A MULTISPECIES STATISTICAL CATCH-ATAGE (MSSCAA) MODEL FOR A MIDATLANTIC SPECIES COMPLEX

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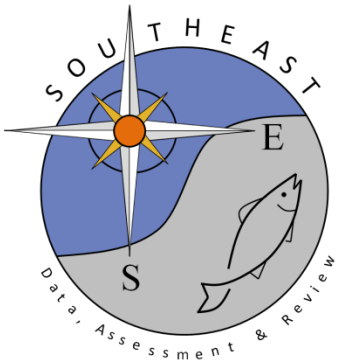

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A MULTISPECIES STATISTICAL CATCH-AT-AGE (MSSCAA) MODEL FOR A MID-ATLANTIC SPECIES COMPLEX

BY

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ABSTRACT

Two of the most ecologically and economically important species in the Mid-Atlantic Bight are Atlantic menhaden and the Atlantic striped bass. These species are important for human prosecuted fisheries, but these two species are also closely linked through ecosystem dynamics that are influenced by interactions between these species such as through predation. Beyond striped bass and menhaden, there are also other important species that are linked in this ecosystem. The focus of this dissertation is to estimate the trophic interactions among several important fish species in the Mid-Atlantic Bight, with an emphasis on the interactions between menhaden and striped bass. These species interactions are estimated by developing a multispecies, statistical catch-at-age model of a community of Mid-Atlantic species that explicitly quantifies the mortality due to predation.

Manuscript I: A model was developed for five important fish species in the Mid-Atlantic Bight. The model includes striped bass (*Morone saxatilis*), Atlantic menhaden (*Brevoortia tyrannus*), bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and scup (*Stenotomus chrysops*). The model was fit to commercial and recreational catch, survey, and diet data from 1985-2012. The model generated time and age varying natural mortality estimates, and allowed for the calculation of species-specific consumption estimates. Predation mortality increased on menhaden at all ages through the timeseries, peaking in the early and mid-2000s, and then declined. Predation mortality for scup was most notable on the first age class,

peaked in the late 1990s and remained high for the remainder of the timeseries. The MSSCAA model performed close to the existing single-species models used for management and better than the multispecies virtual population analysis previously used for these species. The MSSCAA model provided a different view of some important biological information than did the single-species versions of the population models developed for comparisons, in particular with regard to fishing mortality, which was higher for menhaden.

Manuscript II: The model as developed for Manuscript 1 was used to project the five species populations forward under different management scenarios and in both long and medium term time periods. Under all scenarios investigated in the long-term projections, equilibrium levels were achieved by all of the species in the ecosystem. The assumptions going in to the projections were tested and indicated that natural mortality and recruitment are the most important considerations in the suite of assumptions tested. The projections also offer a different view of the population dynamics of the system when factoring in predation mortality. The standard constant natural mortality (*M)* approach to projections produces more optimistic outcomes than when the time and age-varying *M* is accounted for in the projection. This finding shows that accounting for additional dynamics in the ecosystem can add value to the current management process by giving managers a better sense of the structural uncertainty that exists around the various assumptions being made. If time and age-varying natural mortality is the correct state of nature, this should be accounted for in the management action being undertaken.

Manuscript III: Prey-dependent interactions were investigated through the use of a two-species sub-model and projections. The two species used were menhaden and striped bass. The data indicated there may be a link between decreased consumption of menhaden by striped bass and increased natural mortality in the striped bass population. The investigation was extended to look at the impacts that this dynamic has on the two populations by programming the prey-dependent mortality effect into a multispecies estimation model. The parameters from the estimation model were then used to project the population to examine trade-offs that occur under a set of simple management strategies. The trade-offs were found to be important and indicate that there is an interaction between fishing mortality (F) and natural mortality (M) in both the medium and long-term projections. A main finding was that under a no-menhaden fishing scenario, the management outcomes were better for striped bass. This was true under different F strategies for striped bass, as the decreased natural mortality offset F. It is important to note that these management scenarios were developed to illustrate trade-offs and are not offered as actual management recommendations. Analyses like these can offer important information to managers by way of giving them more information to consider when developing measures that attempt to meet goals, as fishing impacts on one population can affect the attainment of goals on other populations.

ACKNOWLEDGMENTS

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PREFACE

This dissertation is written in the manuscript format specified by the University of Rhode Island Graduate School.

Manuscript I is written for the Canadian Journal of Fisheries and Aquatic Sciences and will be submitted for review upon completion of this dissertation.

Manuscript II is written for the ICES Journal of Marine Science and will be submitted for review upon completion of this dissertation.

Manuscript III is written for the North American Journal of Fisheries Management and will be submitted for review upon completion of this dissertation.

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Intended for submission to the Canadian Journal of Fisheries and Aquatic Sciences

A multispecies, statistical catch-at-age model for a mid-Atlantic fish complex

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ABSTRACT

Predation can be the largest source of mortality for fish species and is therefore a critically important process to consider when studying the dynamics of marine fish populations. However, the predation rate is difficult to measure and quantify. Traditionally, population models have either quantified predation externally or have used a general and fixed natural mortality level. To develop a new perspective on the predation component of natural mortality, and extend recent work, a multispecies statistical catch-at-age assessment model (MSSCAA) for a mid-Atlantic species complex is created. The model includes striped bass (*Morone saxatilis*), Atlantic menhaden (*Brevoortia tyrannus*), bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and scup (*Stenotomus chrysops*). The model was fit to commercial and recreational catch, survey, and diet data from 1985-2012. The model generated time and age varying natural mortality estimates, and allowed for the calculation of species-specific consumption estimates. Predation mortality increased on menhaden at all ages through the timeseries, peaking in the early and mid-2000s, and then declined. Predation mortality for scup was most notable on the first age class, peaked in the late 1990s and remained high for the remainder of the timeseries. The MSSCAA model performed close to the existing single-species models used for management and better than the multispecies virtual population analysis previously used for these species. The MSSCAA model provided a different view of some important biological information than did the single-species versions of the population models developed for comparisons, in particular with regard to fishing mortality, which was higher for menhaden.

KEYWORDS

multispecies statistical catch-at-age model, Mid-Atlantic, predation mortality, biological reference points, time and age varying natural mortality

INTRODUCTION

The effectiveness of single-species stock assessment and management has come under scrutiny in recent years. More holistic ecosystem based approaches to stock assessments are required to help inform managers when making the important and complex decisions that are the norm during our current fisheries management process. One of the population dynamic processes that can further the understanding of how populations change in abundance through time is species interactions and the effects these interactions have on population dynamics across species. Tools must be developed to help account for and simulate these population dynamics.

Several modeling approaches have been developed to account for trophic interactions between species. They range from simple dynamic equations that simulate interaction and effect between a predator and a prey species as described by the multispecies Lotka-Volterra competition models to the development of more complex models that account for entire ecosystems, e.g. Ecopath with Ecosim (Buchheister et al. 2017) or Atlantis (Fulton et al. 2014). Somewhere in the middle of these two extremes are multispecies statistical catch-at-age fisheries stock assessment models. These models can account for trophic interactions between species in a relatively realistic manner in much the same way as occurs in a single-species framework, but can also account for the uncertainty that exists in the system through the use of statistical estimation (Collie et al. 2014).

A multispecies statistical catch-at-age model is developed for Atlantic menhaden and a portion of its associated ecosystem. In this framework the additional

chosen species are striped bass, bluefish, weakfish, and scup for the entire coastwide stock range. Multispecies statistical catch-at-age models have been developed and used previous to this work, but this is the first attempt to apply this approach to this suite of species. The use of a statistical model for these species is important due to the uncertainty that exists in the accounting for recreational catch, to accommodate the use of multiple surveys of differing gear types, and the different characteristics of the fisheries that occur on these species.

Recreational catch is monitored through a statistical sampling design for the species examined in this research. This sampling program has changed through time. The original program was called the Marine Recreational Fisheries Statistical Survey (MRFSS) and then was changed in 2008 to the Marine Recreational Information Program (MRIP). The main differences involved a sampling design change between the two programs (https://www.st.nmfs.noaa.gov/recreational-fisheries/index), but conceptually the programs are the same in that they statistically sample the recreational saltwater fishing community. It is believed that recreational harvest has a significant degree of uncertainty associated with the harvest estimates because of this statistical sampling design, thus making statistical estimation within the stock assessment modeling framework a valuable asset for analyzing this system. Beyond the recreational data, the commercial catch and the fishery-independent information are also believed to be subject to observation error, again leading to the adoption of tools that can accommodate these forms of uncertainty in their structure.

There is a need to develop new tools for use in fisheries population stock assessments, and there is a need for these new tools to account for the dynamic nature

of natural mortality, namely predation, in these ecosystems. Modeling multispecies interactions and creating multispecies models is not a new concept. Some of the earliest multispecies work done was to connect virtual population analysis models together using predation functions (Helgason and Gislason 1979; Gislason and Helgason 1985; Sparre 1991; Livingston and Jurado-Molina 2000; Tsou and Collie 2001; Garrison et al. 2010). This modeling approach can be helpful in a complex fisheries modeling environment because the strong assumptions on certain parameters aid in the estimation of the remaining parameters. From this more deterministic modeling technique, statistical approaches were then developed using either age based or length based statistical models. These statistical approaches are more comparable to some of the single-species assessment methods that are now used and have the added benefit of allowing the estimation of uncertainty around the estimated population parameters (Lewy and Vinther 2004; Jurado-Molina 2005; Kinzey and Punt 2009; Van Kirk et al. 2010; Curti et al. 2013). The goal of all of these multispecies approaches is to create more realistic information on which to base fisheries management practices (Gislason 1999; Moustahfid et al. 2009). This research adopts the more progressive statistical approach for its modeling methodology.

Once analytical tools are developed to account for the interactions between species, methods can be developed to set management controls that account for these multispecies dynamics. Using multispecies assessments improves on one of the major underlying assumptions that is often needed for the development of management controls, namely allowing for the use of time and age varying natural mortality rather than a static natural mortality assumption. An additional underlying assumption that is

needed for developing management controls has to do with recruitment. It is important to understand the dynamics of new recruits coming in to the population through time as this has major implications for future population size and the amount of yield that can be achieved from it. This research allows for the investigation of how modeling these species in an ecosystem context changes the perception of the stock, including our understanding of recruitment. Different stock-recruit relationships will be investigated for the multispecies model outputs and these will be compared to the outputs from single-species model versions for the same species to identify what the differences are with regard to recruitment from the two modeling procedures.

Taken in total, the use of this new tool to examine fish populations in a more comprehensive manner will allow for a better understanding of the population dynamics in the species examined, and this context can be compared with some of the existing tools used for fisheries management. The question this study seeks to answer is how does our perception of these fish populations change based on the MSSCAA model relative to some of the more tradition single-species population assessment methods, as well as how does the statistical framework improve upon more deterministic multispecies approaches such as the MSVPA developed for this same suite of species.

METHODS

The multispecies statistical catch-at-age model used for this study is constructed around five species: Atlantic menhaden (*Brevoortia tyrannus*), Atlantic striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and scup (*Stenotomus chrysops*). The species were selected based on a review

of important predator diet information, the availability of age-structured data for the species, and knowledge of the migratory patterns of the species. The migratory pattern aspect allows the confounding factor of temporal and spatial overlap to be mitigated to some degree in that the species selected all have similar seasonal migratory patterns (Atlantic menhaden: SEDAR 2015; Atlantic striped bass: ASMFC 2015; Bluefish: NEFSC 2015; Weakfish: ASMFC 2016; Scup: NEFSC 2015).

In the model, striped bass, weakfish, and bluefish are top predators of both Atlantic menhaden and scup and both Atlantic menhaden and scup are strictly forage species. Cannibalism by any species is not accounted for in this study. All of the symbols and likelihood components for the multispecies model are indicated in Tables 1 and 2 respectively.

Data sources and treatment

As in Curti et al. (2013), there are six input data series categories needed for each species in the model: total fishing catch in weight, total fishery-independent survey catch in number/tow, age proportions for both fishery and fishery-independent survey catches, average individual weight-at-age by year, and age-specific predator diet information. All five of the species examined in this research currently have single-species statistical catch at age models that are used for management. Unless otherwise noted, all of the data inputs used for this research are taken directly from recent stock assessment documents and from direct communication with the stock assessment researchers that work on these species (Atlantic menhaden: SEDAR 2015; Atlantic striped bass: ASMFC 2015; Bluefish: NEFSC 2015; Weakfish: ASMFC 2016; Scup: NEFSC 2015).

For all species, total fishery catches represent landings plus dead discards from both the commercial and recreational fisheries in weight (thousands of metric tons). Assumptions about discard mortality for this study were consistent with assumptions from the reviewed assessments for each species.

Annual catch-at-age in millions of fish for the entire time series were used to calculate age proportions from the catch. The information used to construct age-specific catch from the recreational fishery is generally believed to be more reliable in numbers than it is in weight. Again, for all species used in this study, this time series of information was obtained from the most recent reviewed stock assessment. In contrast to the single-species assessments for these species, which usually model recreational and commercial catches as separate fleets with separately estimated selectivities, all removals were modeled as a single fleet with similar selectivities. This is not a poor assumption for the species selected for this project as each species has one predominant fishery and gear type that prosecutes the fishery (i.e. striped bass is predominately a rod and reel fishery when considering both the commercial and recreational fishery, while menhaden is predominately a commercial purse seine fishery). Therefore, there is most likely one predominate selectivity that governs the age structure of the removals.

In contrast to the work done by Curti et al. (2013), the species used in this study have a diverse series of surveys used to estimate stock abundance through time with differing time-series and consisting of different gear types. To accommodate the multiple surveys yet keep the model structure used in this study as simple and computationally efficient as possible, a hierarchical approach was used to combine the

multiple fishery-independent survey indices into a single index for use in developing the age-structured fishery-independent survey catches in number-per-tow. This approach is similar to that used for Atlantic menhaden (SEDAR 2015) and uses the Bayesian hierarchical model index approach developed for Spanish mackerel (Conn 2010). Not all surveys used for the reviewed single-species assessments were used in this study's combined indices, as some indices used in the single-species assessments are for specific age classes (i.e. young-of-the-year surveys). For this reason, only surveys with good representation of all age classes were used for this study. This decision is consistent with the underlying assumption from the hierarchical approach in that the surveys are tracking the same population and the same population dynamics (proportional change in abundance through time) as the stock. Table 3 shows the indices used by species for this study with the calculated posterior mean of the standard deviation of the process error. Lognormal priors were used for the annual survey estimates for the Bayesian implementation of the annual estimated mean. The annual survey estimates are shown in Table 9. An inconsistent approach was used for weakfish. After consultation with members of the Atlantic States Marine Fisheries Commission (ASMFC) Weakfish Stock Assessment Sub-Committee, a single survey index was used as the abundance index for weakfish, the MRIP CPUE. This index is described in detail in the weakfish stock assessment document (ASMFC 2016). Defaulting to this single index for weakfish was based on the advice that this index received a high weight in the benchmark assessment and was the index that allowed the benchmark assessment model to fit the data for weakfish the best.

Annual fishery-independent, catch-at-age in numbers of fish for the entire time series were used to calculate age proportions from the survey catch. As multiple indices were combined as described in the paragraph above, the age composition data of each survey were combined for the surveys used in this study (Table 3) by year and age class, and these age composition data were applied to the annual combined index to determine number at age through time. As each survey does not contribute equally to the final combined index, an inverse variance weighting procedure was used to weight the age information. The variance was derived from the hierarchical modeling approach, the mean of the posterior standard deviation from the process error was used in the weighting calculation:

$$w_{i,k} = \frac{\left(\frac{1}{\sigma_{i,k}^2}\right)}{\left(\sum_{k=1}^{n} \frac{1}{\sigma_{i,k}^2}\right)} \quad (1)$$

where $w_{i,k}$= weight applied to the age composition information from species specific survey, i = species, σ = the mean of the posterior standard deviation from the process error as calculated by the hierarchical model, k = individual fishery-independent survey weight being calculated, n = total number of surveys being weighted. This weight was then applied to the age composition data for each survey, scaled to account for the fact that not all surveys operate in all years, and then these age composition data were applied to the total index as calculated by the hierarchical model.

Average individual weight-at-age is needed in the model to convert from numbers to biomass units. The weight-at-age information is introduced in the model as a matrix, so the information varies not only by age, but by time as well. This is an

important consideration as a number of the species used in the model have significant shifts in weight-at-age through time.

For the trophic interactions of the multispecies runs, data are needed on species food habits, consumption estimates, and information on biomass throughout the ecosystem. These data include consumption-to-biomass estimates for each species (consumption:biomass or C/B), an estimate of the biomass of "other food" in the ecosystem, and average predator diet information.

Age-specific C/B ratios were obtained by the methodology from Garrison et al. (2010) as developed for the Multispecies Virtual Population Analysis (MSVPA) model developed for this same suite of species. Food consumption rates in fish can vary strongly, particularly between seasons as a function of changing temperatures and metabolic demands. To account for these processes, a consumption model was implemented using the Elliot & Persson (1978) evacuation rate approach. Total yearly (y) consumption for a predator species (i), age (a) during a given season is:

$$C_{y,s}^{i,a} = 24 * E_s^{i.a} * \overline{SC}_s^{i,a} * D_s * w_{y,s}^{i,a} * \overline{N}_{y,s}^{i,a} \quad (2)$$

Where SC_s is the mean stomach-content weight relative to predator body weight in a season (s), D_s is the number of days in the season, $w_{y,s}^{i,a}$ is the average seasonal weight at age for the predator species, and $\overline{N}_{y,s}^{i,a}$ is the abundance of the predator age class during the time interval. The predator and season-specific evacuation rate $E_s^{i.a}$ (hr^{-1}) is given as:

$$E_s^{i,a} = a_{i,a} * \exp\left(b_{i,a} * T_s\right) \quad (2.1)$$

Where T_s is the average seasonal temperature (°C) and $a_{i,a}$ and $b_{i,a}$ are fitted parameters based upon laboratory feeding experiments, field studies, or other sources (Elliot & Persson 1978). The evacuation rate reflects the temperature-dependent metabolic rates of the predator.

These data were updated through 2012 as these species-specific data were available. As noted above, the C/B ratios were developed for the MSVPA with more resolution (i.e. daily C/B ratios by season), but these were averaged across the time series to create a matrix of age-specific C/B ratios by species that were static through time per the procedure of Curti et al. (2013). As the data exist with more resolution, this is an area that may be an extension for future work (time and age varying C/B ratios).

As assumed in Curti et al. (2013) and based on previous work (Sparre 1980, Tsou and Collie 2001), a constant, time-invariant total ecosystem biomass was assumed, permitting the biomass of available other food to vary annually. Prior studies have confirmed that the total biomass in large marine ecosystems can remain relatively stationary through time (Link et al. 2008, Auster and Link 2009, Byron and Link 2010). There were no direct measurements found to develop what this overall biomass estimate should be, so as a starting point, a total biomass estimate from the MSVPA was used. To supplement and support the MSVPA derived total ecosystem biomass value, information derived from an Atlantic Coast Ecopath model was also investigated (Buchheister et al. 2017). Both values were close in magnitude. Testing with the multispecies assessment model indicated that performance was best for the

value derived from the Ecopath model (94,800,000 mt) and therefore this value was the one selected for the base case run of the model.

Stomach-content data were obtained from two main sources. The NEFSC Food Web Dynamics Program, which has systematically sampled predator food habits since 1973 (Link and Almeida 2000) was one source. These food-habits data are structured by predator species and length, but primarily only by prey species because prey lengths and ages are not routinely measured. A subset of the database is structured by both predator and prey lengths, which was used for the following analyses. In addition to the NEFSC Food Web Dynamics Program data, the North East Area Monitoring and Assessment Program (NEAMAP) and Chesapeake Bay Multispecies Monitoring and Assessment Program (CHESMAP) also collect stomach-content data under similar protocols to the NEFSC program. These data were used to supplement the stomach-content data and have an added benefit of increasing the coastal area covered for this dataset (NEAMAP and CHESMAP sample areas further inshore than the NEFSC sampling program). Both datasets have attributes (e.g. the NEFSC data has a long time-series and the NEAMAP data is more inshore so is better able to acquire many of the species used in this study) and drawbacks (e.g. the NEFSC data are from further offshore and the NEAMAP data timeseries is short), but taken together they offer a fairly comprehensive snapshot of the populations. These length-based data for predator and prey from stomach-content information are converted to weight through the use of length-weight relationships as collected in Wigley et al. (2003). Age-specific predator diet habits, input to the model as proportion by weight for each age class, were averaged over 4-year periods to reduce the inherent variability in the

dataset as well as to reduce the amount of missing data and increase the sample size being used for any particular year (Van Kirk et al. 2010), while still capturing the temporal trends.

Standard model formulation

The model used in this study follows a traditional statistical catch-at-age structure as used for many single-species stock assessments. These traditional catch-at-age equations are then linked and interact through a set of trophic interactions. All model equations will not be presented in this document as they follow the equations as developed in Quinn and Deriso (1999), but some of the main equations used will be described for the catch-at-age portions of the model, and the trophic calculations will be presented in detail.

Progression of year class abundance is implemented by the equation:

$$N_{i,a+1,t+1} = N_{i,a,t} e^{-Z_{i,a,t}} \tag{3}$$

where N = species abundance in millions of fish, Z = total mortality, i = species, a = age class, and t = year. As there are plus groups for each species used in this project, the final age class modeled (i.e. when $a = a_{\max}$) needed to be adjusted using the equation:

$$N_{i,a,t+1} = N_{i,a-1,t} e^{-Z_{i,a-1,t}} + N_{i,a,t} e^{-Z_{i,a,t}} \tag{4}$$

Fishery catch-at-age is calculated using Baranov's catch equation:

$$C_{i,a,t} = \frac{F_{i,a,t}}{Z_{i,a,t}} N_{i,a,t} (1 - e^{-Z_{i,a,t}}) \tag{5}$$

where C = fishery catch (recreational, commercial, and dead discards for each) and F = fishing mortality. Fishing mortality-at-age (assuming separable fishing mortality) follows the equation:

$$F_{i,a,t} = s_{i,a}F_{i,t} \quad (6)$$

where s = fishery selectivity. Fishery-independent survey catch ($FIC_{i,t}$) was related to species-specific abundances through the following equation:

$$FIC_{i,t} = q_i r_{i,a} N_{i,t} e^{-\frac{m}{12}Z_{i,t}} \quad (7)$$

This mathematical configuration assumes an age and time-invariant catchability (q_i), age-specific survey selectivity coefficients ($r_{i,a}$), and also accounts for the time of year during which the survey was conducted (m) so total mortality can be applied to the index appropriately. Given the accumulation of multiple indices as described above and their operation across different times of the year, the month in which the survey was conducted was assumed to be mid-year (m=6) in each case. Species-specific catchabilities (q_i) were calculated from the entire time series deviations between the model predicted absolute abundance and model predicted relative abundance (Walters and Ludwig 1994).

Finally, age-specific fishery and survey selectivity coefficients were estimated for each species for all age classes through a double logistic selectivity function, with the exception of weakfish which used a logistic function as this was the selectivity used in the benchmark assessment (ASMFC 2016). This formulation departs from previous work (Curti et al. 2013) and was reconfigured to better simulate what is believed to be the selectivities for the species examined in this study by allowing

doming in the selectivity at age where appropriate, and is also consistent with the selectivity shape used in the approved single-species assessments for these species. The four-parameter double logistic equation used for both the fishery selectivity and the fishery-independent survey selectivity was:

$$Sel_{x,i,a} = \left(\frac{1}{1 + e^{-(a-\alpha_1)/\beta_1}}\right)\left(1 - \frac{1}{1 + e^{-(a-\alpha_2)/\beta_2}}\right) \quad (8)$$

And the two-parameter logistic equation used for weakfish was:

$$Sel_{x,i,a} = \left(\frac{1}{1 + e^{-(a-\alpha_1)/\beta_1}}\right) \quad (9)$$

where $Sel_{x,i,a}$ is the species-specific selectivity at age, x = fishery or fishery-independent information, i = species, a = age class, and α_{1or2} and $\beta_{1\text{or}2}$ are the ascending or descending limb parameters.

Incorporating multispecies formulations

Predation mortality (*M2*) is a sub component of total mortality (*Z*), but more specifically a sub-component of the natural mortality component in *Z*. The simplest equation to describe this is:

$$Z = F + (M1 + M2) \quad (10)$$

where *Z* is total mortality, *F* is fishing mortality, *M1* is residual natural mortality (natural mortality attributed to all other factors with the exception of predation by species included in the model), and *M2* is predation mortality from the species included in the model (Helgason and Gislason 1979). It is important to remember that species in the model that are considered predators only (e.g. striped bass, bluefish, and weakfish) will only have *M1* operating on their population, while species that are

considered prey only (e.g. menhaden and scup) will have both *M1* and *M2* operating on their population.

The *M1* value is an important uncertainty in the model. For this project, *M1* was parameterized by looking back at the MSVPA information for these same species and determining the portion of natural mortality that was occurring (based on that analysis) from predation for menhaden. The assumed natural mortality for the menhaden single-species benchmark assessment was prorated downward based on this proportion. There was less information for scup, therefore *M1* was assumed to account for half of the overall natural mortality of 0.2 as assumed for the benchmark assessment for scup.

There is a recursive property in this formulation of *M2* in that the biomass data element needed for calculating *M2* has total mortality as an element of its calculation, therefore an approximation is used. To approximate the instantaneous rate of *M2*, the biomass of the predator and the prey items are assumed to come from the beginning of each year, prior to being subject to these various forms of mortality (Van Kirk et al. 2010). The equation for the instantaneous *M2* is:

$$M2_{i,a,t} = \frac{1}{N_{i,a,t}W_{i,a,t}} \sum_{j} \sum_{b} CB_{j,b} B_{j,b,t} \frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}} \qquad (10)$$

where $N_{i,a,t}$ = mean number of prey *i* at age *a* and at time *t*, $W_{i,a,t}$ = the weight of prey *i* at age *a* at time *t*, $CB_{j,b}$ = the age-specific (*b*) consumption-to-biomass ratio for predator species *j*, $B_{j,b,t}$ = age-specific biomass of predator *j*, and $\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}$ = the proportion of prey *i* at age *a* in all food available to predator *j* at age *b* in year *t*, which is assumed equal to the proportion of food within the stomach of predator *j* at age *b* in

year *t* composed of prey *i* at age *a* (Lewy and Vinther 2004). Under this formulation, a type-II functional response is assumed. Under this functional response, the predator satiates at a high prey biomass, and the satiation reaches an asymptote (doesn't decline at higher densities) (Sparre 1980).

The next steps for the predation calculation are to develop the various components of the above equation. Availability (ϕ) of prey *i* at age *a* to predator *j* at age *b* is the product of a suitability coefficient ν of prey *i* at age *a* to predator *j* at age *b* and the prey's age and year specific biomass ($B_{i,a,t}$):

$$\phi_{i,a,j,b,t} = \tilde{\nu}_{i,a,j,b,t} B_{i,a,t} \tag{10.1}$$

There are also species included in the model that are not explicitly modeled via the statistical catch-at-age equations in the formulation. These species interactions are described through the equation:

$$\phi_{other,t} = \tilde{\nu}_{other,t} B_{other,t} \tag{10.2}$$

where B_{other} refers to the biomass of the non-modeled prey with the modeled prey biomasses subtracted out (Sparre 1980):

$$B_{other,t} = B_{totalecosystem} - \sum_{i} \sum_{a} B_{i,a,t} \tag{10.3}$$

which is added to the summation of the explicitly modeled prey biomasses after being multiplied by their suitability coefficients. The parameter $B_{totalecosystem}$ is the total weight of all of the species in the ecosystem. This component is constant over time and across species and age. The inclusion of this component allows all of the modeled species to be estimated relative to other prey items in the ecosystem. This can lead to

efficiencies as the predator species in this project have a diverse diet, modeling all of the potential prey items is a large and time intensive task, and adequate data to make inferences about the population dynamics do not exist for all prey species.

The suitability (ν) for each prey item at age is calculated as the product of the size and species-specific preferences of each predator by age class. Here, the size preference and the species preference are assumed independent from each other. The equation for this calculation is:

$$\nu_{i,a,j,b} = \rho_{i,j} g_{i,a,j,b} \tag{10.4}$$

where $\rho_{i,j}$ is the vulnerability of prey species *i* to predator species *j*, and $g_{i,a,j,b}$ is the size-preference function of prey *i* at age *a* to predator *j* at age *b*. The vulnerability, ρ, incorporates all differences in food selection, for example behavioral and spatial differences, that are not attributable to size differences (Gislason and Helgason 1985). As mentioned previously, one of the factors in selecting the species used in this study is that they have significant spatial overlap during the year, making this a reasonable assumption in this case. Species preference is relative to a reference prey species, referred to as "other food" or all of the prey species not explicitly modeled. The vulnerability (ρ) and suitability parameters (ν) are set to one for this "other food" category. The main assumption for using these equations are that the size and the species are the main drivers controlling whether a predator species eats that particular food item and that the other food category is of the preferred size for the predator.

Suitability coefficients (ν) are scaled across all prey species and ages to facilitate comparisons between estimated available prey biomass and food-habits data such that the suitabilities for a predator age class sum to one (Sparre 1980):

$$\tilde{\nu}_{i,a,j,b,t} = \frac{\nu_{i,a,j,b,t}}{\sum_i \sum_a \nu_{i,a,j,b,t} + \nu_{other}} \quad (10.5)$$

The scaling of the suitability coefficients creates a one-to-one direct correspondence between the stomach-contents of the predator and the relative suitable prey biomass.

Size preference ($g_{i,a,j,b}$) of a predator is modeled as a lognormal function of the ratio between predator and prey weights as shown in the following equation:

$$g_{i,a,j,b} = exp\left[-\frac{1}{2\sigma_j^2}\left(ln\frac{w_{j,b}}{w_{i,a}} - \eta_j\right)^2\right] \quad (10.6)$$

where σ and η are size-preference parameters specific to each predator, and w is the age-specific weight of the prey (i) and predator (j) from a specific food habit sample. Species-specific σ and η parameter values are reported in Table 5. Another important assumption implicit in this equation is that there is a single size-preference coefficient for a predator for all prey of a given size regardless of species, but *g* still must differentiate between species and ages given that each prey species has a unique length and weight for a given age (Andersen and Ursin 1977, Helgason and Gislason 1979). As implemented in Curti et al. (2013), the size-preference coefficients are estimated external to the model from empirical food-habit data analysis and are input as known mean and variance parameters.

In this model formulation, the total food available to a given predator in the ecosystem may include species beyond those that are explicitly modeled. One of the benefits of this formulation, as opposed to other formulations that necessitate only using species explicitly modeled in the mathematical framework, is the inclusion of a

non-modeled prey component identified as an overarching ecosystem biomass value ($B_{totalecosystem}$).

The final calculation needed to determine the available prey to a predator is defined by:

$$\phi_{j,b,t} = \phi_{other} + \sum_{i} \sum_{a} \phi_{i,a,j,b,t} \tag{10.7}$$

This is the divisor from equation 10 and completes the steps needed to calculate predation mortality.

Given this formulation, most of the parameters can be derived by interrogating different data sources, which is preferable to making numerous assumptions. The number and weights-at-age for all of the modeled species can be collected from both fishery-independent and dependent sources. These are standard sources of information for many stock assessments. The more unique data elements in a multispecies modeling framework are gathered from diet databases, which are now being routinely (and more systematically) collected in various state, academic, and federal fishery-independent surveys. The diet information (food habits) is derived from stomach-content analysis of the species collected, and the parameters described above that are developed from these data are the consumption-to-biomass ratios, the preferred prey, and preferred prey size information. The most notable parameter described above that is not estimated from data is the total ecosystem biomass (non-modeled prey items). Additionally, some of the elements above are not internally estimated in the model, namely the size-preference parameters, but this element is estimated from actual data

before being input in to the model, and this input value is modeled with estimates of uncertainty.

Parameter estimation and data weighting

One of the attributes of this multispecies model is the statistical estimation process. The estimated model parameters include age-specific abundances in the first year $N_{i,\,a,\,t=1}$ $(Yr1)$, annual recruitment in subsequent years $N_{i,\,a=1,\,t+1}$ $(Age1)$, annual fully recruited fishing mortality rates $F_{i,\,t}$, age-specific fishery $(s_{i,a})$ and survey $(r_{i,a})$ selectivity coefficients, and the vulnerability parameters, $\rho_{i,j}$. Due to the estimation of the population in the first year for all species, the model does not depend on an assumption of equilibrium. Single-species statistical models for all of the species used in this study provide initial estimates of abundance. For all subsequent years, recruitment is estimated as a mean parameter plus a vector of annual deviation parameters that must sum to zero.

All model parameters were estimated with maximum likelihood techniques, programmed in AD Model Builder (ADMB-IDE ver 10.1 2011). In addition to the likelihood approach, a Bayesian-type approach with priors, implemented through penalized likelihoods and bounded parameters, is also used to supplement some of the statistical estimation. The estimation of model parameters allows the assumption that fishery catch, survey catch and food habits data are subject to observation error, which is a critically important extension of this modeling approach relative to previous multispecies formulations, in particular the virtual population analysis approaches that have been used for multispecies modeling (Helgason and Gislason 1979; Gislason and

Helgason 1985; Sparre 1991; Livingston and Jurado-Molina 2000; Tsou and Collie 2001; Garrison et al. 2010).

The total likelihood comprises five components as well as three penalty functions (Table 2). The total fishery catch and total survey catch were assumed to be lognormally distributed. The catch-at-age proportions for both the fishery and the survey information, and predator food habits (average proportions by weight) were assumed to follow multinomial distributions. These are common error distribution assumptions for fisheries stock assessments in general and are also the assumptions used for the single-species assessments for most species modeled in this project.

The objective function weights for each dataset were determined with an iterative approach whereby an initial weighting was applied, output from this initial run was examined, and a subsequent reweighting was undertaken to meet a particular level of uncertainty depending on the dataset. Specifically, weightings for the lognormal components were chosen to achieve approximately a 20% coefficient of variation (CV) for total fishery catch, and a 30-40% CV for total survey catch. The CVs were set such that the uncertainty associated with recreational harvest and discard levels were accounted for. Additionally, a higher CV was assumed for the survey component due to the interannual variability observed in those datasets, and to also account for the additional uncertainty associated with the hierarchical modeling performed on these datasets. Interannual variability results from variation in availability of the species to the survey gear, changes in survey methodology through time, or the fact that surveys may be taking place in spatially discrete areas at different times of year, therefore it is not necessarily the case that these observed changes in

abundance are real, but rather are due to changes in catchability (Pincin et al. 2014). Therefore it is appropriate to allow some significant statistical inference when predicting the various indices in the model. Final model weightings do not necessarily represent the ideal as set forth above, as model convergence was also factored in when selecting the final model configuration.

For the multinomial objective function weighting, the Bayesian approach of McAllister and Ianelli (1997) was followed. Explorations of other weighting procedures were also investigated (namely that proposed in Francis 2011), but the McCallister and Ianelli approach was used for the final model as there were not large differences in the output weights between the two weighting procedures. The weight was chosen to best approximate the average effective sample size for each species, which was then averaged over the entire time series. The effective sample size for species *i* in year *t* was calculated as

$$Neff_{i,t} = \frac{\sum_a \hat{P}_{i,a,t}\left(1 - \hat{P}_{i,a,t}\right)}{\sum_a \left(P_{i,a,t} - \hat{P}_{i,a,t}\right)^2} \tag{11}$$

where $P_{i,a,t}$ is the observed proportion-at-age for species *i* in year *t*, and $\hat{P}_{i,a,t}$ is the predicted proportion-at-age. These effective sample sizes were also set iteratively to get as close to the average effective sample size as possible. This ideal was not achieved in all cases, again model convergence often precluded using these effective sample sizes exactly.

Penalty functions were imposed on initial abundances, annual recruitment and age-specific biomasses (Table 2). These penalties were imposed to keep parameter

estimates from collapsing to zero or producing estimates that were not biologically feasible. The penalty imposed on initial abundances, $Yr1_{pen}$, were calculated with two methods. The first method prevents age-specific abundances from deviating substantially from those predicted by exponential decay across ages, assuming a total mortality equal to the age-specific average. The second approach penalized deviation from the initial input abundance (*Yr1*) values taken from the benchmark models for all species. This second approach was used for the final model configuration. The penalty imposed on annual recruitment, R_{pen}, prevents the coefficient of variation for the log recruitment of any species from becoming greater than a pre-defined threshold value (*Rthresh*). The threshold selected was based on the recruitment and its associated variability from the benchmark models for the species in this study. The penalty imposed on age-specific biomasses, B_{pen}, prevents any age-specific biomass from falling below a pre-defined threshold (*Bthresh*) to prevent the calculations from crashing due to the biomass dropping to zero. The weights for each of these penalties and their corresponding threshold values were selected iteratively.

Retrospective analysis

One analysis was completed to look at the stability of the model. Specifically, a retrospective analysis was done on the multispecies model. A retrospective pattern is a systematic inconsistency among a series of estimates of population size, or related assessment variables, based on increasing periods of data (Mohn 1999). This is a standard analysis performed on many single-species assessments and therefore will be an important test for the MSSCAA model to examine the consistency in output from year to year as more information becomes available to the model.

A four-year peel was performed for the MSSCAA model. Four years was chosen as this is a period where the food habits data do not need to be altered to accommodate the new timeseries length. The food-habit data are binned by four-year periods to allow for some dampening of the inherent variability in the food habit data, and this becomes a limiting factor for the retrospective analysis because once the time series shrinks to less than four years, a reconstruction of the food habit data will be needed, making the year-to-year comparisons impossible.

A sequential year will be dropped from the terminal year of the assessment (2012) for four years, and the model will be rerun for each of those four new datasets. The data being changed for each run will be the total catch, the weight-at-age, the catch-at-age, the total survey catch, and the survey catch-at-age for each species. The outputs examined will be total fishing mortality, biomass, and recruitment.

The severity and direction of the pattern will be determined by using the Mohn's Rho statistic. Mohn's Rho (Mohn 1999) has been commonly used to measure the retrospective patterns for many stocks, including for assessments done on the species examined in this study. The statistic is defined as the sum of relative difference between an estimated quantity from an assessment with a reduced time series and the same quantity estimated from the full time series:

$$\rho = \sum_{t} \frac{X_{t_{new}} - X_{t_{full}}}{X_{t_{full}}} \tag{12}$$

where *X* denotes the variable from the assessment, in this case full fishing mortality, total biomass, or recruitment, *t* denotes the year of comparison, t_{new} denotes the

terminal estimate from an assessment with a reduced time series, and t_{full} denotes the assessment using the full time series. To make the statistic comparable across different numbers of reduced years (i.e. peels), Miller and Legault (2017) reconfigured the estimator to be defined as the average of the peel-specific components:

$$\rho_t = \frac{X_{t_{new}} - X_{t_{full}}}{X_{t_{full}}} \tag{12.1}$$

$$\overline{\boldsymbol{\rho}} = \frac{\mathbf{1}}{\boldsymbol{P}} \sum_{\boldsymbol{t=earliest\ year}}^{\boldsymbol{P}} \boldsymbol{\rho_t} \tag{12.2}$$

Where ρ_t = the peel year specific ρ value and P = the total number of years peeled.

Stock-recruit relationships

Stock-recruitment functions will be required for the projections in Chapter 2. A standard practice for many species is to use a median recruitment assumption in stock projections due to the fact that available data often does not define the parameters of a stock-recruit model (i.e. Ricker or Beverton-Holt) well. The effect of median recruitment and stock recruitment functions will be tested to examine these different states of nature in a multispecies context in the stock projection exercise undertaken in Chapter 2. Three different ways of projecting recruitment will be compiled for comparison. Two stock-recruitment models will be developed; a Beverton-Holt and a Ricker model. The median level of recruitment from the various models will also be reported. Formulations of the stock-recruitment models will be tested in both the multispecies and single-species context and compared. Comparisons of model fit between the two models will be performed using Akaike information criterion (AIC).

As the first year of fish in these models were one year old fish, the *SSB* was shifted backwards one year to line up with the appropriate one-year-old age class when fitting the Beverton-Holt and Ricker models. The stock-recruit model parameters were estimated using the maximum likelihood estimation procedure in R statistical software using the "mle2" function found in the "bbmle" package. An important note on notation for the stock-recruit models below is that the α and β symbols were previously used for the selectivity equations, but these symbols represent different parameters here. Because the stock-recruit equations are usually defined using these Greek symbols in their notation, this was kept consistent with this standard even though duplication exists within this document.

Beverton-Holt stock-recruitment model

The first stock-recruitment model to be investigated will be a Beverton-Holt model (Beverton and Holt 1957). The formulation used is defined by the equation:

$$R_{i,t+1} = \frac{\alpha_i SSB_{i,t}}{\beta_i + SSB_{i,t}} \tag{13}$$

where $R_{i,t+1}$ is recruitment in year t+1, $SSB_{i,t}$ is spawning stock for species i in year t, and α_i and β_i are the species-specific parameters controlling the shape of the function. Data for *SSB* and recruits were taken from the output from either the multispecies or simplified single-species models as described in this document. The error structure was assumed to be normal. This error structure was selected because both normal and lognormal structures were tested and there was only a marginal improvement with the lognormal structure, therefore the normal error structure was used to avoid issues with bias corrections.

Ricker stock-recruitment model

The second stock-recruitment model to be investigated will be a Ricker model (Ricker 1954). The formulation used is defined by the equation:

$$R_{i,t+1} = \alpha_i * SSB_{i,t} * \mathrm{e}^{-\beta_i * SSB_{i,t}} \quad (14)$$

where $R_{i,t+1}$ is recruitment in year *t*+1, $SSB_{i,t}$ is spawning stock for species *i* in year *t*, and α_i and β_i are the species-specific parameters controlling the shape of the function. As noted above, the data for *SSB* and recruits were taken from the output from either the multispecies or simplified single-species models as described in this document. The error structure was assumed to be lognormal, no bias correction was applied.

Median recruitment

In addition to investigating the stock-recruitment relationships explained above, median recruitment levels will also be explored. Median recruitment levels will be investigated for each species and between the single-species and the multispecies model. The recruitment data will again be taken from the output from these different models as developed for this research and compared.

RESULTS

Model fit and comparisons

Model fits are compared to the observed data as a diagnostic test to show the internal performance of the model. Several diagnostic plots are presented to verify that the model is fitting observed data reasonably well. The output from the multispecies model from this project was also compared to outputs from the existing single-species

models for the species examined in this project (meaning the existing stock assessments used for management of these species, hereafter referred to as "benchmark models"), as well as to output from a 2012 updated run for the MSVPA model for these same species as developed by Garrison et al. (2010). This was done to examine consistencies and points of departure between the different approaches. A final comparison was to show differences and similarities between streamlined single-species models which do not contain trophic calculations (modeling frameworks that are simpler than the benchmark models and are used as the underlying species-specific template for the multispecies model) and the multispecies model. This diagnostic is examined to show the influence of the trophic calculations as well as the effect of synthesizing all of the information simultaneously on the model outputs. Additionally, the simplified single-species model can show differences between a simplified single-species model and a more complex single-species model structure as indicated by the comparison to the benchmark assessments.

Model fit

The predicted total annual fishery catch closely followed observed catches with only minor differences (Figure 1). An examination of residuals shows some patterning, but in most cases the residuals are very small in magnitude, overall indicating a good fit to the total catch data (Figure A19). Some lack of fit to the catch data for weakfish is evident.

The fits were less exact for the total annual survey catch, but the multispecies output did follow temporal trends in the observed time series fairly well, though there are some issues between the single-species and multispecies model fits for weakfish (Figure 2). An examination of residuals shows little patterning or problematic

residuals, again with the exception of weakfish, which does indicate some strong patterning and some high magnitude residuals (Figure A20).

For both fishery (Figures A1 – A5) and survey (Figures A6 - A10) age proportions, the predicted trends captured much of the interannual variability seen in the observed dataset. However, the multispecies formulation predicted higher biomass in the older age classes of menhaden and scup, which was inconsistent with the observed age proportions.

Food-habits data were fit without much statistical weight on the observed data. This was done to acknowledge the fact that the food habit data is limited for the species examined in this project. Even with this low weight, there was good correspondence between the observed and predicted data, with the multispecies statistical model predicting smoother curves of increasing proportion of diet for prey items in the food habits of the predators (Figures A12 – A14).

Contributions of the different data elements to the objective function are also presented (Table 4). This information indicates that the fishery-independent survey age-composition data contribute the most to the objective function value, followed by the fishery catch age composition, and then the total fishery-independent survey fit. There is also some contribution from the penalty functions, namely from the initial year penalty function, but these are minor contributions relative to the rest of the information. By species, striped bass followed by bluefish, contribute the most to the objective function value.

Comparison to streamlined single-species and benchmark model output

Comparisons were made between benchmark model output, streamlined single-species model output, and the multispecies statistical model developed for this project. The multispecies total annual fishery catches compared well to the single-species output for the same species (Figure 1). As previously noted, these also correspond well with the observed data for the total annual catch.

Also as noted, the fits were less exact for the total annual survey catch, but the multispecies and single-species output did follow temporal trends in the observed survey time series fairly well, and both models compared well to each other, though there are some issues between the single-species and multispecies model fits for weakfish (Figure 2).

Age-composition data comparisons showed that the single-species and multispecies formulations corroborated each other well. In almost all cases the predictions from the single-species and the multispecies models were similar to each other, with a few notable exceptions. Weakfish in the oldest age classes showed some dissimilarities between the single-species and the multispecies models. With weakfish this was true for both survey and catch age compositions. Menhaden also showed some discrepancies, though these were mainly relegated to the catch age-composition data. For menhaden there was a discontinuity between the single-species and the multispecies models in the oldest age class, with the multispecies model predicting more age six fish annually in both the fishery and the survey (Figures A1 – A10).

Agreement among the various models in predicted total annual abundance varied across species and between models (Figure 3). For menhaden, scup, and striped

bass both single-species and multispecies predictions matched the total abundance estimated in the benchmark models. A notable exception is that the multispecies model predicts higher abundance at times for scup and menhaden, the two prey species. For bluefish and weakfish, total abundance estimated from the multispecies model was generally greater than that estimated from the single-species run, and the single-species runs tended to better align with the benchmark model output.

Similarly for recruitment, trends in predicted recruitment for both model formulations generally followed the same trends, but the magnitude of recruitment between the single-species and the multispecies model were off for menhaden, scup, and weakfish. As was the case for the overall population abundance, the prey species menhaden and scup had multispecies model predictions that indicated higher recruitment than did either the benchmark assessments or the single-species assessments (Figure 4).

Predicted average annual fishing mortality (F) varied across species and between models (Figure 5). In this context, average fishing mortality refers to the average of fishing mortality across all age classes modeled and this averaging of F was kept consistent to make the comparisons across models (multispecies, single-species, and benchmark) coherent. Bluefish and scup had good correspondence between the multispecies model, the benchmark model, and the single-species model. For menhaden the fishing mortality estimated by the multispecies model was higher than the single-species model, and the benchmark fishing mortality estimates were generally less than the models run for this project. Striped bass indicated good correspondence between the single-species and multispecies models with regard to

trend, but these were both below the fishing mortality estimated by the benchmark assessment for the most recent period of time. There was little correspondence in the fishing mortality estimates from any of the three sources (benchmark, multispecies, or single-species models) examined in this study for weakfish.

Estimated selectivity patterns corresponded well between the single-species and multispecies models, with the exception of weakfish, which showed some differences in the selectivity for the survey information (Figures A17 – A18). There seems to be little impact to the estimation of the selectivity function parameters by the incorporation of the trophic calculations in to the modeling framework.

Comparison to MSVPA model output

Only a subset of comparisons can be made between the existing MSVPA model and the multispecies statistical catch-at-age model for the suite of species examined in this study. The species that can be compared are menhaden, striped bass, and weakfish. The reason for this subset of species is because bluefish were not entered into the MSVPA as an age-structured predator, and scup were not entered into the MSVPA as an age-structured prey item. Using output from the last year that the MSVPA was run (terminal year of 2014), comparisons of model output were made between a similar set of years from this study and the MSVPA. Namely, comparisons were made between abundance, average fishing mortality, and the predation portion of mortality for menhaden.

Population abundance between the models had the highest degree of comparability. In general, the multispecies statistical model produced higher population abundances, in particular in the terminal years of the two assessments, with

the multispecies statistical model producing values that are more closely aligned with the benchmark assessments for these species (Figure 9).

Fishing mortality comparisons indicated many differences in model estimates between the two modeling frameworks. In general, the MSVPA generated higher average fishing mortality estimates than did the multispecies statistical model (Figure 9). In many cases the trends in fishing mortality are in opposite directions. Again, it is important to note that the multispecies statistical model more closely aligns with the output from the current benchmark models for these species.

A final comparison was made between the MSVPA and the multispecies statistical model estimates of predation mortality for menhaden. The multispecies statistical model produces higher estimates of predation mortality than does the MSVPA. There is some correspondence in the trends for the two models, but the magnitude of predation mortality produced by the multispecies statistical model are more than twice as high as that produced by the MSVPA in many years (Figure 10).

Multispecies model output

Population abundance produced by the multispecies statistical model follows trends that are in line with the understanding from our current benchmark assessments for these species (Figure 3). For menhaden, the population begins at a high level in the early part of the time series and then declines until the mid-1990s. The population then increases until the end of the time series. Striped bass begins at a low population abundance. Striped bass population abundance then climbs until the late 1990s and has been variable around this higher level until the end of the time series. Bluefish follow a trend similar to that of menhaden, beginning at a high level, declining and then

recovering towards the end of the time series. The most recent five years indicate a period of decline for bluefish. Weakfish, according to the multispecies model, begins at a middle population size level, increases over a short period of time, and then declines for the majority of the time series. There is a short period of time at the end of the time series that indicates some recovery. Scup population abundance begins at a low level and increases through the time series. Scup is at its highest levels in the most recent period of time. Of note is the information that for both menhaden and scup, the multispecies model predicts higher abundances during periods of time than does the benchmark or single-species assessments.

Fishing mortality estimates produced by the multispecies statistical model follows trends that are in line with the understanding from our current benchmark assessments for these species (Figure 5), though in some instances the magnitudes are different. For menhaden, average fishing mortality begins at a low level in the early part of the time series and then increases until the mid-1990s. Fishing mortality then decreases until the end of the time series. Striped bass follows a similar trend. Fishing mortality increases and then plateaus in the mid-1990s until the early 2000s. Fishing mortality on striped bass declines for the final five years of the time series. Bluefish follow a trend of decreasing fishing mortality throughout the time series. Weakfish fishing mortality is similar to bluefish in that it starts off high at the beginning of the time series and then declines. Scup average fishing mortality begins at a high level and decreases through the time series. Scup is at its lowest fishing mortality levels in the most recent period of time.

Estimated predation mortality (*M*2) varied between the two prey species in this study, by prey age, and through time (Figure 6). The three predators in this study are predators only, and are not prey nor do they undergo cannibalism, so time and age varying predation mortality is only being estimated for menhaden and scup. Predation mortality is highest for age-one menhaden, and decreases sequentially as age increases. The only exception to this is in the very first year where predation of age-one is lower than for some of the other age classes. Additionally, predation mortality increases for menhaden beginning in the early 1990s, peaking in the mid-2000s, and declines towards the end of the time series. At its peak, the predation mortality on age-one menhaden approaches 0.7 in a number of years. The terminal year estimate of *M2* for menhaden is 0.40 for age-one and is 0.3 on average (Figure 6). The proportion of total mortality (*Z*) attributed to predation mortality again is highest for age-one menhaden, peaking at around 60% of total mortality being due to predation mortality. The other age classes range from only having 10% of total mortality due to predation up to a peak of approximately 40% (Figure A11).

Predation mortality is highest for scup on age-one as was the case for menhaden, and decreases sequentially as age increases. The drop in predation mortality with age is steeper for scup than it is for menhaden with age-two scup predation mortality decreasing seven fold in some years. There are a number of years where the age-seven scup predation mortality increases above some of the younger age classes, these events are most likely driven by low population size at those ages during those years. Additionally, predation mortality increases for scup beginning in the early 1990s, and remains high with variability towards the end of the time series.

At its peak, the predation mortality on age-one scup approaches and exceeds one in a number of years. The terminal year estimate of *M2* for scup is 1.4 for age-one and is 0.29 on average (Figure 6). The proportion of total mortality (Z) attributed to predation mortality is highest for age-one scup, peaking at above 80% of total mortality being due to predation mortality. The other age classes range from having close to none of the total mortality due to predation up to a peak of approximately 60% (Figure A11).

Food-habit information was queried from the previous MSVPA work done for the same predator species examined in this study (Garrison et al. 2010). The food habits of striped bass predicted by the statistical model creates a smoother curve than does the original input data (Figure A12). The observed data has a decline in proportion of diet that menhaden makes up for striped bass at ages 7 and 8. The estimation by the model from this study does not indicate that same drop in proportion, rather has an increase in proportion of menhaden in the diet as the age of striped bass increases, reaching an asymptote approaching 50% of the overall diet being composed of menhaden. Scup as a prey item for striped bass constitutes a small proportion of the overall diet, with the "other food" category (all prey items not explicitly modeled) constituting close to 50% of the remaining diet. This trend holds throughout the timeframe examined in this study with small modifications in each aggregated year period.

A similar trend from the MSVPA food-habits data to the output from the statistical model from this study was seen for bluefish. The food habits of bluefish, which were modeled in a less refined fashion in the MSVPA, predicted by the

statistical model creates a smoother curve than does the original input data (Figure A13). The estimation by the model from this study predicts an increase in proportion of diet of menhaden as the age of bluefish increases, reaching a peak around 50% of the overall diet being comprised of menhaden at age 5. The proportion of menhaden in the diet then declines slightly for age 6 fish in most years. Scup as a prey item for bluefish constitutes a small proportion of the overall diet, with the "other food" category (all prey items not explicitly modeled) constituting close to 50% of the remaining diet for the oldest age classes. This trend holds throughout the timeframe examined in this study with small modifications in each aggregated year period.

The food-habits of weakfish predicted by the statistical model were similar in trend to the original input data. The estimation by the model from this study predicts an increase in proportion of diet of menhaden as the age of weakfish increases (Figure A14). The magnitude of the proportion of the diet that menhaden constitutes changes in magnitude between aggregated year periods, ranging from close to 0% to around 25% in the oldest age class. As was the case with the other two predators, scup as a prey item for weakfish constitutes a small proportion of the overall diet, with the "other food" category (all prey items not explicitly modeled) constituting 100% to 75% of the remaining diet for the oldest age classes. This trend holds throughout the timeframe examined in this study, though there are some significant changes in magnitude in each aggregated year period.

Consumption of prey as an output of the multispecies model can be represented as thousands of metric tons, and therefore can be viewed in similar currency to catch and other population biomass information. Striped bass consumption

of menhaden closely follows the trajectory of population size for menhaden and trends upward with the increase in population size for striped bass in the time-series (Figure 8). The proportional amount of menhaden in striped bass diets increases as this prey item increases in abundance. By way of magnitude, when striped bass population size was low, the magnitude of menhaden consumption was only 42 thousand metric tons. As the striped bass population size increases through the time series, consumption of menhaden also increases rising to a maximum value of 421 thousand metric tons in 2011. Consumption of scup by striped bass is relatively low for the entire time series, ranging from 0.80 thousand metric tons to a maximum of 55 thousand metric tons in 2009. While this value is comparatively low when reviewed in the context of menhaden, 55 thousand metric tons is much higher than the commercial quota for scup (~8.3 thousand mt in 2017). The remainder of striped bass consumption is attributed to the other prey items that are not explicitly modeled in this study and ranges from 136 to 1,567 thousand metric tons, which occurred in 1999.

Bluefish consumption of menhaden remains relatively flat for the time series examined in this study (Figure 8). The proportional amount of menhaden in bluefish diets decreases in the 1990s, coincident with both a low population period for both menhaden and bluefish. The magnitude of menhaden consumption by bluefish ranges from 114 to 466 thousand metric tons. Consumption of scup by bluefish is relatively low for the entire time series, ranging from 0.90 thousand metric tons to a maximum of 18 thousand metric tons in 2012. The remainder of bluefish consumption is attributed to the other prey items that are not explicitly modeled in this study and ranges from 434 to 1,136 thousand metric tons which occurred in 1985.

Weakfish consumption of menhaden is variable through the time series examined in this study and does not correlate well with weakfish abundance though does correlate to some degree with menhaden population abundance (Figure 8). The proportional amount of menhaden in weakfish diets decreases in the early 1990s, coincident with both a low population period for both menhaden and weakfish. The magnitude of menhaden consumption by weakfish ranges from 4 to 72 thousand metric tons. Consumption of scup by weakfish is low for the entire time series, ranging from 0.1 ton to a maximum of 3 thousand metric tons in 2009. The remainder of weakfish consumption is attributed to the other prey items that are not explicitly modeled in this study and ranges from 123 to 677 thousand metric tons which occurred in 1986.

When viewing consumption by prey item, we see the importance of each predator in the consumption of each prey species. For menhaden, it is striped bass that consumes the most menhaden relative to the other predators examined in this study (Figure 7). Bluefish is the next important predator for menhaden, and bluefish consumed more menhaden than the other predators in this study in the early portion of the time series. Weakfish is also an important predator of menhaden, but given the low population numbers for weakfish during the time series used for this study, its impact on the menhaden population is relatively small.

For scup, again it is striped bass that consumes the most scup relative to the other predators examined in this study (Figure 7). As was the case for menhaden, bluefish consumed more scup than the other predators in this study in the early portion

of the time series when bluefish abundance was high. Weakfish does not appear to be an important predator for scup.

Sensitivity analysis

The retrospective analysis performed well and indicated relatively good stability for most species in the main population metrics examined. Fishing mortality indicated a retrospective pattern where the population total fishing mortality was assumed to be higher in the preceding year when compared to the following year for menhaden. This pattern was generally weak (less than 0.2) as indicated by the Mohn's Rho diagnostic for all five species ($\rho_{menhaden}$ = -0.04, $\rho_{striped\ bass}$ = 0.04, $\rho_{bluefish}$ = 0.02, $\rho_{weakfish}$ = 0.17, ρ_{scup} = 0.11; Figure 16, Table 8).

Total biomass indicated a retrospective pattern where the population total biomass was assumed to be higher in the preceding year when compared to the following year with the exception of striped bass and scup. This pattern was weak as indicated by the Mohn's Rho diagnostic for all species except for menhaden, where it was modest ($\rho_{menhaden}$ = 0.28, $\rho_{striped\ bass}$ = -0.05, $\rho_{bluefish}$ = 0.01, $\rho_{weakfish}$ = 0.03, ρ_{scup} = -0.08). This feature is something often seen in this type of retrospective pattern, namely if fishing mortality is underestimated, biomass is frequently overestimated simultaneously (Figure 17; Table 8). Striped bass indicated a pattern where the biomass was assumed to be lower in the previous model run, as indicated by the negative Mohn's Rho diagnostic.

Recruitment indicated a retrospective pattern where recruitment was assumed to be higher in the preceding year when compared to the following year with the exception of striped bass and bluefish. This population metric had more variability

than the previous two metrics, and showed different patterns and severity depending on the species. The pattern was fairly strong for menhaden and striped bass, and for the other species, the pattern was weak ($\rho_{menhaden} = 0.43$, $\rho_{striped\ bass} = -0.41$, $\rho_{bluefish} = -0.18$, $\rho_{weakfish} = 0.10$, $\rho_{scup} = 0.03$; Figure 18, Table 8).

In a qualitative sense, the retrospective patterns found in the analysis done for this study were on par with or less than those found in the benchmark assessments for these species. It is difficult to make a direct quantitative assessment of this comparison as not all of these benchmark assessments calculated Mohn's Rho statistics or published data that could be analyzed, but when reviewing the information provided in the benchmark assessment documents, the retrospective patterns found in this study were generally the same or better in a diagnostic context.

Stock-recruitment relationships

The Ricker stock-recruit relationship had a better statistical fit than the Beverton-Holt model as indicated by an AIC comparison of the different models (Tables 10 and 11). This held true for both the single-species and multispecies output. The comparison is tenuous for weakfish as there were two instances when the β parameter needed to be fixed, namely for the single-species Ricker model fit and the multispecies Beverton-Holt fit.

Beverton-Holt stock-recruitment relationship and median recruitment values

The Beverton-Holt stock-recruitment model for each species fit the stock-recruitment data in that the model was able to estimate the parameters of the equation, with the exception of weakfish (Figures 11 – 15). For weakfish, the β parameter needed to be bounded in order to get a reasonable relationship, and the parameter

estimated ended up on the lower bound. Despite this poor model diagnostic, this stock-recruitment relationship was used for the comparisons in this section. All of the Beverton-Holt model parameter estimates are reported in Table 6.

The Beverton-Holt relationship for menhaden indicated a gradual increase in recruits as spawning stock biomass increases for all estimation model output examined. The asymptote (defined by the α parameter) for the relationship when run using the single-species model output was lower than when using the multispecies model output (Figure 11, Table 6). Additionally, the shape of the curve was much flatter for the single-species model relationship that it was for the multispecies model. The median recruitment value for menhaden was slightly higher for the multispecies model than the single-species model (Table 6).

The Beverton-Holt relationship for striped bass indicated a strong increase in recruits as spawning stock biomass increases with a flat asymptote for all estimation model output examined. The asymptote (defined by the α parameter) for the relationship when run using the single-species model output was higher than when using the multispecies model output (Figure 12, Table 6). Additionally, the shape of the curve was similar for the two models, as would be expected as predation mortality is not impacting striped bass in the multispecies model. The median recruitment value for striped bass was lower for the multispecies model than the single-species model (Table 6).

The Beverton-Holt relationship for bluefish indicated a strong increase in recruits as spawning stock biomass increases with a flat asymptote for all estimation model output examined. For bluefish, there is not much information to inform the

ascending portion of the curve, so the slope of the increase appears to be fairly uncertain. The asymptote (defined by the α parameter) for the relationship when run using the single-species model output was slightly higher than when using the multispecies model output, but the two values are close (Figure 13, Table 6). Additionally, the shape of the curve was similar for the two models. The median recruitment value for bluefish was the same for the both models (Table 6).

