerous replications = 20
- Supported by Geiger and Parker (1985), Albrecht (1964), Dovel (1971) = 3

Required dissolved oxygen: quality score = 22
Harrell and Bayless (1981) set threshold
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Turner and Farley (1971) = 1

Optimal dissolved oxygen: quality score = 19
O'Malley and Boone (1972) set threshold
- Lab study, not many replications = 15
- Peer reviewed 1
- Chesapeake population = 3

Larvae
Required temperature: quality score = 33
Morgan and Rasin (1981) set entire range
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake population = 3
- Supported by Morgan and Rasin (1973), Kernehan et al. (1981), Dey (1981), Houde et al. (1988), Uphoff Jr. (1989), Boreman (1983), Logan (1985), Regan et al. (1968), Doroshev (1970) = 9

Optimal temperature: average of quality scores for lower and upper limit = (27+23)/2 = 25
Morgan and Rasin (1981) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake population = 3
- Supported by Doroshev (1970), Regan et al. (1986), Rogers et al. (1977) = 3

Rogers et al (1977) set upper limit
- Lab study, numerous replications = 20
- Supported by Morgan and Rasin (1981), Doroshev (1970), Regan et al. (1986) = 3

Required salinity: average of quality scores for lower and upper limit = (22+18)/2 = 20
Albrecht et al. (1964) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Bayless (1972) = 1
Bayless (1972) set upper limit
- Lab study, estimated salinity required due to low resolution = 17
- Supported by Albrecht et al. (1964) = 1

Optimal salinity: average of quality scores for lower and upper limit = (23+21)/2 = 22
Germann and Reeves (1974) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Barwick (1973) and Albrecht et al. (1964) = 2
Morgan and Rasin (1973) set upper limit
- Lab study, numerous replications = 20
- Supported by Bayless (1972) = 1

Required dissolved oxygen: quality score = 22
Turner and Farley (1971) set threshold
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Rogers et al. (1980) = 1

Optimal dissolved oxygen: quality score = 21
Turner and Farley (1971) set threshold
- Lab study, numerous replications = 20
- Peer reviewed = 1

Juvenile
Required temperature: average of quality scores for lower and upper limit = (17+23)/2 = 20
Cook et al. (2006) set lower limit
- Modeling study = 15
- Peer reviewed = 1
- Supported by Matthews et al. (1989) = 1
Cox and Coutant (1981) set upper limit
- Lab study, a numerous replications = 20
- Peer reviewed = 1
- Supported by Cook et al. (2006) and Matthews et al. (1989) = 2

Optimal temperature: quality score = 24

Coutant et al. (1984) set entire range
- Lab study, a numerous replications = 20
- Peer reviewed = 1
- Supported by Cox and Coutant (1981), Meldrin and Gift (1971), Matthews et al. (1989) = 3

Required salinity: quality score = 22
Tagatz (1961) set entire range
- Lab study, lot replications = 20
- Peer reviewed = 1
- Supported by Otwell and Merriner (1975) = 1

Optimal salinity: quality score = 27
Secor et al. (2000) set entire range
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Population = 3
- Supported by Dovel (1971), Rothschild (1990), Bonn et al. (1976) = 3

Required dissolved oxygen: quality score = 22
Chittenden (1972) set threshold
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Coutant (1985) = 1

Optimal dissolved oxygen: quality score = 27
Brandt et al. (2009) set threshold
- Lab study, numerous replications = 20
- Chesapeake Bay population = 3
- Peer reviewed = 1
- Supported by Coutant (1985), Meldrim et al. (1974), Chittenden (1972) = 3

Adults
Required temperature: average of quality scores for lower and upper limit = (21+17)/2 = 19
Kelly and Kohler (1999) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
Coutant and Benson (1990) set upper limit
- Field study = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3

- Supported by Merriman (1941), Wooley and Crateau (1983), Farquhar and Gutreuter (1989) = 3

Optimal temperature: quality score = 25
Talbot (1966) set entire range
- Lab study, numerous replications = 20
- Chesapeake Bay population = 3
- Supported by Coutant and Carroll (1980), Schaich and Coutant (1980) = 2

Required salinity: quality score = 22
Tagatz (1961) set entire range
- Lab study, lot replications = 20
- Peer reviewed = 1
- Supported by Hardy (1978) = 1

