EVALUATING THE EFFECTS OF ATLANTIC MENHADEN MANAGEMENT AND ENVIRONMENTAL CHANGE ON THE NORTHWEST ATLANTIC OCEAN ECOSYSTEM

By

Maxwell Thomas Grezlik

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Fisheries

Committee Membership

Dr. Andre Buchheister, Committee Chair

Dr. Mark Henderson, Committee Member

Dr. Jose Marin Jarrin, Committee Member

Dr. David Chagaris, Committee Member

Dr. Erin Kelly, Program Graduate Coordinator

December 2021

ABSTRACT

EVALUATING THE EFFECTS OF ATLANTIC MENHADEN MANAGEMENT AND ENVIRONMENTAL CHANGE ON THE NORTHWEST ATLANTIC OCEAN ECOSYSTEM

Maxwell Thomas Grezlik

Atlantic Menhaden (*Brevoortia tyrannus*) is an abundant forage fish species whose management has recently shifted from using single species reference points to ecological reference points. This type of management allows for the ecological role (e.g., supporting predators) of the species to be considered when making management decisions, and is part of a growing global movement towards ecosystem-based fisheries management. One model that aided in this transition from single species to ecological reference points was the Northwest Atlantic Continental Shelf (NWACS13) model created using Ecopath with Ecosim (Buchheister et al. 2017). Here, I updated and expanded the NWACS13 model with four years of additional data and used it to address three main objectives. First, I evaluated the effects of different Menhaden fishing mortality rates on the relative biomasses of modeled species groups using 50-year projections. Second, I examined whether single species biomass target reference points would be achieved for five focal species of management interest (Striped Bass, Bluefish, Weakfish, Spiny Dogfish, Atlantic Herring) under different fishing rates for Menhaden and the focal species. Third, I implemented bottom-up, primary production forcing in the ecosystem model to explore the long-term consequences on biomass and catch of a 3.5% and 6% decrease in phytoplankton biomass that represents a range of climate-change effects from the literature. Results indicate that ecological reference points behaved as they were designed, to push Striped Bass biomass toward its target. Nearshore piscivorous birds and pelagic sharks were identified as species of concern and were not included in less complex models. The inclusion of a primary production forcing function strengthened the relationship between Atlantic Menhaden and Striped Bass biomass in model projections, a key interaction evaluated in setting ecological reference points for Atlantic Menhaden. The inclusion of climate change projections identified disproportionate negative impacts on the biomass and catch of several species groups including Weakfish, Atlantic Cod, Striped Bass, Bluefish, and Spiny Dogfish. This model and study can contribute to fisheries management by identifying species or interactions of concern that are sensitive to Menhaden fishing mortality rates. This work contributes to Menhaden management by providing insight into the benefits of adding further complexity to models currently used for management decision making. More broadly, this work contributes to the ecosystem-based management movement and shows how climate impacts can be considered in making management decisions.

ACKNOWLEDGEMENTS

This work was funded by the Lenfest Ocean Program. Additional funding was provided by the Marin and Richmond Rod and Gun Clubs, and the International Women's Fishing Association. Data was provided by NOAA Fisheries, the Atlantic Coastal Cooperative Statistics Program, and the Atlantic States Marine Fisheries Society. Individuals that went above and beyond in assisting this work include Sean Lucey of NOAA fisheries, Katie Drew of the Atlantic States Marine Fisheries Commission, Mike Rinaldi of the Coastal Cooperative Statistics Program, and Jeroen Steenbeek of the Ecopath International Initiative.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Atlantic Menhaden (*Brevoortia tyrannus*; hereafter Menhaden) is a highly abundant species off the U.S. East Coast from Florida to Maine and is managed as one single stock. Menhaden stratify by age and size for most of the year with older, larger individuals found in the northern portions of their range and younger, smaller individuals found in the south. Spawning of Menhaden peaks from December to February with the largest concentrations of spawning individuals found off the coast of North Carolina. Once fertilized, eggs float with currents into estuaries where they hatch. Juveniles mature in estuaries during spring and summer, out-migrating to the ocean and reaching sexual maturity by the fall (Houde 2009). Menhaden filter-feed on phytoplankton and zooplankton both as juveniles and adults (Houde 2009). Menhaden serve as important prey to a number of species, including fishes (e.g., Striped Bass (*Morone saxatilis*), Bluefish (*Pomatomus saltatrix*), Weakfish (*Cynoscion regalis*), Bluefin Tuna (*Thunnus thynnus*), sharks), birds (e.g., osprey, pelicans, cormorants, seabirds), and marine mammals (e.g., dolphins, whales) (SEDAR 2020b). With their large abundance and broad range, Menhaden contribute substantially to the coastal food web along the entire U.S. east coast, acting as a link between primary production and higher trophic levels (Houde 2009).

History of the Fishery

The Atlantic Menhaden fishery is divided into two parts: the reduction fishery and the bait fishery. In the reduction fishery, Menhaden are processed into fish meal, fish oil, and fish solubles, which are used in a variety of commercial products (Anstead et al. 2021). The reduction fishery dates back to the 1800's in New England and reached its peak in 1956, landing 712,100 mt. Since that peak there has been a general decline in landings due to poor to average year classes. Historically there were several fish processing (or "reduction") plants from Florida to Main, but all the plants except for one in VA were closed due to odor abatement regulations and a contraction of the fishery. The reduction fishery accounted for 74% of total landings in 2017 (SEDAR 2020a). In the bait fishery, Menhaden are caught both commercially and recreationally to be used as bait in other fisheries including crab, lobster, and hook-and-line fisheries. The bait fishery landings have generally increased through time as reduction landings decreased, though in 2017 the bait fishery still only represented 25% of the total Menhaden landings (SEDAR 2020a). The bait fishery is expanding rapidly in recent years due to a collapse in the Atlantic Herring population, a common alternative bait to Menhaden in the lobster fishery.

Management History of Atlantic Menhaden

Menhaden are currently managed by Amendment 3 of the Interstate Fishery Management Plan for Atlantic Menhaden (SEDAR 2020b; Anstead et al. 2021). This amendment continued the practice of managing the stock based on single-species reference points but clearly stated the desire to “pursue the development of ecological reference points (ERPs) and revisit allocation methods”. Amendment 3 describes ERPs as “a method to assess the status of Menhaden not only with regard to the sustainability of human harvest, but also with regard to their interactions with predators and the status of other prey species”. ERPs allow for managers to consider Menhaden’s role in the food web when regulating harvest by humans, as opposed to single species reference points which only consider the status of the Menhaden stock. The interest in ERPs for Menhaden management was high given that there has been a longstanding acknowledgment by managers and stakeholders of their ecological importance. When the FMP was reevaluated in 2017 there was strong support for ERPs from stakeholders who value the role of Menhaden in the diets of other economically and culturally important species, with over 126,000 public comments from individuals, organizations, or through form letters (Draft Amendment 3 to the Interstate Fishery Management Plan for Atlantic Menhaden for Public Comment).

In preparation for the benchmark stock assessment in 2020 for Menhaden, the ASMFC assigned the Ecological Reference Points (ERP) working group the task “to develop Menhaden-specific ERPs that account for the abundance of Menhaden and the species role as a forage fish” (Amendment 3 to the FMP, Anstead et al. 2021). ERPs allow management decisions to be made based on both Menhaden’s role in the directed fishery as well as their ecological role as prey for higher trophic levels; and, more broadly, to help advance an ecosystem approach to fisheries management (EAFM) that considers more factors within an ecosystem than just the species of interest (Patrick and Link 2015). Menhaden were assessed in both the Atlantic Menhaden Benchmark Stock Assessment Report (SEDAR 2020a) and the Atlantic Menhaden Ecological Reference Points Stock Assessment Report (SEDAR 2020b). The workgroup followed best practices in model development in that they developed a suite of models all trained to address the same objectives and then set tactical management advice from a model of intermediate complexity (Plagányi et al. 2007, Plagányi et al. 2014). All models developed by the workgroup are described in SEDAR (2020b). In August 2020, the management board unanimously voted to adopt ERPs set by the NWACS-MICE model (Anstead et al. 2021). This model also stemmed from the NWACS13 model but limited the complexity from 61 species groups to 17 species groups of highest interest to the ERP working group.

Ecosystem Management

Ecosystem management refers to a process by which areas are managed at a number of different scales in order to conserve biological resources and ecological services while also sustaining appropriate human uses (Brussard et al. 1998). Ecosystem management has gained support over the past few decades (Link 2010a) and within the context of fisheries management has been explored in two principal ways: an ecosystem approach to fisheries management (EAFM) and ecosystem-based fisheries management

(EBFM) (Patrick and Link 2015). EAFM expands upon single-species management to include ecosystem factors in order to broaden our understanding of ecosystem dynamics and to better inform fisheries management decisions, but management is still focused on the target species (Patrick and Link 2015). EBFM goes further by considering physical, biological, economic, and social tradeoffs involved in managing the ecosystem as an integrated system and compares competing strategies to optimize yields across multiple fish species within the ecosystem (Patrick and Link 2015).

Ecosystem-based fisheries management has gained support over the past two decades but has been difficult to implement for a variety of reasons. Some reasons include a disconnect between management goals and enforceable limits, lack of governance structure to implement and enforce ecosystem management, and the requirement of extensive data in order to implement ecosystem management in a region (Patrick and Link 2015). Management goals tend to be conceptual while enforceable limits are quantitative by necessity. The argument that ecosystem management would require a dramatic and expensive change in management governance structure is common but not necessarily true. Five of the eight regional fishery management councils have developed ecosystem management protocols which are capable of implementation and enforcement under the existing management framework, though the plans have not been acted upon yet (Patrick and Link 2015). Ecosystem management can also be carried out in regions that are not as well-studied as methods and management tools become more advanced and able to account for uncertainties.

Recently, research in this field has focused on operationalizing EBFM. Operational EBFM advice requires the use of models with enough complexity to account for key interactions within an ecosystem while being able to provide tactical advice with a reasonable level of uncertainty. This can be a delicate balance and has been a focus of discussion in recent workshops involving leading scientists from around the world (Karp et al. in preparation). Current recommendations are to limit complexity in models to only what is necessary to address an identified management concern (Link 2010a, Fulton & Link 2014, Plagányi et al. 2014, Collie et al. 2016). More complex models can then be used in support of tactical models (Link et al. 2015, Townsend et al. 2019, Townsend et al. 2020, Howell et al. 2021). Limiting complexity reduces the level of uncertainty associated with management advice, and training multiple models to address the same species or interaction of interest can further minimize uncertainty. Agreement of multiple models increases confidence in model outputs. The suite of models can then be used in conjunction to address alternative research and management questions based on the strengths and limitations of each model. The model presented in this thesis is more complex than several others aimed at informing Menhaden management. This added complexity allows for the examination of interactions and management concerns that other models cannot such as impacts on species groups not included in less complex models, or changes in catch allocation to the two sectors of the fishing industry.

EBFM/EAFM

The NWACS17 model, described in this work, adds to the growing and evolving science of EAFM and EBFM in U.S. waters. Multispecies models or ecosystem models like the NWACS17 model may be necessary to meet mandates for sustainable fisheries management long-term (Link 2010a). Though current legislation falls short of explicitly requiring ecosystem-based management (Marshak et al. 2017), there has been a steady movement toward mandating more holistic management (Rodriguez 2017; FAO 2008; NOAA 2016), and achieving the objectives of all mandates may implicitly require a multispecies approach (Murawski 1991). The Atlantic Ocean Research Alliance (AORA, 2018) found that limited adoption of more holistic management practices in most cases is due to reasons other than a lack of mandates. U.S. and international management bodies continue to push for multispecies considerations in fisheries management plans as well as coastwide and international legislation. Attempts at single-species management for fisheries that target multiple species have produced conflicting management actions, and there are substantial advantages to recognizing the economic, ecological and technical interactions among species that are targeted by the same fishery (e.g., NEFMC 1985).

Multispecies and ecosystem models can outperform single species methods in a variety of ways. Multispecies models offer potential improvements in estimates of natural mortality, predation mortality, and recruitment (e.g., Trijoulet et al. 2020). They offer better understanding of growth rates and spawner-recruit relationships (Hollowed 2000). They can also be used to generate biological reference points (ICES 2011, 2012;

ASMFC 2010; Chagaris et al. 2020; SEDAR 2020b). All of these improvements benefit our ability to assess competition, predation (e.g., consumption or predator limitation), and environmental variability. Link (2010a) listed the types of stocks that are most suitable for multispecies modeling: forage, key linkages between lower and upper trophic levels, species with high trophic efficiency, high tropic linkage density, highly variable, highly migratory, wide ranging, locally dominant, competitors of target species, predators of target species larvae, and potential target species.

Single species stock assessments have some advantages over ecosystem and multispecies models. Single species assessments limit nominal uncertainty by focusing on fewer processes, with more implicit assumptions. Single species assessments avoid the inertia in management systems that limits adoption of multispecies models. Data-collection programs in many cases have been designed to fulfil data requirements of single species assessments in a way that might not be ideal for multispecies models (Hollowed et al. 2000). Single species assessments have also been designed to assess the probability of stock collapse which directly addresses mandates for precautionary fishing (UN FSA 1995) in a way that most multispecies models do not.

Due to the unique benefits of multispecies and single species modeling, a current best practice recommendation is to use single species and multispecies models together in a suite of models (Link 2010a, Plagyani 2007). Single species assessments can be used to provide short-term, tactical management advice, and ecosystem models for the same system can provide longer-term, strategic advice. This can be done through management strategy evaluation (Deroba et al. 2019) or with direct integration into the stock assessment of a target species (SEDAR 2020b). In doing this, mandates are met without drastic deviation from the status quo, however, the full range of potential benefits of multispecies models are not utilized.

Table 1 Different versions of the Northwest Atlantic Continental Shelf model. All models were developed using the Ecopath with Ecosim software and represent the same geographic regions

Model	**Number of species groups**	**Modeled time series**	**Publications**
NWACS 13	61	1982-2013	Buchheister et al. 2017
NWACS MICE	17	1985-2017	Chagaris et al. 2020, SEDAR 2020 ERP Report
NWACS Hybrid	61	1982-2017	SEDAR 2020 ERP Report
NWACS 17	65	1985-2017	This study

Ecosystem Modeling of Atlantic Menhaden

Ecopath is used to create a mass-balanced snapshot of an ecosystem describing where the biomass within an ecosystem is located at a given point in time. Ecopath represents individual species or species aggregations as functional ‘groups’, and each group can be subdivided into age ‘stanzas’ based on characteristics that make the stanzas biologically unique (i.e. size, maturity). Ecosim provides the temporal component, describing how the ecosystem changes over a given time period. EwE has been used as a tool to study ecosystem dynamics and aid in management, with over 800 publications using the software as of January 2018 (Ecopath.org).

Buchheister et al. (2017) created a model, using EwE software, for the Northwest Atlantic Continental Shelf (NWACS) region off of the U.S. East coast with special focus on management of Menhaden. The authors demonstrated that an ecosystem model for the Northwest Atlantic continental shelf could identify tradeoffs associated with alternative ecosystem-based reference points. The model identified groups whose biomasses were negatively affected by increased harvest of Menhaden, groups which were positively affected, and groups which showed negligible response to changes in Menhaden harvest. The model was also able to demonstrate variable biomass and yields of Menhaden resulting from the considered reference points (Buchheister et al. 2017). Despite the insights gained from that work, the model only used data through 2013 and there were some limitations that could be ameliorated to facilitate the model’s utility for management. For example, comparisons between the NWACS13 model and stock assessments for Menhaden and other key predators were hindered by different age-structures among the models. The NWACS13 model also combined the reduction and bait fisheries into a single Menhaden fishery, reducing the scope of potential management strategies that could be simulated using the model. My project seeks to update the

NWACS13 model based on feedback from scientists and managers in order to enhance the utility of the model for management applications.

NWACS17 Contribution to Management

My model was designed to be complimentary to the tools already available to Menhaden managers. Two of the other models available to managers are closely related to the NWACS17 model described in this thesis. Those models, the NWACS MICE and NWACS13 models are briefly described in Table 1. The NWACS MICE model, used to set ERPs for Menhaden management provides tactical management advice to manager in the form of specific reference points. Several models less complex than the NWACS MICE model provide context for those reference points by estimating comparable management targets and thresholds in more traditional ways. The goal of my model is to provide more strategic advice to managers. This advice is more “big-picture” or conceptual when compared to tactical management advice and will come in the form of identifying important processes not included in the NWACS MICE model. These key processes could come in the form of predator-prey interactions or changes in competition with species not included in the NWACS MICE model, impacts of inclusion of a primary production forcing function, or improvements associated with the higher resolution modeling of the fishing industry in the NWACS17 model compared to the NWACS MICE model. Managers will then be able to weight the relative importance of the processes identified and decide if they warrant including in future iterations of the NWACS MICE model.

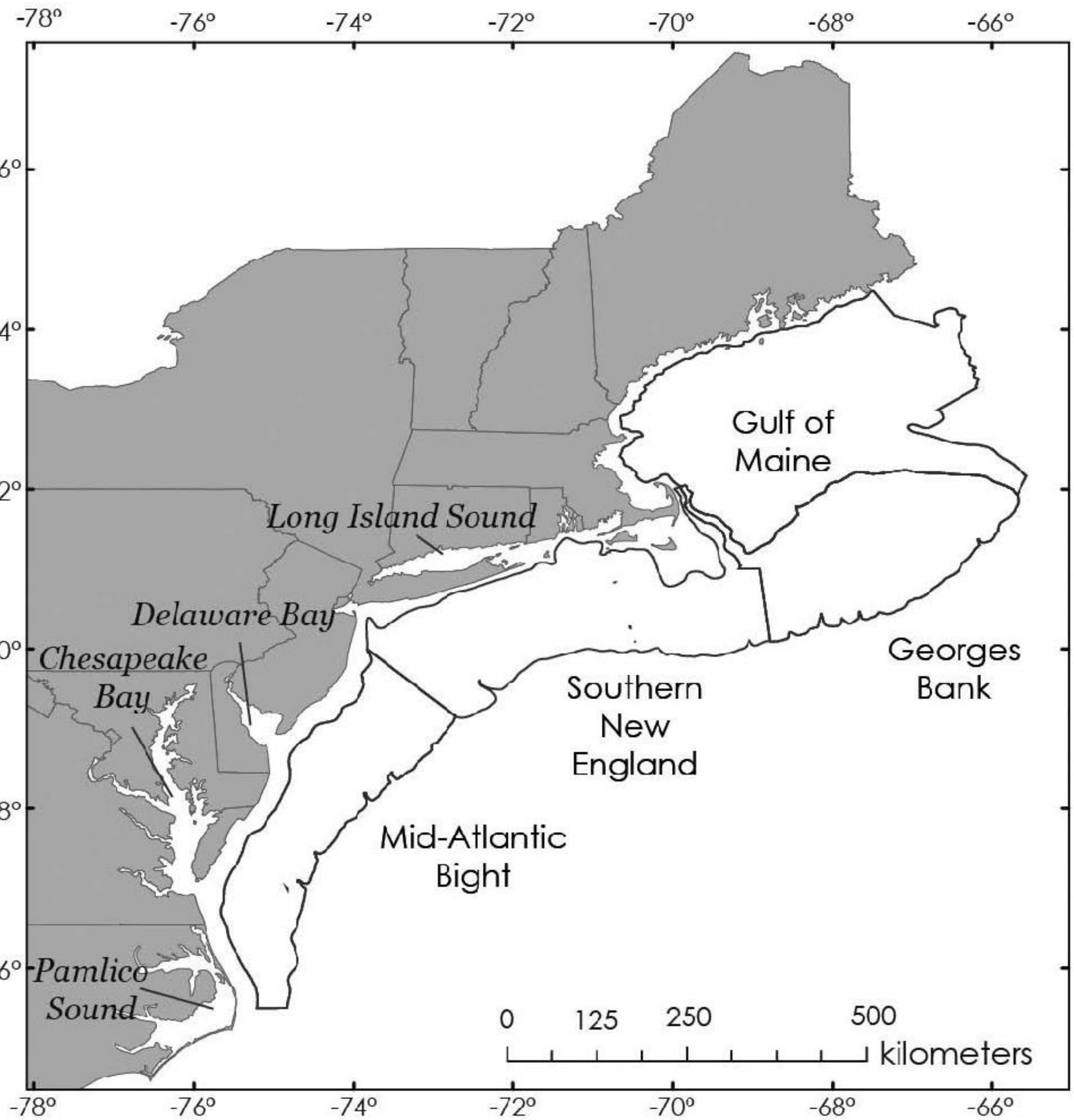

Figure 1 Model region for NWACS13 model and all subsequent versions of the NWACS13 model (Buchheister et al. 2017)

Research Questions

Here I updated and apply the NWACS13, an ecosystem model for the Northwest Atlantic continental shelf, as a tool which will help inform the recent transition towards an EAFM for Menhaden. I have three main research questions for this project. First, how does a change in Menhaden fishing mortality impact the biomass and catch of other species in the ecosystem?   This work will expand upon the previous NWACS13 model by adding four additional years of data, and updating age-structure to allow direct comparisons of outputs between this model, the single species stock assessment model, and multispecies models designed to aid in Menhaden management. Second, are single species biomass target reference points achieved for five focal species of management interest under different fishing rates for Menhaden and the focal species? This evaluation aligns with what was done by the ERP work group when setting target and threshold ERPs for Menhaden management, and allows for direct comparison with their work. Lastly, how are model projections impacted by predicted changes in phytoplankton biomass associated with climate projections in the near future? This was accomplished by adding a primary production forcing function and simulating different levels of decreases in phytoplankton biomass predicted from climate change (Lotze et al. 2019). Similar models have shown that the inclusion of bottom-up forcing functions in EwE models can improve the fit and performance of the model (Ainsworth et al. 2011). This work builds upon the previous NWACS13 ecosystem model. By adding to model capabilities to evaluate a wider variety of stakeholder concerns about the ecosystem and its management, I am able to provide incremental progress towards ecosystem-based management of the system.