The Beverton-Holt relationship for weakfish indicated a gradual increase in recruits as spawning stock biomass increased for all estimation model output examined. The asymptote (defined by the α parameter) for the relationship when run using the single-species model output was higher than when using the multispecies model output (Figure 14, Table 6). Additionally, the shape of the curve was similar for the two models, both indicating a relatively flat curve. The median recruitment value for weakfish was slightly higher for the multispecies model than the single-species model (Table 6). It is important to note that this relationship is suspect as one of the model parameters was hitting a bound.

The Beverton-Holt relationship for scup indicated a strong increase in recruits as spawning stock biomass increases with a flat asymptote for all estimation model output examined. The asymptote (defined by the α parameter) for the relationship when run using the single-species model output was lower than when using the multispecies model output (Figure 15, Table 6). Additionally, the shape of the curve was similar for the two models, but had very different magnitudes. The median recruitment value for scup was higher for the multispecies model than the single-species model (Table 6) and was quite different than the value for the asymptote.

Ricker stock-recruitment relationship

The Ricker stock-recruitment model for each species fit the stock-recruitment data in that the model was able to estimate the parameters of the Ricker equation (Figures 11 – 15). For weakfish, the β parameter needed to be bounded in order to get a reasonable relationship, and the parameter estimated ended up on the lower bound. All of the model parameter estimates are reported in Table 7, while the median values are reported in Table 6. To determine the *SSB* of maximum recruitment from the Ricker curves, the simple approximation as defined by Ricker (1954) will be used which approximates the *SSB* of maximum recruitment from the Ricker curve with the following equation:

$$SSB\ of\ Peak\ Recruitment = \frac{1}{\beta} \tag{15}$$

The Ricker relationship for menhaden indicated a gradual, almost linear increase in recruits as spawning stock biomass increases for all estimation model output examined, and is fairly similar in shape and magnitude to the Beverton-Holt curve. The *SSB* of maximum recruitment for the relationship when run using the single-species model output was higher than when using the multispecies model output (Figure 11, Table 7). The shape of the curve was flatter for the single-species model relationship that it was for the multispecies model indicating an almost linear relationship with virtually no over compensation at higher *SSB* levels.

The Ricker relationship for striped bass indicated a strong increase in recruits as spawning stock biomass increases with an identifiable maximum for all estimation model output examined. The *SSB* that produces maximum recruitment when run using the single-species model output was higher than when using the multispecies model

output (Figure 12, Table 7). Additionally, the shape of the curve was similar for the two models, which should be expected for predator species that do not have predation mortality creating differences between the two modeling approaches.

The Ricker relationship for bluefish indicated a gradual increase in recruits as spawning stock biomass increases with a flat maximum for all estimation model output examined. For bluefish, there is not much information to inform the ascending portion of the curve, so the slope of the increase appears to be fairly uncertain. The *SSB* that produces maximum recruitment when run using the single-species model output was lower than when using the multispecies model output (Figure 13, Table 7). Additionally, the shape of the curve was similar for the two models.

The Ricker relationship for weakfish indicated a gradual, almost linear increase in recruits as spawning stock biomass increases for the single-species model while the multispecies model had a more pronounced curve with a defined maximum. The *SSB* of maximum recruitment for the relationship when run using the single-species model output was higher than when using the multispecies model output (Figure 14, Table 7). The shape of the curve was much flatter for the single-species model relationship that it was for the multispecies model indicating an almost linear relationship with virtually no over compensation at higher *SSB* levels. It is again important to note that the single-species model needed a bounded parameter to fit, and the parameter estimate ended up on the lower bound, thus making the output suspect.

The Ricker relationship for scup indicated a strong increase in recruits as spawning stock biomass increases with a defined maximum and clear over compensation for all estimation model output examined. The *SSB* that produces

maximum recruitment when run using the single-species model output was higher than when using the multispecies model output (Figure 15, Table 7). Additionally, the shape of the curve was similar for the two models. In both cases, this curve seems to be fairly extreme and does not appear to be biologically feasible.

DISCUSSION

The multispecies statistical catch-at-age model performed well according to the model diagnostics examined in this study. The model fit the observed datasets input in to the model well with few exceptions. Model fit to catch and fishery-independent survey information was good, and fits to age-composition data were also good, with some lack of fit showing up in some of the older age classes. Additionally, examination of residual patterns and magnitudes did not indicate any major concerns for most of the species examined in this study. The one species that did not perform as well in a relative sense was weakfish, which showed diagnostic issues with both age composition data fits and some residual patterning in both the catch and survey information.

Single-species models were also created for this study as a comparative diagnostic. These models share the same structure as the statistical multispecies model but lack the trophic calculations that are added into the multispecies modeling framework. The multispecies and single-species models corroborated each other well, with very few differences between the outputs, in particular for the species that were predators only. This is expected, as the trophic calculations do not affect the species that are only operating as a predator, and therefore only have a static natural mortality through time. For the prey species in this study, population abundance and recruitment

are estimated to be higher in the multispecies model than in the single-species model, which is also expected as the trophic calculations are providing a more refined understanding of the time and age varying predation mortality on these prey species. Since natural mortality is allowed to vary by both age and time, there is more information on the population size annually than would be available with time and/or age invariant natural mortality information. In years when predators were consuming more prey items, predation mortality will increase, and the population would need to be larger to accommodate this additional mortality while still allowing for the removals that are occurring from other sources such as from fishing. Again, the poorest performance between the multispecies and single-species models was found with weakfish. It is unclear as to what was causing this lack of corroboration between the two models. There are differences beyond the trophic calculations between the two modeling frameworks such as the way average recruitment is input to the two models, but they are generally minor differences and should not have such large impacts on output. The other possibility is that the additional weightings that are entered for the trophic calculations in the multispecies model are interacting in the likelihood calculations in ways that are not occurring in the single-species model. As an example, weakfish abundance is included in the *M2* calculations, so this interaction of model components could have large effects on the overall likelihood.

The multispecies model's performance relative to benchmark assessments was also investigated. One of the reasons for moving away from the existing MSVPA model for this set of species was the fact that some of the outputs in the last iteration of the MSVPA began to diverge dramatically from the information produced by the

benchmark models for the various species. One of the reasons for this divergence was believed to be the fact that the majority of the benchmark models had moved to statistical catch-at-age modeling frameworks, and therefore were becoming too different to be comparable. The statistical multispecies model, even with its more streamlined structure (i.e. there are no selectivity time blocks or fleet separations in the statistical multispecies model as is the case for all the benchmark models), has good correspondence with the benchmark models for the species in this study. The trends in the information were similar to each other, however there are some differences in the output produced for some important population metrics. Differences are found for menhaden, where the multispecies model predicts higher population size and higher average fishing mortality. The higher fishing mortality is counter intuitive, though it may be that the population abundance increase for this species may not be large enough to offset the increased natural mortality estimated by the model. In addition to menhaden, differences are also found for striped bass, most noticeably in average fishing mortality rates. The multispecies model predicts lower average fishing mortality rates beginning in the mid-1990s. And as was the case for the other comparisons made, weakfish indicated poor correspondence with the benchmark assessment information.

A final comparison was made between overlapping species and timeframes for the statistical multispecies model from this study, and previous MSVPA modeling work. For some of the metrics examined, there is some correlation in output between the models, such as with population abundance, while in other output information there were dramatic differences, such as with fishing mortality. Because there was

agreement in trends and in some cases magnitude of these different population metrics between the benchmark assessments and the statistical multispecies model, there is more confidence in the information produced by the statistical multispecies model than there is for the MSVPA modeling framework. This lack of confidence in the output from the MSVPA (SEDAR 2015), but a continued desire to research the use of multispecies models for developing ecological reference points (http://www.asmfc.org/files/PublicInput/AtlMenhadenAmend3PID_PublicComment.pdf), was one of the main reasons this project was developed, and therefore lack of correspondence between these two multispecies modeling frameworks was both expected and is viewed as a positive outcome of this study.

The MSSCAA model did not show sensitivity to the timeseries of data examined as indicated by the retrospective analysis conducted. The number of years examined was constrained by some of the data inputs, but enough peels were accomplished to give a decent indication of the model's sensitivity to the timeseries of data. Recruitment did show some effect from the differing time series length, but this is not an uncommon feature for many assessments because recruitment, in particular in the most recent time period, is one of the more poorly understood population metrics, and there is usually a need for the model to see the cohort in older ages before the estimation becomes stable. With regard to fishing mortality and biomass, the model performed well in the retrospective analysis. This has important implications if this model were to be used in management, namely that it would be providing stable information through time to managers of the various stocks.

The two prey species used in this study offer good contrast. There are some consistent characteristics between the two species such as the preference of younger ages by the predators and the correlation between predation mortality of these two prey and the size of important predator populations. However, there were also some notable differences such as how quickly scup is abandoned as a prey item as age (and therefore size) increases, most likely due to its morphological characteristics such as a tall profile and sharp spiny dorsal fins, and how menhaden were an important prey item for all of the predators examined while scup was generally preyed on by striped bass but not the other predators. The output produced for the prey examined in this study seemed reasonable and matched well with the other dynamics going on in the system such as the increasing importance of striped bass as a predator as its population rebuilt through the 1990s.

Menhaden abundance decreased from 1985 – 1995, which corresponds with a period of increasing fishing mortality and low predation mortality. The low predation mortality is presumably because striped bass abundance was low and bluefish and weakfish abundance was decreasing. After 2000, menhaden abundance increased with a corresponding decrease in fishing mortality, but predation mortality increased and remained high during this period due to increasing striped bass and bluefish populations. The fact that the menhaden population was able to increase even in the presence of high predation mortality shows that menhaden can withstand large predator fields in their population dynamics when fishing mortality is low. Predation mortality is decreasing for menhaden in the most recent years, likely due to the decreasing striped bass population. Given the population dynamics as described here,

this could be a period where menhaden could withstand moderately higher fishing mortality rates than when the predator populations of bluefish and striped bass are higher.

Scup abundance was at a low level in 1985, which corresponds to a period of high fishing mortality. Fishing mortality dropped off sharply after 1995 and scup abundance responded by increasing, despite the fact that predator populations of striped bass and bluefish were increasing at the same time, driving up predation mortality. Even with predation mortality at a high level in the most recent period of time, scup have been able to maintain a high population size. It appears that predation mortality has replaced fishing mortality on the scup population, but predation mortality has not increased to a level where the population has started to decline. This may in part be due to the increased size structure of the scup population, as once scup reach age 2 and greater, predation mortality drops off sharply, therefore there are plenty of older scup that do not get eaten remaining in the population under this period of low fishing mortality.

In both of these cases it is shown that both predators and prey can coexist at relatively high levels under a low fishing mortality regime. Even if fishing mortality were to increase, as long as the increase was not too extreme, it appears that both prey species in this study would be able to maintain relatively high abundance because all three predators in this study are experiencing some degree of decline, thus allowing there to be a trade-off between predation and fishing mortality. Additionally, the three predators in this study consume scup as prey, but only the smallest age classes of scup are vulnerable. Therefore maintaining a robust age structure in the scup population,

something that can be controlled in fishing practices, would allow the scup population to persist even in the presence of higher predator populations.

Some differences in recruitment can be seen when comparing the single-species models to the multispecies model, but in general, the different modeling frameworks do not change the pattern of recruitment at different stock sizes. Intuitively, the multispecies model predicted higher recruitment, regardless of the recruitment model used for the analysis, for the multispecies model for the prey species. The differences in recruitment between the prey species makes intuitive sense because there are more sources of dynamic removals beyond fishing in the multispecies modeling framework; therefore to produce population levels that can support both the harvest, survey, and consumption information, additional recruits are needed. This same process of increased recruitment would occur in a statistical single-species model, but the procedure used for the single-species models in this study was to assume a static *M* value for the population (as is the standard procedure for most single-species models), thus leading to the differences seen in this study. Additionally, most of the predators prefer prey at smaller sizes and therefore ages, so this adds additional removals on the youngest age classes including the recruits. There is some degree of correlation between *M2* and increased recruitment in the multispecies model for the prey species as another signal of this connection (menhaden correlation between annual average *M2* and recruitment = 0.42; scup correlation between annual average *M2* and recruitment = 0.66). There was also some diversity in recruitment outcomes between the models for the predator species, but these were more modest

differences and were variable, switching between the single-species and the multispecies versions as to which was predicting higher recruitment.

When looking across stock-recruitment models, the Ricker model appears to fit the data better than the Beverton-Holt model in most cases. This has important population dynamics implications in that there is a density dependence, namely over compensation, that will have impacts on these populations at high abundance levels. The Ricker stock recruitment model, which indicates density dependence in recruitment does have a biological basis in that there are mechanisms such as resource limitation, which also supports a Beverton-Holt relationship, and cannibalism that can act on all of these species at high population densities. Additionally, with the exception of menhaden, the median recruitment levels are fairly coherent with the asymptote of the Beverton-Holt curve and the peak of the Ricker curve, therefore the relationship between spawners and recruits is important to the population dynamics if and when spawning stock biomass levels are depleted.

One of the attributes of the modeling approach developed for this work is that it is not required to model all species in the ecosystem, which can be a laborious, and potentially impossible, task. Not modeling all of the species in the ecosystem, however, needs to be considered when making inferences about the results. If a major predator for one of the species is not included in the model, it is important to understand that this creates some of the same concerns as we currently have for a single-species model that does not consider predation mortality at all. Not including every predator is moderated to some degree given that some of the predators in the ecosystem are included, however, missing an important predator could potentially bias

the results and produce unrealistic reference points, leading to a different understanding of the population than is reality, and could result in poor performance of management programs if managers are misled by the information produced by the multispecies model due to missing important ecosystem components. This potential bias is the same as exists for single-species assessments, and would likely manifest in similar ways, such as through the development of a retrospective pattern in the model output. Retrospective patterns are often attributed to misspecifications in the model, or missing removals, so missing the consumption of an important predator could create this type of poor model diagnostic. While the MSSCAA model can have these inherent biases, it is no different in this regard than a single-species model, and as long as care is taken when considering the species to include, and being thoughtful with the parameterization of the residual natural mortality amount, the multispecies approach can still offer benefits in our understanding of natural populations that single-species approaches do not.

The species with the worst model diagnostics was weakfish. Despite the poor diagnostics, the species was kept in the model to allow for comparisons with the previous MSVPA work done on these same set of species. A deeper examination of weakfish would be a fruitful area of research. The benchmark assessment for weakfish (ASMFC 2016) used a Bayesian approach which allowed natural mortality to change through time. One of the causes for this time varying natural mortality could be that weakfish are an important prey item. In this study weakfish was only treated as a predator, but if it is also an important prey item, the MSSCAA model could be a method that could be used to allow for a different approach to the stock assessment

model for weakfish that could use empirical diet information to inform how and why weakfish natural mortality is changing through time. This deeper examination of weakfish population dynamics would be a good extension of this work.

To truly account for the ecosystem in a more robust way, additional considerations are needed. These considerations include the interaction of the species with each other as populations change amongst the species in the ecosystem in the future. These potential effects change the biological reference points (BRP), for instance menhaden natural mortality is impacted by other species in this model, therefore it is important to know how the BRPs change with changing population levels of these other species. These questions are best addressed through population projections which is the next logical extension of this work. The multispecies model provides an excellent platform for this extension.

In conclusion, the hypothesis being tested by this research, namely can the MSSCAA model perform well relative to single-species modeling platforms while giving a better understanding of population dynamics of the ecosystem being examined, was answered. The MSSCAA model showed similar trends in population size and fishing mortality when compared both to a simplified single-species model and the benchmark stock assessment models currently used for management. While the outputs were comparable, the MSSCAA model gives us a better understanding of the population dynamics with regard to new recruitment coming in to the population, and gives a different sense of the scale of the population, and the magnitude of fishing removals that these populations can withstand. It also provides a clearer view of the importance of specific predators on prey populations, the most notable being the

interaction between striped bass and menhaden. There is a clear signal of increased consumption of menhaden as the striped bass population increased, information which would be very useful for fisheries managers when thinking about potential new fishing rules to implement, and providing them better information in order to process their expectations of how these species will respond to this new management. In other words, managers would now have an understanding that it would be likely that menhaden abundances may be lower during periods where striped bass populations are at high abundance, or vice versa.

The MSSCAA model indicated superior performance with regard to the existing MSVPA for the same suite of species. This is a judgement based on how the model performed relative to some of the information considered best available science, namely the benchmark assessments for these species. It is not that this study sought to reproduce the output from the benchmark assessments for these species with the MSSCAA model, however population trends and trends in fishing mortality were more coherent with the current understanding of the population when using the MSSCAA model as opposed to the MSVPA, so while there is not an exact reproduction, the general understanding of what the population is doing through time is better reflected by the MSSCAA model. This would indicate that this model could be introduced as a tool for implementing ecosystem management for this group of species. The MSVPA had been used to inform changing natural mortality for menhaden in the past, but was abandoned due to conflicts in model outputs. The performance of the MSSCAA model as shown by this research could allow for this strategy to be reemployed in future management consideration for these species, and

allow for a more comprehensive and holistic management approach for this ecosystem.

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TABLES

Table 1 – Symbols and terms used in model formulation

Symbol	Definition
i	Species (used to designate prey species)
a	Age class (used to designate prey species age)
j	Predator species
b	Predator species age
t	Year
k	Fishery independent index
n	Number of indices
l	Vector of species specific surveys
m	Month
w_i	Inverse variance weight applied to survey at age information
σ_k	Mean of posterior standard deviation of process error from the hierarchical model
$N_{i,a,t}$	January 1 abundance-at-age (10^6 fish)
$Z_{i,a,t}$	Instantaneous total mortality-at-age per year
$C_{i,a,t}$	Fishery catch-at-age (commercial and recreational harvest and dead discards, 10^6 fish)
$F_{i,a,t}$	Instantaneous fishing mortality-at-age per year
$s_{i,a}$	Fishery selectivity-at-age
$FIC_{i,a,t}$	Fishery independent catch (CPUE)
q_i	Fishery independent catchability
$r_{i,a}$	Fishery independent survey selectivity-at-age
$Sel_{x,i}$	Selectivity generated by logistic or double logistic functions
α_1, α_2, β_1, β_2	Logistic and double logistic ascending or descending limb parameters
$M_{i,a,t}$	Instantaneous natural mortality
$M1_{i,a}$	Instantaneous natural mortality due to everything except fishing and predation mortality (time invariant)
$M2_{i,a,t}$	Instantaneous natural mortality due to predation
$W_{i,a,t}$	Average annual species-specific weight-at-age
$CB_{j,b}$	Consumption to biomass ratio (time invariant)
$B_{i,b,t}$	Biomass-at-age (10^6 kg)
$\phi_{i,a,j,b,t}$	Available prey biomass (10^6 kg)
$\tilde{\nu}_{i,a,j,b,t}$	Scaled prey suitability
$\nu_{i,a,j,b}$	Prey suitability
$B_{totalecosystem}$	Total ecosystem biomass (10^6 kg)
$\rho_{i,j}$	Prey species preference

Table 1 (cont.) – Symbols and terms used in model formulation

Symbol	Definition
$g_{i,a,j,b}$	Predator size preference
η_j	Preferred predator to prey weight ratio
$B_{other,t}$	Total biomass of other food
$P_{i,a,t}$	Proportion-at-age
I	Dataset
LL_I	Log likelihood of dataset I
D_I	Objective function weighting for dataset I
TC	Total fishery catch (10^3 mt)
TS	Total survey catch (CPUE)
CP	Fishery catch age proportions
SP	Survey catch age proportions
FH	Food habits proportions
Pen_i	Total likelihood penalty for each species
Pwt_p	Objective function weighting for penalty p
$Yr1pen$	Year 1 abundance penalty
$Rpen$	Recruitment penalty
$Bpen$	Biomass penalty
$Yr1$	Year 1 abundance-at-age
$Rthresh$	Threshold value for the CV of log recruitment variability
$Bthresh$	Threshold value for age-specific biomass
$Age1$	Recruitment

Table 2 – Components of the likelihood function by assumed distributions and including penalty functions. Small constants (10^{-3}) are added to the lognormal and multinomial calculations to keep the calculations from terminating if they reach zero.

Equation	Definition
$\mathrm{LL_{Total}} = \mathrm{LL_{TC}} + \mathrm{LL_{TS}} + \mathrm{LL_{CP}} + \mathrm{LL_{SP}} + \mathrm{LL_{FH}} + \sum_i Pen_i$	Total log likelihood
$LL_I = D_I * \sum_{t,i,a} \left(ln(I + 10^{-3}) - ln\left(\hat{I} + 10^{-3}\right)\right)^2$	Lognormal distribution component
$LL_I = D_I * \sum_{t,i,a} \left(I + 10^{-3} * ln\left(\hat{I} + 10^{-3}\right)\right)$	Multinomial distribution component
$Pen_i = Pwt_{Yr1_i} * Yr1pen_i + Pwt_{Age1_i} * Rpen_i + Pwt_{B_i} * Bpen_i$	Total penalty
$Yr1pen_i = \sum_a (N_{i,a,t=1} - Yr1_{i,a})^2$	Year 1 penalty
$Rpen_i = 0.01 * (CV\left(N_{i,a=1,t}\right) - Rthresh_i)^2$	Recruitment penalty. Applied when the CV > Rthresh
$Bpen_i = \sum_{a,t} 0.01 * (B_{i,a,t} - Bthresh_i)^2$	Biomass penalty. Applied when B < Bthresh

Table 3 – Fishery-independent indices used for each species and associated process error from hierarchical modeling procedure.

	Menhaden	Striped Bass	Bluefish	Weakfish*	Scup
Survey	NAD	CT Trawl	CT Trawl	MRIP CPUE	NMFS Trawl **
Error	0.56	0.67	0.48		0.43
Survey	SAD	NY Ocean Haul	NMFS Trawl (Albatross)		URI Ventless Fish Pot
Error	0.43	0.57	0.20		0.33
Survey		NJ Ocean Trawl	NMFS Trawl (Bigelow)		CT Trawl (Spring)
Error		0.36	0.43		0.51
Survey			NEAMAP		CT Trawl (Fall)
Error			0.78		0.30
Survey			NC PSIGNS		
Error			0.13		
Survey			MRIP Index		
Error			0.09		

*Weakfish used MRIP CPUE (not Bayesian Hierarchical model) per advice of ASMFC weakfish stock assessment subcommittee members.

**Trawl in calibrated Albatross units, Fall survey

Table 4 – Contributions of the various components by species to the objective function value

Likelihood Component	Menhaden	Striped Bass	Bluefish	Weakfish	Scup
Total fishery catch	19	0.6	22	74	15
Total survey catch	202	127	46	330	113
Fishery catch age proportions	1,901	2,634	2,138	2,400	2,297
Survey catch age proportions	2,208	2,943	3,061	2,623	1,695
Food habits	0	316	708	138	0
Year 1 penalty	0.002	1.15	5.07	18.32	0.70
Recruitment penalty	0	0	0	0	0
Biomass penalty	0	0	0	0	0
Total Likelihood Value	4,331	6,020	5,974	5,564	4,120

Table 5 – Average predator – prey weight ratios (η), the variance in each of these ratios (σ), estimated species preference coefficients (ρ) relative to 1 for "other food"

Parameter	Predator Species	Prey Species	
		Menhaden	Scup
η	Striped Bass	3.97	5.53
	Bluefish	3.1	5.83
	Weakfish	3.89	5.17
σ	Striped Bass	0.95	1.1
	Bluefish	0.62	0.96
	Weakfish	1.43	1
ρ	Striped Bass	59.6	269.1
	Bluefish	67.4	573.8
	Weakfish	16.3	40.8

Table 6 – Parameter estimates for the Beverton-Holt stock-recruitment model and median recruitment levels for all species investigated. Parameters are developed for both the single-species and multispecies model output.

Species	Single-species			Multispecies		
	α	B	Median	α	β	Median
Menhaden	14,853	513	4,109	16,225	458	4,329
Striped Bass	175	14	123	148	11	102
Bluefish	23	8	20	26	18	20
Weakfish	61	12*	15	43	12*	23
Scup	162	6	87	331	5	136

* Weakfish β parameter fixed at lower bound.

Table 7 – Parameter estimates for the Ricker stock-recruitment model and SSB of maximum recruitment (1/ β) for all species investigated. Parameters are developed for both the single-species and multispecies model output.

Species	Single-species			Multispecies		
	α	B	1/ β	α	β	1/ β
Menhaden	28	0.002	594	36	0.002	518
Striped Bass	5	0.010	97	6	0.016	61
Bluefish	0.8	0.014	71	0.6	0.010	96
Weakfish	2.6	0.009*	111	2	0.046	22
Scup	10	0.014	71	27	0.019	52

* Weakfish β parameter fixed at lower bound.

Table 8 – Mohn's Rho statistic ($\bar{\rho}$) for the four-year retrospective peel of the MSSCAA model.

	Full Fishing Mortality	Total Biomass	Recruitment
Menhaden	-0.04	0.28	0.43
Striped Bass	0.04	-0.05	-0.41
Bluefish	0.02	0.01	-0.18
Weakfish	0.17	0.03	0.14
Scup	0.11	-0.07	0.03

Table 9 – Bayesian hierarchical model estimates of annual survey abundances by species.

Year	Menhaden	Striped Bass	Bluefish	Weakfish*	Scup
1985	129.67	26.26	129.93	0.172	113.48
1986	413.94	26.22	145.57	0.639	103.54
1987	331.26	75.48	145.98	0.234	94.88
1988	235.92	72.6	91.98	0.261	85.34
1989	152.35	42.68	87.82	0.126	200.76
1990	121.16	80.52	128.25	0.116	116.2
1991	78.31	84.59	104.33	0.151	145.47
1992	71.55	77.32	107.15	0.106	156.33
1993	64.14	81.6	75.72	0.158	55.3
1994	60.85	94.8	84.4	0.262	42.28
1995	51.14	174.36	93.49	0.385	104.9
1996	60.63	230.14	95.91	0.445	74.27
1997	41.96	243.6	108.11	0.424	57.49
1998	31.39	238.57	96.21	0.356	126.21
1999	71.6	186.22	122.01	0.248	153.31
2000	59.42	230.24	141.33	0.283	709.64
2001	47.04	121.63	146.06	0.19	208.59
2002	56.45	151.51	129.43	0.154	680.31
2003	41.87	268.6	129.39	0.085	244.82
2004	51.79	233.76	158.26	0.141	336.62
2005	98.53	265.49	118.99	0.134	180.36
2006	169.4	154.72	137.68	0.112	301.56
2007	87.31	215.85	154.93	0.058	456.24
2008	73.11	109.1	131.89	0.06	499.34
2009	125.69	143.02	128.56	0.028	452.33
2010	101.74	78.06	125.99	0.055	449.05
2011	222.14	125.3	127.27	0.046	293.4
2012	164.74	166.58	117.8	0.077	461.61

*Weakfish used MRIP CPUE (not Bayesian Hierarchical model) per advice of ASMFC weakfish stock assessment subcommittee members.

Table 10 – AIC comparisons of Beverton-Holt and Ricker stock-recruitment relationships for single-species model output.

Year	Menhaden	Striped Bass	Bluefish	Weakfish	Scup
Beverton-Holt	462.5	306.5	166.1	212.5	295.2
Ricker	455.4	292.1	162.1	187.8	289.1

Table 11 – AIC comparisons of Beverton-Holt and Ricker stock-recruitment relationships for multispecies model output.

Year	Menhaden	Striped Bass	Bluefish	Weakfish	Scup
Beverton-Holt	447.0	298.2	166.4	248.4	335.0
Ricker	439.7	286.9	163.5	225.9	329.1

FIGURES

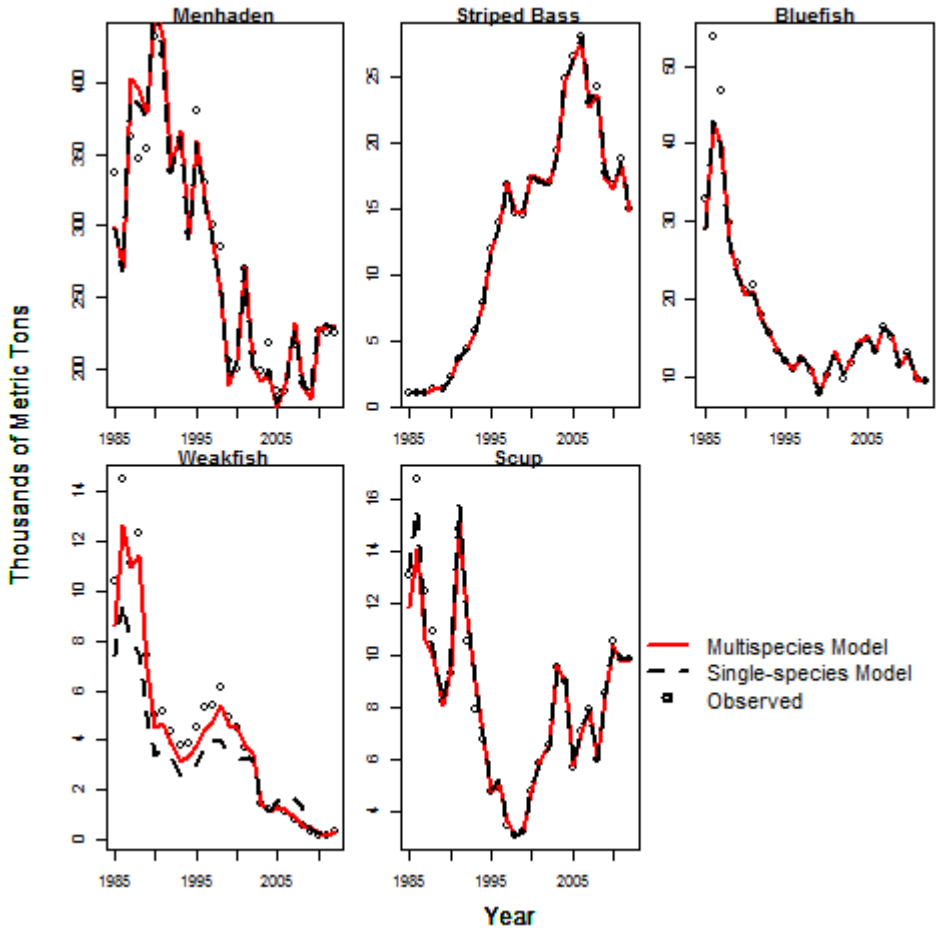

Fig. 1: Observed (open circles), predicted single-species (dashed black line; hereafter single-species refers to the simplified models created for this project, not the benchmark assessments for these species), and predicted multispecies (solid red line) total annual fishery catch.

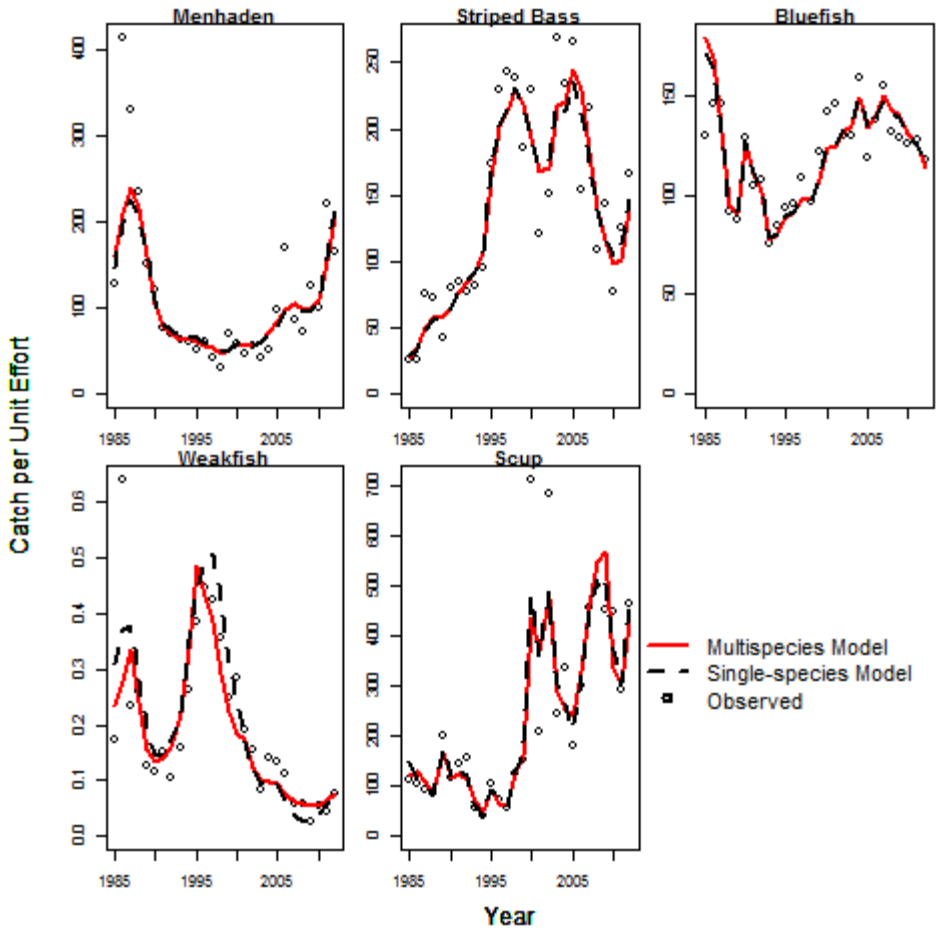

Fig. 2: Observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) total annual survey catch.

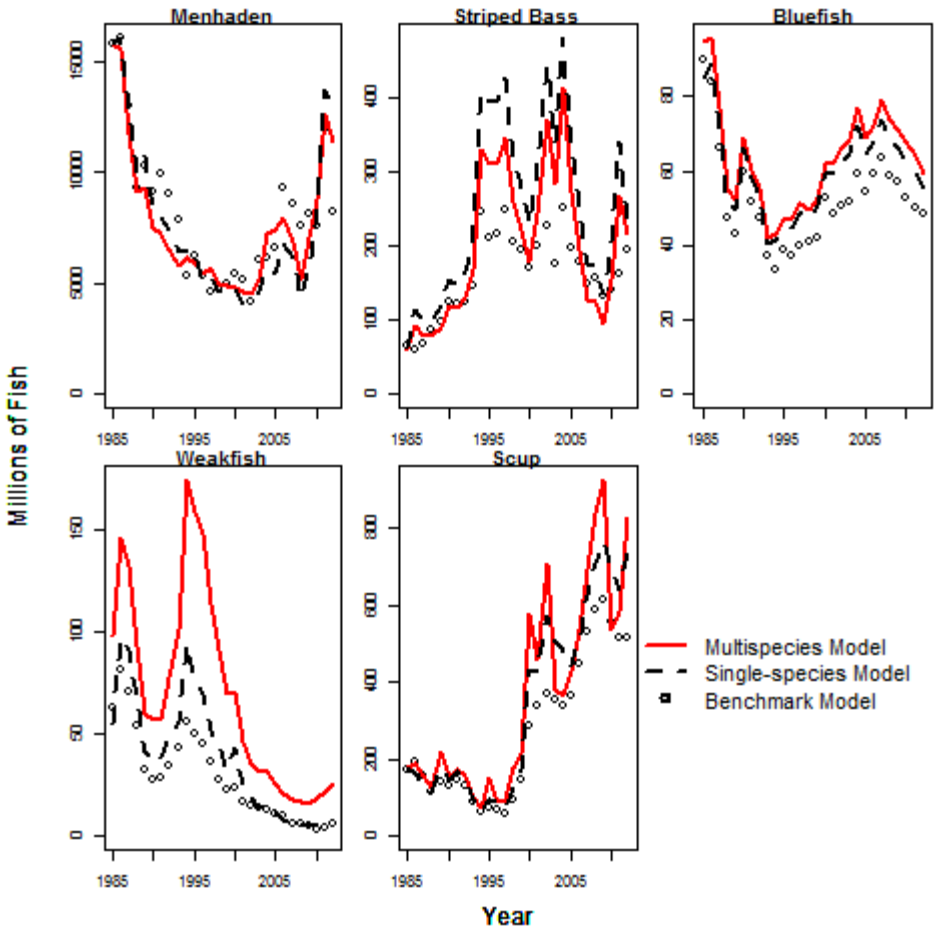

Fig. 3: Predicted annual total abundance by species from single-species (dashed black line) and multispecies (solid red line) models. Data from most recent benchmark assessments presented as open circles for comparison.

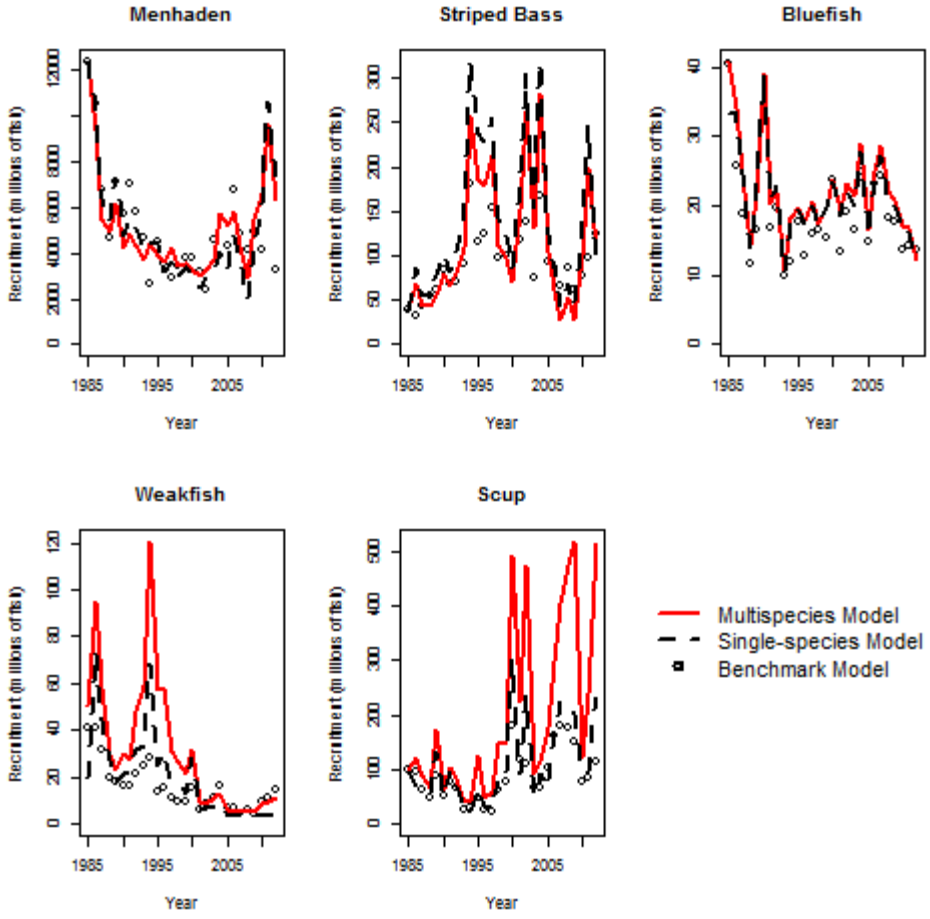

Fig. 4: Predicted annual recruitment (age 1) by species from single-species (dashed black line) and multispecies (solid red line) models. Data from most recent assessments presented as open circles for comparison.

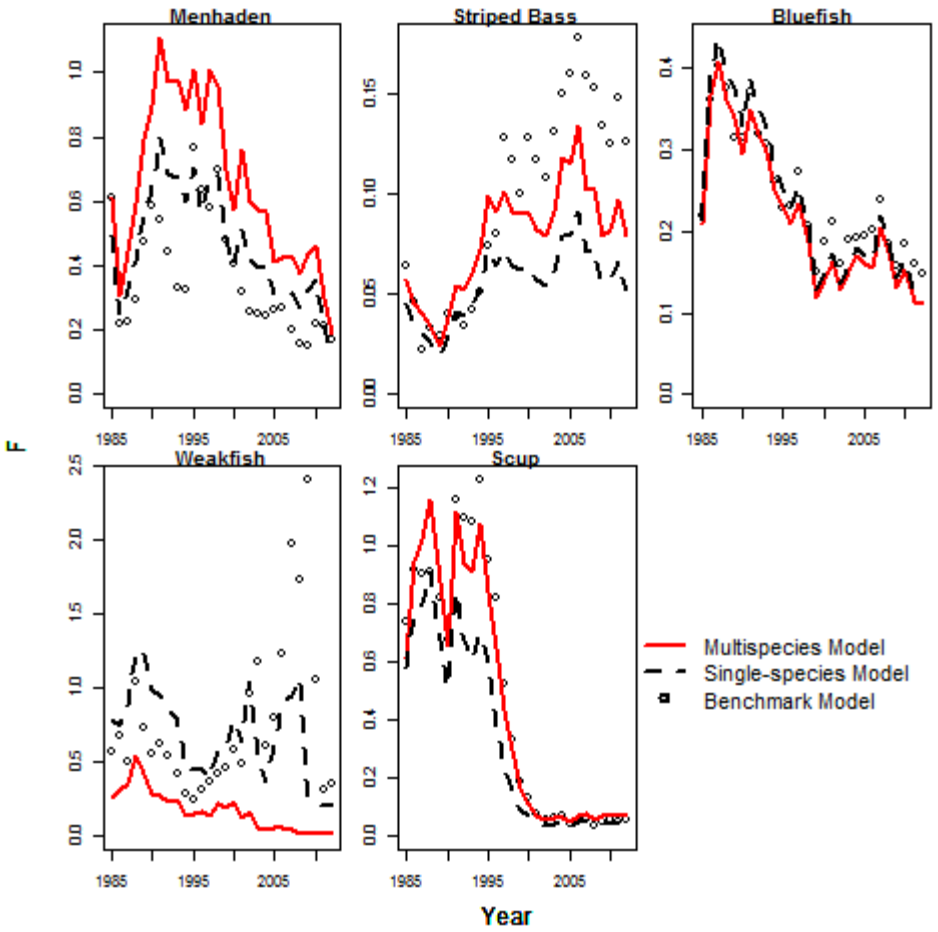

Fig. 5: Predicted annual average fishing mortality (F) by species from single-species (dashed black line) and multispecies (solid red line) models. Data from most recent assessments presented as open circles for comparison.

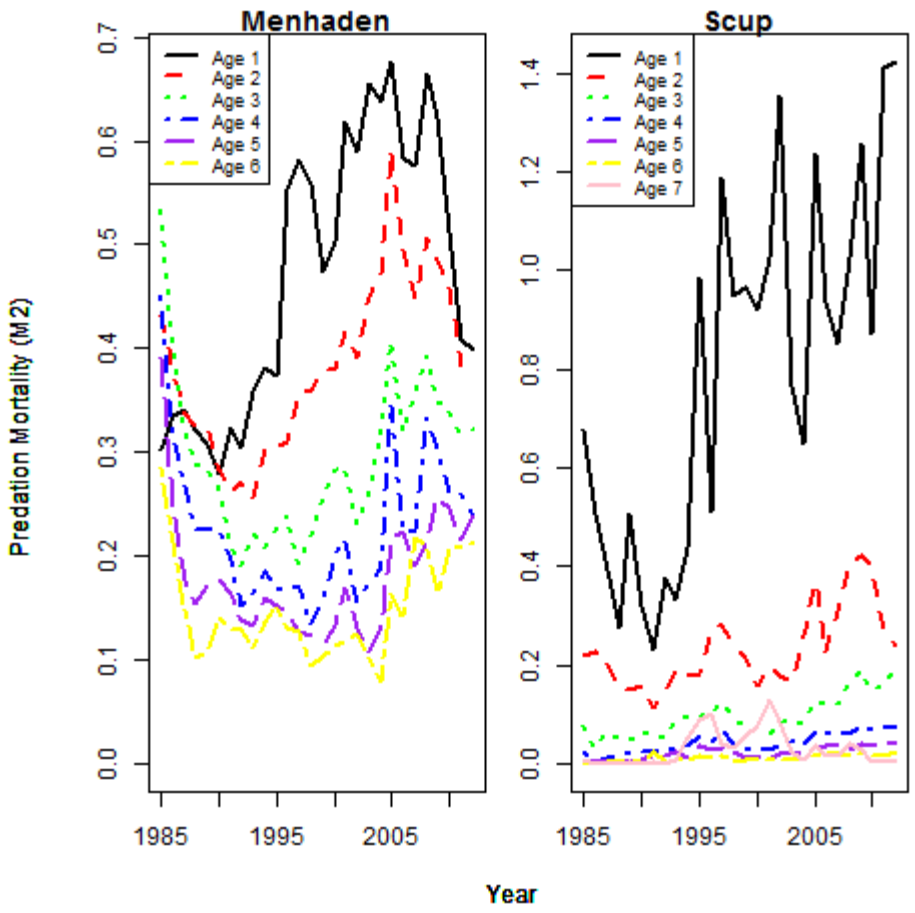

Fig. 6: Predicted annual Predation mortality-at-age (M2) for menhaden and scup.

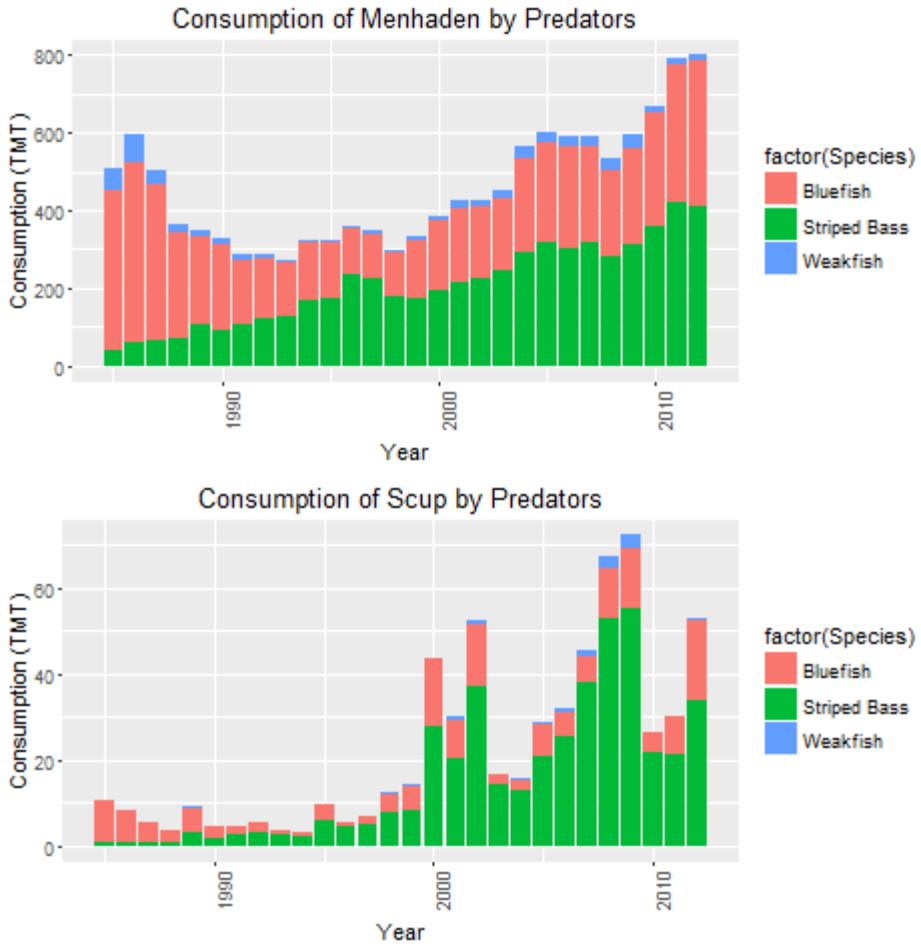

Fig. 7: Predicted annual consumption in thousands of metric tons by predator for menhaden and scup.

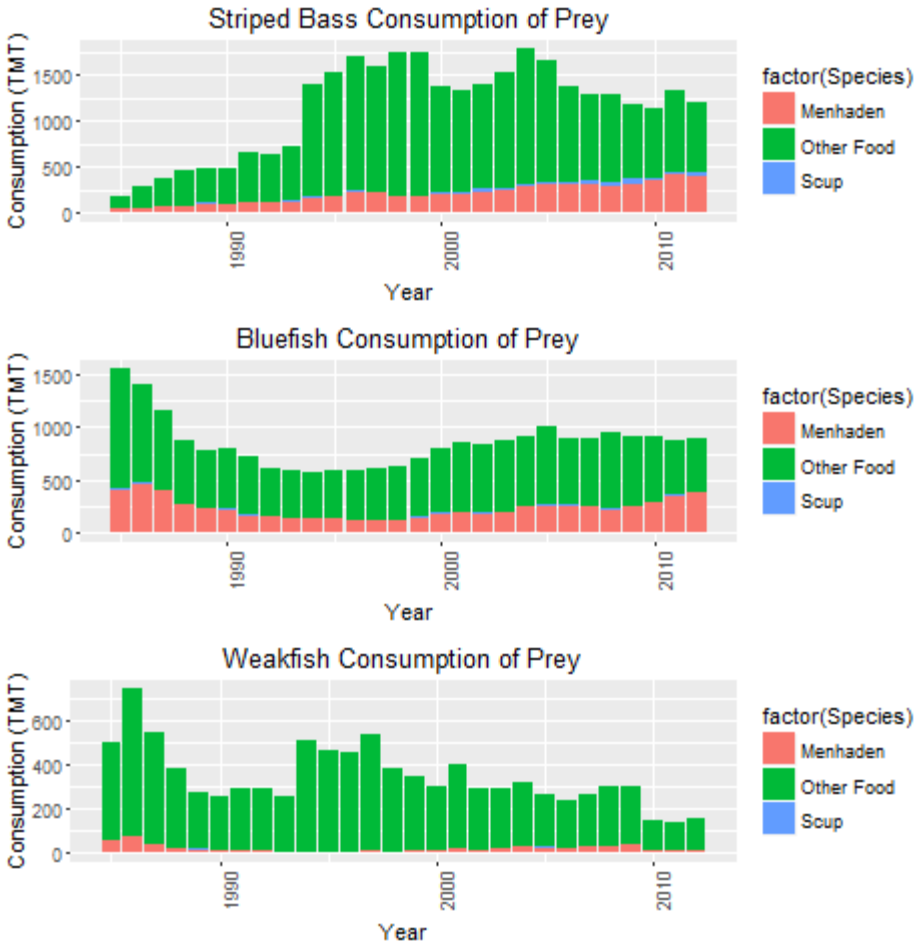

Fig. 8: Predicted annual consumption in thousands of metric tons by prey for striped bass, bluefish, and weakfish.

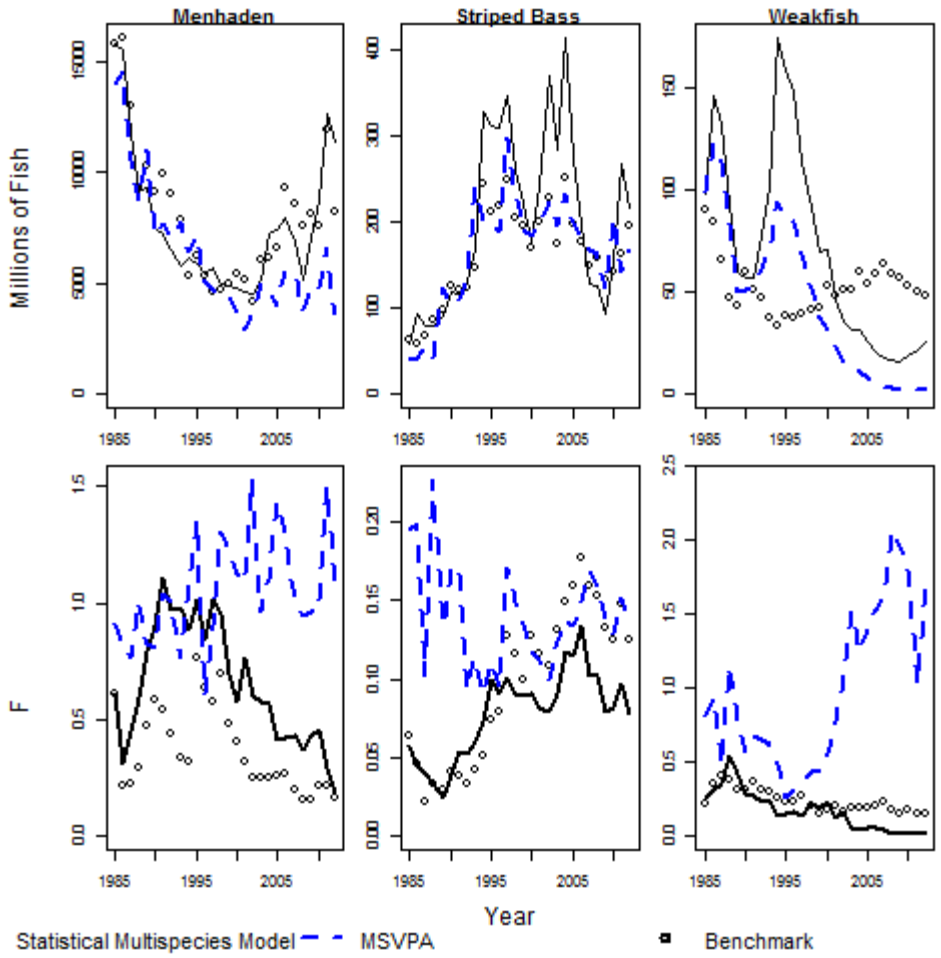

Fig. 9: Comparison of average fishing mortality and total abundance between the MSVPA (blue dashed line), statistical multispecies model (black solid line), and the benchmark assessment (open circles).

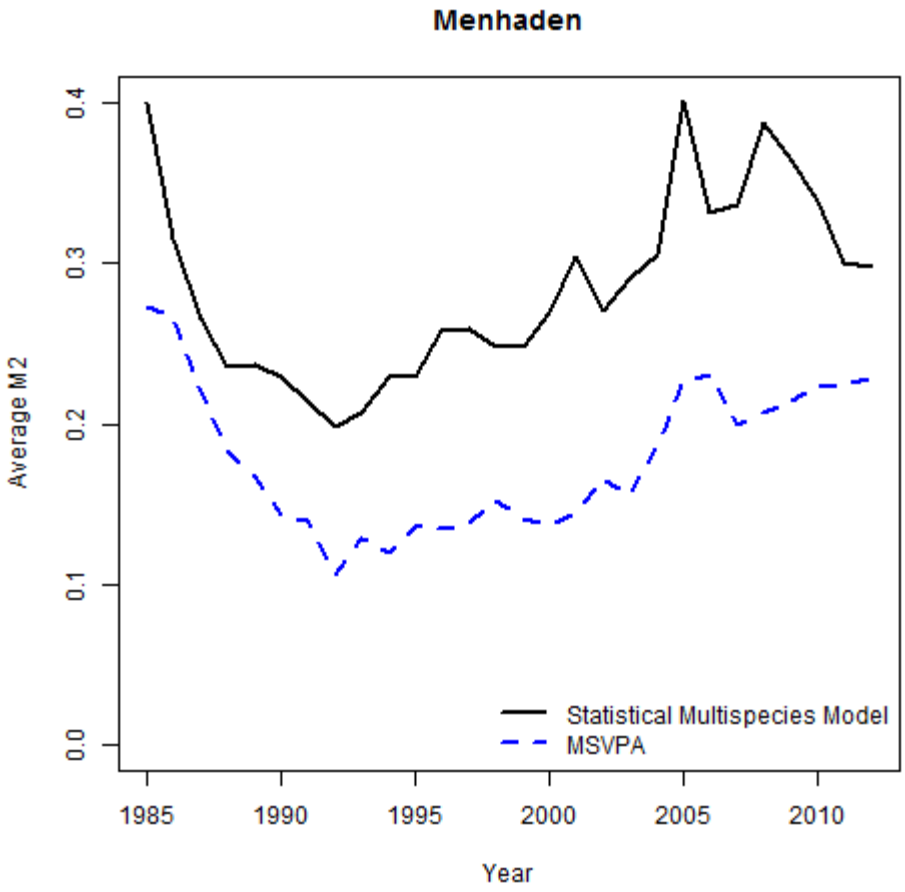

Fig. 10: Comparison of average predation mortality between the MSVPA and statistical multispecies model. Black solid line is the statistical multispecies model, the blue dashed line is the MSVPA.

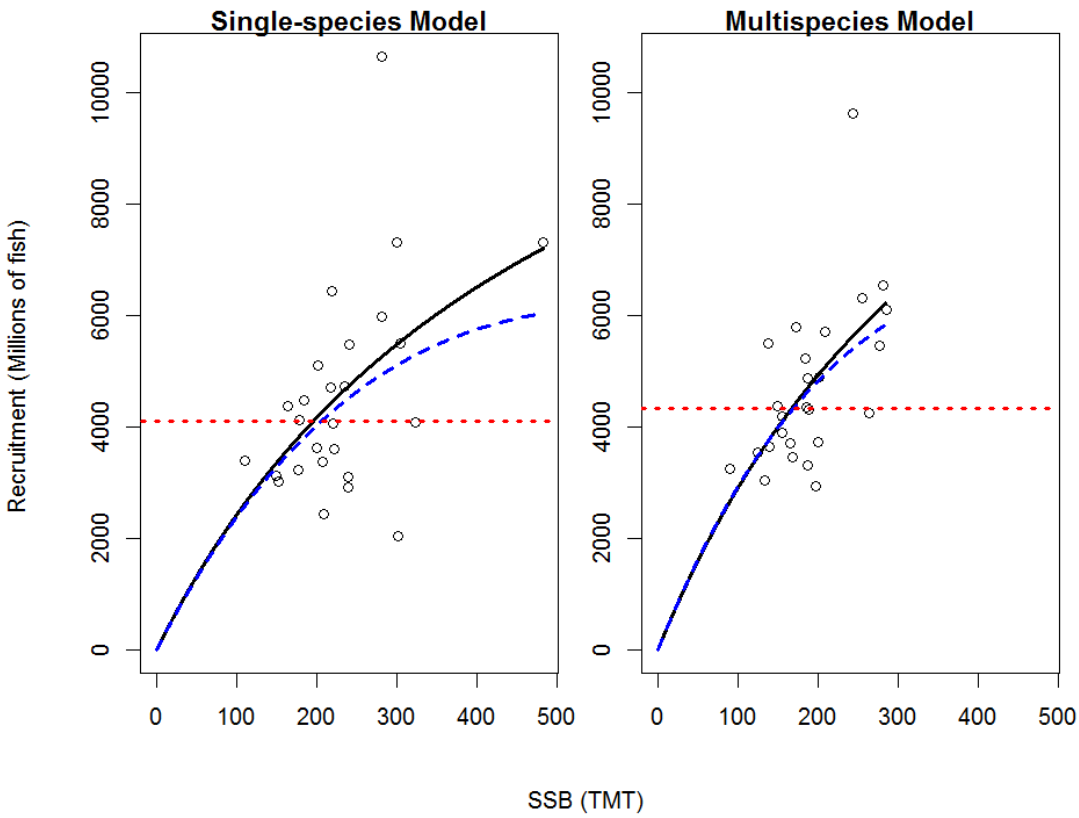

Fig. 11: Beverton-Holt (black solid line) and Ricker (dashed blue line) stock-recruitment relationship for menhaden based off output from the simplified single-species (left side panel) and multispecies (right side panel) stock assessment. The red line represents the median recruitment.

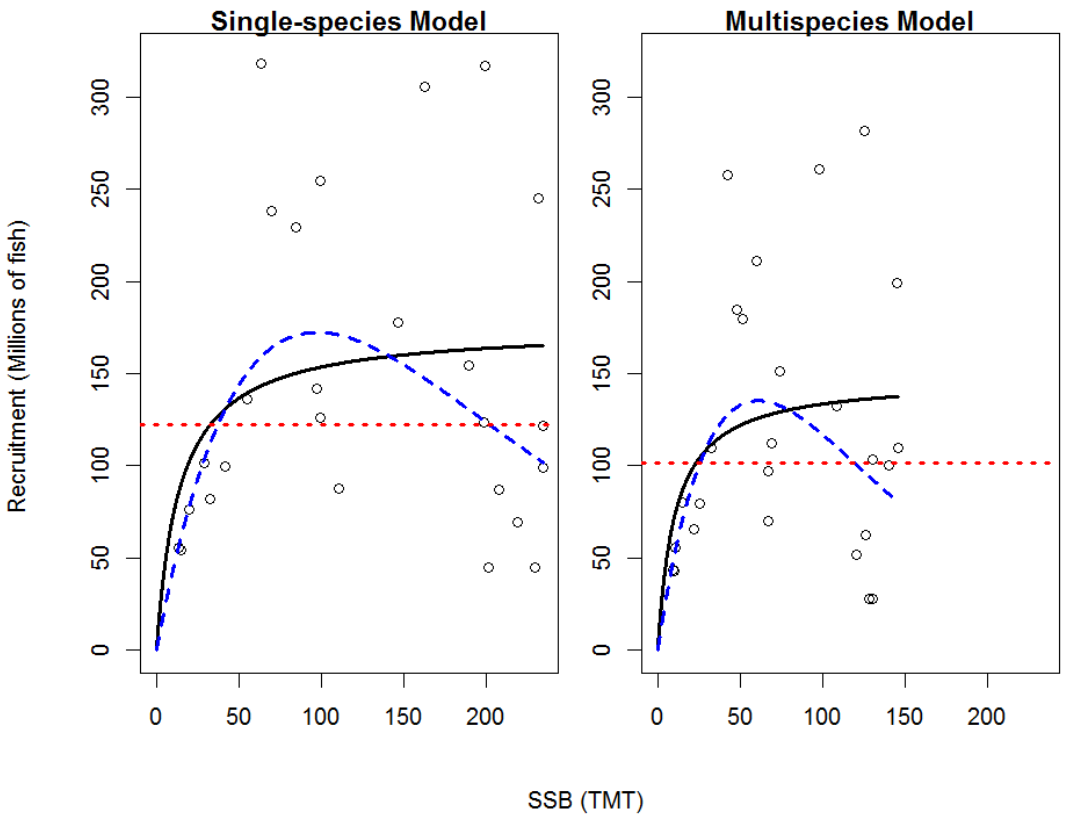

Fig. 12: Beverton-Holt (black solid line) and Ricker (dashed blue line) stock-recruitment relationship for striped bass based off output from the simplified single-species (left side panel) and multispecies (right side panel) stock assessment. The red line represents the median recruitment.

