ABSTRACT

Title of Thesis:	SPATIAL ANALYSIS OF SPOT (*LEIOSTOMUS XANTHURUS*) POPULATION DYNAMICS
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Spot (*Leiostomus xanthurus*) is a forage fish that supports important commercial and recreational fisheries along the U.S. Atlantic coast. Assessment approaches to estimate abundance and mortality of spot for management on the U.S. Atlantic coast have previously not passed peer review. Our objectives were to (1) estimate spatial differences in biomass and mortality rates over time using fisheries-dependent indices and total mortality rates, and 2) estimate Spot abundance and fishing mortality rates in the Chesapeake Bay and the Atlantic coast using spatial population models. We calculated indices of biomass using commercial trip level data from gillnet fisheries and estimated total mortality rates using the Chapman-Robson approach with ageing data from fishery independent and dependent monitoring programs from Maryland to South Carolina. Dynamic factor analysis (DFA) was used to test for spatial differences in trends in biomass and mortality. We developed a two-region statistical catch-at-age model using the Template Model Builder package in R to distinguish the portion of the population along the Atlantic coast (New Jersey to Florida) from the portion in the Chesapeake Bay. We modeled ages 0-3+ for 2002-2019 with age-specific occupancy probabilities for each region. The data inputs for our model included multiple survey indices, commercial and recreational catch, shrimp trawl bycatch, and age composition of each data source. We implemented two models: one where fishing mortality varied between regions (SVM) and another where occupancy probabilities varied over time (TVO). Indices of biomass varied widely across space and time. Spot appeared to have high total annual mortality rates (>80% per year) that have increased in recent years. DFA indicated that stock biomass and mortality rates appeared to follow similar trends across regions. The TVO model was a better fit to the data and produced more biologically plausible estimates than the SVM model. In the TVO model, spot abundance was similar in both regions and has increased since 2015, which was a very poor year class. Patterns in fishing mortality differed between fleets with the commercial fishery declining substantially over time. The results from this work will aid in the development of an upcoming stock assessment for spot to inform management.

SPATIAL ANALYSIS OF SPOT (*LEIOSTOMUS XANTHURUS*) POPULATION DYNAMICS

by
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Table of Contents

List of Tables

List of Figures

Chapter 1: Spatial Trends in Mortality and Biomass for Spot (*Leiostomus xanthurus*)

Introduction

Stock assessments often assume that fish stocks are uniformly distributed and experience the same levels of mortality rates across their entire range, despite evidence of spatial variability (Goethel et al., 2011; Berger et al., 2012; Berger et al., 2017). In reality, this dynamic pool assumption ignores inconsistencies between the spatial structure of a population and the spatial scale over which management is conducted, which can lead to biased management (Kerr et al., 2016). Patterns of fishing mortality area usually not spatially uniform due to fisher choices of fishing locations (e.g., Saul et al., 2020). Additionally, management that is not spatially explicit is more likely to mischaracterize the scale of fish productivity, which may not maximize full utilization of the resource (Kerr et al., 2016). Therefore, understanding the spatiotemporal scale of population structure is important for effective and sustainable fisheries management (Goethel et al., 2011).

The ecosystems of the Mid-Atlantic Bight are highly productive and dynamic, affected by changing estuarine flows, seasonal upwelling, and rapid changes in temperature, salinity, and dissolved oxygen (Farr et al., 2021). Many species that use the Mid-Atlantic Bight exhibit seasonal movements into estuaries. Given the everchanging nature of these disturbances and the role of seasonal migrations in this area, it is important to study spatial patterns that drive population dynamics in this region. Spatial differences in population dynamics are the result of individual-level differences in the ability to adapt to biotic and abiotic conditions that may affect population-level dispersal (Berger et al., 2012). For exploited species, understanding the spatial structure of a population is important because changes in distribution may affect a population's susceptibility to harvest (Berger et al., 2017). Furthermore, understanding localized patterns of fish distribution may explain how populations will respond to environmental change.

Spot (*Leiostomus xanthurus*) is a demersal sciaenid that is distributed along the U.S. Atlantic coast from the Gulf of Maine to the Gulf of Mexico. They are short lived, rapid growers that are early to mature (ASMFC, 2017; Piner & Jones, 2004). They reach a maximum age of six with few fish living older than age two (ASMFC, 2017). Spot undergo seasonal migrations where adults move offshore to spawn in the fall. Larvae are thought to be mostly passively transported into estuaries (Warlen & Chester, 1985; Weinstein & Walters, 1981; Powell and Gordy, 1990). As spot grow and become juveniles, they move into deeper waters of higher salinities (Weinstein, 1984; Weinstein & Walters, 1981; Odell et al., 2017). Spot is managed by the Atlantic States Marine Fisheries Commission (ASMFC), and the fishery primarily operates in state waters from New Jersey to Florida. Spot are primarily targeted by commercial and recreational anglers in south Atlantic waters of the US during the fall months when schools of spot migrate from estuaries into offshore waters (Pacheco, 1962). Historically, harvest was split evenly between the commercial and recreational sectors. However, since 2005 this fishery has been predominantly recreational (ASMFC, 2014). Spot is one of the most frequently caught recreational species in the

U.S. (NOAA, 2022). The seasonal movements exhibited by spot in combination with differences in regional exploitation by fisheries suggest that spatiotemporal methods may be necessary to better understand their population dynamics.

Spot is managed using a data-limited approach because there is not a stock assessment that has been accepted for use in management. The first coastwide benchmark stock assessment for spot was conducted in 2017 by ASMFC, but it did not pass peer review due to conflicting information on population trends (Able et al., 2017). Without a stock assessment to guide the management of Spot, ASMFC adopted a Traffic Light Approach (TLA) in 2014 to monitor the spot population and provide management advice. The TLA calculates the status of commercial and recreational harvest and survey indices of abundance relative to reference levels. For each year, a color (red, yellow, or green) is assigned based on the status. If the proportion of "red" increases above a threshold level, management action is triggered (ASMFC, 2014). At present, indices based on commercial catch-per-unit-effort (CPUE) data are not available for use in the TLA. However, CPUE would be a better indicator of population size because catch alone can fluctuate for many reasons other than population size (Pauly et al., 2013) which would influence TLA status. The TLA has been used to guide spot management since 2014, but stock status remains unknown.

In recent years, the use of data-limited approaches for fisheries management has advanced. For example, with sufficient age composition data, one can use methods such as catch curves to accurately detect changes in mortality rates without needing to estimate catch-at-age (Nelson, 2019). These age-based data-limited approaches can further improve our interpretation of population dynamics without a full stock assessment.

Dynamic factor analysis (DFA) has been increasingly used in fisheries to identify common trends from multiple time series (Peterson et al., 2021a; Peterson et al., 2021b). DFA is a state-space dimension reduction technique used to estimate common trends in a set of time series that are stochastic and contain missing data (Zuur et al., 2003a&b). DFA can also quantify observation error (Peterson et al. 2021a; Peterson et al. 2021b). However, DFA sensitivity to the start and end year of individual time series is poorly understood. The ramifications of incorrectly choosing model years can produce biased estimates that mischaracterize the aggregate population trend. The common trend recommended by DFA may vary substantially with different combinations of years for data sets with short time series.

The goal of our study was to estimate trends in mortality and relative biomass over time for spot from New Jersey to Florida (Figure 1.1) to determine whether the trends differed spatially. We were especially interested in whether trends differed between the Chesapeake Bay and the rest of the U.S. Atlantic coast. Our objectives were to 1) estimate total instantaneous mortality rates; 2) develop standardized indices of biomass using commercial fisheries data; 3) determine whether trends in mortality or biomass varied spatially over time; 4) estimate effects of potential environmental drivers on mortality and biomass trends; and 5) test the sensitivity of DFA trend estimates to different ranges of years for the input data sets.

Methods

Age Data

Ageing data for spot were available from Maryland to South Carolina. Each dataset corresponded to a fishery-independent or fishery-dependent monitoring program that collected biological information. All spot were aged using otoliths, and six data sets had sufficient age information to support the estimation of mortality rates over time (Table 1.1). Ageing workshops have been conducted for other sciaenid species (Atlantic Croaker and Red Drum) to develop ageing protocols. Because these species were straightforward to age, the same protocols also work well for spot (ASMFC, 2008; ASMFC, 2017). Mortality rates were calculated for all years in which ageing data were available.

Commercial fishery age composition data were available from Virginia, North Carolina, and Maryland. The Virginia Marine Resources Commission (VMRC) randomly sampled commercial spot from fish houses and docks in the Chesapeake Bay and coastal Virginia during 1998-2021 using a length-stratified random sampling design (Liao et al., 2022). The majority of VMRC samples came from gill nets (38%), pound nets (36%), and haul seines (25%). The North Carolina Department of Marine Fisheries (NC DMF) sampled spot from fish houses for ageing beginning in the late 1970s. Gear was not known for 86% of aged fish from commercial fisheries, but the remaining NC DMF samples came from ocean and estuarine gill nets, long haul seines, pound nets, or winter trawls. NC DMF subsampled 30 fish per market grade, which were measured and aged (ASMFC, 2017). The Maryland Department of Natural Resources (MD DNR) sampled spot from the commercial pound net fishery in the Chesapeake Bay (ASMFC, 2017). Sampling has been conducted in Maryland since 1993, but fish were aged starting in 2012.

Fishery-independent data sources included the Northeast Area Monitoring & Assessment Program (NEAMAP) survey, the Chesapeake Bay Multispecies Monitoring and Assessment Program survey (ChesMMAP), the South Carolina Trammel net survey, the North Carolina gillnet survey, and the North Carolina Pamlico Sound trawl survey. All surveys follow a stratified random sampling design. NEAMAP is a bottom trawl survey of the mid-Atlantic Bight in near shore waters to a depth of 60 feet that has been conducted since 2007 to maintain coverage of shallow strata following a change in the Northeast Fishery Science Center bottom trawl survey (Latour et al., 2021). Individuals selected for ageing in NEAMAP were sampled using a length-stratified random sampling approach (ASMFC, 2017). ChesMMAP is a bottom trawl survey that began in 2002 and samples up to 80 stations across the Chesapeake Bay every March, June, September, and November. Spot were collected in ChesMMAP for ageing using a length-stratified random sampling design (Bonzek et al., 2022). The South Carolina trammel net survey has been conducted since 1991 to monitor important recreational finfish species in seven estuaries (McDonough et al., 2011). The North Carolina gillnet survey has been conducted since 2001, and the Pamlico Sound trawl survey began in 1987 (ASMFC, 2017; Bangley et al., 2018). For both North Carolina surveys, spot were aged during 1992-2022.

To account for the stratified sampling of age data, we calculated the numbers-at-age by multiplying a vector of the number of fish in each length bin by a year and data source-specific age-length key, which represented the proportion of fish of a given length that were a specific age,

$$\begin{bmatrix} N_{a=0} \\ N_{a=1} \\ N_{a=2} \\ N_{a=3+} \end{bmatrix} = \begin{bmatrix} P_{a=0,L=13-} & P_{a=0,L=14} & \cdots & P_{a=0,L=31+} \\ P_{a=1,L=13-} & P_{a=01L=14} & \cdots & P_{a=1,L=31+} \\ P_{a=2,L=13-} & P_{a=2,L=14} & \cdots & P_{a=2,L=31+} \\ P_{a=3+,L=13-} & P_{a=3+,L=14} & \cdots & P_{a=3+,L=31+} \end{bmatrix} \times \begin{bmatrix} N_{L=13} \\ N_{L=14} \\ \vdots \\ N_{L=31+} \end{bmatrix},$$

where N_a was the number of fish of age a, P was the proportion of fish age a within each length bin, L, and N_L was the number of fish in a given length bin. Lengths were condensed into 1 cm length bins from a minimum bin of 13- cm (spot <14 cm) to a maximum bin of 31+ cm (spot ≥ 31 cm) groups, which were determined based on length bins that represented 1-2% of the cumulative length distribution. Because many more fish were measured than aged, the numbers-at-age for each data source were also rescaled using the number of fish aged.

Commercial Catch-per-Unit-Effort (CPUE) Data

Daily catch reports for spot were obtained from the Atlantic Coastal Cooperative Statistics Program (ACCSP) for all coastal Atlantic states from New Jersey to Florida during 1982-2022. Fishing trips that originated in Maryland or Virginia were further subdivided into trips that occurred within the Chesapeake Bay or the Atlantic Ocean. Catch was recorded in live pounds, and fishing gear was also reported. We used trip as our main unit of effort.

Mortality Rate Estimation

Total instantaneous mortality rates were estimated using the Chapman-Robson method (Chapman and Robson, 1960). The Chapman-Robson approach is one of the most accurate approaches to estimate total instantaneous mortality rates (Z) from catch-at-age data (Millar, 2015; Nelson, 2019). This approach is commonly applied to data-limited fisheries because it estimates the mortality rate of a fish population using only age composition data, assuming constant recruitment and mortality over time.

Based on the peak age of spot in our data, we assumed that the age of full selection was age-1. The Chapman-Robson approach calculates a statistic, X, as the sum of the product of the age past the first age at full selection (a_r) and sample size at age a (n_a),

$$X = \Sigma(a - a_r) \times n_a.$$

The annual survival rate (S) was estimated using the maximum likelihood estimator (Chapman and Robson, 1960),

$$S = \frac{X}{(X + n - 1)},$$

where n was the total sample size (over ages). The total instantaneous mortality rate (Z) was calculated as the negative of the natural logarithm of the annual survival rate (Ricker, 1975),

$$Z = -\ln(S).$$

The annual mortality rate (A) was calculated as 1 minus the survival rate (Ricker, 1975),

$$A = 1 - S.$$

The annual survival, total instantaneous mortality, and annual mortality rates were estimated for each year and each data set for which age data were available. The variance of the estimated survival rates ($var(\hat{S})$) were calculated using the formula provided in Chapman and Robson (1960),

$$var(\hat{S}) = \frac{S \times (S - (\Sigma(X) - 1))}{n + \Sigma(X) - 2}.$$

The Chapman-Robson method assumes that recruitment has been constant, vulnerability to gear remains constant over time and ages, mortality is constant over time and ages, and there is no net immigration or emigration (Chapman and Robson, 1960; Dunn et al., 2002). Additionally, it assumes that ages are accurate. Our approach estimates “apparent” mortality rates because we did not include corrections for migration or selectivity of the gear. All analyses were conducted in R Statistical Software (v4.2.2; R Core Team 2022).

Commercial CPUE Index Standardization

We developed standardized indices of biomass from commercial gillnet catch records for each state using generalized linear models (GLMs; Maunder & Punt 2004). We only used gillnet trips because they represented the majority (70%) of spot commercial fishing trips. The states included New Jersey, Maryland, Delaware, Virginia, North Carolina, and Florida. Fishing trips in Maryland and Virginia were separated into those within the Chesapeake Bay or those in the Atlantic Ocean. Catch data from Delaware and New Jersey were combined into one GLM to minimize the number of years in which data would not be able to be shown due to confidentiality issues. In preparation for standardization, data with zero catch (0.05%) were removed. Our GLMs were conducted separately for each state to allow for differences in variances, and they described the natural logarithm of catch-per-unit-effort (CPUE) as a function of categorical effects for year and month,

$$\log(CPUE) = Intercept + Year_y + Month_m + \varepsilon,$$

where ε was a normally distributed error. The states did not require reporting of effort in a consistent manner. Therefore, we used catch-per-trip as our CPUE metric. Residual diagnostics and leverage were examined to determine if model assumptions were met.

Dynamic Factor Analysis

We applied DFA separately to the time series of mortality rates and the indices of biomass to identify common trends among data sets. DFA models assume that time series are normally distributed with a homogenous variance. Therefore, prior to conducting DFA, the time series were detrended and transformed to be approximately normally distributed. We applied the approach of Peterson et al., (2021a) that allows for back transformation of trends from log-space. The standardization approach was as follows:

1. Multiply each index by a constant that is iteratively determined to meet criteria, where:
    a. The mean of each survey must be >0,
    b. The global standard deviation (GSD) should be 0<GSD<1
    c. The standard deviation of each transformed index should be approximately 1, and
    d. The back-transformed trend should preserve the relative trend of the input surveys;
2. Log transform indices;
3. Center and demean the log transformed indices;
4. Estimate the global standard deviation;

5. Divide each index by the global standard deviation;
6. Fit the DFA model; and
7. Back transform the trend predicted by DFA.

The DFA model was fitted with one or two common trends to the mortality estimates and indices of biomass time series. One and two common trend models were compared using the Akaike Information Criterion corrected for small sample size (AICc). Confidence intervals about the trends were calculated, and the time series were back-transformed out of $\log_e$ space (Peterson et al. 2021a). The DFA models were fitted using the MARSS R package (v3.11.8; Holmes et al., 2023).

The DFA models selected by AICc were rerun with environmental covariates to estimate environmental effects on trends in biomass and mortality. The last year (2022) was dropped from the model due to missing environmental covariate data. The environmental covariates included Atlantic Multidecadal Oscillation index (AMO), North Atlantic Oscillation index (NAO), Gulf stream Index (GSI), and regional bottom temperatures indices for the Northeast and Chesapeake Bay. The AMO, NAO, and GSI indices were obtained from the ecodata package in R (v3.11.8, Bastille and Hardison 2018). Chesapeake Bay temperatures were obtained online from the Chesapeake Bay Program DataHub (Chesapeake Bay Program, 2023). Temperatures from the Northeast came from the Northeast Fisheries Science Center Bottom trawl during 2000—2006 and from the NorthEast Area Monitoring and Assessment Program (NEAMAP) program during 2007—2021. Because the DFA model required that covariates not contain missing data, temperatures for the South Atlantic were excluded due to COVID-19 sampling disruptions during 2020.

We also conducted sensitivity analyses to determine the effect of the combination of years included on the estimated trends. We chose to run eight models with different 10-year time periods, and six longer models that altered the starting and ending years. The sensitivity analyses were conducted using the mortality time series, and models were run with both one and two common trends. Models with one and two common trends were compared using AICc for each sensitivity analysis.

Results

Mortality Rates

Estimated apparent total instantaneous mortality rates for spot averaged 2.26 per year (83% annual mortality; Figure 1.2). The estimated rates were highest in Maryland (Z=3.92 per year) and lowest in North Carolina (Z=1.32 per year), on average. Interannual variability in apparent mortality was relatively low, and patterns among time series were relatively coherent with a generally increasing trend in total mortality from 2015 onwards (Figure 1.2).

The DFA model with two common trends had a slightly lower AICc (1.8 AICc units) than the single trend model for the estimated mortality rates (Table 1.2). The first DFA common trend had more data sources that loaded strongly and positively on it than the second common trend (Table 1.3). The back-transformed first common trend estimated high mortality in the early 2000s that decreased around 2005 and increased again from 2015 onwards (Figure 1.3). The data sources with the highest factor loadings for the first trend included the NEAMAP survey (0.50) and the Virginia fisheries dependent samples (0.63; Table 1.3; Figure 1.4). Factor loadings that approach 1 indicate a closer match to the common trend. The South Carolina Trammel net survey had negative factor loadings for the first trend which indicated an inverse relationship to the common trend (Table 1.3). The back-transformed second common trend indicated initial low levels of mortality in the early 2000s, but an increase in mortality after 2008. Factor loadings for the second trend were highest for the North Carolina Gillnet survey (0.51) and ChesMMAP (0.47; Table 1.3; Figure 1.4). The DFA model with one common trend for mortality rates (Figure 1.5) also tracked individual time series relatively well with loadings between -0.33 and 0.71, and four data sources with loadings exceeding 0.5 (Table 1.3). The back-transformed one-trend model started with high mortality rates that decreased through the early 2000s and increased again in the late 2010s (Figure 1.6).

Commercial CPUE Indices

Estimated biomass indices showed large year-to-year and among state variation (Figure 1.7). The GLM diagnostics did not indicate violations of assumptions for any of the data sets. Despite high variability, indices of biomass may have increased over time in the northern states of New Jersey and Delaware. Biomass indices in both Maryland regions showed a declining trend over time. In Virginia and North Carolina, indices of biomass varied without substantial trends. The index of biomass in Florida was comparatively low for most of the time series but slightly increased in recent years.

For indices of biomass, the DFA model with one common trend had a lower AICc (0.7 AICc units; Table 1.2). The one trend model tracked the individual biomass indices for each state relatively well, according to factor loading values

(Figure 1.8; Table 1.4). Five of the states had positive factor loadings between 0.55 and 0.70 (Table 1.4). However, the Chesapeake Bay portion of Maryland had the weakest factor loading (0.09) and Florida had a negative loading (-0.43). The back-transformed one-trend model showed periods of high biomass in the early 2000s and increasing biomass after a low in 2016 (Figure 1.9). For the DFA model with two common trends, the first trend had slightly higher loading values (four states exceeded a loading of 0.55) than the second trend (all trends had loadings below 0.22; Figure 1.10; Table 1.4). The first back-transformed trend estimated a decline in biomass through the 2000s whereas the second trend estimated an increase in biomass through the 2000s (Figure 1.11).

Dynamic Factor Analysis with Environmental Covariates

None of the environmental covariates improved the models for mortality or biomass according to AICc (Table 1.5). The models with environmental covariates had larger AICc values, with differences ranging from 11-160 AICc units. The environmental covariates also did not help explain the trends in the indices of biomass over time; they all had larger AICc values, with differences ranging from 27-103 AICc units.

Dynamic Factor Analysis Sensitivity Testing

Most of the sensitivity tests for mortality with different ranges of years resulted in a single trend model having the lowest AICc (Table 1.6). For runs with a ten-year time series that also contained many years of missing data (2005-2015, 2006-2016, and 2007-2017), a one trend model consistently had the lowest AICc. For the ten-year time series that had more data available and fewer missing years (2008-2018, 2009-2019, 2010-2020, 2011-2021, 2012-2022), the preferred model varied. Modifying the start or end year by 1-2 years usually resulted in the one trend having the lowest AICc.

Discussion

Our analyses did not detect clear spatial patterns in spot apparent mortality and biomass. If strong spatial patterns existed, we would expect the DFA model to identify trends in biomass and mortality that differed in a consistent and spatially coherent manner. This may be apparent through similar factor loading values for data sources that are near one another. Even though a two-trend DFA had a lower AICc value, several of our time series that sampled in close proximity did not seem to follow similar trends. This was evident in our three North Carolina mortality time series which sampled overlapping areas but had factor loadings that differed among the trends. Furthermore, because the difference in AICc between the one and two trend models was small, and our sensitivity analyses showed that one trend was usually preferred, regional differences were likely minor. Previous studies have found that spot do not exhibit evidence of site fidelity in the lower Delaware Bay (Torre et al., 2017), which may extend to other similar estuaries such as the Chesapeake Bay and explain the lack of consistent spatial patterns in mortality and biomass.

Fishery-independent abundance indices for spot have been reported to be increasing in the late 2000s and 2010s, whereas commercial and recreational harvest have been declining (NC DMF, 2024, Able et al., 2017). A sharp decline in spot commercial catch was presented in the most recent TLA, with the harvest indicator exceeding the lower threshold and triggering management action (ASMFC, 2022). This may agree with the results from our DFA model that showed an increase in total instantaneous mortality rate since 2015. Past work has documented that the relative abundance of spot in Maryland coastal bays showed significant declines from the 1970s to the early-mid 2000s, with the suggestion that the Maryland coastal bays reflect coastwide population trends (Pincin et al, 2014). Furthermore, spot abundance from the ChesMMAP survey declined during 2009-2015 with increases in recent years (post 2015) of primarily small, young fish (Ralph et al., 2022). Schonfeld et al. (2022) found that spot showed a decreasing usage of the Chesapeake Bay relative to the coastal ocean during 2012-2019. ChesMMAP and NEAMAP were used in our study and in Schonfeld et al. (2022), but our analyses made different assumptions about causes of changes over time. Specifically, changes in the age structure resulted in changes in apparent mortality rates over time in our study, whereas changes in CPUE were assumed to be due to changes in movement in Schonfeld et al. (2022). Spot may not be returning to the Chesapeake Bay in as large numbers during their seasonal migration, but it is unclear what is driving this preference (Schonfeld et al., 2022). The high mortality rates we estimated in the Chesapeake Bay may reflect ontogenetic changes in habitat usage and movement instead of changes in mortality. Our estimates of apparent mortality rate for the ChesMMAP data appeared to increase, but when considered in the context of spot migration, it may reflect a change in preference for the Chesapeake Bay as habitat, reflecting changes in movement patterns with age.

We did not identify significant effects of environmental covariates on trends in biomass or mortality. However, it is likely that environmental conditions affect the spot population. Other sciaenids have demonstrated significant trends and associations with environmental covariates (Matthews et al., 2022). Warlen and Chester (1985) found that spot spawn in relatively warm winter waters (17.5-25 C), so as coastal waters warm, spot recruitment output may increase. Winter temperature may also have consequences for the timing and locations of migration and estuarine ingress (Allen et al., 2024). Atlantic croaker (*Micropogonias undulatus*) is closely related to spot and it is encountered in similar fisheries. Atlantic croaker has been documented to have weaker year classes when exposed to colder temperatures that alter feeding preferences (Lankford and Targett, 2001). Additionally, Hare et al. (2010) estimated that when winter temperatures increased, abundance, recruitment, and maximum sustainable yield increased, and their population shifted northward. As a species that prefers warmer waters (Love and May ,2007), spot from the Chesapeake Bay have been documented to be positively associated with increased temperature and salinity (Schaffler et al., 2013; Odell et al., 2017). The potential for spot abundance to increase as waters warm may also be reflected in our results that show an increasing trend in biomass for our New Jersey/Delaware index, and may also explain why the aggregate DFA shows an increasing trend in biomass since 2015. This indicates that they may undergo a northern shift as waters along the coast warm.

Based on our DFA common trends, total instantaneous mortality rate and biomass were both increasing for spot in recent years. In order for this scenario to be true, certain conditions have to be met. For example, recruitment would have to be strong or increasing in order for the population to grow despite increasing mortality rates. This may happen during times when environmental conditions are favorable enough to support high pre-recruit survival, or when spawning biomass is high. This scenario may also be possible if fishery selectivity only targets a portion of the population. As a result, the unexploited portion of the population may have sufficient reproductive potential to allow for strong recruitment. However, this scenario of increasing biomass and mortality may be unreasonable for our analysis due to the assumptions of the Chapman-Robson method. A key assumption of this method is constant recruitment over time. If this were true, it is unlikely that both biomass and mortality could be increasing at the same time. Similarly, the Chapman-Robson method assumes that vulnerability to fishing is constant over time, which would also prevent time-varying selectivity from explaining why both biomass and mortality may be increasing over time.

A main assumption of the Chapman-Robson method is that the population is closed and in equilibrium, but these assumptions, particularly that of a closed population, are possibly violated by our analysis. Spot migrate seasonally, with typically large numbers of younger (postlarvae) spot using lower salinity habitats in the upper reaches of estuaries (Weinstein, 1979; Odell et al., 2017). Age-specific habitat usage likely explains why apparent mortality rates were so high in the Maryland pound net fishery because older fish (>2) were not returning to the Maryland portion of the Chesapeake Bay. The Chapman-Robson estimator also assumes that we have correctly chosen the age at which fish are fully vulnerable to the gear (Chapman and Robson, 1960). We assumed age-1 and older were fully selected, which was also suggested by a study that analyzed spot growth from samples that came from the same commercial fisheries we used (Piner and Jones, 2007). Finally, some of our mortality sources are mixed gear (NC and VA Dependent) which means that selectivity and catchability may not be consistent if the proportion caught in each gear changed over time. However, Nelson (2019) tested cluster sampling bias on the performance of various Z estimators and found the Chapman-Robson estimator to be the least-biased method under a wide range of simulation scenarios. A study by Smith et al. (2012) demonstrated that the Chapman-Robson Z estimate is negatively biased and performs better when a bias correction is applied to the transformation of survival rates to Z. This bias tends to increase with higher Z values, but bias was reduced when sample size was small (N=200). Although we did not apply bias correction, our Z estimates did not have a substantial trend over time and were consistently high which may indicate that including bias correction may improve our estimates. Even though our sample sizes were highly variable for years and data sources, they were usually small (N<200) indicating that this method may perform adequately without the bias correction. Despite the fact that some of our data sources may violate some of the assumptions of the Chapman-Robson method, this analysis still provides useful information about how trends in mortality have changed over time.