MATERIALS AND METHODS

The NWACS13 model I expanded upon was developed using Ecopath with Ecosim version 6.4.3 (Buchheister et al. 2017). The NWACS13 model was parameterized using data from stock assessments, surveys, and literature and it was fit to the time series from 1982-2013. The authors included 61 trophic groups and 8 fishing fleets. The model was then used to compare different ecosystem-based reference points for Menhaden and proxies for single-species reference points over 50-year simulations. Alternative reference points were compared based on the biomass and yield of fished species and the number of species positively and negatively affected by the management practices over the 50-year simulated time series.

Ecopath

Ecopath utilizes two master equations to describe an ecosystem, assuming mass-balance over a one-year time period (Christensen and Walters 2004). One equation describes the production within a group, the other describes the energy balance within a group. The production equation divides total production rate (P_i) for each group *i* into distinct components:

$$P_i = Y_i + M2_i \times B_i + E_i + BA_i + M0_i \times B_i \qquad \text{(Eq. 1)}$$

Where Y_i is the total fishery catch rate for group i, $M2_i$ is the instantaneous predation rate for group i, B_i is the biomass of group i, E_i is the net migration rate (emigration - immigration) for group i, BA_i is the biomass accumulation rate (the change in $t/km^2/year$) for group i, and $M0_i$ is "other mortality". $M0_i$, the "other mortality", can be represented as:

$$M0_i = [P_i (1-EE_i)] / B_i \quad \text{(Eq. 2)}$$

Where EE_i is the "ecotrophic efficiency" of group i, or the proportion of the production of group i which is utilized within the defined ecosystem.

Equation 1 can also be written as (Christensen et al. 2008):

$$B_i \times (P/B)_i \times EE_i - Y_i - E_i - BA_i - \sum_{j=1}^{n} B_j \times (Q/B)_j \times DC_{ji} = 0 \quad \text{(Eq. 3)}$$

Where $(P/B)_i$ is the production to biomass ratio for group i, B_j is the biomass for predator group j, $(Q/B)_j$ is the consumption to biomass ratio for predator j, and DC_{ji} is the fractional contribution of group i to the diet composition of predator group j. This format of the equation allows for the input of three of four parameters (*B*, *P/B*, *Q/B*, and *EE*), and the subsequent calculation of the fourth, unknown, parameter. Catch rate, biomass accumulation rate, and diet composition must be supplied for each group.

The second master equation divides the energy balance of each group based on the principle of conservation of mass and can be represented simply as:

Consumption = *production* + *respiration* + *unassimilated food* (Eq. 4)

This equation divides the consumption of biomass by each group into somatic growth (production), metabolic costs (respiration), and egested waste (unassimilated food).

Equation 4 is used to estimate respiration through input of the other three variables, as respiration is not available for most groups.

Ecosim

Ecosim expands upon the Ecopath software to represent changes within the ecosystem over time. In Ecosim, the biomass dynamics are modeled using a series of coupled differential equations (Christensen et al. 2008). These differential equations are a re-expression of Eq. 3:

$$\frac{dB_i}{dt} = g_i \sum_{j=1}^{n} Q_{ji} - \sum_{j=1}^{n} Q_{ij} + I_i - (M0_i + F_i + e_i)B_i \qquad \text{(Eq. 5)}$$

Where dB_i/dt is the biomass growth rate for group *i* during time interval dt, g_i is the net growth efficiency ($g_i = (P/B)_i/(Q/B)_i$), $M0_i$ is the non-predation or 'other' natural mortality for the group estimated from EE_i ($M0_i = (1-EE_i)P_i/B_i$), F_i is the fishing mortality rate, I_i is the immigration rate that is assumed constant over time, e_i is the emigration rate. In Eq. 5, Q_{ji} represents the total consumption of prey *j* by group *i*, whereas the second summation, Q_{ij}, represents the total consumption of group *i* by all possible predators. Consumption rates (Q_{ji}) are calculated utilizing the "foraging arena" concept in which prey transition between vulnerable and invulnerable states (Walters et al. 1997, Christensen and Walters 2004). Prey are considered in the vulnerable state when they leave refuge to seek food or to reproduce. Prey are considered in the invulnerable state when they return to the refuge and are therefore unavailable to potential predation. The transfer rate between the vulnerable and invulnerable state is termed the vulnerability parameter and ultimately determines the degree to which groups are controlled by top-down (i.e., Lotka-Volterra) or bottom-up (i.e., donor-driven) factors or a combination of the two (Walters et al. 1997, Christensen and Walters 2004).

Within Ecosim, forcing functions can be used to model the impact of physical or other environmental factors on the ecosystem (Christensen and Walters 2004). For example, the model developer can input a time series of data to regulate or modify production, mortality, or consumption for a given predator or prey group. The forcing function can be particularly useful in cases where there were significant changes in the ecosystem which are influenced by factors outside of the model domain (e.g., changes in nutrient inputs into coastal waters, climate change, etc.). I used a forcing function to represent primary production within the ecosystem over the time period being modeled (1985-2017). Inputting empirical data instead of relying on estimates from the model will ensure that changes in the seasonal algal blooms and long-term changes in the biomass of primary producers (e.g., Ainsworth et al. 2011) are incorporated in the model. The inclusion of bottom-up control in the model also increases the number of scenarios that can be projected by the model.

Updates

Here I updated and improved upon the NWACS13 model to complement models used to identify and assess ERPs. These updates were completed in the Ecopath with Ecosim software version 6.6.5, the most recent release of the software at the time of model completion. The most basic update to the NWACS13 model was the addition of four years of data (2014-2017) which became available after the creation of the original model. Another change I made was to update the age structure for Menhaden from the previous age stanzas (3 age-classes, labeled as small, medium, and large in NWACS13) to annual age classes (age 0, age 1, age 2, age 3, age 4, age 5, and age 6+). Moving from the previous stanzas (which aggregated multiple age-classes together) to age classes allows for more direct comparisons between my model and the Menhaden stock assessment model as well as other models being used by the ERP working group. I also updated the fishing fleets evaluated in the model by dividing the Menhaden purse seine fishery into reduction and bait fishery to allow for simulations in which the two fisheries are managed differently (in future studies). A final change to the NWACS13 model was to develop and apply a forcing function within the Ecosim software to more accurately represent primary production in the ecosystem as discussed above. The inclusion of this primary production forcing function allowed the model to simulate how predicted changes to primary production due to climate change will impact the system.

Data Needs

In order to make these changes to the NWACS13 model, a substantial amount of additional data was needed. Where possible, I included data from stock assessment inputs, including fishing mortality rates, biomass estimates, landings, and discards. Diet and biomass data were obtained from the Northeast Fisheries Science Center (NEFSC) trawl survey and the Virginia Institute of Marine Sciences' Northeast Area Monitoring and Assessment Program (NEAMAP). These two trawl surveys provide fisheries independent data on fish diets and biomass over the majority of the area being modeled with the NEFSC trawl survey focusing offshore from depths of 27-366 m (Link and Almeida 2000) and NEAMAP focusing nearshore from depths of 6.1-27.4 m (Bonzek et al. 2014). Fisheries dependent landings data were obtained from the National Marine Fisheries Service (NMFS) and the Atlantic Coastal Cooperative Statistics Program (ACCSP) for any fished species that do not have available stock assessments (www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/index). Species that do not have a stock assessment available were included using values from the NWACS13 model. These values were calculated as weighted averages of four Ecopath models that were previously developed for the system (Link et al. 2006, 2008) as well as primary literature and available reports (Buchheister et al. 2017).

Parameterization and Calibration

Once the new data were obtained and evaluated for quality, parameterization of the updated version of the model began. When parameterizing, I started by following the pre-balance (PREBAL) guidelines and recommendations established by Link (2010b) and continued using quality assurance guidelines from Heymans et al. (2016). These authors highlight the risk of poor-quality modeling that comes with easy-to-use modeling software such as EwE and offer some guidelines as to how to avoid potential pitfalls.

Briefly, Link (2010b) focuses on ways to ensure that a model's structure and data adhere to established ecological and fisheries principles before starting to balance the model. Heymans et al. (2016) reinforces the need for PREBAL rules of thumb and provides guidelines for balancing a model, comparing potential EwE models, fitting to time series, addressing uncertainty, and drawing conclusions from a model.

When building an EwE model with data from a variety of sources it is common that changes will need to be made before model assumptions are met (Heymans et al. 2016). In order to balance the model (i.e., ensuring that mass balance is ensured for each group), I needed to make and justify adjustments to the input data. These adjustments focused on data sources with larger uncertainties and were guided by the 11 terms of reference (ToRs) for the Atlantic Menhaden Single Species Benchmark Stock Assessment and Peer Review as well as the Ecosystem Management Objectives Workgroup's (EMOW) Comprehensive Fundamental Objectives. Both of these references were created by managers to guide modeling efforts for Menhaden management. The 11 ToRs were provided by the ERP working group in order to provide guidelines as to how they would be assessing the usefulness of models created by outside developers. The EMOW's Comprehensive Fundamental Objectives are specific guidelines for effective ecosystem management focused on Menhaden. The 11 ToRs focus on identifying and characterizing uncertainties in ecosystem models, comparing potential reference points, and identifying areas for improvement in ecosystem research. Uncertainties are unavoidable when modeling such a large area; my goal was to minimize these uncertainties by prioritizing higher quality data during the parameterization and balancing process as well as providing a range of possible outcomes when drawing conclusions given the uncertainties present.

Vulnerability parameters in for the Ecosim model were set following the methods described in Chagaris et al. (2020). In this, the most sensitive predator-prey vulnerabilities were allowed to be estimated by the “fit to timeseries” function built into the Ecosim software. The function was then run again to identify the next set of most sensitive vulnerability parameters, which could include one of the original predator prey vulnerabilities. This process was repeated until there was no longer any reduction in the sum of squares for the system as a whole. The number of vulnerability parameters allowed to vary in one iteration was capped at one less than the number of time series the Ecosim model was fit to, as identified as best practice by Heymans et al. (2016). Following this process, the vulnerability parameter minimum was fixed at 1.01 and maximum was capped as described in Chagaris et al (2020). Setting a minimum vulnerability parameter prevented instability in model projections. Capping the vulnerability parameter prevented the maximum predation mortality on any species group from exceeding the natural mortality of that group.

Primary Production Forcing Function

In order to include a primary production forcing function in the Ecosim model, a time series of phytoplankton biomass is needed to fit the Ecosim model to. It became evident that no time series existed for the entire modeled timeline (1985-2017), and therefore I developed a timeseries using three available datasets of chlorophyll *a* concentrations (as a proxy for phytoplankton biomass) for the model domain. From 1977-1987 the MARMAP survey took monthly samples of chlorophyll *a* concentration in the field. The next available time series of chlorophyll *a* is satellite data from NASA's Sea-Viewing Wide Field-of-View Sensor (SeaWIFS) program which started in 1997 and ended December 2010. The Moderate Resolution Imaging Spectroradiometer (MODIS) satellite launched its chlorophyll a concentration measuring satellite in 2002 and has data available until the end of the NWACS17 time series (through 2017). Estimates of chlorophyll *a* concentration during the ten-year gap between the MARMAP and SeaWIFS data sets were generated using the best of several competing generalized linear and additive models that were fit using various candidate environmental and spatiotemporal predictors. The environmental predictors evaluated were sea surface temperature (SST), river discharge, and rainfall. Month and region were included as predictors as well as the interactions between month, region and each environmental factor.

The models were fit using the MODIS chlorophyll a biomass concentration data. This data set consists of samples of chlorophyll a (μg/L) daily at a spatial resolution of 0.05 degrees. Samples within region were averaged to have provide a daily average chlorophyll a concentration by region. The SST data was obtained from NOAA's coastwatch website. This was done by creating data requests for each of the four sub regions (Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight) within the geographic range of the NWACS13 model. This data set consists of SST (°C) measurements at regular spatial intervals across the geographic range specified in the data request at monthly time intervals. Daily rainfall (mm) data was obtained from the Utah State University climate records website, which contains a collection of government and municipal climate records. The stations selected were the Bangor International Airport in northern Maine, the Portland Maine International Jetport, the Islip Li MacArther Airport in New York, the Painter Field Airport on the eastern shore of Virginia, and the Cherry Point Marine Corps Air Station in North Carolina. These stations were selected because they correspond to roughly the middle of one of the model sub regions, or represented roughly the northern and southern extreme of the modeled area. River discharge (cubic feet per second) came from the US geological survey website. The twelve largest rivers by discharge rate were included: the Charles, Connecticut, Delaware, Hudson, James, Mattaponi, Neuse, Pamunkey, Potomac, Rappahannock, Susquehanna, and Tar Rivers. These data sets consist of daily discharge of each river. Once all the data was gathered, one average value was generated for the entire model range for each variable (chlorophyll *a*, SST, rainfall, and river discharge).

Generalized Linear Models (GLMs) as well as Generalized Additive Models (GAMs) were considered. The best model, as identified by Akaike's Information Criterion (AIC), was a GAM that predicted log, standardized, chlorophyll *a* (chla.log.z) using smoothers of month, SST (SST.mean.z), log of rainfall (log.rain.z), log of discharge (log.discharge.z), region, and chlorophyll *a* data source (chla.source: representing MARMAP, MODIS, or SeaWIFS).

gam(chla.log.z ~ s(month,bs='cc') + s(SST.mean.z) + s(log.rain.z) + s(log.discharge.z) + region + chla.source + s(month,by=chla.source,bs='cc') + s(SST.mean.z,by=chla.source) + s(log.rain.z,by=chla.source) + s(log.discharge.z,by=chla.source) + te(month,SST.mean.z,bs='cc') + te(month,log.rain.z,bs='cc') + te(month,log.discharge.z,bs='cc') (Eq. 6)

The basis (bs) for the smooth of some variables was set as a cyclic cubic regression spline (bs='cc'), to force the starting and ending values of the smooths to be equal for monthly predictions). Thin plate regression splines were used otherwise. Interactions of the variables with the chla.source (by=chla.source) allowed for different smooths for each of the two chlorophyll *a* datasets. Similarly, interactions of variables with month were included as a tensor smooth (te). Autocorrelation in residuals of model predictions were tested for using the "acf" function in R and were determined to not be an issue. Predicted values were then back transformed and bias corrected. This model was then used to generate monthly estimates of chlorophyll a that were used as an index of phytoplankton biomass for the ten years of missing data. Projections into the future did not include month effects as fine scale variations were of lesser interest than large scale trends.

Outputs

The updated NWACS13 model was used to conduct deterministic simulations comparable to those examined by the ERP work group. The simulations demonstrated the combined impacts of varying fishing mortality of Menhaden and species of interest to managers. The species of interest were Atlantic Herring, Striped Bass, Bluefish, Weakfish, and Spiny Dogfish. A range of fishing pressure from 0 to 10 times the 2017 fishing mortality of Atlantic Menhaden was evaluated in four different scenarios of fishing pressure for the species of interests. The four scenarios were: 1.) the fishing pressure for all species was kept at status quo (2017) level ("Fsq" scenario), 2.) all species of interest were fished at their target fishing mortality ("Ftar" scenario), 3.) all species of interest were fished at their threshold (i.e., limit) fishing mortality ("Flim" scenario), and 4.) all species of interest were fished at their status quo fishing mortality except for Striped Bass which was fished at target fishing mortality ("Fstriper" scenario). These four scenarios match what was done to evaluate the NWACS MICE model and subsequently set total allowable catch (TAC) for Menhaden (Chagaris 2020, ASMFC 2021). The four scenarios were repeated with the inclusion of a primary production forcing function at 2017 levels as well as two climate projections as discussed above. The combination of four scenarios with four model configurations resulted in sixteen unique model runs.

Outputs from model runs were plotted in various ways. Model fits were assessed by plotting the predicted biomass and predicted catch with the observed data. This was done for the “base” model (with no forcing function) and the “PP0” model that included a primary production forcing function. Atlantic Menhaden total, fishing, and predation mortalities were plotted to demonstrate the relative magnitude of fishing and predation mortality. “Winners and losers” plots were created for the base model to show which groups were most heavily impacted by changes in Menhaden fishing mortality. These plots identified species that showed a relative increase, or decrease, in biomass or catch of 30% compared to 2017 levels. Time series of biomass for the key ERP species were generated to show how projected biomasses change with changing Menhaden fishing scenarios. Tradeoff plots were created for the base and PP0 models to show how the biomass of key species responded to changes in Menhaden fishing mortality. For these plots, the biomass in the terminal year of the projections was calculated relative to the target biomass identified by the stock assessment for the given species (termed “Brel2Btar”). The tradeoff relationships were compared across model configurations (base, PP0) and the four fishing scenarios (Flim, Ftar, Fsq, Fstriper). These tradeoff plots were created following Chagaris et al. (2020) who used similar plots to generate ERPs for Menhaden based on a Menhaden fishing mortality rate which would allow Striped Bass to reach their target and threshold biomass, when striped Bass were fished at their target F rate.

Primary Production Scenarios

The primary production forcing function was used in the ecosystem model to explore the long-term consequences of changes in primary production resulting from three different climate change scenarios. Primary production projections were inspired by the research described in Lotze et al. (2019). Their research used a suite of ecosystem models (including three Ecopath with Ecosim models) to predict how climate change would impact phytoplankton biomass under different Intercontinental Panel on Climate Change (IPCC) emission scenarios. Lotze et al. (2019) predicted declines in phytoplankton biomass of approximately 3.5% and 6.0% over 50 years. Correspondingly, I designed three primary production (PP) scenarios to represent (1) no change in mean annual biomass of phytoplankton (PP0), (2) a 3.5% decline in mean annual phytoplankton biomass (PP3.5), and (3) a 6% decline in mean annual phytoplankton biomass (PP6.0). Results from these projections were explored in two principal ways. First, timeseries of biomass and catch for all ERP focal species combined and of all modeled species combined were visualized for the duration of the projection period. These plots demonstrate the impact of the gradual decrease in phytoplankton biomass forced in the PP3.5 and PP6.0 scenarios as well as the difference in end year projections between model configurations (PP0, PP3.5, PP6.0). The second way in which primary production forcing function outputs were explored was visualizing end year projection data only. These data were filtered to show only groups that demonstrated a more substantial increase or decrease in biomass or catch under the different scenarios. Groups that were disproportionally impacted by the PP scenarios exhibited changes in Biomass or Catch greater than the decrease in phytoplankton biomass (3.5% or 6.0%) in the PP scenario visualized.

RESULTS

Base Model

Fits

The base model had reasonably good fits for both biomass and catch for modeled species groups (Figure 2,Figure 4). The model was generally able to reproduce trends in biomass for focal species and some other ecologically important species (Atlantic Herring, Menhaden, Atlantic mackerel, Butterfish, Bluefish ages 0 and 4+) (Figure 2). Predicted biomass for some groups did not fit the observed data as well (Shrimp, Weakfish age 3+, Haddock, Atlantic croaker) (Figure 2). When the model did not fit the biomass as well, it tended to project no change in biomass (Demersal omnivores in Figure 2), rather than finding a trend that was not found in the raw data. The model predicted catch close to observed data for several groups (Macrobenthos molluscs, Megabenthos other, Atlantic Herring, Alosines, most Menhaden ages, Squid, Bluefish, Striped Bass, and Atlantic cod) (Figure 4). Catch fits were notably poorer for species with less reliable data available (Shrimp, small pelagic other, Spiny Dogfish age 6+, Medium pelagic other, Sharks coastal, Sharks pelagic) (Figure 4). Overestimations for shrimp corresponded with over estimations of catch in two of their key predators, age 6+ Spiny Dogfish and other Demersal piscivores (Figure 4).

The base model explained a large fraction of the total mortality for Atlantic Menhaden groups, particularly for ages 2, 4, 5, and 6+ (Figure 6). In these plots, the sum of fishing and predation mortality (F+M2) was nearly equal to the total mortality (Z). But there was a greater amount of unexplained mortality for ages 0, 1, and 3. Unexplained mortality is the difference between total mortality estimated for the stock assessment and the sum of fishing and predation mortality described by the model. High unexplained mortality is a sign that there are ecological processes accounting for mortality outside what is modeled. Overall, this NWACS17 model explained a greater proportion of Menhaden mortality than previous NWACS models as the model better represents the full range of predators of Menhaden (SEDAR 2020). Predation mortality (M2) was also generally large, as would be expected for a forage species.

Projections

Projections using a range of different Menhaden fishing mortality rates illustrated many tradeoffs in the ecosystem. Projected time-series of biomass for the focal ERP species indicate that some species (Menhaden, striped Bass, weakfish, and spiny Dogfish) were more strongly affected by Menhaden fishing rates than other species (bluefish, Atlantic Herring) (Appendix figures). These species-specific responses are summarized by quantifying the proportional change in their biomass at the end of the 50-year projection relative to their 2017 biomass (termed $B_{rel2017}$) for the base model projections (Figure 7). Not surprisingly, Menhaden exhibited the strongest response to the Menhaden fishing mortality rate scenarios in the base model, with $B_{rel2017}$ranging from a high of 1.3 when Menhaden F was zero to $B_{rel2017}$~0.4 when Menhaden F multiplier is 10. Striped Bass biomass was strongly negatively impacted by increases in Menhaden fishing mortality; for example, $B_{rel2017}$ was ~1.08 when Menhaden were not fished and it dropped to ~0.69 at the highest Menhaden fishing rate (Figure 7). Spiny Dogfish biomass was also negatively impacted by increases in Menhaden fishing mortality, with $B_{rel2017}$ ~0.75 (Figure 7). Weakfish showed an increase in biomass with increasing Menhaden fishing mortality (up to $B_{rel2017}$~1.18), which could be an indirect effect caused by decreased competition (Figure 7). Alosines showed a strong increase in biomass with increasing Menhaden fishing mortality (up to $B_{rel2017}$=3.5), likely caused by a release from competition with Menhaden but also probably affected by higher uncertainty associated with Alosine vulnerability parameters (Figure 8). Biomass of Nearshore Piscivorous Birds was strongly negatively impacted by increases in Menhaden fishing mortality (with $B_{rel2017}$ dropping to ~0.4), while biomass of these birds was projected to more than double if Menhaden were not fished. Pelagic sharks showed a similar but less dramatic trend ($B_{rel2017}$ ranging from 1.2-0.6, across the Menhaden F rates; Figure 8).