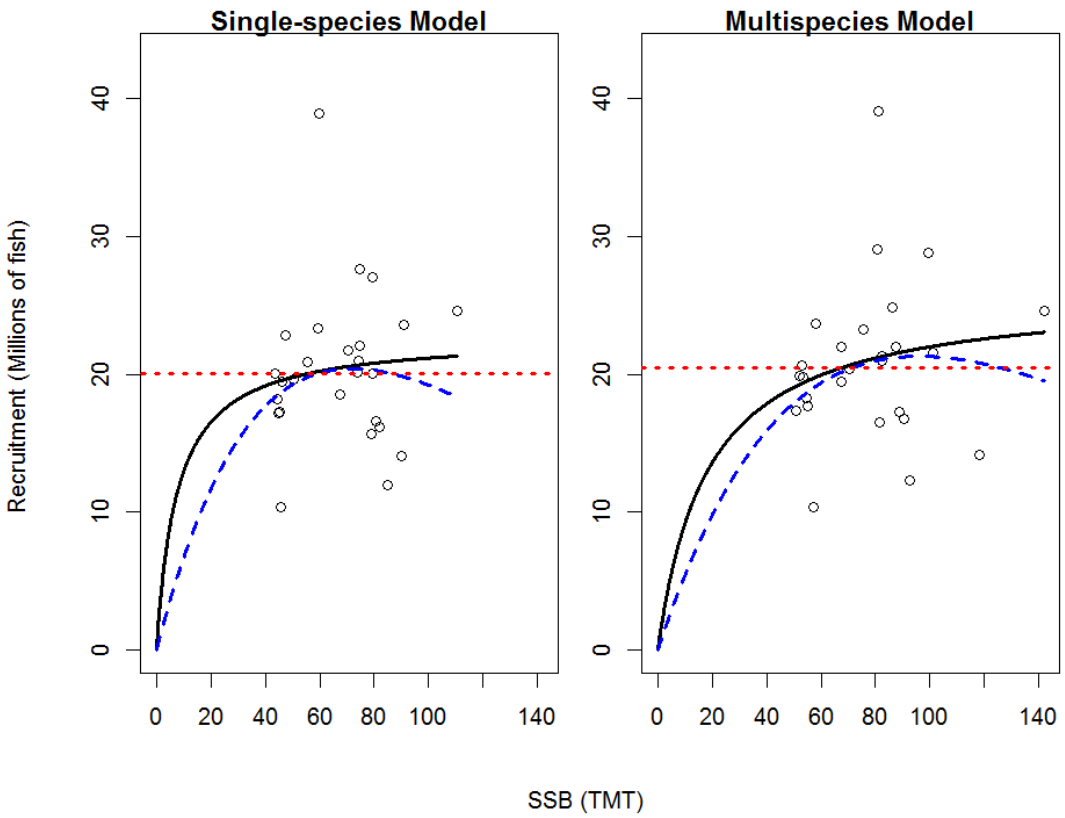

Fig. 13: Beverton-Holt (black solid line) and Ricker (dashed blue line) stock-recruitment relationship for bluefish based off output from the simplified single-species (left side panel) and multispecies (right side panel) stock assessment. The red line represents the median recruitment.

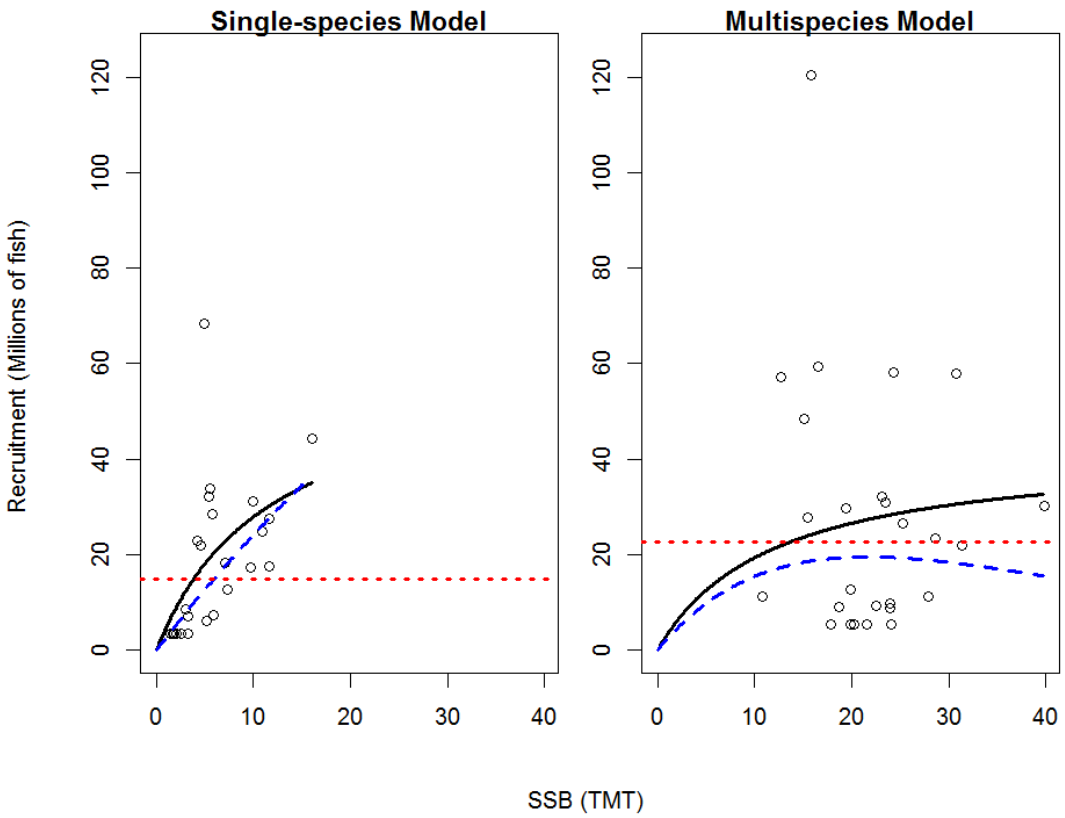

Fig. 14: Beverton-Holt (black solid line) and Ricker (dashed blue line) stock-recruitment relationship for weakfish based off output from the simplified single-species (left side panel) and multispecies (right side panel) stock assessment. The red line represents the median recruitment.

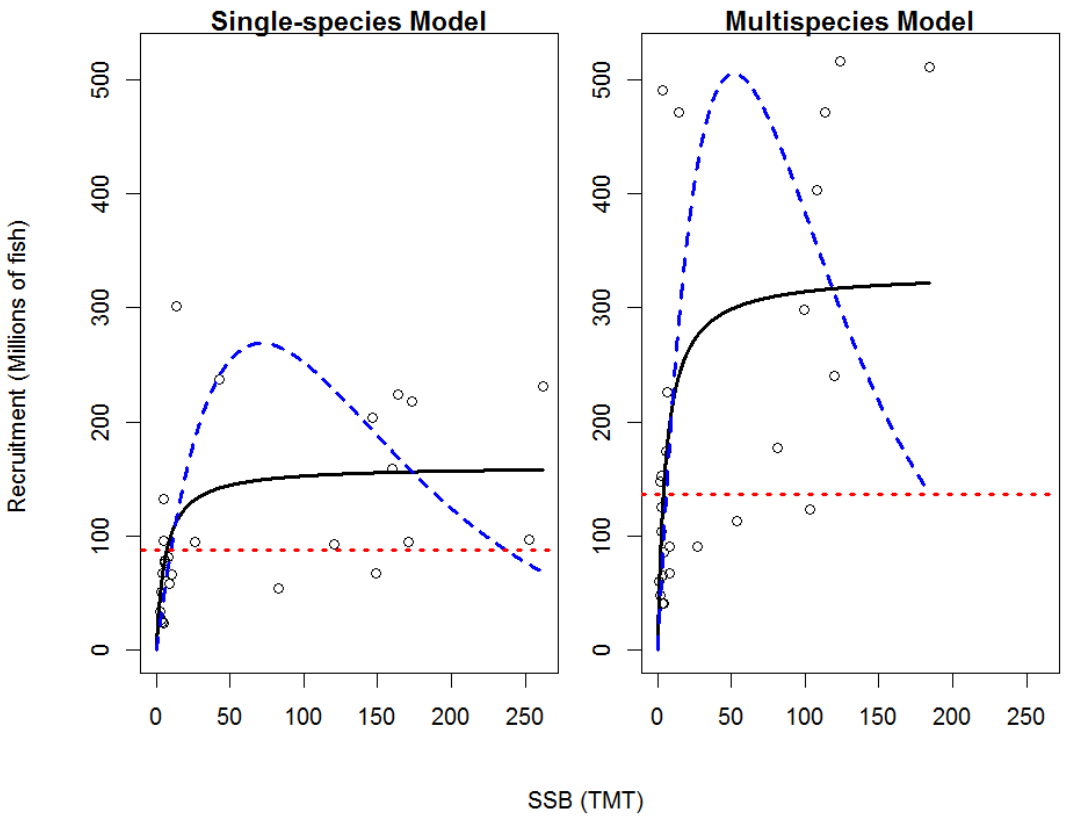

Fig. 15: Beverton-Holt (black solid line) and Ricker (dashed blue line) stock-recruitment relationship for scup based off output from the simplified single-species (left side panel) and multispecies (right side panel) stock assessment. The red line represents the median recruitment.

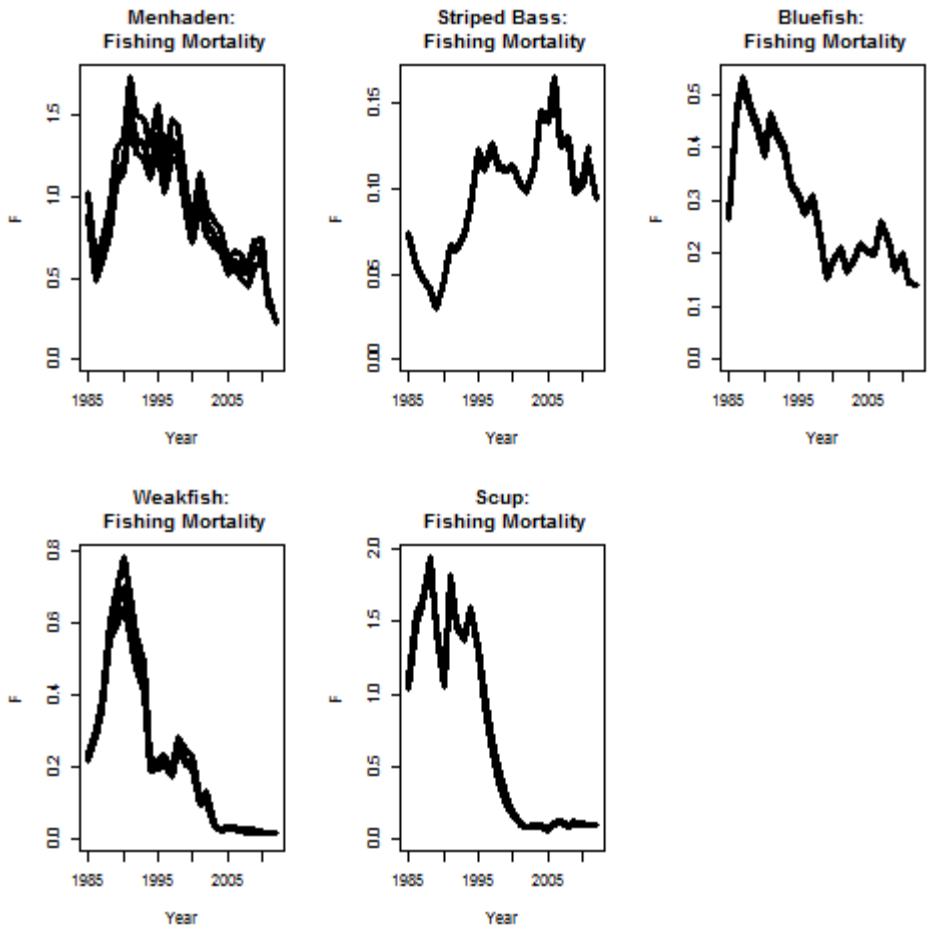

Fig. 16: Retrospective analysis for full fishing mortality for all five species.

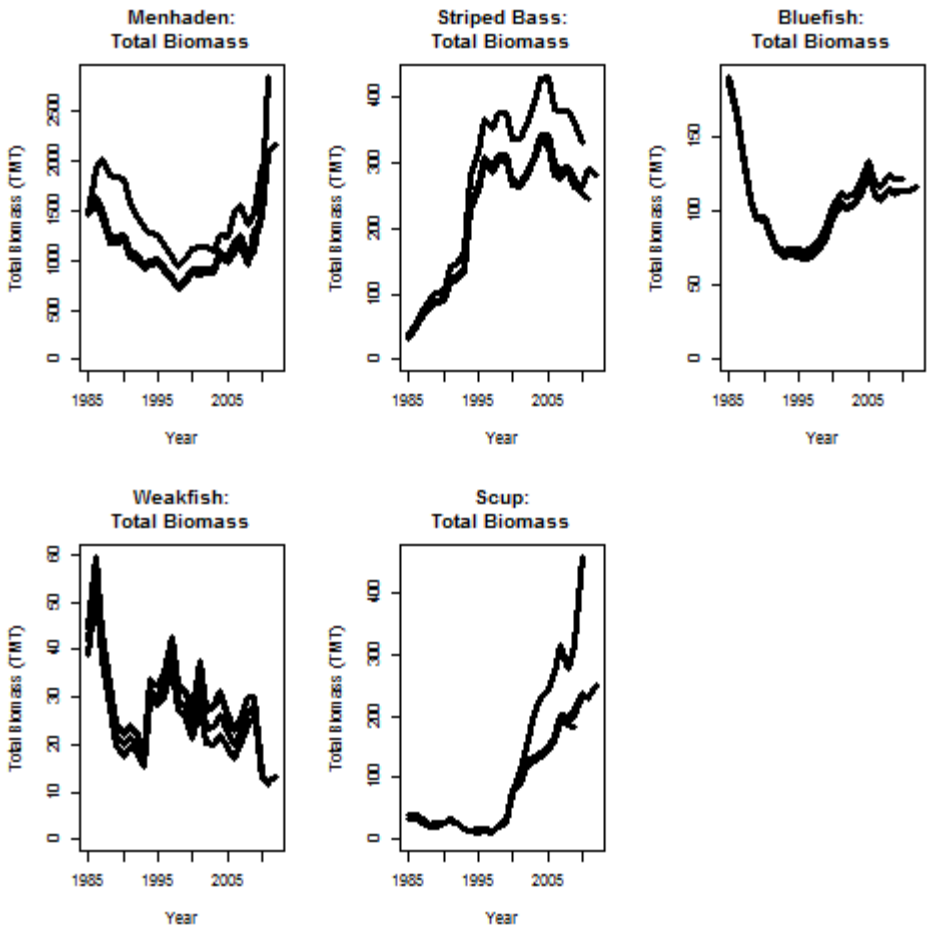

Fig. 17: Retrospective analysis for total biomass for all five species.

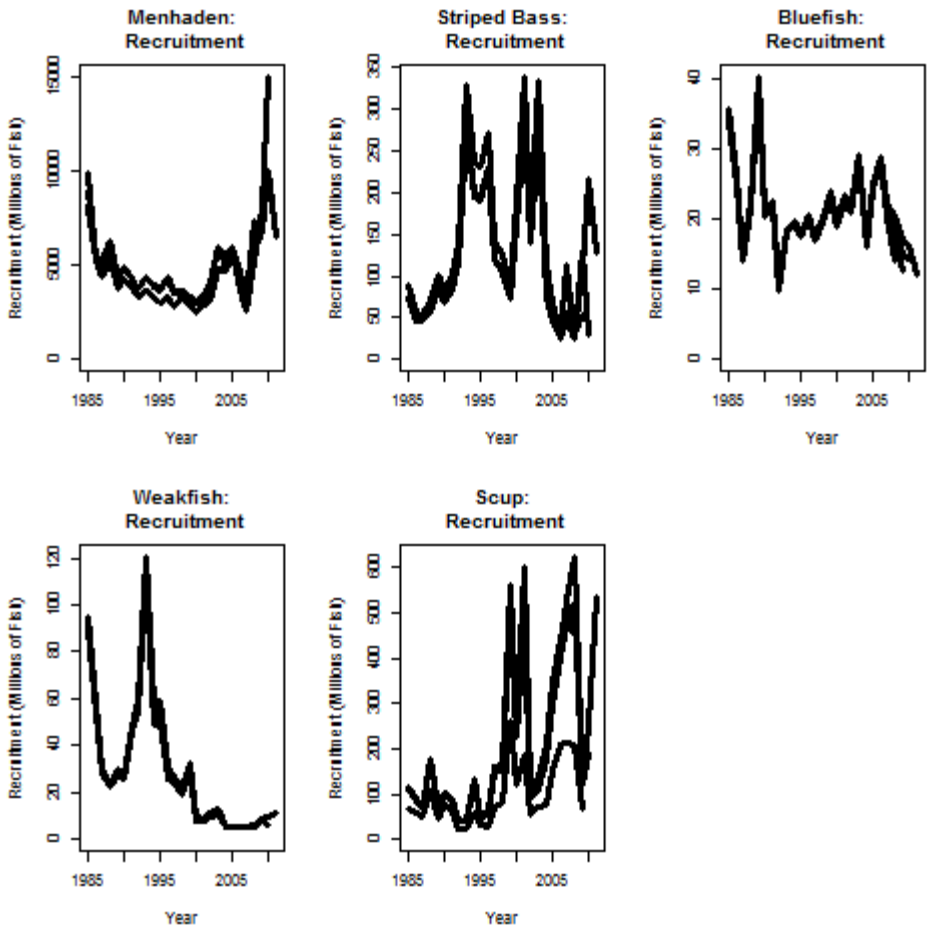

Fig. 18: Retrospective analysis for total biomass for all five species.

APPENDIX

Table A1 – Model estimated population abundance for menhaden (millions of fish)

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1985	12,357.30	2,998.90	134.05	87.01	49.99	146.06
1986	9,363.27	5,419.40	626.59	27.54	21.01	60.59
1987	5,494.79	4,203.87	1,774.85	213.54	10.81	37.44
1988	4,901.49	2,391.23	1,198.04	552.86	74.89	20.60
1989	6,116.55	2,117.35	564.69	320.06	170.06	34.28
1990	4,254.67	2,580.82	385.80	118.63	78.15	58.17
1991	4,872.32	1,811.57	425.72	72.00	25.61	35.38
1992	4,308.92	1,911.53	231.71	64.98	12.52	13.18
1993	3,705.95	1,767.80	290.15	42.80	13.87	6.41
1994	4,375.09	1,438.17	270.73	51.60	9.00	4.98
1995	3,890.90	1,687.36	236.88	54.65	11.79	3.70
1996	3,647.16	1,477.30	235.21	40.12	10.98	3.55
1997	4,197.42	1,194.32	255.00	48.42	9.75	4.02
1998	3,463.80	1,294.94	157.90	44.74	9.71	3.25
1999	3,553.76	1,104.04	183.30	28.80	9.88	3.26
2000	3,260.46	1,292.84	216.20	44.57	8.41	4.37
2001	3,033.84	1,178.52	297.51	59.62	14.41	4.81
2002	3,313.30	944.74	204.28	64.78	15.25	5.72
2003	3,738.95	1,092.64	207.54	57.32	21.22	7.61
2004	5,710.81	1,160.87	234.90	58.71	19.05	11.01
2005	5,233.68	1,808.08	246.34	63.20	19.35	11.56
2006	5,799.12	1,638.23	416.97	73.36	21.31	12.85
2007	4,348.15	1,986.34	407.09	133.25	27.55	14.11
2008	2,938.21	1,498.83	516.65	125.24	49.74	16.94
2009	5,450.73	937.68	395.20	163.53	44.71	28.17
2010	6,551.22	1,792.74	233.48	121.31	56.00	28.97
2011	9,634.72	2,394.67	442.44	70.03	42.06	32.40
2012	6,306.14	4,023.78	790.76	166.06	29.40	34.43

Table A2 – Model estimated population abundance for striped bass (millions of fish)

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13+
1985	39.87	10.29	4.91	1.31	1.01	0.50	0.41	0.24	0.16	0.17	0.02	0.01	0.29
1986	68.24	12.87	5.19	3.07	0.89	0.73	0.38	0.32	0.19	0.13	0.14	0.01	0.25
1987	43.02	22.03	6.50	3.26	2.12	0.65	0.57	0.31	0.26	0.15	0.10	0.11	0.22
1988	43.77	13.89	11.14	4.09	2.26	1.57	0.51	0.46	0.25	0.21	0.13	0.08	0.27
1989	55.53	14.13	7.02	7.02	2.85	1.69	1.24	0.42	0.38	0.21	0.17	0.10	0.30
1990	79.88	17.93	7.15	4.44	4.94	2.15	1.35	1.03	0.35	0.32	0.17	0.15	0.34
1991	65.39	25.79	9.06	4.50	3.08	3.66	1.69	1.10	0.84	0.29	0.26	0.14	0.40
1992	79.49	21.11	13.03	5.68	3.08	2.24	2.81	1.35	0.88	0.67	0.23	0.21	0.45
1993	109.81	25.66	10.66	8.17	3.89	2.24	1.72	2.25	1.08	0.70	0.54	0.18	0.53
1994	257.96	35.45	12.95	6.67	5.55	2.80	1.71	1.37	1.78	0.86	0.56	0.43	0.59
1995	184.91	83.27	17.88	8.07	4.48	3.94	2.10	1.33	1.06	1.39	0.67	0.43	0.81
1996	179.75	59.68	41.93	11.04	5.29	3.07	2.84	1.57	1.00	0.80	1.04	0.50	0.98
1997	211.51	58.01	30.07	25.96	7.29	3.66	2.24	2.16	1.20	0.76	0.61	0.79	1.17
1998	112.07	68.26	29.21	18.55	16.98	4.98	2.64	1.68	1.61	0.89	0.57	0.45	1.53
1999	97.30	36.17	34.39	18.08	12.25	11.75	3.64	2.00	1.27	1.22	0.68	0.43	1.58
2000	69.72	31.40	18.23	21.30	11.96	8.50	8.60	2.77	1.52	0.97	0.93	0.52	1.60
2001	151.48	22.50	15.82	11.28	14.07	8.28	6.20	6.52	2.10	1.15	0.73	0.71	1.69
2002	261.10	48.89	11.34	9.82	7.51	9.85	6.12	4.76	5.01	1.61	0.89	0.56	1.91
2003	132.54	84.28	24.65	7.05	6.56	5.28	7.31	4.72	3.67	3.86	1.24	0.68	1.99
2004	281.62	42.78	42.46	15.26	4.66	4.54	3.86	5.55	3.58	2.79	2.93	0.94	2.13
2005	103.44	90.87	21.52	26.06	9.83	3.12	3.20	2.82	4.06	2.62	2.04	2.14	2.38
2006	62.26	33.38	45.71	13.21	16.83	6.60	2.20	2.35	2.07	2.98	1.92	1.50	3.46
2007	27.52	20.09	16.77	27.91	8.39	11.03	4.54	1.57	1.68	1.48	2.13	1.37	3.79
2008	51.75	8.88	10.11	10.34	18.24	5.73	7.93	3.40	1.18	1.25	1.11	1.59	4.07
2009	28.07	16.70	4.47	6.24	6.76	12.46	4.12	5.93	2.54	0.88	0.94	0.83	4.45

Table A2 cont. – Model estimated population abundance for striped bass (millions of fish)

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13+
2010	100.00	9.06	8.42	2.78	4.17	4.76	9.25	3.18	4.58	1.96	0.68	0.72	4.26
2011	198.95	32.28	4.57	5.23	1.85	2.92	3.52	7.11	2.44	3.52	1.51	0.52	4.02
2012	109.86	64.21	16.26	2.82	3.43	1.27	2.11	2.65	5.35	1.84	2.65	1.13	3.63

Table A3 – Model estimated population abundance for bluefish (millions of fish)

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1985	40.70	17.62	8.98	6.82	4.56	16.00
1986	34.03	25.47	11.26	5.88	4.58	14.47
1987	24.61	17.42	13.51	6.23	3.40	11.95
1988	14.11	11.94	8.80	7.15	3.47	9.35
1989	21.59	7.26	6.37	4.89	4.16	8.06
1990	39.04	11.44	3.98	3.63	2.91	7.79
1991	20.37	21.90	6.61	2.38	2.25	7.06
1992	21.99	10.66	11.86	3.73	1.40	5.91
1993	10.40	11.93	5.97	6.90	2.25	4.75
1994	18.25	5.82	6.87	3.56	4.27	4.61
1995	19.79	10.83	3.54	4.30	2.30	6.01
1996	17.69	12.04	6.74	2.26	2.83	5.74
1997	20.60	11.07	7.69	4.41	1.52	6.02
1998	17.34	12.51	6.88	4.91	2.90	5.21
1999	19.84	11.16	8.20	4.61	3.37	5.78
2000	23.69	13.96	7.94	5.92	3.37	6.86
2001	19.43	16.16	9.66	5.59	4.24	7.54
2002	23.26	12.90	10.90	6.64	3.92	8.54
2003	21.35	16.16	9.07	7.79	4.82	9.28
2004	29.04	14.41	11.07	6.33	5.53	10.33
2005	16.50	19.11	9.64	7.55	4.41	11.44
2006	24.81	10.99	12.93	6.65	5.31	11.54
2007	28.77	16.64	7.48	8.96	4.70	12.30
2008	22.00	18.12	10.69	4.92	6.05	11.98
2009	20.98	14.38	12.05	7.26	3.42	12.97
2010	17.23	14.50	10.07	8.57	5.24	12.19
2011	16.72	11.60	9.91	7.01	6.08	12.76
2012	12.34	11.84	8.31	7.19	5.15	14.19

Table A4 – Model estimated population abundance for weakfish (millions of fish)

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1985	50.54	22.53	10.12	6.60	2.61	5.19
1986	95.22	27.65	11.05	4.97	3.24	3.83
1987	57.89	50.52	12.90	5.16	2.32	3.30
1988	30.13	29.70	22.32	5.70	2.28	2.48
1989	23.47	13.73	10.81	8.12	2.07	1.73
1990	29.79	11.61	5.71	4.50	3.38	1.58
1991	27.71	16.07	5.56	2.74	2.16	2.38
1992	48.43	15.09	7.82	2.71	1.33	2.21
1993	59.32	26.91	7.59	3.93	1.36	1.78
1994	120.38	32.76	13.40	3.78	1.96	1.57
1995	57.21	71.15	18.23	7.46	2.10	1.96
1996	58.23	33.58	39.14	10.02	4.10	2.24
1997	30.92	33.90	18.23	21.25	5.44	3.44
1998	26.62	18.29	18.89	10.15	11.83	4.95
1999	21.98	14.98	9.39	9.70	5.21	8.62
2000	32.20	12.60	7.93	4.97	5.13	7.32
2001	9.33	17.98	6.39	4.02	2.52	6.31
2002	9.07	5.58	10.21	3.63	2.28	5.02
2003	11.19	5.30	3.05	5.57	1.98	3.99
2004	12.72	6.98	3.22	1.85	3.39	3.63
2005	5.42	8.03	4.33	1.99	1.15	4.35
2006	5.42	3.39	4.90	2.64	1.22	3.35
2007	5.42	3.39	2.06	2.98	1.61	2.78
2008	5.42	3.43	2.11	1.29	1.86	2.73
2009	5.42	3.48	2.18	1.34	0.82	2.91
2010	8.78	3.48	2.21	1.39	0.85	2.38
2011	9.75	5.64	2.22	1.41	0.89	2.06
2012	11.21	6.26	3.59	1.41	0.90	1.88

Table A5 – Model estimated population abundance for scup (millions of fish)

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7+
1985	99.28	47.33	16.67	6.58	3.04	1.66	1.81
1986	121.13	39.38	16.38	4.85	2.06	1.21	2.48
1987	90.54	52.69	9.06	2.81	0.88	0.53	2.50
1988	67.56	43.31	11.34	1.32	0.45	0.20	2.14
1989	174.54	35.14	8.32	1.33	0.17	0.09	1.67
1990	64.80	77.06	9.54	1.59	0.27	0.05	1.34
1991	104.36	36.37	26.89	2.60	0.46	0.10	1.11
1992	85.65	57.31	7.65	3.37	0.35	0.09	0.87
1993	40.45	42.44	14.44	1.30	0.61	0.09	0.71
1994	40.45	21.13	10.60	2.49	0.25	0.16	0.59
1995	124.95	18.23	4.37	1.36	0.35	0.05	0.49
1996	48.28	34.46	4.99	0.84	0.28	0.10	0.38
1997	60.10	22.38	10.76	1.33	0.24	0.10	0.34
1998	147.47	14.89	9.05	4.05	0.54	0.12	0.34
1999	152.49	48.09	7.40	4.46	2.13	0.32	0.37
2000	490.85	50.59	28.75	4.67	2.97	1.53	0.57
2001	226.16	172.39	34.10	20.00	3.38	2.29	1.74
2002	471.69	72.09	117.51	25.64	15.62	2.75	3.33
2003	91.20	108.84	51.00	88.86	20.39	12.86	5.12
2004	113.11	37.70	77.30	38.13	69.14	16.63	15.54
2005	177.49	52.59	24.35	57.50	29.69	55.71	28.08
2006	298.46	46.12	31.02	17.80	44.86	24.41	72.33
2007	403.49	104.03	30.37	21.87	13.38	35.51	84.18
2008	471.85	152.63	62.70	21.13	16.09	10.48	103.78
2009	516.52	150.78	85.82	43.75	16.34	13.12	98.35
2010	123.52	130.71	82.38	57.13	32.55	12.96	96.70
2011	239.99	45.90	72.45	56.71	42.72	25.78	97.05
2012	511.68	52.01	28.93	49.50	42.39	33.81	108.12

Table A6 – Model estimated fishing mortality for menhaden

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1985	0.11	0.80	0.76	0.71	0.66	0.61
1986	0.06	0.41	0.38	0.36	0.33	0.31
1987	0.08	0.59	0.55	0.52	0.48	0.45
1988	0.11	0.79	0.74	0.69	0.65	0.60
1989	0.14	1.05	0.99	0.92	0.86	0.79
1990	0.16	1.19	1.12	1.05	0.97	0.90
1991	0.20	1.46	1.38	1.29	1.20	1.11
1992	0.18	1.28	1.21	1.13	1.05	0.97
1993	0.18	1.29	1.22	1.14	1.06	0.98
1994	0.16	1.17	1.10	1.03	0.96	0.88
1995	0.18	1.34	1.26	1.18	1.09	1.01
1996	0.15	1.12	1.05	0.98	0.91	0.84
1997	0.18	1.34	1.26	1.18	1.09	1.01
1998	0.17	1.27	1.19	1.12	1.04	0.96
1999	0.13	0.92	0.87	0.81	0.76	0.70
2000	0.10	0.76	0.71	0.67	0.62	0.57
2001	0.14	1.01	0.95	0.89	0.83	0.76
2002	0.11	0.80	0.75	0.70	0.65	0.60
2003	0.10	0.76	0.71	0.67	0.62	0.57
2004	0.10	0.75	0.71	0.66	0.61	0.57
2005	0.08	0.55	0.51	0.48	0.45	0.41
2006	0.08	0.56	0.53	0.50	0.46	0.43
2007	0.08	0.57	0.53	0.50	0.46	0.43
2008	0.07	0.50	0.47	0.44	0.41	0.38
2009	0.08	0.58	0.54	0.51	0.47	0.44
2010	0.08	0.61	0.57	0.54	0.50	0.46
2011	0.05	0.39	0.37	0.35	0.32	0.30
2012	0.03	0.25	0.23	0.22	0.20	0.19

Table A7 – Model estimated fishing mortality for striped bass

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13+
1985	0.00	0.00	0.02	0.05	0.07	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.04
1986	0.00	0.00	0.01	0.04	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.03
1987	0.00	0.00	0.01	0.04	0.05	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.03
1988	0.00	0.00	0.01	0.03	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.02
1989	0.00	0.00	0.01	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02
1990	0.00	0.00	0.01	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.03
1991	0.00	0.00	0.02	0.05	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.04
1992	0.00	0.00	0.02	0.05	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.04
1993	0.00	0.00	0.02	0.06	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.04
1994	0.00	0.00	0.02	0.07	0.09	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.05
1995	0.00	0.01	0.03	0.09	0.13	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.07
1996	0.00	0.01	0.03	0.08	0.12	0.12	0.13	0.13	0.13	0.13	0.13	0.13	0.06
1997	0.00	0.01	0.03	0.09	0.13	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.07
1998	0.00	0.01	0.03	0.09	0.12	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.06
1999	0.00	0.01	0.03	0.08	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.06
2000	0.00	0.01	0.03	0.08	0.12	0.12	0.13	0.13	0.13	0.13	0.13	0.13	0.06
2001	0.00	0.01	0.03	0.08	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.06
2002	0.00	0.00	0.03	0.07	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.05
2003	0.00	0.01	0.03	0.08	0.12	0.12	0.13	0.13	0.13	0.13	0.13	0.13	0.06
2004	0.00	0.01	0.04	0.11	0.15	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.08
2005	0.00	0.01	0.04	0.11	0.15	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.08
2006	0.00	0.01	0.04	0.12	0.17	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.09
2007	0.00	0.01	0.03	0.10	0.13	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.07

Table A7 cont. – Model estimated fishing mortality for striped bass

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13+
2008	0.00	0.01	0.03	0.09	0.13	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.07
2009	0.00	0.00	0.03	0.07	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.05
2010	0.00	0.01	0.03	0.08	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.06
2011	0.00	0.01	0.03	0.09	0.12	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.07
2012	0.00	0.00	0.03	0.07	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.05

Table A8 – Model estimated fishing mortality for bluefish

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1985	0.27	0.25	0.22	0.20	0.17	0.15
1986	0.47	0.43	0.39	0.35	0.30	0.26
1987	0.52	0.48	0.44	0.39	0.33	0.28
1988	0.46	0.43	0.39	0.34	0.30	0.25
1989	0.44	0.40	0.36	0.32	0.28	0.24
1990	0.38	0.35	0.31	0.28	0.24	0.21
1991	0.45	0.41	0.37	0.33	0.29	0.24
1992	0.41	0.38	0.34	0.30	0.26	0.22
1993	0.38	0.35	0.32	0.28	0.24	0.21
1994	0.32	0.30	0.27	0.24	0.21	0.18
1995	0.30	0.27	0.25	0.22	0.19	0.16
1996	0.27	0.25	0.22	0.20	0.17	0.15
1997	0.30	0.28	0.25	0.22	0.19	0.16
1998	0.24	0.22	0.20	0.18	0.15	0.13
1999	0.15	0.14	0.13	0.11	0.10	0.08
2000	0.18	0.17	0.15	0.13	0.12	0.10
2001	0.21	0.19	0.17	0.15	0.13	0.11
2002	0.16	0.15	0.14	0.12	0.10	0.09
2003	0.19	0.18	0.16	0.14	0.12	0.11
2004	0.22	0.20	0.18	0.16	0.14	0.12
2005	0.21	0.19	0.17	0.15	0.13	0.11
2006	0.20	0.18	0.17	0.15	0.13	0.11
2007	0.26	0.24	0.22	0.19	0.17	0.14
2008	0.22	0.21	0.19	0.17	0.14	0.12
2009	0.17	0.16	0.14	0.12	0.11	0.09
2010	0.20	0.18	0.16	0.14	0.12	0.11
2011	0.15	0.13	0.12	0.11	0.09	0.08
2012	0.14	0.13	0.12	0.10	0.09	0.08

Table A9 – Model estimated fishing mortality for weakfish

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1985	0.17	0.28	0.28	0.28	0.28	0.28
1986	0.20	0.33	0.33	0.33	0.33	0.33
1987	0.24	0.39	0.39	0.39	0.39	0.39
1988	0.36	0.58	0.58	0.58	0.58	0.58
1989	0.27	0.45	0.45	0.45	0.45	0.45
1990	0.19	0.31	0.31	0.31	0.31	0.31
1991	0.18	0.29	0.29	0.29	0.29	0.29
1992	0.16	0.26	0.26	0.26	0.26	0.26
1993	0.16	0.27	0.27	0.27	0.27	0.27
1994	0.10	0.16	0.16	0.16	0.16	0.16
1995	0.10	0.17	0.17	0.17	0.17	0.17
1996	0.11	0.18	0.18	0.18	0.18	0.18
1997	0.10	0.16	0.16	0.16	0.16	0.16
1998	0.15	0.24	0.24	0.24	0.24	0.24
1999	0.13	0.21	0.21	0.21	0.21	0.21
2000	0.15	0.25	0.25	0.25	0.25	0.25
2001	0.08	0.14	0.14	0.14	0.14	0.14
2002	0.11	0.18	0.18	0.18	0.18	0.18
2003	0.04	0.07	0.07	0.07	0.07	0.07
2004	0.03	0.05	0.05	0.05	0.05	0.05
2005	0.04	0.07	0.07	0.07	0.07	0.07
2006	0.04	0.07	0.07	0.07	0.07	0.07
2007	0.03	0.04	0.04	0.04	0.04	0.04
2008	0.01	0.02	0.02	0.02	0.02	0.02
2009	0.01	0.02	0.02	0.02	0.02	0.02
2010	0.01	0.02	0.02	0.02	0.02	0.02
2011	0.01	0.02	0.02	0.02	0.02	0.02
2012	0.02	0.03	0.03	0.03	0.03	0.03

Table A10 – Model estimated fishing mortality for scup

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7+
1985	0.15	0.74	1.06	1.04	0.82	0.39	0.11
1986	0.23	1.14	1.63	1.60	1.26	0.60	0.16
1987	0.25	1.23	1.76	1.72	1.36	0.65	0.18
1988	0.28	1.40	2.00	1.96	1.54	0.74	0.20
1989	0.21	1.05	1.51	1.48	1.16	0.56	0.15
1990	0.16	0.80	1.14	1.11	0.88	0.42	0.11
1991	0.27	1.34	1.92	1.88	1.48	0.71	0.19
1992	0.23	1.13	1.62	1.59	1.25	0.60	0.16
1993	0.22	1.10	1.57	1.54	1.21	0.58	0.16
1994	0.26	1.30	1.85	1.82	1.43	0.68	0.19
1995	0.20	1.01	1.45	1.42	1.12	0.53	0.15
1996	0.16	0.79	1.12	1.10	0.87	0.41	0.11
1997	0.10	0.53	0.75	0.74	0.58	0.28	0.08
1998	0.07	0.36	0.52	0.50	0.40	0.19	0.05
1999	0.04	0.20	0.29	0.28	0.22	0.11	0.03
2000	0.03	0.13	0.19	0.19	0.15	0.07	0.02
2001	0.02	0.09	0.12	0.12	0.09	0.05	0.01
2002	0.01	0.07	0.09	0.09	0.07	0.03	0.01
2003	0.02	0.08	0.11	0.11	0.08	0.04	0.01
2004	0.02	0.08	0.11	0.11	0.09	0.04	0.01
2005	0.01	0.06	0.08	0.08	0.06	0.03	0.01
2006	0.02	0.09	0.13	0.12	0.10	0.05	0.01
2007	0.02	0.10	0.14	0.14	0.11	0.05	0.01
2008	0.01	0.07	0.10	0.09	0.07	0.04	0.01
2009	0.02	0.08	0.12	0.12	0.09	0.04	0.01
2010	0.02	0.09	0.12	0.12	0.10	0.05	0.01
2011	0.02	0.09	0.12	0.12	0.09	0.04	0.01
2012	0.02	0.10	0.14	0.13	0.11	0.05	0.01

Table A11 – Model estimated predation mortality for menhaden

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1985	0.30	0.43	0.53	0.45	0.39	0.29
1986	0.33	0.38	0.40	0.32	0.24	0.21
1987	0.34	0.34	0.32	0.27	0.18	0.15
1988	0.32	0.33	0.29	0.22	0.15	0.10
1989	0.31	0.32	0.28	0.23	0.17	0.11
1990	0.28	0.28	0.27	0.22	0.18	0.14
1991	0.32	0.26	0.21	0.20	0.16	0.13
1992	0.30	0.27	0.19	0.15	0.14	0.13
1993	0.36	0.26	0.22	0.16	0.13	0.11
1994	0.38	0.30	0.21	0.19	0.16	0.14
1995	0.37	0.30	0.23	0.17	0.15	0.15
1996	0.55	0.31	0.24	0.17	0.14	0.13
1997	0.58	0.36	0.19	0.17	0.13	0.13
1998	0.56	0.36	0.22	0.14	0.12	0.10
1999	0.47	0.38	0.26	0.16	0.12	0.10
2000	0.50	0.38	0.28	0.20	0.13	0.11
2001	0.62	0.42	0.29	0.22	0.17	0.12
2002	0.59	0.39	0.23	0.16	0.13	0.13
2003	0.66	0.45	0.26	0.17	0.11	0.10
2004	0.64	0.47	0.32	0.19	0.13	0.08
2005	0.68	0.59	0.41	0.35	0.22	0.16
2006	0.58	0.50	0.32	0.22	0.22	0.14
2007	0.58	0.45	0.35	0.23	0.19	0.22
2008	0.66	0.51	0.39	0.33	0.22	0.21
2009	0.62	0.49	0.35	0.30	0.26	0.16
2010	0.51	0.46	0.34	0.26	0.25	0.21
2011	0.41	0.38	0.32	0.26	0.22	0.21
2012	0.40	0.38	0.32	0.24	0.24	0.21

Table A12 – Model estimated fishing mortality for scup

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7+
1985	0.68	0.22	0.08	0.02	0.01	0.00	0.01
1986	0.51	0.23	0.03	0.01	0.00	0.00	0.00
1987	0.39	0.20	0.07	0.01	0.00	0.00	0.00
1988	0.28	0.15	0.05	0.01	0.00	0.00	0.00
1989	0.51	0.15	0.05	0.02	0.01	0.00	0.00
1990	0.32	0.16	0.07	0.02	0.01	0.00	0.00
1991	0.23	0.11	0.06	0.02	0.01	0.02	0.00
1992	0.38	0.15	0.05	0.03	0.02	0.01	0.00
1993	0.33	0.19	0.09	0.03	0.02	0.01	0.01
1994	0.44	0.18	0.10	0.04	0.01	0.01	0.05
1995	0.99	0.18	0.10	0.06	0.04	0.02	0.09
1996	0.51	0.28	0.10	0.04	0.03	0.01	0.10
1997	1.19	0.28	0.12	0.07	0.03	0.02	0.04
1998	0.95	0.24	0.09	0.04	0.02	0.01	0.03
1999	0.96	0.21	0.07	0.03	0.01	0.01	0.06
2000	0.92	0.16	0.07	0.04	0.01	0.01	0.08
2001	1.03	0.20	0.06	0.03	0.01	0.01	0.13
2002	1.35	0.18	0.09	0.04	0.02	0.01	0.09
2003	0.77	0.17	0.08	0.04	0.02	0.01	0.02
2004	0.65	0.26	0.08	0.04	0.03	0.01	0.01
2005	1.24	0.37	0.13	0.07	0.03	0.02	0.04
2006	0.94	0.23	0.12	0.06	0.04	0.02	0.02
2007	0.85	0.31	0.12	0.07	0.04	0.02	0.02
2008	1.03	0.41	0.16	0.06	0.03	0.02	0.04
2009	1.26	0.42	0.19	0.08	0.04	0.02	0.03
2010	0.87	0.40	0.15	0.07	0.04	0.02	0.00
2011	1.41	0.28	0.16	0.07	0.04	0.02	0.01
2012	1.42	0.24	0.20	0.08	0.05	0.02	0.01

Table A13 – Model estimated total mortality for menhaden

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1985	0.82	1.57	1.58	1.42	1.30	1.13
1986	0.80	1.12	1.08	0.94	0.83	0.76
1987	0.83	1.26	1.17	1.05	0.91	0.84
1988	0.84	1.44	1.32	1.18	1.05	0.94
1989	0.86	1.70	1.56	1.41	1.28	1.14
1990	0.85	1.80	1.68	1.53	1.40	1.28
1991	0.94	2.06	1.88	1.75	1.61	1.48
1992	0.89	1.89	1.69	1.54	1.44	1.34
1993	0.95	1.88	1.73	1.56	1.44	1.33
1994	0.95	1.80	1.60	1.48	1.37	1.26
1995	0.97	1.97	1.78	1.61	1.50	1.40
1996	1.12	1.76	1.58	1.41	1.31	1.22
1997	1.18	2.02	1.74	1.61	1.47	1.38
1998	1.14	1.96	1.70	1.51	1.41	1.29
1999	1.01	1.63	1.41	1.23	1.12	1.04
2000	1.02	1.47	1.29	1.13	1.00	0.93
2001	1.17	1.75	1.52	1.36	1.24	1.12
2002	1.11	1.52	1.27	1.12	1.03	0.97
2003	1.17	1.54	1.26	1.10	0.98	0.92
2004	1.15	1.55	1.31	1.11	1.00	0.89
2005	1.16	1.47	1.21	1.09	0.92	0.82
2006	1.07	1.39	1.14	0.98	0.93	0.81
2007	1.07	1.35	1.18	0.99	0.91	0.89
2008	1.14	1.33	1.15	1.03	0.87	0.83
2009	1.11	1.39	1.18	1.07	0.98	0.84
2010	1.01	1.40	1.20	1.06	0.99	0.91
2011	0.87	1.11	0.98	0.87	0.79	0.75
2012	0.84	0.96	0.85	0.72	0.69	0.64

Table A14 – Model estimated total mortality for striped bass

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13+
1985	1.13	0.68	0.47	0.38	0.32	0.27	0.23	0.23	0.23	0.23	0.23	0.23	0.19
1986	1.13	0.68	0.46	0.37	0.31	0.25	0.21	0.21	0.21	0.21	0.21	0.21	0.18
1987	1.13	0.68	0.46	0.37	0.30	0.24	0.20	0.21	0.21	0.21	0.21	0.21	0.18
1988	1.13	0.68	0.46	0.36	0.29	0.24	0.20	0.20	0.20	0.20	0.20	0.20	0.17
1989	1.13	0.68	0.46	0.35	0.28	0.22	0.18	0.18	0.18	0.18	0.18	0.18	0.17
1990	1.13	0.68	0.46	0.37	0.30	0.24	0.20	0.20	0.20	0.20	0.20	0.20	0.18
1991	1.13	0.68	0.47	0.38	0.32	0.26	0.22	0.22	0.22	0.22	0.22	0.22	0.19
1992	1.13	0.68	0.47	0.38	0.32	0.26	0.22	0.22	0.22	0.22	0.22	0.22	0.19
1993	1.13	0.68	0.47	0.39	0.33	0.27	0.23	0.23	0.23	0.23	0.23	0.23	0.19
1994	1.13	0.68	0.47	0.40	0.34	0.29	0.25	0.25	0.25	0.25	0.25	0.25	0.20
1995	1.13	0.69	0.48	0.42	0.38	0.33	0.29	0.29	0.29	0.29	0.29	0.29	0.22
1996	1.13	0.69	0.48	0.41	0.37	0.31	0.28	0.28	0.28	0.28	0.28	0.28	0.21
1997	1.13	0.69	0.48	0.42	0.38	0.33	0.29	0.29	0.29	0.29	0.29	0.29	0.22
1998	1.13	0.69	0.48	0.42	0.37	0.32	0.28	0.28	0.28	0.28	0.28	0.28	0.21
1999	1.13	0.69	0.48	0.41	0.37	0.31	0.27	0.27	0.27	0.27	0.27	0.27	0.21
2000	1.13	0.69	0.48	0.41	0.37	0.31	0.28	0.28	0.28	0.28	0.28	0.28	0.21
2001	1.13	0.69	0.48	0.41	0.36	0.30	0.26	0.26	0.26	0.26	0.26	0.26	0.21
2002	1.13	0.68	0.48	0.40	0.35	0.30	0.26	0.26	0.26	0.26	0.26	0.26	0.20
2003	1.13	0.69	0.48	0.41	0.37	0.31	0.28	0.28	0.28	0.28	0.28	0.28	0.21
2004	1.13	0.69	0.49	0.44	0.40	0.35	0.31	0.31	0.31	0.31	0.31	0.31	0.23
2005	1.13	0.69	0.49	0.44	0.40	0.35	0.31	0.31	0.31	0.31	0.31	0.31	0.23
2006	1.13	0.69	0.49	0.45	0.42	0.37	0.33	0.33	0.33	0.33	0.33	0.33	0.24
2007	1.13	0.69	0.48	0.43	0.38	0.33	0.29	0.29	0.29	0.29	0.29	0.29	0.22

Table A14 cont. – Model estimated total mortality for striped bass

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13+
2008	1.13	0.69	0.48	0.42	0.38	0.33	0.29	0.29	0.29	0.29	0.29	0.29	0.22
2009	1.13	0.68	0.48	0.40	0.35	0.30	0.26	0.26	0.26	0.26	0.26	0.26	0.20
2010	1.13	0.69	0.48	0.41	0.36	0.30	0.26	0.26	0.26	0.26	0.26	0.26	0.21
2011	1.13	0.69	0.48	0.42	0.37	0.32	0.28	0.28	0.28	0.28	0.28	0.28	0.22
2012	1.13	0.68	0.48	0.40	0.35	0.30	0.26	0.26	0.26	0.26	0.26	0.26	0.20

Table A15 – Model estimated total mortality for bluefish

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1985	0.47	0.45	0.42	0.40	0.37	0.35
1986	0.67	0.63	0.59	0.55	0.50	0.46
1987	0.72	0.68	0.64	0.59	0.53	0.48
1988	0.66	0.63	0.59	0.54	0.50	0.45
1989	0.64	0.60	0.56	0.52	0.48	0.44
1990	0.58	0.55	0.51	0.48	0.44	0.41
1991	0.65	0.61	0.57	0.53	0.49	0.44
1992	0.61	0.58	0.54	0.50	0.46	0.42
1993	0.58	0.55	0.52	0.48	0.44	0.41
1994	0.52	0.50	0.47	0.44	0.41	0.38
1995	0.50	0.47	0.45	0.42	0.39	0.36
1996	0.47	0.45	0.42	0.40	0.37	0.35
1997	0.50	0.48	0.45	0.42	0.39	0.36
1998	0.44	0.42	0.40	0.38	0.35	0.33
1999	0.35	0.34	0.33	0.31	0.30	0.28
2000	0.38	0.37	0.35	0.33	0.32	0.30
2001	0.41	0.39	0.37	0.35	0.33	0.31
2002	0.36	0.35	0.34	0.32	0.30	0.29
2003	0.39	0.38	0.36	0.34	0.32	0.31
2004	0.42	0.40	0.38	0.36	0.34	0.32
2005	0.41	0.39	0.37	0.35	0.33	0.31
2006	0.40	0.38	0.37	0.35	0.33	0.31
2007	0.46	0.44	0.42	0.39	0.37	0.34
2008	0.42	0.41	0.39	0.37	0.34	0.32
2009	0.37	0.36	0.34	0.32	0.31	0.29
2010	0.40	0.38	0.36	0.34	0.32	0.31
2011	0.35	0.33	0.32	0.31	0.29	0.28
2012	0.34	0.33	0.32	0.30	0.29	0.28

Table A16 – Model estimated total mortality for weakfish

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1985	0.60	0.71	0.71	0.71	0.71	0.71
1986	0.63	0.76	0.76	0.76	0.76	0.76
1987	0.67	0.82	0.82	0.82	0.82	0.82
1988	0.79	1.01	1.01	1.01	1.01	1.01
1989	0.70	0.88	0.88	0.88	0.88	0.88
1990	0.62	0.74	0.74	0.74	0.74	0.74
1991	0.61	0.72	0.72	0.72	0.72	0.72
1992	0.59	0.69	0.69	0.69	0.69	0.69
1993	0.59	0.70	0.70	0.70	0.70	0.70
1994	0.53	0.59	0.59	0.59	0.59	0.59
1995	0.53	0.60	0.60	0.60	0.60	0.60
1996	0.54	0.61	0.61	0.61	0.61	0.61
1997	0.53	0.59	0.59	0.59	0.59	0.59
1998	0.58	0.67	0.67	0.67	0.67	0.67
1999	0.56	0.64	0.64	0.64	0.64	0.64
2000	0.58	0.68	0.68	0.68	0.68	0.68
2001	0.51	0.57	0.57	0.57	0.57	0.57
2002	0.54	0.61	0.61	0.61	0.61	0.61
2003	0.47	0.50	0.50	0.50	0.50	0.50
2004	0.46	0.48	0.48	0.48	0.48	0.48
2005	0.47	0.50	0.50	0.50	0.50	0.50
2006	0.47	0.50	0.50	0.50	0.50	0.50
2007	0.46	0.47	0.47	0.47	0.47	0.47
2008	0.44	0.45	0.45	0.45	0.45	0.45
2009	0.44	0.45	0.45	0.45	0.45	0.45
2010	0.44	0.45	0.45	0.45	0.45	0.45
2011	0.44	0.45	0.45	0.45	0.45	0.45
2012	0.45	0.46	0.46	0.46	0.46	0.46

Table A17 – Model estimated total mortality for scup

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7+
1985	0.92	1.06	1.23	1.16	0.93	0.49	0.21
1986	0.83	1.47	1.76	1.70	1.36	0.70	0.26
1987	0.74	1.54	1.92	1.83	1.46	0.75	0.28
1988	0.65	1.65	2.15	2.07	1.65	0.84	0.30
1989	0.82	1.30	1.65	1.60	1.27	0.66	0.25
1990	0.58	1.05	1.30	1.24	0.99	0.52	0.21
1991	0.60	1.56	2.08	2.01	1.60	0.83	0.30
1992	0.70	1.38	1.77	1.71	1.37	0.70	0.26
1993	0.65	1.39	1.76	1.67	1.33	0.69	0.27
1994	0.80	1.58	2.05	1.95	1.54	0.79	0.34
1995	1.29	1.30	1.65	1.58	1.26	0.65	0.33
1996	0.77	1.16	1.32	1.24	1.00	0.53	0.31
1997	1.40	0.91	0.98	0.90	0.71	0.39	0.21
1998	1.12	0.70	0.71	0.64	0.52	0.30	0.19
1999	1.10	0.51	0.46	0.41	0.33	0.21	0.19
2000	1.05	0.39	0.36	0.32	0.26	0.18	0.19
2001	1.14	0.38	0.29	0.25	0.21	0.15	0.24
2002	1.47	0.35	0.28	0.23	0.19	0.14	0.20
2003	0.88	0.34	0.29	0.25	0.20	0.15	0.13
2004	0.77	0.44	0.30	0.25	0.22	0.15	0.12
2005	1.35	0.53	0.31	0.25	0.20	0.15	0.14
2006	1.05	0.42	0.35	0.29	0.23	0.17	0.13
2007	0.97	0.51	0.36	0.31	0.24	0.17	0.13
2008	1.14	0.58	0.36	0.26	0.20	0.15	0.15
2009	1.37	0.60	0.41	0.30	0.23	0.16	0.14
2010	0.99	0.59	0.37	0.29	0.23	0.16	0.12
2011	1.53	0.46	0.38	0.29	0.23	0.16	0.12
2012	1.54	0.44	0.43	0.31	0.25	0.17	0.12

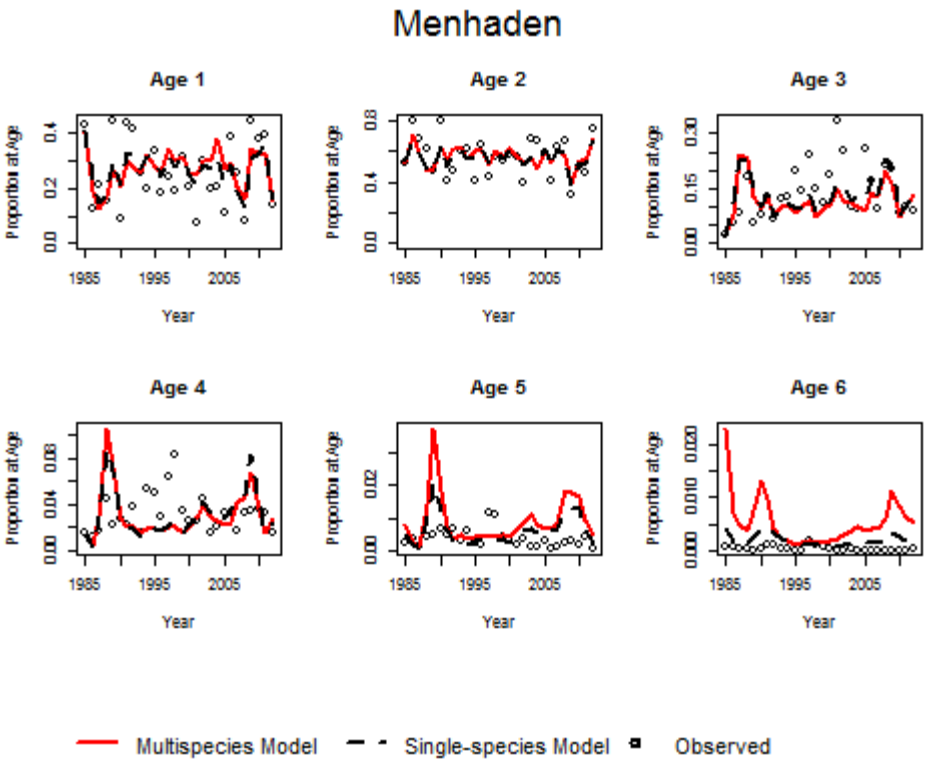

Fig. A1: Atlantic menhaden observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) proportions-at-age of the fishery catch.

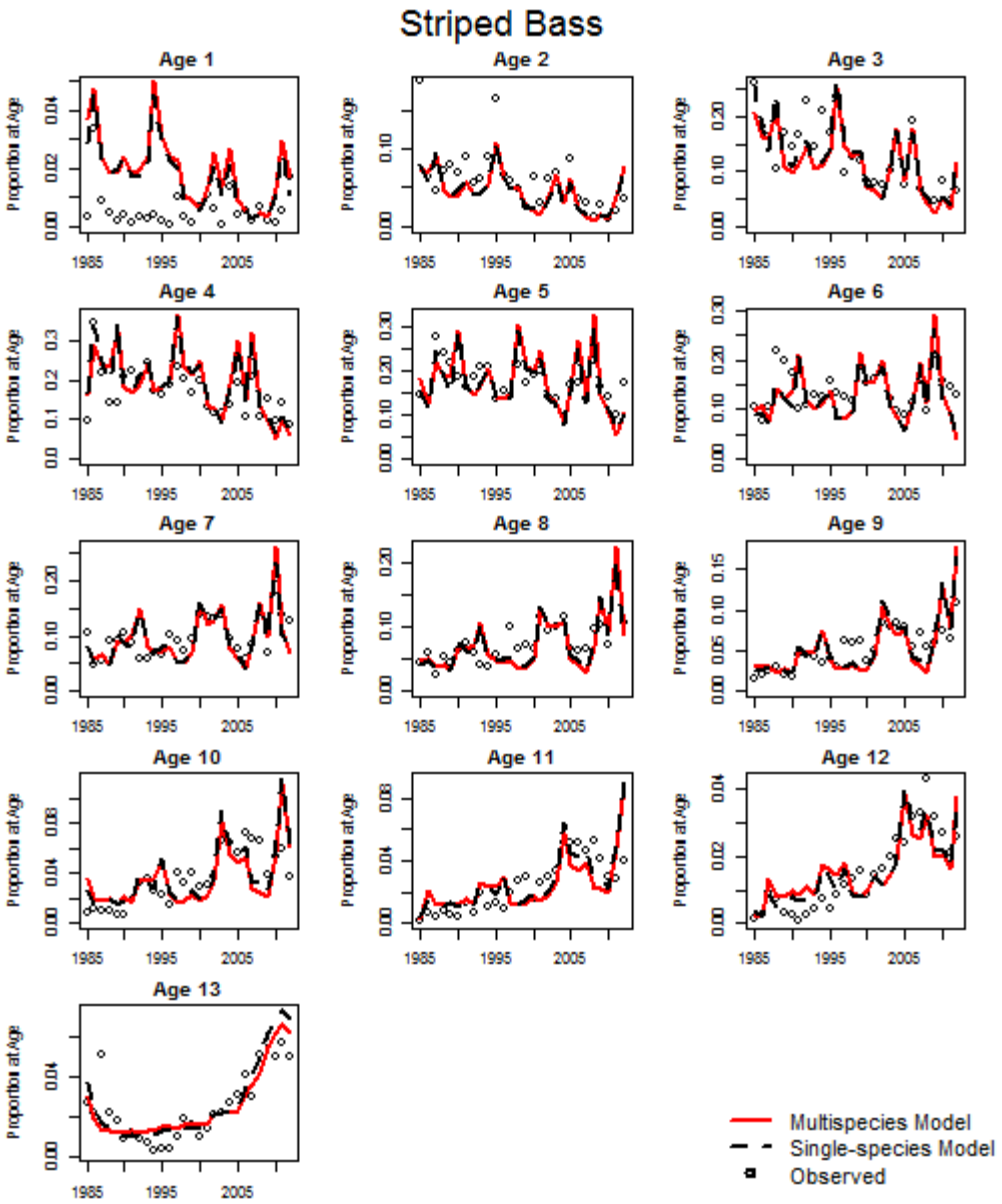

Fig. A2: Atlantic striped bass observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) proportions-at-age of the fishery catch.