Fishery-independent data are typically preferred over fishery-dependent data when constructing indices of abundance because they use standardized methods to survey a fish population (Harley et al., 2001). The main problem, as outlined by

Wilberg et al. (2010), is that changes in management regulations, fishing behavior, and technological advancements may cause catchability to change over time which violates the assumption that CPUE is proportional to population size. Fishery-dependent indices can be problematic because they are likely to have time-varying catchability which may produce estimates that depict high or stable CPUE even though biomass is declining (i.e., hyperstability; Hilborn and Walters, 1992). Hyperstability is caused by non-random fishing, for example, the targeting of fish aggregations (Erisman et al., 2011). We used fishery-dependent data to develop indices of biomass because fishery-dependent data on spot were widely available for the U.S. coast from New Jersey to Florida. Additionally, the previous stock assessment showed conflicting signals between catch and indices (ASMFC, 2022) that we wished to explore. We chose to build indices only using catch data from the gillnet fishery so that catchability would be consistent. However, the restriction of our analysis to gillnet CPUE is a potential limitation because our index may not be tracking certain states well. In the Maryland portion of the Chesapeake Bay, gillnets are largely restricted, and pound nets are the dominant gear used in this fishery. Furthermore, gill nets are banned in state waters of Florida so the CPUE data we used from that state were from federal waters only. While these inconsistencies may weaken confidence in our indices of biomass, for a data-limited species, fishery-dependent indices are valuable, and in some cases, the only way, to assess the population (Kleisner et al., 2012). In the case of spot, fishery-dependent indices were recommended by the peer reviewers of the 2017 stock assessment as a way to resolve interpretation of the commercial and recreational catch time series in the context of increasing indices of biomass (Able et al., 2017). While catch has declined over time, the common trend of biomass estimated by CPUE showed more fluctuation through time and increased after a low in 2016. This might indicate that declines in the commercial catch were not due to declining biomass, but instead due to changes in fishing effort.

We demonstrated that DFA can be used to aggregate indices across spatial areas that can be used in stock assessment models. Furthermore, it can be used as a tool to examine spatial differences in trends. The standardization approach by Peterson et al. (2021a) proved to be easy to implement, which may encourage future use of DFA for index aggregation. Based on the sensitivity analysis results, 10 years of data for a DFA model may be the minimum number of years for time series with many years of missing data because a one trend model was typically preferred for those runs. Zuur et al. (2003) advised that DFA could only make reliable predictions for fisheries data with at least 25-30 years of data. DFA is likely not highly sensitive to specific years included, however, it is more sensitive to missing data. Similarly, Peterson et al. (2021a) reported the recommendation to use complete time-series where possible. Because DFA exhibited some sensitivity to years included, we recommend caution when implementing methods such as DFA that integrate multiple time series, and we recommend exploration of the effect of the years included in the analyses.

The methods we developed to estimate trends in mortality may be useful for improving the TLA guiding spot management. Currently the only indicators used in the TLA are harvest and survey indices. Harvest, in particular, is not thought to be an accurate index of changes in the population over time because changes in biomass may be confounded by changes in fishing mortality. Instead, estimates of commercial or recreational CPUE are more likely to be proportional to biomass, so the replacement of harvest with CPUE could improve the TLA. The TLA may also be strengthened by including a mortality indicator, which is related to fishing mortality. Because spot are relatively easy to age (ASMFC, 2008; ASMFC, 2017), developing estimates of mortality from age structured data would be a straightforward way to track population trends in the TLA. The most recent TLA revealed that reduced harvest levels exceeded the threshold in 2020, triggering management action even though the coastwide indices did not exhibit declines in adult biomass (ASMFC, 2022). These conflicting signals may be improved through the incorporation of CPUE and biological data in the TLA.

In conclusion, we estimated trends in apparent mortality and biomass over time for spot, which is a relatively understudied species despite its common occurrence in commercial and recreational fisheries. Spot shows similar patterns in biomass and mortality from New Jersey to Florida. There has been a notable increase in biomass indices to relatively high levels since 2015. Apparent mortality rates also increased in recent years. Environmental covariates did not explain the observed patterns in biomass or mortality. Despite being a data-limited species, this paper demonstrates that there are several methods to further understand the population without extensive catch-at-age information. These methods should be considered by managers for the next traffic light approach to improve and strengthen data-limited approaches to management.

Tables

Table 1.1: Description of data sources and types used to estimate total instantaneous mortality rates for spot. For each data source, the year, season, ages collected from otoliths, gear type, and geographic region are specified.

Source	Type	Years	Season	Age Range	Gear	Sampling Region
Maryland Commercial Pound Net (MD Pound)	Dependent	2012-2022	May-September	0-2	Pound nets	Inside the Chesapeake Bay
NorthEast Area Monitoring and Assessment Program (NEAMAP)	Independent	2007-2022	Spring (April and May) and Fall (September and October)	0-3	Bottom trawl	Cape Cod, MA south to Cape Hatteras, NC
Chesapeake Bay Multispecies Monitoring and Assessment Program survey (ChesMMAP)	Independent	2002-2022	March, June, September, November	0-4	Bottom Trawl	Chesapeake Bay Main Stem
Virginia Commercial (Va Dep)	Dependent	1998-2021	All year	1-6	Multiple	All regions
North Carolina Gillnet (NC Gill)	Independent	1999-2021	February-December	0-6	Monofilament gillnet (sink and float)	Pamlico sound, Pamlico, Pungo, Neuse, and Cape Fear rivers
North Carolina Pamlico Sound (NC Pam)	Independent	1992-2021	June and September	0-2	Semi-balloon trawl	Pamlico Sound, Pamlico, Pungo, and Neuse Rivers
North Carolina Dependent (NC Dep)	Dependent	1979-2021	All year	0-5	Multiple	All regions
South Carolina Trammel Net Survey (SC Tram)	Independent	2010-2020	March-December	0-4	Trammel net	Salt marsh edge and oyster reef habitat in lower estuarine habitat

Table 1.2: Akaike Information Criterion corrected for small sample size (AICc) values for dynamic factor analysis (DFA) models run with one and two common trends for mortality and biomass trends. Bold values indicate the model with the lowest AICc.

	Mortality DFA	Biomass DFA
One trend AICc	317.0	**333.2**
Two trends AICc	**315.2**	333.9

Table 1.3: Factor loadings for each data source included in the dynamic factor analysis model with one and two common trends for mortality. Data source abbreviations are the same as Table 1.1.

	One trend DFA	**Two trend DFA**	
	Trend 1	Trend 1	Trend 2
NEAMAP	0.71	0.50	0.31
ChesMMAP	0.63	0.04	0.47
MD Pound	0.29	0.34	0.10
VA Dep	0.53	0.63	0.27
NC Dep	-0.003	0.23	-0.02
NC Gill	0.69	0.06	0.51
NC Pam	-0.10	-0.28	0.09
SC Tram	-0.33	-0.20	0.08

Table 1.4: Factor loadings for each state included in the dynamic factor analysis model with one and two common trends for biomass trends. States include New Jersey and Delaware (NJ/DE), the Chesapeake Bay portion of Maryland (MDCB), the Atlantic Ocean portion of Maryland (MDA), the Chesapeake Bay portion of Virginia (VACB), the Atlantic Ocean portion of Virginia (VAA), and North Carolina (NC).

	One trend DFA	**Two trend DFA**	
	Trend 1	Trend 1	Trend 2
NJ/DE	0.62	0.64	-0.13
MDCB	0.09	-0.01	-0.31
MDA	0.56	0.46	-0.08
VACB	0.66	0.63	0.03
VAA	0.58	0.59	0.10
NC	0.71	0.75	0.22
FL	-0.43	-0.31	0.19

Table 1.5: Akaike Information Criterion corrected for small sample size (AICc) values for dynamic factor analysis (DFA) models run with a combination of environmental covariates for mortality and biomass trends. Both models were run for the years 2000-2021. Bold value indicate the model with the lowest AICc value.

Environmental Covariates	Mortality DFA	Biomass DFA
No Covariates	**300.80**	**327.28**
Gulf Stream Index	321.53	333.71
North Atlantic Oscillation Index	311.99	340.81
Atlantic Multi-decadal Oscillation Index	319.28	342.29
Chesapeake Bay Temperature	313.30	341.08
Northeast Temperature	315.49	340.82
All Temperature	460.67	403.65
All Covariates	330.77	347.79

Table 1.6: Akaike Information Criterion corrected for small sample size (AICc) for one and two trend dynamic factor analysis models with different combinations of 10-year periods and different starting and ending years (grey shaded area). This sensitivity analysis was conducted using time series of mortality. Bold values indicate the model with the lowest AICc value.

Years	1 trend model AICc	2 trend model AICc
2005-2015	**167.55**	187.38
2006-2016	**174.97**	194.61
2007-2017	**179.36**	193.35
2008-2018	**190.96**	193.64
2009-2019	202.06	**196.69**
2010-2020	**179.35**	196.43
2011-2021	196.46	**196.18**
2012-2022	**200.13**	206.26
2000-2022	316.98	**315.23**
2000-2021	**302.13**	302.55
2001-2022	**312.64**	313.13
2000-2020	**282.28**	284.54
2001-2021	**295.09**	298.35
2002-2022	**302.85**	306.20

Figures

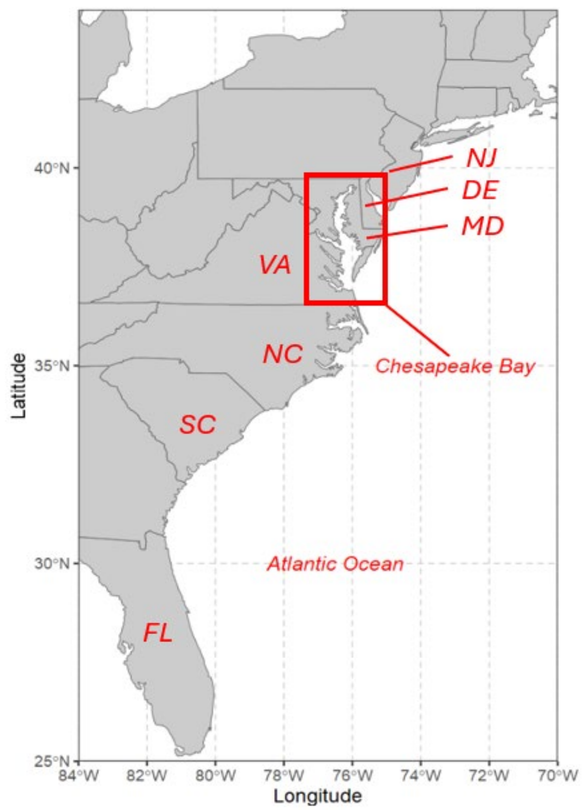

Figure 1.1: Study region examined for spatial trends in mortality and biomass for spot. States with data used in this study inclue New Jersey (NJ), Delaware (DE), Maryland (MD), Virginia (VA), North Carolina (NC), South Carolina (SC), Florida (FL) and are outlined in red. Chesapeake Bay region outlined with a red box.

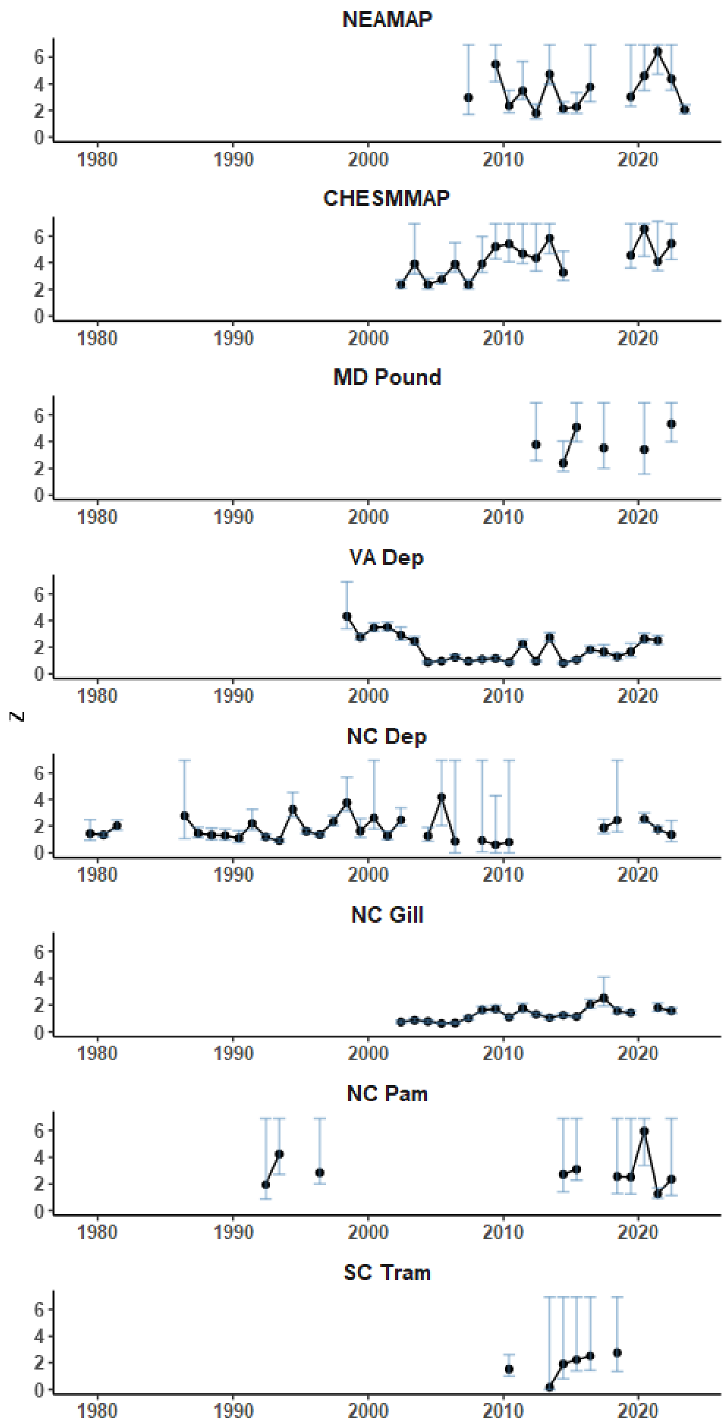

Figure 1.2: Estimated total instantaneous mortality rates (Z, per year) for six data sources with 95% confidence interval error bars. Error bars were calculated for survival rate (S) and constrained in order to convert to Z. Each panel represents a different data source (abbreviations defined in Table 1.1). Estimates of Z were obtained using the Chapman-Robson estimation method.

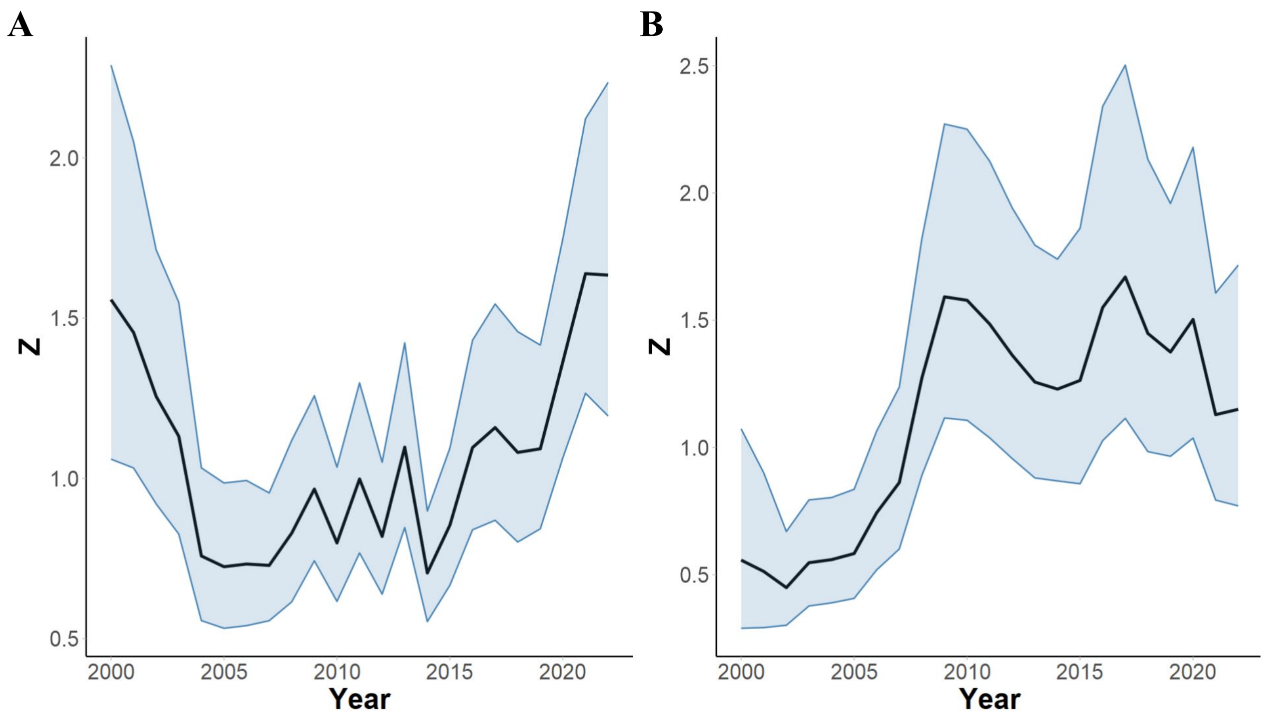

Figure 1.3: Back-transformed common trend one (A) and common trend two (B) of total instantaneous mortality rate and 95% confidence intervals over time from dynamic factor analysis model with two common trends.

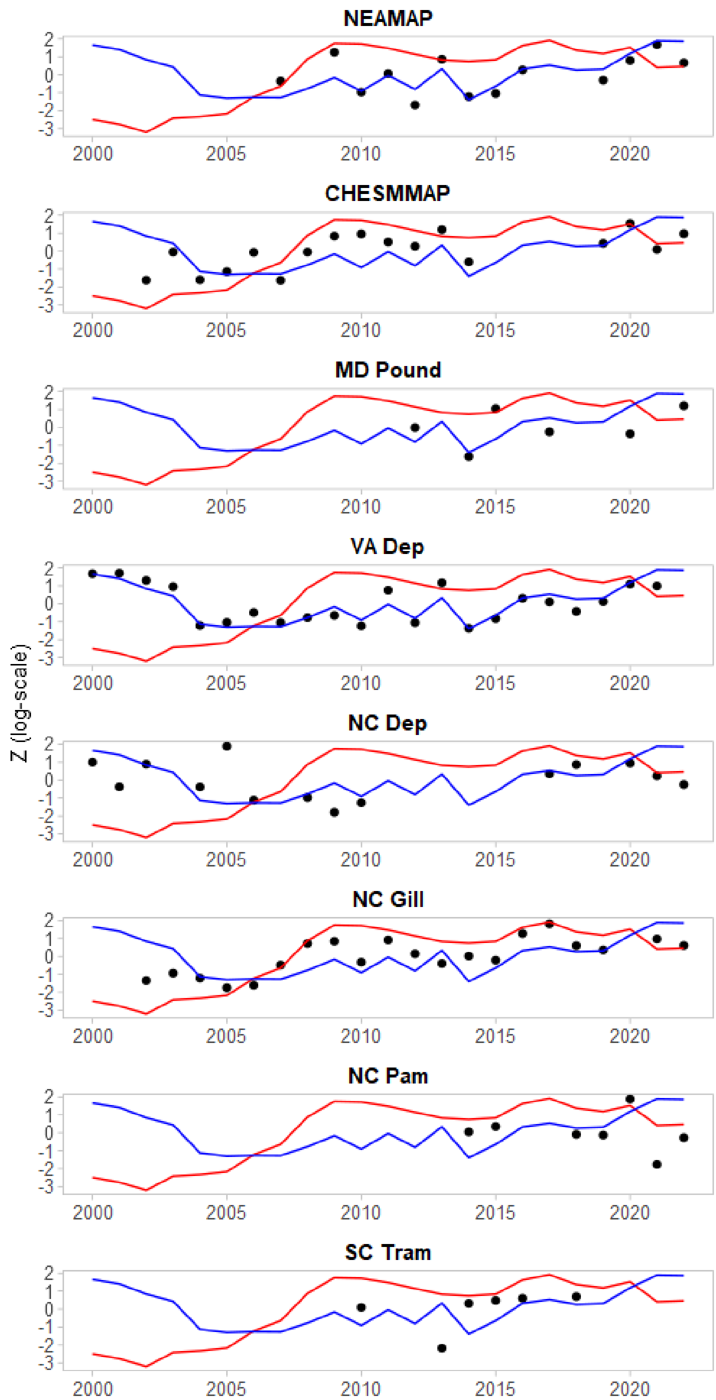

Figure 1.4: Two-trend dynamic factor analysis model with first common trend (blue line) and second common trend (red line) of total instantaneous mortality rate plotted against transformed estimates of total instantaneous mortality rates (black dots). Each panel represents a different data source. Data source abbreviations are the same as Table 1.1.

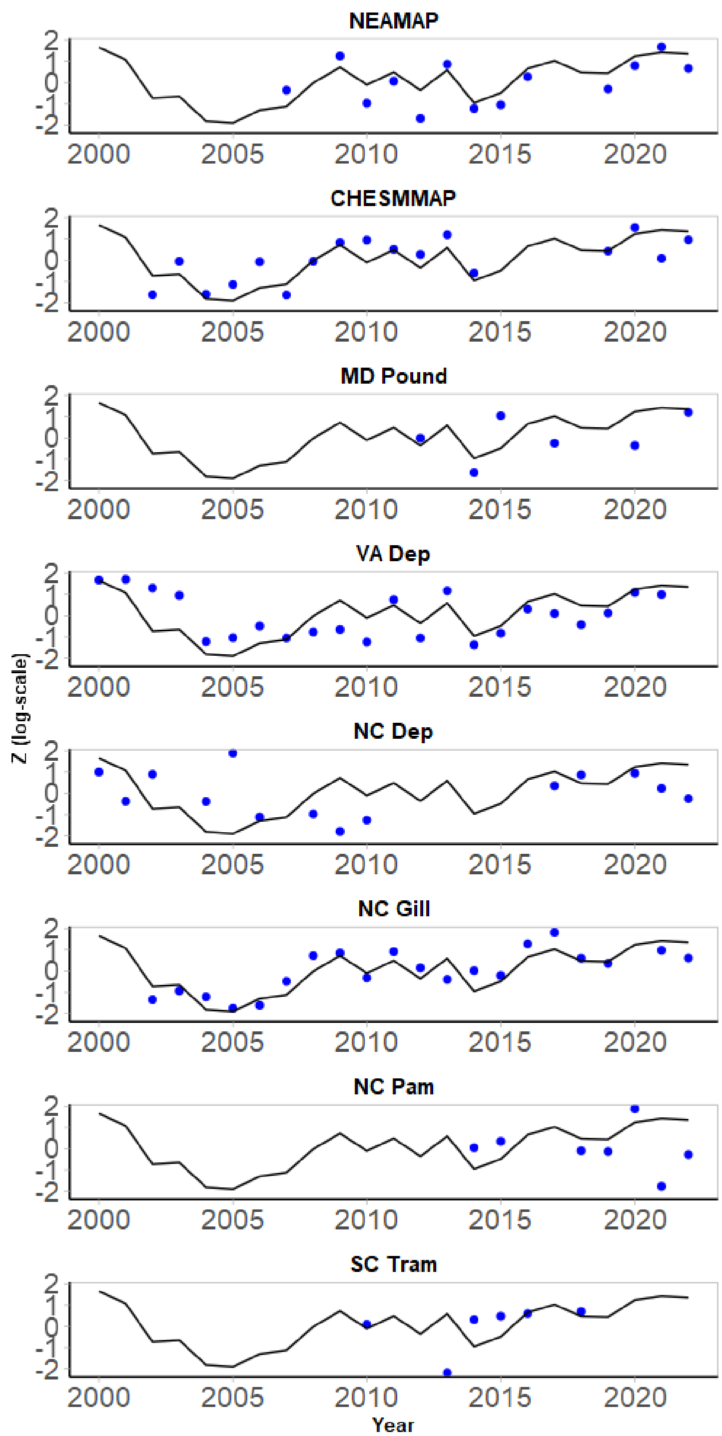

Figure 1.5: Single-trend dynamic factor analysis model with common trend (black line) of total instantaneous mortality rate plotted against transformed estimates of total instantaneous mortality rates (blue dots). Each panel represents a different data source. Data source abbreviations are the same as Figure 2.

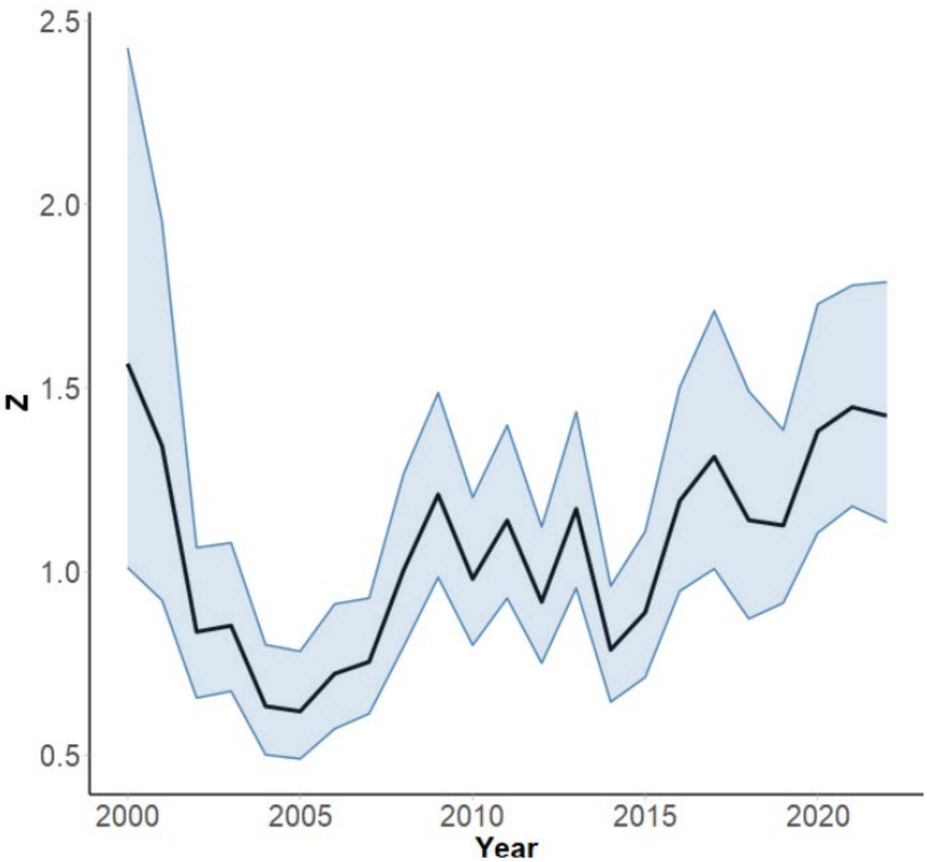

Figure 1.6: Back-transformed common trend of total instantaneous mortality rate and 95% confidence intervals over time from dynamic factor analysis model estimated with one common trend.

