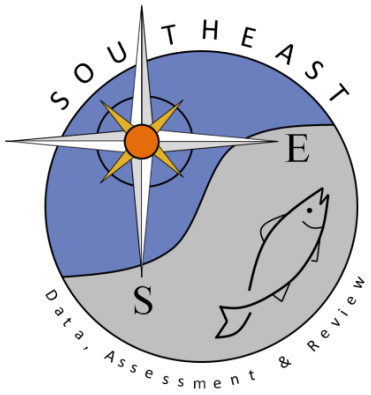
SEDAR 69 Ecological Reference Points Stock Assessment Report

ASMFC

SEDAR102-RD-04

July 2025

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SEDAR

Southeast Data, Assessment, and Review

SEDAR 69

Ecological Reference Points Stock Assessment Report

Atlantic Menhaden

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1. Preface

The development and peer review of the 2019 Atlantic Menhaden Stock Assessment occurred through a joint Atlantic States Marine Fisheries Commission (ASMFC) and Southeast Data, Assessment, and Review (SEDAR) process. From April 2018 to June 2019, the ASMFC coordinated a Data Workshop and three Assessment Workshops in Arlington, Virginia, and Raleigh, North Carolina, while SEDAR coordinated the Review Workshop in Charleston, South Carolina. The report is the culmination of a two-year effort to gather and analyze available data for Atlantic menhaden from the fishery-independent sampling programs of the Atlantic States, commercial purse-seine reduction fishery, and commercial bait fishery. ASMFC developed the stock assessment through its Atlantic Menhaden Technical Committee (TC) and Stock Assessment Subcommittee (SAS). The ASMFC facilitated numerous conference calls and webinars in preparation for the Data, Assessment, and Review Workshops. Participants in the stock assessment process included TC and SAS members, as well as representatives from the fishing industry and Non-Governmental Organizations with an interest in menhaden.

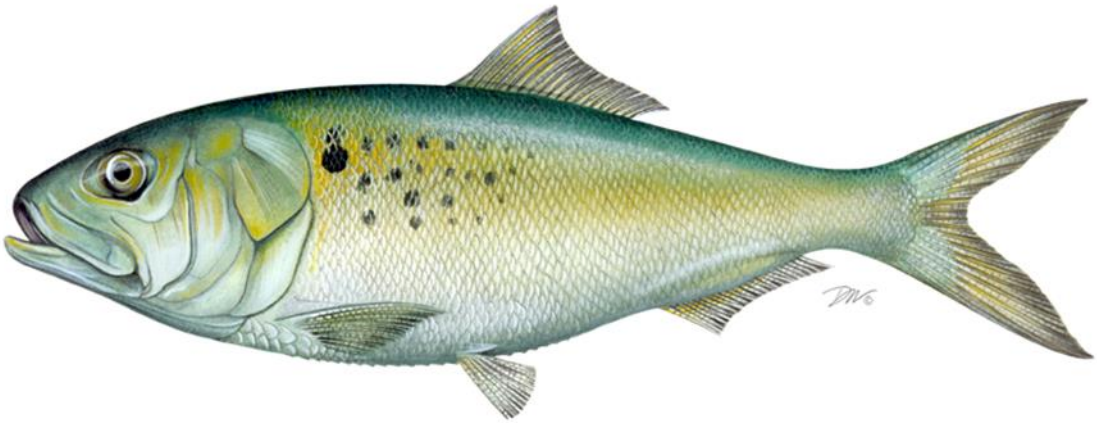
In addition to the single-species menhaden stock assessment report, an Ecosystem Reference Points (ERP) stock assessment report was developed by the ASMFC Ecosystem Reference Points Work Group, and reviewed by the SEDAR 69 Panel. The ASMFC facilitated several webinars and meetings of the Work Group, coinciding with the Menhaden SAS meetings, to develop the ERP Assessment. The ERP report describes ecosystem monitoring and modeling approaches, and provides reference points designed to address multispecies interactions for a subset of stocks managed by the ASMFC, including management of menhaden for forage services in a broader ecosystem management context.

The SEDAR 69 single-species stock assessment report and ERP stock assessment report were generated and provided to three reviewers appointed by the Center for Independent Experts (CIE), as well as a fourth technical reviewer and the review panel chair appointed by ASMFC. The Review Workshop was held in Charleston, South Carolina, from November 4-8, 2019. At the Workshop, reviewers had opportunities to raise questions to the SAS and ERP WG, and provide critiques and constructive comments on the data and models used. A Review Workshop Report (Section III) was generated with comments and overall opinions about the data sources, models, and assessment results. The Review Report, Single-Species Stock Assessment Report, and Ecosystem Reference Points Stock Assessment Report will be provided to the ASMFC Atlantic Menhaden Management Board in February 2020.

The ASMFC and its committees thank the independent peer reviewers for their time and expertise in providing a thorough review of the Atlantic menhaden stock assessment and the Ecosystem Reference Points stock assessment. Additionally, ASMFC expresses its gratitude to all of the individuals who contributed to the completion of both stock assessments.

Atlantic States Marine Fisheries Commission

2019 Atlantic Menhaden Ecological Reference Point Stock Assessment Report



Vision: Sustainably Managing Atlantic Coastal Fisheries

Atlantic States Marine Fisheries Commission

2019 Atlantic Menhaden Ecological Reference Point Benchmark Stock Assessment

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EXECUTIVE SUMMARY

The impact of forage species harvest on predator species and the larger ecosystem has received increasing attention in recent years. Much of this work has concluded that forage fisheries should be managed more conservatively than single-species reference points would suggest. However, much of that work has also been conducted outside the North West Atlantic Continental Shelf ecosystem. The North West Atlantic Continental Shelf ecosystem is complex, with numerous predators and prey overlapping spatially, temporally, and trophically.

Atlantic menhaden have supported one of the largest fisheries in the U.S. since colonial times. The vast majority of landings are turned into fish meal and fish oil for use in a variety of products, and a smaller component is used as bait for other commercial and recreational fisheries. Atlantic menhaden are also an important food source for a wide range of species in the North West Atlantic Continental Shelf ecosystem, including larger fish such as striped bass and bluefin tuna, birds such as bald eagles and osprey, and marine mammals like humpback whales and bottlenose dolphin. Many of these predators support valuable commercial and recreational fisheries or ecotourism industries, in addition to having cultural value.

Managers and stakeholders have expressed strong interest in managing Atlantic menhaden in an ecosystem context. In 2015, the Atlantic States Marine Fisheries Commission held an Ecosystem Management Objectives (EMO) Workshop with managers, scientists, and stakeholders to identify fundamental ecosystem management objectives for Atlantic menhaden. The objectives included sustaining Atlantic menhaden to provide for directed fisheries, sustaining Atlantic menhaden to provide for predators, providing stability for all types of fisheries, and minimizing the risk to sustainability due to a changing environment.

Models and Data

The Commission's Ecological Reference Point Workgroup (ERP WG) was tasked with developing reference points for management use that could account for Atlantic menhaden's role as a forage fish throughout its range. To accomplish this, the ERP WG explored a suite of models to develop ecological reference points and estimate population parameters for Atlantic menhaden. These approaches ranged from simple, with minimal data requirements and few assumptions, to complex, with extensive data needs and detailed assumptions. The approaches included: a time-varying intrinsic growth rate (*r*) surplus production model, a Steele-Henderson surplus production model, a multispecies statistical catch-at-age model, a moderate complexity Ecopath with Ecosim (EwE) model with a limited predator/prey field, and a full ecosystem EwE model.

A suite of five key predator and prey species were identified from diet data and other considerations (referred to as ERP focal species). Atlantic striped bass, bluefish, spiny dogfish, and weakfish were identified as key predator species of Atlantic menhaden. Weakfish was included as both an Atlantic menhaden predator and a prey item for the other predators. Atlantic herring was included as a key alternative prey to Atlantic menhaden for the predators identified. The Steele-Henderson surplus production model explored each of the ERP focal

predators, resulting in a base model that included only Atlantic menhaden and striped bass. The multispecies statistical catch-at-age and the two EwE models included all of the ERP focal species. The intermediate complexity EwE included a few additional trophic groups, while the full EwE incorporated a large number of additional species and groups.

The ERP models were parameterized with the best available data for Atlantic menhaden and the ERP focal species. For Atlantic menhaden, data from the single-species benchmark assessment conducted in parallel with this assessment were used. All ERP focal species had recently undergone benchmark assessments or assessment updates which included the time series of new Marine Recreational Information Program (MRIP) estimates of recreational catch. All ERP focal species had life history, landings, and index data available through 2017, as well as estimates of fishing mortality and population size. Newer data were not available for all of the groups included in the full EwE; as a result, inputs for those groups were extrapolated from the previously published full EwE model, which had a terminal year of 2013.

In addition to the single-species assessment inputs, the ERP WG examined a range of diet datasets – from individual, small-scale studies to larger scale, long-term monitoring programs – to parameterize the multispecies models. The proportion of Atlantic menhaden in the diets of key predators varied by season, location, and age class of predators sampled. The main sources of diet data included the Northeast Area Monitoring and Assessment Program (NEAMAP), the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), and the Northeast Fisheries Science Center Food Habits Database (NEFSC FHD). These programs covered a fairly large proportion of the Atlantic coastal shelf and provided ten to thirty years of diet data collected with consistent methodologies. However, sample sizes often precluded analyses on finer spatial or temporal scales. These databases focused on finfish and shellfish species, not birds or marine mammals. Smaller scale studies were used to supplement the data from these long-term programs for some of the modeling approaches, especially for species that were not well represented in the long-term programs.

Model Results and Comparisons

The ERP WG evaluated the performance of these models, their strengths and weaknesses, and their ability to inform the fundamental ecosystem management objectives identified by the EMO Workshop. To meet the ecosystem management objectives, the models needed to be able to assess both top-down effects of predation on Atlantic menhaden and bottom-up effects of Atlantic menhaden biomass levels on predators in order to quantify tradeoffs between management objectives. The EwE models were the only models that were able to evaluate both factors. The surplus production model with time-varying *r* only estimated changes in productivity without attributing them to a particular cause. The Steele-Henderson model included the effect of striped bass predation on Atlantic menhaden, but did not have a feedback mechanism to predict the effect of Atlantic menhaden harvest on striped bass biomass. Similarly, the current implementation of the multispecies statistical catch-at-age explored here lacked the bottom-up feedback necessary to explore trade-offs between Atlantic menhaden harvest and predator biomass.

The ERP models agreed about the overall trend of Atlantic menhaden population size and exploitation rates over the last 30 years, indicating biomass was increasing and exploitation rate was decreasing. These trends and the magnitude of the estimates were also consistent with the estimates from the single-species assessment. This was not surprising, as all of the ERP models used the same time-series of total removals, life history parameters, and indices of abundance as the single-species model. In addition, the EwE models used some outputs from the single-species model directly as inputs.

All of the ERP models produced MSY- or MSY-proxy reference points. Those reference points were calculated from the current ecosystem conditions, i.e., the estimate of productivity or predator consumption levels from the terminal year of each model. However, these reference point estimates may not meet the management objectives for the ecosystem, because several of the predators included in the ERP models were in an overfished state in the terminal year of the models.

ERP Targets and Thresholds

To establish reference points for Atlantic menhaden that take into account their role as forage fish, the ERP WG recommended using the intermediate complexity EwE model in conjunction with the Atlantic menhaden single-species assessment model.

This approach combined the individual strengths of each model. The single-species model provided the best information on Atlantic menhaden population size and fishing mortality, as it included more detail on size and age structure, fishery selectivity, and recruitment variability than the EwE models. The EwE models provided an evaluation of the impact of proposed harvest scenarios on important predator species in the long-term, which the single-species model could not do.

The intermediate complexity EwE was chosen over the full EwE because the full EwE model results suggested that the reduced predator set of the intermediate complexity EwE model captured the dynamics of the more responsive predators from the full ecosystem model. Striped bass and nearshore piscivorous birds were the most sensitive species in the full EwE models, as they showed larger changes in biomass than other species did in response to increases or decreases in fishing pressure on Atlantic menhaden. The Atlantic menhaden harvest scenarios that sustain the biomass of predators included in the intermediate complexity EwE were thus expected to not cause large declines for other predators that were only included in the full EwE model. In addition, it would be feasible to update the intermediate complexity EwE model on a timeframe suitable for management. The full EwE model required extensive data from stock assessments and other sources for the large number of species and groups included in the model; as a result, updating the model would be a significant effort.

While the final values for the ERP target and threshold will be a management decision that takes into account the management objectives of both Atlantic menhaden and their predators, the tradeoffs between those management objectives can be evaluated with the ERP approach outlined here. To illustrate the potential use of the combined single-species assessment and

intermediate complexity EwE model, the ERP WG put forward example values of an ERP target and an ERP threshold based on existing management objectives for striped bass. Striped bass was the focal species for this analysis because it was the most sensitive fish species to Atlantic menhaden *F*, and focusing on one key predator provided a more tractable example for evaluating tradeoffs among management strategies. Example ERPs based on striped bass biomass should not cause significant declines for other species that were less sensitive to levels of Atlantic menhaden removals.

Multiple combinations of *F* on striped bass and *F* on Atlantic menhaden could keep striped bass populations at their biomass target or threshold (Figure 144). The example ERP target was defined as the maximum *F* on Atlantic menhaden that would sustain striped bass at their biomass target when striped bass were fished at their *F* target. The example ERP threshold was defined as the maximum *F* on Atlantic menhaden that would keep striped bass at their biomass threshold when striped bass were fished at their *F* target. For the example analysis, all other species were fished at their current *F* rates.

The example ERP target and threshold were lower than the current single-species target and threshold (Figure 148). The example ERP target was estimated at a full *F* (i.e., maximum *F*-at-age from the intermediate complexity EwE model) of 0.188, compared to a full *F* of 0.314 for the single-species target. The example ERP threshold was estimated at a full *F* of 0.573, compared to a full *F* of 0.856 for the single-species threshold. The current estimate of full *F* from the single-species model is 0.157, below both the example ERP target and threshold.

This example was based on the *F* and *B* targets laid out in the striped bass fishery management plan. Higher or lower reference points for striped bass will result in higher or lower reference points for Atlantic menhaden. Similarly, this example maintained the other species at their current *F* rates; higher or lower *F* rates on other species would also result in different reference point values for Atlantic menhaden. Managers and stakeholders can evaluate the tradeoffs between Atlantic menhaden harvest, predator harvest, and resulting biomass for all modeled species quantitatively and transparently with this combination of models in order to set the final reference point values and total allowable catch.

Next Steps

This approach represents the first step towards a practical application of an ecosystem approach to fishery management. The ERP WG identified a number of research recommendations dealing with data collection, modeling, and the management process in order to improve the ERP assessment and move the ecosystem approach to management forward.

The ERP models developed for this assessment did not include spatial or seasonal dynamics. Incorporating finer scale dynamics would be possible for some of the models, but would require both additional work on model development and better data. Spatially and seasonally resolved data were lacking, making it difficult to parameterize and calibrate the models on that scale. The ERP WG recommended expanding the collection of diet and condition data along the

Atlantic coast to provide seasonally and regionally stratified annual, year-round monitoring of key predator diets. This would provide information on prey abundance and predator consumption. In addition, ERP WG recommended improving the collection of diet data and monitoring of population trends for non-finfish predators (e.g., birds, marine mammals) and data-poor prey species (e.g., bay anchovies, sand eels, benthic invertebrates) to better parameterize the full ecosystem models.

The ERP WG also recommended further development of the multispecies statistical catch-at-age and the EwE models. In addition to spatial and seasonal dynamics, further development of bottom-up feedback into the multispecies statistical catch-at-age model and stochastic recruitment dynamics into the EwE models would improve the understanding of the relative importance of fishing, trophic interactions, and recruitment dynamics on ecosystem dynamics.

The ERP WG recommended that the intermediate complexity EwE model should be updated in conjunction with the next single-species assessment update in approximately three years and that the next benchmark be conducted in six years in conjunction with the single-species benchmark stock assessment. The other models should be updated and reevaluated as part of the next benchmark assessment if sufficient progress has been made on the modeling research recommendations.

Currently, the timing of individual assessments or updates for Commission-managed species are set independently of each other. The ERP WG in conjunction with other technical groups can develop a timeline for Commission assessments to ensure the most up-to-date data are available for timely ERP assessment updates.

The ERP WG also requested to be tasked by the Atlantic Menhaden Management Board or the Commission's Policy Board with the development of a timeline and framework for continued deployment of ecosystem-based fishery management by the Commission. Atlantic menhaden and their key predators are currently managed by separate Boards within the Commission (and in some cases, in collaboration with NOAA Fisheries). This means that management objectives, including *F* and *B* targets for each species, are set independently of each other. For successful ecosystem-based fishery management, the discussion of trade-offs between Atlantic menhaden and their predators should occur across Boards in order to develop consistent management objectives for individual species and the ecosystem. This will require changes to the way the Commission has historically operated. The Commission also does not have explicit management objectives for species like marine mammals and seabirds. The development of clear, quantitative management objectives for this ecosystem and the evaluation of the trade-offs between Atlantic menhaden harvest and other species need to be a holistic process that engages all managers and stakeholders. The ERP WG recommended that a formal management strategy evaluation be part of this process to identify harvest strategies that will maximize the likelihood of achieving these ecosystem management objectives.

The ERP WG recognized that implementing reference points and tools to address ecosystem issues is a complex and multifaceted problem. The full implementation of ecosystem-based

fisheries management will require significant process and cultural changes to fishery management beyond simply new reference points for Atlantic menhaden. However, these new reference point methods for Atlantic menhaden are a critical first step in that implementation. While the Commission continues to refine the ERP models, collect better data, and consider changes to its management structure and process, managers can set harvest strategies for Atlantic menhaden that take into account their role as forage fish in a transparent and quantitative way.

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TERMS OF REFERENCE REPORT SUMMARY

TOR 1. Review and evaluate the fishery-dependent and fishery-independent data used in the Atlantic menhaden single-species assessment, and justify inclusion, elimination, or modification of those data sets.

The Atlantic menhaden data were thoroughly vetted by the Atlantic Menhaden Technical Committee (TC) and Stock Assessment Subcommittee (SAS), and the available datasets are described in the single-species assessment report. The fishery-dependent data for Atlantic menhaden were robust. The reduction fishery, which accounted for the majority of landings, was well-sampled and both total landings and age composition information were considered precise and reliable. The bait fisheries and the recreational fisheries were not as adequately sampled, and there was a higher degree of uncertainty in the total landings and the age composition information; however, as these fisheries made up only about 10% of total landings, they did not significantly increase the uncertainty of the overall fishery-dependent data used in the assessment.

The fishery-independent data for Atlantic menhaden were more limited and had more uncertainty. Several data sets were available for young-of-year (YOY) abundance indices, but few were long time series. The few long-term YOY indices of abundance that were available were all from a single region, the Chesapeake Bay; however, the Chesapeake Bay is one of the major nursery grounds for Atlantic menhaden. Additionally, several data sets were available to characterize age-1+, or adult, Atlantic menhaden relative abundance. Most surveys that encountered Atlantic menhaden were geographically limited (i.e., occurred in a single state or river/bay) and were not designed to capture menhaden specifically. The hierarchical method of combining multiple separate surveys into a single index of abundance helped overcome some of the geographical limitations. In addition, no SAS-accepted age data were available from the fishery-independent data sources, which increased uncertainty since several indices captured Atlantic menhaden outside the range of sizes seen in the fisheries.

The Ecological Reference Point Working Group (ERP WG) considered the data collected and developed through the single-species assessment to be the best available data for Atlantic menhaden, and used all datasets in the ecological reference point models, with two exceptions. The Southern Adult (SAD) was not used in the biomass dynamic models. Length analysis of the SAD index indicated the index was dominated by age-1 fish, which made it inappropriate for that type of model. The Northern Adult (NAD) and Mid-Atlantic Adult (MAD) indices had a broader size structure and were used in the biomass dynamic models. In addition, the WG accepted the reduction fishery CPUE (RCPUE) index as an index of abundance for use in the surplus production models. Although the WG recognized the SAS's concerns about the index, the long time series and the contrast it provided, which the surplus production models required, outweighed the potential biases.

TOR 2. Characterize precision and accuracy of additional fishery-dependent and fishery-independent data sets, including diet data, used in the ecological reference point models.

The ERP WG relied on the most recent single-species stock assessments wherever possible to provide fishery-dependent and fishery-independent datasets for non-menhaden species. The key predator and prey species identified for the intermediate complexity models (Atlantic herring, Atlantic striped bass, bluefish, spiny dogfish, and weakfish) all had data available through 2017 that had been prepared by the TC or SAS responsible for the single-species assessment. The full ecosystem model included the most recent data for the key predator and prey species, but used the older time series of data from the previously published version of the model for other species.

The key predator and prey species were chosen in part because of the quality of the data available for them. Four of the five species had peer-reviewed statistical catch-at-age models that include fishery-dependent and fishery-independent indices of abundance and reliable estimates of total removals. Spiny dogfish was the one exception; the spiny dogfish assessment was a swept-area biomass estimate from a trawl survey but did include reliable estimates of total catch. For other species, the data were less robust. Important prey items like bay anchovy and sand eels and important predators like birds and whales lacked traditional stock assessments and often did not have reliable estimates of total removals or population abundance or biomass.

The ERP WG examined a range of diet datasets, from individual small-scale studies to larger-scale, long-term monitoring programs. The proportion of Atlantic menhaden in the diets of key predators varied by season, location, and age-class of predators sampled. The main sources of diet data included the Northeast Area Monitoring and Assessment Program (NEAMAP), the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), and the Northeast Fisheries Science Center Food Habits Database (NEFSC FHD). These programs covered a fairly large proportion of the Atlantic coastal shelf, and provided ten to thirty years of diet data collected with consistent methodologies. The key predator and prey species were moderately well-represented in these databases, but sample sizes often precluded analyses on finer spatial or temporal scales. In addition, these databases focused on finfish and shellfish species, not birds or marine mammals. Smaller scale studies were used to supplement the data from these long-term programs for some of the modeling approaches, especially for species that were not well represented in the long-term programs.

TOR 3. Develop models used to estimate population parameters (e.g., F, biomass, abundance) of Atlantic menhaden that take into account Atlantic menhaden's role as a forage fish and analyze model performance.

The ERP WG explored a suite of models to develop ecological reference points and estimate population parameters for Atlantic menhaden, ranging from very simple with minimal data requirements and few assumptions about population drivers to very complex with extensive data needs and detailed assumptions about the mechanisms of population dynamics. These included two surplus production models (one that estimated a time-varying intrinsic growth rate and one that implemented the Steele-Henderson approach of including predator biomass as part of the modeling process), a multispecies statistical catch-at-age model, and two

formulations of Ecopath with Ecosim (EwE), one of intermediate complexity with a limited predator/prey field and one with a full ecosystem.

TOR 4. Develop methods to determine reference points and total allowable catch for Atlantic menhaden that account for Atlantic menhaden's role as a forage fish.
To develop reference points and estimates of total allowable catch that meet the ecosystem management objectives, the models needed to be able to assess both top-down effects of predation on Atlantic menhaden and bottom-up effects of Atlantic menhaden biomass levels on predators. The EwE models were the only models that were able to evaluate both factors; the other explored here models only captured the effects of predation on Atlantic menhaden. Therefore, the ERP WG recommended an approach that combined the single-species assessment model with the intermediate complexity EwE model. The single-species model represented the best information on current Atlantic menhaden population dynamics, including estimates of abundance and fishing mortality, while the intermediate complexity EwE model provided a way to evaluate harvest strategies for Atlantic menhaden in an ecosystem context while still being tractable to update on a management timeline.

The final reference point values used in management will be set by the Atlantic Menhaden Management Board based on their evaluation of the tradeoffs between Atlantic menhaden harvest and predator management objectives; however, the ERP WG developed example ecological targets and thresholds for Atlantic menhaden as a proof-of-concept. Striped bass were found to be one of the most sensitive species across several models, so the ERP WG developed the example target and threshold based on the current striped bass management objectives, as laid out in the striped bass fishery management plan. The ERP target was defined as the maximum fishing mortality rate on Atlantic menhaden that would sustain striped bass at their biomass target when striped bass were fished at their F target; the ERP threshold was defined as the maximum fishing mortality rate on Atlantic menhaden that would keep striped bass at their biomass threshold when striped bass were fished at their *F* target. The single-species projection model would then be used to calculate a TAC based on the ERP target.

The example ERP target and threshold were lower than the current single-species target and threshold. The ERP target was estimated at a full *F* of 0.188, compared to a full *F* of 0.314 for the single-species target. The ERP threshold was estimated at a full *F* of 0.573, compared to a full *F* of 0.856 for the single-species threshold. This example is based on the F and B targets laid out in the striped bass fishery management plan. Higher or lower reference points for striped bass would result in higher or lower reference points for Atlantic menhaden. In addition, other species in the model were fished at their F_{2017} values; increasing or decreasing *F* on the other species would also result in different reference points for Atlantic menhaden.

TOR 5. State assumptions made for all population and reference point models and explain the likely effects of assumption violations on synthesis of input data and model outputs.
Each of the models explored had a different set of assumptions about population and ecosystem dynamics.

The surplus production model with time-varying *r* did not make any explicit assumptions about what was causing changes in productivity: potential factors like changes in M from predation or other sources and variability in recruitment were all combined into changes in *r.* The Steele-Henderson surplus production model assumed that all changes in productivity were driven by the fishery and the key predator species in the model; other sources of mortality were included in the estimate of *r*, but the estimate of *r* was not time-varying. Changes in productivity that result from variability in recruitment or changes in M due to other factors could be attributed to predation by modeled species.

The multispecies statistical-catch-at-age model assumed that changes in M over time are due to changes in predation mortality from modeled predators (M_2); M_2 is a function of predator biomass, diet composition, and consumption-to-biomass ratios. To simplify the ecosystem structure, a limited suite of predator and prey species was used. A pool of other, non-modeled prey biomass was assumed to be constant to allow for diverse predator diets, and an age-varying but time-constant level of *M* from other sources (M_0) was assumed to account for non-modeled predators. Unlike the surplus production models, the multispecies statistical catch-at-age model was able to track observed variability in recruitment by fitting to observed recruitment indices and age composition information. This implementation of the multispecies statistical catch-at-age model was focused on predator impacts on Atlantic menhaden abundance; it did not include bottom-up effects of Atlantic menhaden abundance on predator biomass.

The EwE models are comprised of two model frameworks: the Ecopath model, a static, mass-balance representation of the ecosystem, and Ecosim, where change in biomass is predicted as consumption minus losses to predation, fishing, and migration, with consumption modeled using foraging arena theory. The two formulations of EwE differed in how detailed the trophic structure of the models were; the intermediate complexity model included 17 trophic groups, while the full model included 61 trophic groups. Both models allowed for unexplained, non-modeled mortality in addition to explicit loss to predation and fishing. The EwE models allowed for both top-down impacts of predators on prey species, and bottom-up effects of prey availability on predator biomass. As configured, the EwE models assumed a stock-recruitment relationship existed for all species, and as a result, may overstate the impact of adult mortality on future population abundance for species where recruitment is more environmentally driven.

Modeling of environmental factors was limited by the poor understanding of the relationship between specific environmental drivers and recruitment and mortality. None of the models included explicit environmental drivers in the base model run.

None of the models included spatial dynamics; all data were pooled to a coastwide stock level. As a result, nuances of population dynamics at the regional scale may be lost.

TOR 6. Characterize uncertainty of model estimates and reference points.

Estimates of uncertainty for model parameters and reference points could not be directly compared across models because of differences in the way each model calculated and propagated uncertainty through the estimates. The major source of uncertainty for these models was from the input data and model structure, and these were explored through sensitivity analyses.

The surplus production models were both sensitive to the starting year of the model and the indices used. The magnitude of the estimates of population size and exploitation rate varied significantly between different runs; however, the overall trend and relative stock status (e.g., B/B_{MSY}) were similar across runs. This is a common result with surplus production models.

For the multispecies statistical catch-at-age model, uncertainty about diet data had the greatest effect on the prey species, while the run with the alternative indices had the greater effect on the predator species. The estimate of unexplained M (M_0) used in the model was also a source of uncertainty.

The most sensitive parameters in the EwE models were the vulnerability parameters, which describe the exchange rates of prey from non-vulnerable states into vulnerable foraging "arenas," where they can be consumed by predators. The diet data used as input also had an effect on model results, as with the multispecies statistical catch-at-age, especially in identifying the major predators on Atlantic menhaden. The implementation of EwE used for this assessment did not include the ability to propagate uncertainty in input data such as species or species group biomasses and exploitation rates through to the final population and reference points estimates, so that source of uncertainty has an unknown impact.

TOR 7. Evaluate stock status for Atlantic menhaden from recommended model(s) as related to the respective reference points (if available).

All of the models explored by the ERP WG agreed on the current status of Atlantic menhaden: in 2017, overfishing was not occurring and the stock was not overfished, even when Atlantic menhaden's role as a forage fish was taken into consideration. Current levels of Atlantic menhaden removals were unlikely to cause a decline in predator populations.

TOR 8. Compare trends in population parameters and reference points among proposed modeling approaches, including the results of the single-species benchmark assessment. If outcomes differ, discuss potential causes of observed discrepancies.

All of the ERP models explored here agreed with the single-species assessment model about the overall trend of Atlantic menhaden population size and exploitation rates over the last 30 years: a generally increasing trend in biomass and a decreasing trend in exploitation rate. This consistency in findings is not surprising, since all the ERP models used the same time-series of total removals, life history parameters, and indices of abundance as the single species model, and in some cases (the EwE models) used output from the single-species model directly.

The ERP models produced similar assessments of stock status to the single-species assessment results, which determined that Atlantic menhaden were not overfished and were not experiencing overfishing in 2017. Current levels of Atlantic menhaden removal were not projected to cause declines in predator biomass. However, the ERP models were also consistent in the finding that fishing Atlantic menhaden at the single-species threshold would cause declines in predator biomass or condition.

The example ERP target and threshold developed based on management objectives for striped bass were lower than the single-species *F* target and threshold, but the current *F* for Atlantic menhaden was below the ERP target and threshold as well.

TOR 9. If a minority report has been filed, explain majority reasoning against adopting approach suggested in that report. The minority report should explain reasoning against adopting approach suggested by the majority.
No minority report was filed.

TOR 10. Develop detailed short and long-term prioritized lists of recommendations for future research, data collection, and assessment methodology. Highlight improvements to be made by next benchmark review.
The ERP WG endorsed the research recommendations laid out in the single-species assessment to improve the understanding of Atlantic menhaden population dynamics, especially the recommendations to develop an Atlantic menhaden-specific coastwide fishery-independent index of adult abundance and to continue to investigate environmental covariates related to productivity and recruitment on a temporal and spatial scale.

In addition, the ERP WG identified several short- and long-term research recommendations to improve the ERP assessment in the future. This included enhanced collection of diet and condition data through geographically widespread, annual, year-round monitoring of selected predator diets stratified seasonally and regionally, as well as enhanced collection of abundance and life history data on species such as birds, marine mammals, and non-commercially important finfish and shellfish. Incorporating bottom-up effects into the multispecies statistical catch-at-age model would improve the utility of that model for management use. Better incorporation of stochastic recruitment dynamics into the EwE models would improve the understanding of the relative importance of fishing, trophic interactions, and recruitment dynamics on ecosystem dynamics.

In addition to data and modeling recommendations, the ERP WG also recommended socioeconomic research and management strategy evaluation be conducted. Establishing appropriate ecological reference points requires understanding the tradeoffs between species and stakeholders from a socioeconomic as well as biological standpoint.

TOR 11. Recommend timing of next benchmark assessment and intermediate updates, if necessary relative to biology and current management of the species.

The ERP WG recommended that the moderate complexity EwE model should be updated in conjunction with the next single-species assessment, and that the other models should be updated and reevaluated as part of the next benchmark assessment. The ERP WG recommended the next benchmark be conducted in six years if sufficient progress has been made on the modeling research recommendations.

TERMS OF REFERENCE

For the 2019 ASMFC Atlantic Menhaden
Ecological Reference Point Benchmark Stock Assessment and Peer-Review

Board Approved May 2018

Terms of Reference for the Ecological Reference Point Assessment

1. Review and evaluate the fishery-dependent and fishery-independent data used in the Atlantic menhaden single-species assessment, and justify inclusion, elimination, or modification of those data sets.

2. Characterize precision and accuracy of additional fishery-dependent and fishery-independent data sets, including diet data, used in the ecological reference point models.
    a. Provide descriptions of each data source (e.g., geographic location, sampling methodology, potential explanation for outlying or anomalous data)
    b. Describe calculation and potential standardization of abundance indices.
    c. Discuss trends and associated estimates of uncertainty (e.g., standard errors)
    d. Justify inclusion or elimination of available data sources.
    e. Discuss the effects of data strengths and weaknesses (e.g., temporal and spatial scale, gear selectivities, ageing accuracy, sample size) on model inputs and outputs.

3. Develop models used to estimate population parameters (e.g., F, biomass, abundance) of Atlantic menhaden that take into account Atlantic menhaden's role as a forage fish and analyze model performance.
    a. Briefly describe history of model usage, its theory and framework, and document associated peer-reviewed literature. If using a new model, test using simulated data.
    b. Justify choice of ecological factors (e.g., predator species, other prey species, environmental factors) as appropriate for each model
    c. Describe stability of model (e.g., ability to find a stable solution, invert Hessian)
    d. Justify choice of CVs, effective sample sizes, or likelihood weighting schemes as appropriate for each model.
    e. Perform sensitivity analyses, model diagnostics, and retrospective analyses as appropriate for each model.
    f. Clearly and thoroughly explain model strengths and limitations, including each model's capacity to account for environmental changes

4. Develop methods to determine reference points and total allowable catch for Atlantic menhaden that account for Atlantic menhaden's role as a forage fish.

5. State assumptions made for all population and reference point models and explain the

likely effects of assumption violations on synthesis of input data and model outputs.

6. Characterize uncertainty of model estimates and reference points.

7. Evaluate stock status for Atlantic menhaden from recommended model(s) as related to the respective reference points (if available).

8. Compare trends in population parameters and reference points among proposed modeling approaches, including the results of the single-species benchmark assessment. If outcomes differ, discuss potential causes of observed discrepancies.

9. If a minority report has been filed, explain majority reasoning against adopting approach suggested in that report. The minority report should explain reasoning against adopting approach suggested by the majority.

10. Develop detailed short and long-term prioritized lists of recommendations for future research, data collection, and assessment methodology. Highlight improvements to be made by next benchmark review.

11. Recommend timing of next benchmark assessment and intermediate updates, if necessary relative to biology and current management of the species.

Terms of Reference for the Ecological Reference Point External Peer Review

1. Evaluate the justification for the inclusion, elimination, or modification of data from the Atlantic menhaden single-species benchmark assessment.

2. Evaluate the thoroughness of data collection and the presentation and treatment of additional fishery-dependent and fishery-independent data sets in the assessment, including but not limited to:
    a. Presentation of data source variance (e.g., standard errors).
    b. Justification for inclusion or elimination of available data sources,
    c. Consideration of data strengths and weaknesses (e.g., temporal and spatial scale, gear selectivities, aging accuracy, sample size),
    d. Calculation and/or standardization of abundance indices.

3. Evaluate the methods and models used to estimate Atlantic menhaden population parameters (e.g., F, biomass, abundance) that take into account Atlantic menhaden's role as a forage fish, including but not limited to:
    a. Evaluate the choice and justification of the recommended model(s). Was the most appropriate model (or model averaging approach) chosen given available data and life history of the species?
    b. If multiple models were considered, evaluate the analysts' explanation of any differences in results.
    c. Evaluate model parameterization and specification as appropriate for each

model (e.g., choice of CVs, effective sample sizes, likelihood weighting schemes, calculation/specification of M, stock-recruitment relationship, choice of time-varying parameters, choice of ecological factors).

4. Evaluate the methods used to estimate reference points and total allowable catch.

5. Evaluate the diagnostic analyses performed as appropriate to each model, including but not limited to:
    d. Sensitivity analyses to determine model stability and potential consequences of major model assumptions
    e. Retrospective analysis

6. Evaluate the methods used to characterize uncertainty in estimated parameters. Ensure that the implications of uncertainty in technical conclusions are clearly stated.
7. If a minority report has been filed, review minority opinion and any associated analyses. If possible, make recommendation on current or future use of alternative assessment approach presented in minority report.

8. Recommend best estimates of stock biomass, abundance, exploitation, and stock status of Atlantic menhaden from the assessment for use in management, if possible, or specify alternative estimation methods.

9. Review the research, data collection, and assessment methodology recommendations provided by the TC and make any additional recommendations warranted. Clearly prioritize the activities needed to inform and maintain the current assessment, and provide recommendations to improve the reliability of future assessments.

10. Recommend timing of the next benchmark assessment and updates, if necessary, relative to the life history and current management of the species.

11. Prepare a peer review panel terms of reference and advisory report summarizing the panel's evaluation of the stock assessment and addressing each peer review term of reference. Develop a list of tasks to be completed following the workshop. Complete and submit the report within 4 weeks of workshop conclusion.

1 INTRODUCTION

1.1 Brief Overview

The importance of Atlantic menhaden as a forage fish has long been recognized. As far back as 2004, managers, stakeholders, and the public have had an interest in Atlantic menhaden's role as forage in the ecosystem. Atlantic menhaden are a food source for a variety of species including larger fish such as striped bass (Hartman and Brandt 1995b) and bluefin tuna (Butler et al. 2010), birds such as bald eagles (Mersmann 1989) and osprey (Glass and Watts 2009), and marine mammals like bottlenose dolphin (Gannon and Waples 2004). Many of these predators support valuable commercial and recreational fisheries or ecotourism industries, in addition to having cultural value.

The single-species assessments in 2004 and 2010 used estimates of natural mortality from multispecies virtual population analyses (MSVPA) as input to the single-species model to better quantify the effects of predation on Atlantic menhaden populations (ASMFC 2004, 2010). However, there was still a strong interest in accounting for not only the effects of predation on Atlantic menhaden population dynamics, but also the effects of Atlantic menhaden removals on important predator species.

After an Ecosystem Management Objectives Workshop in 2015 (ASMFC 2015; see also Section 1.4), the Atlantic Menhaden Management Board formally tasked the Commission's Ecological Reference Point Workgroup (ERP WG) with developing reference points for management use that could account for Atlantic menhaden's role as a forage fish. The ERP WG developed a suite of models to provide ecological reference points (ERPs) and parameterized them with the best available data for Atlantic menhaden and key predator species. The ERP WG evaluated the performance of these models, their strengths and weaknesses, and their ability to inform the fundamental management objectives identified by the Board in order to determine the best tool for ecosystem-based management of Atlantic menhaden (Table 1).

Given the results, the ERP WG recommends a hybrid approach combining the current single-species assessment model with an EwE model of intermediate complexity to quantitatively evaluate trade-offs between Atlantic menhaden harvest and biomass levels of key managed predators. The final balance between the level of Atlantic menhaden harvest and maintaining predator biomass levels will be a management decision, but this approach will allow managers and stakeholders to evaluate those tradeoffs both quantitatively and transparently.

1.2 Need for Ecological Reference Points

The impact of fishing forage species on predator species and the larger ecosystem has received increasing attention in recent years. Much of this work has concluded that forage fisheries should be managed more conservatively than single-species reference points would suggest, to both ensure the sustainable harvest of forage fish and to reduce ecosystem impacts from their removal. For example, Smith et al. (2011) recommended maintaining forage fish populations at target biomass of 75% of unexploited biomass to prevent negative consequences to predators,

compared to the approximately 60% level implied by fishing at F_{MSY}. Pikitch et al. (2012) recommended a precautionary approach for forage fish management in order to sustain both predator and prey species, including fishing at 50-75% of F_{MSY} and using a biomass threshold of 30-40% of unexploited biomass, depending on the quality of data available. Hilborn et al. (2017) pushed back on these conclusions, pointing out that the models used to develop those recommendations did not include consideration of environmental drivers of forage fish recruitment, the weak stock-recruitment relationship observed for most forage species, or the differing selectivities of predators and fisheries. As a result, some of the ecosystem models may overstate the ecosystem impact of fishing on forage fish abundance and predators. Despite those conclusions, there remains a general consensus that ecosystem services should be considered when managing forage fisheries.

All stock assessments account for some level of predation mortality in their estimates of *M*. Those that use age-varying natural mortality (such as Lorenzen 1996) incorporate the idea that natural mortality rates are higher at the youngest and smallest age or size classes, which is driven at least in part by higher predation rates on those groups. Some assessments have incorporated time-varying *M*, with approaches like an *M* vector scaled by annual key predator biomasses (northern shrimp, ASMFC 2018), or a random-walk process without an explicit driver (weakfish, ASMFC 2016). Generally, however, most assessments do not capture changes in natural mortality in direct response to predator demand. They also generally do not consider the effects of prey availability on the growth or survival of predators when establishing biological reference points for prey species.

Atlantic menhaden stock assessments have included an age- and time-varying natural mortality component since 2004, but there has been increasing interest from stakeholders and managers in explicitly managing Atlantic menhaden to account for their ecosystem services and changing predator demand. In 2017, when the Board was considering changing the management plan for Atlantic menhaden, ASMFC received 127,698 comments from the public in favor of some form of ecological reference points, compared to 7 comments in favor of single-species reference points.

Ecological reference point models are needed to quantify the effects of Atlantic menhaden harvest on their predators, to examine the impact of predators on Atlantic menhaden removal targets, and to quantitatively evaluate the tradeoffs between Atlantic menhaden harvest and predator biomass. Non-species-specific “rule-of-thumb” advice provided by meta-analyses like Smith et al. (2011) and Pikitch et al. (2012) are based on ecosystems that are not representative of the Atlantic coastal shelf and estuaries. More importantly, such “rules-of-thumb” reference points do not allow for the evaluation of specific trade-offs between forage fishery removals and abundance of important predator species. In order to provide the best management advice for this species and this ecosystem, ecological reference point models developed specifically for the coast-wide Atlantic menhaden stock are needed.

1.3 Regulatory History

See the single-species benchmark stock assessment for a more thorough discussion of Atlantic menhaden regulatory history. Sections from that assessment have been abbreviated below.

Atlantic menhaden management authority is vested in the states because the vast majority of landings come from state waters. All Atlantic coast states and jurisdictions, with the exception of the District of Columbia, have a declared interest in the Atlantic menhaden management program.

The first coastwide fishery management plan (FMP) for Atlantic menhaden was passed in 1981 (ASMFC 1981). The FMP did not recommend or require specific management actions, but provided a suite of options should they be needed. The FMP has undergone a series of revisions and amendments in the subsequent years.

In 1988, the ASMFC concluded that the 1981 FMP had become obsolete and initiated a revision to the plan. The 1992 Plan Revision included a suite of objectives to improve data collection and promote awareness of the fishery and its research needs (ASMFC 1992). Amendment 1, approved in 2001, provided specific biological, social, economic, ecological, and management objectives (ASMFC 2001). Amendment 2, approved in 2012, established a 170,800 metric ton total allowable catch (TAC) for the commercial fishery beginning in 2013 (ASMFC 2012a).

Amendment 3 (2017a) completely replaced Amendment 2 and currently sets the management program for Atlantic menhaden. The Amendment continues to manage the stock via single-species biological reference points until the review and adoption of menhaden-specific ecological reference points as part of the 2019 benchmark stock assessment process. In the interim, the Board used an *ad hoc* approach to set the TAC at 216,000 mt, an increase from the previous years' TACs, but less than what would be recommended if the stock were fished at the single-species target *F* rate, in order to provide a qualitative buffer for ecosystem services.

1.4 Ecological Management Objectives

In 2015, the Commission established the Ecosystem Management Objectives (EMO) Workgroup to identify potential ecosystem management objectives for menhaden-specific ecological reference points. To provide a range of perspectives on Atlantic menhaden management, the multi-disciplinary workgroup included representatives from the Atlantic Menhaden Management Board, stakeholder Advisory Panel, and Technical Committee.

At the EMO Workshop, the Workgroup identified potential ecosystem management objectives, as well as their associated performance measures, through a structured decision-making process (ASMFC 2015). Two types of objectives were identified: fundamental and means. Fundamental objectives are the end goals the group would like to achieve and represent what the group values. Means objectives are intermediary goals necessary to achieve the fundamental objectives, i.e., they represent "means to the ends" of achieving the fundamental objectives. A comprehensive list of fundamental and means objectives was created and then

distilled into a more concise list. The Workgroup developed performance metrics for the refined list of fundamental objectives.

EMO Workshop Fundamental Management Objectives and Performance Measures

Fundamental Objectives	Performance Measures
Achieve broad public support for management	- Unanimous vote of the Atlantic Menhaden Management Board - Positive press releases from all stakeholders - "Informed consent" or acknowledgement that the decisions made were "fair and reasonable" - Participation in the fishery benefits - Absence of legal action - Strong compliance with management measures
Sustain menhaden to provide for fisheries	- Meeting or exceeding (positively) reference points - Non-truncated age distribution - Historical distribution maintained - Avoid unintended economic consequences of management - Employment in fishery - Achieving yield objectives for all fisheries - Achieving abundances that exceed "depleted" status - Reduce regulatory discards
Sustain menhaden to provide for predators	- Same as for fishery, assuming reference points are ecological reference points - Predators in a healthy nutritional state - Distribution of menhaden related to predator requirements (prey availability)
Sustain menhaden to provide for historical and cultural values	- Maintaining "historical" (meaning existing and recent past infrastructure rather than distant past) patterns of employment (spatial, demographic, gear use, etc.)
Sustain menhaden to provide for ecosystem services	- Same as above; represented in the other menhaden "services"
Minimize risk to sustainability due to changing environment	- Analysis would explicitly consider uncertainty about future environmental conditions
Provide stability for all types of fisheries	- Variability for employment and yield - Frequency of substantive management action
Sustain ecosystem resiliency or stability	- Covered by metrics above; if successful in providing for a viable fishery and other food web components that are related to menhaden

The EMO Workgroup also developed the following list of means objectives, which support achieving the fundamental objectives:

- Science
    - Increase knowledge base
    - Better communication of science
    - Account for variation
- Management
    - Define clear objectives
    - Provide timely advice
- Ecosystem
    - Ensure adequate supply of menhaden for:
        - Individual predator groups
        - Food web as a whole
- Account for spatial/temporal variation when using trade-offs
- Minimize the risks of collapse for:
    - Menhaden – the metric of collapse would be a certain level of biomass or fecundity relative to unfished spawning stock biomass or fecundity
    - Fishery – the metric for fishery collapse would depend on the fishery; it would indicate that the fishery is no longer economically viable to fish
    - Irreversible ecosystem change – changes to the food web such that it would not recover to a previous state even with the relaxation of fishing pressure

1.5 Model Selection

As part of the 2015 Benchmark Stock Assessment for Atlantic Menhaden, the ERP WG presented a suite of preliminary ERP models and ecosystem monitoring approaches for feedback (SEDAR 2015). The ERP WG used the peer review recommendations from that assessment and the outcomes of the EMO Workshop to assess the ability of various ERP models to address management objectives and performance measures. The ERP WG focused on those fundamental objectives and performance measures that could be addressed using ecological models. Some objectives, such as "sustain Atlantic menhaden to provide for historical and cultural values" or "achieve broad public support for management," fell outside the purview of the ERP WG. Table 1 summarizes the fundamental objectives and associated performance measures that each ERP model can address.

To best address the management objectives identified at the EMO Workshop (Table 1), the approach selected needed to:

- explicitly examine the trade-off between fishery removal of menhaden and resulting changes in biomass or abundance among important predators;
- provide quantitative and understandable advice on removal levels of Atlantic menhaden under various predator biomass or fishing levels;
- examine the implications and consequences of Atlantic menhaden harvest strategy on important predators, either through predator growth rates and condition or mortality rates;
- be updatable on a timeframe consistent with Atlantic menhaden management.

Approaches were then selected based on: (1) the ability to address multiple management objectives; (2) the ability to predict and monitor performance measures in response to management action; (3) technical merits; and (4) consistency with the advice from the 2015 Peer Review.

Based on this evaluation, the ERP WG placed emphasis on models of intermediate complexity (a multispecies statistical catch-at-age model and an Ecopath with Ecosim model with limited predator and prey components) in developing ecological reference points. However, more complex (a full Ecopath with Ecosim model) and simpler (a Steele-Henderson surplus production model and a surplus production model with time-varying *r*) models were also developed, in order to provide context for the results of the intermediate complexity models and evaluate the tradeoffs between model assumptions, data availability, and the ability to meet management objectives.

In the end, the intermediate complexity Ecopath with Ecosim model was best able to meet the ecosystem management objectives in a timeframe suitable for management, while providing information consistent with the more complex model.

2 ASSESSMENT HISTORY

2.1 Previous Stock Assessments

Since the stock assessment peer review process was adopted by the ASFMC in 1998, Atlantic menhaden have been assessed several times as a single species (ASMFC 1999, 2004, 2010, 2012b; SEDAR 2015; ASMFC 2017b). The most recent peer-reviewed benchmark stock assessment was SEDAR 2015, which was updated in 2017.

Explicit multispecies considerations have been a part of the single-species assessments since 2004. To better quantify the effects of predation on Atlantic menhaden the single-species assessments in 2004 and 2010 used the *M*-at-age estimates from MSVPA as input to the single-species model. Issues with MSVPA model performance and the effort to develop explicit ecological reference point models resulted in moving away from the time-varying *M*-at-age to a time-constant *M*-at-age in the 2015 assessment (SEDAR 2015). The process of developing ecological reference points for Atlantic menhaden began as part of the 2015 single-species assessment, but the work was not ready to be peer-reviewed at that time.

2.2 Summary of Previous Assessment Models

The Beaufort Assessment Model (BAM) was used to provide management advice during the 2015 benchmark stock assessment (SEDAR 2015) and the 2017 update. BAM is a statistical catch-at-age model that estimates population size-at-age and recruitment, using 1955 as the start year, and then projects the population forward in time. The model estimates trends in the population, including abundance-at-age, recruitment, spawning stock biomass, egg production, and fishing mortality rates. BAM was configured to be a fleets-as-areas model with each of the fleets broken into areas to reflect differences along the coast. This means that both reduction

and bait fleets were split into north and south regions because the fisheries operated differently along the coast and through time.

In 2001, ASMFC began developing the Expanded Multispecies Virtual Population Analysis model (MSVPA-X), an extension of the ICES MSVPA, which was peer-reviewed in 2006 (NEFSC 2006, Garrison et al. 2010). The MSVPA-X model, like the original MSVPA, was a set of single-species VPA models that were linked by a feeding model, which allowed for the calculation of M_2, predation mortality on Atlantic menhaden. The extended version allowed for the use of tuning indices and improved the consumption, feeding, and size-selectivity models. The MSVPA-X model explicitly modeled Atlantic menhaden, striped bass, bluefish, and weakfish, and included a pool of "other prey", which could be broken down into more specific groups if necessary.

The MSVPA-X was intended to better quantify predator and prey interactions and to account for these effects on Atlantic menhaden, specifically through the development of time-varying *M* estimates for use in single-species assessments. It was not intended to replace the single-species assessments, set reference points, or set harvest limits for the modeled species, but rather to inform the single species assessment for Atlantic menhaden. Estimates of *M* for Atlantic menhaden from the MSVPA-X were used in BAM for the 2004 and 2010 assessments. The MSVPA-X was updated for the 2015 assessment, but the estimates of *M* were not used in the base run of BAM. This was due to concerns about the MSVPA-X performance (SEDAR 2015) not matching the biomass trajectory of important predators. More importantly, the MSVPA-X could not match the trajectory of BAM biomass estimates with the more complex and detailed BAM parameterization and was sensitive to small changes in predator/prey overlap and prey preference parameters. The uncertainty from the MSVPA-X was used to set the scale of the uncertainty surrounding *M* in the Monte Carlo bootstrap runs done for the base run. The resulting *M*-at-age from the MSVPA-X was also used as a sensitivity analysis during the 2015 benchmark for the single species assessment.

The 2015 assessment also began work on the task of developing ecological reference points for Atlantic menhaden. A suite of ERP and ecosystem monitoring approaches were identified and characterized by the timeframe for completion, the type of ERPs they would provide, and what management objectives they would meet. The 2015 Peer Review Panel recommended: 1) fully engaging managers and stakeholders in a Management Strategy Evaluation process, and 2) placing emphasis on models of intermediate complexity as potential tools for examining trade-off among predators and prey. The 2015 assessment and the EMO Workshop report (Section 1.4) formed the basis of the 2019 ERP Assessment.

It is important to note that all the approaches examined were based on the unit stocks for both predators and prey. While regional approaches are possible, both data needs and the desire to provide stock-level advice for Atlantic menhaden made regional approaches unviable at this time. Rates of production, fishery removals, predator removals, and changes in predator/prey abundance can be different at the regional level than the dynamics on a stock-wide scale. Despite this and given the above constraints, the methods and approaches developed provide management advice on a stock-wide level only.

2.3 Biological Reference Points

Atlantic menhaden are currently managed with single-species reference points, based on the historical performance of the population during 1960 to 2012, a period during which the Technical Committee (TC) considers the population to have been sustainably fished. The F_{TARGET} is defined as the median geometric mean *F* on ages 2-4 from 1960-2012, and the $F_{THRESHOLD}$ is the maximum geometric mean *F* for ages 2-4 during that period. To determine overfished status, a fecundity target and threshold are used (rather than a spawning stock biomass target and threshold). The fecundity target and threshold are defined as the mature egg production one would expect when the population is being fished at the target or threshold fishing mortality rates, respectively. Based on the assessment update (ASMFC 2017), Atlantic menhaden were neither overfished nor experiencing overfishing under these reference points.

