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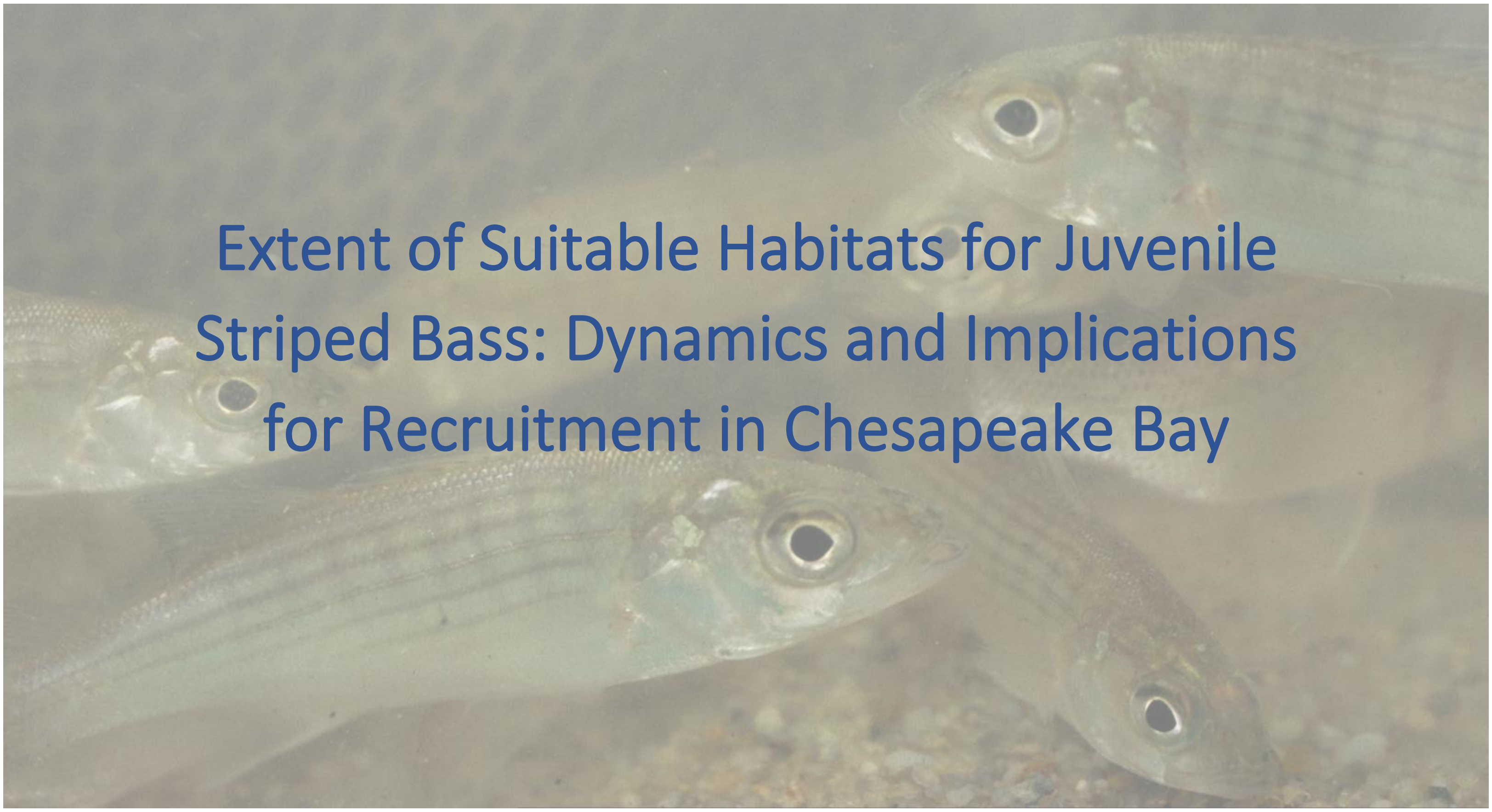

Extent of Suitable Habitats for Juvenile Striped Bass: Dynamics and Implications for Recruitment in Chesapeake Bay

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Executive Summary

The production of striped bass *Morone saxatilis* in Chesapeake Bay supports recreational and commercial fisheries along the Atlantic coast of the United States, but factors that contribute to high abundances of juvenile life stages are not fully understood. In this study, we characterized and quantified suitable and optimal habitat conditions in the Chesapeake Bay for two age groups of juvenile striped bass in discrete portions of the Bay: young-of-the-year (age-0) fish in shoreline and nearshore habitats, and resident sub-adults (age-1 to -4) in the mainstem and Bay-wide. We coupled information from 24 years of monthly fisheries surveys with hindcasts from a 3-D hydrodynamic model of the Bay and a numerical model of dissolved oxygen (DO) conditions. These models provided estimates of habitat conditions for 1996 to 2019 for 33 metrics of temperature, salinity, current speed, depth, DO, and physical features of habitats. Boosted regression trees were used to identify influential habitat covariates for each group, and those covariates were used to develop nonparametric habitat suitability models based on environmental conditions at the time and location of sampling. Habitat suitability indices (HSI), ranging from 0 (poor habitat) to 1 (high-quality habitat), were assigned to each grid in the 3-D model for each season in 1996 to 2019. We quantified suitable (HSI $\geq$ 0.5) and optimal (HSI $\geq$ 0.7) on a seasonal and annual basis, and across a range of environmental conditions (wet vs. dry years; warm vs. cool years). We also estimated the persistence of suitable habitats through time as the percent of years during which conditions were suitable at a given site; persistence allowed us to identify areas of the Bay and tidal tributaries that consistently supported suitable conditions for juvenile striped bass.

Specific habitat conditions that defined suitable and optimal habitats for age-0 and age 1-4 striped bass varied across seasons and among years, reflecting changes in water quality conditions in Chesapeake Bay and changes in habitat use by striped bass during their first few years of life. Metrics of water quality, especially dissolved oxygen, were consistently identified as important covariates for juvenile striped bass; these conditions are of greater importance in determining habitat suitability than specific physical features, especially for a highly mobile species, and may be used to inform existing decision-support tools. In our study, we found no evidence that habitat use by striped bass in Chesapeake Bay was moderated by a strict threshold for any given covariate, and average to above-average abundances of striped bass were encountered in sub-suitable conditions; thus, habitat use resulted from a combination of abiotic, and likely biotic, conditions.

The use of hydrologic characterizations (i.e., wet/dry) to understand availability of suitable habitats for juvenile striped bass appeared to be limited because such effects were season-specific. The extent of suitable habitat in fall and winter for age-0 striped bass increased during the wet year relative to average or dry years, but wet/dry years had no noticeable effect on habitat extents in spring or summer. The extent of suitable habitat for age 1-4 fish increased in spring and fall during the wet year, but habitat extents in summer during wet and dry years were not appreciably different. Thermal characterizations (i.e., warm/cool) were somewhat more consistent in their ability to assess changes in the extent of suitable habitats. For age-0 fish, suitable habitat extents were greater in the cool year relative to the warm year, and this was true across all seasons. In contrast, suitable habitat extents were similar during warm, average, and cool years for age 1-4 fish, suggesting this age group was less responsive to thermal changes than the age-0 group.

Our examination of suitable habitats indicated that shallow, nearshore areas in summer and habitats in the mainstem in spring, fall, and winter offered consistently suitable conditions for age-0 and age 1-4 fish. Mainstem channels, tributary channels, and the region along the eastern shore of the Bay offered

persistent habitats that were suitable for age 1-4 fish in spring and fall. These results emphasize the need to protect habitats throughout the Bay.

Neither age group exhibited a statistically significant relationship between relative abundance and the extent of suitable habitats, however, for nearly all ages and seasons, relative abundance increased with greater extent of suitable habitats suggesting that detection of this relationship requires additional annual observations. A significant decrease in the extent of suitable habitat through time (1996 to present) was observed in spring and early summer, reflecting a change in suitable environmental conditions; with additional study years, declines in the relative abundance of age-0 and age 1-4 fish may be observed as suitability of habitats continues to decline. Given the high degree of interannual variability in abundance that is characteristic of estuarine-dependent species like striped bass, the availability and quantity of suitable and high-quality habitats at the scale of individual tributaries and Bay-wide may play an important role in production of this species.

Introduction

Striped bass *Morone saxatilis*, an icon of the Chesapeake Bay, support recreational and commercial fisheries along the Atlantic coast of the United States. The abundance of the Atlantic coastal stock, however, has declined in recent years and the stock is currently overfished with overfishing occurring (ASMFC 2019). The coastal migratory stock is comprised primarily of adult fish originating from nursery areas in the Chesapeake Bay, Delaware Bay, Hudson River, and to a lesser extent, Roanoke River (EBFM Striped Bass Species Team 2009; Wirgin et al. 2020). Fish produced in Chesapeake Bay, however, contribute a significant proportion to the coastal stock (Berggren and Lieberman 1978; Fabrizio 1987; Gauthier et al. 2013), and overall stock dynamics most closely resemble patterns of age-0 abundance in Chesapeake Bay (Richards and Rago 1999). Despite recent years of average production of age-0 fish, the female spawning stock biomass declined below the threshold level in 2013 and has remained below the threshold (ASFMC 2019). Recruitment success (defined as the relative abundance of age-0 fish) in striped bass is determined by many factors, including the demography of the spawning stock (Secor 2000; Secor 2007), and multiple environmental drivers that affect the growth and survival of early-life stages. Indeed, fluctuations in environmental conditions can contribute to large variability in the production of age-0 fish and hence, variability in annual year-class strength (Houde 2016). Similar to many other marine fishes, the link between spawning stock biomass and recruitment to the fishery is weak or unknown, in part due to environmental variability (Szuwalski et al. 2015). In this study, we seek to understand the effects of environmental conditions on the quality of habitats used by young striped bass, and ultimately, how the extent of suitable habitats may affect abundance of this species in Chesapeake Bay.

Habitat use by many estuarine fishes varies with ontogeny such that newly hatched fishes, young fishes, and mature adults may not use the same habitats. As fish grow, movements between habitats occur in response to abiotic factors (Able and Fahay 1998), as well as biotic influences. For anadromous fishes like striped bass, eggs hatch in the upper freshwater reaches of tidal tributaries and as they grow, larval and juvenile stages move downriver into brackish environments (Setzler-Hamilton et al. 1981). In Chesapeake Bay tributaries, survival of larval striped bass and subsequent recruitment to the juvenile stage is largely moderated by spring water temperature and freshwater flow (the frequency and magnitude of pulsed discharges, specifically), where cool, wet springs are associated with strong year classes (North and Houde 2001; North et al. 2005; Martino and Houde 2004; 2010). The timing of peak zooplankton abundance, which is influenced by winter temperatures, may also impact larval survival (Millette et al. 2019). Recruitment success of anadromous striped bass has also been tied to the retention of larvae in the estuarine turbidity maximum (ETM; North and Houde 2001), where abundant prey, refuge from predation, and optimal temperature and salinity conditions for growth may occur (North and Houde 2001; 2003). As such, ETMs in the Chesapeake Bay and its major tributaries are considered nursery areas for larval striped bass.

Factors that affect survival and production of fish beyond the larval stage, and the mechanisms that support high abundances of juvenile life stages, however, are not fully understood (Martino and Houde 2010). For this study, we define 'juvenile' stage as the phase immediately following the larval stage and up to the age at maturity; therefore, juvenile striped bass comprise fish of multiple age classes, namely, age-0 to age-4. To capture differences in life-history dynamics, we henceforth use the term 'young-of-the-year' (YOY) for age-0 fish, and 'resident sub-adults' for age-1 to -4 fish; note that it is likely that some individuals within the age-1 to -4 group are sexually mature. Male striped bass reach maturity at age 2 to 3 (Merriman 1941) and about half of the females are mature by age 3 (Gervasi et al. 2019), though previous studies suggested that half of the females reach maturity at slightly older ages (ages 4 and 5, Merriman 1941; ages 5 and 6, Berlinsky et al. 1995). Striped bass remain in estuarine habitats for the first 2 to 4 years of life before they mature, and before some join the migratory contingent offshore (Richards and Rago 1999; Secor and Piccoli 2007). Notably, these fish are smaller than the minimum size limit for the recreational fishery in Chesapeake Bay (18 inches).

Currently, essential habitats for juvenile striped bass are broadly characterized as shallow estuarine waters with slow current speeds and dissolved oxygen levels greater than 2 to 3 mg O_2/L (Coutant and Benson 1990). Estuarine environments, however, are characterized by physical, hydrodynamic, and habitat complexity, as well as large fluctuations in conditions across space and time (Bever et al. 2016; Boutin and Targett 2019). As a result, the extent and quality of suitable habitats for juvenile striped bass likely also vary, partly in response to variations in seasonal and annual environmental conditions (Murdy et al. 1997; Schloesser and Fabrizio 2019; Fabrizio et al. 2021). Although juveniles are tolerant of a wide range of water-quality conditions, growth is optimized at intermediate salinities (~7 psu) and warm temperatures (24-27°C for fish 80-300 mm TL; Coutant et al. 1984). We hypothesize that habitat constraints in Chesapeake Bay may affect habitat use and the abundance of YOY and resident sub-adult striped bass. In particular, habitats that provide refuge from predation and promote enhanced feeding opportunities for YOY fish facilitate the supply of age-1 and older fish to the population, and the availability, quantity, and quality of these habitats are critical for sustaining the stock. We note that the decline in the production of age-0 striped bass observed in the 1970s and 1980s in Chesapeake Bay is partially attributed to poor water quality in spawning and nursery (YOY) habitats (Richards and Rago 1999). The limited availability of suitable habitat may affect juvenile striped bass, although suitable habitat extents for juvenile striped bass have not been estimated to date. Indeed, reduced availability of suitable habitats due to eutrophication and elevated nutrient inputs (e.g., oxy-thermal habitat compression) is hypothesized to contribute to increased natural mortality rates of adult striped bass in Chesapeake Bay (Coutant 1985; Itakura et al. 2021). In addition to recognized ‘high-quality’ habitats (e.g., sea grass, saltmarsh, oyster reefs; Lefcheck et al. 2019), areas that support particular ranges of conditions or processes known to be favorable to young fishes are essential for overall productivity (Able et al. 2012; Colombano et al. 2020).

The maintenance and protection of habitats used by juvenile stages should be considered in the development of effective management plans (Marshak and Brown 2017) for fishes such as striped bass. Suitable habitats can be defined by habitat features and conditions that contribute to production (e.g., as measured by the annual abundance of age-0 striped bass). In the Chesapeake Bay, research to date has largely focused on habitat use by adult striped bass (e.g., Kraus et al. 2015a; Itakura et al. 2021) or the effects of specific drivers on spatial distributions of adult striped bass (e.g., hypoxia; Constantini et al. 2008; Buchheister et al. 2013), but habitat use by juvenile striped bass (ages 0 to 4) is largely unexplored. Furthermore, the persistence of suitable habitats may provide insight on the stability of juvenile production across tributaries in Chesapeake Bay. An assessment of the persistence of suitable habitats may also inform restoration and conservation efforts by identifying critical locations that consistently support suitable conditions.

Here, we comprehensively describe and quantify habitat conditions that promote survival and production of juvenile striped bass in Chesapeake Bay; for this study, we broadened the consideration to individuals of ages 0 to 4. Because habitat requirements and use vary between YOY (age-0) and late-stage (ages 1 to 4) juveniles, this study will examine dynamics of habitat suitability for these two distinct age groups. Our objectives were to:

(1) quantify habitat conditions that promote the survival and production of YOY (age-0) and resident sub-adult (age-1 to age-4) striped bass;

(2) assess how habitat conditions change through time;

(3) identify areas that consistently supported suitable habitats (persistence); and

(4) relate changes in habitat area and suitability over time to recruitment as measured by the relative abundance of YOY fish or relative abundance of resident sub-adult fish.

To address these objectives, we used observations from multiple fishery-independent surveys spanning 24 years (1996 to 2019), coupled with a pair of numerical models of Chesapeake Bay and its tributaries. These numerical models provided a suite of habitat covariates that described both dynamic (temperature, salinity, current speed, dissolved oxygen) and static physical features of habitats (distance to shore, seabed composition), which we considered for quantitatively describing habitats used by striped bass. We developed nonparametric habitat models for each age group based on environmental conditions at the time of the catch, and then quantified the extent of suitable and optimal habitat for the Chesapeake Bay system as a whole. We estimated the persistence of suitable habitats by calculating the percent of years during which conditions were suitable at a particular site and used this to identify areas of the Bay and tributaries that consistently supported suitable environmental conditions for juvenile striped bass. This data-driven approach employs habitat suitability index (HSI) modeling – a recognized tool used here to assess spatiotemporal variation in habitat quality by relating field observations (catches of striped bass) to environmental predictors (Georgian et al. 2019; Fabrizio et al. 2021). HSI modeling, which does not require assumptions about the underlying mechanisms that support high abundances at suitable sites, allows for visualization and quantification of seasonally suitable habitats. Finally, nonparametric regressions were used to assess the relationship between abundance of striped bass and seasonal and annual estimates of suitable habitat extent; these regressions were applied to information for YOY and resident sub-adult striped bass for the period 1996 to 2019.

Methods

We employed abundance data from multiple fishery-independent surveys coupled with abiotic conditions estimated from two numerical models of Chesapeake Bay and its tributaries as inputs into an integrated modeling framework. These surveys represent a diversity of sampling gears and methodologies and together provide spatially broad samples from mainstem and tributaries of the Bay over the full analysis period.

Fishery-Independent Surveys

Survey Protocols

Geo-located catch data of age 0-4 striped bass were acquired from five ongoing fishery-independent surveys managed by the Virginia Institute of Marine Science (VIMS; n=3) and Maryland Department of

Natural Resources (MDDNR; n=2). Gear utilized by these five surveys include seine nets (n=2) and otter trawls (n=3). Each dataset provided catch (i.e., numbers and size of individual fish) and site-specific information by sampling event (i.e., latitude and longitude coordinates, sample date, and time). A sampling event, therefore, corresponds to an individual seine haul or trawl tow. Where available, abiotic data collected during sampling (i.e., bottom temperature, bottom salinity, surface temperature, and surface salinity) were also acquired to validate modeled habitat conditions. In total, 48,394 individual sampling events during the 24-year period, 1996 to 2019, were considered in the modeling framework described below.

The dataset from the VIMS Juvenile Striped Bass seine survey included 39 fixed sites in the Rappahannock, James, and York rivers from five sampling events conducted between June and September of each year (1996-2017); although data were available for 2018 and 2019, we withheld these data for subsequent external validation of our modeling approach. Sampling occurred at 18 index sites and 21 auxiliary sites that serve to provide wider geographic coverage and increase sample sizes within river systems (Figure 1); the distinction between index and auxiliary sites is not germane to this study. MDDNR's Juvenile Striped Bass seine survey sampled 22 fixed sites in the Choptank, Nanticoke, Potomac, and Patuxent rivers, as well as other small bays and tributaries on the eastern shore and at the head of Chesapeake Bay during three sampling events between June and September of each year (Figure 1). The VIMS and MDDNR seine surveys deployed a 30.5-m X 1.24-m bar mesh (6.4 mm) minnow seine perpendicular to the shoreline until either the net was fully extended or a depth of approximately 1.2 m was reached; the onshore brail was left in a fixed position while the offshore brail was pulled down-current and back to shore, sweeping a quarter-circle quadrant. For the MDDNR survey and the VIMS index sites, replicate hauls were collected at each site, however, data from only the first haul were retained for analysis because of the lack of statistical independence of the first and second hauls. Additional details on sampling protocol for the VIMS and MD seine surveys can be found in Buchanan et al. 2021 and at https://dnr.maryland.gov/fisheries/pages/striped-bass/juvenile-index.aspx.

The VIMS Juvenile Fish trawl survey (hereafter, VIMS trawl survey) sampled sites in the Rappahannock, James, and York rivers as well as the Virginia portion of the Bay on a monthly basis from January to December using a random stratified design; about 1,224 sites were sampled each year between 1996 and 2019 (fewer sites were sampled in some years due to weather or vessel issues; Figure 2). This survey deployed a semi-balloon bottom trawl with a 5.8-m headrope for five minutes at each site; additional details on sampling protocol are available in Tuckey and Fabrizio (2021). The MDDNR Blue Crab summer trawl survey (hereafter, MDDNR trawl survey) sampled fixed sites in several MD tributaries monthly between May and October using a semi-balloon bottom trawl with 4.8-m headrope for six minutes at each site; samples were available from 1996 to 2019 (Figure 2). Additional details on protocol are available at https://dnr.maryland.gov/fisheries/pages/blue-crab/trawl.aspx.

The Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) survey was designed to sample late juvenile and adult fishes in the mainstem of Chesapeake Bay. Five distinct sampling events occurred each year from 2002 to 2018 (March, May, July, September, November) at 80 sites in MD and VA waters of the mainstem Bay (Figure 3). This survey began in 2002, so no data exist prior to that date, and data for the year 2019 were not available due to an ongoing calibration study as a result of a vessel change. Sites were selected with a random stratified design, where the mainstem of the Bay was divided into five regions: regions 1-3 coincided with the Maryland waters and regions 4 and 5 corresponded with Virginia waters. This survey used a two-bridle, four-seam bottom trawl with 13.7-m headrope and conducted a 20-minute tow at each site. Additional details on survey protocols can be found in Bonzek et al. (2022).

Assignment of Fish to Age Groups

The properties of suitable habitat for each age group (age-0 = YOY; age 1-4 = resident sub-adults) were described separately because habitat requirements differ for fish through ontogeny. Observed fish lengths were used to allocate catches to the corresponding age group using an age-length key that we developed (described below). Some surveys measured a subsample of fish at each site. The MDDNR seine survey recorded the total number of striped bass collected at each site, then recorded length (total length, mm) of a random subsample of up to 30 individuals per site. Similarly, the MDDNR trawl survey recorded length for a random subsample of up to 20 individuals (total length, mm). The other three surveys subsampled the catch for length measurements (fork length, mm) only in the event of a large catch. In cases where fish were subsampled prior to being measured, a multiplier was calculated to estimate the expected total number of fish of a particular size. For such calculations, the multiplier was used to assign lengths to all counted fish in proportion to the individuals that were measured.

To assign individual fish to an age group, recorded lengths must first be expressed in the same metric (i.e., either fork length [FL] or total length [TL]). We developed a conversion factor (Eq. 1) appropriate for the size range of fish encompassed in this study (37-600 mm FL) by regressing measurements of fork length on total length from the same fish:

$$\text{FL (mm)} = -3.160978 + 0.9377*\text{TL(mm)} \qquad (1)$$

Specifically, we used paired FL and TL observations from the same fish (n=673) measured by the Virginia Marine Resources Commission (VMRC; O. Phillips, *pers. comm.*), the VIMS seine and trawl surveys, the VIMS spring gill-net spawning and stock monitoring program, and the VIMS spring pound-net spawning stock monitoring program (C. Bonzek, *pers. comm.*) to develop an appropriate conversion factor (Eq. 1). Estimates of FL for fish smaller than approximately 120 mm TL may have exhibited a slight positive bias. Whereas seine surveys primarily sampled age-0 fish, trawl surveys encountered multiple age classes of striped bass. Assignment to age-class based on observed or estimated FL required the development of an age-length key because a comprehensive age-length key for Chesapeake Bay striped bass was not available. To develop an initial age-length key, we used observed fork lengths (mm) and otolith-derived ages from striped bass collected by the ChesMMAP survey (C. Bonzek, *unpublished data*). Otolith-derived ages were preferable over scale-based measurements because scale-based ages are likely to have a positive bias for fish younger than age 5 (Welch et al. 1993; Liao et al. 2013). Preliminary analyses revealed substantial overlap in length frequencies for fish in age classes 1 to 4, and between resident sub-adult fish (age 1-4) and adult fish (age 5 and older). We therefore employed a model-based approach using a logistic regression with Firth bias-correction (Firth 1993) to address separation, in order to estimate the length threshold between age-4 and age-5 striped bass, where age was a function of fork length, year, and the year*length interaction. This threshold (determined to be 401 mm FL) represents the length at which the probability that a given fish is allocated to the age 1-4 group is sufficiently conservative (90% or higher, with a confidence interval of 81% to 90%) to include the majority of age-4 fish while minimizing the number of older individuals that may be incorrectly assigned to the age 1-4 group. The threshold value was also assessed by comparing the average and median habitat conditions (water depth, temperature, and salinity) occupied by age 1-4 fish as defined by the 90% confidence threshold versus a more conservative confidence threshold (85% or 80%). We found no significant difference in average or median habitat conditions occupied by fish allocated to the age 1-4 group using the 80%, 85%, or 90% confidence thresholds; this result further validated that we were not including older fish, with possibly different habitat requirements, within the 1-4 age group. Examination of the age-length relationships for age 1-4 striped bass in Chesapeake Bay across time indicated that this relationship was relatively stable throughout our 24-year period and between seasons, which provided support for the use of a single age-4 threshold rather than year-specific thresholds. Because no age data were available from ChesMMAP prior to 2002, we assumed that the age-length relationship for fish captured between 1996 and 2001 resembled that of fish captured in 2002 and subsequent years. If this assumption is not valid and fish exhibited faster growth during 1996-2001, then we would expect to underage fish based on fork length (i.e., a fish deemed to be 4 years old would actually be 5 years old), but our assessment indicates that this likelihood was low.

Because fish were captured throughout the year, we estimated monthly length threshold values to allocate fish into the corresponding age group (age-0 or age 1-4) based on the observed or estimated fork length in the month of capture. Insufficient numbers of age-0 catch in the ChesMMAP data prevented the use of a similar model-based approach to determine the length threshold between age-0 and age-1 fish. Therefore, age-0 thresholds were based on existing monthly length thresholds used by the VIMS trawl survey and were validated by observations from the VIMS seine survey. Although there is a possibility that individual age-0 fish may have exceeded these length thresholds on occasion, the proportion of fish in this scenario was likely small (Figure 4).

Standardized Catches

Once fish were assigned to the appropriate age group by fork length as described above, the proportion of striped bass in each age group that was encountered in each survey was calculated (Table 1). We used four datasets to quantify habitat for age-0 and age-1-4 fish; information from seine and trawl surveys was used to independently assess habitats used by age-0 fish, and information from trawl surveys was used to assess habitats used by age-1-4 fish. The first dataset comprised the age-0 fish captured by seine surveys in MD and VA. The second dataset comprised the age-0 fish captured by the VIMS and MDDNR trawl surveys; these two surveys captured a considerable proportion of age-0 fish in any given year (~85% of striped bass captured by each survey were age-0 fish; Table 1). Although we explored several methods to standardize and combine age-0 catch rates from trawl and seine surveys, we were unable to combine standardized catches from these different gear types in an effective manner. Therefore, we considered age-0 information from these two datasets separately: seine surveys provided information on habitat requirements of age-0 striped bass in waters adjacent to the shoreline, whereas trawl surveys provided information on habitat requirements of age-0 fish in deeper waters. Consideration of age-0 fish from the VIMS trawl survey also allowed us to describe suitable habitats for age-0 fish during their first winter in residence in the Bay because this survey samples year-round.

Habitat associations of age 1-4 fish were assessed using catch rates from three trawl surveys: dataset number three used observations from the small trawls (i.e., VIMS and MDDNR trawl surveys) and dataset number four which used observations from the large trawl (ChesMMAP). Together, the three trawl surveys effectively targeted different sizes of striped bass, and therefore different ages, within the age 1-4 group (Figure 5). This outcome reflects differences in gear size as well as spatial and temporal differences in sampling regimes. In summary, four independent datasets were used to model habitat associations and to quantify the extent of suitable habitats occupied by age-0 and age 1-4 fish (Table 2).

We standardized the catches from each survey using catch per unit effort (CPUE), where effort was estimated by the area swept by the gear. Area swept for trawl surveys (km^2) was calculated as the product of the effective width of the net opening, estimated as 55% of the headline spread (km), and the length of the tow (km), which was estimated by the geodetic distance between the GPS coordinates that demarcated the beginning and end of each tow. For seine surveys, area swept (m^2) was calculated as $1/4\pi * D^2$ where D represents the distance the net was extended offshore, in meters (Martino and Houde 2012). Observations where the seine net was extended less than 12 m offshore were removed from further consideration (n=1,344) because a previous study demonstrated that detection probabilities for age-0 striped bass were variable and low (<60%) when the effective net length was less than 12 m (Williams and Fabrizio 2011).

Numerical Models for Chesapeake Bay

Description of Two Numerical Models

A hydrodynamic model (Fabrizio et al. 2021) and a numerical model of dissolved oxygen (DO; Du and Shen 2014) were used to hindcast estimates of both dynamic (time-varying) and static habitat conditions at every location in the Chesapeake Bay system and every hour between 1996 and 2019.