Optimal salinity: average of quality scores for lower and upper limit = (14+16)/2 = 15
Rothschild (1990) set lower limit
- Field study = 10
- Peer reviewed =1
- Chesapeake Bay population = 3
Walter et al. (2003) set upper limit
- Field Study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Chapoton and Sykes (1961), Diodati and Richards (1996) = 2

Required dissolved oxygen: quality score = 19
Chittenden (1971a) set threshold
- Lab study, unpublished data = 15
- Chesapeake Bay population = 3
- Supported by Coutant (1985) = 1

Optimal dissolved oxygen: quality score = 21
Chittenden (1971a) set threshold
- Lab study, unpublished data = 15
- Chesapeake Bay population = 3
- Supported by Cheek et al. (1985), Coutant (1985), Brandt et al. (2009) = 3

D. Bay Anchovy (*Anchoa mitchilli*)
Eggs
Required temperature: quality score = 17

Dovel (1971) set entire range
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by (Dovel 1981), Dalton (1987), Rilling and Houde (1999) = 3

Optimal temperature: quality score = 17
Dovel (1971) set entire range
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Dalton (1987), Rilling and Houde (1999), and Peebles (2002)= 3

Required salinity: average of quality scores for lower and upper limit = (19+19)/2 = 19
Dovel (1971) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Dovel (1981), Olney (1983), Rilling and Houde (1999), Dovel (1967), Peebles (2002) = 5
Olney (1983) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Dovel (1981), Dovel (1971), Rilling and Houde (1999), Dovel (1967), Peebles (2002) = 5

Optimal salinity: average of quality scores for lower and upper limit = (17+20)/2 = 18
Dovel (1971) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Olney (1983), Lippson et al. (1979), Rilling and Houde 1999 = 3
Rilling and Houde (1999) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Dovel (1971), Lippson et al. (1979), Olney (1983), North and Houde (2004), Jung and Houde (2003), Jung and Houde (2004) = 6

Required dissolved oxygen: quality score = 24
Chesney and Houde (1989) set threshold
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Optimal dissolved oxygen: quality score = 24
Chesney and Houde (1989) set threshold
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Larvae
Required temperature: average of quality scores for lower and upper limit = (17+28)/2 = 22.5
Olney (1983) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Dovel (1971), Rilling and Houde (1999), Dokken et al. 1984= 3
Houde (1974) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Dovel (1971), Dokken (1984), Olney (1983), Rilling and Houde (1999) = 4

Optimal temperature: average of quality scores for lower and upper limit = (15+25)/2 = 20
Dovel (1971) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Houde (1974) = 1
Houde (1974) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Dovel (1971) = 1

Required salinity: average of quality scores for lower and upper limit = (17+17)/2 = 17
Dovel (1971) set lower limit
  - Field study, high resolution = 10
  - Peer reviewed = 1
  - Chesapeake Bay population = 3
  - Supported by Dokken (1984), Olney (1983), Rilling and Houde (1999) = 3
Olney (1983)
  - Field study, high resolution = 10
  - Peer reviewed = 1
  - Chesapeake Bay population = 3
  - Supported by Dokken (1984), Dovel (1971), Rilling and Houde (1999) = 3

Optimal salinity: quality score = 15
Dovel (1971) set entire range
  - Field study, high resolution = 10
  - Peer reviewed = 1
  - Chesapeake Bay population = 3
  - Supported by Dovel (1981) = 1
Required dissolved oxygen: quality score = 25
Chesney and Houde (1989) set threshold
  - Lab study, numerous replications = 20
  - Peer reviewed = 1
  - Chesapeake Bay population = 3
  - Supported by Breitburg (1994) = 1

Optimal dissolved oxygen: quality score = 15
North and Houde (2004) set threshold
  - Field study, high resolution = 10
  - Peer reviewed = 1
  - Chesapeake Bay population = 3
  - Supported by Keister et al. (2000) = 1

Juveniles
Required temperature: average of quality scores for lower and upper limit = (16+26)/2 = 21
Dovel (1971) set lower limit
  - Field study, high resolution = 10
  - Peer reviewed = 1
  - Chesapeake Bay population = 3
  - Supported by Chung and Strawn (1982), Kimura et al (2000) = 2
Terpin et al. (1976) set upper limit
  - Lab study, numerous replications = 20

- Chesapeake Bay populations = 3
- Supported by Dovel (1971), Chung and Strawn (1982), Kimura et al (2000) = 3