The relative impact of Menhaden fishing mortality rates on select ERP species' biomasses (striped Bass, bluefish, spiny Dogfish, Atlantic Herring) were also expressed relative to the current biomass targets for each species, and results were compared across different fishing and primary production scenarios (Figure 9, Figure 10, Figure 11, Figure

12). For striped Bass, their 50-yr projected biomass relative to their biomass target ($B_{rel2Btar}$) declined consistently with increasing Menhaden F for all examined scenarios (Figure 9). However, the base model does not project that Striped Bass would reach their target biomass (i.e., $B_{rel2Btar} = 1$) under any combination of Menhaden F or fishing scenarios for the ERP focal species (Figure 9). The model also projects that the difference between fishing all ERP focal species at their Flim, Ftar, or Fsq has little impact on the biomass of Striped Bass, but the Fstriper scenario resulted in consistently higher $B_{rel2Btar}$ values across all Menhaden F using the Base model (Figure 9). Bluefish $B_{rel2Btar}$ is relatively unimpacted by changes in Menhaden fishing mortality and, similar to Striped Bass, is not projected to surpass their target biomass (Figure 10). The base model is predicting a large impact on Bluefish biomass when fishing ERP focal species at Flim or Ftar (with $B_{rel2Btar} \sim 0.6$) compared to the Fsq and Fstriper scenarios (with $B_{rel2Btar} \sim 0.4$; Figure 10). Spiny Dogfish is projected to reach its target biomass at a Menhaden fishing mortality multiplier of 0.12-5.0 depending on fishing mortality of ERP focal species (Figure 11). Again, the model projects a difference in biomass depending on fishing pressure on ERP focal species, but this time Flim and Ftar scenarios result in lower $B_{rel2Btar}$ of Spiny Dogfish compared to Fsq and Fstriper scenarios (Figure 11). Atlantic Herring biomass is not projected to reach its target biomass under any combination of fishing mortality of Menhaden and the ERP focal species (Figure 12). Atlantic Herring $B_{rel2Btar}$ has relatively flat relationship with Menhaden fishing pressure and ERP fishing scenarios, given that the magnitude of the changes across scenarios were relatively small (with $B_{rel2Btar}$ differences typically less than 0.03 across Menhaden F; Figure 12). This is most likely because the impact of Menhaden fishing pressure on Atlantic Herring biomass is an indirect one, resulting from release from competition. This release from competition is dampened or exacerbated with changes in the biomass of shared predators.

Primary Production Forcing Function

Fits

Model fits for both biomass and catch with the inclusion of bottom-up control via a primary production forcing function were strong (Figure 3). Surprisingly, there was a 15.5% increase in total sum of squares from the base model to the PP0 model, which included a primary production forcing function. It is worth noting that the fit-to-timeseries tool within EwE initially fit a PP0 model with a smaller sum of squares than the base model. The increase in sum of squares came when the model was adjusted to produce ecologically feasible projections for all species groups. This was done by decreasing predator-prey vulnerability parameters until biomasses did not increase to greater than 10 times the highest seen in the historic time series. The increased capabilities of a model that includes a primary production forcing function justify exploring the model further, even with the poorer fit overall. The seasonality of phytoplankton biomass (induced by the forcing function and observed chl *a* data) is evident in biomass fits of lower trophic level species groups (Squid, Shrimp, Atlantic Herring) but not in higher trophic species groups (Striped Bass, Spiny Dogfish) (Figure 3). The month effect also becomes less evident with increasing age within a species (Atlantic Menhaden, Bluefish, Summer flounder) (Figure 3). Biomass fit for Striped Bass ages 2-6 and 7+ were improved slightly with the inclusion of the primary production forcing function (Figure 3). Catch fits were strongest for focal species (Atlantic Menhaden, Bluefish) (Figure 5). Catch for Striped Bass was underestimated for both ages 2-6 and 7+ (Figure 5), and not as good as the fits for the base model (Figure 4). Catch for several groups was overestimated (Shrimp, Alosines, Atlantic mackerel, Weakfish age 3+, Spiny Dogfish age 6+, Demersal benthivores) (Figure 5). Species groups with low data availability showed lack in trend in catch (Sharks – coastal and pelagic, Medium pelagic, Large pelagic, megabenthos filterers) (Figure 5).

<u>Projections</u>

The inclusion of a primary production forcing function (PP0) had several impacts in projections compared to the base model (BASE). The inclusion of a primary production forcing function resulted in different vulnerability parameters than the base model. This configuration of the model leads to projections of much greater gain in biomass with low Menhaden fishing pressure for both Menhaden (Figure 25) and Striped Bass (Figure 26) compared to the base model. PP0 results in a lower total biomass projected for Bluefish but no change in the impact Menhaden fishing pressure has on Bluefish biomass projections (Figure 27). Projections of Atlantic Herring also show a decrease in biomass with inclusion of a primary production forcing function (Figure 30). A higher total biomass is projected for Weakfish (Figure 28) and Spiny Dogfish (Figure 29) in the PP0 model compared to the base model. PP0 projects that Striped Bass (Figure 9) and Spiny Dogfish (Figure 11) will be more responsive to changes in Menhaden fishing morality than does the base model. PP0 projects Bluefish (Figure 10) will be more responsive to changes in BERP focal species fishing mortality than the base model but not more responsive to changes in Menhaden fishing mortality. PP0 projects Atlantic Herring (Figure 12) will be slightly more responsive to Menhaden fishing mortality though the relative change is small.

Projections of declines in phytoplankton biomass (PP3.5 and PP6.0) tended to have impacts relatively comparable to the magnitude of the phytoplankton decline. Projections of total ERP group biomass demonstrated decreases in biomass and catch for PP3.5 and PP6.0 roughly proportional to the decrease in phytoplankton biomass (3.5% and 6.0%) compared to PP0 (Figure 13). The same pattern was evident for the predicted catches of the ERP focal groups (Figure 14). Projections for total biomass in the model showed decreases in biomass greater than the decrease in phytoplankton biomass when comparing PP3.5 and PP6.0 to PP0 (Figure 15), though decrease in total catch was roughly proportional to the decrease in phytoplankton biomass (Figure 16). Groups projected to increase in biomass (terminal year biomass compared to terminal year biomass in PP0) with a decrease in phytoplankton biomass (both PP3.5 and PP6.0) were Demersal omnivores, Alosines, and other primary producers (Figure 17 and Figure 18). Several groups were projected to decrease in biomass greater than the decrease in phytoplankton biomass in a given model configuration (Figure 17 and Figure 18). For PP3.5, these groups were: Large pelagics (HMS), Seabirds, Microzooplankton, Bluefish, Sharks – pelagic, Striped Bass, Nearshore piscivorous birds, Micronekton, Atlantic cod, Medium pelagic – other, and Weakfish (Figure 17). For PP6.0, these groups were: Pinnipeds, Atlantic mackerel, small pelagic – other, squid, sharks – coastal, Atlantic Herring, Anchovies, Spiny Dogfish, Atlantic Menhaden, Large pelagics (HMS), Microzooplankton, Seabirds, Bluefish, Sharks – pelagic, Striped Bass, Nearshore piscivorous birds, Micronekton, Atlantic cod, Medium pelagic – other, and Weakfish (Figure 18)

DISCUSSION

Base Model

The base model and corresponding plots were generated with the goal of informing management for the Atlantic Menhaden. As management for the species has moved toward an EAFM, managers at the ASMFC have utilized a suite of models to base management decisions off a greater understanding of the role of the species within the ecosystem. The NWACS17 model was designed to work with the existing suite of models to inform Menhaden management. The model shows both direct and indirect impacts of changes in Menhaden fishing pressure on the ERP focal species. Striped Bass is the most strongly impacted predator species of the ERP focal species. Other species, such as Bluefish and Weakfish see an increase in biomass with increases in Menhaden fishing pressure (Figure 7). This is most likely an indirect impact within the ecosystem due to release from competition with other predators like Striped Bass. All of these impacts can be assessed by one or more of the existing models used in the ERP stock assessment for Menhaden management (ASMFC 2020). One benefit of the NWACS17 model is that it is more readily compared to single species stock assessments than NWACS13 because the age structure of both Menhaden and key predators (Striped Bass, Bluefish, and Weakfish) have been expanded to match the age structure in their corresponding single species assessments.

The NWACS17 model will also benefit Menhaden management by providing an updated assessment of impacts of Menhaden fishing mortality on species not included in the list of ERP focal species. In the 2020 ERP stock assessment for Menhaden management this role was filled by the NWACS13 model. The NWACS17 model updates that management advice with the most up to date data available. Nearshore piscivorous birds and pelagic sharks were the two groups most negatively impacted by increases in Menhaden fishing pressure. The impact on Nearshore piscivorous birds is likely a direct effect as Menhaden makes up over 30% of the diet for this species group. The impact on pelagic sharks is likely an indirect effect as Menhaden makes up roughly 2% of the diet for this species group. Neither of these groups were selected as a focal group for the ERP working group and therefor were not identified as species of concern in the ERP stock assessment. This information is still worth noting, however, as both groups are economically and ecologically important. Nearshore piscivorous birds support a large ecotourism industry while pelagic sharks attract recreational anglers to fishing towns throughout the modeled region. Both groups play important roles as high trophic-level and apex predators in the system. Including this information in reports could inspire their inclusion in the list of focal species in subsequent iterations of modeling efforts as we move towards EBFM. The NWACS17 model projects strong increases in biomass of Alosines with increase in Menhaden fishing pressure (Figure 8). This is an indirect impact most likely resulting from a release from competition with Menhaden for food resources, decrease in predators that prey on both Alosines and Menhaden, or both. This strong increase in Alosine biomass could mitigate the negative impacts on biomass of increased Menhaden fishing pressure for predator species that prey on both Alosines and Menhaden. This could be a reason to include Alosines in the ERP focal species for the next iteration of assessment, similar to the inclusion of bay anchovy and Atlantic Herring in the NWACS-MICE. However, the data quality for Alosines was poor and greater efforts in estimating their biomass and trophic dynamics would help reduce uncertainty with this group.

The base model is well suited to provide complimentary management advice to that of the other models available for Menhaden. This model has the ability to model the reduction and bait fisheries separately. This gives managers the ability to evaluate impacts of a redistribution of catch allocation between the two sectors. The base model also identifies species impacted by changes in Menhaden fishing mortality which are not included in less complex models available to managers. If managers and stakeholders find these species to be of importance, this could warrant including them in future iterations of the less complex models available. These forms of strategic management advice compliment tactical advice from other models consistent with best practices (Plaganyi et al. 2007, Link et al. 2020).

The movement towards EAFM for Menhaden management was inspired by known interactions within the environment, namely the predator-prey interaction between

Menhaden and economically and culturally important Striped Bass. This predator prey interaction was the main focus when setting ecological reference points for Menhaden. The interaction is evident in the NWACS17 model though the impact of changes in Menhaden fishing pressure is dampened in the larger model as compared to the NWACS MICE model (Chagaris et al. 2020). This suggests that either Striped Bass are switching to other prey species when access to Menhaden is limited or other prey species are released from competition with Menhaden and are able to supplement the diet of their predators. Either way, these feasible changes in the ecosystem are lost in less complex models and demonstrate the value of considering higher complexity models when weighing potential actions for strategic management.

Comparison With NWACS13 Model

Unsurprisingly, the NWACS17 model has many similarities with its predecessor the NWACS13 model. In both models, Striped Bass shows a strong response to changes in Menhaden fishing mortality. This relationship has been understood qualitatively by managers and fishermen alike for many years before computing power advanced to the point where the relationship could be more quantitively explored. Quantitative analyses of this predator prey interaction (e.g., Buchheister et al. 2017, SEDAR 2020b, Chagaris et al. 2020) were the inspiration for the current ERP target and threshold Menhaden fishing mortality. Feedback on the NWACS13 model also inspired efforts on the NWACS17 model discussed here. Expanding the model from size classes based on ontogenetic changes in diet to annual age classes for Menhaden allows for direct comparison with stock assessments while maintaining the predator prey interactions. The inclusion of the primary production forcing function brings in bottom-up control within the ecosystem. To my knowledge, this is the first time this has been done for an EwE ecosystem model for the region. The gained function allows for more thorough investigations in food web dynamics in the ecosystem as well as the ability to explore more potential future scenarios, such as climate change scenarios. Managers and stakeholders in the Menhaden fishery have expressed the need for climate considerations in management decisions for years (SEDAR 2020b) but so far there is no way to quantify climate impacts associated with Menhaden management. Climate will have a significant impact on the modeled region within the fifty-year projections made by this model and others used in Menhaden management. Climate impacts, especially associated with rising ocean temperature, will be particularly important to consider in the modeled region as it has been shown to be warming faster than the global average (Frumhoff et al. 2007).

In all, it is encouraging that the updated NWACS17 model agrees with many of the major findings from the NWACS13 model. The gain of function from updates and expansion of the model makes the model more useful for managers, expanding upon the ability of the NWACS13 model's ability to address questions that other established models for Menhaden cannot do. The NWACS17 model, like the NWACS13 model when it was completed, was designed to address more management objectives of the ERP working group than any other model developed. As more management objectives arise the model can be further expanded to provide broad, strategic advice on managing Menhaden.

Comparison With NWACS MICE Model

The NWACS19 model has many similarities with the NWACS MICE model (Chagaris et al. 2020) but the differences in model structure allow for complementary exploration between the two models. Encouragingly, the two models agreed qualitatively in projecting how increasing Menhaden fishing mortality would impact the ERP focal species, though the degree to which the species were impacted did not always agree. The two models both identified the predator prey interaction between Striped Bass and Menhaden as the strongest. This is primarily a result of the two models using the same diet data. The available fisheries independent diet data shows that Menhaden make up about a third of the diet of Striped Bass. The reduction is Striped Bass biomass at greater fishing mortalities of Menhaden is therefore not surprising. What is interesting is that the interaction is stronger in the NWACS MICE model than the NWACS17 model. This is most likely the result of a fuller representation of Striped Bass diet in the NWACS17 model and/or slightly different vulnerability parameters. Crustaceans make up a large portion of Striped Bass diet depending on the age of Striped Bass (roughly half the diet of age 0-1 Striped Bass but decrease significantly with age). This group is included in the NWACS17 model but not in the NWACS MICE model. This allows for the negative impact on Striped Bass biomass caused by increasing Menhaden fishing mortality to be mitigated in the NWACS17 model by the Striped Bass preying upon crustaceans more heavily. This prey switching makes sense ecologically but may be lost to some degree when limiting complexity in the model with the goal of tactical management like what was done with the NWACS MICE model.

In addition to providing more context to linkages found in the NWACS MICE model, the NWACS17 model also identifies linkages not included in the NWACS MICE model. The NWACS17 model projects negative impacts on the biomass of nearshore piscivorous birds and pelagic sharks and positive impacts on the biomass of alosines associated with increased Menhaden fishing mortality. These linkages are not included in the NWACS MICE model because the groups were not identified in the ERP focal species list. Identification of strong linkages for these species could lead to their inclusion in the next iteration of the NWACS MICE model. The nearshore piscivorous birds bring revenue to the region through ecotourism and are a group of concern for a large number of shareholders. The strong positive impact of increased Menhaden fishing mortality on alosine biomass could be reason enough to include them in the next iteration of the NWACS MICE model, especially if nearshore piscivorous birds are included. Alosines make up <2% of the diet of current ERP focal species, which is why they were not included in the list of ERP focal species. If nearshore piscivorous birds were included in the NWACS MICE model, however, it would make sense to include alosines as they make up 11% of the diet of nearshore piscivorous birds and their inclusion would lead to more realistic projections of biomass. These potential changes to the NWACS MICE model, identified by the more complex NWACS17 model highlights the benefit of developing a suite of models as is best practice in EAFM (Townsend et al. 2020, Link et al. 2020)

Primary Production Forcing Function

The addition of a primary production forcing function within the model increases the capabilities of the model and realism of model outputs. The inclusion of a primary production forcing function strengthens the predator-prey relationship between Menhaden at its predators Striped Bass and Spiny Dogfish compared to the BASE model in that changes in Menhaden fishing mortality results in a greater change in biomass of these predators when comparing the BASE model to the PP0 (Figure 9 and Figure 11). These relationships were identified in several of the models developed by the ERP work group. Seeing similar trends in model projections of different models provides some confidence in model configuration. The predator-prey interaction with Striped Bass and Menhaden is of particular interest as this tradeoff was directly used to set ERPs in the NWACS MICE models.

Climate-Driven Primary Production Scenarios

The inclusion of climate-driven primary production projection scenarios highlighted the added capabilities of including a primary production forcing function while also providing a first step toward a defined management goal for Atlantic Menhaden. Biomass and catch in the ecosystem are projected to decline under the climate scenarios explored by the model (Figure 15, Figure 16). Several species are identified as disproportionately impacted by climate change in these model configurations (Figure 17, Figure 18, Figure 19, Figure 20). Among the species disproportionately impacted are Striped Bass, Atlantic cod, and nearshore piscivorous birds. These species are all important economically, ecologically, and culturally in the region. Striped Bass is of particular interest as the predator-prey interaction between this species and Menhaden is used to set ERPs under current management. Identifying the sensitivity of this group to climate change may warrant climate considerations in other models available for Menhaden management.

It is important to note that the emission scenarios explored in the Lotze et al. (2019) paper and in this work assumed aggressive reduction in emissions. The "business as usual" limited climate action scenarios were not explored in this work or the research that inspired this exploration though they may be more realistic in the 50-year projection explored here.

The work described here represents a first step toward making climate-informed management decisions for Menhaden and the modeled region. For a full assessment of climate impacts on management decisions many more factors would need to be included (impacts of temperature, ocean acidification, shifting distributions, sea level rise, etc.). The process described here quantifies only the impact of decreasing phytoplankton biomass, similarly to what was described in Lotze et al. (2019). If stakeholders are interested in these early climate considerations, it would warrant more effort to quantify more well-rounded climate impact scenarios.

Caveats and Qualifications

Model development in Ecopath with Ecosim is an evolving field with plenty of room for improvement. Some issues faced during model development are well known (Heymans et al. 2016, Link 2010b) and were addressed as much as possible before model balancing began. Other issues, and possible solutions to those issues, became evident throughout the effort. Perhaps the most glaring issue that became evident throughout the balancing process is the inherent decision-making process necessary to balance the Ecopath model. This process can and should be informed by data quality and management questions the model is being designed to address. The fact remains, however, that no two model developers would design identical models if model balance were not achieved with raw data. Moreover, a model the size of the NWACS17 model would be impossible to duplicate from scratch even for the same modeler, without detailed notes of what had been done. This issue of reproducibility and standardization of model balancing process was part of the inspiration for Rpath (Lucey et al. 2020). Rpath is a package within R to create an Ecopath with Ecosim model that has been completed after the NWACS17 model was created. By creating an EwE model in R, sensitivity analysis can be more easily conducted on any input value. Such sensitivity analyses demonstrates how heavily outputs are influenced by a given input value and bolsters confidence in model predictions.

As with any shift from the status quo, the use of ecosystem models in tactical management has faced scrutiny and not without merit. Some researchers criticize the NWACS MICE model and the ecological reference points because it lacks more complete size- and age-specific data, information on fishery selectivity, and variability in recruitment (Cadrin Review of SEDAR 69). The NWACS17 model partially addresses these shortcomings, but additional work would be needed to fully account for these concerns. The Menhaden age structure for the NWACS17 model is the same as the single species stock assessment (Beaufort Assessment Model or BAM), which is a finer level of granularity than the NWACS MICE and hybrid models. This allows for direct comparisons between model outputs of the BAM and the NWACS17 model, but also introduces considerable uncertainty when parsing diet of predators into Menhaden age classes. The NWACS17 model partially addresses concerns about fishery selectivity by using annual age classes and modeling the reduction and bait fisheries for Atlantic Menhaden separately. This allows for projections to be generated where the two fisheries are managed differently from one another. If managers were interested in basing management decisions off fishing fleet specific projections, additional granularity would be needed to better represent bycatch and spatial dynamics of the fisheries of interest. Future work would be needed to incorporate annual Menhaden recruitment deviations into the NWACS17 model.

Future Research

While this research advances the science of ecosystem modeling for Atlantic Menhaden it also highlights the need for further research. Future efforts in ecosystem modeling for Atlantic Menhaden management should focus on dealing with uncertainty associated with model outputs and expanding capabilities of the model. In some cases, future efforts could accomplish both goals. Anstead et al. (2021) highlights the need to "embrace incremental progress" in the movement toward EBFM. Much as the NWACS17 can be seen as the next step from the NWACS13 model and in some ways the NWACS MICE model, future additions will need to be constructed incrementally.

Dealing with uncertainty in model outputs can be done in many forms with clear first steps to advance the science. One first step would be to improve data quality on species groups included in the model in order to reduce uncertainty with model outputs.

Priority for data quality improvement should be placed on species that have been identified as sensitive to changes in Menhaden fishing mortality such as nearshore piscivorous birds. This group has been shown to be sensitive to availability of Menhaden using the NWACS models, but the diet of this group remains under-studied. Data quality improvements would also help to address the concern of recruitment variability in the NWACS17 model and similar models. These data quality improvements could include more detailed data on phytoplankton biomass or rates of primary production, and higher data quality of juvenile species groups, especially for forage fish which are highly sensitive to changes in primary production.