The Anchor QEA UnTRIM Chesapeake Bay model (hereafter, AQ Chesapeake Bay model) is a 3-dimensional hydrodynamic model of Chesapeake Bay that was developed using the UnTRIM hydrodynamic model (Casulli and Zanolli 2002, 2005). The UnTRIM model has been applied previously to large estuaries in the United States, such as Chesapeake Bay (Shen et al. 2006; Sisson et al. 2010; Wang et al. 2015; Fabrizio et al. 2021) and San Francisco Bay (Cheng and Casulli 2002; Bever and MacWilliams 2013; MacWilliams et al. 2015; Bever et al. 2016). The UnTRIM model uses an unstructured horizontal grid that allows the model to accurately resolve the complex shoreline and bathymetry of the Bay and tributaries. Thus, the UnTRIM numerical approach has been well tested in estuaries and is well suited to perform hydrodynamic, water level, salinity, and temperature modeling in the Bay. Similar to the AQ Chesapeake Bay model, the DO model was used to hindcast estimates of surface and bottom DO throughout the Bay and for each day between 1996 and 2019. Outputs from the numerical model of DO were previously used to describe normoxic and hypoxic habitat conditions throughout the Chesapeake Bay (Fabrizio et al. 2021). The 1-km resolution of this model is similar to the 0.600-km resolution of the Chesapeake Bay Environmental Forecast System (CBEFS) model used to forecast hypoxia in the bay (https://www.vims.edu/research/products/cbefs/cbay/index.php), but unlike the CBEFS model, the hindcast DO model allowed us to reconstruct dissolved oxygen conditions back to 1996.

AQ Chesapeake Bay Model: Grid, Bathymetry, and Boundaries

The AQ Chesapeake Bay model extends from the Atlantic Ocean through the Bay to the Conowingo Dam, the Delaware side of the C&D Canal, and into each of the tributaries (Figure 6). The model takes advantage of the grid flexibility allowed in an unstructured mesh by gradually varying grid cell sizes, beginning with large grid cells in the Atlantic Ocean and gradually transitioning to finer grid resolution in the northern portion of the Bay and the upper reaches of the tributaries. This approach offers significant advantages both in terms of numerical efficiency and accuracy, and it allows for local grid refinement for detailed analysis of local hydrodynamic conditions, while still incorporating the overall hydrodynamics of the larger estuary in a single model. Grid-cell side lengths are approximately 2 km at the ocean boundary, 500 m at the Bay Bridge in Maryland and become gradually smaller with distance in the landward direction and into the tributaries. The model uses fixed vertical layers (Z-grid) with a vertical grid resolution of 0.5 m to a depth of 40 m below zero North American Vertical Datum of 1988 (NAVD88) and 1 m thereafter. High-resolution bathymetric data from two sources were incorporated into the model bathymetry. The Federal Emergency Management Agency (FEMA) Region III bathymetric and topographic Digital Elevation Model (DEM) developed for storm surge analyses was used throughout the model domain (Forte et al. 2011). This DEM is a 10-m DEM on the North American Datum of 1983 (NAD83) coordinate system, and the vertical datum was referenced to NAVD88. Bathymetric data from the U.S. Army Corps of Engineers (USACE) Baltimore District were used for many of the main navigation channels in the Bay and Baltimore Harbor to best include the bathymetry of dredged navigation channels (USACE 2016).

The AQ Chesapeake Bay model has two open boundaries: one at the Atlantic Ocean and one at the Delaware side of the C&D Canal. Observed water levels from the National Oceanic and Atmospheric Administration (NOAA) Chesapeake Bay Bridge Tunnel (CBBT; 8638863) and Kiptopeke (KPT; 8632200) stations at the southwestern end of the Bay mouth were used to specify water levels at the ocean boundary (Figure 6). Observed water levels from CBBT were used when available, otherwise water levels from KPT were used. The observations were multiplied by an amplification factor to account for the difference in tidal range between observed CBBT and KPT tides and tides along the ocean boundary, and a phase lead was applied to account for the phase difference between CBBT and KPT and the model boundary. The amplification factors and phase leads were selected to minimize the phase and amplitude difference between the observed and modeled water levels at both the NOAA CBBT (8638863) and NOAA Kiptopeke (8632200) stations. Water levels at the Delaware side of the C&D Canal were specified using observed water levels from the NOAA Reedy Point (8551910) station, with an amplification and phase lead applied to minimize the phase and amplitude difference between the observed and modeled water levels at the NOAA Chesapeake City (8573927) station.

The salinity and water temperature at the ocean boundary were specified based on monthly climatology values. World Ocean Atlas 2013 monthly climatological values were set at the middle day each month and linearly interpolated in time to produce continuous time series at the ocean boundary that repeated each year. Average daily salinity and water temperature observations from the U.S. Geological Survey (USGS) Delaware River at Reedy Island Jetty (01482800) station were used as the salinity and water temperature at the Delaware side of the C&D Canal.

AQ Chesapeake Bay Model: Data Inputs

River inflows to the model domain included 12 tributary inflows, representing the majority of the riverine freshwater flow into the Bay. These river inflows were the Appomattox River, James River, Pamunkey River, Mattaponi River, Rappahannock River, Potomac River, Patuxent River, Patapsco River, Susquehanna River, Chester River, Choptank River, and Nanticoke River. USGS discharge data were scaled based on the ratio of the gauged area to the overall drainage area to specify the freshwater discharges for the model input, as was done by Xu et al. (2012). Salinity of the inflows was set to zero practical salinity units (PSU), except for the Susquehanna River inflow, which was set to 0.1 PSU based on data from the Chesapeake Bay Interpretive Buoy System (CBIBS) Susquehanna location. Temperature of the inflows was set using available data based on proximity to the inflow locations and availability. Data used for the inflow temperature included USGS streamflow temperature, time series of temperatures from upriver CBIBS locations, National Estuarine Research Reserve locations, Maryland Continuous Monitoring locations, Virginia Estuarine and Coastal Observing System locations, and monthly to bimonthly temperature vertical profiles collected by the long-term Water Quality Monitoring Program (WQMP).

Wind, evaporation, precipitation, air temperature, incoming solar radiation, and relative humidity were specified using 3-hourly gridded North American Regional Reanalysis (NARR) products. For evaporation and precipitation, only the gridded NARR points over water were considered. NARR incoming radiation includes the effect of cloud cover, so the cloud cover for the heat flux calculation was set to zero. Evaporation and precipitation were treated as sink and source terms, respectively, in the surface layer of each hydrodynamic model grid cell. Previous work has shown the NARR wind speed underestimates the wind speed over the Bay (Scully 2013). To help minimize the NARR underestimation of the wind speed, the NARR wind speed was adjusted based on relationships developed between the NARR wind speeds and observed wind speeds from the National Data Buoy Center, similar to the approach described by Bever et al. (2021). Wind forcing was applied at the water surface as a wind stress. The wind drag coefficient was varied based on local wind speed according to the formulation of Large and Pond (1981).

Salinity and temperature vertical profiles collected as part of the WQMP were used to specify salinity and water temperature initial conditions. These data are available through the Chesapeake Bay Program data hub (CBP 2017). A transect of vertical profiles spanning from the Bay mouth to the Susquehanna River was used to specify the along-estuary and vertical salinity and temperature gradients in the mainstem of the Bay. Similar transects in the James, York, Rappahannock, Potomac, Patuxent, Chester, and Choptank rivers and Eastern Bay were also used to specify initial conditions.

AQ Chesapeake Bay Model: Model Simulation and Outputs

The AQ Chesapeake Bay model was used to simulate a 24-year period spanning 1996 through 2019 for this study. The model was initialized in August 1995, providing 4.5 months for the model to spin up before January 1, 1996. The model was used to predict water level, currents, salinity, and temperature throughout the Bay and tributaries. Model output was processed to develop environmental variables for use with fisheries data and for developing maps and areas of fish habitat.

The maps of habitat suitability and environmental variables detailed in subsequent sections of this report were generated based on the hydrodynamic model grid. The hydrodynamic model grid is a complex mixture of irregularly spaced triangles and quadrilaterals, and the plotting of maps based on the hydrodynamic model grid is not straightforward. To provide files that can be efficiently used in a GIS-based program to make maps of habitat suitability, the values from the hydrodynamic model grid were mapped to a regularly spaced grid of squares. A regularly spaced grid with 100 m resolution (squares of 100 m side lengths) was created that completely covered the Bay and tributaries. Because the entire area of each of the regularly spaced squares was not always within the Bay (portions of some squares were over land), the wetted area of each regularly spaced square was calculated based on the shoreline of the hydrodynamic model and a zero NAVD88 elevation cutoff.

Each regularly spaced square was further subdivided into 10 m squares to allows us to determine the habitat suitability value associated with each regularly spaced grid and to estimate persistence of suitable habitat. These 10 m squares are referred to here as subcells. The values from the hydrodynamic model were interpolated to the subcells, and then all of the subcells that were over water were averaged to obtain a representative value for the corresponding regularly spaced square. The habitat suitability values on the regularly spaced grid can then be used with the wetted area of each regularly spaced grid cell to estimate the area of habitat within the range of 'suitability', described further below.

AQ Chesapeake Bay Model: Model Validation

Validation was achieved by comparing the model outputs to the abiotic data collected as part of the fisheries sampling programs and to vertical profile data from the WQMP. Irby et al. (2016) documented the accuracy of multiple models in the Bay for 2004 and 2005 using vertical profile data from 13 of the WQMP stations in the mainstem of the Bay. A detailed comparison of the accuracy of the AQ Chesapeake Bay model to the models evaluated in Irby et al. (2016) was provided in Anchor QEA (2020). Anchor QEA (2020) also evaluated the model accuracy for time series data at CBIBS locations.

Salinity and temperature from the 24-year simulation were validated using a combination of data sources to provide a robust validation. The model was validated to long-term trawl survey observations of salinity and temperature in each year individually from 1996 through 2019, to provide a direct evaluation of the environmental conditions predicted by the model that were then used in combination with the fish catch data, similar to that done by MacWilliams et al. (2016). Validation to the VIMS trawl survey data included 28,634 individual model-data comparisons and validation to the ChesMMAP trawl survey data included 6,261 individual model-data comparisons (Figure 7). The AQ Chesapeake Bay model was validated to the same 13 WQMP stations in the mainstem of the Bay (Figure 7) as used in Irby et al. (2016) and used 38 WQMP stations for the large western tributaries.

The model estimates were validated using methods detailed in MacWilliams et al. (2015) and Irby et al. (2016), using the means and correlation of the observed and estimated values, model skill (Willmott 1981), and target diagram statistics (Jolliff et al. 2009) to assess the accuracy of the model. The target diagram statistics determine how the mean and variability of the model estimates related to those of the observed data. Jolliff et al. (2009) and Hofmann et al. (2011) provide detailed descriptions of target diagrams and their use in assessing model skill. This approach uses the bias and the unbiased Root-Mean-Square Difference (*ubRMSD*) between the observations and predictions, which are normalized by the standard deviation in the observations ($bias_N$ and $ubRMSD_N$) to assess the accuracy of the model predictions. The $ubRMSD_N$ was multiplied by the sign of the difference in the observed and predicted standard deviations to indicate overprediction (positive) or underprediction (negative) of the observed variability. On target diagrams, the Y axis is the $bias_N$ while the X-axis is the $ubRMSD_N$. The radial distance from the origin to each data point is the normalized total Root-Mean-Square Difference ($RMSD_N$, calculated as $RMSD_N = \sqrt{bias_N^2 + ubRMSD_N^2}$). The $RMSD_N$ is a dimensionless number, where values less than 1.0 indicate the model estimates were more accurate than simply estimating the mean of the observations. Thresholds established by MacWilliams et al. (2015) provide general guidance on classifying the accuracy of hydrodynamic model estimates, with an $RMSD_N$ less than 0.25 indicating very accurate estimates, 0.25 to 0.5 indicating accurate estimates, 0.5 to 1.0 indicating acceptable estimates, and greater than 1.0 indicating relatively poor agreement between the model estimates and observations.

The validation of model-predicted salinity and temperature to the co-located VIMS trawl survey data for each year from 1996 through 2019 demonstrated that the salinity and temperature observed at the same time as the fisheries sampling was accurately estimated, with the $RMSD_N$ being less than 0.44 for salinity and 0.23 for temperature (Figure 8). The predicted salinity was slightly biased high at higher salinity values, and the predicted temperature was very slightly biased low at low temperature. The validation of model-estimated salinity and temperature to the co-located ChesMMAP trawl survey data for each year from 2002 through 2018 demonstrated that the salinity and temperature observed at the same time as the fisheries sampling was acceptably to accurately estimated, with the $RMSD_N$ being less than 0.74 for salinity and 0.31 for temperature (Figure 9). The model-estimated salinity was slightly biased high at higher salinity values, and the model-estimated temperature was very slightly biased low at low temperature.

Data from the WQMP were used to validate predicted salinity and temperature in each year in the mainstem and the tributaries separately. Mainstem bottom salinity was most accurately predicted during the years 1996 through 2001 and 2005 through 2019 (Figure 10A). The predicted bottom mainstem salinity was less accurate from 2002 through 2004 than in the other years. Mainstem bottom temperature was accurately estimated in each year (Figure 10B). This study expanded the model validation to include tributary WQMP locations. Both bottom salinity (Figure 10C) and bottom temperature (Figure 10D) in the tributaries were accurately predicted by the model.

The detailed validation of the predicted salinity and temperature demonstrated that the model accurately predicted temperature and salinity in the major tributaries and accurately predicted the salinity and temperature co-located with the fisheries catch data. The AQ Chesapeake Bay model is sufficiently accurate for understanding environmental conditions in fish habitats over multiple spatial and temporal scales.

AQ Chesapeake Bay Model: Pairing Catch Data with Model Outputs

We used the geo-located midpoint of each tow as the location to estimate dynamic and static variables from the AQ Chesapeake Bay model. Water depth recorded during each tow in the MDDNR trawl survey was used to estimate the actual geographic location closest to the targeted fixed station location at the time of sampling. For the seine surveys, we used the reported station location as the location for extracting habitat variables from the AQ Chesapeake Bay model. Some sampling locations in the seine surveys were very close to the edge of the model grid, i.e., close to tributary inflows to the model. As a result, model outputs for some of these locations were highly dependent on model inputs, particularly inflow temperature, and may have deviated from exact conditions at a given day and time. Finally, a small number of survey locations (n<10) were outside the extent of the model grid, so modeled values for these sites were not provided or used in subsequent analyses. Both static and dynamic conditions were output for consideration in habitat suitability models and to estimate area of suitable habitat for two age groups of striped bass throughout the Bay.

AQ Chesapeake Bay Model: Dynamic (time-varying) Variables

Estimates of temperature (n=4), salinity (n=4), current speed (n=6), and tidal-averaged water depth obtained from the AQ Chesapeake Bay model were considered dynamic variables (Table 3). These variables were output as both instantaneous values at the time and location of each sampling, as well as a time-averaged value of the 24.8 hours (i.e., one tidal cycle) prior to sampling to represent environmental conditions encountered by fish in the period directly preceding sampling. Tidal-averaged and depth-averaged metrics were also generated for temperature, salinity, and current speed, as well as maximum depth-averaged current speed. Covariates that reflect bottom (1 m above seabed) and surface (1 m below surface) temperature and salinity were considered to indicate conditions sampled by particular gears (e.g., surveys that employ a bottom trawl); temperature and salinity stratification were calculated as the difference between bottom and surface values. Covariates that represent vertical gradients (difference between near bed and surface) and the horizontal gradient (maximum difference between adjacent model grid cells) in current speed were also supplied by the AQ Chesapeake Bay model. Finally, dynamic water depth was estimated at the time and location of sampling as the average depth in a given spatial grid. Covariates that vary through time may provide insight into seasonal or interannual variability in habitat conditions. Additionally, the aquatic environment changes tidally and striped bass are likely responding to the suite of conditions experienced prior to capture. By using dynamic variables, those conditions can be assessed and compared with point estimates taken at the time of capture.

AQ Chesapeake Bay Model: Static Variables

Static variables do not change with time to an extent that will meaningfully affect fish habitat, and as such these variables were assumed to be constant in time but variable across space. The two static variables considered were distance to shoreline and sediment composition, expressed as seabed percent fine sediment (Table 3). Distance to shore was calculated as the straight-line distance from the sample site to the nearest shore. A seabed grain-size distribution was developed for the entire Bay and tributaries based on observed surface seabed grains size data (Moncure and Nichols 1968; Byrne 1983; Kerhin et al. 1988; Velinsky 1994; Maryland Geological Survey 1996; Reid et al. 2005) as part of the development of the AQ Chesapeake Bay hydrodynamic, wave, and sediment transport model. This Bay-wide surface grain-size distribution map was used to estimate a seabed percent fine sediment at each fisheries sampling location. The static distance-to-shoreline metric provides an indication of the proximity of fish habitats to shorelines; as fish grow, they may use habitats that are further away from vegetated shorelines and marshes, which may provide refuge for smaller fishes (Fabrizio et al. 2021). Similarly, the static sediment-composition metric can help resolve areas used by young fishes for foraging; young striped bass include a number of benthic organisms in their diet and as such, sediment composition may reveal areas that support benthic production. In general, static variables provide insight about the spatial distribution of fish.

Dissolved Oxygen Model for Chesapeake Bay

A second high-resolution numerical model of DO conditions (Du and Shen 2014; Fabrizio et al. 2021) was extended in time by incorporating monthly field observations of DO from fisheries surveys (VIMS trawl, ChesMMAP, VIMS and MDDNR seine) and monthly to bimonthly observations from the tidal WQMP stations between 1996 and 2019. Observed bottom and surface water DO concentrations were spatially interpolated and assigned to a 1 km^2 rectangular grid using inverse-distance weighting. This resolution was selected to better represent smaller tributaries known to be critical habitats for striped bass. This method assumes that observations close to one another in space and time are more alike than those that are farther apart. Each measured point therefore has an area of local influence that decreases with distance. DO values were then temporally interpolated from monthly to daily time steps via linear regression, thus bottom and surface DO values could be coupled with a sampling event by extracting values from the closest grid cell for a given day. A third variable, DO stratification, was calculated as the difference between surface and bottom DO. We considered DO stratification as a metric of the strength of the DO gradient in the water column; such gradients may dictate habitat use by striped bass. In Chesapeake Bay, resident striped bass aged 2 to 5 years avoid deep areas that experience hypoxia during summer (Kraus et al. 2015a). Instead, these fish use habitats in the surface layers (above the hypoxic volume) or in shallow areas close to shore that exhibit normoxic conditions; temperatures in these normoxic waters, however, may exceed 25°C (Kraus et al. 2015a) and may thereby impose a metabolic toll (Lapointe et al. 2014).

In the fisheries surveys that recorded DO in the field, observed data were compared against the interpolated DO values to verify their validity. A subset of years were used for this comparison for age-0 (n=4,481 observations) and age 1-4 fish (n=3,668 observations). Approximately 4% of the DO observations recorded from the seine surveys indicated bottom DO conditions were $\leq$ 5 mg O_2/L but the model-based estimates were >5 mg O_2/L. Similarly, potentially questionable model estimates occurred in about 2.5% of observations from the VIMS and MDDNR trawl surveys over the entire time series for bottom DO, and <1% for surface DO. A previous application of the interpolated DO model (Fabrizio et al. 2021) found that the 1 km^2 spatial resolution and daily time step may not capture localized instantaneous DO conditions measured at the time of sampling. However, we assert that at least 95% of hindcasts from this model are acceptable and accurate.

Selection of Habitat Covariates

Using Boosted Regression Trees to Identify Influential Covariates

Boosted regression trees (BRTs, Elith et al. 2008) were applied to identify and select the subset of habitat covariates that influenced abundance of age-0 and age 1-4 striped bass. BRTs aim to improve the performance of a single model by fitting many models and combining (i.e., “boosting”) them to optimize predictive performance. Note that this data-driven approach contrasts with the *a priori* specification of covariates to describe habitat characteristics. BRTs partition observations into increasingly similar groups based on threshold values of predictors – habitat covariates – through the recursive selection of a random subset of the data (the training set). In this manner, cross-validation is used to assess model fit by ensuring that trees were applicable to the remaining data (the test set). BRTs can accommodate missing values, different scales of measurement, nonlinear relationships, and interactions which are common features of ecological data. BRTs quantify the importance of a given covariate with a measure of relative influence, a weight which indicates whether the model improved as a result of its inclusion. All habitat covariates considered in BRT analyses were examined for collinearity and standardized to allow for direct comparison of their influence (Schielzeth 2010). This targeted selection of a subset of covariates is not only computationally efficient but allows the resulting model to be generalizable beyond the survey data used to develop the BRT model.

Because environmental conditions and habitat features that describe suitable habitats are likely to differ between age groups and surveys, BRTs were applied independently to each of the four datasets. For the trawl survey datasets (age-0 small trawl, age 1-4 small trawl, age 1-4 ChesMMAP), 30 possible covariates from the AQ Chesapeake Bay model and three covariates from the numerical DO model were considered in BRT analyses (Table 3). This full suite of 33 covariates included tidal-averaged and non-tidal averaged values; to reduce computational time and correlations between covariates, BRTs were applied to each trawl survey dataset with either tidal-averaged (n=20) or non-tidal averaged (n=18) covariates, and the subset that resulted in the greatest deviance reduction (a measure of model performance where low deviance indicates better performance) was used for subsequent analyses. Both subsets included static habitat metrics (i.e., distance to shore, percent fine sediment) as well as dynamic water depth. For the seine survey dataset (age-0 seine), covariate selection using BRTs was restricted to a subset of six covariates to describe habitat conditions for fish sampled by seine surveys: surface temperature, surface salinity, surface dissolved oxygen, and three metrics of current speed. This decision reflects the spatial limitation associated with beach seines; this gear samples relatively shallow waters directly adjacent to the shoreline, rendering some covariates inapplicable (e.g., distance to shore) or inconsequential (e.g., temperature stratification). In addition, at small spatial scales closer to shore, the robustness of some of the AQ Chesapeake Bay model estimates of habitat conditions decreases.

Habitat covariates identified as influential explained variation in relative catch rates (CPUE), where the number of fish captured per standard tow or per standard seine haul were modeled as a Poisson response in the BRTs. Catches of age-0 fish from the VIMS seine survey were standardized to a mean area swept (1/4π * [23.95 m]^2, where 23.95 was the mean net extension offshore) and expressed as the number of fish per area swept. Catches of age-0 fish from the MDDNR seine survey were standardized by expressing CPUEs as fish per area swept equivalent to the VIMS seine area swept and rounded to the nearest integer. Similarly, catches of age-0 and age 1-4 striped bass from the VIMS trawl survey were standardized by expressing the catches as numbers of fish per five-minute tow and catches from the MDDNR trawl survey, which samples for six minutes, were expressed in five-minute equivalents and rounded to the nearest integer. Finally, catches of age 1-4 fish in the ChesMMAP survey were expressed as numbers of fish per 20-minute tow, without modification.

Optimization and Fitting of BRTs

Prior to the application of BRTs, three model parameters were specified: bag fraction, learning rate, and tree complexity. The bag fraction refers to the proportion of data randomly selected from each model run, with the remainder serving as the cross-validated dataset; this stochasticity helps reduce the variance of the final model. The bag fraction is recommended to range between 0.5 and 0.75 (Elith et al. 2008); previous work suggested that 0.75 was a sufficient level for fisheries catch data (Fabrizio et al. 2021). The learning rate describes the contribution of each tree to the model (i.e., how quickly the model approximates the observed data), whereas tree complexity indicates the level of interaction possible among covariates. Optimization of these three parameters helps balance model fit and performance to prevent overfitting. As optimization can be computationally intensive, a subset of three years of survey data that represented a range of abundance ('low', 'average' and 'high' years) were used in optimization runs (age-0: 2010, 2011, 2012; age 1-4: 2004, 2010, 2016). A series of learning rates (0.0005, 0.005, 0.0075, 0.01, 0.02, 0.03, 0.04, 0.05, and 0.075) and tree complexities (1, 3, 5, and 10) were considered for each of the four datasets. The cross-validated deviance and the minimum predictive error produced by each combination of parameter values were graphically examined and the combination of learning rate and tree complexity that produced the lowest deviance and predictive error was selected (Elith et al. 2008); this approach was performed separately for each dataset. Only those runs for which at least 1,000 trees were fit were considered (Elith et al. 2008).

We fit BRTs to the datasets on fish catch (numbers of fish per standardized area sampled) and environmental covariates following the approach outlined in Elith et al. (2008) and Elith and Leathwick (2017), and using the optimal learning rates, tree complexities, and bag fraction identified for each dataset:

(1) age-0 fish from the VIMS and MDDNR seine surveys, 1996-2017, learning rate of 0.0075, tree complexity of 3, and bag fraction 0.75;

(2) age-0 fish from the VIMS and MDDNR trawl surveys, 1996-2019, learning rate of 0.005, tree complexity of 5, and bag fraction 0.75;

(3) age-1-4 fish from the VIMS and MDDNR trawl surveys, 1996-2019, learning rate of 0.0075, tree complexity of 10, and bag fraction 0.75; and

(4) age 1-4 fish from the ChesMMAP survey, 2002-2018, learning rate of 0.02, tree complexity of 3, and bag fraction 0.75.

We used the scree plot and the relative importance metric to identify habitat covariates that best described habitat characteristics for each of the four datasets for striped bass. Habitat predictors that explained at least 5% of the variation in fish abundance in a given dataset were retained for use in habitat suitability modeling. All BRT analyses, including the optimization runs, were conducted with the R package ‘dismo’ and the gbm.step procedure (R Core Team 2022).

Habitat Suitability Models

The Need for Seasonal Models of Habitat Suitability

The key habitat predictors identified by BRT analyses were used to develop four nonparametric habitat suitability models for age-0 (seine model and trawl model) and age-1-4 striped bass (two trawl models). Changes in seasonal conditions (e.g., temperature or precipitation) may affect the suitability of estuarine habitats for juvenile striped bass (Manderson et al. 2014), and as such, we considered development of seasonal models to reflect the dynamic nature of estuarine conditions and the availability of fish of a given age to the sampling gear at different times of year. Habitat suitability models were developed and estimates of suitable habitat were produced for specific seasons, the definition of which varied among datasets (Table 2). For age-0 fish captured by seines, seasons were defined as ‘early’ (June-July) and ‘late’ (August-September) summer to reflect the rapid growth and development of these fish, and the potentially different habitats used during this first summer of life. For age-0 fish captured by the VIMS and MDDNR trawl surveys, we identified four periods: early summer (May-July), late summer (August-October), fall/winter (November-January), and spring (February-April). These seasons were designed to follow a cohort post-hatching through its first full year of life. We defined three seasonal periods for age 1-4 fish captured by the VIMS and MDDNR trawl surveys: spring (March-June), summer (July-October), fall/winter (November-February). Note that habitat suitability estimates during seasons that included information from fish captured between the months of November and April were based solely on catches from the VIMS trawl survey because the Maryland trawl survey does not sample during these months. Finally, because the ChesMMAP survey conducts five distinct monthly surveys each year, a similar three-period approach was established to describe habitat suitability for age 1-4 fish in this survey to align with the periods of data collection: spring (March-June includes the March and May surveys), summer (July-October includes the July and September surveys) and fall (November). Notably, the survey design for ChesMMAP dictated that the “fall” period includes November only to avoid biasing habitat estimates toward conditions that were not sampled (i.e., December-February) and therefore, not encountered by these fish.

Suitability Indices (SIs)

We used the histogram approach to develop suitability indices (SIs) that ranged between 0 (poor) and 1 (high quality) and that corresponded with a range of conditions, for example, an SI of 0.9 may correspond with tidal-averaged bottom temperatures between 18.2 and 19.5°C. To delineate these ranges, we grouped observations of each influential habitat covariate using a disjoint clustering method; this method allowed us to identify ‘natural’ clusters within the full range of observed values in a given season. This approach was implemented using the *‘FastClus’* procedure in SAS/STAT software (version 9.4). The number of clusters for each covariate was allowed to vary (but not exceed 10), with each cluster having a minimum of 40 observations so that the sample size would adequately represent the average fish abundance observed in habitats defined by the range of conditions for each cluster. Clusters were then used to estimate the corresponding SI as described in Tanaka and Chen (2015) and Fabrizio et al. (2021):

$$SI_{ij} = \frac{CPUE_{ij} - CPUE_{i,min}}{CPUE_{i,max} - CPUE_{i,min}} \qquad (2)$$

where $CPUE_{ij}$ is the mean fish abundance observed in cluster *j* of covariate *i*, and $CPUE_{i,min}$ and $CPUE_{i,max}$ are the minimum and maximum catches observed across all clusters. For the seine dataset, CPUE was expressed as the geometric mean fish abundance in order to minimize bias from a number of very large, and possibly influential, catches. Equation (2) ensured that SI scores range between 0 and 1.0. In summary, SI scores were developed for each of the influential covariates for each season (e.g., 'early summer') and dataset.