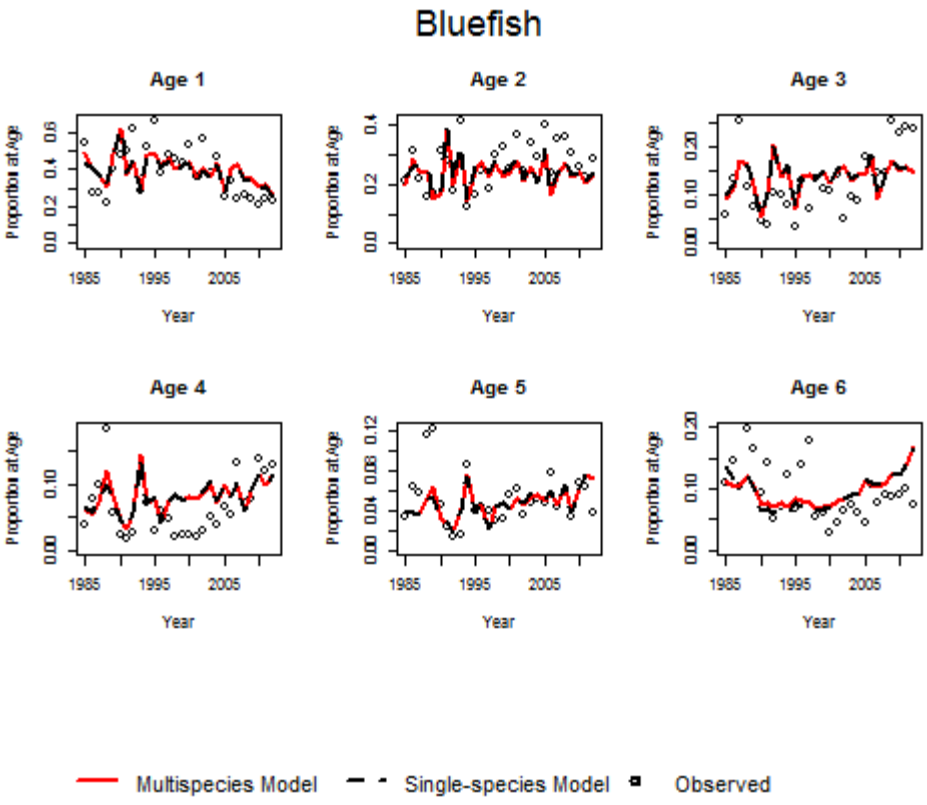

Fig. A3: Bluefish observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) proportions-at-age of the fishery catch.

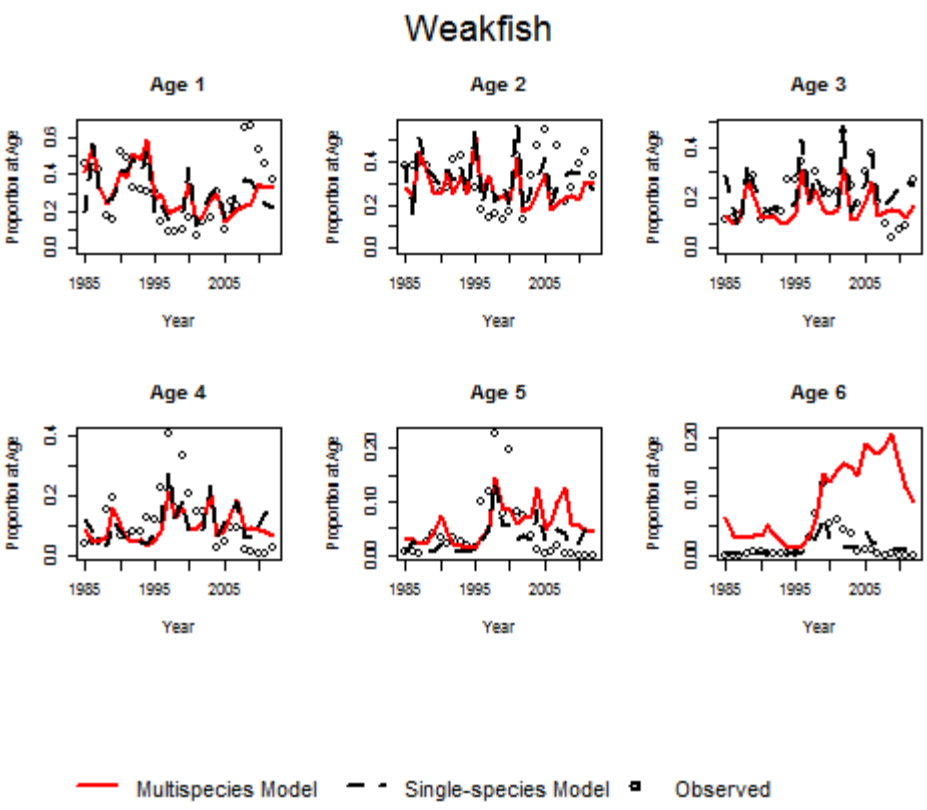

Fig. A4: Weakfish observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) proportions-at-age of the fishery catch.

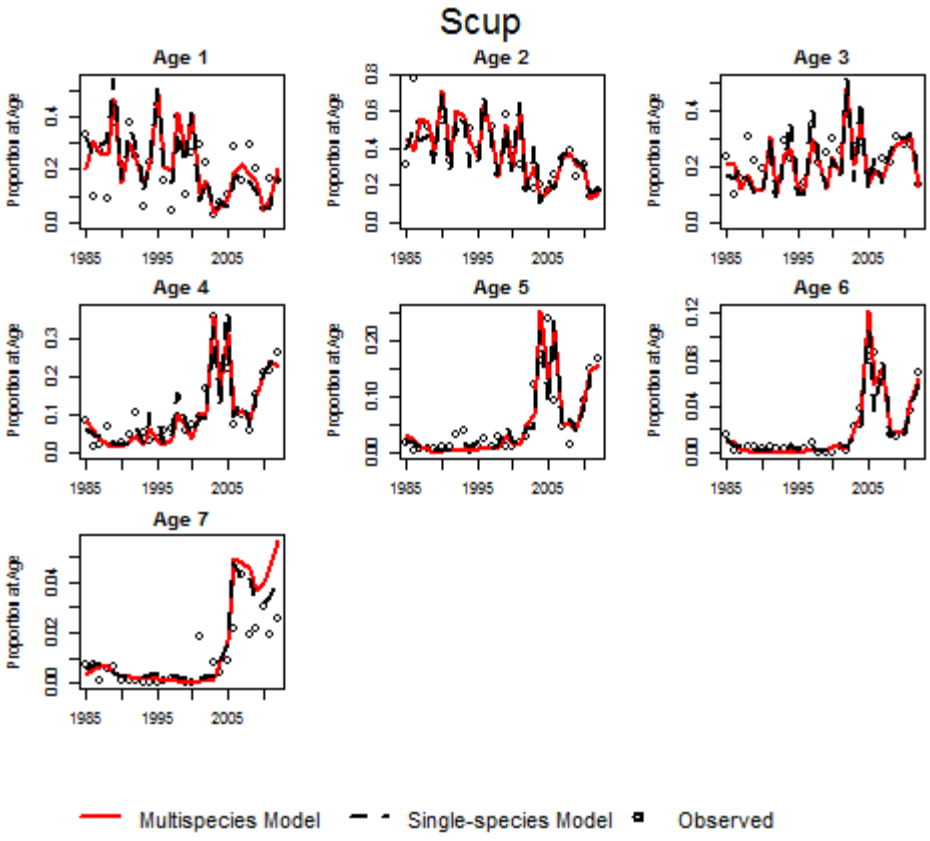

Fig. A5: Scup observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) proportions-at-age of the fishery catch.

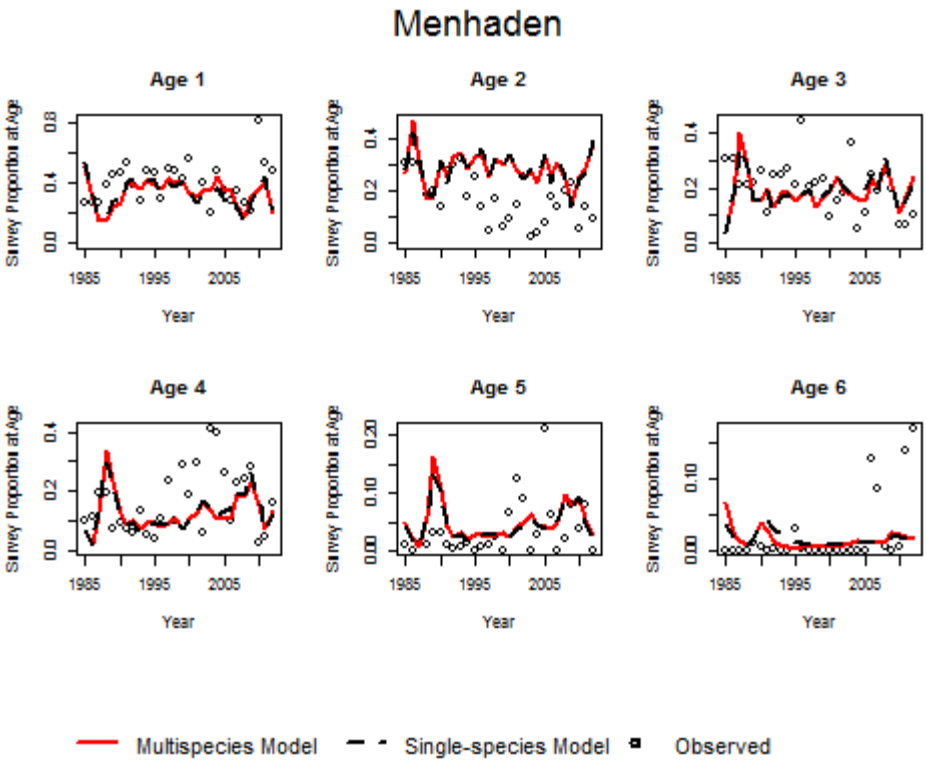

Fig. A6: Atlantic menhaden observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) proportions-at-age of the fishery-independent survey catch.

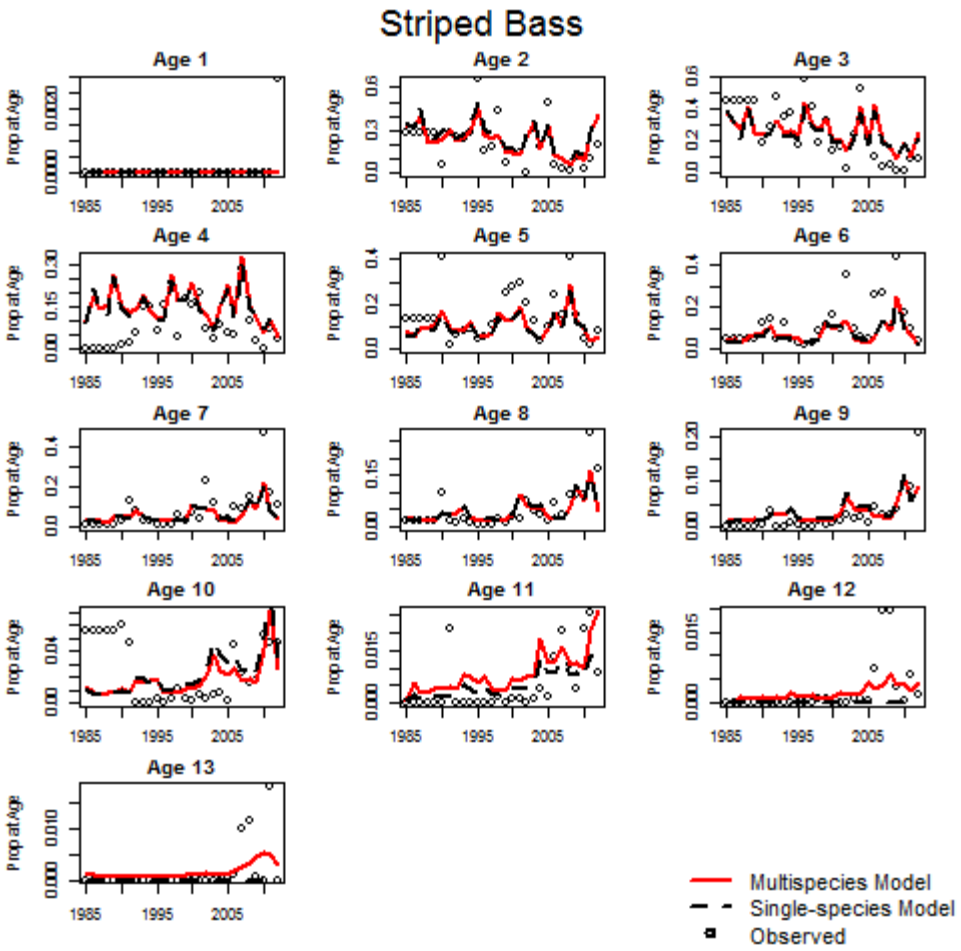

Fig. A7: Atlantic striped bass observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) proportions-at-age of the fishery-independent survey catch.

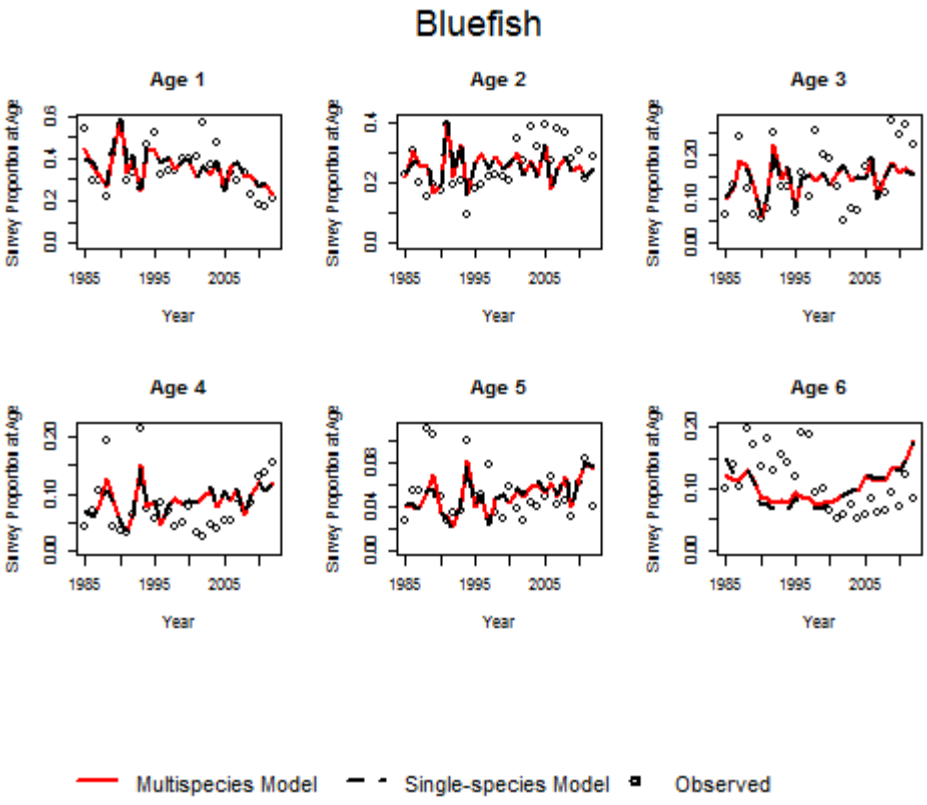

Fig. A8: Bluefish observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) proportions-at-age of the fishery-independent survey catch.

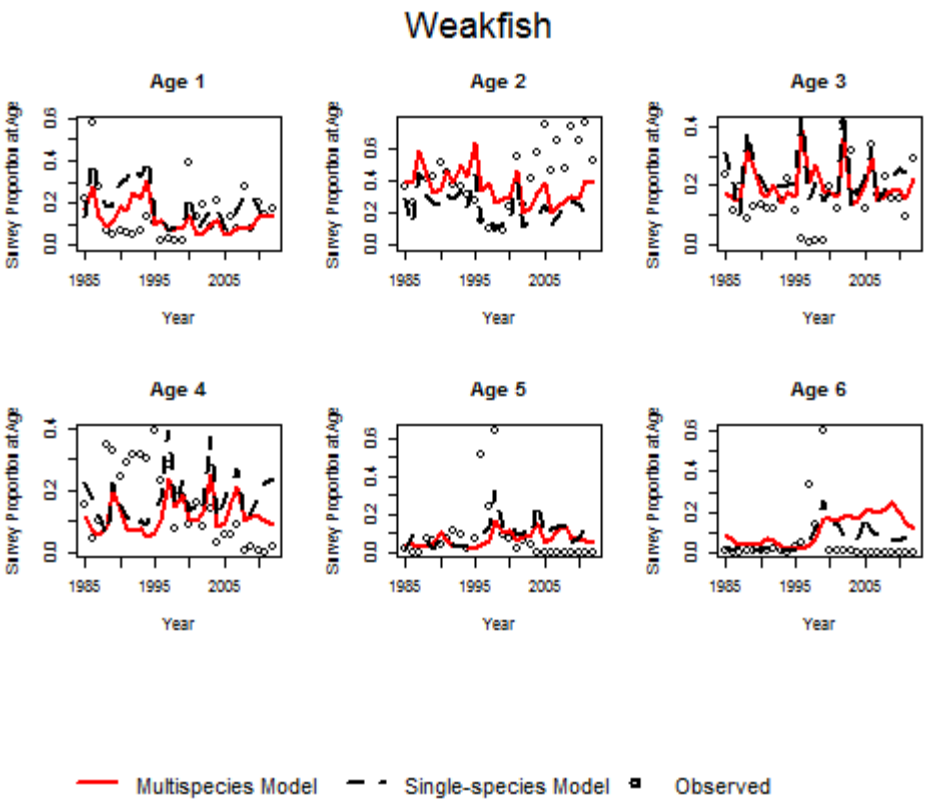

Fig. A9: Weakfish observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) proportions-at-age of the fishery-independent survey catch.

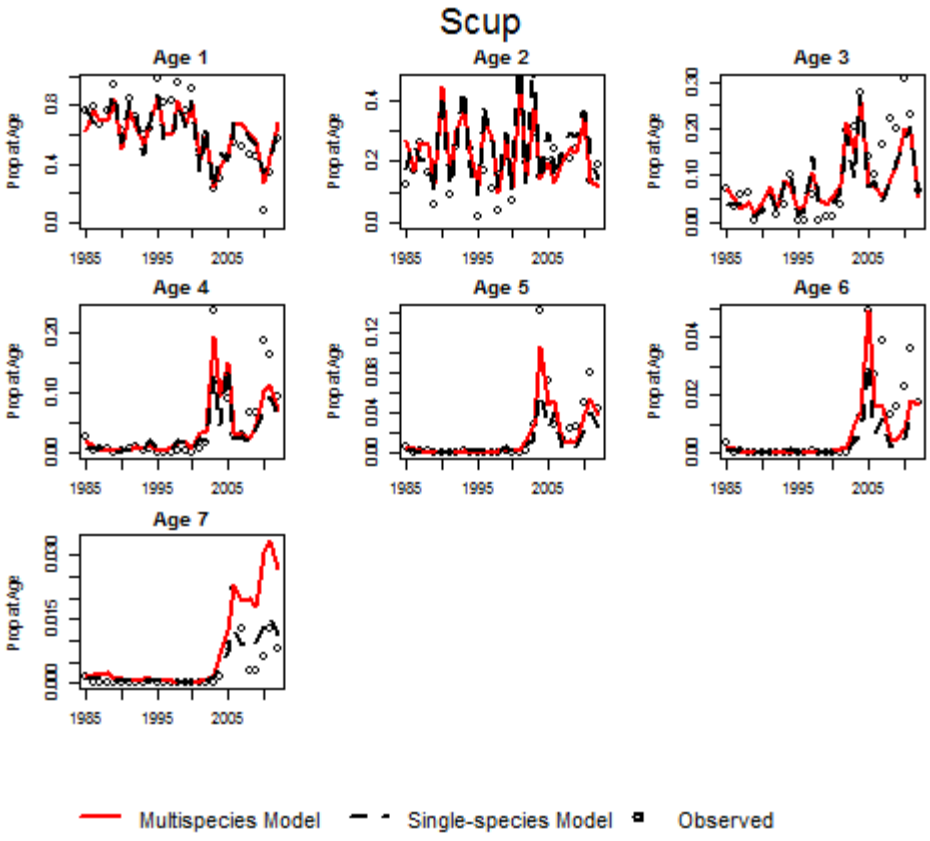

Fig. A10: Scup observed (open circles), predicted single-species (dashed black line), and predicted multispecies (solid red line) proportions-at-age of the fishery-independent survey catch.

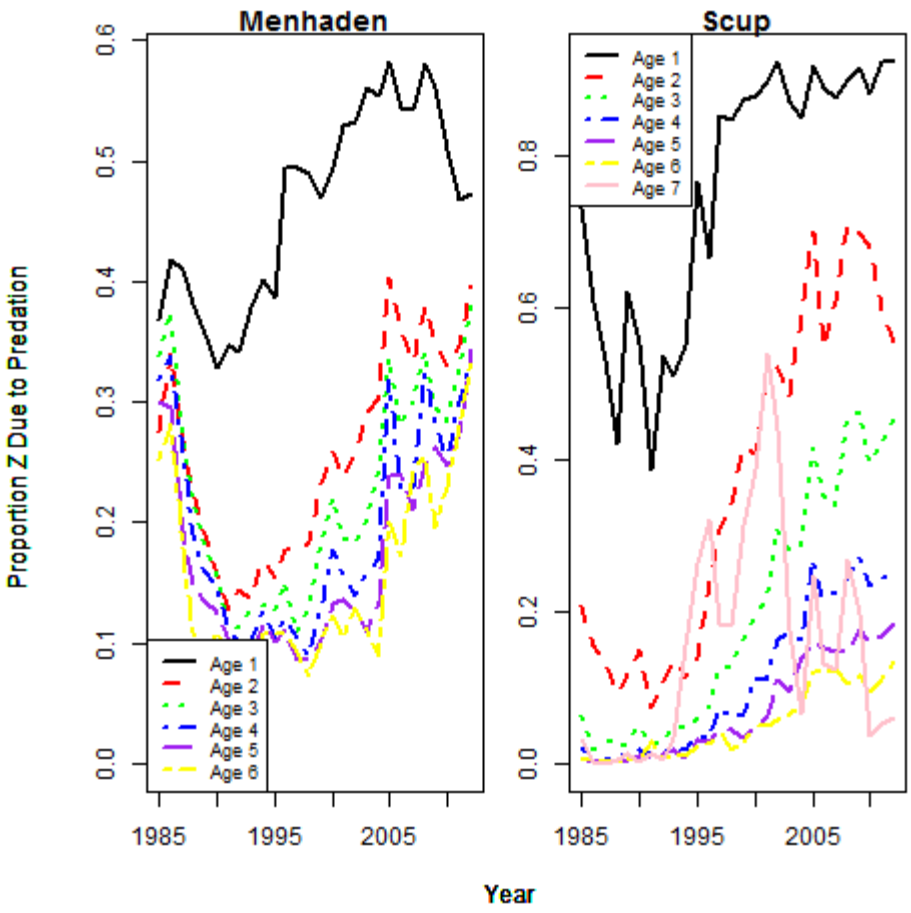

Fig. A11: Predicted annual proportion of total mortality-at-age (Z) due to predation mortality (M2) for menhaden and scup.

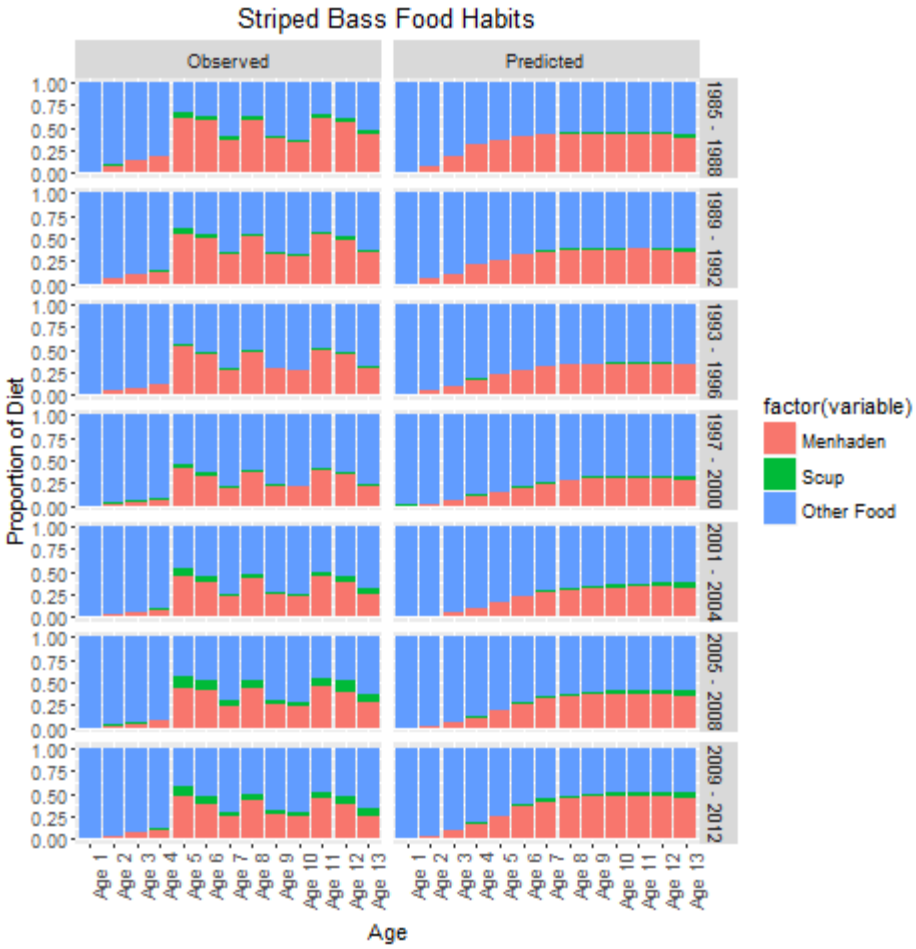

Fig. A12: Observed and predicted food habit information for striped bass by time block represented as proportion of total diet.

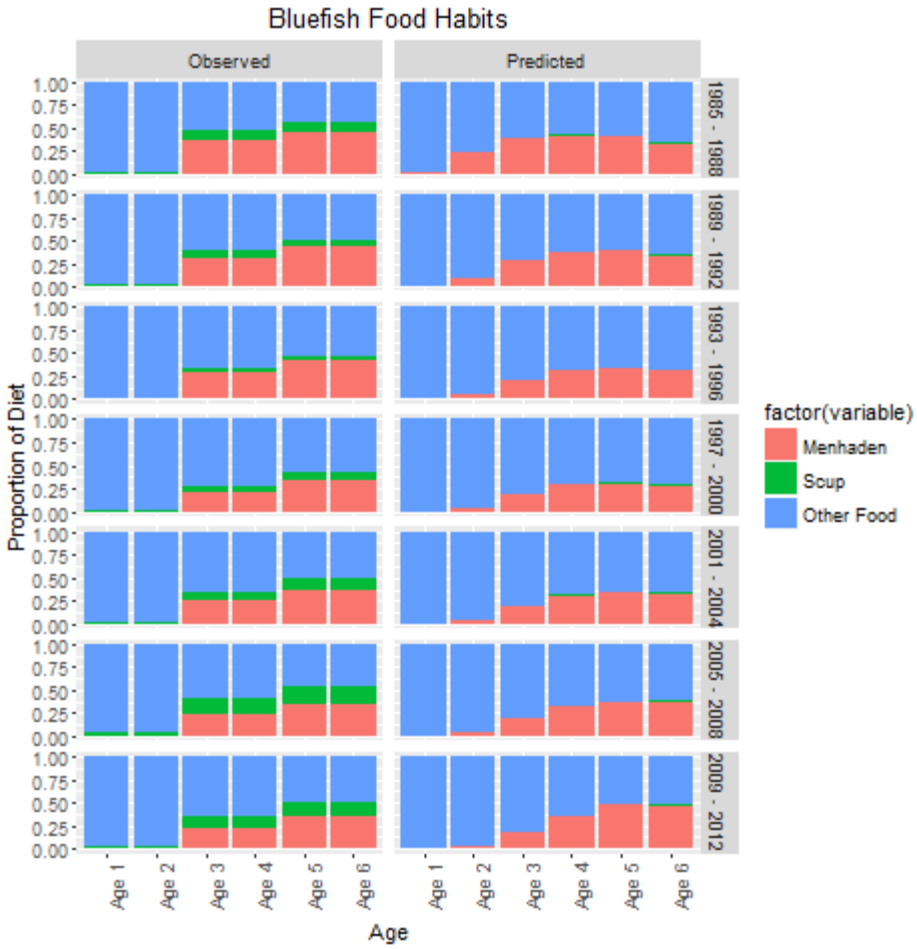

Fig. A13: Observed and predicted food habit information for bluefish by time block represented as proportion of total diet.

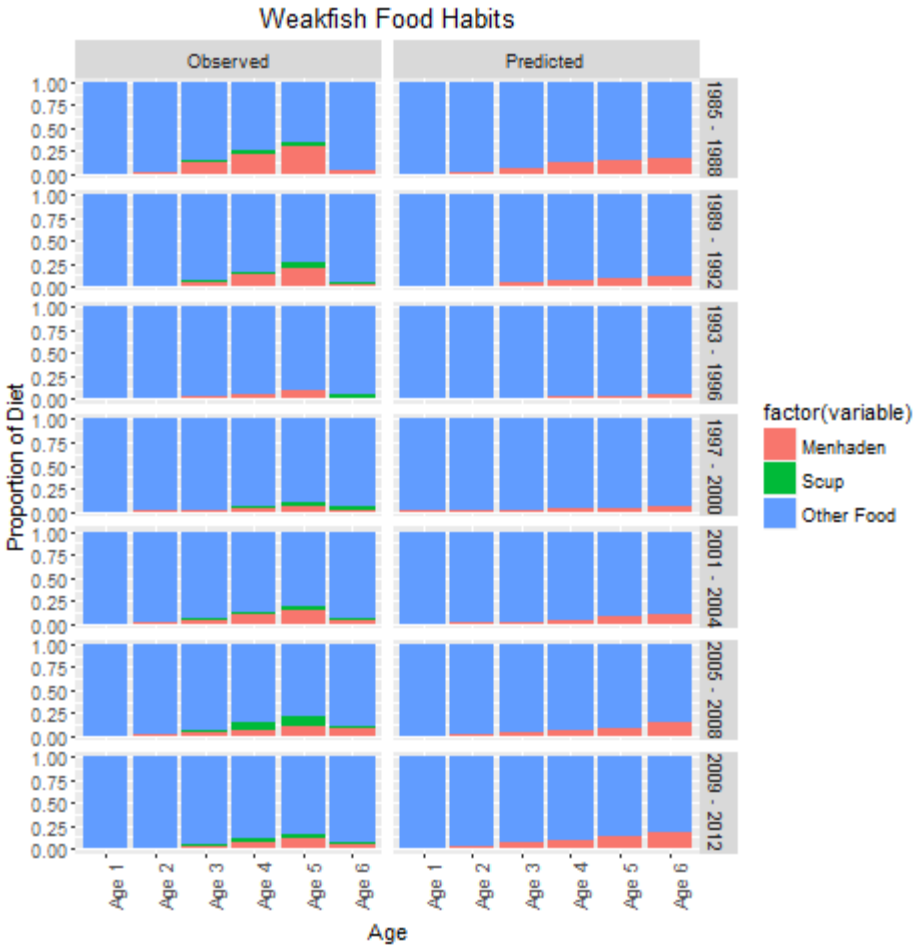

Fig. A14: Observed and predicted food habit information for weakfish by time block represented as proportion of total diet.

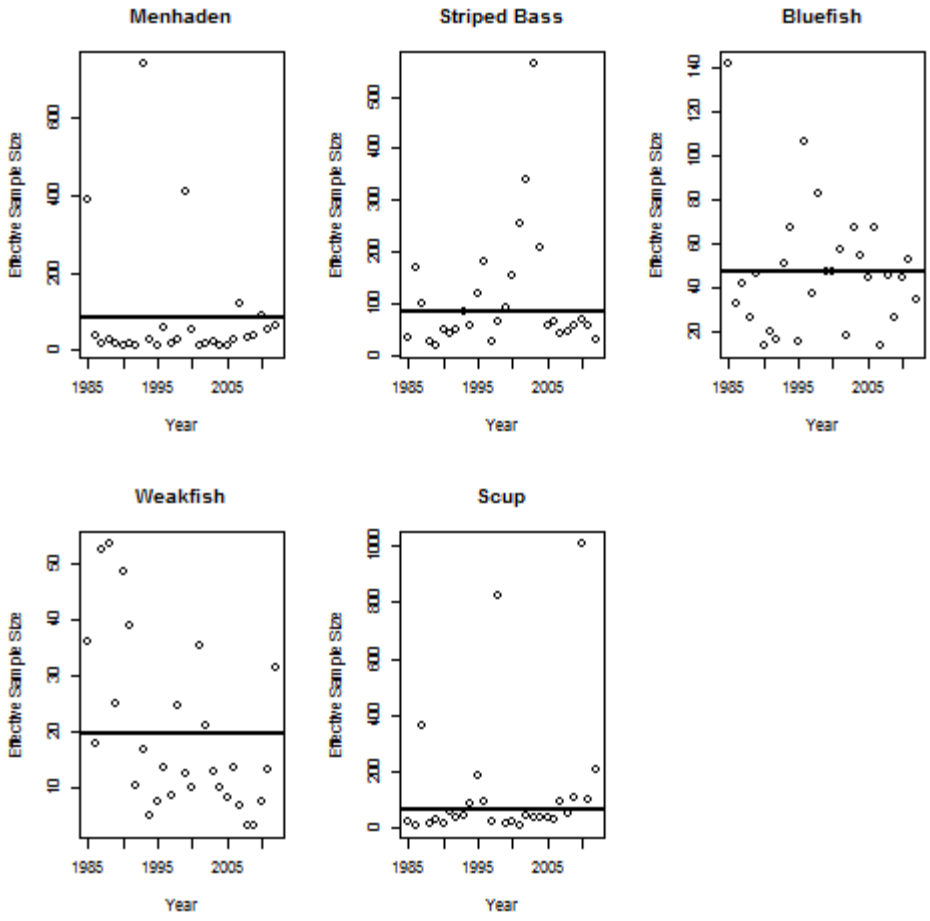

Fig. A15: Effective sample sizes for the catch at age information.

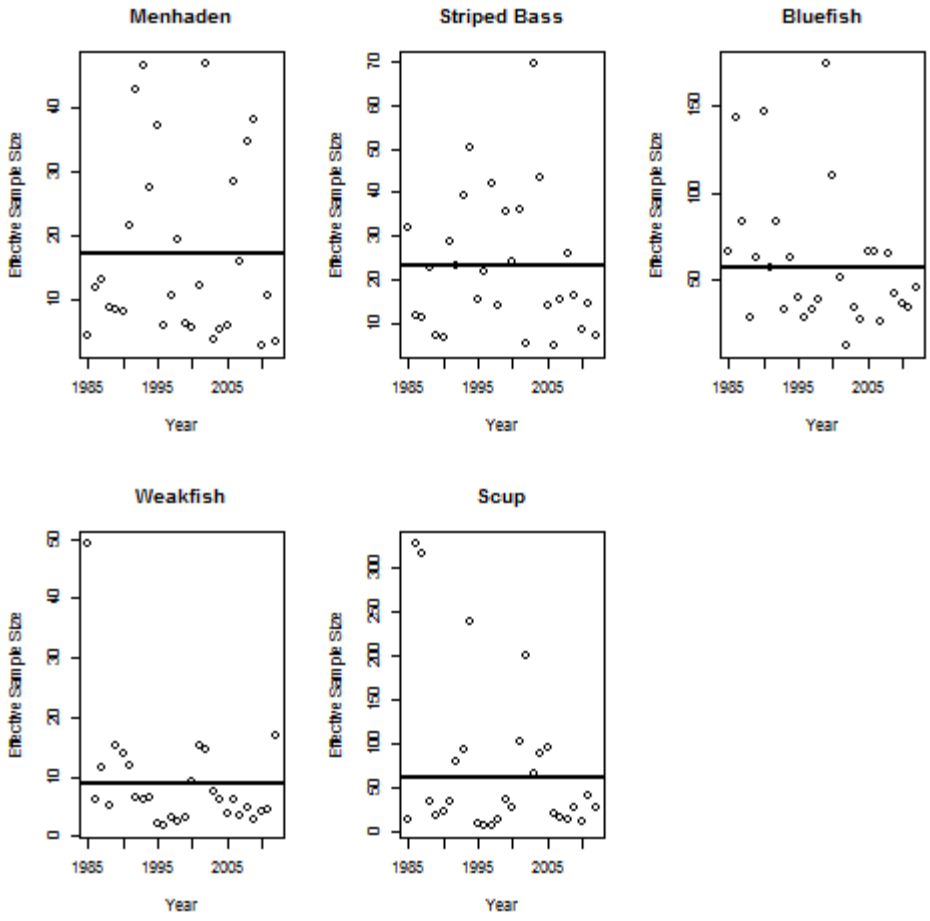

Fig. A16: Effective sample sizes for the fishery-independent survey age information.

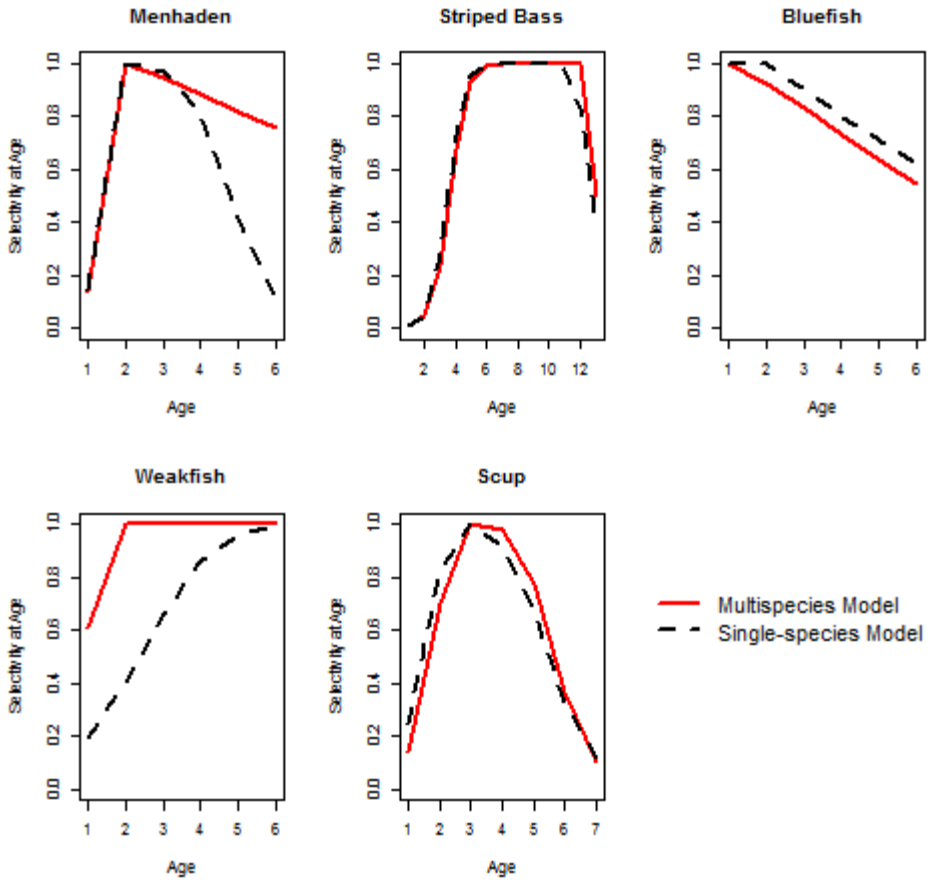

Fig. A17: Estimated selectivities for the single-species (black dashed line) and statistical multispecies (red solid line) models for the fishery catch information.

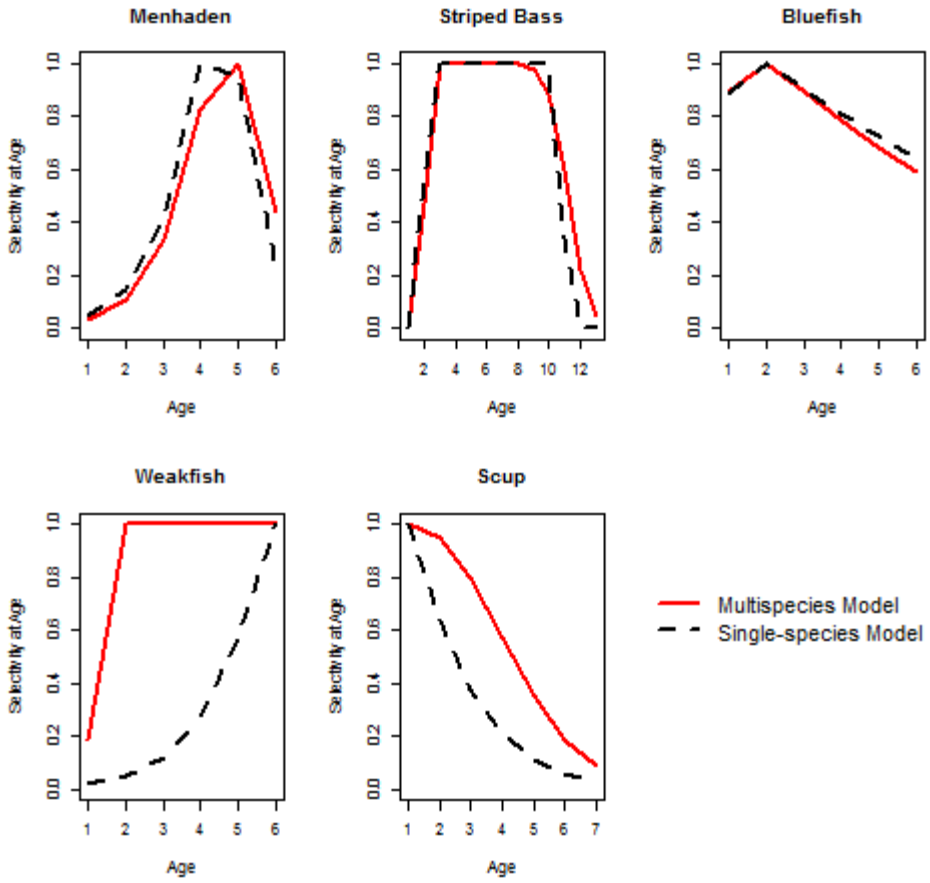

Fig. A18: Estimated selectivities for the single-species (black dashed line) and statistical multispecies (red solid line) models for the fishery-independent survey information.

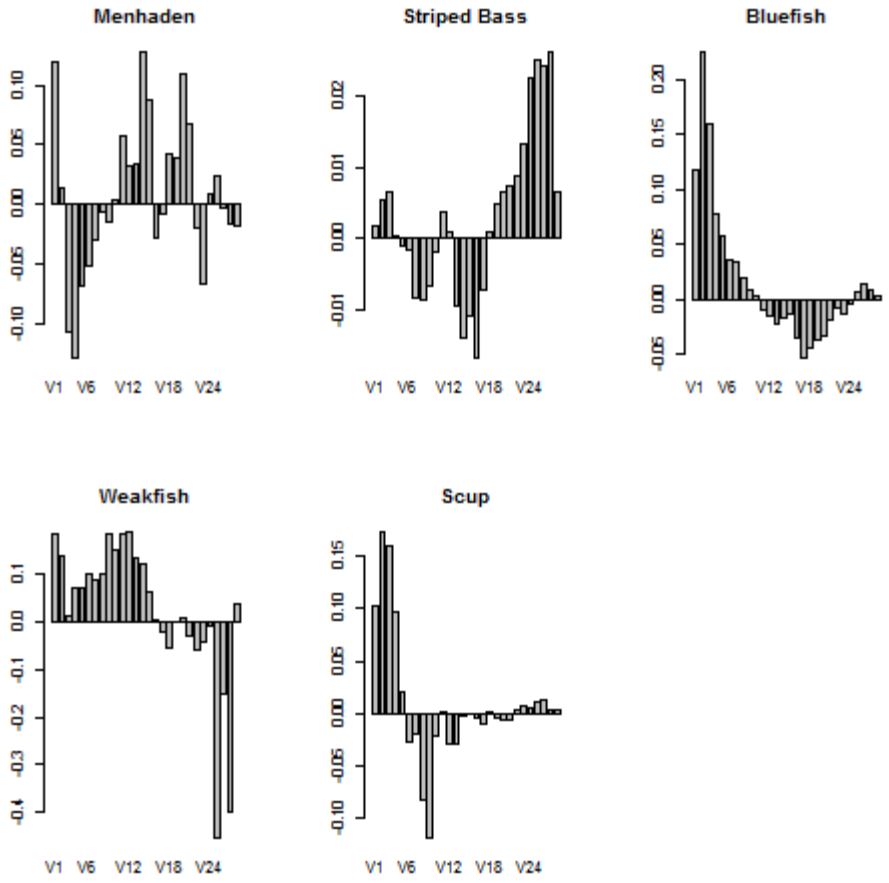

Fig. A19: Residuals for the model fit to the fishery catch information by species.

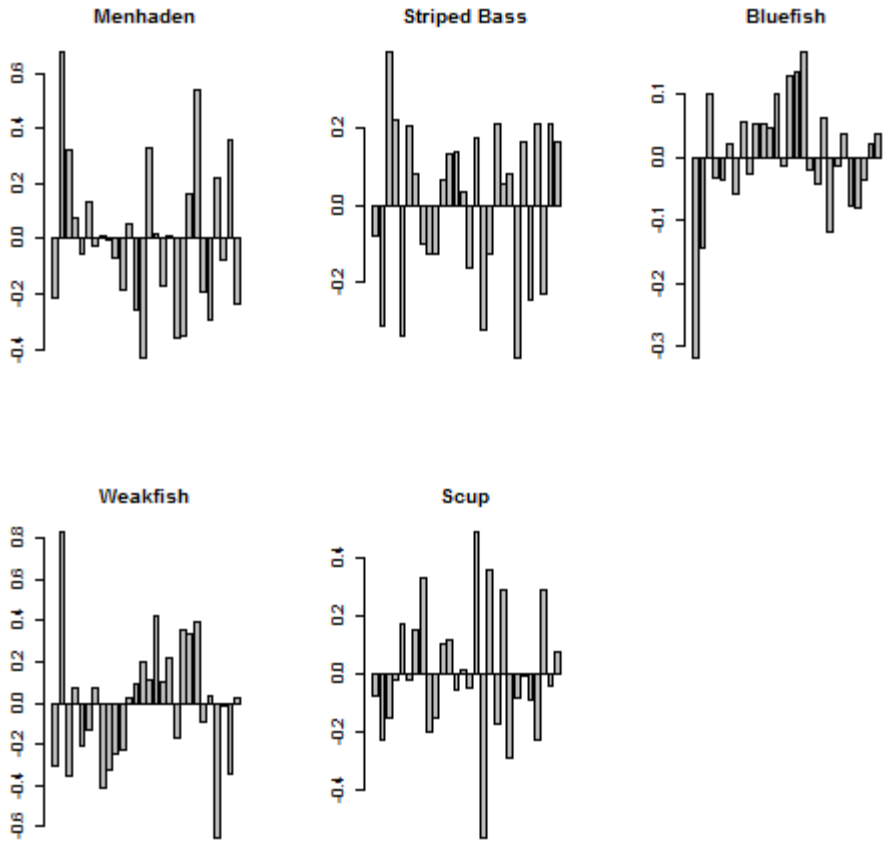

Fig. A20: Residuals for the model fit to the fishery-independent survey information by species.

MANUSCRIPT – II

Intended for submission to the ICES Journal of Marine Science

Projecting population metrics based on a multispecies, statistical catch-at-age model.

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ABSTRACT

As multispecies modeling tools are developed, there is a need to use the parameters generated by these multispecies analytical models to project the populations forward in time in an ecosystem context. A multispecies statistical catch-at-age model was developed for a mid-Atlantic suite of species including two prey populations (Atlantic menhaden and scup) and three top predators (Atlantic striped bass, bluefish, and weakfish). This model and its output were used as the basis for projecting the populations simultaneously into the future under different assumptions. Under all scenarios investigated in the long-term projections, equilibrium levels were achieved by all of the species in the ecosystem. The assumptions going in to the projections were tested and indicated that natural mortality and recruitment are the most important considerations in the suite of assumptions tested. The projections also offer a different view of the population dynamics of the system when factoring in predation mortality. The standard constant natural mortality (*M)* approach to projections produces more optimistic outcomes than when the time and age-varying *M* is accounted for in the projection. This finding shows that accounting for additional dynamics in the ecosystem can add value to the current management process by giving managers a better sense of the structural uncertainty that exists around the various assumptions being made. If time and age-varying natural mortality is the correct state of nature, this should be accounted for in the management action being undertaken.

KEYWORDS

multispecies statistical catch-at-age model, projection, predation mortality, biological reference points, time and age varying natural mortality

INTRODUCTION

The development of analytical population models for fish stocks is the preferred way by which stock status and population health is determined for the population being examined. The common practice is to analyze species on a stock-by-stock basis. Interest in multispecies models has grown, with managers placing an emphasis on ecosystem management as a new approach of interest in fisheries. Several multispecies modeling approaches have been developed to begin to create the infrastructure needed to assess fish populations in a multispecies context, including several multispecies statistical catch-at-age approaches (Lewy and Vinther 2004; Jurado-Molina 2005; Kinzey and Punt 2009; Van Kirk et al. 2010; Curti et al. 2013). As these multispecies modeling tools are developed, there is a need to use the parameters generated by these multispecies analytical models to project the populations forward in time in an ecosystem context.

These multispecies projections will allow for the setting of important management metrics, such as quotas, for important fish stocks, and will allow the managers to do this in the context of the ecosystem. Allowing the populations to be projected simultaneously and allowing them to interact through important population dynamic features such as predation, will give the necessary information to better understand the yield possible from the various components of the ecosystem, while better accounting for the interactions between the populations in that system. Developing tools that allow for this dynamic interaction also allows for the explicit understanding of the tradeoffs in population production. Managers will be able to look

at the impacts across species in the ecosystem through the management choices made on their population of focus.

A multispecies statistical catch-at-age model was developed for a mid-Atlantic suite of species including two prey populations (Atlantic menhaden and scup) and three top predators (Atlantic striped bass, bluefish, and weakfish). This model was based on the formulation developed by Curti et al. (2013), but was altered to allow for differences in some of the population characteristics specific to the species modeled, such as the allowance for domed selectivities and changing some of the penalized parameters in the model. This model produces many standard outputs that are both time and age varying, such as fishing mortality (F), biomass (B), catch (C), and abundance (N), and allows for the dynamic estimation of natural mortality (M) by age and year, which is unique to the multispecies formulation. This model and its output was used as the basis for projecting the populations simultaneously into the future under different assumptions.

When projecting population assessments into the future, several assumptions must be made. One of the key assumptions is how to parameterize M in the projections. The standard approach to this assumption in population projections is the same as that used in single-species assessments, namely to assume a time and/or age invariant M to allow for ease in the estimation of the other parameters (Brodziak et al. 2011; Deroba and Schueller 2013). Using a multispecies formulation provides new information with which to base this assumption, namely the multispecies model provides information about how M changes in time and by age. Additionally, parameters are developed in the multispecies model that can allow for the projection

of *M* dynamically into the future based on the number of predators in the ecosystem being modeled and their respective consumption rates.

Two different approaches to using the multispecies model information in projections will be investigated. One way multispecies model output can be used in projections is to use a standard approach of taking *M* and projecting forward with it in a static way. In the multispecies context, this static *M* can be based on the dynamic *M* produced by the multispecies model. An average of this dynamically estimated *M* can be used for the projections. This strategy follows that used for Atlantic menhaden in the past, when the MSVPA model (Garrison et al. 2010) for these species was still deemed useful for management (ASMFC 2011). This approach is useful for short to medium-term projections if predator abundance remains relatively consistent. The advantage of the multispecies model output in this context is that an average for a period believed to be appropriate and applicable to the period being projected can be used. The main way this will be examined will be by using the dynamic *M* estimates from the multispecies model, and taking an average of the time and age varying information for use in the forward projections. In addition to the average *M*-at-age estimates themselves, the variability in the *M* values through time will be used in the stochastic processes of the forward projections.

The second approach will be to use the estimated parameters from the predation functions in the multispecies model to project under dynamic *M* conditions that are predicated by the various populations and their different roles in the ecosystem. These types of projections better inform the tradeoffs between different management decisions on the different populations. These two approaches will be

compared to each other to examine how the understanding of the ecosystem changes based on the types of population dynamics and the various assumptions included in the projections.

In addition to the comparisons of different *M* assumptions, long-term projections will be performed. These projections will be used to compare the importance of two recruitment assumptions, one being that there is an underlying stock-recruit relationship, the other assumes that there is no relationship between spawners and recruits, and that a median recruitment level will be seen in the population regardless of underlying spawning stock size. This second assumption is used routinely in the projections using the single-species benchmark models for the species examined in this study (Atlantic menhaden: SEDAR 2015; Atlantic striped bass: ASMFC 2015; Bluefish: NEFSC 2015; Weakfish: ASMFC 2016; Scup: NEFSC 2015). The two projections will be examined to determine the relative importance of recruitment assumptions in the context of time and age varying natural mortality.

As an extension of the examination of important uncertainties when projecting populations forward in time, uncertainty in weight-at-age will also be investigated. The empirical weight-at-age for the species examined here change in time. How that weight-at-age will change in the future is an unknown, and a standard practice is to make an assumption about the appropriate value of this parameter when performing projections on these populations. These assumptions can range from using the weight-at-age from the terminal year of the assessment as being indicative of the current state of the population, to using an average over some relevant period of time for the projection. This exercise will examine the importance of the weight-at-age uncertainty

in the context of the uncertainty in natural mortality, allowing for a judgement on the importance of these two parameters to be made.

Another interesting concept that can be examined in a multispecies projection framework is the interaction between species and the effect of this on biological reference points. For this study, we will use a common *F* reference point, $F_{40\%\ msp}$ ($F_{40\%}$), or the fishing mortality rate that decreases per recruit spawning stock biomass (*SSB*) to 40% of the unfished per recruit *SSB* (Clark 1991, 2002). To calculate this $F_{40\%}$ value, the *M* from the terminal year of the multispecies assessment will be used. These "proxy" type reference points are used when the spawner-recruit relationship is poorly defined. This type of reference point assumes that an equilibrium level can be reached by the population under no fishing, and the management reference point is meant to constrain harvest to a level that is assumed to allow the fished population to remain sustainable. There are other common reference points used in fisheries, such as F_{msy} (fishing mortality of maximum sustainable yield), but this study will focus on the "F_{msy} proxy" reference point of $F_{40\%}$ as this is the type of reference point that is currently used for the species examined in this study. Dynamically changing *M* makes calculating reference points challenging. As suggested by Legault and Palmer (2016), using a time varying *M* should only be undertaken when strong empirical evidence suggests it is occurring. In this case, the strong empirical evidence is the diet information from the important predators in the ecosystem, and this therefore justifies the use of a time varying *M* for the analysis, and by using this feature in the projections, context can be provided in how the reference points change through time as interactions occur between fishing and predators in the ecosystem. In this context

the appropriateness of using per-recruit reference points can also be examined, as was done by Legault and Palmer (2016).

Looking at this information collectively allows for inferences to be made about the additional value in the information received when using multispecies information for projecting a population forward, which is important for understanding how different management scenarios will impact a species, but also how the management choice for one species cascades through the ecosystem. This study will test the hypothesis that using multispecies information is important and can lead to a different sense of the population, and the fishing it can sustain through time. This will be tested by running an ecosystem forward under different scenarios. As the information from the different scenarios is generated, the output will be viewed and contrasted to see how the different assumptions might lead to different management choices.

METHODS

Data into and output from a run of a Multispecies Statistical Catch-at-age model (MSSCAA) as developed for Chapter 1 of this dissertation were used as the basis for these projections, including the data for *SSB*, recruits, and recruitment deviations. The model outputs were exported from ADMB software (ADMB-IDE ver 10.1 2011) and imported to R statistical software (R Core Team 2016) for the projection calculations.

The starting conditions of the projection analysis include initial numbers at age, which were the estimated numbers at age, N_0, for the terminal year of the multispecies stock assessment model. To allow for variability in the projection starting

population, a bootstrap procedure was used for recruitment as described above, and for numbers-at-age for ages 2+. The bootstrap procedure adds a deviation to the starting numbers-at-age, the deviation being based on sampling from a normal distribution with a mean of 0 and a standard deviation set at the standard deviation seen in the population for the time period examined. This deviation was bounded to prevent very large deviations from occurring randomly through the sampling process.

Numbers at age after the initial year were calculated as:

$$N_{i,a+1,y+1} = N_{i,a,y} e^{-Z_{i,a,y}} \quad (1)$$

where Z is age and year specific mortality and equals natural mortality for each age for that year plus the fishing mortality rate times the fishery selectivity at age, $N_{i,a,y}$ is the population by age and year, and the subscript i is the species. Fishery selectivity was a vector as estimated for each species from the multispecies stock assessment.

For the constant-F scenarios used for this project, the landings associated with the chosen F strategy were calculated. These annual landings were calculated using the Baranov catch equation and weight of landings.

$$C_a = \frac{F_a}{F_a + M_a}\left(1 - e^{-(F_a + M_a)}\right)N_a \quad (2)$$

Where C is catch, F_a is fishing mortality at age, M_a is natural mortality at age, and N_a is the population at the start of the year. In this case, the Baranov catch equation is

used so that *F* is the input variable and catch is estimated from the input *F*. The catch and population in numbers are converted into biomass units, and the weight-at-age for each species is assumed to be equal to the species specific average weight-at-age. This weight-at-age is projected forward in both a static fashion and also in a stochastic manner in one scenario.

Spawning stock biomass (*SSB*) was calculated for each species and was based on the biomass-at-age as estimated for each year in the projection multiplied by the maturity-at-age vector from the terminal year of the multispecies stock assessment model. In this case, all *SSB* is represented in the estimate and is therefore comprises both male and female biomass. Spawning was assumed to occur mid-year for all of the species in the model, therefore the *SSB* was decreased by total mortality for half a year.

In several of the projection scenarios, recruitment was projected without an underlying stock-recruitment function and was based on the median recruitment observed from the entire time series for each species. Recruitment variability was included whereby for each year a deviation in recruitment was selected randomly with replacement from the deviations estimated in the multispecies stock assessment model. This may be an overly restrictive assumption in that it will be impossible to have recruitment overfishing in a population, however this strategy was chosen due to the lack of good stock-recruitment information, and because this is the standard approach for all of the species in this complex of species in their normal single-species assessment procedures.

In some scenarios, a stock-recruitment function was used. For the stock-recruitment function, a Ricker model was used (Ricker 1954). This stock-recruit model was found to fit the data best in the analysis done for Chapter 1 of this dissertation as determined by AIC analysis. There is also a biological basis for this stock-recruit model for the species used in this study as well in that many of the predators exhibit cannibalism and food resource limitation could also occur on these species if the stock increases to high population levels. The formulation used is defined by the equation:

$$R_{i,t+1} = \alpha_i * SSB_{i,t} * e^{-\beta_i * SSB_{i,t}} + e^{\varepsilon} \quad (3)$$

where $R_{i,t+1}$ is recruitment in year t+1, $SSB_{i,t}$ is spawning stock for species i in year t, α_i and β_i are the species-specific parameters controlling the shape of the function, and ε is a term that adds in recruitment variability in each year and is drawn from a normal distribution with a mean of zero and a standard deviation based on the recruitment deviations from the time-series of the stock assessment model. The selection of the Ricker model for the stock-recruitment relationship was based on the findings from Chapter 1 that the Ricker model fit the stock-recruitment data better than the Beverton-Holt stock-recruit function, therefore this was the most appropriate model to use for this analysis.

Long-term projections

An initial set of projections was run under two recruitment assumptions and no fishing mortality to determine unfished biomass levels. These projections were run for 200 years to allow the populations to reach equilibrium. The projections were

parameterized as above with the exception of the recruitment and fishing mortality assumptions, and these projection runs were done using the dynamic *M* formulation.

The first recruitment assumption was to use an underlying stock-recruitment function. While the relationship between spawners and recruits for all of the species examined is uncertain, this projection was run in the context of examining the importance of the recruitment assumption versus not assuming any stock-recruit relationship.

The second recruitment assumption was to run the projections without an underlying stock-recruitment function and was based on the median recruitment observed from the entire time series for each species. Recruitment variability was included whereby for each year a deviation in recruitment was selected randomly with replacement from the deviations estimated in the multispecies stock assessment model. This deviation was then added to the overall median recruitment.

For both of these recruitment assumptions, the projection was run allowing *M* to be calculated dynamically. The description of the dynamic *M2* calculations follow the procedure used in Chapter 1 of this dissertation. The projections are run in a stochastic fashion. The projection parameters were bootstrapped for two-hundred iterations for the long-term projections, with the initial population and recruitment bootstrapped with uncertainty based on the timeseries from the multispecies model from Chapter 1. Outputs included the median, 5th and 95th percentiles for spawning stock biomass, fishing mortality, recruitment, landings, and natural mortality for the prey species.

Two other long-term projections were also run. One projection was set up the same as the above projection with median recruitment, but instead of setting $F = 0$, F was set to meet the management goal of maintaining an F rate at the F_{msy} proxy of $F_{40\%}$ as calculated by the multispecies assessment model. This $F_{40\%}$ calculation uses a more standard approach of using a static M assumption, namely the M from the terminal year of the assessment, in the spawner-per-recruit (SPR) calculations. There is an inconsistency between the assumption of a static M for the $F_{40\%}$ calculation in the context of dynamically changing M in the projections, but this was done to allow a fair comparison between the different scenarios, some of which are assuming a static M in the projection. Additionally, this gives all the scenarios a similar F rate goal for comparison. These projections were run for 200 years with 200 bootstrap runs.

A final long-term projection scenario was run using a static M assumption, median recruitment, and F set to 0. The mean M-at-age from the entire time series from the multispecies model was used as the static M vector to use in the projections. These projections were run for 200 years with 200 bootstrap runs. This is not a very realistic set of assumptions, however these are some of the same assumptions made in a standard projection methodology, and therefore this scenario was included to provide some context with the other more realistic scenarios.

Medium-term projections

After the two long-term projections were run, a series of medium-term projections were run to compare some different assumptions and uncertainties. These projections were run for a total of 10 years with an assumption of a constant F strategy during that time period. The F was set to meet the management goal of maintaining an

F rate at the F_{msy} proxy of $F_{40\%}$ as calculated by the multispecies assessment model, as was done for one of the long-term projection scenarios above. The medium-term projections are run in a stochastic fashion. The projection parameters were bootstrapped for five-hundred iterations for the medium-term projections and the projection period used was ten years. Outputs included the median, 5th and 95th percentiles for spawning stock biomass, fishing mortality, recruitment, landings, and natural mortality for the prey species.