After the 2015 assessment, ASMFC considered using interim ecological reference points for Atlantic menhaden until this assessment could be completed. These interim reference points would have been based on generic or "rule-of-thumb" guidelines proposed in the literature such as a biomass target of 75% unfished biomass (Smith et al. 2011) or *F*=50%*M* (Pikitch et al. 2012). In the end, the Board decided not to change the definitions of the reference points until Atlantic menhaden specific ERPs could be developed, and instead applied an *ad hoc* buffer to the quota, setting the TAC lower than what the single-species target *F* rate would have allowed (ASMFC 2017b).

3 PREDATOR AND PREY SPECIES

3.1.1 Diet Data Sources

The ERP WG examined a range of diet datasets, from large-scale, long-term monitoring programs to individual small-scale studies. The proportion of Atlantic menhaden in the diets of key predators varied by year, season, location, and age class of predators sampled, making the selection of diet data sources important in model parameterization.

Fish stomach-content data were obtained from three main sources: the Northeast Fisheries Science Center (NEFSC) Food Web Dynamics Program, the North East Area Monitoring and Assessment Program (NEAMAP), and Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP). The NEFSC program has systematically sampled predator food habits since 1973 (Link and Almeida 2000). The food-habits data are structured by predator species and length, but prey lengths and ages are not routinely measured. A subset of the database is structured by both predator and prey lengths, which was used for part of the following analyses. NEAMAP and ChesMMAP also collect stomach-content data under similar protocols to the NEFSC program; NEAMAP has collected data since 2008 and ChesMMAP since 2002. These data were used to supplement the stomach-content data and have an added benefit of increasing the coastal area covered for this dataset (NEAMAP and ChesMMAP sample areas further inshore than the NEFSC sampling program).

Both datasets have strengths (e.g., the NEFSC data has a long time-series and the NEAMAP data are more inshore so is better able to acquire many of the species used in this study) and weaknesses (e.g., the NEFSC data are from further offshore and the NEAMAP data timeseries is short) but taken together they offer a fairly comprehensive snapshot of the populations. However, sample sizes often precluded analyses on finer spatial or temporal scales. These databases focused on finfish and shellfish species, not birds or marine mammals. Smaller scale studies were used to supplement the data from these long-term programs for some of the modeling approaches, especially for species that were not well represented in the long-term programs.

3.1.2 Identification of Key Predator and Prey Species

Two of the ERP models presented in this report are models of intermediate complexity, which focus on a limited number of key predator and prey species. To identify this suite of key predator and prey species, the ERP WG considered a number of factors, including: the importance of a species' role as a Atlantic menhaden consumer (as indicated by the diet data), the importance of a species' role as an alternative prey to Atlantic menhaden (as indicated by the diet data), the quality and availability of life history and fishery data for the species, and the relevance of the species to ASMFC management.

Predator Species

Diet data were used to identify key predators during the last benchmark assessment as part of the update to the MSVPA-X (SEDAR 2015). The methods and conclusions from that assessment were reviewed by the ERP WG and used to inform the choice of key predators used in this assessment. The NEFSC Food Habits Database (FHDB) (1981-2012) was queried for all species with Atlantic menhaden recorded in their gut contents. Only twelve species had records of Atlantic menhaden in their gut contents: striped bass, bluefish, spiny dogfish, weakfish, smooth dogfish, spiny butterfly ray, clearnose skate, goosefish, Atlantic angel shark, dusky shark, sandbar shark, and Atlantic herring. Of the twelve predators whose diets contained Atlantic menhaden, there were some notable outliers, such as Atlantic herring, which does not typically feed on Atlantic menhaden, and spiny butterfly ray, which had one individual stomach that contained 86% of the total prey weight for that species and 100% of that stomach was Atlantic menhaden. The ERP WG decided to remove these outliers from the list of key predators, along with Atlantic angel shark, dusky shark, and sandbar shark, all of which had less than 50 stomachs sampled throughout the entire time series (the next lowest sample number of stomachs was about 800; species with notably fewer samples would not provide an accurate representation of diets when compared to the rest of the data available). The remaining predators were considered by the group for inclusion into the models.

The annual Atlantic menhaden consumption (C) of each predator was estimated using the methodology from Butler et al. (2009), defined as:

$$C = B \times P \times DR \times W \times T \quad (3.1)$$

Where:

B = Biomass of predators (B) calculated from scaled up swept area biomasses from the NEFSC Survey 1981-2012. This calculation assumed that catchability is equal to 1.0 and that the survey covers the inshore and offshore extent of each species' range.

P = the proportion of each predator stock in the model domain calculated using swept area biomass from the NEFSC Survey and scaled up to the full range of the species to estimate total biomass. For offshore strata, a GIS program was used to pare out tows that were offshore of the model domain. All strata with at least one tow in the model domain were then divided by the total tows conducted in that stratum to get the proportion of tows in that domain. Model domain biomass divided by expanded total biomass by range was calculated to get the proportion of each predator in the model domain.

DR = Daily ration (in kg prey per kg predator per day) generated using direct estimates from literature and calculations using parameters from the literature. Direct estimates for similar species or overall average of other species that were not as similar were used when necessary.

W = the proportion of total prey in weight that is Atlantic menhaden generated using data from the NEFSC FHDB, ChesMMAP survey, and NEAMAP survey.

T = the portion of the year (in days) that predator and prey are both in the model domain calculated using the NJ Ocean Trawl Survey. It was assumed Atlantic menhaden were always present somewhere in the model domain throughout the year. The NJ Ocean Trawl Survey catches all predators, so it was used as a proxy of when predators were in the model domain. Only 2% of the stations fell outside domain so all of them were used. The average biomass per season across years 1990-2012 was used to calculate when predators were present in the domain. All proportions were standardized to 1.0 then divided by the maximum. The NJ Ocean Trawl Survey occurs 5 months out of each year so biomass for months in which sampling did not occur was linearly interpolated based on the closest surrounding months' biomass. For any month with less than 1% of the max, the predator was assumed not present. Time (days) in the model domain was then finally calculated from months where the predator was present in the model domain.

Spiny dogfish, striped bass, and bluefish had the highest Atlantic menhaden consumption (Table 2). In addition, those species also had reliable data on catch and indices of abundance, as well as recently updated assessments with estimates of biomass and fishing mortality from peer-reviewed stock assessments. All three are managed either solely (striped bass) or cooperatively (spiny dogfish and bluefish) by the Commission, so providing quantitative information on these species would be relevant to management. All three of these predators were included in the group of key predators.

Weakfish and smooth dogfish alternated between the fourth and fifth most important Atlantic menhaden predator, depending on the ranking system, but weakfish more consistently ranked as the fourth. The ERP WG debated including smooth dogfish and/or weakfish given their relatively low menhaden consumption rates compared to the top three predator species. The ERP WG decided not to include smooth dogfish because of data availability challenges, including the lack of age data to support an age-structured model. The ERP WG decided to include weakfish due to the decline in population through the years which could provide important contrast, given that it is the only one of the predator species that has shown significant declines in population size over the time series. Predation mortality and/or increased competition for Atlantic menhaden from striped bass have been proposed as a factor in weakfish population declines (NEFSC 2009). Weakfish also had more robust data to support modeling efforts, and are solely managed by the Commission, so information on the ecosystem effects of Atlantic menhaden fishing on weakfish would be more relevant to management.

Marine Mammals

Overall lack of data and taxonomic resolution in marine mammal diet data limits incorporation of marine mammals as predators for multispecies/food web/ecosystem models of Atlantic menhaden. A paper by Smith et al. (2015) is the only broad, systematic review of marine mammal diets (i.e., consumption rates) for the US Atlantic Coast; note that it also includes some studies outside of the area. The paper develops annual consumption rates of marine mammals on key marine species. In the paper, marine mammal diet compositions were allocated to 12 standard prey groups of similar taxonomy (squid, mesopelagic fish, clupeids, scombrids, small gadids, large gadids, shrimp, zooplankton, benthic invertebrates, sandlance, flatfish, and miscellaneous fish). Because the data for diet composition were from a wide array of references using multiple sampling types (mostly scat and stomach analysis from bycaught and stranded animals), finer taxonomic resolution was not possible for this systematic review of marine mammal diets that included ~110 papers and reports. A literature review in web of science showed no additional research papers (from 2008-2018) with information on Atlantic menhaden in marine mammal diets. Of the 110 articles reviewed by Smith et al. (2015), only 3 studies specifically identified Atlantic menhaden in the diet. All 3 studies were on bottlenose dolphin. Bottlenose dolphin are the only species of marine mammal with adequate taxonomic resolution in the diet data to support inclusion of dolphins as a predator in a multi-species model; however, the proportion of Atlantic menhaden in bottlenose dolphin diets (4% or less) suggests that they are not important predators of Atlantic menhaden.

Prey Species

The key ERP predators identified here are generalists, consuming a wide range of other prey items in addition to Atlantic menhaden. The ERP models of intermediate complexity include a pool of "other prey biomass," but also allow for the modeling of other, specific prey species in addition to Atlantic menhaden. To identify an additional key prey species to be modeled explicitly, the ERP WG used similar criteria to what was used for key predator identification. Atlantic herring was chosen as an alternate prey species because it was a major component of the diets of the key predators. In addition, unlike several other prey species – such as bay anchovy, sand eels, and benthic invertebrates – Atlantic herring was recently assessed with an

age-structured model. As a result, reliable catch data, indices of abundance, age structure, biomass, and fishing mortality were available.

4 LIFE HISTORY

4.1 Atlantic Menhaden

See the single-species benchmark stock assessment for a more thorough discussion of Atlantic menhaden life history. Sections from that assessment have been abbreviated below.

Stock Definitions

Atlantic menhaden inhabit nearshore and inland tidal waters from Florida to Nova Scotia, Canada. Atlantic menhaden are considered a single stock. Historically there was considerable debate relative to stock structure of Atlantic menhaden on the US East Coast, with a northern and southern stock hypothesized based on meristics and morphometrics (Sutherland 1963; June 1965). Based on size-frequency information and tagging studies (Nicholson 1972 and 1978; Dryfoos et al. 1973), the Atlantic menhaden resource is believed to consist of a single unit stock or population. Genetic studies (Anderson 2007; Lynch et al. 2010) support the single stock hypothesis.

Migration Patterns

There have been several studies examining Atlantic menhaden migration patterns (Roithmayr 1963; Dryfoos et al. 1973; Nicholson 1978; ASMFC 2004). Adults begin migrating inshore and north in early spring following the end of the major spawning season off the Carolinas during December-February. The oldest and largest fish migrate farthest, reaching southern New England by May and the Gulf of Maine by June. Adults that remain in the south Atlantic region for spring and summer migrate south later in the year, reaching northern Florida by fall. In the fall, Atlantic menhaden begin a migration to the Carolinas and spawn as a population in the winter months, although spawning occurs along the migration route earlier in the year (Ahrenholz 1991; Berrien and Sibunka 1999).

Historical tagging data from 1966-1969 was recently reanalyzed by Liljestrand et al. (2019a, 2019b), which indicated that while the pattern of Atlantic menhaden's movement was similar to previous findings, the magnitude of movement during the winter in the northern region differed. For example, previous literature (Roithmayr 1963; Nicholson 1971) stated that the majority of Atlantic menhaden in the north migrate south to overwinter in North Carolina whereas Liljestrand et al. suggested about 55% of Atlantic menhaden in the northern region migrates southward. Therefore, there may be less southward movement of Atlantic menhaden in the winter than previously described by the literature and more residency in the northern area throughout the year.

Age and Growth

In 1955, the NOAA Laboratory at Beaufort, North Carolina, began monitoring the Atlantic menhaden purse-seine fishery for size and age composition of the catch (June and Reintjes 1959). Scales were selected as the ageing tool of choice for Atlantic menhaden due to ease of

processing and reading and an age validation study confirming reliable age marks on scales (June and Roithmayer 1960). The Beaufort lab to date still ages all the reduction and bait fishery samples. The maximum age used in this assessment is 10 years, although Atlantic menhaden over age 6 are rarely found in the fisheries.

In the single-species assessment, a time-invariant relationship for length-weight was used. Annual estimates of fork length-at-age were interpolated from the annual, cohort-based von Bertalanffy growth fits with a bias correction in order to represent the population at the start of the fishing year (March 1) for use in estimating population fecundity. Age-6 fish average around 375 mm in fork length and 600 grams in weight over the time series.

Maturity and Fecundity

Using data from the NEAMAP Southern New England/Mid-Atlantic Nearshore Trawl Survey to evaluate maturity-at-age, it was determined that maturity is a length-based process as opposed to an age-based process. A logistic regression was fit to the maturity and length data from the commercial reduction fishery database. Time-varying lengths-at-age for the population were used along with the logistic regression to provide time-varying maturity at age for 1955-2017 for the single-species assessment. Generally, 5-15% of age-1 fish were mature, approximately 50% were mature by age-2, and 95-100% were mature by age-5 (Figure 1).

Since SEDAR 40 (2015), work has been completed by VIMS (R. Latour and J. Gartland, unpublished data) to address a single-species research recommendation and update fecundity values for use in BAM. Based on the analysis of the study, Latour and Gartland concluded that Atlantic menhaden are indeterminate batch spawners. Additionally, estimates of age-specific annual fecundity for Atlantic menhaden spanning age-0 to age-6+ were provided for SEDAR 69 (2019). Female fecundity-at-age for each year was fixed in BAM and was based on a function of mean weight by age for the population. The annual fecundity-at-age in year *i* (AF_{ai}) was estimated as:

$$AF_{ai} = RBF * WT_{ai} * SF * PM_{ai} \quad (4.1)$$

where *RBF* (relative batch fecundity) was 236.92 eggs/g ovary-free body weight, *SF* (spawning frequency) was 11.70 spawns/season, and where WT_{ai} (weight-at-age) and PM_{ai} (maturity-at-age) were the weight-at-age *a* and proportion of fish mature at age *a* for a given *i* at the start of the fishing year (i.e., March 1). The updated fecundity values from Latour and Gartland resulted in higher estimated fecundity from SEDAR 2015. Refer to the single-species assessment Section 2.6 and Appendix 14.1 for more details.

Natural Mortality

In the previous Atlantic menhaden stock assessment (SEDAR 2015), *M* was determined using the method of Lorenzen (1996), which was scaled to an historical analysis done on historical tagging data. Since SEDAR 40 (2015), the historical tagging data have been digitized and a new analysis was conducted by Liljestrand et al. (2019a, 2019b), which provided updated values. The new analysis uses methods that were not available during the original collection of the data set.

For the 2019 single-species benchmark assessment (SEDAR), several methods for estimating *M* were explored, including several age-constant *M* estimates and age-varying *M* approaches. Ultimately, an age-varying but time-invariant approach using the methods of Lorenzen (1996) and scaled to the new tagging estimates from Liljestrand (2019a, 2019b) was used. This resulted in estimates of *M* ranging from 1.76 for age-0 fish to 0.72 for age-6 fish (Figure 1). See SEDAR 69 (2019) for further details.

Habitat

Estuarine and nearshore waters along the Atlantic coast from Florida to Nova Scotia serve as important habitat for juvenile and/or adult Atlantic menhaden. Adult Atlantic menhaden spawn in oceanic waters along the continental shelf, as well as in sounds and bays in the northern extent of their range. Winds and tides transport larvae shoreward from the shelf toward nursery grounds in the estuaries. After hatching from buoyant eggs, the larvae are transported by ocean currents to fresh and brackish-water estuaries where much of the early development takes place. Juvenile habitat is unconsolidated bottom consisting mostly of sand and mud, with various mixtures of organic material. In more northerly areas, juveniles can be found in rocky coves, with mixtures of cobble, rock, and sand bottoms. Sub-adult habitat is found in temperate, nearshore marine and estuarine areas that have a bottom composition of sand and mud, and more organic material than in marine areas. Adult habitat ranges from a bottom composition of sand, mud, and organic material to marine sand and mud with increasing amounts of rocks in the more northerly areas. Adults appear to prefer water temperatures near 18°C; adult migrations and movement may be attributed to seeking waters within a certain temperature range.

4.2 Atlantic Herring

Stock Definitions

Atlantic herring (*Clupea harengus*) is a schooling pelagic clupeid which ranges from North Carolina to Labrador in the Western Atlantic. In US waters the Georges bank-Gulf of Maine stock are fall spawners that range from NC through the Gulf of Maine (GOM) and out to Georges Bank (GB). There are two main spawning components for this meta-stock, one centered on GB, and the other in coastal portions of the GOM (Shepard et al. 2009; NEFSC 2012; NEFSC 2018a).

Migration Patterns

When not spawning, these sub-components intermingle in the summertime along the Maine coast with the GB component located both in the inshore GOM and offshore on GB. Sometime after spawning in their respective areas, both sub-components travel south to overwinter from Block Island Sound to the Virginia Capes. Return migration back to their summertime feeding grounds occurs in early to mid-spring. There is thought to be some mixing between the GOM-GB stock and the adjacent Canadian 4WX stock. While the rate of mixing is unknown, the magnitude is thought to be rather small (NEFSC 2018).

Age and Growth

Life span is generally thought to be 14 years for Atlantic herring in the absence of fishing (NEFSC 2018). The average size-at-age of Atlantic herring has declined over time, most notably for older ages; the average weight at age of an age-8 fish from 1965-1986 was 0.35 kg, while the average weight at age of an age-8 fish from 1995-2017 was 0.2 kg. The time-series average was 0.28 kg (Figure 2).

Maturity and Fecundity

Atlantic herring are 65% mature at age-3, 90% by age-4 and 100% mature by age-5 (Figure 2; NEFSC 2018a). Atlantic herring lay sticky sinking eggs over gravel or sand in shallow portions of the GOM and GB in the fall with larval settlement and recruitment to Age 1 occurring in the early spring. As such the birthdate for all cohorts occurs January 1st in any given year (NEFSC 2018a).

Natural Mortality

Atlantic herring are important prey items for a variety of fish, birds, mammals, and other predators (NEFSC 2018a). Some of these predators, such as striped bass and bluefish, are also important predators of menhaden. Despite this, the most recent assessment for Atlantic herring assumed a 0.35 natural mortality static across age and year based largely on model diagnostics and a lack of change in consumption by important predators (Figure 2) (NEFSC 2018a).

Habitat

Atlantic herring are a pelagic species found in the open ocean, but the benthic zone is especially important for their reproduction. In U.S. waters, herring spawn mainly in two areas: the Gulf of Maine and Georges Bank/Nantucket Shoals. Spawning grounds are located in high-energy environments with strong tidal currents and high salinity. Eggs require water temperatures ranging from 7 to 15°C and depths from 5 to 90 m, and will not survive if covered by mud or fine sand.

Larvae have been observed in depths up to 1,500 m, but are generally found in depths in the 41 to 220 m range and temperatures below 12.5°C in the Gulf of Maine, Georges Bank, and southern New England. Juveniles are commonly found in waters with temperatures from 2.5 to 14.5°C, depths between 4-300 m, and salinities ranging from 20 to 32 ppt. Adults occupy the same geographic range and similar habitats as juveniles, but typically prefer more saline (> 28 ppt) waters.

4.3 Striped Bass

Stock Definitions

Atlantic striped bass (*Morone saxatilis*) are found along the eastern coast of North America from the St. Lawrence River in Canada to the St. Johns River in Florida (ASMFC 1990). Atlantic striped bass are anadromous, returning to their natal rivers to spawn. As a result, the Atlantic striped bass population includes multiple biologically distinct stocks. Stocks which occupy coastal rivers from the Albermarle Sound/Roanoke River system in North Carolina south to the St. Johns River in Florida are believed to be primarily endemic and riverine, as historical tagging

data suggest they do not presently undertake extensive Atlantic Ocean migrations as the more northern stocks do.

The habitat of the coastal migratory striped bass population includes the coastal and estuarine areas from Maine through Virginia and the coastal waters of North Carolina. The coastal migratory striped bass population is assessed and managed as a single stock, although it is known to be comprised of multiple biologically distinct stocks, predominantly the Chesapeake Bay stock, the Delaware Bay stock, and the Hudson River stock.

Migration Patterns

Atlantic migratory striped bass exhibit two types of migration: a spawning migration in late winter to early spring where mature adults move from ocean waters to the spawning grounds at the heads of estuaries and in their tributaries (Shepherd 2007; Zurlo 2014), and a north-south migration in coastal ocean waters during the rest of the year, with fish moving northward into New England and Gulf of Maine waters during the summer and southward to waters off of Virginia and North Carolina during the winter (Kneebone et al. 2014). Juveniles remain in their natal estuaries until they are about three years old, when they begin to leave the estuaries and join the coastal migratory population (Nichols and Miller 1967). The extent of the migration that individual striped bass undertake varies depending on the sex, size, and stock of the fish (Hill et al. 1989; Secor and Piccoli 2007; Callihan et al. 2014).

Age and Growth

Generally, longevity of striped bass has been estimated as approximately 30 years, with a maximum observed age of 31 years based on otoliths (Secor 2000). Striped bass are capable of attaining moderately large size, reaching as much as 125 pounds (57 kg) (Tresselt 1952), and fish weighing 50-60 pounds (23-27 kg) are not exceptional (Figure 3). Growth rates and maximum size are significantly different for males and females. Both sexes grow at the same rate until 3 years old; beginning at age-4, females grow faster than males. Females grow to a considerably larger size than males; striped bass over about 30 pounds (14 kg) are almost exclusively female (Bigelow and Schroeder 1953).

Maturity and Fecundity

Female striped bass begin to mature at age-4. They are 45% mature by age-6 and 100% mature by age-9 (Figure 3; NEFSC 2019). Males mature at younger ages, reaching 100% maturity by age-4 (NEFSC 2013).

The number of mature ova in female striped bass varies by age, weight, and fork length. Jackson and Tiller (1952) found that fish from Chesapeake Bay produced from 62,000 to 112,000 eggs/pound of body weight, with older fish producing more eggs than younger fish. Raney (1952) observed egg production varying with size, with a 3-pound (1.4 kg) female producing 14,000 eggs and a 50-pound (23 kg) specimen producing nearly 5,000,000.

Natural Mortality

Striped bass are a long-lived species, suggesting natural mortality is relatively low. In the 2013 benchmark assessment, age-specific *M* estimates for ages 1-6 were derived from a curvilinear model fitted to tag-based *Z* estimates (assuming *Z*=*M*) for fish younger than age 3 from New York and tag-based *M* estimates (Jiang et al. 2007) for age 3-6 striped bass from Maryland calculated for years prior to 1997 (NEFSC 2013). This resulted in a maximum *M*-at-age of 1.13 for age 1 fish declining to *M*=0.19 for age-6 fish (Figure 3). *M* for ages 7+ was assumed equal to 0.15, consistent with Hoenig's (1983) regression on maximum age.

An increasing prevalence of mycobacteriosis in the Chesapeake Bay since 1997 could be causing increases in natural mortality (Ottinger and Jacobs 2006). Although fish who are infected with the disease show overall decreased health (Overton et al. 2003), the slow progression of the disease may take years to become lethal in infected fish, thus allowing for multiple spawning opportunities, making determination of the population level impacts of the disease difficult (Jacobs et al. 2009). Various hypotheses have been put forward to explain the increasing prevalence of mycobacteriosis, including lack of forage and increasing water temperatures in Chesapeake Bay (Jacobs et al. 2009).

Habitat

Atlantic striped bass move between a variety of habitats in their life cycle. Generally, spawning and early development occurs at the heads of estuaries and in their tributaries, fish mature in estuaries, and move into the ocean as adults. Habitat selection and migratory behavior in striped bass is influenced by temperature and photoperiod (Able and Grothues 2007; Wingate and Secor 2007; O'Connor et al. 2012; Manderson et al. 2014). Striped bass are not usually found more than 6 to 8 km offshore (Bain and Bain 1982). Fishery-independent and fishery-dependent data suggest striped bass distribution on their overwintering grounds during December through February has changed significantly since the mid-2000s, with the migratory portion of the stocks moving well offshore in the U.S. Exclusive Economic Zone (EEZ, >3 miles offshore) (NEFSC 2018).

4.4 Bluefish

Stock Definitions

Bluefish (*Pomatomus saltatrix*) are a coastal, pelagic species found in temperate and tropical marine waters throughout the world (Goodbred and Graves 1996; Juanes et al. 1996). Bluefish in the western North Atlantic are managed as a single stock (NEFSC 1997; Shepherd and Packer 2006). Genetic data support a unit stock hypothesis (Graves et al. 1992; Goodbred and Graves 1996; Davidson 2002). The management unit is defined as the portion of the stock occurring along the Atlantic Coast from Maine to the east coast of Florida.

Migration Patterns

Bluefish spawn offshore, and juveniles settle in estuarine and nearshore shelf habitat (Kendall and Naplin 1981; Marks and Conover 1993; Able et al. 2003). Traveling in loose groups of fish aggregated by size, bluefish typically migrate north as far as Maine in the spring/summer and south as far as Florida in the fall/winter (Wilk 1977; Klein-MacPhee 2002; Shepherd et al. 2006).

Age and Growth

The maximum observed age for bluefish is 14 years (NEFSC 2015). Bluefish grow nearly one-third of their maximum length in their first year (Richards 1976; Wilk 1977). Estimates of L_∞ from the literature range from 87 cm – 128 cm (Lassiter 1962; Barger 1990; Terceiro and Ross 1993; Salerno et al. 2001; Robillard et al. 2009). Bluefish average weight is 5-6 kg at ages 6+ (Figure 4). There is no evidence of sexual dimorphism in growth.

Maturity and Fecundity

Bluefish mature quickly, with approximately half of the population mature at age-1 and close to one hundred percent mature (97%) by age-2 (Figure 4; NEFSC 2015). Bluefish are characterized as iteroparous spawners with indeterminate fecundity and spawn continuously during their migration (Robillard et al. 2008). This results in distinctive spring and summer cohorts within a year.

Natural Mortality

In past stock assessments, a value of 0.2 has been assumed as the instantaneous natural mortality (*M*) for bluefish over all ages and years (Figure 4; NEFSC 2015). This is in the range of estimates from age-constant methods based on maximum age or growth parameters such as Hoenig (1983), Jensen (1996), Hewitt and Hoenig (2005), and Then et al. (2014).

Habitat

Bluefish larvae occur near the edge of the continental shelf in the south Atlantic Bight, in open oceanic waters in the mid-Atlantic Bight, and over mid-shelf depths farther north (Shepherd and Packer 2006). Spring-spawned larvae are subject to advection to northern waters by the Gulf Stream (Shepherd and Packer 2006). Adult and juvenile bluefish are found primarily in waters less than 20m deep along the Atlantic coast (Shepherd and Packer 2006). Adults use both inshore and offshore areas of the coast and favor warmer water temperatures although they are found in a variety of hydrographic environments (Ross 1991; Shepherd and Packer 2006). Bluefish can tolerate temperatures ranging from 11.8°-30.4°C, however they exhibit stress, such as an increase in swimming speed, at both extremes (Olla and Studholme 1971; Klein-MacPhee 2002). Temperature and photoperiod are the principal factors directing activity, migrations, and distribution of adult bluefish (Olla and Studholme 1971).

4.5 Spiny Dogfish

Stock Definitions

Spiny dogfish (*Squalus acanthias*) are a small shark species that inhabit both sides of the North Atlantic and North Pacific Oceans, mostly in the temperate and subarctic areas. Spiny dogfish are considered a unit stock in the Northwest Atlantic Ocean (US and Canadian waters), ranging from Labrador to Florida, and are most abundant from Nova Scotia to Cape Hatteras (Rago et al. 1998).

Migration Patterns

Spiny dogfish are highly migratory (Compagno 1984) and migrate north in the spring and summer and south in the fall and winter. In the winter and spring, they congregate primarily in

Mid-Atlantic waters but also extend onto the shelf break of southern Georges Bank. In the summer, they are located farther north in Canadian waters and move inshore into bays and estuaries. By autumn, spiny dogfish have migrated north with high concentrations in Southern New England, on Georges Bank, and in the Gulf of Maine. They remain in northern waters throughout autumn until water temperatures begin to cool and then return to the Mid-Atlantic. Juvenile spiny dogfish school by size until sexually mature and then aggregate by both size and sex.

Age and Growth

Spiny dogfish are long-lived. The maximum recorded age for this species was 35 years for males and 40 years for females in the northwest Atlantic (Nammack et al. 1985). Female spiny dogfish are larger than males and can reach up to 125 cm in length (NEFSC 2006). L_∞ has been estimated at 100.5 cm for females (Nammack et al. 1985), corresponding to a weight of 5 kg at the oldest ages (Figure 5).

Maturity and Fecundity

Spiny dogfish mature late and have low fecundity. Female spiny dogfish reach sexual maturity at 12 years (~75 cm) (Figure 5), while males reach sexual maturity at six years (~60 cm). Mating occurs in the winter months and the pups are delivered on the offshore wintering grounds. Females give birth every two years with litters ranging from 2 to 15 pups. While carrying one litter, the female will begin developing eggs for the fertilization of her next litter. After an 18- to 24-month gestation period, pups are released live and fully formed at about 20-33 cm (Burgess 2002).

Natural Mortality

Natural mortality for spiny dogfish has been estimated at 0.092, based on a maximum expected age of 50 years (Rago et al. 1998) (Figure 5).

Habitat

Spiny dogfish are predominately epibenthic species, with no known associations to any particular substrate, submerged aquatic vegetation, or any other structural habitat (McMillan and Morse 1999). Data from fishery independent surveys can be used to define habitat based on water temperature and depth on the Atlantic coast. Juvenile and adult spiny dogfish showed similar patterns in habitat preference. Both life stages are most commonly caught in waters with bottom temperature ranges from 6-17^{o}C, and bottom depth ranges from 10m – 150m (ASMFC 2002).

4.6 Weakfish

Stock Definitions

Weakfish (*Cynoscion regalis*) can be found along the Atlantic coast from Florida through Massachusetts, but the core of their distribution is from North Carolina to New York. Genetic data suggest weakfish are a single stock (Graves et al. 1992; Cordes and Graves 2003), but tagging data and meristic/life history information suggest there may be spatial structure or sub-stock

structure in the population (Crawford et al. 1988). However, since stock boundaries could not be determined with confidence from the available literature, weakfish continued to be assessed and managed as a single species within this range (ASMFC 2016). Tringali et al. (2011) found that there was an active zone of introgressive hybridization between weakfish and sand seatrout (*C. arenarius*) in Florida, centered in the Nassau and St. Johns Rivers, with the genome proportions of "pure" weakfish estimated at 48% in Nassau County and 17% in Duval County, and that "pure" weakfish were rare southward.

Migration Patterns

Weakfish exhibit a north-inshore/south-offshore migration pattern, although in the southern part of their range they are considered resident. Shepherd and Grimes (1983) observed that migrations occur in conjunction with movements of the 16-24^{o} C isotherms. Warming of coastal waters during springtime triggers a northward and inshore migration of adults from their wintering grounds on the continental shelf from Chesapeake Bay to Cape Lookout, North Carolina (Mercer 1983). The spring migration brings fish to nearshore coastal waters, coastal bays, and estuaries where spawning occurs. Weakfish move southward and offshore in waves as temperatures decline in the fall (Manderson et al. 2014; Turnure et al. 2014).

Age and Growth

The historical maximum age recorded using otoliths is 17 years for a fish collected from Delaware Bay in 1985 (ASMFC 2016). Weakfish growth is rapid during the first year, and age-1 fish typically cover a wide range of sizes, a result of the protracted spawning season. Lowerre-Barbierri et al. (1995) found length at age to be similar between sexes, with females attaining slightly greater length at age than males. Estimates of L_{∞} ranged from 89.3 cm – 91.7 cm depending on study area (Hawkins 1988; Villoso 1990; Lowerre-Barbierri et al. 1995). Weakfish in the catch averaged 5-6 kg at the oldest ages (Figure 6).

Maturity and Fecundity

Weakfish mature early, with 90-97% of age-1 fish estimated to be mature (Figure 6) Lowerre-Barbieri et al. 1996; Nye et al. 2008). Although the majority of age-1 fish were mature, age-1 weakfish spawned less frequently, arrived later to the estuary, and had lower batch fecundity than did older fish (Nye et al. 2008). Batch fecundity ranged from 75,289 to 517,845 eggs/female and significantly increased with both total length and somatic weight (Lowerre-Barbieri et al. 1996). Weakfish have a protracted spawning season and individual fish spawn multiple times in a season; spawning occurs from March to September in North Carolina (peaking from April to June) (Merriner 1976), but the season is shorter (May to mid-July/August) in Chesapeake Bay and Delaware Bay (Shepherd and Grimes 1984; Lowerre-Barbieri et al. 1996).

Natural Mortality

Recent assessments of weakfish indicate natural mortality has increased over time (NEFSC 2009; ASMFC 2016). Catch has declined significantly since the mid-1990s and remained at low levels in recent years under restrictive management, while recruitment indices have been stable over the

time series; however, the population has not recovered. ASMFC (2016) used a Bayesian model to estimate time-varying natural mortality, and found that *M* was low (*M*=0.14-0.17) during the 1980s and early 1990s, but began to increase sharply in the late 1990s; it was estimated at 0.92-0.95 from 2003 – 2013 (Figure 6). There are several hypotheses about what caused the increase in *M*, including increasing predation or competition from increasing striped bass and spiny dogfish populations and large-scale environmental drivers like Atlantic Multidecadal Oscillation, but no definitive conclusions can be made (NEFSC 2009).

Habitat

Weakfish are found in shallow marine and estuarine waters along the Atlantic coast. They can be found in salinities as low as 6 ppt (Dahlberg 1972) and temperatures ranging from 17^{o} to 26.5^{o} C (Merriner 1976). Weakfish spawn in estuarine and nearshore habitats throughout their range, and larval and juvenile weakfish generally inhabit estuarine rivers, bays, and sounds, commonly associated with sand or sand/grass bottoms (Mercer 1983). Adult weakfish overwinter offshore on the continental shelf from Chesapeake Bay to North Carolina.

5 FISHERY DEPENDENT DATA SOURCES

5.1 Marine Recreational Information Program (MRIP) Changes

Data on recreational catch for modeled species comes from the Marine Recreational Information Program (MRIP, formerly the Marine Recreational Fisheries Statistics Survey or MRFSS). MRIP uses a combination of effort surveys that are designed to estimate the number of fishing trips taken in various regions of the US and dockside angler intercept surveys that are designed to estimate catch-per-trip and size frequencies of recreationally caught species. Data from these surveys are used to calculate total catch (broken down by harvest and live releases) and the size frequency of landed fish. MRIP estimates are available from 1981 to the present.

Prior to 2018, the estimates of angler effort (i.e., angler trips) used to calculate annual recreational catch and harvest of Atlantic striped bass were derived from the Coastal Household Telephone Survey (CHTS), a random-digit-dial telephone survey. The CHTS was replaced in 2018 by the mail-based Fishing Effort Survey (FES), due to concerns about the inefficient design, coverage bias, and declining response rates of the CHTS. The CHTS and FES were conducted simultaneously for three years (2015-2017), during which the FES produced much higher estimates of fishing effort, and therefore much higher estimates of recreational catch. The results of these years of “side-by-side” surveys were used to develop a calibration model to convert historic CHTS estimates to the scale of the new FES.

All recreational data used in the ERP models has been calibrated to the new FES scale, and the time series of biomass and *F* estimates used as input for some models for these species are from assessments that used the new calibrated MRIP data.

5.2 Atlantic Menhaden

The Atlantic menhaden commercial fishery has two major components, a purse-seine reduction sector that harvests fish for fish meal and oil and a bait sector that supplies bait to other commercial and recreational fisheries. Fishery-dependent data for the Atlantic menhaden purse-seine reduction fishery, including landings, lengths, weights, and ages, have been collected by the Beaufort Laboratory of the National Marine Fisheries Service since 1955. The fishery has changed over the time series from peak landings in the 1950s and several processing plants to lower landings, the implementation of a total allowable catch (TAC), and one remaining processing plant in recent years. Bait landings and biosampling data including lengths and ages were compiled by NOAA Fisheries historically, but have been housed and validated by the Atlantic Coastal Cooperative Statistical Program (ACCSP) since 1985. The Beaufort Laboratory does all the commercial ageing of Atlantic menhaden samples.

There has been a TAC for Atlantic menhaden in place since 2013. Landings in the reduction fishery are currently at their lowest levels in the time series. In contrast, bait landings have increased in recent years as demand has grown because of recent limitations in other species used as bait (e.g., Atlantic herring). In 2017, coastwide landings were comprised of 74% from the reduction fishery and 25% from the bait fishery. Recreational removals comprised 1% of the coastwide landings and are combined with the bait fishery landings for the assessment. Recreational removals are not well captured by MRIP; there is not a known directed recreational fishery for Atlantic menhaden, although they may be caught by recreational anglers for use as bait for other gamefish. A 100% mortality was applied to the reported live recreational releases, so that total recreational removals were equal to the sum of landings and live releases. Total removals have generally declined over time, from a high of 738 thousand mt in 1956 to a time series low of 169 thousand mt in 2013. Total removals rebounded slightly after that, with total removals in 2017 at 175 thousand metric tons (Figure 7).

5.3 Atlantic Herring

Fishery dependent data for Atlantic herring consists of catch and biological sampling for age, length, weight, and spawning condition/fecundity (NEFSC 2018a). Landings are derived from electronic logbooks reported by the harvesters and verified through dealer reports. At-sea observers and portside samples measure both discards and incidentally landed bycatch, respectively. Discards at-sea are generally low for the industrialized fishery for Atlantic herring. Biological samples are also taken from the fishery at the time of off-loading. These samples are processed for length, weight and later aged and staged. Resulting data are then available for the stock assessment process.

Total removals of Atlantic herring peaked at 478 mt in 1968, before declining to a time series low of 44.6 mt in 1983. Total removals were mostly stable from 1990 – 2010, averaging 114 mt, but have declined in recent years to 50.2 million metric tons in 2017 (Figure 8).

5.4 Striped Bass

Striped bass are a predominantly recreationally caught species, with recreational harvest and release mortality making up approximately 90% of total removals in recent years. It is assumed that 9% of striped bass that are released alive die as a result of being caught, so that total recreational removals are equal to the recreational harvest plus 9% of the recreational live releases. Live releases have accounted for 85 to 90% of the total recreational catch in most years, with release mortality comprising 40-50% of the total recreational removals. The size frequency of recreationally landed fish comes from MRIP and is supplemented with state programs such as volunteer angler logbook programs. Data on sizes of striped bass released alive come from state-specific sampling, volunteer angler logbook programs, and the American Littoral Society (ALS) volunteer angler tagging program.

For the commercial sector, strict quota monitoring is conducted by states through various state and federal dealer and fishermen reporting systems, and landings are compiled annually from those sources by state biologists. Biological data (e.g., length, weight, etc.) and age structures from commercial harvest are collected from a variety of gear types through state-specific port sampling programs. Harvest numbers are apportioned to age classes using length frequencies and age-length keys derived from biological sampling. Commercial discards were estimated using tag return data from commercial and recreational sectors; for the Chesapeake Bay and the Delaware Bay these estimates were scaled by estimates of discards from a short-term observer program in the Delaware Bay.

Total removals were low at the beginning of the assessment time series due to the poor condition of the stock and the restrictive management measures put in place to rebuild it (Figure 9). As the stock rebuilt and regulations were eased, removals increased from a low of 1,580 mt in 1987 to a high of 37,391 mt in 2013. Removals were relatively stable from 2003-2013, averaging around 34,000 mt, but began to decline after 2013. From 2014-2017, removals averaged 27,375 mt due to a combination of stock declines and management action.

5.5 Bluefish

Bluefish is a predominately recreational species, with recreational removals making up about 85-92% of the total removals. It is assumed that 15% of bluefish that are released alive die as a result of being caught, so that total recreational removals are equal to the recreational harvest plus 15% of the recreational live releases. The proportion of bluefish released alive has increased over the time series from about 20% in early years to about 65% in recent years. Recreational landings are sampled for length as part of the MRIP program. The MRIP length samples were used to expand recreational landings per half year. Recreational discards were characterized using lengths from bluefish tagged and released in the ALS volunteer tagging program, as well as information provided by volunteer angler programs in Rhode Island, Connecticut, and New Jersey.

Commercial landings data were queried from the ACCSP Data Warehouse, which houses commercial data from state and federal data collection programs, including dealer reports and harvester reports. Biological samples were collected from commercial fisheries by the NEFSC

port sampling program and state programs in Virginia, North Carolina, and Florida. Commercial discards were assumed to be negligible.

Bluefish removals were highest at the beginning of the assessment time series, peaking at 84,200 mt in 1987; by 1993 landings had declined to 26,940 mt, and remained relatively stable after that, averaging 27,000 mt from 1996 – 2017 (Figure 10).

5.6 Spiny Dogfish

Commercial fishermen catch spiny dogfish using longlines, trawls, and purse seines. Fishermen target female spiny dogfish because the females grow larger than males and tend to school together. The commercial fishery supplies the European food fish markets that use spiny dogfish for fish and chips.

Spiny dogfish landings are reported in the stock assessment as a total from commercial, recreational, Canadian, and distant water landings, or Northwest Atlantic Fisheries Organization (NAFO) Areas 2-6 (Sosebee and Rago 2017). US landings include those from US and distant water commercial fisheries and recreational landings and discards were obtained from MRIP. Canadian and distant water landings were obtained from the NAFO catch statistics database (Sosebee and Rago 2017). Landings were variable but high in the 1970s and then decreased through the early 1980s. The National Marine Fisheries Service (NMFS) encouraged commercial fishermen to target the bountiful stocks of spiny dogfish in the 1980s and 1990s when stocks of other commercially valuable fish in the Northeast declined. Therefore, landings were high in the 1990s, peaking at 27.8 mt in 1996, and then in the late 1990s, landings declined (Figure 11). In 1998, NMFS determined that spiny dogfish were overfished and implemented stringent harvest restrictions in federal waters to allow the stock to rebound. After federal and state regulations were implemented in the early 2000s, landings declined to a low of 3.2 mt in 2003. As the stock began to improve, landings began to increase in the 2010s. In 2017, commercial landings were estimated at 11.1 mt (Figure 11). Commercial landings are comprised of about 98% female spiny dogfish (Sosebee and Rago 2017).

5.7 Weakfish

For weakfish, the proportion of removals coming from the recreational sector has increased over time, increasing from about 10% of total removals at the beginning of the time series to approximately 50% of total removals in recent years. It is assumed that 10% of weakfish that are released alive die as a result of being caught, so that total recreational removals are equal to the recreational harvest plus 10% of the recreational live releases. The proportion of weakfish released alive has increased over the time series from less than 10% in early years to more than 90% in recent years. Recreational landings are sampled for length as part of the MRIP program. The MRIP length samples were used to expand recreational landings per half year. Recreational discards were characterized using lengths from the MRIP sampling of released fish on headboat vessels; prior to that program, it was assumed that the length frequency of fish released alive was the same as the length frequency of harvested fish.

Weakfish commercial landings data came from state-specific harvest records collected through a mandatory reporting system where available, or from the NMFS commercial landings database. Estimates of commercial discards were developed from the Northeast Fishery Observer Program data. Biosamples were collected through state sampling programs, and pooled length frequencies were developed for sub-regions based on geographic location and commercial size limits. Florida landings for both the commercial and recreational sector were corrected for hybridization using the observed proportion "pure" weakfish in the catch from Tringali et al. (2011).

Weakfish landings have declined significantly over the assessment time series; total landings in 2017 were 391 mt, just 2% of their 1986 value of 19,515 mt (Figure 12).

6 ATLANTIC MENHADEN INDICES OF ABUNDANCE

6.1 Fishery-Independent Indices

6.1.1 Background of Analysis and Model Description

When several population abundance indices provide conflicting signals, hierarchical analysis can be used to estimate a single population trend. The abundance indices for Atlantic menhaden were combined into regional composite indices using hierarchical modeling as described in Conn (2009). This method assumes each index samples a relative abundance but that the abundance is subject to sampling and process errors. It can be used on surveys with different time series, but it does assume that indices are measuring the same relative abundance and that the surveys have similar selectivities. The Conn method was also used to combine individual abundance indices into regional indices in SEDAR 2015 and ASMFC 2017b.

6.1.2 Model Configuration and Results

The Atlantic Menhaden Stock Assessment Subcommittee (SAS) developed an Atlantic menhaden young-of-year (YOY) index from 16 fishery-independent surveys and three regional adult indices from various fishery-independent surveys: a northern adult index (NAD), a Mid-Atlantic adult index (MAD), and a southern adult index (SAD). Refer to the single-species benchmark (2019) for full methods for the indices of relative abundance in numbers to support the BAM and MSSCAA models.

The NAD hierarchical biomass index predicted variable abundance throughout the time series with notable peaks in 1999, 2002, and the mid-2010s (Figure 13). Despite the higher abundance occurring in 2014-2015, the final two years of the index (2016-2017) indicate a decreasing adult abundance. All three of the individual abundance indices used in the NAD indicated a declining abundance in the terminal years. The MAD hierarchical index predicted high abundance in the beginning of the time series followed by low abundance in the early 1990s (Figure 13). From 1985 until the Virginia's Gill Net (VA GN) began in 1998, the MAD relied on only the Maryland Gill Net survey (MD GN) and thus there are larger errors associated with those years. The index then bounces around from the mid-1990s to the 2010s. Despite high abundance in 2014-2015, the final two years of the index (2016-2017) indicate a decreasing adult abundance just like the

NAD indicated. Both of the individual abundance indices used in the MAD indicated a declining abundance in the terminal years. The SAD hierarchical index predicted high abundance in 1990 followed by low abundance from 1991-2004, followed by an increase to a high in 2006 (Figure 13). The index is variable from 2006-2015 with a low abundance in 2016 and a slight uptick in the terminal year of 2017. All three of the individual abundance indices used in the SAD indicated an increasing or neutral abundance in the terminal year.

To develop biomass indices for the surplus production models, the length frequencies from the individual surveys were converted into weight frequencies using the time-invariant length-weight relationship developed for the single-species benchmark (SEDAR 2019). The individual GLM indices were converted into biomass using the weight frequencies and then combined regionally using the methods of Conn (2009). Biomass Conn indices were very similar in pattern to the Conn indices in numbers.

6.2 Fishery-Dependent Indices

The ERP WG developed two long-term indices of abundance for Atlantic menhaden: a commercial reduction fishery CPUE index (RCPUE index) and a commercial bait fishery catch per unit effort (CPUE) index, the Potomac River Fisheries Commission (PRFC) index. The Atlantic Menhaden SAS considered fishery dependent indices of abundance in past assessments, including the PRFC index, but did not use them in the single-species assessment due to concerns about the reliability of the index as a measure of relative abundance. These concerns included how to define a consistent unit of effort, the limited spatial scale (of the PRFC index), the potential for hyperstability (of the RCPUE index), and other factors. Although the WG acknowledged the SAS's concerns about these indices, the long time series and the contrast they provided, which the surplus production models required, outweighed the potential biases.

The two indices had similar trends since 1990, but showed differing trends from 1970-1990 (Figure 13). The ERP WG decided to use the RCPUE index for ERP model base runs because of its larger spatial coverage, its consistently recorded unit of effort, its known variance structure, support from supplemental analyses that showed relatively strong correlations with other sources of data, and the ability to standardize the data through explanatory covariates (week, factory, vessel size), among other factors. However, sensitivity analyses with the PRFC index were conducted.

6.2.1 Commercial Reduction Catch Per Unit Effort (RCPUE) Index

A long-term index of abundance spanning 1955-2017 was generated for Atlantic menhaden using catch and effort data from dealer reporting in the reduction fishery (RCPUE index). CPUE was defined as landings (1,000 t) per net tonnage-days fished to account for variability over time in fishing effort and size of fishing vessels used. An index of abundance (RCPUE) was generated by estimating the year effects of a lognormal generalized linear model that predicted CPUE as a function of year, week in year, and plant; week and plant were included in the model to account for changes in the location and number of reduction plants over time and seasonality of the fishery. A similar index using more detailed effort data contained in Captain's

Daily Fishing Reports spanning 1985-2017 was generated and found to be highly correlated (r = 0.92) with the long-term RCPUE index.

6.2.2 Potomac River Fishery Commission Commercial Bait Catch Per Unit Effort (PRFC) Index

A long-term index of abundance spanning 1964-2017 was generated for Atlantic menhaden using pound net landings and effort data collected by the Potomac River Fisheries Commission (PRFC). The PRFC index was calculated as annual ratios of total pound net landings (in mt) to total pound net days fished.

Landings with associated effort (pound net days fished) were available, but discontinuous (1976-1980 and 1988-2018). During 1964-1993, the PRFC required a license for each pound net and did not restrict number of pound net licenses sold. Since pound nets were expensive and labor intensive to fish, it was reasonable to assume that each licensee would maintain stable fishing practices and, as a result, number of licenses could approximate effort. When licenses were capped at 100 in 1993, this estimator may have stopped representing effort in the same manner as before the cap (fishermen may have bought more licenses than needed to keep from being excluded from fishing). Prior to the imposition of the cap, licenses had steadily fallen by half between 1985 and 1993 (to 72). After the cap was imposed, 100 licenses were issued every year; however, not all 100 licenses were necessarily fished.

Previous single-species stock assessments (ASMFC 2004, ASMFC 2012b) used a linear regression to fill missing years of effort. Recently, the PRFC obtained and computerized more detailed data on pound net landings and effort, which allowed index values to be calculated for 1964-1975 and 1981-1987 (A. C. Carpenter, PRFC, personal communication).

To generate estimates of pound net days fished (*DF*) for missing years (those with only license effort data), a linear regression was fitted to *DF* as a function of the number of licenses (*L*):

$$DF = 2794.5 + 19.214 \cdot L \quad (6.1)$$

which had an R^2 value of 0.505 and was significant at an α-level of 0.014 (n = 11).

Pound net days fished predicted by this equation were used to convert landings (in mt) per license to landings per pound net days fished for years without pound net days estimates. A trend was not evident for 1976 – 1978, so the regression intercept was used for pound net days fished for years prior to 1979. For all other years (1979 – 1993), the equation was used to estimate pound net days fished.

7 NON-MENHADEN INDICES OF ABUNDANCE

The single-species assessments for all of these species use multiple (often 5 or more) indices of relative abundance. In order to keep the multispecies models tractable, the ERP WG consulted with the other species' TCs to select the most representative subset of indices. The ERP WG limited the non-menhaden species to one index of recruitment and two age-0+ indices of abundance, with one additional age-0+ index chosen for a sensitivity run.

7.1 Atlantic Herring

The Atlantic herring TC recommended using the NEFSC fall bottom trawl survey as an index of age-1+ abundance. This survey catches Atlantic herring across age-classes but does miss some of the youngest Atlantic herring inshore in the GOM (NEFSC 2018a). This survey has been operational since 1963.

Because of the vessel change from the RV Albatross to the RV Bigelow in 2009, the fall index was separated in the most recent assessment. This results in two separate indices for Atlantic herring: Fall Albatross 1985-2008 and Fall Bigelow 2009-present (NEFSC 2018a).

The ASMFC Summer Shrimp survey was selected as a sensitivity run. The Summer Shrimp survey has operated with consistent gear and methodology in the Gulf of Maine since 1984. It uses a combination of fixed and stratified random stations. Although the survey targets northern shrimp, data for other species is also collected.

There is no dedicated YOY index for Atlantic herring.

The NEFSC Fall Albatross and Summer Shrimp surveys showed similar trends, increasing from lower levels at the beginning of the time series and showing peaks in the mid-1990s before declining again (Figure 8). The NEFSC Fall Bigelow has generally varied without trend since 2009 (Figure 8).

7.2 Striped Bass

For the recruitment index, the Striped Bass TC recommended the composite YOY index for the Chesapeake Bay. The composite index was developed from two separate but methodologically similar seine surveys conducted in the Maryland and Virginia waters of the Chesapeake Bay, combined into a single index using the Conn (2009) method. The index represents recruitment for the Chesapeake Bay stock, which is the major contributor to the coastal metapopulation of striped bass. The index showed several strong year classes in the late 1980s and early 1990s, a period of generally below average recruitment from the early 2000s to 2010, and strong year classes in 2011, 2014, and 2015 (Figure 9).

For age-1+ indices, the Striped Bass TC recommended the Connecticut Long Island Sound Trawl Survey (CT LISTS) and the MRIP CPUE index. Both of these indices have long time series with good contrast in the data, and represent the coastal migratory metapopulation of striped bass, unlike the spawning stock surveys, which represent individual stocks. The Maryland Spawning Stock Survey (MD SSN) was selected as a sensitivity run, as it represents the Chesapeake Bay stock and has a relatively long time series.

CT LISTS is a stratified random trawl survey that occurs in Long Island Sound; the fall component of the survey was used to develop the index. Length frequencies were converted to age composition information using regional age-length keys. The MRIP CPUE was developed

from the raw intercept data collected by MRIP. Trip records were subset to trips that occurred in ocean waters from Virginia through Maine from May – October. Striped bass trips were identified using a guild approach as trips that caught either striped bass or another similar species. Similar species were identified on a state-by-state basis as the species with the highest Jaccard coefficient, which measures how often any given species is caught with striped bass compared to how often they are caught separately. For most states, bluefish or Atlantic mackerel (*Scomber scombrus*) were the most commonly co-encountered species. A negative binomial GLM was used to develop the index from the trip data. Recreational harvest-at-age for the ocean during those months were combined with the full recreational release-at-age numbers (i.e., not scaled by the discard mortality rate) to develop age structure information for this index. The MD SSN is a multi-panel gillnet survey that occurs on the spawning grounds in the Maryland portion of the Chesapeake Bay during the spawning season. For more details on survey methods and index calculations, see NEFSC (2019).