Calculation of the Habitat Suitability Index

The SIs for each of the covariates were combined to generate a composite habitat suitability index (HSI) for each grid cell and corresponding sampling locations. The HSI was also expressed on a scale of 0 to 1.0 and calculated as the mean of the individual SIs (Brown et al. 2000, Tanaka and Chen 2015) across multiple habitat covariates:

$$HSI = \frac{SI_1 + SI_2 + \cdots + SI_i}{i} \qquad (3)$$

where SI_1 represents the suitability index for habitat covariate #1, SI_2 represents the suitability index for habitat covariate #2, and *i* represents the number of covariates identified from BRTs. To avoid overweighting the HSI for a particular habitat condition, only covariates that did not exhibit high correlations with other covariates ($r^2 \leq 0.8$) were considered. Multiple models of the mean (i.e., geometric, arithmetic, and weighted arithmetic) were considered in the formulation of the HSI because a single estimation method may not be appropriate for all species (Yu et al. 2019; Fabrizio et al. 2021). The arithmetic mean model of the HSI is presented in Eq. 3. The weights applied in the weighted arithmetic model were obtained from the measures of relative influence from the BRT analyses. Each of the four datasets therefore resulted in four HSI models, two for age-0 striped bass and two for age 1-4 striped bass.

HSI models were calibrated by graphical examination of average relative abundance and HSI values for each season. The expectation is that mean relative abundance of striped bass increases as the HSI approaches 1.0, or as habitat conditions become more suitable (Tanaka and Chen 2015). We used trimmed means (5%) to estimate mean relative abundance to reduce the influence of extreme catches observed in some datasets.

Verification of HSIs

To verify covariate selection and HSI formulation, each of the four models was cross-validated with 10 bootstrapped replicates. Replicates were generated as random subsamples of fishery observations in a respective dataset stratified across years, regions (i.e., Chesapeake Bay tributaries), and seasons, and partitioned into training (70%) and test (30%) datasets. BRTs were again fitted to the data and the HSIs were predicted for each training dataset; note that each bootstrapped subsample may identify different influential covariates or a different number of covariates relative to the initial run. The bootstrapped

HSIs were compared with those from the original model, and the formulation with the lowest root mean square error (RMSE) was selected. The RMSE is a metric used to evaluate model performance and was calculated as the standard deviation of the residuals, or the difference between the predicted and observed HSI for each location. This analysis allowed us to determine the appropriateness of the selected covariates and the HSI formulation (e.g., arithmetic vs geometric mean).

Extent of Suitable Habitats

Habitat suitability models were used to characterize and delineate suitable habitats based on the range of conditions that were occupied (HSI>0) or not occupied (HSI=0) by age-0 or age 1-4 striped bass. An HSI value was assigned to each hydrodynamic model grid cell to quantify the extent of suitable habitat for each season and year and for each dataset. Several thresholds of suitability (e.g., HSI > 0.4, HSI > 0.5, etc.) were used to estimate the extent of suitable habitats in the Chesapeake Bay system and these estimates were examined graphically to inform our selection of an appropriate threshold of suitability. A threshold HSI value of 0.5 was selected to delineate unsuitable (HSI < 0.5) from suitable (HSI $\geq$ 0.5) habitats; similarly, optimal habitats were those where the HSI was at least 0.7. The threshold value of 0.5 was also used by Fabrizio et al. (2021) and Theuerkauf and Lipcius (2016) to delineate suitable habitats. HSI models were used to generate maps that visually depicted the location and spatial extent of unsuitable (0.00-0.49), suitable (0.50-0.69) and optimal (>0.70) habitats for each age group using the 0.5 and 0.7 thresholds. Maps and estimates of the extent of suitable and optimal habitats (km^2) were generated for the entire Chesapeake Bay system, Maryland waters, Virginia waters, and 10 specific regions representing the major spawning and rearing areas for YOY striped bass (Fabrizio et al. 2018). These areas are the James, Rappahannock, York, Potomac, Patuxent, Chester, Choptank, and Pocomoke rivers, a region on Maryland's Eastern shore that encompassed the Nanticoke and Wicomico rivers and Fishing Bay (hereafter called the "Nanticoke area"), and a region denoted Upper Bay that comprised the area near the Susquehanna flats to Conowingo Dam (refer to Figure S2 in supplemental materials). Estimation of suitable habitat areas in these regions demonstrated how habitat suitability models can be used to estimate seasonal and interannual variability in fish habitat at multiple spatial scales, and to estimate the extents of suitable habitats in areas that are not currently sampled by fisheries surveys (e.g., Potomac River).

Preliminary mapping of HSIs estimated for age-0 fish captured by seines depicted a high degree of small-scale variation that was difficult to interpret at the scale of the Chesapeake Bay region. The sampling domain of the seine surveys (close to the shoreline, and less than 2 meters deep) limited the extent to which estimates of suitable habitat could be spatially interpolated Bay-wide, for example, age-0 striped bass are not expected to occupy habitats in the mainstem of the Bay in early or late summer, yet our models suggested the existence of suitable habitat in the mainstem of the Bay. Given the behavior and distribution of age-0 striped bass in summer, such projections of habitat were deemed unreliable. Therefore, estimates of suitable habitat for age-0 fish from the VIMS and MDDNR seine surveys were restricted to habitats along the shorelines with a depth of 2 meters or less. Because dynamic water depth depended on both the grid-cell size and bathymetry at a given sampling location, subsequent estimates of suitable habitat were based on areas where the median water depth across a given season was at least 2 m in depth. This demarcated areas that represented suitable shoreline habitats that were consistently available to YOY striped bass in summer.

To quantify and depict the extent of suitable habitat for a range of specific environmental conditions, six years in the time series (1996-2019) were selected to represent relatively low, high, and average thermal (warm, average, cool) and hydrologic (wet, average, dry) conditions in the Chesapeake Bay. The identification of wet, average, and dry years was based on river discharge data from nine USGS River Inflow Monitoring (RIM) tributaries to the Bay (Moyer and Blomquist 2020; USGS 2021). These RIM tributaries represent the majority of the riverine freshwater discharge to the Bay. The USGS reports the annual average discharge for "water years", defined as October 1 through September 30. The use of water years instead of calendar years is appropriate for this analysis because Bay-wide salinity responds relatively slowly to freshwater discharge. High freshwater discharge in the fall (e.g., in November) will influence the salinity experienced by fish in January. The yearly average freshwater discharge rate to the Bay was extracted from the USGS RIM data and plotted to identify relatively wet (higher discharge), average (average discharge), and dry (lower discharge) years (Figure 11). We identified 1999, 2007, and 2019 as dry, average, and wet years, respectively. Next, we used the observed water temperatures at Thomas Point Light (obtained from the National Data Buoy Center, Station TPML2; NDBC 2021) to evaluate the annual median observed water temperature (Figure 12). We used the median temperature to remain consistent with the way we estimated average conditions from the hydrodynamic model. The years 2002, 2012, and 2014 were identified as average, warm, and cool years, respectively. Because of these designations, we were unable to apply this analysis to the age 1-4 fish captured by the ChesMMAP survey (fisheries observations for 1999 and 2019 were unavailable for this survey).

Some areas of the Bay and tributaries may have suitable habitats in most years, while other areas only intermittently or never have suitable habitats. A metric of persistence can provide insight on the locations that consistently (or never) exhibit conditions that support striped bass. We estimated persistence of suitable habitats for each model grid cell by calculating the percentage of years when the HSI was greater than or equal to 0.5 for each season and age group combination.

Finally, we tested the hypothesis that the extent of suitable habitat did not vary through time. To address this question, the annual areal extent of suitable habitat (HSI>0.5) was rank-transformed and regressed against year; we used a nonparametric approach due to the limited number of observations (years). We used an *a priori* α level of 0.05 for the tests of the significance of the slope parameter (which estimates the change in suitable habitat area per year); we also reported P values. Nonparametric regression analyses were conducted with the '*rank*' and '*glm*' procedures in SAS/STAT software.

Relationship Between Relative Abundance of Striped Bass and Extent of Suitable Habitats

We explored the relationship between the extent of suitable habitats and the relative abundance of age-0 or age 1-4 striped bass to determine if season-specific annual changes in habitat extent were related to the observed relative abundance. For datasets that incorporated information from multiple fishery surveys (e.g., age-0 striped bass captured by the VIMS trawl survey and the MDDNR trawl survey), a Bayesian hierarchical method (Conn 2010) was used to extract a single Bay-wide standardized estimate of relative abundance for each season and each dataset. This approach yielded an index that reflected the pattern exhibited by the multiple separate indices, and accounted for variation in catchability, spatial distribution, and variance within individual surveys (i.e., process and sampling error, respectively; Conn 2010). A composite index is preferable for analyzing multiple, "noisy" indices, especially when those indices are not highly correlated. Prior to applying the Conn (2010) method, seasonal relative abundances that reflected CPUE (fish/km^2 or fish/m^2) were standardized to a mean of 1.0 across time (24 years, 1996-2019 for the VIMS/MDDNR trawl surveys; 22 years, 1996-2017 for the VIMS/MDDNR seine surveys; and 17 years, 2002-2018 for the ChesMMAP survey). These standardized abundances do not reflect differences in estimated mean catch rates among surveys within a given year but allow for a comparison of patterns in abundance among surveys and across time. Calculations were performed using WinBugs (version 1.4.3) accessed through the R package *R2WinBUGS* (R Core Team 2022).

To relate the standardized Bay-wide abundance of age-0 or age 1-4 striped bass to variation in the Bay-wide extent of suitable habitats (areas [km^2] with $HSI \geq 0.5$), seasonal and annual abundance indices were rank transformed prior to regressing the indices against habitat extent. As before, we used a nonparametric regression approach to explore these relationships. We assumed that the effect of habitat extent on fish abundance was constant through time (i.e., the relationship was stationary), which was reasonable for this relatively short (<25 years) time series. For models that utilized data from the VIMS and MDDNR trawl surveys, only the standardized relative abundance index from the VIMS survey was used to assess the relationship in winter (November-January) and spring (February-April) for age-0 fish, and in fall (November-February) for age 1-4 fish, because the MDDNR trawl survey does not sample during these months. As a result, abundance was regressed against the extent of suitable habitats in Virginia waters only, not the entire system. We used an *a priori* α level of 0.05 for the tests of the significance of the slope parameter (which estimates the change in standardized abundance per km^2 of suitable habitat); we also reported *P* values. Nonparametric regression analyses were conducted with the '*rank*' and '*glm*' procedures in SAS/STAT software.

Results and Interpretation

The following section characterizes and quantifies habitat for each habitat suitability model generated for YOY and resident sub-adult striped bass. Conditions that defined suitable and optimal habitats for age-0 and age 1-4 striped bass varied across seasons and among years. This variation reflected changes in environmental conditions throughout the year and among years, but also changes in habitat use that occurred throughout this period of life. Some of this variation may have also reflected differences in sampling designs (e.g., random stations in Virginia and fixed stations in Maryland).

As used here, 'suitability' was a function of the specific covariates selected for analysis, as well as other factors affecting the estimation of abundance, such as the availability of fish of a given size to a particular gear and detection probabilities at certain sites or under certain conditions. Such concerns apply to all sampling gear and add to uncertainty in suitability models.

A threshold value of 0.5 was used to delineate unsuitable ($SI < 0.5$) from suitable ($SI \geq 0.5$) habitats; optimal habitats were those where $SI \geq 0.7$. Specific habitat conditions that corresponded to suitability indices of 0.5 or greater varied for each model.

Verification of HSI approach

In all four habitat models, bootstrapped BRTs generally identified the same or similar covariates from the 10 replicates of the model.

For the model applied to age-0 fish collected by seines, the weighted arithmetic mean had the lowest RMSE which indicated this formulation best approximated the original HSI model (Figure 13; $t=15.01$, $P<0.05$). Weights for individual covariates were obtained from measures of relative influence produced by the BRT analysis and used to fit the original HSI; the proportion of variance explained was used as the weight and values were as follows: maximum depth-averaged current speed (0.3606), surface dissolved oxygen (0.2638) and horizontal gradient in the current speed (0.1539).

Bootstrapped habitat suitability models using three formulations for the HSI (arithmetic mean, geometric mean, and weighted arithmetic mean) for age-0 fish captured by small trawls were compared with those from the original model, and mean RMSEs for the three formulations were not significantly different; however, the least square mean of the geometric mean HSI (0.22) was greater than the arithmetic (0.16) or weighted arithmetic (0.17), indicating that either the arithmetic or weighted arithmetic formulation was best. No difference was observed between the mean RMSEs for the arithmetic and weighted arithmetic means (t=-0.24, *P*=0.81); therefore, we selected the arithmetic mean formulation in the interest of parsimony (Figure 13). The mean RMSE for the geometric formulation of the HSI was significantly greater than the arithmetic and weighted arithmetic mean for bootstrapped suitability models for age 1-4 fish captured by small trawls (t=2.44, *P*<0.05) and age 1-4 fish captured by the ChesMMAP survey (t=3.19, *P*<0.05). No significant difference was observed between the RMSE based on arithmetic and weighted arithmetic mean HSI for the models using fish captured by either the small trawls (t=0.10, *P*=0.92) or ChesMMAP trawl (t=0.04, *P*=0.97), so we again selected the arithmetic mean formulation in the interest of parsimony (Figure 13).

Note that the geometric mean HSI was not selected for the formulation of the HSIs for either age-0 or age 1-4 fish. The geometric mean HSI is best when a single factor dictates habitat suitability, but this construct is too conservative for a highly mobile species such as striped bass that uses a variety of habitats, particularly during the rapid growth and development that occurs during the first few years of life. The arithmetic mean or weighted arithmetic mean HSI is best when species of interest tolerate broader variations in environmental conditions, including sub-optimal or marginal habitats for limited periods of time. For example, if DO in an area is low, other environmental conditions may be suitable and fish may use these habitats. Therefore, the suite of variables considered (and likely those not considered, such as food availability) define suitability of habitats, and based on our results, we found no evidence that habitat use in age-0 or age 1-4 striped bass is moderated by a strict threshold in a single covariate.

We found that the HSI was properly calibrated for the four datasets. The trimmed mean relative abundance increased as the weighted arithmetic HSI approached 1.0 for the model for age-0 fish captured by seines (Figure 14). The trimmed mean relative abundance also increased as the arithmetic HSI approached 1.0 for age 1-4 fish captured by small trawls and by the ChesMMAP trawl (Figure 14B, Figure 15A-B). For each model, habitats that supported abundances at or above average during the full time period were consistently represented by HSI values $\geq$ 0.5 across seasons.

Age-0 (YOY) Striped Bass in Shoreline Habitats (VIMS and MDDNR Seine Surveys)

Influential habitat covariates

Six habitat covariates were considered in the seine model and three were identified as influential covariates (Table 4): surface dissolved oxygen, maximum depth-averaged current speed, and the horizontal gradient in the current speed. These three predictors explain approximately 78% of the variation in abundance of age-0 striped bass in the seine surveys between 1996 and 2017. The identification of instantaneous metrics for describing habitats of importance to seine-captured YOY striped bass reflects that these fish may move in and out of shallow areas with the tide; as such, tidal-averaged covariates were not likely to describe conditions encountered at the time of sampling. The large amount of explained variation in relative abundance indicates that local conditions played an important role in defining habitats in shallow, seine-able waters close to the shoreline.

Dissolved oxygen was important in defining habitats for YOY striped bass that inhabited shoreline areas. In the Chesapeake Bay, higher temperatures during summer have increased the prevalence of hypoxic ($\leq$ 2 mg O_2/L) or anoxic (0 mg O_2/L) conditions by facilitating stratification and reducing oxygen solubility. Despite the fact that areas of low DO are semi-consistent features in some areas of the Bay, interannual variability in these features results, in part, from changes in spring rainfall. DO concentrations may also fluctuate widely in estuarine environments across a range of spatial and temporal scales. In shallow, shoreline habitats occupied by age-0 striped bass, diel fluctuations in DO can present conditions that range from hyperoxia ($\geq$15 mg O_2/L) during the day, to hypoxia or anoxia overnight, with the lowest DO concentrations observed just after dawn (Tyler et al. 2009, Dixon et al. 2017). Additionally, these low DO conditions can extend to the benthos. Episodic hypoxic conditions can alter the quality of shallow estuarine habitats for juvenile fishes and DO may therefore be a critical predictor of suitable habitat for age-0 striped bass, particularly during warm months. DO is generally considered a limiting resource, because a decrease in DO may limit a fish’s capacity to expend energy through metabolically expensive activities like swimming, foraging, and growth (Nelson and Lipkey 2015). As a result, low DO concentrations may contribute to direct mortality or restrict available habitat for young fishes. Although natural processes of primary production and algal respiration contribute to hypoxic conditions, the severity and duration of these events has increased due to increased nutrient loadings to the Bay (Diaz and Rosenburg 2008; Breitburg et al. 2018); hypoxic events are further enhanced as temperatures continue to warm in the Chesapeake Bay (Hinson et al. 2021). Whereas surface temperature was not identified as an influential covariate for describing shoreline habitats used by age-0 striped bass, the inherent strong positive correlation between water temperature and dissolved oxygen concentration indicates that temperature likely played a role in defining suitable habitats for these fish.

Two current speed metrics, maximum depth-averaged current speed and horizontal gradient in the current speed, were influential habitat covariates for age-0 striped bass in shoreline habitats. YOY fish are likely to prefer shallow waters characterized by slower current speeds. Note that most estimates of current speed from the AQ Chesapeake Bay model are for locations further from shore than the location sampled by the seine surveys. Regardless, in shallow environments close to shore, strong vertical gradients or stratified conditions with respect to current speed are unlikely to occur. As a result, the maximum depth-averaged current speed may provide insight on age-0 fish preference for high or low velocity regions; high current speeds may be briefly tolerable as long as the maximum speed does not exceed a particular threshold. This suggests that an upper limit of current speed may be useful to delineate shoreline areas able to support age-0 striped bass. Horizontal gradients may function to aggregate prey concentrations, and although no metrics that directly represented prey resources were considered in BRT analyses, suitable habitats will need to provide ample, high-quality prey.

Characterization of suitable habitats

For age-0 striped bass in shallow shoreline habitats in early summer (June-July), suitable habitats were those with maximum depth-averaged current speeds less than 0.644 m/s and horizontal gradients in the current speed less than 0.000532 m/s. Age-0 striped bass occupied habitats with surface dissolved oxygen greater than or equal to 3.84 mg O_2/L, and optimal (SI$\geq$0.7) habitats were characterized by DO concentrations greater than or equal to 8.91 mg O_2/L. In late summer (August-September), suitable habitats for age-0 fish in shoreline areas were defined by maximum depth-averaged speeds between 0.422 and 0.563 m/s and horizontal gradients between 0.0006 and 0.001 m/s. Suitable habitats for age-0 fish in late summer were characterized by surface DO concentrations greater than or equal to 3.84 mg O_2/L. In contrast with early summer, optimal (SI$\geq$0.7) habitats in late summer were defined by DO concentrations greater than or equal to 3.97 mg O_2/L (refer to Figure S1 in supplemental materials).

Although suitable shoreline habitats across seasons were characterized by normoxic surface DO concentrations, age-0 fish were observed at a wide range of DO concentrations including those below normoxia. Growth in striped bass may be depressed when DO concentrations decline to about 4 mg O_2/L (Coutant 1985; EBFM Striped Bass 2009), however, juveniles were routinely captured in areas with low and hypoxic ($\leq$2 mgO_2/L) conditions. We hypothesize that age-0 fish in areas characterized by low concentrations of surface DO may be using a specific prey resource or using these areas as refugia from predation, indicating that areas with supposedly marginally suitable DO conditions may yet provide useful habitat for this age group. Our approach enabled us to identify shoreline areas that were occupied by age-0 striped bass, however, the relationship between habitat suitability and specific habitat functions, such as foraging and growth, remain unknown.

Extent of suitable habitat and persistence through time

The extent (km^2) of suitable habitat for age-0 striped bass in shoreline habitats varied both seasonally and annually (Table 5). The average extent of suitable (HSI $\geq$ 0.5) and optimal (HSI $\geq$ 0.7) shoreline habitat was consistently greater in early summer relative to late summer across the ten regions we examined. In early summer, the mean proportional extent of suitable shoreline habitats in Maryland waters was approximately comparable to that in Virginia (difference=1.4%). We observed a similar pattern in late summer such that an approximately equivalent mean proportional extent of suitable habitat was found in Maryland and Virginia waters (difference=<1%). The average proportional extent of optimal habitat was also similar between regions in early and late summer. On average, in any given year between 1996 and 2017, 6.95% of the shallow shoreline habitats across the entire Bay system were considered suitable in early summer, and 1.55% were considered suitable in late summer for age-0 striped bass. Notably, several regions, all in Maryland waters, supported areas of suitable shoreline habitat greater than the Bay-wide proportional average (Table 5), including the Upper Bay in early summer (10.7%), the Nanticoke area in early summer (14.5%) and late summer (3.3%), and the Pocomoke River in early summer (14.1%) and late summer (3.6%). This suggests that these regions were particularly critical for the production of age-0 fish, and that proportionally, tributaries on the Eastern shore may play a larger role in supporting YOY striped bass than previously understood. This pattern, however, was not observed in other Maryland regions. For example, the mean estimated proportional extent of suitable habitat was below the Bay-wide average in both seasons in the Patuxent River (Table 5). Aside from the Patuxent River, all other regions consistently contained suitable habitats for age-0 striped bass that proportionally were similar to or greater than the Bay-wide average in early summer. The Potomac and York rivers supported an above-average proportional extent of suitable habitat in early summer but aligned with the Bay-wide average in late summer. Finally, the Choptank, Rappahannock, and James rivers also supported an above-average proportional extent of suitable habitat in early summer, but this declined below the Bay-wide proportional average in late summer (Table 5).

The extent of suitable habitat in early summer decreased significantly from 1996 to 2017 (Table 8; $F_{EarlySummer}$=6.04, $P_{EarlySummer}$=0.02). This decrease appears to be driven by a decline in the extent of suitable habitat area in Virginia waters (F=13.53, *P*<0.01), and in the Rappahannock River in particular (F=6.08, *P*=0.02) during the period of study. Conditions in shoreline habitats changed since 1996, and this change occurred during a critical period in which a decline in suitable habitat availability could have affected the relative abundance of age-0 striped bass. In contrast, the extent of suitable shoreline habitat in late summer exhibited no significant linear change between 1996 and 2017. We note that the extent of suitable area in late summer was lower than that observed in early summer, suggesting that as fish grow, suitable shoreline habitats may become limiting for YOY striped bass in many regions of the Bay. Suitable habitats for age-0 fish captured by seines, were necessarily constrained to shoreline areas; persistence (HSI $\geq$ 0.5 in at least 50% of years) of suitable areas was similar in Maryland and Virginia, suggesting that the annual availability of suitable habitats throughout the Bay is important for the continued production of the Chesapeake Bay population of striped bass.

Relationship between extent of suitable habitat and relative abundance of YOY striped bass

Indices of relative abundance for YOY striped bass in shoreline habitats were highly variable among years and between seasons (Figure 16). Abundance of age-0 fish in MD and VA shoreline habitats followed the same general pattern in early (June-July) and late (August-September) summer, with 1996 a particularly high abundance year for age-0 fish in MD, and 2011 a high abundance year for age-0 fish in VA (Figure 16). In contrast, 2002 and 2012 were low abundance years in both MD and VA.

Despite the significant decline in the extent of suitable habitat in early summer since 1996, with an alpha level of 0.05, we were unable to detect a significant linear relationship between the Bay-wide extent of suitable shoreline habitat ($\leq$2 m depth) and the rank-transformed estimate of Bay-wide age-0 abundance; this was true in early summer ($F_{EarlySummer}$=2.43, $P_{EarlySummer}$=0.13) and late summer ($F_{LateSummer}$=3.28, $P_{LateSummer}$=0.09; Table 9). It is possible that the observed decline in suitable shoreline habitats over time in Virginia (specifically, in the Rappahannock River) had minimal impact on the Bay-wide annual abundance of age-0 fish. High levels of productivity (i.e., consistently high catches of age-0 striped bass) occurred in early summer in the Upper Bay and in Maryland tributaries, but this was not where suitable habitat extents declined. Nevertheless, the data suggested that a relationship may indeed exist between Bay-wide index of ranked abundance of age-0 fish and the extent of suitable habitats (recall *P*-levels of 0.13 and 0.09). In general, the Bay-wide index of ranked abundance increased with greater extent of suitable habitats in both seasons (Figure 20A and B), with a few notable exceptions: 2002 and 2013 exhibited a high extent of suitable shoreline habitat but the index of ranked abundance in early summer was relatively low. Interestingly, we detected a significant, positive linear relationship between extent of optimal (HSI$\geq$0.7) shoreline habitats and ranked abundance in late summer (F=5.51, *P*=0.03; Figure 21B). Years in which indices of abundance were high (1996, 2001, 2003, 2011) were also characterized by greater extents of optimal habitats during late summer, despite the fact that average areal extents of habitats with an HSI $\geq$ 0.7 were an order of magnitude lower than estimates of the extent of suitable (HSI $\geq$ 0.5) habitats, and considerably less than the extents of optimal habitats in early summer (Table 5). As the extent of optimal-quality shoreline habitats (i.e., areas with HSI values $\geq$ 0.7) increased, higher abundances of age-0 striped bass were supported, particularly in late summer. We note that the relationship between abundance of YOY striped bass and the extent of suitable and optimal shoreline habitats may become detectable with additional years of data (> 22 years), especially given the high degree of interannual variability in abundance that is characteristic of estuarine-dependent species like striped bass.

Age-0 (YOY) Striped Bass in Nearshore Habitats (VIMS and MDDNR Trawl)

Influential habitat covariates

Of the suite of possible predictors considered for age-0 fish captured by small trawls, tidal-averaged predictors performed best (i.e., these predictors exhibited the greatest reduction in deviance of the BRT models). Four predictors were identified as influential in describing variation in abundance in age-0 striped bass captured by trawls (Table 4): bottom dissolved oxygen, dissolved oxygen stratification, the tidal-averaged current speed 1-m below the surface, and the tidal-averaged horizontal gradient in the current speed. Together, these four predictors explained approximately 48% of variation in abundance; other covariates individually explained less than 5% of the variation in relative abundance and were therefore, not retained.

Similar to the results for age-0 striped bass in shoreline habitats, metrics of dissolved oxygen and current speed were identified as important variables for age-0 striped bass captured by trawls. In this model, the identification of bottom DO (as opposed to surface DO) as an influential covariate reflected the portion of the water column sampled by the two bottom trawl surveys. Bottom DO appeared to be a critical covariate for describing suitable habitats for age-0 striped bass captured by trawls throughout the bay. This was especially true in summer, and although no metrics of temperature were identified as influential covariates in this model, we suggest that temperature was likely to be important in defining suitable habitats because of its significant positive relationship with DO. DO stratification (calculated as the difference between surface and bottom DO) in these models may provide insight on the volume of habitat available to both fish and prey: low stratification values suggest uniformity throughout the water column and hence, greater volume compared with high stratification where habitat compression may occur due to large differences in surface and bottom conditions.

Characterization of suitable habitats

Low current speeds, low bottom DO concentrations, and strong DO stratification (i.e., higher surface DO) characterized suitable habitats in early and late summer for age-0 striped bass captured by small trawls. Suitable habitats for age-0 striped bass in early summer (May-July) were characterized by horizontal gradients in the current speed less than 0.000738 m/s, tidal-averaged near-surface current speeds between 0.003 and 0.098 m/s, bottom dissolved oxygen concentrations of 2.94 mg O_2/L and lower, and fairly stratified DO conditions with a difference between surface and bottom DO ranging from 4.66 to 10.35 mg O_2/L. In late summer (August-October), suitable habitats for age-0 fish captured by trawls were in areas with a horizontal gradient in the current speed less than or equal to 0.000128 m/s, and tidal-averaged near-surface current speeds less than or equal to 0.124 m/s. Suitable late summer habitats were those where bottom DO concentrations were less than or equal to 3.96 mg O_2/L, and DO stratification was between 3.2 and 9.53 mg O_2/L. In fall/winter (November-January), suitable habitats for age-0 fish captured by the VIMS trawl survey were characterized by horizontal gradients less than or equal to 0.00069 m/s, near-surface tidal-averaged current speeds between 0.201 and 0.426 m/s, bottom DO concentrations between 10.97 and 14.5 mg O_2/L, and DO stratification between 1.65 and 5.07 mg O_2/L. Finally, spring (February-April) conditions in suitable habitats sampled by the VIMS trawl survey were similarly defined by horizontal gradients less than or equal to 0.00073 m/s, tidal-averaged near-surface current speeds between 0.177 and 0.486 m/s. Suitable spring bottom DO concentrations ranged between 9.26 and 14.31 mg O_2/L, and DO stratification ranged from 0.33 to 6.76 mg O_2/L (refer to Figure S1 in supplemental materials).