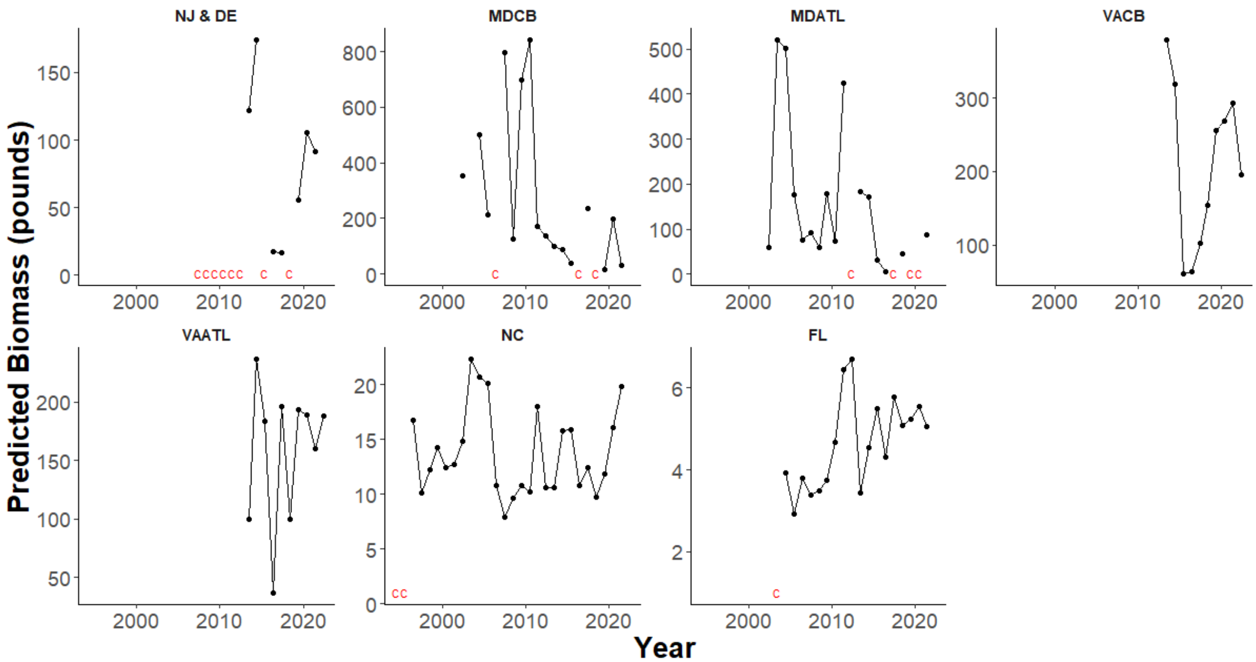

Figure 1.7: Standardized catch per trip indices of biomass for the spot gillnet fishery by state (non-confidential). States include New Jersey and Delaware combined (NJ & DE), the Chesapeake Bay portion of Maryland (MDCB), the Atlantic Ocean Portion of Maryland (MDATL), the Chesapeake Bay portion of Virginia (VACB), Atlantic Ocean portion of Virginia (VAATL), North Carolina (NC), and Florida (FL). Red Cs indicate years with confidential data.

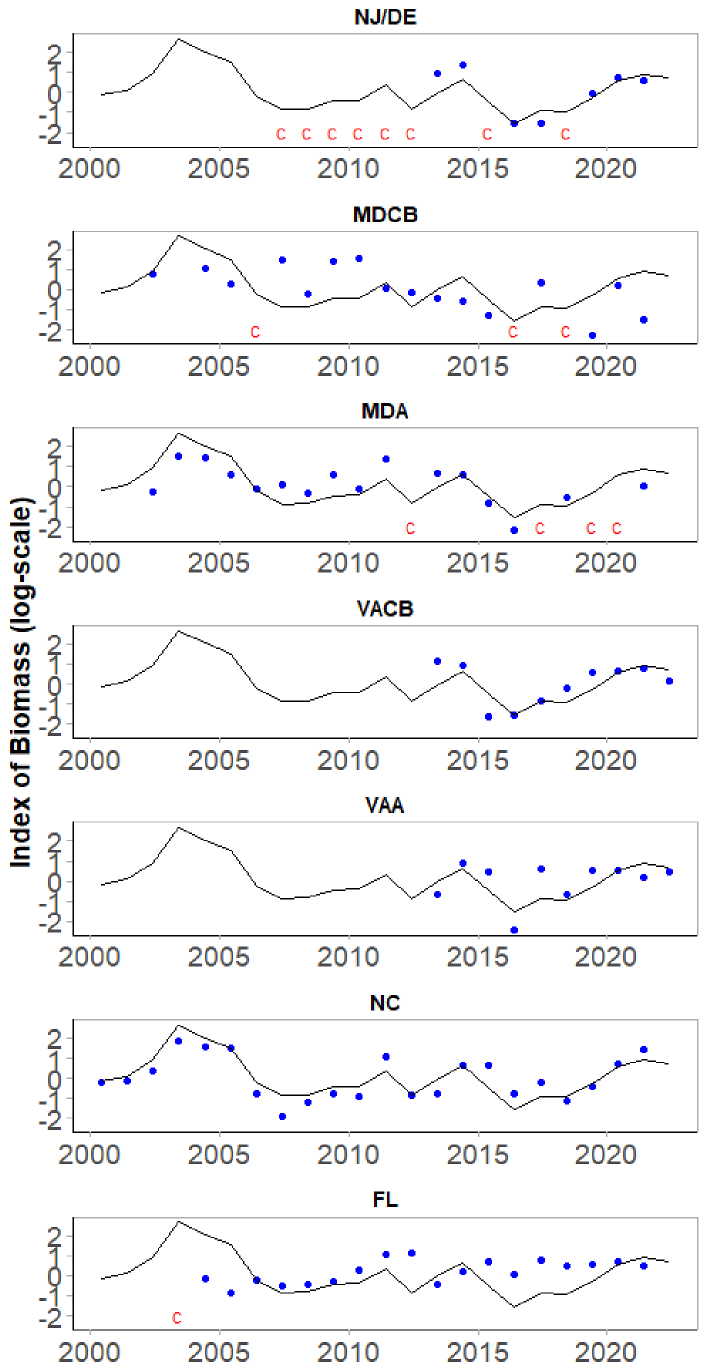

Figure 1.8: Single trend dynamic factor analysis (DFA) model with common trend (black line) of biomass plotted against transformed estimates of biomass (blue dots). Each panel represents a different data source. Data source abbreviations are the same as Figure 1.7. Red Cs indicate years with confidential data.

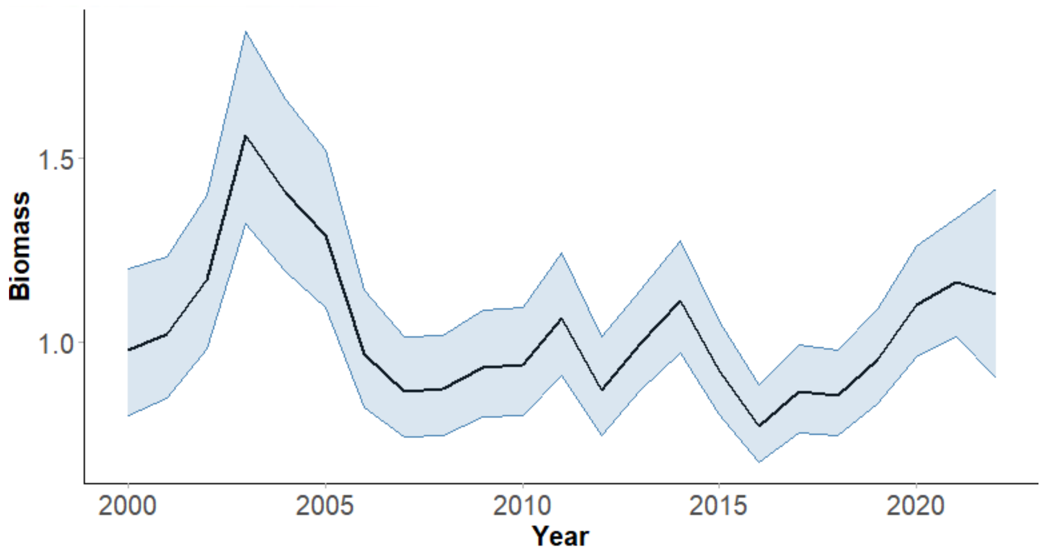

Figure 1.9: Back-transformed common trend of the index of biomass and 95% confidence intervals estimated from a dynamic factor analysis model with one common trend.

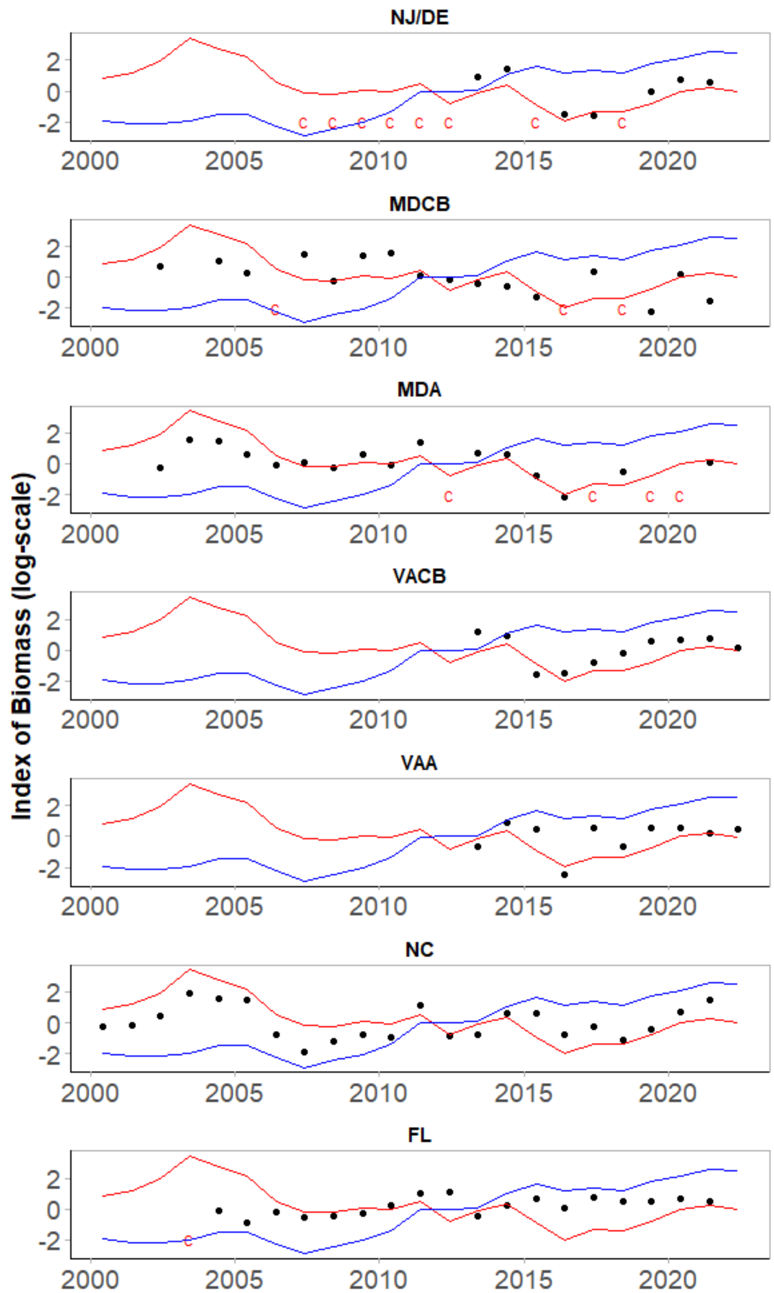

Figure 1.10: Two-trend dynamic factor analysis (DFA) with first common trend (blue line) and second DFA common trend (red line) of biomass plotted against transformed estimates of biomass (black dots). Each panel represents a different data source. Data source abbreviations are the same as Figure 1.7. Red Cs indicate years with confidential data.

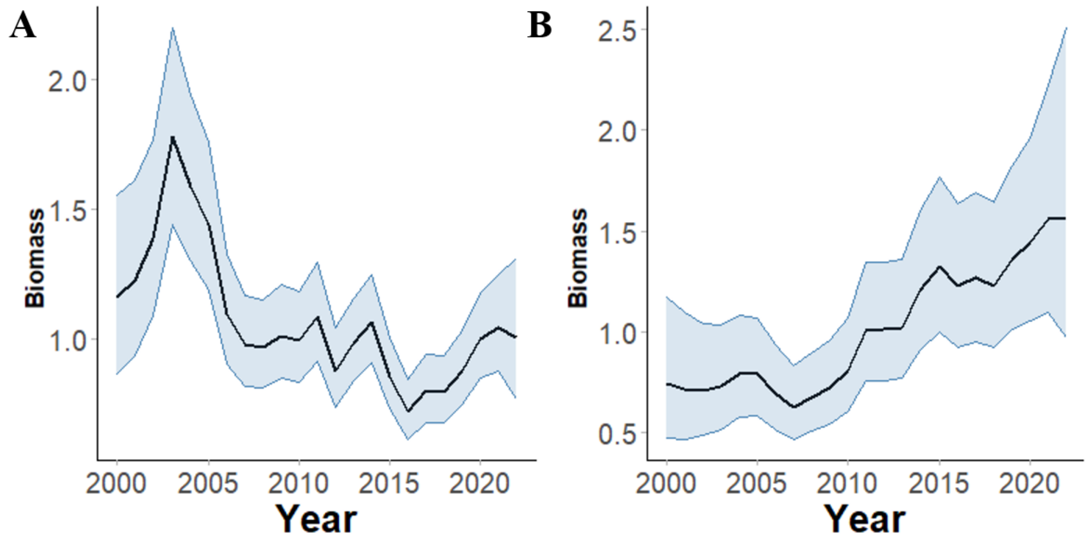

Figure 1.11: Back-transformed common trend one (A) and common trend two (B) of biomass and 95% confidence intervals over time estimated from a dynamic factor analysis model with two common trends.

Chapter 2: Estimating Spot abundance and fishing mortality rates in the Chesapeake Bay and the Atlantic coast using a spatial population model.

Introduction

Traditional stock assessments make three assumptions about a population being modeled: 1) populations are closed so there is no net immigration or emigration, 2) the population is homogenous and well mixed across its range, and 3) vital rates (growth, survival, and reproduction) are homogenous across the stock area (Cadrin, 2020; Cadrin et al., 2023). These assumptions are often violated because life history patterns and fishing practices drive nuances in spatial structure (Cadrin and Secor, 2009). The majority of stock assessments used to support management advice assume no spatial structure (Berger et al., 2017) because the process of incorporating spatial structure is often considered not practical, possible, important, or convenient (Cadrin, 2020). The use of spatial stock assessments has also been limited because of the long tradition of using single-area models and the increased data demands of spatial approaches (Goethel et al., 2011). However, non-spatial models may not adequately capture the complexity of real-world population dynamics, resulting in assessments that have biased estimates and misperceptions of stock status that can eventually lead to failures in fisheries management (Cadrin, 2020). Furthermore, trends in abundance or biomass can be misinterpreted if the spatial scale of management is not aligned with the true population distribution (Cadrin 2020; Goethel et al., 2023). This mismatch can result in management measures that do not achieve their intended goal, further highlighting the importance of correctly defining geographic boundaries. Finally, spatial stock assessments can be beneficial when working with multiple data sources that are collected from small-scale regions that do not cover the entirety of a species' range.

Methods to incorporate spatial structure have rapidly advanced since early efforts by Beverton and Holt (1957) to characterize the importance of defining spatial structure in assessments. Prior to the 1990s, stock assessment scientists struggled to implement dynamic spatial models because they lacked advanced computational resources, statistical software, and had fewer options to acquire data at finer spatial scales (Goethel et al., 2011). Currently, there is increased awareness of spatial stock assessment techniques and their advantages for improving biological reference points (Punt, 2019); however, they are still underutilized (Berger et al., 2017). Spatially-explicit stock assessment models are beneficial because they can vary in complexity depending on population structure and data availability (Berger et al., 2017). They can also be implemented in almost any assessment framework (e.g., Pincin and Wilberg, 2012), but they are most commonly applied to statistical catch-at-age models (Maunder and Punt, 2013).

Spatial assessment models allow for the estimation of population parameters in each region specified in the model. This allows for the ability to compare population size, fishing mortality rate, and recruitment among regions for a better understanding of population dynamics and the effects of fishing over time. Typically, spatial stock assessment models describe movement as the probability that a fish will move from one region to another given its age (Goethel, 2011; Punt, 2019). These movement parameters are often assumed to be constant over time and are most often informed by tagging data (Punt, 2019). Alternative approaches for including spatial habitat use in stock assessment models have also been considered, particularly in whale assessments (Punt, 2017). The incorporation of time-varying movement in spatial assessment models is important to consider but has not received substantial attention.

The Chesapeake Bay is the largest estuary in the United States, and it is an economically and ecologically valuable resource. Seasonal fluctuations in temperature, freshwater input, dissolved oxygen, and other physical characteristics cause diverse assemblages of fishes to utilize the estuary at different times throughout the year (Latour et al., 2017). Up to 90% of fishes in the Chesapeake Bay are transient, occupying this region for short periods of time to seek nursery habitat, refuge from predation, or feeding opportunities (Murdy et al., 1997). It is therefore important to characterize the spatial dynamics of fishes that use the Chesapeake Bay at some point during their life cycle. Accurate information about fish abundance in the Chesapeake Bay is important to effectively manage fisheries and mitigate future impacts of ecosystem change. Therefore, spatially-explicit models may be a useful tool for better understanding this system.

Spot (*Leiostomus xanthurus*) is a sciaenid that is distributed along the U.S. Atlantic coast from the Gulf of Maine to the Gulf of Mexico. It is short lived, fast growing, and early to mature. It reaches a maximum age of six and achieves about 84% of their cumulative growth in their first year (ASMFC, 2017; Piner & Jones, 2004). Its maximum average size is approximately 34 cm, but individuals may grow larger at higher latitudes (ASMFC, 2017). Spot undergo seasonal migrations where adults move offshore to spawn in the fall. Larvae are thought to be mostly passively transported into estuaries (Warlen & Chester, 1985; Weinstein & Walters, 1981). As spot grow, they move into deeper waters of a higher salinity (Weinstein, 1984; Weinstein & Walters, 1981). Spot is considered estuarine dependent and is one of the most abundant fishes encountered in these systems, making them widely available as forage (Friedl et al., 2013). Spot is managed on the U.S. east coast by the Atlantic States Marine Fisheries Commission (ASMFC), and the fishery historically operated in state waters from New Jersey to Florida during the fall months when schools of spot migrate from estuaries into offshore waters (Pacheco, 1962). Historically, harvest was split evenly between the commercial and recreational sectors. However, since 2005 the spot fishery has been predominantly recreational (approximately 30% commercial and 70% recreational, ASMFC, 2022), and in recent years, it is one of the most frequently caught recreational species in the U.S. (National Oceanic and Atmospheric Administration (NOAA), 2022). Spot also comprises a large portion of South Atlantic shrimp trawl fishery bycatch and discards (ASMFC, 2017). The first coastwide benchmark stock assessment for spot was conducted in 2017 by ASMFC, but it did not pass peer review due to data uncertainties and conflicting information on population trends (Able et al., 2017).

The goal of our study was to estimate abundance and fishing mortality rates over time for spot in two regions, the Chesapeake Bay and U.S. Atlantic coastal waters from New Jersey through Florida, and to determine whether spatial patterns of spot abundance were due to changes in mortality rates or movement. Our objectives were to 1) develop a statistical catch-at-age model with spatially-varying mortality

(SVM) in template model builder (TMB); 2) adapt the SVM model into a model with time-varying occupancy (TVO); 3) compare the SVM and TVO models using standard diagnostics and a pre-determined set of qualitative plausibility criteria; and 4) evaluate sensitivity of each model to alternative levels of natural mortality.

Methods

We developed a statistical catch at age (SCAA) model that was spatially structured to model spot in two regions: the Chesapeake Bay and the remainder of the U.S. Atlantic Coast from New Jersey to Florida (Figure 2.1). We modeled ages-0-3+, where 3+ was an aggregate age group that included all spot age-3 and older. The model operated on an annual time step because the fishery largely occurs in the late summer and fall and data are sparse in the winter and early spring. We modeled spot during 2002-2019. Although spot ageing data in some states goes as far back as 1989, we did not have an index of abundance to inform the Chesapeake Bay region prior to 2002. To avoid dealing with missing data caused by COVID-19 sampling disruptions in 2020, we ended our model in 2019. The model included three fleets, commercial, recreational, and shrimp trawl bycatch. Recreational and commercial fishing occurred in both regions, but shrimp trawling did not occur in the Chesapeake Bay. Our base model allowed for spatially-varying mortality (referred to as the SVM model) by fixing the occupancy probabilities to be constant over time but allowing fishing mortality rate to vary over time between regions. We adapted this model into a time-varying occupancy model (referred to as the TVO model) that allowed the occupancy probabilities to change over time, but annually varying fishing mortality rates for commercial and recreational fisheries were the same across regions. Our model was developed using Template Model Builder (TMB: Kristensen et al., 2016). During the development process, we tested our estimation model using data simulated with minimal error, and found it was able to estimate simulated values.

Data

Fishery Catch

Fishery removals (landed catch and estimated dead discards) were summarized by gear and region. Daily commercial catch reports for spot were obtained from the Atlantic Coastal Cooperative Statistics Program (ACCSP) for all states from New Jersey to Florida during 1982-2022. Fishing trips that originated in Maryland or Virginia were further subdivided into trips that occurred within the Chesapeake Bay or the Atlantic Ocean based on landing location. Catch was recorded in live pounds (whole weight) and converted to kilograms. We compiled commercial catch into yearly summaries for each region. Discards from commercial fisheries were estimated by ASMFC (2017) using observer data from the Northeast Fisheries Observer program. Gillnets discarded a median of 2,769 fish and trawls discarded a median of 58,682 fish (ASMFC, 2017). Discards were higher in Mid-Atlantic trawl fisheries, but both sources made up less than 10% of all coastwide fishery removals combined in a given year. These data were not available to us, so commercial discards were assumed to be zero. We considered using North Carolina and Virginia “scrap” fishery landings as a source of commercial mortality, but they made up a very small proportion of non-shrimp trawl commercial removals (<0.1%) and were not used in the model.

Recreational catch data were obtained through the Marine Recreational Information Program (MRIP) online query tool (NOAA, 2023). Recreational data for the Chesapeake Bay had an average percent standard error (PSE) of 74.3% across years and categories of catch, and recreational data for the coast had an average of 77.5%. Total recreational catch in each region was the sum of observed harvest, reported harvest, and dead discards. We calculated dead discards from estimated discards assuming a 15% recreational release mortality rate (ASMFC, 2017).

Because large numbers of spot are caught as bycatch in shrimp trawl fisheries on the U.S. Atlantic coast, we used estimates of bycatch from this fishery as another source of fishing mortality. The average number of spot discarded in the shrimp trawl fishery per year were calculated using observer coverage data from the Southeast Shrimp Trawl Observer Program (SESTOP) for 2008-2019. Years prior to 2008 were hindcasted using catch rate data for spot from the Southeast Area Monitoring and Assessment Program (SEAMAP) survey, which uses a shrimp trawl. Discard rate estimates were then applied to reported effort data to estimate total shrimp trawl discards. Bycatch discards in numbers were modelled with a negative binomial generalized linear model (J. Kipp, ASMFC, personal communication; ASMFC 2017). All shrimp trawl bycatch was assumed to be age-0 (ASMFC, 2017).

Fishery-Independent Indices

Data from multiple surveys were used to develop regional indices of abundance for spot (Table 2.1). To inform abundance in the Chesapeake Bay we used the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) survey and the Virginia Institute of Marine Science (VIMS) Juvenile Finfish Trawl Survey. ChesMMAP is a bottom trawl survey that began in 2002 and samples up to 80 stations in the mainstem of the Chesapeake Bay every March, June, September, and November using a stratified random design (Bonzek et al., 2022; VIMS, 2023a). Indices of abundance from ChesMMAP were developed using generalized linear models in the glmmTMB R package (Brooks et al., 2017). We built a model for summer (June and July) and fall (September and November) to allow for differences in variances. Models were tested for zero inflation, and zero inflation factors were included when necessary. The equation described the natural logarithm of the expected value of catch-per-unit-effort (CPUE) as a linear function of year with effort as an offset,

$$log(CPUE) = Intercept + Year_y + log\ (Effort) \quad ,$$

where CPUE followed a negative binomial distribution CPUE~NB(μ,θ). The unit of effort used was area swept in m^2.

Since 1955, the VIMS Juvenile Finfish Trawl Survey conducted monthly sampling (excluding January and March) of juvenile fishes in the Virginia portion of the Chesapeake Bay and its tributaries (Tuckey and Fabrizio, 2023). All spot from this survey were considered to be age-0. The VIMS juvenile trawl survey was standardized using a weighted geometric mean catch-per-tow using data from July to October (Tuckey and Fabrizio, 2023).

To inform abundance along the Atlantic coast, we used the Northeast Area Monitoring and Assessment program (NEAMAP) survey and a coastal aggregate index. NEAMAP is a bottom trawl survey in the mid-Atlantic Bight in near shore waters to a depth of 18 meters that has been conducted since fall 2007. It was implemented to maintain coverage of shallow strata following a change in the Northeast Fishery Science Center bottom trawl survey (Latour et al., 2021). We used the spring survey (April and May). The NEAMAP spring index was calculated as the weighted geometric mean of catch per standard area swept weighted by the strata area (Bonzek et al., 2017; VIMS, 2023b). Data from 2013 and 2017 were dropped because of unusually high catch numbers (6 and 21 times the time series average). This was likely the result of a small number of tows with high catches, which may not reflect true trends in abundance (Bonzek et al., 2017).

A fall coastal aggregate index was developed to estimate biomass by combining several trawl surveys using a Vector Autoregressive Spatio-Temporal Model (VAST; R. Mestav, VIMS, personal communication). The surveys included the SEAMAP coastal trawl, NEAMAP, the New Jersey Ocean Stock Assessment Program Trawl Survey, and the Northeast Fisheries Science Center Bottom Trawl Survey. Combined, these bottom trawl surveys covered the region of the Atlantic coast from Cape Hatteras, NC to Canada during the fall (September – November). The coastal aggregate represented the estimated biomass over the area covered by the combined surveys (Cape Canaveral, Florida to Nova Scotia).

Age Data

Age and length frequency data from commercial fisheries were available from Virginia, North Carolina, and Maryland. All spot were aged using otoliths. Ageing workshops have been conducted for other sciaenid species (Atlantic Croaker and Red

Drum) to develop ageing protocols. Because these closely related species were straightforward to age, the same protocols also work well for spot (ASMFC, 2008; ASMFC, 2017). The Virginia Marine Resources Commission (VMRC) randomly sampled commercial spot from fish houses and docks in the Chesapeake Bay and coastal Virginia annually. The majority of samples came from gill nets (38%), pound nets (36%), and haul seines (25%). The North Carolina Department of Marine Fisheries (NC DMF) sampled spot from fish houses for ageing. Gear was not known for 86% of aged fish from commercial fisheries, and the remaining NC DMF samples came from gill nets, haul seines, pound nets, or trawls. NC DMF subsampled 30 fish per market grade, which were measured and aged (ASMFC, 2017). The Maryland Department of Natural Resources (MD DNR) sampled spot from the commercial pound net fishery in the Chesapeake Bay (ASMFC, 2017) with ageing beginning in 2012. No age data were available from the recreational fishery, but length composition data were available from MRIP (NOAA, 2023). Fishery-independent ageing data were available from ChesMMAP and NEAMAP. For both ChesMMAP and NEAMAP, individuals selected for ageing were sampled using a length-stratified random sampling approach (ASMFC, 2017).