Both of these indices showed similar trends, starting out low at the beginning of the time series and increasing through the 1990s (Figure 9). They peaked around the early 2000s and have been gradually declining since. The MD SSN has varied without trend over that time period (Figure 9); however, it shows the same expansion of the age structure during the 1990s and the contraction in recent years that the CT LISTS and MRIP CPUE do.

7.3 Bluefish

For a recruitment index, the Bluefish TC recommended the composite YOY index developed from state seine surveys that are conducted in bays and estuaries from Virginia to New Hampshire, using the Conn (2009) method. The composite index showed years of strong and weak recruitment at the beginning of the time series, with less variability in more recent years (Figure 10).

For the age-0+ indices, the Bluefish TC recommended the North Carolina Pamlico Sound Independent Gillnet Survey (NC PSIGNS) and the MRIP CPUE. These are the only two bluefish indices that are not dominated by age-0 fish and are therefore able to provide information on population age structure. In addition, the MRIP CPUE has the longest time series and widest spatial extent of the indices used in the assessment. The TC recommended using the NEFSC Fall Bottom Trawl Survey conducted on the R/V Albatross (NEFSC Fall Albatross) as a sensitivity run, since it had the widest spatial extent of the fishery independent indices.

NC PSIGNS uses a stratified random sampling design, based on area and water depth, to deploy arrays of gillnets with different mesh sizes. Sampling is conducted from mid-February to mid-December, and all months are used in the index. Length frequency data were converted to age composition information with seasonal age-length keys. The MRIP CPUE was calculated from the raw intercept data collected by MRIP. The MRIP data were subset to directed bluefish trips; that is, trips where the angler caught bluefish or reported they were targeting bluefish. Trips from Florida to Maine from all months were included. A negative binomial GLM was used to develop the index from the trip data. MRIP harvest-at-age for the ocean during those months

were combined with the full recreational release-at-age numbers (i.e., not scaled by the discard mortality rate) to develop age structure information for this index. The NEFSC has conducted a stratified random bottom trawl survey since 1963 from North Carolina into the Gulf of Maine; in 2009, the survey switched vessels from the R/V Albatross to the R/V Bigelow. This vessel change resulted in changes to the trawl gear and survey protocol. NEFSC fall inshore strata from Cape Hatteras, NC to Cape Cod, MA were used to develop separate indices for bluefish for the Albatross and Bigelow years. For more information on these indices, see NEFSC (2015).

All three indices showed similar trends: a slight decline from 1985 to 1995 then a slight increasing trend to 2005, after which the NC PSIGNS and MRIP CPUE have been mostly stable (Figure 10).

7.4 Spiny Dogfish

The NEFSC calculates a biomass estimate for spiny dogfish based on area swept from their spring bottom trawl survey (Figure 11). The index does not have a value for 2014 due to mechanical problems on the FSV Bigelow that delayed the spring bottom trawl and resulted in the loss of critical strata for the index. The time series indicates that biomass was lower in the late 1960s-1970s and then increased but was variable through the 1980s and 1990s. The index decreased to a low in 2004 and has increased but been variable since then.

7.5 Weakfish

The Weakfish TC recommended using the composite YOY index developed from state trawl surveys for juvenile finfish that occur in bays and estuaries from North Carolina to Rhode Island, using the Conn (2009) method. The composite YOY generally varied without a strong trend, being below average in the 1980s and most recent years, and above average from 1992-2006 (Figure 12).

The Weakfish TC noted that there were differences in trends between indices that occurred offshore and indices that were conducted inshore, with offshore indices being more variable and with weaker trends that were inconsistent with the inshore surveys. This may be due to mismatches between survey timing and inshore/offshore movements of weakfish in some years. Based on input from the Weakfish TC, the ERP WG decided to use the MRIP CPUE and the Delaware Bay 30’ Trawl Survey (DE 30ft Trawl) as the base run age-0+ indices, both of which are inshore indices, and the NC PSIGNS index as an inshore sensitivity run and the New Jersey Ocean Trawl (NJ OT) as an offshore sensitivity run.

The MRIP CPUE for this assessment was calculated from the raw intercept data collected by MRIP for states from North Carolina to New York. Weakfish trips were identified using a guild approach as trips that caught either weakfish or another similar species. Similar species were identified on a state-by-state basis as the species with the five highest Jaccard coefficients, which measures how often any given species is caught with striped bass compared to how often they are caught separately. For most states, Atlantic croaker (*Micropogonias undulates)*,

spot, and summer flounder (*Paralichthys dentatus*) were the most commonly co-encountered species. A negative binomial GLM was used to develop the index from the trip data. MRIP harvest-at-age for the ocean during those months were combined with the full MRIP release-at-age numbers (i.e., not scaled by the discard mortality rate) to develop age structure information for this index. ALS volunteer tagging data were used as a proxy for the length frequencies of fish released alive for the period of years between the implementation of coastwide minimum size limits and the implementation of the MRIP at-sea headboat sampling. NC PSIGNS is described above for bluefish. The NJ OT is a stratified random trawl survey conducted five times per year (January, April, June, August and October) in nearshore ocean waters from the entrance of New York Harbor south, to the entrance of the Delaware Bay. A GLM-based index was derived using a negative binomial distribution of the August and October abundance data with mean depth and bottom salinity as the covariates. New Jersey's age length keys were applied to this survey's mean catch at length indices to derive an index-at-age. For more details on these indices, see ASMFC (2016).

The MRIP CPUE and the DE 30ft Trawl showed similar trends, increasing from the late 1980s through the mid-1990s before declining to low levels (Figure 12). For the MRIP CPUE, the peak in the mid-1990s never reached the levels of the index in the early 1980s. The NC PSIGNS index showed a similar declining trend from the start of its time series in 2001 through 2017 (Figure 12). The NJ OT fluctuated without a general trend but did show a similar peak in 1994 (time series high) and 1995, followed by low values for most of the rest of the time series with smaller peaks in 2000, 2004 and 2011 (Figure 12).

8 SINGLE-SPECIES ASSESSMENTS AND STOCK STATUS

For the key predator and prey species, the most recent stock assessments were used to provide estimates of population size, fishing mortality, and reference points. For species where the terminal year of the most recent published stock assessment was prior to 2017 (namely, bluefish and weakfish), preliminary assessment updates were used to provide biomass estimates on the correct scale; the values from those assessment updates may not match the final assessment update values used in management.

The single-species assessments use target and threshold values based on spawning stock biomass, but the EwE models use total biomass. In addition, the scale of biomass and fishing mortality are not the same between the EwE models and the single-species models, so direct comparisons with the target and threshold values are not possible. To address this issue, spawning stock biomass targets and thresholds were converted to total biomass targets and thresholds, and the percent change between terminal year *B* and *F* and target and threshold *B* and *F* was calculated so that the EwE model results could be scaled appropriately (see also the sections on the EwE models for why this was necessary and how these values were used). Reference points, *B* equivalents, and *B* and *F* scalars are shown in Table 3 and Table 4.

8.1 Atlantic Menhaden

Atlantic menhaden are assessed with a statistical catch-at-age model, the Beaufort Assessment Model (BAM). According to the 2019 benchmark stock assessment (see single species assessment document), Atlantic menhaden were not overfished and overfishing was not occurring in 2017, the terminal year of the assessment. The F_{TARGET} was defined as the median of the geometric mean *F* on ages 2-4 from 1960 – 2012, and the $F_{THRESHOLD}$ was the maximum value of the geometric mean *F* on ages 2-4, over that time series. The overfished determination is based on total population fecundity. The spawning potential ratio associated with the F_{TARGET} and $F_{THRESHOLD}$ are converted into total fecundity values to represent the FEC_{TARGET} and $FEC_{THRESHOLD}$, respectively.

Total age-1+ biomass has fluctuated over time from an estimated high of over 6.8 million mt in 1959 to a low of 1.4 million mt in 1973 (Figure 14). Biomass was estimated to have been largest during the late-1950s and late-2010s, with lows occurring during the 1960s, 1970s, and 1980s. From 1980 to the present, biomass has increased in trend. Biomass likely increased at a faster rate than abundance because of the increase in the number of older fish at age and an increase in weight-at-age. Biomass in 2017 was 4.7 million mt.

Population fecundity (i.e., total egg production) was the measure of reproductive output used to assess overfished status. Population fecundity (*FEC*, number of maturing ova) was highest in the early 1960s and from the 1990s to the present (Figure 14). The largest values of population fecundity were in 1955, 1961, and 2012. Throughout the time series, age-2 and age-3 fish have produced most of the total estimated number of eggs spawned annually. Fecundity in 2017 was estimated at 2.6 quadrillion eggs, above both the threshold (1.46 quadrillion eggs) and the target (1.94 quadrillion eggs).

Fishing mortality rate over time was reported as the geometric mean fishing mortality rate at ages-2 to -4 to account for changes in selectivity over time. Geometric mean fishing mortality rate was highest in the 1970s and 1980s and has been declining since approximately 1990 (Figure 14). *F* in 2017 (0.11) was below both the $F_{THRESHOLD}$ (0.60) and the F_{TARGET} (0.22).

8.2 Atlantic Herring

Atlantic herring are assessed with a statistical catch-at-age model, the ASAP program from the NEFSC Toolbox. According to the 2018 benchmark stock assessment (NEFSC 2018a), Atlantic herring were not overfished and overfishing was not occurring in 2017, the terminal year of the assessment. The *F* threshold is the F_{MSY} proxy, $F_{40\%SPR}$. The SSB target (the B_{MSY} proxy) is calculated by using AgePro to project the population forward under $F=F_{40\%SPR}$ until it stabilizes, with recruitment drawn from the observed time series; the long-term equilibrium SSB under these conditions is the SSB target. The SSB threshold is 50% of the SSB target. The ratio of SSB to age-1+ biomass over the entire assessment time-series was used to convert the SSB targets and thresholds to age-1+ biomass targets and thresholds for the ERP models that use total biomass.

Total age-1+ biomass ranged from a peak of 2,035,800 mt in 1967 to a low of 169,860 mt in 1982 (Figure 15). Total biomass in 2017 was 239,470 mt. SSB showed a similar pattern, ranging from a high of 1,352,700 mt in 1967 to a low of 53,084 mt in 1982 (Figure 15). SSB in 2017 was 141,473 mt, above the SSB threshold of 94,500 mt.

F was reported as the average *F* over ages 7 and 8, as those ages are fully selected by the mobile gear fishery, which has accounted for the majority of total landings since 1986. *F* ranged from a low 0.13 in 1965 to a high of 1.04 in 1975 (Figure 15). *F* in 2017 equaled 0.45, below the *F* threshold of 0.51.

8.3 Striped Bass

Striped bass are assessed with a statistical catch-at-age (SCA) model. According to the 2018 benchmark stock assessment (NEFSC 2019), Atlantic striped bass were overfished and overfishing was occurring in 2017, the terminal year of the assessment. The reference points currently used for management are based on the 1995 estimate of female SSB. The 1995 female SSB is used as the SSB threshold because many stock characteristics (such as an expanded age structure) were reached by this year and the stock was declared recovered. The SSB target is 125% of the SSB threshold. The *F* target and *F* threshold are defined as the *F* needed to maintain the population at the SSB target and SSB threshold respectively. The estimate of age-2+ biomass in 1995 from the single species model was used as the $B_{THRESHOLD}$ proxy for the ERP models that use total biomass, and 125% of that value was defined as the B_{TARGET} proxy.

Total age-1+ biomass of striped bass increased from a low of 38,149 mt in 1982 and increased to a peak of 334,661 mt in 1999 before beginning to decline (Figure 16). Total biomass was 173,663 mt in 2017. Female SSB started out at low levels and increased steadily through the late-1980s and 1990s, peaking later than total biomass at 113,602 mt in 2003 before beginning to gradually decline; the decline became sharper in 2012 (Figure 16). Female SSB was estimated at 68,476 mt in 2017, below the SSB threshold of 91,436 mt and below the SSB target of 114,295 mt.

Total *F* has been increasing for both the ocean fleet and the Chesapeake Bay fleet since 1990. Total *F* in 2017 was 0.31, above both the *F* threshold of 0.24 and the *F* target of 0.20 (Figure 16).

8.4 Bluefish

Bluefish are assessed with a statistical catch-at-age model, the ASAP program from the NEFSC Toolbox. Bluefish assessment data used for this assessment was from a preliminary assessment update with data through 2017; for the final values, see NEFSC 2019b. The trends are the same, with some small differences in magnitude between the preliminary update and the final 2019 update. In 2017, the preliminary assessment update indicated bluefish were overfished and overfishing was occurring. The SSB target (the B_{MSY} proxy) is calculated by using AgePro to project the population forward under $F=F_{THRESHOLD}$ until it stabilizes, with recruitment drawn from the observed time series; the long-term equilibrium SSB under these conditions is the SSB

target. The SSB threshold is 50% of the SSB target. The equilibrium age-1+ biomass from this projection was used as the B_{TARGET} proxy for the ERP models that use total biomass, and 50% of that value was the $B_{THRESHOLD}$ proxy.

Total age-1+ biomass declined from the beginning of the time series until the mid-1990s before beginning to increase; total biomass has trended downward in recent years (Figure 17). The preliminary estimate of total biomass in 2017 was 117,107 mt. SSB has shown a similar trend, with the preliminary estimate of SSB in 2017 at 107,282 mt, below the SSB threshold (Figure 17).

F is reported as *F* at age 2, the age of full selectivity for bluefish. *F* declined over the time series until 2008, when it began to increase (Figure 17). *F* has been above the *F* threshold for the entire time series. The preliminary estimate of *F* in 2017 was 0.34, above the *F* threshold.

8.5 Spiny Dogfish

Spiny dogfish are assessed using a swept-area biomass estimate derived from the NEFSC Spring Bottom Trawl Survey. Biological reference points are derived from a stock-recruitment relationship derived from the survey data and a population projection model. Based on the 2018 updated, spiny dogfish were not overfished and overfishing was not occurring in 2018 (NEFSC 2018b). The SSB target (B_{MSY} proxy) is SSB_{MAX}, the biomass of female spiny dogfish greater than 80cm that results in the maximum projected recruitment based on a Ricker stock-recruitment model derived from NEFSC trawl survey data. The SSB threshold is 50% of the SSB target. The SSB target is converted from the survey SSB CPUE scale (biomass-per-tow of female spiny dogfish greater than 80cm) to total swept area SSB. The ratio of SSB per tow to total biomass-per-tow over the entire time series was used to convert the female SSB target and threshold to a total biomass target and threshold for the ERP models that use total biomass.

Estimates of total biomass have been variable over the time series, showing an increase from the late 1970s to the early 1990s before declining (Figure 18). Total biomass has generally been increasing since 2004, but 2017 was 414,900 mt the lowest value seen in the last 10 years. Survey data by sex are not available prior to 1980, so the female SSB time series is more limited. Female SSB is reported as the three year average of the annual survey estimates, so the trend is smoother, but generally similar to the total biomass trend: declining from the early 1990s to the early 2000s, then increasing again (Figure 18). The year-specific estimate of female SSB in 2017 was 24,400 mt, the lowest in the time series. However, the indices for all size and sex classes decreased, likely indicating a year specific availability issue rather than a major decline in biomass. The 3-year average of the female swept area SSB was 112,000 mt in 2017, lower than in recent years but still above the SSB threshold of 79,644 mt but below the SSB target of 159,288 mt.

F is reported as female catch on exploitable female biomass; males make up a tiny component of the overall fishery. Observer estimates of commercial discards are not available prior to 1990, so the time series of *F* is shorter than the total biomass and SSB time series. *F* has

generally been declining since the mid-1990s, but has been increasing in recent years (Figure 18). *F* was 0.20 in 2017, below the *F* threshold of 0.24.

8.6 Weakfish

Weakfish are assessed using a Bayesian statistical catch-at-age model that estimates a time-varying natural mortality rate. Weakfish were found to be depleted in 2015 with total mortality above the *Z* threshold, based on the 2016 benchmark assessment (ASMFC 2016). Biological reference points for total mortality were developed using a SPR-based approach with natural mortality set at the time-series average estimated by the Bayesian model. The SSB threshold was developed by projecting the population forward under average *M* and no fishing mortality. The SSB threshold was defined as 30% of that unfished SSB; 30% of unfished age-1+ biomass was used as the proxy biomass threshold for the ERP models that used total biomass. A preliminary assessment update was conducted in a maximum likelihood framework model (ASAP, from the NEFSC Toolbox), using the previous time-varying estimates of *M*, in order to incorporate the new MRIP estimates of recreational catch. The overall trend in *F* and SSB from the preliminary update was similar to the benchmark assessment trends, but the scale was somewhat different due to the higher recreational catch estimates.

The preliminary update indicates that total age-1+ biomass has declined since the beginning of the time series, from a high of 33,457 mt in 1986 to a low of 1,634 mt in 2014 (Figure 19). The population rebounded somewhat in the mid-1990s, but has been steadily declining since then. The preliminary estimate of total biomass in 2017 was 3,210 mt, an increase since 2014, but still well below the time-series mean. Spawning stock biomass showed very similar trends to age-1+ biomass, since weakfish are 90% mature at age 1 (Figure 19). The preliminary estimate of SSB in 2017 was 3,114 mt, below the SSB threshold of 8,815 mt.

Full *F* for weakfish declined through the early 1990s before increasing again; *F* spiked in 2008, but has been below average since then (Figure 19). *F* in 2017 was 0.23, below the proxy $F_{\text{THRESHOLD}}$ of 0.93.

9 BEAUFORT ASSESSMENT MODEL (BAM) DESCRIPTION AND CONFIGURATION

The Beaufort Assessment Model (BAM) has been used to assess Atlantic menhaden since 2010 (SEDAR 2010; SEDAR 2015). BAM is a statistical catch-at-age model that estimates population size-at-age and recruitment, using 1955 as the start year, and then projects the population forward in time. The model estimates trends in the population, including abundance-at-age, recruitment, spawning stock biomass, egg production, and fishing mortality rates. BAM was configured to be a fleets-as-areas model with each of the fleets broken into areas to reflect differences along the coast.

BAM estimates of age-1+ biomass have fluctuated over time from an estimated high of over 6,794,000 mt in 1959 to a low of 1,379,000 mt in 1973. From 1980 to the present, biomass has been increasing in trend. Population fecundity (number of maturing ova, used as the metric for

spawning capacity of the stock) was highest in the early 1960s and from the 1990s to the present. Age-0 recruits of Atlantic menhaden were highest during the 1950s. An extremely large year class was also predicted for 1958. Recruitment has appeared to be rather stable during the late 1970s to the present. Fishing mortality rate over time was reported as the geometric mean fishing mortality rate at ages-2 to -4, the dominant age-classes in the fishery, to account for differences in selectivity patterns over time. Geometric mean fishing mortality rate was highest in the 1970s and 1980s and has been declining since approximately 1990.

For more detailed information on the BAM configuration and results, see the single-species assessment report.

10 SURPLUS PRODUCTION MODEL WITH TIME-VARYING *r* (SPMTVR) (SUPPORTING)

An alternative to explicit incorporation of ecosystem processes in stock assessments is the use of single species models that implicitly estimate changes with time-varying parameters. Age- and length-structured stock assessments often implicitly account for anthropogenic and environmental effects on stock dynamics through the estimation of time-varying parameters such as natural mortality, growth, selectivity, and catchability (Fu and Quinn II 2000; Wilberg et al. 2010; Wilberg et al. 2011; Methot and Wetzel 2013; Nielsen and Berg 2014; Xu et al. 2019). In situations with less reliable data, the use of surplus production models with time-varying parameters may provide an alternative to explicit modeling of ecosystem drivers (Nesslage and Wilberg 2012, 2019). Using only a time series of catch and at least one index of abundance, surplus production models estimate stock biomass, carrying capacity, and the population's intrinsic growth rate (Prager 1994). The intrinsic growth rate of the population encompasses the growth response of the stock to its surrounding ecosystem, including mortality processes such as predation and recruitment processes affected by environmental conditions. If allowed to vary over time, surplus production model parameters can implicitly capture the effects of shifting drivers on fish stocks without having to explicitly model the underlying mechanisms, especially when time series are of sufficient length to cover periods of major anthropogenic or environmental change are available (Nesslage and Wilberg 2019).

A surplus production model with a time-varying intrinsic growth rate (SPMTVr) was fitted to Atlantic menhaden catch and indices of Atlantic menhaden biomass to generate annual estimates of fishery exploitation rate and total Atlantic menhaden biomass. The SPMTVr used is a modified Schaefer surplus production model with observation error (Polacheck et al. 1993; Quinn and Deriso 1999), which follows a logistic population growth process,

$$\hat{B}_{t+1} = \hat{B}_t + \hat{r}_t \hat{B}_t \left(1 - \frac{\hat{B}_t}{\hat{K}}\right) - C_t, \quad (10.1)$$

such that $\hat{B}_t$ is estimated Atlantic menhaden biomass at time t, $\hat{K}$ is carrying capacity, C_t is catch at time t, and $\hat{r}$ is the intrinsic population growth rate estimated annually according to a random walk on the log scale:

$$\log_e \hat{r}_{t+1} = \log_e \hat{r}_t + \omega_t, \quad (10.2)$$

with annual deviations, ω_t, from a normal distribution with a mean of zero and an SD of 0.1. A random walk was selected to generate annual deviations in *r* because random walk estimation processes have been shown to perform well under a variety of circumstances with trends over time, whereas other forms of annual deviations such as white noise are more limited in their application (Wilberg and Bence 2006).

The estimated index of biomass, $\hat{I}_t$, was the product of catchability and biomass,

$$\hat{I}_t = \hat{q}\hat{B}_t, \tag{10.3}$$

where $\hat{q}$ was survey catchability. Total catch was assumed known without error. Parameter estimates were obtained by minimizing the concentrated negative log likelihood function,

$$-LL_1 = \frac{n}{2}\log_e\left(\sum\left(\log_e(I_t) - \log_e\left(\hat{I}_t\right)\right)^2\right). \tag{10.4}$$

Multiplicative lognormal observation errors were assumed for the index of biomass. A normal (on the loge scale) prior, LL_2, was included on initial biomass,

$$-LL_2 = 0.5\left(\frac{\log_e(B_{t=1}) - \log_e(prior)}{sd}\right)^2 \tag{10.5}$$

such that $\hat{B}_{t=1}$ was the estimated biomass in the first year, prior was the prior point estimate, and *sd* was the standard deviation of the lognormal prior distribution. An additional term, -LL_3,

$$-LL_3 = \frac{1}{2\sigma^2}\sum \omega_t^2, \tag{10.6}$$

was included to account for the annual random walk deviations, such that annual deviations were normally distributed with a mean of zero and a known variance.

The SPMTVr estimates dynamic, MSY-based reference points that reflect changing stock productivity (Nesslage and Wilberg 2019). A dynamic overfishing threshold was produced by calculating 75% of annual U_{MSY} estimates (calculated as $\frac{r_t}{2}$). 75% of U_{MSY} was selected because it has been suggested as a general overfishing limit for forage species (Pikitch et al. 2012). Use of 75% of U_{MSY} in the terminal year as a reference point for management assumes that the *r* in the terminal year will continue (i.e., that there is substantial temporal autocorrelation in the population productivity). Biomass at 50% of B_{MSY} (B_{MSY} calculated as $\frac{K}{2}$) was defined as a potential overfished threshold for Atlantic menhaden given its common use in US federal fisheries management.

The SPMTVr was extensively simulation tested using a linked, age-structured, predator-prey model of Atlantic menhaden and striped bass (Nesslage and Wilberg 2019). The SPMTVr generally produced more accurate, less variable estimates of exploitation rate and biomass than traditional Schaefer surplus production models with static intrinsic growth.

10.1 Treatment of Indices & Input Data

The base model configuration of the SPMTVr included total annual landings (1,000t) during 1957-2017 and three adult indices of abundance (RCPUE, NAD, and MAD).

10.2 Parameterization

The intrinsic population growth rate in 1957 was estimated and annual deviations from that rate in each subsequent year. Other estimated parameters included catchability of each of the three indices of abundance, initial biomass, and carrying capacity. All estimated parameters were bounded (Table 5). Estimates of mean fishing mortality across the species' range (F = 0.55yr^{-1}) and natural mortality (M = 1.18yr^{-1}) generated from an historical tagging study conducted in the late 1960s (Liljestrand et al. 2019) were used along with a reported catch of 630,300 t in 1957 to estimate a starting value for initial biomass of 2,424,000 t. In addition, a normal prior was placed on the logarithm of initial biomass with a mean equal to the estimate of biomass in 1957 and a standard deviation of 0.15.

The starting value for the RCPUE index CV was assumed to be 0.5. For fishery-independent indices, CVs were assumed to be the time series average CV for the NAD (CV = 0.71) and MAD (CV = 0.70). Log-scale standard deviations for each index were adjusted iteratively to determine the final weights applied to each index (Francis 2011). The SD of the annual r deviations, ω_t, was set at 0.1 based on previous research in the use of random walk processes (Wilberg and Bence 2006; Nesslage and Wilberg 2012); however, model performance with random walk SDs of 0.05 and 0.2 were explored as well (Section 10.4.2).

10.3 Results

10.3.1 Diagnostics

The base run of the SPMTVr converged on a stable solution and parameter estimates did not approach bounds. The SPMTVr fit overall trends in abundance indices but overestimated RCPUE at the beginning of the time series and underestimated RCPUE at the end of the time series. Also, the model underestimated MAD at the beginning of the time series (Figure 20).

10.3.2 Population Estimates

The model estimated that biomass in 1957 (2,182,820 t) was near carrying capacity (2,182,790 t). The estimated trend in population intrinsic growth rate ranged from values of 0.76 to 0.88 at the beginning of the time series then dropped to values in the range of 0.55 to 0.68 from the 1990s to present (Figure 21). Estimated biomass declined sharply in the late 1950s to mid-1960s then increased through the end of the time series with a small period of decline in the early 1990s (Figure 22). Estimated exploitation rate increased through the 1950s, then largely declined from the 1960s through the end of the time series (Figure 23).

The SPMTVr produced a static biomass reference point (50% of B_{MSY} = 546,000 t), suggesting the stock was overfished from 1963-1969 but has remained above that reference point for the remainder of the time series (Figure 22). The model also produced a dynamic exploitation rate reference point (75% of annual U_{MSY}) that ranged from 0.21-0.33 yr^{-1}, suggesting that the exploitation rate exceeded 75% U_{MSY} prior to mid-1980s but that the stock was not experiencing overfishing from 1999 onward (Figure 23). The model estimated a time-varying TAC (Figure 24) with a 2017 estimate of 443,662 t.

10.3.3 Uncertainty

CVs of model parameter estimates based on asymptotic standard errors are reported in Table 5.

10.4 Sensitivity Analyses

Sensitivity analyses were conducted to examine the effects of model start year, alternative model configuration (alternate starting values for B_{1957} and the SD of *r* deviations), and alternative abundance indices (Figure 25 - Figure 26). In summary, all model configurations agreed that the stock was not overfished and was not experiencing overfishing in the terminal year of the model (Figure 27 top); however, the models differed substantially in estimated stock status trajectory over the time series (Figure 27 bottom).

10.4.1 Sensitivity to Input Data

Model sensitivity to the exclusion of early years with relatively high landings was examined by starting the model in 1964 instead of 1957. This alternative model estimated the magnitude of *r* was much lower (0.3-0.4), but *r* declined over time as in the base model (Figure 21). Biomass estimates were similar in trend but about double the magnitude (Figure 25). Similar to the base model, exploitation rate exhibited a decline over time since 1964, but was approximately half the magnitude (Figure 26).

Model sensitivity to an alternate primary index of abundance was also examined by exchanging the RCPUE with the PRFC fishery-dependent index and starting the model in 1964. This alternative model estimated a large spike in *r* in the 1970s that was not as pronounced in the RCPUE-based model, indicating a period of very high productivity during that time that is not evident in the RCPUE index (Figure 21). Use of the PRFC index resulted in estimates of biomass and exploitation rate which were largely similar to that of the base run with the exception of the 1970s during which biomass doubled and exploitation rate halved (Figure 25 - Figure 26).

A sensitivity run was also conducted in which the MARMAP/EcoMon ichthyoplankton indices of spawning biomass were added; however, the model did not exhibit good convergence criteria (results not shown).

10.4.2 Sensitivity to Configuration

Sensitivity of the base model to the SD of annual *r* deviations, ω_t, was examined using lower (0.05) and higher (0.2) values. Estimates of biomass and exploitation rate were largely similar to the base model despite an expected slight flattening in the trend in *r* with a lower SD (0.05) and slightly more exaggerated trend in *r* with a higher SD (0.2).

Sensitivity to the starting value and mean of the prior on initial biomass was also examined. First, use of a likelihood penalty was explored in which exploitation rates in 1967-1969 were

penalized for straying too far from the estimated values from an historical tagging study (Liljestrand et al. 2019). This model did not exhibit good convergence criteria, but produced similar estimates to that of another alternative model in which the starting value and mean of the prior on initial biomass was set equal to the BAM estimate of biomass in 1957 (Figure 21, Figure 25, Figure 26 & Figure 27). This model estimated very low, declining exploitation rates and high, increasing biomass compared with all other model configurations.

11 STEELE-HENDERSON SURPLUS PRODUCTION MODEL (SUPPORTING)

Steele-Henderson models are surplus production models with additional sigmoidal type III predation functions that estimate predation losses from one or more predators (Collie and Spencer 1993). They quantify the extent that modeled predators and fishing influence a prey species. When applied generally, the Steele-Henderson model reproduced rapid shifts in productivity exhibited by marine populations (regime shifts; Steele and Henderson 1984; Spencer 1997). Steele-Henderson models have been used to explore the role of predation on management of haddock (Spencer and Collie 1997), weakfish (NEFSC 2009), and Atlantic menhaden (Crecco 2010; Uphoff and Sharov 2018).

Steele-Henderson models represent an increase in mechanistic specificity over the time-varying *r* surplus production model: where the SPMTVr model did not specify a cause for time-varying productivity, the Steele-Henderson models assume that changes in productivity beyond what a traditional surplus production model would predict are driven by predator biomass. A Steele-Henderson model has the same data requirements as a surplus production model, plus it needs predator biomass estimates or indices to generate estimates of predation losses through a type III functional response (Collie and Spencer 1993; Crecco 2010). A Steele-Henderson model could be considered a "minimal realistic model" and the key feature of this approach is that only predators likely to have important impacts on the prey of interest are considered (Punt and Butterworth 1995; Yodzis 2001).

The Haddon (2001) version of a Schaefer surplus production model was adapted to the Steele-Henderson model formulation. An observation error model was used that assumed all residual errors were in the index observations and the equation used to describe the time-series was deterministic and without error (Haddon 2001). Biomass dynamics of Atlantic menhaden with losses from harvest and major predators were described by the following discrete time-step equation:

$$B_t = B_{t-1} + r \cdot B_{t-1}\left(1 - \frac{B_{t-1}}{K}\right) - H_{t-1} - \sum_j D_{j,t-1} + \varepsilon \qquad (11.1)$$

where B_t was age-1+ Atlantic menhaden biomass in year t; B_{t-1} = age-1+ biomass in the previous year, r = intrinsic rate of population increase; K = carrying capacity (unfished biomass); H_{t-1} = harvest in the previous year; $\sum D_{j,t-1}$ = the sum of estimated predation losses from predators in the previous year (estimated for each predator j by Equation 11.2, below); and ε = observation error (Collie and Spencer 1993; Spencer and Collie 1995). Initial biomass was estimated directly

for the starting year as a separate parameter and then projected forward by the Steele-Henderson model. A fishing-only version of the model (i.e., traditional Schaefer biomass dynamic model) was created from equation 11.1 by excluding predation loss terms ($\sum D_{j,t-1}$).

Annual consumption of Atlantic menhaden biomass by each candidate predator in the Steele-Henderson model was estimated by a type III functional response as

$$D_{j,t-1} = \frac{d_j \cdot P_{j,t-1} \cdot (B_{t-1})^2}{A_j^2 + (B_{t-1})^2} \quad (11.2)$$

where d_j was estimated maximum per biomass consumption for predator *j*; $P_{j,t-1}$ was predator *j* biomass at time *t-1*; A_j was estimated Atlantic menhaden biomass where predator *j* satiation begins (Collie and Spencer 1993; Spencer and Collie 1995) and B_{t-1} represented age-1+ Atlantic menhaden biomass. Predator biomass was an input and the remaining three terms were estimated by the model.

This configuration of the Steele-Henderson model was tested on the same simulated dataset used to evaluate the time-varying *r* model. See Appendix B for more a detailed description of the Steele-Henderson model configuration and results.

11.1 Treatment of Indices & Input Data

The base model configuration of the Steele-Henderson included three age 1+ Atlantic menhaden biomass indices: fishery-dependent RCPUE (1985-2017), and fishery-independent MAD (1985-2017) and NAD (1990-2017). The MAD and NAD indices were scaled into RCPUE units using a ratio of averages approach based on years in common (1990-2017).

The Atlantic menhaden single-species assessment time-series of landings in weight was used to characterize removals. Estimates of biomass from the most recent single-species assessments (see Section 8) for the candidate predators were used to characterize predator population trends. Biomass for each predator was defined as the sum of biomass in each age or size class capable of eating age-1+ Atlantic menhaden. Based on an examination of diet length composition data by Uphoff and Sharov (2018), this was age-3+ for striped bass and age-1+ for bluefish; for spiny dogfish, it was sizes 36 cm+ (Scharf et al. 2000).

11.2 Parameterization

Model Parameters

The Steele-Henderson model was implemented in an Excel spreadsheet, and a genetic algorithm plug-in (Evolver; Palisade Corporation 2010) was used to estimate model parameters that minimized the difference between the observed and predicted indices of relative abundance for Atlantic menhaden:

$$\sum_{i,t} \left(\ln(I_{i,t}) - \ln(q_i \cdot B_t) \right)^2 \quad (11.3)$$

where $I_{i,t}$ is the value of index i in year t, q_i is a catchability coefficient for index i, and B_t is the age-1+ biomass of Atlantic menhaden in year t.

The genetic algorithm used by the Evolver software continuously introduces novel parameter values (i.e., "mutations") during the model fitting procedure. As such, model optimization was concluded after a set time limit (3 minutes), as opposed to numerical convergence criteria. If the progress optimization summary graph indicated the sums of squares converged on an asymptote, the run was used. If the graph indicated it was not reached, then another run of 3-minutes was made and progress was evaluated again. None of the runs required more than 6 minutes for the sums of squares to converge on an asymptote.

The model fitting algorithm required bounds for each parameter (Palisade Corporation 2016) and the ranges used were broad. Parameter r varied from 0.1 (very low) to 3.0 (a value associated with chaotic behavior of populations described by logistic equations; May 1974). The range of K fell between 100,000 and 10,000,000 mt, a range that fell below lowest observed landings to about 23-times the highest landings. Initial biomass ranged from 50,000 to 2,500,000 mt. The same ranges of estimates of d (0 – 17-times predator weight) for striped bass and bluefish estimated by Uphoff and Sharov (2018) were used for the three candidate predators. The range in parameter A was set equal to the range for K. Mid-range values were used as starting values for all models, excluding sensitivity analyses (described below).

Akaike information criterion for small sample sizes (AICc) were used to evaluate fishing-only and Steele-Henderson models with different predators that related changes in Atlantic menhaden biomass to fishing alone or to fishing and predation (Burnham and Anderson 2001)

Predator Selection

The ERP focal species of striped bass, bluefish, and spiny dogfish were screened for consideration as major predators using correlation analyses of Atlantic menhaden indices (RCPUE, MAD, and NAD) and predator biomass estimates from single-species assessments. Correlation analysis provided weak evidence of potential predator-prey interactions, and Steele-Henderson models were developed with each predator separately, and with combinations of predators. The fit of the index time-series and the AIC_c from the Steele-Henderson models with different predators and the fishing-only surplus production model were used to determine which predators to include in the base model, along with evaluation of the magnitude of M_2 from the Steele-Henderson model. Striped bass was determined to be the sole major predator for the base Steele-Henderson model based on these criteria (Table 6).

Estimates of *ad libitum* consumption of prey at optimal temperature as grams of prey per gram of striped bass per day derived from Hartman and Brandt (1995a; 1995b) bioenergetics models (C_{MAX}) provided a means to judge a maximum value for parameter d for striped bass in the initial parameterization of the Steele-Henderson model.

Reference Points

Moustahfid et al. (2009a) explored the use of biomass dynamic models that included predation losses and applied the concept of maximum useable production (MUP; Overholtz et al. 2008; Moustahfid et al. 2009b) instead of maximum sustainable yield (MSY). MUP reference points were generated for Steele-Henderson models using the formula developed by Moustahfid et al. (2009a):

$$B_{MUP} = \frac{K}{2} \tag{11.4}$$

MUP represents the surplus production available to modeled predators and the fishery. The surplus production available to the fishery (*SF*) can be partitioned out as maximum usable production minus recent average predator consumption:

$$SF = MUP - D \tag{11.5}$$

Instantaneous annual fishing mortality at MUP (F_{MUP}) was estimated as:

$$F_{MUP} = \frac{SF}{B_{MUP}} \tag{11.6}$$

The Steele-Henderson model also calculated *F* and time-varying natural mortality from modeled predators (M_2) based on annual harvest and consumption:

$$F_t = \frac{H_{t-1}}{\frac{1}{2}(B_{t-1}+B_t)} \tag{11.7}$$

$$M_{2t} = \frac{D_{t-1}}{\frac{1}{2}(B_{t-1}+B_t)} \tag{11.8}$$

A time-varying total mortality (Z_2) could be calculated from *F* and M_2:

$$Z_{2t} = F_t + M_{2t} \tag{11.9}$$

Estimates of Z_2 / Z_{MUP} and F / F_{MUP} greater than 1.0 would exceed the mortality thresholds, while B / B_{MUP} ratios less than one would indicate the stock is overfished.

Patterson (1992) established a general relationship of biomass of exploited small pelagic fishes to F / Z and proposed that F / Z higher than 0.4 would lead to declines in stock size, so for this analysis, 0.4 was used as a threshold to evaluate F / Z_2.

Direct feedback from prey to predator is not a feature of a Steele-Henderson model and an empirical approach was employed to develop a threshold based on major predator condition. Indicators of condition were not routinely estimated for major predators, so annual weights-at-age were used as a condition metric for major predators assessed by catch-at-age models (bluefish and striped bass). Changes in striped bass weight-at-age may have been a coarse

indicator of condition since fasting striped bass replace lipids (the energy currency in marine fish; Rose and O'Driscoll 2002) with water in a linear fashion (Jacobs et al. 2013).

Correlation analysis (Pearson correlation coefficients, ρ; $P \leq 0.05$) was used to estimate strength of associations of D_t / P_t estimated by the base Steele-Henderson model with weight-at-age in the same year, and one, two, and three years before (i.e., an immediate response in weight to feeding vs. lagged responses). Correlations with weight-at-age were considered biologically significant if they occurred over continuous blocks of ages rather than sporadically.

If a major predator had a block of ages with D_t / P_t correlated with weights-at-age, the series of weights for a given age within the block were standardized to their age-specific time-series mean. Then a linear regression of D_t / P_t from the base Steele-Henderson model and standardized weight-at-age for all ages within the time block was used to predict the point where D_t / P_t results in average weight (standardized weight-age-age = 1.0). This point was considered a threshold consumption level for predator condition. Data were further examined to determine the risk that below average weight would occur when D_t / P_t was at or below the threshold and to see if a potential D_t / P_t target was suggested where the chance of a predator being below average weight was substantially less. For striped bass, this analysis resulted in a potential target for D_t / P_t of 2.2, which was consistently met or exceeded once Z_2 / Z_{MUP} fell below 0.87.

11.3 Results

11.3.1 Diagnostics

Based on AIC_c, a fishing biomass dynamic model and a Steele-Henderson model featuring striped bass were equally likely the best models given the data; both models had an AIC_c of -156. Neither the base fishing-only model nor the base striped bass Steele-Henderson model (base Steele-Henderson model) fit the individual indices well. The r^2 for the striped bass Steele-Henderson model was 0.18 for the fit of the observed and estimated RCPUE indices, 0.12 for NAD, and 0.33 for MAD. Residuals appeared normally distributed with a mean near zero and serial patterning was not evident. Trends in estimated indices were similar between the fishing only and striped bass Steele-Henderson models, but the fishing only model trend was smoother (Figure 28). The Steele-Henderson model was able to account for some year-to-year variability (Figure 28), but the model does not include any process error (i.e. recruitment deviations) and so it was not expected to fit the fine scale inter-annual variability in the observed indices.

Bioenergetics-based annual C_{MAX} estimates derived by Uphoff and Sharov (2018) for striped bass ranged from 12.7 to 15.6-times striped bass body weight and the median equaled 14.6; the Steele-Henderson model estimated the striped bass-specific parameter *d* to be 11.0. Buckel et al. (1999) estimated annual C_{MAX} for bluefish (17.8), while the Steele-Henderson model estimated *d* at 5.1. Similar information for spiny dogfish was not available.

11.3.2 Population Estimates

Estimates of *r* and *K* were quite different between the fishing-only and the base Steele-Henderson model which included striped bass a predator (Table 6). The estimate of *r* was higher for the Steele-Henderson model (2.27) than the fishing only model (0.32) and K was about 3-times lower for the Steele-Henderson model (Table 6). Adding striped bass predation to harvest resulted in a general shift in depiction from a stock with low productivity and high biomass to one with high productivity and low biomass. The estimate of MSY from the fishing only model was 273,184 mt, while the estimate of MUP from the Steele-Henderson model was 608,517 mt. It is not uncommon with biomass dynamic models that data can be well explained as coming from a small, productive stock or a large, unproductive one since estimates of *r* and *K* are often highly negatively correlated (Walters and Martell 2004).

The base Steele-Henderson model indicated that biomass was initially high (B / B_{MUP} ~ 1.5), then declined steadily into the late 1990s (B / B_{MUP} ~ 0.7), increased sharply to near 1.0 by 2000, and finally increased to about 1.25 in 2014 and remained there through 2017 (Figure 29). Biomass was below its threshold during 1990-2001.

Base Steele-Henderson model estimates of landings as a proportion of annual surplus production available to the fishery indicated that the ratio exceeded 1.0 seven times between 1990 and 2010; it has been between 0.69 and 0.86 since 2013 (Figure 30). Relative *F* was above the F_{MUP} threshold intermittently during 1990-2010 with the base Steele-Henderson model; the model identified 1995-1998 as the period of highest *F* (Figure 31). Relative M_2 (M_2 / Z_{MUP}) rose from less than 0.20 in 1985 to a plateau of 0.60-0.70 that was maintained from the mid-1990s to 2010. It then dropped to approximately 0.50 by 2013 and remained there through 2017 (Figure 32). Relative Z_2 (Z_2 / Z_{MUP}) was below the threshold during 1985-1989. Relative Z_2 estimated by the base Steele-Henderson model consistently exceeded the threshold from 1990 to 1997 and intermittently through 2010, but declined below the threshold and remained at about 0.80 after 2012 (Figure 33).

Estimates of F / Z_2 indicated that *F* was the major influence on the stock until the late 1990s (base Steele-Henderson model; Figure 34). Estimates of F / Z_2 from the base Steele-Henderson model were generally below the threshold after 1998, but were at or near it during 2001-2002 and 2011-2012.

Striped bass consumption

The range of D_t / P_t was 1.1 – 3.8 for the base Steele-Henderson model. Estimates from the base Steele-Henderson model started high during 1985-1987 (3.5-3.8), fell to a nadir (1.1) during 1997-1998, quickly rose to near 2.0 by 2001, dipped to 1.6 in 2002, rose again, remained near 2.0 during 2003-2011, climbed to about 2.8 in 2014, and remained there through 2017. D_t / P_t estimates were lower than the annual consumption estimates derived from bioenergetics models, which ranged from 4.2 – 6.3 (Uphoff and Sharov 2018).

Forage Status of Ages 1+ Atlantic Menhaden for Striped Bass in 2017

Based on the base Steele-Henderson model, ages 1+ Atlantic menhaden were at low risk of not maintaining their forage role for striped bass in 2017. Atlantic menhaden harvest was low relative to historic levels and estimated striped bass biomass in 2017 was at its lowest since recovery. This combination led to relatively low predatory and fishery demand. None of the proposed indicators (B / B_{MUP}, Z_2 / Z_{MUP}, D_t / P_t, F / Z_2, F / F_{MUP}, and H_t / SF) exceeded threshold conditions in 2017 and the risk that they did (based on jackknifed distributions for 2017) was estimated as 0% (Table 7). None of the 90% intervals overlapped a threshold. If the suggested target conditions ($D_t / P_t \geq 2.2$ and $Z_2 / Z_{MUP} < 0.87$) in the previous section are considered, then the risk of not meeting these targets was also zero.

11.3.3 Uncertainty

Bounds of the 90% intervals of r, K, B_{1985}, A, and MUP were within 5% of the estimated values, while d was less precise (9%). High precision of model parameters lead to precise estimates of ages 1+ Atlantic menhaden biomass (Figure 35), D (total biomass consumed by striped bass; Figure 36), M_2 (Figure 37), F (Figure 38), Z_2 (Figure 39), and D_t / P_t (Figure 40).

11.3.4 Simulation Testing

The Steele-Henderson model using Evolver underwent limited testing with the simulated data set used to test the time-varying r surplus production model (25 runs for each scenario). The results indicated that the Steele-Henderson model could fit the simulated index fairly well and had a low relative error for prey biomass and exploitation rate, but overestimated M_2 (Figure 41). The magnitude of M_2 overestimation varied over the time series and depended on the scenario (e.g., increasing, decreasing, or constant predator time series). Because the Steele-Henderson model estimates a time-constant r value, annual variability in productivity caused by variability in recruitment (as in the simulated data) or other factors may be subsumed into the estimates of M_2. The simulation testing suggested that the magnitude of the estimates of M_2 from this model could be positively biased. Estimates of consumption-related parameters can be evaluated for plausibility with estimates from other studies of predator consumption (as was done with the base runs) or M of forage species. Better starting values for consumption might have resulted in better simulation model performance and further work on this with the simulated data is needed.

11.4 Sensitivity Analyses

Runs were made with initial values 20% higher or lower than the midpoints used as the common starting value. The PRFC index was substituted for the RCPUE index (MAD and NAD indices were standardized to PRFC index units using the same approach used for RCPUE). Retrospective bias of the base run was investigated by sequentially removing up to the last four years (2014-2017) from analysis. Additional runs were made that removed one of the indices from analysis to investigate an individual index's influence. Index pairs considered were RCPUE and NAD, RCPUE and MAD, and NAD and MAD.

Since the genetic algorithm did not provide a defined endpoint for convergence, the base Steele-Henderson model was run for one hour to look at run time sensitivity. Three runs were made with different limits on Steele-Henderson model parameter *d*: *d* was confined to a range estimated from bioenergetics; *d* was allowed a higher maximum (starting range for *d* was 0-20.0); and the default penalty function in Evolver was imposed for *d* if estimates exceeded the maximum (17.0). These three runs were prompted by concerns about parameter *d* being at its maximum constraint for one of the predators in Uphoff and Sharov (2018).

Sensitivity runs resulted in a "population" of base Steele-Henderson models with well-correlated parameters that produced the same general depiction of Atlantic menhaden (high *r* and low *K*) as the base Steele-Henderson model (Table 8). Estimates of *r* ranged from 1.66 to 2.56; *K*, $9.7^5 – 1.4 \cdot 10^6$; mt B_{1985}, $7.1 \cdot 10^5 – 1.1 \cdot 10^6$ mt; *d*, 7.8 – 17.0 (two were at maximum constraint) and *A*, $7.8 \cdot 10^5 – 2.0 \cdot 10^6$ mt (Table 8). Correlations among Steele-Henderson model parameters of the base Steele-Henderson model and six sensitivity runs were high for *r*, *K*, B_{1985}, and *A*, and for *d* and *A* ($\rho \geq 0.90$ or ≤ -0.91; $p \leq 0.0064$; Table 9). Parameter *d* was modestly correlated with *r* ($\rho = 0.67$, $p = 0.10$) and *K* ($\rho = 0.63$, $p = 0.15$); High correlation of *r* and *K* led to estimates of MUP among the seven runs with a maximum difference of 4% from the base run (Table 8).

Steel-Henderson model estimates of B / B_{MUP} (Figure 42), Z_2 / Z_{MUP} (Figure 43) and D_t / P_t during 1985-2017 (Figure 44) were very similar across sensitivity runs. Substantially different conclusions about status were unlikely among the Steele-Henderson model runs. Differences among annual estimates of B / B_{MUP}, Z_2 / Z_{MUP}, and D_t / P_t from the sensitivity runs were small (Table 10).

A striped bass Steele-Henderson model using the PRFC index (PRFC Steele-Henderson model) fit the data similarly well to the base model (Figure 45). The r^2 for the PRFC Steele-Henderson model was higher for the fishery-dependent index (PRFC: 0.35), but lower for the fishery-independent indices (NAD: 0.01; MAD: 0.25) Residuals appeared normally distributed and serial patterning was not evident.

Different conclusions about stock status were not likely if the PRFC index was substituted for the RCPUE index during 1985-2017. Trends in B / B_{MUP}, Z_2 / Z_{MUP}, and D_t / P_t were very similar between the base run and the PRFC Steele-Henderson model. Estimates of B / B_{MUP} from the PRFC Steele-Henderson model were generally higher than for the base run (Figure 46), while estimates of Z / Z_{MUP} from the PRFC Steele-Henderson model were generally lower than for the base run (Figure 47). Estimates of D_t / P_t were similar (Figure 48).

Removal of a single index from the time-series increased variability (SSQ / N) by about a third over the base run for the two pairings that included RCPUE and the variability of the run featuring only fishery-independent indices was nearly double that of the base run (Table 11). All pairing combinations resulted in parameters that would generalize Atlantic menhaden as a highly productive stock. If the MAD index was included in the time-series, *r* ranged between 2.01 and 2.27; *r* equaled 1.26 for the run without the MAD index (RCPUE and NAD; Table 11).

Estimates of K were similar for runs that included RCPUE (~1.1 to 1.4 · 10^6 mt) and higher (~1.8 · 10^6 mt) for the run with only fishery-independent indices (Table 11).

Removal of the RCPUE index (i.e., fishery-independent indices remained) resulted in D_t / P_t estimates that exceeded the maximum estimated for striped bass from bioenergetics models during 1985-1989 (Uphoff and Sharov 2018) and fell between the minimum and maximum during 1990-1993 and 2013-2017 (Figure 49). These estimates were considered unlikely and assessment based on the two fishery-independent indices alone would be biased. Estimates of D_t / P_t from the remaining three runs with RCPUE were considered plausible. The RCPUE and NAD run indicated that fewer ages 1+ Atlantic menhaden were consumed by Ages 3+ striped bass (low D_t / P_t), while the base run and run with RCPUE and MAD were similar and D_t / P_t was about 2-3 times that of the RCPUE and NAD run (Figure 49).

The RCPUE and MAD Steele-Henderson model estimates of B / B_{MUP} were very close to the base run (Figure 50). All four runs indicated that B / B_{MUP} was above the threshold during 1985-1990. The base run, RCPUE and MAD run, and the RCPUE and NAD run fell below the B / B_{MUP} threshold during the 1990s. The base and two-index runs that included RCPUE remained near the threshold through 2011 and then climbed above 1.20 and remained there. The RCPUE and NAD run diverged from the base run in the early 1990s and for the remainder of the time-series provided a more optimistic view of B / B_{MUP} that was an additional 0.10 - 0.20 greater than the base run. Estimates of B / B_{MUP} from the MAD and NAD run reflected the unrealistically high estimates of consumption and were 0.15 to 0.25 lower than the base run after striped bass recovered in 1995 (Figure 50). Trends in Z_2 / Z_{MUP} were the converse of those described for B / B_{MUP} (Figure 51).

11.5 Retrospective Analyses

Removal of up to four years from the end of the time-series in retrospective runs had minimal impact. Variability (SSQ / N) remained close to that of the base run (Table 11). Most parameters estimated were well correlated ($\rho > 0.90$ or < -0.90 for r, K, and B_{1985}, K and A, and A and d) among the retrospective runs. All combinations resulted in parameters that would generalize Atlantic menhaden as a small, productive stock (Table 11). Retrospective bias was not apparent in B / B_{MUP} (Figure 52), Z_2 / Z_{MUP} (Figure 53) and D_t / P_t (Figure 54) when up to four years were removed from the end of the 1985-2017 time series.

11.6 Projections

Stochastic projections using the base Steele-Henderson model were made for 2018-2041. They explored four scenarios: (1) continuation of 2017 harvest with major predators at 2017 levels (status quo projection), (2) major predator biomass increases to recovered status (Table 3) and Atlantic menhaden are fished at one half their target F (major predator recovery, half-target F projection); (3) major predator biomass increases to recovered status and Atlantic menhaden are fished at their target F (major predator recovery, target F projection); and (4) predator biomass increases to a point where a proposed consumption threshold is met and Atlantic

menhaden are fished at their current harvest (predator consumption threshold, current harvest projection). For Steele-Henderson model projections featuring predator recovery, a ten-year period was arbitrarily chosen for recovery and then predator biomass was held steady for another ten years. Terminal estimates represented "equilibrium" conditions for each projection.

Two distributions provided the best depiction of jackknifed base Steele-Henderson model parameters. A Laplace distribution (also known as a double exponential distribution) fit *K, d, A*, and Atlantic menhaden ages 1+ biomass on January 1, 2018, best. The distribution of *r* was best described by a log logistic distribution. Jackknifed estimates of the four Steele-Henderson parameters needed for projections (*r*, *K*, *d*, and *A*) were weakly to moderately correlated (Table 12). Graphs of distributions are presented in Figure 55 – Figure 57 . Table 13 provides a summary of location, scale, and shape values assigned to distribution functions for each simulated parameter.