The association of age-0 striped bass with habitats exhibiting low DO concentrations or hypoxia is not surprising. Fish are known to occupy hypoxic habitats for a limited period of time to utilize prey resources or evade predation (Dixon et al. 2017). In the St. Lawrence estuary, juvenile striped bass disperse to sub-optimal habitats (based on several environmental metrics, including DO) in late summer to avoid intraspecific competition (Vanalderweireldt et al. 2020). Laboratory experiments indicate that the hypoxia tolerance of individual juvenile striped bass (119-183 mm TL) is highly variable and may increase with repeated or chronic exposure to hypoxia (Nelson and Lipkey 2015; Kraskura and Nelson 2020); we note, however, that laboratory-exposed fish were larger than the age-0 fish observed in our trawl surveys during summer. Hypoxia tolerance of juvenile striped bass is significantly higher at rest than when swimming (Nelson and Lipkey 2015), suggesting that individuals may 'hunker down' to wait out hypoxic episodes. Another possible explanation for the association of age-0 striped bass and hypoxic habitats concerns feeding opportunities that may be enhanced in hypoxic habitats. Low bottom DO is related to the extent of impervious surface in a watershed such that increased runoff contributes to higher nutrient concentrations, eutrophication (Uphoff et al. 2011), and possibly secondary production. Age-0 striped bass in these habitats may capitalize on abundant prey fields that develop in response to higher phytoplankton concentrations. A high degree of DO stratification may contribute to trophic partitioning within the water column (Ludsin et al. 2009), where stressed prey resources near the bottom may provide foraging opportunities for age-0 striped bass; normoxic conditions in the upper water column can be used by fish to offset metabolic costs associated with foraging in hypoxic bottom waters. Age-0 striped bass that exhibit this feeding behavior in summer, however, may be more vulnerable to capture by bottom trawls (Kraus et al. 2015b; Thambithurai et al. 2019), but such relationships have not been examined for Chesapeake Bay fishes. Age-0 striped bass in Chesapeake Bay are routinely exposed to low DO conditions across multiple time scales, including seasonal and diel periods of hypoxia. Tolerance of low DO concentrations is likely important to the survival of young striped bass in coastal rivers and estuaries that experience recurring hypoxia.

The range in conditions at sites sampled in Maryland and Virginia by bottom trawls was similar, but subtle differences were found; habitats sampled in Maryland were typically shallower, closer to shore, warmer in summer, and cooler in fall than those sampled in Virginia. Although the Maryland trawl survey samples in early and late summer only, the annual total catch (in numbers) of age-0 striped bass in Virginia was only 51% of that in Maryland, despite the fact the Virginia survey operated year-round. Therefore, conditions in shallower, warmer sites in Maryland, where higher relative abundances of fish were observed, contributed to the identification of covariates and the range of conditions that determined habitat suitability for age-0 fish captured by trawls during summer. Differences in sampling design may also contribute to the availability of age-0 fish to the gear: in May, age-0 fish are more readily available to the Maryland trawl that samples shallower waters closer to shore in comparison to the VIMS trawl that samples in deeper waters, on average. In Virginia, age-0 striped bass are more susceptible to capture later in the summer; indeed, catches from August to November are used to estimate an index of relative abundance for striped bass based on the Virginia trawl survey. Overall, these two trawl surveys are only moderately effective at targeting this age group: age-0 striped bass are captured in only about 12% of tows completed between 1996 and 2019 in Maryland and Virginia.

Extent of suitable habitat and persistence through time

The average extent (km^2) of suitable (HSI $\geq$ 0.5) and optimal (HSI $\geq$ 0.7) habitats for age-0 striped bass captured by bottom trawls was higher in early summer (May-July) compared with late summer (August-October) across all regions examined except for the Rappahannock River, which supported equivalent extents of suitable habitat across both seasons (Table 5). We did not observe optimal habitats in either early or late summer in the Upper Bay, Nanticoke area, and the James River (Table 5). In early summer, the highest average estimates of proportional suitable habitat extents were observed in the Chester (71%) and Potomac (45%) rivers. Estimates of the proportional suitable habitat in Maryland in early summer were greater than in Virginia (difference=45.5%). In late summer, the proportional extent of suitable habitats declined in Maryland and Virginia, but still remained higher in Maryland. In total, an average of 39.1% of the entire Bay system was considered suitable habitat for age-0 striped bass in early summer, and 28.5% was considered suitable habitat in late summer. On average 16.4% and 9.2% of the Bay was considered optimal in early and late summer, respectively.

In fall and winter (November-January), the average proportional extent of suitable (and optimal) habitats decreased substantially across all regions of the Bay, with only 3.1% of the Bay having HSI values $\geq$ 0.5 (Table 5). The only region that maintained a proportion of suitable habitat in fall and winter that was similar to that in summer was the Upper Bay, where about 21% of this area was deemed suitable habitat in fall/winter. During this time of year, the proportion of suitable habitat for age-0 striped bass in several regions in the Maryland portion of the Bay declined to zero or near-zero, including the Chester, Choptank, Patuxent, and Pocomoke rivers, as well as the Nanticoke area. In spring (February-April), the average proportional extent of suitable habitat was approximately 6% greater in Virginia than in Maryland (Table 5). The major tributaries in Virginia (the Rappahannock, York, and James rivers) and the Potomac River all showed an increase in suitable and optimal habitats during this season compared with fall/winter; likewise, the Upper Bay also exhibited an increase in the proportion of suitable and optimal habitats available for age-0 fish in spring, with 39% deemed suitable and 7.5% deemed optimal on average (Table 5). Notably, models of suitable habitat in fall/winter and spring were developed from catches of age-0 fish from only the VIMS trawl survey. About 18.8% of age-0 striped bass in the VIMS trawl survey were captured in fall/winter and 23.7% were captured in spring. Although the Maryland trawl survey samples between May and October only, the catch of age-0 striped bass from this survey was nearly double that observed in Virginia year-round. As a result, it is possible that the conditions encountered by the Maryland trawl survey during warm months (i.e., low DO) influenced the selection of habitat covariates used in the HSI model; these covariates, however, may not be ideal for describing suitable habitat conditions during other times of the year. Additionally, trawl surveys may be less effective in capturing striped bass as they approach 12 months of age because these 'older' fish may evade capture or may not be vulnerable to the gear (i.e., these fish may use the entire water column versus using primarily demersal environments or environments that can be sampled with a seine. Therefore, we caution the use of estimates of suitable habitat extent in fall/winter and spring for age-0 fish captured by trawls until such time as our results can be corroborated. We found relatively less suitable habitat for age-0 fish captured by trawls in fall/winter and spring, however, no significant linear change in Bay-wide habitat extent for age-0 striped bass from 1996 to 2019 was detected in any season (Table 8). Suitable habitats for age-0 striped bass captured in the trawl surveys persisted in shallow, nearshore areas during summer but extended further into the mainstem of the Bay in fall/winter and spring; persistence was defined as areas where the HSIU0.5 in at least 50% of years (1996-2019).

Precipitation conditions (e.g., wet, dry, average) affected the extent of suitable and optimal habitats for age-0 striped bass captured by small trawls; however, patterns were season-dependent. In fall/winter, very little suitable or optimal habitat was observed and what was present was found in the upper bay, the Potomac River, and the Virginia rivers during the dry year. The extent of suitable habitat increased in the Bay in Maryland and along the eastern portion of the Bay in Virginia in the average and wet years. In spring, the extent of suitable habitat was similar across seasons regardless of precipitation conditions with suitable habitats found along shallow habitats in the bay and in all of the tributaries in Maryland and Virginia. In early summer, the extent of suitable and optimal habitats increased greatly and included much of the bay, though a decrease in extent of suitable habitat was observed in the tributaries. This pattern was consistent across precipitation conditions. In late summer, the extent of suitable and optimal habitats decreased compared with early summer and was found mostly in the bay in Maryland and the Potomac River.

The extent of suitable and optimal habitats increased from relatively small extents in fall/winter to large extents in early summer in the cool, average, and warm years. Overall, the cool year tended to have greater extents of suitable habitat compared with the average and warm years. In fall/winter, suitable habitats were found in the upper portions of the bay and the upper portions of the tributaries in Maryland and Virginia with more suitable habitat found during the cool year compared with the average or warm years. In spring, the extent of suitable habitat increased and included all of the tributaries, the upper Bay and portions of the lower Bay in Virginia with more suitable and optimal habitat in the cool year compared with the average and warm years. In early summer there was a shift in the location of suitable and optimal habitat with most of the tributaries and bay in Maryland and the lower Potomac River containing suitable and optimal habitat, whereas the extent of suitable habitat decreased in the Virginia bay and tributaries. The shift in the location of suitable habitat was observed in the cool, average and warm years. In late summer during the cool year, most of the bay in Maryland had suitable or optimal habitats. In late summer in the warm year, the Potomac River also have suitable and optimal habitats, along with the bay in Maryland.

Relationship between extent of suitable habitat and relative abundance of YOY striped bass

Across years and between seasons, indices of relative abundance for YOY striped bass in the small trawl surveys were highly variable (Figure 17). Patterns of age-0 abundance in early summer (May-July) and based on trawl surveys revealed that peaks in relative abundance in MD waters occurred in 1996, 2001, 2003, and 2011, and in VA waters, relative abundance peaked in 1996, 2003, 2005, 2011, and 2014. In late summer (August-October), peaks in MD waters occurred in 1996, 2001, 2003, and 2011, and in VA peaks in late summer were observed in 1996, 2001, 2008, and 2011 (Figure 17). The indices of relative abundance in fall/winter (November-January) and spring (February-April) were based on catches from the VIMS trawl survey only and relative abundance was also highly variable across years; more than half of the years indicated that relative abundance was below average (Figure 17). Because these seasons reflected catches from only a single survey, this may or may not reflect the overall pattern of relative abundance for age-0 striped bass during these months. For example, HSIs from the Upper Bay and Potomac River indicated some of the highest proportional and absolute extents of suitable habitat for age-0 striped bass during winter and spring (Table 5), but we are not aware of fisheries surveys in these areas to validate that these areas do indeed support high abundances of age-0 striped bass during these seasons.

We were unable to detect a statistically significant relationship between the Bay-wide extent of suitable habitat and the rank-transformed estimates of age-0 abundance for fish captured by trawls in early ($F_{EarlySummer}$=1.77, $P_{EarlySummer}$=0.20) or late summer ($F_{LateSummer}$=1.30, $P_{LateSummer}$=0.27; Table 9). Likewise, no statistically significant relationship was detected between ranked abundance of age-0 striped bass in Virginia waters and the extent of suitable habitats in Virginia waters in fall/winter ($F_{Fall/Winter}$=2.25, $P_{Fall/Winter}$=0.15) or spring (F_{Spring}=2.59, P_{Spring}=0.12). Across all seasons, however, the index of ranked abundance increased with increasing extent of suitable habitats (Figure 22), suggesting that a relationship may exist between suitable habitat extent and abundance of age-0 striped bass observed in these surveys. We were unable to detect a statistically significant relationship likely due to small sample sizes, that is, we would need to consider more than 22 years of observations. As such, we recommend re-evaluation of these relationships as additional years of observations become available.

Age 1-4 (Resident Sub-Adult) Striped Bass (VIMS and MDDNR Trawl)

Influential habitat covariates

The tidal-averaged predictors resulted in the greatest deviance reduction of BRT models for the small trawl surveys. Seven covariates were identified as influential for describing habitats used by age 1-4 striped bass captured by the small trawls (Table 4): tidal-averaged bottom salinity, bottom dissolved oxygen, water depth, tidal-averaged salinity stratification, dissolved oxygen stratification, tidal-averaged horizontal gradient in the current speed, and percent fine sediment. Together, these seven predictors explained 68% of variation in the relative abundance of age 1-4 fish captured by the small trawls.

Bottom salinity and bottom dissolved oxygen concentrations reflected environmental conditions encountered by the fish sampled by the bottom trawls and at sites where fish were not present. Metrics of dissolved oxygen and current speed were identified as important habitat covariates for age 1-4 striped bass, similar to YOY striped bass. Other covariates of importance for age 1-4 striped bass were water depth and sediment bed composition, suggesting a spatial component for defining environmental conditions and features of suitable habitats for striped bass during this period in their life. As fish grow and develop, changes in diet and physiological tolerances allow fish to use different habitats around the Bay and across time. Age-1 striped bass undergo a diet shift from primarily invertebrate prey to fish prey, depending on growth rate and local prey densities (Overton et al. 2009). A shift in habitat use by resident sub-adults was observed between summer, when they used relatively shallow, low salinity environments, and fall, when they occupied deeper waters. The salinity stratification covariate measured the difference in surface and bottom salinity.

Suitable and optimal habitats reflected seasonal variation in environmental conditions, as well as differences in size selectivity of the gear used by two trawl surveys (Figure 5). The VIMS and MDDNR trawl surveys captured the smaller striped bass within this age group and thus, these surveys may not be ideal for representing suitable habitats for resident sub-adult striped bass up to age-4. As a highly mobile species, older and larger striped bass are more capable of evading capture by small bottom trawls; as such, relative abundances of age 1-4 fish detected in either survey alone or combined likely did not reflect the abundance of striped bass of this age group in the Bay. In particular, age-3 and -4 fish were underrepresented in the catches from the small trawl surveys (Figure 5). Differences in sampling design also affected the availability and vulnerability of resident sub-adult fish to the trawls used by VIMS and MDDNR. For example, approximately 13% of all striped bass captured by the VIMS trawl survey were considered age 1-4 fish based on length, however, these fish were encountered in only about 6% of tows conducted from 1996 to 2019; moreover, the majority (78%) of these individual tows captured only one or two fish. Taken together, the VIMS trawl survey and the MDDNR trawl survey encountered age 1-4 striped bass in approximately 8% of tows; 40% or greater of these catches were only one or two fish. Because each trawl survey encountered a different size range of fish from the age 1-4 age group, and fish were captured infrequently overall, the range of environmental conditions identified as "suitable" may or may not be applicable to a given age class within the age group.

Characterization of suitable habitats

Suitable habitats for age 1-4 striped bass captured by the small trawls in spring were characterized by tidal-averaged bottom salinities between 2.36 and 9.0 psu; tidal-averaged salinity stratification less than or equal to 1.225 psu; horizontal gradients in the current speed less than or equal to 0.000153 m/s; bottom DO concentrations less than or equal to 3.64 mg O_2/L; and DO stratification that ranged between 5.2 and 10.35 mg O_2/L. Spring suitable habitats were shallower than 3.74 m and were characterized by 24.6 to 97.1% fine sediment. In summer, suitable habitats were represented by tidal-averaged bottom salinities between 4.03 and 11.35 psu; tidal-averaged salinity stratification less than or equal to 1.73 psu; horizontal gradients in the current speed less than or equal to 0.000191 m/s; bottom DO concentrations less than or equal to 4.69 mg O_2/L; and DO stratification between 3.99 and 9.53 mg O_2/L. Suitable summer habitats were similarly shallower than 3.33 m and were characterized by substrates with 22.7 to 82.3% fine sediment. In the fall, suitable habitats for age 1-4 striped bass in Virginia waters were characterized by tidal-averaged bottom salinity less than or equal to 17.34 psu; tidal-averaged salinity stratification between 0.924 and 9.98 psu; horizontal gradients in the current speed less than or equal to 0.000732 m/s; bottom DO concentrations between 10.89 and 14.50 mg O_2/L; and DO stratification between 0.61 and 5.07 mg O_2/L. These habitats were deeper than 13.26 m and were comprised of bottom substrates with 53.2 to 75.3% fine sediments (refer to Figure S1 in supplemental materials).

Suitable habitats in spring and summer represented conditions observed in the tributaries and several small embayments in Maryland waters: shallow areas with lower bottom salinity and DO, higher DO stratification, minimal salinity stratification, and slower current speeds. Areas sampled by the MD DNR trawl survey were typically shallower, closer to shore, and warmer in summer than habitats sampled by the VIMS trawl survey. In fall, habitat suitability was based on catches from Virginia waters only, where greater depths, higher bottom salinity and DO, and greater stratification in salinity occur relative to Maryland waters. Suitable habitats in fall were found in the mainstem of the Bay and the main channel of the major tributaries.

Extent of suitable habitat and persistence through time

The suitability of habitats throughout the Chesapeake Bay and its tributaries varied seasonally and annually for age 1-4 striped bass (Table 6). The average Bay-wide proportional extent of suitable (HSI $\geq$ 0.5) habitat for age 1-4 fish captured by small trawls was higher in summer (July-October) relative to spring (March-June) or fall (November-February). In spring and summer, the mean proportional extent of suitable habitat in Maryland waters exceeded that in Virginia waters in spring (difference=29.6%) and summer (difference=30%). In fall, this difference declined somewhat. Overall, in a given year between 1996 and 2019, an average of 21% of the entire Bay system was considered suitable in spring for age 1-4 fish, 27% was suitable in summer, and 11% was suitable in fall. Optimal (HSI $\geq$ 0.7) habitats followed seasonal and regional patterns that were similar to those for suitable habitats (Table 6). The Chester

River consistently supported the greatest mean proportional extent of suitable habitat in spring and summer (~70% in each season). During summer, approximately 45-50% of the Choptank, Patuxent, Potomac, and Rappahannock rivers contained suitable habitats for age 1-4 striped bass. The Bay-wide extent of suitable habitats in spring significantly decreased between 1996 and 2019 (F_{Spring}=13.55, P_{Spring}<0.01; Table 8). This Bay-wide decline was driven by the significant decline in the extent of suitable habitat in Maryland waters (F=13.13, *P*<0.01), specifically the Patuxent River (F=7.00, *P*=0.01). The extent of suitable habitat for age 1-4 fish in summer and fall exhibited no significant linear pattern between 1996 and 2019 (F_{Summer}=2.13, P_{Summer}=0.16; F_{Fall}=0.00, P_{Fall}=0.96; Table 8), however, the data suggested that a decline in suitable habitats in summer may be occurring. Additional years of observations will help us understand if the decline in suitable habitat extent observed in spring will carry forward to summer as well. From 1996 to 2019, suitable habitats persisted in at least 50% of years in shallow nearshore areas in summer (particularly in Maryland) and in the central channels in the Bay mainstem and major tributaries and along the Eastern shore in spring and fall.

Precipitation conditions (wet, average, dry) affected the location and extent of suitable habitats for age 1-4 striped bass captured by small trawls, with the greatest extent of suitable and optimal habitats observed during the wet year in spring and fall. Suitable and optimal habitats for age 1-4 fish captured by small trawls in spring were observed during wet, average, and dry years but were primarily confined to the Maryland portion of the Bay during the dry year. Average and wet years were characterized by greater extents of suitable and optimal habitats for age 1-4 fish in spring. Suitable habitat areas in spring were found in the Maryland portion of the Bay, the Potomac River, and in Virginia tributaries as well as nearshore habitats throughout the system. Optimal habitat areas in spring during the average and wet years were primarily found in the Potomac River and the Maryland portion of the Bay. In summer, the extents of suitable and optimal habitats for age 1-4 fish captured by the small trawls were similar for dry, average, and wet years and these habitats were located nearshore. The offshore extent of suitable habitats for age 1-4 fish in summer was somewhat greater in wet years, but these differences were small. In fall, the extent of suitable habitats for age 1-4 fish captured by small trawls was lower during the dry year relative to what we observed in the average year. The wet year was characterized by a noticeably greater extent of suitable habitats for age 1-4 fish in fall; optimal habitats in fall during the average year were observed only in the Choptank River but were present in the Choptank River and other tributaries during the wet year.

The location and extent of suitable habitats under varying thermal conditions (warm, average, cool) were somewhat invariant, indicating that other environmental factors may have played a larger role in determining suitability of habitats. The extent of suitable and optimal habitats for age 1-4 fish captured by small trawls in spring was similar for warm, average, and cool years and these habitats were generally found nearshore; optimal habitats were confined to the northern portion of the Bay in spring. In summer, suitable and optimal habitats for age 1-4 fish captured by small trawls were found nearshore throughout the Bay and tributaries in warm, average, and cool years. A slightly greater extent of optimal habitat was observed in the cool year relative to the average and warm years, but this may be an artefact of selection of a single year to represent conditions during cool years. In fall, the extent of suitable habitats for age 1-4 fish captured by small trawls was similar for warm and cool years and these habitats were primarily in the main channel of the Bay and in tributary channels in Maryland and Virginia.

Relationship between extent of suitable habitat and relative abundance of age 1-4 striped bass

Indices of relative abundance for resident sub-adult striped bass (age 1-4) varied by season and region in Chesapeake Bay (Figure 18). In spring (March-June), an inconsistent pattern was observed between relative abundance of fish in Maryland and Virginia waters, with many of the early years showing an opposing pattern, and with relative abundances in Virginia consistently higher than in Maryland since 2012. This suggested that processes that affect abundance and habitat use in spring varied across regions of the Bay. The spring decline in relative abundance of age 1-4 fish in Maryland since 2012 is consistent with the observed decline in the extent of suitable habitats in spring throughout the Chesapeake Bay (Table 8). In summer (July-October), the pattern in relative abundance was similar between regions; despite years of high relative abundance in VA in 1997 and 2004, and in MD in 1997, 2001, and 2004, relative abundance of age 1-4 fish in VA and MD waters appeared to be at or below average (1.0) since about 2008. The index of abundance for fall represented data from the VIMS trawl survey only and was highly variable (Figure 18).

We found a significant decrease in the Bay-wide extent of suitable habitats ($HSI \geq 0.5$) in spring for age 1-4 fish captured by small trawls, however, we were unable to detect a significant linear relationship between habitat area and rank-transformed abundance during 1996 to 2019 ($F_{Spring}=2.85$, $P_{Spring}=0.11$; Table 9). It is possible that the significant decline in suitable habitats in spring (Table 8) may pose a greater threat to certain age-classes within this age group, but this relationship cannot be elucidated using a single index of abundance for multiple ages. We also did not detect a significant relationship between ranked abundance and the extent of suitable Bay-wide habitats in summer ($F_{Summer}=1.60$, $P_{Summer}=0.22$; Table 9) or the extent of suitable habitats in Virginia waters in fall ($F_{Fall}=0.00$, $P_{Fall}=0.97$; Table 9). In spring and summer, indices of ranked abundance increased with greater extent of suitable habitats, suggesting that a relationship may indeed exist between habitat extent and abundance of age 1-4 striped bass (Figure 23). We hypothesize that due to the observed variability, additional years of observation may allow us to detect a statistically significant relationship between relative abundance and suitable habitats in spring and summer.

Age 1-4 (Resident Sub-Adult) Striped Bass (ChesMMAP)

Influential habitat covariates

The tidal-averaged subset of predictors resulted in the greatest deviance reduction in the BRT models for age 1-4 fish captured by the ChesMMAP survey. Four covariates were selected (Table 4): bottom dissolved oxygen; water depth; tidal-averaged salinity stratification; and depth-averaged, tidal-averaged temperature. These four covariates explained approximately 54% of the variation in relative abundance of age 1-4 striped bass captured by this survey.

Similar environmental conditions and habitat features were selected to delineate suitable habitats for age 1-4 striped bass captured by the ChesMMAP survey as those captured by the small trawl surveys. This similarity may have resulted from partial overlap in sampling locations throughout the mainstem of the Bay sampled by the ChesMMAP and VIMS trawl surveys. The selection of water depth as an influential covariate, in particular, was likely a function of both the large spatial domain of this survey and differences in the distribution of age 1-4 fish in the Bay. Notably, this was the only BRT model that identified a metric of temperature as one of the most influential covariates for describing suitable habitats. Because striped bass are not confined to the near-bed region, the depth-averaged temperature metric may reflect that fish respond most strongly to the overall average water-column temperature. As striped bass grow, physiologically optimum temperature ranges shift to lower temperatures, near 20-24°C for subadults in their second year (Coutant and Carroll 1980), with older subadults typically avoiding temperatures greater than about 25°C when cooler waters are available (Coutant and Benson 1990). A telemetry study, however, indicated that in summer, sub-adult striped bass avoid hypoxic areas and occupy warm (> 25°C) habitats when cooler habitats are unavailable (Kraus et al. 2015a). Such studies suggest that thermal habitat use by striped bass is context dependent, such that dissolved oxygen concentration and prey availability (Kraus et al. 2015a) alter habitat selection by sub-adult striped bass.

Characterization of suitable habitats

Suitable habitats in the mainstem of the Bay for age 1-4 striped bass captured by the ChesMMAP survey were characterized by deeper waters, cooler temperatures, and variable salinity stratification in spring; shallow waters, variable (but warmer) temperatures, and lower bottom DO in summer; and intermediate depths, temperatures, and dissolved oxygen in November. Suitable habitats for age 1-4 fish captured in spring by the ChesMMAP survey were at depths of 18.6 to 31.3 m and were characterized by depth-averaged tidal-averaged temperature between 2.23 and 4.48 °C; tidal-averaged salinity stratification less than or equal to 4.25 or greater than or equal to 6.54 psu; and bottom dissolved oxygen concentrations between 5.48 and 8.94 mg O_2/L. In summer, age 1-4 striped bass were found in shallower habitats where depth ranged from 3.1 to 7.35 m; depth-averaged tidal-averaged temperatures ranged between 9.85 and 29.44 °C; tidal-averaged salinity stratification was less than or equal to 2.75 psu; and bottom DO concentrations were less than or equal to 5.60 mg O_2/L. Suitable habitats for age 1-4 fish captured by the ChesMMAP survey in November ('fall') were characterized by depths between 3.5 and 15.1 m; depth-averaged tidal-averaged temperatures between 7.62 and 12.28 °C; salinity stratification less than or equal to 2.39 psu; and DO concentrations between 8.60 and 14.07 mg O_2/L (refer to SI histograms in supplemental materials)

In contrast to what we observed for age 1-4 fish captured by small trawls in spring, habitats suitable for resident sub-adults captured by the ChesMMAP survey were restricted to the central mainstem channel, and this partially reflected the design of this survey. Higher catch rates in the ChesMMAP survey were observed in Maryland waters across all seasons, but especially in spring. Overall, habitat suitability was representative of general environmental conditions in the mainstem of the Bay and likely resemble conditions found in the tributaries. We did not, however, extend estimates of HSIs into the tributaries or shallow areas nearshore because we lacked observations on environmental conditions from ChesMMAP trawl samples in such areas. Thus, we were unable to validate the spatial extension of model predictions into tributaries and shallow bay waters.

Extent of suitable habitat and persistence through time

Estimates of the extent of suitable and optimal habitats for age 1-4 fish captured by the ChesMMAP survey were truncated in space and time due to concerns about the transferability of the model to shallow tributaries and to years preceding the initiation of the survey. Spatially, estimates were restricted to the mainstem of the Bay to align with the sampling domain of the survey. Temporally, estimates were limited to survey years 2002 to 2018. We did not project estimates of habitat conditions prior to 2002 because significantly lower mean water temperatures were observed in earlier years and as such, these lower temperatures were outside the domain of the suitability metrics derived from observations between 2002 and 2018 (Figure 12). We noted several years prior to 2002 that were characterized by unique environmental conditions that were not encountered by fish captured by the ChesMMAP survey since 2002. Although the ChesMMAP survey comprised five distinct sampling events in March, May, July, September, and November, estimates of suitable habitat and corresponding maps for spring and summer included the 'middle' months of April and August. Even though sampling did not occur at these times, environmental conditions during the 'shoulder' months likely encompassed conditions in the 'middle' months that were not sampled.

The average proportional extent of suitable and optimal habitats for age 1-4 fish captured by the ChesMMAP trawl in November and in summer exceeded that in spring (Table 7). In fall in particular, 87.7% of the mainstem Bay was considered suitable ($HSI \geq 0.5$) for age 1-4 striped bass, and 66.9% was considered optimal ($HSI \geq 0.7$). In contrast, spring was characterized by very little to no optimal habitat in Maryland or Virginia waters of the mainstem Bay. The proportional extent of suitable habitats for age 1-4 fish in Virginia and Maryland waters was similar, with slightly higher proportions observed in Virginia in spring (difference=3.5%) and November (difference=7.6%). In summer, however, the mean proportional extent of suitable habitats in Maryland waters of the mainstem Bay was greater than that in Virginia waters of the mainstem Bay (difference=23.5%). No significant linear change in suitable habitat extents in the Bay mainstem between 2002 and 2018 was detected in any season (Table 8; $F_{Spring}=0.05$, $P_{Spring}=0.83$; $F_{Summer}=0.73$, $P_{Summer}=0.41$; $F_{Nov}=0.90$, $P_{Nov}=0.36$). Suitable habitats for age 1-4 fish captured by the ChesMMAP survey persisted throughout the central main channel in fall, and in comparatively shallower waters in the mainstem in spring and summer in at least 50% of years (2002-2018).

Relationship between extent of suitable habitat and relative abundance of age 1-4 striped bass

Patterns in relative abundance of age 1-4 striped bass captured by the ChesMMAP survey in the mainstem of the Bay differed among seasons; relative abundance was fairly stable around the mean in spring, and more variable in summer and fall (Figure 19). A distinct peak was observed in 2005 across all seasons and again in 2012 and 2017, but only for summer and fall. Note that, the index of abundance for spring 2003 could not be estimated due to equipment failures at the time of sampling (C. Bonzek, *pers. comm.*).

We were unable to detect a significant relationship between the extent of suitable habitats in the mainstem of the Bay and the rank-transformed estimates of age 1-4 relative abundance based on ChesMMAP catches in any season (Table 9; $F_{Spring}=1.52$, $P_{Spring}=0.24$; $F_{summer}=0.06$, $P_{summer}=0.81$; $F_{Nov}=0.51$, $P_{Nov}=0.48$). Oddly, ranked abundance in spring exhibited a slight decline with increasing extents of suitable habitats, but this relationship was not significant. Relative abundances in summer and November were variable (Figure 19), and the extent of suitable (and optimal) habitats in summer and November exceeded estimates of suitable habitat extents in spring, suggesting that habitat was not limiting for age 1-4 striped bass during summer and November.