Natural mortality (*M*) was modeled using two different scenarios. The first scenario represents a more traditional technique of using a static *M* assumption for each year of the projection. Under this set of scenarios, the mean *M*-at-age from the entire time series from the multispecies model was used as the static *M* vector to use in the projections. Using the entire time-series was chosen to provide this scenario as an interim method between a static assumed quantity and a dynamic quantity. Another choice could have been to use an average from a more recent period, but this full time-series assumption was chosen to provide contrast with the other two scenarios in the analysis. While this is characterized as a standard practice, such as the practice used for most single-species model projections, there is still a progression from this standard approach for the prey species examined here in that the *M* value is based off of a dynamically calculated *M* from the multispecies model, whereas this metric is usually an assumed quantity that remains static in both the assessment model and the projections in a single-species context.

The second scenario uses a dynamic calculation of *M* for each year in the projection. The main assumption for this scenario is that the prey suitabilities (ν), as

calculated by the multispecies stock assessment model, remain constant for the time period of the projections, and are taken from the terminal year of the multispecies assessment model. Under this formulation, a type-II functional response is assumed. Under this functional response, the predator satiates at a high prey biomass, and the satiation reaches an asymptote (doesn't decline at higher densities) (Sparre 1980). This dynamic *M2* value is summed with the residual natural mortality estimate (*M1*, natural mortality not attributed to predation) to complete the natural mortality calculation.

A medium-term projection was run to test the effect of another projection assumption, namely variability in weight-at-age. In these projections, a mean weight at age was used but was allowed to vary stochastically based on the variance in the entire time series of empirical weight-at-age information. This was accomplished by sampling from a normal distribution with the mean set at the mean weight-at-age for the species for the time-series and the standard deviation set at the standard deviation of the empirical weight-at-age for the entire time-series. The variability is included by calculating a deviation from the mean weight-at-age for each species annually.

A final comparative projection was run that assumed dynamic natural mortality for the projection period. The main difference between this scenario and the other scenarios outlined above is that this projection assumes a spawner-recruit function, the Ricker model as used for the long-term projections. As with the other scenarios, the constant *F* strategy is to assume $F_{40\%}$ for all of the species.

Time-varying natural mortality and the effect on biological reference points

A final test was undertaken to examine how *F* proxy values react in a system where the natural mortality rate is changing. Using the long-term projection with

dynamic F for the prey species, the prey populations were set at their $F_{40\%}$ biological reference point, but for this exercise, $F_{40\%}$ was recalculated for menhaden in each year. The predators were set at their $F_{40\%}$ levels as was the procedure for the original projections. As programed in the assessment program ASAP (NEFSC 2017), the F reference points are computed through a bisection algorithm that is repeated 20 times (producing an accuracy of approximately $1*10^{-05}$).

RESULTS

Long-Term Projections

Projections with Stock-Recruit Relationship

As noted, the stock-recruit relationship used for this exercise was a Ricker stock-recruitment model. For the long-term projections with $F = 0$ where the natural mortality (M) varied for prey species through the projection time period with the inclusion of a stock-recruitment function, there was generally a period where the recruitment and spawning stock biomass (SSB) levels varied followed by both population metrics settling to an equilibrium level. For menhaden, there was a decrease in SSB over the 200-year projection period from 736 tmt to 598 tmt by year 200 (Table A1). Striped bass had an increase in SSB during the projection period, increasing from 143 tmt to 178 tmt in year 200 (Table A2). Bluefish also had an increase in SSB during the projection period, going from 121 tmt to 212 tmt in year 200 (Table A3). Weakfish reached equilibrium rapidly, increasing from 12 tmt to 32 tmt by year 50 and then remained stable at that level through year 200 (Table A4). Finally, scup had a rapid decrease in SSB during the projection period, decreasing from 160 tmt to 75 tmt by year 200 (Table A5).

Recruitment showed variability patterns similar to the patterns seen in the *SSB* across species, with a period of variability followed by a period of stability at an equilibrium level. The variability was in the opposite direction when compared to the oscillations in *SSB*. Menhaden recruitment began at 6,565 million fish and ended at 6,695 million fish (Table A1), so while there were some significant swings in the early part of the time period, recruitment was fairly stable for menhaden. Striped bass recruitment began at 82 million fish and ended at 59 million fish (Table A2). Bluefish recruitment declined during the projection period, beginning at 22 million fish and ended at 15 million fish (Table A3). After a period of rapid decline, bluefish recruitment remained stable for the majority of the projection period with less variability than the other species. Weakfish recruitment began at 17 million fish and ended at 19 million fish (Table A4) and was stable for the majority of the projection period. Scup recruitment increased significantly in the beginning of the time period and stabilized at a high recruitment level. Scup recruitment began at 120 million fish and ended at 467 million fish (Table A5).

For these long-term projections, *M* was occurring dynamically on the prey species menhaden and scup. There was an initial increase in *M* for menhaden, with ages one and two having the highest *M* occurring on them. After the initial increase, the *M* rates stabilized for the remainder of the projection (Figure 7, Table A6). At the end of the projection period, *M* was high on all ages in this scenario, with *M* being approximately 2 on ages one and two. Similarly for scup, *M* increased on all ages through the entire projection period. The *M* rate was highest on age one and dropped

off quickly for the older ages (Figure 8, Table A7). By the end of the projection period, *M* was high on age-one, being approximately 2.6.

Median Recruitment

For the long-term projections with $F = 0$ where the natural mortality varied for prey species through the projection time period with the assumption of no stock-recruitment relationship and median recruitment, there were mixed trends across the species. For menhaden, there was a rapid decrease in *SSB* over the 200-year projection period, settling at a very low equilibrium value. Menhaden *SSB* decreased from 710 tmt to 62 tmt by year 200 (Figure 1, Table A8). All three of the predator species increased dramatically under no fishing and their median recruitment levels. Striped bass *SSB* increased from 143 tmt and ended at 371 tmt in year 200, more than doubling in size (Figure 2, Table A9). Bluefish *SSB* increased from 121 tmt to 301 tmt in year 200, also increasing by more than 2 times its starting population size (Figure 3, Table A10). Weakfish *SSB* started at 14 tmt and ended at 58 tmt in year 200, more than tripling in size (Figure 4, Table A11). Scup did not fare well with all of the predators at these large population sizes. Scup had a sharp decrease in *SSB* during the projection period. Scup *SSB* started at 160 tmt and declined to 0 tmt in year fifty of the projection (Figure 5, Table A12). While the population dropped very low, it was not extinct but at very low *SSB* levels that were less than 1 tmt.

As was the case for the previous long-term projection, *M* was occurring dynamically on the prey species menhaden and scup. There was an initial increase in *M* for menhaden, with ages one and two having the highest *M* occurring on them. After the initial increase, the *M* rates stabilized for the remainder of the projection (Figure 7, Table A13). At the end of the projection period, *M* was high on all ages in

this scenario, with *M* being approximately 2 on ages-one and two. Similarly for scup, *M* increased on all ages through the entire projection period. The *M* rate was highest on age-one and dropped off quickly for the older ages (Figure 8, Table A14). By the end of the projection period, *M* was very high on age-one, being approximately 6.5.

Long Term Projection with $F_{40\%}$

Another long-term projection was run under the median recruitment assumption, but allowing fishing to occur at the $F_{40\%}$ level. The $F_{40\%}$ levels used for each species can be seen in Table 1, and were calculated based on the terminal year *M* from the multispecies stock assessment model from Chapter 1. The patterns with the prey and predator species remained, namely that the prey species declined and the predators increased. In this case though, neither of the prey species declined to 0. Menhaden started the projection at 572 tmt and declined to 214 tmt by year 200, a large decline but not nearly as big a decline as when the predators were not experiencing fishing mortality (Figure 1, Table A15). Striped bass, bluefish, and weakfish all increased as was the case under no fishing, but the increases were much less than in the no fishing case. Striped bass *SSB* began at 139 tmt and ended at 149 tmt (Figure 2, Table A16). Bluefish began at 114 tmt and ended at 124 tmt (Figure 3, Table A17), and weakfish began at 13 tmt and ended at 22 tmt (Figure 4, Table A18). Scup again declined, but did not decline to 0. Scup began the projection at 153 tmt and ended at 17 tmt (Figure 5, Table A19).

Natural mortality (*M*) was occurring dynamically on the prey species menhaden and scup in this projection scenario. There was an initial increase in *M* for menhaden, with ages one and two having the highest *M* occurring on them. After the initial increase, the *M* rates stabilized for the remainder of the projection (Figure 7,

Table A20). At the end of the projection period, *M* was high on ages one and two in this scenario, with *M* being approximately 1 on ages one and two, about half of what it was under the no fishing scenario. For scup, *M* increased on all ages through the entire projection period. The *M* rate was highest on age one and dropped off quickly for the older ages (Figure 8, Table A21). By the end of the projection period, *M* was high on age-one, approximately 2.4, but this was lower than in the no fishing scenario.

Long Term Projection with Static M

A final long-term projection was run under the median recruitment assumption and $F = 0$. The difference for this projection was that *M* was set at a static level based off the average from the entire time series from the multispecies assessment. In this case, all of the species increased through the time period. Menhaden started the projection at 732 tmt and increased to 969 tmt by year 200 (Figure 1, Table A22). The predators should generally exhibit the same trends as those seen in the median recruitment long-term projection scenario described above, but small variations were seen in the outcome due to the stochasticity in the projections. Striped bass *SSB* began at 145 tmt and ended at 368 tmt (Figure 2, Table A23). Bluefish began at 120 tmt and ended at 300 tmt (Figure 3, Table A24), and weakfish began at 14 tmt and ended at 53 tmt (Figure 4, Table A25). Finally, scup began the projection at 160 tmt and ended at 238 tmt (Figure 5, Table A26).

Medium-term Projections

Static natural mortality

The first medium-term projection investigated was to set $F_{40\%}$ (Table 1) as the management scenario to use in the medium-term time period. The natural mortality assumption for this scenario was set based on an average of the entire time series from

the multispecies stock assessment model. In this projection scenario, the predator species were flat to slightly increasing through the projection period, while the prey species declined modestly. Menhaden *SSB* decreased from 585 tmt to 346 tmt (Figure 9, Table 4). Striped bass *SSB* was flat during the projection period. Striped bass *SSB* started at 139 tmt and ended at 133 tmt (Figure 10, Table 5). Bluefish had a modest increase in *SSB* during the projection period. Bluefish *SSB* increased from 113 tmt to 123 tmt (Figure 11, Table 6). Weakfish also had an increase in *SSB* during the projection period (Figure 12, Table 7). Weakfish *SSB* increased from 12 tmt to 22 tmt. Finally, scup *SSB* decreased during the projection period (Figure 13, Table 8). Scup *SSB* decreased from 154 tmt to 117 tmt.

Given the changes seen in *SSB* during the projection period, the landings for the species modeled also change to maintain the management goal of $F_{40\%}$. Menhaden landings decreased from 412 tmt to 221 tmt (Figure 9, Table 4). Striped bass landings remained flat, going from 15 tmt to 17 tmt (Figure 10, Table 5). Bluefish landings were also flat, starting at 13 tmt and ending at 14 tmt in year 10 (Figure 11, Table 6). Weakfish landings increased from 3 tmt to 5 tmt (Figure 12, Table 7). Finally, scup landings decreased from 15 tmt to 10 tmt (Figure 13, Table 8).

Recruitment and natural mortality was stable for all species modeled per the assumption of the projections, though recruitment was allowed to vary stochastically based on the variance for the entire time series from the stock assessment model.

Dynamic natural mortality

The second medium-term projection investigated also set $F_{40\%}$ (Table 1) as the management scenario to use in the medium-term time period. The natural mortality assumption for this scenario could vary based on the predation calculations

as defined in Chapter 1. In this projection scenario, the predator species were exactly as described in the previous section as predation mortality was not occurring on the predators in this study (Figures 10 – 12; Table 5 – 7). The prey species in this scenario declined modestly, though the decline was larger than when the assumption was set at static *M* through the projection period. Menhaden *SSB* decreased from 573 tmt to 238 tmt (Figure 14, Table 9). Scup *SSB* decreased from 154 tmt to 71 tmt (Figure 15, Table 10).

Given the changes seen in *SSB* during the projection period, the landings for the prey species modeled also changed to maintain the management goal of $F_{40\%}$. Menhaden landings decreased from 405 tmt to 158 tmt (Figure 14, Table 9). Finally, scup landings decreased from 15 tmt to 3 tmt (Figure 15, Table 10).

Recruitment was stable for all species modeled per the assumption of the projections, though recruitment was allowed to vary stochastically based on the variance for the entire time series from the stock assessment model. For the prey species however, *M* changed through the projection period. Menhaden *M* increased steadily through the projection period for all age classes. Age one and two saw the highest *M* on them, with age one starting with an *M* equal to 0.88 and ending at *M* equal to 1.06 (Figure 14, Table 11). Scup *M* also increased steadily through the time period. For scup, the main age class that was impacted by *M* was age one. Age one scup started with an *M* of 1.66 and ended with a high *M* of 2.22 by year ten (Figure 15, Table 12).

Varying weight-at-age

The final medium-term projection investigated was to set $F_{40\%}$ (Table 1) as the management scenario to use in the medium-term time period and the natural mortality

assumption was set based on an average of the entire time series from the multispecies stock assessment model. The difference for this projection was that weight-at-age could vary stochastically during the projection period. In this projection scenario, the predator species were flat to slightly increasing through the projection period, while the prey species declined modestly. These trends were little changed from the previous scenario using static *M*, though the variance around the median values for *SSB* and landings increased (see Table 20 as an example). Menhaden *SSB* decreased from 577 tmt to 346 tmt (Figure 16, Table 13). Striped bass *SSB* was flat during the projection period. Striped bass *SSB* started at 141 tmt and ended at 134 tmt (Figure 17, Table 14). Bluefish had a modest increase in *SSB* during the projection period (Figure 18, Table 15). Bluefish *SSB* increased from 114 tmt to 124 tmt. Weakfish also had an increase in *SSB* during the projection period (Figure 19, Table 16). Weakfish *SSB* increased from 12 tmt to 21 tmt. Finally, scup *SSB* decreased during the projection period (Figure 20, Table 17). Scup *SSB* decreased from 154 tmt to 112 tmt.

Given the changes seen in *SSB* during the projection period, the landings for the species modeled also changed to maintain the management goal of $F_{40\%}$. Menhaden landings decreased from 406 tmt to 220 tmt (Figure 16, Table 13). Striped bass landings remained flat, going from 15 tmt to 17 tmt (Figure 17, Table 14). Bluefish landings were also flat, starting at 13 tmt and ending at 14 tmt in year 10 (Figure 18, Table 15). Weakfish landings increased from 3 tmt to 5 tmt (Figure 19, Table 16). Finally, scup landings decreased from 15 tmt to 10 tmt (Figure 20, Table 17).

Recruitment and natural mortality was stable for all species modeled per the assumption of the projections, though recruitment was allowed to vary stochastically based on the variance for the entire time series from the stock assessment model.

Static natural mortality set at benchmark assessment levels

This medium-term projection set $F_{40\%}$ (Table 1) as the management scenario to use in the medium-term. The natural mortality assumption for this scenario was set based on the assumption used in the current benchmark single-species assessments for the species examined (Table 2). In this projection scenario, the predator species were flat to slightly increasing through the projection period, while the prey species declined modestly. The predator plots are the same as in Figures 29 – 31. Similar to the other projections run for menhaden, *SSB* decreased from 597 tmt to 378 tmt (Figure 21, Table 18). Different than the other scup projections investigated, scup *SSB* increased during the projection period (Figure 22, Table 19). Scup *SSB* increased from 149 tmt to 158 tmt.

Given the changes seen in *SSB* during the projection period, the landings for the species modeled also changed to maintain the management goal of $F_{40\%}$. Menhaden landings decreased from 419 tmt to 242 tmt (Figure 21, Table 18) and scup landings increased from 15 tmt to 20 tmt (Figure 22, Table 19).

Recruitment and natural mortality was stable for all species modeled per the assumption of the projections, though recruitment was allowed to vary stochastically based on the variance for the entire time series from the stock assessment model.

Time-varying natural mortality and biological reference points

When F40% is recalculated in each year, we see that there is variation in what the new reference point would be in each year for menhaden but it is not dramatic over

the ten-year projection. The range of possible biological reference points go from an *F* of 0.74 to 0.77 for menhaden (Figure 23). This difference is not overly meaningful in a biological or a management sense as it would be difficult to detect changes this small, but the exercise still illustrates the point that the reference point is not static in a scenario where *M* is allowed to vary through time, making managing based on this dynamic information challenging.

DISCUSSION

Initially some long-term projections were run to look at how the populations of the species examined in this study behave over a long period of time under different states of nature. The unique investigation from this study is that the projections allow the species to interact through predation during the projection period, adding more realism in to the population projections. An important first-order observation was that under all of the scenarios investigated in the long-term projections, equilibrium levels were achieved by all of the species in the ecosystem, an important finding given that we know all of the species coexisted historically prior to fishing commencing. In the cases using the median recruitment assumption however, the prey populations dropped to very low levels, reaching a low stable population size, but only because the populations were fed by the assumption that there would always be a median recruitment coming in to the population. This result calls in to question the use of median recruitment as a reasonable assumption in long-term projections when thinking about these populations in an ecosystem context.

In the context of this ecosystem approach to projecting fish populations, several important assumptions were tested to investigate the impact that these

assumptions might have on long-term effects to the populations when they are allowed to interact. The first notable outcome was that the assumption about recruitment has important implications for the populations. The existence of a presumed stock-recruit relationship in the projections had very different outcomes than in the projections where a median and constant recruitment assumption was made. For the prey species, populations were maintained at a higher level in the long term when a stock-recruit relationship was assumed. The predators on the other hand have much less optimistic population trajectories when a stock-recruit relationship was assumed compared with the median recruitment assumption. It is this interaction, namely that the predator populations do not increase to relatively high population levels under a stock-recruit assumption, which allows the prey species to maintain relatively robust population sizes. This could in part be driven by the choice of the Ricker stock-recruit model, but there are reasons to believe this may be the appropriate stock-recruit relationship in part due to the superior model fit to the data as shown in Chapter 1 of this dissertation, the fact that cannibalism has been found to occur in certain high density circumstances for two of the most important predators examined in this study (bluefish (Schilling et al 2017) and striped bass (Paller and Lewis 1987)), and resource limitation at high densities. Under the median recruitment scenario, the predator populations rose to very high levels under no fishing, and due to this, the prey populations were unable to maintain their population levels at high numbers, with scup dropping to extremely low levels. This effect is caused by the high *M* endured by the prey populations when all of the predators are at extremely high population levels. As prey populations decrease to low numbers, the dynamic *M* projections account for this to some degree through the

availability (ϕ) calculations, but vulnerability (ρ), and thereby suitability (ν) would likely change as well. In these projections these parameters are set per the terminal year of the assessment and so remain static in the projections. In reality, the vulnerability would likely decrease, decreasing the prey items suitability, which could feed back to the dynamic *M* calculations and add an additional dynamic not captured in these projections. While the assumption of static vulnerability and suitability are likely fair assumptions in a shorter-term projection, the assumption is likely not valid in a long-term projection when the prey population changes dramatically.

An additional examination was undertaken to look at other possible mechanisms that might keep predator populations down, and what effect this might have on the prey population over a long period. The scenario where fishing was implemented on the populations showed that this was a mechanism whereby the prey populations could remain at higher equilibrium population levels than when predator populations were not undergoing fishing and could increase to high population levels. Even though the prey species were also experiencing fishing mortality, the equilibrium populations for the prey under this scenario were higher because the predator populations were kept from reaching as high a level as when they were not experiencing fishing mortality.

When these scenarios and their effects are viewed comprehensively, we see that the underlying assumption in the projections about recruitment is an important consideration. This is a widely known caveat for fisheries population projections, but it was shown to have additional importance in an ecosystem context because of the dramatically different long-term consequences to the populations, in particular the

prey populations. In addition to shedding new light on how the selection of the recruitment assumption is important, we also see that there must be a missing aspect to the population dynamics that is not captured in this exercise. These populations have likely coexisted historically, and the prey species have likely done so at levels higher than shown in the no-fishing scenarios examined here. This may be due to missing some removal dynamic on the predator populations that keeps them from reaching the high levels seen in this research under no fishing. The comparison between the long-term projections with fishing and without, but with dynamic natural mortality shows that removal of predators through fishing impacts the prey populations positively, but given that fishing has not always existed, other removal mechanisms must be in play on the predator populations that are not captured in this research. One possible explanation is a feedback mechanism between prey and predators, meaning that as prey populations decline, predator populations are negatively impacted. This potential prey-to-predator feedback will be explored in the next chapter of this dissertation. A second possibility might be that the predators switch when prey populations become low. This would implicate a different functional response in predation than the one assumed here (type-2 functional response (Holling 1959)). Specifically, a type-3 functional response between predators and prey could be examined in future research to see the effects that this has on the various species populations. In these projections, *M* continues to increase as the prey population declines because the predators have a consistent preference for a certain species, which does not change over time. Therefore if a different functional response were assumed and if other prey species were added to the ecosystem being modeled beyond the two examined here, very

different dynamic might result, allowing the prey populations to reach equilibrium at a higher, more realistic level. A functional response that is different than that assumed in this study would likely be important as prey populations reach low population sizes, but in a scenario where the prey population is at a moderate to high level, as is the case for the prey species examined in this study, or for shorter-term projection timeframes, using the functional response assumed in this study adds an important dynamic that is missing in standard management projections and will likely improve the projection performance. This improved performance could be tested through simulation experiments or by starting the projection at a period prior to the terminal year of the assessment and then comparing how well a standard projection with static *M* and one with dynamic *M* calculations perform relative to the data for the remainder of the timeseries.

One note on the stock-recruit relationship is that for both menhaden and scup, the long-term equilibrium recruitment is much higher than that seen under median recruitment. Investigations into different stock-recruit relationships in Chapter 1 indicated that the Ricker model fit the data better for the species examined in this study (this improvement was modest for a couple of the species), which is why it was the chosen model for this research, however future investigations could explore the stock-recruitment relationship in an ecosystem context in more detail given that it is shown to have an important impact to the populations examined here. This examination could explore the relative importance of adding an environmental variable in to the stock-recruit relationship and contrast that with projections

incorporating dynamic *M* to see the relative importance of these two population dynamics drivers.

Other important assumptions were tested over a shorter time frame, which is more realistic to the current management time frame. The scenarios that add in dynamic natural mortality show a different picture than do the scenarios that use a static natural mortality assumption for the projection period. This dynamic only impacts the prey species, but both scup and menhaden show declines in both *SSB* and landings in these scenarios. This makes sense because the dynamic *M* scenarios are accounting for an additional variable that impacts removals. For these scenarios, the predator populations remain relatively stable, with stable recruitment and declining prey population sizes, leading to an increase in *M* over the projection period for the prey species. This leads to lower landings rates needed to keep the prey populations at the chosen *F* rate.

In both scenarios, dynamic *M* and an average static *M* based on multispecies model output, there is still a progression from the common *M* assumption being used in most single-species assessments. When contrasting the two scenarios that are basing the prey population *M* on the multispecies assessment (either in a static or dynamic way) with a projection that is similar to the current management structure, we see that the standard constant *M* approach produces more optimistic outcomes with regard to projected *SSB* and landings than when the time and age varying *M* is accounted for in the projection (Table 22). This finding shows that accounting for additional dynamics in the ecosystem can add value to the current management process by giving managers a better sense of how the various assumptions being made can bias the output they are

using to set management measures. Time and age varying natural mortality is most likely the correct state of nature, therefore this should be accounted for in the management action being undertaken. This accounting could result in decreasing *F* rates on prey populations, or conversely increasing *F* rates on predator populations.

When looking at the importance of other underlying projection assumptions relative to the importance of natural mortality, namely uncertainty in weight-at-age for the species examined, we see that allowing for stochasticity in weight-at-age does little to change the outcome of the projections relative to the natural mortality or recruitment assumptions. The scenario explored here was to simply add in noise to the projections with regard to weight-at-age, however if there were a systematic change in weight-at-age, such as through a density-dependent effect, this may have produced a more pronounced effect on the population dynamics, such as not allowing the predator populations to achieve such high population sizes under the no-fishing scenarios. For the scenarios examined in this study though, we see that the two main assumptions that need the most thought when constructing projections are natural mortality and recruitment; the other assumption does not produce the effects that recruitment and natural mortality do in the context of information being used to manage important marine species.

How the proxy reference point $F_{40\%}$ changes through time was also examined. As the various populations change, there are subsequent impacts to some of the other populations in the ecosystem, namely the prey species that have predation mortality operating on their populations. If these dynamics are not accounted for, as is the case when a static *F* proxy level is set as a management goal, the expected management

outcomes may not be achieved. This is illustrated by the changing $F_{40\%}$ values through time seen in Figure 23. In the case of menhaden as illustrated in this study, these changes are not large, therefore the management impacts would not be too severe, but if *M* were to change more dramatically, for instance during the period of time when the striped bass fishery was under a moratorium and rebuilt fairly rapidly over a decade, this would be a more significant concern. This is one of the challenges faced by managers as they begin to progress towards an ecosystem based approach to management. Because all of the elements in the ecosystem interact, the attribute of stability in management becomes more elusive, in that to meet management goals, the goals must be changed as the ecosystem changes. This instability could be overcome, however, through simulation work and setting the management measures at levels that will meet management goals over a longer period of time, though not so long a period that large amounts of yield are lost. In other words, projections could be made using a tool like that developed for this study, and the management goal could be set at the most conservative $F_{40\%}$ value as calculated in a medium-term projection period. However, as shown by Collie et al. (2016), if the reference points can be updated periodically (e.g. every five years) this risk-averse approach would not be needed.

When discussing the output from the projections, it is important to note some important caveats. Projections should be interpreted in light of the model assumptions and key aspects of the data. In general, projections of fish stocks are highly uncertain, particularly in the long term (e.g., beyond 5 years), because of all of the assumptions that need to made about the future state, and uncertainties surrounding those assumptions. Although these projections included many major sources of uncertainty,

they importantly do not include structural (model) uncertainty. The results are conditioned on one set of functional forms used to describe population dynamics, selectivity, recruitment, etc., many of which are assumed to be similar to the terminal year of the underlying stock assessment model, or as in the case of the stock-recruitment models used in certain scenarios in this paper, based on functional forms that may or may not reflect the empirical data very well (Brooks and Legault 2016, Weidenmann and Jensen 2016). In addition to the modeling aspects, the fisheries prosecuting the species examined in this project were assumed to continue fishing at their estimated current proportions of total effort, using the estimated current selectivity patterns. As well as the fisheries proceeding in a similar fashion to the terminal year of the assessment, if future recruitment is characterized by runs of large or small year classes, possibly due to environmental or ecological conditions, stock trajectories will likely be affected. Finally, the projections apply the Baranov catch equation to relate *F* and landings using a one-year time step, as in the underlying multispecies stock assessment. The Baranov catch equation implicitly assumes that mortality occurs throughout the year. This assumption is violated when seasonal closures or other fishery management changes like this occur, which would introduce additional and unquantified uncertainty into the projection results. As shown by Legault and Ehrhardt (1997), this bias can be significant depending on the natural mortality rate and the extent of the seasonality in the fishery.

In conclusion, this study has shown that accounting for time and age varying *M* is an important dynamic to capture in projections, because not accounting for it can bias the setting of management measures. Accounting for changing *M* through time

allows for management to set harvest levels that will not lead to unfavorable outcomes, like large stock declines, if appropriate recruitment assumptions are also made. Additionally, this research has highlighted the importance of accounting for *M* in the context of other important assessment assumptions. When looking at uncertainty in weight-at-age, *M* is a more important driver of uncertainty than is uncertainty in weight-at-age. Therefore, accounting for time-varying *M* in projections adds value for managers when setting future management goals by providing them information on how management and population changes in other populations will impact the management of their target species, and allows them an opportunity to better inform their assessment of risk to the population in their management goals over time. This work highlights an ability to run a projection, calculate a management metric such as an SPR based fishing mortality rate, and base the final management metric on a period of time in the projection period that will allow for a successful management outcome over time. The work also indicates that an approach that accounts for this additional uncertainty, even if it is only to use the time and age varying natural mortality produced by a multispecies stock assessment in a more standard static way (i.e. the averaged *M* that was used in a static fashion), will add realism and could allow for better outcomes from the selected management measures if there is empirical information available to parameterize the model adequately and if the most important species in the dynamics of the target population are captured by the model. Despite the value achieved by accounting for time and age varying *M*, recruitment was shown to be as important as *M* by way of uncertainties in the projections, so this is an area that also needs additional research. This research could focus on developing good stock-

recruit models that account for environmental variables, or could focus on creating techniques for setting management measures that are robust to variable recruitment through time.

Other areas of future research include more examination of the population dynamics of weakfish. Weakfish have been modeled using a Bayesian approach which allows for time varying *M* (ASMFC 2016). One of the reasons for this time varying *M* may be that weakfish are also an important prey item in the ecosystem. Food-habit databases could be examined to determine if weakfish show up as an important prey item for predators, and this could be the signal that points to a missing dynamic in weakfish population models. Using a tool like that used for this study, weakfish could be modeled to be both a predator and a prey species to see if this changes the characteristics of the population dynamics seen in this study, or if it shows results analogous to the Bayesian stock assessment model results with regard to time-varying *M*.

An additional area that was shown to be an important influence on the projection performance is recruitment. Recruitment assumptions were shown to have important impacts to projection performance depending on the length of time used in the projections. This is a general truism for many management projections (Brooks and Legault 2016, Weidenmann and Jensen 2016), but investigating influences that could lead to better predictive power for recruitment such as identifying important environmental covariates influencing a species recruitment success or by adjusting the projection and stock assessment update schedule to eliminate the influence of

recruitment variability will lead to better performance for projections such as those made in this study.

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TABLES

Table 1: Fishing mortality level assumption for the various projections by species ($F_{40\%}$).

Species	Menhaden	Striped Bass	Bluefish	Weakfish	Scup
$F_{40\%}$	0.50	0.11	0.17	0.25	0.21

Table 2: Natural mortality level assumption for the various species from the single-species benchmark assessments.

Age	Menhaden	Striped Bass	Bluefish	Weakfish	Scup
1	0.82	1.13	0.2	0.43	0.2
2	0.65	0.68	0.2	0.43	0.2
3	0.57	0.45	0.2	0.43	0.2
4	0.52	0.33	0.2	0.43	0.2
5	0.5	0.25	0.2	0.43	0.2
6	0.48	0.19	0.2	0.43	0.2
7		0.15			0.2
8		0.15			
9		0.15			
10		0.15			
11		0.15			
12		0.15			
13		0.15			

Table 3: Average M-at-age used for the time invariant natural mortality projection runs.

Age	Menhaden	Striped Bass	Bluefish	Weakfish	Scup
1	0.88	1.13	0.2	0.43	0.90
2	0.71	0.68	0.2	0.43	0.33
3	0.58	0.45	0.2	0.43	0.20
4	0.49	0.33	0.2	0.43	0.14
5	0.43	0.25	0.2	0.43	0.12
6	0.39	0.19	0.2	0.43	0.11
7		0.15			0.13
8		0.15			
9		0.15			
10		0.15			
11		0.15			
12		0.15			
13		0.15			

Table 4: Projected spawning stock biomass, recruitment, fishing mortality, and landings for menhaden under $F_{40\%}$ scenario and static M.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	585	4078.72	0.50	412
30	500	4078.72	0.50	303
31	420	4078.72	0.50	254
32	382	4078.72	0.50	235
33	364	4078.72	0.50	225
34	356	4078.72	0.50	223
35	346	4078.72	0.50	218
36	342	4078.72	0.50	217
37	344	4091.36	0.50	219
38	346	4078.72	0.50	221

Table 5: Projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under $F_{40\%}$ scenario and static M.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	139	103.72	0.11	15
30	129	103.72	0.11	14
31	123	103.72	0.11	14
32	117	103.72	0.11	15
33	124	100.92	0.11	15
34	130	103.72	0.11	15
35	131	103.72	0.11	15
36	131	103.72	0.11	16
37	133	103.72	0.11	16
38	133	103.72	0.11	17

Table 6: Projected spawning stock biomass, recruitment, fishing mortality, and landings for bluefish under $F_{40\%}$ scenario and static M.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	113	20.68	0.17	13
30	112	20.87	0.17	13
31	113	21.06	0.17	13
32	115	20.68	0.17	14
33	116	20.68	0.17	14
34	118	20.68	0.17	14
35	121	21.06	0.17	14
36	122	20.68	0.17	14
37	123	20.68	0.17	14
38	123	20.68	0.17	14

Table 7: Projected spawning stock biomass, recruitment, fishing mortality, and landings for weakfish under $F_{40\%}$ scenario and static M.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	12	27.68	0.25	3
30	13	27.68	0.25	3
31	15	27.68	0.25	4
32	17	31.40	0.25	4
33	19	27.68	0.25	5
34	20	27.68	0.25	5
35	21	27.68	0.25	5
36	21	27.68	0.25	5
37	21	27.68	0.25	5
38	22	27.68	0.25	5

Table 8: Projected spawning stock biomass, recruitment, fishing mortality, and landings for scup under $F_{40\%}$ scenario and static M.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	154	105.19	0.21	15
30	148	105.19	0.21	12
31	142	105.19	0.21	11
32	136	105.19	0.21	10
33	131	105.19	0.21	11
34	129	105.19	0.21	10
35	124	105.19	0.21	10
36	121	105.19	0.21	11
37	119	105.19	0.21	10
38	117	105.19	0.21	10

Table 9: Projected spawning stock biomass, recruitment, fishing mortality, and landings for menhaden under $F_{40\%}$ scenario and dynamic M.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	573	4078.72	0.50	405
30	474	4078.72	0.50	285
31	372	4078.72	0.50	227
32	316	4078.72	0.50	197
33	286	4078.72	0.50	184
34	271	4078.72	0.50	177
35	258	4078.72	0.50	168
36	246	4078.72	0.50	161
37	238	4091.36	0.50	158
38	238	4078.72	0.50	158

Table 10: Projected spawning stock biomass, recruitment, fishing mortality, and landings for scup under $F_{40\%}$ scenario and dynamic *M*.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	154	105.19	0.21	15
30	147	105.19	0.21	11
31	134	105.19	0.21	8
32	121	105.19	0.21	6
33	111	105.19	0.21	5
34	101	105.19	0.21	5
35	92	105.19	0.21	4
36	84	105.19	0.21	4
37	77	105.19	0.21	4
38	71	105.19	0.21	3

Table 11: Projected natural mortality at-age for menhaden under $F_{40\%}$ scenario and dynamic *M*.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
29	0.88	0.76	0.64	0.52	0.51	0.47
30	0.92	0.81	0.69	0.56	0.55	0.50
31	0.95	0.83	0.72	0.58	0.57	0.52
32	0.97	0.84	0.72	0.57	0.56	0.52
33	1.00	0.85	0.72	0.58	0.57	0.52
34	1.02	0.87	0.74	0.59	0.58	0.53
35	1.04	0.89	0.75	0.60	0.59	0.54
36	1.05	0.90	0.76	0.60	0.59	0.54
37	1.05	0.90	0.76	0.60	0.59	0.54
38	1.06	0.91	0.77	0.61	0.60	0.55

Table 12: Projected natural mortality at-age for scup under $F_{40\%}$ scenario and dynamic *M* and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
29	1.66	0.35	0.31	0.18	0.15	0.12	0.11
30	1.86	0.39	0.34	0.19	0.16	0.13	0.11
31	1.98	0.42	0.36	0.20	0.16	0.13	0.11
32	1.99	0.42	0.36	0.21	0.17	0.13	0.11
33	2.03	0.43	0.37	0.21	0.17	0.14	0.11
34	2.10	0.42	0.37	0.21	0.17	0.13	0.11
35	2.15	0.42	0.36	0.20	0.16	0.13	0.11
36	2.17	0.41	0.35	0.20	0.16	0.13	0.11
37	2.21	0.41	0.35	0.20	0.16	0.13	0.11

Table 13: Projected spawning stock biomass, recruitment, fishing mortality, and landings for menhaden under $F_{40\%}$ scenario, static M, and variable weight.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	577	4078.72	0.50	406
30	497	4078.72	0.50	302
31	423	4078.72	0.50	254
32	383	4078.72	0.50	234
33	363	4078.72	0.50	224
34	352	4078.72	0.50	221
35	345	4078.72	0.50	216
36	342	4078.72	0.50	214
37	341	4091.36	0.50	216
38	346	4078.72	0.50	220

Table 14: Projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under $F_{40\%}$ scenario, static M, and variable weight.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	141	103.72	0.11	15
30	130	103.72	0.11	14
31	123	103.72	0.11	14
32	116	103.72	0.11	15
33	123	100.92	0.11	15
34	129	103.72	0.11	15
35	130	103.72	0.11	15
36	133	103.72	0.11	16
37	133	103.72	0.11	17
38	134	103.72	0.11	17

Table 15: Projected spawning stock biomass, recruitment, fishing mortality, and landings for bluefish under $F_{40\%}$ scenario, static M, and variable weight.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	114	20.68	0.17	13
30	112	20.87	0.17	13
31	114	21.06	0.17	13
32	114	20.68	0.17	14
33	116	20.68	0.17	14
34	118	20.68	0.17	14
35	120	21.06	0.17	14
36	121	20.68	0.17	14
37	123	20.68	0.17	14
38	124	20.68	0.17	14

Table 16: Projected spawning stock biomass, recruitment, fishing mortality, and landings for weakfish under $F_{40\%}$ scenario, static *M*, and variable weight.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	12	27.68	0.25	3
30	13	27.68	0.25	3
31	15	27.68	0.25	3
32	17	31.40	0.25	4
33	18	27.68	0.25	4
34	19	27.68	0.25	4
35	20	27.68	0.25	5
36	21	27.68	0.25	5
37	21	27.68	0.25	5
38	21	27.68	0.25	5

Table 17: Projected spawning stock biomass, recruitment, fishing mortality, and landings for scup under $F_{40\%}$ scenario, static *M*, and variable weight.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	154	105.19	0.21	15
30	145	105.19	0.21	12
31	146	105.19	0.21	11
32	132	105.19	0.21	10
33	128	105.19	0.21	10
34	123	105.19	0.21	10
35	124	105.19	0.21	10
36	120	105.19	0.21	11
37	115	105.19	0.21	11
38	112	105.19	0.21	10

Table 18: Projected spawning stock biomass, recruitment, fishing mortality, and landings for menhaden under $F_{40\%}$ scenario and benchmark *M* assumption.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	597	4078.72	0.50	419
30	527	4078.72	0.50	322
31	449	4078.72	0.50	273
32	411	4078.72	0.50	254
33	394	4078.72	0.50	244
34	387	4078.72	0.50	243
35	378	4078.72	0.50	238
36	374	4078.72	0.50	237
37	377	4091.36	0.50	239
38	378	4078.72	0.50	242

Table 19: Projected spawning stock biomass, recruitment, fishing mortality, and landings for scup under $F_{40\%}$ scenario and benchmark *M* assumption.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	149	105.19	0.21	15
30	136	105.19	0.21	13
31	136	105.19	0.21	14
32	139	105.19	0.21	17
33	142	105.19	0.21	19
34	147	105.19	0.21	19
35	150	105.19	0.21	20
36	153	105.19	0.21	21
37	157	105.19	0.21	20
38	158	105.19	0.21	20

Table 20: Weight-at-age variance table for menhaden.

Yr	SSB (1000 mt)		Landings (1000 mt)	
	5th	95th	5th	95th
1	453	759	304	549
1 without weight uncertainty	486	703	338	504
2	387	655	231	422
2 without weight uncertainty	417	624	250	411
3	337	582	199	370
3 without weight uncertainty	350	557	207	360
4	301	541	179	354
4 without weight uncertainty	316	519	191	346
5	285	512	173	338
5 without weight uncertainty	295	503	180	335

Table 21: Time-varying $F_{40\%}$ for menhaden.

Yr	$F_{40\%}$
29	0.740088
30	0.740929
31	0.742003
32	0.743083
33	0.744771
34	0.746955
35	0.749882
36	0.75212
37	0.754279
38	0.756211
39	0.758388
40	0.760508
41	0.762099
42	0.76261
43	0.764059
44	0.764691
45	0.765629
46	0.766445
47	0.766935
48	0.767477
49	0.768657
50	0.768086
51	0.768278
52	0.769023
53	0.769115
54	0.769353
55	0.769519
56	0.768829
57	0.769686
58	0.769949
59	0.769846
60	0.770216
61	0.769564
62	0.770707
63	0.770535

Table 22: Table comparing results in SSB levels and landings across the four scenarios tested for menhaden.

Scenario	SSB (1000 mt)	Landings (1000 mt)
Dynamic M	3,272	2,120
Static M	3,985	2,527
Variable Weight	3,969	2,507
Benchmark assessment assumed M	4,272	2,711

FIGURES

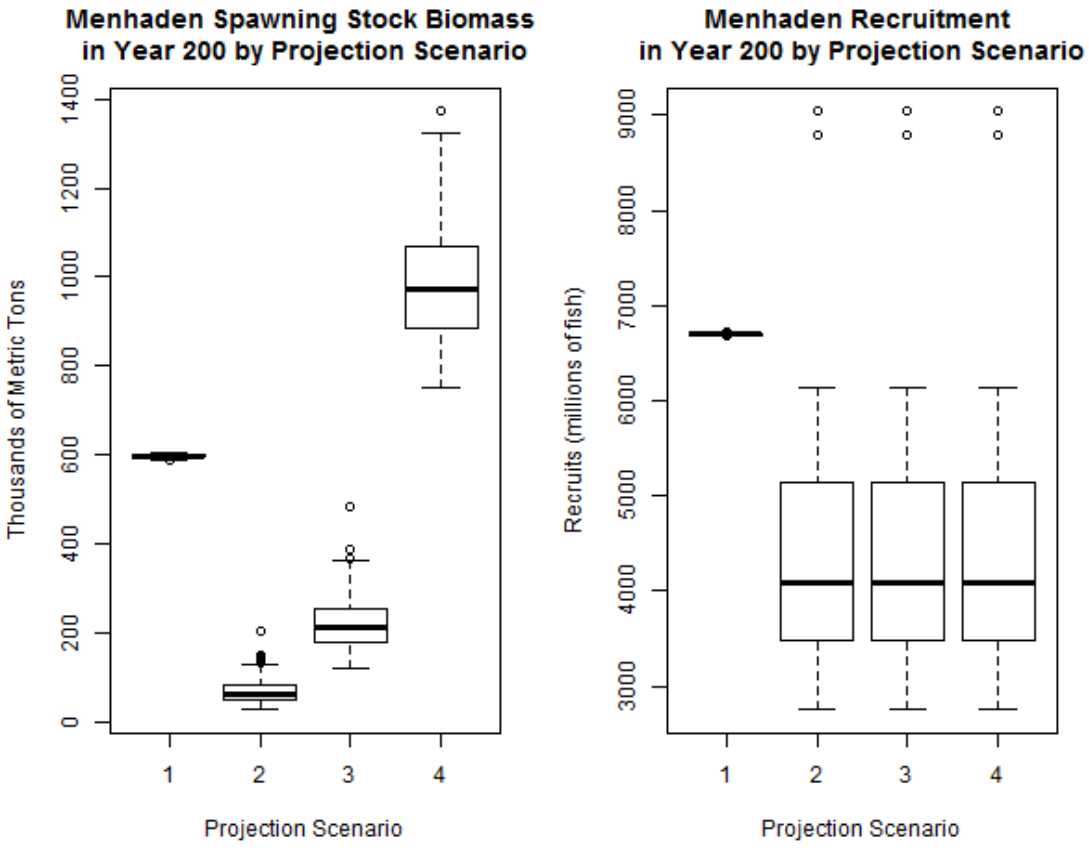

Fig. 1: Spawning stock biomass and recruitment for menhaden from year 200 of the projection. Projection scenario 1 is $F = 0$, stock recruitment relationship, and dynamic M. Projection scenario 2 is $F = 0$, median recruitment, and dynamic M. Projection scenario 3 is $F = F_{40\%}$, median recruitment, and dynamic M. Projection scenario 4 is $F = 0$, median recruitment, and static M.

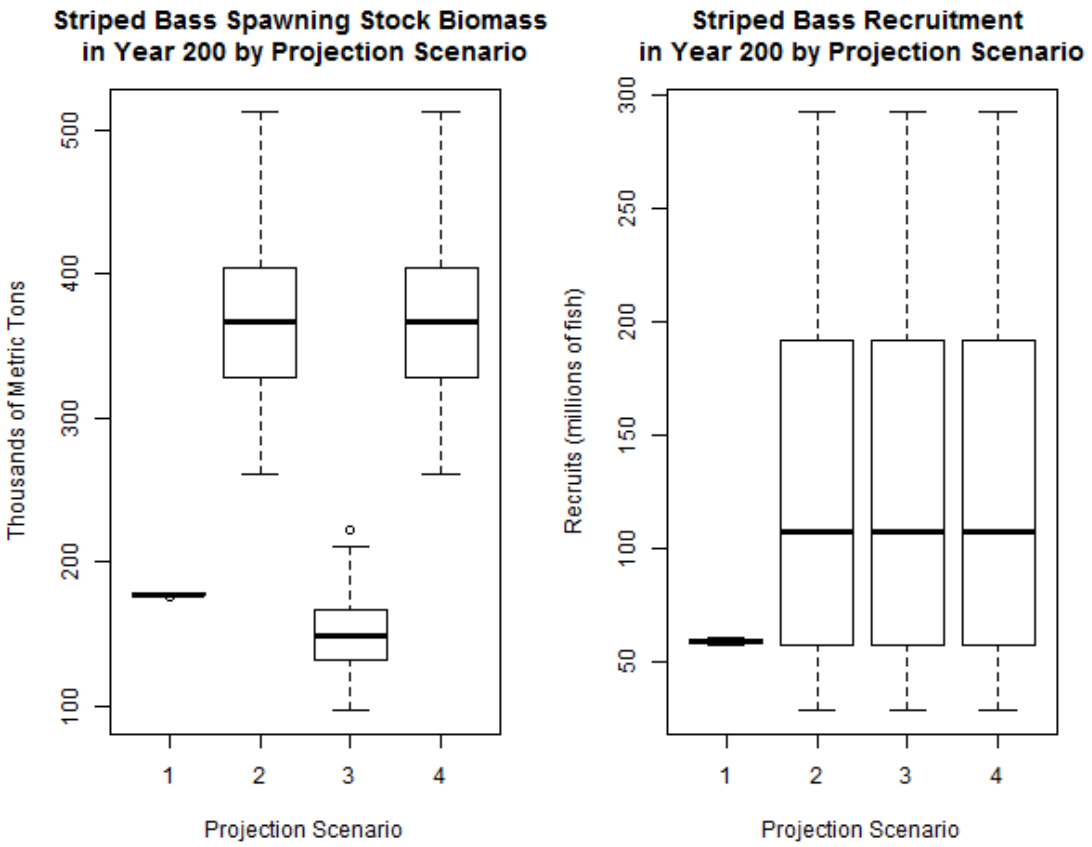

Fig. 2: Spawning stock biomass and recruitment for striped bass from year 200 of the projection. Projection scenario 1 is $F = 0$, stock recruitment relationship, and dynamic M. Projection scenario 2 is $F = 0$, median recruitment, and dynamic M. Projection scenario 3 is $F = F_{40\%}$, median recruitment, and dynamic M. Projection scenario 4 is $F = 0$, median recruitment, and static M.

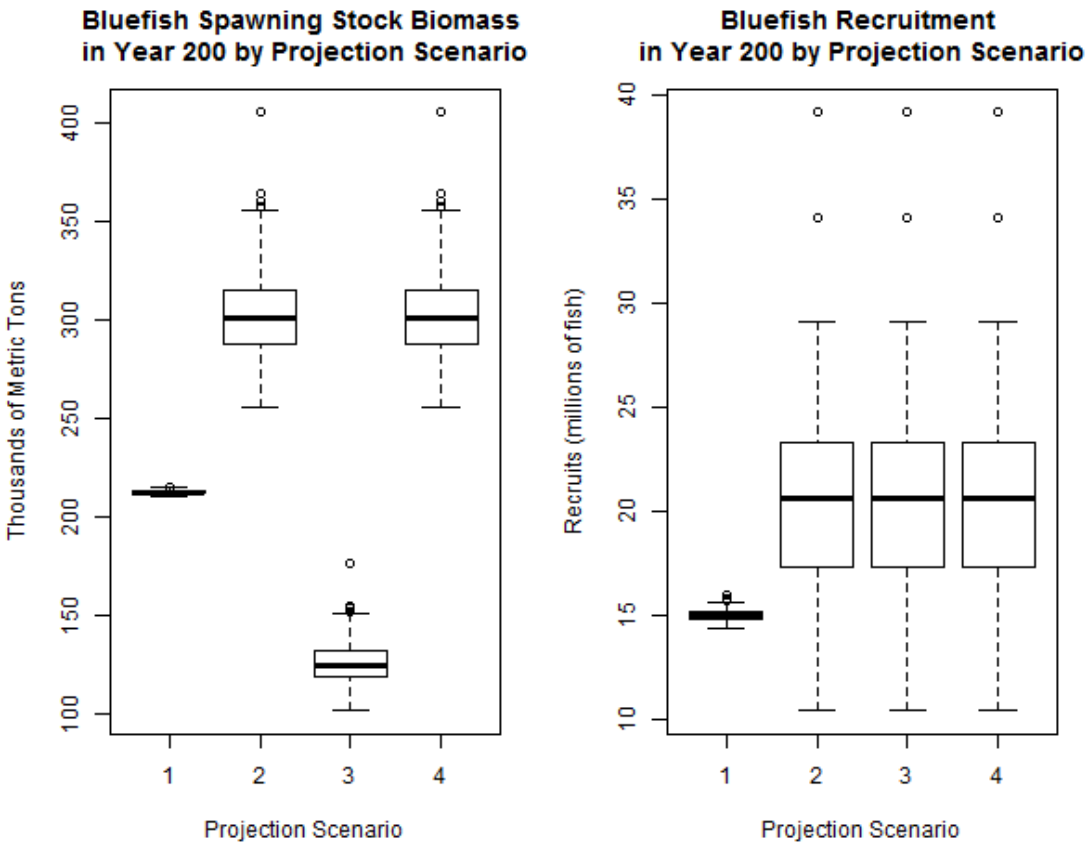

Fig. 3: Spawning stock biomass and recruitment for bluefish from year 200 of the projection. Projection scenario 1 is $F = 0$, stock recruitment relationship, and dynamic M. Projection scenario 2 is $F = 0$, median recruitment, and dynamic M. Projection scenario 3 is $F = F_{40\%}$, median recruitment, and dynamic M. Projection scenario 4 is $F = 0$, median recruitment, and static M.

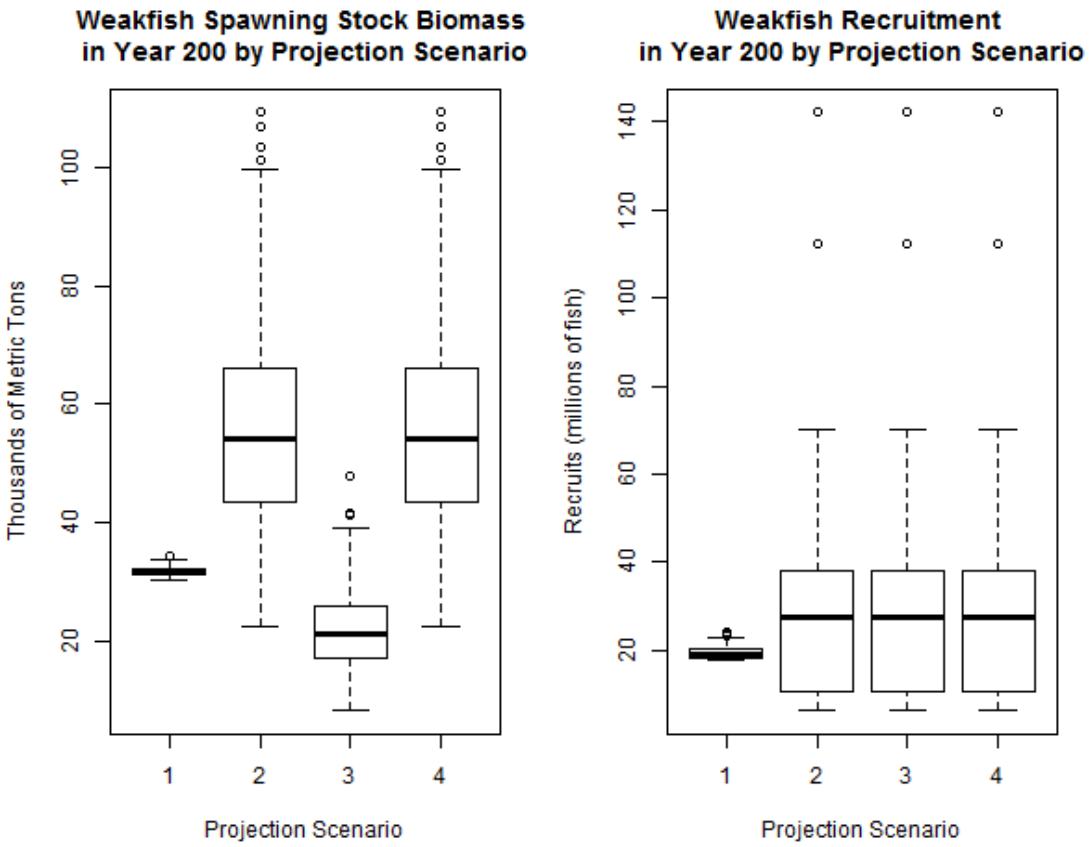

Fig. 4: Spawning stock biomass and recruitment for weakfish from year 200 of the projection. Projection scenario 1 is $F = 0$, stock recruitment relationship, and dynamic M. Projection scenario 2 is $F = 0$, median recruitment, and dynamic M. Projection scenario 3 is $F = F_{40\%}$, median recruitment, and dynamic M. Projection scenario 4 is $F = 0$, median recruitment, and static M.

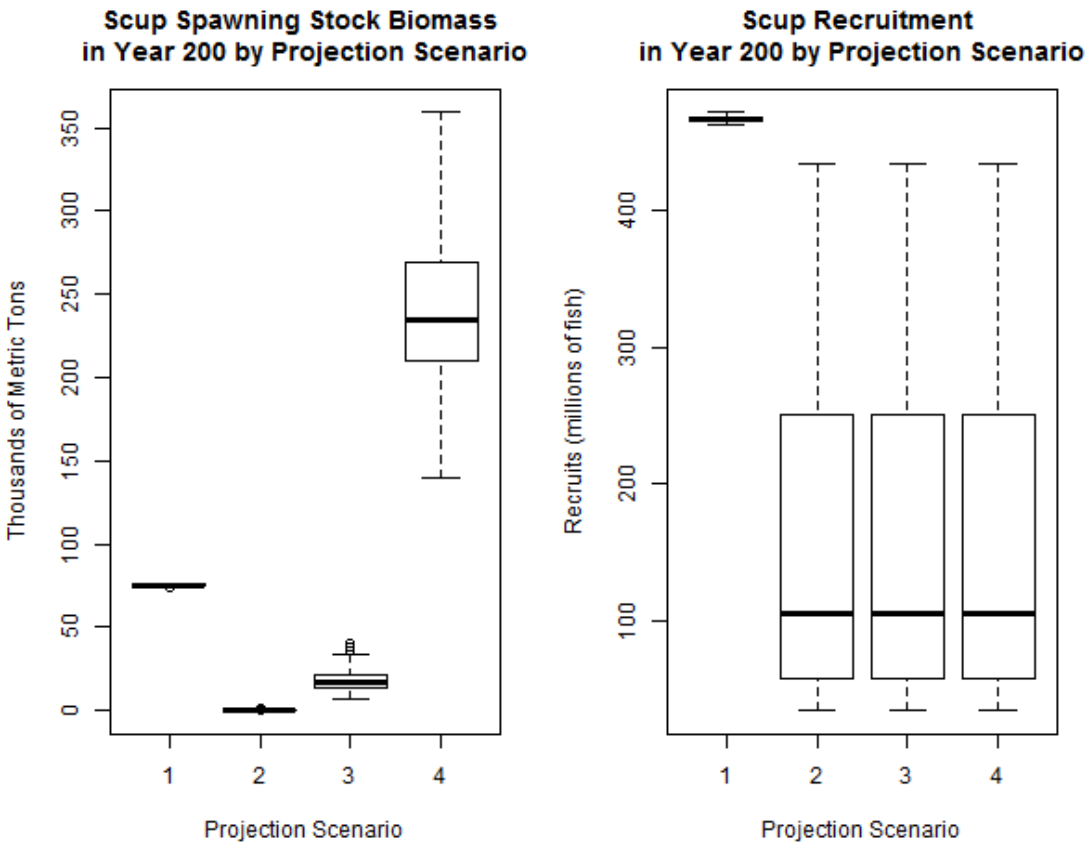

Fig. 5: Spawning stock biomass and recruitment for scup from year 200 of the projection. Projection scenario 1 is $F = 0$, stock recruitment relationship, and dynamic M. Projection scenario 2 is $F = 0$, median recruitment, and dynamic M. Projection scenario 3 is $F = F_{40\%}$, median recruitment, and dynamic M. Projection scenario 4 is $F = 0$, median recruitment, and static M.

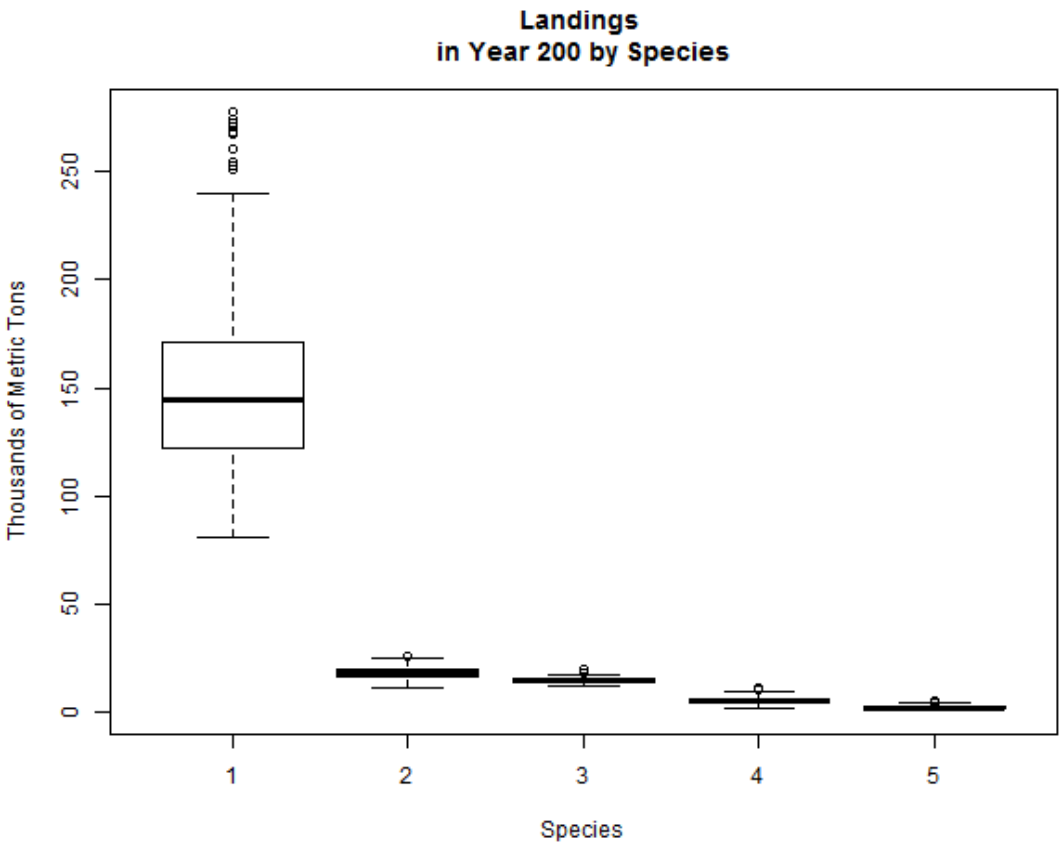

Fig. 6: Landings from year 200 of the projection for Projection Scenario 3 ($F = F_{40\%}$, median recruitment, and dynamic M). Species 1 = menhaden, Species 2 = striped bass, Species 3 = bluefish, Species 4 = weakfish, and Species 5 = scup.

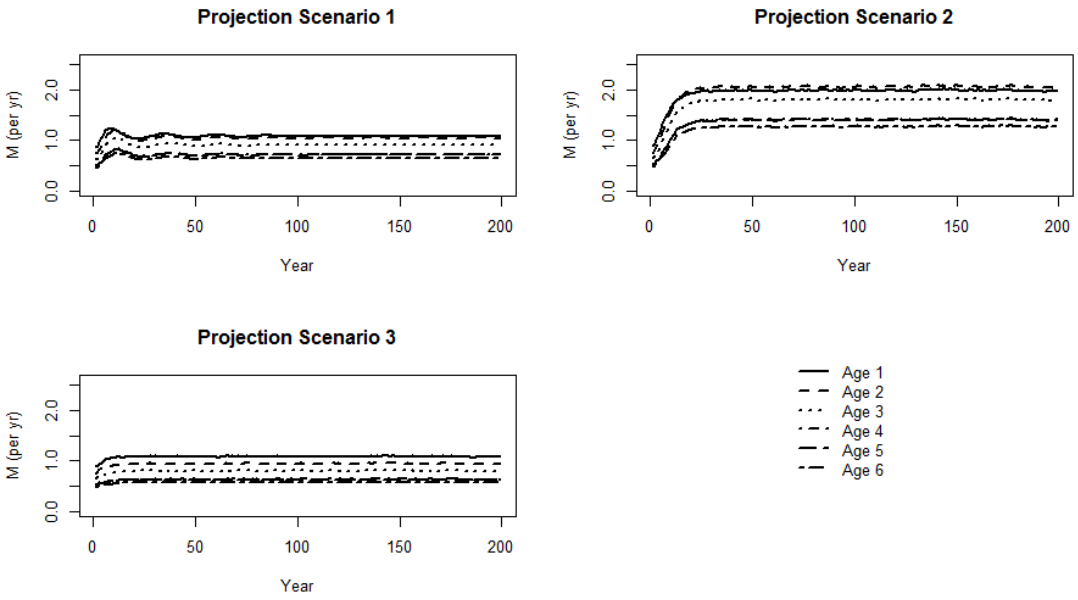

Fig. 7: Projected *M*-at-age for menhaden across the three different projection scenarios with dynamic *M*. Projection scenario 1 is $F = 0$, stock recruitment relationship, and dynamic *M*. Projection scenario 2 is $F = 0$, median recruitment, and dynamic *M*. Projection scenario 3 is $F = F_{40\%}$, median recruitment, and dynamic *M*.