For commercial data, sufficient age or length data were not available to create state-specific age compositions. Therefore, we developed regional age-length keys (ALKs) for the Chesapeake Bay and the Atlantic coast by aggregating the available age data from North Carolina, Virginia, and Maryland. Age-length data from Virginia were assigned to the coast or Chesapeake Bay based on whether the catch occurred outside or inside of the Chesapeake Bay. All age data from Maryland were from catches inside the Chesapeake Bay, and all data from North Carolina were from outside the Chesapeake Bay. ALKs were calculated as the proportion of spot at age in each 1 cm length bin for each year and region.

Proportions-at-age for commercial and recreational catches in each region were calculated by applying the ALKs to regional length frequencies. Regional length frequencies for the commercial fishery were weighted based on the amount of catch from each state. Length frequency data were available from the same commercial data sources specified above. Approximately 86% of the commercial ages for the Chesapeake Bay region came from Virginia and 14% from Maryland. Approximately 78% of the commercial ages for the coastal region came from North Carolina and 22% from Virginia. Lengths were reported differently by state with most states reporting total length except for North Carolina, which reported a combination of total length and fork length. Using the individual length data from North Carolina for samples that had total and fork length, fork length was converted to total length using a linear regression,

$$Total\ Length = 0.57 + 1.07 \times Fork\ Length.$$

This linear regression was used to convert all fork length records without associated total length. Estimated total lengths were combined with measured total length data to build the length composition for North Carolina. Lengths for the ALKs and length compositions were condensed into 1-cm length bins from a minimum bin of 13- cm (length <14 cm) to maximum bin of 31+ cm (length ≥ 31 cm) groups, which were determined based on length bins that represented 1-2% of cumulative length distribution. To get proportions-at-age for each region, the length frequency vector was multiplied by the ALK matrix,

$$\begin{bmatrix} N_{a=0} \\ N_{a=1} \\ N_{a=2} \\ N_{a=3+} \end{bmatrix} = \begin{bmatrix} P_{a=0,L=13-} & P_{a=0,L=14} & \cdots & P_{a=0,L=31+} \\ P_{a=1,L=13-} & P_{a=01L=14} & \cdots & P_{a=1,L=31+} \\ P_{a=2,L=13-} & P_{a=2,L=14} & \cdots & P_{a=2,L=31+} \\ P_{a=3+,L=13-} & P_{a=3+,L=14} & \cdots & P_{a=3+,L=31+} \end{bmatrix} \times \begin{bmatrix} N_{L=13} \\ N_{L=14} \\ \vdots \\ N_{L=31+} \end{bmatrix},$$

where N_a was the number of fish of age a, P was the proportion of fish age a within each length bin, L, and N_L was the number of fish in a given length bin. Ages were not available from the recreational fishery, so we applied the commercial ALK to the recreational length composition data to calculate the recreational age compositions. This application of the commercial data ALKs to the recreational length frequencies assumed that growth was the same between fish caught by both fleets. The recreational length composition were aggregated over states and compiled into two regions using data collected by MRIP (J. Kipp, ASMFC, personal communication).

For each survey (NEAMAP and ChesMMAP) and season, we compiled ALKs, length compositions, and proportions at age using the same methods as for the fishery-dependent data. Because NEAMAP was one of the surveys used in the aggregate index, we assumed that age data from the NEAMAP fall survey represented the age composition of the aggregate index.

Model Description

The model tracked abundance-at-age of spot over time within each region. Movement of spot was modeled as a pulse at the beginning of each year, such that a proportion of total abundance at each age was allocated to each region. Total abundance (*TN*) at the beginning of year *y* for age *a*, was calculated as the sum of abundance at the beginning of the year ($\widetilde{N}$) across regions for ages > 0,

$$TN_{y,a} = \sum_r \widetilde{N}_{r,y,a}.$$

For age-0, total abundance at the beginning of the year was equal to estimated recruitment (*R*),

$$TN_{y,0} = R_y,$$

where R in year, *y*, was an estimated parameter. Abundance for each region at the beginning of the year after movement (*N*) was calculated as the product of total abundance and the region and age-specific occupancy probability (*P*),

$$N_{r,y,a} = TN_{y,a}P_{r,y,a}.$$

The occupancy probability (*P*) was an estimated parameter that represented the proportion of fish at a given age in each region at the beginning of the year. Abundance in region *r*, at the beginning of the next year before movement followed the exponential mortality model,

$$\widetilde{N}_{r,y+1,a+1} = N_{r,y,a} \times e^{-Z_{r,y,a}},$$

where *Z* was the total instantaneous mortality rate. For age-3+, abundance in region *r* at the beginning of the next year before movement was the sum of the survivors of age-2 individuals to age-3 and the survivors of the age-3+ individuals,

$$N_{r,y+1,a=3+} = N_{r,y,a=2} \times e^{-Z_{r,y,a=2}} + N_{r,y,a=3+} \times e^{-Z_{r,y,a=3+}}.$$

The 3+ age group for the first year was assumed to be in equilibrium where *N* in region, *r,* was equal to the product of the occupancy probability (*P*) and total abundance,

$$N_{r,1,3} = P_{r,3} \times TN_{1,3}.$$

Equilibrium abundance for the remaining ages, *a,* for the first year was,

$$N_{r,1,a} = P_{r,a} \times TN_{1,a}.$$

TN by age and region in the first year was assumed to be in equilibrium

$$TN_{1,3} = \frac{TN_{1,3}}{1 - S_{eq}},$$

where S_{eq} was the weighted survival rate with weights equal to the sum of the proportion, *P*, in region *r*, times the survival rate in region *r* for age-3+,

$$S_{eq} = \sum P_{r,3} \times e^{-Z_{r,3}}.$$

The occupancy probabilities-at-age for the Chesapeake Bay were estimated on the logit scale, and the occupancy probabilities for the coast were calculated as,

$$P_{r=2,a} = 1 - P_{r=1,a}.$$

The total instantaneous mortality rate was calculated as the sum of fishing mortality (*F*) over fleets and the age-specific natural mortality rate (*M*),

$$Z_{r,y,a} = M_a + \sum_f F_{r,y,a}.$$

M at age was estimated using a mortality-length model developed by Lorenzen (2005) and rescaled with a constant (0.145) to approximately match the age-constant natural mortality value estimate, 0.91, calculated using the approach of Then et al. (2014) with a maximum age of 6 (Table S2).

Fishing mortality rate ($\tilde{F}$) for fully selected ages was estimated as an individual parameter for each fleet (commercial, recreational, and shrimp; *f*) and year (*y*). The age-specific fishing mortality rate (*F*) for a given fleet, year, and age (*a*) was the product of fully selected fishing mortality rate and the fleet-, region-, and age-specific selectivity (*Sel*),

$$F_{f,r,y,a} = \tilde{F}_{f,r,y} \times Sel_{f,r,a}.$$

Selectivity for the recreational and commercial fisheries was specified equal to one for some ages and was estimated for the other ages (Table 2.2). Shrimp trawl fishery was assumed to select only age-0 spot, so selectivity was specified as one for age-0 and zero for all other ages.

Fishing for spot primarily occurs in the late summer through the fall. Therefore, we modified the catch equation to allow for natural mortality outside of the fishing season and both fishing and natural mortality during the fishing season. Catch at age (*CAA*) for fleet *f*, region *r,* year *y,* and age *a*, was estimated as the product of the proportion of mortality during the fishing season due to fishing by fleet *f*, the fraction of individuals that died during the fishing season, and the abundance at the beginning of the fishing season,

$$CAA_{f,r,y,a} = \frac{F_{f,y,r,a}}{\sum_f F_{f,r,y,a} \;\; + M \times Dur_M} \times \left(1 - e^{-(\sum_f F_{f,r,y,a} F_{total} + M \times Dur_M)}\right) \times N_{r,y,a} \times e^{-M \times Bef_M},$$

where Dur_M was the fraction of natural mortality that happened during the fishery and Bef_M was the fraction of natural mortality that happened before the fishery began.

Indices of abundance were calculated in a similar manner to catch by allowing for some mortality before the survey occurred. Specifically, the index of abundance at age (IAA) for index *i*, region *r*, year *y*, and age *a*, was estimated as the product of catchability (*q*), abundance, survey selectivity, and modified by the fraction of natural and fishing mortality that occurred prior to the survey,

$$IAA_{i,r,y,a} = q_i \times N_{r,y,a} \times Sel_{i,r,a} \times e^{-(M \times Frac_M + F \times Frac_F)},$$

where $Sel_{i,r,a}$ was the selectivity at age parameter for index i, and q_i was the catchability parameter for index i. $Frac_M$ was the fraction of natural mortality that occurred before the survey and $Frac_F$ was the fraction of fishing mortality that occurred before the survey. $Frac_M$ and $Frac_F$ depended on the timing of the survey in relation to the fishery (Table 2.3).

Proportions-at-age for fishery catches were calculated for each region and fleet as:

$$PAA_{f,r,y,a} = \frac{CAA_{f,r,y,a}}{\sum_a CAA_{f,r,y,a}}.$$

Proportions-at-age for each survey used the same equation with IAA replacing CAA.

Parameters were estimated by minimizing the objective function (NLL_{Obj}), which was the sum of the negative log likelihood functions for each data source and penalties on some of the estimated parameters,

$$NLL_{Obj} = -ln(L_{Catch}) - ln(L_{Index}) - ln(L_{CatchPAA}) - ln(L_{SurveyPAA}) - ln(L_{Penalties}),$$

where $L_{Penalties}$ was the sum of all penalties described in Table 2.4.

Lognormal errors were assumed for the survey indices ($-ln(L_{Index})$) and the fishery catch ($-ln(L_{Catch})$), and the negative log likelihood for the proportions-at-age ($-ln(L_{CatchPAA}); -ln(L_{SurveyPAA})$) used a robust multinomial distribution (Fournier et al., 1990; Fisch et al., 2021). Model fit was assessed using Pearson residuals for catch and surveys and standardized residuals for proportions at age. Coefficient of variations (i.e., log-scale standard deviations; CV) for the lognormal distributions and effective sample sizes (Neff) for the robust multinomial distributions were determined by iterative re-weighting for each survey (Francis, 2011). Neff describes the information in the proportions-at-age if sampling is random, and it cannot be larger than the number of fish aged in a year. Typically, higher Neff values indicate more confidence in ageing data. Neff values were restricted to a minimum value of 5-10, but values in the 10-20 range were considered to be better because they reflected the low samples size and lower confidence in the proportions at age relative to the survey indices. We were less concerned with ageing error because spot are considered easy to age, however, we were more concerned that our ageing data was not a representative sample of the population. To reflect that uncertainty, we used lower Neff values. Because no fish were aged from the recreational fishery, we restricted Neff for this fleet to be lower than that for the commercial fishery. CV values represented our confidence in the reliability of a data set. Smaller CV values indicate less error in the data (relative to the true unknown values) and will force the model to fit better. The commercial catch had a lower CV than the recreational or shrimp bycatch fleets because we believed that the commercial catch summaries were more reliable than the other fleets. CV and Neff were constant over time. Final values of the CVs and Neffs are presented in Table S1.

We used several penalties to constrain parameters such that they were estimable and to ensure that the model produced biologically plausible estimates. Therefore, we implemented several penalties that were in three categories: 1) parameter estimates should be similar to other related parameter estimates, 2) fishing mortality rates are unlikely to be extremely high or low, and 3) the spatial distribution of spot recruitment should be somewhat similar to estuarine primary productivity and the proportions of recreational and commercial catch. Penalized likelihood components of the objective function and their respective equations, means, and standard deviations are described in Table 2.4. Normal distributions were assumed for all penalties, but for some parameters the penalty was applied to a transformed value. The occupancy probability parameters (*P*) had several penalties because we did not have data to inform these values. Instead, we used an estimate of the proportion of primary production in the Chesapeake Bay relative to other estuaries on the U.S. East Coast to penalize the occupancy probability for age-0. ASMFC (2004) calculated the weighted average of primary productivity and estimated that 69% of the estuarine primary production occurred in the Chesapeake Bay. The average occupancy probability for age-0 spot in the Chesapeake Bay over years was penalized to match productivity levels ($-ln(L_{P0})$, Eq. 4.1). Spot are estuarine dependent as juveniles (Odell et al., 2017), and primary productivity should positively relate to their prey. Additionally, proportions for ages 1-3+ were penalized using a mean value of 0.5 ($-ln(L_{Psplit})$, Eq. 4.2) because commercial and recreational fishery catches were similar between the Chesapeake Bay and coastal regions. P was additionally penalized to minimize differences between ages ($-ln(L_{Pagediff})$, Eq. 4.3). These penalties were included because we do not expect large proportions of the population to be concentrated in one region for a given age based on fishery catches, and we do not expect the occupancy probabilities to vary substantially from one age to the next. Fishing mortality rates for spot are not likely to undergo large jumps from one year to the next because fishing effort in likely not highly variable year-to-year. Therefore, we constrained $\tilde{F}$ to penalize year-to-year changes for each fleet within a region ($-ln(L_{F-cdiff})$, Eq. 4.4; ($-ln(L_{F-rdiff})$, Eq. 4.5; ($-ln(L_{F-sdiff})$, Eq. 4.6).

Similarly, the models included penalties on between-age differences in the occupancy probabilities in both regions. These penalties on the differences between parameters do not provide information on the scale of the parameter estimates and should be relatively uninformative for estimates of abundance or fishing mortality rates. $\tilde{F}$ for the recreational fishery in the Chesapeake Bay and shrimp trawl bycatch were additionally penalized to avoid extremely high (e.g., 20 yr^{-1}) values that were estimated in preliminary model runs ($-ln(L_{Frecbay})$, Eq. 4.7, ($-ln(L_{Fshrimp})$, Eq. 4.8) by including a normal penalty on the $\log(\tilde{F})$ with a mean of 0.5 and an SD of 0.2. The purpose of this penalty was to inform the model that very high or low values of $\tilde{F}$ were unlikely. Finally, recreational selectivity patterns for commercial and recreational fisheries were penalized to minimize differences between the Chesapeake Bay and the coast because we assumed that age-specific fishing selectivity patterns would be similar between regions ($-ln(L_{sel})$, Eq. 4.9).

We implemented two versions of the model that differed in estimated parameters and penalties. The SVM model assumed that occupancy probabilities-at-age were constant over time while fishing mortality rates for each fleet and fishery selectivity differed between regions. The TVO model allowed occupancy probability parameters, P, to vary over time while holding fishing mortality rates and selectivity patterns constant between regions for the recreational and commercial fleets. Time-varying occupancy probabilities were estimated by modeling P for each age as a random walk on the logit scale,

$$logit(P_{y+1,a}) = logit(P_{y,a}) + Pdevs_{y,a},$$

where the annual deviations in the occupancy probabilities ($Pdevs_{y,a}$) were penalized using a normal distribution ($-ln(L_{pdevs})$, Eq. 4.10). Except for the changes specified, the structure of the TVO model was the same as the SVM model (all other penalties were the same).

The SVM and TVO models were compared using a set of qualitative plausibility criteria related to biological plausibility and model fit (Table 2.5). We deemed a model to be biologically plausible if spot were not extremely concentrated in one region. Also, occupancy probabilities within a region should be similar between ages because it is unlikely that fish close in age have drastically different movement patterns. Additionally, selectivity patterns should not have inexplicable patterns and fishing mortality rates should not exceed 2 yr^{-1} for a single fleet because it is unlikely that spot fishing mortality rates were that high during the study period. We believe this is realistic because spot are a low value fish that is usually not the target species. Because they are so widely distributed, it would be difficult to concentrate fishing effort to remove large quantities of the population. Lastly, the model should be able to fit catch and indices relatively well and avoid any major patterning in age composition residuals.

Sensitivity Analysis

We conducted sensitivity analyses for both models to test the effect of different values of age-specific natural mortality rates. Our base models used Lorenzen (2005) M estimates that were rescaled to average the maximum age M estimate using the Then et al. (2014) approach with an added constant (0.145). We explored another version of each model with “low” M, which reduced the base model

M values by 0.145 (Table S2). Similarly, we ran “high” M model which used the base M estimates increased by 0.145.

Results

Both the SVM and TVO models appeared to converge on unique parameter estimates with satisfactory convergence diagnostics, and standard errors of parameter estimates for both models were estimable. While the SVM model had a lower objective function value, the TVO model better fit most of the data sources and satisfied more of the plausibility criteria (Tables 2.5 and 2.6). The objective function of the SVM model was 36.76 for the negative log likelihood only and 0.51 with penalties included (Table 2.6). The objective function of the TVO model was 19.78 for the negative log likelihood only and 81.94 with penalties included (Table 2.6). The TVO model fit all of the data sources better than the SVM model except for the commercial catch, commercial catch proportions-at-age, and the NEAMAP spring survey index, based on the negative log likelihood values. Both models had similar fits to the NEAMAP proportions-at-age. The SVM model produced implausibly high estimates of fishing mortality for the recreational fishery ($F>3.0$ yr^{-1} in 2016). The models had similar trends in residuals for most data sets, but the SVM model usually had larger standardized residuals, which indicated a worse fit than the TVO model.

Fit to Data

The SVM and TVO models fit commercial catch in both regions similarly, closely following the declining trend over time (Figure S1). However, the SVM model could better match the high commercial catches, which led to a lower NLL (-

54.64 compared to 31.48; Table 2.6; Figure S2). The fit of both models to the recreational catch data was not as close as the commercial data (Figure S1). Both models struggled to match the trend in each region, particularly a large stretch of years in the middle of the time series for the Chesapeake Bay. However, the TVO model came closer to matching the trend and had a lower NLL than the SVM model (3.59 compared to 17.69; Table 2.6; Figure S2). Both models had no obvious patterns in Pearson residuals for the commercial and recreational fleets (Figures S4 and S5). Both models fit the shrimp trawl bycatch similarly well, capturing the general variability over time but not matching most of the points. The TVO model was slightly better at matching high catches which led to a lower NLL (44.87 compared to 39.92, Table 2.6; Figure S2). Both models had Pearson residuals with a slight pattern and some outliers (Figure S4 and S5).

The TVO model fit all surveys better than the SVM model, except for the NEAMAP index, according to NLL (Table 2.6; Figure S2). Both seasons of ChesMMAP increased early in the 2000s to very high levels around 2010 before dropping to very low levels around 2015 (Figure S3). Neither model was able to capture the trend over time and fit the highest catches. Both models had a poor fit to data, especially in the fall, but the TVO fit moderately better. Pearson residuals showed trends relative to the estimated values for both seasons of ChesMMAP (Figures S4 and S5). For the NEAMAP survey, the TVO model estimated high CPUE in 2013, an outlier year that we removed from the model. CPUE for NEAMAP declined from a high in 2014, which both models struggled to characterize (Figure S3). Pearson residuals of both models did not show any patterns for NEAMAP

(Figures S4 and S5). The TVO model fit the aggregate index better than the SVM, better capturing the increasing trend over time and the variability. The TVO model had a lower NLL than the SVM model, and the Pearson residuals appeared more random for the TVO model (Figures S4 and S5). There was a large outlier in the YOY survey in 2010, which both models were unable to fit (Figure S3). The VIMS juvenile trawl report explained that spot was one of most abundant species encountered by the survey and 2010 was an above average recruitment year (Tuckey and Fabrizio, 2023), indicating that this outlier may represent actual recruitment. The TVO model was mostly able to fit the trend in this survey, which increased through the early 2000s and dropped to very low levels in 2015 before increasing again. The SVM model was not able to fit the trend over time and had a larger NLL value. The Pearson residuals were difficult to interpret because of the large outlier for 2010.

According to NLL, the TVO model fit the age composition data better for all data sources except the commercial fishery. The SVM and TVO models fit the age composition of the commercial catch similarly in both regions, with standardized residuals ranging up to 5 for both regions and models (Figure S7-S10). For both regions and models, the proportion-at-age 3+ was overestimated and was slightly more of a problem in the TVO model. Additionally, both models struggled to fit age-0 in the beginning of the time series and in the years 2018-2019 when the amount of age-0 fish in the data was particularly high. The SVM model had slightly fewer patterns in the commercial proportions-at-age residuals (particularly for age-1), which likely contributed to its lower NLL value. Fit to the recreational age composition was similar between the TVO and SVM models (Figures S11-S14), with the TVO model having a better NLL. Standardized residuals ranged up to 5 for both regions and models and tended to be slightly higher for the coastal region in both models. Like the commercial age composition, both models overestimated the proportions for age-3+ in most years and underestimated the proportion of age-0 during 2018-2019 when the data had unusually high proportions of age-0. For both seasons of ChesMMAP, the models were largely only fitting ages-0 and 1 because there were few older spot encountered in the survey (Figures S15-S18). As a result, residual patterns for ages-0 and 1 were largely mirror images of one another. Both models had similar fits to the ChesMMAP summer age compositions, with TVO having a slightly better NLL due to slightly smaller residual values. For both models, the summer survey fit worse than the fall survey. Neither season had patterning in residuals over time, however, residuals were larger for the summer season with the exception of outliers in the fall survey. The fall survey had two major outlier years, 2011 and 2015, that the model could not fit. Differences between the SVM and TVO model fit to NEAMAP were very small and their NLL values were the closest of all data sources (within 0.3 NLL units; Figures S19 and S20). Both models had a tendency to overestimate age-1 and underestimate age-2. The model especially struggled to fit 2011-2012. Standardized model residuals were generally less than 2 for both models for the NEAMAP index. The aggregate index age composition was somewhat better fit by the TVO model according to NLL (Figures S21 and S22). Residuals were less than 2.5 for the SVM model and less than 8 for the TVO model. However, the large residuals for the TVO model were in 2011 and 2013. The SVM model tended to underestimate age-0 and overestimate age-1. Both models had residual patterns between ages-0 and 1 that were mirror images of one another.

Recruitment, Abundance, and Occupancy Probabilities

The models estimated substantially different average recruitment by region and trends in recruitment over time (Figure 2.2). For both regions, the TVO model estimated higher levels of recruitment than the SVM model. Both models identified 2012 as the year with the highest recruitment and 2015 as a year of the lowest recruitment. Both models also estimated that recruitment has increased since 2015. Estimated recruitment showed substantial year-to-year variability in both models. The TVO model estimated higher recruitment in the Chesapeake Bay, whereas, the SVM model estimated higher recruitment along the Atlantic Coast. Differences in recruitment and occupancy probabilities led to substantial differences in abundance between the models. The TVO model estimated higher abundance than SVM model, but the largest difference was in the Chesapeake Bay (Figure 2.3). For both regions and models, abundance increased until peaking in 2012, quickly dropping to a time series low in 2015, and increasing until 2019. The TVO model had relatively similar estimated abundance in the two regions, and the SVM model estimated higher abundance along the coast.

The estimated occupancy probabilities were substantially different between the models (Figure 2.4). The proportion of fish in the Chesapeake Bay was consistently higher in the TVO model compared to the SVM model (TVO ~ 60% and SVM~30%). The TVO model estimated a higher proportion of age-0 spot in the Chesapeake Bay than the SVM model, but the occupancy probabilities of older fish

(2-3+) were higher than for age-0 and 1 in the Chesapeake Bay in the SVM model. The TVO model also had relatively consistent occupancy probabilities over time except for 2014-2015, where the estimated occupancy probability for all ages dropped to < 40%.

Fishing Mortality Rates

The models estimated substantially different average fishing mortality rates and trends in fishing mortality over time (Figure 2.5). The SVM model estimated consistently higher values of F than the TVO model, especially in the Chesapeake Bay where F was highest and declines were steeper. For the commercial fishery, the SVM and TVO models estimated a decreasing trend in F. Trends along the coast were similar between the two models, but average F was lower for the TVO than SVM. Trends in the recreational fishery differed between the SVM and TVO models. This was especially evident in the Chesapeake Bay where values fluctuated around 1.0 yr^{-1} but steadily increased to very high values larger than 3.0 yr^{-1} around 2015-2016 for the SVM model. Estimated F along the coast had values that were much lower than the Chesapeake Bay (fluctuated around 0-0.2 yr^{-1} and peaked at 0.6 yr^{-1}). Trends in F were similar between the Chesapeake Bay and the coast for the SVM model and increased over time but decreased in recent years. Estimated F and selectivity-at-age for the commercial and recreational fleets were the same in both regions in the TVO model, so values and trends over time were the same between regions. The TVO model estimated lower values of F that ranged from 0.05 to 0.15 yr^{-1} that were less variable over time. The SVM and TVO models estimated different trends in shrimp trawl bycatch F over time, but F was higher, on average, in the SVM model. For the

SVM model, F started low (<1.0 yr^{-1}), increased until peaking in 2010 (~1.5 yr^{-1}), and was relatively stable after 2014. For the TVO model, F started high (~1.0 yr^{-1}) and decreased to lower levels (~0.4 yr^{-1}) in the mid-2010s. Both models predicted similar trends in F at age for both regions of the commercial fishery where age 3+ fish were highly selected for. The two models estimated different trends in F at age for the recreational fishery. The SVM model predicted peak selectivity to be for age-2 with all other ages similar except age-0, which had very low selectivity. The TVO model, however, predicted peak selectivity to be for age-1, with all other ages being substantially lower.

Sensitivity Analysis

Averages of estimated abundance, recruitment, fishing mortality, and occupancy probabilities for each sensitivity run are compared to base models in Table 2.7. Changing the M-at-age vector resulted in minor changes in model estimates in some cases but substantial changes in others. The low M SVM model had very similar diagnostics and estimates as the base SVM model. Trends in abundance for the low M SVM model were similar to the base SVM model, but estimated abundance was 35% lower in the Chesapeake Bay and 16% lower on the coast in the low M SVM model, on average. Estimated F was higher for the low M SVM model compared to the base SVM model for the recreational Chesapeake Bay and shrimp trawl fleets; weighted average Fs were nearly double for the recreational fishery in the Chesapeake Bay. Estimated recruitment and occupancy probabilities were, however, similar between the base and low M SVM models. The high M SVM model differed substantially from the base SVM model. Estimated abundance in the high M

SVM model had a similar trend over time as the base SVM model, but abundance was 108% higher in the Chesapeake Bay and 48% higher in the coast for the high M SVM, on average. Estimated F for all fleets was lower in the high M SVM model than the base SVM model. The high M SVM model also estimated higher average recruitment than the base SVM model. The estimated occupancy probabilities for the Chesapeake Bay in the high M SVM model were more similar to the base TVO model than the base SVM model.

The low M TVO model was somewhat different than the base TVO model. Estimated abundance in the low M TVO model was substantially lower than the base TVO model by 124% in the Chesapeake Bay and 104% in the coast. Estimated Fs were higher for each fleet in the low M TVO model, especially the recreational and shrimp trawl bycatch fleets. Estimated recruitment was lower for the low M TVO model, but the occupancy probabilities were only moderately larger. The high M TVO model and the base TVO model demonstrated similar trends in estimated abundance, recruitment, and F. Estimated occupancy probabilities from the high M TVO model estimated higher abundance of spot in the Chesapeake Bay across all ages compared to the base TVO model.

Discussion

We implemented two novel spatial models of spot population dynamics on the U.S. Atlantic coast that allowed for estimation of abundance in the Chesapeake Bay. The main difference between the models was whether fishing mortality varied between regions, or the occupancy probabilities varied over time. We used two categories of plausibility criteria to evaluate model performance: biological plausibility and model fit. Because the TVO model had a better fit to catch and indices and more realistic recreational fishing mortality rates in the Chesapeake Bay, we believe it is the better model option for spot. Furthermore, the TVO model estimated occupancy probabilities that were closer to the proportions of commercial and recreational catch in the two regions. Shrimp trawl bycatch is thought to comprise the majority of spot removals by numbers (ASMFC, 2020). The shrimp trawl bycatch F estimated by the SVM model was >1.5 yr^{-1} at its peak. This level of shrimp trawl bycatch F is plausible, but the TVO model estimated lower shrimp trawl bycatch Fs that may be more reasonable. The TVO model also estimated occupancy probabilities that were more similar across regions and ages and were more similar to the regional proportions in the commercial and recreational catches than the SVM model. These details, alongside the SVM model's poorer fit to indices, made it model appear less plausible overall.