Summary and Recommendations for Future Directions

HSI models are useful tools to identify and visualize locations and times that have the potential to support high abundances of juvenile striped bass, defined here as ages 0 to 4. The use of hydrodynamic models and other numerical models to estimate environmental conditions has multiple benefits (Bever et al. 2016; Fabrizio et al. 2021). First, the projection of habitat suitability indices could be made to areas not currently sampled by fishery surveys when these areas comprised environmental and physical conditions that were similar to those that were sampled. Second, numerical models allowed for the consideration of covariates that represented a wide array of environmental conditions that are not typically observed in the field (e.g., current speed, tidal-averaged bottom temperature).

Our approach provided an opportunity to examine changes in the extent of suitable (and optimal) habitat conditions for age-0 and age-1-4 striped bass through time and across space. We visualized patterns of suitable habitat on a seasonal and annual basis, quantified the extent of suitable habitats Bay-wide and in specific tributaries or areas, and examined the relationship between habitat extent and fish abundance. For juvenile striped bass, habitat suitability was a function of the specific covariates selected, and the availability and vulnerability of individual fish to a particular gear. Importantly, spatiotemporal differences in survey design and changes in fish behavior and habitat use across ages added complexity in model development and interpretation. Here, we provide a list of our principal findings, offer our thoughts on areas of consideration for future applications, and end with a discussion of technical recommendations.

1. Water quality conditions were key predictors of habitat suitability for juvenile striped bass

Water-quality conditions may be of greater importance in determining habitat suitability than specific physical features particularly for highly mobile species such as striped bass. Influential covariates used to describe the suitability of habitats for YOY and resident sub-adults were exclusively dynamic environmental metrics, and not static features of the environment (i.e., distance to shore or seabed composition). This distinction was manifested as patterns in habitat suitability that varied seasonally and interannually at a given location. Moreover, metrics of dissolved oxygen concentration were included in all habitat suitability models. This highlights the importance of DO, as well as the role of co-varying temperature, in delineating suitable habitats for age 0 and age 1-4 striped bass. Interestingly, several metrics of current speed were also identified as influential variables, particularly for age-0 fish. Current speed is not typically measured at the time of fish sampling, but this may be a metric for future consideration by existing long-term surveys, particularly those that sample age-0 fish. Further investigation into these metrics and their role in defining fish habitat may help identify actionable thresholds to maintain a minimum extent of suitable habitat Bay-wide. Anticipated changes due to continued warming and increased precipitation in the Chesapeake Bay watershed (Najjar et al. 2010) will likely affect water-quality conditions and may have significant effects on the extent of suitable and optimal habitats for juvenile striped bass, particularly spring and early summer. Continued support of the Chesapeake Bay Total Maximum Daily Load (TMDL) and associated water-quality standards will be critical to sustain current progress and attain new goals to protect vital habitats and ensure sustainable fisheries and climate resiliency.

2. Juvenile striped bass used less-than-ideal habitats

Each survey routinely encountered average to above-average abundances of striped bass in areas with conditions that would ostensibly be considered unsuitable, such as areas with low dissolved oxygen. Indeed, age 0-4 striped bass appeared to tolerate broad variations in some environmental conditions, and this finding was supported by the selection of the arithmetic mean formulation for the HSI. This formulation suggested that conditions dictated by a single covariate were not limiting habitat use, and instead, habitat use reflected a combination of conditions, none of which was limiting. Thus, we found no evidence that habitat use in striped bass was moderated by a strict threshold in any given covariate; if conditions for one covariate were unsuitable, other covariates may present suitable or even optimal conditions and striped bass would occupy such habitats.

Our approach allowed us to visualize and quantify habitats that have the potential to support higher abundances of fish, but habitat suitability models by their nature cannot elucidate the value (e.g., feeding, predation refuge, growth) of particular habitats to fishes. Furthermore, the designation of a particular habitat as suitable does not necessarily indicate that fish will be present; likewise, the absence of fish does not necessarily indicate that conditions in a particular habitat are unsuitable. In the case of absences, detection probabilities may help explain some absences, whereas other absences may be true absences. The use of these habitats by striped bass may suggest that the availability or extent of better, more suitable habitats was limited, which may occur when fish density is high, and resources are limited. During our study period (1996-2019), abundances of juvenile striped bass were high during a handful of years and high densities may not have been achieved or resources may not have been limiting. Food availability, competition, and other factors such as predation pressure also likely influenced fish-habitat relationships. Future analyses may wish to consider additional ecological complexity to fully describe suitable conditions for striped bass, however, we note that such data (e.g., prey abundance) may be lacking at the spatial and temporal time scales necessary to resolve habitat conditions for juvenile fish.

3. Localized, tributary-specific conditions may be important for supporting juvenile striped bass

Across age groups, seasons, and years, the extent of suitable habitats varied between regions in Maryland and Virginia that represented the major tributaries and embayments for spawning and rearing of striped bass. An assessment of habitat suitability on a regional scale allowed us to examine tributary-specific trends in the extent of suitable habitats over time. For example, high proportions of available habitats in some tributaries like the Potomac River and smaller bays on the Eastern shore (i.e., the Nanticoke area) were characterized as suitable habitats for juvenile striped bass; these areas may be critical for supporting juvenile striped bass in the Bay. We recommend efforts to expand or develop fishery surveys in these areas; where possible, future and existing surveys should use gear types that more effectively target striped bass from these age classes (e.g., finer mesh; midwater trawl) to ensure that survey catch rates are representative of relative abundance. Our assessment of the persistence of suitable habitats through time indicated that restoration and conservation efforts will need to focus Bay-wide as locations that consistently support suitable conditions for juvenile striped bass include shallow, nearshore areas, channels, and tributaries throughout Chesapeake Bay. We observed a significant decline in the extent of suitable habitats for age-0 fish captured by seines in early summer (June-July), and for age 1-4 fish captured by small trawls in spring (March-June), suggesting that the suitability of habitats declined for YOY and resident sub-adult striped bass in the Bay. These changes are occurring relatively early in the year, when we may expect to observe declines in relative abundances of age-0 and age 1-4 fish. These declines were driven by a loss of habitat in specific regions. This further highlights the importance of understanding local, tributary-specific conditions, and the critical role of restoration efforts at the local scale in addition to Bay-wide efforts. Future investigations may seek to examine the relationship between extent of suitable habitat and land cover or shoreline modification to further link trends in habitat conditions to local land-based activities in the watershed.

4. Ecology and life history add complexity to interpretations from multiple suitability models

Juvenile striped bass use a variety of habitats in estuarine environments, particularly during the period of rapid growth and development (i.e., age-0). Our use of multiple age groups (age-0 and age 1-4) attempted to capture some of this variation, however, fish also occupied different habitats on a seasonal basis as they grew, even within a single age class. This complexity posed a challenge to understanding fish-habitat relationships for a mobile species. In addition, spatial and temporal differences in sampling design among fisheries surveys created further complexities in the interpretation of habitat suitability maps for age-0 and age 1-4 striped bass. Future investigations of habitat suitability for Chesapeake Bay fishes should carefully consider the unique life history of the target species when framing modeling approaches; we caution that life-history based requirements may not be properly addressed with currently existing data or numerical models. For example, different questions may require environmental and hydrodynamic data at variable spatial resolutions. This is particularly relevant for shallow water habitats along the shoreline, where fine-scale data will be necessary to understand localized conditions. In particular, the sampling scale and model estimates for some covariates (e.g., percent fine sediment) may not be representative of shoreline conditions – that is, conditions in waters that are sampled with beach seines. Currently, the approach we used in this study could be applied at a fine scale for a particular region (e.g., Baltimore Harbor), but is too computationally intensive for a Bay-wide assessment.

5. Consistent patterns in the relationship between abundance and the extent of suitable habitat suggest suitable habitat may be limiting

Although we were unable to detect a statistically significant ($\alpha = 0.05$) relationship between relative abundance and the extent of suitable habitat in any season or age group combination, our findings strongly suggest that a relationship may indeed exist between Bay-wide index of abundance and habitat extent for age-0 striped bass captured by seines and trawls, and for age 1-4 striped bass captured by small trawls. Across seasons and datasets, we observed a pattern of increasing abundance with increasing extent of suitable habitat. Conditions along shoreline habitats and those habitats used by larger fish appear to be changing, particularly in spring and early summer when a decline in suitability of habitats may contribute to observed declines in relative abundances of age-0 and age 1-4 fish. The strength of evidence across seasons and multiple datasets indicates that habitat may become limiting for juvenile striped bass, and we recommend re-evaluation of these relationships as additional years of observations become available.

Technical recommendations

We used catch data from multiple fishery-independent surveys that represented a variety of sampling gears, sampling designs, and methodologies. Together, these surveys provided broad spatial coverage in the mainstem and tributaries of the Bay, but each survey targeted and observed different sizes and ages of striped bass. A collated inventory of data sources, stewards, sampling methodology, spatial and temporal domain, and metadata (e.g., life stage, size ranges) for striped bass in Chesapeake Bay would benefit future studies focused on this species. Additionally, two existing data sources that were unable to be used in this project may provide insights and expand our understanding of habitat suitability for striped bass in novel locations and for different life stages. First, seine and electrofishing surveys in the upper reaches of the Potomac and Anacostia rivers are conducted by the District of Columbia Department of Energy and the Environment (DC DOEE), but currently have critical data gaps (specifically, distance of net extension offshore, time of sampling) that preclude the ability to standardize catches or link catches with hydrodynamic model outputs. Second, an extensive time series of observations on egg presence/absence from MDDNR's Striped Bass Egg Survey may be used to describe and map conditions in striped bass spawning habitats, but requires that someone digitize, curate, and review the database prior to release; we understand that such efforts are currently underway. Finally, while various sources of fishery-dependent data may provide additional information on habitat use by older striped bass, several challenges remain with the use of such data, including imprecise location information, missing or inaccurate information on length, missing information on time of capture; such data, however, may warrant further exploration or consideration.

The three trawl surveys considered in this project (VIMS, MDDNR and ChesMMAP) used bottom trawls of different sizes, sampled at different temporal resolutions, and sampled from domains of varying spatial coverage. These surveys targeted fish of different sizes and ages, and our approach necessitated multiple models to capture the associated life-history dynamics of these different age classes. Although scale-based age data were available from MDDNR and otolith-based data were available from the ChesMMAP survey, a comprehensive age-length key for striped bass in Chesapeake Bay was not currently available. This was especially true for smaller-sized fish (<200 mm fork length). We developed an age-length key focused on ages 0 to 4 for this project, but such a key is needed for older age classes as well. We found that pooling multiple age-classes into the age 1-4 fish group added complexity in parsing out the ontogenetic changes in habitat use that occur during this formative time in the life cycle of striped bass. By pooling these age classes, we assumed similar behaviors and habitat use among individuals ranging in age from 1 to 4, which we believe is unreasonable. Whereas many of the age 1-4 fish may be year-round residents of Chesapeake Bay, a portion of the 3- and 4-year old fish are likely mature fish that may have already engaged in coastal migratory behaviors; classification of these individuals as 'juveniles' is not accurate. We recommend that future analyses refrain from pooling multiple age classes into a single group unless it can be shown that behaviors and habitat use do not vary among these age classes.

Annual estimates of the extent of suitable habitat could be used to develop annual habitat indices in Chesapeake Bay in support of resource management, but current estimates are available for 1996 to 2019 only. Numerical models to estimate current environmental conditions in the Bay will need to be updated with recent meteorological and hydrological data to allow calculation of water column conditions throughout the Chesapeake Bay in years beyond 2019. These extensions with nowcast numerical models would permit estimation of habitat suitability for age-0 or age 1-4 striped bass in 2020 and beyond. Updating the input files for the hydrodynamic model entails acquisition of data for tributary inflows, Atlantic Ocean open boundary conditions, and meteorological conditions. Those data must then undergo quality assurance tests after which they are converted into the formats used for hydrodynamic model inputs. Some of the necessary input data are currently available, however the meteorological data used for model inputs are typically delayed by 2 to 6 months (i.e., data for July 2022 may not be available until January 2023). Thus, updates to this analysis to extend the length of the simulation period up to the most recently available data would result in at least a 6-month lag. Additionally, field observations of DO from the fishery surveys and tidal monitoring stations around the Bay would need to be used to update the numerical DO model. Continued sampling by fisheries-independent surveys would provide catch data with which HSI models could be developed and applied to 2020 and beyond. The nowcast models provide a platform from which we could deliver habitat suitability information that is more current than what was possible in this study and as such, presents an opportunity to develop habitat indicators for striped bass, and possibly other species.

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Table 1. Approximate proportion of the catch in each of the five fishery-independent surveys that corresponds to each age group for striped bass (age-0 = YOY or age 1-4 = resident sub-adult). Monthly length thresholds for age-0 fish used in the VIMS trawl and seine surveys were used to distinguish age-0 from age-1 fish, where a model-derived threshold (401 mm FL) was used to distinguish age-4 from age-5 and older fish. Grey shaded cells indicate cases where a particular survey was not used to model habitat conditions for a particular age group.

Survey	**Age 0**	**Age 1-4**	**Age 5+**
ChesMMAP	0.04	0.77	0.17-0.19
VIMS Trawl	0.86	0.13	<0.02
MDDNR Trawl	0.85	0.14	<0.01
VIMS Seine	0.99	0.01	0
MDDNR Seine	0.99	0.01	0

Table 2. Summary of four independent datasets used to quantify and describe age-0 and age-1-4 habitats. N denotes the total number of observations in each dataset considered in boosted regression tree (BRT) analyses for the specified time period. Note that for the age-0 dataset that incorporates data from the VIMS and MD small trawls, 'winter' and 'spring' only utilize data from the VIMS juvenile trawl survey. Additionally, survey design for the ChesMMAP dataset dictates that "Fall" include only the month of November to avoid biasing habitat estimates toward conditions that were not sampled.

Age Group	Survey Sources	N	Seasons of Focus
Age-0	VIMS and MDDNR Seine	5117	Early Summer (Jun-Jul) Late Summer (Aug-Sep)
	VIMS and MDDNR Trawl	33783	Early Summer (May-Jul) Late Summer (Aug-Oct) Fall/Winter (Nov-Jan) Spring (Feb-Apr)
Age 1-4	VIMS and MDDNR Trawl	33783	Spring (Mar-Jun) Summer (Jul-Oct) Fall (Nov-Feb)
	ChesMMAP	6257	Spring (Mar-Jun) Summer (Jul-Oct) Fall (Nov)

Table 3. Summary of environmental variables considered for use in habitat suitability models for age-0 and age 1-4 striped bass. Thirty predictors were obtained from the AQ Chesapeake Bay model (hydrodynamic model), and three additional predictors were obtained from an interpolated model of dissolved oxygen (spatio-temporal model; Du and Shen 2014). D: Daily values; I: instantaneous values; S: static variables; TA: tidal-averaged values.

Category	Habitat Variable	Type	Source	Time Period
Salinity	Surface salinity	Dynamic	Hydrodynamic model	I/TA
	Near-bed salinity	Dynamic	Hydrodynamic model	I/TA
	Depth-averaged salinity	Dynamic	Hydrodynamic model	I/TA
	Salinity stratification	Dynamic	Hydrodynamic model	I/TA
Water temperature	Surface temperature	Dynamic	Hydrodynamic model	I/TA
	Near-bed temperature	Dynamic	Hydrodynamic model	I/TA
	Depth-averaged temperature	Dynamic	Hydrodynamic model	I/TA
	Temperature stratification	Dynamic	Hydrodynamic model	I/TA
Current speed	Near-surface current speed	Dynamic	Hydrodynamic model	I/TA
	Near-bed current speed	Dynamic	Hydrodynamic model	I/TA
	Vertical gradient in the current speed	Dynamic	Hydrodynamic model	I/TA
	Depth-averaged current speed	Dynamic	Hydrodynamic model	I/TA
	Horizontal gradient in the depth-averaged current speed	Dynamic	Hydrodynamic model	I/TA
	Maximum depth-averaged current speed	Dynamic	Hydrodynamic model	I
Morphology	Water depth	Dynamic	Hydrodynamic model	I
	Distance to shoreline	Static	Hydrodynamic model	S
	Seabed percent fine sediment	Static	Hydrodynamic model	S
Dissolved Oxygen	Bottom dissolved oxygen	Dynamic	Spatio-temporal model	D
	Surface dissolved oxygen	Dynamic	Spatio-temporal model	D
	Dissolved oxygen stratification	Dynamic	Spatio-temporal model	D

Table 4. Summary of influential variables identified by boosted regression tree (BRT) analysis for age-0 and age 1-4 striped bass, denoted by X and summed in parentheses in each column. Note that only a subset of six variables were considered in BRT analyses applied to data from the seine surveys (non-shaded) to reflect that these surveys sample relatively shallow waters directly adjacent to the shoreline.

	Age-0 VIMS/MDDNR Seine (3)	**Age-0 VIMS/MDDNR Trawl (4)**	**Age 1-4 VIMS/MDDNR Trawl (7)**	**Age 1-4 ChesMMAP (4)**
Physical				
Water Depth	▨		X	X
Distance to Shore	▨			
% Fine Sediment	▨		X	
Temperature				
Bottom Temperature	▨			
Surface Temperature				
Depth-Averaged Temperature	▨			X
Temperature Stratification	▨			
Salinity				
Bottom Salinity	▨		X	
Surface Salinity				
Depth-Averaged Salinity	▨			
Salinity Stratification	▨		X	X
Current Speed				
Max Depth-Averaged Current Speed	X			
1-Meter Below Surface Current Speed	▨	X		
1-Meter Above Bottom Current Speed	▨			
Depth-Averaged Current Speed				
Current Speed Vertical Stratification	▨			
Horizontal Gradient in Depth-Avg Current Speed	X	X	X	
Dissolved Oxygen				
Bottom dissolved oxygen	▨	X	X	X
Surface dissolved oxygen	X			
DO Stratification	▨	X	X	

Table 5. Average suitable (HSI ≥ 0.5) and optimal (HSI ≥ 0.7) habitat area (km^2) by region and season for age-0 striped bass from the VIMS and MDDNR seine and trawl surveys. Average habitat extent is calculated for the entirety of Chesapeake Bay, Maryland, Virginia, and 10 tributaries that represent major spawning and rearing grounds for striped bass. Numbers after each region indicate total area of each region. Seine model reflects suitable habitat estimates for depths ≤2 meters along the shoreline.

	Seine (1996 - 2017)		Trawl (1996 - 2019)			
	Early Summer (Jun - Jul)	Late Summer (Aug - Sep)	Early Summer (May - Jul)	Late Summer (Aug - Oct)	Fall/Winter (Nov - Jan)	Spring (Feb - Apr)
Region						
Upper Bay (327 km^2)						
HSI ≥ 0.5	35.12	5.84	66.42	23.04	69.80	129.32
HSI ≥ 0.7	3.74	0.90	0	0	6.00	24.65
Chester River (179 km^2)						
HSI ≥ 0.5	12.38	0.19	127.40	91.78	7.73	12.14
HSI ≥ 0.7	1.63	<0.01	66.26	18.36	0.01	0.09
Choptank River (319 km^2)						
HSI ≥ 0.5	29.96	1.48	104.32	83.63	2.95	55.17
HSI ≥ 0.7	1.30	0.03	30.45	12.18	0	2.42
Nanticoke area (234 km^2)						
HSI ≥ 0.5	33.99	7.61	51.23	23.46	1.56	35.50
HSI ≥ 0.7	1.79	0.04	0	0	0	0.99
Pocomoke River (103 km^2)						
HSI ≥ 0.5	14.59	3.69	21.59	4.86	0	5.24
HSI ≥ 0.7	1.21	<0.01	0.11	<0.01	0	0.03
Patuxent River (117 km^2)						
HSI ≥ 0.5	6.69	0.80	77.36	60.92	0.29	9.85
HSI ≥ 0.7	0.70	0.04	34.29	8.77	0	0.06
Potomac River (1,174 km^2)						
HSI ≥ 0.5	98.36	18.08	530.96	358.18	60.50	272.99
HSI ≥ 0.7	1.69	0.19	158.24	81.98	1.78	16.29
Rappahannock River (348 km^2)						
HSI ≥ 0.5	28.78	3.44	64.44	66.28	18.60	165.13
HSI ≥ 0.7	2.75	<0.01	10.80	8.46	0.32	17.80
York River (195 km^2)						
HSI ≥ 0.5	18.76	2.97	10.05	8.38	10.41	98.48
HSI ≥ 0.7	0.16	0.18	0.05	0.05	0.03	10.10
James River (631 km^2)						
HSI ≥ 0.5	45.75	5.75	50.92	23.78	45.41	277.68
HSI ≥ 0.7	1.63	0.14	0	0	1.30	27.60
Maryland (6,047 km^2)						
HSI ≥ 0.5	462.09	82.25	3,655.21	2,742.62	252.78	789.21
HSI ≥ 0.7	65.75	1.22	1,656.82	1,013.74	7.98	49.02
Virginia (5,253 km^2)						
HSI ≥ 0.5	323.67	93.18	761.04	474.98	101.91	1,301.01
HSI ≥ 0.7	31.46	0.51	194.28	29.31	1.43	75.42
Entire Bay (11,300 km^2)						
HSI ≥ 0.5	785.75	175.43	4,416.25	3,217.61	345.68	2,090.22
HSI ≥ 0.7	97.21	1.73	1,851.10	1,043.05	9.70	124.43

Table 6. Average suitable (HSI ≥ 0.5) and optimal (HSI ≥ 0.7) habitat area (km^2) by region and season for age 1-4 striped bass from the VIMS and MDDNR trawl surveys. Average habitat extent is calculated for the entirety of Chesapeake Bay, Maryland, Virginia, and 10 tributaries that represent major spawning and rearing grounds for striped bass (1996 - 2019). Numbers after each region indicate total area.

Region		Spring (Mar - Jun)	Summer (Jul - Oct)	Fall/Winter (Nov - Feb)
Upper Bay (327 km^2)				
	HSI ≥ 0.5	44.07	82.03	31.08
	HSI ≥ 0.7	0.09	0.74	0.17
Chester River (179 km^2)				
	HSI ≥ 0.5	126.41	132.34	31.90
	HSI ≥ 0.7	33.72	45.85	0.25
Choptank River (319 km^2)				
	HSI ≥ 0.5	124.68	192.06	43.51
	HSI ≥ 0.7	8.59	37.23	1.17
Nanticoke area (234 km^2)				
	HSI ≥ 0.5	63.32	109.82	17.42
	HSI ≥ 0.7	0.15	3.38	0
Pocomoke River (103 km^2)				
	HSI ≥ 0.5	29.85	34.53	0.04
	HSI ≥ 0.7	0	0	0
Patuxent River (117 km^2)				
	HSI ≥ 0.5	37.30	57.61	35.75
	HSI ≥ 0.7	3.69	11.75	0.88
Potomac River (1,174 km^2)				
	HSI ≥ 0.5	373.34	471.25	221.04
	HSI ≥ 0.7	35.61	96.17	3.58
Rappahannock River (348 km^2)				
	HSI ≥ 0.5	60.37	158.49	81.65
	HSI ≥ 0.7	0.14	19.48	1.48
York River (195 km^2)				
	HSI ≥ 0.5	14.65	53.20	26.27
	HSI ≥ 0.7	0	2.61	0.40
James River (631 km^2)				
	HSI ≥ 0.5	110.22	157.80	82.12
	HSI ≥ 0.7	0.43	2.73	1.14
Maryland (6,047 km^2)				
	HSI ≥ 0.5	2,116.54	2,473.62	895.17
	HSI ≥ 0.7	364.52	517.44	8.23
Virginia (5,253 km^2)				
	HSI ≥ 0.5	284.06	589.14	359.38
	HSI ≥ 0.7	0.61	26.35	3.66
Entire Bay (11,300 km^2)				
	HSI ≥ 0.5	2,400.60	3,062.76	1,254.56
	HSI ≥ 0.7	365.12	543.79	11.88

Table 7. Average suitable (HSI ≥ 0.5) and optimal (HSI ≥ 0.7) habitat area (km^2) by region and season for age 1-4 striped bass from the ChesMMAP survey (2002 - 2018). Numbers after each region indicate total area excluding the major tributaries. Spatially, estimates were restricted to the mainstem of the Bay to align with the domain of this particular survey.

Region		Spring (Mar - Jun)	Summer (Jul - Oct)	Fall (Nov)
Upper Bay (327 km^2)				
	HSI ≥ 0.5	0.17	302.24	326.66
	HSI ≥ 0.7	0	94.17	326.63
Maryland Bay (3,921 km^2)				
	HSI ≥ 0.5	231.04	2,412.41	3,286.92
	HSI ≥ 0.7	7.80	559.56	2,604.67
Virginia Bay (4,079 km^2)				
	HSI ≥ 0.5	385.01	1,551.77	3,732.01
	HSI ≥ 0.7	9.41	72.72	2,743.45
Entire Bay (8,000 km^2)				
	HSI ≥ 0.5	616.05	3,964.18	7,018.93
	HSI ≥ 0.7	17.21	632.28	5,348.12

Table 8. Nonparametric ranked regression of suitable habitat extent (HSI $\geq$ 0.5) Bay-wide and time (year; 1996-2017 for VIMS/MD seine, 1996-2019 for VIMS/MD trawl and 2002-2018 for ChesMMAP). Extent of suitable habitat was calculated as the sum of areas (km^2) with HSI $\geq$ 0.5 within Chesapeake Bay, or in Virginia waters in seasons denoted with *. In the ChesMMAP model, analyses were restricted to the extent of suitable habitat in the mainstem of the Bay. The model fit to the data was $Yi = \beta0 + \beta1X1i + \varepsilon i$ where Yi is the rank-transformed response (extent of suitable habitat), β0 is the overall average response (intercept), β1 is the regression coefficient (slope), X1i is the value of the predictor for observation I (year), and εi is the random, unexplained error. N is the sample size (number of years) and F is the value of the F-statistic used to test model significance.

	Season	**N**	**F**	**p**	**Direction**
Age-0 VIMS/MD Seine	Early Summer (Jun-July)	22	6.04	0.02	Decrease
	Late Summer (Aug-Sept)	22	2.54	0.13	No change
Age-0 VIMS/MD Trawl	Early Summer (May-July)	24	2.60	0.12	No change
	Late Summer (Aug-Oct)	24	0.80	0.38	No change
	Fall/Winter (Nov-Jan_) *VIMS only_	24	0.00	0.97	No change
	Spring (Feb-Apr) _*VIMS only_	24	1.47	0.24	No change
Age 1-4 VIMS/MD Trawl	Spring (Mar-Jun)	24	13.55	<0.01	Decrease
	Summer (July-Oct)	24	2.13	0.16	No change
	Fall/Winter (Nov-Feb) *_VIMS only_	24	0.00	0.96	No change
ChesMMAP	Spring (Mar-Jun)	17	0.05	0.83	No change
	Summer (July-Oct)	17	0.73	0.41	No change
	Fall (Nov)	17	0.90	0.36	No change

Table 9. Nonparametric ranked regression of relative abundance and the extent of suitable habitat extent (HSI $\geq$ 0.5) Bay-wide (or in Virginia waters in seasons denoted with *). In the ChesMMAP model, comparisons were restricted to extent of suitable habitat in the mainstem of the Bay. The model fit to the data was $Yi = \beta 0 + \beta 1X1i + \varepsilon i$ where Yi is the rank-transformed response (relative abundance), β0 is the overall average response (intercept), β1 is the regression coefficient (slope), X1i is the value of the predictor for observation I (extent of suitable habitat), and εi is the random, unexplained error. N is the sample size (number of years) and F is the value of the F-statistic used to test model significance.

	Season	**N**	**F**	**p**
Age-0 VIMS/MD Seine	Early Summer (Jun-July)	22	2.43	0.13
	Late Summer (Aug-Sept)	22	3.28	0.09
Age-0 VIMS/MD Trawl	Early Summer (May-July)	24	1.77	0.20
	Late Summer (Aug-Oct)	24	1.30	0.27
	Fall/Winter (Nov-Jan*) **VIMS only*	24	2.25	0.15
	Spring (Feb-Apr) **VIMS only*	24	2.59	0.12
Age 1-4 VIMS/MD Trawl	Spring (Mar-Jun)	24	2.85	0.11
	Summer (July-Oct)	24	1.60	0.22
	Fall (Nov-Feb) **VIMS only*	24	0.00	0.97
ChesMMAP	Spring (Mar-Jun)	17	1.52	0.24
	Summer (July-Oct)	17	0.06	0.81
	Fall (Nov)	17	0.51	0.48

Figure 1. Sample sites of the VIMS Juvenile Striped Bass seine survey and MDDNR's Juvenile Striped Bass seine survey. The VIMS seine survey sampled at 39 fixed sites in the Rappahannock, James, and York rivers from five sampling events conducted between June and September of each year. Sampling occurred at 18 index sites and 21 auxiliary sites that serve to provide wider geographic coverage and increase sample sizes within river systems. The MDDNR seine survey sampled 22 fixed sites in the Choptank, Nanticoke, Potomac, and Patuxent rivers, as well as other small bays and tributaries on the eastern shore and at the head of Chesapeake Bay during three sampling events between June and September of each year. Both surveys collect replicate hauls at each site (but only at index sites in the VIMS survey); data from only the first haul were retained for analysis.