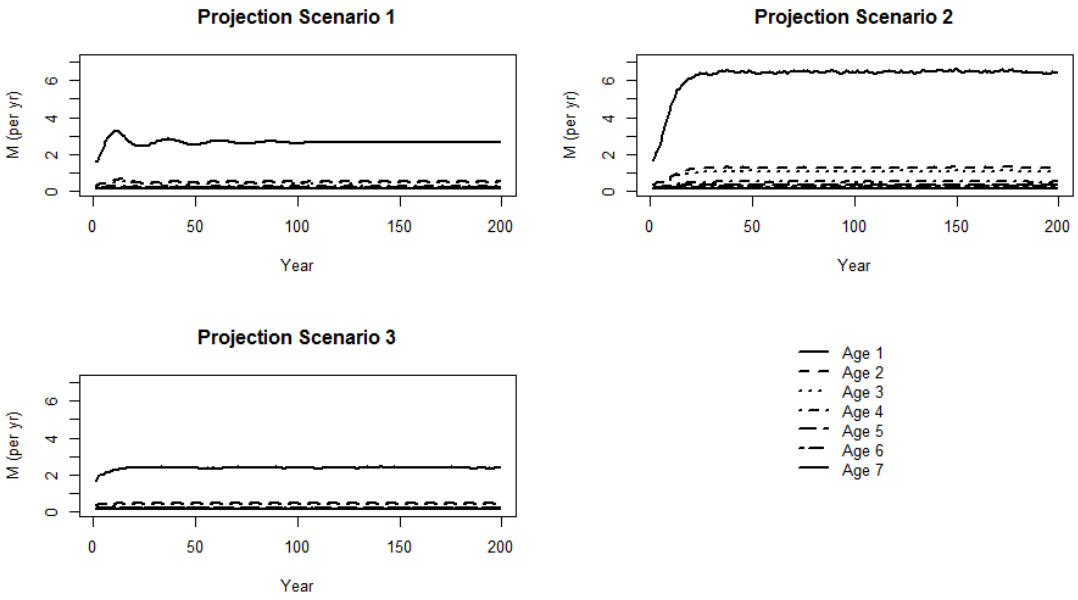

Fig. 8: Projected *M*-at-age for scup across the three different projection scenarios with dynamic *M*. Projection scenario 1 is $F = 0$, stock recruitment relationship, and dynamic *M*. Projection scenario 2 is $F = 0$, median recruitment, and dynamic *M*. Projection scenario 3 is $F = F_{40\%}$, median recruitment, and dynamic *M*.

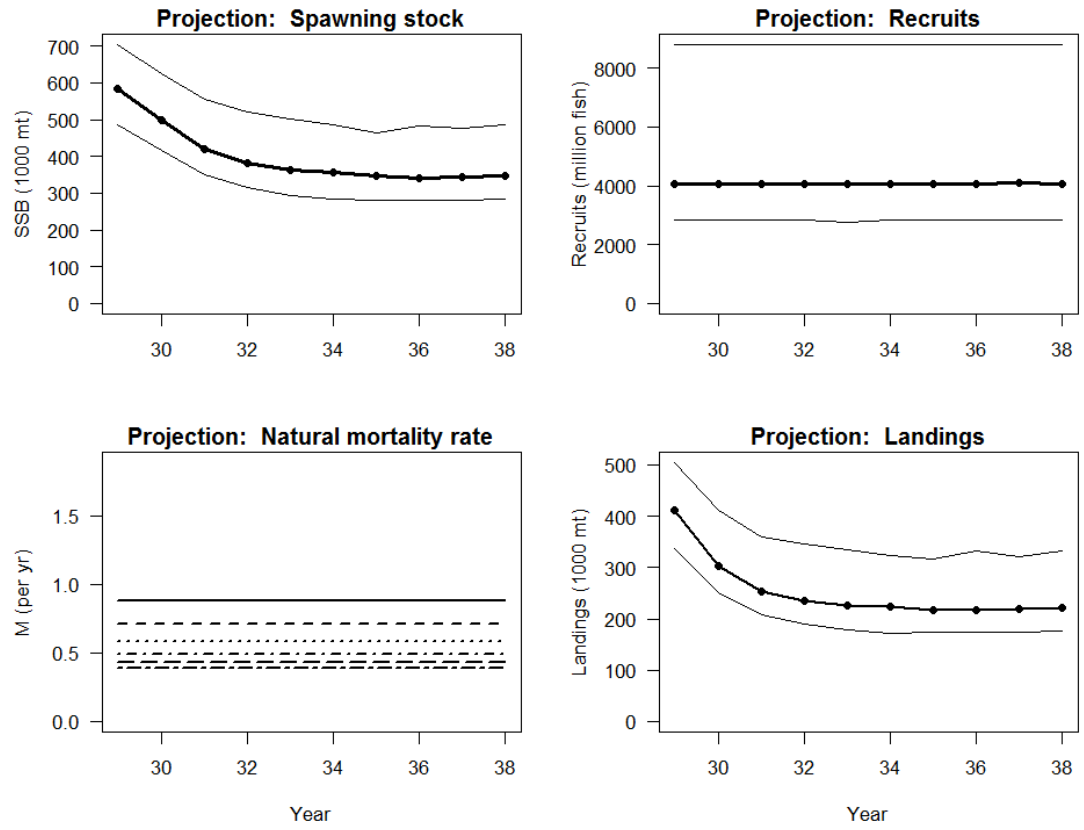

Fig. 9: Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for menhaden under $F_{40\%}$ scenario and static M. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

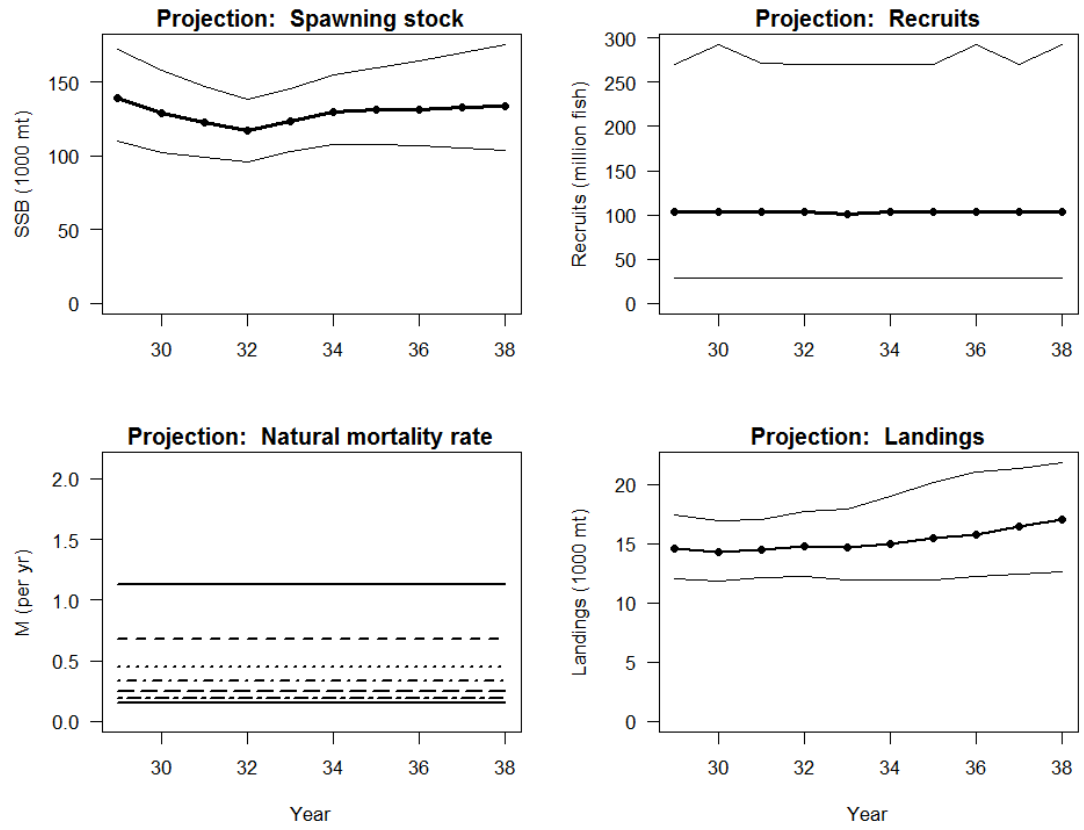

Fig. 10: Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under $F_{40\%}$ scenario and static M. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

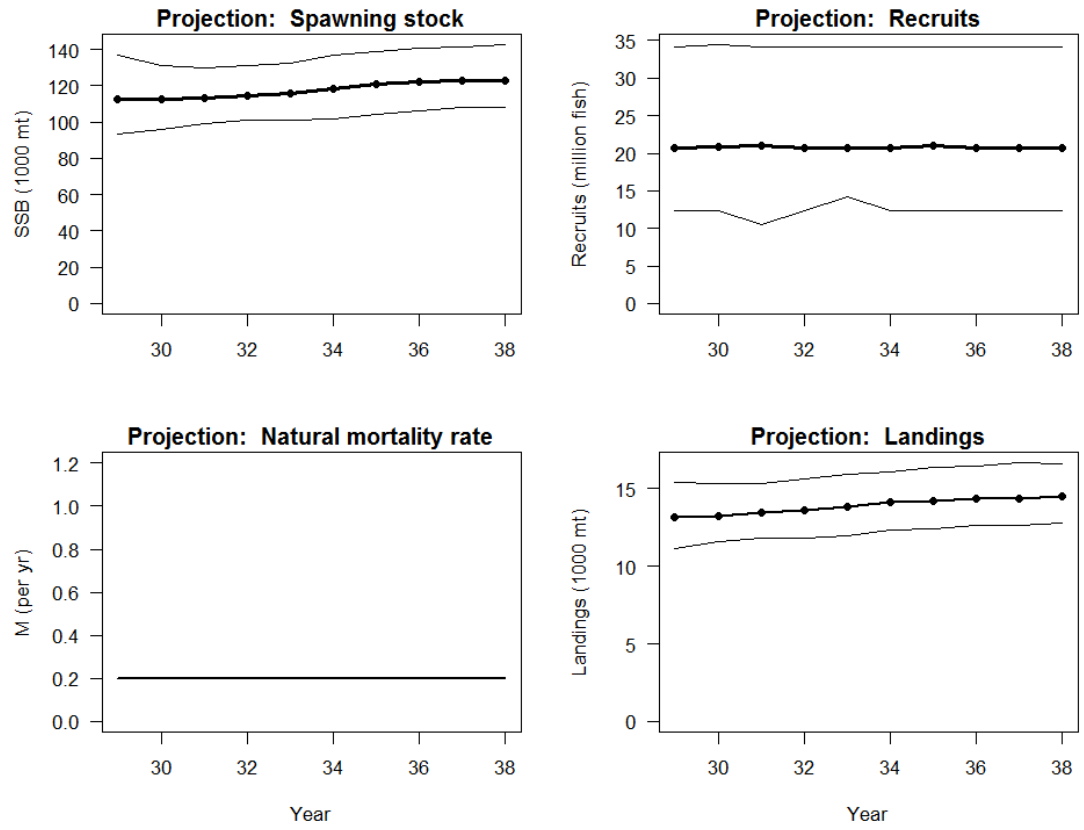

Fig. 11: Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for bluefish under $F_{40\%}$ scenario and static M. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

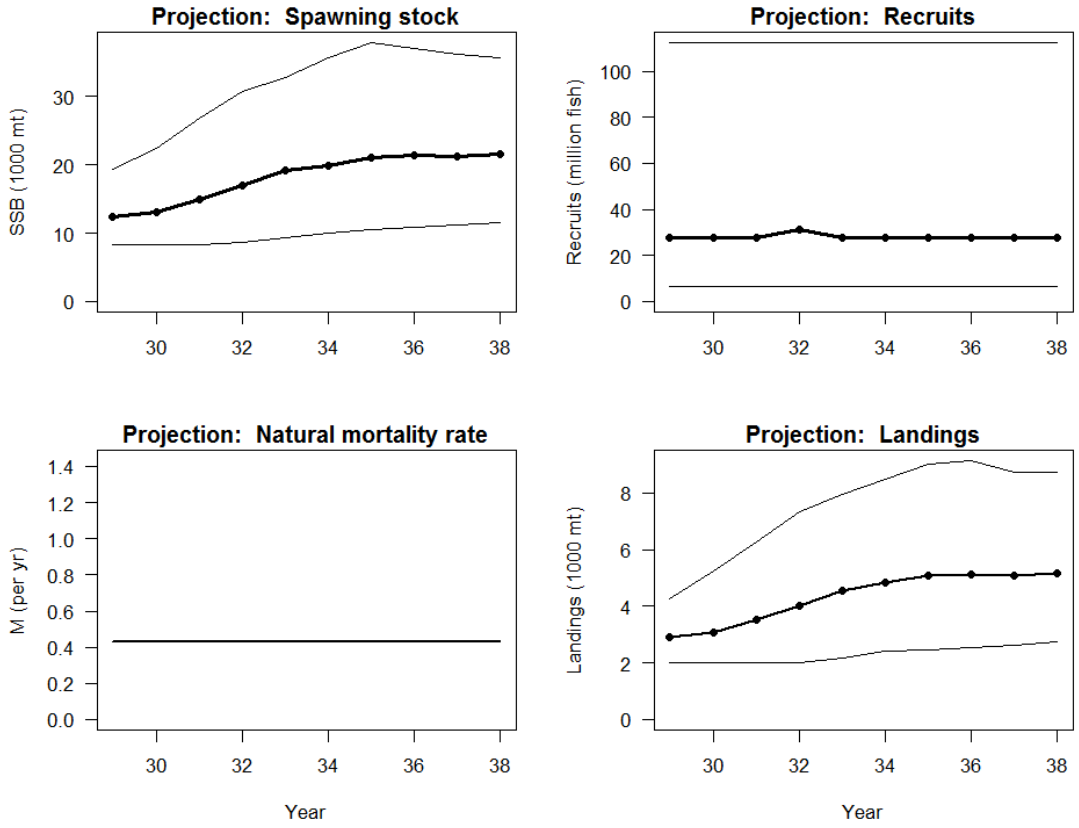

Fig. 12: Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for weakfish under $F_{40\%}$ scenario and static M. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

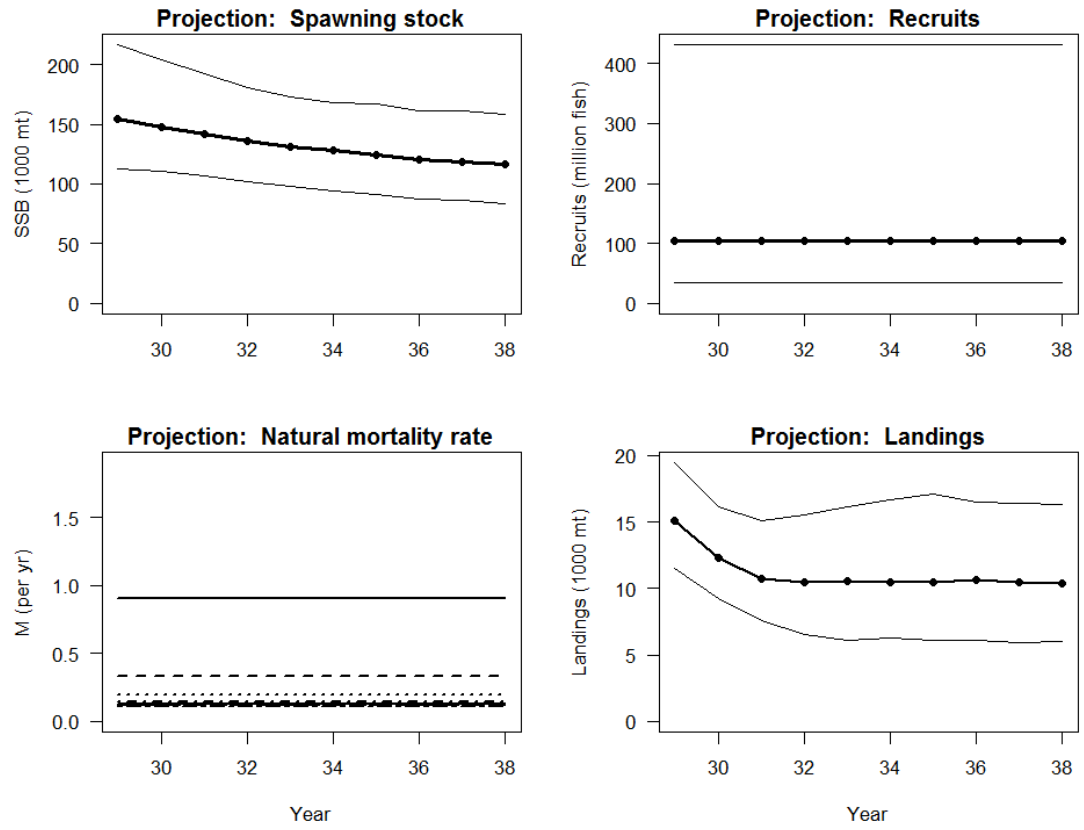

Fig. 13: Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for scup under $F_{40\%}$ scenario and static M. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

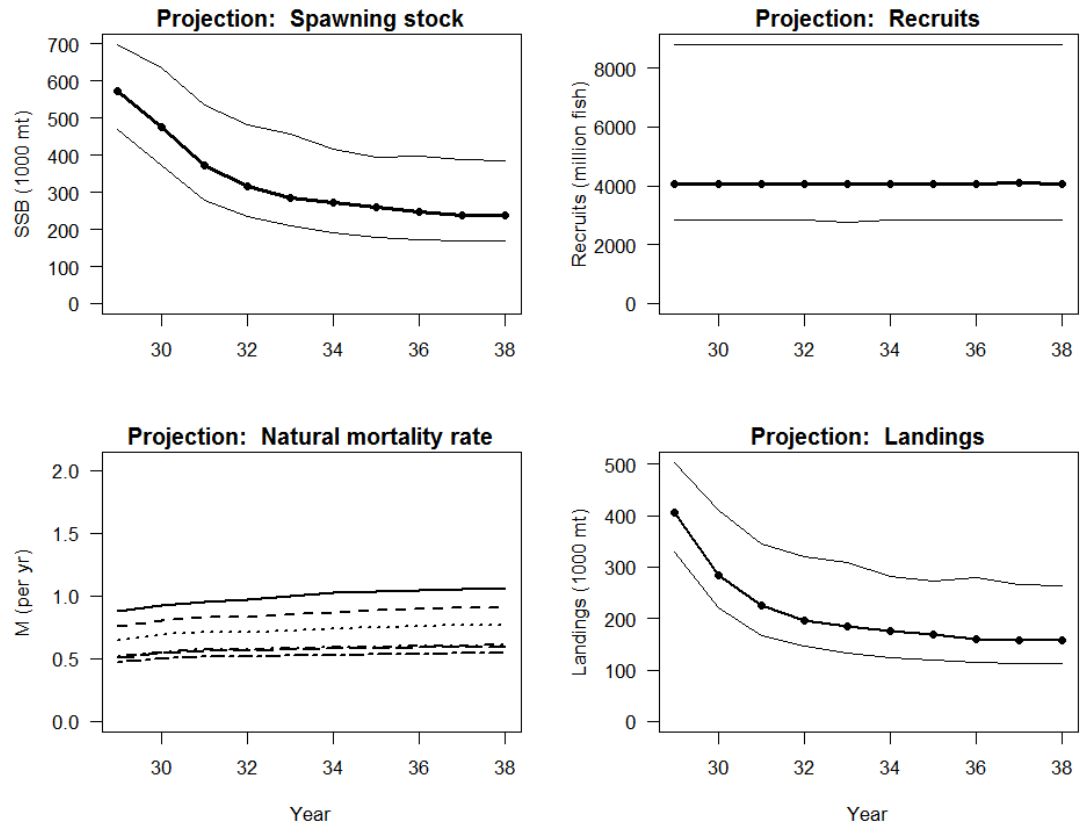

Fig. 14: Projected spawning stock biomass, recruitment, fishing mortality at-age, and landings for menhaden under $F_{40\%}$ scenario and dynamic M. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

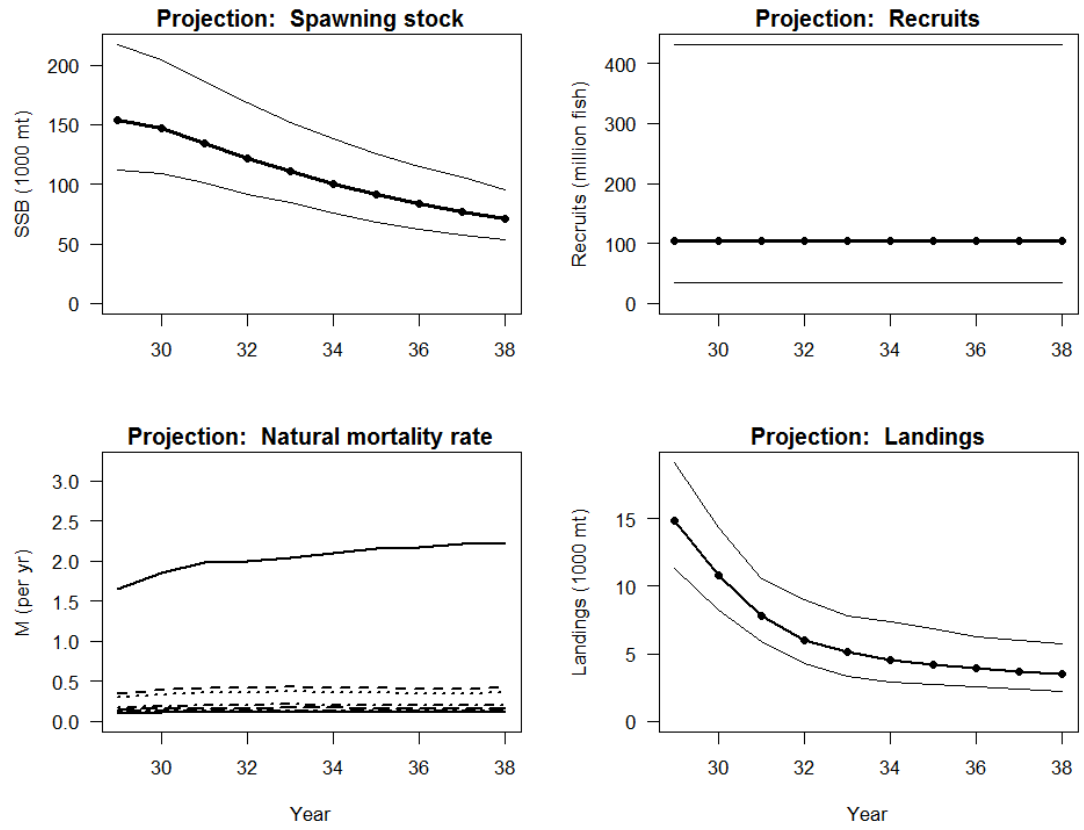

Fig. 15: Projected spawning stock biomass, recruitment, fishing mortality, and landings for scup under $F_{40\%}$ scenario and dynamic M. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

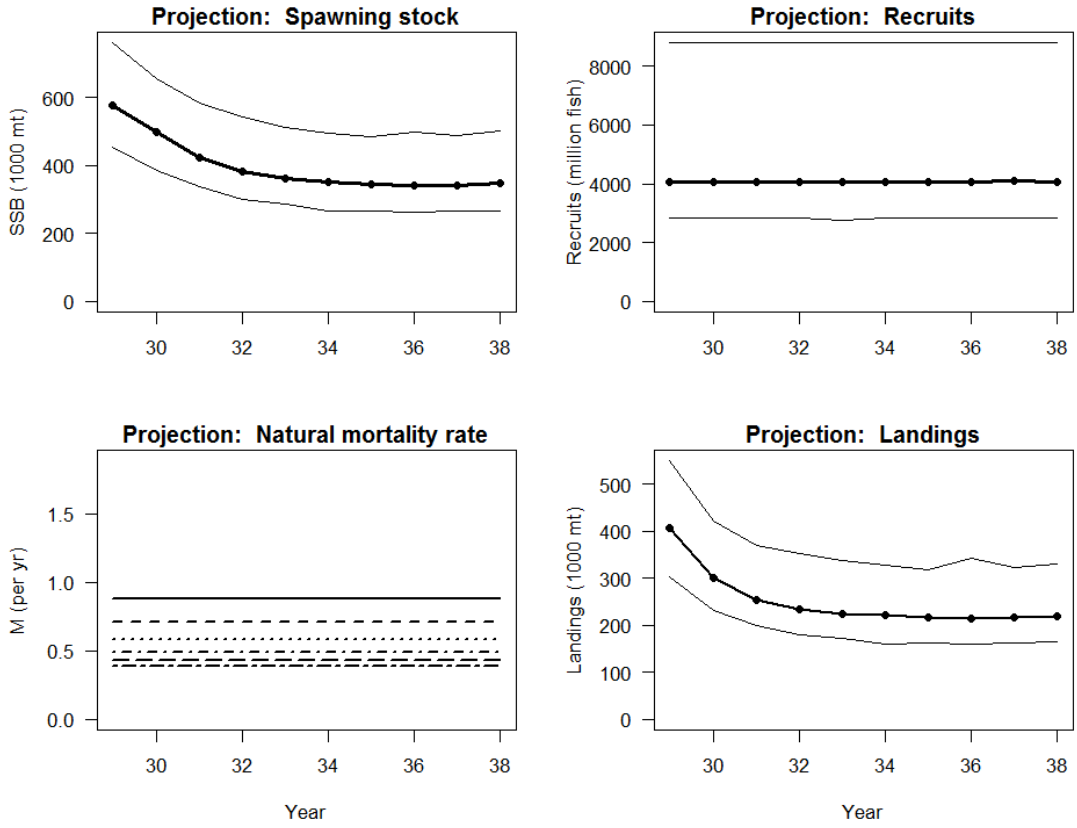

Fig. 16: Projected spawning stock biomass, recruitment, natural mortality, and landings for menhaden under $F_{40\%}$ scenario and static *M,* and adding in uncertainty to weight-at-age. For the *SSB*, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

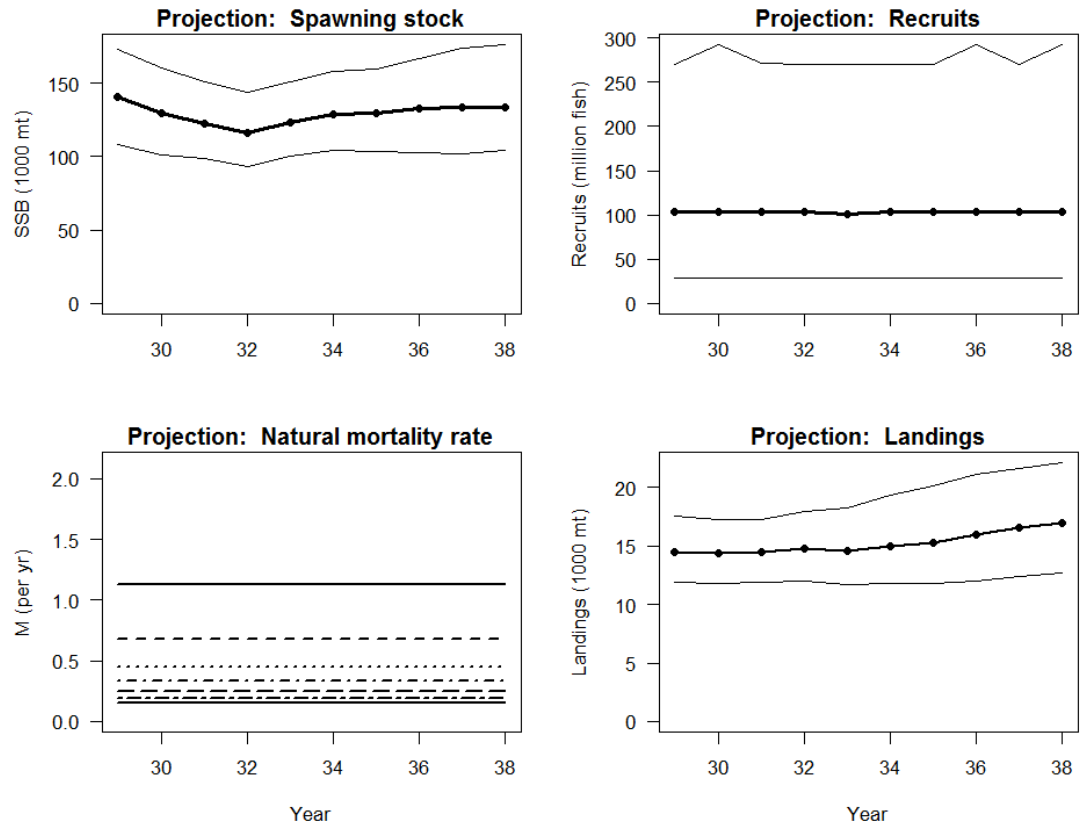

Fig. 17: Projected spawning stock biomass, recruitment, natural mortality, and landings for striped bass under $F_{40\%}$ scenario and static *M,* and adding in uncertainty to weight-at-age. For the *SSB*, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

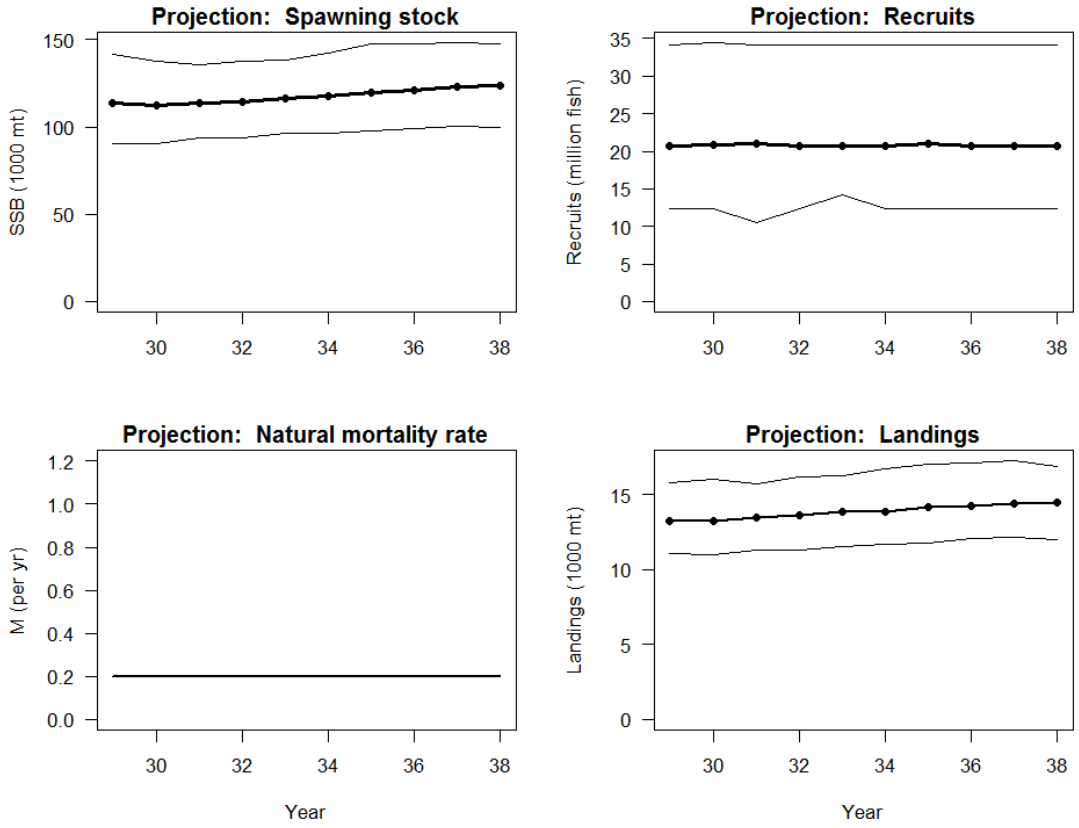

Fig. 18: Projected spawning stock biomass, recruitment, natural mortality, and landings for bluefish under $F_{40\%}$ scenario and static *M,* and adding in uncertainty to weight-at-age. For the *SSB*, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

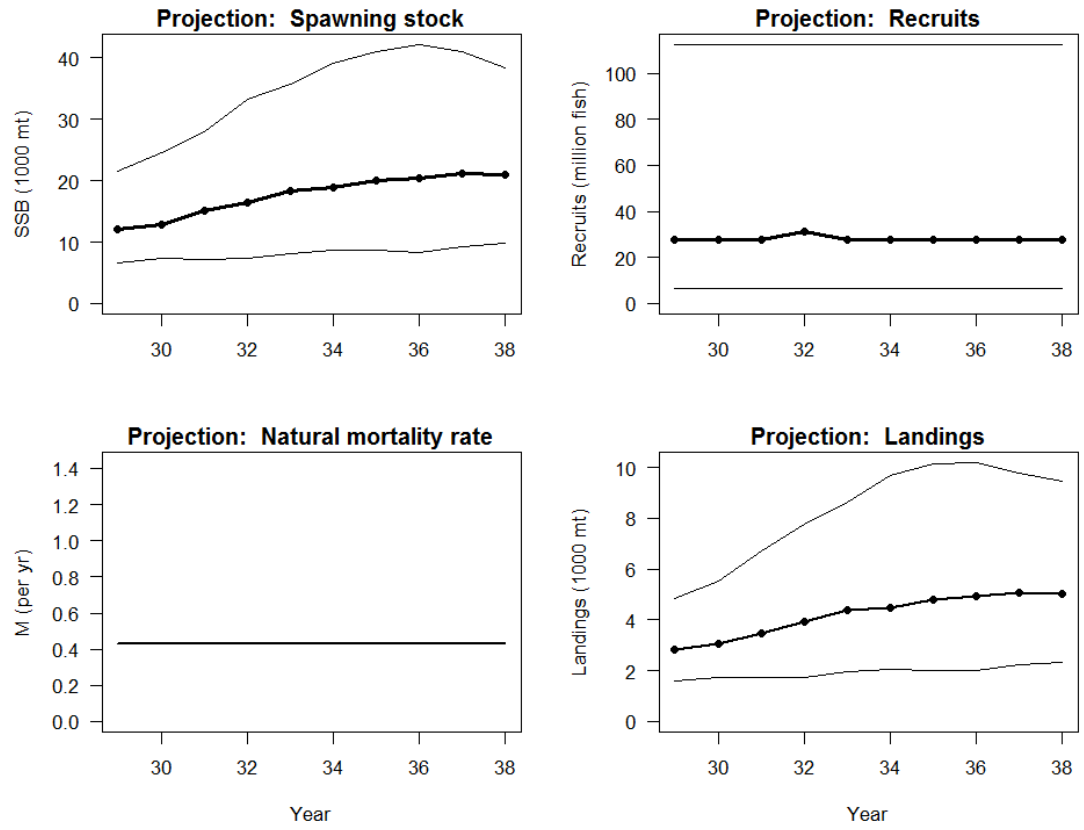

Fig. 19: Projected spawning stock biomass, recruitment, natural mortality, and landings for weakfish under $F_{40\%}$ scenario and static *M,* and adding in uncertainty to weight-at-age. For the *SSB*, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

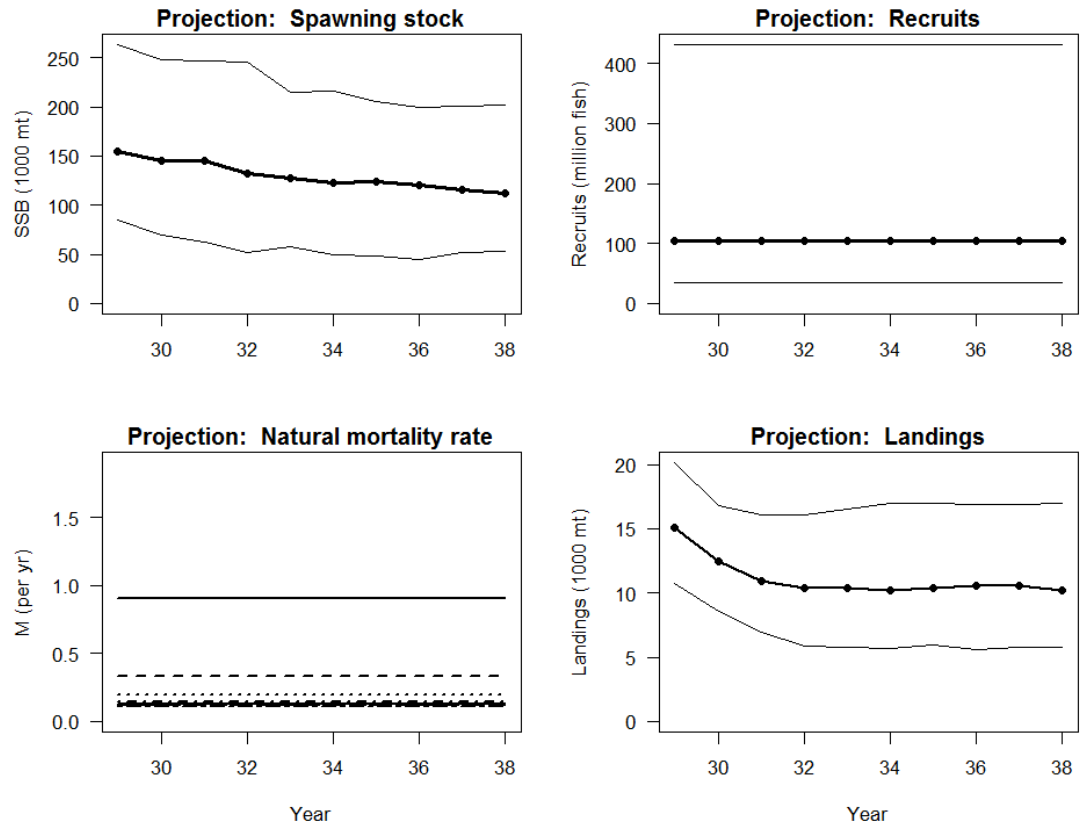

Fig. 20: Projected spawning stock biomass, recruitment, natural mortality, and landings for scup under $F_{40\%}$ scenario and static *M,* and adding in uncertainty to weight-at-age. For the *SSB*, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

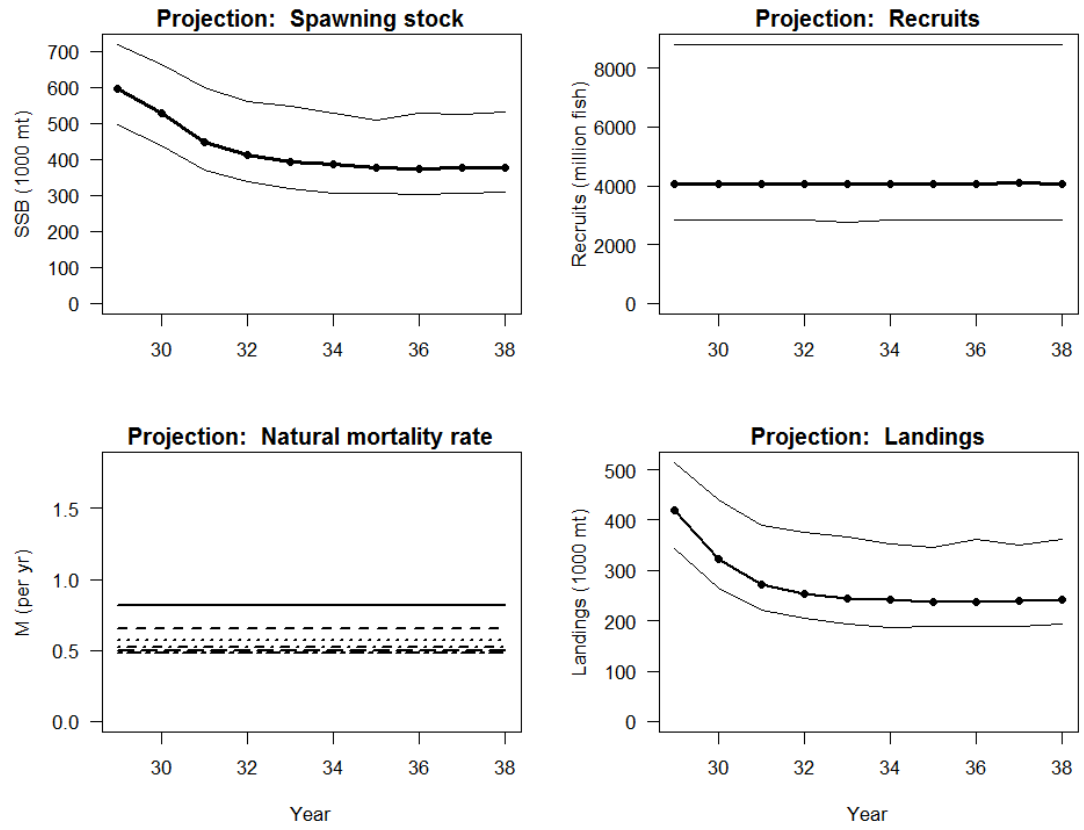

Fig. 21: Projected spawning stock biomass, recruitment, natural mortality, and landings for menhaden under $F_{40\%}$ scenario and benchmark M. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

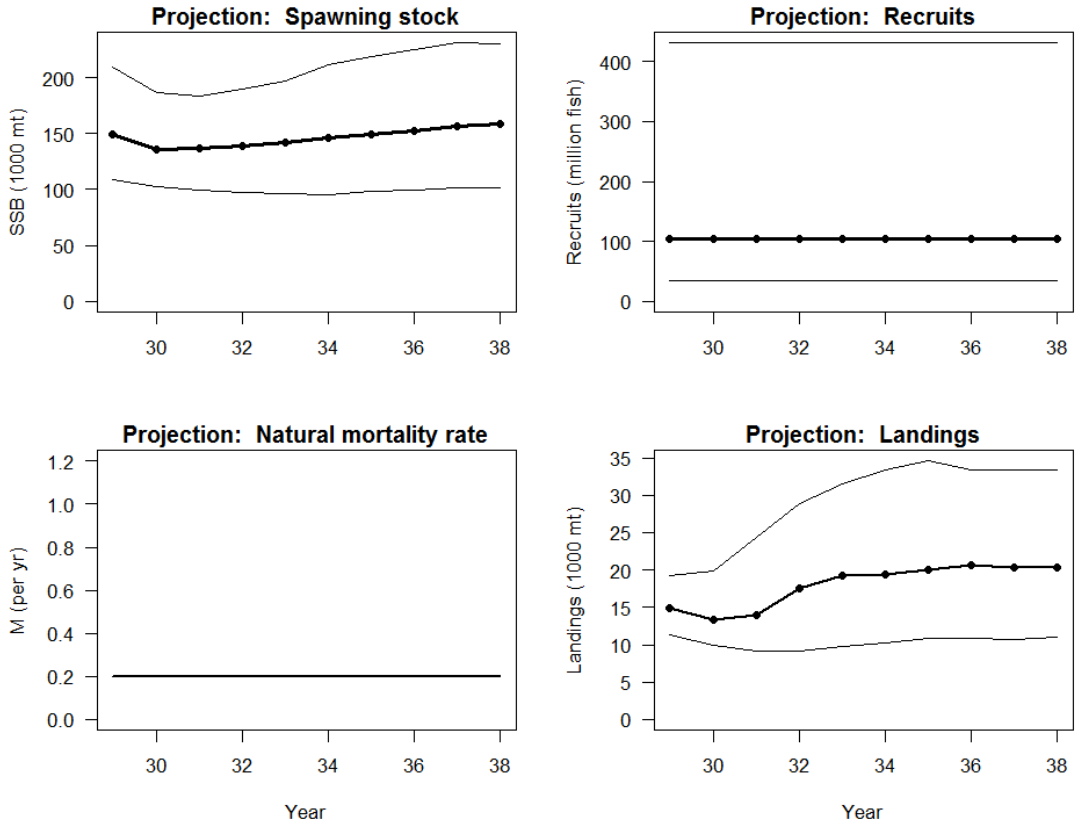

Fig. 22: Projected spawning stock biomass, recruitment, natural mortality, and landings for scup under $F_{40\%}$ scenario and benchmark M. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

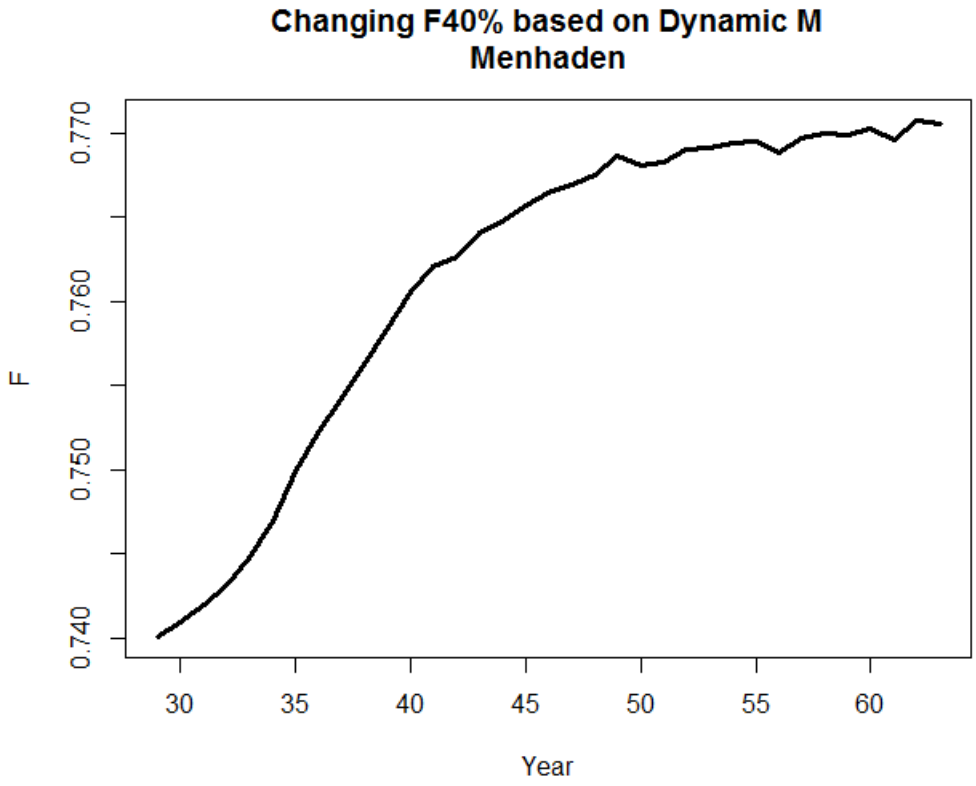

Fig. 23: Time varying $F_{40\%}$ for menhaden.

APPENDIX

Table A1: Projected spawning stock biomass, recruitment, fishing mortality, and landings for menhaden under *F*=0 scenario and dynamic *M* with a stock recruitment relationship. The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	736	6565.65	0.00	0
30	963	6315.49	0.00	0
31	1044	5330.28	0.00	0
32	978	4943.80	0.00	0
33	855	5258.76	0.00	0
224	598	6696.46	0.00	0
225	598	6695.89	0.00	0
226	598	6696.13	0.00	0
227	598	6695.29	0.00	0
228	598	6695.21	0.00	0

Table A2: Projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under *F*=0 scenario and dynamic *M* with a stock recruitment relationship. The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	143	82.72	0.00	0
30	146	83.41	0.00	0
31	152	81.35	0.00	0
32	157	76.38	0.00	0
33	177	72.50	0.00	0
224	178	58.58	0.00	0
226	178	58.93	0.00	0
227	178	58.88	0.00	0
228	178	58.89	0.00	0

Table A3: Projected spawning stock biomass, recruitment, fishing mortality, and landings for bluefish under *F*=0 scenario and dynamic *M* with a stock recruitment relationship. The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	121	22.29	0.00	0
30	134	21.76	0.00	0
31	152	21.13	0.00	0
32	171	19.86	0.00	0
33	190	18.40	0.00	0
224	212	15.06	0.00	0
225	212	15.02	0.00	0
226	213	15.03	0.00	0
227	212	15.03	0.00	0
228	213	15.05	0.00	0

Table A4: Projected spawning stock biomass, recruitment, fishing mortality, and landings for weakfish under *F*=0 scenario and dynamic *M* with a stock recruitment relationship. The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	12	16.99	0.00	0
30	14	18.60	0.00	0
31	17	19.35	0.00	0
32	20	19.98	0.00	0
33	23	20.59	0.00	0
224	32	19.10	0.00	0
225	32	19.13	0.00	0
226	32	19.08	0.00	0
227	32	19.12	0.00	0
228	32	19.14	0.00	0

Table A5: Projected spawning stock biomass, recruitment, fishing mortality, and landings for scup under *F*=0 scenario and dynamic *M* with a stock recruitment relationship. The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	160	120.49	0.00	0
30	167	191.91	0.00	0
31	167	174.84	0.00	0
32	161	176.90	0.00	0
33	155	189.98	0.00	0
224	75	467.18	0.00	0
225	75	467.15	0.00	0
226	75	466.94	0.00	0
227	75	466.76	0.00	0
228	75	466.74	0.00	0

Table A6: Projected natural mortality at-age for menhaden under *F*=0 scenario and dynamic *M* with a stock recruitment relationship. The table presents the first and final 5 years of the 200-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
29	0.86	0.74	0.63	0.51	0.50	0.46
30	0.89	0.76	0.65	0.52	0.51	0.47
31	0.95	0.81	0.69	0.56	0.55	0.50
32	1.05	0.88	0.75	0.59	0.58	0.54
33	1.14	0.97	0.82	0.65	0.64	0.58
224	1.08	1.04	0.91	0.72	0.71	0.65
225	1.08	1.04	0.91	0.72	0.71	0.65
226	1.08	1.04	0.91	0.72	0.71	0.65
227	1.08	1.04	0.91	0.72	0.71	0.65
228	1.08	1.04	0.91	0.72	0.71	0.65

Table A7: Projected natural mortality at-age for scup under *F*=0 scenario and dynamic *M* with a stock recruitment relationship. The table presents the first and final 5 years of the 200-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
29	1.59	0.34	0.29	0.17	0.14	0.12	0.11
30	1.68	0.36	0.31	0.18	0.15	0.13	0.11
31	1.87	0.39	0.34	0.19	0.16	0.13	0.11
32	2.10	0.42	0.37	0.21	0.17	0.13	0.11
33	2.39	0.47	0.41	0.22	0.18	0.14	0.11
224	2.64	0.50	0.43	0.23	0.18	0.14	0.11
225	2.63	0.50	0.43	0.23	0.18	0.14	0.11
226	2.63	0.50	0.43	0.23	0.18	0.14	0.11
227	2.63	0.50	0.43	0.23	0.18	0.14	0.11
228	2.63	0.50	0.43	0.23	0.18	0.14	0.11

Table A8: Projected spawning stock biomass, recruitment, fishing mortality, and landings for menhaden under *F*=0 scenario, dynamic *M*, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	710	4060.33	0.00	0
30	836	4078.72	0.00	0
31	807	4078.72	0.00	0
32	726	4078.72	0.00	0
33	620	4078.72	0.00	0
224	66	4104.00	0.00	0
225	66	4078.72	0.00	0
226	66	4078.72	0.00	0
227	63	3991.04	0.00	0
228	62	4078.72	0.00	0

Table A9: Projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under *F*=0 scenario, dynamic *M*, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	143	107.29	0.00	0
30	146	91.89	0.00	0
31	152	103.72	0.00	0
32	157	100.92	0.00	0
33	177	103.72	0.00	0
224	375	103.72	0.00	0
225	373	102.32	0.00	0
226	372	102.32	0.00	0
227	369	103.72	0.00	0
228	371	103.72	0.00	0

Table A10: Projected spawning stock biomass, recruitment, fishing mortality, and landings for bluefish under *F*=0 scenario, dynamic *M*, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	121	20.68	0.00	0
30	134	20.68	0.00	0
31	152	20.68	0.00	0
32	168	20.68	0.00	0
33	188	20.68	0.00	0
224	298	20.68	0.00	0
225	299	20.68	0.00	0
226	300	20.87	0.00	0
227	299	20.68	0.00	0
228	301	20.68	0.00	0

Table A11: Projected spawning stock biomass, recruitment, fishing mortality, and landings for weakfish under *F*=0 scenario, dynamic *M*, and no stock recruit relationship (median recruitment). The table presents the final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	14	27.68	0.00	0
30	18	31.40	0.00	0
31	24	29.54	0.00	0
32	31	31.40	0.00	0
33	38	27.68	0.00	0
224	56	27.68	0.00	0
225	57	27.68	0.00	0
226	57	27.68	0.00	0
227	57	27.68	0.00	0
228	58	27.68	0.00	0

Table A12: Projected spawning stock biomass, recruitment, fishing mortality, and landings for scup under *F*=0 scenario, dynamic *M*, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	160	105.19	0.00	0
30	167	105.19	0.00	0
31	167	105.19	0.00	0
32	159	105.19	0.00	0
33	151	105.19	0.00	0
224	0	105.19	0.00	0
225	0	105.19	0.00	0
226	0	105.19	0.00	0
227	0	124.15	0.00	0
228	0	114.67	0.00	0

Table A13: Projected natural mortality at-age for menhaden under F=0 scenario and dynamic M and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
29	0.89	0.76	0.65	0.52	0.51	0.47
30	0.93	0.81	0.69	0.55	0.54	0.50
31	1.02	0.87	0.75	0.60	0.59	0.54
32	1.12	0.95	0.81	0.64	0.63	0.58
33	1.22	1.05	0.88	0.69	0.68	0.62
224	1.99	2.04	1.80	1.41	1.40	1.27
225	1.98	2.06	1.81	1.42	1.41	1.27
226	1.99	2.07	1.82	1.41	1.40	1.27
227	2.00	2.07	1.81	1.42	1.41	1.28
228	1.99	2.06	1.81	1.42	1.41	1.28

Table A14: Projected natural mortality at-age for scup under F=0 scenario and dynamic M and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
29	1.68	0.35	0.30	0.18	0.15	0.12	0.11
30	1.86	0.38	0.33	0.19	0.15	0.13	0.11
31	2.10	0.43	0.37	0.21	0.17	0.13	0.11
32	2.36	0.46	0.40	0.22	0.17	0.14	0.11
33	2.67	0.52	0.45	0.24	0.19	0.14	0.11
224	6.43	1.27	1.07	0.50	0.35	0.23	0.14
225	6.47	1.29	1.09	0.51	0.35	0.23	0.14
226	6.56	1.30	1.09	0.51	0.35	0.23	0.14
227	6.55	1.31	1.10	0.51	0.36	0.23	0.14
228	6.49	1.29	1.09	0.51	0.35	0.23	0.14

Table A15: Projected spawning stock biomass, recruitment, fishing mortality, and landings for menhaden under $F_{40\%}$ scenario, dynamic *M*, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	572	4060.33	0.50	404
30	476	4104.00	0.50	284
31	379	4078.72	0.50	233
32	326	4104.00	0.50	204
33	304	4041.93	0.50	192
223	213	4078.72	0.50	144
224	214	4016.48	0.50	147
225	210	4041.93	0.50	141
226	214	4078.72	0.50	143
227	214	4078.72	0.50	144

Table A16: Projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under $F_{40\%}$ scenario, dynamic *M*, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	139	100.92	0.11	15
30	129	103.72	0.11	14
31	122	103.72	0.11	14
32	116	103.72	0.11	15
33	122	103.72	0.11	15
223	145	103.72	0.11	17
224	146	103.72	0.11	18
225	148	105.50	0.11	17
226	149	105.50	0.11	18
227	149	107.29	0.11	18

Table A17: Projected spawning stock biomass, recruitment, fishing mortality, and landings for bluefish under $F_{40\%}$ scenario, dynamic *M*, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	114	20.68	0.17	13
30	113	20.68	0.17	13
31	113	20.68	0.17	13
32	115	20.68	0.17	14
33	116	21.06	0.17	14
223	124	20.68	0.17	14
224	124	20.87	0.17	15
225	124	20.68	0.17	15
226	124	20.68	0.17	15
227	124	20.45	0.17	15

Table A18: Projected spawning stock biomass, recruitment, fishing mortality, and landings for weakfish under $F_{40\%}$ scenario, dynamic *M*, and no stock recruit relationship (median recruitment). The table presents the final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	13	27.68	0.25	3
30	13	25.93	0.25	3
31	15	31.40	0.25	4
32	17	27.68	0.25	4
33	18	27.68	0.25	4
223	21	27.68	0.25	5
224	21	26.80	0.25	5
225	21	27.68	0.25	5
226	21	31.40	0.25	5
227	22	27.68	0.25	5

Table A19: Projected spawning stock biomass, recruitment, fishing mortality, and landings for scup under $F_{40\%}$ scenario, dynamic *M*, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	153	105.19	0.21	15
30	147	124.15	0.21	11
31	136	103.99	0.21	8
32	122	105.19	0.21	6
33	112	105.19	0.21	5
223	18	105.19	0.21	2
224	17	105.19	0.21	2
225	18	105.19	0.21	2
226	18	105.19	0.21	2
227	17	105.19	0.21	2

Table A20: Projected natural mortality at-age for menhaden under $F_{40\%}$ scenario and dynamic *M* and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
29	0.88	0.76	0.64	0.52	0.51	0.47
30	0.91	0.80	0.69	0.55	0.54	0.50
31	0.94	0.83	0.71	0.57	0.56	0.52
32	0.96	0.83	0.71	0.57	0.56	0.52
33	1.00	0.85	0.72	0.58	0.57	0.52
223	1.09	0.94	0.80	0.63	0.62	0.57
224	1.08	0.94	0.80	0.63	0.62	0.57
225	1.09	0.95	0.81	0.64	0.63	0.58
226	1.08	0.94	0.80	0.63	0.62	0.57
227	1.10	0.95	0.80	0.64	0.63	0.57

Table A21: Projected natural mortality at-age for scup under $F_{40\%}$ scenario and dynamic *M* and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
29	1.66	0.35	0.30	0.18	0.15	0.12	0.11
30	1.84	0.39	0.34	0.19	0.16	0.13	0.11
31	1.96	0.41	0.36	0.20	0.16	0.13	0.11
32	1.97	0.41	0.36	0.20	0.16	0.13	0.11
33	2.02	0.42	0.37	0.21	0.17	0.14	0.11
223	2.34	0.45	0.39	0.21	0.17	0.14	0.11
224	2.39	0.46	0.39	0.21	0.17	0.14	0.11
225	2.40	0.47	0.40	0.22	0.17	0.14	0.11
226	2.37	0.47	0.40	0.22	0.17	0.14	0.11

Table A22: Projected spawning stock biomass, recruitment, fishing mortality, and landings for menhaden under $F = 0$ scenario, static M, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	732	4060.33	0.00	0
30	899	4104.00	0.00	0
31	954	4078.72	0.00	0
32	981	4104.00	0.00	0
33	1006	4041.93	0.00	0
223	958	4078.72	0.00	0
224	960	4016.48	0.00	0
225	957	4041.93	0.00	0
226	959	4078.72	0.00	0
227	969	4078.72	0.00	0

Table A23: Projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under $F = 0$ scenario, static M, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	145	100.92	0.00	0
30	148	103.72	0.00	0
31	154	103.72	0.00	0
32	158	103.72	0.00	0
33	176	103.72	0.00	0
223	358	103.72	0.00	0
224	359	103.72	0.00	0
225	364	105.50	0.00	0
226	366	105.50	0.00	0
227	368	107.29	0.00	0

Table A24: Projected spawning stock biomass, recruitment, fishing mortality, and landings for bluefish under $F = 0$ scenario, static M, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	120	20.68	0.00	0
30	133	20.68	0.00	0
31	150	20.68	0.00	0
32	170	20.68	0.00	0
33	189	21.06	0.00	0
223	301	20.68	0.00	0
224	300	20.87	0.00	0
225	300	20.68	0.00	0
226	301	20.68	0.00	0
227	300	20.45	0.00	0

Table A25: Projected spawning stock biomass, recruitment, fishing mortality, and landings for weakfish under $F = 0$ scenario, static M, and no stock recruit relationship (median recruitment). The table presents the final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	14	27.68	0.00	0
30	18	25.93	0.00	0
31	23	31.40	0.00	0
32	30	27.68	0.00	0
33	35	27.68	0.00	0
223	55	27.68	0.00	0
224	54	26.80	0.00	0
225	55	27.68	0.00	0
226	55	31.40	0.00	0
227	53	27.68	0.00	0

Table A26: Projected spawning stock biomass, recruitment, fishing mortality, and landings for scup under $F = 0$ scenario, static M, and no stock recruit relationship (median recruitment). The table presents the first and final 5 years of the 200-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	160	105.19	0.00	0
30	169	124.15	0.00	0
31	174	103.99	0.00	0
32	179	105.19	0.00	0
33	186	105.19	0.00	0
223	239	105.19	0.00	0
224	240	105.19	0.00	0
225	238	105.19	0.00	0
226	239	105.19	0.00	0
227	238	105.19	0.00	0

MANUSCRIPT – III

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Prey-dependent effects on predator populations.

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ABSTRACT

Empirical information was examined to test for prey-dependent effects between the available biomass of Atlantic menhaden (*Brevoortia tyrranus*) on the striped bass (*Morone saxatailis*) population. The data indicated there may be a link between decreased consumption of menhaden by striped bass and increased natural mortality in the striped bass population. The investigation was extended to look at the impacts that this dynamic has on the two populations by programming the prey-dependent mortality effect into a multispecies estimation model. The parameters from the estimation model were then used to project the population to examine trade-offs that occur under a set of simple management strategies. The trade-offs were found to be important and indicate that there is an interaction between fishing mortality (F) and natural mortality (M) in both the medium and long-term projections. A main finding was that under a no-menhaden fishing scenario, the management outcomes were better for striped bass. This was true under different F strategies for striped bass, as the decreased natural mortality offset F. It is important to note that these management scenarios were developed to illustrate trade-offs and are not offered as actual management recommendations. Analyses like these can offer important information to managers by way of giving them more information to consider when developing measures that attempt to meet goals, as fishing impacts on one population can affect the attainment of goals on other populations.