The SVM and TVO models displayed notable similarities and differences. Estimated abundance in both models increased in both regions by very similar percentages since 2015 (SVM: 136% in the Chesapeake Bay and 139% in the Atlantic Ocean; TVO: 132% in the Chesapeake Bay and 118% in the Atlantic Ocean). Despite following a similar trend over time, the estimated abundance in each region was very different. The TVO model estimated higher abundance in the Chesapeake Bay than along the coast due to differing occupancy probabilities. These differences in abundance led to large differences in fishing mortality rates between the models, with the SVM model having higher Fs for every fleet and region. Shrimp trawl bycatch fishing mortality rate had the most notable difference in trend, in which the

SVM model estimated lower values of F that increased over time, but the TVO showed an opposite pattern. However, both models captured a major decline over time in the commercial fishery, a relatively large year class in 2012, and a relatively weak year class in 2015. Both models encountered challenges fitting all of the data simultaneously due to data conflicts, particularly between the commercial age composition and abundance indices. Many of the surveys predominantly encountered age-0 spot, while the models consistently underestimated age-0 spot in the recreational and commercial catch. This conflict between the data sources was likely why neither model could match the trend in abundance in the Chesapeake Bay indices. For example, most surveys consistently indicated a weak 2015-year class, whereas fishery age compositions showed high proportions of age-1 fish in 2016. Francis (2011) suggested that data weighting should be used to force a model to fit indices better because the purpose of conducting this type of modeling is to calculate estimates of abundance. However, when considering our abundance indices, they might not be truly representative of the stock to make extensive weighting appropriate. Because all of our Chesapeake Bay surveys largely encountered fish ages 0-1, they mostly describe recruitment which is more likely to be highly variable over time. The extreme variation present in these surveys (up to four units on the log scale in some years) may not be reasonable because older ages are not fully represented in surveys. However, this is partially accounted for by fixing selectivity at age for the older ages.

We had to penalize the fishing mortality and occupancy probability parameters for the model to obtain a unique best set of parameter estimates because we did not have data on spot occupancy or movement at the spatial scale needed to inform the model. Without penalties, both models estimated very high values of F (e.g., >10.0 yr^{-1}) for at least one fleet in one region. Also, estimated occupancy probabilities seemed implausibly low (e.g., 1%) in the Chesapeake Bay given the approximately 50:50 split of the recreational and commercial catch. Lastly, unconstrained models resulted in large differences in the occupancy probabilities from one age to the next within a region. When we tightened penalties on the occupancy probabilities, we achieved model estimates that seemed more realistic. We decided that using penalized likelihood models was favorable to other data-limited methods that make stronger assumptions about population dynamics.

We used the aggregate coastal index that combined multiple trawl surveys on the U.S. Atlantic Coast as a measure of absolute abundance available to the surveys. The two largest surveys included were NEAMAP and SEAMAP. Only three years of spot age data were available from SEAMAP, so we used proportions at age from the NEAMAP fall survey in the model because it was available for a longer period of time. Even though NEAMAP does not cover the southern extent of spot's range, this assumption seems justified because the SEAMAP age composition was similar to NEAMAP. Although we estimated the aggregate index as a measure of absolute abundance by fixing survey catchability at 1, we still allowed the model to have flexibility for biomass to differ from the index because we estimated selectivity for ages 1 and 2. The model estimated low selectivity values for older ages because they encountered fewer of these fish (Figure S6). As a result, the model estimated higher levels of coastal abundance than the aggregate survey (44-277% larger for the TVO model; 15-84% larger for the SVM model). Fixing catchability and selectivity of age-0 spot in the aggregate index at 1 is likely a conservative assumption because it is unlikely that the aggregate index covers all spot habitat on the coast and that all age-0 spot are caught if they are in the path of a trawl. However, we believe that the aggregate survey extensively covered most of the spot habitat in the coastal region, although several inland estuaries are unsampled by the surveys included in the aggregate. Although post-larval and juvenile spot are highly concentrated in coastal estuaries in the spring, they usually leave the estuaries during the fall (Weinstein, 1979; Weinstein and Brooks, 1983; Music and Pafford, 1984). Without full coverage of all estuaries, there could be fish in these unsampled areas that are not being accounted for in the aggregate index.

Use of a penalized maximum likelihood approach complicated model selection in this study. The Akaike information criterion (AIC) is commonly used for model selection (Burnham and Anderson, 2002). AIC combines a measure of fit to the data (the log likelihood) with a measure of model complexity, approximated by the number of parameters. If the negative log likelihoods of two models are the same, use of AIC will select the model with fewer parameters (i.e., lower complexity). In our case, the SVM model had fewer parameters. However, AIC is not appropriate for selecting between our models because many of the parameters were penalized. When a model penalizes parameters, the number of estimated parameters is not an accurate approximation of model complexity (Spiegelhalter et al., 2002), complicating the interpretation of AIC. In lieu of using AIC, we directly compared the negative log likelihoods from each model. A lower value of NLL indicates a better fit of a model to the data. The TVO model better fit the data as indicated by a lower negative log likelihood value. Additionally, the TVO model is likely better than the SVM model because it satisfied more of our plausibility criteria. F is also likely to vary between regions, but because this species has no tagging information to inform the occupancy probabilities, it was necessary to have common fishing mortality rates-at-age across regions for the commercial and recreational fisheries to estimate time-varying occupancy probabilities.

The TVO model indicated some degree of changing use of habitat in the Chesapeake Bay by spot over time. Schonfeld et al. (2022) found that the relative habitat usage of the Chesapeake Bay by spot had decreased during 2008-2019. Using some of the same surveys as our study (ChesMMAP and NEAMAP), Schonfeld et al. (2022) constructed a common trend of relative habitat usage that showed similar increases around 2012 and decreases around 2015 that we observed in our Chesapeake Bay abundance estimates. Because recent trends in the fishery and abundance indices have caused management concern, they suggested that the declining ratio of spot in the Chesapeake Bay is not driven by increases in coastal abundance. Spot may not be returning to the Chesapeake Bay in as large numbers during their seasonal migration, but it is unclear what is driving this preference. An additional study by Schonfeld et al. (2024) found that the concurrency of multiple climate driven stressors in the Chesapeake Bay could cause declines in relative abundance of spot. Tuckey and Fabrizio (2023) also report that recruitment indices for spot have declined in the Chesapeake Bay over the past 50 years, but year-class strength appears to be determined by environmental factors in the coastal ocean.

The majority of spot studies typically occur on a small spatial scale, therefore, population dynamics are difficult to compare to our study. Apart from the 2017 stock assessment, our study is one of the first to characterize spot population dynamics for the U.S. Atlantic stock. Similar to our results, the 2017 stock assessment peer review also indicated conflicting information on population trends. They found that catch in some fisheries declined while the indices of abundance increased (Able et al., 2017). Looking more closely at the commercial fishery which has seen the largest decline, the decline was likely caused by reductions in the haul seine fishery, which used to be more prominent historically (ASMFC, 2017). Since 2014, spot has been managed using a traffic light approach (TLA) to guide management. The TLA calculates the status of the stock using commercial and recreational harvest and survey indices relative to reference levels. Management action is triggered if thresholds are exceeded for a sufficient number of metrics. When first initiated, the TLA indicated declines in harvest that were not observed in the abundance indices (ASMFC, 2022). During 2015-2019, harvest was sufficiently low to indicate concern in four of five years for the Mid-Atlantic region and for the South Atlantic region. During 2015-2019, abundance indices were below their thresholds of concern in four of five years for the Mid-Atlantic and three of five years in the South Atlantic region (ASMFC, 2022). These results triggered management to implement bag limits in the recreational fishery and a 1% reduction in commercial catch. Estimates of abundance from our models showed qualitatively different patterns of stock status than the TLA because estimated abundance increased since 2015, which tracked the indices of abundance used in both models. Compared to both spatial models, the TLA is a non-population dynamics approach that is not able to reconcile trends across different data sets. The TLA presents a more concerning picture of the stock than the TVO or SVM models. Furthermore, the TLA breaks up the coastal regions into two zones (north versus south) whereas the TVO and SVM model the population in one coastal region and the Chesapeake Bay. The TVO could be improved by separating the coastal region into the north and south to match fishing effort, however, data are probably too limited to inform a three-region spatial model.

Continued development of a spatially-explicit stock assessment for spot will be challenging due to data limitations. A challenge we faced was that age data for spot fishery catches were only available from Virginia, North Carolina, and Maryland commercial fisheries. To have adequate samples for age-length keys, we aggregated the data from three states to inform an entire region. Because recreational age data were not available, we had to use the commercial age length key to create recreational age compositions. This treatment of the recreational fishery data assumed that growth of spot was the same for fish captured in both fisheries. The current data may be insufficient to support a robust spatial model, particularly due to limited information on age-specific movement and habitat use and relatively few observations of older fish (ages 2+) in surveys. Without more information on older fish, the model estimated low selectivities for surveys (or they were specified to be zero due to a lack of observations). Ideally, tagging studies and more extensive surveys that encounter older fish or unsampled coastal estuaries would be needed to develop a stronger spatially structured SCAA model. Alternative approaches, such as treating fleets as proxies for spatial areas, could be explored to address this gap (Cope and Punt, 2011;

Punt et al., 2014), but this would not help clarify spatial trends in abundance indices. Because the survey indices in the Chesapeake Bay showed different patterns than those on the coast, there may be evidence of spatial structure or time-varying habitat use in this population. Several studies have emphasized the benefits of incorporating movement between regions in stock assessments, which can significantly improve estimates of stock size, fishing mortality, and recruitment (McGilliard et al., 2015; Goethel, 2011). Other approaches may also help to inform the estimation of the occupancy probabilities. For example, the geographic size of the Chesapeake Bay and the Atlantic coastlines could be used to inform the occupancy probabilities. Similarly, including the Chesapeake Bay surveys in the VAST model could help inform the proportions of fish in each area.

The population model estimates generally agreed with the trends in biomass over time from Chapter 1, but they disagreed with the fishing mortality rate estimates. We found that the fishery catches were likely not tracking abundance, which resolved a key uncertainty highlighted in the 2017 stock assessment. Trends in biomass over time from both chapters were similar with increasing biomass during 2005-2012, decreasing biomass during 2013-2015 or 2016, and an increasing trend thereafter. However, trends in mortality rates from Chapter 1 differed from the SVM and TVO model trends in mortality. The Chapman-Robson analysis showed increasing total instantaneous mortality rate in recent years, yet fishing mortality rate from the TVO and SVM models showed a decline in recent years for the commercial and recreational fleets. Due to the complexity of the spatial model which was able to combine multiple data sources, and the concerns regarding violations of assumptions for the Chapman-Robson analysis, the spatial models are likely a more accurate reflection of changes in mortality rates. The work from both chapters provides new insights into the spot population along the Atlantic Coast which can be used going forward to improve their management.

In conclusion, we developed spatially-structured statistical catch-at-age models that advance our understanding of the population dynamics of spot, which is a relatively understudied species despite its common occurrence in commercial and recreational fisheries. We developed a unique approach to spatial population modeling by allowing for time-varying occupancy probabilities. The lack of tagging data is a common problem that prevents people from implementing spatial models (Goethel et al., 2011; Punt, 2019). Through a combination of using an absolute abundance index for the coast and penalties on the occupancy parameters, we were able to successfully implement a spatial catch-at-age model without using tagging data. We demonstrated that spatial modeling can be a useful tool to better understand a complex system such as the Chesapeake Bay, which is increasingly important to understand the future effects of environmental change. These methods should be considered for further development in the next stock assessment to improve and strengthen spot management.

Tables

Table 2.1: Description of fisheries independent data sources including the survey name, area sampled, ages of spot caught, gear, years sampled, months sampled, and region applied in the model. Young-of-the-year (i.e., age-0) surveys are indicated as YOY.

Survey Name	Location	Age	Gear	Years	Season	Region in model
Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP)	Mainstem of the Chesapeake Bay	0-3+ (Very few age-3)	Trawl	2002-2019	March, June, September, and November	Chesapeake Bay
Northeast Area Monitoring and Assessment Program (NEAMAP)	Mid-Atlantic	0-3+ (very few age 3)	Trawl	2008-2019	Spring, Fall	Coast
Virginia Institute of Marine Science (VIMS) Juvenile Finfish Trawl Survey (YOY)	Virginia portion of the Chesapeake Bay	0	Trawl	1989-2019	Fall	Chesapeake Bay
Aggregate Coast Index	Atlantic Coast	0-3+	Trawl	2002-2019	Fall	Coast

Table 2.2: Description of estimated and fixed selectivity-at-age parameters for each fleet or survey, where 1 indicates ages that had selectivity specified at 1, 0 indicates ages that had selectivity specified at 0, and "estimated" refers to parameters that are estimated by the model.

Fishery or Survey	Age 0	Age 1	Age 2	Age 3+
Commercial Bay and Coast	estimated	1	1	1
Recreational Bay and Coast	estimated	1	estimated	estimated
ChesMMAP Summer	1	estimated	estimated	0
ChesMMAP Fall	1	estimated	estimated	0
NEAMAP Spring	0	1	estimated	0
Aggregate	1	estimated	estimated	0

Table 2.3: *Seasonal timing of surveys represented by the fraction of fishing mortality (F) and natural mortality (M) that occurred before the survey. The commercial and recreational fisheries were assumed to occur during August-November. Survey abbreviations are defined in Table 2.1.*

Survey	Timing of survey	Parameter value F	Parameter value M
ChesMMAP Summer	June-July	0	6/12
NEAMAP Spring	April-May	0	4/12
ChesMMAP Fall	September-November	6/12	9/12
Aggregate	Fall (September-October)	6/12	9/12

Table 2.4: Penalties for model parameters including the occupancy probabilities (P) and fishing mortality rate (F) with their means and standard deviations. Parameters were penalized using normal distributions. X indicates the value that was used to calculate the penalty including any transformations.

Number	Penalties	Equation	Mean	Standard Deviation
4.1	Penalize average of P0 (P for age 0) in the Chesapeake Bay $(-ln(L_{P0}))$	$X = \sum_{y} \frac{P_{y,Chesapeake\ Bay}}{18}$	0.69	0.1
4.2	Keep P for ages 1-3+ close to 0.5 $(-ln(L_{Psplit}))$	$X = P_{y,a}$	0.5	0.2
4.3	Minimize differences in P between ages $(-ln(L_{Pagediff}))$	$X = P_{y,a} - P_{y,a+1}$	0	0.05
4.4	Minimize year to year differences in commercial F $(-ln(L_{F-cdiff}))$	$X = \log(\tilde{F}_{commercial,r,y}) - \log(\tilde{F}_{commercial,r,y+1})$	0	0.2
4.5	Minimize year to year differences in recreational F $(-ln(L_{F-rdiff}))$	$X = \log(\tilde{F}_{recreational,r,y}) - \log(\tilde{F}_{recreational,r,y+1})$	0	0.2
4.6	Minimize year to year differences in shrimp F $(-ln(L_{F-sdiff}))$	$X = \log(\tilde{F}_{shrimp,r,y}) - \log(\tilde{F}_{shrimp,r,y+1})$	0	0.2
4.7	Minimize recreational bay F $(-ln(L_{Frecbay}))$	$X = \log(\tilde{F}_{recreational,r,y})$	-0.69	1
4.8	Minimize Shrimp F $(-ln(L_{Fshrimp}))$	$X = \tilde{F}_{shrimp,r,y}$	0.5	1
4.9	Minimize difference between coast and bay recreational selectivity $(-ln(L_{Sel}))$	$X = \log(Sel_{a,r}) - \log(Sel_{a,r+1})$	0	0.2
4.10	Random walk for P to vary over time $(-ln(L_{Pdevs}))$	$X = logit(P_{devs})$	0	0.2

Table 2.5: *Qualitative plausibility table used to evaluate and compare the spatially-varying mortality (SVM) model and the time-varying occupancy model (TVO).*

Criteria	**SVM**	**TVO**
Biological Plausibility		
Occupancy probabilities not very high or low	Low proportion in the Chesapeake Bay relative to the coast	Yes
Occupancy probabilities for neighboring ages should be similar	Yes	Yes
Selectivity pattern with implausible jumps between ages	Yes	Yes
Fishing mortality rate (F) should not be too high (F>2 kills the majority of fish in a region)	Very high F for the recreational fishery in the Chesapeake Bay and shrimp trawl bycatch	F is reasonable
Model Fit		
Good fit to catch	Commercial good	Commercial good; Better fit to recreational and shrimp trawl bycatch than SVM
Reasonable fit to indices	Cannot match extremes in all surveys	Cannot match extremes in all surveys; Better fit to most surveys than SVM; Much better fit to aggregate than SVM
Avoid major patterns in age composition residuals (avoid standardized residuals >4, runs, many outliers)	Issues discussed in results section, largely the same for both models. SVM slightly larger residuals for several data sources	
Pearson residual plots should appear random without extreme values (> 4)	ChesMMAP trending, outliers in aggregate and YOY	ChesMMAP trending, outliers in aggregate and YOY

Table 2.6: *Objective function value, negative log likelihood components (NLL), and penalties for the spatially-varying mortality (SVM) model and the time-varying occupancy (TVO) model.*

Likelihood component	**SVM**	**TVO**
Data		
Objective function value	0.51	81.94
Total NLL	36.76	19.78
Commercial	−54.64	31.48
Recreational	17.69	3.59
Shrimp trawl bycatch (Shrimp)	44.87	39.92
ChesMMAP summer (CMJJ)	59.07	40.74
ChesMMAP Fall (CMSN)	95.17	68.15
NEAMAP (NMS)	4.81	5.67
Aggregate	81.51	22.96
YOY	21.94	18.81
PAA Commercial	−50.67	20.48
PAA Recreational	−90.43	−101.86
PAA ChesMMAP summer (PAA CMJJ)	5.39	−7.54
PAA ChesMMAP Fall (PAA CMSN)	−51.49	−54.58
PAA NEAMAP	−26.20	−26.52
PAA Aggregate	−20.26	−41.52
Penalties		
P random walk deviations (P devs)	−46.95	44.15
Average P for age 0 in Chesapeake Bay (P0)	7.99	0.18
Average P for ages 1-3+ near 0.5 (P difference)	−16.41	-29.20
P age differences	−103.75	−85.43
Shrimp trawl bycatch F (Shrimp F)	18.70	17.05
Commercial F difference	80.56	81.32
Recreational F difference	1.79	−5.67
Shrimp F difference	1.04	4.88
Recreational F	21.87	36.97
Recreational Selectivity	−1.08	−2.07

Table 2.7: Average values of recruitment, abundance, fishing mortality rate (F), and occupancy probability (P) for sensitivity analyses of alternative natural mortality rate (M) values for the time-varying occupancy (TVO) and spatially-varying mortality (SVM) models. N at age were summed across ages before averaging. F values were calculated as a weighted average of abundance in each age class in a given year.

Estimate	Base SVM Model	SVM Low M	SVM High M	Base TVO Model	TVO Low M	TVO High M
Recruitment Bay	134.4	92.0	445.9	613.5	155.2	696.0
Recruitment Coast	359.7	304.4	555.2	506.3	183.7	566.5
Abundance Bay	173.0	121.4	586.7	878.3	203.1	935.9
Abundance Coast	441.4	373.3	726.0	716.1	223.3	757.4
F Commercial Bay	0.1	0.17	0.02	0.01	0.06	0.01
F Commercial Coast	0.18	0.02	0.01	0.01	0.05	0.01
F Recreational Bay	0.28	0.52	0.05	0.03	0.18	0.03
F Recreational Coast	0.6	0.07	0.03	0.03	0.14	0.03
F Shrimp Trawl Bycatch	0.73	0.84	0.43	0.42	1.45	0.43
P Age 0 (Bay)	0.27	0.23	0.44	0.46	0.46	0.55
P Age 1 (Bay)	0.32	0.29	0.45	0.44	0.55	0.56
P Age 2 (Bay)	0.33	0.32	0.45	0.44	0.56	0.56
P Age 3+ (Bay)	0.33	0.32	0.45	0.44	0.56	0.56

Figures

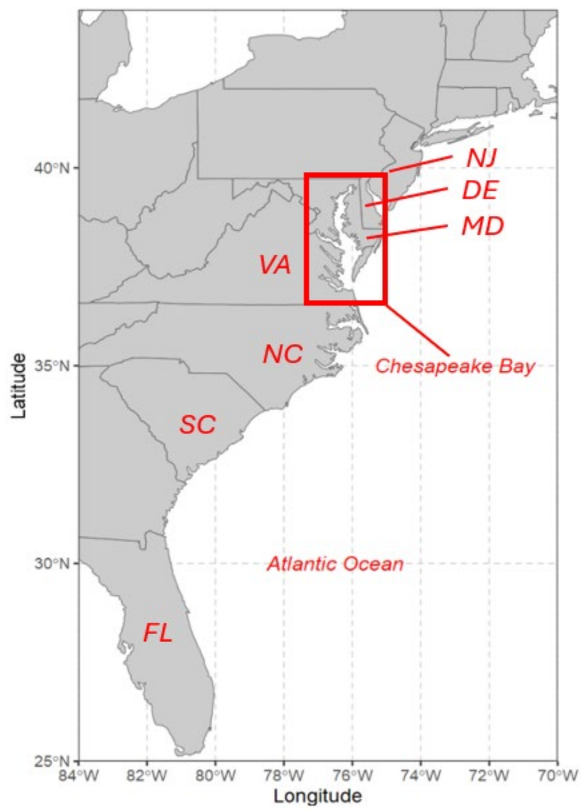

Figure 2.1: *Study region for spatial population model of spot in the U.S. Atlantic. Chesapeake Bay region (outlined in red) included Maryland (MD) and Virginia (VA). The Atlantic Coast region includes New Jersey (NJ), Delaware (DE), MD, VA, North Carolina (NC), South Carolina (SC), and Florida (FL) including all of the estuaries in this region except for the Chesapeake Bay.*

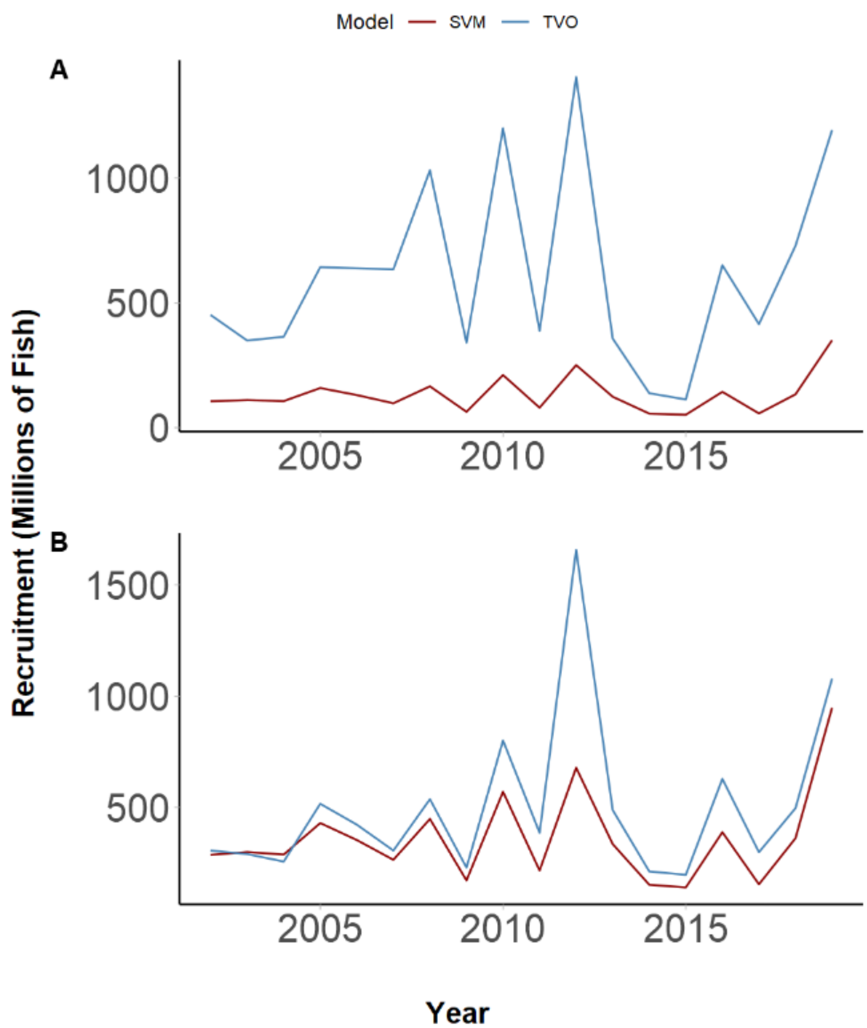

Figure 2.2: *Estimated recruitment of spot over time for the spatially-varying mortality (SVM) model (red line) and the time-varying occupancy (TVO) model (blue line) in the Chesapeake Bay (A) and the Atlantic coast (B).*

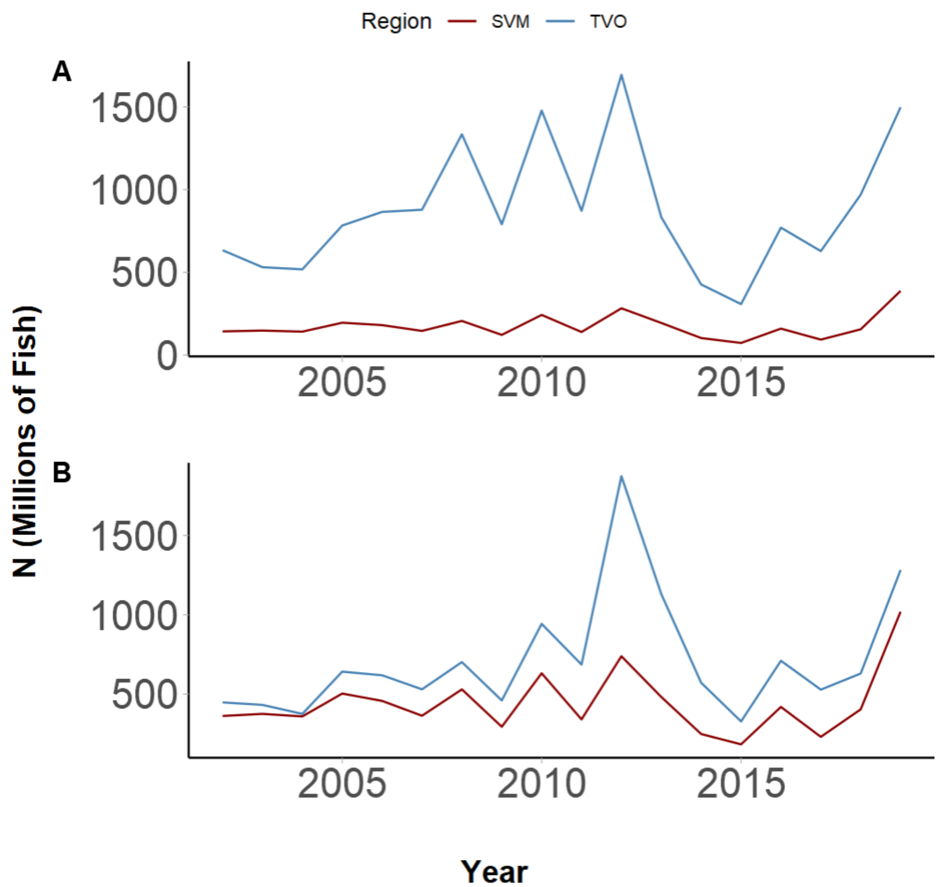

Figure 2.3: *Estimated abundance (N) over time in the Chesapeake Bay (A) and the remainder of the U.S. Atlantic Coast (B) from the spatially-varying mortality (SVM) model (red line) and the time-varying occupancy (TVO) model (blue line).*