Optimal temperature: quality score = 26
Terpin et al. (1976) set entire range
- Lab study, numerous replications = 20
- Chesapeake Bay populations = 3
- Supported by Dovel (1971), Houde and Zastrow (1991), Lou and Brandt (1993) = 3

Required salinity: average of quality scores for lower and upper limit = (16+13)/2 = 14.5
Dovel (1971) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Kimura et al (2000), Kilby (1995) = 2
Kilby (1995) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Dovel (1971), Kimura et al (2000) = 2

Optimal salinity: average of quality scores for lower and upper limit = (16+16)/2 = 16
Dovel (1971) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Houde and Zastrow (1991), Jung and Houde (2003) = 2
Houde and Zastrow (1991) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Dovel (1971), Jung and Houde (2003) = 2

Required dissolved oxygen: quality score = 11
Taylor et al. (2007) set threshold
- Field study, high resolution = 10
- Peer reviewed = 1

Optimal dissolved oxygen: quality score = 15
Ludsin et al. (2009) set threshold
- Field study, high resolution = 10

- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Taylor et al. (2007) = 1

Adults

Required temperature: average of quality scores for lower and upper limit = (13+14)/2 = 13.5

Dovel (1981) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Roessler (1970), Gelwick et al. (2001) = 2

Roessler (1970) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Dovel (1981), Chung and Strawn (1982), Gelwick et al. (2001) = 3

Optimal temperature: average of quality scores for lower and upper limit = (14+20)/2 = 17

Houde and Zastrow (1991) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3

Luo and Brandt (1993) set upper limit
- Modeling study = 15
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Houde and Zastrow (1991) = 1

Required salinity: average of quality scores for lower and upper limit = (17+14)/2 = 15.5

Massmann (1954) set lower limit
- Field study = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Dovel (1971), Roessler (1970), Gelwick et al. (2000) = 3

Roessler (1970) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Dovel (1981), Gelwick et al. (2000), Massmann (1954) = 3

Optimal salinity: quality score = 14

Houde and Zastrow (1991) set entire range
- Field study, high resolution = 10

- Peer reviewed = 1
- Chesapeake Bay population = 3

Required dissolved oxygen: quality score = 12
Taylor et al. (2007) set threshold
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Gelwick et al. (2001) = 1

Optimal dissolved oxygen: quality score = 15
Ludsin et al. (2009) set threshold
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Taylor et al. (2007) = 1

E. Bluefish (*Pomatomus saltatrix*)
Eggs
Required temperature: average of quality scores for lower and upper limit = (15+16)/2 = 15.5
Farhey et al. (1999) set lower limit
- Technical Report, high resolution = 10
- Includes Chesapeake Population = 3
- Supported by Norcross et al. (1974), Smith et al. (1994) = 2
Smith et al. (1994) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Includes Chesapeake Population = 3
- Supported by Farhey et al. (1999), Norcross et al. (1974) = 2

Optimal temperature: quality score = 16
Farhey et al. (1999) set entire range
- Technical Report, high resolution = 10
- Peer reviewed = 1
- Includes Chesapeake Population = 3
- Supported by Norcross et al. (1974), Smith et al. (1994) = 2
Required salinity: average of quality scores for lower and upper limit = (15+15)/2 = 15
Norcross et al (1974) set lower limit
- Field study, high resolution = 10
- Chesapeake Bay population = 3
- Peer reviewed = 1

- Supported by Kendall and Walford (1979) = 1

Kendall and Walford (1979) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Includes Chesapeake Bay population = 3
- Supported by Norcross et al (1974) = 1

Optimal salinity: quality score = 14
Norcross et al. (1974) set entire range
- Field study, high resolution = 10
- Chesapeake Bay population = 3
- Peer reviewed = 1

Required dissolved oxygen: quality score = N.A.

Optima dissolved oxygen: quality score = N.A.