Another next step in dealing with model uncertainty would be to conduct a management strategy evaluation (MSE). MSEs involve comparisons of tradeoffs in performance metrics associated with proposed management strategies using simulations in the presence of uncertainties (Punt et al. 2014). A management strategy refers to the data collection scheme, the specific analysis applied to the data, and the harvest control rules used to plan management actions (Butterworth 2007). MSEs can be used to identify harvest strategies that will maximize the likelihood of achieving the identified ecosystem management objectives. MSEs have been used to inform policy around the world for many fisheries, such as fisheries for South African anchovy (Bergh and Butterworth 1987), sardine (Geromont et al. 1999), cape hake (Rademeyer et al. 2008), rock lobster (Johnston and Butterworth 2005), and horse mackerel (Furman and Butterworth

2012). MSEs in the past have focused on single species management strategies but have also been applied to ecosystem management, such as one conducted on the European Commission's North Sea Multi-Annual Plan (Mackinson et al. 2018) and on Atlantic Herring (*Clupea harengus*) (Deroba et al. 2018). An MSE for the NWACS17 model could be conducted within the EwE software by utilizing the MSE Batch plug in or by utilizing one of the packages in R designed to conduct MSEs (GMSE, MSEtool).

More exciting from the prospective of the model developer are future efforts to expand model capabilities. A clear next step would be the addition of spatial structure within the model. Spatial structure would require the addition of an Ecospace model. Ecospace has been developed alongside Ecopath and Ecosim and therefore could readily build upon the NWACS17 model. An Ecospace model would essentially create a unique Ecopath with Ecosim model for a given number of spatial blocks and allow biomass of species to move around the modeled ecosystem according to ecological and ontogenetic principles. The addition of spatial structure within the model could also help reduce uncertainty in model output as seasonal changes in species distributions and trophic dynamics can be better represented.

Expansion and progression of this and similar models faces several hurdles moving forward. One hurdle will be increased data requirements in order to expand the models. In order to accomplish the goal of spatially explicit Ecopath with Ecosim and Ecospace models, high-quality spatial data is required. Similarly, the output of higher resolution temporal output is only possible with the input of higher resolution temporal data. For species where at-sea-observer data is available, this type of model expansion could be relatively straight forward. For less well-studied species, however, model expansion could come with an increase in model uncertainty which is already a concern with ecosystem models. A second major hurdle facing the use of ecosystem models in management is updateability. To be useful for managers, models must be updateable on the same time frame as benchmark stock assessments are. Larger models take a significant amount of time and expertise to develop. Simple updates can be done fairly quickly but any change in complexity to the model requires the model to be recalibrated, significantly increasing the time needed to prepare the model. This overlaps with a third hurdle facing ecosystem models in management which is a financial hurdle. Added complexity in models requires added expertise and time devoted to model development and generating output. Models included in the benchmark stock assessment for Atlantic Menhaden were created by state and academic researchers funded by federal and state agencies, non-profit organizations like the Lenfest Ocean Program, the Maryland Sea Grant, or pro bono to accomplish this work. Regular model updates and further expansion will require more stable forms of funding.

CONCLUSION

The significance of the NWACS17 can best be understood when considering its role among the other models available for Menhaden management advice. All of the models available have advantages and disadvantages. These advantages and disadvantages are the reason the BERP working group decided the best management advice would be produced with a suite of models. The NWACS17 model is the most complex of the models available for Menhaden management advice. This level of complexity makes the NWACS17 model most useful for demonstrating large trends in predictions and checking for concerns with species and fisheries not included in the less complex models. Moving forward, this model can continue to be used to address concerns related to climate and consider when it would be beneficial to add complexity to the NWACS MICE model.

The NWACS17 model represents further incremental progress in the movement toward ecosystem-based fisheries management. This model leverages the strongest points of the models it was built upon and adds capabilities that are unique in all models available for the species and region of interest. These added capabilities allow for the novel investigation of research objectives that have gone unaddressed for years. This model will be beneficial to managers when they reevaluate ERPs and current management of Atlantic Menhaden. Further expansions of this model will build upon the capabilities described here and continue to advance the science of ecosystem modeling and management.

FIGURES

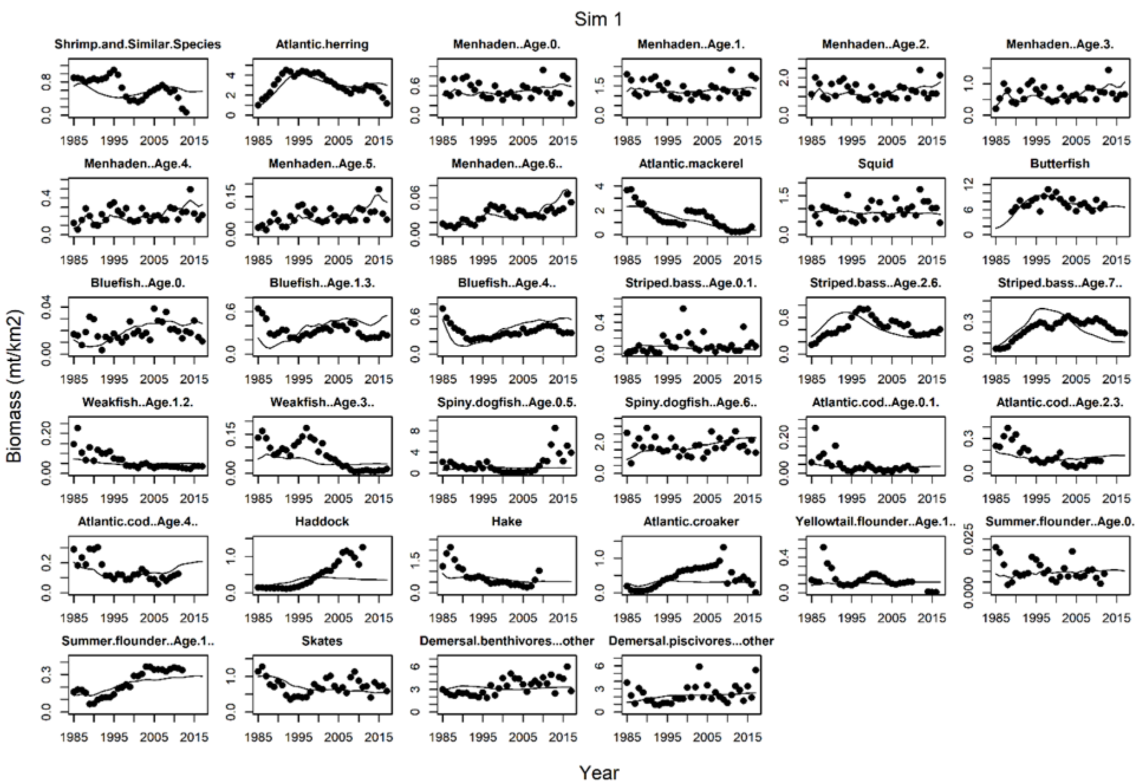

Figure 2 Biomass fits for BASE model run. Points show observed data, line shows model fit

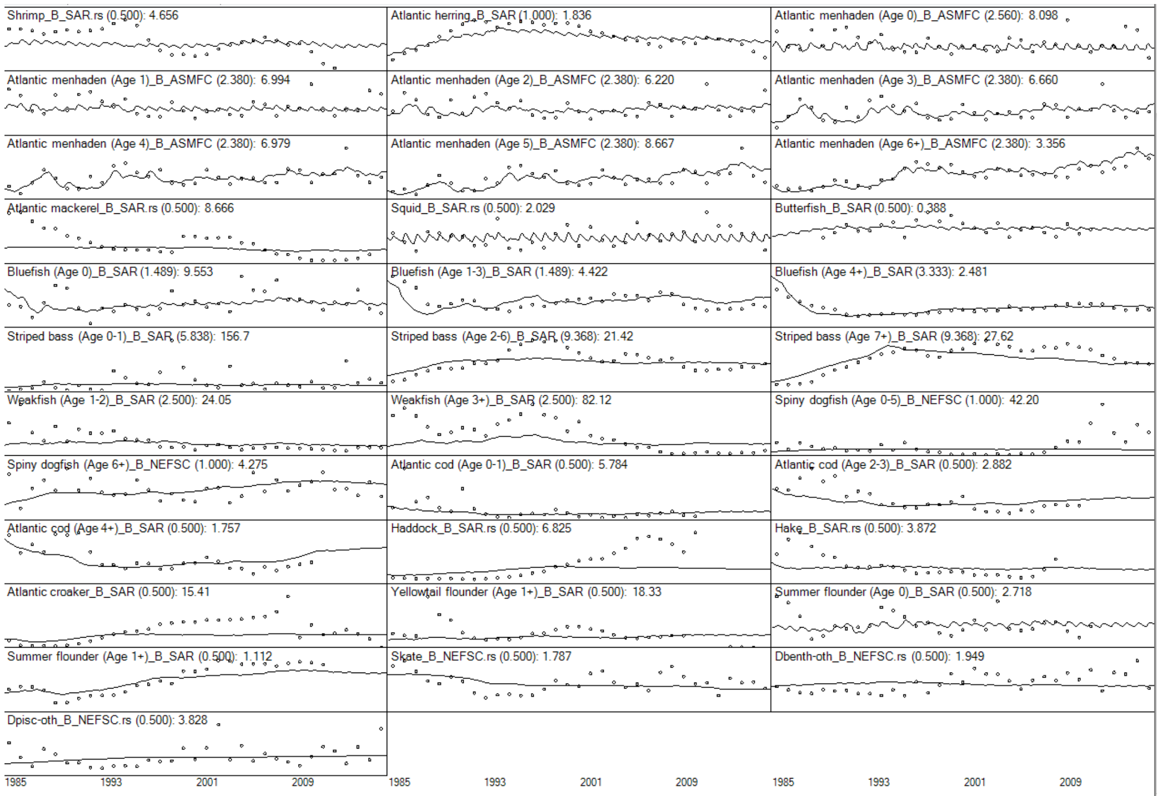

Figure 3 Biomass fits for PP0 model run. Points show observed data, line shows model fit

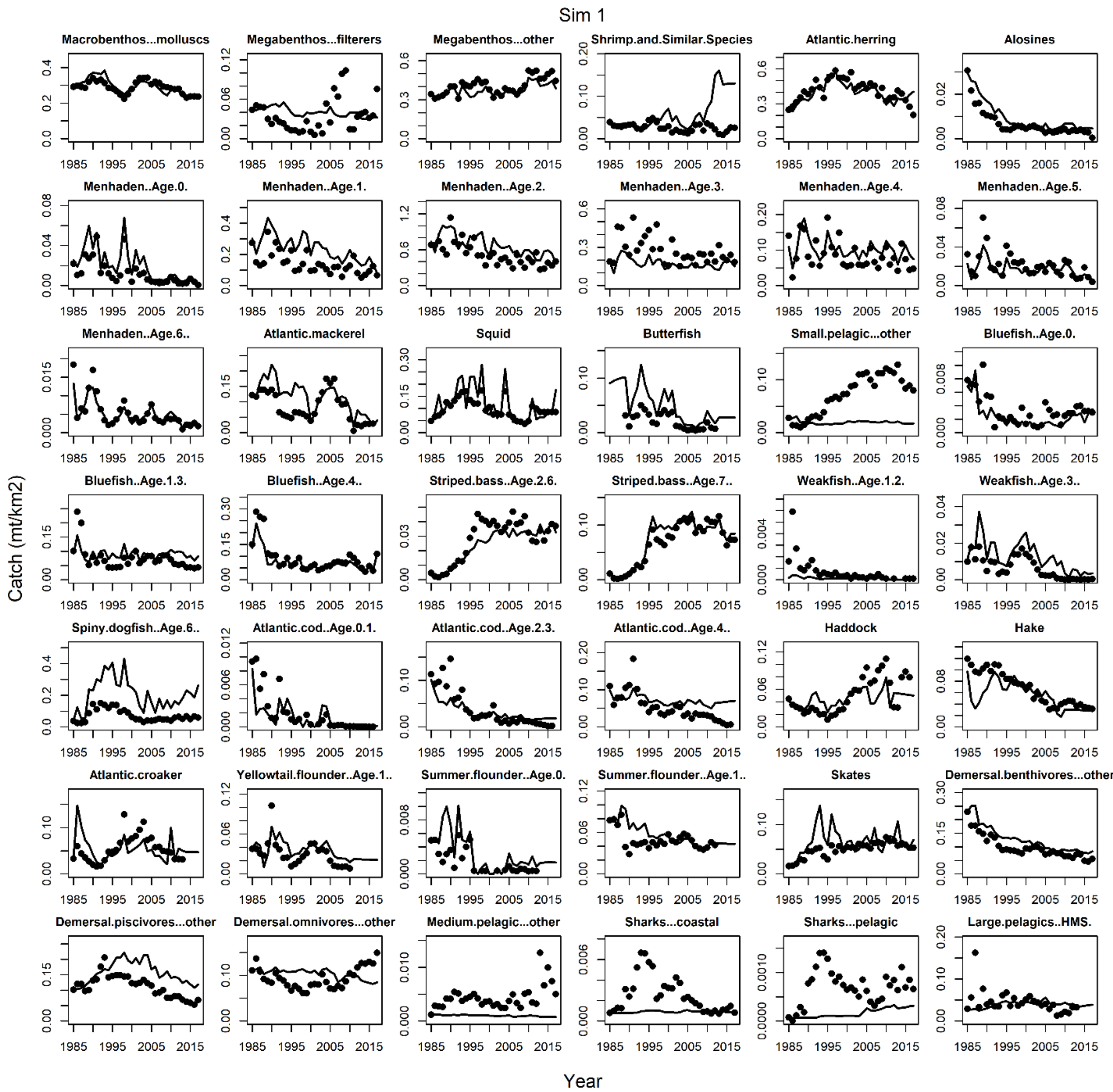

Figure 4 Catch fits for BASE model run. Points show observed data, line shows model fit

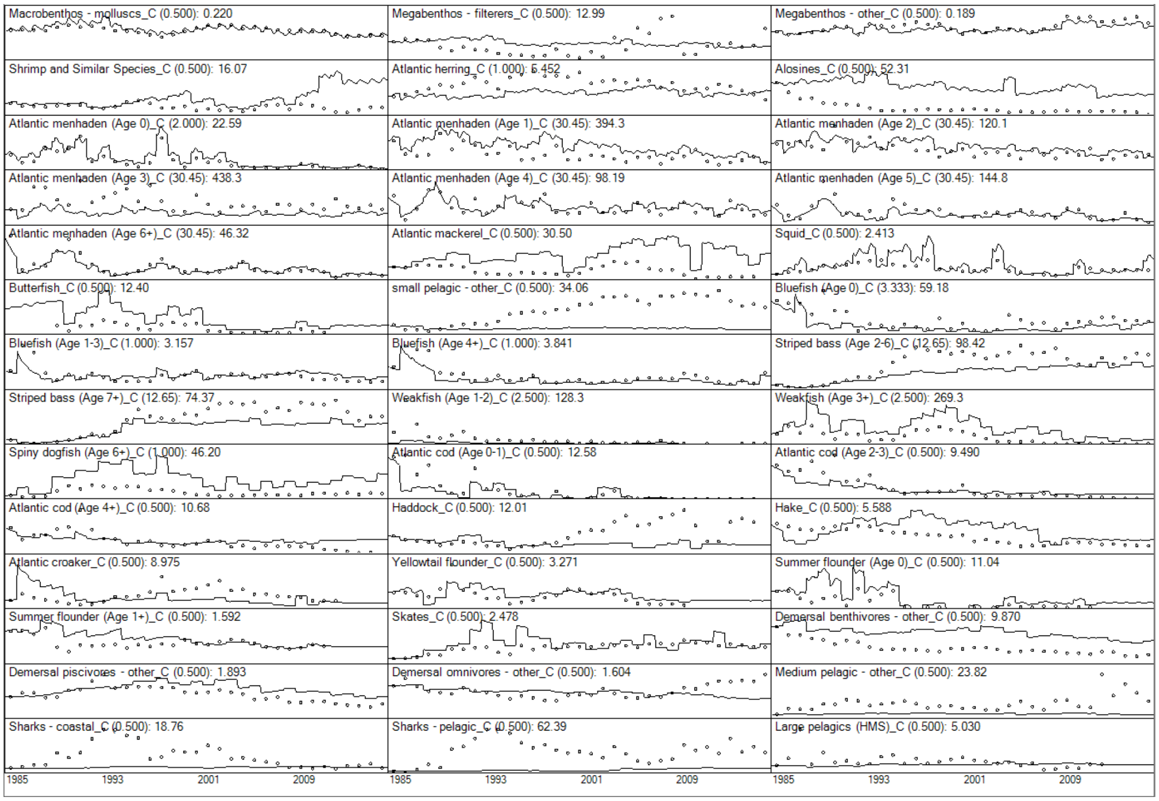

Figure 5 Catch fits for PP0 model run. Points show observed data, line shows model fit

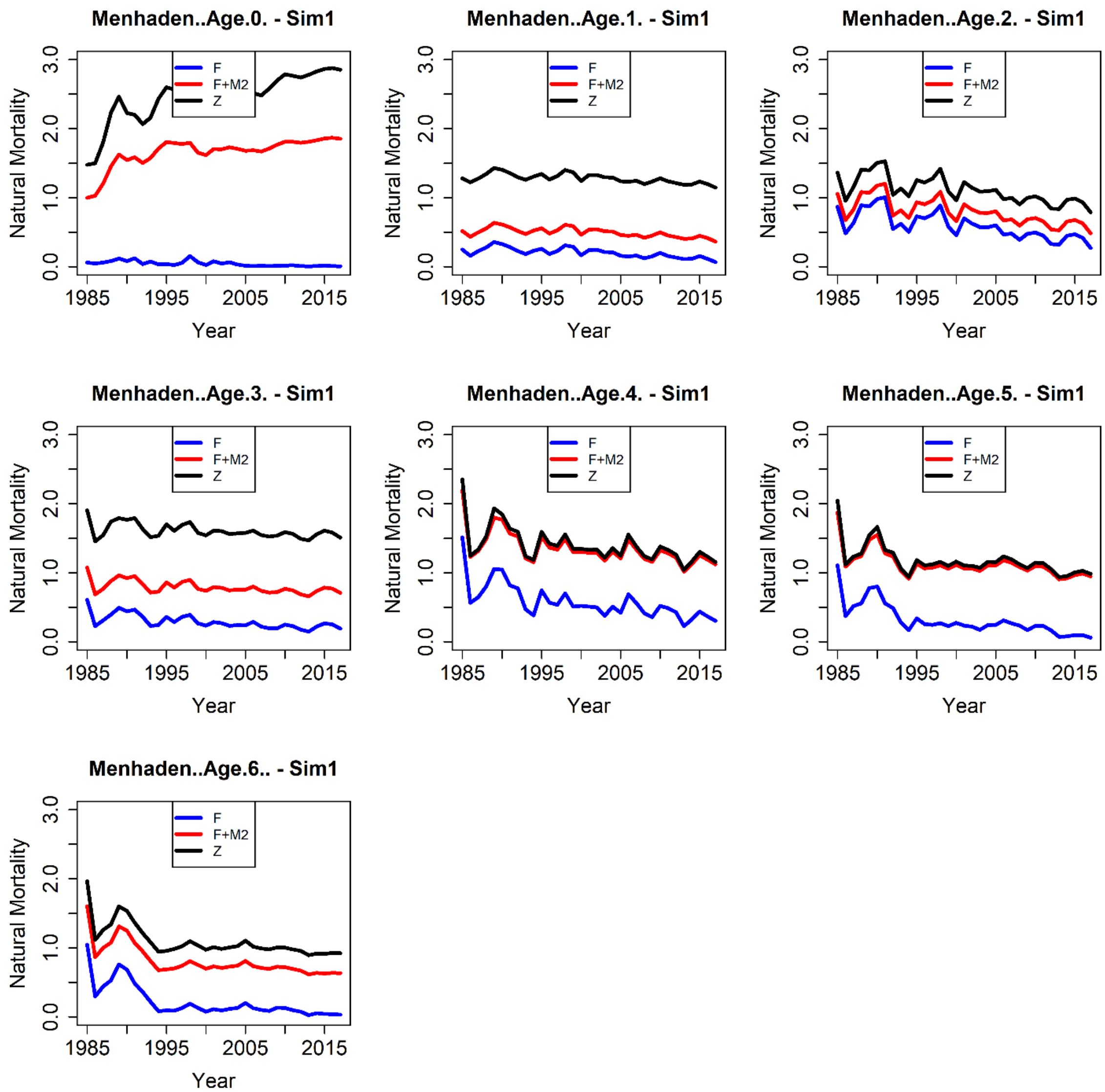

Figure 6 Mortality for Atlantic Menhaden in the BASE model run. Z (top line) represents total mortality, F (bottom line) represents fishing mortality, F+M2 (middle line) represents fishing mortality plus the predation mortality explained by the model

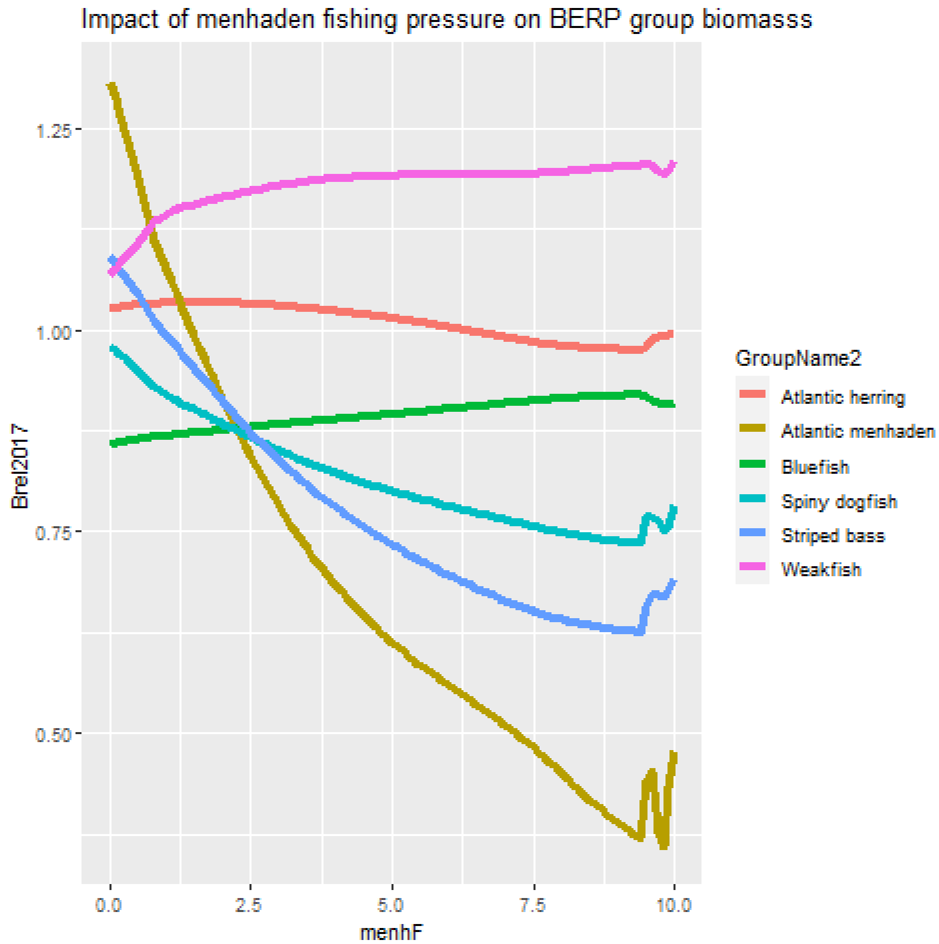

Figure 7 Impact of variable Menhaden fishing mortality on biomass of ERP focal species. Brel2017 is Biomass relative to the Biomass in 2017 for each ERP focal species. Lines from top to bottom on the right-hand side of the plot represent Weakfish, Atlantic Herring, Bluefish, Spiny Dogfish, Striped Bass, and Atlantic Menhaden.