KEYWORDS

multispecies statistical catch-at-age model, projection, prey-dependent feedback, biological reference points, time and age varying natural mortality

INTRODUCTION

When investigating ecosystem interactions there is often a focus on the impacts of predation on prey populations as an important top-down control on population dynamics (Helgason and Gislason 1979; Tsou and Collie 2001; Curti et al. 2013). There is also a need to understand some of the dynamics in bottom-up processes as well, namely the impacts that declining prey abundance has on predator populations, if any. This notion of prey dependency of predators has been investigated by researchers before and these investigations have focused on the effects of declining prey on predator growth (Gislason 1999; Lewy and Vinther 2004; Latour et al. 2012; Holsman et al. 2015; Cormon et al. 2015; Hilborn et al. 2017).

There may be a second effect that can occur by way of prey feedback on predator population dynamics beyond growth, and this could be an effect on increasing or decreasing natural mortality (Walters et al. 1999; Hixon and Jones 2005; Anderson et al. 2017). If this effect were occurring, other indicators, such as growth, may not become apparent because the animals are removed from the population before they can influence empirical indicators of growth such as weight-at-age.

These concepts have been researched for striped bass (*Morone saxatilis*), where it is believed that the decline in a preferred and important prey item, Atlantic menhaden (*Brevoortia tyrannus*) can have negative consequences for the striped bass population by way of increasing disease or decreasing fitness, which could lead to decreased growth and potentially increased natural mortality (Uphoff 2003; Overton et al. 2003; Jiang et al. 2007; Gauthier et al. 2008; Jacobs et al. 2009; Latour et al. 2012). The link is that menhaden are a preferred prey item for striped bass and are a

nutritionally superior food item for striped bass. Lacking this important food item in the diet of striped bass is thought to lead to switching to nutritionally inferior prey items, which results in the inability to fight off diseases, negative impacts to the growth rate of striped bass, increases in the prevalence of poor condition indicators such as emaciation and skin lesions, as well as potentially leading to decreased survival (Uphoff 2003; Overton et al. 2003; Jiang et al. 2007; Gauthier et al. 2008; Jacobs et al. 2009, Sadler 2010).

The menhaden population declined during the 1990s, which coincided with the recovery of the striped bass population, with striped bass remaining at a high biomass level between late 1980s through the late 1990s (Atlantic menhaden: SEDAR 2015; Atlantic striped bass: ASMFC 2015). In the late 1990s, striped bass in poor condition increased in Chesapeake Bay (Overton et al. 2003; Gauthier et al. 2008), leading to research on the potential causative agents, with some implicating the lack of menhaden in the striped bass diet as a potential cause for the poor condition in these fish (Uphoff 2003). The main causative agent when linking decreased consumption of menhaden to mortality for striped bass is caused through a disease called mycobacteriosis. Mycobacteriosis is a subacute to chronic disease common in wild and captive fishes worldwide. Mortality resulting from mycobacteriosis has been reported in wild striped bass populations (Gauthier et al. 2008), and is commonly observed in aquaculture (Nigrelli and Vogel 1963, Hedrick et al. 1987, Bruno et al. 1988), and it is generally assumed that mycobacteriosis in fishes is chronic, progressive, and ultimately fatal (Van Duijn 1981, Frerichs 1993, Overton et al. 2003, Decostere et al. 2004). Jacobs et al. (2009) linked poor diet condition to increased

prevalence and severity of mycobacteriosis in striped bass. Therefore if menhaden are not available due to a decrease in population size, or due to competition for limited menhaden prey when striped bass populations are at high densities, this could increase mycobacteriosis and lead to an increase in striped bass mortality. Tagging studies (Jiang et al. 2007; Sadler 2010) and epidemiological models (Gauthier et al. 2008) provide evidence that support the hypothesis that increased natural mortality of striped bass in Chesapeake Bay has occurred since the late 1990s, potentially caused by mycobacteriosis. While these studies were all focused in the Chesapeake Bay, high natural mortality of striped bass in the Chesapeake could have serious implications for the entire coastwide population of striped bass and the management of this species along the Atlantic coast since this stock area is the main contributor to Atlantic coast fisheries for striped bass (Richards and Rago 1999; Sadler 2010).

Empirical information will be examined to investigate linkages between the availability of menhaden as a prey item for striped bass, and the potential feedback this might have by way of impacts to growth of the striped bass population or impacts to natural mortality of striped bass. Data generated from a multispecies statistical catch-at-age model will be used to illustrate the change in biomass of the prey item (menhaden) as well as the amount of menhaden consumed by striped bass through time. This prey biomass and consumption time-series data will then be compared to a time-series of striped bass weight-at-age information, as well as two independently generated natural mortality indicators that have been developed for striped bass (Sadler 2010) to look for potential links between the dynamics in the two populations. This information will then be used to investigate the trade-offs that can occur between

these two populations based on the top-down predation effects of striped bass on menhaden, fishing on these populations, and the prey-dependent feedback of menhaden on striped bass.

METHODS

Investigations of prey-dependent predator growth

The first set of analyses examined empirical information to see if there was an apparent link between biomass of menhaden through time and weight-at-age of striped bass as a proxy for prey impacts to growth. Data into and output from a two-species (menhaden and striped bass) run of a Multispecies Statistical Catch-at-age model (MSSCAA) as developed for Chapter 1 of this dissertation were used as the basis for these analyses. Mean weight-at-age for striped bass are plotted along with the biomass trend of striped bass through time (Figure 1). It can be seen that weight at-age was relatively flat through time, though potentially shows a period of variable decline as the striped bass population grew in the 1990s. The model outputs were exported from ADMB software (ADMB-IDE ver 10.1 2011) and imported to R statistical software (R Core Team 2016) for the calculations. To test for signals between these two datasets, a set of pairwise correlation analyses were performed using the "corr.test" function from the "psych" package, applying a Holm correction when testing for significance of the correlations. The data were arranged by aligning biomass-at-age of menhaden as estimated by the multispecies model versus weight-at-age of striped bass, running each pairwise correlation between one age class of menhaden biomass against each age class' annual average weight for striped bass. This same procedure was repeated for various aggregated age classes of menhaden biomass as well (i.e

biomass of age 1 and 2 menhaden, biomass of age 1, 2, and 3 menhaden, etc.). The idea was to see if a certain subset of menhaden relative to striped bass weight-at-age was most important.

A second analysis was done to investigate the existence of a relationship between changes in weight-at-age, availability of prey, and size of the predator population. In this analysis, a theoretical relationship between the two metrics was developed (Horbowy and Luzenczyk 2017), defined by the equation:

$$Relative\ Weight - at - age = \frac{\alpha * B_{prey}}{\beta * B_{prey} + B_{pred}} \quad (1)$$

Where α and β are the parameters controlling the shape of the curve, B_{prey} is the total biomass of menhaden, and B_{pred} is the biomass of striped bass for ages 2 – 13. This model was used to predict the relative weight-at-age of striped bass using menhaden biomass as a predictor. If there is a relationship between the two metrics, this should be indicated by the prediction following the relative weight-at-age through time.

Analyses were then conducted looking at another metric of the amount of menhaden available to striped bass as prey. Per the method of Uphoff and Sharov (2018), this analysis used a ratio of menhaden biomass consumed per striped bass biomass. Both of these population metrics were generated by the two-species multispecies statistical catch-at-age model. The ratio was developed by dividing the amount of menhaden biomass consumed annually by striped bass by the total annual biomass of striped bass for ages 3 through 12 in that same year. The age classes selected for the analysis are the age classes that consume menhaden in significant amounts, and the final year class of striped bass was dropped as it is a plus group and

represents multiple ages 13 and greater. The reason for dropping the plus group from the analysis is because the average age class-specific weight-at-age could be influenced by the age structure within this plus group, thereby confounding the analysis of the consumption ratio and striped bass weight-at-age.

$$Consumption\ Ratio = \frac{Consumption\ of\ menhaden\ by\ striped\ bass}{Total\ Biomass\ of\ striped\ bass} \quad (2)$$

This time-varying ratio was then compared to the weight-at-age of striped bass in those same years, and a pairwise correlation analysis was again conducted as described above to look for a signal in these two datasets.

Investigations of prey-dependent predator mortality

The consumption ratio as described above was used to investigate any apparent signal between the natural mortality (*M*) of striped bass and changes in the amount of menhaden consumed by striped bass. Two externally generated estimates of striped bass *M* were examined for this analysis. These estimates of *M* were developed during the 2009 stock assessment process for striped bass (ASMFC 2009). Two of the *M* estimates in this document had longer time series and allowed for the representation of both the pre-migratory portion of the population and the migratory portion of the population. The age classes represented by these two time series of *M* have an additional justification in that they represent the age classes that are the highest consumers of menhaden in their diet. Based on the information contained in the stock assessment document, the pre-migratory *M* vector represents fish from age 3 to age 8, and the migratory portion represents fish through the remainder of the age classes (for a total of 13 year classes, with age 13 being a plus group). As noted by Matsche et al.

(2010), prevalence of mycobacteriosis was low in the coastal migratory component of the striped bass stock, therefore there is a logic to developing two separate relationships for these two segments of the striped bass population. These time series of *M* were examined relative to the consumption ratio using the same correlation analysis procedures as above.

Projecting the population with prey-to-predator feedback

Once it was determined that there was a plausible connection between the indicator of menhaden availability or consumption with striped bass growth or mortality, a model was developed between the appropriate metrics for use in a predictive manner. A Weibull function was deemed an appropriate model to use for the mortality component of the analysis. A two-parameter Weibull function was defined by:

$$M1 = 1 - e^{-\left(\frac{consumption\ ratio}{\eta}\right)^{\beta}} \quad (3)$$

Where *M1* is natural mortality, the consumption ratio is defined in equation 2 above, η is the scale parameter of the Weibull function and controls how quickly the function increases or decays across the metric being used (in this case consumption ratio), and β is the shape parameter and controls whether the function increases, declines or remains flat. The Weibull function has been used in numerous survival analyses, some specific to striped bass, and was deemed appropriate for this application (Heisey et al. 2006; Gauthier et al. 2008; Bolker 2008).

The predictive model as defined above was then used in a two-species version of the five-species model from Chapter 1. This model framework is the same as that

developed in Chapter 1; it included striped bass as a predator and menhaden as the prey species, and excluded other species from the analysis. This is justified because the strongest interaction as seen in Chapter 1 was between striped bass and menhaden.

The starting conditions of the projection analysis include initial numbers at age, which were the estimated numbers at age, N_0, for the terminal year of the multispecies stock assessment model.

Numbers at age after the initial year were calculated as:

$$N_{i,a+1,y+1} = N_{i,a,y} e^{-Z_{i,a,y}} \quad (4)$$

where $Z_{i,a,y}$ is species, age, and year-specific total mortality and equals natural mortality for each age for that year plus the fishing mortality rate times the fishery selectivity-at-age, $N_{i,a,y}$ is the species specific population by age and year. Fishery selectivity was a vector as estimated for each species from the multispecies stock assessment model.

These numbers at age were converted to annual species-specific biomass using the equation:

$$B_{i,a,y} = N_{i,a,y} * w_{i,a} \quad (5)$$

where $N_{i,a,y}$ is either the initial population-at-age from the terminal year of the multispecies stock assessment model or the population-at-age calculated by equation 4, and $w_{i,a}$ is the species-specific weight-at-age, which was set at the weight-at-age from the terminal year of the multispecies stock assessment model.

Fishing mortality was set at a constant level in the projections, and so for the constant *F* scenarios used for this project, the landings associated with the chosen *F* strategy were calculated. These annual landings were calculated using the Baranov catch equation:

$$C_{i,a,y} = \frac{F_{i,a,y}}{F_{i,a,y} + M_{i,a,y}}\left(1 - e^{-(F_{i,a,y}+M_{i,a,y})}\right)B_{i,a,y} \quad (6)$$

where $C_{i,a,y}$ is species-specific annual catch-at-age, $F_{i,a,y}$ is species-specific annual fishing mortality-at-age, $M_{i,a,y}$ is species-specific annual natural mortality-at-age, and $B_{i,a,y}$ is the species-specific annual population biomass-at-age.

Recruitment was projected without an underlying stock-recruitment function and was based on the median recruitment observed from the entire time series for each species. Recruitment variability was included whereby for each year a deviation in recruitment was selected randomly with replacement from the deviations estimated in the multispecies stock assessment model. This may be an overly restrictive assumption in that it will be impossible to have recruitment overfishing in a population, however this strategy was chosen due to the fact that this is the standard approach for these species in their normal single species assessment procedures (Atlantic menhaden: SEDAR 2015; Atlantic striped bass: ASMFC 2015), and because this will keep recruitment in the populations close to values seen in the timeseries of information available, thereby not conflating the feedback being tested with model derived large or small recruitment events that may not have been witnessed in the population dynamics previously.

Spawning stock biomass (*SSB*) was calculated for each species and was based on the biomass-at-age as estimated for each year in the projection multiplied by the maturity-at-age vector from the terminal year of the multispecies stock assessment model. In this case, all *SSB* is represented in the estimate and is therefore comprises both male and female biomass. Spawning was assumed to occur mid-year for all species in the model; therefore the *SSB* was decreased by total mortality for half a year.

Natural mortality (*M*) was modeled using a dynamic calculation of *M* for each year in the projection for the prey species (menhaden). The main assumption for this scenario is that the prey suitabilities (v), as calculated by the multispecies stock assessment model, remain constant for the time period of the projections, and are taken from the terminal year of the multispecies assessment model. All of the natural mortality calculations were the same as those presented in Chapter 1. The dynamic *M2* value was summed with the residual natural mortality estimate (*M1*, natural mortality not attributed to predation) to complete the natural mortality calculation.

For the predator, striped bass, time and age varying *M1* was calculated based on the outcome of the investigation in to the prey-dependent feedback on *M*. Taking the results of the Weibull model defining the relationship between prey abundance and predator mortality as described in Equation 3, a ratio of menhaden biomass consumption to striped bass total biomass was developed for the projection time period. This time-varying ratio was then used in the Weibull function as defined above to predict the new *M1* estimate for striped bass. Striped bass was assumed to not undergo any predation mortality (i.e. $M2 = 0$), therefore this new mortality estimate

was applied to the *M1* portion of the assumed separable *M* estimate. The model predicts an average (not age specific) *M1* rate, therefore this average level of *M1* was compared to the assumed level of *M1* as developed by the last benchmark stock assessment for striped bass, which was a Lorenzen (Lorenzen 2005) age varying estimate of *M1* (Table 2). The proportional difference between the *M1* vector at age as assumed for the benchmark assessment and the newly generated *M1* value from this research was used to prorate all of the striped bass age class *M1* values up to their new estimate. Further, two Weibull models were run for the different segments of the population, and this separate estimate of the change in *M1* was applied to the appropriate age classes. These newly generated *M1* estimates were then used in the projections for the predator. The formulation for this is:

$$Relative\ change = \frac{(PredM1_x - OrigM1_x)}{OrigM1_x} \quad (7)$$

$$NewM1_a = (1 + \ Relative\ change) * M1_a) \quad (8)$$

Where $PredM1_x$ is the new predicted average natural mortality for portion of the population *x* (either premigratory or migratory) from Equation 3, $OrigM1_x$ is the average natural mortality from the age classes corresponding to the natural mortality-at-age from the Lorenzen curve natural mortality estimates used for the benchmark single-species striped bass model (Table 2) grouped by the age classes that correspond to the premigratory and migratory portion of the population, and $M1_a$ is the natural mortality-at-age, again from the single-species striped bass benchmark assessment. An important note is that ages-1 and 2 were not analyzed for this portion of the study. This is because the age classes represented by the external *M* estimates generally start

at age three, and furthermore, ages-1 and 2 striped bass do not consume menhaden to a large extent, therefore changes in the menhaden population should not impact these two age classes of striped bass.

The parameters from the simplified two-species multispecies model were used in projections of the striped bass and menhaden populations. In the multispecies model and projections, there was a dynamic interaction between predator and prey, and this interaction was both top-down (predator consuming prey) and bottom-up (prey population interacting with predator population through growth or mortality). Several projections were run with varying combinations of fishing mortality occurring on each of the species. All projections assumed a constant *F* management strategy during the projection time period on both the predator and the prey, but this constant *F* was set to meet different potential management goals. The *F* rate for striped bass was set at 0.1, 0.2, and 0.3. In combination with these *F* strategies used for the predator species, two scenarios were set for the prey species (menhaden). The first was to set *F* equal to 0 and the second was to set a high *F* rate on menhaden of 0.9. These are extreme values but were selected to illustrate the potential effects that these strategies have on the two species. These combinations of measures will allow for the examination of the trade-offs between allowing for more removal of prey and its indirect feedback on the predator population. Two different projection periods were examined, 100 and 10 years.

The projections were run in a stochastic fashion in R statistical software (R Core Team 2016). The projection parameters were bootstrapped for 500 iterations for the medium-term projections, and 200 iterations for the long-term projections. Outputs

included the median, 5th and 95th percentiles for spawning stock biomass over time, recruitment over time, landings over time, and natural mortality for the species.

Interactions between predator and prey populations

An exploration of the interaction between the two species in the model was also undertaken. As the biomass of the prey species changes, this changes the available prey for the predator. When there are both top-down and bottom-up interactions occurring, this causes the species to interact through natural mortality, so as one species declines in abundance, this could cause the predation mortality to increase on the prey species in the model, which can then feed back to the predator population. A series of projections were run from an *F* rate of 0 to 4 in steps of 0.1 for both menhaden and striped bass resulting in 1,681 separate runs. The projections were run for thirty years, and the last year from the projection was used for the comparisons. This was done to allow the variability in the projections from things like recruitment to dampen as well as giving the *F* rate a chance to impact the populations.

Once the projections were completed, the information was arranged in two matrices (one for menhaden and one for striped bass) with menhaden *F* rates going from 0 to 4 by row and striped bass *F* rates going from 0 to 4 by column. The data in each matrix was the species specific resulting biomass level for the combination of *F* rates. A contour plot was then generated from this information to show the impacts to the two species biomass levels as the *F* rates changed on each population.

RESULTS

Investigations of prey-dependent predator growth

For both the investigations of menhaden biomass levels (Table A2 – A3) and the ratio of menhaden consumed by striped bass against striped bass weight-at-age (Table A4), no significant correlations were found. This finding was consistent for all combinations of menhaden biomass-at-age examined relative to all age classes of striped bass. Additionally, the predictive model with menhaden biomass as a predictor of striped bass weight-at-age also did not indicate any effect of menhaden biomass on striped bass weight-at-age changes through time (Figure 2). This indicated that there was no signal in the empirical data to suggest that there was an effect between menhaden biomass levels or levels of menhaden consumed by striped bass and the growth rates of striped bass as measured by changes in mean weight-at-age of striped bass through time. Given this finding, no subsequent analyses were conducted on prey-dependent growth for striped bass.

Investigations in to prey-dependent predator mortality

The investigation of the ratio of menhaden consumed by striped bass against external tagging estimates of *M* for striped bass did find significant correlation between the two metrics (Table A5). Given this finding, the analysis was extended to fit the Weibull model (Equation 3) to the external natural mortality and consumption ratio data. The model fit the data and showed a trend whereby the predicted average *M* declines as the consumption of menhaden by striped bass increases (Figures 4 and 5). This trend held for both the pre-migratory and migratory portions of the population, however the pre-migratory portion showed a higher magnitude of impact relative to the migratory age classes of striped bass.

Two-species estimation model with dynamic *M1*

Once the relationship was established, the parameters of the Weibull model were incorporated into a two-species multispecies statistical catch-at-age model. Two model diagnostic plots are presented to show that the model was able to fit the empirical data relatively well (Figures 6 and 7). Due to differences in the estimation of selectivity between the two-species and the five-species model, the selectivity parameters were set at the values calculated in the five-species model and not estimated in the two-species model. A set of Weibull model parameters were fit to the two-species model information (Table A6). The model was run with these parameters, which calculated changes in *M1* for striped bass that depended on changes in the amount of menhaden that striped bass consumed. The trend in *M*-at-age indicated a period of higher *M* in the striped bass population as the menhaden population was declining in the 1980s while there was a coincident increase in the striped bass population (Figure 8). These two factors combined to decrease the ratio in menhaden consumed by striped bass (Figure 3), leading to the increase in *M1* for striped bass. The middle of the time series showed variability in *M1*, and then the trend reversed later in the time series as the striped bass population stabilized and showed some modest decrease, while the menhaden population increased. The striped bass population dynamics responded by indicating a lowering in *M1*-at-age.

Projecting the population with prey to predator feedback

Long-term projections

The first long-term scenario involved implementing no fishing mortality on menhaden and implementing three increasing fishing mortality levels on striped bass (F=0.1, F=0.2, and F=0.3). Over the long term, the striped bass population declined, but did not drop to zero in any scenarios given the median recruitment assumption for

all scenarios. Under $F = 0.1$, the striped bass SSB began at 212 tmt and ended after the 100-year projection at 89 tmt. Correspondingly, the landings dropped from 21 tmt to 12 tmt during the projection period (Figure 9, Table A7). Under $F = 0.2$, the SSB began at 203 tmt and ended after the 100-year projection at 21 tmt. Correspondingly, the landings dropped from 39 tmt to 9 tmt during the projection period (Figure 9, Table A8). Under $F = 0.3$, the SSB began at 194 tmt and ended after the 100-year projection at 8 tmt. Correspondingly, the landings dropped from 57 tmt to 8 tmt during the projection period (Figure 9, Table A9).

The natural mortality for all the long-term scenarios increased through the projection period. It is important to note that, as described in the methods, the *M* on the first two age classes of striped bass does not interact dynamically with menhaden; therefore these two age classes remain at a static assumption throughout the projection period for all the scenarios. In the case of no fishing on menhaden and low fishing mortality on striped bass ($F = 0.1$) the projection started with values that were close to the assumption used for the single-species benchmark, given that menhaden biomass was high (Figure 10, Table A10). As the high population of striped bass with low overall mortality preys on menhaden, the menhaden population responded by decreasing, and this impacts the *M* for striped bass. Striped bass *M* increased across age classes three through thirteen, increasing on average by 48% on the pre-migratory age classes (3 – 8) relative to the base assumption from the single-species model *M*, and increased by 33% on the migratory portion of the population. The trend is the same under the medium fishing mortality scenario ($F = 0.2$) for striped bass resulting in a 108% increase on the pre-migratory age classes and a 60% increase on the

migratory age classes (Figure 10, Table A11). The final high-*F* scenario (*F* = 0.3) followed this trend as well with beginning values of *M* being lower than the single-species assumed values and ending with an increase from the original assumption, however the proportional increase is less than in the low and medium *F* scenarios, with an increase of 148% and 80% on the pre-migratory and migratory portions of the population respectively (Figure 10, Table A12).

The second set of long-term scenarios implemented high fishing mortality on menhaden (*F* = 0.9) and implemented same three increasing fishing mortality levels on striped bass (*F*=0.1, *F*=0.2, and *F*=0.3) as was done above. Over the long term, the striped bass population declined to low numbers in some cases, but did not drop to zero given the median recruitment assumption for all scenarios. Additionally, the population of striped bass declined more rapidly than under the no fishing mortality scenario for menhaden. Under *F* = 0.1, the SSB began at 212 tmt and ended after the 100-year projection at 24 tmt. Correspondingly, the landings dropped from 21 tmt to 5 tmt during the projection period (Figure 9, Table A13). Under *F* = 0.2, the SSB began at 203 tmt and ended after the 100-year projection at 7 tmt. Correspondingly, the landings dropped from 39 tmt to 5 tmt during the projection period (Figure 9, Table A14). Under *F* = 0.3, the SSB began at 194 tmt and ended after the 100-year projection at 4 tmt. Correspondingly, the landings dropped from 57 tmt to 5 tmt during the projection period (Figure 9, Table A15).

The natural mortality for all the long-term scenarios increased through the projection period. In the case of high fishing on menhaden (*F* = 0.9) and low fishing mortality on striped bass (*F* = 0.1) the projection began with values that are close to

the assumption used for the single-species benchmark (Figure 10, Table A16). By the end of the projection period, striped bass *M* increased across age classes two through thirteen, increasing by 140% on the pre-migratory age classes (3 – 8) from the original *M* assumption from the single-species assessment and increased by 73% on the migratory portion of the population. The trend is the same under the medium fishing mortality scenario ($F = 0.2$) for striped bass resulting in a 193% increase on the pre-migratory age classes and a 107% increase on the migratory age classes (Figure 10, Table A17). The final high-*F* scenario ($F = 0.3$) followed this trend as well with beginning values of *M* being close to but higher than the single-species assumed values and ending with an increase from the original assumption. This proportional increase is higher than in the low and medium *F* scenarios, with an increase of 220% and 120% on the pre-migratory and migratory portions of the population respectively (Figure 10, Table A18). Across all scenarios for the case of high fishing mortality on menhaden, the effect on *M* for striped bass is higher than in the case of no fishing on menhaden.

The trade-offs between the different long-term scenarios can be seen in the tables for the long-term scenarios (Table 3 and 4). For both landings and SSB, the management outcomes are more favorable for striped bass for the no menhaden fishing scenarios. The optimal scenario for striped bass landings is a scenario with no menhaden fishing and low *F* on striped bass, as this produces 1,218 tmt over the projection period. The optimal scenario for SSB is the same scenario, with no fishing on menhaden and low *F* for striped bass, producing 89 tmt at the end of the projection period. For both landings and SSB, the largest trade-off was seen in the low fishing

mortality scenario for striped bass, where the proportional difference between a scenario with no fishing and high fishing mortality on menhaden was a 46% increase in landings and a 73% increase in SSB for the no fishing on menhaden scenario.

Medium-term projections

A series of medium-term projections were run to see population outcomes in the shorter-term relative to the 100-year projections. The combination of fishing mortality choices matched those performed for the long-term projections. The first medium-term scenario implemented no fishing mortality on menhaden and implemented three increasing fishing mortality levels on striped bass (F=0.1, F=0.2, and F=0.3). Over the medium-term, the striped bass population declined across all scenarios. Under F = 0.1, the SSB began at 213 tmt and ended after the 10-year projection at 106 tmt. Correspondingly, the landings dropped from 21 tmt to 13 tmt during the projection period (Figure 11, Table A19). Under F = 0.2, the SSB began at 204 tmt and ended after the 10-year projection at 50 tmt. Correspondingly, the landings dropped from 39 tmt to 15 tmt during the projection period (Figure 12, Table A20). Under F = 0.3, the SSB began at 195 tmt and ended after the 10-year projection at 24 tmt. Correspondingly, the landings dropped from 57 tmt to 13 tmt during the projection period (Figure 13, Table A21).

The natural mortality for all the medium-term scenarios increased through the projection period. In the case of no fishing on menhaden and low fishing mortality on striped bass (F = 0.1) the projection began with values that were close to the assumption used for the single-species benchmark (Figure 11, Table A22). By the end of the projection period, striped bass M increased across age classes two through

thirteen, increasing by 48% on the pre-migratory age classes (3 – 8) relative to the base *M* assumption from the single-species model, but decreased by 33% on the migratory portion of the population. The trend was the same under the medium fishing mortality scenario ($F = 0.2$) for striped bass resulting in a 77% increase on the pre-migratory age classes and a 47% decrease on the migratory age classes (Figure 12, Table A23). The final high-*F* scenario ($F = 0.3$) followed this trend as well with beginning values of *M* being lower than the single-species assumed values and ended with an increase from the original assumption, with an increase of 116% and 67% on the pre-migratory and migratory portions of the population respectively (Figure 13, Table A24).

The second set of medium-term scenarios implemented high fishing mortality on menhaden ($F = 0.9$) and implemented the same three increasing fishing mortality levels on striped bass (F=0.1, F=0.2, and F=0.3). Over the medium term, the striped bass population declined in all scenarios. Additionally, and as was the case in the long-term projections, the population of striped bass declined more rapidly than under the no fishing mortality scenario for menhaden. Under $F = 0.1$, the SSB began at 213 tmt and ended after the 10-year projection at 87 tmt. Correspondingly, the landings dropped from 21 tmt to 11 tmt during the projection period (Figure 14, Table A25). Under $F = 0.2$, the SSB began at 204 tmt and ended after the 10-year projection at 40 tmt. Correspondingly, the landings dropped from 39 tmt to 12 tmt during the projection period (Figure 15, Table A26). Under $F = 0.3$, the SSB began at 195 tmt and ended after the 10-year projection at 18 tmt. Correspondingly, the landings dropped from 57 tmt to 10 tmt during the projection period (Figure 16, Table A27).

The natural mortality for all of the medium-term scenarios increased through the projection period. In the case of high fishing pressure on menhaden and low fishing mortality on striped bass ($F = 0.1$) the projection began with values that were close to the assumption used for the single-species benchmark (Figure 14, Table A28). By the end of the projection period, striped bass M increased across age classes two through thirteen, increasing by 74% relative to the base M assumption from the single species model on the pre-migratory age classes (3 – 8) and increased by 47% on the migratory portion of the population. The trend was the same under the medium fishing mortality scenario ($F = 0.2$) for striped bass resulting in a 114% increase on the pre-migratory age classes and a 67% increase on the migratory age classes (Figure 15, Table A29). The final high-F scenario ($F = 0.3$) followed this trend as well with beginning values of M being higher than the single-species assumed values, and the proportional increase was higher than in the low and medium F scenarios, with an increase of 158% and 87% on the pre-migratory and migratory portions of the population respectively (Figure 16, Table A30). Across all scenarios for the case of high fishing mortality on menhaden, the effect on M for striped bass increased M relative to the case of no fishing on menhaden.

The trade-offs between the different medium-term scenarios can be seen in the table for the medium-term scenarios (Table 5 and 6). For both landings and SSB, the management outcomes were more favorable for striped bass in the no menhaden fishing scenarios. The optimal trade-off scenario for landings was a scenario with no menhaden fishing and low F on striped bass, as this produces a 7% increase in landings over the projection period between the no menhaden fishing and high

menhaden fishing scenarios. Despite the optimal trade-off, the maximum landings occur in the high fishing on striped bass scenarios as the populations are being depleted. The optimal scenario for SSB, as was the case for the long-term projections, was one with no fishing on menhaden and low *F* for striped bass, producing 106 tmt by the end of the the projection period. For landings, the largest trade-off was seen in the low fishing mortality scenario for striped bass, where the proportional difference between a scenario with no fishing and high fishing mortality on menhaden was a 7% increase in landings between these two scenarios. SSB showed a 25% increase in the no fishing on menhaden and high fishing pressure on striped bass scenario, making this the biggest trade-off across scenarios. The trade-offs were more modest over the medium-term than in the long-term trade-offs examined.

Long-term projections – Effects on Menhaden

Two long-term scenarios were investigated for their impacts on menhaden. Under $F = 0.1$ for striped bass and $F = 0$ for menhaden, menhaden SSB began at 838 tmt and ended after the 100-year projection at 2,491 tmt (Figure 17). Under $F = 0.3$ for striped bass and $F = 0$ for menhaden, menhaden SSB began at 838 tmt and ended after the 100-year projection at 4,988 tmt (Figure 17).

The natural mortality for the two long-term scenarios investigated for menhaden had different trends. Under $F = 0.1$ for striped bass and $F = 0$ for menhaden, *M* had a short period of increase and then declined to a stable but low level of *M* relative to the starting values (Figure 18). Under $F = 0.3$ for striped bass and $F = 0$ for menhaden, *M* declined through the projection period to values lower than the starting values, and lower than in the lower *F* scenario for striped bass (Figure 18).

Interactions between predator and prey populations

Predator and prey interactions across a range of fishing mortalities general showed significant interplay at low fishing mortality levels for each species, after which further increases did not indicate further inter-species effects (Figures 19 and 20). For the case of menhaden, a fishing mortality rate of 0.1 corresponded to a biomass level between 790 and 1190 tmt when striped bass fishing mortality was 0.05 or less, and this increased to a range between 1590 and 1190 tmt when striped bass fishing mortality was increased to a range of 0.09 to 0.19, while menhaden were still under a 0.1 fishing mortality scenario. Menhaden biomass was maximized to greater than 1990 tmt when menhaden fishing mortality was lower than 0.1 and striped bass fishing mortality was greater than 0.19.

Conversely for striped bass, a fishing mortality rate of 0.1 corresponded to a biomass level greater than 230 tmt when menhaden fishing mortality was less than 0.025, and this decreased to a range between 230 and 190 tmt in striped bass biomass (still under a 0.1 fishing mortality rate for striped bass) when menhaden fishing mortality was increased to a range of 0.025 to 0.05. Striped bass biomass continued to decrease as menhaden fishing mortality increased to 0.13, at which point further increases on menhaden fishing mortality did not impact biomass levels of striped bass anymore.

DISCUSSION

Despite the numerous research projects on the topic (Uphoff 2003; Overton et al. 2003; Jacobs et al. 2009; Latour et al. 2012) that indicated a local effect of lack of forage reducing striped bass weight-at-age, this study did not find any strong signals

between changes in menhaden biomass levels in the coastwide stock and decreased growth in striped bass as observed in the mean weight-at-age through time. This does not indicate that this feedback does not exist between these two species, however there does not appear to be a signal in the data examined for this study, which is at the scale of the coastwide population. Many of the studies that have examined this relationship between diet and growth of striped bass have been focused in the Chesapeake Bay, and there may be a more localized effect that is easier to observe given that there is an abundance of data and long-term monitoring programs that occur in the Chesapeake that can be analyzed. However, when broadening that view to the coastwide populations as done for this study, a signal in the empirical data was not found.

While prey-dependent growth in striped bass was not discovered when looking at the coastwide population, a different feedback mechanism was revealed. When examining the consumption of menhaden by striped bass as determined by a multispecies stock assessment model, a significant correlation was discovered, indicating that there may be a link between decreased consumption of menhaden by striped bass and apparent increased natural mortality in striped bass. There is support in the literature for this linkage (Uphoff 2003, Jiang et al. 2007, Sadler 2010, Jacobs et al. 2009) and there is also a causative agent in mycobacteriosis, which is implicated in this increased mortality (Gauthier et al. 2008, Overton et al. 2003). Given the apparent relationship between increased natural mortality when consumption of menhaden by striped bass declines, the effects that this feedback might have on these two important finfish species was further investigated by programing this dynamic in to a multispecies stock assessment model and then using the parameters generated by the

model to project these population dynamics into the future under different management scenarios.

A continuum of management scenarios was developed for both the medium-term and long-term to examine the trade-offs that might be present under different management scenarios over different time periods. The interest lies in how the top-down and bottom-up processes impact the population of interest under different management implementations as it may not be straight forward depending on how the dynamics work. The scenarios selected were picked to illustrate the dynamics, therefore it is not intended that the fishing mortalities at the levels chosen for this exercise be implemented. These cases were chosen to illustrate the possible dynamics and what the boundaries of those dynamics might be.

For the cases examined here, it was evident under all scenarios that when fishing mortality was high on menhaden, the population of striped bass declined more rapidly than when there was no fishing mortality on menhaden when accounting for this bottom-up process. Additionally, the outcomes from the management strategies chosen for striped bass all improve under a no-fishing scenario on menhaden relative to when there is high fishing mortality on menhaden. The cause of this is, as fishing mortality is increased on striped bass, the impact of those removals are mitigated to some extent by the relative lowering of M due to there being ample menhaden around to consume, so this other removal mechanism on the population, namely M, is decreased, thereby slowing the decline and improving the population metrics such as SSB and landings.

This same interaction between predator and prey was seen in the species interaction graphs, where for a given fishing mortality of striped bass, the biomass level would be higher for lower levels of fishing mortality on menhaden. The converse was true for menhaden in that for a given fishing mortality on menhaden, the biomass level would be higher given an increasing level of fishing mortality on striped bass. This interaction again shows both the bottom up and top down controls on the interacting populations.

A second finding that holds across all scenarios examined is the trade-offs occurring between striped bass and menhaden through time. In the cases of low *F* on striped bass, the striped bass population starts the projection at a high level, which in turn, because predation mortality on menhaden increases, drives the menhaden population down. As the menhaden population declines, the ratio of consumption of menhaden biomass to the population biomass of striped bass declines, and this impacts striped bass by increasing *M* and decreasing the population over the medium term. There seems to be a critical population level for menhaden around 200 tmt. If the population of menhaden drops to this point, the impact on *M*-rates for striped bass increases, though in all cases the striped bass population does find a new equilibrium level. The magnitude of this equilibrium depends on the striped bass *F* scenario examined.

Another scenario showing similar declines but for different reasons is the case where *F* is high on striped bass. Here it is fishing that is driving the population low from the beginning of the projection, where the menhaden population does not decline to the extent that is seen in the low *F* on both menhaden and striped bass scenarios.

Regardless of the scenario, once the striped bass population declines, important fishing removals on menhaden are released, and the menhaden population is able to rebound to high levels in all cases. Even with the high abundance of menhaden in these scenarios, *M1* increases for striped bass due to the fact that their population is at such a low level, exacerbated by the age structure being truncated to the youngest age classes of striped bass, so the consumption of menhaden decreases relative to the number of young striped bass left in the population.

When viewing the management trade-offs across all scenarios, the cases where there was no fishing on menhaden produced more favorable outcomes for striped bass than when fishing mortality was high on menhaden regardless of what the *F* was on striped bass.

When landings are considered, the most significant trade-off is shown under the low *F* on striped bass scenarios in both the medium and long-terms. The magnitude of the tradeoff is substantial in the long term when there is a low level of *F*, however the magnitude of this trade-off is much less over the medium term. While lower in the medium-term, an ability to achieve a net gain of seven percent is significant in a management context. It is also of interest to see that in the long-term, there is a small difference (~10%) between the low and medium *F* strategies for striped bass under the no menhaden fishing scenario, showing that there is some compensation occurring between the two sources of removals.

The picture is different when reviewing SSB. For SSB the scenario in the long-term that produced the highest SSB over the projection period was the no fishing on menhaden and low fishing mortality on striped bass case, however in the medium term

it was the high *F* on striped bass and no fishing on menhaden that produced the largest trade-off in SSB. Over both the medium and long terms, the low *F* on striped bass and no menhaden fishing produced the highest SSB level by the end of the projection. This indicates that low fishing on striped bass would always be a good strategy to protect the spawning stock, however the relative benefit between that and other *F* strategies decreases over time due to the interaction between *F* and *M*.

Even though the studies looking at impacts to natural mortality examined in this research project focused on the Chesapeake Bay, this area is of critical importance to the entire coastal population as the largest producer area for striped bass on the east coast (ASMFC 2015). There is reason to believe that this prey-dependent effect occurs to some degree throughout the population (Jiang 2007, Sadler 2010); however, even if it doesn't, the impacts that occur in the Chesapeake can have repercussions on the entire coastwide population (Gauthier 2008). Therefore, the exploration of these prey-dependent effects to the striped bass population are relevant and can provide valuable information to managers by showing that indirect effects from management on other species in the ecosystem can have cascading effects on other species, thus affecting the performance of the management program on these other species. As shown in this study, when fishing mortality is high on an important prey item for striped bass, this can affect the amount of yield received and can impact the population by way of reducing spawning stock. If these indirect linkages are not accounted for, management that is implemented may not perform as expected, or worse, management could be inadvertently set in a more risk-prone way that could have long-term negative consequences for the population.

One area that warrants further examination is exploring other models to define the density-dependent effect seen on striped bass mortality. Other studies investigating disease influenced mortality on fish species have examined other models such as Pareto, Gompertz, and log-logistic models (Gauthier 2008, Heisey et al. 2006), but the two-parameter Weibull model was examined here to keep the analysis as parsimonious as possible so that the effects on the dynamics were tractable given all the other complexities in the population dynamics model. This work could be extended to test other models and to compare those models to test for improved diagnostic performance of the estimation model.

In conclusion, the empirical information examined in this study indicates that there may be a link between decreased consumption of menhaden by striped bass and increased natural mortality in the striped bass population. The investigation was then extended to look at the impacts that this dynamic has on the two populations by programming the prey-dependent mortality into a multispecies estimation model which focused on the two species of interest. Once the estimation model was generated, the parameters from the estimation model were used to project the population forward in time to examine trade-offs that occur under a set of simple management strategies. These trade-offs were found to be important and analyses like these can offer important information to mangers by way of giving them more information to consider when developing measures that attempt to meet goals. The indirect impacts across species can impact the outcome of those goals and should be considered carefully to allow for more realistic expectations.

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TABLES

Table 1: External estimates of natural mortality (*M1*) from the 2009 benchmark stock assessment for striped bass.

Year	Pre-migratory ages	Migratory ages
1987	0.15	0
1988	0.27	0.07
1989	0.03	0.09
1990	0.49	0.30
1991	0.28	0.24
1992	0.38	0.17
1993	0.52	0.23
1994	0.37	0.20
1995	0.55	0.21
1996	0.24	0.24
1997	0.62	0.21
1998	0.91	0.19
1999	0.83	0.28
2000	1.11	0.37
2001	0.83	0.46
2002	0.56	0.47
2003	0.41	0.39
2004	1.3	0.44
2005	0.98	0.43
2006	1.11	0.38
2007	1.21	0.46
2008	0.76	0.43

Table 2: Striped bass annual average *M1* as assumed for the MSSCAA model.

Age Class	Natural Mortality Value
Age 1	1.13
Age 2	0.68
Age 3	0.45
Age 4	0.33
Age 5	0.25
Age 6	0.19
Age 7	0.15
Age 8	0.15
Age 9	0.15
Age 10	0.15
Age 11	0.15
Age 12	0.15
Age 13+	0.15

Table 3: Table showing the trade-off in landings between two menhaden *F* scenarios (*F* = 0 and *F* = 0.9) and three striped bass *F* scenarios (*F* = 0.1, *F* = 0.2, and *F* = 0.3). This table shows the long-term trade-offs in the sum of landings of striped bass and are reported in thousands of metric tons.

	Striped Bass		
	Low *F*	**Medium *F***	**High *F***
No *F* on menhaden	1,218	1,095	1,040
High *F* on menhaden	653	691	758

Table 4: Table showing the trade-off in *SSB* between two menhaden *F* scenarios (*F* = 0 and *F* = 0.9) and three striped bass *F* scenarios (*F* = 0.1, *F* = 0.2, and *F* = 0.3). This table shows the long-term trade-offs in the terminal year *SSB* of striped bass and are reported in thousands of metric tons.

	Striped Bass		
	Low *F*	**Medium *F***	**High *F***
No *F* on menhaden	89	21	8
High *F* on menhaden	24	7	4

Table 5: Table showing the trade-off between two menhaden *F* scenarios (*F* = 0 and *F* = 0.9) and three striped bass *F* scenarios (*F* = 0.1, *F* = 0.2, and *F* = 0.3). This table shows the medium-term trade-offs in the sum of landings of striped bass and are reported in thousands of metric tons.

	Striped Bass		
	Low *F*	**Medium *F***	**High *F***
No *F* on menhaden	153	228	267
High *F* on menhaden	142	213	250

Table 6: Table showing the trade-off between two menhaden *F* scenarios (*F* = 0 and *F* = 0.9) and three striped bass *F* scenarios (*F* = 0.1, *F* = 0.2, and *F* = 0.3). This table shows the medium-term trade-offs in the terminal year SSB of striped bass and are reported in thousands of metric tons.

	Striped Bass		
	Low *F*	**Medium *F***	**High *F***
No *F* on menhaden	106	50	24
High *F* on menhaden	87	40	18

FIGURES

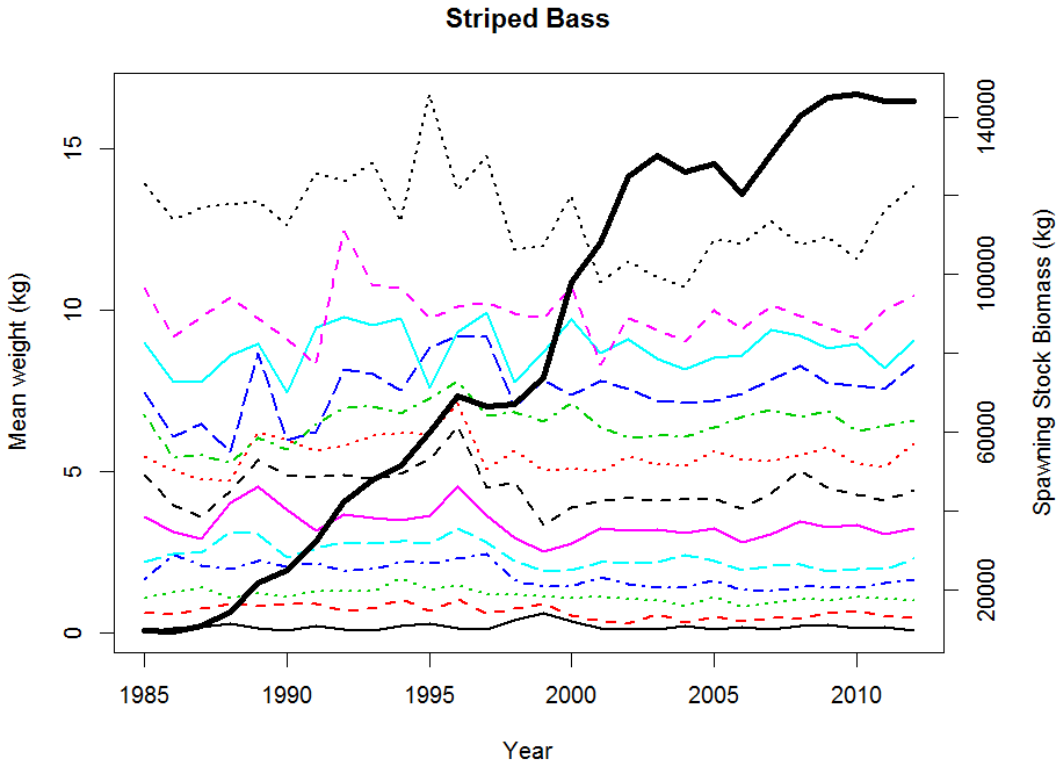

Fig. 1: Striped bass weight-at-age with striped bass SSB trajectory superimposed (thick solid black line).

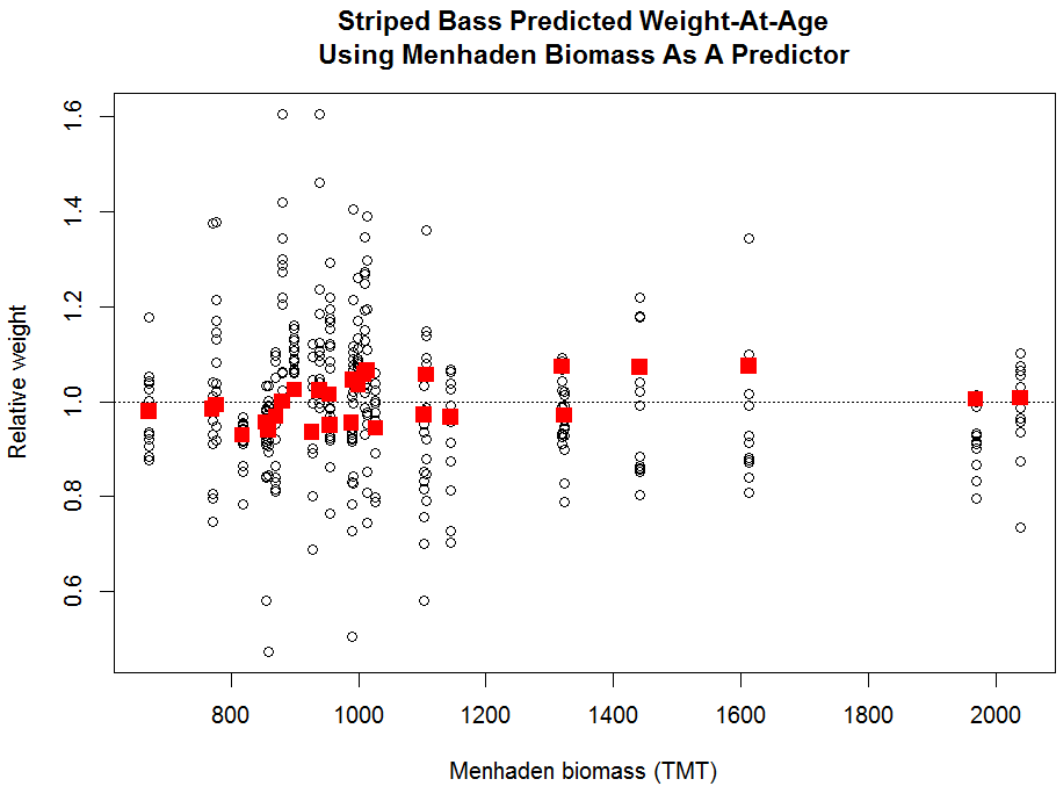

Fig. 2: Striped bass predicted (red filled squares) and observed (open circles) relative weight at age.

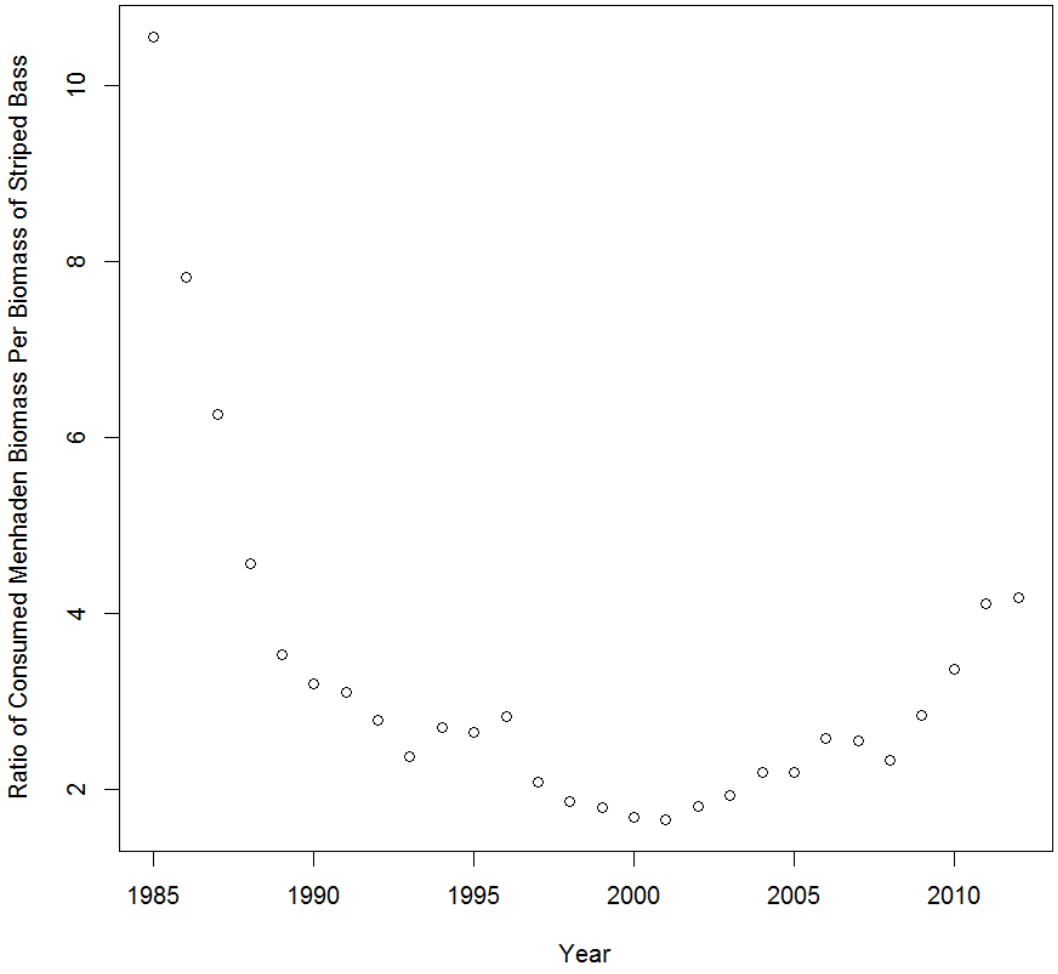

Fig. 3: Ratio of consumed menhaden biomass per striped bass total biomass for ages 3 through 12 from the two-species multispecies model through time.

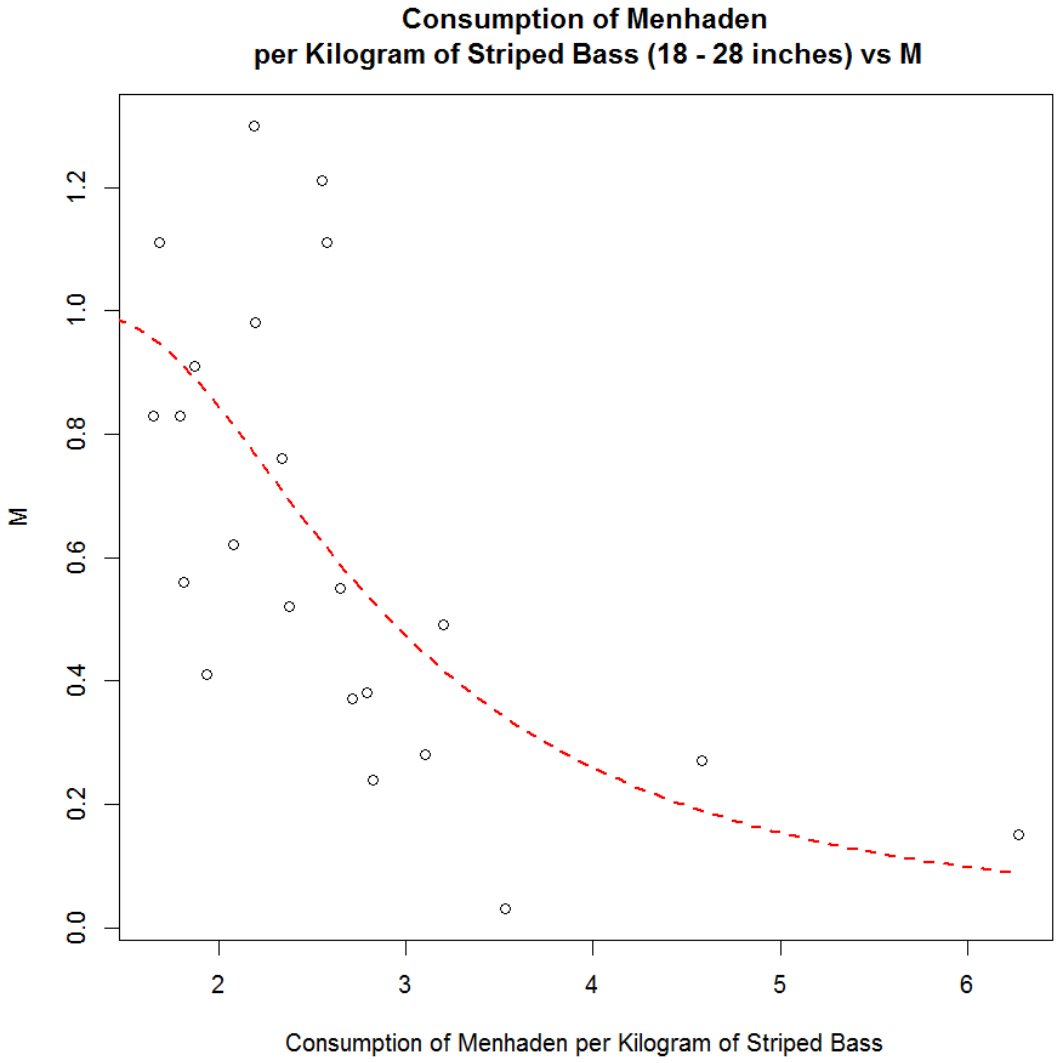

Fig. 4: Fit between the predicted Weibull model (red dashed line) and the ratio of consumed menhaden to striped bass biomass for the two-species multispecies model. This plot represents the pre-migratory portion of the population.

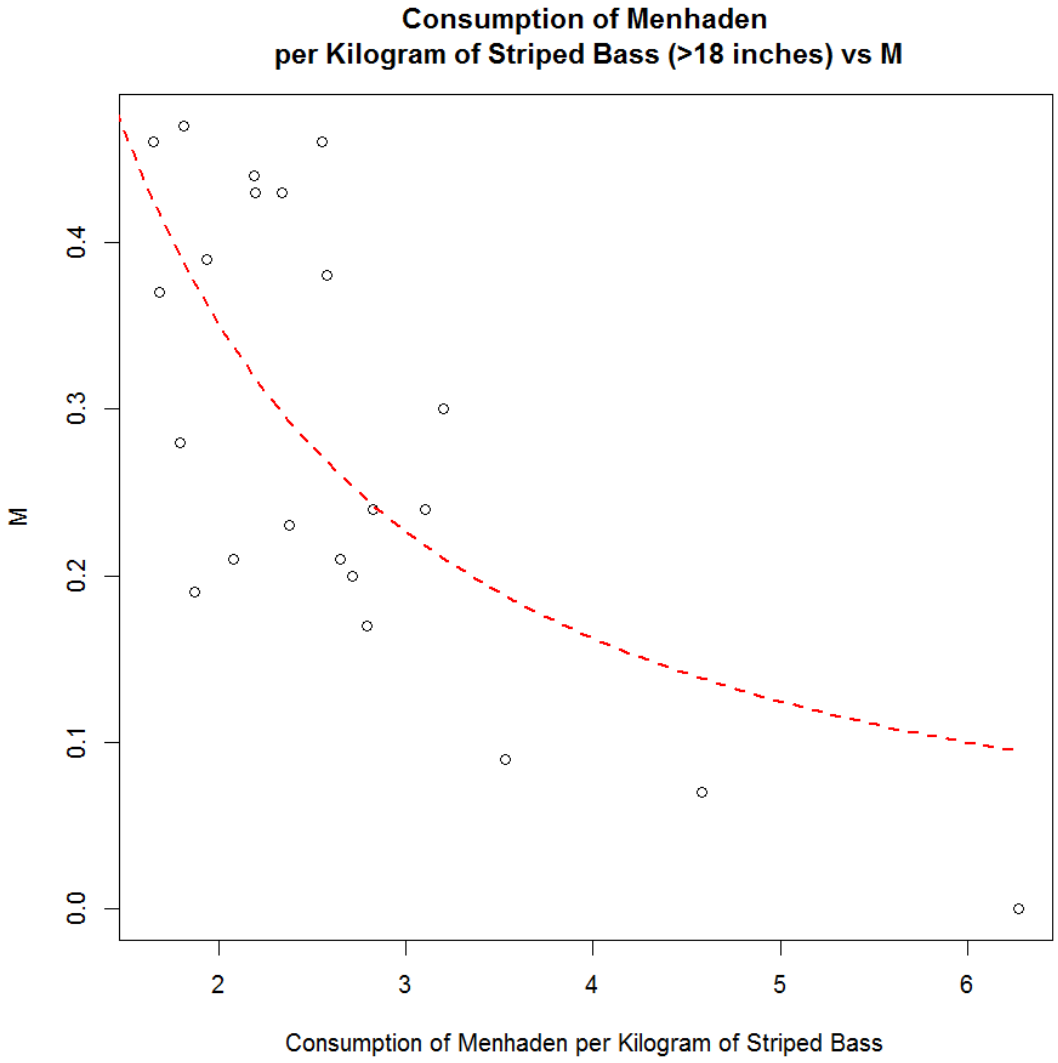

Fig. 5: Fit between the predicted Weibull model (red dashed line) and the ratio of consumed menhaden to striped bass biomass for the two-species multispecies model. This plot represents the migratory portion of the population.

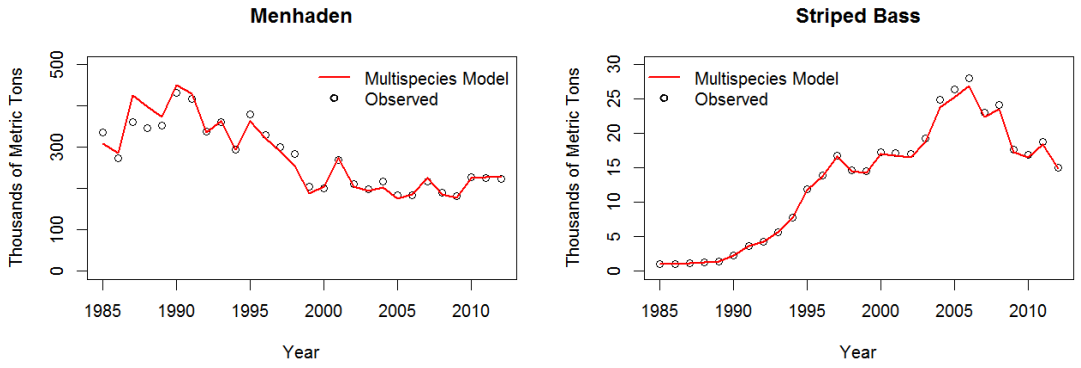

Fig. 6: Observed and predicted catch from the 2-species multispecies model with time varying *M1* for striped bass.

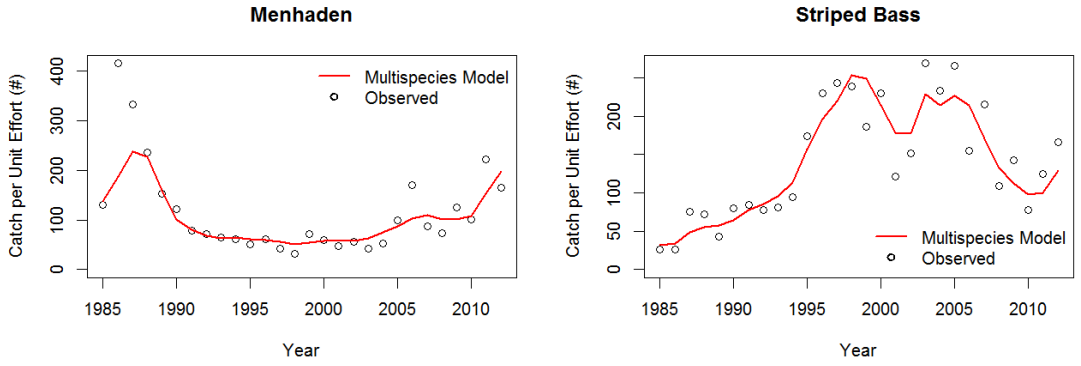

Fig. 7: Observed and predicted fishery independent catch per unit effort from the 2-species multispecies model with time varying *M1* for striped bass.