Larvae
Required temperature: average of quality scores for lower and upper limit =
(14+15)/2 = 14.5
Farhey et al. (1999) set lower limit
- Techincal Report, high resolution = 10
- Includes Chesapeake Population = 3
- Supported by Kendall and Walford (1979) = 1
Kendall and Walford (1979) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Includes Chesapeake Bay population = 3
- Supported by Farhey et al. (1999) = 1

Optimal temperature: quality score = 16
Kendall and Walford (1979) set entire range
- Field study, high resolution = 10
- Peer reviewed = 1
- Includes Chesapeake Bay population = 3
- Supported by Farhey et al. (1999), Deuel et al. (1966) = 2

Required salinity: quality score = 14
Kendall and Walford (1979) set entire range
- Field study, high resolution = 10
- Peer reviewed = 1
- Includes Chesapeake Bay population = 3
Optimal salinity: quality score = 14

Kendall and Walford (1979) set entire range
- Field study, high resolution = 10
- Peer reviewed = 1
- Includes Chesapeake Bay population = 3

Required dissolved oxygen: quality score = N.A.

Optimal dissolved oxygen: quality score = N.A.

Juveniles
Required temperature: average of quality scores for lower and upper limit =
(14+23)/2 = 18.5
Lund (1971) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Includes Chesapeake Bay populations = 3
Olla et al. (1975)
- Lab study, numerous replications = 20
- Includes Chesapeake Bay populations = 3

Optimal temperature: quality score = 29
Olla et al. (1975) set entire range
- Lab study, numerous replications = 20
- Includes Chesapeake Bay populations = 3
- Supported by Kendall and Walford (1979), Farhey et al. (1999), Brooks and Gear (2001), Creaser and Perkins (1994), Nyman and Conover (1988), Hartman and Brandt (1995) = 6

Required salinity: average of quality scores for lower and upper limit = (23+13)/2 =
18
Buckel et al. (1995) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Baird 1873 and Lippson and Lippson (2006) = 2
Farhey et al. (1999) set upper limit
- Technical Report, field surveys = 10
- Chesapeake Bay populations included = 3

Optimal salinity: quality score = 14
Gear (2002) set entire range
- Technical Report, based upon VIMS trawl surveys = 10
- Chesapeake Bay population = 3
- Supported by Brooks and Gear (2001) = 1

Required dissolved oxygen: quality score = 14
Gear (2002) set threshold
- Technical Report, based upon VIMS trawl surveys = 10
- Chesapeake Bay population = 3
- Supported by Brooks and Gear (2001) = 1

Optimal dissolved oxygen: quality score = 14
Middaugh et al. (1981) set threshold
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Farhey et al. (1999), Brooks and Geer (2001) and Geer (2002) = 3

Adults
Required temperature: average of quality scores for lower and upper limit = (15+21)/2 = 18
Lund (1971) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Includes Chesapeake Bay populations = 3
- Supported by Farhey et al. (1999) = 1
Olla et al. (1975) set entire range
- Lab study, numerous replications, but conducted for juveniles = 17
- Includes Chesapeake Bay populations = 3
- Supported by Farhey et al. (1999) = 1

Optimal temperature: quality score = 29
Olla and Studholme (1971) set entire range
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Includes Chesapeake populations = 3
- Supported by Olla et al. (1975), Olla and Studholme (1975), Farhey et al. (1999), Able (2007), Lund and Maltezos (1970) = 5

Required salinity: average of quality scores for lower and upper limit = (23+13)/2 = 18
Buckel et al. (1995) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Baird (1873) and Lippson and Lippson (2006) = 2
Farhey et al. (1999) set upper limit
- Technical Report, field surveys = 10

- Chesapeake Bay populations included = 3

Optimal salinity: average of quality scores for lower and upper limit = (12+16)/2 = 14
Grothues and Able (2007) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Faryhay et al. (1999) = 1
Faryhay et al. (1999) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Includes Chesapeake Population = 3
- Supported by Grothues and Able (2007) = 2

Required dissolved oxygen: quality score = 12
Grothues and Able (2007) set threshold
- Field survey, high resolution = 10
- Peer reviewed = 1
- Supported by Swanson and Sinderman (1979) = 1

Optimal dissolved oxygen: quality score = 12
Grothues and Able (2007) set threshold
- Field survey, high resolution = 10
- Peer reviewed = 1
- Supported by Swanson and Sinderman (1979) = 1

F. Atlantic Sturgeon (*Acipenser oxyrinchus*)
Eggs
Required temperature: quality score = N.D.

Optimal temperature: average of quality scores for lower and upper limit = (25+24)/2
= 24.5
Smith et al. (1981) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Smith et al. (1980), Mohler et al. (2003), Vladykov and Greeley (1963), Dean (1984) = 4
Mohler et al. (2003) set upper limit
- Lit review, lab studies = 20
- Supported by Smith et al. (1980), Smith et al. 1981, Vladykov and Greeley (1963), Dean (1984) = 4

Required salinity: quality score = 13

Van Eenanaam et al. (1996) set entire range
- Field study, high resolutions = 10
- Peer reviewed = 1
- Supported by Dovel (1978) and Borodin (1925) = 2

Optimal salinity: quality score = N.D.