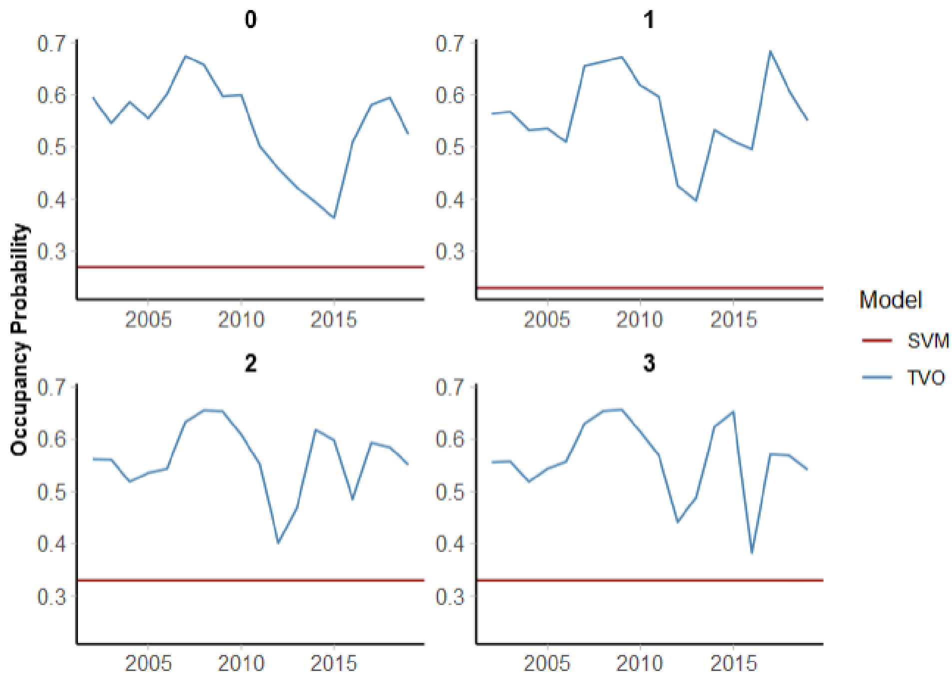

Figure 2.4: *Estimated occupancy probabilities-at-age of spot in the Chesapeake Bay over time from the time-varying occupancy model (TVO, blue line) and the spatially-varying mortality model (SVM, red line). Numbers above each panel refer to the age of spot, and age 3 represents all spot age 3 and older.*

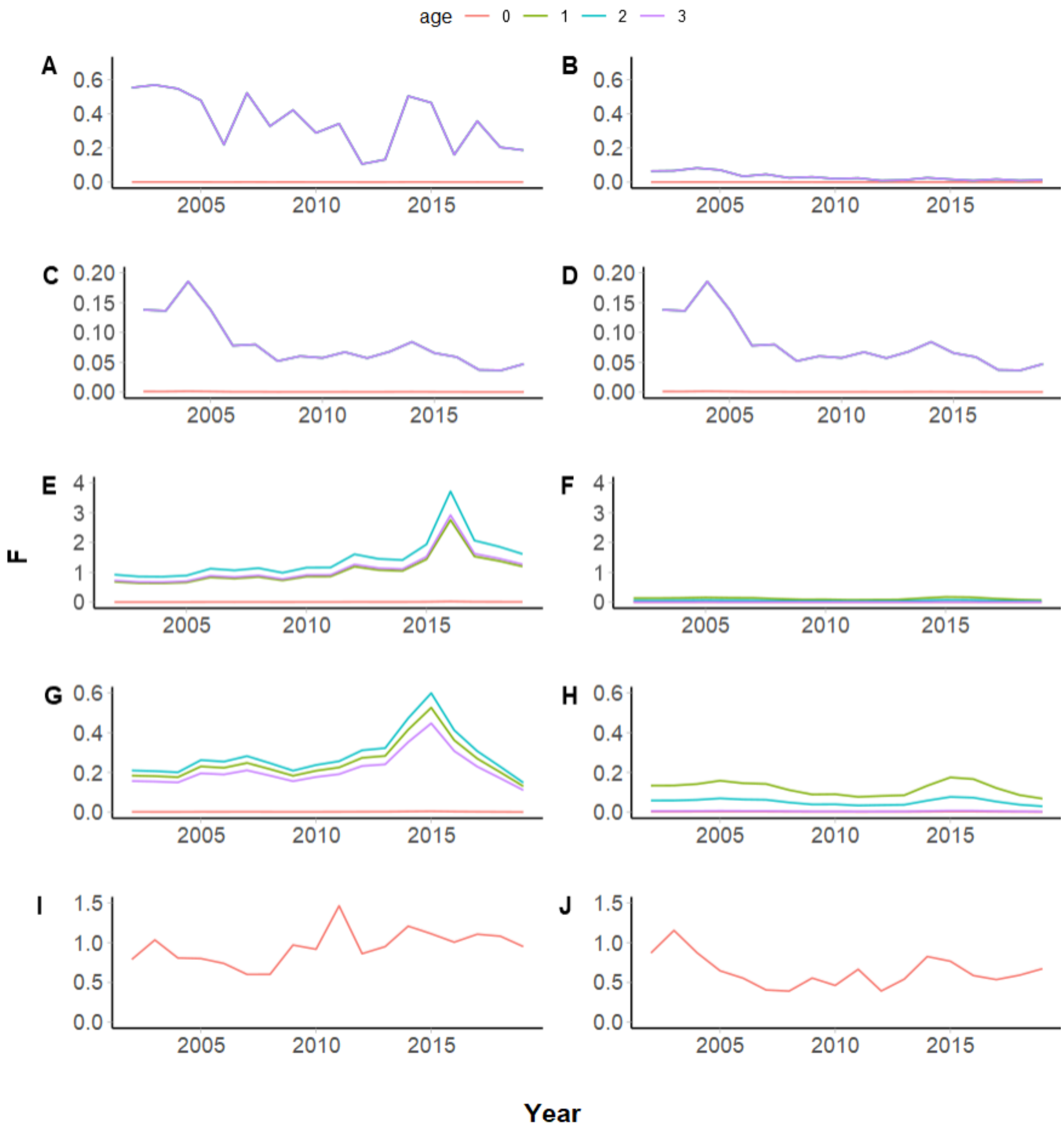

Figure 2.5: *Estimated fishing morality rates-at-age (F yr^{-1}) for the Chesapeake Bay commercial fishery (A and B), coast commercial fishery (C and D), Chesapeake Bay recreational fishery (E and F), coast recreational fishery (G and H), and shrimp trawl bycatch (I and J). The left column is the spatial-varying mortality model and the right column is the time-varying occupancy model. Ages are indicated by the colors.*

Supplemental Tables

Table S1. Effective sample sizes (Neff) and log-scale standard deviations (CV) used to weight the data sources in the negative log likelihood functions. The same values were used in both the spatially-varying mortality and time-varying occupancy models.

Data Source	Neff	CV
Commercial	20	0.05
Recreational	10	0.2
Shrimp Trawl		0.2
ChesMMAP Summer	20	0.4
ChesMMAP Fall	20	0.4
NEAMAP	10	0.4
Aggregate	20	0.2
YOY		0.7

Table S2. Natural mortality (M) values-at-age (yr^{-1}) for the base model runs and sensitivity analyses. The low and high values for the sensitivity analyses were calculated as the base value ± 0.145.

Run	Age 0	Age 1	Age 2	Age 3+
Base	1.00	0.925	0.8	0.83
Low M (Lorenzen (2005) values)	0.86	0.78	0.73	0.69
High M	1.15	1.07	1.02	0.98

Supplemental Figures

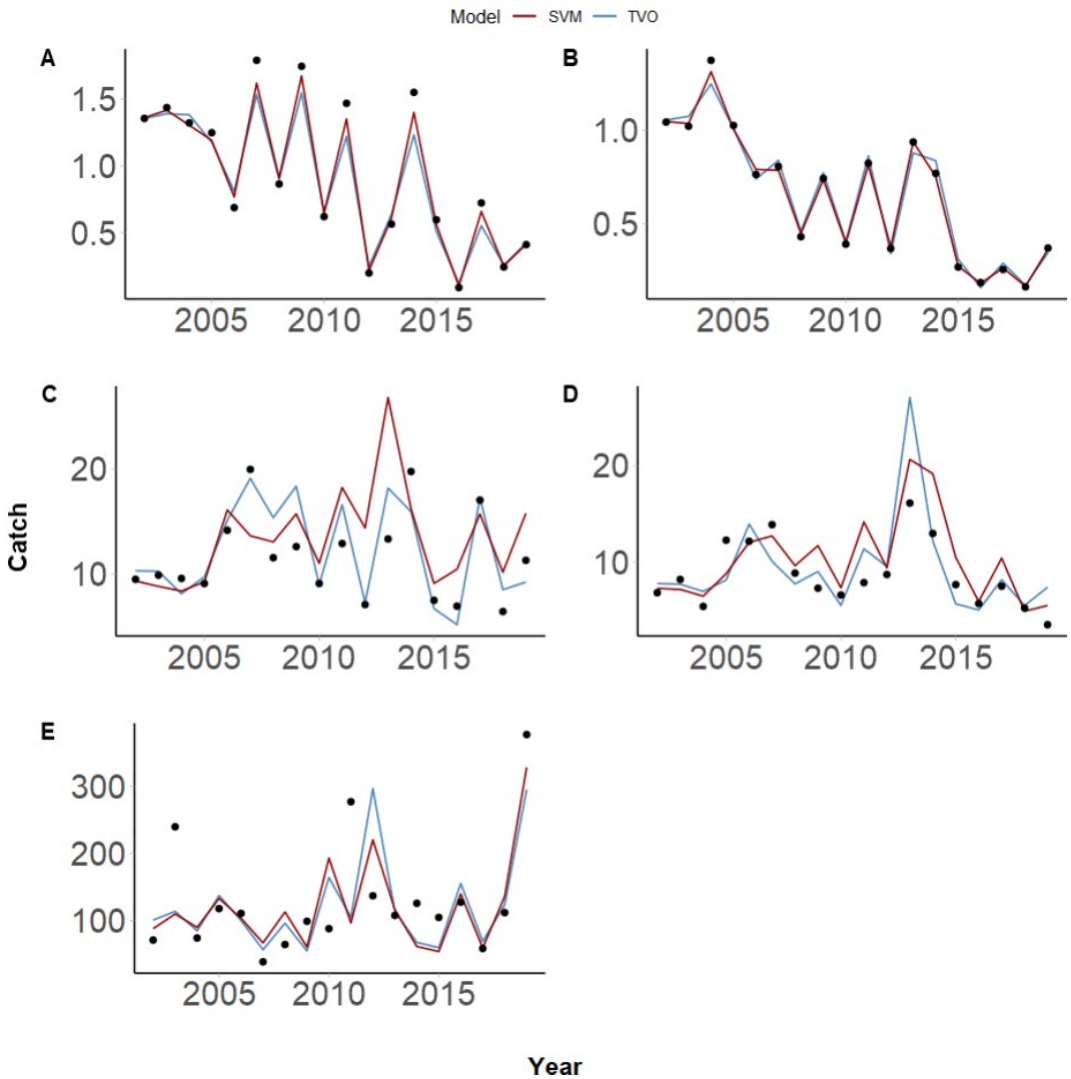

Figure S1. Fit of spatially-varying mortality (SVM) model (red line) and time-varying occupancy (TVO) model (blue line) to fishery catch data (black points) for spot. Fishery catch data included commercial for the Chesapeake Bay (A), commercial coast (B), recreational Chesapeake Bay (C), recreational coast (D), and shrimp trawl bycatch (E). Commercial catch is in millions of kilograms, and recreational catch and shrimp trawl bycatch are in millions of fish.

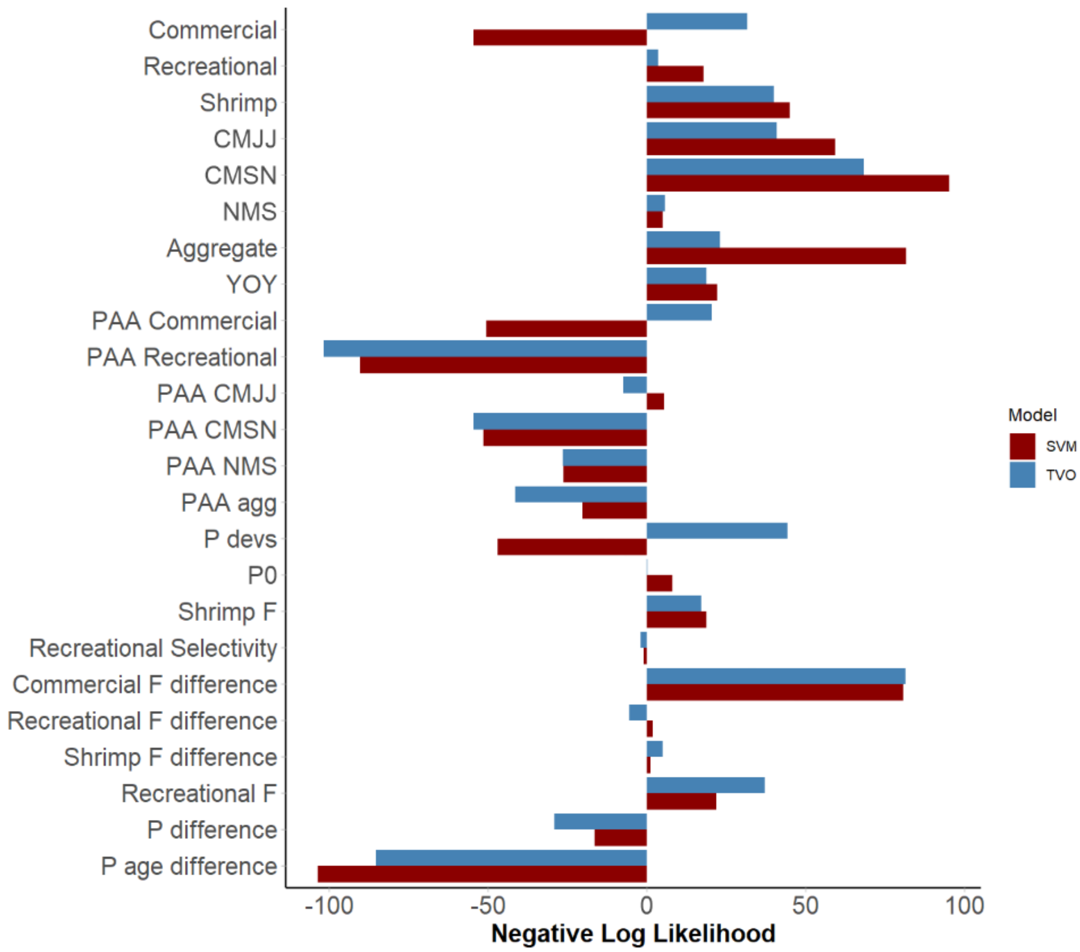

Figure S2. Components of the total likelihood objective function for both the spatially-varying mortality (SVM) model and the time-varying occupancy (TVO) model. Abbreviations and penalty names can be found in Table 2.6.

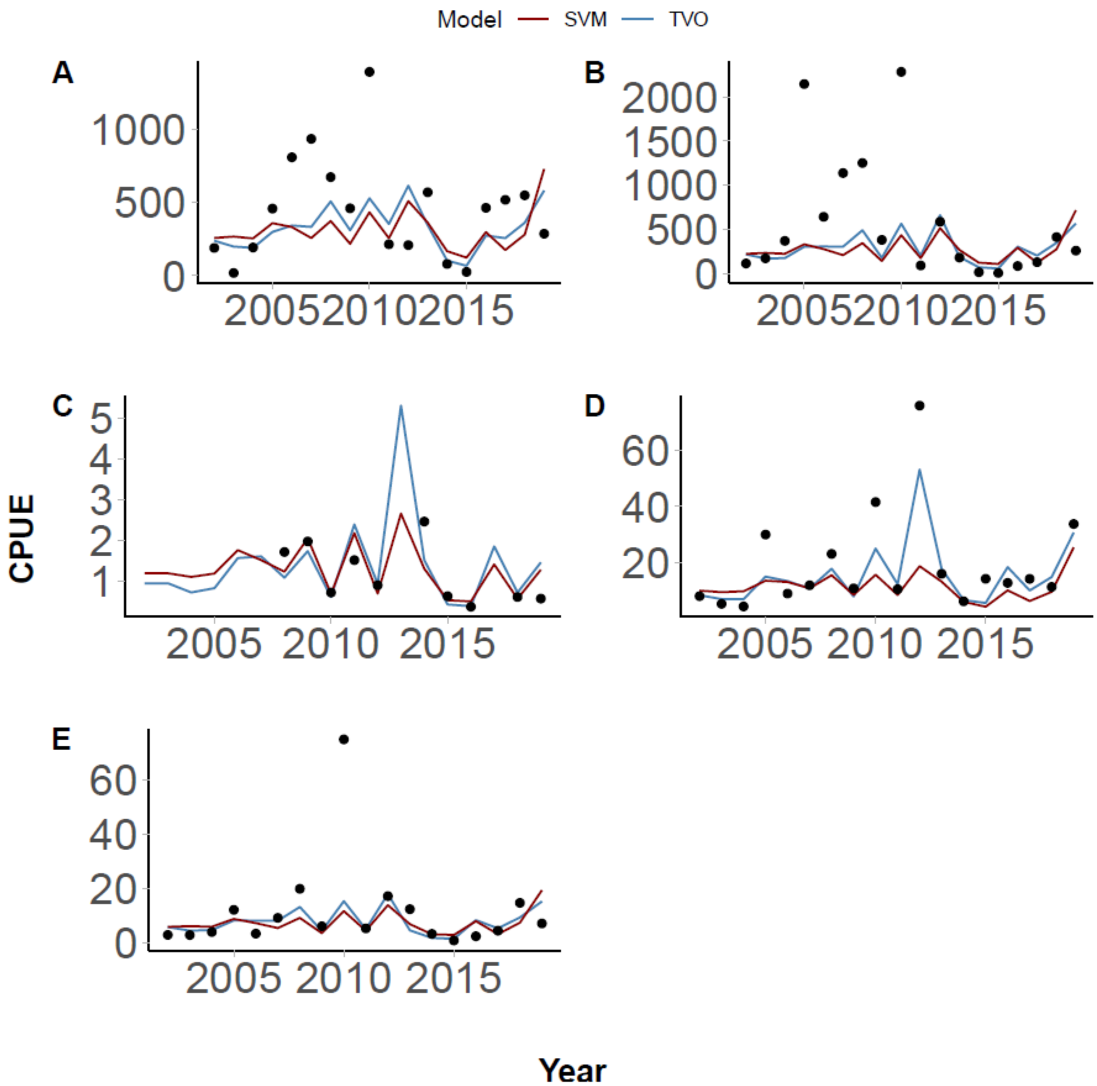

Figure S3. Fit of spatially-varying mortality (SVM) model (red line) and time-varying occupancy (TVO) model (blue line) to fishery independent indices (black points) for spot. Fishery independent indices included ChesMMAP Summer in numbers of fish per hectare (A), ChesMMAP Fall in numbers of fish per hectare (B), NEAMAP Spring in geometric mean numbers of fish (C), Aggregate index in millions of kilograms (D), and the young of the year index in weighted geometric mean numbers (E). Survey abbreviations are defined in Table 2.1.

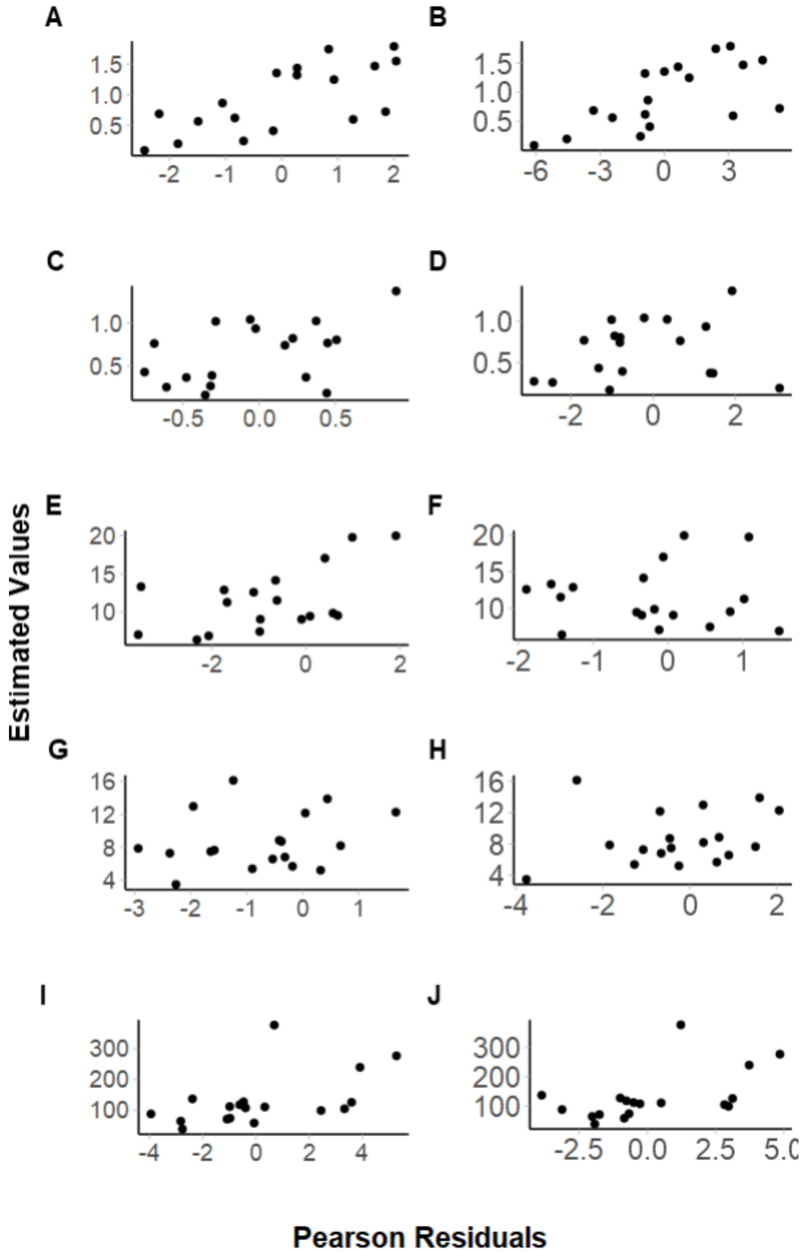

Figure S4. Pearson residuals versus estimated values for the spatially-varying mortality (SVM; left column) and time-varying occupancy (TVO; right column) models. Data sources include the commercial catch in the Chesapeake Bay (A and B), commercial catch on the coast (C and D), recreational catch in the Chesapeake Bay (E and F), recreational catch on the coast (G and H), and shrimp trawl bycatch (I and J).

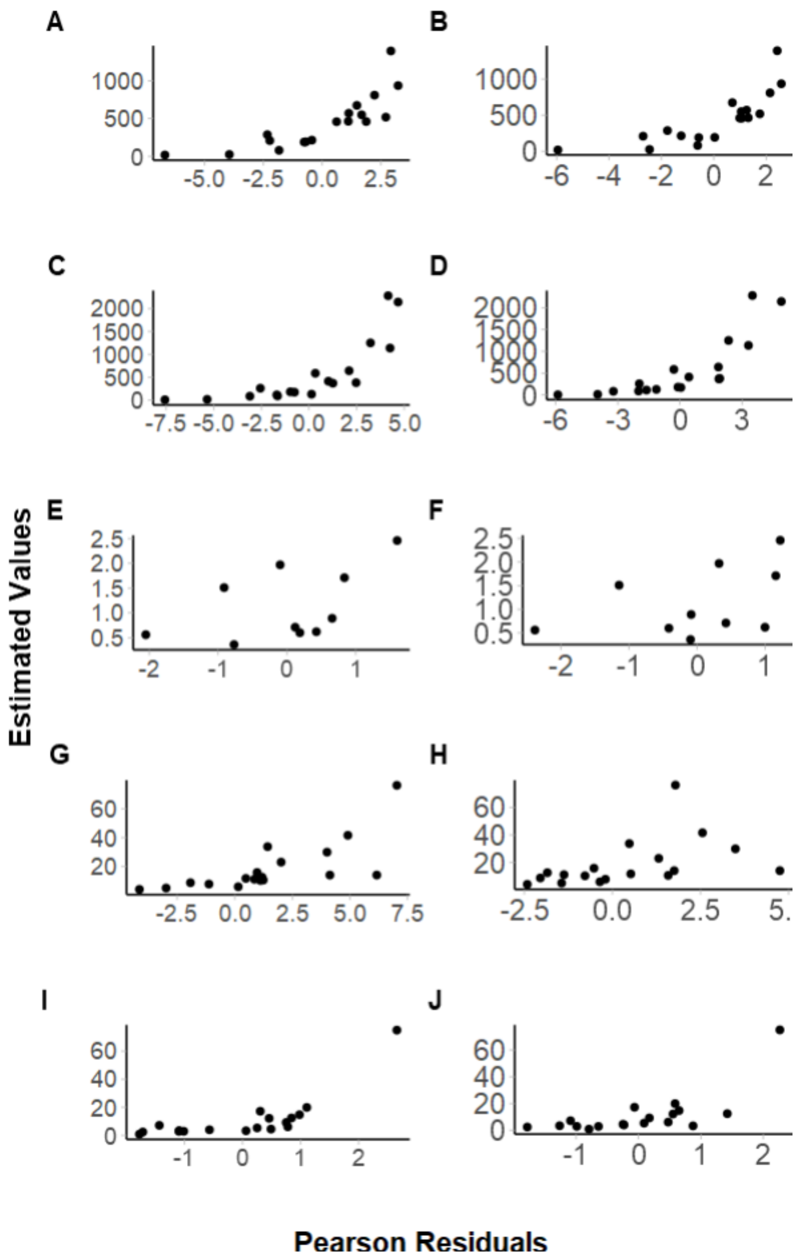

Figure S5. Pearson residuals versus estimated values for the spatially-varying mortality (SVM; left column) and time-varying occupancy (TVO; right column) models. Data sources ChesMMAP summer index of abundance (A and B), ChesMMAP fall index of abundance (C and D), NEAMAP index of abundance (E and F), aggregate index of abundance (G and H), YOY index (I and J).

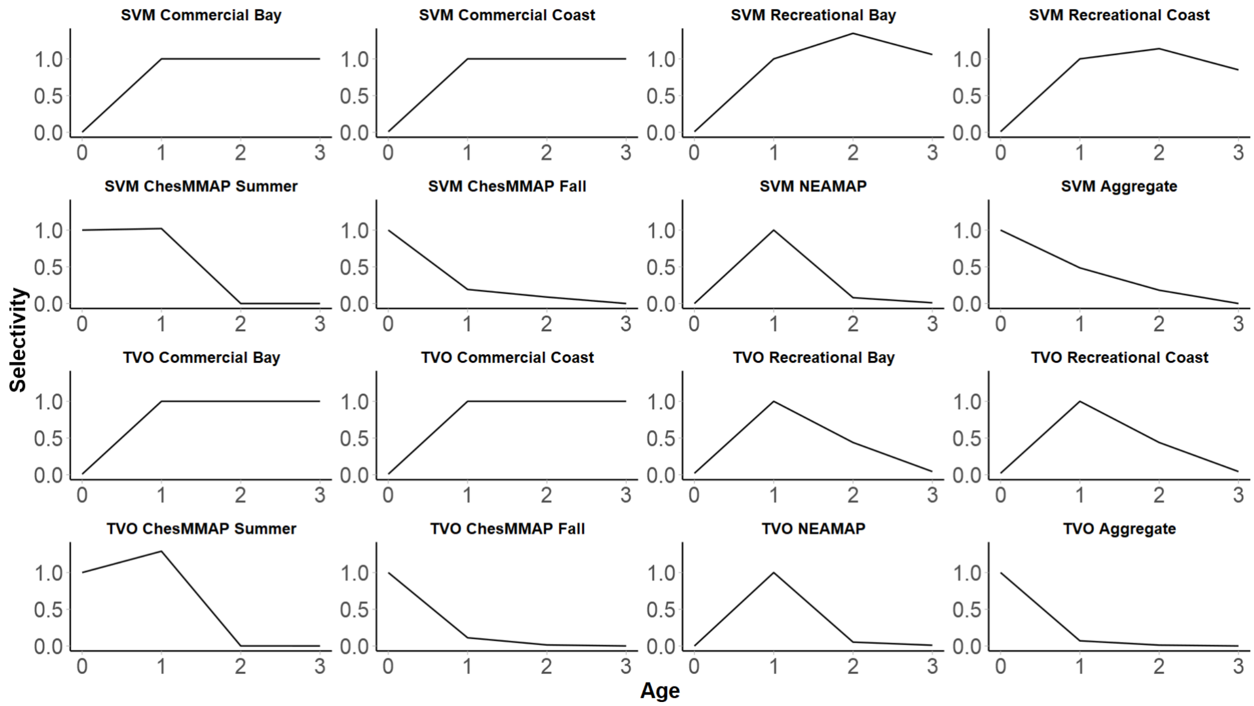

Figure S6. Selectivity patterns for the spatially-varying mortality (SVM) and time-varying occupancy (TVO) model.