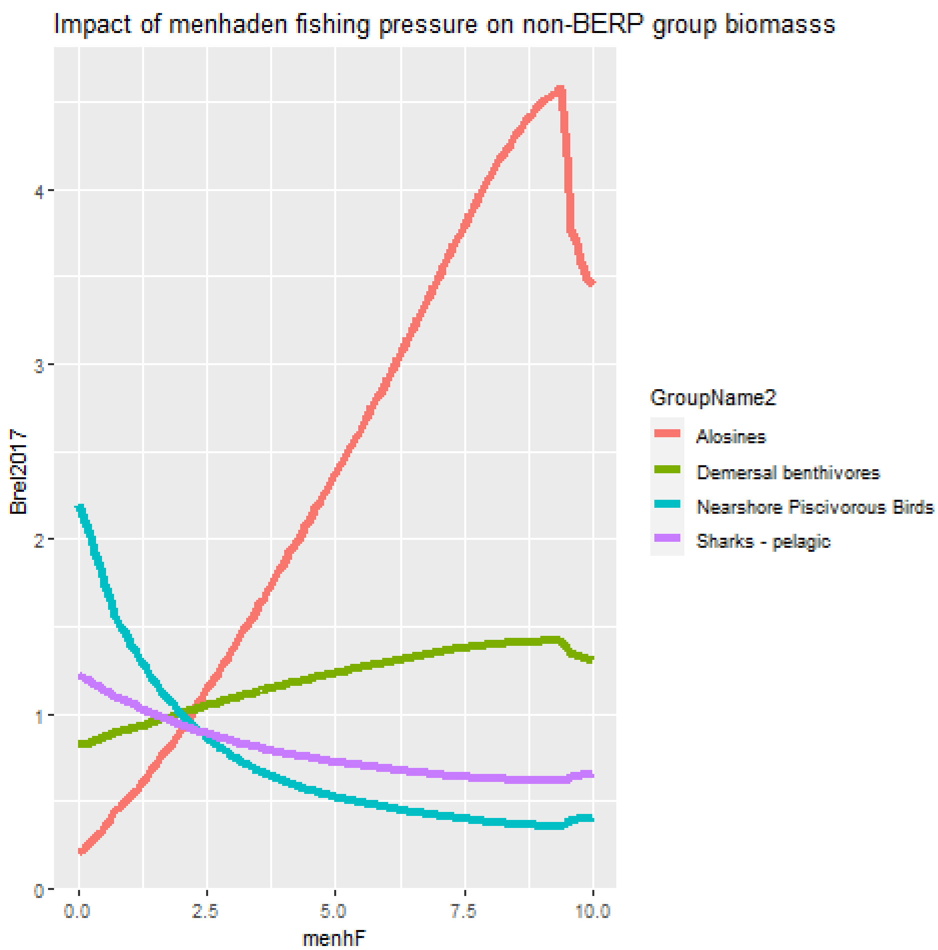

Figure 8 Impact of variable Menhaden fishing mortality on biomass of species not included in the ERP focal species list. Brel2017 is Biomass relative to the Biomass in 2017 for each species. Lines from top to bottom on the right-hand side of the plot represent Alosines, Demersal benthivores, Sharks – pelagic, and Nearshore piscivorous birds.

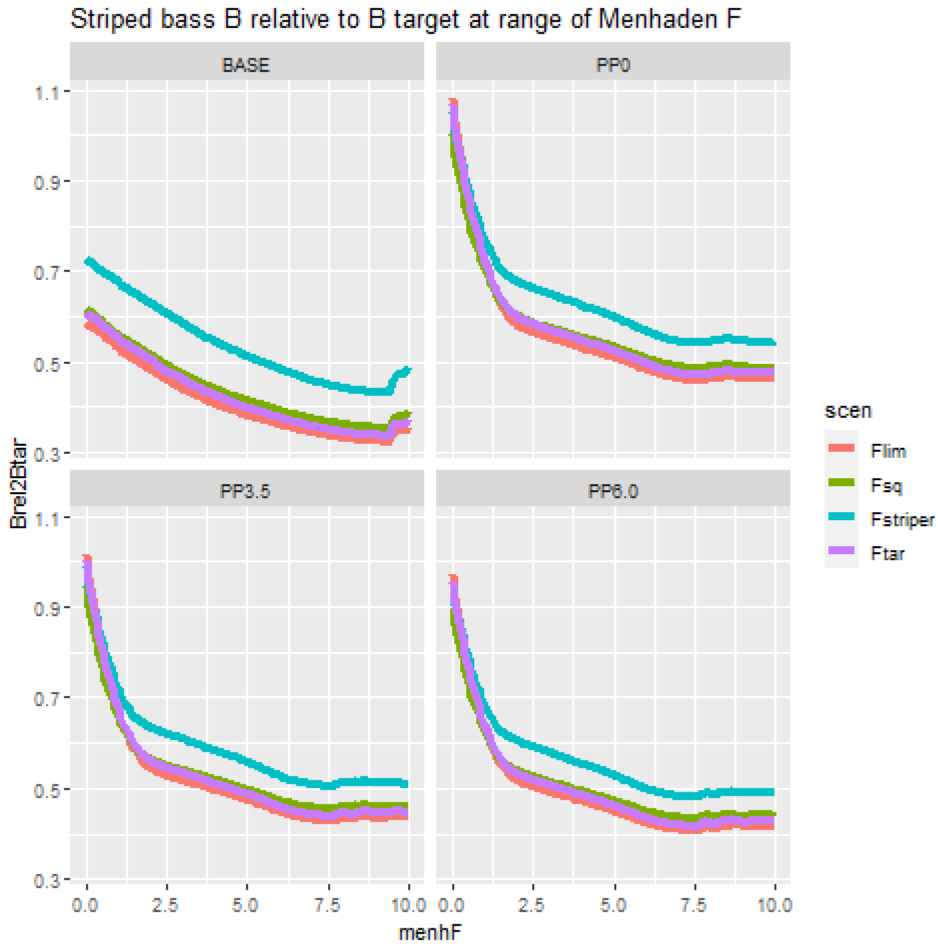

Figure 9 Striped Bass biomass relative to biomass target at a range of Atlantic Menhaden fishing mortality. Colors represent ERP focal species fishing mortality scenario. Lines from top to bottom on the right hand side of the plot represent Fstriper, Fsq, Ftar, Flim.

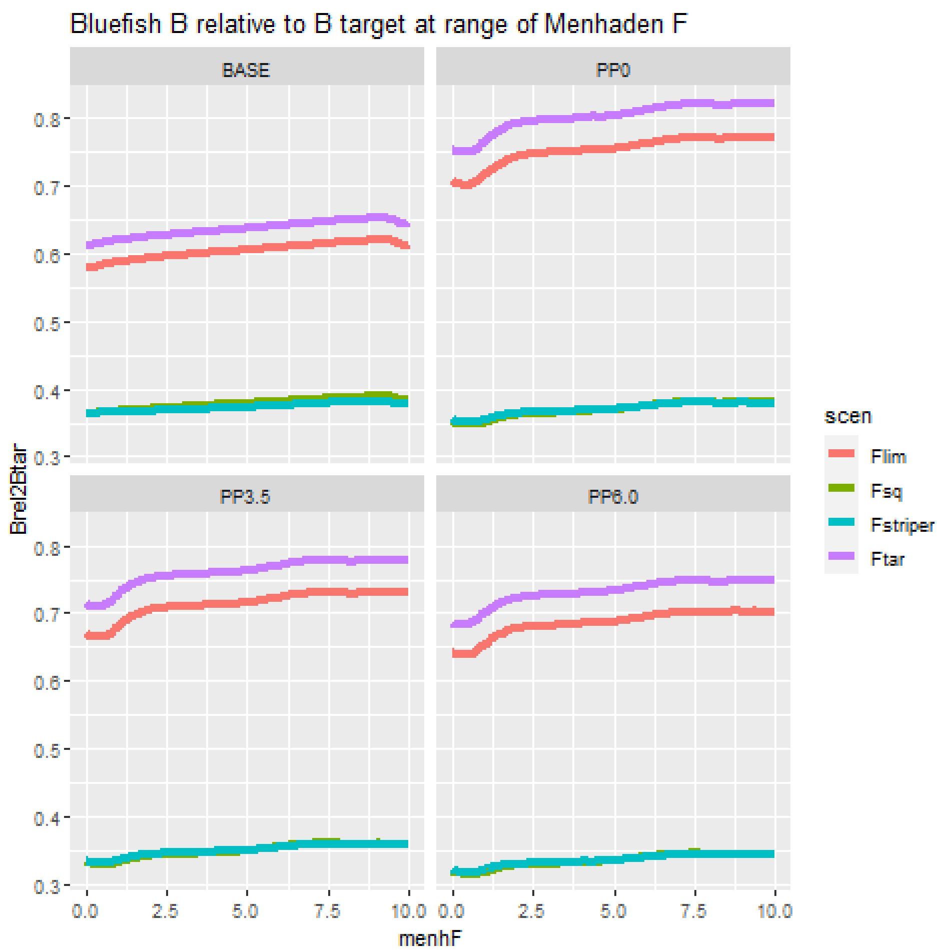

Figure 10 Bluefish biomass relative to biomass target at a range of Atlantic Menhaden fishing mortality. Colors represent ERP focal species fishing mortality scenario. Lines from top to bottom on the right-hand side of the plot represent Ftar, Flim, Fsq, and Fstriper.

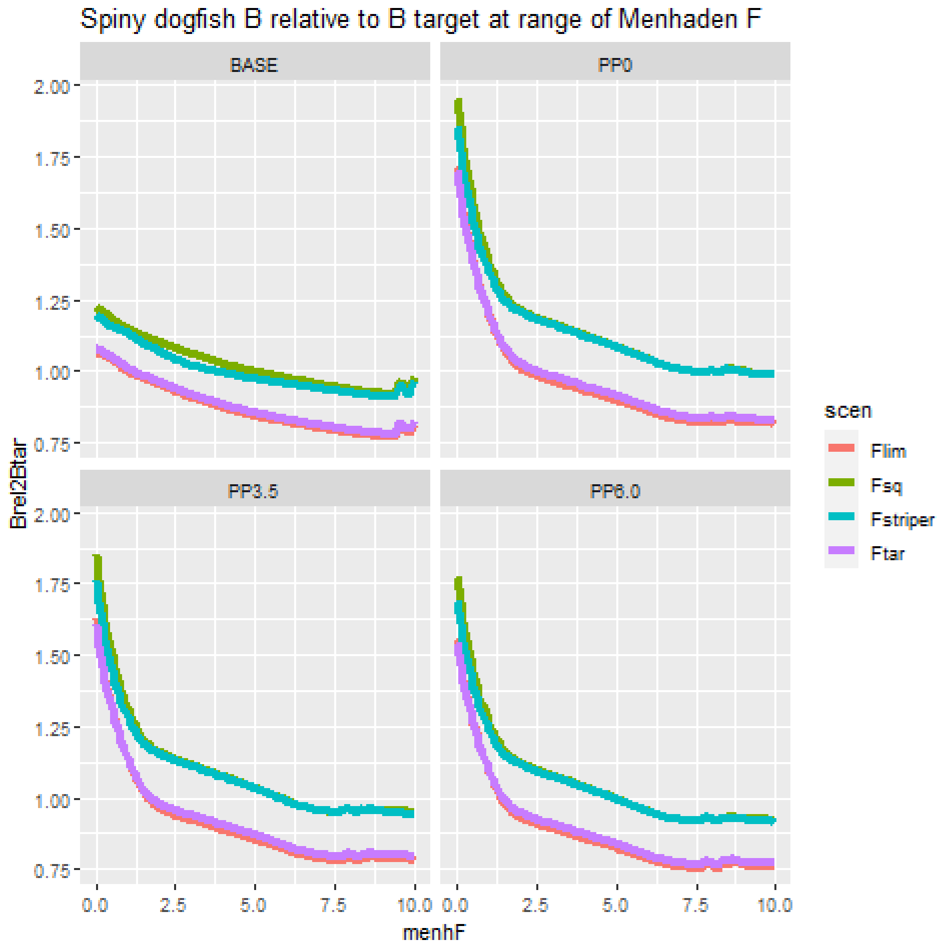

Figure 11 Spiny Dogfish biomass relative to biomass target at a range of Atlantic Menhaden fishing mortality. Colors represent ERP focal species fishing mortality scenario. Lines from top to bottom on the right-hand side of the plot represent Fsq, Fstriper, Ftar, Flim.

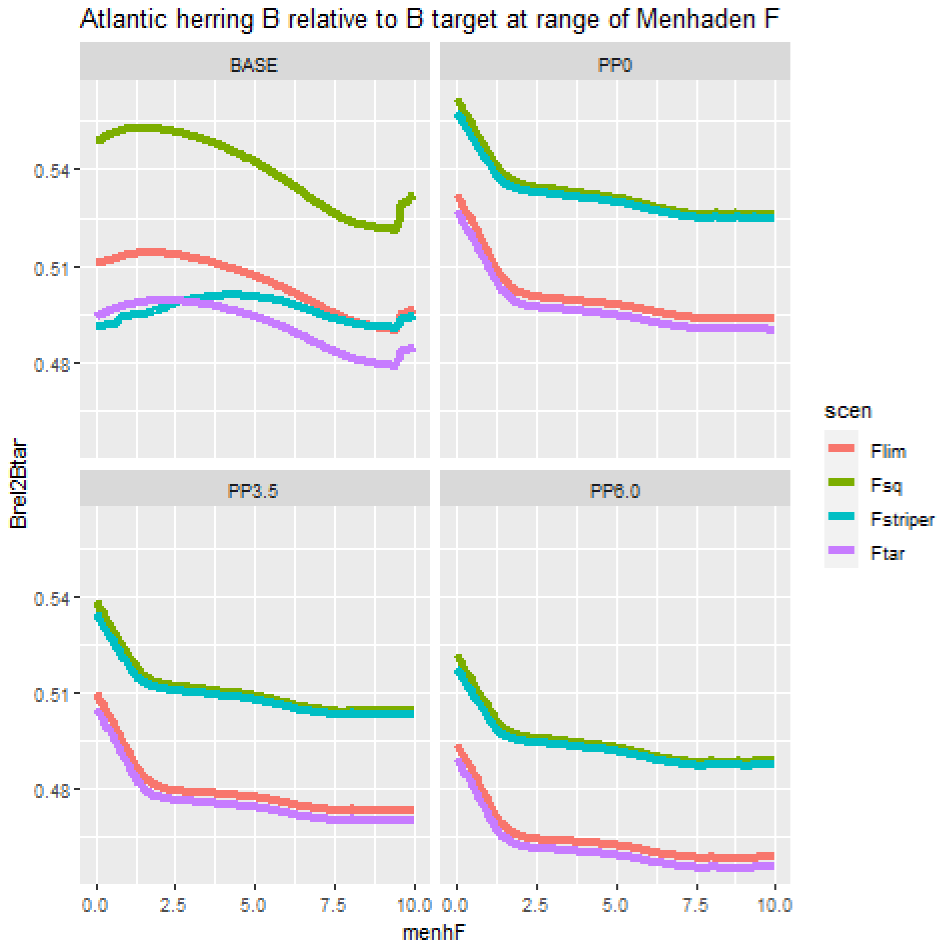

Figure 12 Atlantic Herring biomass relative to biomass target at a range of Atlantic Menhaden fishing mortality. Colors represent ERP focal species fishing mortality scenario. Lines from top to bottom in the BASE model projections on the left-hand side of the plot are Fsq, Flim, Ftar, and Fstriper. In the PP0, PP3.5, and PP6.0 plots, the order from top to bottom is Fsq, Fstriper, Flim, and Ftar.

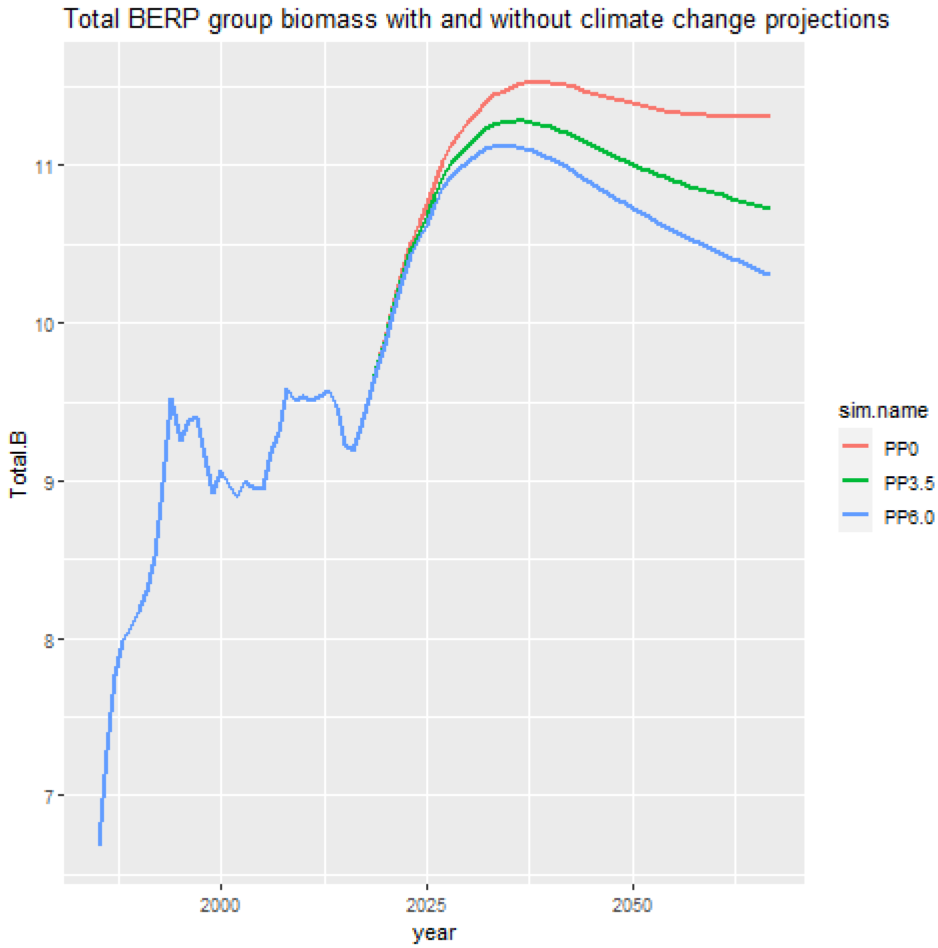

Figure 13 ERP focal species biomass projections under status quo fishing mortality scenario. Colors represent primary production biomass projections. Lines representing projections from top to bottom are PP0, PP3.5, and PP6.0.