Required dissolved oxygen: quality score = N.D.

Optimal dissolved oxygen: quality score = N.D.

Larvae
Required temperature: quality score = 11
Bath et al. (1981) set entire range
- Field study, high resolution = 10
- Peer reviewed = 1

Optimal temperature: average of quality scores for lower and upper limit = (22+23)/2
= 22.5
Mohler et al. (2003) set lower limit
- Lit review, lab studies = 20
- Supported by Hardy and Litvak (2004), Kelly and Arnold (1999) = 2
Hardy and Litvak (2004) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Mohler et al. (2003), Kelly and Arnold (1999) = 2

Required salinity: quality score = 11
Bath et al. (1981)
- Field study, high resolution = 10
- Peer reviewed = 1

Optimal salinity: quality score = N.D.

Required dissolved oxygen: quality score = N.D.

Optimal dissolved oxygen: quality score = N.D.

Juvenile - YOY

Required temperature: average of quality scores for lower and upper limit =
(24+14)/2 = 19
Dovel and Breggren (1983) set lower limit
- Lit review, lab and field studies = 10
- Peer reviewed = 1

- Supported by Niklitschek and Secor (2005), Kieffer and Kynard (1993),
        Bain et al. (2000) = 3
Niklitschek and Secor (2005) set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Optimal temperature: quality score = 24
Niklitschek and Secor (2009) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Required salinity: average of quality scores for lower and upper limit = (24+35)/2 =
29.5
Niklitschek and Secor (2009) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
Niklitschek (2001) set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Population = 3
- Multivariable physiological relationship = 5
- Supported by Niklitschek and Secor (2009), Brundage and Meadows
        (1982), Dovel and Berggren (1983), Smith (1985b), Haley et al. (1996),
        Bain et al. (2000) = 6

Optimal salinity: quality score = 24
Niklitschek and Secor (2009) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Required dissolved oxygen: quality score = 24
Niklitschek (2001) set threshold
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Optimal dissolved oxygen: quality score = 24
Niklitschek (2001) set threshold
- Lab study, numerous replications = 20

- Peer reviewed = 1
- Chesapeake Bay population = 3

Juvenile – Yearling

Required temperature: average of quality scores for lower and upper limit = (24+11)/2 = 17.5

Dovel and Breggren (1983) set lower limit
- Lit review, lab and field studies = 10
- Peer reviewed = 1

Niklitschek and Secor (2005) set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Optimal temperature: quality score = 24

Niklitschek and Secor (2009) set entire range
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Required salinity: quality score = 25

Niklitschek and Secor (2005) set entire range
- Lab study, in depth = 2
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Secor et al. (2000) = 1

Optimal salinity: quality score = 24

Niklitschek and Secor (2009) set entire range
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Required dissolved oxygen: quality score = 25

Secor and Gunderson (1998) set threshold
- Lab study, in depth = 2
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Niklitschek and Secor (2009) = 1

Optimal dissolved oxygen: quality score = 25

Secor and Gunderson (1998) set threshold
- Lab study, in depth = 2

- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Niklitschek and Secor (2009) = 1

Adult
Required temperature: quality score = 14
Brundage and Meadows (1982) set entire range
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Population = 3

Optimal temperature: quality score = N.D.

Required salinity: quality score = 15
Brundage and Meadows (1982) set entire range
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Population = 3
- Supported by Kieffer and Kynard (1993) = 1

Optimal salinity: quality score = N.D.
Required dissolved oxygen: quality score = N.D.