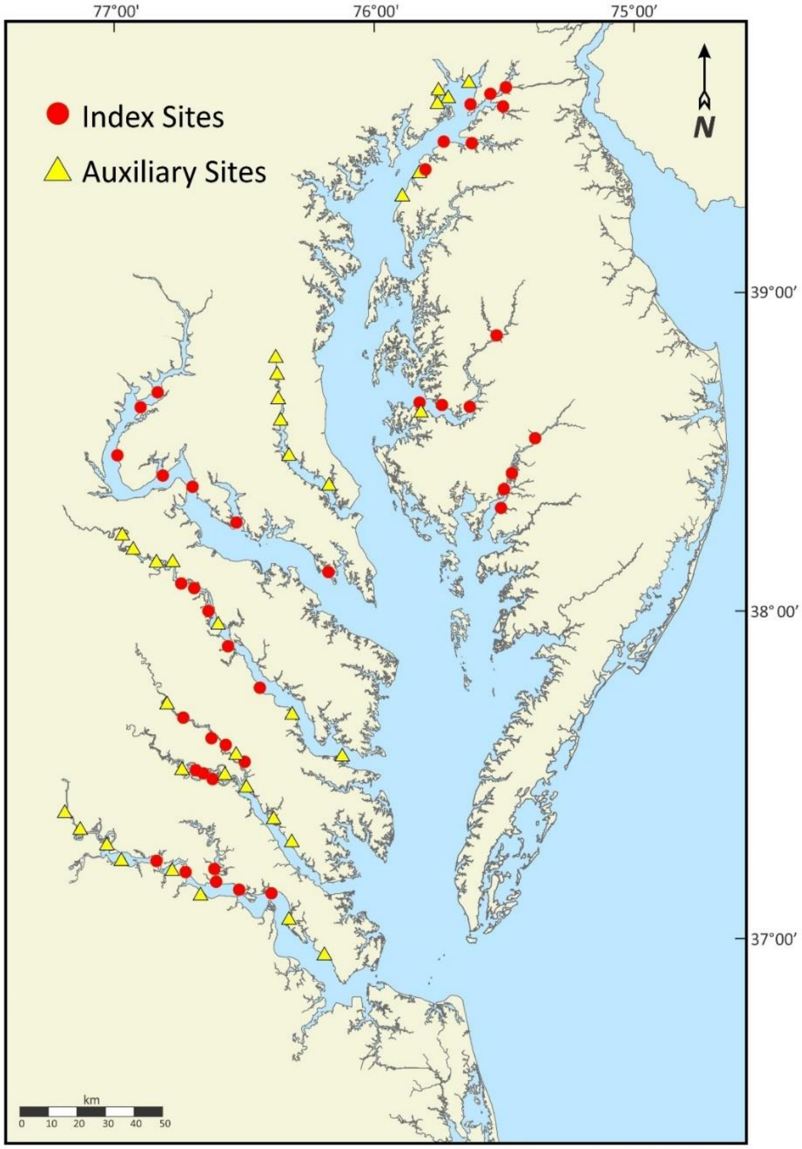


Figure 2. Sample sites by the VIMS Juvenile Fish trawl survey and MDDNR Blue Crab summer trawl survey. The VIMS trawl survey sampled sites on a monthly basis using a random stratified design; a representative month is depicted here. Approximately 1,224 sites were sampled each year between 1996 and 2019 (fewer sites were sampled in some years due to weather or vessel issues). The MDDNR trawl survey) sampled fixed sites monthly between May and October.

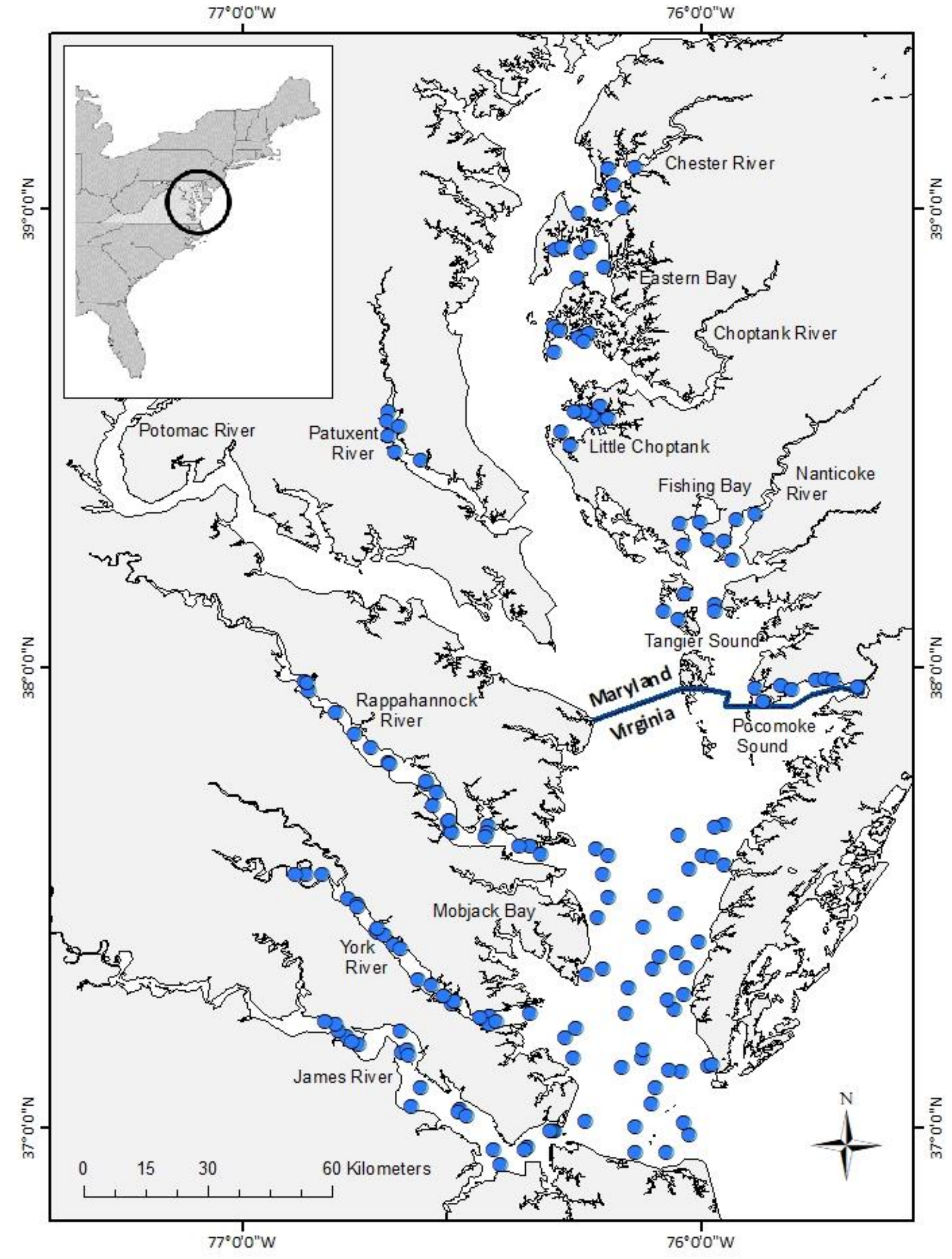


Figure 3. Example of sampling locations (March 2015) for a cruise ([black dot], n ≈ 80) and sampling coverage for a full year ([white dot], n ≈ 400) for the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP). Horizontal lines delineate 5 regional strata; shading denotes the 3 depth strata

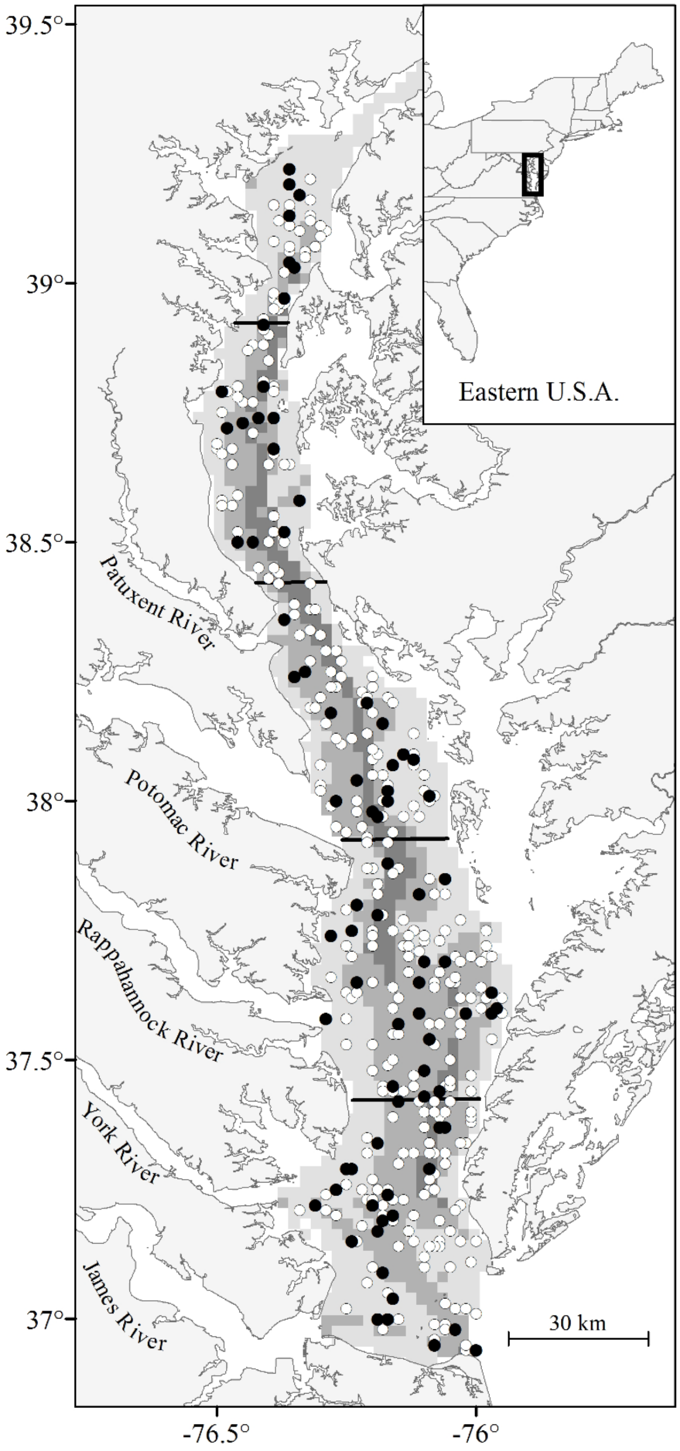
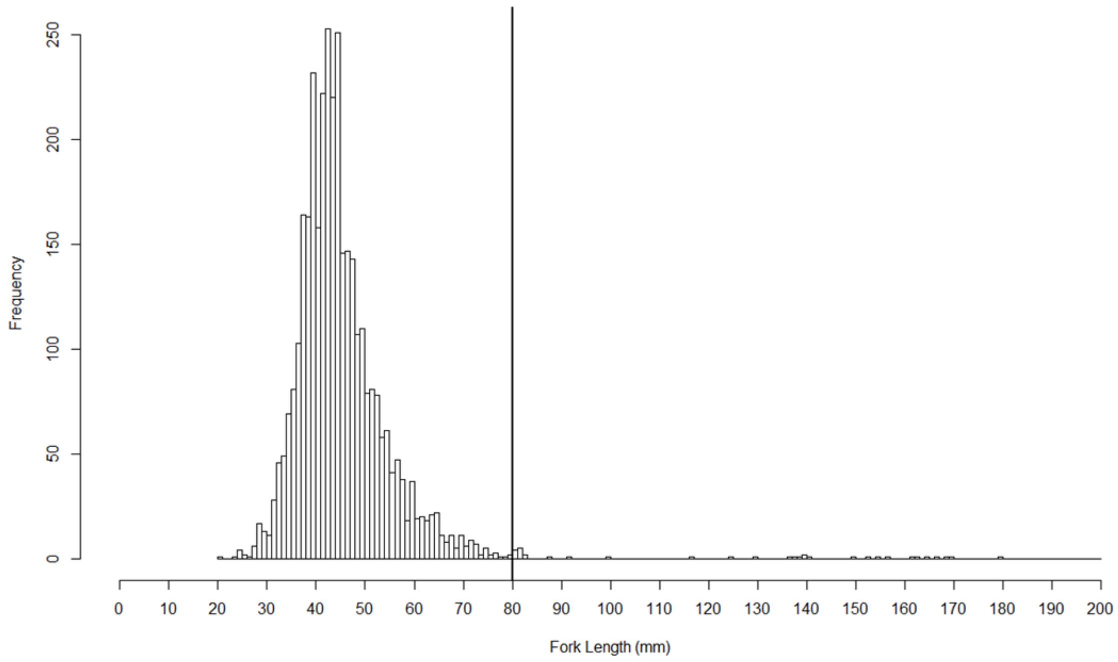


Figure 4. Length frequency histograms of age-0 striped bass in the VIMS striped bass seine survey in June (A) and July (B). Vertical lines denote the monthly length threshold (mm FL) used to distinguish age-0 from older fish during summer months.

(A)



(B)

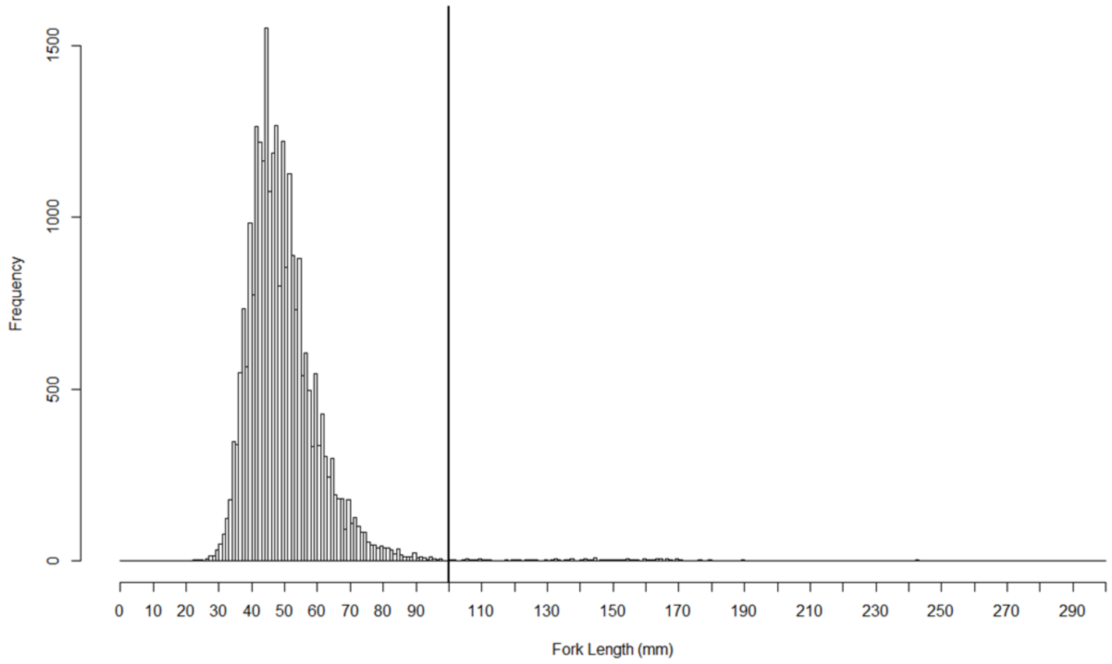


Figure 5. Length frequency counts by survey of age 1-4 striped bass, where 401 mm FL denotes the age-4 threshold value indicating a 90% likelihood that an individual fish is assigned to this group based on size. Each trawl survey effectively target different sizes, and therefore different ages, of striped bass within this age group that reflect differences in gear size and sampling design (MDDNR trawl survey 63-392 mm FL; VIMS trawl survey 88-401 mm FL; ChesMMAP 99-401 mm FL). Dotted vertical lines indicate mean fork length.

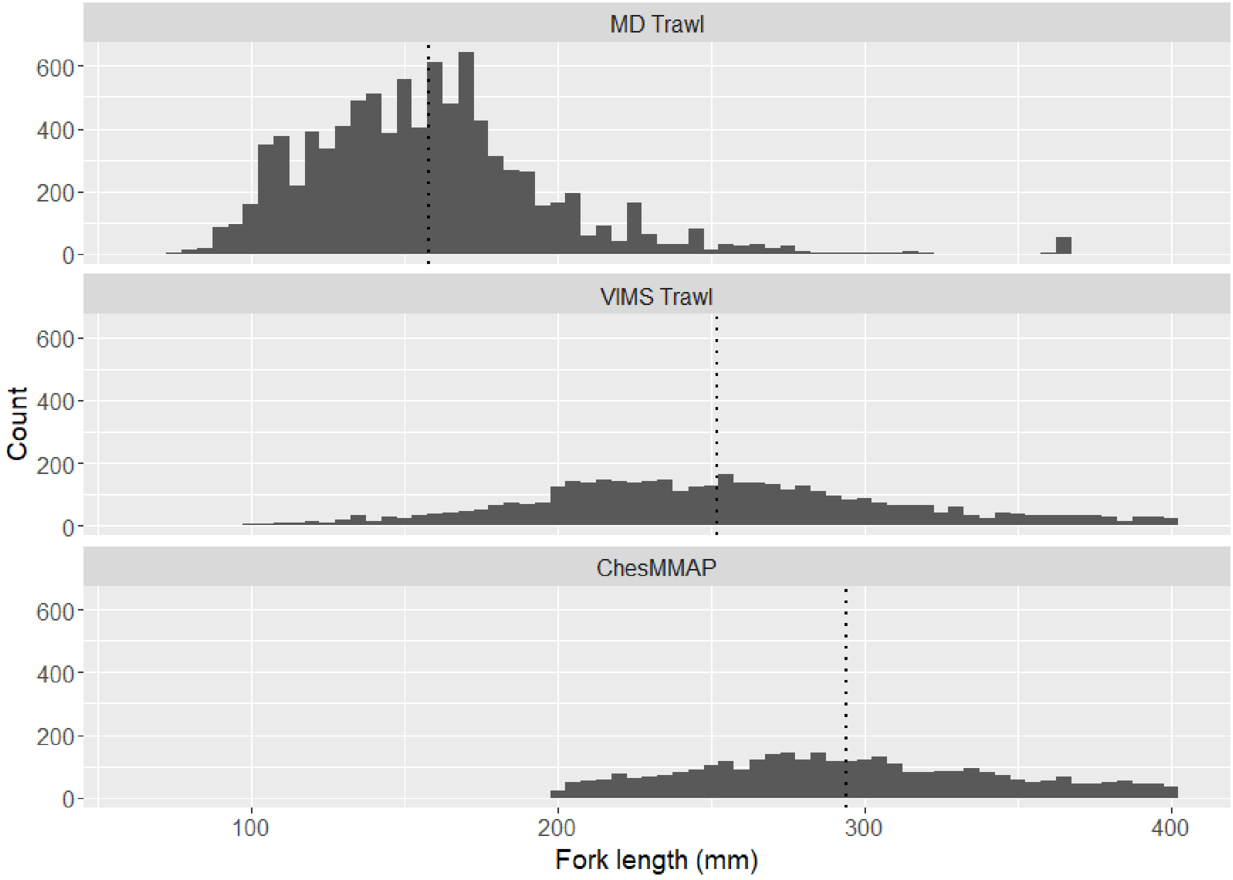


Figure 6. Model domain and boundary conditions for the AQ Chesapeake Bay model which was used to hindcast environmental conditions for age-0 and age 1-4 striped bass spanning the years 1996-2019.

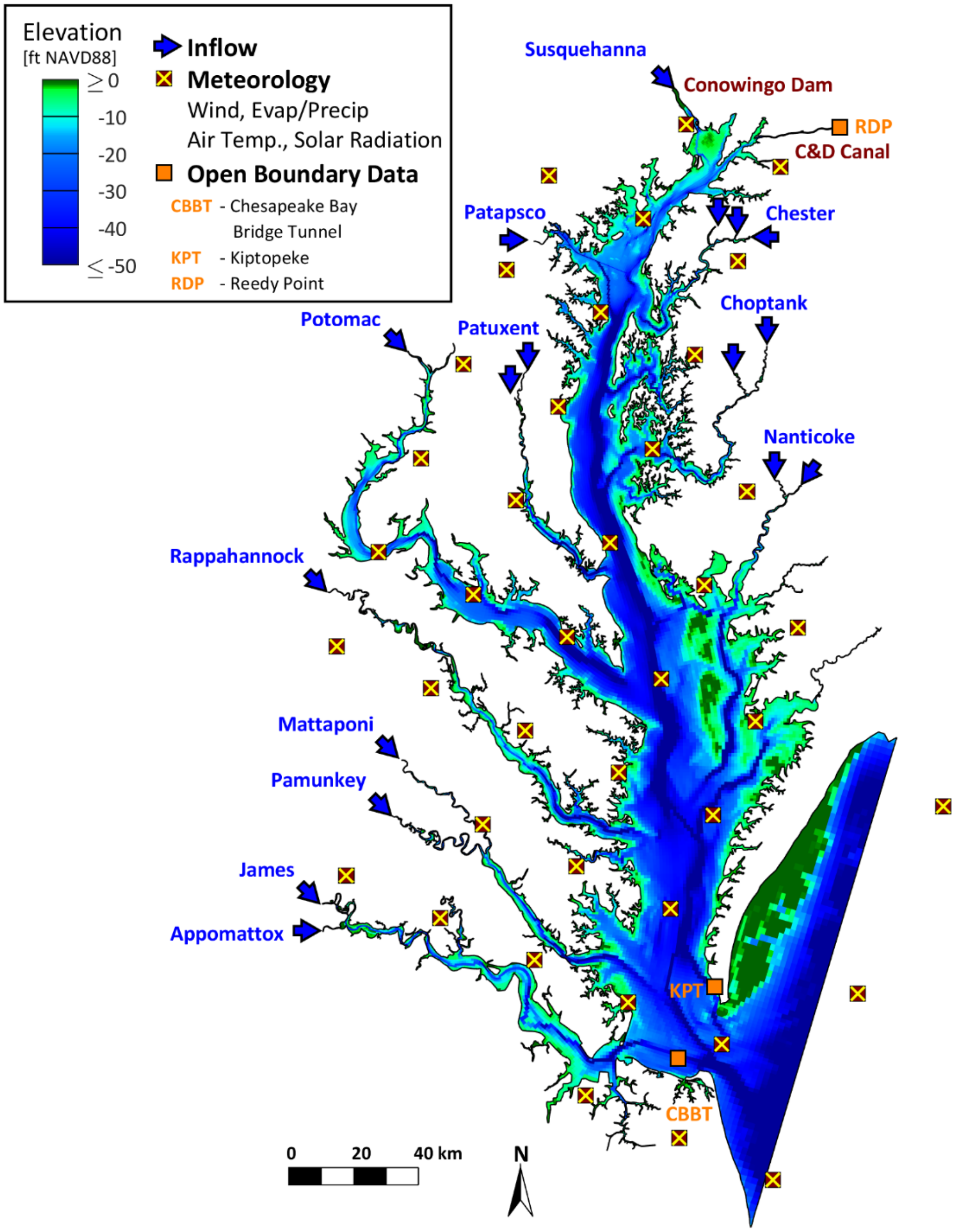


Figure 7. Locations used to validate outputs for the AQ Chesapeake Bay hydrodynamic model.

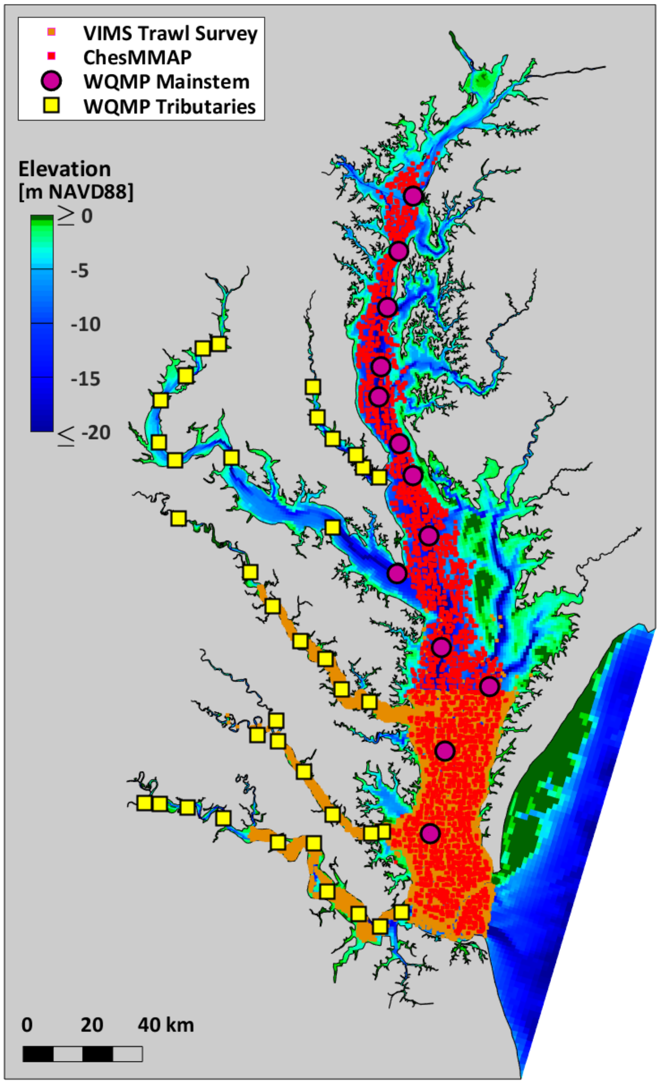


Figure 8. Scatter Plots Comparing Model Estimates to Data Collected During the VIMS Trawl Survey Fisheries Sampling for (A) Bottom Salinity and (B) Bottom Temperature During 2012 and Target Diagrams Showing Each Year for (C) Bottom Salinity, (D) Bottom Temperature, (E) Surface Salinity, and (F) Surface Temperature.

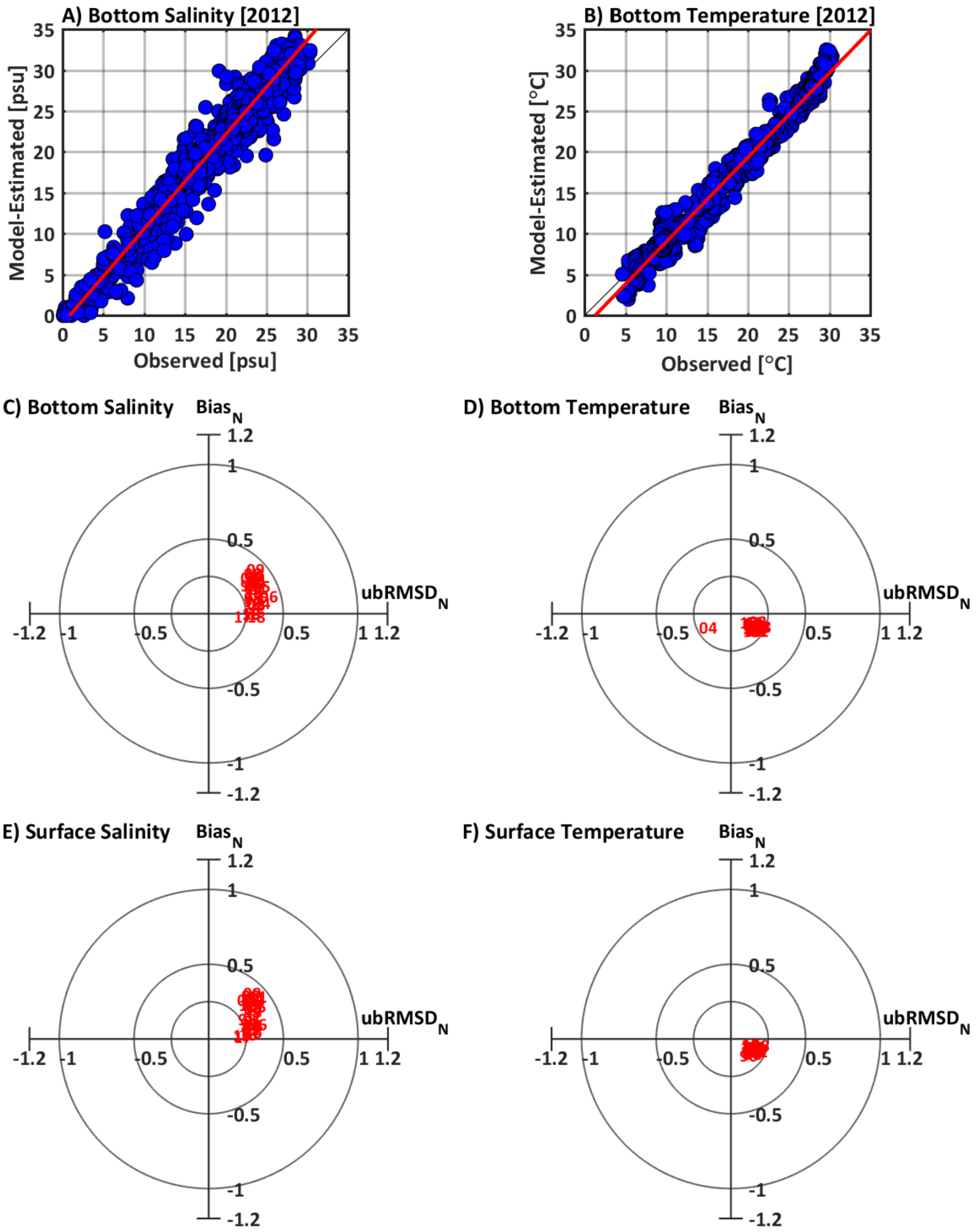


Figure 9. Scatter Plots Comparing Model Estimates to Data Collected During the ChesMMAP Trawl Survey Fisheries Sampling for (A) Bottom Salinity and (B) Bottom Temperature During 2012 and Target Diagrams Showing Each Year for (C) Bottom Salinity, (D) Bottom Temperature, (E) Surface Salinity, and (F) Surface Temperature.