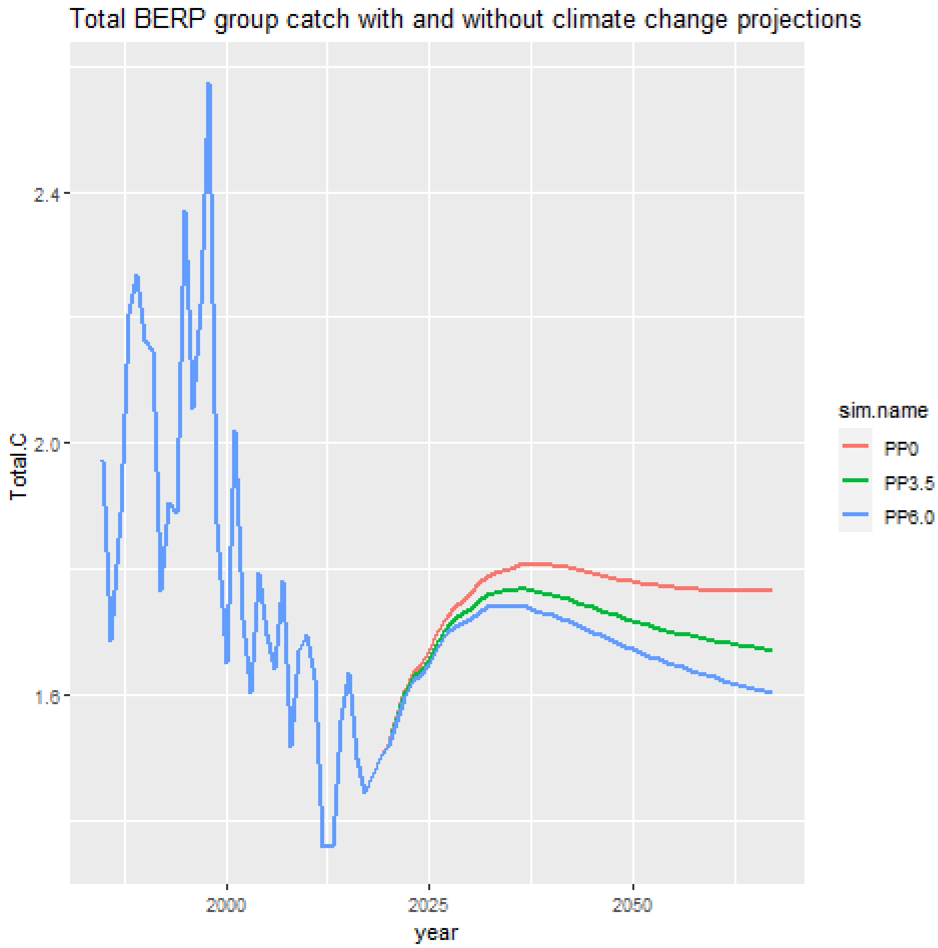

Figure 14 ERP focal species catch projections under status quo fishing mortality scenario. Colors represent primary production biomass projections. Lines from top to bottom in the projection are PP0, PP3.5, and PP6.0

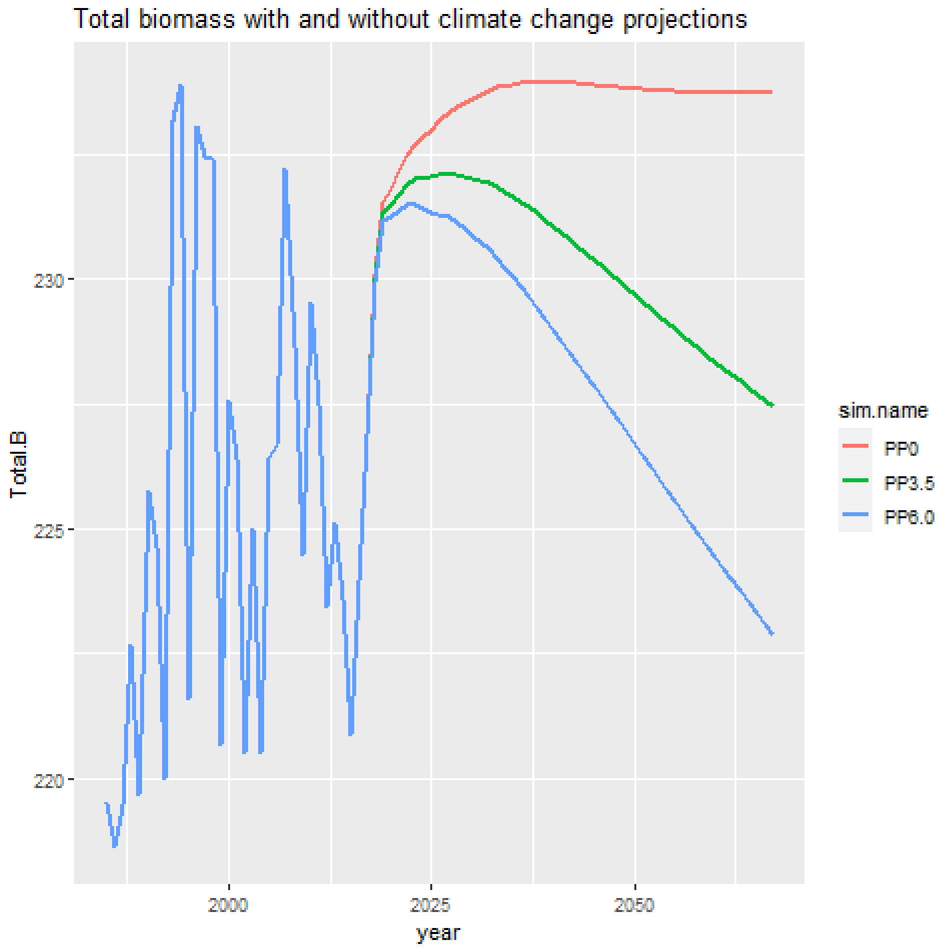

Figure 15 Total non-phytoplankton biomass projection of the system under status quo fishing scenario. Colors represent phytoplankton biomass projections. Lines from top to bottom in the projection are PP0, PP3.5 and PP6.0.

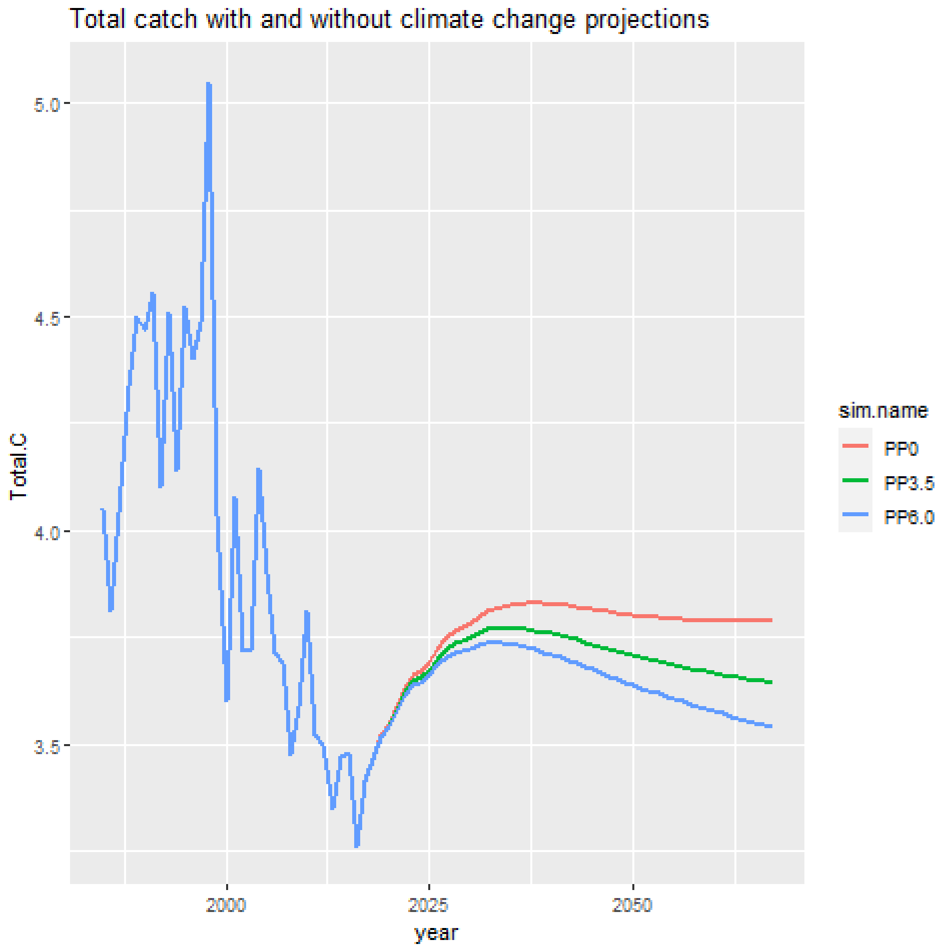

Figure 16 Total non-phytoplankton catch within the system under status quo fishing scenario. Colors represent phytoplankton biomass projections. Lines from top to bottom in the projection are PP0, PP3.5, and PP6.0.

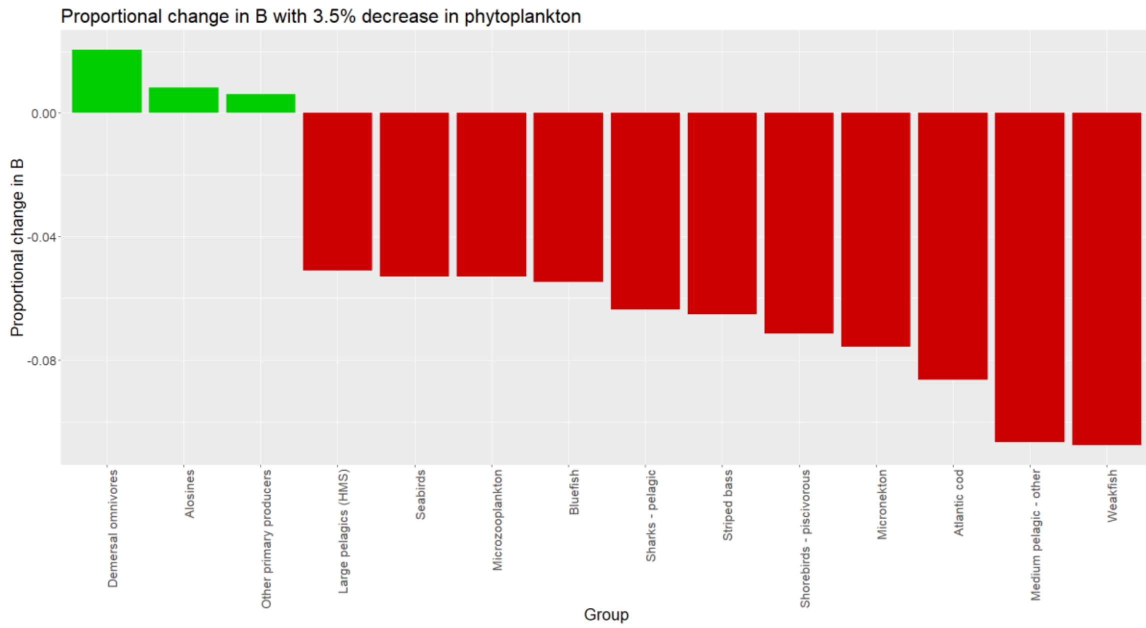

Figure 17 Proportional change in biomass with 3.5% decrease in phytoplankton biomass compared to the PP0 end year projection biomass.

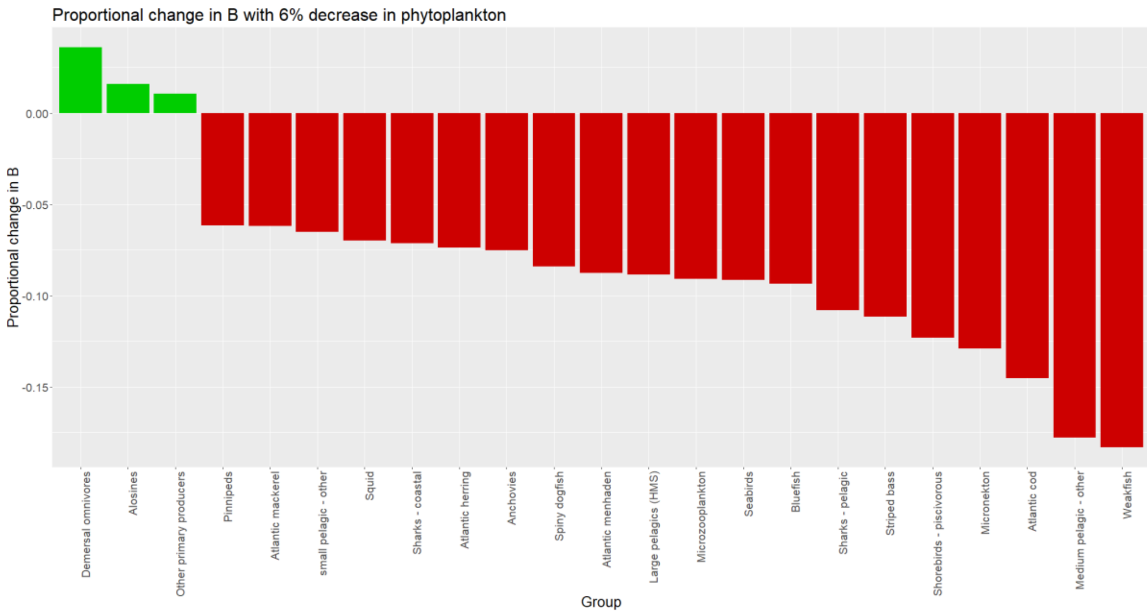

Figure 18 Proportional change in biomass with 6.0% decrease in phytoplankton biomass compared to the PP0 end year projection biomass.

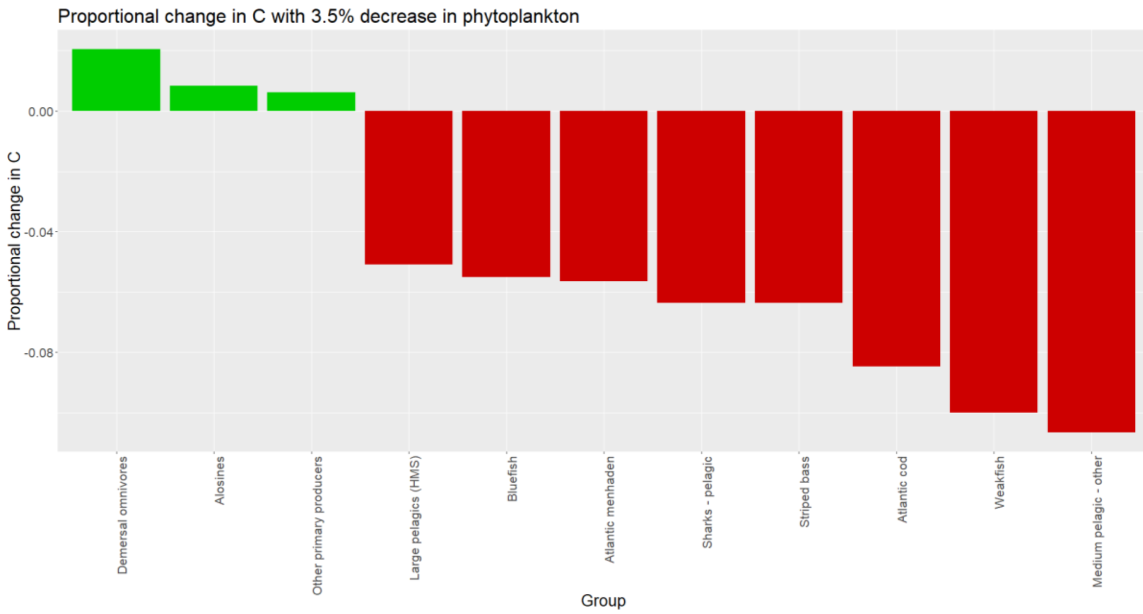

Figure 19 Proportional change in catch with 3.5% decrease in phytoplankton biomass compared to the PP0 end year projection biomass.

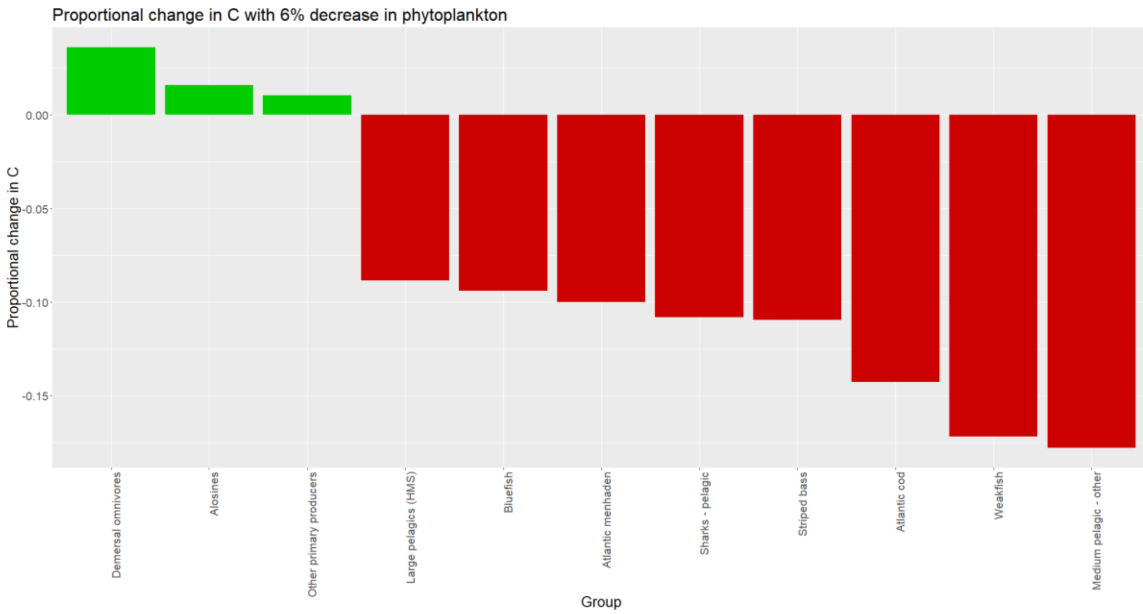

Figure 20 Proportional change in catch with 6.0% decrease in phytoplankton biomass compared to the PP0 end year projection biomass.

REFERENCES

Ainsworth, C. H., Samhouri, J. F., Busch, D. S., Cheung, W. W. L., Dunne, J., and Okey, T. A. 2011. Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries, ICES Journal of Marine Science, Volume 68, Issue 6, July 2011, Pages 1217–1229, https://doi.org/10.1093/icesjms/fsr043

Anstead KA, Drew K, Chagaris D, Cieri M, Schueller AM, McNamee JE, Buchheister A, Nesslage G, Uphoff JH Jr, Wilberg MJ, Sharov A, Dean MJ, Brust J, Celestino M, Madsen S, Murray S, Appelman M, Ballenger JC, Brito J, Cosby E, Craig C, Flora C, Gottschall K, Latour RJ, Leonard E, Mroch R, Newhard J, Orner D, Swanson C, Tinsman J, Houde ED, Miller TJ and Townsend H. 2021. The Path to an Ecosystem Approach for Forage Fish Management: A Case Study of Atlantic Menhaden. Front. Mar. Sci. 8:607657. doi: 10.3389/fmars.2021.607657

ASMFC. 2010. Atlantic Menhaden stock assessment and review panel reports. Atlantic States Marine Fisheries Commission, Stock Assessment Rep. No. 10-02.

ASMFC (Atlantic States Marine Fisheries Commission). 2012. Amendment 2 to the Interstate Fishery Management Plan for Atlantic Menhaden. ASMFC, Arlington, Virginia.

Bonzek, C. F., Gartland, J., Gauthier, D. J., & Latour, R. J. (2017) Northeast Area Monitoring and Assessment Program (NEAMAP) 2016 Data collection and analysis in support of single and multispecies stock assessments in the Mid-Atlantic: Northeast Area Monitoring and Assessment Program Near Shore Trawl Survey. Virginia Institute of Marine Science, William & Mary. https://doi.org/10.25773/7206-KM61

Brussard, P. F., Reed, M.J., Tracy, R.C.. Ecosystem management: what is it really? Landscape and Urban Planning. Volume 40, Issues 1–3. 1998. Pages 9-20. ISSN 0169-2046. https://doi.org/10.1016/S0169-2046(97)00094-7.

Buchheister, A., and R. J. Latour. 2015. Diets and trophic guild structure of a diverse fish assemblage in Chesapeake Bay, USA. Journal of Fish Biology 86:967–992.

Buchheister, A., T. J. Miller, E. D. Houde, D. H. Secor, and R. J. Latour. 2016. Spatial and temporal dynamics of Atlantic Menhaden (Brevoortia tyrannus) recruitment in the Northwest Atlantic Ocean. ICES Journal of Marine Science 73:1147–1159.

Buchheister, A., Miller, T. J., and Houde, E. D. (2017a). Evaluating ecosystem-based reference points for Atlantic Menhaden. Mar. Coast. Fish. 9, 457–478. doi: 10.1080/19425120.2017.1360420

Buchheister, A., Miller, T. J., Houde, E. D., and Loewensteiner, D. A. (2017b). Technical Documentation of the Northwest Atlantic Continental Shelf (NWACS) Ecosystem Model. Report to the Lenfest Ocean Program University of Maryland Center for Environmental Sciences Report TS 694-17. Washington, DC: University of Maryland.

Butterworth, D. S., and É. E. Plagányi. 2004. A brief introduction to some approaches to multispecies/ecosystem modelling in the context of their possible application in the management of South African fisheries. Afr. J. Mar. Sci. 26:53-61. https://doi.org/10.2989/18142320409504049

Chagaris, D., K. Drew, A. Schueller, M. Cieri, J. Brito, and A. Buchheister. 2020. Ecological reference points for Atlantic Menhaden established using an ecosystem model of intermediate complexity. Front. Mar. Sci. 7:606417. https://doi.org/10.3389/fmars.2020.606417

Christensen, V., and C. J. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling 172:109–139.

Christensen,V., C. J.Walters,D. Pauly, and R. Forrest. 2008. Ecopathwith Ecosim, version 6, user guide. Lenfest Ocean Futures Project, Washington, D.C.

Christensen, V., and C. J. Walters. 2011. Progress in the use of ecosystem modeling for fisheries management. Pages 189–208 in V. Christensen and J. Maclean, editors. Ecosystem approaches for fisheries management: a global perspective. Cambridge University Press, New York.

Coll, M., A. Bundy, and L. J. Shannon. 2009. Ecosystem modelling using the Ecopath with Ecosim approach. Pages 225–291 in B. A. Megrey and E. Moksenss, editors. Computers in fisheries research. Springer, Dordrecht, The Netherlands.

Collie, J. S., and A. K. DeLong. 1999. Multispecies interactions in the Georges Bank fish community. Pages 187–210 in Ecosystem approaches for fisheries management. University of Alaska Sea Grant, AK-SG-99-01, Fairbanks.