Biomass of ages 3+ striped bass in 2018 was set at the estimate for 2017 (134,796 mt). Striped bass biomasses for 2018 and subsequent years were assumed to be normally distributed and were assigned a CV of 6% based on variation of biomass estimates in the recent assessment. Striped bass recovery is based on an SSB target. Target ages 1+ striped bass biomass at target SSB for projections was estimated for ages 1+. The median proportion of ages 1+ striped bass biomass that was comprised of ages 3+ (0.84) during the period the stock has been considered recovered (1995-2017) was multiplied by the target estimate for ages 1+ to approximate target biomass of ages 3+ striped bass (260,685 MT) capable of eating ages 1+ Atlantic menhaden at target SSB.

The status quo projection indicated very low risk that ages 1+ Atlantic menhaden's forage role would not be maintained (Table 14). At "equilibrium", the 90% CI's of B / B_{MUP}, Z_2 / Z_{MUP}, and D_t / P_t did not overlap their proposed thresholds and estimated risk of breaching these thresholds was 0%. Projected D_t / P_t averaged 2.89 (45% higher than the threshold), a value associated with higher than average weights (i.e., better condition) of ages 6+ striped bass (Table 14). Maintaining the forage role of ages 1+ Atlantic menhaden for striped bass was likely.

The projection where striped bass biomass increased to recovered status (ages 3+ biomass nearly doubles) and Atlantic menhaden are fished at status quo *F* (F_{2017}) represented a high-risk strategy (Table 14). Substantial portions of 90% intervals of all three metrics overlapped their thresholds. Risk of breaching the B / B_{MUP} threshold was 80%; risk of breaching the Z_2 / Z_{MUP} threshold, 55%; and the risk of breaching the D_t / P_t threshold, 85%. Average yield would be 26% less than in 2017 and average D_t / P_t was 10% less than the threshold, indicating consumption was not sufficient to maintain striped bass individual weight at or above the time series average (Table 14). Maintaining the forage role of ages 1+ Atlantic menhaden for striped bass was unlikely with this strategy.

The projection where striped bass biomass increased to recovered status and Atlantic menhaden were fished at their target *F* had the highest risk (Table 14). Ninety percent intervals

of all three metrics came close to completely overlapping their thresholds. Risk of breaching the B / B_{MUP} threshold was 100%; breaching the Z_2 / Z_{MUP} threshold, 95%; and the risk of breaching the D_t / P_t threshold was 100%. Yield was 26% greater than in 2017 and average D_t / P_t was 30% less than the threshold (Table 14). Maintaining the forage role of ages 1+ Atlantic menhaden for striped bass was unlikely.

The projection with predator biomass increasing to a point where their consumption threshold is met and Atlantic menhaden harvested at their current level represented a high risk option, but not as risky as the previous two (Table 14). Ninety percent intervals of all three metrics overlapped their thresholds near the interval midpoint. Risk of breaching the B / B_{MUP} threshold was 45%; risk of breaching the Z_2 / Z_{MUP} threshold, 60%; and the risk of breaching the D_t / P_t threshold was 50%. Striped bass biomass was 83% of the target to maintain D_t / P_t at its threshold (Table 14). Risk that the forage role of ages 1+ Atlantic menhaden for striped bass would not be met was high. Atlantic menhaden harvest in this projection would be considered low by historical standards and striped bass biomass had to be below its current target in order to meet threshold (not target) D_t / P_t.

12 MULTISPECIES STATISTICAL CATCH-AT-AGE MODEL (VADER) (SUPPORTING)

Some of the earliest multispecies modeling work connected virtual population analysis (VPA) models together with predation functions (Helgason and Gislason 1979; Gislason and Helgason 1985; Sparre 1991; Livingston and Jurado-Molina 2000). This modeling approach can be helpful in a complex fisheries modeling environment because the strong assumptions on certain parameters aid in the estimation of the remaining parameters. From this more deterministic modeling technique, statistical approaches were then developed using either age-based, or length-based statistical models. These statistical approaches are more comparable to some of the single-species assessment methods that are now used and have the added benefit of allowing the estimation of uncertainty around the estimated population parameters (Lewy and Vinther 2004; Van Kirk et al. 2010; Curti et al. 2013). The goal of these multispecies approaches is to create more realistic information for fisheries management (Gislason 1999; Moustahfid et al. 2009a). The multispecies statistical catch-at-age model (hereafter referred to as Virtual Assessment for the Description of Ecosystem Responses, or VADER) developed for this assessment adopted the more progressive statistical approach for its modeling methodology and was built on the foundational work of Curti et al. (2013) and McNamee (2018).

12.1 Treatment of Indices & Input Data

The VADER model was constructed around the six ERP focal species: Atlantic menhaden, striped bass, bluefish, weakfish, Atlantic herring, and spiny dogfish. The species were selected based on a review of important predator diet information, the availability of age-structured data for the species, and knowledge of the migratory patterns of the species (see also Section 3.1.2). The confounding factor of temporal and spatial overlap was mitigated to some degree by the fact that the ERP focal species all have similar seasonal migratory patterns (Section 4). However, Atlantic herring and spiny dogfish do not overlap as significantly as the other species – an important consideration when interpreting the output from this assessment model, which does not explicitly account for spatiotemporal overlap in predators and their prey.

In the model, striped bass, bluefish, and spiny dogfish were top predators of both Atlantic menhaden and Atlantic herring. Both Atlantic menhaden and Atlantic herring were strictly forage species. Weakfish served as both a predator of Atlantic menhaden and Atlantic herring, as well as a prey species for striped bass, bluefish, and spiny dogfish. Cannibalism by any species was not accounted for in this study. All symbols and likelihood components for the multispecies model are indicated in Table 15 and Table 16 respectively.

As in Curti et al. (2013), there were six types of input data needed for each species in the model: total fishery removals in weight, fishery-independent indices of abundance, age proportions for both fishery removals and fishery-independent survey catches, average weight-at-age by year, and age-specific predator diet information. With the exception of spiny dogfish, single-species statistical catch-at-age models are used for management of all of the ERP focal species. Spiny dogfish are assessed using a swept-area biomass approach. Unless otherwise noted, all data inputs used were taken directly from recent stock assessment documents and from direct communication with the stock assessment scientists that work on these species (Section 8).

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

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

In contrast to the work done by Curti et al. (2013), many of the ERP focal species have multiple surveys – with differing time series and gear types – that are used to estimate stock abundance over time. To accommodate multiple surveys while keeping the model structure as simple and computationally efficient as possible, a subset of the available surveys for each species was used. For each species, one YOY survey was selected along with two adult indices, when available (Table 17). This subset was identified using ASMFC TC guidance on the most appropriate indices of abundance for their respective species. Data for these indices – including

the number per tow in each year, uncertainty around the index values, and age composition data – was taken from the stock assessment documents and most recent assessment information. Given that Atlantic menhaden are the focus of this work, the YOY index and all three of the adult indices from the single-species benchmark assessment were used. Only two indices were used for Atlantic herring and one index for spiny dogfish, with no YOY indices for either species. See Section 7 for more details on the surveys used.

Average individual weight-at-age was needed to convert from numbers to biomass units. The weight-at-age information was introduced in the model as a matrix, so the information varies not only by age, but by time as well. This is an important consideration as several of the ERP focal species have significant shifts in weight-at-age through time.

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

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

$$C_y^{i,a} = 24 * E_s^{i.a} * \overline{SC}_y^{i,a} * D_y * w_y^{i,a} * \bar{N}_y^{i,a} \qquad (12.1)$$

Where SC_y is the mean stomach-content weight relative to predator body weight in a year (*y*), D_y is the number of days in the year, $w_y^{i,a}$ is the average yearly weight at age for the predator species, and $\bar{N}_y^{i,a}$ is the abundance of the predator age class during the year. The predator-specific evacuation rate $E_{i,a}$ (hr^{-1}) is given as:

$$E_{i,a} = a_{i,a} * \exp\left(b_{i,a} * T_y\right) \qquad (12.1.1)$$

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

These data were updated through 2017 as these species-specific data were available. As noted above, the *C*/*B* ratios were developed for the MSVPA with more resolution (i.e. daily *C*/*B* ratios by season), but were aggregated across the whole year for this model to create a matrix of age-specific *C*/*B* ratios by species that varied through time based on the annual temperature. The method for calculating the Mean Annual Sea Surface Temperature (SST) for the US East Coast

Shelf for 1985-2017 was calculated using daily mean SST on a 0.25° spatial grid from the NOAA Optimum (OI) SST V2 High Resolution Dataset. OISST is also known as Reynolds' SST. OISST provides global fields that are based on a combination of ocean temperature observations from satellite, Advanced Very High Resolution Radiometer (AVHRR) infrared satellite SST data, and in situ platforms (i.e., ships and buoys). The input data are irregularly distributed in space and must first be placed on a regular grid. Then, statistical methods (optimum interpolation, OI) are applied to fill in where there are missing values. The methodology includes a bias adjustment step of the satellite data to in situ data prior to interpolation (Reynolds 2007).

The High Resolution SST data were provided by the NOAA/Ocean and Atmospheric Research/ Earth System Research Laboratory/Physical Sciences Division from their website at https://www.esrl.noaa.gov/psd/. Specifically, netcdf files with global mean daily SST for 1985-2017 were downloaded from: https://www.esrl.noaa.gov/psd/cgi-bin/db_search/DBListFiles.pl?did=132&tid=68373&vid=2423

A spatial polygon covering the US East Coast Shelf was used to clip regional data from the global data sets. The daily mean values for the region were used to calculate an annual mean for each year. All analyses were performed using the R software environment for statistical computing and graphics (R Core Team 2018 – specific packages used are included in the references). Algorithms for clipping OISST data and calculating mean annual SST were adapted from algorithms used for the NOAA\Northeast Fisheries Science Center's Ecosystem Status Report (Ecosystem Assessment Program 2012 and Sean Hardison, pers. comm).

As assumed in Curti et al. (2013) and based on previous work (Sparre 1980; Tsou and Collie 2001), a constant, time-invariant total ecosystem biomass was assumed. As a result, the total ecosystem biomass was constant over time, but the biomass of the individual modeled species could vary annually. Prior studies have confirmed that the total biomass in large marine ecosystems can remain relatively stationary through time (Link et al. 2008; Auster and Link 2009; Byron and Link 2010). There were no direct measurements found indicating what this overall biomass estimate should be, so a total biomass estimate from the MSVPA was used as a starting point. To supplement and support the MSVPA derived total ecosystem biomass value, information derived from an Atlantic coast Ecopath model was also investigated (Buchheister et al. 2017). Both values were close in magnitude. Testing with the multispecies assessment model indicated that performance was best for the value derived from the Ecopath model (94,800,000 mt) and therefore this value was the one selected for the base case run of the model.

Stomach-content data were obtained from three main sources: the NEFSC Food Web Dynamics Program, NEAMAP, and ChesMMAP also collect stomach-content data under similar protocols to the NEFSC program (Section 3.1.1). These length-based data for predator and prey from stomach-content information were converted to weight through the use of length-weight relationships as collected in Wigley et al. (2003). Age-specific predator diet habits, input to the model as proportion by weight for each age class, were averaged over 3-year periods to reduce the inherent variability in the dataset, as well as to reduce the amount of missing data and

increase the sample size being used for any year (Van Kirk et al. 2010), while still capturing the temporal trends.

Even with binning, there are still gaps and sample size issues in the data for this portion of the model. A Bayesian technique was used to account for this. A multinomial probit model was developed for the diet data, using the implementation in the MNP package in R (Imai and van Dyk 2005). Under the multinomial probit model, a multivariate normal distribution on the latent variables is assumed, $W_i = (W_{i1}, \dots, W_{ip-1})$.

$$W_i = X_i\beta + \epsilon_i, \epsilon_i \sim N(0, \Sigma), for\ i = 1, \dots, n \quad (12.2)$$

where X_i is a $(p-1)$ x k matrix of covariates, β is k x 1 vector of fixed coefficients, ϵ_i is $(p-1)$ x 1 vector of disturbances, and Σ is a $(p-1)$ x $(p-1)$ positive definite matrix. For the model to be identified, the first diagonal element of Σ was constrained, $\sigma_{11} = 1$. The response variable, Y_i, is the index of the prey choice of predator i among the alternatives in the choice set (here it was the prey items Atlantic menhaden, weakfish, Atlantic herring, and "other food") and was modeled in terms of this latent variable, W_i , via

$$Y_i(W_i) = \begin{cases} 0, & if\ max(W_i) < 0 \\ j, & if\ max(W_i) = W_{ij} > 0 \end{cases}, for\ i = 1, \dots, n, and\ j = 1, \dots, p-1 \quad (12.3)$$

where Y_i equal to 0 corresponded to a base category.

The matrix X_i may include both choice-specific and predator-specific variables. A choice specific variable is a variable that has a value for each of the p choices (in our case this is 4 choices for each prey species in the model plus an "other" category), and these p values may be different for each predator. Choice-specific variables are recorded relative to the baseline choice (in this case weakfish was used as the base case) and thus there are $(p-1)$recorded values for each predator. In this way a choice-specific variable is tabulated as a column in X_i. Predator-specific variables, on the other hand, take on a value for each individual predator, but are constant across the choices, e.g., the age of the individual predator. These variables are tabulated via their interaction with each of the choice indicator variables. Thus, a predator-specific variable corresponds to $(p-1)$ columns of X_i and $(p-1)$components of β .

The prior distribution follows the methods of Imai and van Dyk (2005). The prior distribution for the multinomial probit model is

$$\beta \sim N\left(0, A^{-1}\right) \text{ and } p(\Sigma) \propto |\Sigma|^{-\frac{(\nu+p)}{2}} \left[trace\left(S\Sigma^{-1}\right)\right]^{-\frac{(\nu-p)}{2}} \quad (12.4)$$

where A is the prior precision matrix of β, ν is the prior degrees of freedom parameter for Σ, and the $(p-1)$ x $(p-1)$ positive definite matrix A is the prior scale for Σ; the first diagonal element of S is assumed to be one. The prior distribution on Σ is proper if $\geq (p-1)$, the prior mean of Σ is approximately equal to S if $\nu \geq (p-2)$, and the prior variance

of Σ increases as ν decreases as long as this variance exists. An improper prior on β was allowed, which was $p(\beta) \propto 1$ (i.e. $A = 0$).

This model was run on the existing dataset, and then used to predict for each combination of predator, year-bin, and predator age group. In some cases, no data existed for certain combinations (a certain predator, in a certain year-bin, at a certain age class), and therefore a prediction was not possible. In these cases, a simpler model without year-bin was also run, and when a combination was missing from the dataset, the global preference of prey for the predator was used instead of the year-bin specific preference, meaning the preference of the predator at that age class across the entire dataset was used to fill this data gap.

Spiny Dogfish

Spiny dogfish input data were a special case. Spiny dogfish inputs were constructed from several sources, due to the fact that spiny dogfish do not have an age-structured assessment. Separate male and female indices from the spring NEFSC Survey were obtained from NEFSC (personal communication, Katherine Sosebee). These were standardized in number per tow and adjusted for any gear or vessel changes. Separate sexed age-length keys were constructed using von Bertalanffy relationships found in Nammack et al. 1985 and following methodology from Curti 2012. Sexed landings were retrieved from Sosebee and Rago 2018 (2018 spiny dogfish status update) and were from the U.S., Canadian, and Foreign fisheries. Since the single species assessment used these values and there was a period of time in the early 2000s when Canadian fisheries had high landings, all of these sources were included (see Table 5 in Sosebee and Rago 2018). Landings were added to sexed dead discards from NMFS port sampling but only back to 1991. Dead discard numbers from Table 3 in the 2018 status update were used for 1985-1990 (this table indicates that this time period was hindcast from SARC 43). These numbers were broken down by sex using the formulas in Table 6 from the 2018 status update using averages of 1991-1993.

Spiny dogfish catch-at-age was calculated using survey index as a length frequency (which assumed that survey length frequencies were the same as the commercial/recreational catch for the landings in the U.S., Canada, and foreign fisheries), age-length keys from Nammack et al. (1985) (time-invariant, the same age-length key was used for each year), and catch in numbers. A plus group was decided after review of Nammack et al. (1985), where growth curve plateaus for males at 20+. Sexed spiny dogfish weight-at-age was also calculated separately using this information. Male and female catch-at-age and weight-at-age were combined to generate a weighted total catch-at-age and weight-at-age using a sex ratio.

The maturity-at-age matrix was assumed to be knife-edge at 12 years old, consistent with Curti (2012) and Nammack et al. 1985. A static and time-invariant natural mortality of 0.092 was used based on a life span of 50 years from TRAC (2010) and Curti (2012). Initial year one biomass estimates in 1985 were from the TRAC (2010) and adjusted for catchability based on Sagarese et al. (2016). These were converted to numbers-at-age using the catch-at-age to partition the biomass into age bins and the weight-at-age to convert to numbers.

12.2 Parameterization

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

Progression of year class abundance was implemented by the equation:

$$N_{i,a+1,t+1} = N_{i,a,t} e^{-Z_{i,a,t}} \tag{12.5}$$

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

$$N_{i,a,t+1} = N_{i,a-1,t} e^{-Z_{i,a-1,t}} + N_{i,a,t} e^{-Z_{i,a,t}} \tag{12.6}$$

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

$$C_{i,a,t} = \frac{F_{i,a,t}}{Z_{i,a,t}} N_{i,a,t} (1 - e^{-Z_{i,a,t}}) \tag{12.7}$$

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

$$F_{i,a,t} = s_{i,a} F_{i,t} \tag{12.8}$$

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

$$FIC_{i,t} = q_i r_{i,a} N_{i,t} e^{-\frac{m}{12} Z_{i,t}} \tag{12.9}$$

This mathematical configuration assumes an age and time-invariant catchability (q_i), age-specific survey selectivity coefficients ($r_{i,a}$), and also accounts for the time of year during which the survey was conducted (m) so total mortality can be applied to the index appropriately. Species-specific catchabilities (q_i) were calculated from the entire time series deviations between the model predicted absolute abundance and model predicted relative abundance (Walters and Ludwig 1994).

Finally, age-specific fishery and survey selectivity coefficients were estimated for each species for all age classes through the choice of either a logistic or double logistic selectivity function, depending on the choices made by the single-species stock assessment teams. YOY surveys

assumed age specific selectivity, with selection being 1 for the first age class and 0 for all other age classes. This formulation departed from previous work (Curti et al. 2013) and was reconfigured to better simulate the selectivities for the modeled species by allowing doming in the selectivity-at-age, which provided more consistency with the selectivity shapes used in the single-species assessments. The four-parameter double logistic equation used for both the fishery selectivity and the fishery-independent survey selectivity was:

$$Sel_{x,i,a} = \left(\frac{1}{1 + e^{-(a-\alpha_1)/\beta_1}}\right)\left(1 - \frac{1}{1 + e^{-(a-\alpha_2)/\beta_2}}\right) \quad (12.10)$$

And the two-parameter logistic equation used was:

$$Sel_{x,i,a} = \left(\frac{1}{1 + e^{-(a-\alpha_1)/\beta_1}}\right) \quad (12.11)$$

where $Sel_{x,i,a}$ is the species-specific selectivity at age, *x* = fleet or survey, *i* = species, *a* = age class, and α_{1or2} and $\beta_{1\mathrm{or}2}$ are the ascending or descending inflection point and slope parameters, respectively.

Predation mortality (M_2) is a sub component of total mortality (Z), but more specifically a sub-component of the natural mortality component in Z. The simplest equation to describe this is:

$$Z = F + M_0 + M_2 \quad (12.12)$$

where Z is total mortality, F is fishing mortality, M_0 is residual natural mortality (natural mortality attributed to all other factors except predation by species included in the model), and M_2 is predation mortality from the species included in the model (Helgason and Gislason 1979). Species that were modeled as predators only (e.g. striped bass, bluefish, and spiny dogfish) only had M_0 operating on their populations, while species that were modeled as prey (e.g. Atlantic menhaden, Atlantic herring, and weakfish) had both M_0 and M_2 operating on their populations.

The M_0 value was an important source of uncertainty in the model. Initial values for M_0 were taken from the MSVPA information on the ERP focal species, where available, to determine the portion of natural mortality that was occurring from predation. The assumed total natural mortality from the single-species benchmark assessments for the prey species in this model were prorated downward based on this proportion. Additional analyses looked at the objective function values under different M_0 selections, as well as the difference between the VADER biomass outputs and the single-species biomass outputs. These methods were used to identify the best choice for this parameter in VADER, which was determined to be a 20% decrease from the single species total natural mortality assumptions for the prey species.

There is a recursive property in this formulation of M_2 in that the biomass data element needed for calculating M_2 has total mortality as an element of its calculation, therefore an approximation was used. To approximate the instantaneous rate of M_2, the biomass of the

predator and the prey items were assumed to come from the beginning of each year, prior to being subject to these various forms of mortality (Van Kirk et al. 2010). The equation for the instantaneous M_2 is:

$$M_{2i,a,t} = \frac{1}{N_{i,a,t}W_{i,a,t}} \sum_j \sum_b CB_{j,b}B_{j,b,t}\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}} \quad (12.13)$$

where $N_{i,a,t}$ = mean number of prey *i* at age *a* and at time *t*, $W_{i,a,t}$ = the weight of prey *i* at age *a* at time *t*, $CB_{j,b}$ = the age-specific (*b*) consumption-to-biomass ratio for predator species *j*, $B_{j,b,t}$ = age-specific biomass of predator *j*, and $\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}$ = the proportion of prey *i* at age *a* in all food available to predator *j* at age *b* in year *t*, which was assumed equal to the proportion of food within the stomach of predator *j* at age *b* in year *t* composed of prey *i* at age *a* (Lewy and Vinther 2004). Under this formulation, a type-II functional response was assumed, where the predator satiates at a high prey biomass, and the satiation reaches an asymptote (i.e., does not decline at higher densities) (Sparre 1980).

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

$$\phi_{i,a,j,b,t} = \tilde{v}_{i,a,j,b,t}B_{i,a,t} \quad (12.13.1)$$

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

$$\phi_{other,t} = \tilde{v}_{other,t}B_{other,t} \quad (12.13.2)$$

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

$$B_{other,t} = B_{\mathrm{ECO}} - \sum_i \sum_a B_{i,a,t} \quad (12.13.3)$$

which is added to the summation of the explicitly modeled prey biomasses after being multiplied by their suitability coefficients. The parameter B_{ECO} is the total biomass of all of the species in the ecosystem. This component is constant over time and across species and age. The inclusion of this component allowed all of the modeled species to be estimated relative to other prey items in the ecosystem. This led to efficiencies because the ERP focal predators have a diverse diet, modeling all potential prey items (including other fish as well as invertebrates) would be a large and time intensive task, and adequate data to make inferences about the population dynamics were not available for all prey species.

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

$$\nu_{i,a,j,b} = \rho_{i,j} g_{i,a,j,b} \tag{12.13.4}$$

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

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

$$\tilde{\nu}_{i,a,j,b,t} = \frac{\nu_{i,a,j,b,t}}{\sum_i \sum_a \nu_{i,a,j,b,t} + \nu_{other}} \tag{12.13.5}$$

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

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

$$g_{i,a,j,b} = exp\left[-\frac{1}{2\sigma_j^2}\left(ln\frac{w_{j,b}}{w_{i,a}} - \eta_j\right)^2\right] \tag{12.13.6}$$

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

In this model formulation, the total food available to a given predator in the ecosystem may include species beyond those that are explicitly modeled. One of the benefits of this formulation, as opposed to other formulations that necessitate only using species explicitly modeled in the mathematical framework, is the inclusion of a non-modeled prey component identified as an overarching ecosystem biomass value (B_{ECO}).

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

$$\phi_{j,b,t} = \phi_{other} + \sum_{i} \sum_{a} \phi_{i,a,j,b,t} \qquad (12.13.7)$$

This is the divisor from Equation 12.13 and completes the steps needed to calculate predation mortality.

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

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

All model parameters were estimated with maximum likelihood techniques, programmed in AD Model Builder (ADMB-IDE ver 10.1 2011). In addition to the likelihood approach, a Bayesian-type approach with priors, implemented through penalized likelihoods and bounded

parameters, was also used to supplement some of the statistical estimation. The estimation of model parameters allowed the inclusion of the assumption that fishery catch, survey catch, and food habits data are subject to observation error; this is a critically important expansion relative to previous multispecies formulations, in particular the virtual population analysis approaches that have been used for multispecies modeling (Helgason and Gislason 1979; Gislason and Helgason 1985; Sparre 1991; Livingston and Jurado-Molina 2000; Tsou and Collie 2001; Garrison et al. 2010).

The total likelihood comprises five components as well as three penalty functions (Table 16). The total fishery and total survey catch were assumed to be lognormally distributed. The catch-at-age proportions for both the fishery and the survey information, and predator food habits (average proportions by weight) were assumed to follow a Dirichlet multinomial distribution. These are common error distribution assumptions for fisheries stock assessments in general and were also the assumptions used for the single-species assessments for most ERP focal species.

Weightings for the lognormal components were species-specific (Table 18 - Table 23). The CVs were set such that the uncertainty associated with recreational harvest and discard levels were accounted for and were higher for species with higher recreational catch (i.e. striped bass and bluefish). Additionally, a higher CV was assumed for the survey component due to the interannual variability observed in those datasets, in each case the CV was set consistent with the choice made by the single-species assessment working group. Interannual variability can result from variation in availability of the species to the survey gear, changes in survey methodology through time, or the fact that surveys may be taking place in spatially discrete areas at different times of year; therefore it is not necessarily the case that these observed changes in abundance are real, but rather are due to changes in catchability (Pincin et al. 2014). As a result, it is appropriate to allow some significant statistical inference when predicting the various indices in the model.

For the Dirichlet objective function, sample sizes came from two sources depending on the species (Table 18 - Table 23). In cases where the total samples taken for the composition data were known, those data were used (Atlantic menhaden and Atlantic herring); total samples represented numbers of trips or survey tows sampled, not numbers of fish collected. For the other species, the effective sample sizes as used in the single-species assessments for the various composition data were used; these were generally calculated from number of trips or survey tows/hauls sampled.

Penalty functions were imposed on initial abundances, annual recruitment and age-specific biomasses (Table 16). These penalties were imposed to keep parameter estimates from collapsing to zero or producing estimates that were not biologically feasible. The penalty imposed on initial abundances, $Yr1_{PEN}$, was calculated with two methods. The first method prevented age-specific abundances from deviating substantially from those predicted by exponential decay across ages, assuming a total mortality equal to the age-specific average. The

second approach penalized deviation from the initial input abundance (*Yr1*) values taken from the benchmark models for all species. This second approach was used for the final model configuration. The penalty imposed on annual recruitment, *Rpen*, prevented the coefficient of variation for the log recruitment of any species from becoming greater than a pre-defined threshold value ($R_{THRESHOLD}$). The threshold selected was based on the recruitment and its associated variability from the benchmark models for the species in this study. The penalty imposed on age-specific biomasses, B_{PEN}, prevented any age-specific biomass from falling below a pre-defined threshold ($B_{THRESHOLD}$) to prevent the calculations from crashing due to the biomass dropping to zero. The weights for each of these penalties and their corresponding threshold values were selected iteratively.

12.3 Results

12.3.1 Diagnostics

Model fits were compared to the observed data as a diagnostic test to show the internal performance of the model. Additionally, the output was also compared with a run that had the trophic calculations turned off (representing multiple simplified single-species assessments). Several diagnostic plots are presented to verify that the model is fitting observed data reasonably well. Model parameter estimates and their associated standard deviations and are reported in Table 24 - Table 28.

The predicted total annual fishery catch closely followed observed catches with only minor differences for all species (Figure 58). Some lack of fit to the catch data for weakfish and spiny dogfish was evident.

The fits were less exact for the indices, but the multispecies output did follow temporal trends in the observed time series fairly well (Figure 59 – Figure 64).

For both fishery (Figure 65 – Figure 70) and survey (Figure 71 – Figure 82) age proportions, the predicted trends captured much of the interannual variability seen in the observed dataset. The model did a good job at capturing the age proportions for the catch; however, the model did not fit Atlantic herring and spiny dogfish as well in a relative sense. The model did poorly at predicting the survey age proportions in some instances. The model predicted more older Atlantic menhaden than were observed in the population for the NAD and SAD surveys. The model overpredicted the youngest ages of striped bass in the MRIP CPUE survey and the fit declined as age increased for the CT LISTS survey. The model did not fit the youngest age class for bluefish in either survey used in the model. The fit to the Albatross and Bigelow surveys for Atlantic herring was poor for the youngest age class. Finally, the fit to the Albatross survey for spiny dogfish decreased with increasing age.

Food-habits data were fit without much statistical weight on the input data. This was done to acknowledge the fact that the food habit data were limited for the species examined in this project. Even with this low weight, there was good correspondence between the input values and predicted data, with the multispecies statistical model predicting smoother curves of

increasing proportion of diet for prey items in the food habits of the predators (Figure 83 – Figure 86).

Contributions of the different data elements to the objective function are presented in Table 29. This information indicates that the fishery catch-age composition data contributed the most to the objective function value, followed by the fishery-independent survey age-composition, and then the total fishery-independent survey fit. There was also some contribution from the penalty functions, namely from the initial year penalty function, but these were minor contributions relative to the rest of the information. By species, Atlantic menhaden, followed by striped bass, contributed the most to the objective function value.

12.3.2 Population Estimates

Population abundance produced by the multispecies statistical model followed trends that were in line with the understanding from the current benchmark assessments for the ERP focal species (Figure 87). For Atlantic menhaden, the population began at a high level in the early part of the time series and then declined until the mid-1990s. After this, the population increased and then oscillated up and down without trend until the end of the time series. Striped bass began at a low population abundance. Striped bass population abundance then climbed until the late 1990s and was variable around this higher level until the end of the time series, with a decreasing trend. Bluefish followed a trend similar to that of Atlantic menhaden, beginning at a high level, declining, and then recovering towards the end of the time series. The most recent five years indicated a period of decline for bluefish. Weakfish, according to the multispecies model, began at a middle population size level, increased over a short period of time, and then declined for the majority of the time series. There was a short period of time at the end of the time series that indicated some recovery. Atlantic herring population abundance began at a low level and increased through the time series, with a period of decline in the last decade. The spiny dogfish population abundance began at a median level and increased in to the 1990s. The population then went through a period of decline, with a slight recovery in the final decade of the time series.

Fishing mortality estimates produced by the multispecies statistical model followed trends that are in line with the understanding from the current benchmark assessments for the ERP focal species (Figure 88), though in some instances the magnitudes were different. For Atlantic menhaden, fully recruited fishing mortality began at a high level in the early part of the time series and then decreased until the late-1980s. Fully recruited fishing mortality increased into the early 2000s, but then decreased again until the end of the time series. Striped bass fishing mortality started high, decreased sharply early in the time series, and then increased until the end of the time series. Bluefish followed a trend of decreasing fully recruited fishing mortality throughout the time series, with the exception of a sharp increase in the very beginning of the timeseries. Weakfish fully recruited fishing mortality started off low at the beginning of the time series and then increased to a peak in the mid-2000s. It has been declining since. Atlantic herring fully recruited fishing mortality began at a high level and decreased through the mid-1990s. It increased to a peak in 2010, and then decreased to the end of the timeseries. Spiny

dogfish fully recruited fishing mortality began at a high level and decreased through the early-2000s. It then increased to the end of the timeseries.

Population biomass produced by the multispecies statistical model followed trends similar to the current benchmark assessments for the ERP focal species (Figure 89). For Atlantic menhaden, the population began at a high level in the early part of the time series and then declined until the mid-1990s. The population biomass increased and then oscillated up and down without trend until the end of the time series. Striped bass began at a low population biomass. Striped bass population biomass then climbed until the late 1990s and has been variable around this higher level until the end of the time series, with a decreasing trend. Bluefish biomass began at a high level, declining and then recovering towards the end of the time series. Weakfish biomass began at a high level, increased over a short period of time, and then declined for the majority of the time series. There was a short period of time at the end of the time series that indicated some recovery. Atlantic herring population biomass began at a low level and increased through the time series, with a period of decline since the early 2000s. The spiny dogfish population biomass began at a low level and increased in to the mid-1990s. The population then went through a period of decline through the end of the time series.

Recruitment estimates produced by the multispecies statistical model indicated events similar to the current benchmark assessments for the ERP focal species (Figure 90). For Atlantic menhaden, recruitment was high in the beginning of the time series, but then declined and oscillated around a low level; the most recent time period saw some higher than average recruitment events. Striped bass began with low recruitment, and then had a period of high recruitment in the middle of the time series. Recruitment was low since this time period, punctuated by two or three above average recruitment events at the end of the time series. Bluefish had a very high recruitment event early in the time series, followed by a period of lower recruitment with multiple above average recruitment events during this time period. Weakfish had two very large recruitment events in the early part of the time series, but has been in a period of very low recruitment since 2000. Atlantic herring recruitment has been without trend, with some very large events occurring throughout the time series. Spiny dogfish saw high recruitment in the early part of the timeseries, but has been in a period of lower but stable recruitment since 1995.

Estimated predation mortality (M_2) varied between the prey species in this study, by prey age, and through time (Figure 91). The predator-only ERP focal species were not prey nor did they undergo cannibalism, so time- and age-varying predation mortality was only estimated for Atlantic menhaden, weakfish, and Atlantic herring. Predation mortality was highest for age-0 Atlantic menhaden and decreased sequentially as age increased. Predation mortality increased for Atlantic menhaden beginning in the early 1990s, peaking in the mid-2000s, and declined towards the end of the time series. At its peak, the predation mortality on age-0 Atlantic menhaden approached 0.14 in several years. The terminal year estimate of M_2 for Atlantic menhaden was 0.06 for age-0 and was 0.03 on average for all other age classes. The proportion of total mortality (Z) attributed to predation mortality was highest for age-0 and age-1 Atlantic menhaden, peaking at around 10% of total mortality due to predation mortality (Figure 92). The

other age classes ranged from only having 1% of total mortality due to predation up to a peak of approximately 4% (Figure 92). It is important to note that these predation rates were much lower than previous studies on Atlantic menhaden predation (Garrison et al 2010). This is in large part due to the diet data and the way it was processed for this model.

Predation mortality was highest for Atlantic herring on age-1, as was the case for Atlantic menhaden, and decreased sequentially as age increased. Predation mortality increased for Atlantic herring beginning in the early 1990s, and decreased from 2007 to the end of the time series. At its peak, the predation mortality on age-1 Atlantic herring approached 0.14. The terminal year estimate of M_2 for Atlantic herring was 0.08 for age-1 and was 0.06 on average (Figure 91). The proportion of total mortality attributed to predation mortality is highest for age-1 Atlantic herring, peaking at above 30% of total mortality due to predation mortality. The other age classes ranged from having close to 4% of the total mortality due to predation up to a peak of approximately 20% (Figure 92).

Predation mortality was highest for weakfish on age-0 as was the case for Atlantic menhaden and Atlantic herring, and decreased sequentially as age increased. Additionally, predation mortality increased for weakfish beginning in the mid-1990s, and generally decreased after 2000 to the end of the time series, though there was variability depending on which age class is being examined. At its peak, the predation mortality on age-0 weakfish approached 0.25. The terminal year estimate of M_2 for weakfish was 0.14 for age-0 and was 0.05 on average for all other age classes (Figure 91). The proportion of total mortality attributed to predation mortality was highest for age-0 weakfish, peaking at above 20% of total mortality due to predation mortality. The other age classes ranged from having close to 2.5% of the total mortality due to predation up to a peak of approximately 15% (Figure 92).

Although predation mortality was always highest on age-0 and age-1 fish, different species showed different patterns in terms of total mortality ($F + M_0 + M_2$) at age (Figure 93). For Atlantic menhaden, total mortality was highest on age-0 fish and decreased at older ages across the time series; for Atlantic herring, the pattern was reversed, with total mortality being the lowest on age-0 fish and increasing with age. For weakfish, the pattern changed over time, with total mortality being highest on age-0 and age-1 in some years and highest on older ages in years with higher F.

Food-habit information was queried from the diet information from the NMFS trawl survey, the NEAMAP survey, and the ChesMMAP survey and was processed through a Bayesian multinomial probit model to account for the dearth of data in many instances. The food habits of striped bass predicted by VADER created more consistent proportions across time than the original input data; the food habits showed that prey not explicitly modeled make up the largest proportion of striped bass diet, with Atlantic menhaden making up the next most important proportion (Figure 83). Atlantic herring and weakfish constituted a small proportion of the overall diet for striped bass. The “other food” category (all prey items not explicitly modeled) constituting close to 80% of the remaining diet. This trend held throughout the timeframe examined in this study with small differences in each aggregated year period.

A similar trend in the output from the statistical model from this study was seen for bluefish, weakfish, and spiny dogfish (Figure 84 - Figure 86). The estimation by the model predicted proportionally very little consumption of the prey explicitly included in the model, with the "other food" category constituting over 95% of the remaining diet. This trend= held throughout the timeframe examined in this study with small modifications in each aggregated year period.

Consumption of prey as an output of the multispecies model can be represented as thousands of metric tons, and therefore can be viewed in similar currency to catch and other population biomass information. Striped bass consumption of Atlantic menhaden closely followed the trajectory of population size for Atlantic menhaden and trended upward with the increase in population size for striped bass in the time-series (Figure 94). The proportional amount of Atlantic menhaden in striped bass diets increased as this prey item increased in abundance. When striped bass population size was low, the magnitude of Atlantic menhaden consumption was only 50 thousand metric tons (Figure 95). As the striped bass population size increased through time, consumption of Atlantic menhaden also increased, rising to a maximum value of ~200 thousand metric tons in 2010. Consumption of Atlantic herring by striped bass was relatively low for the entire time series, ranging from close to one thousand metric tons to a maximum of ~30 thousand metric tons in 1996. Striped bass was the predominant predator on weakfish, but overall the magnitude was very low.

Bluefish consumption of Atlantic menhaden remained relatively flat and low for the time series examined in this study (Figure 94). The proportional amount of Atlantic menhaden in bluefish diets decreased in the 1990s, coincident with a low population period for both Atlantic menhaden and bluefish. The magnitude of Atlantic menhaden consumption by bluefish ranged from ~25 to 100 thousand metric tons (Figure 95). Consumption of Atlantic herring by bluefish was relatively low for the entire time series, ranging from 20 thousand metric tons to a maximum of 25 thousand metric tons. The remainder of bluefish consumption was attributed to the other prey items that are not explicitly modeled and ranged from ~750 to 1,800 thousand metric tons, which occurred in 1985.

Weakfish consumption of Atlantic menhaden was variable through the time series examined in this study and correlated well with weakfish and Atlantic menhaden population abundance (Figure 94). The proportional amount of Atlantic menhaden in weakfish diets decreases in the early 1990s, coincident with a low population period for both Atlantic menhaden and weakfish. The magnitude of Atlantic menhaden consumption by weakfish ranged from 0.4 to 8 thousand metric tons (Figure 95). Consumption of Atlantic herring by weakfish was low for the entire time series, ranging from 0.03 thousand metric tons to a maximum of 0.4 thousand metric tons in 2009. The remainder of weakfish consumption was attributed to the other prey items that were not explicitly modeled in this study and ranges from 77 to ~800 thousand metric tons, which occurred in 1993.

Spiny dogfish consumption of Atlantic menhaden was variable and low through the time series (Figure 94). The magnitude of Atlantic menhaden consumption by spiny dogfish ranged from

0.2 to 5 thousand metric tons (Figure 95). Consumption of Atlantic herring and weakfish by spiny dogfish was low for the entire time series, ranging from 0.05 thousand metric tons to a maximum of 4 thousand metric tons in 2016 for Atlantic herring and 0.004 to 0.3 thousand metric tons for weakfish. The remainder of spiny dogfish consumption was attributed to the other prey items that were not explicitly modeled in this study and ranges from 8 to ~120 thousand metric tons, which occurred in 2000.

When viewing consumption by prey item, the importance of each predator in the consumption of each prey species can be seen. Striped bass consumed the most Atlantic menhaden relative to the other predators examined in this study (Figure 95). Bluefish was the next most important predator for Atlantic menhaden; bluefish also consumed more Atlantic menhaden than the other predators in this study in the early portion of the time series. Weakfish was also an important predator of Atlantic menhaden; however, given the low population numbers for weakfish during the time series used for this study, its impact on the Atlantic menhaden population was relatively small.

For Atlantic herring, it was bluefish that consumed the most Atlantic herring relative to the other predators examined in this study, followed by striped bass (Figure 95). As was the case for Atlantic menhaden, bluefish consumed more Atlantic herring than the other predators in this study in the early portion of the time series when bluefish abundance was high. Weakfish did not appear to be an important predator for Atlantic herring, and spiny dogfish only contributed significant amounts of predation in certain years.

For weakfish, it was striped bass that consumed the most weakfish relative to the all other predators examined (Figure 95). Spiny dogfish was the only other predator that appeared to contribute significantly to the predation of weakfish, but this was only in certain years, and was at a much lower magnitude than striped bass.

Estimates of recruitment, total abundance, total biomass, and fishing mortality were virtually indistinguishable for runs with tropic calculations turned on and the runs with the trophic calculations turned off for non-prey species (striped bass, bluefish, and spiny dogfish) (Figure 87 – Figure 90). For prey species (Atlantic menhaden, Atlantic herring, and weakfish), runs with the trophic calculations turned off had higher estimates of recruitment, total abundance, and total biomass, but generally similar estimates of *F*, although there were some differences early in the time series for Atlantic menhaden and later in the time series for weakfish (Figure 87 – Figure 90). This was most likely due to differences in the estimates of natural mortality used in the model. For runs with the trophic calculations turned off, the single-species assessment value of *M* was used; for runs with the trophic calculations turned on, a scaled down estimate of the single-species *M* was used as the input non-modeled-predation natural mortality component (M_0) for prey species, and the model calculated an additional component of natural mortality attributed to the predators in the model (M_2). The estimates of M_2 were a small component of total *M*, and in effect, the runs with the trophic calculations turned off used a higher *M* value for prey species than the runs with the trophic calculations turned on, resulting in higher estimates of recruitment and abundance, but relative similar estimates of *F*, as would be

expected. The natural mortality for species that acted only as predators was the same in both sets of runs, as the trophic calculations did not include effects on predators; as a result, the estimates of recruitment, population size, and *F* were very similar between the two runs.

12.4 Sensitivity Analyses

Two main sensitivity analyses were conducted for VADER. The first was to test the model's performance relative to a change in the input surveys. As noted, only a subset of indices used in the single-species assessments were included in the base run of VADER. Because of this, sensitivity runs were conducted to determine the importance of these choices; age-1+ indices in the base run were replaced with an alternate age-1+ index as identified by the single-species TCs (Table 17).

A second sensitivity analysis was conducted to test the sensitivity of the model to the input diet data. Instead of the Bayesian multinomial probit model as described and used for the base run, the food habits data (diet proportion of each prey for each predator) output from the previously performed MSVPA-X model (Garrison et al 2010) was used as the food habits input dataset. The food habits as produced by the MSVPA-X used numerous additional sources that were not incorporated in to this model due to missing datasets, and this in turned changed the food habit information significantly, in particular for striped bass. Given these differences, testing the effect on the output was an important sensitivity to undergo.

Generally, the run with the alternative indices had the greatest effect on the predator only species, while the alternative diet data had the greatest effect on the prey species. Annual total abundance showed some differences relative to the base run in the runs with the alternate indices for striped bass, bluefish, and spiny dogfish; however, neither of the sensitivity runs (alternate indices and alternate food habits) indicates a large effect on the model output (Figure 96). For the case of Atlantic menhaden and Atlantic herring, the alternate diet data had significant impacts on the abundance output, with the alternate diet data run increasing the total abundance for these two species. For spiny dogfish, neither sensitivity run indicated much difference from the base run.

Annual fully recruited fishing mortality indicated some departure from the base run from the alternate indices for striped bass, bluefish, weakfish, and Atlantic herring, while Atlantic menhaden and spiny dogfish showed little difference (Figure 97). Weakfish indicated a very different trend in *F* at the end of the time series. For the alternate diet run the biggest effects occurred on the species that are prey in the model (Atlantic menhaden, Atlantic herring), with Atlantic menhaden indicating higher *F* earlier in the time period and lower in the most recent period, and Atlantic herring showing lower *F* rates from this run for the entire time series. Weakfish indicated pretty good coherence to the base run when examining the alternate diet run.

Annual total biomass showed little effect from the alternate indices run across all species (Figure 98). For the alternate diet run the biggest effects occurred on striped bass, bluefish, weakfish, and Atlantic herring; however, there was no consistency in trend, with some species

indicating higher abundance and some lower. The effect was more modest or non-existent for the other species.

Annual recruitment was significantly affected by the alternate diet run for Atlantic menhaden and Atlantic herring, with the alternate diet run showing increased recruitment for these species across the time series (Figure 99). The alternate indices only indicated a modest effect relative to the base run, with the biggest impact occurring in weakfish, which generally showed less biomass over the time period under this model configuration.

Average predation mortality (the average predation mortality (M_2) across all age classes) was examined for the alternate diet run relative to the base run. The alternate indices were not examined in this comparison. There were large effects across all three prey species (Figure 100). Atlantic menhaden and Atlantic herring indicated significantly higher predation mortality under the alternate diet information, while weakfish indicated significantly lower predation mortality. This highlights the importance of the diet information as an input to the multispecies model.

12.5 Retrospective Analysis

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

A three-year peel was performed for the VADER model. Three years was chosen because this was a period where the food habits data did not need to be altered to accommodate the new timeseries length. The food-habit data were binned by three-year periods to allow for some dampening of the inherent variability in the food habit data. The food-habit data bins were a limiting factor for the retrospective analysis because, if the time series was reduced by more than three years, a reconstruction of the food habit data would have been needed, making year-to-year comparisons difficult.

A sequential year was dropped from the terminal year of the assessment (2017) for three years, and the model was rerun for each of those three new datasets. The data changed for each run included the total catch, the weight-at-age, maturity, the catch-at-age, the total survey catch, and the survey catch-at-age for each species, along with uncertainty estimates for each of these elements (sample sizes and CVs). The outputs examined were total fishing mortality, biomass, and recruitment.

The severity and direction of the pattern was determined by using the Mohn's Rho statistic. Mohn's Rho (Mohn 1999) has been commonly used to measure the retrospective patterns for many stocks, including for assessments done on the species examined in this study. The statistic

is defined as the sum of relative difference between an estimated quantity from an assessment with a reduced time series and the same quantity estimated from the full time series:

$$\rho = \sum_{t} \frac{X_{t_{new}} - X_{t_{full}}}{X_{t_{full}}} \tag{12.14}$$

where *X* denotes the variable from the assessment (in this case full fishing mortality, total biomass, or recruitment), *t* denotes the year of comparison, t_{new} denotes the terminal estimate from an assessment with a reduced time series, and t_{full} denotes the assessment using the full time series. To make the statistic comparable across different numbers of reduced years (i.e. peels), Miller and Legault (2017) reconfigured the estimator to be defined as the average of the peel-specific components:

$$\rho_t = \frac{X_{t_{new}} - X_{t_{full}}}{X_{t_{full}}} \tag{12.14.1}$$

$$\bar{\rho} = \frac{1}{P} \sum_{t=earliest\ year}^{P} \rho_t \tag{12.14.2}$$

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

The retrospective analysis performed well and indicated relatively good stability for the species in the main population metrics examined. Fishing mortality indicated a retrospective pattern where the population total fishing mortality was overestimated for Atlantic menhaden, bluefish, and spiny dogfish, and underestimated for the other species. These patterns were generally weak (less than 0.13) as indicated by the Mohn's Rho diagnostic for all six species ($\rho_{menhaden}$ = -0.12, $\rho_{striped\ bass}$ = 0.04, $\rho_{bluefish}$ = -0.002, $\rho_{weakfish}$ = 0.12, $\rho_{herring}$ = 0.03, $\rho_{dogfish}$ = -0.03; Figure 101).

Total biomass indicated a retrospective pattern where the population total biomass was overestimated for weakfish and spiny dogfish and underestimated for the other species. These patterns were weak as indicated by the Mohn's Rho diagnostic for all species ($\rho_{menhaden}$ = -0.03, $\rho_{striped\ bass}$ = -0.10, $\rho_{bluefish}$ = -0.03, $\rho_{weakfish}$ = 0.08, $\rho_{herring}$ = -0.07, $\rho_{dogfish}$ = 0.04). This feature is something often seen in this type of retrospective pattern, namely if fishing mortality is underestimated, biomass is frequently overestimated simultaneously, and vice versa (Figure 102).

Recruitment indicated a retrospective pattern where recruitment was overestimated for bluefish and spiny dogfish and underestimated for the other species. This population metric had more variability than the previous two metrics, and showed different patterns and severity depending on the species. The pattern was fairly strong for striped bass, bluefish, and Atlantic

herring, and for the other species, the pattern was weak to modest ($\rho_{menhaden}$ = -0.16, $\rho_{striped\ bass}$ = -0.32, $\rho_{bluefish}$ = 0.28, $\rho_{weakfish}$ = -0.12, $\rho_{herring}$ = -0.59, $\rho_{dogfish}$ = 0.19; Figure 103).

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

12.6 Projections

Data into and output from the base run of the VADER model, as described above, were used as the basis for these projections, including the data for SSB, recruits, and recruitment deviations. The model outputs were exported from ADMB software (ADMB-IDE ver 10.1 2011) and imported to R statistical software (R Core Team 2016) for the projection calculations.

The starting conditions of the projection analysis include initial numbers at age, which were the estimated numbers at age, N_0, for the terminal year of the multispecies stock assessment model. To allow for variability in the projection starting population, a bootstrap procedure was used for recruitment and for numbers-at-age for ages older than the modeled recruits. The bootstrap procedure added a deviation to the starting numbers-at-age, the deviation was based on sampling from a normal distribution with a mean of 0 and a standard deviation set at the standard deviation seen in the population for the time period examined. This deviation was bounded to prevent very large deviations from occurring randomly through the sampling process.

Numbers at age after the initial year were calculated as:

$$N_{i,a+1,y+1} = N_{i,a,y} e^{-Z_{i,a,y}} \tag{12.15}$$

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

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

$$C_a = \frac{F_a}{F_a + M_a}\left(1 - e^{-(F_a + M_a)}\right)N_a \tag{12.16}$$

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

was the input variable and catch was estimated from the input *F*. The catch and population in numbers were converted into biomass units, and the weight-at-age for each species was assumed to be equal to the species-specific average weight-at-age. This weight-at-age was projected forward in a static fashion.

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

Recruitment was projected without an underlying stock-recruitment function and was based on the median recruitment observed from the entire time series for each species. Recruitment variability was included whereby for each year a deviation in recruitment was selected randomly with replacement from the deviations estimated in the multispecies stock assessment model. This may have been overly restrictive assumption in that it was impossible to have recruitment overfishing in a population, however this strategy was chosen due to the lack of good stock-recruitment information and because this is the standard approach in stock assessments of most of the ERP focal species. The projection methods allowed for the inclusion of a Ricker stock recruitment curve as an option, but this was not used for the projections described here.

Projections were run for 100 years to allow the populations to reach equilibrium. The projections were parameterized as above with the exception of the fishing mortality assumptions that were defined a priori, and these projection runs were done using a dynamic *M* formulation.

The projection was run allowing *M* to be calculated dynamically. The description of the dynamic M_2 calculations followed the procedure as defined in Equations 12.13 – 12.13.7. The projections were run in a stochastic fashion. The projection parameters were bootstrapped for two-hundred iterations for the long-term projections, with the initial population and recruitment bootstrapped with uncertainty based on the timeseries from the multispecies model. Outputs included the median, 5th and 95th percentiles for spawning stock biomass, recruitment, landings, and natural mortality for the prey species.

Fishing mortality (*F*) was set to meet the management goal of maintaining an *F* rate at predetermined scenarios of management interest. Four scenarios were conducted as follows:

1. The projections were run setting *F* for the predators and non-menhaden prey (weakfish and Atlantic herring) at their target *F* rates (striped bass = 0.2, bluefish = 0.14, weakfish = 0.55, Atlantic herring = 0.46, and spiny dogfish = 0.22). Atlantic menhaden in this scenario was set at its status quo *F* rate, meaning the *F* rate in 2017 as calculated by the current single-species model (Atlantic menhaden = 0.11).

2. A second projection was run setting *F* for the predators and non-menhaden prey (weakfish and Atlantic herring) at their target *F* rates as above. Atlantic menhaden in this scenario was set at its target *F* rate (Atlantic menhaden = 0.22).
3. A third projection was run setting *F* for the predators and non-menhaden prey (weakfish and Atlantic herring) at their status quo *F* rates as determined from the current single-species assessments (striped bass = 0.31, bluefish = 0.34, weakfish = 0.23, Atlantic herring = 0.45, and spiny dogfish = 0.15). Atlantic menhaden in this scenario was set at its status quo *F* rate, as defined above.
4. A final projection was run setting *F* for the predators and non-menhaden prey (weakfish and Atlantic herring) at their status quo *F* rates as defined above. Atlantic menhaden in this scenario was set at its target *F* rate, as defined above.

Projection Results

In scenario 1 as defined above (Atlantic menhaden at status quo *F*, other species at their *F* targets), the prey species SSB were flat to declining and the predators increased or were flat, with the exception of spiny dogfish, which declined. Atlantic menhaden started the projection at ~700 tmt and increased to ~800 tmt of SSB by year 100 (Figure 104). Atlantic herring began the projection at ~280 tmt and ended at ~225 tmt of SSB (Figure 105). Striped bass SSB began at ~50 tmt and ended at ~90 tmt (Figure 106). Bluefish began at ~100 tmt and ended at ~290 tmt of SSB (Figure 107). Weakfish began at ~12 tmt and ended at ~10 tmt of SSB (Figure 108). Spiny dogfish began at ~70 tmt and ended at ~20 tmt of SSB (Figure 109).