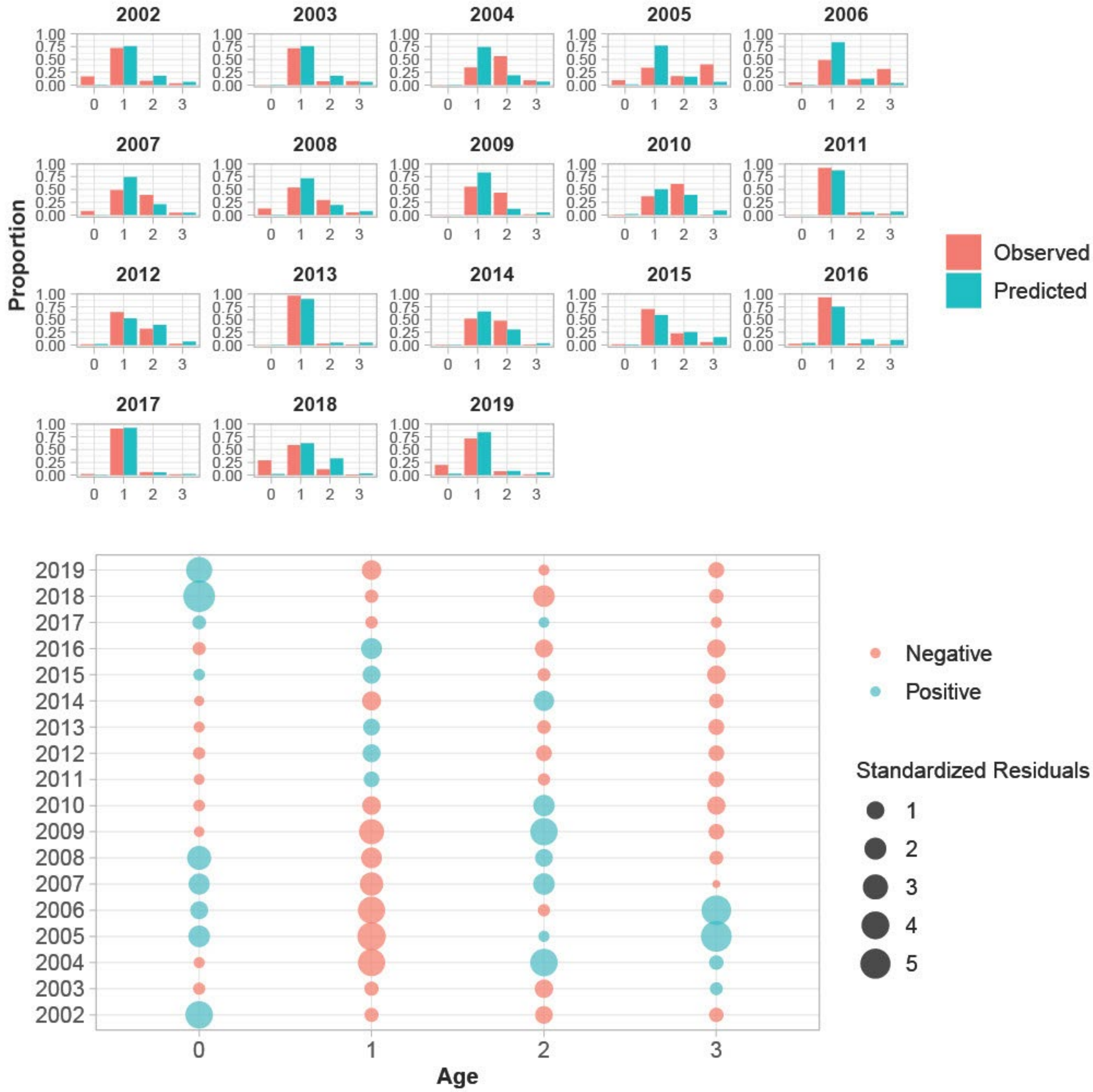

Figure S7. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for commercial catches in the Chesapeake Bay from the spatially-varying mortality (SVM) model.

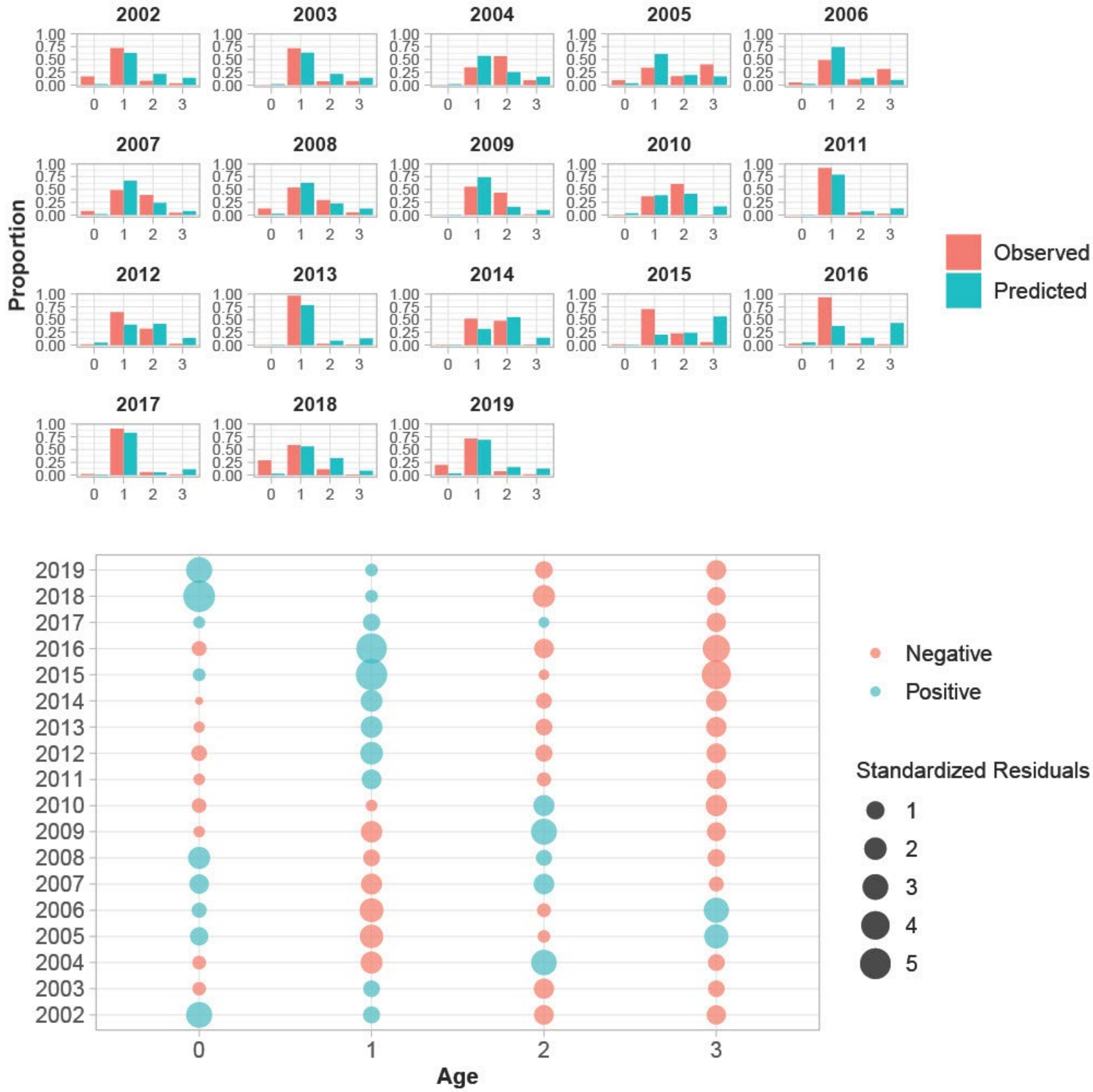

Figure S8. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for commercial catches in the Chesapeake Bay from the time-varying occupancy (TVO) model.

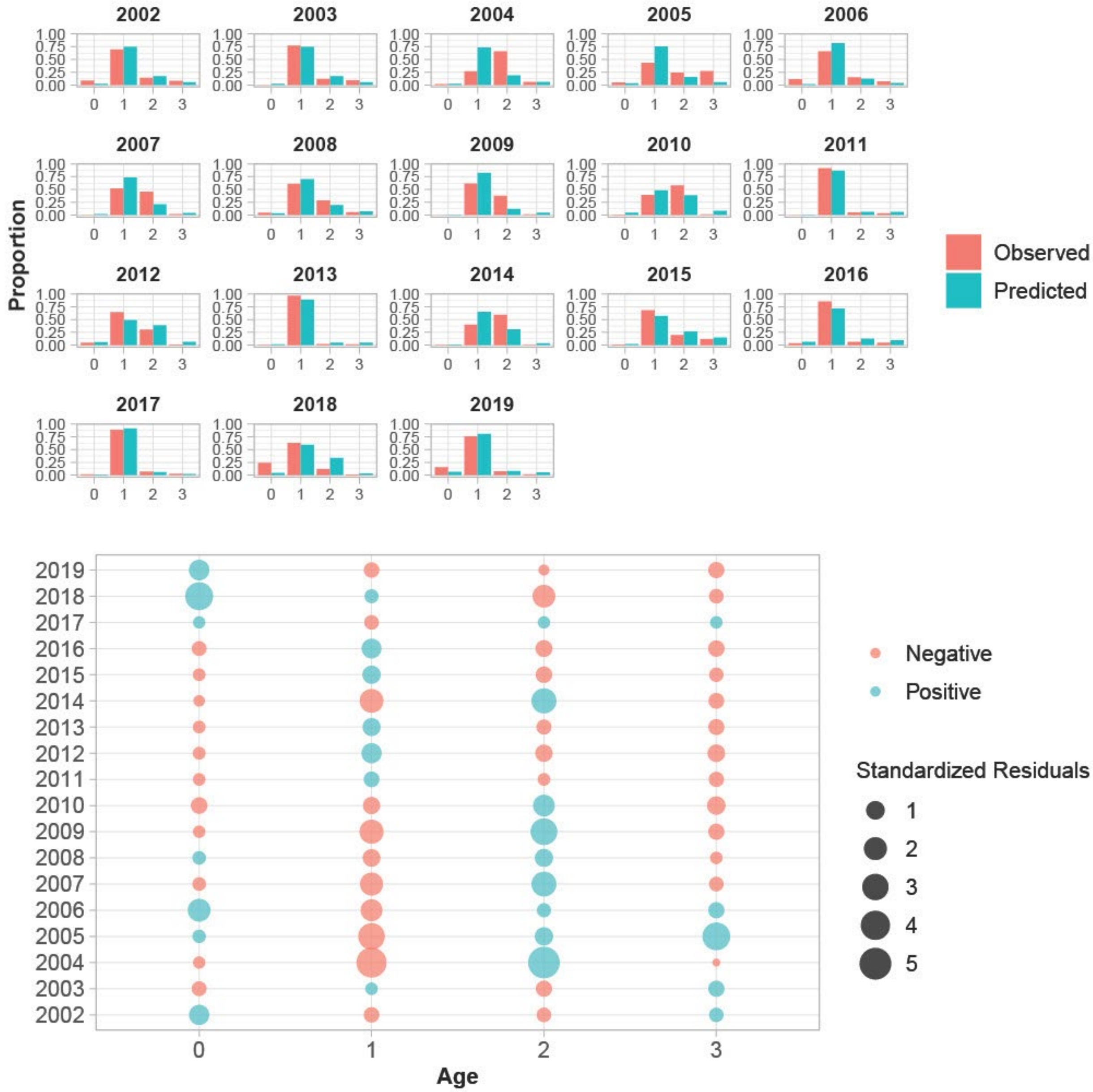

Figure S9. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for commercial catches in the coast from the spatially-varying mortality (SVM) model.

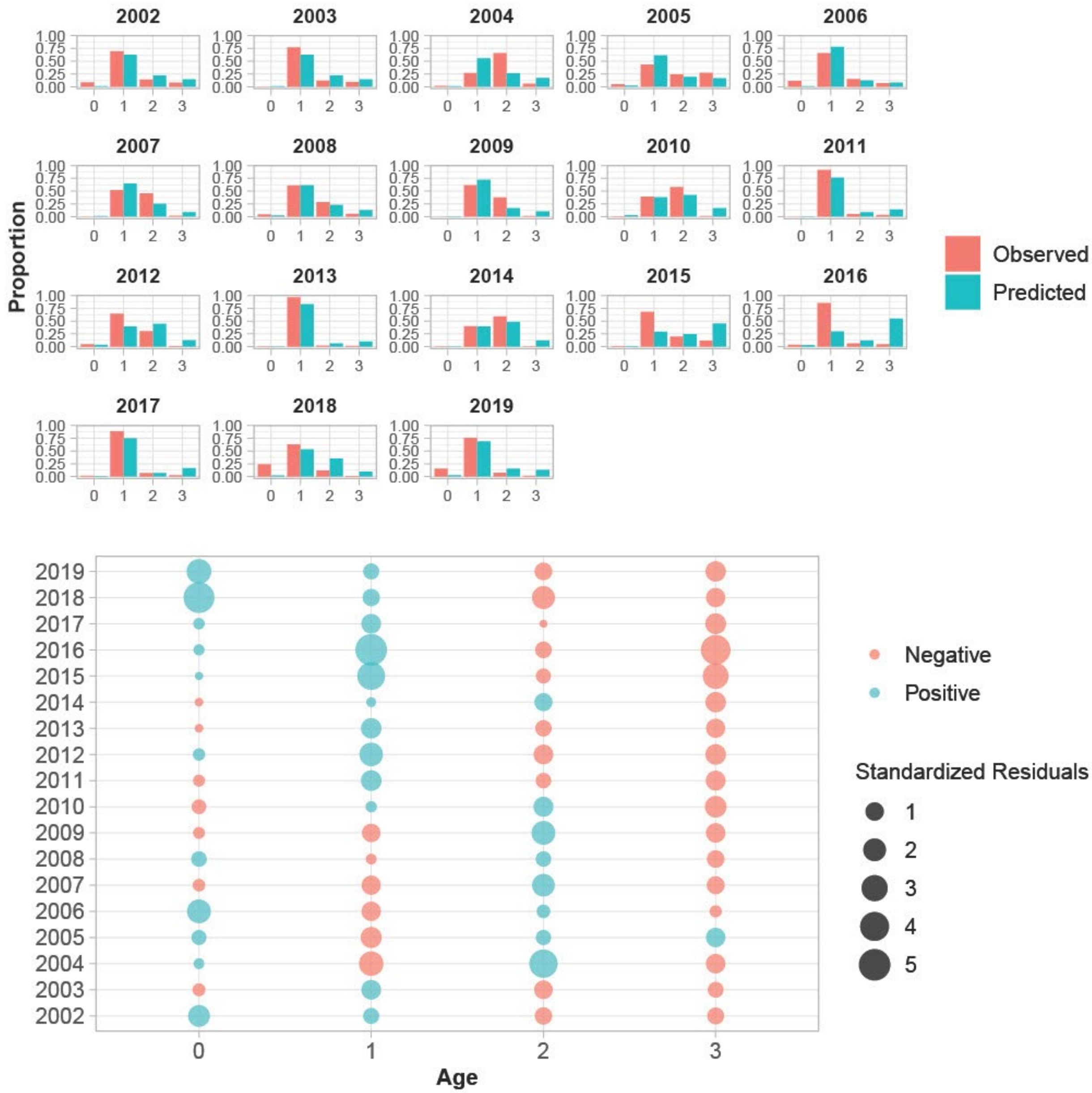

Figure S10. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for commercial catches in the coast from the time-varying occupancy (TVO) model.

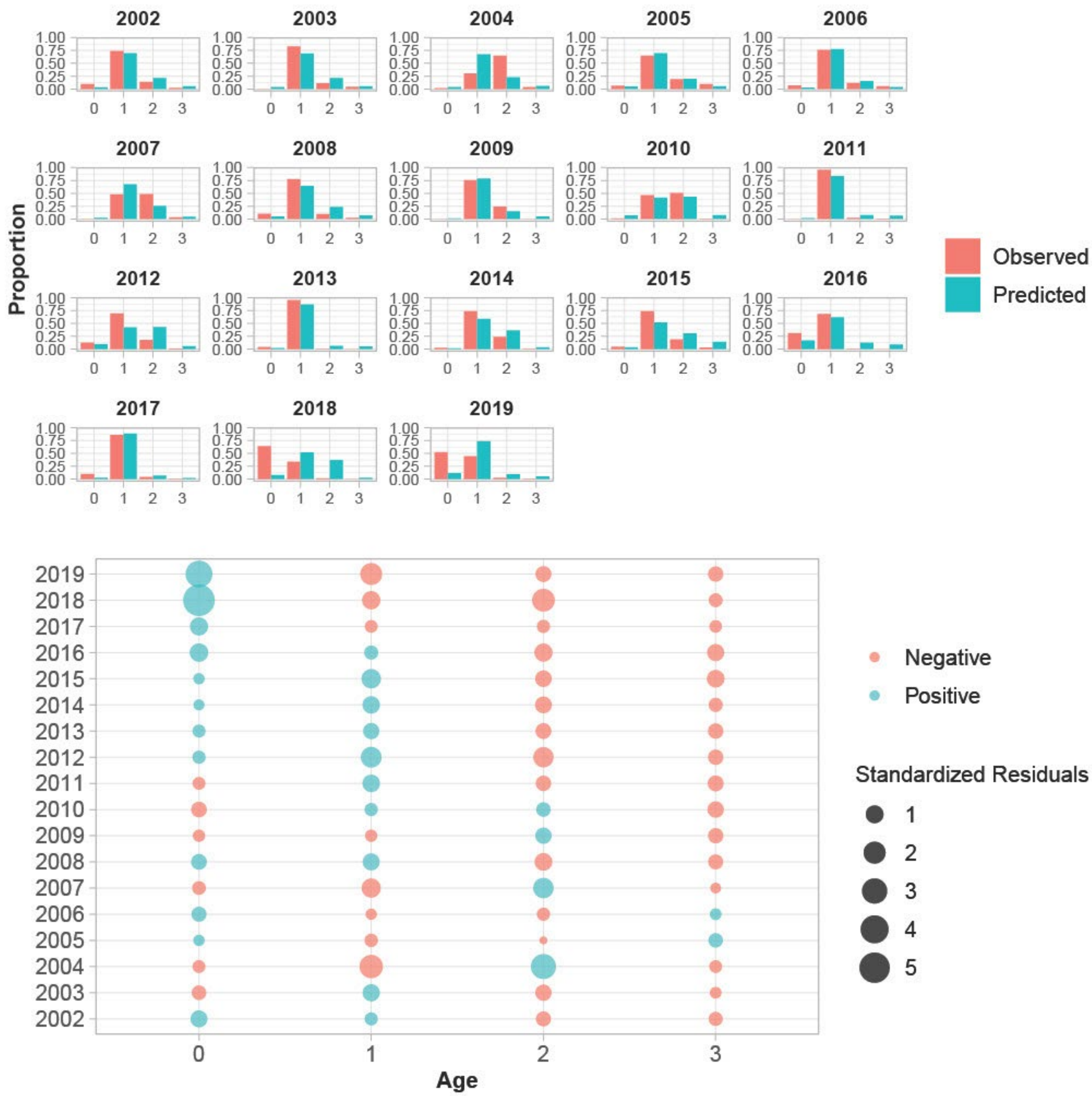

Figure S11. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for recreational catches in the Chesapeake Bay from the spatially-varying mortality (SVM) model.

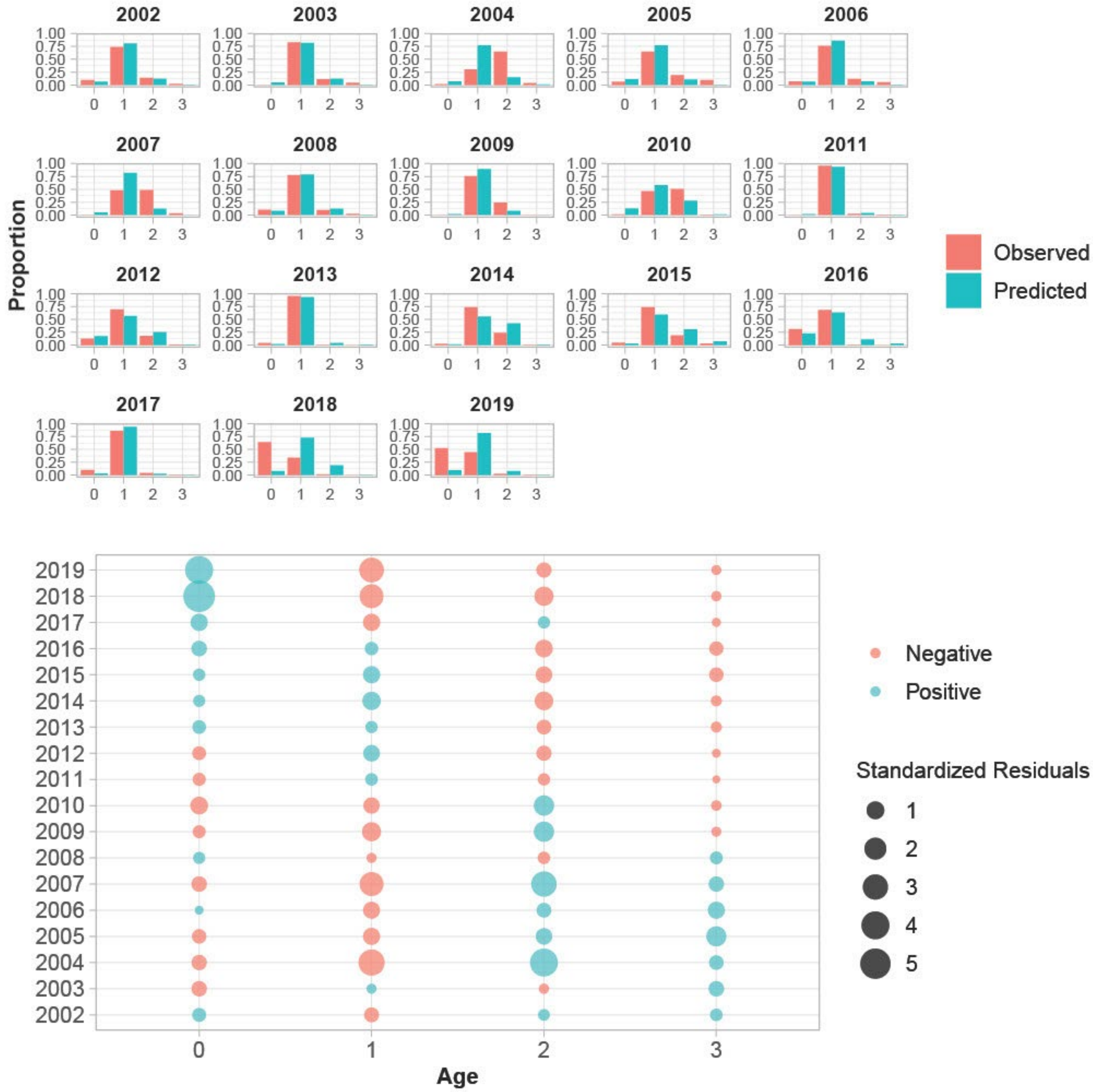

Figure S12. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for recreational catches in the Chesapeake Bay from the time-varying occupancy (TVO) model.

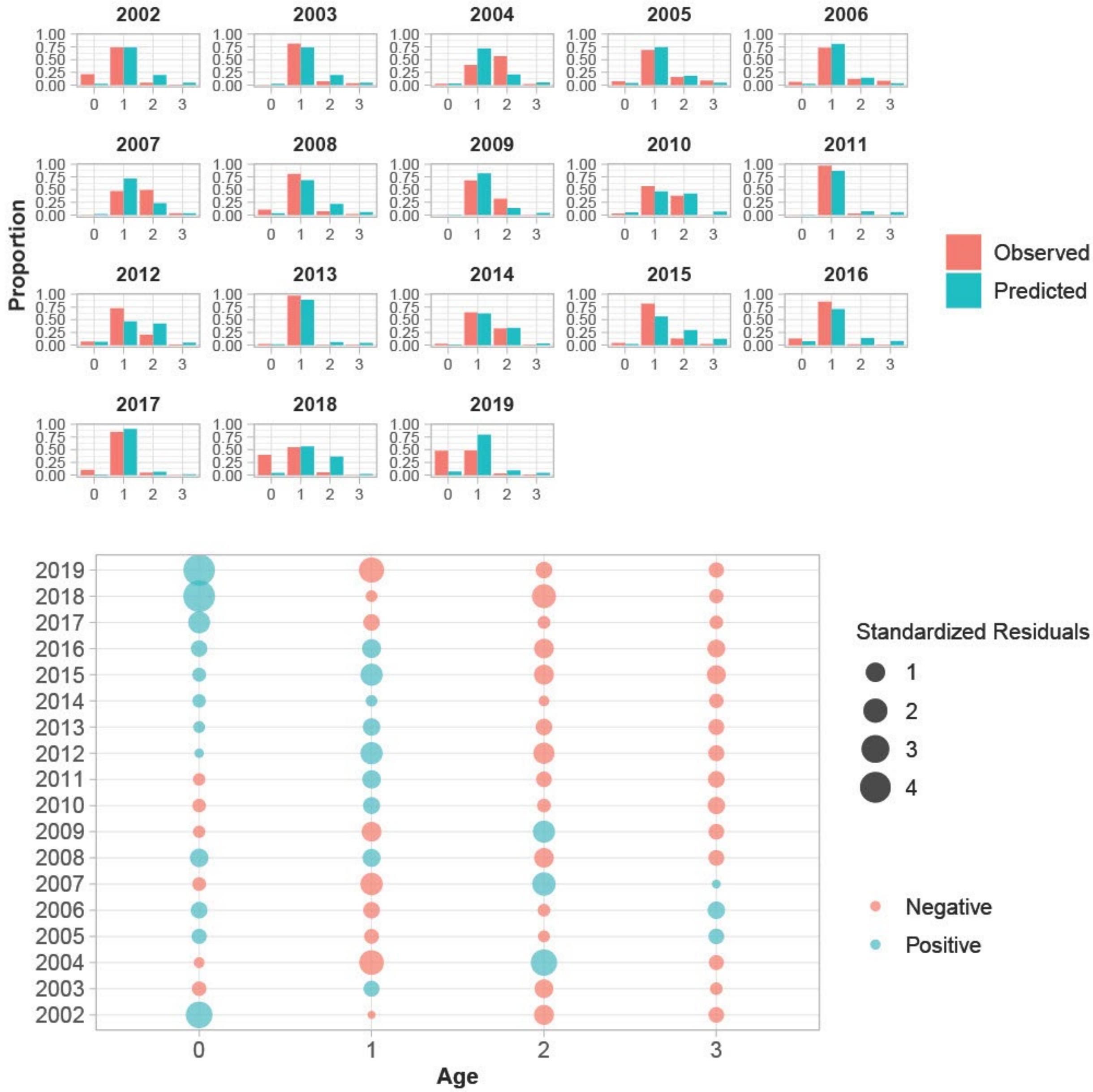

Figure S13. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for recreational catches in the coast from the spatially-varying mortality (SVM) model.