Collie, J. S., Botsford, L. W., Hastings, A., Kaplan, I. C., Largier, J. L., Livingston, P. A., Plagányi, É., Rose, K. A., Wells, B. K., and Werner, F. E. 2016. Ecosystem models for fisheries management: finding the sweet spot. Fish Fish. 17:101-125. https://doi.org/10.1111/faf.12093

Deroba, J. J., S. K. Gaichas, M.-Y. Lee, R. G. Feeney, D. Boelke, and B. J. Irwin. 2019. The dream and the reality: meeting decision-making time frames while incorporating ecosystem and economic models into management strategy evaluation. Can J. Fish. Aquat. Sci. 76:1112-1133. https://doi.org/10.1139/cjfas-2018-0128

Essington, T. E. 2007. Evaluating the sensitivity of a trophic mass-balance model (Ecopath) to imprecise data inputs. Canadian Journal of Fisheries and Aquatic Sciences 64:628–637.

Fogarty, M. J. 2014. The art of ecosystem-based fishery management. Canadian Journal of Fisheries and Aquatic Sciences 490:479–490.

Frumhoff, P, Mccarthy, J., Melillo, J., Moser, S., Wuebbles, D., Wake, C., Spanger-Siegfried, E., 2008. An integrated climate change assessment for the Northeast United States. Mitigation and Adaptation Strategies for Global Change. 13. 419-423. 10.1007/s11027-007-9138-x.

Fulton, E. A., and J. S. Link. 2014. Modeling approaches for marine ecosystem-based management. In The Sea. Vol. 16. Marine ecosystem-based management (M.J. Fogarty and J.J. McCarthy, eds.), p. 121-170. Harvard University Press, Boston, Massachusetts.

Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R. J., Smith, A. D. M., and Smith, D. C. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish Fish. 12:171-188. http://doi.org/10.1111/j.1467-2979.2011.00412.x

Geers, T. M., E. K. Pikitch, and M. G. Frisk. 2016. An original model of the northern Gulf of Mexico using Ecopath with Ecosim and its implications for the effects of fishing on ecosystem structure and maturity. Deep-Sea Res. II 129:319-331. https://doi.org/10.1016/j.dsr2.2014.01.009

Harvey, C. J., Reum, J. C. P., Poe, M. R., Williams, G. D., and Kim, S. J. 2016. Using Conceptual Models and Qualitative Network Models to Advance Integrative

Assessments of Marine Ecosystems. Coast. Manage. 44(5):486-503. https://doi.org/10.1080/08920753.2016.1208881

Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., et al. (2016). Best practice in Ecopath with Ecosim food-web models for ecosystembased management. Ecol. Model. 331, 173–184. doi: 10.1016/j.ecolmodel.2015. 12.007

Hilborn, R., Amoroso, R. O., Bogazzi, E., Jensen, O. P., Parma, A. M., Szuwalski, C., et al. (2017). When does fishing forage species affect their predators? Fish. Res. 191, 211–221. doi: 10.1016/j.fishres.2017.01.008

Hollowed, A. B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J., and Rice, J. C. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES J. Mar. Sci. 57:707-719. https://doi.org/10.1006/jmsc.2000.0734

Hollowed, A. B., S. R. Hare, and W. S. Wooster. 2001. Pacific Basin climate variability and patterns of Northeast Pacific marine fish production. Prog. Oceanogr. 49:257-282. https://doi.org/10.1016/s0079-6611(01)00026-x

Houde, E.D., Fish larvae. Marine Ecological Processes: A derivative of the Encyclopedia of Ocean Sciences. Academic Press. 286-296., Burlington, Vermont

Howell, D., Schueller, A. M., Bentley, J. W., Buchheister, A., Chagaris, D., Cieri, M., Drew, K., Lundy, M. G., Pedreschi, D., Reid, D. G., and Townsend, H. 2021. Combining ecosystem and single-species modeling to provide ecosystem-based fisheries management advice within current management systems. Front. Mar. Sci. 7:607831. http://doi.org/10.3389/fmars.2020.607831

ICES. 2004. Report of the study group on multispecies assessment in the Baltic (SGMAB). ICES CM 2004/H:06.

ICES. 2010. Report of the ICES Advisory Committee, 2010. ICES Advice.

ICES. 2012. Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak (WGNSSK), 27 April - 3 May 2012, ICES Headquarters, Copenhagen. ICES CM 2012/ACOM:13, 1346 p.

ICES. 2020a. Baltic fisheries assessment working group (WGBFAS). ICES Sci. Rep. 2(45), 643 p. https://doi.org/10.17895/ices.pub.6024

ICES. 2020b. Working group on the assessment of demersal stocks in the North Sea and Skagerrak (WGNSSK). ICES Sci. Rep. 2(61),1140 p. https://doi.org/10.17895/ices.pub.6092

ICES. 2021. Working group on multispecies assessment models (WGSAM; outputs from 2020 meeting). ICES Sci. Rep. 3(10), 231 p. https://doi.org/10.17895/ices.pub.7695

Kinzey, D., and A. E. Punt. 2009. Multispecies and single-species models of fish population dynamics: comparing parameter estimates. Nat. Resour. Model. 22:67-104. https://doi.org/10.1111/j.1939-7445.2008.00030.x

Link J. S., Almeida F. P.. An overview and history of the food web dynamics program of the Northeast Fisheries Science Center, Woods Hole, Massachusetts, 2000N. OAA Technical Memorandum, NMFS-NE-159

Link, J., Overholtz, W., O'Reilly, J., Green, J., Dow, D., Palka, D., et al. (2008). The Northeast US continental shelf Energy Modeling and Analysis exercise (EMAX): ecological network model development and basic ecosystem metrics. J. Mar. Syst. 74, 453–474. doi: 10.1016/j.jmarsys.2008.03.007

Link, J. S. 2010a. Ecosystem-based fisheries management: confronting tradeoffs. Cambridge University Press, New York.

Link, J. S. 2010b. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. Ecological Modelling 221:1580–1591.

Link, J. S., Ihde, T. F., Townsend, H. M., Osgood, K. E., Schirripa, M. J., Kobayashi, D. R., Gaichas, S., Field, J. C., Levin, P. S., Aydin, K. Y., and Harvey, C. J. (eds.). 2010. Report of the 2nd National Ecosystem Modeling Workshop (NEMoW II): bridging the credibility gap - dealing with uncertainty in ecosystem models. NOAA Tech. Memo. NMFS-F/SPO-102, 72 p.

Link, J. S., T. F. Ihde, C. J. Harvey, S. K. Gaichas, J. C. Field, J. K. T. Brodziak, H. M. Townsend, and R. M. Peterman. 2012. Dealing with uncertainty in ecosystem models: the paradox of use for living marine resource management. Progress in Oceanography 102:102–114.

Link, J. S., Mason, D., Lederhouse, T., Gaichas, S., Hartley, T., Ianelli, J., Methot, R., Stock, C., Stow, C., and Townsend, H. 2015. Report from the joint OAR-NMFS Modeling Uncertainty Workshop. NOAA Tech. Memo. NMFS-F/SPO-153, 31 p.

Link, J. S., G. Huse, S. Gaichas, and A. R. Marshak. 2020. Changing how we approach fisheries: A first attempt at an operational framework for ecosystem approaches to fisheries management. Fish Fish. 21:393-434. https://doi.org/10.1111/faf.12438

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W. L., Galbraith, E. D., Barange, M., Barrier, N., Bianchi, D., Blanchard, J. L., Bopp, L., Büchner, M., Bulman, C. M., Carozza, D. A., Christensen, V., Coll, M., Dunne, J. P., Fulton, E. A., Jennings, S., Jones, M, Mackinson, S, Maury, O, Niiranen, S, Oliveros-Ramos, R, Roy, T, Fernandes, J, Schewe, J, Shin, Y, Silva, T, Steenbeek, J, Stock, C, Verley, P, Volkholz, J, Walker, N, Worm, B. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. Proceedings of the National Academy of Sciences of the United States of America (26). https://doi.org/10.1073/pnas.1900194116

Lucey, S.M., Gaichas, S.K., Aydin, K.Y.. 2020. Conducting reproducible ecosystem modeling using the open source mass balance model Rpath, Ecological Modelling, Volume 427, 109057, ISSN 0304-3800, https://doi.org/10.1016/j.ecolmodel.2020.109057

McNamee, J. E. (2018). A Multispecies Statistical Catch-At-Age (MSSCAA) Model for a Mid-Atlantic Species Complex. Kingston, RI: University of Rhode Island.

National Marine Fisheries Service [NMFS], (2016). Ecosystem-Based Fisheries Management Policy of the National Marine Fisheries Service National Oceanic and Atmospheric Administration. NMFS Policy Directive 01-120. Beaufort, NC: NMFS.

National Marine Fisheries Service [NMFS], (2019). Forecast for the 2019 Gulf and Atlantic Menhaden Purse-Seine Fisheries and Review of the 2018 Fishing Season. Beaufort, NC: National Marine Fisheries Service Sustainable Fisheries Branch.

NOAA (National Oceanic and Atmospheric Administration). 2014a. NOAA National Marine Fisheries Service commercial fisheries statistics. Available: http://www.st.nmfs.noaa.gov/commercial-fisheries/index. (August 2015).

NOAA (National Oceanic and Atmospheric Administration). 2014b. NOAA National Marine Fisheries Service recreational fisheries statistics. Available: http://www.st.nmfs.noaa.gov/recreational-fisheries/index. (August 2015).

Patrick, W. S., and J. S. Link. 2015. Myths that continue to impede progress in ecosystem-based fisheries management. Fisheries 40:155–160.

Pauly, D., Christensen, V., and Walters, C. (2000). Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. 57, 1–10. doi: 10.1007/s00773-016-0388-8

Peck, M. A., S. Neuenfeldt, T. E. Essington, V. M. Trenkel, A. Takasuka, H. Gislason, M. Dickey-Collas, K. H. Andersen, L. Ravn-Jonsen, N. Vestergaard, S. F. Kvamsdal,A.Gardmark, J. Link, and J. C. Rice. 2014. Forage fish interactions: a symposium on "creating the tools for ecosystem-based management of marine resources." ICES Journal of Marine Science 71:1–4.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., et al. (2004). Ecosystem based fishery management. Science 305, 346–347. doi: 10.1126/science.1098222

Pikitch, E. K., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Essington, T. E., et al. (2012). Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs. Washington, DC: Lenfest Ocean Program.

Pikitch, E. K., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Essington, T. E., et al. (2018). The strong connection between forage fish and their predators: a response to Hilborn et al. (2017). Fish. Res. 198, 220–223. doi: 10.1016/j.fishres. 2017.07.022

Pikitch, E. K., C. Santora, E. A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, P. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E. D. Houde, J. Link, P. A. Livingston, M. Mangel, M. K. McAllister, J. Pope, and K. J. Sainsbury. 2004. Ecosystem-based fishery management. Science 305:346–347.

Plagányi, É. E. 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper. No. 477. 108 p. FAO, Rome.

Plagányi, É. E., Punt, A. E., Hillary, R., Morello, E. B., Thébaud, O., Hutton, T., Pillans, R. D., Thorson, J. T., Fulton, E. A., Smith, A. D. M., Smith, F., Bayliss, P., Haywood, M., Lyne, V., and Rothlisberg, P. C. 2014. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. Fish Fish. 15:1-22. https://doi.org/10.1111/j.1467-2979.2012.00488.x

SEDAR, (2015). SEDAR 40 – Atlantic Menhaden Stock Assessment Report. North Charleston, SC: SEDAR.

SEDAR, (2020a). SEDAR 69 – Atlantic Menhaden Benchmark Stock Assessment Report. North Charleston, SC: SEDAR.

SEDAR, (2020b). SEDAR 69 – Atlantic Menhaden Ecological Reference Points Stock Assessment Report. North Charleston, SC: SEDAR.

Sissenwine, M. P., and N. Daan. 1991. An overview of multispecies models relevant to management of living resources. ICES Mar. Sci. Symposia 193:6-11.

Townsend, H., Aydin, K., Brodie, S., DePiper, G., deReynier, Y., Harvey, C., Haynie, A., Hazen, E., Kaplan, I., Kasperski, S., Kearney, K., Large, S., Lucey, S., Masi, M., Ortiz, I., Reum, J., Stawitz, C., Tommasi, D., Weijerman, M., Whitehouse, A., Woodworth-Jefcoats, P., Lynch, P., Osgood, K., and Link, J. (eds.). 2020. Report of the 5th National Ecosystem Modeling Workshop (NEMoW 5): progress in ecosystem modeling for living marine resource management. NOAA Tech. Memo. NMFS-F/SPO-205, 72 p.

Townsend, H., Harvey, C. J., deReynier, Y., Davis, D., Zador, S. G., Gaichas, S., Weijerman, M., Hazen, E. L., and Kaplan, I. C. 2019. Progress on implementing ecosystem-based fisheries management in the United States through the use of ecosystem models and analysis. Front. Mar. Sci. 6: 641. http://doi.org/10.3389/fmars.2019.00641

Trijoulet, V., G. Fay, and T. J. Miller. 2020. Performance of a state-space multispecies model: What are the consequences of ignoring predation and process errors in stock assessments? J. Appl. Ecol. 57:121-135. http://doi.org/10.1111/1365-2664.13515

Walters, C., V. Christensen, B. Fulton, A. D. M. Smith, and R. Hilborn. 2016. Predictions from simple predator–prey theory about impacts of harvesting forage fishes. Ecological Modelling 337:272–280.

Walters, C., V. Christensen, and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries 7:139–172.

Walters, C. J., and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Canadian Journal of Fisheries and Aquatic Sciences 50:2058–2070.

Whipple, S. J., J. S. Link, L. P. Garrison, and M. J. Fogarty. 2000. Models of predation and fishing mortality in aquatic ecosystems. Fish Fish. 1:22-40. http://doi.org/10.1046/j.1467-2979.2000.00007.x