G. Soft Shell Clam (*Mya arenaria*)
Juvenile
Required temperature: average of quality scores for lower and upper limit =
(22+26)/2 = 24
Borget (1983) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Supported by Loi and Wilson 1979 = 1
Kennedy and Muhursky (1971) set upper limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Harrigan (1956), Loi and Wilson (1979) = 2

Optimal temperature: quality score = 27
Harrigan (1956) set entire range
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Population = 3

- Supported by Stewart and Bamford (1976), Kennedy and Mihursky (1972), Anderson (1978) = 3

Required salinity: average of quality scores for lower and upper limit = (28+17)/2 = 22.5
Chanley (1958) set lower limit
- Lab study, numerous replications = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Lucy (1976), Perkins (1974), Castagna & Chanley (1973), Matthiesen (1960) = 4

Castagna & Chanley (1973) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Chanley (1958), Lucy (1976), Brousseau (1978a) = 3

Optimal salinity: quality score = 22
Matthiesen (1960) set entire range
- Lab study, numerous replications 20
- Peer reviewed = 1
- Supported by Stewart and Bamford (1976) = 1

Required dissolved oxygen: quality score = 23
Theede et al. (1969) set threshold
- Lab experiment, numerous replications = 20
- Peer reviewed = 1
- Supported by Ricketts and Calvin (1967), Newell and Hidu (1986) = 2

Optimal dissolved oxygen: quality score = 22
Savage 1975 set threshold
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Van Dam (1935) = 1

H. Winter Flounder (*Pseudopleuronectes americanus*)
Juvenile
Required temperature: average of quality scores for lower and upper limit = (24+25)/2 = 24.5
Pearcy (1962) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1

- Supported by Armstrong (1997), Hoff and Westman (1966), Lazzari
  (2008) = 3

Hoff and Westman (1966) set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Pearcy (1962), McCracken (1963), Armstrong (1997),
  Lazzari (2008) = 4

Optimal temperature: average of quality scores for lower and upper limit = (26+26)/2
= 26
Casterlin and Reynolds (1982) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Armstrong (1997), Stoner et al. (2001), Manderson et al.
  (2002), Olla et al. (1969), Meng et al. (2000) = 5

Manderson et al. 2002 set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Olla et al. 1969, Armstrong 1997, Meng et al. (2000), Stoner
  et al. 2001, Steifhoff et al. (2006), = 5

Required salinity: average of quality scores for lower and upper limit = (23+14)/2 =
18
Pearcy (1962) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Armstrong (1997), Howell et al. (1999) = 2

Meng et al. (2000) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Armstrong (1997), Howell et al. (1999), Lazzari (2008) = 3

Optimal salinity: average of quality scores for lower and upper limit = (11+24)/2 =
17.5
Armstrong (1997) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1

Manderson et al. (2002) set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Armstrong (1997), Frame (1973), Stoner et al. (2001) = 3

Required dissolved oxygen: quality score = 22

Ziskowski et al. (1991) set threshold
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Bejda (1992) = 1

Optimal dissolved oxygen: quality score = 25
Stierhoff et al. (2006) set threshold
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Bejda (1992) = 1

I. Menhaden (*Brevoortia tyrannus*)
Juvenile
Required temperature: average of quality scores for lower and upper limit =
(24+23)/2 = 23.5
Burton et al. (1979) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
Lewis and Hettler (1968) set upper limit
- Lab study, in depth =20
- Peer reviewed = 1
- Supported by Terpin et al. (1999), Young and Gibson (1973) = 2

Optimal temperature: average of quality scores for lower and upper limit = (22+20)/2
= 21
Terpin et al. (1999) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Brandt and Mason (2011) = 1
Brandt and Mason (2003) set upper limit
- Modeling study = 15
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Terpin et al. (1999) = 1

Required salinity: average of quality scores for lower and upper limit = (15+22)/2 =
18.5
Gunter (1961) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1

- Supported by Hettler (1976), Engel et al. (1987), Friedland et al. (1996), Massman et al. (1954) = 4

Engel et al. 1987 set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Gunter (1961), Hettler (1976) = 2

Optimal salinity: quality score = 24
Hettler (1976) set entire range
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Friedland et al. (1996), Gunter (1961), Massman et al. (1954) = 3

Required dissolved oxygen: quality score = 24
Burton et al (1980) set threshold
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Optimal dissolved oxygen: quality score = 19
Brandt and Mason (2003) set threshold
- Modeling study = 15
- Peer reviewed = 1
- Chesapeake Bay population = 3

J. Atlantic Croaker (*Micropogonias undulates*)
Juvenile
Required temperature: average of quality scores for lower and upper limit =
(25+15)/2 = 20
Shwartz (1964) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Population = 3
- Supported by Lankford and Targett (2001) = 1
Parker 1971 set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Knudesen and Herke (1978), Haven (1957), Miller et al. (2003), Bearden (1964) = 4