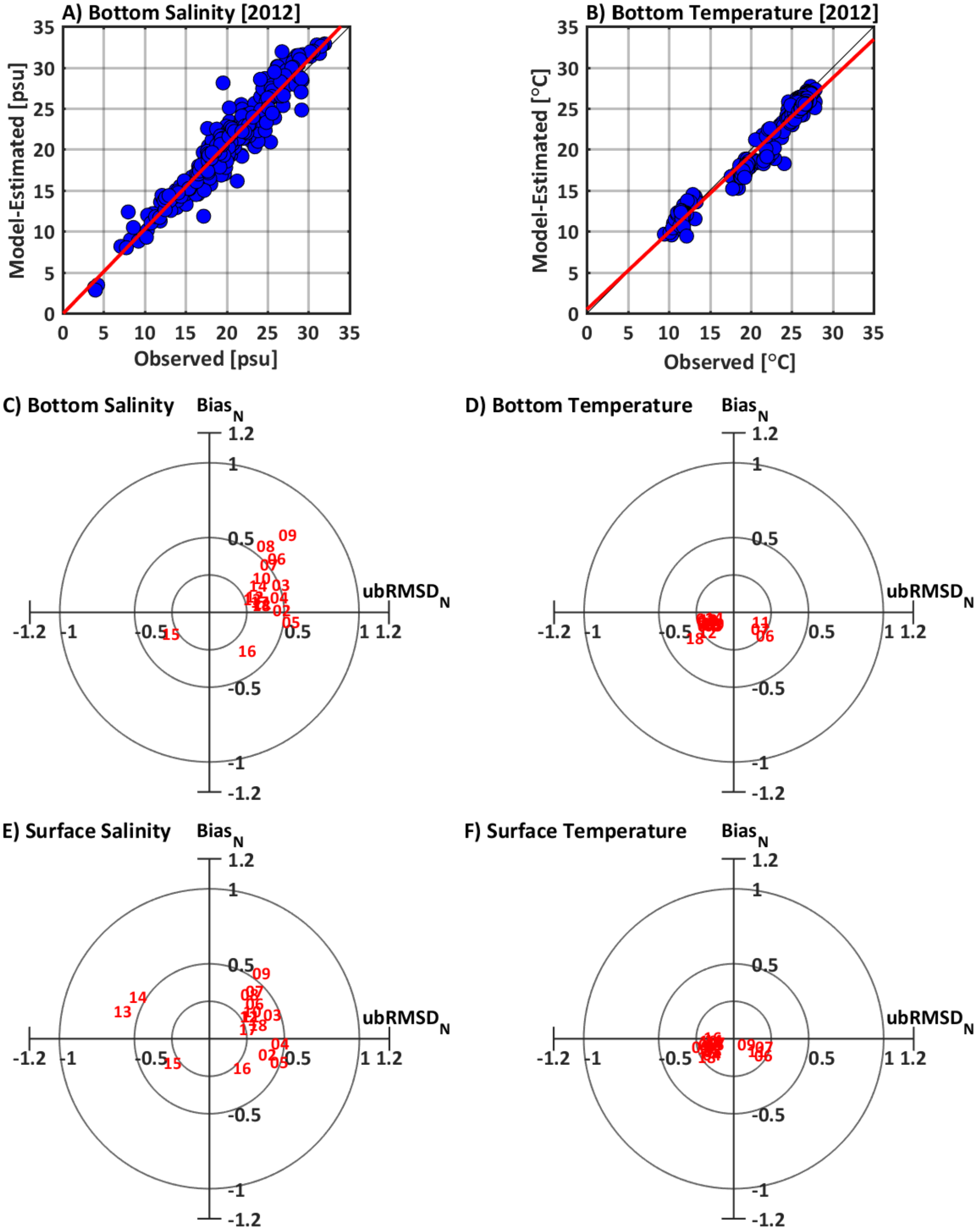
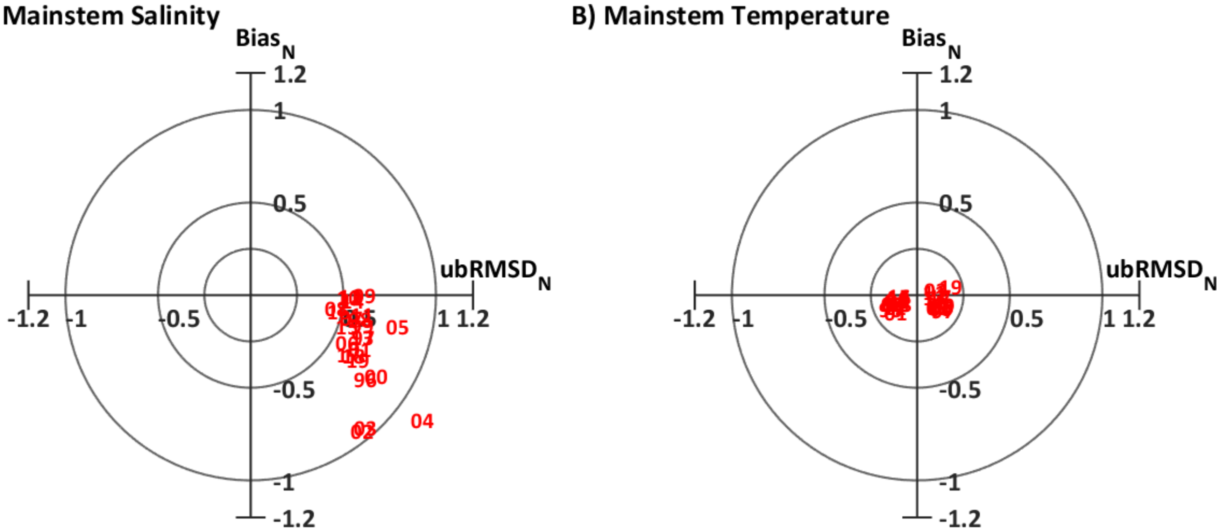
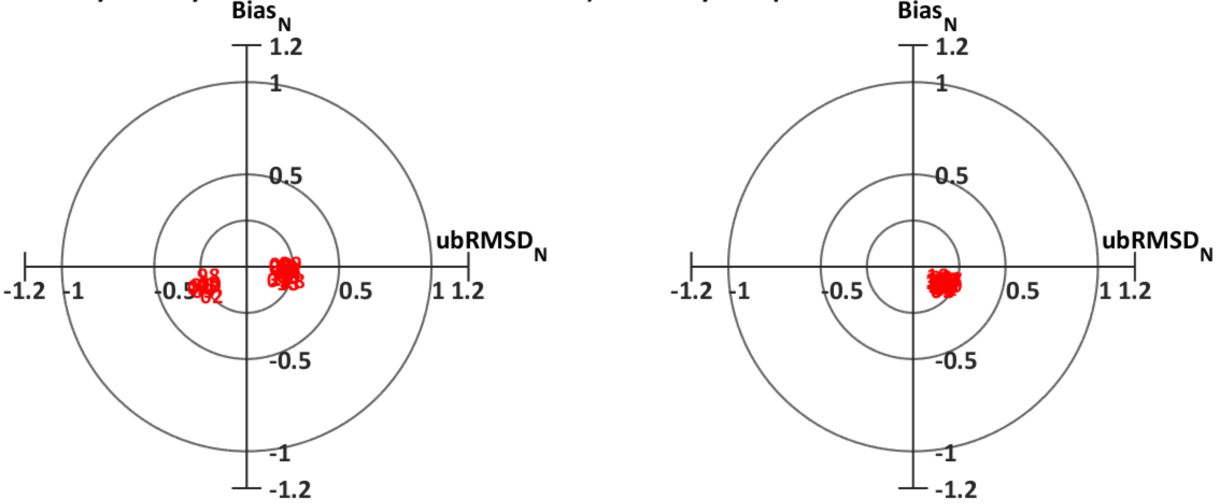


Figure 10. Target Diagrams Comparing Model Estimates to Data Collected During the WQMP for (A) Mainstem Salinity, (B) Mainstem Temperature, (C) Tributary Salinity, and (D) Tributary Temperature.


A) Mainstem Salinity

B) Mainstem Temperature


C) Tributary Salinity

D) Tributary Temperature

Figure 11. Yearly average freshwater discharge rates from the nine RIM tributaries. The dark horizontal line denotes the median value, and the lighter horizontal lines denote plus and minus two standard deviations around the median. 1999, 2007, and 2019 were identified as dry, average, and wet years, respectively.

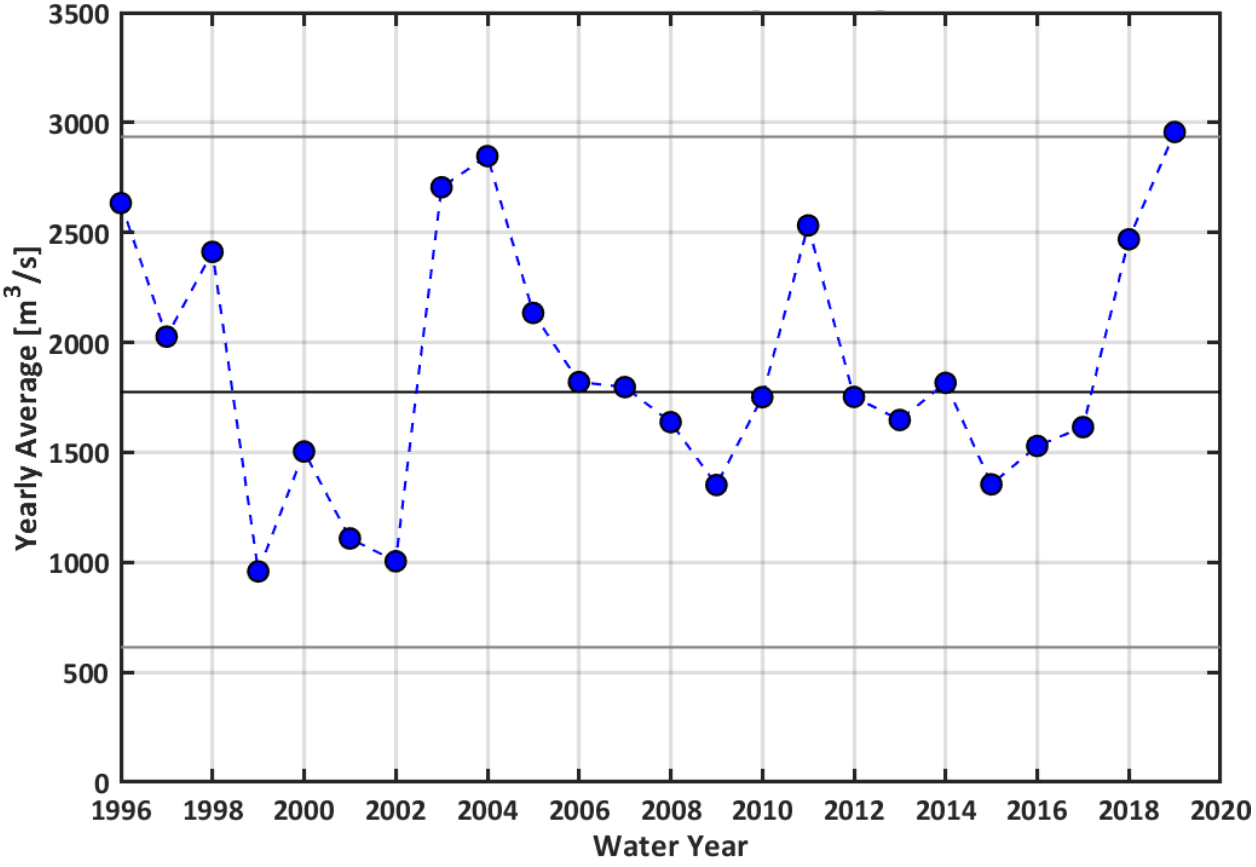


Figure 12. Yearly median water temperature at Thomas Point Light. The years 2002, 2012, and 2014 were identified as average, warm, and cool years, respectively.

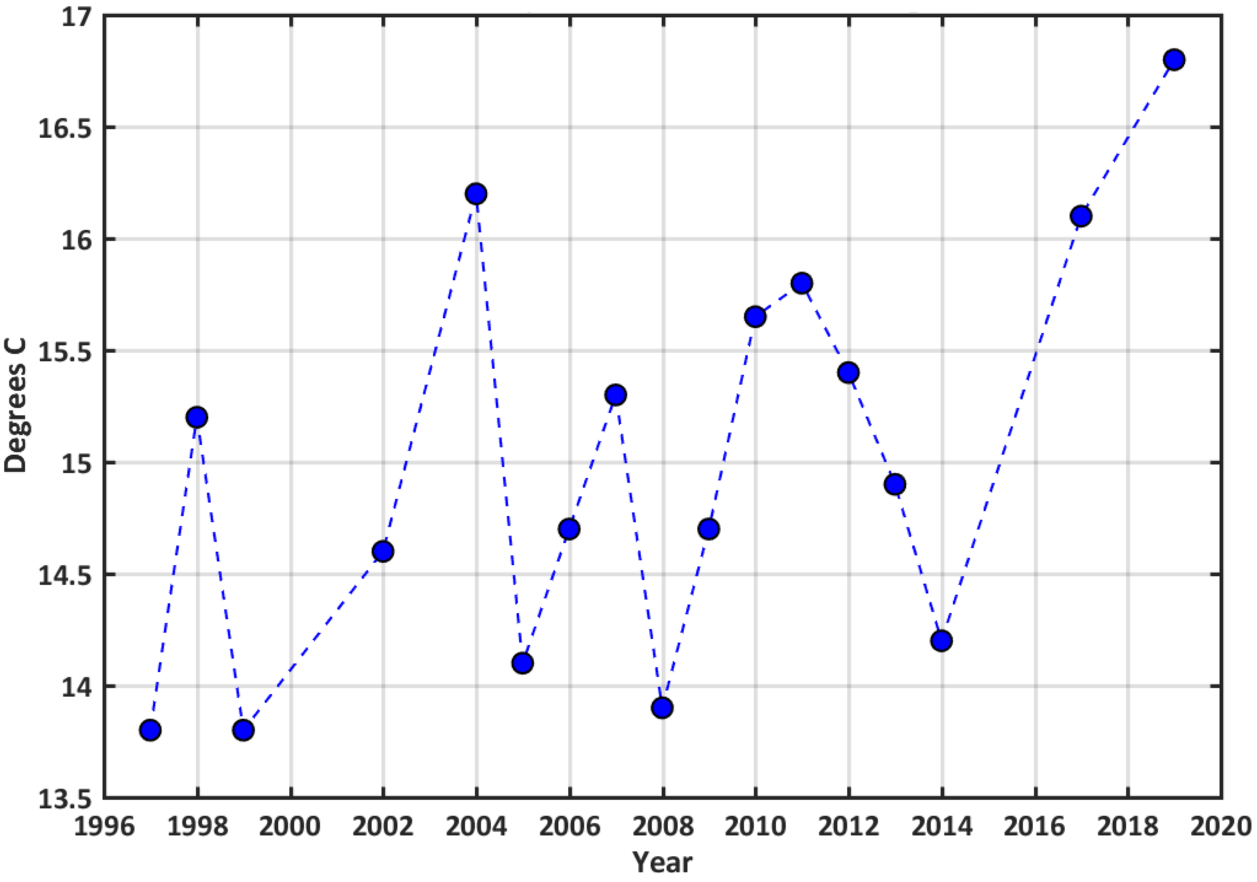


Figure 13. Box-and-whisker plots of the root mean-square error (RMSE) for three formulations of the habitat suitability index (HSI) estimated from 10 bootstrap replicates in each model for age-0 and age 1-4 striped bass. Bootstrap replicates were partitioned into training (~70%) and test (~30%) sets: the training set was used to identify influential covariates and to estimate the habitat suitability index (HSI); the test set was used to predict the HSI, which was then compared with the HSI from the training set and used to calculate RMSEs. The diamond symbol in the plot displays the mean, the horizontal blue line is the median, the top and bottom of the boxes are the quartiles, the whiskers represent 1.5 times the interquartile range, and the open circles denote outliers. Lower values of the mean RMSE indicate better model performance.

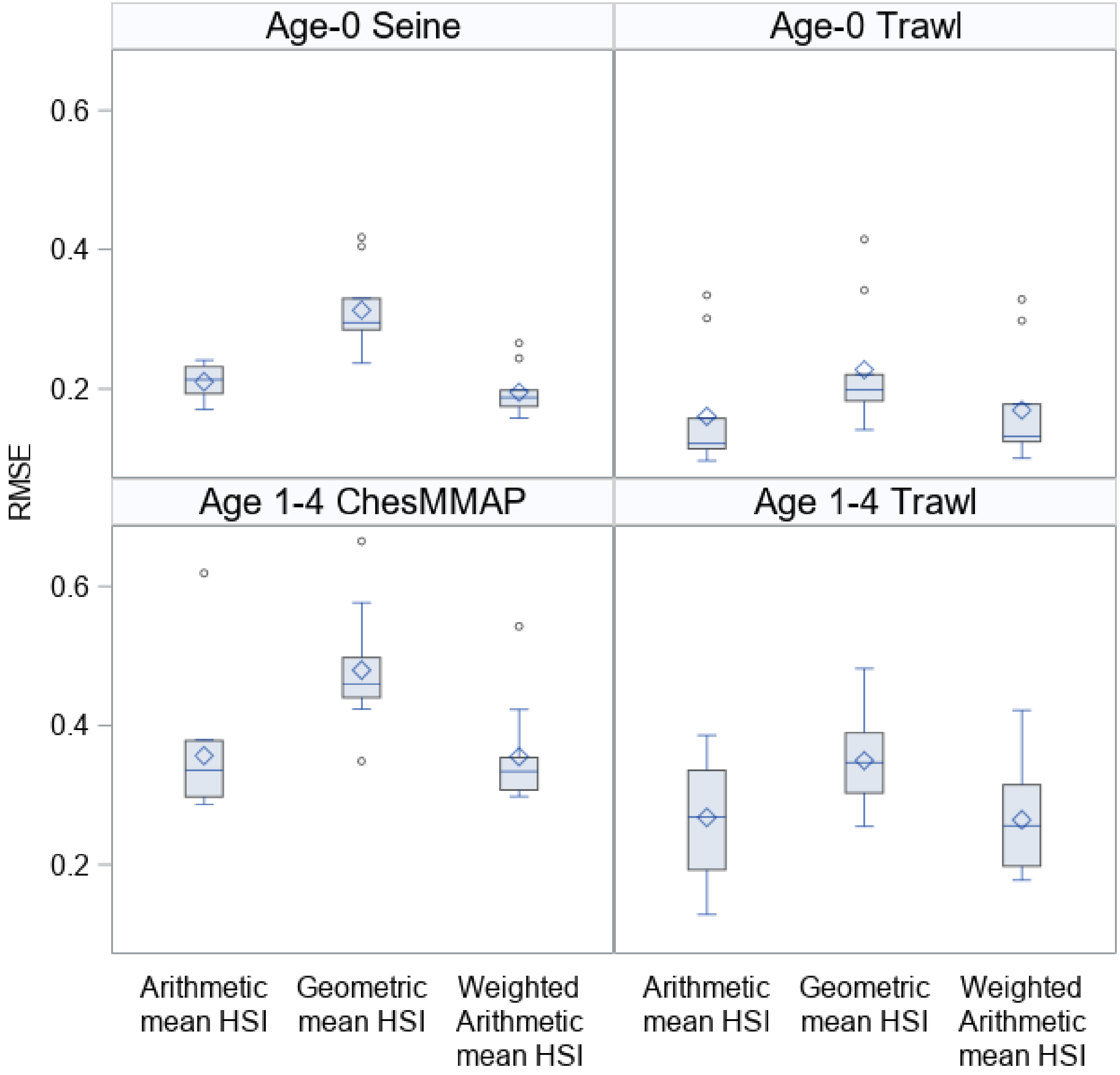
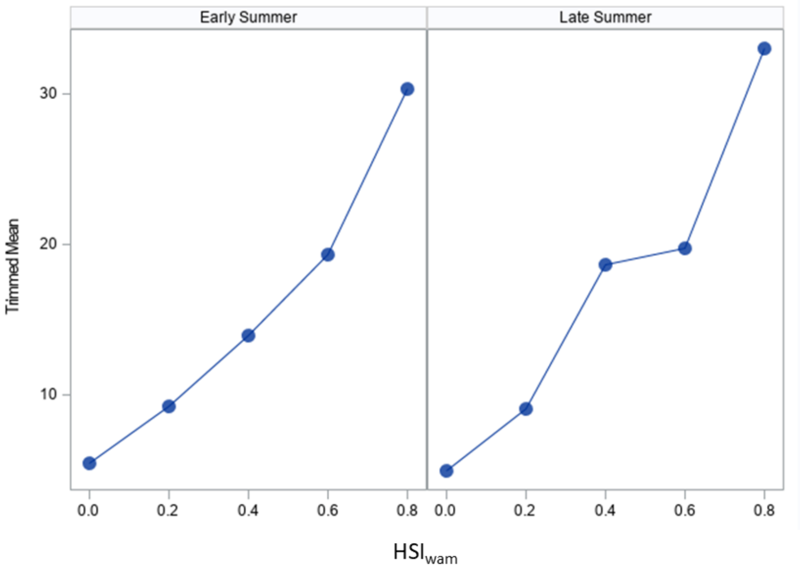


Figure 14. Relationship between HSI and trimmed mean catches for (A) age-0 striped bass in the VIMS and MDDNR seine surveys, 1996-2017; and (B) age-0 striped bass in the VIMS and MDDNR trawl surveys, 1996-2019. For the seine model, the HSI_{wam} is shown, whereas the HSI_{am} is shown for the trawl model (see text). Note the different y-axes.

(A)



(B)

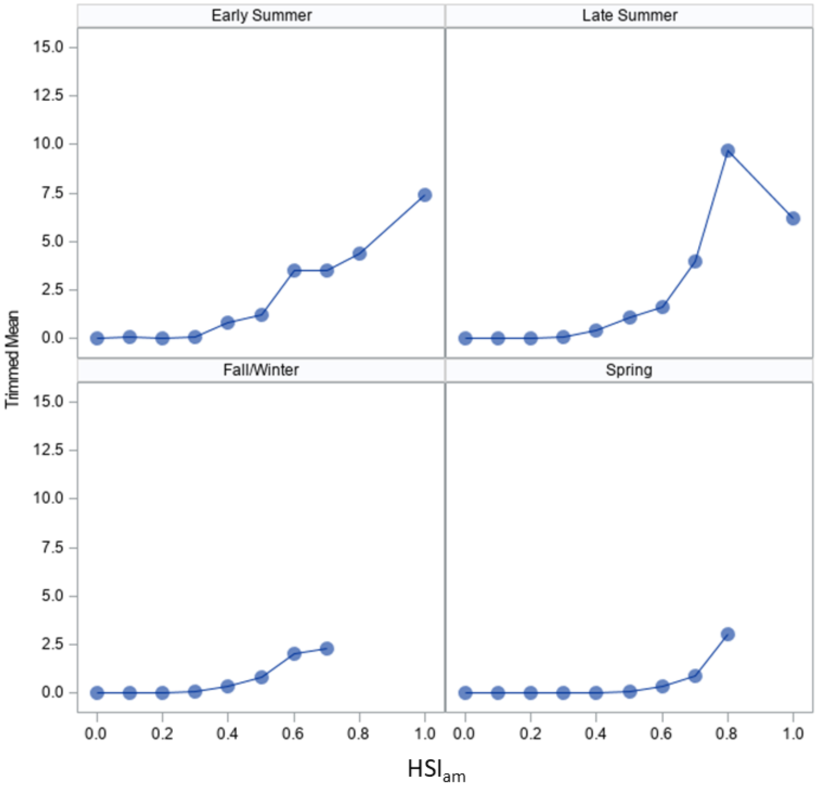
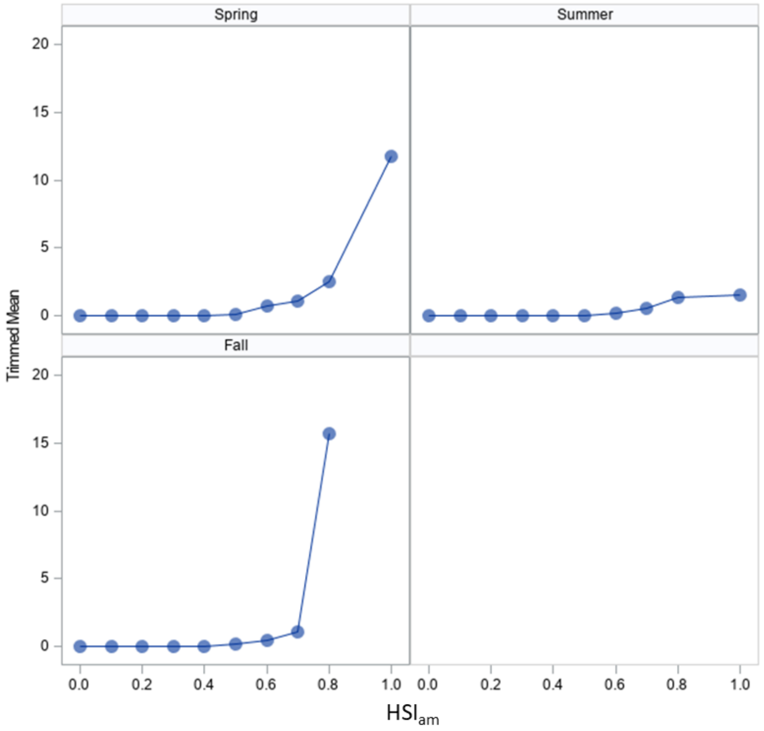


Figure 15. Relationship between HSI and trimmed mean catches for (A) age 1-4 striped bass in the VIMS and MDDNR trawl surveys, 1996-2019; and (B) age 1-4 striped bass in the ChesMMAP survey, 2002-2018. Both models show the HSI_{am} (see text). Note the different y-axes.