Natural mortality (*M*) was occurring dynamically on the prey species Atlantic menhaden, Atlantic herring, and weakfish in this projection scenario. There was an initial increase in *M* for Atlantic menhaden, with ages-0 and 1 having the highest *M* occurring on them. After the initial increase, the *M* rates stabilized for the remainder of the projection (Figure 104). For Atlantic herring, *M* increased in the first few years on all ages and then stabilizes. The *M* rate was similar across ages (Figure 105). For weakfish, *M* increased slightly in the first few years on all ages and then stabilized (Figure 108).

In scenario 2 as defined above (all species at their *F* targets), the prey species SSB declined and the predators increased or were flat, with the exception of spiny dogfish, which declined. Atlantic menhaden started the projection at ~700 tmt and decreased slightly to ~650 tmt of SSB by year 100 (Figure 110). Atlantic herring began the projection at ~280 tmt and ended at ~220 tmt of SSB (Figure 111). Striped bass SSB began at ~50 tmt and ended at ~90 tmt (Figure 112). Bluefish began at ~100 tmt and ended at ~290 tmt of SSB (Figure 113). Weakfish began at ~12 tmt and ended at ~9 tmt of SSB (Figure 114). Spiny dogfish began at ~70 tmt and ended at ~20 tmt of SSB (Figure 115).

There was an initial slight increase in *M* for Atlantic menhaden, with ages-0 and 1 having the highest *M* occurring on them. After the initial increase, the *M* rates stabilized for the remainder of the projection (Figure 110). For Atlantic herring, *M* increased in the first few years on all ages and then stabilizes. The *M* rate was similar across ages (Figure 111). For weakfish, *M* increased slightly in the first few years on all ages and then stabilized (Figure 114).

In scenario 3 as defined above (all species at status quo *F*), the prey species SSB increased and the predators increased, with the exception of spiny dogfish, which declined. For the predators, the increase was less than in the previous two scenarios, and spiny dogfish declined more modestly. Atlantic menhaden started the projection at ~700 tmt and increased to ~900 tmt of SSB by year 100 (Figure 116). Atlantic herring began the projection at ~280 tmt, had a short period of decline, and ended at ~300 tmt of SSB (Figure 117). Striped bass SSB began at ~50 tmt and ended at ~60 tmt (Figure 118). Bluefish began at ~100 tmt and ended at ~105 tmt of SSB (Figure 119). Weakfish began at ~12 tmt and ended at ~17 tmt of SSB (Figure 120). Spiny dogfish began at ~70 tmt and ended at ~45 tmt of SSB (Figure 121).

The *M* rate for Atlantic menhaden was flat for the entire time series, with ages-0 and 1 having the highest *M* occurring on them (Figure 116). For Atlantic herring, *M* was stable for the time series. The *M* rate was similar across ages (Figure 117). For weakfish, *M* increased slightly in the first few years on all ages and then stabilized (Figure 120).

In scenario 4 as defined above (Atlantic menhaden at *F* target, others at status quo *F*), the prey species SSB was flat or increasing and the predators increased modestly, with the exception of spiny dogfish, which declined. As in scenario 3, the increase was less than in scenarios 1 and 2 and spiny dogfish declined more modestly as well. Atlantic menhaden started the projection at ~700 tmt and increased to ~700 tmt of SSB by year 100 (Figure 122). Atlantic herring began the projection at ~280 tmt, had a short period of decline, and ended at ~300 tmt of SSB (Figure 123). Striped bass SSB began at ~50 tmt and ended at ~60 tmt (Figure 124). Bluefish began at ~100 tmt and ended at ~105 tmt of SSB (Figure 125). Weakfish began at ~12 tmt and ended at ~17 tmt of SSB (Figure 126). Spiny dogfish began at ~70 tmt and ended at ~45 tmt of SSB (Figure 127).

The *M* rate for Atlantic menhaden was flat for the entire time series, with ages-0 and 1 having the highest *M* occurring on them (Figure 122). For Atlantic herring, *M* was stabile for the time series. The *M* rate was similar across ages (Figure 123). For weakfish, *M* was stabile for the timeseries (Figure 126).

13 INTERMEDIATE COMPLEXITY ECOPATH WITH ECOSIM MODEL (NWACS-MICE) (PREFERRED)

A full Northwest Atlantic Continental Shelf (NWACS) ecosystem model was developed using EwE by Buchheister et al. (2017a, 2017b) to inform Atlantic menhaden management in an ecosystem context and an updated version of this model was produced for this assessment (Section 14). To provide an intermediate level of complexity, a Model of Intermediate Complexity for Ecosystem assessment, or MICE model (Plaganyi et al. 2014; Collie et al. 2016; Punt et al. 2016) based on the full NWACS model was developed using EwE. The NWACS-MICE model was restricted in complexity to focus on key species that interact with one another through food web interactions and are also regularly assessed and managed by ASMFC. As a proof of concept, a simple Atlantic menhaden-striped bass EwE model was first developed and reviewed by the ERP WG in summer 2018. This single predator model was later expanded by

the ERP WG to include bluefish, weakfish, spiny dogfish, and Atlantic herring, all of which undergo regular population assessments and/or were determined to be important predators on Atlantic menhaden (see Section 3.1.2: Identification of Key Predator and Prey Species). Anchovies (*Anchoa spp.*) were added to the NWACS-MICE model because they represent a major prey item for bluefish and are prey for other modeled species. Benthic invertebrates, zooplankton, phytoplankton, and detritus were also included in the NWACS-MICE model. Therefore, the NWACS-MICE model strikes a level of complexity slightly above VADER but below the full NWACS model. It also serves to link the dynamics of individual stock assessments with feedbacks to predators so that harvest policies for multiple species can be simulated simultaneously and tradeoffs evaluated.

13.1 Ecopath with Ecosim Modeling Framework

The EwE trophic dynamic modeling package facilitates management of basic biomass and food web data for whole ecosystems and has been widely used for analysis of aquatic resources (Pauly et al. 2000; Christensen and Walters 2004; Colléter et al. 2015). The Ecopath component of EwE is a static, mass-balance view of the ecosystem that allows for age structure representation and provides the initial state for dynamic modeling. One of the main assumptions of the modeling framework is that the system is mass-balanced over the course of the year. Ecopath assumes mass balance between groups based on how production is allocated among fishing, predation, other mortality, and migration. The basic data requirements for Ecopath are biomass, total mortality or production rate, consumption rate, diet composition, landings, and discards for each trophic group. Ecopath relies in part on setting up a system of linear equations in which three of the following four parameters are inputted for each group (solving for the fourth): biomass, production/biomass ratio, consumption/biomass ratio, and ecotrophic efficiency (EE). Typically, EE is estimated for each group, and EE is defined as the proportion of the production that is utilized in the modeled ecosystem and accounted for by fishing, predation, migration, and biomass accumulation. For full details on the underlying theory, assumptions, equations, and model mechanics, see the original sources (Walters et al. 1997; Christensen and Walters 2004; Christensen et al. 2008).

In Ecosim, biomass dynamics are modeled on a monthly time step as a series of differential equations, where change in biomass is predicted as consumption minus losses to predation, fishing, and migration (Walters et al. 1997). In Ecosim, consumption is modeled based on the foraging arena theory, which states that predator–prey interactions are restricted to spatial and temporal arenas (Ahrens et al. 2012). Models can include both environmental forcing functions, which drive long term and seasonal patterns of primary production, and mediation effects, which allow a third-party organism to either facilitate or protect against a predator-prey interaction.

The most sensitive parameters in Ecosim models are the vulnerability parameters, V_{ij}, which describe the exchange rates of prey *i* from not vulnerable states into vulnerable "foraging arenas," where they can be consumed by predator *j*. The V_{ij} parameters control the amount of prey biomass available for consumption and are input in Ecosim as multipliers on Ecopath base

predation mortality rates (M_{2ij}) to represent the maximum possible predation mortality rate (M_{2MAX}) that can be exerted on a prey item at high predator biomasses. The V_{ij} parameters must be greater than or equal to 1. Low values restrict flow into the vulnerable state, which thereby limits consumption and prevents any biomass gains in the predator. High V_{ij} values imply strong top-down effects and can lead to dynamic instability in Ecosim models. To simulate a population, increase of an overexploited or invasive predator species with a low initial biomass and low M_{2ij} on their prey, the V_{ij} parameters must be quite high in order for consumption (and therefore biomass) of the predator to increase.

Ecosim models are typically fit to time series data by first identifying the most sensitive V_{ij} and then searching for the values that minimize the sum of squares between predicted and observed values. A weight may be assigned to each data series used in calibration. The weighting scheme may vary, but usually follows conventional approaches of estimating the variability in observed data (i.e. 1/cv). The weights may be adjusted upwards to emphasize fits to species of particular interest. Examples of model fitting procedures are described in the literature (Buchheister et al. 2017b, Chagaris et al. 2015, Heymans et al. 2016). New sensitivity routines in EwE are under development that allow for propagation of uncertainty in input data through all Ecosim simulation routines. Additionally, the multisim framework can facilitate rapid analysis of alternative vulnerability exchange rate parameters (see Chagaris et al. 2017 for an example using this approach).

13.2 Ecopath Model Description

Spatial Domain

The spatial domain for the model is the NWACS ecosystem, which spans the continental shelf of the Northwest Atlantic Ocean from North Carolina to Maine (Figure 128). The model domain includes four continental shelf subregions, following the regional strata of the NEFSC trawl survey: Mid-Atlantic Bight, Southern New England, Georges Bank, and Gulf of Maine. Our model also represents the estuaries along the coastline, such as the Chesapeake Bay, Delaware Bay, and Long Island Sound (Figure 128), given that diet and biomass data from estuaries were included in the model parameterization. Although the domain does not encompass the entire distributional range of Atlantic menhaden (from Florida to Nova Scotia), it is similar to the range in the MSVPA-X developed for Atlantic menhaden (Garrison et al. 2010) and to existing Ecopath models for the region (Link et al. 2008). This domain relies on the natural faunal and oceanographic break in NC (Longhurst 1998), while also including the bulk of historical Atlantic menhaden fishing effort concentrated in Chesapeake Bay and the Mid-Atlantic (SEDAR 2015). The area of the model domain (used to calculate biomass densities) was 246,662 km^2.

Temporal Structure

The NWACS-MICE Ecopath model base year is 1985, which is the earliest year included in all stock assessments for the ERP focal species.

Trophic Structure

The NWACS-MICE model simulates the dynamics of 17 biomass pools, including striped bass (3 age stanzas), Atlantic menhaden (2 age stanzas), spiny dogfish, bluefish (2 age stanzas),

weakfish (2 age stanzas), Atlantic herring (2 age stanzas), anchovies, benthic invertebrates, zooplankton, phytoplankton, and detritus (Table 30). Multiple age stanzas were included for key species to represent trophic ontogeny, fishery selectivity, and size/age dependent predation.

Fishing Fleets
In Ecopath, a separate "fleet" was included for each group, where each fleet only captures one species (i.e. bycatch is not included), total landings are combined over gear types/sectors, and discards are not modeled separately.

13.2.1 Basic Inputs

The basic data requirements for Ecopath are biomass (*B*), production to biomass rate (*P/B*; equivalent to the total mortality rate, *Z*), consumption to biomass rate (*Q/B*), diet composition, and landings for each trophic group. Biomass accumulation rates, which describe the instantaneous rate of change of a functional group's biomass to account for groups that are not in equilibrium, can also be provided.

Biomass
Biomass inputs (million metric tons) were obtained either directly from stock assessments or by simply adding the biomass of lower trophic level groups from the full NWACS model. For all the assessed species, biomass was taken directly from the single species assessment report files as the mid-year 1985 biomass (when available) or calculated as the mean 1985 biomass-at-age,

$$\overline{B_a} = w_a * N_a * \frac{(1-e^{-Z_a})}{Z_a}, \quad (13.1)$$

and summed over ages for each Ecopath age stanza. For multistanza groups in Ecopath, biomass is only input for a single age stanza (usually the oldest) and then calculated by Ecopath for other stanzas based on input growth and mortality parameters. Details for biomass calculations of each group are provided below.

- Striped bass were last assessed in 2018, with data through 2017, using a statistical catch-at-age model. The 1985 mean biomass of age 6+ striped bass was estimated using Equation 13.1 and the January 1 N-at-age, *Z*-at-age, and Rivards weights from the statistical catch-at-age model. Age 6+ biomass input was estimated to be 18,486 mt, and biomass for age 0-1, and age 2-5 striped bass was calculated by Ecopath as 36,158 mt and 8,415 mt respectively (Table 30).
- Atlantic menhaden biomass was derived from the 2019 BAM assessment model that simulated Atlantic menhaden population dynamics from 1955-2017. The BAM report file provided estimates of 1985 mid-year biomass at age. These estimates were simply summed for adult (age 1+) Atlantic menhaden for a biomass input of 1,704,469 mt. Juvenile (age-0) Atlantic menhaden biomass was calculated by Ecopath to equal 281,721 mt.
- Spiny dogfish are assessed using biomass estimates from density and area swept by the NEFSC spring bottom trawl survey. These estimates were available from 1968-2017 and

exhibit high interannual variability. In 1985, the total biomass of spiny dogfish (all sexes and size classes) was estimated to be 1,056,700 mt from the trawl survey. This value is the second highest observed in the time series and about 4x higher than the average biomass in preceding years. When input to Ecopath, this resulted in severe mass imbalance for spiny dogfish prey. Therefore, the average biomass of 1984 and 1986 was used as the input to Ecopath, which was estimated to be 271,555 mt.

- Bluefish biomass inputs were derived from the 2019 statistical catch-at-age model developed using the age structured assessment program (ASAP). Mean annual biomass in 1985 was calculated using Equation 13.1 and N-at-age, *Z*-at-age, and weight-at-age matrices from the ASAP base run of the preliminary assessment update. Input 1985 biomass for adult bluefish (age 1+) was calculated as 219,654 mt and juvenile bluefish biomass (age-0) was calculated by Ecopath to be 4,325 mt.
- Weakfish biomass was derived from preliminary runs of the 2019 ASAP model using the N-at-age, *Z*-at-age, and weight-at-age matrices to obtain mean annual biomass. Biomass for adult weakfish (age 1+) was estimated by ASAP to be 12,703 mt and the juvenile weakfish stanza (age-0) biomass was estimated at 1,222 mt by Ecopath.
- Atlantic herring were last assessed in 2018 using ASAP. Numbers-at-age in 1985 were converted to mean biomass at age using Equation 13.1. Adult Atlantic herring (age 2+) biomass was estimated to be 149,741 mt and the juvenile biomass (age 0-1) was calculated by Ecopath to be 8,322 mt.
- Anchovy biomass was taken directly from the full NWACS model and converted to units of million metric tons. The biomass of anchovies in the full NWACS model (Buchheister et al. 2017a, 2017b) was reported to be 1.1 mt/km^2 with a model area of 246,662 km^2. This converts to a biomass of 271,328 mt for the NWACS-MICE model.
- Benthic invertebrate biomass was calculated by summing the biomass of polychaetes, crustaceans, molluscs, other macrobenthos, filter feeders, other megabenthos, and shrimp from the NWACS model (groups 9-15 from the full NWACS) and multiplying by model area. Input biomass of benthic invertebrates was estimated to be 14,546,250 mt.
- Zooplankton biomass was calculated as the sum of five biomass groups from the full NWACS and includes microzooplankton, small copepods, large copepods, gelatinous zooplankton, and micronekton. Input biomass of zooplankton in the MICE model was estimated to be 13,558,763 mt.
- Phytoplankton and detritus biomasses were taken directly from the full NWACS and multiplied by the model area. Biomass inputs for phytoplankton and detritus are 8,596,470 mt and 12,974,000 mt, respectively.

Biomass Accumulation Rates

The species included in the NWACS-MICE Ecopath model are not necessarily required to be in steady-state during the Ecopath base year (1985). In fact, it is more reasonable to assume that species biomass is changing during the base year period. To represent non steady-state in Ecopath, biomass accumulation rates were used. The biomass accumulation rate is a flow term, also expressed as a rate of change (i.e. proportion of input biomass), where a negative value signifies biomass depletion during the model period and a positive value indicates biomass gains. If the biomass for a group is known, e.g., at the beginning of the year and at the

beginning of the next year, biomass accumulation can be calculated as the difference between these values.

The biomass accumulation rate parameters have several important effects on the model. First, they can be used to adjust the calculated biomass for non-leading (typically younger) age stanzas to better match the population structure in the base year of the stock assessment. In this case, a high biomass accumulation rate will shift the age distribution to younger ages leading to more biomass in those age stanzas and possibly lower ecotrophic efficiencies (EEs). Second, biomass accumulation rate inputs have a clear effect during the first few years of an Ecosim simulation. Higher biomass accumulation rates will lead to initial increases in Ecosim simulations, often leading to better fits when a species is increasing rapidly as a result of rebuilding efforts (or vice versa when a species is being rapidly depleted and the biomass accumulation rate is negative).

Biomass accumulation was entered for all assessed species except weakfish and spiny dogfish (Table 30). For multistanza groups, a single biomass accumulation rate is input for all stanzas (i.e. one biomass accumulation rate parameter for all striped bass stanzas). Typically, the input biomass accumulation rate was calculated from stock assessment model timeseries output as (B_{1986}/B_{1985})-1, where *B* is the total biomass (mid-year or mean) over all ages. For Atlantic menhaden, the biomass accumulation rate was calculated based on age 1+ biomass only. For bluefish, the biomass accumulation rate was reduced by half from -0.128 to -0.064 to balance the model. Atlantic herring input the biomass accumulation rate was calculated as the 3-yr mean biomass accumulation rate (average over 1984-1986) and reduced by half from 0.275 to 0.137 to provide better estimates of biomass and fishing mortality for the younger age stanza.

Mortality

Mortality rates in Ecopath are entered as annual total instantaneous mortality, *Z*, where *Z=F+M*. Age-specific *M* was available from the stock assessments as a function of body size using the Lorenzen equations (Lorenzen 1996) and scaled so that the mean *M* for fully selected ages equals a target *M* based on longevity (Hoenig 1983). For multistanza groups, the general approach to estimating natural mortality for each age stanza was to take the average *M* over all ages in each stanza weighted by the 1985 mean (or mid-year) numbers-at-age (Table 30).

$$M_s = \frac{\sum(M_a \cdot N_a)}{\sum N_a} \tag{13.2}$$

Here, M_s is the natural mortality rate for the Ecopath age stanza *s* and the summations are over all ages *a* included in stanza *s*. In the case of Atlantic herring, the most recent assessment used a constant *M* and so the age-varying *M* vector was taken from the previous stock assessment that used the Lorenzen estimator. Spiny dogfish and anchovy *M*s were taken directly from the full NWACS model and the *M* (or production to biomass ratio P/B) of the invertebrate and zooplankton groups were taken as the average P/B of the inclusive groups from the full NWACS

model, weighted by the biomass of those groups. Lastly, the P/B ratio for phytoplankton was taken directly from the full NWACS model.

For harvested groups (Atlantic menhaden, striped bass, bluefish, weakfish, spiny dogfish, and Atlantic herring), *F* was calculated from stock assessment output as the sum of landings for each stanza divided by the average (or mid-year) biomass of each stanza. These *F* rates were added to numbers weighted mean *M* to obtain the input *Z* values. For species without landings (anchovy, benthos, zooplankton), the input *Z* was equal to *M*.

Diet Composition

In Ecopath, a diet matrix is required that describes the proportion of each prey *i* in the diet of predator *j*, DC_{ij}. The diet matrix of the full NWACS model was simplified for the MICE model by first summing the DC_{ij} across NWACS-MICE prey groups and then averaging across NWACS-MICE predators, weighted by total consumption (B*Q/B) of each predator. Any DC_{ij} for a prey type not included in the MICE model was assigned to diet import (Table 31). Diet import provides a convenient workaround to modeling all the prey items of every species. Essentially, it allows for some proportion of the diet to be obtained from outside the modeled system and this part of their consumption is held constant over time in Ecosim. For example, striped bass age 6+ have a diet import of 0.269, meaning that 26.9% of their consumption comes from groups not included in the model. In Ecosim, that proportion of their total consumption will remain constant over time, i.e. they will always be able to achieve 26.9% of their base food intake.

Consumption Rates

Consumption rates, Q/B, are input for all consumer groups (Table 30); for multi-stanza species it is entered for the leading stanza only and calculated for other stanzas based on input biomass, mortality, and growth parameters. In all cases, Q/B was taken directly from the full NWACS model. For aggregate groups (inverts and zooplankton) the Q/B was taken as the weighted average Q/B for inclusive groups from the full NWACS model weighted by the biomass of each group.

Unassimilated Food

The unassimilated food parameter, *U*, represents the proportion of consumption that is not assimilated into biomass and therefore becomes part of the detrital pool. The *U* values were obtained from the full NWACS model, which were left at the recommended defaults for fish (0.2), benthic invertebrates (0.5), and zooplankton (0.3).

Landings

Landings were included for striped bass, Atlantic menhaden, spiny dogfish, bluefish, weakfish, and Atlantic herring (Table 30). Landings were derived from stock assessment outputs by summing the landings-at-age across fleets and then summing across ages for each stanza.

13.2.2 Balancing

The process of adjusting parameters in an Ecopath model to ensure mass balance is known as "balancing". One of the key diagnostics is that all groups should have EE values < 1.

13.2.3 Ecopath Outputs

Mortality Rates

Fishing mortality, *F*, in Ecopath is calculated simply as input landings divided by input biomass. Thus, the fishing mortality rates should match exactly those from the stock assessment, albeit converted to $F=C/\bar{B}$ by summing landings over ages and dividing by mid-year or average annual biomass. However, because the biomass of younger (non-leading) age stanzas is calculated in Ecopath assuming a stable age distribution, it is often not possible to obtain the exact *F* from a given year in the age-structured assessment models. Adjusting the biomass accumulation rate parameter in Ecopath allows for a better approximation of the age specific biomass and therefore *F* in the stock assessments, but some divergence is still expected for non-leading stanzas. Fishing mortalities for the Ecopath base year 1985 are provided in Table 32. Fishing mortality rates on fully selected age stanzas were 0.171 for striped bass, 0.193 for Atlantic menhaden, 0.019 for spiny dogfish, 0.148 for bluefish, 0.222 for weakfish, and 0.395 for Atlantic herring.

Predation mortality, M_2, in Ecopath is calculated as the total consumption of prey *i* by predator *j* divided by biomass of the prey.

$$M_{2i} = \frac{\sum B_j QB_j DC_{ij}}{B_i} \quad (13.3)$$

Total predation mortality for Atlantic menhaden in Ecopath (1985 base year) was 0.121 for juveniles and 0.031 for adults (Table 32). These low M_2 rates are due to low predator biomass, exclusion of other predators from the model, modest contributions to predator diets, and high Atlantic menhaden biomass. The result is that a large portion of the total mortality of Atlantic menhaden in the MICE model is unexplained (Figure 129), i.e. not attributable to fishing or predation. This is important because the top-down predation effects on Atlantic menhaden are expected to be muted under such configuration unless predator biomass increases drastically. The partitioning of Atlantic menhaden mortality in the MICE model should be contrasted with that in the full NWACS model (Section 14), which includes a broader suite of predators.

Predation mortality for the other forage group of interest, Atlantic herring, was higher than Atlantic menhaden, with M_2=0.895 for juveniles and M_2=0.377 for adults. Even though Atlantic herring contribute to a smaller portion of the predator diets compared to Atlantic menhaden, their predation mortality rates are higher because biomass is an order of magnitude lower than Atlantic menhaden.

Predation mortality rates were low (<0.002) for the adult age stanzas of predator groups (striped bass, spiny dogfish, bluefish), which is expected for larger individuals but is also due to the exclusion of any potential predators of large bodied fish (sharks, dolphins, larger fish) from

the model. Weakfish, which function in the model as both a predator and a prey, had a slightly higher predation mortality in the adult stanza (M_2=0.08) than the aforementioned groups. Predation mortality on juvenile stanzas was generally higher than adults, with juvenile bluefish and weakfish having a high M_2, 1.6 and 1.3 respectively. Predation on striped bass juveniles is poorly explained by the model and represents only about 10% of the total mortality, with virtually no predation on the sub-adults.

Bluefish, spiny dogfish, and striped bass accounted for most of the predation mortality in the Ecopath model (Table 33, Figure 130). In fact, bluefish accounted for the largest percentage of predation mortality on Atlantic menhaden, juvenile bluefish, and weakfish. Predation mortality on Atlantic herring was highest for spiny dogfish, followed by bluefish. Striped bass contributed to at least 20% of the predation mortality on juvenile striped bass, Atlantic menhaden, and juvenile weakfish.

Mixed Trophic Impacts

Mixed trophic impact analysis provides a method to assess the direct and indirect effect that changes in biomass of a group will have on biomass of other groups in the system (Ulanowicz and Puccia 1990). The mixed trophic impact is calculated in Ecopath using a standard matrix inversion routine and shows the net effect that a very small increase in biomass of one group has on other groups, through direct and indirect interactions, in a steady-state system. If diet compositions change over time with predator-prey abundances, the interactions that contribute to mixed trophic impact will also change, and so this analysis should not be used for prediction but rather as a form of sensitivity analysis to identify groups that are expected to have quantitative impacts in the model. The mixed trophic impact should not be interpreted in an absolute sense but are relative and can be compared across groups.

The mixed trophic impact of the NWACS-MICE model illustrates that increases in Atlantic menhaden biomass are expected to have positive effects on striped bass, and to a lesser extent bluefish and weakfish (Figure 131). Relatively speaking, the impact of increasing Atlantic menhaden biomass is more positive than that of Atlantic herring for these predators. Conversely, increases in predator biomass are expected to have negative effects on most species, with bluefish having negative impacts on almost all other species. A counterintuitive result is that increasing striped bass age 6+ is estimated to have a net positive effect on juvenile Atlantic menhaden and juvenile weakfish.

13.3 Ecosim Model Description

The NWACS-MICE Ecosim model was calibrated to time series of observed abundance and catch from 1985-2017 using fishing mortality as a forcing function. The general strategy was to fit several Ecosim models under alternative assumptions about prey switching, feeding time adjustment rates, and upper and lower limits to the vulnerability parameters. After a fitted model was obtained, a series of forward projection scenarios (40 years) were conducted to screen single species reference points for Atlantic menhaden, evaluate tradeoffs between

Atlantic menhaden and striped bass, and develop ecological reference points for Atlantic menhaden.

13.3.1 Treatment of Indices & Time Series Data

Indices of Relative Abundance

A total of 18 indices of abundance were used to calibrate the NWACS-MICE Ecosim model (Table 34). These indices were recommended by each species' respective ASMFC TCs as the most representative and were obtained directly from the stock assessment output files, except for spiny dogfish, which was obtained from the assessment report (NEFSC 2018b). The selected indices were derived from fisheries independent surveys and recreational catch rates. Some species included more than one index and most indices spanned the entire simulation period. Time series weights were derived from the year-specific CV for each survey, which were already available in the stock assessments. The time series weights were calculated as the inverse of the mean CV over all available years (i.e. 1/ $\overline{cv}$), such that more precise data streams have higher weights and thus more influence on model fit.

Catch Time Series

Catch time series were assembled from the stock assessment report files as the landings in weight, summed over all gears and age classes for each stanza. In most cases, annual CVs for landings were available from the stock assessment and the combined CV for all years and fleets was calculated as the average of all CV, weighted by the landings. The time series weight in Ecosim was taken as the inverse of the combined landings CV, which generally resulted in higher weights than the abundance data. Due to the scaling issues associated with the stable age calculations in multi-stanza groups, the catch time series for juvenile stanzas of Atlantic menhaden, bluefish, and Atlantic herring were treated as relative catch and were scaled (internally by Ecosim) to the Ecopath base landings. Spiny dogfish landings were used as a forcing time series because *F* was unavailable for that species.

Fishing Mortality Time Series

Fishing mortality was used a forcing time series in Ecosim for all harvested species except spiny dogfish, which used catch forcing instead. Fishing mortality time series were derived from the stock assessment as $F_y = C_y/\bar{B}_y$, where C_y is the total landings summed over ages and gears for each species/stanza and $\bar{B}_y$ is the mean (or mid year) biomass for each species/stanza. In Ecosim, it is important that *F* in the first year of the time series is equal to the Ecopath base *F*. As mentioned above, however, this is not always possible for younger ages of multi-stanza groups whose biomass (and therefore *F*) is calculated based on stable age assumption and differs from that in the stock assessment used to derive *F*.

13.3.2 Ecosim Calibration Procedure

General Overview of Fitting Ecosim Models

When fitting Ecosim models, there are three broad types of parameters to consider, state variables, flows, and forcing functions. State variables, e.g. biomasses, are the components that this assessment is predominantly interested in; they are solved for as time derivatives in Ecosim. The Ecopath diet matrix describes the initial flow of energy between state variables, and in Ecosim the flows are expressed using foraging arena theory equations. Forcing functions in Ecosim are external factors that drive the system, such as environmental drivers, fishing effort, or fishing mortality. Forcing functions are calculated external to the model and imposed as a time series.

The Ecopath model represents the initial state for time-dynamic simulations. Initial state parameters (biomass, mortality, consumption, diet, landings) are input to Ecopath by the user and not estimable in Ecosim. Thus, to evaluate the effect of initial state parameters on model fit one must manually adjust the input values or use Ecosim Monte Carlo simulations and provide uncertainty around the input parameters. The Monte Carlo routine will, optionally, save the parameters that improve fits to time series, but it is constrained by mass balance (each Monte Carlo trial is evaluated for mass balance and discarded if not) and does not include a minimization search and so is computationally inefficient for fitting models. It is recommended to thoroughly evaluate the pre-balance diagnostics (Link 2010) in Ecopath before going to Ecosim and then only adjust the initial inputs sparingly and on a case-by-case basis (as a last resort) to improve model stability and fit.

In Ecosim, there are two sets of parameters that describe the consumption model according to foraging arena equations. The first set of Ecosim parameters are the vulnerability exchange rates, V_{ij}. These regulate consumption, and therefore regulate biomass gains. Consumption for a predator is mortality for its prey, and so the V_{ij} also serve as limits on predation mortality at high predator biomass. Ecosim models are sensitive to the V_{ij} values. The V_{ij} can be estimated in Ecosim using the fit to time series interface to reduce the sum of squares differences between predicted and observed time series of biomass and catch. These are the only parameters estimated by Ecosim to minimize a goodness-of-fit measure.

The second set of parameters are found on the group info tab, and these include maximum *P*/*B*, foraging time adjustments (FTA), predator effect on foraging times, and prey switching. The FTA parameters are important for allowing compensatory improvements in survival at low stock sizes by allowing groups to spend less time feeding at low densities and thus be exposed to less predation. Prey switching is said to occur when predator diet proportions change more rapidly (or slowly) than relative abundances. Prey switching can occur in two ways in Ecosim. First, predators will switch from prey that are declining in abundance, due to density dependent foraging time of prey [FTA>0], which is implied in NWACS-MICE for all juvenile stanzas. Second, predators may explicitly switch between prey types by modifying the rate of effective search (a_{ij}) in relation to changes in abundance of prey using a power function $a_{ijt} = a_{ij} \cdot B_i^{P_j} \cdot K_{ij}$, where Pj = [0,2], and K_{ij} is a scaling constant.

The group info parameters are set by the user and not estimable in Ecosim fit to time series. A recommended configuration is to set FTA=0.5 for the youngest age of multi-stanza groups and FTA=0 for all other groups, with prey switching turned off (=0). To evaluate the effect of alternative values for FTA or prey switching, one must manually adjust the parameter and run the model. However, the vulnerability parameters are dependent on the group info configuration and so it is advised (but not required) to re-estimate the vulnerabilities each time one of these values is changed (see scenarios below).

Lastly, Ecosim forcing functions are input as either time series multipliers or absolute values. For environmental forcing functions (e.g. chlorophyll, temperature), they are typically applied as mean-scaled multipliers on baseline PB parameters (in the case of primary producers), or as multipliers on V_{ij}, search rate, or arena size parameters – thus allowing a forcing function to modify the predator-prey functional response. Most commonly, Ecosim forcing functions are applied to simulate changes in nutrient loading, chlorophyll production, and fishing mortality. In the case of environmental forcing, variables such as temperature or salinity must be accompanied with a habitat preference function for affected groups. Additionally, fishing mortality may be forced by including a time series of species-specific *F* values, a time series of fleet-specific fishing effort that functions as a multiplier on the Ecopath *F* for each fleet and species, or by forcing removals (i.e. forced catch).

Estimating Vulnerability Parameters

When fitting an Ecosim model, it is important to first determine the appropriate number of vulnerabilities to estimate. As a conservative approach, it has been recommended to only estimate *K-1* parameters (Heymans et al. 2016), where *K* is the number of reference time series (i.e. observed biomass and catch) used to tune the model. Alternatively, estimating fewer parameters may lead to a better model based on AIC criteria and this can be tested by estimating different numbers of parameters in a stepwise fashion (Scott et al. 2016).

Fitting an Ecosim model begins by first identifying the most sensitive V_{ij} parameters and then estimating those parameters to improve the model's goodness-of-fit as assessed by the sum of squares of predicted biomass and catch from observed time series. The sensitivity search proceeds by adjusting each vulnerability slightly, one at a time, to see how much the sum of squares changed. The *K-1* most sensitive vulnerabilities are then selected, i.e. "turned on" for parameter estimation. In the NWACS-MICE model, no more than 27 (*K*-1) vulnerability parameters were estimated during a single tuning iteration.

Ecosim models are prone to local minima in SS, thus requiring repeated vulnerability searches in order to find model convergence. Therefore, a methodology was implemented where the sensitivity and estimation routine was repeated until no further improvement in the sum of squares and AIC was obtained. This was done by searching for and estimating the most sensitive 27 V_{ij}, keeping those estimated values, and then searching for and estimating another set of 27 V_{ij}, and so on until the sum of squares and AIC have stabilized. At each iteration, the model may identify and estimate a different set of 27 V_{ij}, such that the total number of V_{ij} estimated is greater than 27. This approach is analogous to estimating parameters in phases –

whereby the most important parameters are estimated first and when those are in an appropriate parameter space, additional ones are turned on. Typically, convergence on a solution would be obtained after 5-7 iterations (Figure 132) and approximately 70-80 V_{ij} would have been estimated. This amounts to between 2-3 estimated parameters per time series, and around 75% of all possible V_{ij}. The vulnerabilities were reset to their default value of 2 and the repeated search was initiated after any changes were made to Ecopath inputs, group info, or forcing functions.

Vulnerability Bounds

The most sensitive parameters in Ecosim models are the vulnerability parameters, V_{ij}, which control the amount of prey biomass available for consumption. They are input in Ecosim as multipliers on Ecopath base predation mortality rates (M_{2ij}) to represent the maximum possible predation mortality rate (M_{2MAX}) that can be exerted on a prey item at high predator biomasses. For this reason, the V_{ij} parameters are also referred to as "predation rate limits".

It is often the case that Ecosim will estimate extremely high values of V_{ij} ($1x10^9$) in the fitting process, which may result in theoretical predation rates far above the prey's Z when predator biomass is high. While this may improve the sum of squares measure-of-fit over the period of observed data, the high V_{ij} could lead to dynamic instability, exaggerated top-down effects, and groups crashing entirely under extreme fishing scenarios. To correct for this, vulnerability caps were applied after the repeated search was completed. M_{2MAX}, and therefore the V_{ij}, can be expressed as some proportion of the prey's M, such that $V_{ij} = (M_{2MAX} * M)/M_{2BASE}$. For example, an M_{2MAX} of $0.5*M$ means that a single predator will not account for more than 50% of the natural mortality of that single prey. Through an iterative approach, it was found that values of M_{2MAX} around $0.75*M$ to $1.0*M$ provided the best fit to the data (i.e. compared sum of squares across scenarios where M_{2MAX} varied from $0.25M$ to $2M$ for all V_{ij}). Additionally, V_{ij} estimated at the lower bound of 1.0 can be problematic in projections scenarios and often causes species to be unresponsive to fishing. Small increases (going from 1.0 to 1.1) can have noticeable effects in projections scenarios that apply high F rates (see Section 13.4.3: Equilibrium MSY).

Applying the vulnerability caps will increase the sum of squares and result in a poorer fit to the data by that measure of fit. However, the vulnerability caps may provide a model with better dynamics in the projection scenarios and more comparable productivity patterns relative to the stock assessments. Additionally, a search procedure that included penalized bounds on the V_{ij} might result in a lower sum of squares with values not on the bound. The decision of what constitutes the "best fit" model should not be based solely on the sum of squares measure of fit but rather the full suite of diagnostics including MSY curves and stock-recruit plots.

13.3.3 MICE Model Simulations

Over 30 different Ecosim configurations were fit during development and testing of the NWACS-MICE model. Those scenarios evaluated model fit under different inputs for foraging time adjustments, prey switching, vulnerability caps, primary production anomalies, and recruitment deviations. Not all of the 30 scenarios are presented in this report; instead, seven

alternative scenarios that represent the best fit and most parsimonious model configurations are summarized (Table 35). Only the first four scenarios in Table 35 were intended to be used for management purposes (default configuration and prey switching), whereas the last three (primary production anomaly and recruitment deviations) served as robustness tests during model development and parameter estimation. The last three scenarios are listed here only as a record of their existence in case future model iterations might wish to include primary production drivers or recruitment anomalies. Further work is needed to a) compare and validate the PP anomalies against actual changes in primary production observed through coastal and ocean monitoring systems (e.g. satellites, river gauges); and b) properly adjust for M_0 forcing effect when EE is high (and M_0).

The prey switching scenario sim3.5 is the preferred base run to be used for development of ERPs. While sim3 had a lower sum of squares than the other three, sim3.5 was preferred because the vulnerabilities estimated at the upper bound (1e10) are replaced with the vulnerability caps (M_{2MAX} =M) and those estimated at the lower bound (1.0) were replaced with values ranging from 1.02 to 1.5 to remove dynamic instability in projections with high F rates.

Baseline configuration (sim1 and sim1.1)
The baseline configuration (sim1) has FTA set to 0.5 for all of the youngest age stanzas and 0 for all others, with no prey switching (P_j=0). An alternative baseline run (sim1.1) applies the upper vulnerability cap of (M_{2MAX} =M).

Prey Switching (sim3 and sim3.5)
The model was fit under prey switching P_j values of 0, 0.5, 1, and 1.5 applied to all Atlantic menhaden predators. Of the values considered, P_j=1 (sim3) resulted in the lowest sum of squares at the end of the repeated search. An alternative prey switching model (sim3.5) was tested that includes the upper and lower vulnerability caps (M_{2MAX} =M) as well as changes to foraging time adjustments for striped bass so that F_{TARGET} projections were more comparable to the stock assessments.

Primary Production Anomalies (sim9 and sim9.1)
Ecosim can be invoked to search for time series values of annual relative primary productivity in order to further improve the fits to observed data. The underlying assumption is that primary production is variable over time and causes changes in relative abundance throughout the food web. The NWACS-MICE model was fit with primary production anomalies estimated using a 3-year smoothing spline function (sim9) and with annual primary production anomaly estimates (sim9.1). The primary production anomaly scenarios should not be considered for base run or management advice because the estimated historical primary production pattern may be a spurious trend with no relation to known primary production patterns. Rather, these scenarios were produced to examine whether management advice generated by the model is robust if bottom-up drivers are explicitly included.

Recruitment Deviations (sim12.3)

Assuming that recruitment deviations estimated in the stock assessment models can be interpreted as years of good or poor survival, those deviations can be included as a forcing function on mortality of juvenile age stanzas in Ecosim. Doing so allows the model to represent year class variability over time, but makes no inference as to the mechanism. Recruitment deviations were available for all assessed species as log transformed deviations. These were converted to an index of relative mortality as the inverse of the back transformed log deviation, scaled to a mean of 1 and applied as multipliers on M_0 for all juvenile stanzas. The vulnerabilities were again fit following the repeated search procedure described above. One caveat when using M_0 forcing is that groups with high EE (and low M_0) might not respond to very large multiples of M_0 because it is still only affecting a small portion of Z. In extreme cases (EE>0.8), the M_0 forcing function may need to be rescaled to obtain the desired response in Z. The last two scenarios are those fitted with recruitment deviations applied as M_0 forcing on juvenile stanzas. Recruitment deviation models with prey switching P_j values of 0, 0.5, 1, and 1.5 applied to all Atlantic menhaden predators were fit. Of the values considered, P_j=1.5 (sim12.3) resulted in the lowest sum of squares at the end of the repeated search.

13.4 Ecosim Outputs

13.4.1 Fits to time series

The NWACS-MICE Ecosim model produced reasonably good fits to the relative abundance time series (Figure 133 and Figure 134), with the exception of juvenile Atlantic menhaden and weakfish. The inability to fit to juvenile Atlantic menhaden and weakfish might be explained by the absence of bottom-up drivers in the model that would describe the decline in abundance of juvenile Atlantic menhaden and the increase in weakfish abundance during the mid-1990s. The NWACS-MICE Ecosim model fit the catch trends very well (Figure 135), for all species except juvenile Atlantic menhaden, which is essentially a scaling issue associated with multistanza calculations of juvenile biomass under stable age distribution assumption.

13.4.2 Emergent Stock Recruit relationships

Ecosim models do not include an explicit stock-recruit equation, rather stock-recruit relationships are an emergent property of Ecosim models with multi-stanza age groups (Walters and Martell 2004). A Beverton-Holt or Ricker type stock-recruit curve is generated when the juveniles have non-zero feeding time adjustment, combined with high EE and/or high proportion of other mortality sensitive to feeding time (set to 1 in all scenarios). This represents density-dependent changes in juvenile mortality rate associated with changes in feeding time and predation risk. The shape of the stock-recruit curve is determined by the degree of compensatory increase in juvenile survival at low densities. Compensatory effects are increased (i.e. higher steepness and constant recruitment across broad range of spawning stock size) by setting the V_{ij} of juvenile prey items close to 1.

The stock-recruitment relationship for Atlantic menhaden was revealed by simulating a severe increase and decrease in fishing mortality so as to generate the paired adult and juvenile abundances across a wide range of stock sizes. Stock-recruit curves were generated for each

scenario after all fitting and V_{ij} adjustments were complete (Figure 136). The Ecosim stock-recruitment curves tend to show a positive relationship between recruits and adults at low stock sizes, which begins to level off at high stock sizes. In particular, the scenarios with primary production anomaly (sim9 and 9.1) exhibit more of a Beverton-Holt, or possibly a Ricker, curve. Other scenarios showed low compensatory response in juvenile survival and exhibited more of a straight line out of the origin. This figure is provided to make clear that a stock recruit relationship does exist in Ecosim models. Further research should be conducted to understand how density-dependent processes combined with bottom-up drivers affect our estimates of stock-recruit relationships in both multi species and single species models.

13.4.3 Equilibrium MSY

Estimates of equilibrium MSY and F_{MSY} are obtained by running long term Ecosim simulations over a range of *F* or effort values. Each species is analyzed separately and there are two options when invoking the Equilibrium MSY search in Ecosim, stationary and dynamic (Walters et al. 2005). In the stationary analysis, all predators and prey of the species being evaluated are held constant at their Ecopath inputs and do not respond dynamically to changes in the target species. In the non-stationary, dynamic simulations, predators and prey are allowed to respond to changes in abundance of the target species. This sometimes leads to compensatory responses in the target species that might, for example, allow for maximum yield at higher *F* of forage species when predators respond negatively or switch to other prey.

The equilibrium MSY analysis revealed a dynamic instability in sim3 that was associated with vulnerability parameters estimated on the lower bound of 1.0 (Figure 137). Small increases to those values were made in sim3.5 and this instability was removed. This is a primary justification for choosing sim3.5 as the preferred run over sim3, even though it had a higher SS.

Striped bass F_{MSY} was estimated in all four scenarios and ranged between 0.154-0.171 (excluding sim3) (Figure 137, Table 36). Atlantic menhaden F_{MSY} was approximately 0.65 in the scenarios without prey switching and 0.954 and 0.837 for sims 3 and 3.5 respectively. The higher F_{MSY} with prey switching is obtained because predators will quickly switch away from Atlantic menhaden when they are declining allowing for compensatory reductions in M_2. With the exception of sim3, bluefish F_{MSY} was estimated between 0.72-0.86. Weakfish F_{MSY} estimates are unreliable, but estimated at 0.8 for sim 3.5. Lastly, there was good agreement in F_{MSY} of Atlantic herring, with values ranging between 0.24 and 0.4.

13.5 Projections

13.5.1 Single-species proxy reference points

The biomass and fishing mortality reference points from the stock assessment are defined in a variety of ways with different metrics and currencies, making it impossible to apply those values directly in Ecosim. Therefore, a ratio approach was used to calculate proxy reference points that can be applied and evaluated in Ecosim. This was done by multiplying the single

species ratios B_{ref}/B_{2017} or F_{ref}/F_{2017} by the corresponding Ecosim predicted B_{2017} and F_{2017} (forcing). Single species reference points and their Ecosim proxies are provided in Table 37.

13.5.2 *F* target and *F* threshold scenarios

For species with defined target and threshold fishing mortality rates, long-term projections under each *F* reference point were conducted, while holding all other species constant at their 2017 *F*. This was done to test if Ecosim can replicate similar dynamics to the stock assessment with regards to how species respond to changes in fishing pressure. Because a ratio approach based off 2017 values was used to convert single species reference points to Ecosim, biomass from each scenario was scaled to its own predicted 2017 estimate.

For striped bass, the projected biomass for sim1 was far below its associated targets and thresholds, whereas sims 1.1, 3, and 3.5 all approximated the biomass target and threshold; sim3.5 showed a higher biomass under the threshold scenario (Figure 138).

Target and threshold fishing mortality rates were evaluated for Atlantic menhaden, but no biomass reference points were available. The Atlantic menhaden projections under F_{TARGET} were all similar, except for sim3, which was slightly lower with some dynamic instability (Figure 139). The scenarios with prey switching (sims 3 and 3.5) predicted higher biomass under $F_{THRESHOLD}$ than the non-switching scenarios (sims 1 and 1.1). This is because predators will quickly switch away from Atlantic menhaden to other prey as Atlantic menhaden are declining resulting in less predation mortality.

Bluefish target and threshold projections were similar across all scenarios with the exception of sim3 (Figure 140). Sim3 was the only scenario that reached the biomass target, with all others remaining below the target but above the threshold. By testing additional configurations, it was determined that there is tension in the model between bluefish and striped bass, such that no configuration could be found that allowed both of them to reach their biomass targets simultaneously in these scenarios. Also, there is disconnect between the bluefish *F* and *B* reference points, where the $B_{THRESHOLD}$ is half of the target, but the $F_{THRESHOLD}$ is only 10% higher than the F_{TARGET}. Therefore, the target and threshold scenarios for bluefish are very similar.

13.5.3 Screening BAM *F* reference points

Short-term projection scenarios (2018-2021) were conducted using the BAM under three scenarios: 1) harvest each year is equal to the current TAC of 216,000 mt; 2) harvest is set equal to a level that has a 50% probability of reaching the single-species *F* target; and 3) harvest is set equal to a level that has a 50% probability of reaching the single-species *F* threshold. The projections were run using the BAM Monte Carlo bootstrap routine to capture the uncertainty associated with *M* and fecundity. For each scenario, a total of 4,864 *F* vectors were provided from BAM representing a distribution of *F* values to be evaluated in Ecosim.

The fishing mortality rates coming out of the BAM projections are equal to the full *F* used in the assessment, and based on population size in numbers. To apply proxy scenarios in Ecosim, the ratio of F_y/F_{2017} for projection years was multiplied by the terminal year F_{2017} in Ecosim (equal to 0.048 for adult Atlantic menhaden, as $C/\overline{B}$). For each scenario, 500 BAM trials were selected at random and converted to Ecosim *F* input files (one file for each trial) using the multisim plugin to automate the simulations. In the Ecosim projections, all other species were held constant at their 2017 status quo *F* rates. Long term (40 year) projections were run by extending the BAM scenarios to 2057 using the mean *F* from the BAM projection years (2018-2021). Biomass trajectories from these scenarios are shown in Figure 141.

Results of this analysis are summarized for each BAM *F* scenario as the proportion of *F* trials that caused each predator to change by *X*%, where *X* ranged from -50% to 50% in 5% increments. Change in biomass was calculated relative to the status quo scenario (ΔB_{REL}), where $\Delta B_{REL} = (B_{TRIAL}-B_{2017})/B_{2017}$, and *B* for each trial and the status quo is equal to the biomass after 4 or 40 years. Additionally, the median ΔB_{REL} is provided. The analysis provides information on the level of risk of predator declines associated with single-species Atlantic menhaden reference points developed by the BAM. Small changes of less than 10% are deemed to be low risk and within the bounds of measurement uncertainty.

The Ecosim model predicted that harvesting Atlantic menhaden at the current TAC of 216,000 mt is not expected to cause any predators to decline by more than 10% over the short and long term (Table 38, Figure 142 - Figure 143). After 40 years of fishing at the current TAC, striped bass biomass was predicted to decline by 5-10% in 16% of trials (Table 38, Figure 143).

The F_{TARGET} scenario represents an increase in Atlantic menhaden fishing mortality from F_{2017}. In this scenario, the proportion of trials leading to declines in predator biomass increased slightly compared to the TAC scenario (0% column in Table 38). No predators were predicted to decline by 10% over the short term (four years) (Table 38, Figure 142). Over the long-term (40 years), striped bass was still the only predator with predicted negative effects with 10% of trials predicting biomass declines of 10-15%.

Impacts on other predators begin to be observed when Atlantic menhaden are fished at $F_{THRESHOLD}$. In this scenario, nearly all trials led to at least some decline in biomass for all species relative to status quo; however, striped bass was the only predator to exhibit declines greater than 10% over the short term. Under the Atlantic menhaden $F_{THRESHOLD}$ scenarios, striped bass biomass was reduced in the short term by at least 10-15% in 58% of the trials and biomass was reduced by 15%-20% in 12% of the trials (Table 38, Figure 142). Over the long term, striped bass biomass was predicted to decline by 10-15% in 90% of trials, by 15-20% in 75% of the trials, and by 20% or more in 56% of trials (Table 38, Figure 143). In other words, there is a greater than 56% probability that fishing Atlantic menhaden at their *F* threshold will cause striped bass biomass to decline by at least 20%.

This analysis indicates that the current TAC and F_{TARGET} scenarios developed by the BAM are not likely to cause negative effects on predators (biomass declines of greater than 10%) over the

short term (4 years). Over the long term, and assuming striped bass are fished at status quo *F*, the Atlantic menhaden F_{TARGET} scenario showed a low probability (0.10) that striped bass would decline by 10% or more. While the median change in biomass relative to 2017 for all species in the first two scenarios are either zero or negative, they do not fall below -10%. It is not until Atlantic menhaden are fished to their biomass threshold that more substantial impacts on predators are predicted by Ecosim, with the most severe impacts on striped bass. Even in this scenario, the predicted median decline for striped bass is -11% after 4 years and -21% after 40 years. This information is intended to gauge the level of risk associated with single species reference points developed by BAM.

13.5.4 Predator-prey surface plots

Species in Ecosim are connected to one another through food web interactions, such that the predicted biomass of any given species is a function of its own fishing mortality rate as well as that of its predators and prey. Specifically, the biomass of striped bass is a function of striped bass *F* and Atlantic menhaden *F*. To elucidate this relationship, series of simulations was run under different combinations of *F* for striped bass and Atlantic menhaden (all other species held constant at 2017 status quo). In these simulations, striped bass *F* rates ranged from 0 to 2 times F_{2017} and Atlantic menhaden *F* rates ranged from 0 to 10 times the current F_{2017}. For striped bass, which has two harvested age stanzas, the *F* multipliers were applied to each stanza (i.e. an *F* multiplier of 0.5 would be a 50% reduction in 2017 *F* for all harvested stanzas).

For each simulation, a biomass ratio for striped bass was calculated as age 6+ biomass in the terminal year divided by the target age 6+ biomass (1.58 x predicted 2017 age 6+ biomass). Thus, *B* ratios < 1 are below the target, *B* ratios between 0.75 and 1 are above the threshold and below the target, and *B* ratios > 1 are above the target. Similarly, the biomass of bluefish was predicted as a function of striped bass and Atlantic menhaden *F*. For bluefish, the biomass target and threshold were calculated as 2.36 times the current biomass, and for weakfish the terminal year biomass was expressed relative to the threshold biomass that is 3.58 times higher than current biomass B_{2017} predicted by Ecosim.

It is important to note that current striped bass *F* is above the *F* threshold and that biomass is below the biomass threshold. The analysis shows that at current striped bass *F* (where *F* multiplier = 1 on the y-axis of Figure 144), the stock will remain below the threshold regardless of Atlantic menhaden *F* rates. This indicates that striped bass fishing mortality is currently above that which would achieve biomass target and any efforts to improve stock status should be focused on reducing *F* on striped bass.

The estimated striped bass target *F* from the striped bass stock assessment is about 35% lower than current *F*. At striped bass target *F* (*F* multiplier ≈0.65), striped bass biomass would reach the target under current Atlantic menhaden *F* rates. Striped bass biomass would remain above the threshold over Atlantic menhaden *F* rates ranging from zero to approximately 4 times F_{2017} (Figure 144), i.e. if striped bass were fished at F_{TARGET}, Atlantic menhaden harvest could be

increased from the 2017 rate by up to 4 fold and striped bass biomass would remain above the threshold but below the target.