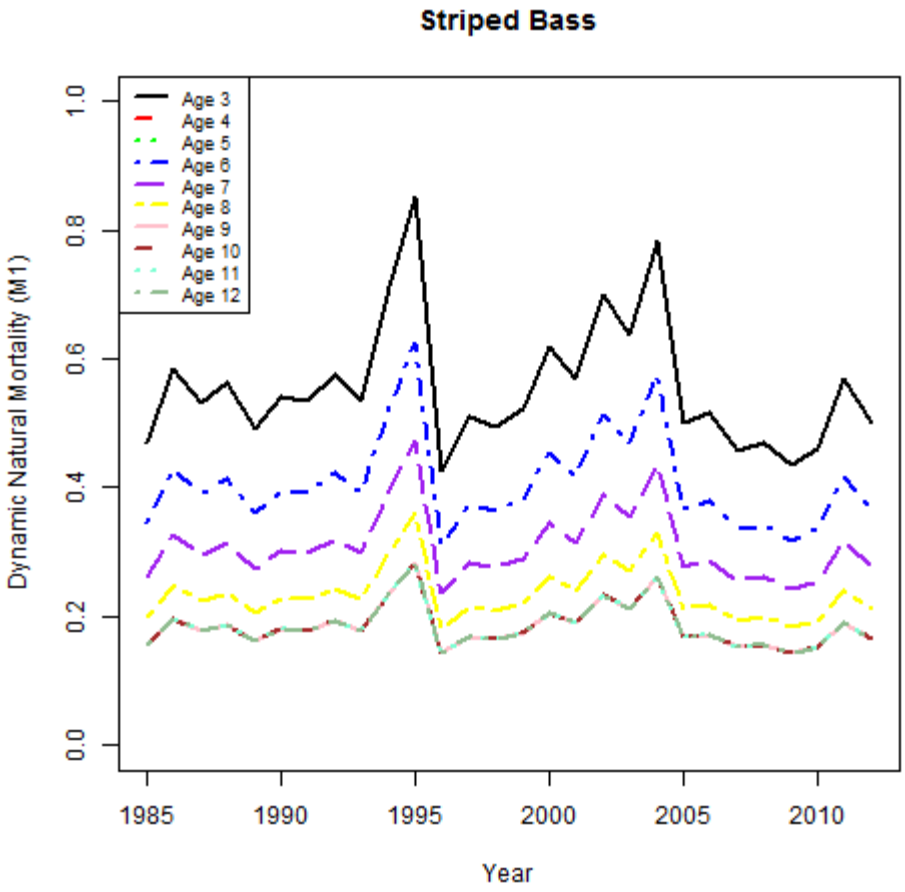

Fig. 8: Predicted *M1-at-age* for striped bass from the 2-species multispecies model. The lines for ages 7 – 12 overlay on top of each other as they show the same trend and magnitude through time.

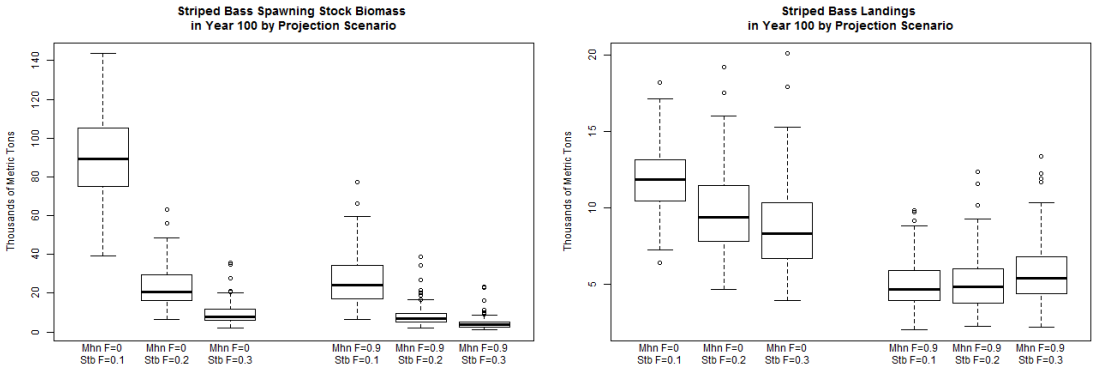

Fig. 9: Long-term projected spawning stock biomass and landings for striped bass under the six menhaden and striped bass mortality combinations. This projection assumes median recruitment.

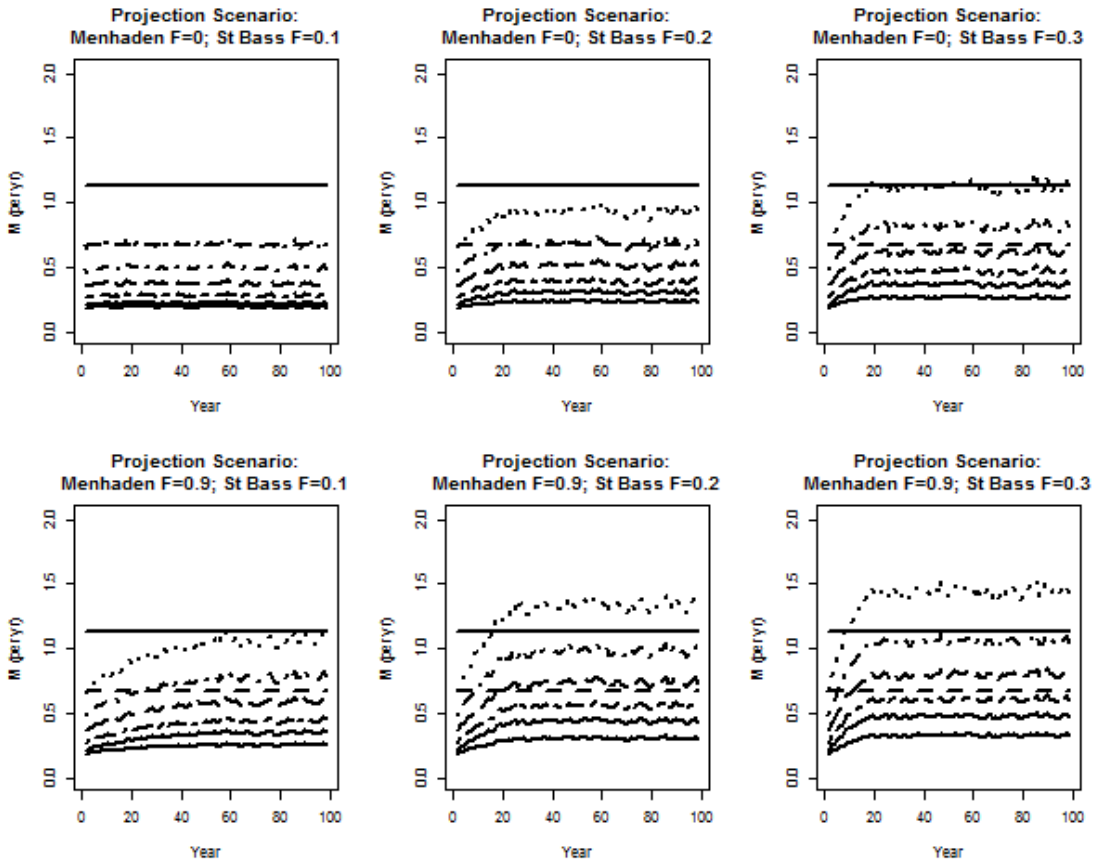

Fig. 10: Long-term projected natural mortality at-age for striped bass by projection scenario. This projection assumes median recruitment. The different lines represent *M*-at-age. Note: ages 1 and 2 are static through time.

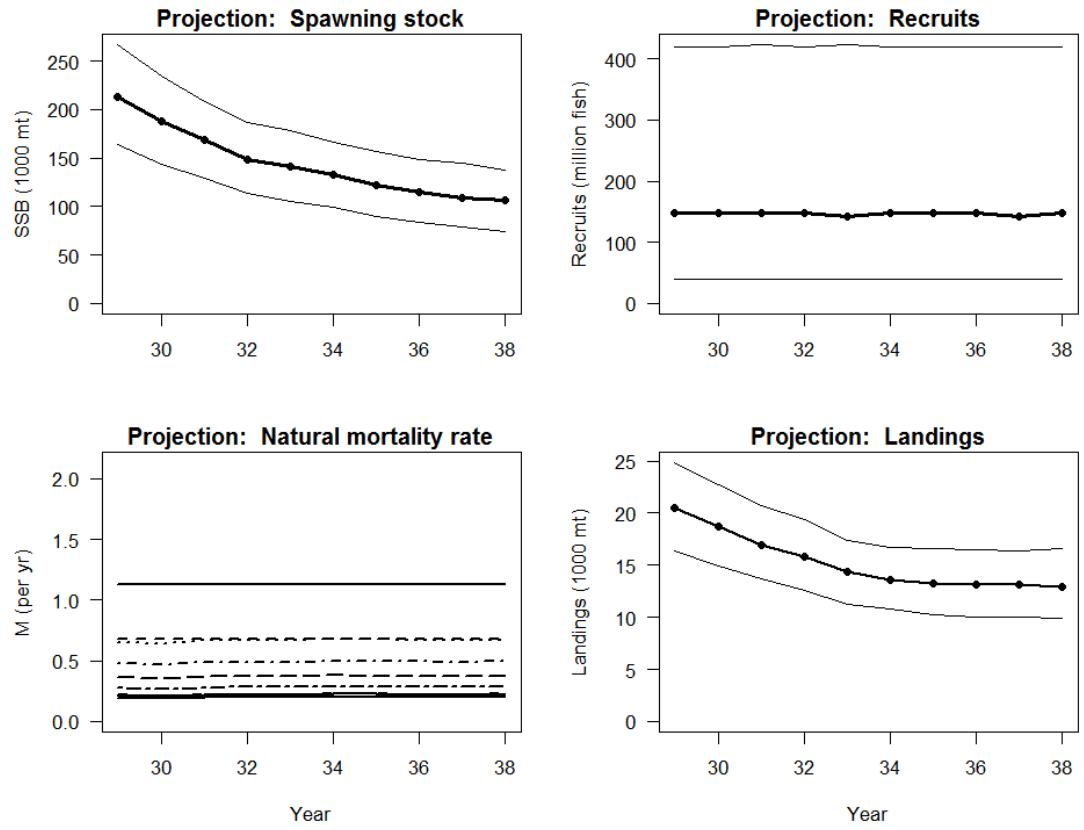

Fig. 11: Medium -term projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under $F = 0$ for menhaden and $F = 0.1$ for striped bass. This projection assumes median recruitment. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

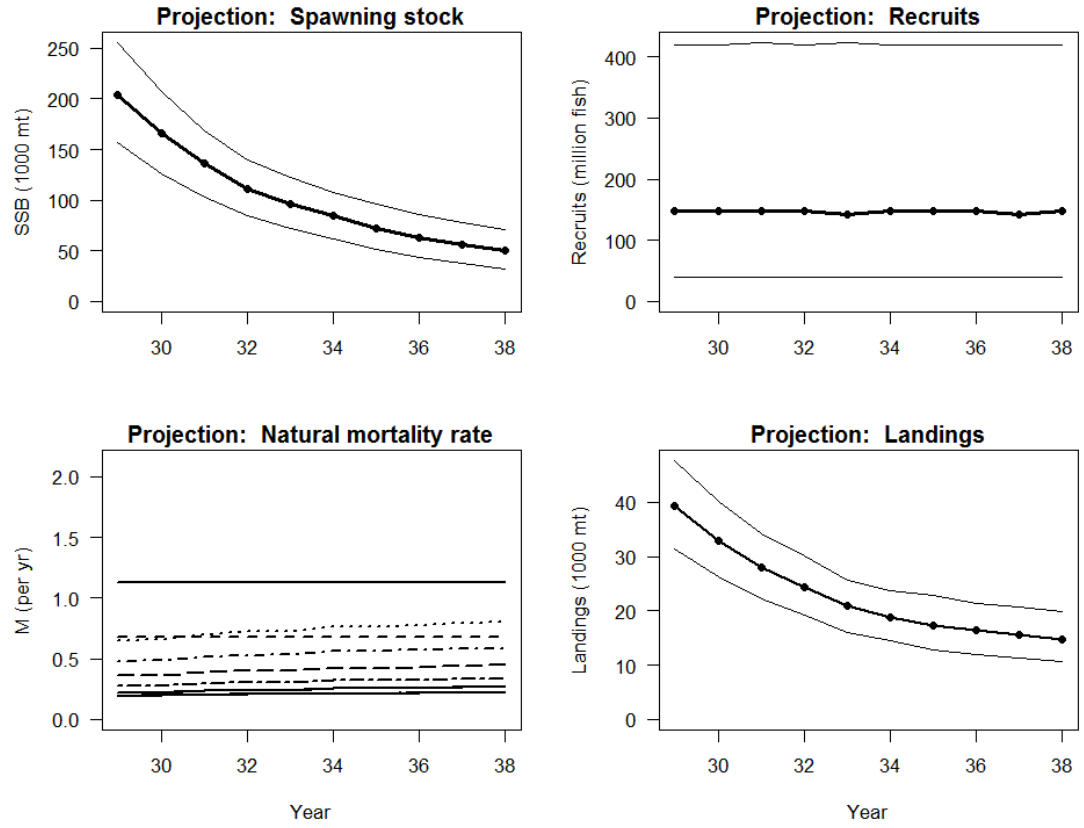

Fig. 12: Medium -term projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under $F = 0$ for menhaden and $F = 0.2$ for striped bass. This projection assumes median recruitment. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

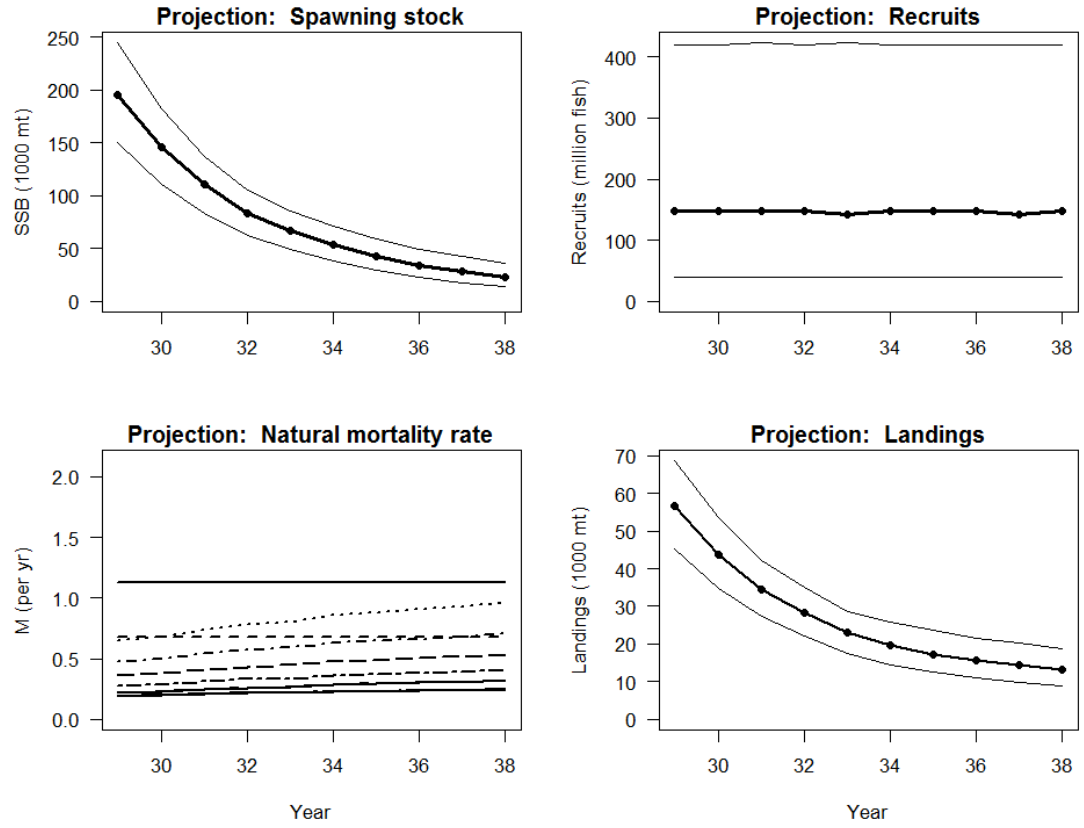

Fig. 13: Medium-term projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under $F = 0$ for menhaden and $F = 0.3$ for striped bass. This projection assumes median recruitment. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

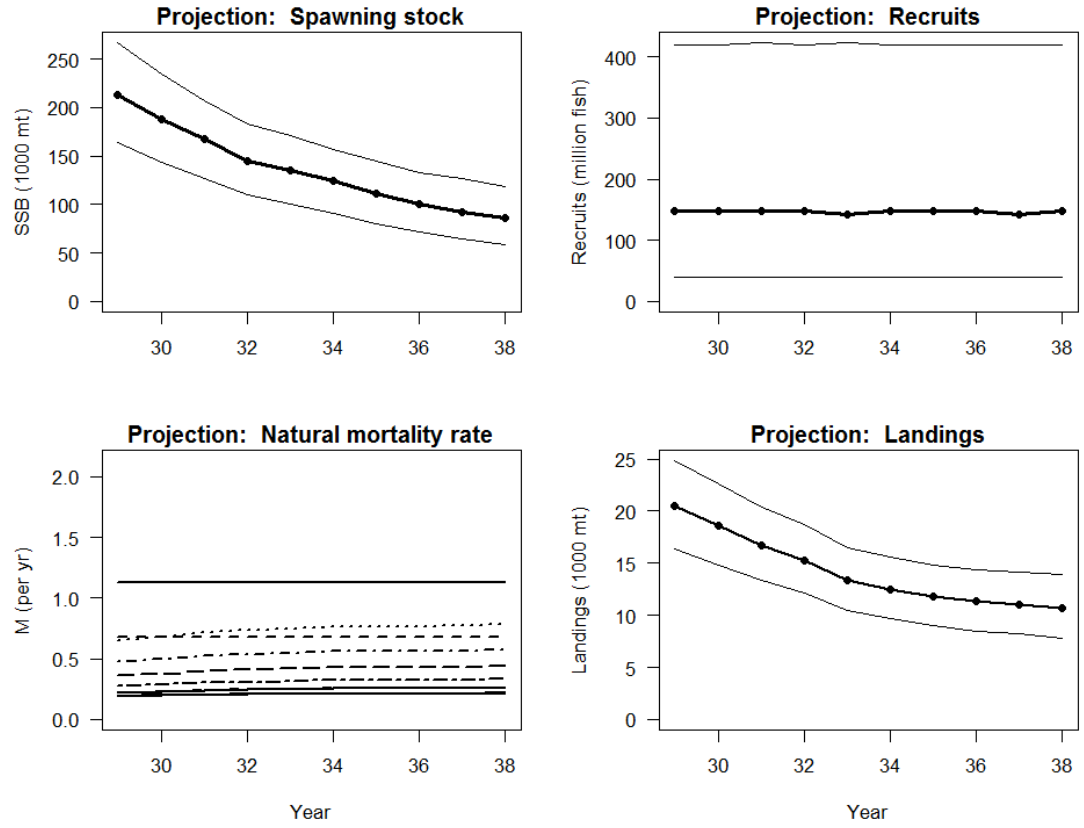

Fig. 14: Medium-term projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under $F = 0.9$ for menhaden and $F = 0.1$ for striped bass. This projection assumes median recruitment. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

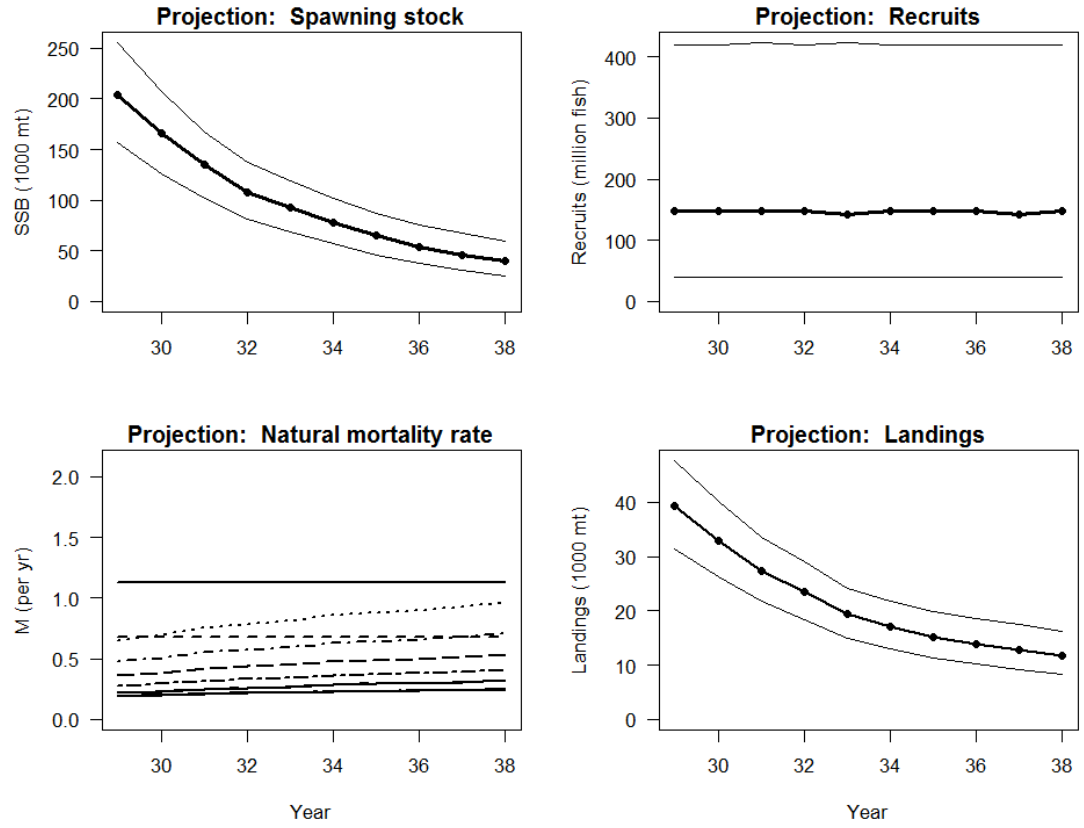

Fig. 15: Medium -term projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under $F = 0.9$ for menhaden and $F = 0.2$ for striped bass. This projection assumes median recruitment. For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent M-at-age.

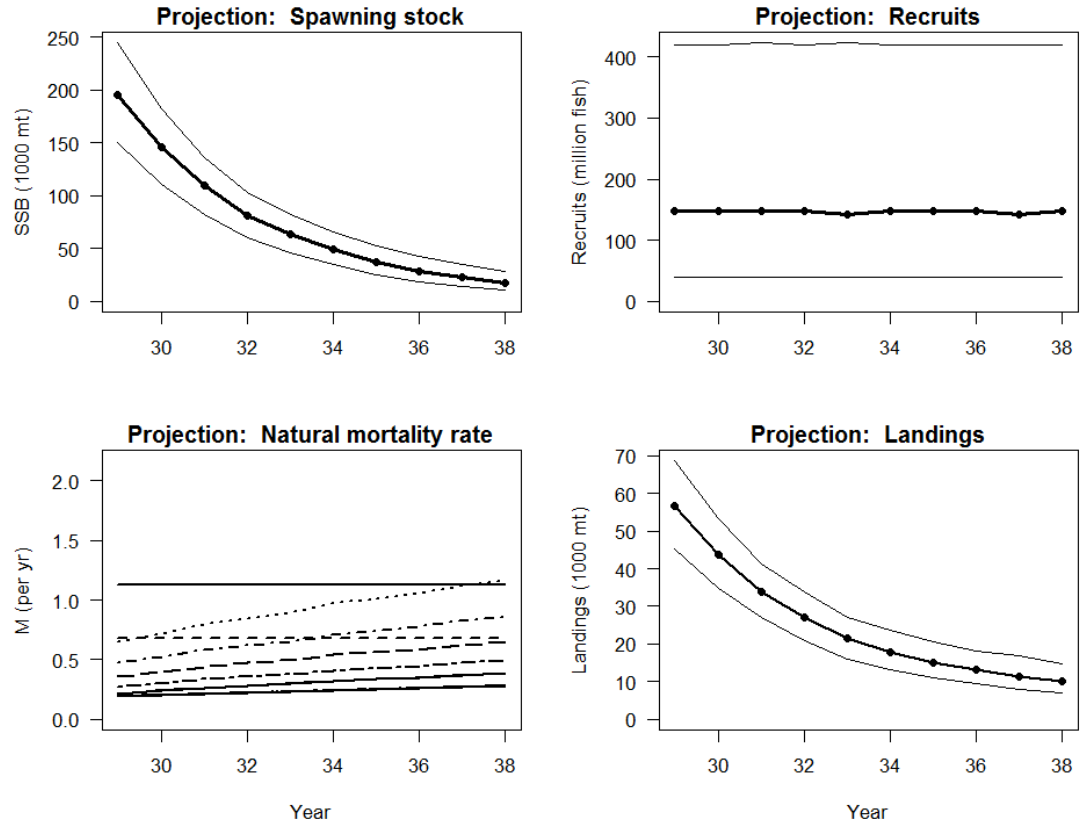

Fig. 16: Medium -term projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under $F = 0.9$ for menhaden and $F = 0.3$ for striped bass. This projection assumes median recruitment. For the *SSB*, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

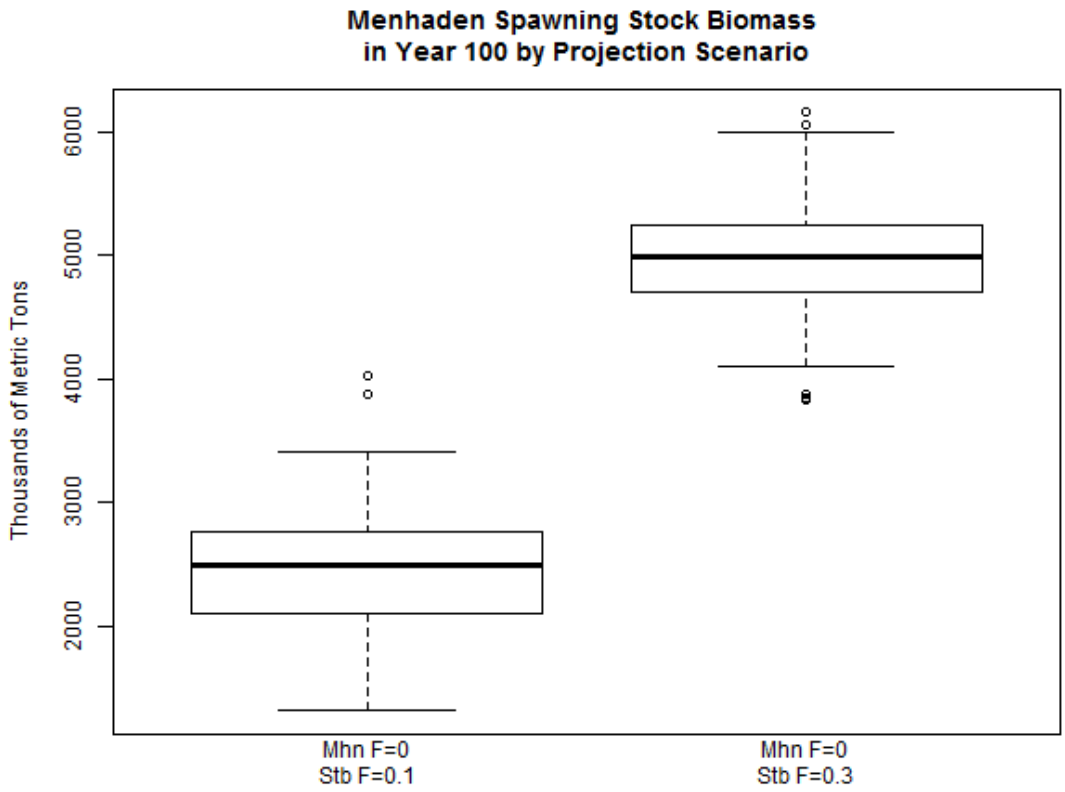

Fig. 17: Long -term projected spawning stock biomass for menhaden under two projection scenarios. This projection assumes median recruitment.

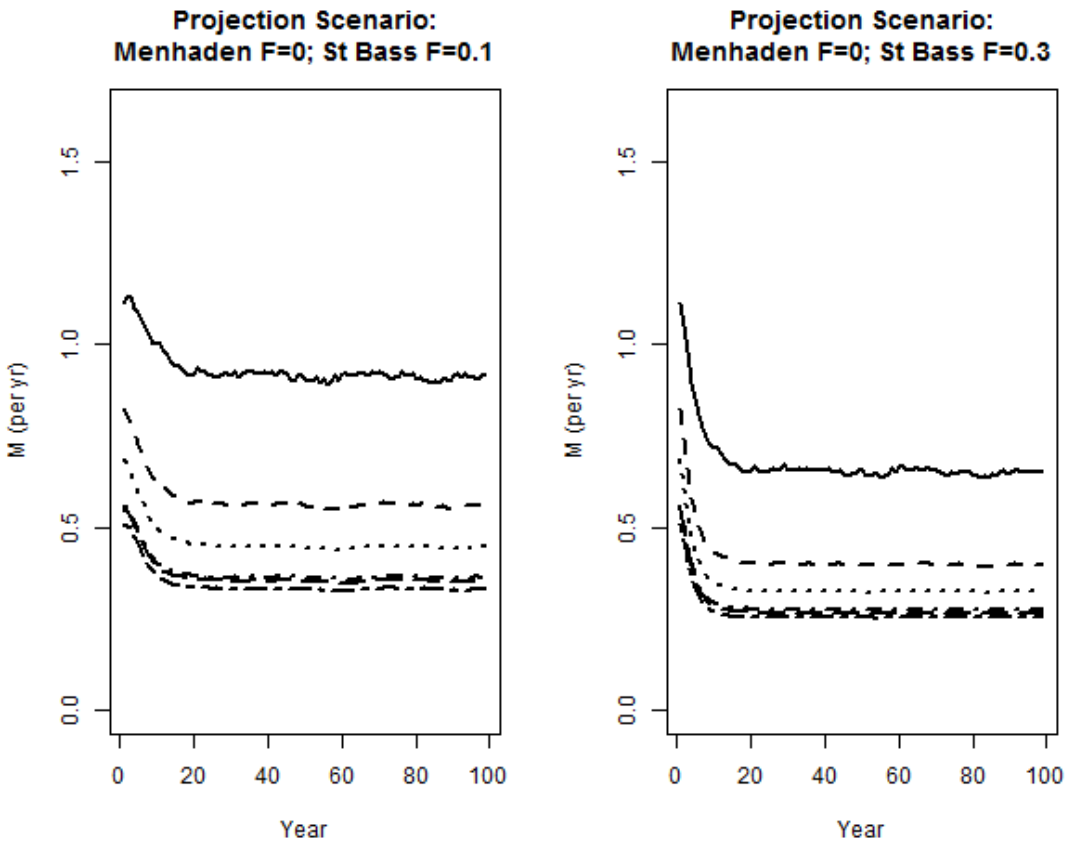

Fig. 18: Long -term projected natural mortality at-age for menhaden under two different projection scenarios. This projection assumes median recruitment. The different lines represent *M*-at-age.

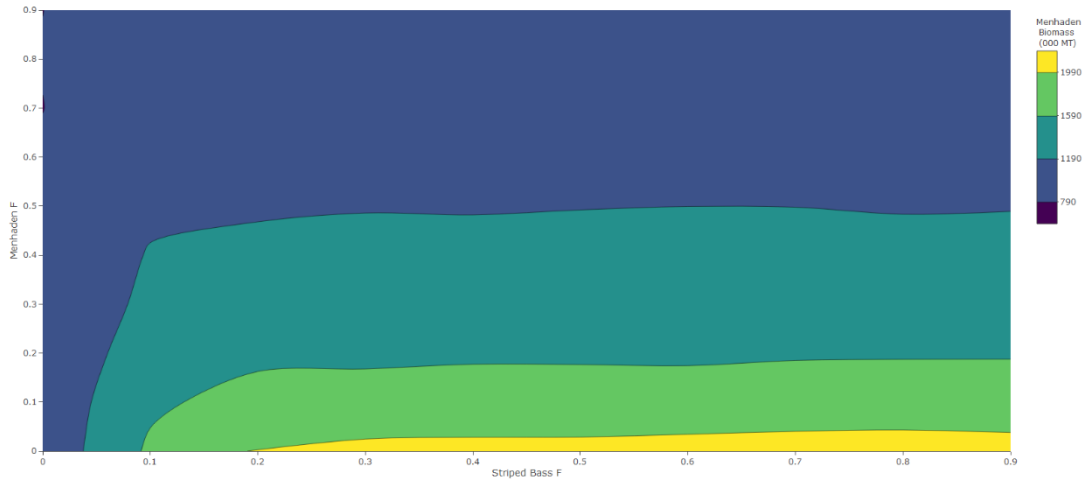

Fig. 19: The effect of different combinations of F on striped bass and menhaden on the biomass of menhaden. The different colored contours in the plot represent different levels of menhaden biomass in thousands of metric tons, while the x and y axes show the level of species specific F for that area of the plot.

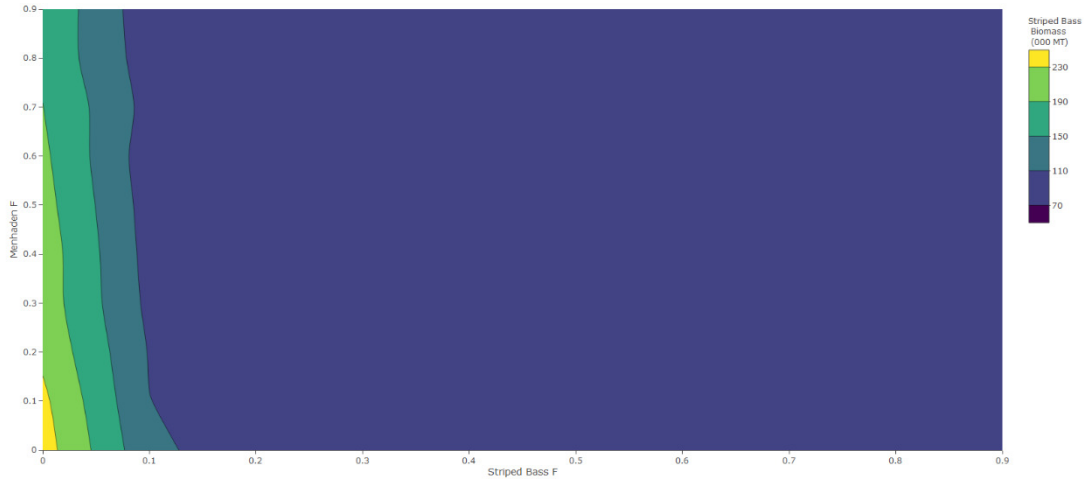

Fig. 20: The effect of different combinations of F on striped bass and menhaden on the biomass of striped bass. The different colored contours in the plot represent different levels of striped bass biomass in thousands of metric tons, while the x and y axes show the level of species specific F for that area of the plot.

APPENDIX

Table A1: Striped bass weight-at-age for the years of 1985 through 2012.

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13+
1985	0.06	0.61	1.07	1.66	2.19	3.59	4.91	5.46	6.77	7.45	9	10.69	13.91
1986	0.14	0.57	1.27	2.4	2.44	3.12	3.95	5.05	5.44	6.09	7.75	9.16	12.78
1987	0.2	0.77	1.41	2.11	2.5	2.91	3.61	4.74	5.52	6.49	7.77	9.78	13.15
1988	0.31	0.91	1.1	1.98	3.12	4.02	4.38	4.7	5.24	5.62	8.58	10.4	13.27
1989	0.16	0.83	1.22	2.23	3.06	4.53	5.37	6.23	6.04	8.68	8.94	9.74	13.36
1990	0.08	0.89	1.14	2.05	2.35	3.83	4.91	5.96	5.7	5.97	7.44	9.08	12.6
1991	0.21	0.92	1.29	2.17	2.62	3.17	4.81	5.64	6.46	6.24	9.46	8.3	14.22
1992	0.1	0.69	1.31	1.93	2.81	3.67	4.9	5.79	6.96	8.15	9.77	12.44	13.97
1993	0.07	0.76	1.31	1.99	2.77	3.58	4.8	6.11	7.03	8.01	9.53	10.76	14.55
1994	0.24	1.05	1.69	2.21	2.85	3.5	4.94	6.2	6.8	7.53	9.73	10.69	12.73
1995	0.28	0.7	1.35	2.18	2.77	3.65	5.38	6.16	7.27	8.86	7.57	9.73	16.66
1996	0.14	1.05	1.47	2.32	3.23	4.52	6.39	7.11	7.81	9.2	9.31	10.1	13.7
1997	0.13	0.62	1.18	2.46	2.81	3.64	4.51	5.07	6.73	9.17	9.94	10.24	14.78
1998	0.39	0.77	1.2	1.62	2.25	2.95	4.69	5.66	6.82	7.03	7.76	9.87	11.87
1999	0.62	0.9	1.11	1.44	1.91	2.51	3.36	5.03	6.56	7.85	8.69	9.76	11.98
2000	0.37	0.55	1.1	1.45	1.96	2.79	3.89	5.09	7.11	7.37	9.7	10.7	13.55
2001	0.16	0.38	1.12	1.75	2.21	3.25	4.12	5.02	6.36	7.79	8.65	8.29	10.87
2002	0.12	0.31	1.06	1.51	2.18	3.17	4.19	5.48	6.03	7.56	9.09	9.75	11.52
2003	0.1	0.6	1	1.4	2.2	3.2	4.1	5.2	6.1	7.2	8.5	9.4	11
2004	0.23	0.33	0.84	1.4	2.43	3.11	4.14	5.17	6.07	7.12	8.18	9.03	10.71
2005	0.13	0.5	1.14	1.64	2.22	3.23	4.18	5.64	6.38	7.21	8.51	10	12.19

Table A1 (cont.): Striped bass weight-at-age for the years of 1985 through 2012.

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13+
2006	0.18	0.38	0.81	1.35	1.96	2.8	3.84	5.35	6.7	7.41	8.58	9.4	12.05
2007	0.1	0.46	0.94	1.3	2.1	3.07	4.31	5.32	6.89	7.84	9.39	10.12	12.77
2008	0.21	0.45	1.04	1.43	2.14	3.47	5.05	5.51	6.69	8.26	9.19	9.82	12
2009	0.26	0.62	1.03	1.41	1.92	3.29	4.49	5.74	6.87	7.73	8.81	9.47	12.24
2010	0.16	0.7	1.11	1.41	1.99	3.34	4.27	5.21	6.27	7.65	8.97	9.15	11.59
2011	0.2	0.52	1.04	1.55	2	3.08	4.1	5.13	6.41	7.54	8.2	9.98	13.08
2012	0.08	0.48	1.01	1.67	2.3	3.25	4.44	5.88	6.57	8.31	9.05	10.41	13.84

Table A2: Matrix of correlation values between menhaden biomass-by-age and striped bass weight-at-age. None of the correlations are significant ($\alpha = 0.05$) based on multiple pairwise analysis with Holm adjustment.

Striped bass weight-at-age	Menhaden Biomass Age 1	Menhaden Biomass Age 2	Menhaden Biomass Age 3	Menhaden Biomass Age 4	Menhaden Biomass Age 5	Menhaden Biomass Age 6
1	-0.18	-0.38	-0.05	0.1	-0.07	-0.34
2	-0.3	-0.13	0.02	0.18	0.17	0.1
3	-0.37	0.02	0.15	-0.1	-0.09	-0.07
4	-0.42	0.21	0.18	0.05	0.14	0.15
5	-0.42	-0.03	0.06	0.3	0.31	-0.04
6	-0.13	-0.02	-0.17	0.26	0.56	0.21
7	-0.07	0	-0.29	-0.08	0.24	0.1
8	-0.01	0.07	-0.31	-0.33	0.1	-0.04
9	0.16	-0.15	-0.41	-0.5	-0.36	-0.35
10	0.2	-0.11	-0.25	-0.39	0.03	-0.37
11	0.06	-0.19	-0.25	-0.1	-0.03	-0.26
12	0.09	0	-0.08	0.1	-0.05	-0.07
13	-0.03	0.22	0.06	0.03	0	0.11

Table A3: Matrix of correlation values between menhaden aggregated biomass and striped bass weight-at-age. None of the correlations are significant ($\alpha = 0.05$) based on multiple pairwise analysis with Holm adjustment.

Striped bass weight-at-age	Menhaden Biomass Age 1 -2	Menhaden Biomass Age 1-3	Menhaden Biomass Age 1-4	Menhaden Biomass Age 1-5	Menhaden Biomass Age 1-6
1	-0.34	-0.34	-0.32	-0.33	-0.34
2	-0.29	-0.26	-0.23	-0.22	-0.21
3	-0.25	-0.18	-0.2	-0.2	-0.2
4	-0.17	-0.1	-0.1	-0.08	-0.08
5	-0.31	-0.27	-0.22	-0.2	-0.19
6	-0.1	-0.15	-0.1	-0.07	-0.05
7	-0.05	-0.15	-0.16	-0.14	-0.13
8	0.04	-0.07	-0.12	-0.11	-0.11
9	0.03	-0.11	-0.19	-0.21	-0.23
10	0.07	-0.01	-0.08	-0.07	-0.09
11	-0.07	-0.15	-0.17	-0.17	-0.18
12	0.06	0.04	0.05	0.05	0.04
13	0.11	0.12	0.12	0.12	0.13

Table A4: Correlation values between consumed menhaden biomass per striped bass biomass (column heading "Ratio") and striped bass weight-at-age. None of the correlations are significant ($\alpha = 0.05$) based on multiple pairwise analysis with Holm adjustment.

Striped bass weight-at-age	Ratio
1	-0.28
2	0.08
3	0.09
4	0.25
5	0.06
6	0.12
7	0
8	-0.16
9	-0.32
10	-0.31
11	-0.23
12	0.1
13	0.23

Table A5: Correlation values between consumed menhaden biomass per striped bass biomass (column heading "Ratio") and striped bass natural mortality as developed through tagging models in the Chesapeake Bay. The correlations are highly significant ($\alpha = 0.05$) based on multiple pairwise analysis with Holm adjustment.

Portion of the population	Ratio
Pre-migratory	-0.58
Migratory	-0.72

Table A6: Parameter values for the Weibull model by segment of the population.

Portion of the population	Scale parameter: α	Shape parameter: β
Pre-migratory	2.53	-2.64
Migratory	1.04	-1.29

Table A7: Long-term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under *F*=0 for menhaden and *F*=0.1 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	*F*(/yr)	Landings (1000 mt)
29	212	147.79	0.10	21
30	188	142.91	0.10	19
31	168	147.79	0.10	17
32	148	151.91	0.10	16
33	140	142.91	0.10	14
123	88	147.79	0.10	12
124	89	147.79	0.10	12
125	91	147.79	0.10	12
126	92	137.96	0.10	12
127	89	147.79	0.10	12

Table A8: Long-term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under *F*=0 for menhaden and *F*=0.2 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	*F*(/yr)	Landings (1000 mt)
29	203	147.79	0.20	39
30	164	142.91	0.20	33
31	135	147.79	0.20	28
32	109	151.91	0.20	24
33	95	142.91	0.20	21
123	21	147.79	0.20	10
124	21	147.79	0.20	10
125	23	147.79	0.20	9
126	22	137.96	0.20	9
127	21	147.79	0.20	9

Table A9: Long-term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under *F*=0 for menhaden and *F*=0.3 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	*F*(/yr)	Landings (1000 mt)
29	194	147.79	0.30	57
30	144	142.91	0.30	44
31	109	147.79	0.30	35
32	81	151.91	0.30	28
33	65	142.91	0.30	23
123	8	147.79	0.30	9
124	9	147.79	0.30	9
125	9	147.79	0.30	8
126	9	137.96	0.30	8
127	8	147.79	0.30	8

Table A10: Long-term projected natural mortality at-age for striped bass under F=0 for menhaden and F=0.1 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
30	1.13	0.68	0.64	0.47	0.36	0.27	0.21	0.21	0.19	0.19	0.19	0.19	0.19
31	1.13	0.68	0.65	0.48	0.36	0.28	0.22	0.22	0.19	0.19	0.19	0.19	0.19
32	1.13	0.68	0.68	0.50	0.38	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
33	1.13	0.68	0.68	0.50	0.38	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
123	1.13	0.68	0.66	0.48	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
124	1.13	0.68	0.68	0.50	0.38	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
125	1.13	0.68	0.71	0.52	0.39	0.30	0.24	0.24	0.20	0.20	0.20	0.20	0.20
126	1.13	0.68	0.71	0.52	0.39	0.30	0.24	0.24	0.20	0.20	0.20	0.20	0.20
127	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20

Table A11: Long-term projected natural mortality at-age for striped bass under F=0 for menhaden and F=0.2 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
30	1.13	0.68	0.66	0.48	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
31	1.13	0.68	0.68	0.50	0.38	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
32	1.13	0.68	0.73	0.53	0.40	0.31	0.24	0.24	0.21	0.21	0.21	0.21	0.21
33	1.13	0.68	0.74	0.54	0.41	0.31	0.25	0.25	0.21	0.21	0.21	0.21	0.21
123	1.13	0.68	0.92	0.67	0.51	0.39	0.31	0.31	0.24	0.24	0.24	0.24	0.24
124	1.13	0.68	0.95	0.69	0.53	0.40	0.32	0.32	0.24	0.24	0.24	0.24	0.24
125	1.13	0.68	0.99	0.73	0.55	0.42	0.33	0.33	0.25	0.25	0.25	0.25	0.25
126	1.13	0.68	0.99	0.72	0.55	0.42	0.33	0.33	0.25	0.25	0.25	0.25	0.25
127	1.13	0.68	0.94	0.69	0.52	0.40	0.31	0.31	0.24	0.24	0.24	0.24	0.24

Table A12: Long-term projected natural mortality at-age for striped bass under F=0 for menhaden and F=0.3 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
30	1.13	0.68	0.68	0.50	0.38	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
31	1.13	0.68	0.72	0.52	0.40	0.30	0.24	0.24	0.21	0.21	0.21	0.21	0.21
32	1.13	0.68	0.78	0.57	0.43	0.33	0.26	0.26	0.22	0.22	0.22	0.22	0.22
33	1.13	0.68	0.81	0.60	0.45	0.34	0.27	0.27	0.22	0.22	0.22	0.22	0.22
123	1.13	0.68	1.09	0.80	0.60	0.46	0.36	0.36	0.27	0.27	0.27	0.27	0.27
124	1.13	0.68	1.10	0.81	0.61	0.46	0.37	0.37	0.27	0.27	0.27	0.27	0.27
125	1.13	0.68	1.18	0.86	0.65	0.50	0.39	0.39	0.28	0.28	0.28	0.28	0.28
126	1.13	0.68	1.16	0.85	0.65	0.49	0.39	0.39	0.28	0.28	0.28	0.28	0.28
127	1.13	0.68	1.12	0.82	0.62	0.47	0.37	0.37	0.27	0.27	0.27	0.27	0.27

Table A13: Long-term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under F=0.9 for menhaden and F=0.1 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	212	147.79	0.10	21
30	188	142.91	0.10	19
31	167	147.79	0.10	17
32	145	151.91	0.10	15
33	134	142.91	0.10	13
123	24	147.79	0.10	5
124	24	147.79	0.10	5
125	25	147.79	0.10	5
126	25	137.96	0.10	5
127	24	147.79	0.10	5

Table A14: Long -term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under F=0.9 for menhaden and F=0.2 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	203	147.79	0.20	39
30	164	142.91	0.20	33
31	134	147.79	0.20	28
32	107	151.91	0.20	23
33	91	142.91	0.20	19
123	7	147.79	0.20	5
124	8	147.79	0.20	5
125	8	147.79	0.20	5
126	7	137.96	0.20	5
127	7	147.79	0.20	5

Table A15: Long -term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under F=0.9 for menhaden and F=0.3 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	194	147.79	0.30	57
30	144	142.91	0.30	43
31	108	147.79	0.30	34
32	79	151.91	0.30	27
33	62	142.91	0.30	21
123	4	147.79	0.30	6
124	4	147.79	0.30	6
125	4	147.79	0.30	5
126	4	137.96	0.30	5
127	4	147.79	0.30	5

Table A16: Long-term projected natural mortality at-age for striped bass under F=0.9 for menhaden and F=0.1 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
30	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
31	1.13	0.68	0.71	0.52	0.40	0.30	0.24	0.24	0.20	0.20	0.20	0.20	0.20
32	1.13	0.68	0.74	0.54	0.41	0.31	0.25	0.25	0.21	0.21	0.21	0.21	0.21
33	1.13	0.68	0.75	0.55	0.42	0.32	0.25	0.25	0.21	0.21	0.21	0.21	0.21
123	1.13	0.68	1.04	0.76	0.58	0.44	0.35	0.35	0.26	0.26	0.26	0.26	0.26
124	1.13	0.68	1.07	0.78	0.59	0.45	0.36	0.36	0.26	0.26	0.26	0.26	0.26
125	1.13	0.68	1.12	0.82	0.62	0.47	0.37	0.37	0.27	0.27	0.27	0.27	0.27
126	1.13	0.68	1.11	0.81	0.62	0.47	0.37	0.37	0.27	0.27	0.27	0.27	0.27
127	1.13	0.68	1.08	0.79	0.60	0.46	0.36	0.36	0.26	0.26	0.26	0.26	0.26

Table A17: Long-term projected natural mortality at-age for striped bass under F=0.9 for menhaden and F=0.2 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
30	1.13	0.68	0.69	0.50	0.38	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
31	1.13	0.68	0.75	0.55	0.42	0.32	0.25	0.25	0.21	0.21	0.21	0.21	0.21
32	1.13	0.68	0.79	0.58	0.44	0.33	0.26	0.26	0.22	0.22	0.22	0.22	0.22
33	1.13	0.68	0.82	0.60	0.46	0.35	0.27	0.27	0.22	0.22	0.22	0.22	0.22
123	1.13	0.68	1.32	0.97	0.73	0.56	0.44	0.44	0.31	0.31	0.31	0.31	0.31
124	1.13	0.68	1.34	0.98	0.74	0.56	0.45	0.45	0.31	0.31	0.31	0.31	0.31
125	1.13	0.68	1.40	1.03	0.78	0.59	0.47	0.47	0.32	0.32	0.32	0.32	0.32
126	1.13	0.68	1.39	1.02	0.77	0.59	0.46	0.46	0.32	0.32	0.32	0.32	0.32
127	1.13	0.68	1.32	0.97	0.74	0.56	0.44	0.44	0.31	0.31	0.31	0.31	0.31

Table A18: Long-term projected natural mortality at-age for striped bass under F=0.9 for menhaden and F=0.3 for striped bass. The table presents the first and final 5 years of the 100-year projection.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
30	1.13	0.68	0.71	0.52	0.39	0.30	0.24	0.24	0.20	0.20	0.20	0.20	0.20
31	1.13	0.68	0.79	0.58	0.44	0.33	0.26	0.26	0.22	0.22	0.22	0.22	0.22
32	1.13	0.68	0.85	0.62	0.47	0.36	0.28	0.28	0.23	0.23	0.23	0.23	0.23
33	1.13	0.68	0.90	0.66	0.50	0.38	0.30	0.30	0.23	0.23	0.23	0.23	0.23
123	1.13	0.68	1.43	1.05	0.79	0.60	0.48	0.48	0.33	0.33	0.33	0.33	0.33
124	1.13	0.68	1.46	1.07	0.81	0.62	0.49	0.49	0.34	0.34	0.34	0.34	0.34
125	1.13	0.68	1.49	1.09	0.83	0.63	0.50	0.50	0.35	0.35	0.35	0.35	0.35
126	1.13	0.68	1.50	1.10	0.83	0.63	0.50	0.50	0.35	0.35	0.35	0.35	0.35
127	1.13	0.68	1.44	1.05	0.80	0.61	0.48	0.48	0.33	0.33	0.33	0.33	0.33

Table A19: Medium-term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under *F*=0 for menhaden and *F*=0.1 for striped bass.

Yr	SSB (1000 mt)	Recruits (millions of fish)	*F*(/yr)	Landings (1000 mt)
29	213	147.79	0.10	21
30	188	147.79	0.10	19
31	169	147.79	0.10	17
32	149	147.79	0.10	16
33	141	142.91	0.10	14
34	132	147.79	0.10	14
35	122	147.79	0.10	13
36	115	147.79	0.10	13
37	109	142.91	0.10	13
38	106	147.79	0.10	13

Table A20: Medium -term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under *F*=0 for menhaden and *F*=0.2 for striped bass.

Yr	SSB (1000 mt)	Recruits (millions of fish)	*F*(/yr)	Landings (1000 mt)
29	204	147.79	0.20	39
30	166	147.79	0.20	33
31	137	147.79	0.20	28
32	111	147.79	0.20	24
33	97	142.91	0.20	21
34	84	147.79	0.20	19
35	72	147.79	0.20	17
36	63	147.79	0.20	16
37	56	142.91	0.20	16
38	50	147.79	0.20	15

Table A21: Medium -term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under *F*=0 for menhaden and *F*=0.3 for striped bass.

Yr	SSB (1000 mt)	Recruits (millions of fish)	*F*(/yr)	Landings (1000 mt)
29	195	147.79	0.30	57
30	147	147.79	0.30	44
31	110	147.79	0.30	35
32	83	147.79	0.30	28
33	67	142.91	0.30	23
34	54	147.79	0.30	20
35	42	147.79	0.30	17
36	34	147.79	0.30	16
37	28	142.91	0.30	14
38	24	147.79	0.30	13

Table A22: Medium -term projected natural mortality at-age for striped bass under *F*=0 for menhaden and *F*=0.1 for striped bass.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.65	0.48	0.36	0.27	0.22	0.22	0.19	0.19	0.19	0.19	0.19
30	1.13	0.68	0.64	0.47	0.36	0.27	0.21	0.21	0.19	0.19	0.19	0.19	0.19
31	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
32	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
33	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
34	1.13	0.68	0.68	0.50	0.38	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
35	1.13	0.68	0.68	0.50	0.38	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
36	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
37	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
38	1.13	0.68	0.67	0.49	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20

Table A23: Medium -term projected natural mortality at-age for striped bass under *F*=0 for menhaden and *F*=0.2 for striped bass.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.65	0.48	0.36	0.27	0.22	0.22	0.19	0.19	0.19	0.19	0.19
30	1.13	0.68	0.66	0.48	0.37	0.28	0.22	0.22	0.20	0.20	0.20	0.20	0.20
31	1.13	0.68	0.70	0.51	0.39	0.30	0.23	0.23	0.20	0.20	0.20	0.20	0.20
32	1.13	0.68	0.72	0.53	0.40	0.30	0.24	0.24	0.21	0.21	0.21	0.21	0.21
33	1.13	0.68	0.73	0.53	0.40	0.31	0.24	0.24	0.21	0.21	0.21	0.21	0.21
34	1.13	0.68	0.76	0.56	0.42	0.32	0.25	0.25	0.21	0.21	0.21	0.21	0.21
35	1.13	0.68	0.76	0.56	0.42	0.32	0.25	0.25	0.21	0.21	0.21	0.21	0.21
36	1.13	0.68	0.78	0.57	0.43	0.33	0.26	0.26	0.22	0.22	0.22	0.22	0.22
37	1.13	0.68	0.79	0.58	0.44	0.33	0.26	0.26	0.22	0.22	0.22	0.22	0.22
38	1.13	0.68	0.80	0.59	0.44	0.34	0.27	0.27	0.22	0.22	0.22	0.22	0.22

Table A24: Medium -term projected natural mortality at-age for striped bass under *F*=0 for menhaden and *F*=0.3 for striped bass.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.65	0.48	0.36	0.27	0.22	0.22	0.19	0.19	0.19	0.19	0.19
30	1.13	0.68	0.68	0.50	0.38	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
31	1.13	0.68	0.74	0.54	0.41	0.31	0.25	0.25	0.21	0.21	0.21	0.21	0.21
32	1.13	0.68	0.78	0.57	0.43	0.33	0.26	0.26	0.22	0.22	0.22	0.22	0.22
33	1.13	0.68	0.80	0.59	0.45	0.34	0.27	0.27	0.22	0.22	0.22	0.22	0.22
34	1.13	0.68	0.86	0.63	0.48	0.36	0.29	0.29	0.23	0.23	0.23	0.23	0.23
35	1.13	0.68	0.88	0.65	0.49	0.37	0.29	0.29	0.23	0.23	0.23	0.23	0.23
36	1.13	0.68	0.90	0.66	0.50	0.38	0.30	0.30	0.24	0.24	0.24	0.24	0.24
37	1.13	0.68	0.93	0.68	0.52	0.39	0.31	0.31	0.24	0.24	0.24	0.24	0.24
38	1.13	0.68	0.97	0.71	0.54	0.41	0.32	0.32	0.25	0.25	0.25	0.25	0.25

Table A25: Medium -term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under F=0.9 for menhaden and F=0.1 for striped bass.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	213	147.79	0.10	21
30	188	147.79	0.10	19
31	168	147.79	0.10	17
32	145	147.79	0.10	15
33	135	142.91	0.10	13
34	124	147.79	0.10	12
35	111	147.79	0.10	12
36	101	147.79	0.10	11
37	93	142.91	0.10	11
38	87	147.79	0.10	11

Table A26: Medium -term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under F=0.9 for menhaden and F=0.2 for striped bass.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	204	147.79	0.20	39
30	166	147.79	0.20	33
31	135	147.79	0.20	27
32	108	147.79	0.20	23
33	93	142.91	0.20	20
34	78	147.79	0.20	17
35	65	147.79	0.20	15
36	54	147.79	0.20	14
37	46	142.91	0.20	13
38	40	147.79	0.20	12

Table A27: Medium -term projected spawning stock biomass, recruitment, fishing mortality, and landings for striped bass under F=0.9 for menhaden and F=0.3 for striped bass.

Yr	SSB (1000 mt)	Recruits (millions of fish)	F(/yr)	Landings (1000 mt)
29	195	147.79	0.30	57
30	147	147.79	0.30	44
31	109	147.79	0.30	34
32	81	147.79	0.30	27
33	64	142.91	0.30	21
34	50	147.79	0.30	18
35	38	147.79	0.30	15
36	29	147.79	0.30	13
37	23	142.91	0.30	11
38	18	147.79	0.30	10

Table A28: Medium-term projected natural mortality at-age for striped bass under F=0.9 for menhaden and F=0.1 for striped bass.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.65	0.48	0.36	0.27	0.22	0.22	0.19	0.19	0.19	0.19	0.19
30	1.13	0.68	0.68	0.50	0.38	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
31	1.13	0.68	0.71	0.52	0.40	0.30	0.24	0.24	0.21	0.21	0.21	0.21	0.21
32	1.13	0.68	0.73	0.54	0.41	0.31	0.24	0.24	0.21	0.21	0.21	0.21	0.21
33	1.13	0.68	0.75	0.55	0.42	0.32	0.25	0.25	0.21	0.21	0.21	0.21	0.21
34	1.13	0.68	0.77	0.56	0.43	0.32	0.26	0.26	0.21	0.21	0.21	0.21	0.21
35	1.13	0.68	0.77	0.56	0.43	0.32	0.26	0.26	0.21	0.21	0.21	0.21	0.21
36	1.13	0.68	0.77	0.56	0.43	0.32	0.26	0.26	0.21	0.21	0.21	0.21	0.21
37	1.13	0.68	0.77	0.57	0.43	0.33	0.26	0.26	0.21	0.21	0.21	0.21	0.21
38	1.13	0.68	0.78	0.58	0.44	0.33	0.26	0.26	0.22	0.22	0.22	0.22	0.22

Table A29: Medium-term projected natural mortality at-age for striped bass under F=0.9 for menhaden and F=0.2 for striped bass.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.65	0.48	0.36	0.27	0.22	0.22	0.19	0.19	0.19	0.19	0.19
30	1.13	0.68	0.70	0.51	0.39	0.29	0.23	0.23	0.20	0.20	0.20	0.20	0.20
31	1.13	0.68	0.75	0.55	0.42	0.32	0.25	0.25	0.21	0.21	0.21	0.21	0.21
32	1.13	0.68	0.78	0.58	0.44	0.33	0.26	0.26	0.22	0.22	0.22	0.22	0.22
33	1.13	0.68	0.81	0.60	0.45	0.34	0.27	0.27	0.22	0.22	0.22	0.22	0.22
34	1.13	0.68	0.86	0.63	0.48	0.36	0.29	0.29	0.23	0.23	0.23	0.23	0.23
35	1.13	0.68	0.88	0.64	0.49	0.37	0.29	0.29	0.23	0.23	0.23	0.23	0.23
36	1.13	0.68	0.90	0.66	0.50	0.38	0.30	0.30	0.23	0.23	0.23	0.23	0.23
37	1.13	0.68	0.92	0.68	0.51	0.39	0.31	0.31	0.24	0.24	0.24	0.24	0.24
38	1.13	0.68	0.96	0.71	0.53	0.41	0.32	0.32	0.25	0.25	0.25	0.25	0.25

Table A30: Medium-term projected natural mortality at-age for striped bass under F=0.9 for menhaden and F=0.3 for striped bass.

Yr	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13
29	1.13	0.68	0.65	0.48	0.36	0.27	0.22	0.22	0.19	0.19	0.19	0.19	0.19
30	1.13	0.68	0.72	0.53	0.40	0.30	0.24	0.24	0.21	0.21	0.21	0.21	0.21
31	1.13	0.68	0.79	0.58	0.44	0.34	0.26	0.26	0.22	0.22	0.22	0.22	0.22
32	1.13	0.68	0.85	0.62	0.47	0.36	0.28	0.28	0.23	0.23	0.23	0.23	0.23
33	1.13	0.68	0.89	0.65	0.50	0.38	0.30	0.30	0.23	0.23	0.23	0.23	0.23
34	1.13	0.68	0.97	0.71	0.54	0.41	0.32	0.32	0.25	0.25	0.25	0.25	0.25
35	1.13	0.68	1.01	0.74	0.56	0.43	0.34	0.34	0.25	0.25	0.25	0.25	0.25
36	1.13	0.68	1.06	0.77	0.59	0.45	0.35	0.35	0.26	0.26	0.26	0.26	0.26
37	1.13	0.68	1.12	0.82	0.62	0.47	0.37	0.37	0.27	0.27	0.27	0.27	0.27
38	1.13	0.68	1.16	0.85	0.65	0.49	0.39	0.39	0.28	0.28	0.28	0.28	0.28