Optimal temperature: quality score = 12

Parker (1971) set entire range
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Milagrese et al. (1982) = 1

Required salinity: average of quality scores for lower and upper limit = (17+14)/2 = 15.5
Haven (1957) set lower limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay Population = 3
- Supported by Milagrese et al. (19820, Bearden (1964), Parker (1971) = 3
Bearden (1964) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Haven (1957), Milagrese et al. (1982), Simmons (1958) = 3

Optimal salinity: average of quality scores for lower and upper limit = (26+26)/2 = 26
Peterson et al. (1999) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Parker (1971), Moser and Gerry, Abud (1991), Miller et al. (2003), Milagrese et al. (1982) = 5
Abud (1992) set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Parker (19710, Moser and Gerry (1989), Peterson et al. (1999), Miller et al. (2003), Milagrese et al. (1982) = 5

Required dissolved oxygen: quality score = N.A.

Optimal dissolved oxygen: quality score = 14
Bell and Eggleston (2005) set threshold
- Field study, high resolution = 10
- Peer reviewed = 1
- Supported by Eby et al. (2005), Craig and Crowder (2002), Eby and Crowder (2000) = 3

K. Weakfish (*Cynoscion regalis*)
Juvenile
Required temperature: average of quality scores for lower and upper limit = (25+16)/2 = 20.5
Shwartz (1964) set lower limit

- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Population = 3
- Supported by Hildebrand and Cable (1934) = 1

Richards and Castagna (1970) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Massman et al. (1958), Thomas (1971) = 2

Optimal temperature: average of quality scores for lower and upper limit = (24+26)/2 = 25

Shwartz (1964) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Population = 3

Lankford and Targett (1994) set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Terpin et al. (1977), Wilk (1979) = 2

Required salinity: average of quality scores for lower and upper limit = (24+14)/2 = 19

Lankford and Targett (1994) set lower limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3

Richards and Castagna (1970) set upper limit
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3

Optimal salinity: quality score = 25

Lankford and Targett (1994) set entire range
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Massmann et al. 1958 = 1

Required dissolved oxygen: quality score = 24

Brady et al. (2009) set threshold
- Lab study, in depth = 20

- Peer reviewed = 1
- Chesapeake Bay population = 3

Optimal dissolved oxygen: quality score = 27
Stierhoff et al. (2009) set threshold
- Lab study, in depth = 20
- Peer reviewed = 1
- Chesapeake Bay population = 3
- Supported by Brady et al. (2009), Ebby and Crowder (2002), Tyler and Targett (2007) = 3

L. White Perch (*Morone Americana*)
Juvenile
Required temperature: average of quality scores for lower and upper limit = (22+24)/2 = 23
Johnson and Evans (1990) set lower limit
- Lab study, in depth = 2
- Peer reviewed = 1
- Supported by Stanley 1983 = 1
Kellogg and Gift (1983) set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Hall et al. (1978), Meldrim and Gift (1971), Dorfman and Westman (1970) = 3

Optimal temperature: average of quality scores for lower and upper limit = (24+24)/2 = 24
Hanks and Secor (2011) set lower limit
- Lab study, in depth = 20
- Chesapeake Bay Population = 3
- Peer reviewed = 1
Kellogg and Gift (1983) set upper limit
- Lab study, in depth = 20
- Peer reviewed = 1
- Supported by Terpin et al. (1977), Hall et al. (1978), Stanley (1983) = 3

Required salinity: quality score = 19
Nemerson and Able (2004) set entire range
- Field study, high resolution = 10
- Peer reviewed = 1
- Chesapeake Bay population = 3

- Supported by Kraus and Secor (2004), Kraus and Secor (2005), Stanley (1983), Hanks and Secor (2011) = 5

Optimal salinity: quality score = 27
Hanks and Secor (2011) set entire range
- Lab study, in depth = 20
- Chesapeake Bay Population = 3
- Peer reviewed = 1
- Supported by Kraus and Secor (2004), Kraus and Secor (2005), Stanley (1983) = 3

Required dissolved oxygen: quality score = 20
Dorfman and Westman (1970) set threshold
- Lab study, in depth = 20

Optimal dissolved oxygen: quality score = 26
Hanks and Secor (2011)
- Lab study, in depth = 20
- Chesapeake Bay Population = 3
- Peer reviewed = 1
- Supported by AuClair (1954), Stanley (1983) = 2

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