(A)



(B)

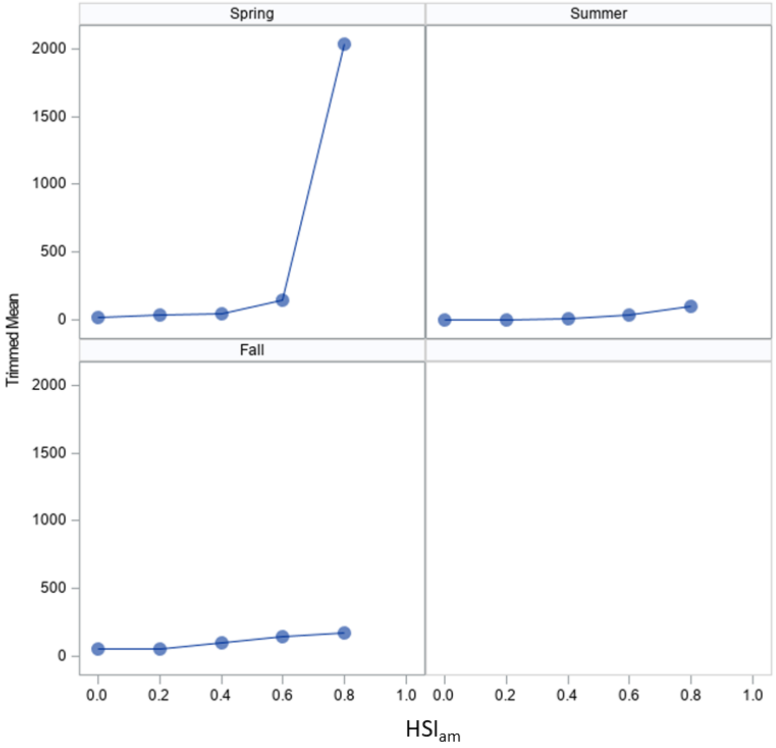
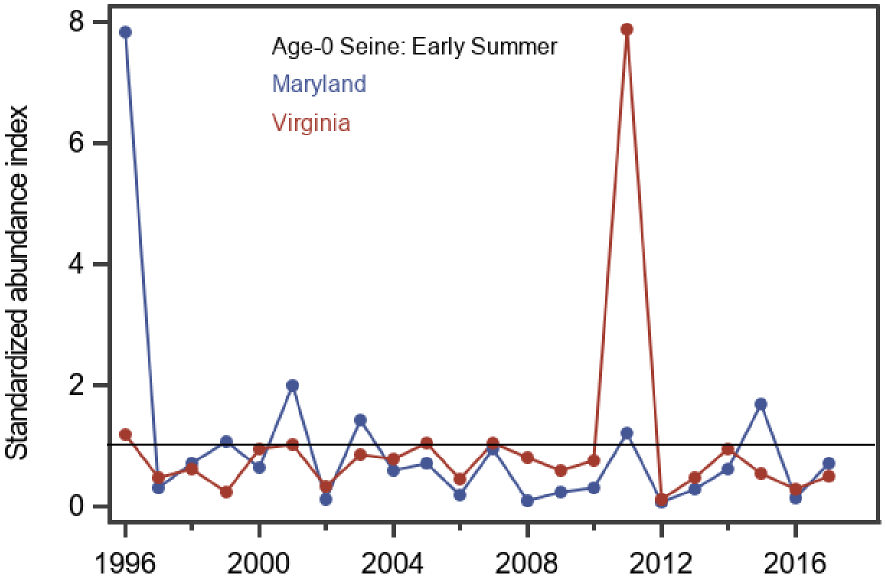


Figure 16. Standardized index of relative abundance by season for age-0 (YOY) striped bass in Maryland (blue) and Virginia (red) waters. Seasonal relative abundance was estimated as mean catch per unit effort (CPUE) calculated as the number of fish divided by area swept by the seine (number/m2). CPUE was standardized by season to a mean of 1.0 across 22 years (1996-2017) to allow for comparison between surveys, denoted by the solid horizontal line. Note that standardized abundances do not reflect differences in absolute abundance in a given year. Seasons are as follows: Early summer (June-July) and Late summer (August-September).



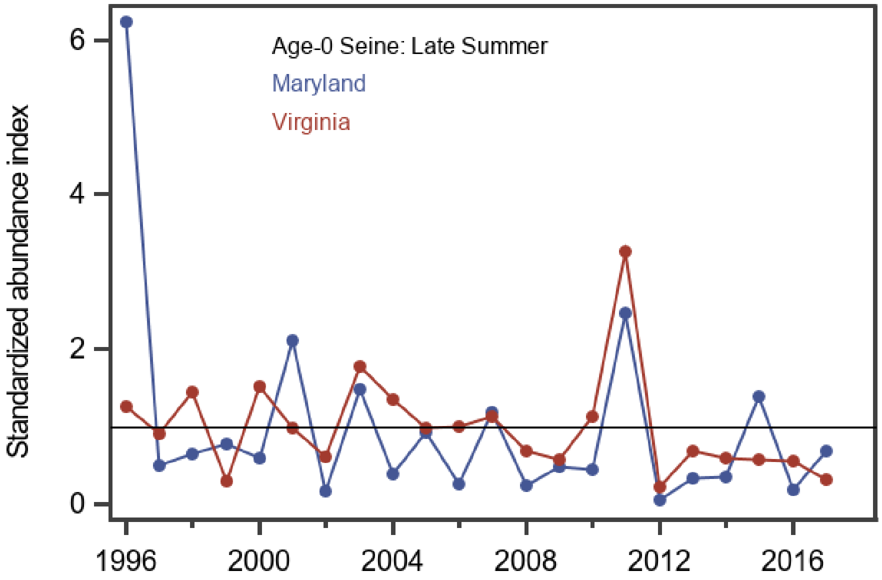


Figure 17. Standardized index of relative abundance by season for age-0 (YOY) striped bass in Maryland (blue) and Virginia (red) waters. Seasonal relative abundance was estimated as mean catch per unit effort (CPUE) calculated as the number of fish divided by area swept by the trawl (number/km2). CPUE was standardized by season to a mean of 1.0 across 24 years (1996-2019) to allow for comparison between surveys, denoted by the solid horizontal line. Note that standardized abundances do not reflect differences in absolute abundance in a given year. For age-0 fish in the trawl survey in winter and spring, only the standardized index for Virginia is shown because Maryland does not sample during these months. Seasons are: Early summer (May-July), late summer (August-October), winter (November-January) and spring (February-April).

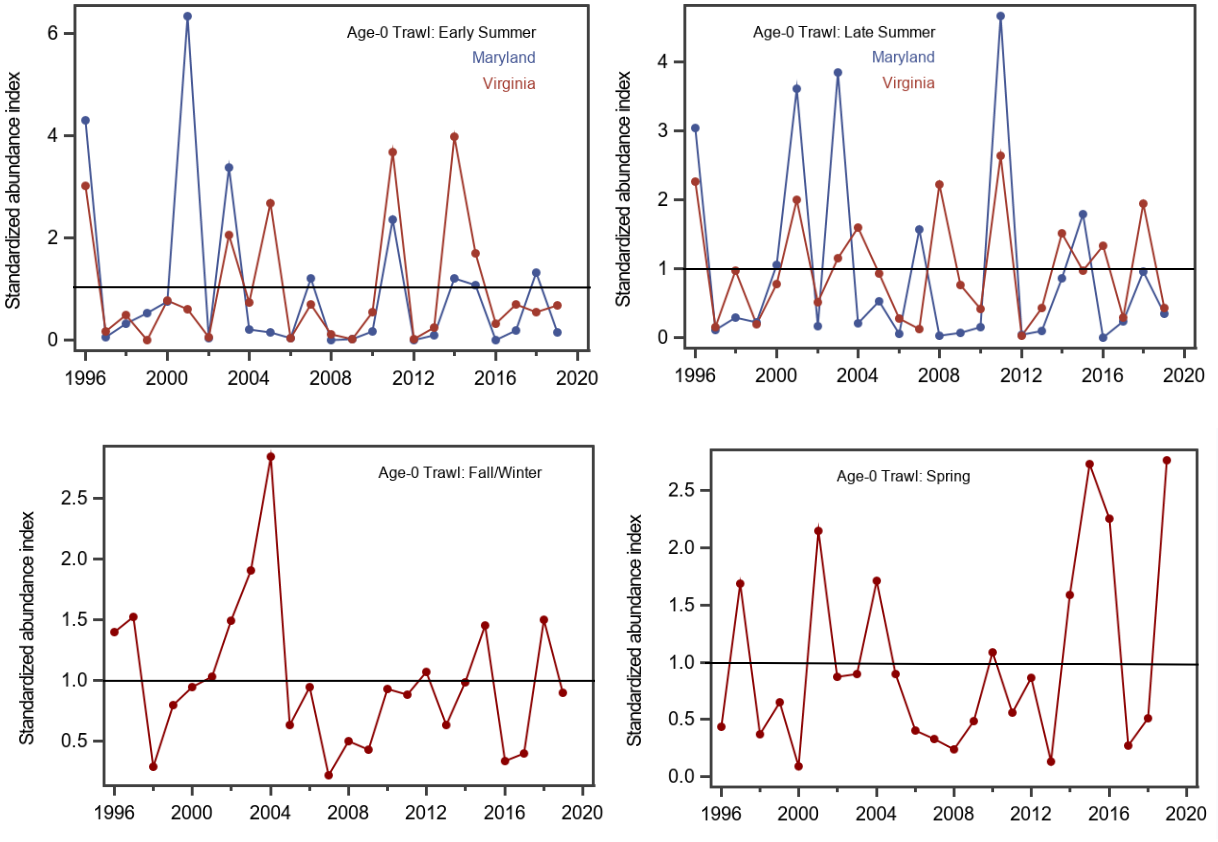


Figure 18. Standardized index of relative abundance by season for age-1-4 (resident sub-adult) striped bass in Maryland (blue) and Virginia (red) waters. Seasonal relative abundance was estimated as mean catch per unit effort (CPUE) calculated as the number of fish divided by area swept by the trawl (number/km^2). CPUE was standardized by season to a mean of 1.0 across 24 years (1996-2019) to allow for comparison between surveys, denoted by the solid horizontal line. Note that standardized abundances do not reflect differences in absolute abundance in a given year. Only the standardized index for Virginia is shown in ‘fall’ (November-February) because Maryland does not sample during these months. ‘Spring’ corresponds to March-June, ‘Summer’ corresponds to July-October, and ‘Fall’ encompasses the months of November to February.

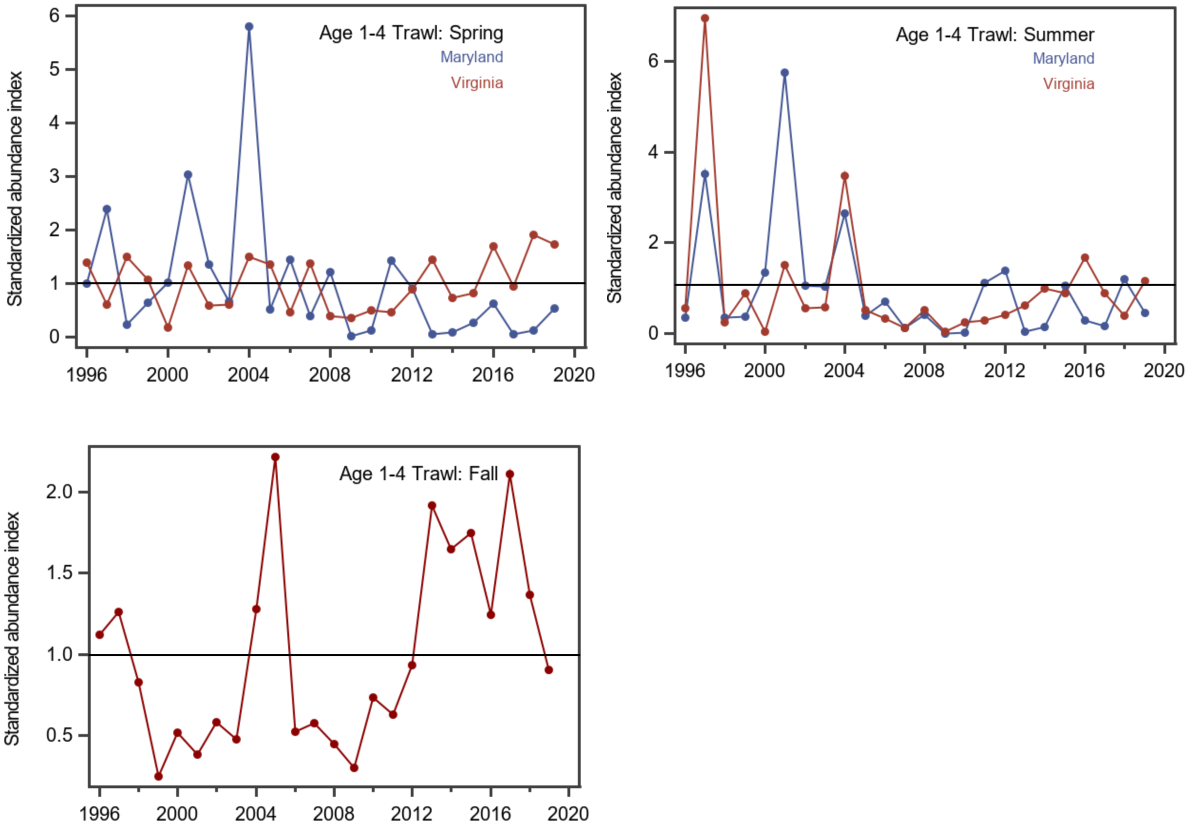


Figure 19. Standardized index of relative abundance by season for age-1-4 (resident sub-adult) striped bass in the mainstem of the Bay (green). Seasonal relative abundance was estimated as mean catch per unit effort (CPUE) calculated as the number of fish divided by area swept by the trawl (number/km^2). CPUE was standardized by season to a mean of 1.0 across 17 years (2002-2018) in the ChesMMAP (CMP) model, denoted by the solid horizontal line. Note that standardized abundances do not reflect absolute abundance in a given year. ‘Spring’ corresponds to March-June and ‘Summer’ corresponds to July-October, but ‘Fall’ only represents the month of November given this survey’s sampling regime. Note that spring 2003 was removed from the index of abundance due to equipment failures during the May 2003 cruise.

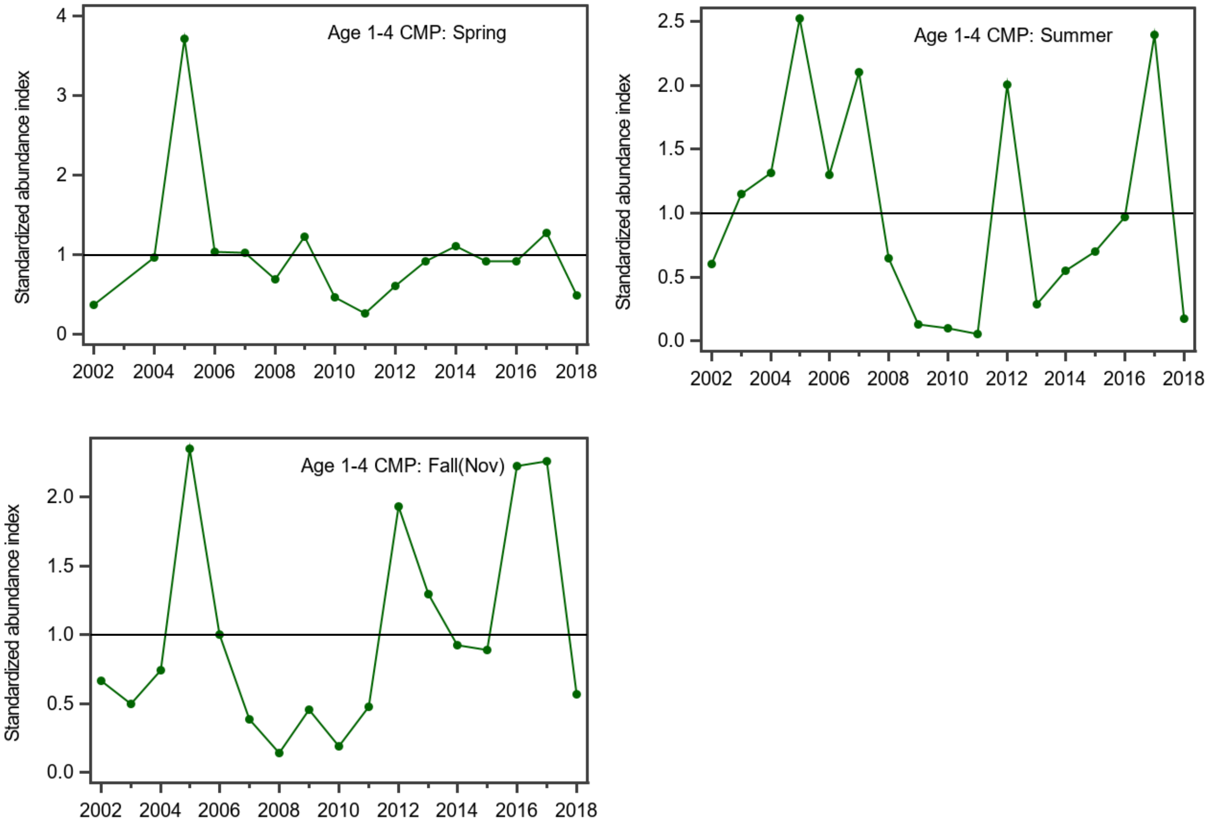
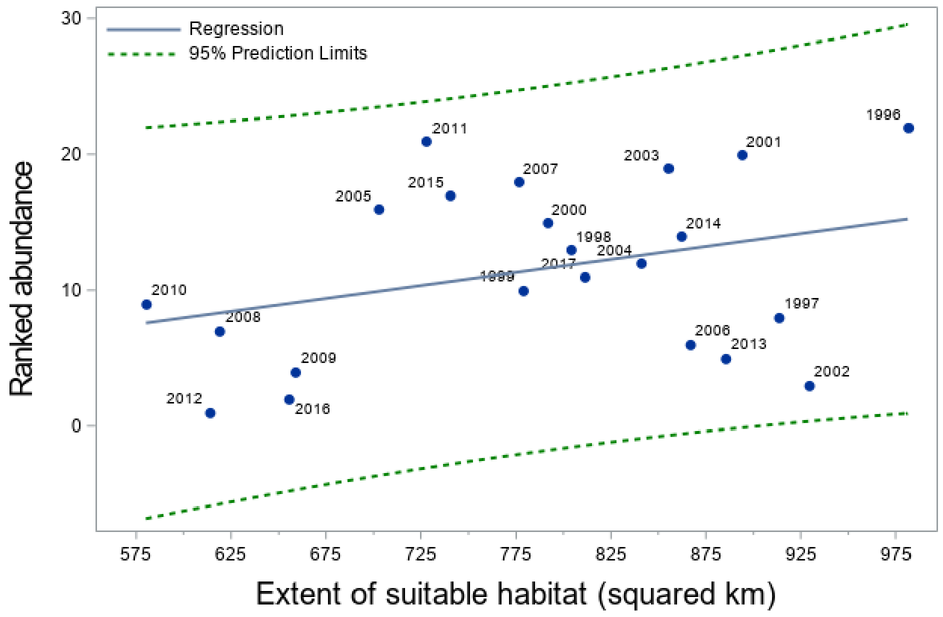


Figure 20. Nonparametric relationship between ranked abundance of age-0 striped bass in the seine surveys and extent of suitable shoreline (up to 2 m depth) habitat (km^2) in Chesapeake Bay in (A) early summer, and (B) late summer, 1996-2017. Observations (years) are depicted by blue circles; the solid line is the nonparametric regression fit to the observations, and the dashed line is the 95% prediction limit. Values of HSI $\geq$ 0.5 were considered suitable habitat. This relationship was not significant at $p<0.05$ in either season.

(A)



(B)

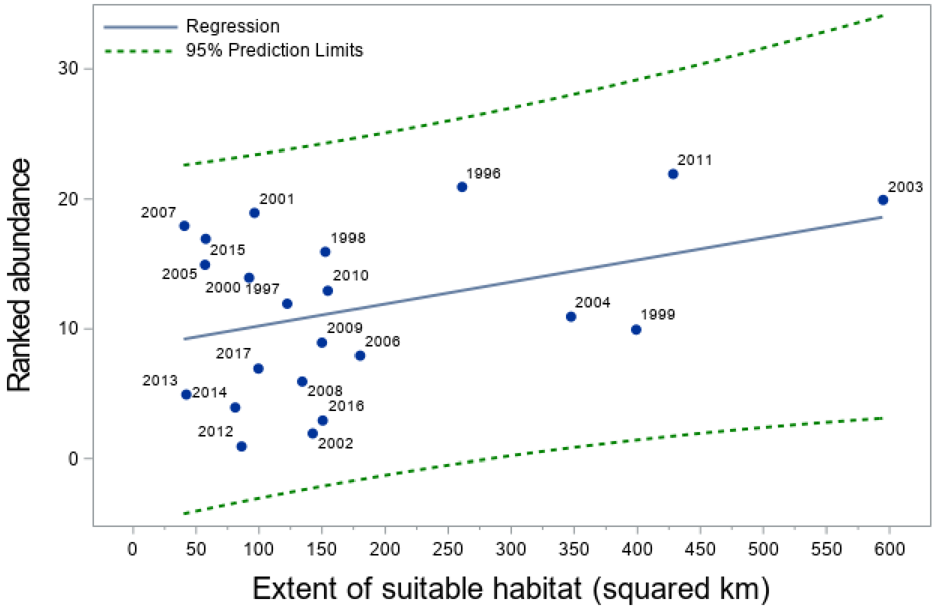
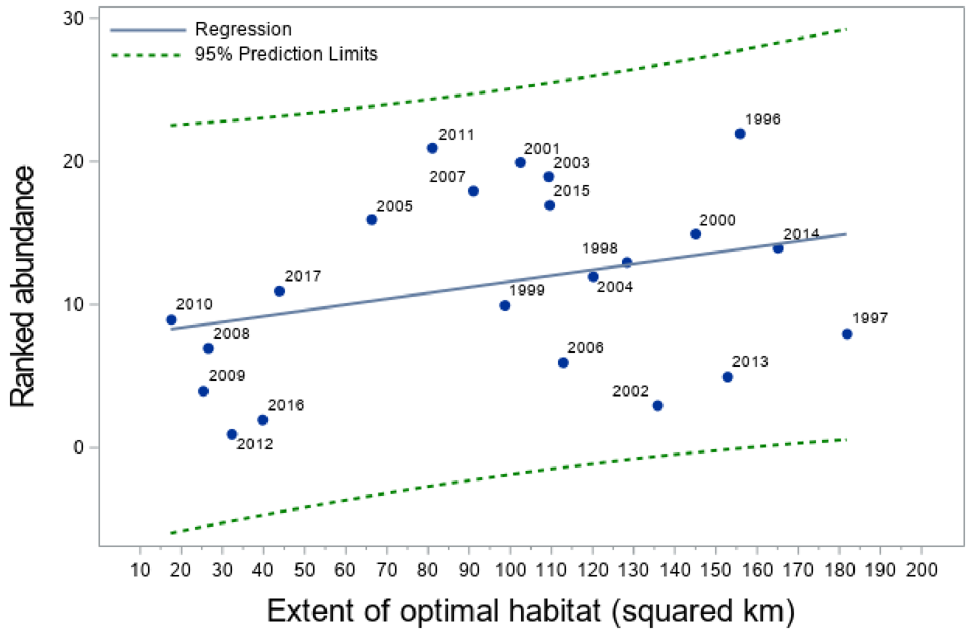


Figure 21. Nonparametric relationship between ranked abundance of age-0 striped bass in the seine surveys and extent of optimal shoreline (up to 2 m depth) habitat (km^2) in Chesapeake Bay in (A) early summer, and (B) late summer, 1996-2017. Observations (years) are depicted by blue circles; the solid line is the nonparametric regression fit to the observations, and the dashed line is the 95% prediction limit. Values of HSI $\geq$ 0.7 were considered optimal habitat. We detected a significant linear relationship between extent of optimal (HSI>0.7) habitats and ranked abundance in late summer (B; F=5.51, p=0.03).

(A)



(B)

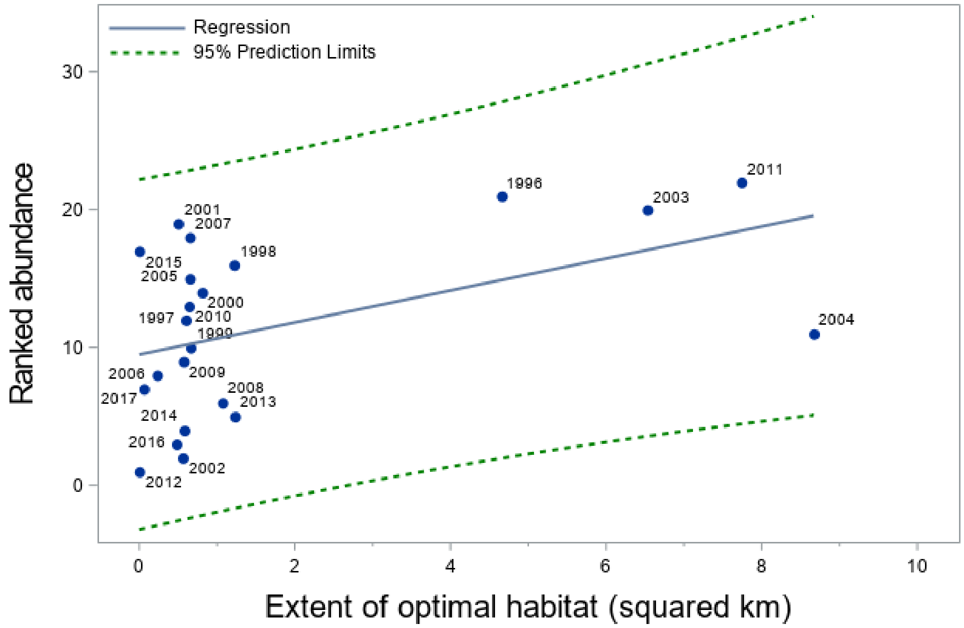


Figure 22. Nonparametric relationship between ranked abundance of age-0 striped bass in the trawl surveys and extent of suitable habitat (km^2) in Chesapeake Bay in (A) early summer and (B) late summer; and ranked abundance of age-0 striped bass in the VIMS trawl survey and extent of suitable habitat (km^2) in Virginia waters in (C) fall/winter and (D) spring, 1996-2019. Observations (years) are depicted by blue circles; the solid line is the nonparametric regression fit to the observations, and the dashed line is the 95% prediction limit. Values of HSI $\geq$ 0.5 were considered suitable habitat.

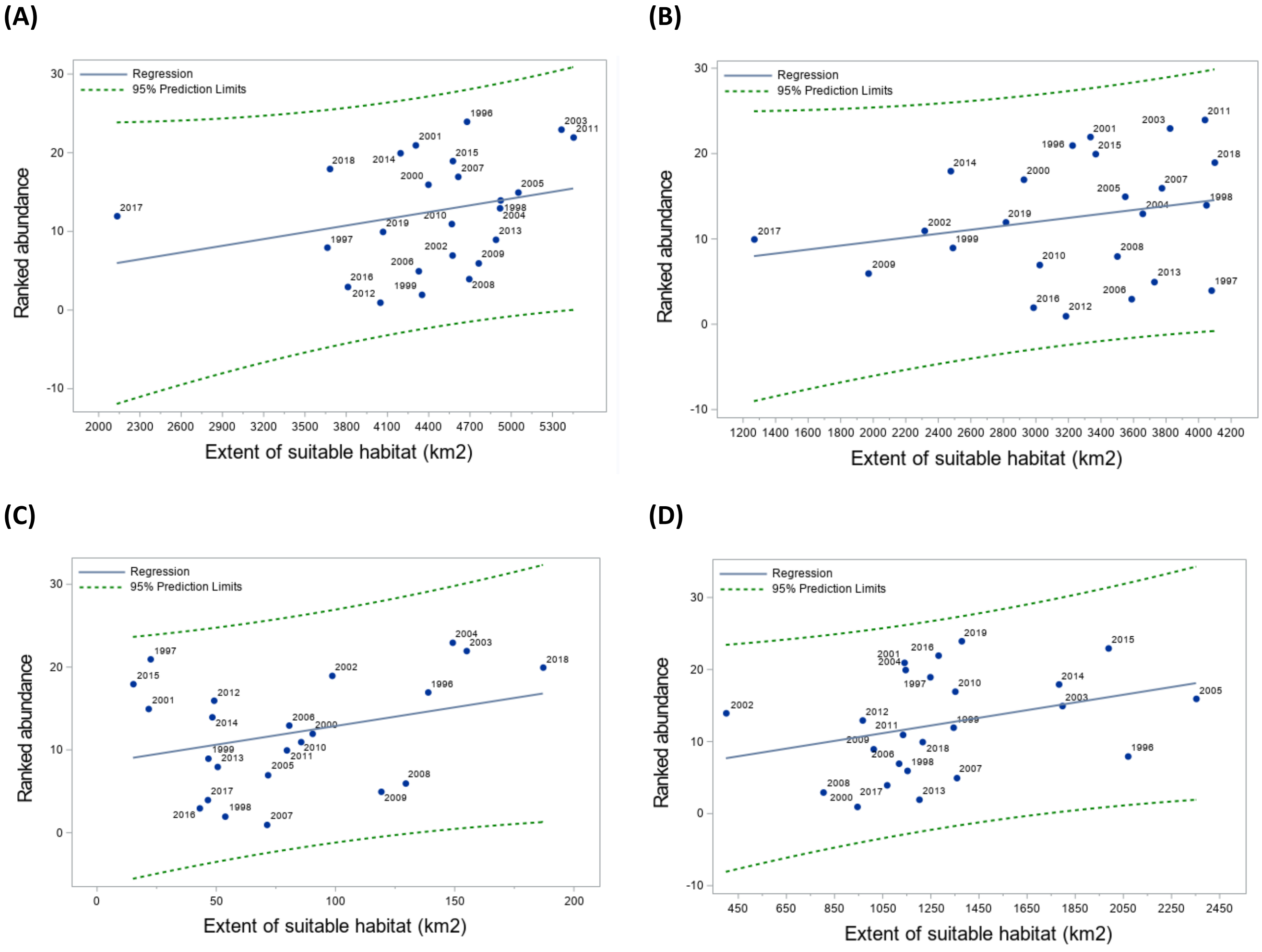


Figure 23. Nonparametric relationship between ranked abundance of age 1-4 striped bass in the trawl surveys and extent of suitable habitat (km^2) in Chesapeake Bay in (A) spring and (B) summer, 1996-2019. Observations (years) are depicted by blue circles; the solid line is the nonparametric regression fit to the observations, and the dashed line is the 95% prediction limit. Values of HSI $\geq$ 0.5 were considered suitable habitat.

(A)