APPENDIX

Appendix A: Additional figures

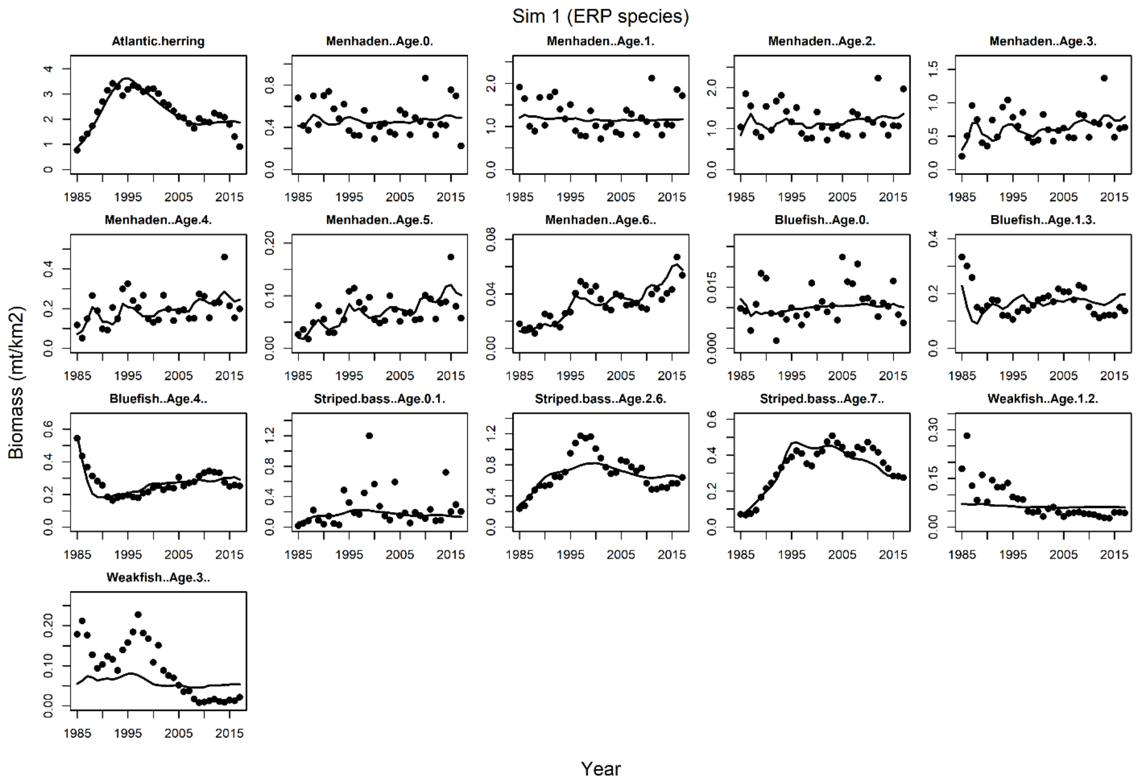

Figure 21 Biomass fits for ERP focal species from BASE model run

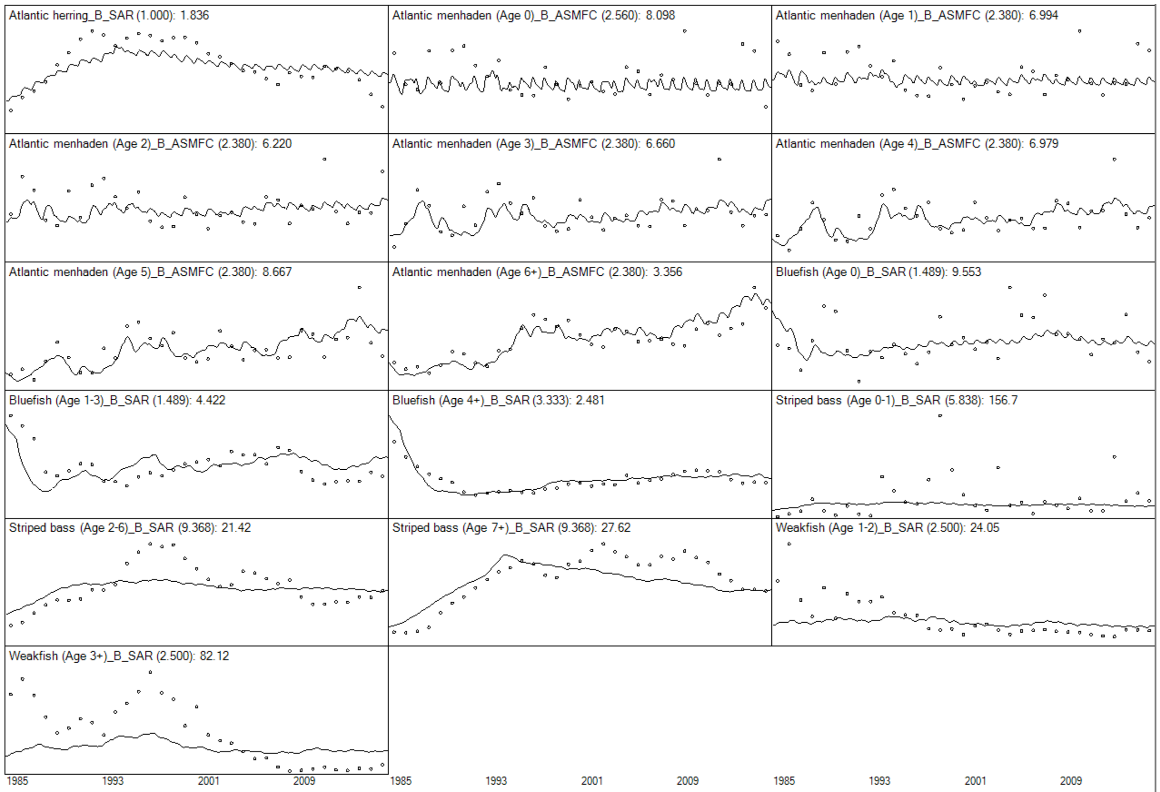

Figure 22 Biomass fits for ERP focal species from PP0 model run

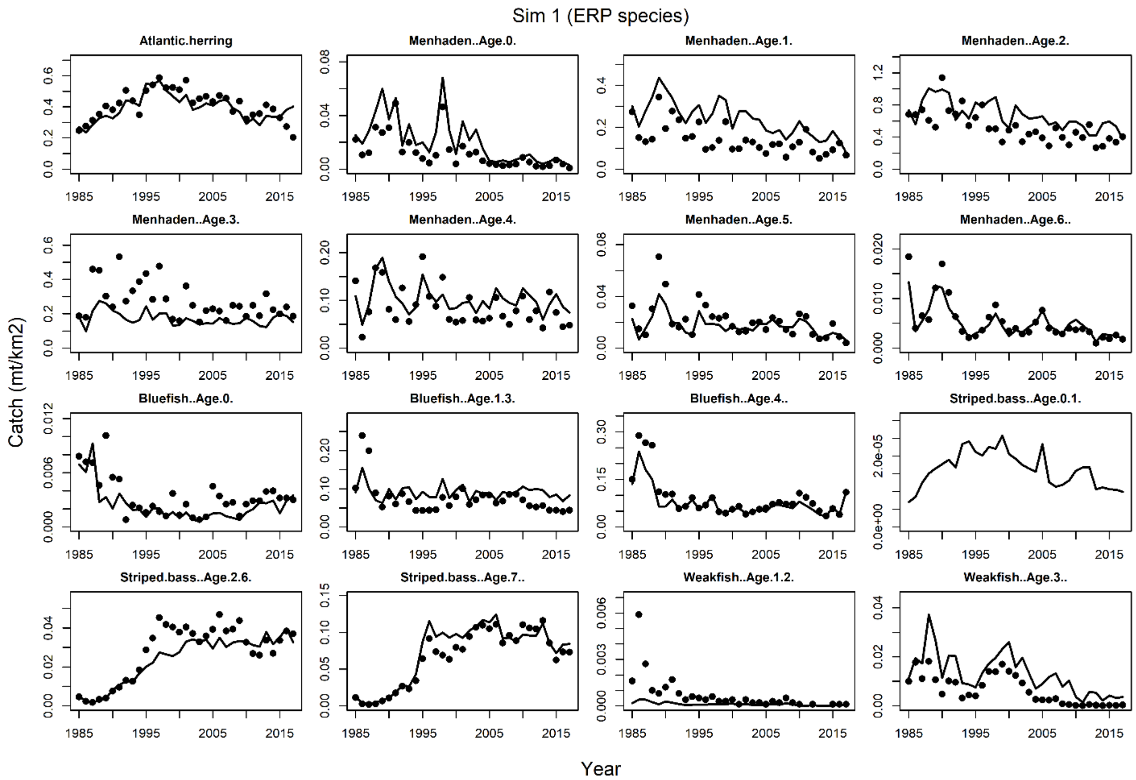

Figure 23 Catch fits for ERP focal species in the BASE model run

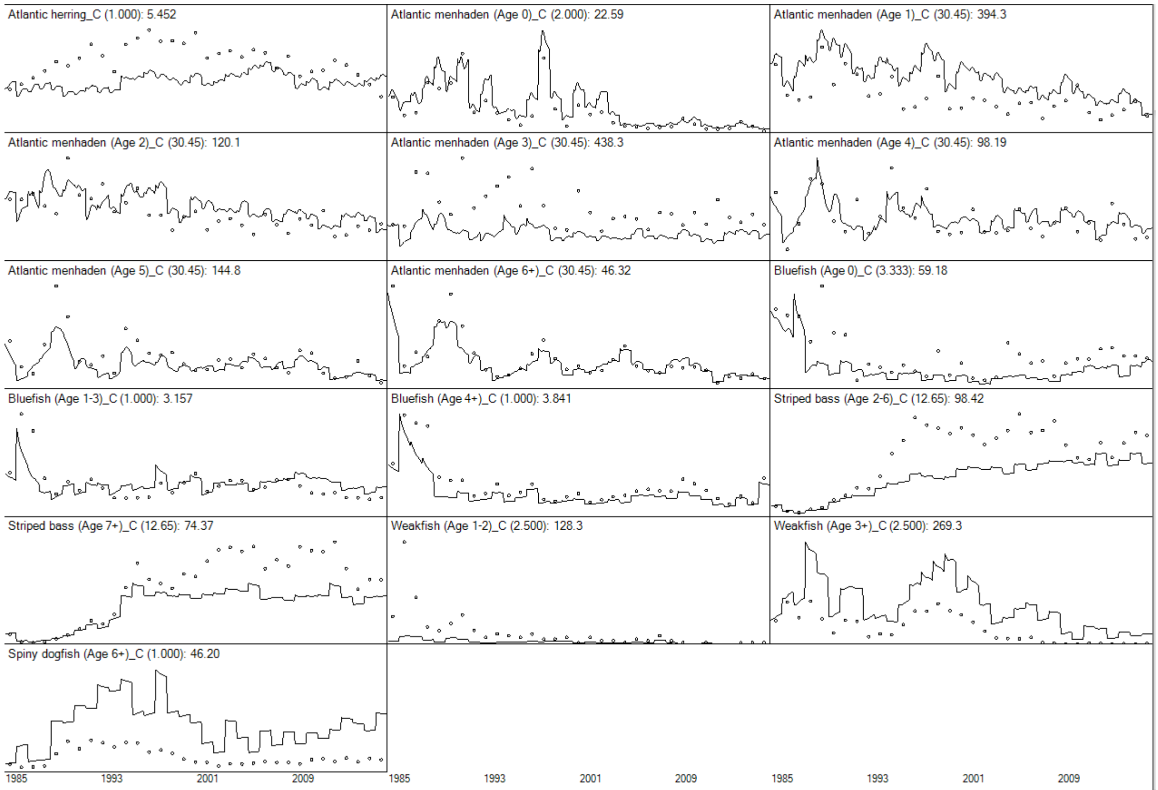

Figure 24 Catch fits for ERP focal species from PP0 model run

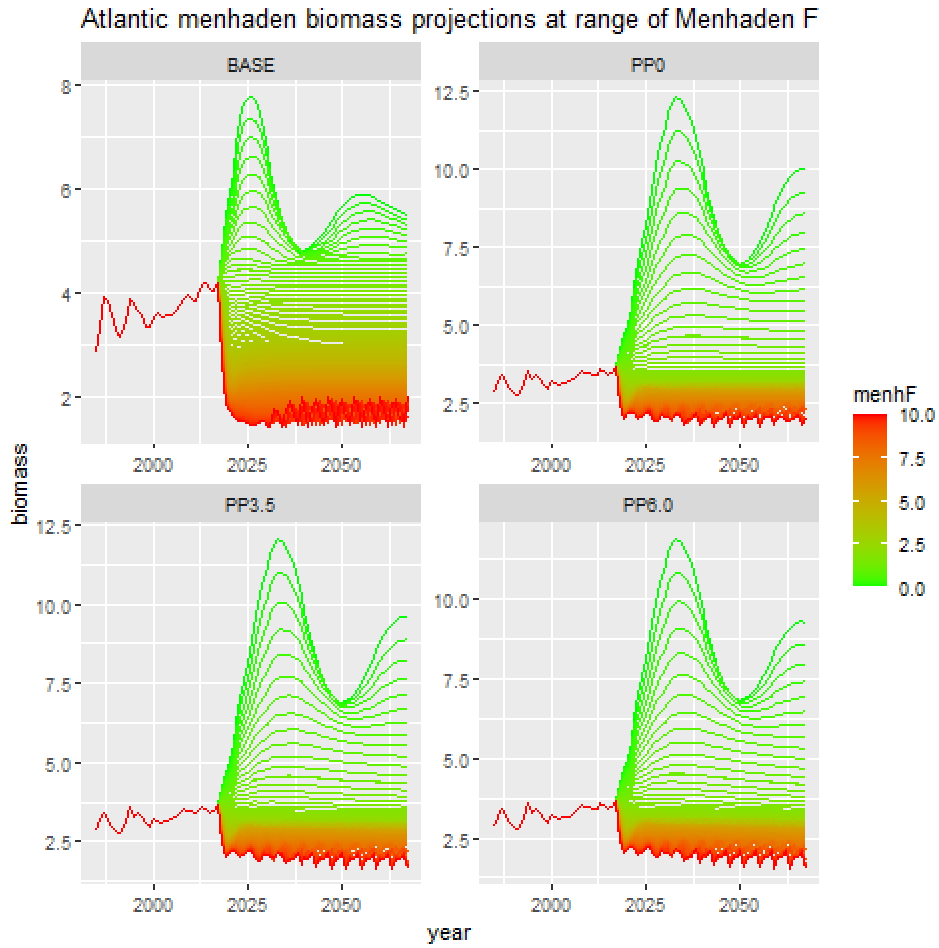

Figure 25 Atlantic Menhaden biomass projections at a range of Atlantic Menhaden fishing mortality multipliers (menhF represents multiplier from 2017 fishing mortality rate).

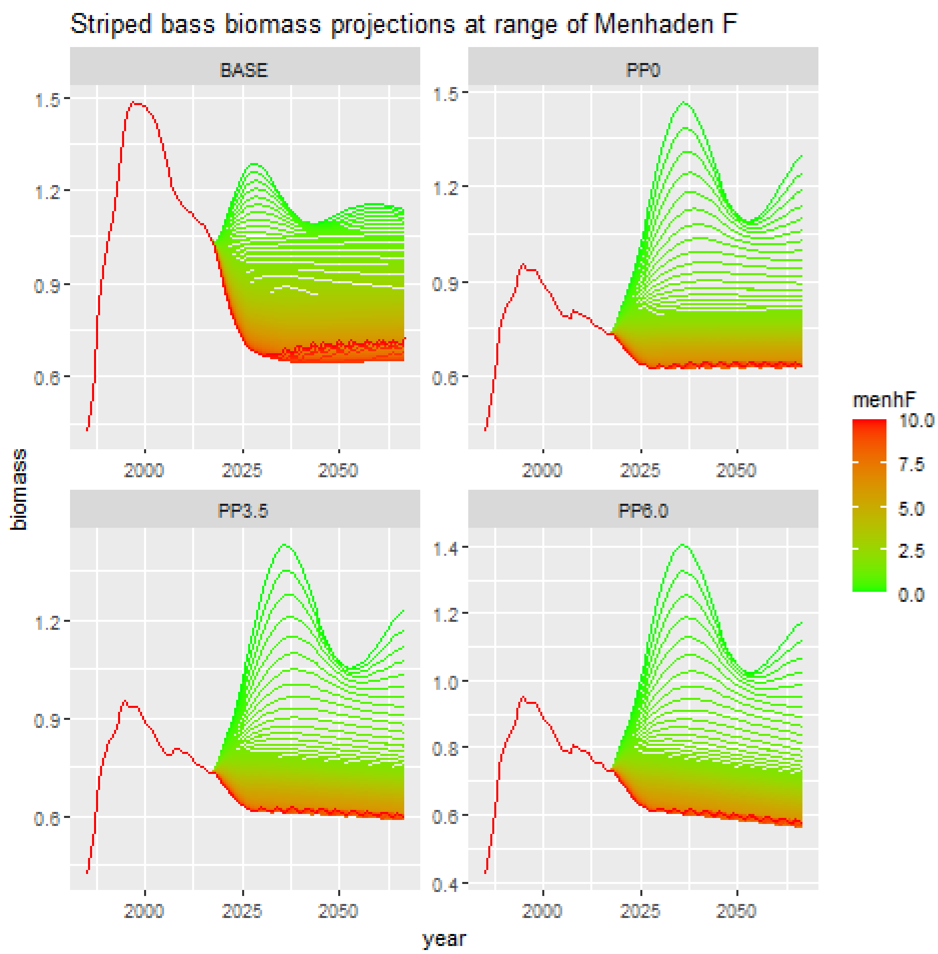

Figure 26 Striped Bass biomass projections at a range of Atlantic Menhaden fishing mortality multipliers (menhF represents multiplier from 2017 fishing mortality rate).

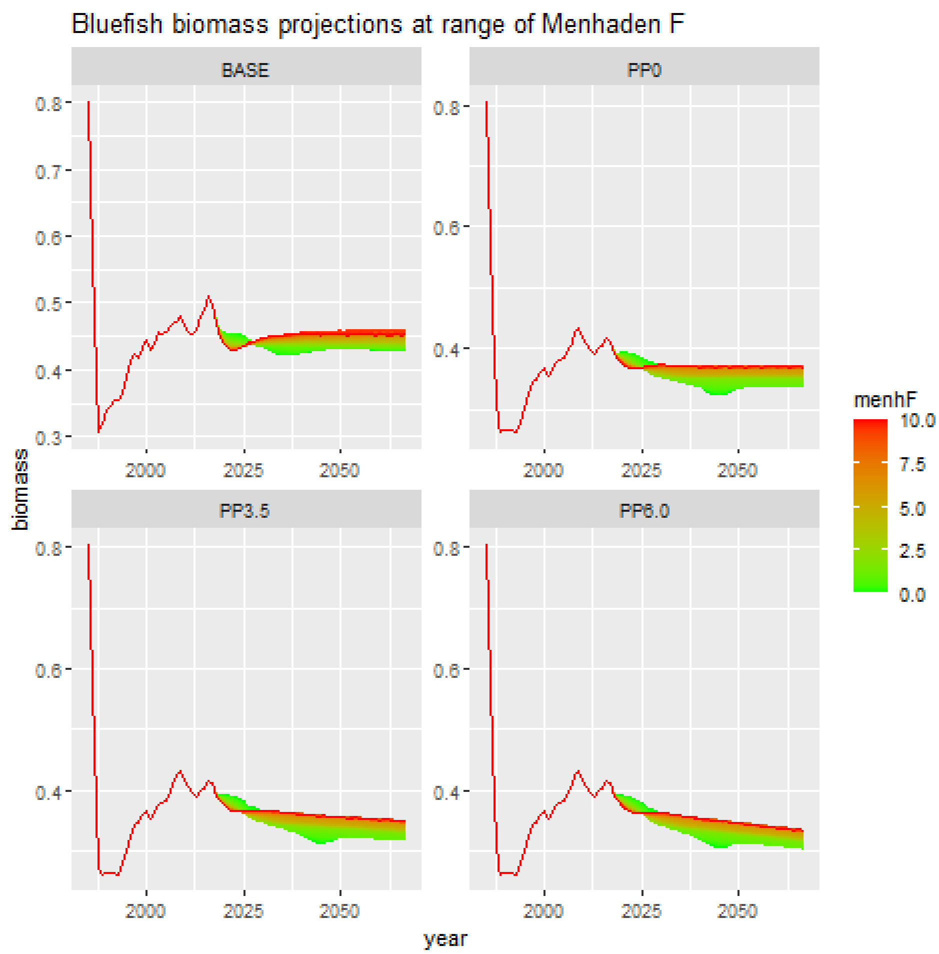

Figure 27 Bluefish biomass projections at a range of Atlantic Menhaden fishing mortality multipliers (menhF represents multiplier from 2017 fishing mortality rate).

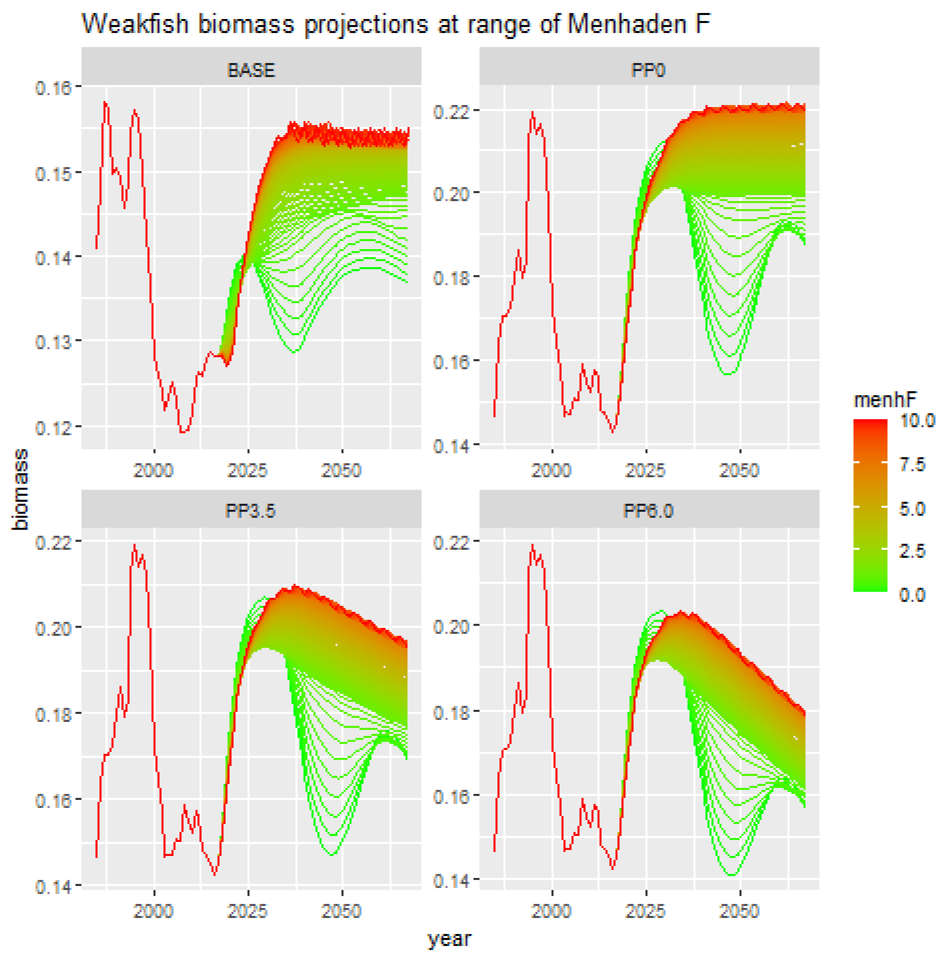

Figure 28 Weakfish biomass projections at a range of Atlantic Menhaden fishing mortality multipliers (menhF represents multiplier from 2017 fishing mortality rate).

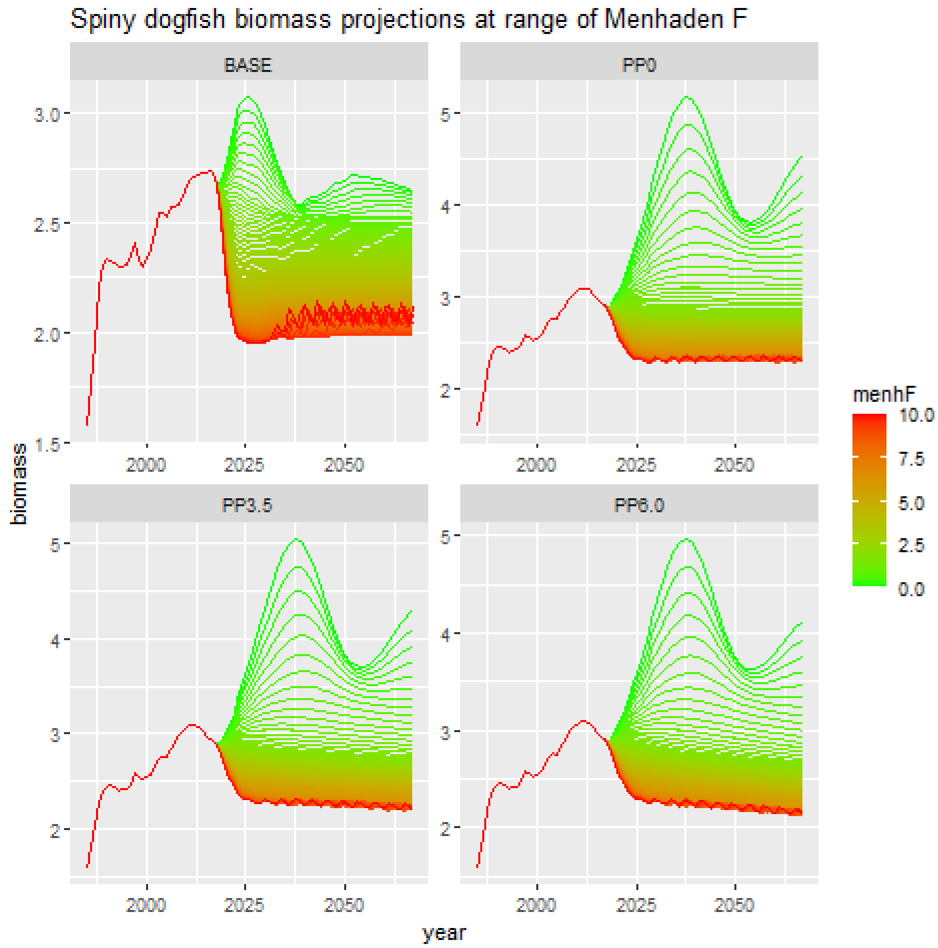

Figure 29 Spiny Dogfish biomass projections at a range of Atlantic Menhaden fishing mortality multipliers (menhF represents multiplier from 2017 fishing mortality rate).

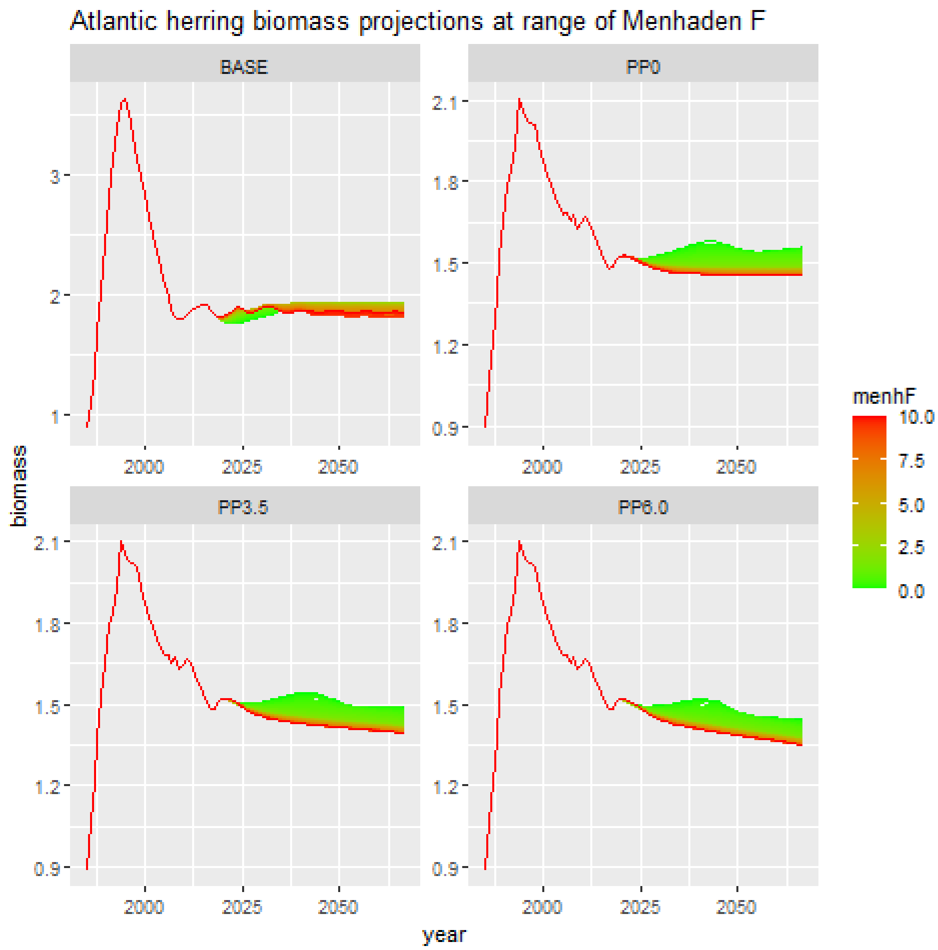

Figure 30 Atlantic Herring biomass projections at a range of Atlantic Menhaden fishing mortality multipliers (menhF represents multiplier from 2017 fishing mortality rate).