The harvest of Atlantic menhaden and striped bass is likely to have effects on other species such as bluefish and weakfish that are preyed upon by striped bass and/or compete with them for prey. Bluefish was below the target across all Atlantic menhaden and striped bass *F* combinations, suggesting (as with striped bass) that bluefish *F* needs to be reduced in order to reach their target (Figure 145). Higher *F* rates on striped bass led to higher biomass of bluefish as a result of reduced predation and competition (striped bass prey on juvenile bluefish and also have diet overlap with bluefish). With striped bass fished out of the system, Atlantic menhaden harvest has very little effect on bluefish biomass. In contrast, when striped bass *F* is reduced, biomass of bluefish declines, with the lowest biomass predicted in scenarios with both reduced striped bass *F* and high Atlantic menhaden *F*. This highlights an important prediction by the model – that effects of Atlantic menhaden harvest on predators are only likely to be observed when predator biomasses are high and there is more competition for food.

Similarly, weakfish biomass is lowest at low striped bass *F* (Figure 146). However, in the low striped bass *F* scenarios, weakfish biomass increases with higher Atlantic menhaden *F*. This peculiar result might indicate that the indirect effects (i.e. lower predation and competition) resulting from the impact of Atlantic menhaden harvest on striped bass biomass (Figure 144) are stronger than the direct effects of Atlantic menhaden harvest on weakfish. That is, when striped bass biomass is high, reducing it by way of increased Atlantic menhaden harvest will result in a net benefit to weakfish. On the other hand, when striped bass biomass is low (high *F* scenarios), increasing Atlantic menhaden harvest has a slight negative effect on weakfish (Figure 146).

13.5.5 NWACS-MICE Ecological Reference Points

Of all the modeled fish species, striped bass was the most responsive to changes in Atlantic menhaden *F*. As a result, striped bass were used as an indicator of the impacts of Atlantic menhaden fishing pressure on the ecosystem for the development of ecological reference points. This is supported by analysis from the full NWACS model that evaluated a broader suite of fish species and found that striped bass was the most sensitive Atlantic menhaden fish predator. The full NWACS model also predicted that piscivorous shorebirds were also sensitive to Atlantic menhaden harvest, and those impacts are not considered in the MICE model.

Analysis to develop ERP *F* target and *F* threshold was based on striped bass biomass responses to changes in Atlantic menhaden *F* while maintaining striped bass at F_{TARGET}. All other modeled species were kept constant at current *F* rates. The proposed ERP target (ERP F_{TARGET}) is the maximum Atlantic menhaden *F* that maintains striped bass biomass at their biomass target, when striped bass are fished at their *F* target. The proposed ERP threshold (ERP $F_{THRESHOLD}$) is the maximum Atlantic menhaden *F* that maintains striped bass biomass at their biomass threshold, when striped bass are fished at their *F* target. Here, the ERP target and threshold apply to Atlantic menhaden *F*.

Projections were run from 2018 to 2057 over a range of Atlantic menhaden *F*s while keeping striped bass fixed at F_{TARGET} (0.635*F_{2017}). Figure 147 shows the simulations over time and Figure 148 shows the terminal year striped bass biomass ratio against Atlantic menhaden *F*. Here, striped bass age 6+ biomass is treated as a proxy for SSB based reference points, since females mature between ages 4-8. Ecosim *F* rates were converted back to BAM units by multiplying the Ecosim *F* ratio (ERP F_{TARGET}/F_{2017}) by the current full *F* of 0.157 from BAM.

The Atlantic menhaden ERP *F* target is 0.06, a 20% increase from current Atlantic menhaden *F*. Conveniently, the BAM equivalent ERP *F* target of 0.188 is equal to current F_{TAC} scenarios from the BAM MC runs (averaged over all years and MC trials). The Atlantic menhaden ERP *F* threshold of 0.183 (=BAM full *F* of 0.573) is about 30% lower than the BAM *F* threshold.

As such, it can be concluded that 1) the proposed current Atlantic menhaden TAC is equal to the ERP *F* target for Atlantic menhaden and should maintain striped bass at target biomass when striped bass are fished at their *F* target; 2) fishing Atlantic menhaden at the proposed BAM *F* target will maintain striped bass above the threshold but below the target; and 3) the current BAM *F* threshold for Atlantic menhaden is too high to maintain striped bass at or above their biomass threshold.

This example was based on the *F* and *B* targets laid out in the striped bass fishery management plan. Higher or lower reference points for striped bass will result in higher or lower reference points for Atlantic menhaden. In addition, this example maintained the other species at their current *F* rates; higher or lower *F* rates on other species would also result in different reference point values for Atlantic menhaden. This equilibrium approach for developing ERPs assumed a constant environment during the projection years. Major changes to biomass of other predators and to bottom-up drivers could alter the productivity of Atlantic menhaden and result in different ERPs.

14 FULL ECOPATH WITH ECOSIM MODEL (NWACS-FULL) (SUPPORTING)

Buchheister et al. (2017a, 2017b) previously developed an NWACS ecosystem model using EwE to inform Atlantic menhaden management within an ecosystem context. This NWACS model simulated 61 trophic groups and eight fishing fleets, using data from 1982 to 2013 (Buchheister et al. 2017a, 2017b). For this assessment, the published model was used to derive a new, updated model (the NWACS-FULL model) to support the evaluation of Atlantic menhaden ERPs. An externally funded research project is currently underway to update time series of all available species in the model; however, the timing of this project did not coincide with the Atlantic menhaden ERP process as it will not be completed for another 1-2 years. As a result, a hybrid approach was developed, where only the time series for the six ERP focal species were updated (1982-2017) and incorporated into the NWACS-FULL model. The NWACS-FULL model provides a holistic ecosystem perspective, addressing the broader impacts of Atlantic menhaden fishing on the ecosystem and all of its predators, including birds, marine mammals, and other fishes not accounted for in the other ERP models.

14.1 Ecopath Model Description

14.1.1 Ecopath with Ecosim Modeling Framework

See Section 13.1 for a description of the EwE modeling framework.

14.1.2 The NWACS Ecosystem Model

Spatial Structure

See Section 13.2 for a description of the NWACS spatial structure.

Temporal Structure

The model was parameterized using available data for the ecosystem from 1982 to 2013. The initial year 1982 was chosen because this is the first year of available catch data for many of the single species stock assessments. All-time series for the ERP focal species (Atlantic menhaden, striped bass, bluefish, weakfish, spiny dogfish, and Atlantic herring) were updated to span 1982-2017 using stock assessment data (See NWACS-MICE Section 13.2.1). For all other groups, forcing time series were extended to 2017 using the values from 2013. A project is underway to update these groups with the best available data through 2017, but the timeline of that project did not align with the Atlantic menhaden stock assessment process.

Trophic Structure

The trophic structure of the model represents the principal groups in the ecosystem – from detritus and phytoplankton to marine mammals and seabirds – using 61 different groups (Table 39). Groups are aggregated taxa based on similar functional or taxonomic characteristics, with a higher degree of aggregation for lower trophic levels (e.g., phytoplankton, zooplankton, and benthic invertebrates) and highest trophic levels (e.g., sharks, marine mammals, seabirds). The degree of taxonomic resolution at lower and higher trophic levels largely followed the structure used for the Energy Modeling and Analysis eXercise (EMAX) models (Link et al. 2006, 2008). Given that the initial application of the NWACS model was for Atlantic menhaden, important Atlantic menhaden predators (e.g., striped bass, bluefish, weakfish) are represented as individual species, as are alternative prey for those predators (e.g., Atlantic herring, Atlantic mackerel, anchovies). Other fish species (e.g., Atlantic cod (*Gadus morhua)*, summer flounder, spiny dogfish) that are of particular management concern or ecological significance were also retained explicitly in the model.

Several fishes were partitioned into multiple age stanzas to account for documented ontogenetic differences in diets (e.g., Garrison and Link 2000; Smith and Link 2010; Buchheister and Latour 2015) or changes in habitat or migration behaviors. Stanzas were defined based on age, but associated length cutoffs were also assigned to allow length-based data to be partitioned appropriately among stanzas (e.g., trawl survey catches and diets based on predator length). Length cutoffs for each age were approximated using length-at-age relationships from scientific trawl surveys or from literature studies. For simplicity and consistency in naming of multi-stanza groups, stanzas were labeled as either small (S), medium (M), or large (L), but they represent different ages and lengths for each species (Table 39).

All groups were modeled using biomass densities (mt/km^2).

Fishing Fleets
Multiple fishing fleets were modelled to account for the dynamics of fishing operations in the region. Modelled fleets were defined as the predominant fishing gears used within the model domain, based on landings data from NOAA. The eight modeled fishing fleets were labeled as dredge, trawl, trap, gill net, purse seine, recreational, longline, and other.

14.1.3 Basic Inputs

The basic data requirements for Ecopath are biomass (*B*), production to biomass rate (*P/B*; equivalent to the total mortality rate, *Z*), consumption to biomass rate (*Q/B*), diet composition, and landings for each trophic group. Biomass accumulation rates (BA_i/B), which describe the instantaneous rate of change of a functional group's biomass to account for groups that are not in equilibrium, can also be provided. A summary of the general approaches and data sources used to parameterize the original NWACS model is provided below. Full details are available in the NWACS documentation (Buchheister et al. 2017b) and paper (Buchheister et al. 2017a). Additional detail on the parameterization for the ERP focal species updated in the NWACS-FULL model, can be found in Section 13.2.1.

The model was developed using several data sources, including fishery-independent surveys, single species stock assessments, primary and gray literature, and existing ecosystem models from the Northwest Atlantic shelf and its estuaries. The NWACS model also adopted many parameters from the EMAX project (Link et al. 2006, 2008). The EMAX project developed four Ecopath models for the Mid-Atlantic Bight, Southern New England, Georges Bank, and the Gulf of Maine; these parameters were used for many of the lower and higher trophic levels that did not have stock assessment data. The NWACS-FULL model has a greater taxonomic resolution for the fish groups (typically in the middle to high trophic levels) than the EMAX models. Stock assessment and fisheries independent survey data were used to parameterize these groups, when possible.

Biomass
When available, biomass estimates for fished groups were obtained from the most recent stock assessment for a given group. Data from multiple assessments were combined in cases where there were multiple stocks within the modeled domain (e.g., Gulf of Maine and Georges Bank Atlantic cod). In the situations with multiple stocks, absolute biomasses (in mt) were summed, whereas *P/B* and *Z* were calculated as biomass-weighted averages. In cases where a stock's distribution extends beyond the modelled domain (e.g., some species inhabit the South Atlantic Bight in addition to the Mid-Atlantic Bight), biomass was apportioned into the model domain based on regional catch or biomass proportions (if available). However, in most of these instances (e.g., Atlantic croaker), the entire stock biomass was used for the model because the contribution of the South Atlantic Bight catch (or biomass) was negligible and would not have a

substantial impact. All absolute biomasses were divided by the model area (246,662 km^2) to obtain the biomass density in mt/km^2. Biomasses for the ERP focal species were obtained from the most recent stock assessments updated through 2017 as described in Section 13.2.1.

Fisheries-independent trawl survey data were obtained from the NEFSC to parameterize the biomasses of non-assessed species. The NEFSC trawl survey is a longstanding fisheries independent monitoring program that has been conducted from 1963 – present, and samples depths from 27-366 m on the continental shelf (Azarovitz 1981). All species captured by the NEFSC trawl were re-classified into the NWACS group definitions, and catchability-corrected biomass estimates were generated following Link et al. (2006). Catchability coefficients (*q*) were assumed to be constant and were estimated using a Bayesian approach that incorporates information on catchability from previous studies. Details on the estimation of catchability coefficients are available in Link et al. (2006). For multispecies groups (e.g., Demersal benthivores-other) that are composed of multiple individual species with different *q* values, the median *q* was used.

Eight species were modeled using multiple stanzas (Table 39), with data obtained from stock assessments. Generally, age-specific biomass estimates were available and summed based on the defined age classes. In the absence of age-specific biomasses, these were calculated from abundance-at-age and weight-at-age data if possible.

Biomass Accumulation Rates

Biomass accumulation rates (BA_i/B) were calculated for all assessed species. Biomass accumulation rates describe the instantaneous rate of change of a functional group's biomass, and they account for groups that are not in equilibrium with their sources of mortality. Negative values indicate a declining biomass and positive values indicate an increasing biomass within the Ecopath model. Biomass accumulation rates were calculated as the rate of change in biomass per year from 1982-1983 [$(B_{1983}- B_{1982})/ B_{1983}$], based on data availability. Biomass accumulation rates were entered as relative rates (yr^{-1}) for all trophic groups, but they can also be expressed in absolute terms (with units in mt km^{-1} yr^{-1}).

Production/Biomass and Mortality

P/B rates for lower and higher trophic levels (i.e., non-assessed species) were primarily obtained from the EMAX models (Link et al. 2006, 2008). For assessed species, instantaneous total mortality rate estimates (*Z*) for each group or age class were calculated as the sum of fishing mortality rate (*F*) and natural mortality (*M*) estimates from the stock assessments. Often *M* was assumed to be constant in the assessments, but if age-specific *M* values were available, an average for each age stanza was calculated. *F* rates were calculated as *C*/*B* using time series from stock assessments (Christensen and Walters 2004). For full details on the calculation of mortality estimates for the ERP focal species, see section 13.2.1 .

Diet Composition

Diets for the NWACS-FULL model were taken from the published NWACS model, which were obtained from the previous EMAX models, fisheries survey data, and the literature. Diets from

the EMAX models were used for many lower trophic level groups and higher trophic level groups that are not typically captured in fisheries surveys. Diets for nodes 17-52 (Table 39) were obtained primarily from the NEFSC and the NEAMAP trawl surveys, which conduct extensive diet sampling within the model domain in deeper (>27 m) and shallower (<37 m) waters respectively. For multi-stanza groups, predators were defined based on the size-cutoffs for each age class, but prey were not classified by age or size because that information was not available in the databases. Any unidentified material was divided among identified prey based on their relative proportions, for each unidentified group. Further details can be found in Buchheister et al. (2017a, 2017b).

Given the central objectives pertaining to Atlantic menhaden, diet estimates for Atlantic menhaden and three dominant predators (striped bass, weakfish, and bluefish) were augmented with literature studies. Diets for the three predators were obtained from the MSVPA-X diet database (Garrison et al. 2010; SEDAR 2015). In addition to data from 21 literature studies, the database includes the diet data from the NEFSC and NEAMAP surveys (mentioned previously), as well as the ChesMMAP survey (Bonzek et al. 2008). Following the methods of the MSVPA (SEDAR 2015), length- and region-specific diets were calculated as an average from these multiple sources weighted by sample sizes, study area, and number of years. The outputted MSVPA diets were region-specific for the MSVPA regions (Gulf of Maine, Southern New England, Mid-Atlantic Bight, Chesapeake Bay, and North Carolina). These regional diets were averaged using region-specific biomasses of each predator species as determined from the NEFSC trawl survey. Given differences in regional definitions, the MSVPA regions identified as Chesapeake Bay, North Carolina, and Mid-Atlantic Bight were assumed to be equally representative of the NWACS Mid-Atlantic Bight region.

Predator diets were modified to apportion the contribution of any multi-stanza prey groups across age-classes. For example, a 13% contribution of Atlantic menhaden to the diet of medium striped bass was allocated among the three Atlantic menhaden age-classes. These allocations were based on predators' size selectivity information when available (including all ERP focal species) and on general guidelines when size selectivity information was not available (Buchheister et al. 2017b).

Consumption Rates

Consumption rate (*Q/B*) values were primarily obtained from the EMAX models (Link et al. 2006, 2008), other ecosystem models (e.g., Christensen et al. 2009), or empirical relationships (Pauly 1989; Palomares and Pauly 1998).

Unassimilated Food

The ratio of unassimilated material to consumed biomass (*UA/Q*) represents the fraction of consumed biomass that is egested and not used for production or respiration. The assimilation efficiency is 1 – *UA/Q*. A *UA/Q* value of 0.2 was assumed for carnivorous fishes and higher trophic levels (Christensen et al. 2008). For lower trophic levels, estimates of *UA/Q* from the EMAX models were used, although several of these were increased during the balancing process to balance the detritus group.

Landings
Catch data were obtained from NOAA online databases and stock assessments. Commercial landings data by weight were downloaded for the entire east coast of the USA by year, species, state, and gear type (NOAA 2014a, http://www.st.nmfs.noaa.gov/commercial-fisheries/index). State-specific landings from North Carolina to Maine were summed to obtain landings for the NWACS model domain. The 127 unique gear types in the database were classified into seven gear types that were used as fishing fleets in the NWACS model (dredge, trawl, trap, gill net, purse seine, longline, and other). An eighth fleet, representing recreational fisheries, was also included using recreational landings data obtained from NOAA by state, year, and species (NOAA 2014b, http://www.st.nmfs.noaa.gov/recreational-fisheries/index). Recreational data included estimates of catch that was brought back to the dock and could be identified by trained interviewer (Type A) and catch that was used for bait, released dead, or filleted as identified by anglers (Type B1).

For assessed species, the landings data from the assessment reports were preferentially used, as these datasets were more detailed, tended to be larger, and were presumably more accurate. Landings data from assessments included dead discards for a more complete estimate of biomass removal. Total catch for each group was apportioned among the eight fishing fleets based on the fractional catches obtained from the NOAA databases. For all multi-stanza groups (except spiny dogfish), catch-at-age matrices from the stock assessment were used to partition catch among stanzas.

14.1.4 Balancing

Model fitting, stability, and sensitivity to parameters are addressed in the NWACS documentation (Buchheister et al. 2017b) and paper (Buchheister et al. 2017a). As with all ecosystem models, there is no single, objective method for arriving at a final model that best replicates historical trends in relative biomass or catch. To the extent possible, the NWACS model was developed following the general guidelines and best-practices for building, parameterizing, balancing, and calibrating EwE models, as recommended in the literature (Christensen et al. 2008; Heymans et al. 2016).

The process of adjusting parameters in an Ecopath model to ensure mass balance is known as "balancing". One of the key diagnostics is that all groups should have EE values < 1. Given that the balanced version of the published NWACS model was used as the starting point, the NWACS-FULL relies on all of the balancing decisions made previously, which are described by Buchheister et al. (2017a). Additional balancing was required after the data were updated for the ERP focal species. Several small changes were made, including changes to the diet matrix and minor adjustments to P/B, Q/B, and BA/B. There were two changes that were more substantial but deemed justifiable. First, Atlantic herring 1982 biomass was increased from 0.466 mt/km^2 (mid-year biomass calculated from the stock assessment) to 0.8 mt/km^2 (+72%) to account for the large amount of predation on this species by a diverse group of predators.

This amount of increase was only 16% greater than the Jan 1 biomass in 1982. This change can also help account for age-0 fish that are not included in the assessment. Second, the starting *B* of large spiny dogfish was decreased by 51% from 2.45 to 1.2 mt/km^2. Spiny dogfish were an outlier based on a pre-balancing analysis (PREBAL; Link 2010) with high biomasses in the system given their trophic level (Figure 149). This 51% reduction still kept the group at the high end of log(biomass) for their given trophic level. Also, the *B* for large spiny dogfish was very variable with a 3-year mean *B* (1981-1983) of 1.57 mt/km^2, so this change was deemed reasonable.

14.1.5 Ecopath Outputs

The balanced Ecopath model output is presented in Table 40. The food web was highly interconnected and complex, with a total of 970 trophic links in the system and an average of 15.9 links per trophic group (Figure 150, Table 41). Atlantic menhaden were consumed by a total of 22 predator groups (36% of the modeled trophic groups) and they contributed to a substantial portion of the diet of some predators, notably 30% for large striped bass and 33% for nearshore piscivorous birds.

14.2 Ecosim Model

14.2.1 Treatment of Time Series Data

The input data needed for the time-dynamic Ecosim model included time series of relative biomass, catch, fishing mortality, and fishing effort. Time series of catch and relative biomass were used as reference time series, whereas fishing mortality (for all groups with stock assessments) and fishing effort (for groups that are not assessed) were included as forcing time series. Relative biomass time series were obtained from stock assessment reports (for assessed species), or from the NEFSC trawl survey for all other fish groups. For assessed species, data from stock assessment reports were used to obtain catch and fishing mortality time series. Data from NOAA landings databases were used to obtain catch time series for non-assessed fishes and non-assessed, commercially-harvested invertebrate species. Fishing effort by fleet was assumed to be proportional to changes in fleet-specific total catch through time, and it was used to drive non-assessed trophic groups. Fishing mortality was used to drive changes in groups with stock assessment data, which included the groups of greatest commercial importance and of greatest relevance to the research objectives. For all groups (including those with multi-stanzas) that had assessments, fishing mortality rates were calculated as catch divided by biomass ($F = C/B$). If the baseline Ecopath biomass value for a group was changed during the Ecopath balancing procedure (section 14.1.4), then the *F* was calculated using the biomass time series scaled to the balanced Ecopath biomass. For any fishing mortality time series that did not extend for the full 1982-2017 time period, a 3-4 year mean of the nearest assessed years was used to extrapolate any missing values. This was typically only needed for <5 years; however, Atlantic mackerel, butterfish, and Atlantic croaker had longer periods of missing *F*s, with 6-9 years missing at either the beginning or end of the time series.

For the ERP focal species, all-time series were updated through 2017 using the most recent stock assessment data (see Section 13.3.1). For these species, the mid-year biomass estimates from the assessment models were used as reference time series instead of indices of abundance.

14.2.2 Calibration Steps

The NWACS-FULL model was calibrated to the observed, reference time series using an iterative approach. See Section 13.3.2 for full details on the approach. Briefly, the "Fit to Time Series" utility in Ecopath was used in which the most sensitive vulnerabilities for K-1 different predator-prey interactions were estimated by reducing the sum of squares of the model fits. K refers to the number of observed time series used to fit the model (K=68 for this model). This process was done iteratively until there were no substantial reductions in sum of squares or AIC. No more than 67 vulnerabilities were fitted during each tuning iteration, but different vulnerability values could be estimated during each iteration. As many as 229 different vulnerabilities were estimated using this process. This amounts to between ~3 estimated parameters per time series, or ~23% of all possible vulnerabilities (i.e. the number of predator-prey interactions in the diet matrix).

Scenarios
Eight different versions of the NWACS-FULL model (referred to as simulations, or Sims) were developed to examine the sensitivity of model results to specific decisions (Table 42). The eight versions are combinations of decisions pertaining to three components: the diet matrix, the vulnerability constraints, and manual changes pertaining to model dynamics. Sims 1 and 5 involved re-fitting the model using the iterative calibration procedure. The other 6 model versions did not require calibration to observed time series but instead applied vulnerability caps or included manual tuning adjustments made after model fitting. Sums of squares and AIC values were obtained for Ecosim simulation and used for comparison of model fits.

We explored two different options for the diet matrix. The base diet matrix was taken from the published NWACS model (Buchheister 2017b). A second diet option involved increasing the contribution of Atlantic menhaden in the diets of their predators as a way to increase Atlantic menhaden EE in the model and to examine dynamics when Atlantic menhaden importance is increased. Diets were increased to what was deemed to be the upper range of possible values, as informed by available data. For example, Atlantic menhaden contribution to spiny dogfish diet was increased from <1% (the value from NEFSC trawl survey used in the base diet matrix) to ~16% (which is the value from NEAMAP trawl survey). These dietary differences for spiny dogfish represent a range of possible, realistic diet values from extensive food habits surveys that sample in habitats of different depth (offshore vs. nearshore).

Vulnerability caps were examined to investigate the effect of these parameters on the Ecosim model. After completing the fitting process, vulnerabilities could range from 1 to 10^{10}. Vulnerability caps were established to restrict the upper end by assuming that the maximum M_2 that a predator can exert on any individual prey is equal to 75% of the total M experienced by the prey in the base year of the model (see section 13 for more detail). These changes

resulted in all predator-prey v<5300. An arbitrary minimum vulnerability value of v=1.01, instead of v=1, was also employed.

The third consideration for alternative model versions was whether or not manual adjustments were made to the vulnerabilities of Atlantic menhaden and the other ERP focal species. Any vulnerability parameter with Atlantic menhaden as a predator was capped at v=4 to 5 such to make the Atlantic menhaden stock recruitment relationship have a Beverton-Holt shape as opposed to one weak density dependent compensation, which was more typical of the other model versions (Figure 151). This involved changing just four vulnerability parameters in the models. Also, the minimum vulnerabilities for each ERP focal species were also adjusted to generate more reasonable F_{MSY} values. The minimum vulnerability value for a selected ERP focal species was evaluated iteratively using the "F_{MSY}" tool within Ecopath. For example, minimum vulnerabilities (v_{min}) for all age-classes of striped bass would be changed from v=1 to v=1.1, and the F_{MSY} tool would be used to evaluate the relative catch of striped bass at varying levels of F on each of the striped bass groups. Often, with v_{min} =1, the species could sustain unrealistically high levels of fishing without having a decline in relative catch. The expectation was to have a dome shaped relative catch curve that indicates a theoretical F_{MSY} value. The v_{min} values for a given ERP focal species would be iteratively adjusted to obtain a dome-shaped curve. This was done separately for each ERP focal species, yielding v_{min} values between 1.03 and 1.1. A more formal and rigorous analysis could be conducted in the future where all yield curves are evaluated simultaneously instead of individually.

14.3 Ecosim Outputs

14.3.1 Fits to time series

Ecosim predictions from 1982-2017 generally corresponded well to observed historical trends in biomass (Figure 152). The observed time series of biomass were fitted as relative biomass as opposed to absolute biomass for each of the eight simulations, and Ecosim internally scales each relative biomass timeseries for each simulation. On the plot, the observed biomasses are scaled according to Sim 1, therefore the fits for the other simulations are slightly better than depicted (Figure 152). Generally, the different simulations tended to generate similar predictions, albeit with some changes in scale or pattern (e.g., Atlantic herring, butterfish, weakfish, cod, haddock, croaker, summer flounder). Model predictions also typically smoothed over higher-frequency interannual changes (e.g., Atlantic menhaden, squid, spiny dogfish), because no information was provided in the model to capture such variability (e.g., recruitment deviations, primary production anomalies). In the case of some species (often when better F data was not available), predictions remained relatively flat despite trends in the observed time series (e.g., shrimp, Atlantic mackerel, hake, skates, demersal piscivores). Fits for the ERP focal species tended to be good with some exceptions (weakfish-M, spiny dogfish-S) (Figure 153).

There was a greater diversity in model fits to the catch time series (Figure 154). Catches for many groups were predicted well (e.g., shrimp, ERP focal species, cod, croaker, demersal piscivores). In several cases model predictions matched the patterns but not the scale or vice

versa (Figure 154). For some groups (e.g., Megabenthos other, Hake, Summer flounder, skates, sharks), both the scale and pattern of simulations deviated from the observed catches. In many of the cases of poor model fit, the lack of fit is partly attributable to absence of detailed information on fishing mortality for these groups and poor catch data; for many of these groups, fishing pressure was forced in the model using patterns of fishing effort from generalized fleets (that capture numerous groups) rather than being forced with a group-specific fishing mortality. Fits to ERP focal species tended to be reasonable at least for some simulations (Figure 155). In some instances, vulnerabilities were adjusted manually in an attempt to improve the catch fit for a species (e.g., Atlantic herring); however, this led to substantial reductions in the quality of the fit for another species (e.g., striped bass) (Figure 155), highlighting that there are tradeoffs in the quality of fit for some groups in complex models. The trophic linkages responsible for these tradeoffs should be examined closer through targeted diet studies and sensitivity analysis.

Results of the fits for all 8 model versions (Sims 1-8) suggested that Sim 1 and 5 were the best fitting models based on AIC (Table 42). However, Sim 2 and Sim 6 were chosen as the best models for evaluation because they included the manual adjustments that generated more realistic stock recruitment dynamics for Atlantic menhaden and more feasible F_{MSY} dynamics. Heymans et al. (2016) recommends sacrificing the overall fit to some groups in order to obtain more biologically reasonable dynamics for focal species.

14.3.2 Mortalities and Diets

Mortality rates for Sim 2 and Sim 6 indicate the relative contributions of fishing (F), predation mortality (M_2), and unexplained mortality (M_0) to total mortality (Z) (Figure 156). F represents a small proportion of total instantaneous mortality for small and medium Atlantic menhaden (<3% in 2017) and ~12% for large, age-3+ Atlantic menhaden, and these patterns did not differ greatly among the eight simulations (Figure 157). The contribution of M_2 to the total mortality differed between sim 2 and sim 6 (Figure 156) because of the increased contribution of Atlantic menhaden to predator diets (Table 42). M_0 (the difference between Z and $F + M_2$) was much greater for Sim 2 than Sim 6 particularly for small, age-0 Atlantic menhaden (Figure 156). For both Sim 2 and 6, Z has increased over the time series for small age-0 Atlantic menhaden, stayed relatively constant for medium age-1-2 Atlantic menhaden, and declined slightly for large, age-3+ Atlantic menhaden.

A variety of predators contribute to Atlantic menhaden M_2, but the dominant groups differed between Sim 2 and Sim 6. For Sim 2, bluefish, striped bass, miscellaneous demersal omnivores and piscivores, marine mammals, and birds were important sources of predation, depending on the Atlantic menhaden age class (Figure 158). For Sim 6, spiny dogfish became the most important predator (Figure 159) because Atlantic menhaden contribution to spiny dogfish diet was increased from <1% (value from NEFSC trawl survey) to ~16% (value from NEAMAP trawl survey) and spiny dogfish are a biomass-dominant group in the system. These dietary differences for spiny dogfish represent a range of possible, realistic diet values from extensive food habits surveys that sample in habitats of different depth (offshore vs. nearshore).

14.3.3 Emergent Stock Recruit relationships

The emergent stock-recruitment relationship for Atlantic menhaden were evaluated using methods recommended by (Christensen et al. 2008) and described in Section 13.4.2. Ecosim models do not include an explicit stock-recruitment equation, but Beverton-Holt or Ricker type stock-recruitment curve may emerge for multi-stanza groups depending on Ecosim parameters settings, particularly the vulnerabilities. The stock-recruitment relationship for Atlantic menhaden was examined by simulating a severe increase and decrease in fishing mortality that would generate paired biomass estimates of small (age-0) and large (age-3+) Atlantic menhaden across a wide range of stock sizes. Stock-recruitment curves were generated for each scenario. Manual adjustments were made to the vulnerability caps of Atlantic menhaden as a predator (capped at v=4 to 5) to achieve a Beverton Holt shape for Sims 2, 4, 6, and 8 (Figure 151).

14.3.4 Equilibrium MSY

An analysis was conducted to estimate and evaluate F_{MSY} values for Atlantic menhaden using the base (1982) conditions of Sim 2 and Sim 6 of the NWACS-FULL model. The methods employed are similar to those described in Section 13.4.3. However, given that fishing occurs on multiple Atlantic menhaden age-stanzas (e.g., age-1-2 and age-3+), some modifications were necessary. The Sim 2 and 6 models were adjusted by creating a single Atlantic menhaden fishing fleet that only targeted Atlantic menhaden. Using the "F_{MSY}" tool in Ecopath simulations were conducted in which the fishing effort of the Atlantic menhaden fleet was applied for 40 years using an effort multiplier (ranging from 0-5). Simulations allowed for full compensation in the system such that predators and prey would respond dynamically to the changes in Atlantic menhaden fishing. These simulations rely on the base 1982 Ecopath parameterization and the Ecosim parameters from the calibrated simulations (e.g., vulnerabilities), and project forward from 1982 for equilibrium conditions. Thus, any relative and effort values coming out of the Equilibrium MSY analysis are relative to 1982.

Relative biomass and catch for several species groups were affected by different Atlantic menhaden fishing rates (Figure 160). Biomasses of Atlantic menhaden, striped bass, and nearshore piscivorous birds exhibited the strongest declines, whereas some groups had increases in biomass (e.g., alosines, pinnipeds, summer flounder) (Figure 160). Catch trends were similar to those of biomass for non-menhaden species. Atlantic menhaden catch peaked with an effort multiplier (relative to 1982) between 2.5-3.4 for Sim 2 with corresponding F_{MSY} estimates of 0.735 (age-1-2) and 0.926 (age-3+) (Figure 160, Table 43).In Sim 6, Atlantic menhaden maximum sustainable yield occurred with an effort multiplier between 1.3 and 1.9 with F_{MSY} estimates of 0.41 (age-1-2) and 0.48 (age-3+) (Figure 160, Table 43). This analysis shows that if predators are more dependent on Atlantic menhaden, harvest policies of Atlantic menhaden may need to be more conservative to meet the management goals for those species.

14.4 Projections

The NWACS-FULL model was used for two sets of forward projections. The first set of projections examined four different fishing scenarios (at status quo or target *F* for Atlantic menhaden and the ERP focal species). The second set of projections explored numerous Atlantic menhaden fishing scenarios (from no fishing to excessive fishing) under different fishing conditions for the ERP focal species.

14.4.1 Projection Scenarios 1 (at status quo and target *F*).

The first set of projections involved maintaining fishing mortality rates at either status quo or target levels for Atlantic menhaden and for all other ERP focal species (striped bass, bluefish, weakfish, spiny dogfish, and Atlantic herring). All other modeled species were kept at their status quo levels of fishing mortality or fishing effort (from 2013, because their time-series were not updated through 2017). The four scenarios were (1) status quo fishing on Atlantic menhaden and status quo fishing on the ERP focal species (SQ Menh – SQ Others), (2) status quo fishing on Atlantic menhaden and target *F* rates for the ERP focal species (SQ Menh – TARG Others), (3) target *F* rate for Atlantic menhaden and status quo fishing on the ERP focal species (TARG Menh – SQ Others), (4) target *F* rate for Atlantic menhaden and target *F* rates for the ERP focal species (TARG Menh – TARG Others). Projections were run for 50 years.

Due to the differences in what *F* rates represent in the single species stock assessments and Ecosim, proxies for all single species *F* reference points were developed using the proportional change of the target *F* from F_{2017} (Table 4). For example, target *F* rates for Atlantic menhaden from BAM are based on abundance and calculated as the geometric mean *F* for ages 2-4, whereas EwE *F* rates are based on biomass and constrained to the age classes in the model. Based on the BAM, *F* rates from 2017 (F_{2017}=0.11) would need to be doubled to reach the Atlantic menhaden target *F* (F_{TARGET}=0.22). Therefore, the target *F* rate in EwE was scaled by doubling the 2017 *F* rate for each of the modeled Atlantic menhaden age classes. This was done to obtain all target *F* rates for projection scenarios (Table 4).

Results of these projections indicated that, with the exception of bluefish, projected biomasses for Atlantic menhaden and the other ERP focal species are not expected to change dramatically (Figure 161). Scenarios where bluefish (and the other ERP focal species) *F* rates were set at target levels generated a strong recovery of bluefish, greater than the 136% increase needed to reach their target biomass. This indicates that for bluefish, their fishing mortality rate has a strong impact on the population response (Figure 161); however, recovery was not seen for other species like striped bass, which did not recover to their target B level. While there may be some ecological explanation for this, it equally, if not more likely that the inability of striped bass to recover to B_{TARGET} in Ecosim is due to parameter estimates and the unbounded nature of the vulnerability search in Ecosim.

Projection results were also used to isolate the effect that Atlantic menhaden fishing would have on the ERP focal species. This was done by comparing the biomass of species in the "TARG Menh – SQ Others" scenario with the status quo (SQ Menh – SQ Others) scenario. Specifically,

the percent biomass difference (B_{DIFF}) was calculated as $B_{DIFF} = [(B_{TRIAL,y}/B_{2017,y})-1]*100$, where $B_{TRIAL,y}$ is the biomass for the "TARG Menh – SQ Others" (trial) scenario in year y, and $B_{2017,y}$ is the biomass for the status quo scenario in year y. B_{DIFF} was calculated following a projection of 4 years (y=2021) and 40 years (y=2057), using both Sim 2 and Sim 6. Identical calculations were also made for catch relative to the status quo scenario (C_{DIFF}).

Results of the projection analysis (expressed as B_{DIFF} percentages) indicate that the majority of the modeled groups are not expected to have dramatic changes in either *B* or *C* relative to the status quo scenario if Atlantic menhaden are fished at their target *F* rate (Table 44). For Sim 2, B_{DIFF} and C_{DIFF} were ≤5% for all species (excluding Atlantic menhaden) after 4 years. However, the biomass of striped bass and nearshore piscivorous birds were 7% and 9% lower than the status quo fishing scenario after 40 years (using Sim 2) indicating a greater sensitivity to Atlantic menhaden fishing (Table 44). Atlantic menhaden catch was 82% greater after 40 years in the *F* target scenario relative to status quo. The magnitude of B_{DIFF} and C_{DIFF} were greater using Sim 6 of the NWACS-FULL Model (which had higher importance of Atlantic menhaden to predator diets); B_{DIFF} after 40 years was negative for most species (except Alosines and Atlantic cod), with the greatest impact on bluefish (-10%), striped bass (-11%), and nearshore piscivorous birds (-14%) (Table 44).

14.4.2 Projection scenarios 2 (at various Atlantic menhaden *F* rates)

The second set of projections using the NWACS-FULL model examined a range of Atlantic menhaden fishing mortality rates. Projections were conducted under two alternative conditions for the focal ERP focal species: *F* rates for the ERP focal species were collectively maintained at either the threshold *F* (i.e., limit *F*) ($F_{THRESHOLD}$) or at the target *F* (F_{TARGET}). Under each of these 2 conditions, simulations were run at 14 different Atlantic menhaden *F* rates. Specifically, Atlantic menhaden F_{2017} rates for all three age stanzas were scaled using an *F*-multiplier (i.e., $F = F_{2017}*F$-multiplier) where *F*-multipliers were equal to 0, 0.3, 0.6, 1, 1.5, 2, 3, 4, 7, 10, 15, 20, 30, and 40. This was done to explore a broad range of Atlantic menhaden *F* rates and to ensure that the complete Atlantic menhaden yield curve was obtained (although for reference, the maximum observed *F* from 1982-2017 for medium, age-1-2 Atlantic menhaden was only ~10 times the 2017 value). *F*-multipliers of 1, 2, and 5.5 correspond to F_{2017}, F_{TARGET}, and $F_{THRESHOLD}$ for Atlantic menhaden, respectively. Projections were run for 50 years and the relative equilibrium biomass (B/B_{2017}) was calculated, where B was the equilibrium biomass for a given *F* scenario and B_{2017} was the equilibrium biomass for the status quo Atlantic menhaden fishing scenario (i.e., when the *F*-multiplier=1). Equilibrium catches are presented relative to the maximum equilibrium catch across all Atlantic menhaden fishing scenarios (C/C_{MAX}), which would occur under the *F*=0 or $F_{EXTINCTION}$. Patterns were similar across the $F_{THRESHOLD}$ and F_{TARGET} conditions, therefore only the results for the F_{TARGET} projections are presented.

Results of these projections indicate that only bluefish and spiny dogfish would achieve their biomass targets when the ERP focal species are fished at F_{TARGET} (Figure 162). Bluefish and spiny dogfish had relative biomass values approximately twice their biomass thresholds and approximately equal to their biomass target (Figure 162) under the different Atlantic menhaden fishing mortality scenarios. Atlantic herring, striped bass, and weakfish B were all below their *B*

thresholds, even when there was no fishing on Atlantic menhaden (~60%, ~50%, and ~30% of *B* thresholds, respectively) (Figure 162). Aside from Atlantic menhaden, bluefish and striped bass showed the greatest response to Atlantic menhaden fishing rates (Figure 162, Figure 163).

In addition to Atlantic menhaden, striped bass, and bluefish, some other modeled trophic groups also exhibited substantial responses to Atlantic menhaden fishing (Figure 164). Striped bass and nearshore piscivorous birds declined 69% and 77%, respectively, as Atlantic menhaden were fished out of the system (Figure 164, Table 45). Biomass of demersal piscivores, seabirds, haddock, large pelagics (HMS), and coastal sharks decreased between 10 and 15% without Atlantic menhaden in the system (Figure 164, Table 45). Atlantic cod and medium pelagic fishes exhibited biomass increases (51% and 18%) at the highest Atlantic menhaden *F* scenarios due to release from predation or competition (Figure 164, Table 45). It should be noted, however, that the lack of spatial consideration might result in an overestimation of the competitive effects on Atlantic cod.

Trends of relative catch (C/C_{MAX}) under the different Atlantic menhaden projection scenarios (Figure 165, Table 45) generally show similar trends as for biomass. Striped bass is the most sensitive species with maximum declines near 75%, but most negatively affected species have catches declining by <20% at the highest Atlantic menhaden *F* rates. Catches of Atlantic Cod and Medium pelagics were predicted to increase as a result of their biomass increases. Atlantic menhaden catch was obviously the most responsive to Atlantic menhaden *F* with maximum sustainable yield occurring at ~15 times the F_{2017} values for the species (Figure 165). This would equate to approximate F_{MSY} values for age-1-2 and age-3+ Atlantic menhaden of 0.57 and 1.68 respectively.

Projection analyses can be used to compare and evaluate potential effects of alternative Atlantic menhaden reference points on the relative biomass and yield of different trophic groups (Table 45). These analyses also indicate the species most sensitive to Atlantic menhaden fishing, as indicated previously. Compared to status quo Atlantic menhaden fishing, fishing Atlantic menhaden at F_{TARGET} is not anticipated to generate substantial losses to biomass of most other groups (2-5%), except for striped bass and nearshore piscivorous birds, which declined by 8 and 9% (Table 45). Catch of Atlantic menhaden was 84% of the theoretical maximum (if Atlantic menhaden were unfished). Fishing at $F_{THRESHOLD}$ resulted in declines of biomass of 4-8% of some groups, with again greater declines for striped bass (28%) and nearshore birds (32%), relative to F_{2017} (Table 45). Results for the F_{MSY} and $F_{EXTINCTION}$ scenarios are included for comparison to highlight the magnitude of change predicted by the model under these more extreme conditions (Table 45).

It is important to note that the values for the F_{MSY} estimates should be examined cautiously. F_{MSY} values were sensitive to vulnerability parameters, and additional analyses are recommended to examine how Atlantic menhaden F_{MSY} values change with the model's parameterization. Also, the F_{MSY} estimates from this projection analysis using *F*-multipliers (F_{MSY} =0.57 for age-1-2 Atlantic menhaden, and F_{MSY} =1.68 for age-3+ Atlantic menhaden) differ from those of Table 43 because of the slightly different methods employed and the different

assumptions regarding fishing rates for the other species. Here, the ERP focal species were assumed to be fished at target *F* levels; all other groups were fished at 2017 status quo *F* levels, whereas the values in Table 43 assume 1982 fishing mortality rates. This highlights that F_{MSY} estimates for Atlantic menhaden (or any species) will be conditional on the fishing mortality rates of all other trophic groups within a system.

14.5 Uncertainties and sensitivities

Ecosystem models have inherent uncertainties that are broader than single species models, but they are a valuable tool for addressing ecosystem considerations for managers. Hilborn et al. (2017) criticized ecosystem models that aren't case-specific and that don't address important factors in systems (e.g. size selective predation, environmental variability, high natural variability of forage fishes, weak stock-recruitment relationships, and the spatial dynamics of trophic interactions) (but see Pikitch et al. 2018). The NWACS model (and other model derivatives like the NWACS-MICE model) has (or can) address several of the Hilborn et al. (2017) concerns because 1) it is case-specific, developed specifically with Atlantic menhaden in mind, 2) it accounts for size selective predation, and 3) the model can be used as a foundation to explore the topics of environmental variability, recruitment variability and spatial dynamics that are a challenge for any modeling framework, as can be seen from the explorations using the NWACS-MICE model.

A full uncertainty analysis of this model update remains to be completed. Alternative model parameterizations may lead to different model behavior (Mackinson 2014). However, previous MC simulations with the NWACS model (Buchheister et al. 2017a), in which base Ecopath biomass parameters were allowed to vary with a CV of 0.2, suggested that the general patterns of individual group responses were maintained. Ultimately, a more comprehensive sensitivity analyses should be conducted to evaluate more specific, targeted concerns including, for example, uncertainty in predator diets, vulnerability estimates, and other parameters. These were addressed to some extent here and in the MICE model.

As noted previously, any F_{MSY} estimates derived from EwE projections should be examined cautiously given their sensitivities to the vulnerability parameters. Additional analyses are recommended to examine how F_{MSY} values for Atlantic menhaden and other key species change with the model's parameterization. The fact that a species' F_{MSY} estimates are conditional on *F* rates for other modeled species (e.g., predators) also reinforces the need to consider tradeoffs when managing fisheries in an ecosystem context.

We noted that some of the ERP focal species (striped bass, Atlantic herring, and weakfish) did not recover in projections when these species were fished at their target *F* rates and when Atlantic menhaden were not fished (Figure 162). Additional manual modification of Ecosim parameters for these species could lead to projections with recovery for these species, but this would likely be at the expense of goodness-of-fit to historical data.

There remained a substantial amount of unexplained mortality for Atlantic menhaden (Figure 156), which was unexpected given the inclusion of all trophic groups, the inclusion of a directed

Atlantic menhaden fishery, and the broad spatial scale of the model. There are multiple hypotheses that could contribute to this pattern. First, the dietary contribution of Atlantic menhaden could be higher than used in Sim 2 (as explored in Sim 6), but this did not appear to address the unexplained mortality of age-1-2 and age-3+ Atlantic menhaden. Second, the overall biomass of Atlantic menhaden in the system could be lower than the estimate used from the BAM output, as the scale of biomass in single species stock assessment models can be harder to determine as opposed to biomass trends. Third, the mortality rates used for Atlantic menhaden could be too high. Fourth, the model may not be fully capturing the spatiotemporal dynamics of Atlantic menhaden-predator interactions, for example by not representing periods or locations of particularly intensive predation. The truth is likely some combination of these hypotheses, and future work is needed to explore these hypotheses in an attempt to reduce the amount of unexplained mortality (and thus increase the EE) for Atlantic menhaden in the model. A more complete accounting of total Atlantic menhaden mortality could potentially increase the effect of Atlantic menhaden fishing on other species in the system as seen when comparing the projection results of Sim 6 with Sim 2 (Table 44).

14.6 Main findings

The NWACS-FULL model can provide long-term strategic advice that is focused on broad-scale assessments of directions and patterns of change for diverse species groups (Christensen and Walters 2011). This model leverages and integrates single-species stock assessment models to provide a fuller, more thorough description of a complex ecosystem. This is done by explicitly accounting for predator-prey feedbacks that are not possible with many other models and quantifying the tradeoffs among different management decisions and scenarios.

This model identified striped bass and nearshore piscivorous birds as the two groups most strongly linked to the dynamics of Atlantic menhaden, and thus they should be of particular focus for managers. For example, striped bass and nearshore piscivorous bird biomasses were estimated to decline by 8% and 9% (respectively) if Atlantic menhaden F was increased from F_{2017} to F_{TARGET} (while ERP focal species were fished at their target levels). Striped bass and nearshore piscivorous bird biomasses would decrease more substantially by 28 and 32% if Atlantic menhaden F was changed from F_{2017} to $F_{THRESHOLD}$ (Table 45). Prioritizing consideration of striped bass (over other species) in the multispecies and ecosystem models included in this report is warranted based on the results of the NWACS-FULL model. This finding reinforces the linkage between Atlantic menhaden and striped bass indicated by past research, by the other models in this report, and by managers and stakeholders.

Some other modeled groups (e.g., bluefish, weakfish, demersal piscivores, seabirds, haddock, large pelagics, and coastal sharks) were also shown to be negatively affected by increased Atlantic menhaden fishing but their responses at Atlantic menhaden F_{TARGET} were negligible relative to F_{2017} (Table 45). Negative effects on these species groups tended to be most substantial at higher Atlantic menhaden F rates (e.g., F_{MSY}, $F_{EXTINCTION}$). The model also indicates that a few groups (e.g., medium pelagic fishes, and Atlantic cod) could benefit from increased Atlantic menhaden fishing, due to indirect ecosystem effects.

Many of the groups negatively affected by increased Atlantic menhaden fishing are those with relatively poor data (e.g., nearshore piscivorous birds, seabirds, large pelagics, coastal sharks, demersal piscivores); thus, the model results can help prioritize research needs for these species. For example, the nearshore piscivorous birds (including blue herons, bald eagles, brown pelicans, cormorants, and osprey) have the capacity to consume large amounts of prey per capita due to higher metabolism and Q/B, but their coastal biomass and diet dependencies have not been well quantified (Bryan Watts, College of William and Mary, personal communication). Other studies have shown sensitivity of seabirds to changes in forage fish abundance and management (Cury et al. 2011; Pikitch et al. 2012), and the NWACS-FULL results suggest that a better understanding of bird-Atlantic menhaden linkages would be an important ecosystem consideration for management.

In quantifying the tradeoffs in biomasses and catches of various species groups and fisheries, this model highlights that outcomes are contingent not only on the fishing rates for Atlantic menhaden, but also on the fishing rates of other species such as their predators. Taking a true ecosystem-based approach to managing Atlantic menhaden would ideally require collaboration and coordination among managers for multiple species (e.g., Atlantic menhaden and striped bass) or the system as a whole. However, the mechanisms and process are not yet in place to do this effectively in the current single-species management framework. Models and analyses like those presented in this report could be used to help advance discussion or implementation of a more comprehensive ecosystem-based management strategy for the ERP focal species or the entire ecosystem (e.g., Essington et al. 2016). Given competing interests and uncertainties, this could be a challenging process but it can be facilitated by structured decision-making approaches (e.g., Miller et al. 2010, Irwin et al. 2011) and formal management strategy evaluation (e.g., Mackinson et al. 2018), which could use the NWACS model to explore management alternatives dynamically.

15 MODEL COMPARISONS

15.1 Biomass

To compare population size estimates across models, total age-1+ biomass was used. For the surplus production models, this was equivalent to the total biomass estimates from each model. For the BAM and the VADER model, this was the sum of the beginning of the year biomass at age for ages 1-6+; the mid-year age-1+ biomass was also calculated for a metric that was more equivalent to the output of the NWACS models. For the NWACS models, total age-1+ biomass was used as the biomass in the “adult” age class from the NWACS-MICE model (which used only two age classes: age-0 and age-1+) and the sum of the “medium” and “large” size/age classes for the NWACS-FULL model (which used three size/age classes, with the “small” size class equivalent to age-0). The MCMC confidence intervals from the single-species assessment were used as a measure of the minimum uncertainty when comparing the single-species assessment estimates to the ERP assessment estimates.

Overall, all models showed similar trends in age-1+ biomass estimates and were on similar scales, both in comparison to each other and to the BAM single-species assessment results (Figure 166).

The magnitude of the estimates from the surplus production models (time-varying *r* and Steele-Henderson) were sensitive to the starting year (Figure 167). This is not surprising, since the strongest contrast in the index time-series was in the earliest year (1955-1965; Figure 13). However, on a relative scale, the surplus production models showed very similar trends to each other and to the BAM trends, regardless of the starting year (Figure 167). All three models showed a decline from the late 1950s to a low in the early 1960s before increasing through the end of the time series, although the surplus production models began increasing sooner than the BAM. The surplus production estimates of biomass were less variable than the BAM estimates, which is consistent with the structure of each of the models.

The multispecies statistical catch-at-age model, VADER, more closely tracked the BAM total biomass output and the biomass estimates were generally within the minimum uncertainty bounds of the MCMC confidence intervals for the BAM estimates (Figure 168). Both models showed an increase from 1985 to the early 1990s followed by a decline into the early 2000s and then recovery to levels higher than 1985. The VADER followed more of the variability in the BAM output than the biomass dynamics models.

The NWACS models followed the overall trend and magnitude of the BAM estimates, but, like the surplus production models, did not show the same variability as the BAM estimates (Figure 169). The NWACS models are biomass dynamic models and therefore do not capture the variability in recruitment that is captured by the statistical catch-at-age model structure. The NWACS-FULL model used biomass estimates from the BAM as input; however, the NWACS-MICE model used fishery independent indices instead of BAM output but was still able to recover similar overall trajectories as the BAM and the other ERP models.

15.2 Mortality

15.2.1 Exploitation Rate

Exploitation rate was used to compare measures of fishing mortality across models with different structures as well as different units. Exploitation rate was calculated as predicted total age-1+ removals in weight divided by beginning of the year age-1+ biomass. Age-0 fish make up approximately 1% of total Atlantic menhaden removals over the entire time series, which is why age-0 biomass was excluded. The MCMC confidence intervals from the single-species assessment were used as a measure of the minimum uncertainty when comparing the single-species assessment estimates to the ERP assessment estimates.

All models showed similar magnitude and the same declining trends since the mid-1980s (Figure 170). However, the surplus production models showed a different trend from the BAM estimates in the earliest part of the time-series, the mid-1950s through the mid-1970s (Figure

171). The surplus production models estimated the highest exploitation rates over the entire time series in the early 1960s, followed by a steady decline through the end of the time series. The BAM estimates peaked in the mid-1970s to the mid-1980s before declining. The BAM estimates were lower relative to both the surplus production model estimates and its own time-series high during the 1960s, although still higher than the estimates from the most recent years. This is due in part to differences in the input data; the surplus production model used the fishery-dependent RCPUE index as well as the fishery independent indices, while the base run of the BAM did not. When the RCPUE was included in the BAM, the trend in estimates of exploitation rate in the early part of the time-series was more similar to the surplus production models, peaking at the same time as the surplus production models and declining consistently through the rest of the time-series, with a smaller peak in the 1980s (Figure 172). The estimate of exploitation rate from this run of the BAM were still lower than the estimates from the surplus production models. The VADER and the NWACS models do not extend back that far, so no comparisons with those models were possible for this time period.