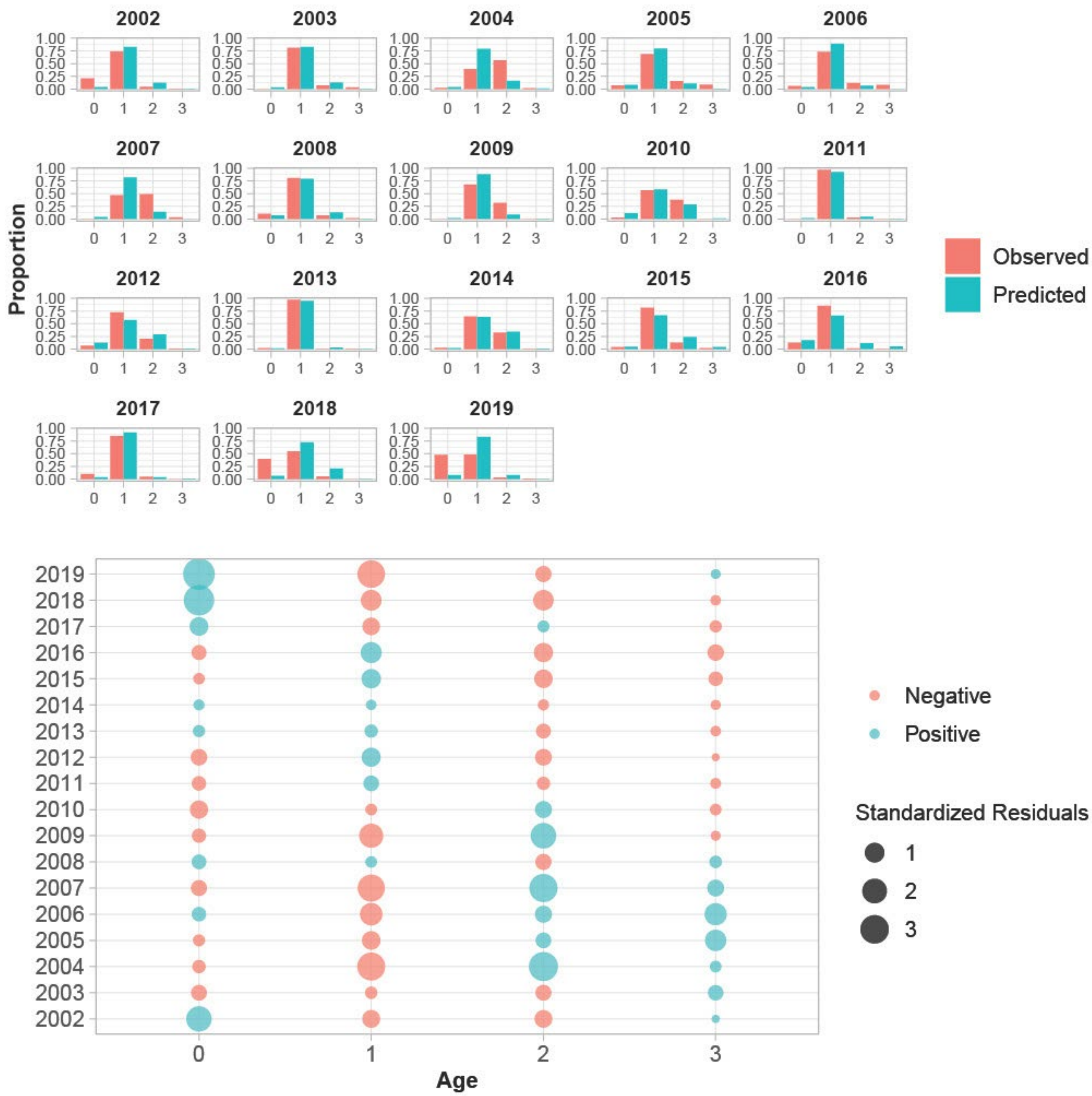

Figure S14. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for recreational catches in the coast from the time-varying occupancy (TVO) model.

Figure S15. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for the ChesMMAP summer survey from the spatially-varying mortality (SVM) model.

Figure S16. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for the ChesMMAP summer survey from the time-varying occupancy (TVO) model.

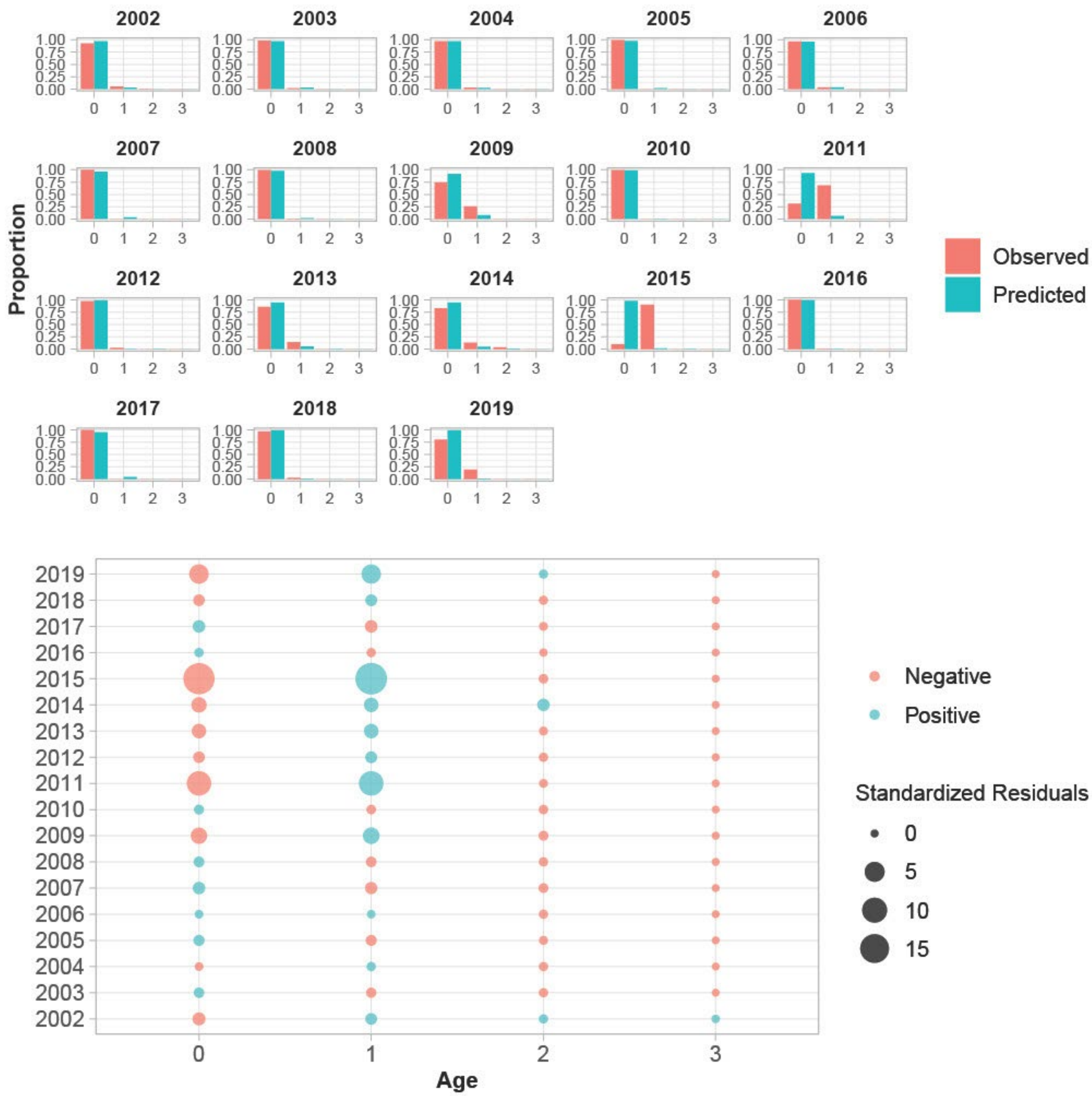

Figure S17. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for the ChesMMAP fall survey from the spatially-varying mortality (SVM) model.

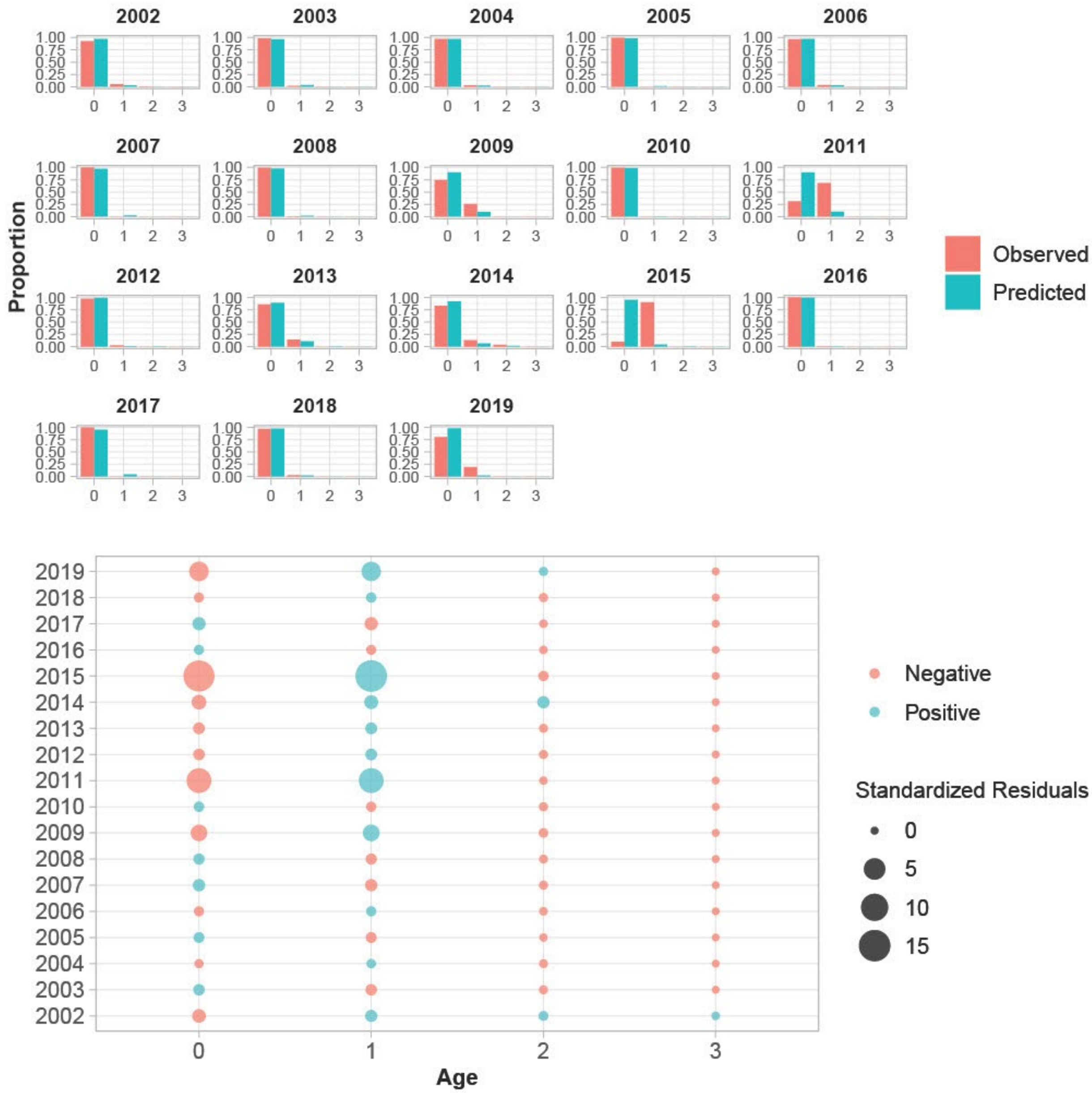

Figure S18. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for the ChesMMAP fall survey from the time-varying occupancy (TVO) model.

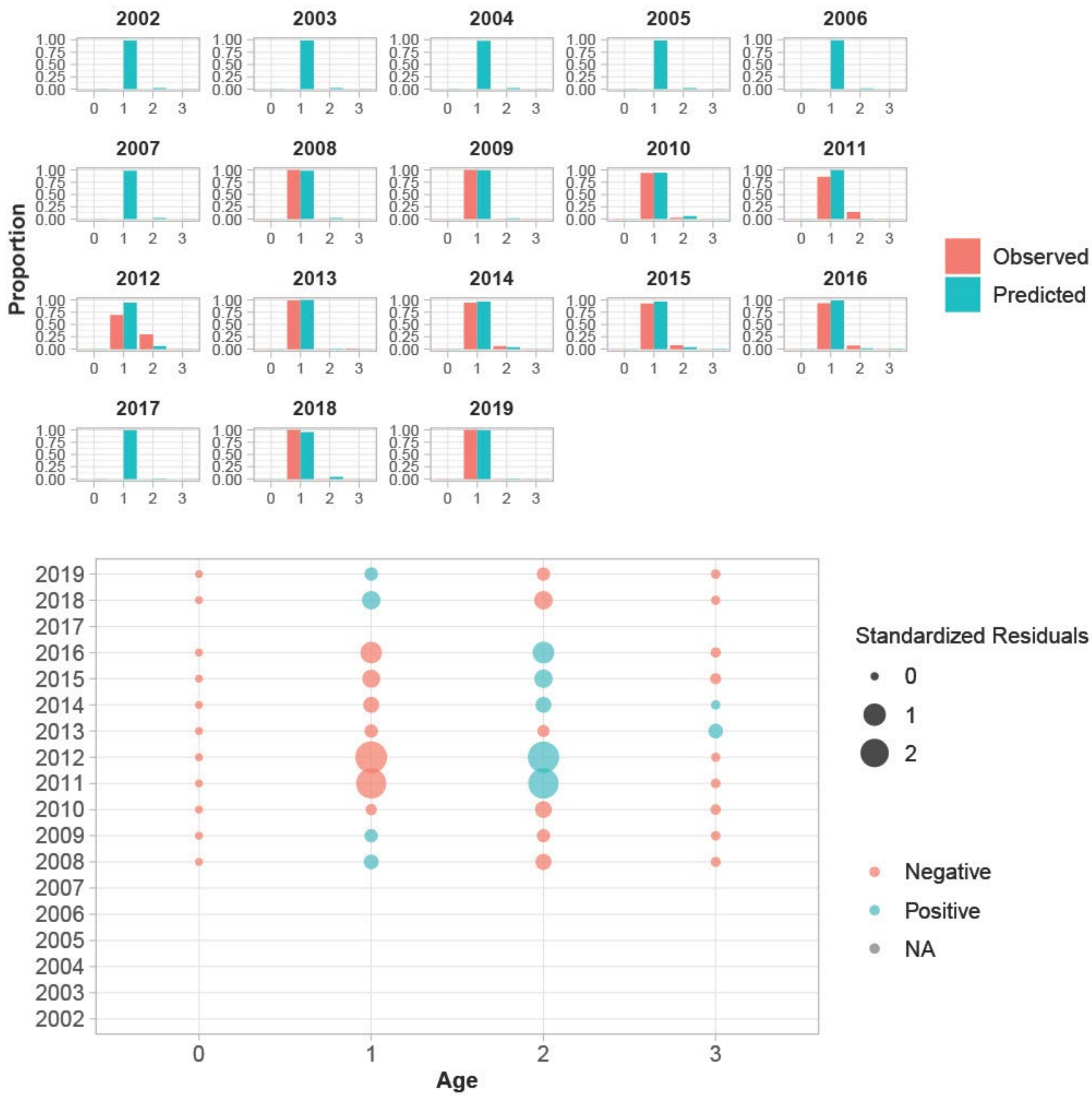

Figure S19. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for NEAMAP from the spatially-varying mortality (SVM) model.

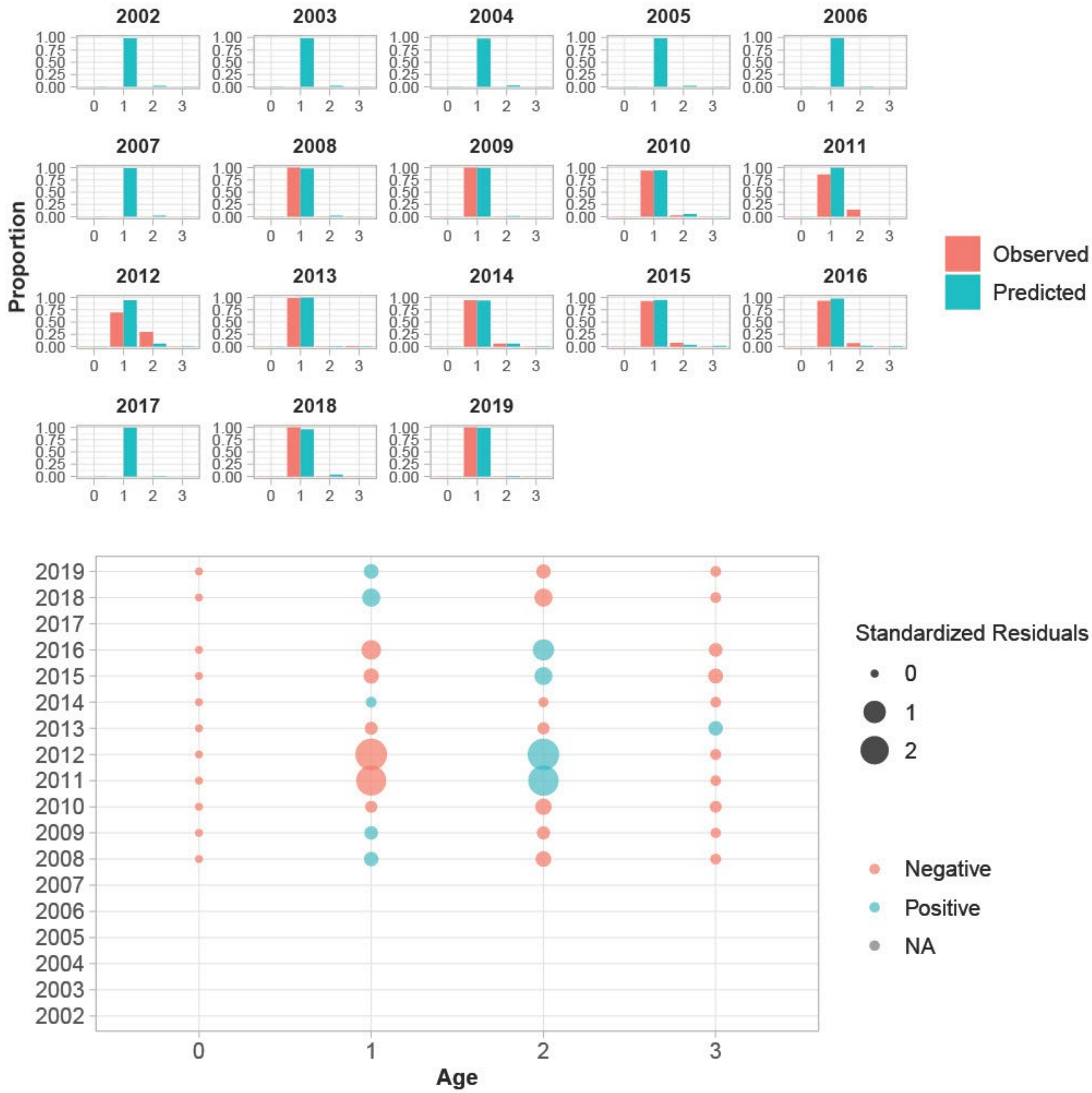

Figure S20. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for NEAMAP from the time-varying occupancy (TVO) model.

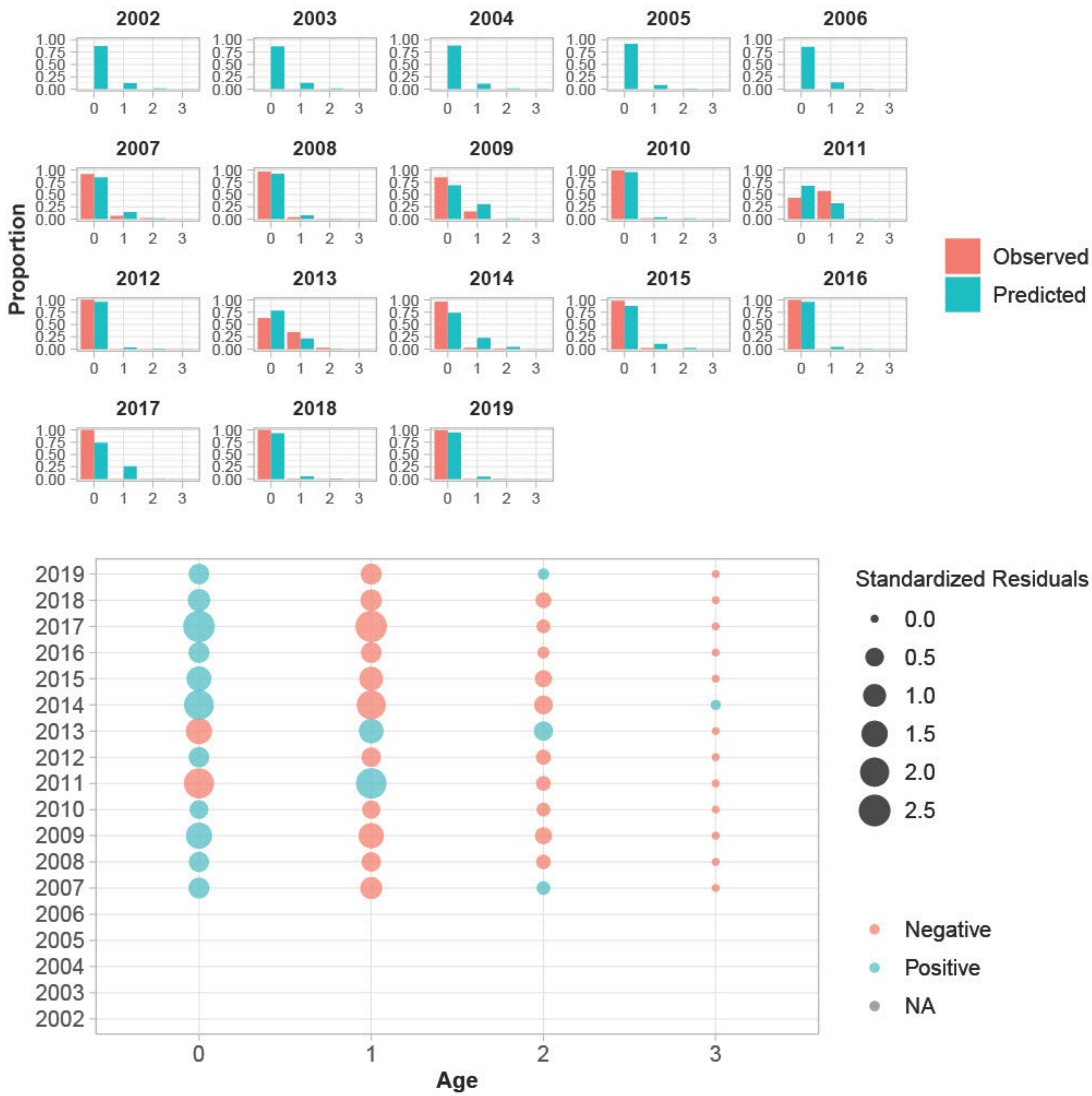

Figure S21. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for the aggregate index from the spatially-varying mortality (SVM) model.

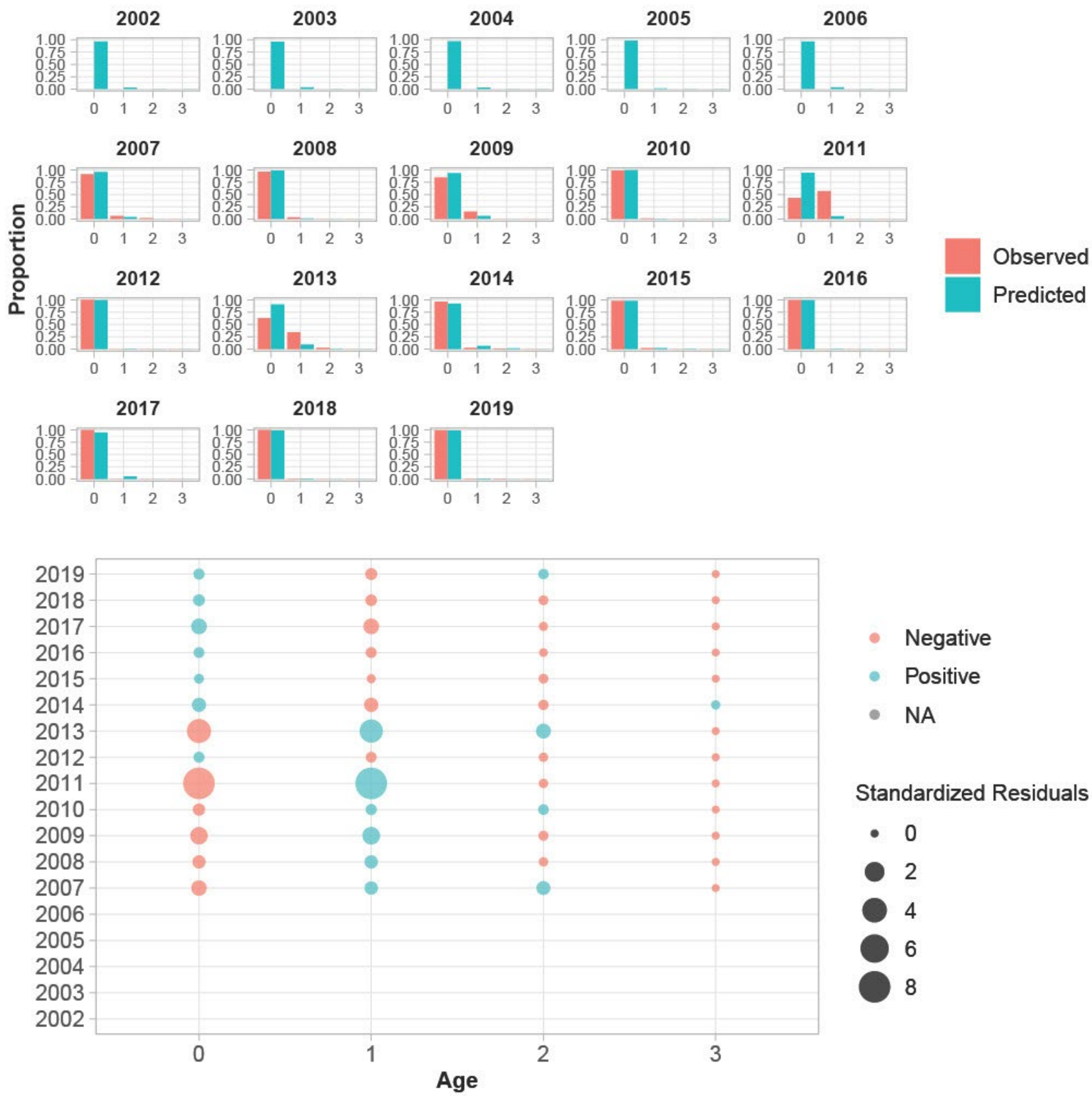

Figure S22. Observed and predicted proportions-at-age (upper bar charts), and standardized residuals for proportions-at-age (lower panel) for the aggregate index from the time-varying occupancy (TVO) model.

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