The VADER estimates of exploitation rate were very similar to the BAM estimates and generally within the MCMC confidence intervals of the BAM estimates (Figure 173).

The NWACS estimates of exploitation rate were very similar to the BAM estimates (Figure 174), but this was because exploitation rate or fishing mortality rate from the BAM output were used as input to the NWACS models, so the comparison is not truly meaningful.

15.2.2 Non-Fishing Mortality

15.2.2.1 Modeled Predation Mortality

The Steele-Henderson surplus production model, the VADER model, and the NWACS models estimated natural mortality from the predation of modeled species, referred to as M_2. To compare estimates of M_2 across models, a biomass-weighted average M_2 was calculated for the age-structured models (the VADER and full NWACS models), while the full M_2 from the Steele-Henderson model and the full M_2 on age-1+ Atlantic menhaden was used for the less structured models. The time-varying *r* surplus production model and the BAM did not separate out different components of natural mortality, so comparisons were not possible for those models.

The Steele-Henderson, VADER, and NWACS-MICE model generally showed similar trends over time, with M_2 peaking in the late 1990s to early 2000s before declining (Figure 175). This is likely driven by the trend in striped bass biomass over this time period. In contrast, the full NWACS model showed a gradual increase over the entire time-series. The magnitude of M_2 estimates varied across models, with the Steele-Henderson and VADER models estimating the highest M_2, followed by the full NWACS model, and then the NWACS-MICE model.

15.2.2.2 Total Non-Fishing Mortality

Modeled predation mortality (M_2) is only part of total natural mortality (M) in these models. To compare estimates of M across models, a biomass-weighted average M was calculated for the

age-structured models (the VADER and full NWACS models) while the full *M* on age-1+ Atlantic menhaden was used for the NWACS-MICE. A biomass-weighted average *M* on age-1+ was also calculated for the BAM, although this *M* is of course input to the single-species model, not estimated. The time-varying *r* and the Steele-Henderson surplus production models included natural mortality (total or non-modeled predation) in the estimate of the intrinsic growth parameter, so comparisons were not possible for those models.

Overall, modeled predation mortality (M_2) made up a small component of total natural mortality, even for the full NWACS model (compare the scale of Figure 175 to Figure 176). Total natural mortality showed relatively little trend across all models over the last 30 years (Figure 176). Estimates of *M* were more variable for the VADER model than for the NWACS models, and all three ERP models estimated higher *M* than was used as input for the single-species model.

15.2.3 Total Mortality

Total mortality (*Z*) is the sum of natural mortality and fishing mortality. The BAM and VADER models calculated total mortality by age, while the other models calculated total mortality for age classes (full NWACS model) or the entire age-1+ population (Steele-Henderson model and NWACS-MICE models). In order to compare estimates of *Z* across models, biomass-weighted average *Z* across all age-1+ age classes was calculated for BAM, VADER, and the full NWACS model. The time-varying surplus production model did not estimate natural mortality.

The estimates of *Z* from the Steele-Henderson model were much lower than the estimates of *Z* from the other models (Figure 177). This is to be expected, given the differences in model structure: the Steele-Henderson model only estimated predation mortality from striped bass and combined other sources of natural mortality into the estimate of *r*, the intrinsic growth rate. The other models had explicit estimates or input of all sources of natural mortality, so their estimates of total mortality were higher.

In general, the models did not show much contrast in *Z* over the time series. The Steele-Henderson, VADER, and the NWACS-MICE model showed a slight declining trend from about 2000 onward, likely corresponding to declines in the striped bass population and the decline in Atlantic menhaden landings, while the full NWACS and the BAM estimates were relatively steady over this period.

15.3 Model Strengths and Weaknesses

The suite of models explored by the ERP WG resulted in similar estimates of biomass, exploitation rate, and stock status in both a single-species and multispecies context. However, each model varied in the type of advice it was able to provide, and not all models met all the ecological management objectives for Atlantic menhaden. As suggested in Section 1.5, the ERP WG determined that the ERP approach selected needed to:

- explicitly examine the trade-off between fishery removal of Atlantic menhaden and resulting trade-offs among important predators
- provide quantitative and understandable advice on removal levels of Atlantic menhaden under various predator biomass or fishing levels
- examine the implications and consequences of Atlantic menhaden harvest strategy on important predators; either through predator growth rates or survivability
- be updatable on a timeframe consistent with Atlantic menhaden management

The time-varying *r* surplus production model was able to identify changes in productivity over time and adjust the sustainable exploitation rate to take those changes into account. However, the model did not attribute changes in productivity to predation or any other specific cause, and therefore could not be used to evaluate tradeoffs between Atlantic menhaden harvest and ecosystem services.

The Steele-Henderson surplus production model attributed changes in productivity to predation, but only to striped bass as currently configured. It could, however, provide reference points that allowed for sustainable Atlantic menhaden harvest in consideration of changing striped bass dynamics. However, it could not directly capture the consequences of Atlantic menhaden harvest to the predator populations (in this case striped bass). External proxy metrics of predator condition relative to consumption levels would need to be implemented to assess the effects of Atlantic menhaden harvest on predators, which would require additional monitoring, research, and analysis to identify metrics and understand their implications for predator population dynamics.

Similarly, the current implementation of the VADER model lacks bottom-up feedback and cannot fully address the trade-offs. However, it was capable of incorporating changes in productivity due to both predation mortality and variability in recruitment.

The NWACS approaches show promise in meeting the needs of Atlantic menhaden management (Table 46). The NWACS-MICE has the desired level of complexity needed for transparent and quantitative examination of trade-offs. The NWACS-FULL model's reliance on model output from other assessments and the sheer quantity of data (some of it of poor quality) that is required make it unwieldy for providing updated advice in a timeframe suitable for management. However, the NWACS-FULL is the only model that can provide a complete evaluation of ecosystem sensitivities to Atlantic menhaden harvest policies.

Both NWACS-FULL and NWACS-MICE agree across many scenarios and sensitivities. More importantly, the NWACS-FULL model suggested that the reduced predator set of the NWACS-MICE model captured the dynamics of the more responsive predators from the full ecosystem model well. The NWACS-FULL model indicated nearshore piscivorous birds were as sensitive as striped bass to Atlantic menhaden harvest rates, while other predators not included in the NWACS-MICE model such as seabirds and demersal piscivores were less sensitive and more similar to bluefish and spiny dogfish in their response to Atlantic menhaden harvest rates. Harvest scenarios that sustain the biomass of predators included in the NWACS-MICE model

were thus expected to not cause large declines for other predators that were only included in the NWACS-FULL model.

Dynamics of variable recruitment, year-class strength, and changes in fleet selectivities are nuances not well captured in the biomass dynamics approach of NWACS models, but these nuances are important in fully understanding Atlantic menhaden population dynamics.

None of the models included explicit environmental drivers in the base model run. The BAM, the surplus production model with time-varying *r,* and the VADER model could account for environmentally-driven variation in productivity or recruitment in the observed data without an explicit mechanism by estimating the annual intrinsic growth rate or recruitment annually. However, without a mechanism, these models had no way to predict changes in productivity or recruitment into the future under different environmental conditions. Modeling of environmental factors was limited by the poor understanding of the relationship between specific environmental drivers and recruitment and mortality. Ecosim models were designed to incorporate information on bottom-up drivers. The NWACS-MICE model considered primary production anomalies in an alternative run, and future versions should aim to develop an independent time series of primary production for this system that could be directly included in the model.

In addition, none of the models included spatial or seasonal dynamics. The available diet data indicate there are seasonal and regional differences in diet composition along the Atlantic coast, but the current data, as well as the understanding of Atlantic menhaden migration patterns, are not currently sufficient to support modeling at such a fine scale. As a result, nuances of population dynamics at these scales may be lost. The EwE modeling software includes a spatially-explicit component, Ecospace. The NWACS-MICE model provides an opportunity to quickly develop and test an Ecospace model to capture the seasonal-spatial dynamics, which would facilitate development of Ecospace in the full NWACS model.

16 REFERENCE POINTS

In the previous benchmark assessment report, the ERP workgroup examined a number of different ecological based reference points approaches (SEDAR 2015). These included ecosystem indicators, nutrition reference points for important predators, BAM based single species reference points coupled with rule-of-thumb harvest control rules (HCR), as well as the approaches examined in the current report. Most of the approaches not developed in the current report were discarded after SEDAR 40 (2015) and the EMO Workshop because they only provided qualitative advice, did not fully address managers concerns, or required extensive research and monitoring programs to be initiated.

One exception to this was the BAM based single species reference points coupled with rule-of-thumb HCRs. This approach used the current single-species assessment for Atlantic menhaden (BAM) with a series of potential HCRs as outlined by Smith et al. (2011) and Pikitch et al. (2012).

Smith et al. (2011) recommended maintaining forage fish populations at target biomass of 75% of unexploited biomass to prevent negative consequences to predators, compared to the approximately 60% level implied by fishing at F_{MSY}. Pikitch et al. (2012) recommended a precautionary approach for forage fish management in order to sustain both predator and prey species, including fishing at 50-75% of F_{MSY} and using a biomass threshold of 30-40% of unexploited biomass, depending on the quality of data available.

At the behest of the Board, the EMO workgroup developed the recommendations of Pikitch et al. (2012) for management consideration (see ASMFC 2017) as an interim step while ERPs were under development. However, the ERP workgroup noted a number of difficulties in applying the rule-of-thumb approaches to the coastwide stock of Atlantic menhaden in their ecosystem context. Chief among the issues was that the Pikitch et al. (2012) rule-of-thumb reference points and harvest control rules were derived from ecosystems or locations/seasons where a majority of the trophic energy passed through a handful of species. They were not well tested in ecosystems like the Mid-Atlantic, which have a diverse forage base and a suite of generalist predators. Additionally, Pikitch et al. (2012) ERPs could not quantitatively examine the tradeoffs and risk to predators resulting from Atlantic menhaden fishery removals, a vital function that both managers and stakeholders were interested in examining. As a result, the ERP WG recommended developing ERP models using data specific to Atlantic menhaden and its ecosystem instead.

16.1 Model Reference Points

The suite of models explored by the ERP WG are capable of producing MSY-based reference points (or MSY-proxy reference points such as %SPR). What sets these reference points apart from the single-species equivalents is the consideration of changing productivity over time, whether that is explicitly modeled as predation or simply estimated.

The time-varying *r* model produced estimates of U_{MSY} that take into account changes in productivity over time. Although productivity is lower in recent years than it was at the beginning of the time-series, declining removals have brought the exploitation rate under the threshold of 75%U_{MSY}, indicating that Atlantic menhaden are not currently experiencing overfishing. Biomass is also above the B_{MSY} target, indicating the stock is not overfished.

The Steele-Henderson model produced reference points in terms of “maximum usable production” (MUP) instead of the traditional “maximum sustainable yield” (MSY) concept. Proxy metrics of striped bass condition relative to consumption were developed as targets to relate levels of consumption to striped bass population health, as there is no bottom-up feedback within this model. The Steele-Henderson surplus production model also indicated Atlantic menhaden are not overfished ($B_{2017}/B_{MUP} > 1$) and are not experiencing overfishing ($F_{2017}/F_{MUP} < 1$). Condition metrics indicated current striped bass consumption of Atlantic menhaden was sufficient to sustain the 2017 striped bass population in a healthy condition.

The VADER model and the two NWACS models produced MSY or MSY-proxy reference points based on the time-varying mortality components of these models. The estimates of F_{MSY} from the NWACS models were higher than the estimates of *F* in 2017 for all age stanzas.

In all, the ERP models produced similar assessments of stock status to the single-species assessment results, which determined that Atlantic menhaden were not overfished and were not experiencing overfishing in 2017, relative to the reference points calculated by each model. However, the values of these reference points are determined by the ecosystem conditions (e.g., productivity levels, predator consumption levels) under which they are calculated. While the models were able to calculate reference point values for different levels of productivity or predation, there is no one "right" answer or reference point value; the sustainable level of Atlantic menhaden mortality depends on the management objectives for the predators and the ecosystem, which is ultimately a decision for managers. Therefore, the ERP WG recommended a method for developing an ERP target and threshold, rather than a specific value, to allow managers and stakeholders to evaluate the tradeoffs between Atlantic menhaden harvest and predator biomass.

16.2 ERP Target and Threshold

The ERP WG recommended using the NWACS-MICE model to develop fishing mortality targets and thresholds for Atlantic menhaden that help account for Atlantic menhaden's role in the ecosystem. The final values for the ERP target and threshold will be a management decision that takes into account the management objectives of both Atlantic menhaden and their predators. However, the ERP WG put forward example values of an ERP target and an ERP threshold based on existing management objectives for striped bass.

Striped bass was the focal species for this analysis because it was one of the most sensitive species to Atlantic menhaden *F*, and it allowed for a tractable description of tradeoffs for key groups in the system. ERPs based on striped bass biomass should also sustain other species in the ecosystem that were less sensitive to levels of Atlantic menhaden removals.

The ERP target was defined as the maximum *F* on Atlantic menhaden that would sustain striped bass at their biomass target when striped bass were fished at their *F* target. The ERP threshold was defined as the maximum *F* on Atlantic menhaden that would keep striped bass at their biomass threshold when striped bass were fished at their *F* target. All other species were maintained at their current *F* rates.

The example ERP target and threshold were lower than the current single-species target and threshold. The single-species assessment reported *F* reference points and annual values as the geometric mean of ages 2-4, rather than the full *F* (i.e., maximum *F*-at-age) values; the equivalent full *F* values for the single-species *F* target, threshold, and 2017 estimate are presented here for comparison with the full *F* values derived from the NWACS-MICE model. The ERP target was estimated at a full *F* of 0.188, compared to a full *F* of 0.314 for the single-species target. The ERP threshold was estimated at a full *F* of 0.573, compared to a full *F* of 0.856 for the single-species threshold. The current estimate of full *F* from the BAM model is 0.157, below

both the example ERP target and ERP threshold, indicating Atlantic menhaden are not experiencing overfishing from an ecosystem perspective.

This example was based on the *F* and *B* targets laid out in the striped bass fishery management plan. Higher or lower reference points for striped bass will result in higher or lower reference points for Atlantic menhaden. In addition, this example maintained the other species at their current *F* rates; higher or lower *F* rates on other species would also result in different reference point values for Atlantic menhaden. Managers and stakeholders can select final reference point values after examining the tradeoffs between Atlantic menhaden harvest, predator harvest rates, and predator biomass levels.

17 DISCUSSION

17.1 Synthesis of Findings

The ERP WG explored several different models capable of producing ecological reference points for Atlantic menhaden, ranging from mechanistically very simple with minimal data inputs (time-varying *r* surplus production model) to mechanistically very complex with intensive data needs (full NWACS model). All of the ERP models explored here agreed about the overall trend of Atlantic menhaden population size and exploitation rates over the last 30 years, a generally increasing trend in biomass and a decreasing trend in exploitation rate. These trends and the magnitude of the estimates were also very consistent with the estimates from the single-species assessment. This should not be surprising, since all the ERP models used the same time-series of total removals, life history parameters, and indices of abundance as the single species model, and in some cases (the NWACS models) used output from the single species model directly. However, the true value of these kinds of ecological models is not the ability to recreate a single-species assessment, but their ability to put those dynamics into an ecosystem context and develop reference points that take into account management objectives of other ecosystem components. These models produced reference points and management advice that were consistent across the different approaches as well.

The time-varying *r* model indicated that although productivity is lower in recent years than it was at the beginning of the time-series, declining removals have brought the exploitation rate under the threshold of 75%U_{MSY}, so Atlantic menhaden are not currently experiencing overfishing. Biomass is also above the B_{MSY} target, indicating the stock is not overfished.

The Steele-Henderson surplus production model also indicated Atlantic menhaden are not overfished ($B_{2017}/B_{MUP} > 1$) and are not experiencing overfishing ($F_{2017}/F_{MUP} < 1$). Proxy metrics of striped bass condition relative to consumption indicated striped bass consumption of Atlantic menhaden in 2017 was sufficient to sustain the current striped bass population in a healthy condition.

The VADER model indicated that Atlantic menhaden biomass would increase if fished under status quo *F*, even as predator biomass increased. At the single-species *F* target, Atlantic menhaden biomass decreased by less than 10% under increasing predator levels, but stabilized

at that level in the long-term projections. The VADER model did not include bottom-up effects of Atlantic menhaden abundance on predators, so in these scenarios, the increases or decreases in predator biomass is strictly a result of increasing or decreasing predator *F* to the target level. The combination of predation mortality and fishing mortality were sustainable for Atlantic menhaden in these projections, but the VADER model as currently configured could not evaluate the effects of Atlantic menhaden biomass on predator populations.

The NWACS-MICE and NWACS-FULL models projected that current levels of Atlantic menhaden harvest are unlikely to lead to declines in key predator species from their current levels.

The consistency of results across ERP approaches presented here suggest that Atlantic menhaden dynamics are only moderately sensitive to changes in predator dynamics and that minor changes in Atlantic menhaden harvest rates are not expected to have major negative effects on most predators. This is most likely due to current Atlantic menhaden management and aspects of Atlantic menhaden ecology and population dynamics. The ERP results are also consistent with the single-species assessment results, which determined that Atlantic menhaden were not overfished and were not experiencing overfishing. However, the ERP models indicated that fishing Atlantic menhaden at the single-species *F* threshold would cause declines in predator biomass, particularly for striped bass and nearshore piscivorous birds.

Atlantic menhaden are not managed with the traditional single-species approach of maximizing yield via F_{MSY} or an F_{MSY} proxy. Instead, the current single-species reference points for Atlantic menhaden are based on the historical performance of the fishery and the stock from 1960-2012. This approach captured the mean Atlantic menhaden dynamics across a large range of predator and fishery dynamics. Also, the Atlantic Menhaden Management Board has set the TAC lower than what would be allowed if fishing at *F* target, an *ad hoc* buffering approach that was adopted in recognition of the uncertainty surrounding Atlantic menhaden's role as a forage fish. The single-species assessment indicated fishing mortality rates on Atlantic menhaden are low and having been declining over time, and biomass and fecundity have increased. As a result, current levels of Atlantic menhaden harvest are unlikely to cause declines in predator species, as the ERP models indicate.

The impact to predators by fishing Atlantic menhaden is somewhat mitigated by the availability of other prey items in the same ecological niche. The nearshore environment of the Northwestern Atlantic has a very diverse forage base that includes Atlantic and river herrings, bay anchovy, sandeels, sardines, and many other small forage fishes. Additionally, most of the important predators on Atlantic menhaden are generalists; Atlantic menhaden may be a significant component of the diet for some predator size classes in some seasons and areas, but on a population scale, Atlantic menhaden are an important but not dominant component (i.e., do not comprise 50% or more) of predators' diets. In short, this ecosystem is not "wasp-waisted" like many of the ecosystems that formed the basis of previous literature on the subject (e.g., Smith et al. 2011, Pikitch et al. 2012); there is a diverse array of forage fishes to meet the demand of a generalist predator base.

ERP and BAM results suggest that most of the predation mortality on Atlantic menhaden occurs on the youngest and smallest age classes, typically ages 0-1. Given that the fishery harvest is dominated by ages 2+, and the highly variable nature of recruitment, it appears that the main driver for Atlantic menhaden availability to predators is recruitment success. That success is only marginally tied to adult population size; a host of environmental parameters may be more important across the population size of Atlantic menhaden so far seen, as suggested by Hilborn et al. (2017). Furthermore, Atlantic menhaden's life history lends itself to resiliency under exploitation. They are highly fecund, and larval data indicate they spawn nearly year-round across the coast, providing a buffer against unfavorable environmental conditions (Simpson et al. 2016). The majority of the population matures before peak selectivity in the fishery, allowing most individuals to spawn for at least one year before they are fully vulnerable to the fishery.

17.2 Synthesis of Management Advice

The ERP WG recommends using the BAM single-species assessment model in conjunction with the NWACS-MICE model to establish sustainable harvest levels for Atlantic menhaden that take into account their role as forage fish.

This approach combined the individual strengths of each model: BAM provided the single-species information, which incorporates the more nuanced structure and recruitment variability of the statistical catch at-age model, and the NWACS-MICE model provided an evaluation of the impact of proposed harvest scenarios on important predator species. The relative harvest strategy from the NWACS-MICE model that meets management objectives for Atlantic menhaden and the key predators can then be translated into a TAC using the single-species model. The NWACS-MICE model was chosen as the ERP model for this analysis as it included both top-down effects of predation on Atlantic menhaden biomass and bottom-up effects of Atlantic menhaden population size on predator biomass. The NWACS-FULL model was the only other model that explicitly included both types of feedback within the ecosystem, but the data demands of the NWACS-FULL model would make updating it on the frequent timeframe necessary for management difficult. The NWACS-FULL model indicated that striped bass was the most sensitive fish species, consistent with the NWACS-MICE model, suggesting that harvest strategies developed through the NWACS-MICE model that are sustainable for striped bass should also be sustainable for the major predatory fishes in the system. The NWACS-FULL model indicated that nearshore piscivorous birds, which includes species like osprey and herons, were also sensitive to Atlantic menhaden harvest. Based on the results of the scenarios examined in the NWACS-FULL model, nearshore piscivorous bird responses are expected to be similar to striped bass responses. As a result, harvest strategies developed with the NWACS-MICE model that maintain or rebuild striped bass biomass are likely to have a similar positive effect on nearshore piscivorous birds, though the model would not capture the potential effects on nearshore piscivorous birds in the full ecosystem context.

There are downsides, however, to this approach. As outlined in ASMFC (2017), translation between two models with different levels of complexity such as different age structures, recruitment assumptions, and selectivities, can increase uncertainty. Likewise, propagating

error for both models through the translation process can also pose challenges and make it more difficult to assess the risk and uncertainty associated with each management strategy. More work on this topic is needed, but these issues could be resolved in consultation with managers about their preferred level of risk.

As the NWACS-MICE surface plots show (Figure 144-Figure 146), there is no one "right answer" to the ecological reference point question. Sustainable harvest for Atlantic menhaden depends on the management objectives of both the predator species and Atlantic menhaden. The approach used to develop the NWACS-MICE surface plots provide a tool for managers to evaluate the tradeoffs between levels of Atlantic menhaden harvest, levels of predator harvest, and resulting biomass for all modeled species, not just striped bass. Managers have already performed this type of evaluation in a qualitative way with the *ad hoc* buffering approach used in recent Atlantic menhaden management. The tool presented would allow for this evaluation in a quantitative, transparent way, which is the overarching goal of the ecological reference point process.

18 RESEARCH AND MODELING RECOMMENDATIONS

The ERP WG endorsed the research recommendations laid out in the single-species assessment to improve the understanding of Atlantic menhaden population dynamics, especially the recommendations to develop an Atlantic menhaden-specific coastwide fishery-independent index of adult abundance and to continue to investigate environmental covariates related to productivity and recruitment on a temporal and spatial scale.

In addition, the ERP WG identified a number of research needs to improve the multispecies modeling efforts and the development of ecological reference points for Atlantic menhaden, as well as process considerations to fully implement ecosystem-based fishery management.

18.1 Future Research and Data Collection

18.1.1 Short term

1. Expand collection of diet and condition data along the Atlantic coast to provide seasonally and regionally stratified annual, year-round monitoring of key predator diets to provide information on prey abundance and predator consumption. This could be done through existing data collection programs.

18.1.2 Long term

1. Improve monitoring of population trends and diet data in non-finfish predators (e.g., birds, marine mammals) and data-poor prey species (e.g., bay anchovies, sand eels, benthic invertebrates, zooplankton, and phytoplankton) to better characterize the importance of Atlantic menhaden and other forage species to the ecosystem dynamics.

18.2 Modeling Needs

18.2.1 Short term

1. Conduct a management-strategy evaluation (MSE) to identify harvest strategies that will maximize the likelihood of achieving the identified ecosystem management objectives.
2. Continue development of the NWACS-MICE model to incorporate recruitment deviations (from external models or primary productivity time series) to better capture the productivity dynamics of Atlantic menhaden and other species.
3. Continue development of the VADER model to include bottom-up effects of Atlantic menhaden abundance on key predator species.
4. Continue development of the NWACS-FULL model to bring other species up to date and continue exploring the impacts of fishing on higher trophic level predators like birds and mammals.

18.3 Management Process Needs

18.3.1 Short term

1. Develop a coordinated timeline of assessments and assessment updates for Commission-managed species in order to provide the most up-to-date multispecies inputs for the NWACS-MICE model during ERP assessment updates.

18.3.2 Long term

1. Develop a plan to coordinate management of Atlantic menhaden and their predator species across management Boards. This will require changes to the way the Commission has historically operated. These species are currently managed by separate Boards within the Commission, and management objectives, including *F* and *B* targets for each species, are set independently of each other. For successful ecosystem-based fishery management, consistent management objectives for individual species and the ecosystem should be set holistically with the engagement of all managers and stakeholders.

18.4 Timing of Future Assessments

The ERP WG recommended updating the NWACS-MICE model in conjunction with the next single-species assessment update (in approximately three years), and recommended a full ERP model benchmark in six years if sufficient progress has been made on the modeling research recommendations. The ERP benchmark process should include updating and reevaluating the other models considered here, as well as any other promising models that could address management objectives, to continue to improve the understanding of Atlantic menhaden's role in the ecosystem.

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20 TABLES

Table 1. ERP models explored and the fundamental management objectives they address.

	FUNDAMENTAL OBJECTIVES											
	Sustain menhaden to provide for fisheries				Sustain menhaden to provide for predators				Provide stability for all types of fisheries		Minimize risk to sustainability due to changing environment	
	PERFORMANCE MEASURES				PERFORMANCE MEASURES				PERFORMANCE MEASURES		PERFORMANCE MEASURES	
	Abundance/ biomass of menhaden	Menhaden yield objectives	Age Composition	Historical distribution (Age comp as proxy)	Abundance/ biomass of predators	Predator yield objectives	Predator nutrition	Prey availability relative to predator distribution	Stability in yield for directed menhaden fisheries	Stability in yield for non-menhaden fisheries	*Model explicitly considers uncertainty about future environment for menhaden*	*Model explicitly considers uncertainty about future environment for predators*
Single-Species Models												
BAM Statistical Catch-at-Age Model (current model)	X	X	X	X					X		*	
Multi-Species Models												
Surplus Production												
Steele-Henderson	X	X					X (proxy)		X		*	*
Time-varying r	X	X							X		*	*
Multi-species Catch-at-Age (MSSCA)	X	X	X	X	X	X	X (proxy)	*	X	X	*	*
Ecopath with Ecosim (EwE)	X	X	X	X	X	X	X (proxy)	*	X	X	*	*
*: Indicates it is possible to modify the model to meet that performance objective, but would require extensive additional work												

Table 2. Annual population-level consumption and associated ranked levels of consumption for the top five predator species consuming Atlantic menhaden based on the NEFSC Food Habits Database. Consumption is shown in most multi-year averages (note: multi-year averages are for the most recent x number of years noted working back from 2012) and averages for the whole analysis time period from 1981-2012. Shaded cells indicate species that were not included in the final list of key ERP predators.

	Annual population-level consumption				Ranked levels of consumption			
	1 year	5 year	10 year	All years '81+	1 year	5 year	10 year	All years
Spiny dogfish	142,944,946	96,031,910	85,632,752	80,475,599	1	1	1	1
Striped bass	4,052,220	30,601,675	17,793,908	7,816,855	2	2	2	2
Bluefish	1,465,923	2,049,989	2,196,640	2,608,901	3	3	3	3
Weakfish	463,150	376,622	1,007,166	787,034	4	5	4	4
Smooth dogfish	446,791	588,205	900,819	757,217	5	4	5	5
Atlantic angel shark	345,432	180,740	139,435	141,519	6	7	7	6
Clearnose skate	34,830	31,340	18,387	9,554	8	8	8	10
Dusky shark	-	-	3,483	100,672	-	-	10	8
Goosefish	258,958	211,633	145,905	124,572	7	6	6	7
Sandbar shark	-	7,199	5,530	15,533	-	9	9	9
Spiny butterfly ray	4,245,350	4,639,049	6,437,951	4,737,723	2*	3*	3*	3*

*: Spiny butterfly ray consumption estimates were not included in the ranking because of the extremely small sample size of stomachs available for the analysis.

Table 3. Single-species reference points and total biomass equivalents. *: Estimates for bluefish and weakfish are based on preliminary assessment updates and may not match values used in management.

Species	SSB Target Definition	SSB Target	B Target Proxy
Atlantic herring	Projected SSB when fishing at $F_{40\%SPR}$	189,000 mt	448,000 mt
Bluefish	Projected SSB when fishing at $F_{40\%SPR}$	261,591 mt*	276,892 mt*
Spiny dogfish	Biomass of females > 80cm	159,288 mt	511,776 mt
Striped bass	125% of female SSB in 1995	114,295 mt	277,361 mt
Weakfish	Not defined	N/A	N/A

Species	SSB Threshold Definition	SSB Threshold	B Threshold Proxy
Atlantic herring	½ SSB target	94,500 mt	224,000 mt
Bluefish	½ SSB target	130,795 mt*	138,446 mt*
Spiny dogfish	½ SSB target	79,644 mt	255,888 mt
Striped bass	Female SSB in 1995	91,436 mt	221,889 mt
Weakfish	30% of unexploited SSB	8,815 mt*	11,489 mt*

Species	*F* Target Definition	*F* Target
Atlantic menhaden	Median of mean age 2-4 *F* 1960-2012	0.22
Atlantic herring	Not defined; use 90% of *F* threshold as proxy	0.46
Bluefish	Not defined; use 90% of *F* threshold as proxy	0.14
Spiny dogfish	Not defined; use 90% of *F* threshold as proxy	0.22
Striped bass	*F* rate projected to achieve SSB target	0.20
Weakfish	$Z_{SPR30\%}$ =0.98; based on *M*=0.43	F=0.55*

Species	*F* Threshold Definition	*F* Threshold
Atlantic menhaden	Maximum of mean age 2-4 *F* 1960-2012	0.60
Atlantic herring	$F_{40\%MSY}$	0.51
Bluefish	$F_{40\%MSY}$	0.16*
Spiny dogfish	*F* rate projected to achieve SSB target	0.24
Striped bass	*F* rate projected to achieve SSB threshold	0.24
Weakfish	$Z_{SPR20\%}$=1.36; based on *M*=0.43	F=0.93*

Table 4. Single-species estimates of total biomass and *F* in 2017 and percent change needed to achieve target and threshold values. *: Estimates for bluefish and weakfish are based on preliminary assessment updates and may not match values used in management.

Species	Status Quo Biomass	% Change to reach B Threshold	% Change to reach B Target
Atlantic menhaden	4,677,129 mt	N/A	N/A
Atlantic herring	239,472 mt	-6%	+87%
Bluefish	117,107 mt*	+18%	+136%
Spiny dogfish	641,132 mt	-60%	-20%
Striped bass	173,663 mt	+41%	+77%
Weakfish	3,209 mt*	+258%	N/A

Species	Status Quo F	*F* Multiplier to reach Threshold	% Change to reach *F* threshold	*F* Multiplier to reach Target	% Change to reach *F* target
Atlantic menhaden	0.11 (ages 2-4)	5.455	+445%	2.000	+100%
Atlantic herring	0.45 (ages 7-8)	1.133	+13%	1.022	+2%
Bluefish	0.34 (Full F) *	0.471	-53%	0.412	-59%
Spiny dogfish	0.15 (Full F)	1.600	+60%	1.467	+47%
Striped bass	0.31 (Full F)	0.774	-23%	0.645	-35%
Weakfish	0.23 (Full F)*	4.043	+304%	2.391	+139%

Table 5. Estimated parameters, starting values, bounds, parameter estimates, and coefficient of variation (CV) from the SPMTVr model.

Parameter	Description	Starting value	Lower/upper bounds	SPMTVr Estimate	SPMTVr CV
r_{1957}	Intrinsic growth rate (1957)	0.7	0.0001/2.1	0.74	0.96
K	Carrying capacity (1,000 t)	6,828,000	1,000/20,000	2,182,790	0.02
B_{1957}	Initial biomass (1,000 t)	2,424,000	200/10,000	2,182,820	0.02
q_{RCPUE}	Catchability (RCPUE index)	0.001	$1x10e^{-8}$/0.005	0.00076	0.03
q_{NAD}	Catchability (NAD index)	0.001	$1x10e^{-8}$/0.005	0.00057	0.04
q_{MAD}	Catchability (MAD index)	0.001	$1x10e^{-8}$/0.005	0.00057	0.03

Table 6. Summary of results for index-based fishing-only and Steele-Henderson predator-prey surplus production models with candidate predators. Shaded cells indicate parameters at constraint. Parameter *r* is the intrinsic rate of increase; *K* is maximum biomass of ages 1+ Atlantic menhaden; B_{1985} is the initial biomass in 1985 of ages 1+ Atlantic menhaden; *d* is maximum Atlantic menhaden biomass consumption per predator biomass; *A* of ages 1+ Atlantic menhaden where predator satiation begins; and MT = metric tons. Estimates with parameter *d* = 0 do not produce M_2.

Model Predator 1 Predator 2	Fishing	Fishing Bass	Fishing Bluefish	Fishing Dogfish	Fishing Bass Bluefish
AIC_c	-156	-156	-149	-154	-149
SSQ / N	0.170	0.161	0.170	0.170	0.170
			Parameters		
r	0.32	2.27	0.30	0.32	3.00
K (MT)	3,430,522	1,071,224	4,998,378	3,433,550	4,456,472
B_{1985} (MT)	3,022,384	775,014	2,977,523	3,022,199	3967296.312
q	0.00000030	0.00000110	0.00000032	0.00000030	0.00000019
Predator 1 d		11.0	5.1	0	14.0
Predator 1 A (mt)		1,143,513	4,933,403	10,000,000	507,280
Predator 2 d					0
Predator 2 A (mt)					10,000,000

Table 7. Summary of stock status metrics, conditions for breaching their thresholds, estimated risk of exceeding their thresholds, and mean and 5th and 95th percentiles in 2017 from the Steele-Henderson surplus production model.

			Statistic		
Metric	Threshold	Risk (%)	Mean	5th %	95th %
B / B_{MUP}	≤ 1.0	0	1.27	1.26	1.29
Z_2 / Z_{MUP}	≥ 1.0	0	0.73	0.71	0.74
D_t / P_t	≤ 2.0	0	2.87	2.72	2.96
F / Z_2	≤ 0.4	0	0.31	0.30	0.32
F / F_{MUP}	≥ 1.0	0	0.62	0.60	0.64

Table 8. Parameter estimates from the Steele-Henderson surplus production model for base and sensitivity runs. See Section 11.4 for descriptions of sensitivity runs. Parameter *r* is the intrinsic rate of increase; K is maximum biomass of ages 1+ Atlantic menhaden; B_{1985} is the initial biomass in 1985 of ages 1+ Atlantic menhaden; d is maximum Atlantic menhaden biomass consumption per predator biomass; A of ages 1+ Atlantic menhaden where predator satiation begins; MUP = maximum usable production, and mt = metric tons.

	Parameter					
Model run	*r*	*K* (mt)	B_{1985} (mt)	*d*	*A* (mt)	MUP (mt)
Base	2.27	1,071,224	775,014	11.0	1,143,513	608,517
Long	2.56	971,189	706,019	7.0	783,581	621,302
d bio	2.01	1,200,251	871,548	15.6	1,548,475	602,859
d wider	1.66	1,402,670	1,092,780	17.0	2,025,389	582,062
d constraint	2.21	1,093,466	787,412	12.6	1,263,289	605,021
minus 20%	2.05	1,175,749	910,940	9.0	1,151,076	602,375
plus 20%	2.22	1,089,415	777,844	17.0	1,477,231	604,163

Table 9. Correlations among model parameters for base and sensitivity runs of the Steele-Henderson surplus production model. *n*=7.

Parameter	Statistic	r	K	1985 biomass	Bass d
K	*ρ*	-0.99			
	p-value	<.0001			
1985 biomass	*ρ*	-0.96	0.99		
	p-value	0.0004	<.0001		
d	*ρ*	-0.67	0.63	0.50	
	p-value	0.1018	0.1315	0.2522	
A	*ρ*	-0.91	0.90	0.83	0.90
	p-value	0.0044	0.0053	0.0217	0.0064

Table 10. Summarized percentage differences between Steele-Henderson model base run and sensitivity analyses estimates of B / B_{MUP}, Z / Z_{MUP}, and D_t / P_t estimates for 1985-2017.

Sensitivity run	Base	Long run	d penalty	d bioen	d wide	minus 20%	plus 20%
				B / B_{MUP}			
Maximum	4.5%	-0.5%	4.5%	4.5%	3.6%	0.9%	2.9%
Minimum	-7.7%	-4.8%	-0.6%	-0.6%	-7.0%	-5.7%	1.7%
5th %	-4.4%	-4.6%	0.1%	0.1%	-6.2%	-5.0%	1.7%
95th %	3.3%	-1.3%	3.4%	3.4%	3.0%	-0.4%	2.8%
Median	1.2%	-3.7%	2.6%	2.6%	0.1%	-2.3%	2.4%
Average	0.0%	-3.4%	2.3%	2.3%	-0.6%	-2.6%	2.3%
				Z / Z_{MUP}			
Maximum	8.2%	7.5%	8.2%	-1.1%	3.3%	4.7%	-0.7%
Minimum	-5.7%	0.8%	4.7%	-5.0%	-5.6%	0.6%	-5.7%
5th %	-4.4%	1.4%	4.9%	-4.7%	-4.6%	0.8%	-4.9%
95th %	7.3%	7.4%	7.7%	-1.6%	2.7%	4.0%	-0.9%
Median	1.5%	4.1%	6.5%	-3.0%	-0.6%	2.9%	-2.5%
Average	1.2%	4.5%	6.5%	-3.0%	-0.5%	2.7%	-2.9%
				D_t / P_t			
Maximum	14.2%	9.5%	5.2%	5.2%	14.2%	9.1%	4.5%
Minimum	-10.8%	-6.5%	-8.5%	-8.5%	-10.8%	-5.3%	-7.8%
5th %	-6.1%	-6.1%	-6.3%	-6.3%	-1.6%	-2.8%	-6.5%
95th %	8.0%	8.1%	4.2%	4.2%	9.9%	6.5%	3.7%
Median	1.2%	-2.6%	1.0%	1.0%	6.3%	2.3%	0.8%
Average	1.0%	1.0%	1.3%	1.5%	2.7%	1.2%	0.2%

Table 11. Parameter estimates for base (1985-2017) and retrospective runs of the Steele-Henderson surplus production model. Parameter *r* is the intrinsic rate of increase; K is maximum biomass of ages 1+ Atlantic menhaden; d is maximum Atlantic menhaden biomass consumption per predator biomass; A of ages 1+ Atlantic menhaden where predator satiation begins; MUP = maximum usable production, and mt = metric tons.

	Parameters					
	r	*K*	B_{1985} (mt)	*d*	*A* (mt)	SSQ / N
Base run	2.27	1,071,224	775,014	11.0	1,143,513	0.16
End year			Retrospective			
2013	1.98	1,267,432	944,767	16.9	1,692,663	0.15
2014	2.40	1,042,689	767,328	12.8	1,178,648	0.15
2015	2.13	1,128,231	820,564	10.4	1,169,501	0.16
2016	2.33	1,042,940	742,861	11.6	1,132,136	0.16
Index pairs			Index removal			
RCPUE-MAD	2.01	1,140,899	824,306	17.0	1,688,439	0.21
RCPUE-NAD	1.26	1,360,902	767,694	7.7	2,138,622	0.22
NAD-MAD	2.12	1,769,138	1,459,544	17.0	1,363,111	0.31

Table 12. Correlations of Steele-Henderson model parameters used in projections. Parameter *r* is the intrinsic rate of increase; *K* is maximum biomass of ages 1+ Atlantic menhaden; *d* is maximum Atlantic menhaden biomass consumption per predator biomass; A of ages 1+ Atlantic menhaden where predator satiation begins.

Parameter	r	K	d
K	-0.50		
d	0.11	0.39	
A	-0.59	0.44	0.55

Table 13. Summary of parameters, their distribution, and shape, scale, and location values for their probability density functions used in Monte Carlo simulations of four management scenarios for the Steele-Henderson surplus production model.

Parameter	Species	Distribution	Shape	Scale	Location
r	Menhaden	Log logistic	$\alpha = 0.10$	$\beta = 7.75$	$\gamma = 2.19$
K	Menhaden	Laplace		$\sigma = 15{,}713$	u = 1,064,665
d	Bass	Laplace		$\sigma = 0.30$	u = 11.0
A	Bass	Laplace		$\sigma = 17{,}155$	u = 1,140,035
2018 biomass	Menhaden	Laplace		$\sigma = 8{,}903$	u = 676,885
2018 biomass	Bass	Normal		CV = 0.06	u = 134,796

Table 14. Summary of Steele-Henderson surplus production model projection results. Bass = Ages 3+ striped bass. Atlantic menhaden = Ages 1+ Atlantic menhaden. All parameters reported are for terminal year estimates that were considered "equilibrium" estimates for a strategy. 5% and 95% = bounds of the 90% percentile interval for simulated results. mt = metric tons.

Species	Parameter	Mean	5%	95%	Threshold breach risk
Strategy		Status Quo			
Bass	Biomass (mt)	134,000			
Menhaden	Harvest (mt)	175,000			
Menhaden	B / B_{MUP}	1.28	1.22	1.33	0%
Menhaden	Z / Z_{MUP}	0.72	0.67	0.78	0%
Bass	D_t / P_t	2.89	2.7	3.09	0%
Strategy		Status quo F for menhaden, bass recover			
Bass	Biomass (mt)	260,000			
Menhaden	Harvest (mt)	132,000			
Menhaden	B / B_{MUP}	0.95	0.85	1.05	< 80%
Menhaden	Z / Z_{MUP}	1.05	0.81	1.34	< 55%
Bass	D_t / P_t	1.83	1.49	2.13	< 85%
Strategy		Menhaden target F, bass recover			
Bass	Biomass (mt)	260,000			
Menhaden	Harvest (mt)	226,000			
Menhaden	B / B_{MUP}	0.82	0.74	0.89	100%
Menhaden	Z / Z_{MUP}	1.19	1.00	1.42	< 95%
Bass	D_t / P_t	1.40	1.18	1.61	100%
Strategy		Menhaden at current harvest, bass D_t / P_t at threshold			
Bass	Biomass (mt)	215,000			
Menhaden	Harvest (mt)	175,000			
Menhaden	B / B_{MUP}	1.01	0.92	1.10	< 45%
Menhaden	Z / Z_{MUP}	0.99	1.10	1.21	< 60%
Bass	D_t / P_t	2.01	2.23	2.23	< 50%

Table 15. Symbols and terms used in the VADER model formulation.

Symbol	Definition
i	Species (used to designate prey species)
a	Age class (used to designate prey species age)
j	Predator species
b	Predator species age
t	Year
k	Fishery independent index
n	Number of indices
I	Vector of species-specific surveys
m	Month
$N_{i,a,t}$	January 1 abundance-at-age (10^6 fish)
$Z_{i,a,t}$	Instantaneous total mortality-at-age per year
$C_{i,a,t}$	Fishery catch-at-age (commercial and recreational harvest and dead discards, 10^6 fish)
$F_{i,a,t}$	Instantaneous fishing mortality-at-age per year
$s_{i,a}$	Fishery selectivity-at-age
$FIC_{i,a,t}$	Fishery independent catch (CPUE)
q_i	Fishery independent catchability
$r_{i,a}$	Fishery independent survey selectivity-at-age
$Sel_{x,i}$	Selectivity generated by logistic or double logistic functions
α_1, α_2, β_1, β_2	Logistic and double logistic ascending or descending limb parameters
$M_{i,a,t}$	Instantaneous natural mortality
$M0_{i,a}$	Residual natural mortality (time invariant)
$M2_{i,a,t}$	Instantaneous natural mortality due to predation
$W_{i,a,t}$	Average annual species-specific weight-at-age
$CB_{j,b}$	Consumption to biomass ratio (time invariant)
$B_{i,b,t}$	Biomass-at-age (10^6 kg)
$\phi_{i,a,j,b,t}$	Available prey biomass (10^6 kg)
$\tilde{\nu}_{i,a,j,b,t}$	Scaled prey suitability
$\nu_{i,a,j,b}$	Prey suitability
B_{eco}	Total ecosystem biomass (10^6 kg)
$\rho_{i,j}$	Prey species preference

Table 16 (Continued). Symbols and terms used in the VADER model formulation

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

Table 16. Components of the VADER model likelihood function by assumed distributions and including penalty functions for the VADER model. Small constants (10^{-3}) are added to the lognormal and multinomial calculations to keep the calculations from terminating if they reach zero.

Equation	Definition
$\mathrm{LL}_{\mathrm{Total}} = \mathrm{LL}_{\mathrm{TC}} + \mathrm{LL}_{\mathrm{TS}} + \mathrm{LL}_{\mathrm{CP}} + \mathrm{LL}_{\mathrm{SP}} + \mathrm{LL}_{\mathrm{FH}} + \sum_i Pen_i$	Total log likelihood
$LL_I = \sum_{t,i} \frac{1}{2} * ln\left(\frac{\hat{I} + 10^{-4}}{I + 10^{-4}}\right)^{ln(cv^2)}$	Lognormal distribution component
$LL_I = -\Gamma(nsamp * e^{dpar}) - \sum_{t,i,a} \Gamma\left((nsamp * I) + \left((nsamp * e^{dpar}) * \hat{I}\right)\right) + \sum_{t,i,a} \Gamma\left((nsamp * e^{dpar}) * \hat{I}\right)$	Dirichlet multinomial distribution component
$Pen_i = Pwt_{Yr1_i} * Yr1pen_i + Pwt_{Age1_i} * Rpen_i + Pwt_{B_i} * Bpen_i$	Total penalty
$Yr1pen_i = \sum_a (N_{i,a,t=1} - Yr1_{i,a})^2$	Year 1 penalty
$Rpen_i = 0.01 * (CV(N_{i,a=1,t}) - Rthresh_i)^2$	Recruitment penalty. Applied when the CV > *Rthresh*
$Bpen_i = \sum_{a,t} 0.01 * (B_{i,a,t} - Bthresh_i)^2$	Biomass penalty. Applied when *B* < *Bthresh*

Table 17. Indices used for each species for the Base and Alternate runs of the VADER model.

Bluefish		
	Used in Base run	Used in sensitivity run
NEFSC Albatross		X
MRIP CPUE	X	X
NC PSIGNS/P915	X	
Composite YOY	X	
Weakfish		
	Used in Base run	Used in sensitivity run
MRIP CPUE	X	
DE 30' Trawl	X	
NJ Ocean Trawl		X (offshore)
Composite YOY	X	
NC PSIGNS/P915		X (inshore)
Atlantic Herring		
	Used in Base run	Used in sensitivity run
Shrimp Survey		X
NEFSC Fall Albatross (1985-2008)	X	
NEFSC Fall Bigelow (2009-2017)	X	
Striped bass		
	Used in Base run	Used in sensitivity run
Composite YOY	X	
MD Spawning Stock		X
MRIP CPUE	X	
CT LISTS	X	
Atlantic menhaden		
	Used in Base run	Used in sensitivity run
SAD	X	X
MAD	X	X
NAD	X	X
Composite YOY	X	X
Spiny Dogfish		
	Used in Base run	Used in sensitivity run
NMFS Trawl (converted to Albatross units)	X	X

Table 18. Effective sample size and CVs for Atlantic menhaden catch and indices used in the VADER model.

	Atlantic menhaden									
	Catch		YOY		NAD		MAD		SAD	
Year	CV	Sample Size	CV	Sample Size	CV	Sample Size	CV	Sample Size	CV	Sample Size
1985	0.05	213	0.4	0	0	0	1.15	89	0	0
1986	0.05	146	0.4	0	0	0	1.14	89	0	0
1987	0.05	191	0.4	0	0	0	1.18	89	0	0
1988	0.05	185	0.4	0	0	0	1.14	0	0	0
1989	0.05	173	0.4	0	0	0	1.18	89	0	0
1990	0.05	171	0.4	0	0.4	18	1.15	0	0.4	22
1991	0.05	194	0.4	0	0.4	12	1.16	0	0.4	29
1992	0.05	142	0.4	0	0.4	24	1.16	0	0.4	23
1993	0.05	137	0.4	0	0.4	24	1.19	0	0.4	26
1994	0.05	132	0.4	0	0.4	18	1.14	0	0.4	10
1995	0.05	125	0.4	0	0.4	14	1.13	0	0.4	15
1996	0.05	116	0.4	0	0.4	34	1.2	0	0.4	21
1997	0.05	114	0.4	0	0.4	30	1.22	0	0.4	25
1998	0.05	115	0.4	0	0.4	18	0.4	89	0.4	29
1999	0.05	107	0.4	0	0.4	43	0.43	0	0.4	13
2000	0.05	92	0.4	0	0.4	30	0.36	89	0.4	12
2001	0.05	125	0.4	0	0.4	36	0.38	89	0.4	30
2002	0.05	110	0.4	0	0.4	51	0.43	89	0.4	32
2003	0.05	101	0.4	0	0.4	25	0.36	0	0.4	108
2004	0.05	115	0.4	0	0.4	48	0.38	0	0.4	47
2005	0.05	99	0.4	0	0.4	62	0.39	89	0.4	112
2006	0.05	105	0.4	0	0.4	33	0.42	89	0.4	134
2007	0.05	133	0.4	0	0.4	63	0.42	89	0.4	51
2008	0.05	111	0.4	0	0.4	52	0.45	89	0.4	527
2009	0.05	101	0.4	0	0.4	40	0.41	89	0.4	565
2010	0.05	111	0.4	0	0.4	25	0.39	89	0.4	554
2011	0.05	109	0.4	0	0.4	58	0.38	89	0.4	613
2012	0.05	93	0.4	0	0.4	60	0.44	89	0.4	610
2013	0.05	72	0.4	0	0.4	40	0.4	96	0.4	590
2014	0.05	89	0.4	0	0.4	58	0.38	96	0.4	621
2015	0.05	111	0.4	0	0.4	70	0.45	74	0.4	645
2016	0.05	108	0.4	0	0.4	50	0.43	86	0.4	527
2017	0.05	107	0.4	0	0.4	46	0.41	95	0.4	619

Table 19. Effective sample size and CVs for striped bass catch and indices used in the VADER model.

	Striped Bass							
	Catch		YOY		MRIP CPUE		CT LISTS	
Year	CV	Sample Size	CV	Sample Size	CV	Sample Size	CV	Sample Size
1985	0.1	70	0.4	0	0.4	36	0	0
1986	0.1	70	0.4	0	0.4	36	0	0
1987	0.1	70	0.4	0	0.4	36	0.4	12
1988	0.1	70	0.4	0	0.4	36	0.4	12
1989	0.1	70	0.4	0	0.4	36	0.4	12
1990	0.1	70	0.4	0	0.4	36	0.4	12
1991	0.1	70	0.4	0	0.4	36	0.4	12
1992	0.1	70	0.4	0	0.4	36	0.4	12
1993	0.1	70	0.4	0	0.4	36	0.4	12
1994	0.1	70	0.4	0	0.4	36	0.4	12
1995	0.1	70	0.4	0	0.4	36	0.4	12
1996	0.1	70	0.4	0	0.4	36	0.4	12
1997	0.1	70	0.4	0	0.4	36	0.4	12
1998	0.1	70	0.4	0	0.4	36	0.4	12
1999	0.1	70	0.4	0	0.4	36	0.4	12
2000	0.1	70	0.4	0	0.4	36	0.4	12
2001	0.1	70	0.4	0	0.4	36	0.4	12
2002	0.1	70	0.4	0	0.4	36	0.4	12
2003	0.1	70	0.4	0	0.4	36	0.4	12
2004	0.1	70	0.4	0	0.4	36	0.4	12
2005	0.1	70	0.4	0	0.4	36	0.4	12
2006	0.1	70	0.4	0	0.4	36	0.4	12
2007	0.1	70	0.4	0	0.4	36	0.4	12
2008	0.1	70	0.4	0	0.4	36	0.4	12
2009	0.1	70	0.4	0	0.4	36	0.4	12
2010	0.1	70	0.4	0	0.4	36	0.4	12
2011	0.1	70	0.4	0	0.4	36	0.4	12
2012	0.1	70	0.4	0	0.4	36	0.4	12
2013	0.1	70	0.4	0	0.4	36	0.4	12
2014	0.1	70	0.4	0	0.4	36	0.4	12
2015	0.1	70	0.4	0	0.4	36	0.4	12
2016	0.1	70	0.4	0	0.4	36	0.4	12
2017	0.1	70	0.4	0	0.4	36	0.4	12

Table 20. Effective sample size and CVs for bluefish catch and indices used in the VADER model.

	Bluefish							
	Catch		YOY		MRIP CPUE		NC PSIGNS	
Year	CV	Sample Size	CV	Sample Size	CV	Sample Size	CV	Sample Size
1985	0.15	24	0.71	0	0.11	30	0	0
1986	0.15	24	0.75	0	0.11	30	0	0
1987	0.15	24	0.57	0	0.1	30	0	0
1988	0.15	24	0.44	0	0.11	30	0	0
1989	0.15	24	0.43	0	0.1	30	0	0
1990	0.15	24	0.43	0	0.1	30	0	0
1991	0.15	24	0.43	0	0.1	30	0	0
1992	0.15	24	0.5	0	0.1	30	0	0
1993	0.15	24	0.48	0	0.09	30	0	0
1994	0.15	24	0.49	0	0.09	30	0	0
1995	0.15	24	0.44	0	0.09	30	0	0
1996	0.15	24	0.48	0	0.09	30	0	0
1997	0.15	12	0.47	0	0.1	10	0	0
1998	0.15	12	0.48	0	0.1	10	0	0
1999	0.15	12	0.53	0	0.1	10	0	0
2000	0.15	12	0.43	0	0.1	10	0	0
2001	0.15	12	0.42	0	0.1	10	0.13	10
2002	0.15	12	0.4	0	0.1	10	0.17	10
2003	0.15	12	0.43	0	0.1	10	0.15	10
2004	0.15	12	0.41	0	0.11	10	0.18	10
2005	0.15	48	0.38	0	0.1	45	0.17	20
2006	0.15	48	0.4	0	0.1	45	0.2	20
2007	0.15	48	0.41	0	0.1	45	0.15	20
2008	0.15	48	0.39	0	0.1	45	0.14	20
2009	0.15	48	0.44	0	0.1	45	0.14	20
2010	0.15	48	0.4	0	0.1	45	0.13	20
2011	0.15	48	0.42	0	0.1	45	0.19	20
2012	0.15	48	0.41	0	0.1	45	0.16	20
2013	0.15	48	0.4	0	0.11	45	0.19	20
2014	0.15	48	0.33	0	0.1	45	0.14	20
2015	0.15	48	0.42	0	0.1	45	0.15	20
2016	0.15	48	0.41	0	0.1	45	0.22	20
2017	0.15	48	0.45	0	0.1	45	0.17	20

Table 21. Effective sample size and CVs for weakfish catch and indices used in the VADER model.

	Weakfish							
	Catch		YOY		MRIP CPUE		DE30 Trawl	
Year	CV	Sample Size	CV	Sample Size	CV	Sample Size	CV	Sample Size
1985	0.12	50	0.45	0	0.3	25	0	0
1986	0.12	50	0.43	0	0.26	25	0	0
1987	0.18	50	0.37	0	0.29	25	0	0
1988	0.2	50	0.38	0	0.28	25	0	0
1989	0.12	50	0.33	0	0.33	25	0	0
1990	0.14	50	0.3	0	0.33	25	0	0
1991	0.12	50	0.3	0	0.32	25	0.62	25
1992	0.13	50	0.3	0	0.35	25	0.62	25
1993	0.12	50	0.34	0	0.31	25	0.62	25
1994	0.12	50	0.32	0	0.29	25	0.64	25
1995	0.11	50	0.34	0	0.27	25	0.62	25
1996	0.13	50	0.3	0	0.27	25	0.62	25
1997	0.11	50	0.32	0	0.27	25	0.63	25
1998	0.11	50	0.31	0	0.27	25	0.63	25
1999	0.11	50	0.3	0	0.28	25	0.62	25
2000	0.1	50	0.29	0	0.28	25	0.64	25
2001	0.12	50	0.3	0	0.3	25	0.63	25
2002	0.11	50	0.3	0	0.32	25	0.63	25
2003	0.15	50	0.31	0	0.36	25	0.63	25
2004	0.17	50	0.29	0	0.31	25	0.62	25
2005	0.12	50	0.3	0	0.33	25	0.62	25
2006	0.13	50	0.3	0	0.36	25	0.62	25
2007	0.13	50	0.3	0	0.45	25	0.62	25
2008	0.21	50	0.32	0	0.44	25	0.63	25
2009	0.14	50	0.29	0	0.57	25	0.62	25
2010	0.14	50	0.31	0	0.43	25	0.62	25
2011	0.15	50	0.3	0	0.43	25	0.62	25
2012	0.14	50	0.3	0	0.39	25	0.62	25
2013	0.13	50	0.3	0	0.46	25	0.62	25
2014	0.15	50	0.3	0	0.44	25	0.62	25
2015	0.16	50	0.31	0	0.4	25	0.62	25
2016	0.2	50	0.31	0	0.34	25	0.62	25
2017	0.13	50	0.3	0	0.48	25	0.62	25

Table 22. Effective sample size and CVs for Atlantic herring catch and indices used in the VADER model.

	Atlantic Herring					
	Catch		NEFSC Albatross		NEFSC Bigelow	
Year	CV	Sample Size	CV	Sample Size	CV	Sample Size
1985	0.1	15	0.95	0	0	0
1986	0.1	6	0.95	0	0	0
1987	0.1	8	0.79	16	0	0
1988	0.1	9	0.95	14	0	0
1989	0.1	9	0.91	15	0	0
1990	0.1	13	0.95	9	0	0
1991	0.1	10	0.95	14	0	0
1992	0.1	14	0.51	18	0	0
1993	0.1	13	0.88	17	0	0
1994	0.1	7	0.45	18	0	0
1995	0.1	8	0.73	22	0	0
1996	0.1	9	0.64	25	0	0
1997	0.1	10	0.72	20	0	0
1998	0.1	11	0.23	27	0	0
1999	0.1	10	0.41	22	0	0
2000	0.1	10	0.52	16	0	0
2001	0.1	10	0.56	16	0	0
2002	0.1	10	0.82	20	0	0
2003	0.1	10	0.95	20	0	0
2004	0.1	9	0.5	20	0	0
2005	0.1	10	0.54	16	0	0
2006	0.1	10	0.95	20	0	0
2007	0.1	10	0.41	21	0	0
2008	0.1	9	0.73	19	0	0
2009	0.1	8	0	0	0.95	9
2010	0.1	8	0	0	0.37	9
2011	0.1	8	0	0	0.63	9
2012	0.1	8	0	0	0.27	9
2013	0.1	9	0	0	0.4	8
2014	0.1	9	0	0	0.44	7
2015	0.1	8	0	0	0.3	9
2016	0.1	6	0	0	0.82	9
2017	0.1	7	0	0	0.71	6

Table 23. Effective sample size and CVs for spiny dogfish catch and indices used in the VADER model.

	Spiny Dogfish			
	Catch		NEFSC Albatross	
Year	CV	Sample Size	CV	Sample Size
1985	0.05	70	0.95	0
1986	0.05	70	0.95	0
1987	0.05	70	0.79	16
1988	0.05	70	0.95	14
1989	0.05	70	0.91	15
1990	0.05	70	0.95	9
1991	0.05	70	0.95	14
1992	0.05	70	0.51	18
1993	0.05	70	0.88	17
1994	0.05	70	0.45	18
1995	0.05	70	0.73	22
1996	0.05	70	0.64	25
1997	0.05	70	0.72	20
1998	0.05	70	0.23	27
1999	0.05	70	0.41	22
2000	0.05	70	0.52	16
2001	0.05	70	0.56	16
2002	0.05	70	0.82	20
2003	0.05	70	0.95	20
2004	0.05	70	0.5	20
2005	0.05	70	0.54	16
2006	0.05	70	0.95	20
2007	0.05	70	0.41	21
2008	0.05	70	0.73	19
2009	0.05	70	0.95	9
2010	0.05	70	0.37	9
2011	0.05	70	0.63	9
2012	0.05	70	0.27	9
2013	0.05	70	0.4	8
2014	0.05	70	0.44	7
2015	0.05	70	0.3	9
2016	0.05	70	0.82	9
2017	0.05	70	0.71	6

Table 24. Parameter estimates and standard deviations from the VADER model for predation interactions, average recruitment and average fishing mortality.

Parameter	Description	Estimate	Standard Deviation
iRho[1]	Predation Interaction Parameter – striped bass on menhaden	2.19	0.11
iRho[2]	Predation Interaction Parameter – bluefish on menhaden	0.37	0.43
iRho[3]	Predation Interaction Parameter – weakfish on menhaden	-0.05	0.54
iRho[4]	Predation Interaction Parameter – spiny dogfish on menhaden	0.93	0.17
iRho[5]	Predation Interaction Parameter – striped bass on weakfish	3.27	0.43
iRho[6]	Predation Interaction Parameter – bluefish on weakfish	-1.00	0.00
iRho[7]	Predation Interaction Parameter – spiny dogfish on menhaden	2.81	1.23
iRho[8]	Predation Interaction Parameter – striped bass on Atl herring	2.17	0.23
iRho[9]	Predation Interaction Parameter – bluefish on Atl herring	2.03	0.32
iRho[10]	Predation Interaction Parameter – weakfish on Atl herring	-0.94	2.48
iRho[11]	Predation Interaction Parameter – spiny dogfish on Atl herring	2.87	0.22
aAge1[1]	Average Recruitment Menhaden	10.61	0.05
aAge1[2]	Average Recruitment Striped Bass	4.60	0.04
aAge1[3]	Average Recruitment Bluefish	4.06	0.04
aAge1[4]	Average Recruitment Weakfish	4.53	0.12
aAge1[5]	Average Recruitment Herring	8.20	0.09
aAge1[6]	Average Recruitment Spiny Dogfish	3.62	0.05
aFt[1]	Average F Menhaden	-1.05	0.09
aFt[2]	Average F Striped Bass	-1.55	0.05
aFt[3]	Average F Bluefish	-0.97	0.06
aFt[4]	Average F Weakfish	-0.72	0.08
aFt[5]	Average F Herring	-0.65	0.14
aFt[6]	Average F Spiny Dogfish	-2.27	0.05

Table 25. Parameter estimates and standard deviations from the VADER model for initial abundance at age for Atlantic menhaden, striped bass, bluefish, and weakfish.

Parameter	Description	Estimate	Standard Deviation
iYr1[1]	Year 1 Menhaden Age 1	11.98	0.00
iYr1[1]	Year 1 Menhaden Age 2	10.38	0.00
iYr1[1]	Year 1 Menhaden Age 3	8.54	0.00
iYr1[1]	Year 1 Menhaden Age 4	6.31	0.00
iYr1[1]	Year 1 Menhaden Age 5	5.80	0.00
iYr1[1]	Year 1 Menhaden Age 6	4.35	0.01
iYr1[1]	Year 1 Menhaden Age 7	4.40	0.01
iYr1[2]	Year 1 Striped Bass Age 1	3.65	0.01
iYr1[2]	Year 1 Striped Bass Age 2	2.50	0.03
iYr1[2]	Year 1 Striped Bass Age 3	1.79	0.05
iYr1[2]	Year 1 Striped Bass Age 4	0.75	0.11
iYr1[2]	Year 1 Striped Bass Age 5	0.41	0.12
iYr1[2]	Year 1 Striped Bass Age 6	-0.06	0.14
iYr1[2]	Year 1 Striped Bass Age 7	-0.34	0.16
iYr1[2]	Year 1 Striped Bass Age 8	-1.79	0.34
iYr1[2]	Year 1 Striped Bass Age 9	-2.50	0.49
iYr1[2]	Year 1 Striped Bass Age 10	-2.32	0.45
iYr1[2]	Year 1 Striped Bass Age 11	-2.64	0.56
iYr1[2]	Year 1 Striped Bass Age 12	-2.59	0.56
iYr1[2]	Year 1 Striped Bass Age 13	-2.87	0.83
iYr1[2]	Year 1 Striped Bass Age 14	-2.48	0.92
iYr1[2]	Year 1 Striped Bass Age 15	-1.78	0.52
iYr1[3]	Year 1 Bluefish Age 1	4.19	0.01
iYr1[3]	Year 1 Bluefish Age 2	4.20	0.01
iYr1[3]	Year 1 Bluefish Age 3	3.31	0.01
iYr1[3]	Year 1 Bluefish Age 4	2.54	0.03
iYr1[3]	Year 1 Bluefish Age 5	2.26	0.04
iYr1[3]	Year 1 Bluefish Age 6	1.66	0.07
iYr1[3]	Year 1 Bluefish Age 7	3.05	0.02
iYr1[4]	Year 1 Weakfish Age 1	4.50	0.00
iYr1[4]	Year 1 Weakfish Age 2	3.88	0.01
iYr1[4]	Year 1 Weakfish Age 3	2.49	0.03
iYr1[4]	Year 1 Weakfish Age 4	1.87	0.05
iYr1[4]	Year 1 Weakfish Age 5	1.27	0.10
iYr1[4]	Year 1 Weakfish Age 6	0.65	0.18
iYr1[4]	Year 1 Weakfish Age 7	0.99	0.12

Table 26. Parameter estimates and standard deviations from the VADER model for initial abundance at age for Atlantic herring and spiny dogfish and Dirichlet parameters.

Parameter	Description	Estimate	Standard Deviation
iYr1[5]	Year 1 Herring Age 1	8.11	0.00
iYr1[5]	Year 1 Herring Age 2	8.05	0.00
iYr1[5]	Year 1 Herring Age 3	6.26	0.00
iYr1[5]	Year 1 Herring Age 4	5.79	0.00
iYr1[5]	Year 1 Herring Age 5	4.70	0.00
iYr1[5]	Year 1 Herring Age 6	3.97	0.01
iYr1[5]	Year 1 Herring Age 7	1.27	0.14
iYr1[5]	Year 1 Herring Age 8	2.91	0.03
iYr1[6]	Year 1 Spiny Dogfish Age 1	5.01	0.00
iYr1[6]	Year 1 Spiny Dogfish Age 2	4.52	0.01
iYr1[6]	Year 1 Spiny Dogfish Age 3	3.39	0.02
iYr1[6]	Year 1 Spiny Dogfish Age 4	2.31	0.05
iYr1[6]	Year 1 Spiny Dogfish Age 5	1.81	0.08
iYr1[6]	Year 1 Spiny Dogfish Age 6	1.71	0.08
iYr1[6]	Year 1 Spiny Dogfish Age 7	1.58	0.09
iYr1[6]	Year 1 Spiny Dogfish Age 8	1.51	0.10
iYr1[6]	Year 1 Spiny Dogfish Age 9	1.46	0.10
iYr1[6]	Year 1 Spiny Dogfish Age 10	1.42	0.11
iYr1[6]	Year 1 Spiny Dogfish Age 11	1.37	0.11
iYr1[6]	Year 1 Spiny Dogfish Age 12	1.33	0.12
iYr1[6]	Year 1 Spiny Dogfish Age 13	1.30	0.12
iYr1[6]	Year 1 Spiny Dogfish Age 14	1.27	0.13
iYr1[6]	Year 1 Spiny Dogfish Age 15	1.24	0.13
iYr1[6]	Year 1 Spiny Dogfish Age 16	1.22	0.13
iYr1[6]	Year 1 Spiny Dogfish Age 17	1.21	0.14
iYr1[6]	Year 1 Spiny Dogfish Age 18	1.21	0.14
iYr1[6]	Year 1 Spiny Dogfish Age 19	1.23	0.14
iYr1[6]	Year 1 Spiny Dogfish Age 20	1.25	0.14
iYr1[6]	Year 1 Spiny Dogfish Age 21	1.72	0.09
log_dm_Cac[1]	Dirichlet Parameter Catch at age Menhaden	-1.71	0.13
log_dm_Cac[2]	Dirichlet Parameter Catch at age Striped Bass	5.00	0.00
log_dm_Cac[3]	Dirichlet Parameter Catch at age Bluefish	5.00	0.00
log_dm_Cac[4]	Dirichlet Parameter Catch at age Weakfish	-1.08	0.15
log_dm_Cac[5]	Dirichlet Parameter Catch at age Herring	5.00	0.00
log_dm_Cac[6]	Dirichlet Parameter Catch at age Spiny Dogfish	-0.11	0.09
log_dm_Sac[1]	Dirichlet Parameter Survey at age Menhaden	-2.07	0.09
log_dm_Sac[2]	Dirichlet Parameter Survey at age Striped Bass	5.00	0.00
log_dm_Sac[3]	Dirichlet Parameter Survey at age Bluefish	-0.05	0.13
log_dm_Sac[4]	Dirichlet Parameter Survey at age Weakfish	-0.69	0.14
log_dm_Sac[5]	Dirichlet Parameter Survey at age Herring	5.00	0.00
log_dm_Sac[6]	Dirichlet Parameter Survey at age Spiny Dogfish	5.00	0.00

Table 27. Parameter estimates and standard deviations from the VADER model for fishery selectivity parameters.

Parameter	Description	Estimate	Standard Deviation
sel_params[1]	Fishery Selectivity Parameter – menhaden α1	2.50	0.00
sel_params[2]	Fishery Selectivity Parameter – menhaden β1	3.30	0.11
sel_params[3]	Fishery Selectivity Parameter – menhaden α2	5.00	0.00
sel_params[4]	Fishery Selectivity Parameter – menhaden β2	1.00	0.00
sel_params[5]	Fishery Selectivity Parameter – striped bass α1	5.15	0.06
sel_params[6]	Fishery Selectivity Parameter – striped bass β1	1.00	0.00
sel_params[7]	Fishery Selectivity Parameter – striped bass α2	14.72	326.94
sel_params[8]	Fishery Selectivity Parameter – striped bass β2	2.83	188.49
sel_params[9]	Fishery Selectivity Parameter – bluefish α1	1.17	0.08
sel_params[10]	Fishery Selectivity Parameter – bluefish β1	2.00	0.00
sel_params[11]	Fishery Selectivity Parameter – bluefish α2	6.08	0.38
sel_params[12]	Fishery Selectivity Parameter – bluefish β2	1.00	0.00
sel_params[13]	Fishery Selectivity Parameter – weakfish α1	3.32	0.09
sel_params[14]	Fishery Selectivity Parameter – weakfish β1	1.50	0.00
sel_params[15]	Fishery Selectivity Parameter – herring α1	3.31	0.20
sel_params[16]	Fishery Selectivity Parameter – herring β1	1.00	0.00
sel_params[17]	Fishery Selectivity Parameter – herring α2	7.00	0.00
sel_params[18]	Fishery Selectivity Parameter – herring β2	1.00	0.00
sel_params[19]	Fishery Selectivity Parameter – spiny dogfish α1	6.00	0.00
sel_params[20]	Fishery Selectivity Parameter – spiny dogfish β1	0.43	0.03

Table 28. Parameter estimates and standard deviations from the VADER model for survey selectivity parameters.

Parameter	Description	Estimate	Standard Deviation
FICsel_params[8]	Survey Selectivity Parameter – NAD α1	3.80	0.15
FICsel_params[9]	Survey Selectivity Parameter- NAD β1	2.18	0.13
FICsel_params[10]	Survey Selectivity Parameter – MAD α1	4.00	0.00
FICsel_params[11]	Survey Selectivity Parameter – MAD β1	2.56	0.09
FICsel_params[12]	Survey Selectivity Parameter – MAD α2	3.67	0.85
FICsel_params[13]	Survey Selectivity Parameter – MAD β2	3.50	0.01
FICsel_params[14]	Survey Selectivity Parameter – SAD α1	1.32	0.01
FICsel_params[15]	Survey Selectivity Parameter – SAD β1	6.50	0.00
FICsel_params[16]	Survey Selectivity Parameter – SAD α2	2.00	0.00
FICsel_params[17]	Survey Selectivity Parameter – SAD β2	1.86	0.23
FICsel_params[33]	Survey Selectivity Parameter – MRIP α1	4.18	0.08
FICsel_params[34]	Survey Selectivity Parameter - MRIP β1	1.00	0.00
FICsel_params[35]	Survey Selectivity Parameter – CTLIST α1	4.00	0.00
FICsel_params[36]	Survey Selectivity Parameter – CTLIST β1	0.77	0.05
FICsel_params[37]	Survey Selectivity Parameter – CTLIST α2	13.00	0.00
FICsel_params[38]	Survey Selectivity Parameter – CTLIST β2	1.00	0.00
FICsel_params[46]	Survey Selectivity Parameter – MRIP α1	2.00	0.00
FICsel_params[47]	Survey Selectivity Parameter - MRIP β1	5.00	0.00
FICsel_params[48]	Survey Selectivity Parameter – PSIGNS α1	2.00	0.00
FICsel_params[49]	Survey Selectivity Parameter – PSIGNS β1	5.00	0.00
FICsel_params[50]	Survey Selectivity Parameter – PSIGNS α2	3.21	0.31
FICsel_params[51]	Survey Selectivity Parameter – PSIGNS β2	2.00	0.00
FICsel_params[59]	Survey Selectivity Parameter – MRIP α1	3.58	0.13
FICsel_params[60]	Survey Selectivity Parameter - MRIP β1	1.50	0.00
FICsel_params[61]	Survey Selectivity Parameter – DE30 α1	1.76	0.15
FICsel_params[62]	Survey Selectivity Parameter – DE30 β1	1.50	0.00
FICsel_params[63]	Survey Selectivity Parameter – Alb α1	5.10	0.29
FICsel_params[64]	Survey Selectivity Parameter – Alb β1	1.00	0.00
FICsel_params[65]	Survey Selectivity Parameter – Bigelow α1	4.56	0.54
FICsel_params[66]	Survey Selectivity Parameter – Bigelow β1	1.00	0.00
FICsel_params[67]	Survey Selectivity Parameter – Alb α1	6.00	0.00
FICsel_params[68]	Survey Selectivity Parameter – Alb β1	0.43	0.04

Table 29. Contributions of the various components by species to the VADER model objective function value

Likelihood component	Menhaden	Striped Bass	Bluefish	Weakfish	Atlantic Herring	Spiny Dogfish
Total fishery catch	1.5	1.2	7.6	111.3	0.4	43.2
Total survey catch	34.2 30.8 252.9 54.3	12.3 27.5 29.6	13.1 20.9 11.3	97.2 47.0 25.5	17.3 3.1	23.2
Fishery catch age proportions	5,004.3	5,533.0	1,716.8	2,554.2	546.5	7,162.1
Survey catch age proportions	1,681.2 2,796.7 5,345.2	2,667.3 760.0	2,058.2 453.3	1,249.5 879.2	708.3 115.7	1,587.2
Food habits	0	487.0	98.8	75.8	0	326.0
Year 1 penalty	3.0e-005	18.6	0.1	6.4	6.9e-005	147.7
Recruitment penalty	0	0	0	5.9	0	0.01
Biomass penalty	0	0	0	0	0	0
Total Likelihood Value	15,201	9,518.23	4,380.2	5,039.9	1,391.4	9,141.8

Table 30. Ecopath inputs representing the base year of 1985 for the NWACS-MICE model. BA rate is biomass accumulation rate and *Q/B* is consumption per biomass. For multistanza groups, the adult age stanza is considered to be age 1+ unless otherwise noted.

n	Group name	Biomass (1e6 mt)	BA rate (/year)	Z or PB (/year)	Q/B (/year)	Total Landings (1e6 mt)
1	striped bass 0-1	0.008	0.113	1.132	7.152	
2	striped bass 2-5	0.036	0.113	0.582	3.004	0.001
3	striped bass 6+	0.018	0.113	0.335	1.820	0.003
4	menhaden juv	0.282	0.114	1.764	9.402	0.005
5	menhaden adult	1.704	0.114	1.454	3.804	0.329
6	spiny dogfish	0.272	0.000	0.321	1.810	0.005
7	bluefish juv	0.004	-0.064	2.069	12.331	0.001
8	bluefish adult	0.220	-0.064	0.656	3.139	0.032
9	weakfish juv	0.001	0.000	1.453	9.977	
10	weakfish adult	0.013	0.000	1.310	3.770	0.003
11	Atlantic herring 0-1	0.008	0.137	1.371	10.829	0.002
12	Atlantic herring 2+	0.150	0.137	0.823	3.700	0.059
13	anchovies	0.271	0.000	2.200	7.333	
14	benthos	14.546	0.000	2.432	12.469	
15	zooplankton	13.559	0.000	45.850	154.600	
16	phytoplankton	8.596	0.000	186.436		
17	Detritus	12.974	0.000			

Table 31. Diet matrix for the NWACS-MICE model with columns as predators and rows as prey. The numbers in the column and row headings correspond to the groups listed in Table 30. Imp = diet import.

Pred/ Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1		0.001	0.002			0.001	0.001	0.000							
2			0.001												
3															
4	0.020	0.078	0.076			0.003	0.009	0.027	0.013	0.025					
5	0.020	0.079	0.228			0.002		0.049		0.018					
6						0.001									
7		0.001	0.001					0.010							
8			0.001					0.001							
9	0.002	0.004					0.001	0.001	0.001	0.006					
10								0.001		0.001					
11		0.002	0.011			0.008		0.003			0.003	0.002			
12		0.022	0.051			0.062		0.029			0.003	0.004			
13	0.112	0.232	0.254			0.007	0.444	0.212	0.436	0.445	0.027	0.027			
14	0.514	0.353	0.101			0.218	0.024	0.032	0.204	0.169	0.177	0.177	0.101	0.090	0.001
15	0.146	0.016	0.002	0.420	0.570	0.234	0.011	0.009	0.238	0.164	0.784	0.784	0.684	0.021	0.261
16		0.001	0.003	0.301	0.223			0.002	0.001	0.000			0.155	0.229	0.490
17				0.278	0.206								0.060	0.413	0.199
Imp.	0.186	0.213	0.269	0.000		0.465	0.510	0.624	0.107	0.172	0.006	0.006		0.246	0.048

Table 32. Ecopath estimates of trophic level, ecotrophic efficiency, and mortality rates from the NWACS-MICE model.

n	Group name	Trophic level	Ecotrophic Efficiency	Fishing mortality	Predation Mortality	Other Mortality
1	striped bass 0	3.307	0.089	0.000	0.101	1.031
2	striped bass 2-5	3.540	0.037	0.020	0.001	0.561
3	striped bass 6+	3.787	0.511	0.171	0.000	0.164
4	menhaden juv	2.562	0.080	0.019	0.121	1.623
5	menhaden adult	2.762	0.154	0.193	0.031	1.230
6	spiny dogfish	3.385	0.063	0.019	0.001	0.301
7	bluefish juv	3.959	0.855	0.173	1.596	0.300
8	bluefish adult	3.906	0.229	0.148	0.002	0.506
9	weakfish juv	3.624	0.919	0.022	1.313	0.118
10	weakfish adult	3.686	0.231	0.222	0.080	1.008
11	Atlantic herring 0-1	3.320	0.834	0.248	0.895	0.228
12	Atlantic herring 2+	3.320	0.938	0.395	0.377	0.051
13	anchovies	3.027	0.433	0.000	0.952	1.248
14	benthos	2.108	0.521	0.000	1.266	1.165
15	zooplankton	2.337	0.899	0.000	41.207	4.643
16	phytoplankton	1.000	0.669	0.000	124.635	61.802
17	Detritus	1.000	0.370		0.000	0.000

Table 33. Predation mortality matrix from the NWACS-MICE model with columns as predators and rows as prey. The numbers in the column and row headings correspond to the groups listed in Table 30.

Pred/ Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1		0.0126	0.0079			0.0392	0.0064	0.0347							
2			0.0009												
3															
4	0.0042	0.0301	0.0091			0.0046	0.0017	0.0669	0.0006	0.0043					
5	0.0007	0.0050	0.0045			0.0006		0.0200		0.0005					
6						0.0012									
7		0.0246	0.0077					1.5634							
8			0.0002					0.0022							
9	0.0979	0.3474					0.0437	0.5916	0.0101	0.2220					
10								0.0761		0.0041					
11		0.0225	0.0435			0.4606		0.2356			0.0279	0.1047			
12		0.0158	0.0114			0.2029		0.1320			0.0015	0.0132			
13	0.0249	0.0927	0.0315			0.0134	0.0872	0.5395	0.0196	0.0785	0.0090	0.0556			
14	0.0021	0.0026	0.0002			0.0074	0.0001	0.0015	0.0002	0.0006	0.0011	0.0067	0.0138	1.1258	0.1041
15	0.0006	0.0001	0.0000	0.0821	0.2725	0.0085	0.0000	0.0004	0.0002	0.0006	0.0052	0.0320	0.1004	0.2847	40.4197
16		0.0000	0.0000	0.0928	0.1685			0.0001	0.0000	0.0000			0.0359	4.8343	119.5028

Table 34. Time series of abundance and catch used in the Ecosim component of the NWACS-MICE model.

Group Name	Index Type	Index Name	Years	Weight
striped bass 0	rel. biomass	composite YOY index	1985-2017	3.476
striped bass 2-5	rel. biomass	recreational cpue	1985-2017	2.015
striped bass 2-5	rel. biomass	Connecticut Long Island Sound trawl survey	1987-2017	2.686
striped bass 6+	rel. biomass	recreational cpue	1985-2017	2.015
striped bass 6+	rel. biomass	Connecticut Long Island Sound trawl survey	1987-2017	2.686
menhaden juv	rel. biomass	composite YOY index	1985-2017	1.981
menhaden adult	rel. biomass	composite northern adult index	1990-2017	1.476
menhaden adult	rel. biomass	composite mid Atlantic adult index	1985-2017	1.419
menhaden adult	rel. biomass	composite southern adult index	1990-2017	1.787
spiny dogfish	rel. biomass	NEFSC trawl survey	1985-2017	2.500
bluefish juv	rel. biomass	composite YOY index	1985-2017	2.202
bluefish adult	rel. biomass	recreational cpue	1985-2017	9.925
bluefish adult	rel. biomass	NC Pamlico Sound inshore gillnet survey	2001-2017	6.082
weakfish juv	rel. biomass	composite YOY index	1985-2017	3.137
weakfish adult	rel. biomass	recreational cpue	1985-2017	2.867
weakfish adult	rel. biomass	Delaware 30' trawl survey	1991-2017	1.603
Atlantic herring 2+	rel. biomass	NEFSC Fall survey Albatross	1985-2008	1.412
Atlantic herring 2+	rel. biomass	NEFSC Fall survey Bigelow	2009-2017	1.842
striped bass 2-5	catch	total landings from stock assessment	1985-2017	12.655
striped bass 6+	catch	total landings from stock assessment	1985-2017	12.655
menhaden adult	catch	total landings from stock assessment	1985-2017	21.666
bluefish adult	catch	total landings from stock assessment	1985-2017	6.938
weakfish juv	catch	total landings from stock assessment	1985-2017	7.458
weakfish adult	catch	total landings from stock assessment	1985-2017	7.458
Atlantic herring 2+	catch	total landings from stock assessment	1985-2017	10.000
menhaden juv	rel. catch	total landings from stock assessment	1985-2017	21.666
bluefish juv	rel. catch	total landings from stock assessment	1985-2017	6.938
Atlantic herring 0-1	rel. catch	total landings from stock assessment	1985-2017	10.000
spiny dogfish	forced catch	total landings from stock assessment	1985-2017	1.000

Table 35. Ecosim scenarios for the NWACS-MICE model.

Scenario	Description	Start SS	End SS
sim1	Default configuration with foraging time adjustment set to 0.5 for all juvenile stanzas and prey switching = 0.	2582	1200
sim1.1	sim 1 with vulnerability caps, M_0 changing with foraging time, and foraging time changing with predator abundance for juvenile striped bass	2582	1269
sim3	Aimed at evaluating the sensitivity to prey switching (parameter set at 1, when default value is 0).	2590	1088
sim3.5	Sim3 with vulnerability caps applied and juvenile striped bass with risk sensitive foraging and M_0 constant relative to foraging time.	2590	1186
sim9	fit 17 vulnerabilities and 11 PP splines	2582	1031
sim9.1	fit 28 vulnerabilities and 33 PP splines	2582	1096
sim 12.3	Fit to time series with recruitment deviation, prey switching 1.5 for menhaden predators	2461	1062

Table 36. Equilibrium F_{MSY} values from the NWACS-MICE model.

Group	sim1	sim1.1	sim3	sim3.5
striped bass ages 6+	0.171	0.154	0.305	0.171
menhaden adult	0.657	0.637	0.954	0.837
bluefish adult	0.856	0.723	NA	0.729
weakfish adult	NA	NA	1.097	0.794
Atlantic herring 2+	0.237	0.237	0.395	0.335

Table 37. Biomass and fishing mortality reference points from single species stock assessments with conversions for sim 3.5 of the NWACS-MICE model.

Biomass Reference Points								
Species	**Single Species B_{2017}**	**Single Species B_{TARGET}**	**Single Species $B_{THRESHOLD}$**	**B_{TARGET}/ B_{2017}**	**$B_{THRESHOLD}$/ B_{2017}**	**Ecosim B_{2017}**	**Ecosim B_{TARGET}**	**Ecosim $B_{THRESHOLD}$**
Striped bass (age 6+)	97,046	153,244	119,722	1.58	1.23	0.110	0.174	0.136
Menhaden (adult)	3,581,000	NA	NA	NA	NA	2.344	NA	NA
Spiny dogfish	641,132	511,776	255,888	0.80	0.40	0.314	0.251	0.125
Bluefish (adult)	92,794	198,717	99,359	2.14	1.07	0.104	0.223	0.112
Weakfish (adult)	3,209	NA	11,489	NA	3.58	0.007	NA	0.026
Atlantic herring (age 2+)	239,472	448,000	224,000	1.87	0.94	0.453	0.848	0.424
Fishing Mortality Reference Points								
Species	**Single Species F_{2017}**	**Single Species F_{TARGET}**	**Single Species $F_{THRESHOLD}$**	**F_{TARGET}/ F_{2017}**	**$F_{THRESHOLD}$/ F_{2017}**	**Ecosim F_{2017}**	**Ecosim F_{TARGET}**	**Ecosim $F_{THRESHOLD}$**
Striped bass (age 6+)	0.310	0.197	0.240	0.635	0.774	0.294	0.187	0.228
Menhaden (adult)	0.110	0.220	0.600	2.000	5.455	0.049	0.098	0.267
Spiny dogfish	0.150	0.220	0.240	1.467	1.600	0.035	0.052	0.056
Bluefish (adult)	0.340	0.160	0.320	0.471	0.941	0.384	0.181	0.361
Weakfish (adult)	0.230	0.550	0.930	2.391	4.043	0.069	0.165	0.278
Atlantic herring (age 2+)	0.450	0.460	0.510	1.022	1.133	0.283	0.290	0.321

Table 38. Proportion of trials with change in biomass (ΔB_{REL}) at or below a given percentage and median ΔB_{REL} from 500 Ecosim projections for each *F* scenario from the NWACS-MICE model.

	Years out	-20%	-15%	-10%	-5%	0%	5%	10%	15%	20%	Median ΔB_{REL}
Atlantic menhaden *F=Current TAC*											
striped.bass.adult	4 yr	0.00	0.00	0.00	0.00	0.68	1.00	1.00	1.00	1.00	-0.01
	40 yr	0.00	0.00	0.00	0.16	0.70	0.98	1.00	1.00	1.00	-0.02
spiny.dogfish	4 yr	0.00	0.00	0.00	0.00	0.61	1.00	1.00	1.00	1.00	0.00
	40 yr	0.00	0.00	0.00	0.00	0.30	1.00	1.00	1.00	1.00	0.00
bluefish.adult	4 yr	0.00	0.00	0.00	0.00	0.67	1.00	1.00	1.00	1.00	0.00
	40 yr	0.00	0.00	0.00	0.00	0.70	1.00	1.00	1.00	1.00	-0.01
weakfish.adult	4 yr	0.00	0.00	0.00	0.00	0.71	1.00	1.00	1.00	1.00	0.00
	40 yr	0.00	0.00	0.00	0.00	0.86	1.00	1.00	1.00	1.00	0.00
Atl.herring.adult	4 yr	0.00	0.00	0.00	0.00	0.70	1.00	1.00	1.00	1.00	0.00
	40 yr	0.00	0.00	0.00	0.00	0.30	0.99	1.00	1.00	1.00	0.01
Atlantic menhaden *F=F$_{TARGET}$*											
striped.bass.adult	4 yr	0.00	0.00	0.00	0.02	0.86	1.00	1.00	1.00	1.00	-0.03
	40 yr	0.00	0.00	0.10	0.57	0.88	1.00	1.00	1.00	1.00	-0.06
spiny.dogfish	4 yr	0.00	0.00	0.00	0.00	0.76	1.00	1.00	1.00	1.00	0.00
	40 yr	0.00	0.00	0.00	0.00	0.12	1.00	1.00	1.00	1.00	0.01
bluefish.adult	4 yr	0.00	0.00	0.00	0.00	0.84	1.00	1.00	1.00	1.00	-0.01
	40 yr	0.00	0.00	0.00	0.00	0.88	1.00	1.00	1.00	1.00	-0.01
weakfish.adult	4 yr	0.00	0.00	0.00	0.00	0.88	1.00	1.00	1.00	1.00	-0.01
	40 yr	0.00	0.00	0.00	0.00	0.89	1.00	1.00	1.00	1.00	0.00
Atl.herring.adult	4 yr	0.00	0.00	0.00	0.00	0.88	1.00	1.00	1.00	1.00	0.00
	40 yr	0.00	0.00	0.00	0.00	0.12	0.73	1.00	1.00	1.00	0.04
Atlantic menhaden *F=F$_{THRESHOLD}$*											
striped.bass.adult	4 yr	0.00	0.12	0.58	0.86	1.00	1.00	1.00	1.00	1.00	-0.11
	40 yr	0.56	0.75	0.90	0.97	1.00	1.00	1.00	1.00	1.00	-0.21
spiny.dogfish	4 yr	0.00	0.00	0.00	0.00	0.99	1.00	1.00	1.00	1.00	0.00
	40 yr	0.00	0.00	0.00	0.00	0.00	0.66	1.00	1.00	1.00	0.04
bluefish.adult	4 yr	0.00	0.00	0.00	0.56	1.00	1.00	1.00	1.00	1.00	-0.05
	40 yr	0.00	0.00	0.00	0.39	1.00	1.00	1.00	1.00	1.00	-0.05
weakfish.adult	4 yr	0.00	0.00	0.00	0.05	1.00	1.00	1.00	1.00	1.00	-0.03
	40 yr	0.00	0.00	0.00	0.00	0.99	1.00	1.00	1.00	1.00	-0.01
Atl.herring.adult	4 yr	0.00	0.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	0.00
	40 yr	0.00	0.00	0.00	0.00	0.00	0.07	0.27	0.54	0.90	0.14

Table 39. Ecosystem model trophic groups used in the NWACS-FULL model. Trophic groups are arranged by node number and arranged into broader categories. Eight species were modeled using multi-stanza groups that were identified as small (S), medium (M), or large (L), and the defining ages (in years) and fork lengths (cm) for each of the eight species is listed.

		Small		Medium		Large	
Node	Node Name	age	size	age	size	age	size
Primary Producers							
1	Phytoplankton						
2	Other primary producers						
Bacteria							
3	Bacteria						
Zooplankton							
4	Microzooplankton						
5	Small copepods						
6	Large copepods						
7	Gelatinous zooplankton						
8	Micronekton						
Benthic Invertebrates							
9	Macrobenthos - polychaetes						
10	Macrobenthos - crustaceans						
11	Macrobenthos - molluscs						
12	Macrobenthos - other						
13	Megabenthos - Filterers						
14	Megabenthos - other						
15	Shrimp and Similar Species						
Forage Fishes							
16	Mesopelagics						
17	Atlantic herring						
18	Alosines						
19-21	Atlantic menhaden	0	<14	1-2	14-24	3+	>24
22	Anchovies						
23	Atlantic mackerel						
24	Squid						
25	Butterfish						
26	small pelagic - other						
Fishes							
27-29	Bluefish	0	<30	1-3	30-60	4+	>60
30-32	Striped bass	0-1	<25	2-6	25-70	7+	>70
33-35	Weakfish	0	<20	1-2	20-40	3+	>40
36-37	Spiny dogfish	0-5	<60			6+	>60
38-40	Cod	0-1	<20	2-3	20-50	4+	>50
41	Haddock						
42	Hakes						
43	Atlantic croaker						
44-45	Yellowtail flounder	0	<20			1+	>20
46-47	Summer flounder	0	<25			1+	>25
48	Skates						
49	Demersal benthivores - other						
50	Demersal piscivores - other						
51	Demersal omnivores - other						
52	Medium pelagic - other						
Apex Predators							
53	Sharks - coastal						
54	Sharks - pelagic						
55	Large pelagics (HMS)						
56	Pinnipeds						
57	Baleen whales						
58	Odontocetes						
59	Seabirds						
60	Shorebirds - piscivorous						
Detritus							
61	Detritus						

Table 40. Basic inputs and outputs for Sim2 of the NWACS-FULL model. Values include biomass accumulation (BA) rates, total instantaneous mortality (*Z*) or production to biomass (*P/B*), consumption to biomass (*Q/B*), trophic level (*TL*), ecotrophic efficiency (*EE*), fishing mortality rate (*F*), predation mortality rate (M_2), and other mortality (M_0).

N	Group	Biomass (mt/km2)	BA rate (/yr)	Z or P/B (/year)	Q/B (/yr)	Total Landings (mt/km2)	TL	EE	F	M_2	M_0
1	Phytoplankton	30.000	0.000	180.700	0.000	0.000	1.000	0.943		170.357	10.343
2	Other primary producers	1.621	0.000	55.570	0.000	0.009	1.000	0.900	0.006	50.007	5.557
3	Bacteria	7.700	0.000	91.250	380.208	0.000	2.000	0.941		85.867	5.383
4	Microzooplankton	7.000	0.000	85.000	283.400	0.000	2.264	0.934		79.351	5.649
5	Small copepods	16.000	0.000	46.000	140.000	0.000	2.152	0.992		45.624	0.376
6	Large copepods	17.966	0.000	46.000	150.000	0.000	2.388	0.978		44.994	1.006
7	Gelatinous zooplankton	6.349	0.000	40.000	145.326	0.000	3.085	0.590		23.612	16.388
8	Micronekton	7.654	0.000	14.250	85.497	0.000	2.723	0.675		9.612	4.638
9	Macrobenthos - polychaetes	17.452	0.000	2.500	17.500	0.002	2.377	0.800	0.000	2.001	0.499
10	Macrobenthos - crustaceans	7.000	0.000	3.600	21.000	0.000	2.535	0.763		2.747	0.853
11	Macrobenthos - molluscs	8.340	0.000	2.200	13.949	0.275	2.246	0.835	0.033	1.805	0.362
12	Macrobenthos - other	21.000	0.000	2.000	16.059	0.000	2.349	0.865	0.000	1.731	0.269
13	Megabenthos - filterers	5.500	0.000	1.200	6.660	0.041	2.120	0.868	0.007	1.034	0.158
14	Megabenthos - other	4.498	0.000	2.300	15.533	0.350	2.895	0.739	0.078	1.622	0.600
15	Shrimp and Similar Species	0.470	0.144	2.000	6.660	0.021	2.751	0.833	0.046	1.477	0.333
16	Mesopelagics	0.090	0.000	1.100	3.700	0.000	3.238	0.961		1.057	0.043
17	Atlantic herring	0.800	0.000	1.700	5.300	0.285	3.495	0.952	0.357	1.262	0.081
18	Alosines	0.200	0.000	1.300	4.400	0.025	3.367	0.876	0.123	1.016	0.161
19	Atlantic menhaden (S)	1.340	0.234	1.766	15.860	0.018	2.533	0.151	0.013	0.252	1.500
20	Atlantic menhaden (M)	5.562	0.234	1.498	6.993	1.194	2.685	0.200	0.215	0.085	1.198
21	Atlantic menhaden (L)	1.135	0.234	1.229	4.160	0.418	2.837	0.453	0.368	0.189	0.672
22	Anchovies	1.100	0.000	2.200	7.333	0.000	3.060	0.973		2.141	0.059
23	Atlantic mackerel	1.740	0.000	0.550	2.170	0.052	3.546	0.786	0.030	0.402	0.118
24	Squid	1.267	0.407	5.720	19.000	0.042	3.859	0.958	0.033	5.041	0.239
25	Butterfish	1.488	0.020	1.312	4.230	0.024	3.833	0.888	0.079	1.066	0.147
26	Small pelagic - other	1.400	0.000	1.200	4.000	0.004	3.397	0.910	0.003	1.089	0.108
27	Bluefish (S)	0.015	-0.173	2.500	17.977	0.008	4.435	0.907	0.537	1.730	0.233
28	Bluefish (M)	0.257	-0.173	0.893	5.786	0.102	4.406	0.585	0.397	0.125	0.371
29	Bluefish (L)	0.618	-0.173	0.461	3.139	0.150	4.498	0.606	0.243	0.036	0.182

Table 40 continued. Basic inputs and outputs for Sim2 of the NWACS-FULL model.

N	Group	Biomass (mt/km2)	BA rate (/yr)	Z or P/B (/year)	Q/B (/yr)	Total Landings (mt/km2)	TL	EE	F	M_2	M_0
30	Striped bass (S)	0.018	0.011	1.130	7.543	0.000	3.795	0.307		0.347	0.783
31	Striped bass (M)	0.126	0.011	0.536	2.973	0.005	3.934	0.100	0.037	0.017	0.483
32	Striped bass (L)	0.071	0.011	0.325	1.820	0.012	4.072	0.558	0.176	0.005	0.144
33	Weakfish (S)	0.006	-0.083	2.800	13.520	0.000	3.923	0.849		2.378	0.422
34	Weakfish (M)	0.055	-0.083	0.913	4.869	0.001	3.977	0.398	0.022	0.341	0.550
35	Weakfish (L)	0.082	-0.083	0.845	2.813	0.037	4.063	0.533	0.449	0.001	0.395
36	Spiny dogfish (S)	0.303	0.050	0.200	3.600	0.000	4.188	0.719		0.144	0.056
37	Spiny dogfish (L)	1.200	0.050	0.200	1.810	0.025	4.263	0.296	0.038	0.022	0.141
38	Atlantic cod (S)	0.055	-0.228	1.087	5.059	0.010	3.630	0.910	0.174	0.815	0.098
39	Atlantic cod (M)	0.144	-0.228	1.125	2.603	0.132	3.948	0.936	0.920	0.133	0.073
40	Atlantic cod (L)	0.277	-0.228	0.700	1.500	0.122	4.318	0.658	0.441	0.020	0.239
41	Haddock	0.254	0.000	0.700	3.000	0.082	3.634	0.924	0.323	0.325	0.053
42	Hake	1.000	0.000	1.296	3.850	0.109	4.164	0.869	0.109	1.017	0.169
43	Atlantic croaker	0.350	0.000	0.994	3.550	0.027	3.569	0.298	0.079	0.218	0.698
44	Yellowtail flounder (S)	0.007	0.000	2.700	12.168	0.000	3.569	0.975		2.633	0.067
45	Yellowtail flounder (L)	0.187	0.000	0.850	2.900	0.085	3.536	0.658	0.457	0.102	0.291
46	Summer flounder (S)	0.011	0.119	2.400	10.379	0.009	4.206	0.873	0.837	1.258	0.304
47	Summer flounder (L)	0.159	0.119	1.050	2.900	0.084	4.516	0.543	0.525	0.044	0.480
48	Skates	1.000	0.000	0.250	0.900	0.011	3.805	0.807	0.011	0.191	0.048
49	Demersal benthivores - other	2.300	0.000	0.600	2.000	0.119	3.555	0.977	0.052	0.535	0.014
50	Demersal piscivores - other	1.300	0.000	0.450	1.500	0.089	4.079	0.747	0.068	0.268	0.114
51	Demersal omnivores - other	1.100	0.000	0.550	1.833	0.101	3.885	0.991	0.092	0.453	0.005
52	Medium pelagic - other	0.021	0.000	0.450	1.838	0.001	4.707	0.658	0.056	0.240	0.154
53	Sharks - coastal	0.008	0.000	0.200	1.247	0.001	4.601	0.564	0.099	0.014	0.087
54	Sharks - pelagic	0.016	0.000	0.113	0.690	0.000	4.644	0.194	0.003	0.019	0.091
55	Large pelagics (HMS)	0.070	0.000	0.579	6.794	0.027	4.494	0.671	0.386	0.003	0.191
56	Pinnipeds	0.035	0.000	0.075	5.581	0.000	4.530	0.118		0.009	0.066
57	Baleen whales	0.464	0.000	0.040	3.217	0.000	3.541	0.012		0.000	0.040
58	Odontocetes	0.060	0.000	0.040	14.301	0.000	4.611	0.922		0.037	0.003
59	Seabirds	0.007	0.000	0.279	80.000	0.000	4.264	0.373		0.104	0.175
60	Shorebirds - piscivorous	0.007	0.000	0.279	80.000	0.000	3.997	0.005		0.001	0.278
61	Detritus	52.600	0.000	0.000	0.000	0.000	1.000	0.871			

Table 41. Diet composition matrix for Sim2 of the NWACS-FULL model. Columns indicate the predators (labeled by node number) and rows are prey. (Page 1 of 3)

Node	Prey \ predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Phytoplankton	0.243	0.225	0.744	0.668	0.107	0.233	0.131	0.177	0.424	0.236	0.692		0.067	0.026			0.278	0.221
2	Other primary producers	0.023						0.015	0.012	0.010	0.013	0.006						0.023	0.018
3	Bacteria		0.196			0.025		0.313	0.166	0.201	0.244	0.120	0.270	0.397	0.015				
4	Microzooplankton		0.054	0.111	0.060	0.031									0.075			0.140	0.180
5	Small copepods			0.011	0.114	0.303	0.149		0.015						0.439	0.399	0.601	0.140	0.180
6	Large copepods				0.065	0.432	0.323		0.033						0.429			0.140	0.180
7	Gelatinous zooplankton				0.042	0.035										0.021	0.002		
8	Micronekton						0.059	0.015	0.014	0.009	0.019			0.134	0.013	0.365	0.227		
9	Macrobenthos - polychaetes							0.005	0.099		0.021		0.133			0.001	0.002		
10	Macrobenthos - crustaceans				0.001			0.003	0.001		0.001		0.046	0.026		0.139	0.134		
11	Macrobenthos - molluscs							0.001	0.010	0.001	0.011		0.110			0.002			
12	Macrobenthos - other				0.001			0.014	0.084	0.011	0.011		0.146	0.061		0.001	0.005		
13	Megabenthos - filterers							0.003	0.014	0.010	0.001		0.012						
14	Megabenthos - other							0.001	0.002	0.001	0.007		0.012			0.003	0.002		
15	Shrimp and Similar Species													0.001		0.030	0.005		
16	Mesopelagics																		
17	Atlantic herring															0.005			
18	Alosines																		
19	Atlantic menhaden (S)																		
20	Atlantic menhaden (M)																		
21	Atlantic menhaden (L)																		
22	Anchovies															0.027	0.003		
23	Atlantic mackerel																		
24	Squid					0.000													
25	Butterfish																		
26	Small pelagic - other															0.004	0.019		
27	Bluefish (S)																		
28	Bluefish (M)																		
29	Bluefish (L)																		
30	Striped bass (S)																		
31	Striped bass (M)																		
32	Striped bass (L)																		
33	Weakfish (S)																		
34	Weakfish (M)																		
35	Weakfish (L)																		
36	Spiny dogfish (S)																		
37	Spiny dogfish (L)																		
38	Atlantic cod (S)																		
39	Atlantic cod (M)																		
40	Atlantic cod (L)																		
41	Haddock																		
42	Hake															0.001			
43	Atlantic croaker																		
44	Yellowtail flounder (S)																		
45	Yellowtail flounder (L)																		
46	Summer flounder (S)																		
47	Summer flounder (L)																		
48	Skates																		
49	Demersal benthivores - other																		
50	Demersal piscivores - other															0.001			
51	Demersal omnivores - other																		
52	Medium pelagic - other																		
53	Sharks - coastal																		
54	Sharks - pelagic																		
55	Large pelagics (HMS)																		
56	Pinnipeds																		
57	Baleen whales																		
58	Odontocetes																		
59	Seabirds														0.001				
60	Shorebirds - piscivorous																		
61	Detritus	0.734	0.526	0.135	0.049	0.068	0.235	0.498	0.374	0.333	0.436	0.182	0.270	0.314	0.001			0.278	0.221
	Import																		

Table 41. (Continued) Diet composition for Sim2 of the NWACS-FULL model. Columns indicate the predators (labeled by node number) and rows are prey. (Page 2 of 3)

Node	Prey \ predator	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	Phytoplankton	0.163	0.130																		
2	Other primary producers	0.014	0.025						0.002	0.001		0.001	0.003	0.001		0.001					
3	Bacteria																				
4	Microzooplankton	0.220																			
5	Small copepods	0.220	0.300	0.400		0.028	0.454				0.027			0.005	0.002	0.001			0.002		
6	Large copepods	0.220	0.300		0.152		0.172				0.027			0.005	0.002	0.001			0.002		
7	Gelatinous zooplankton			0.023	0.008	0.507	0.018	0.002	0.004	0.006					0.001	0.002	0.220	0.151			
8	Micronekton		0.084	0.365	0.509	0.112	0.186	0.009	0.009		0.092	0.016	0.002	0.229	0.174	0.131	0.096	0.020	0.150	0.024	0.003
9	Macrobenthos - polychaetes		0.010	0.002		0.019	0.001	0.001	0.002	0.001	0.019	0.034	0.028	0.009	0.010	0.005	0.019	0.005	0.075	0.024	0.016
10	Macrobenthos - crustaceans		0.091	0.128	0.118	0.314	0.135	0.016	0.017	0.013	0.461	0.229	0.033	0.139	0.124	0.107	0.043	0.019	0.473	0.147	0.029
11	Macrobenthos - molluscs					0.002				0.001	0.005	0.041	0.016	0.001	0.002		0.112	0.074	0.016	0.061	0.055
12	Macrobenthos - other				0.021	0.006	0.004	0.001			0.005	0.002	0.003			0.001	0.004	0.004	0.087	0.096	0.014
13	Megabenthos - filterers											0.008	0.001				0.025	0.089	0.015	0.044	0.036
14	Megabenthos - other				0.004			0.005	0.015	0.015	0.019	0.038	0.021	0.015	0.017	0.028	0.014	0.021	0.030	0.184	0.144
15	Shrimp and Similar Species			0.011	0.001	0.001	0.001	0.001	0.001	0.001	0.005	0.001		0.039	0.027	0.009	0.012	0.007	0.053	0.061	0.019
16	Mesopelagics				0.001			0.001	0.003	0.003							0.004	0.001			
17	Atlantic herring			0.003					0.031	0.032		0.023	0.062				0.048	0.043		0.067	0.222
18	Alosines								0.019	0.016	0.010	0.008	0.012		0.001	0.002		0.008		0.002	0.009
19	Atlantic menhaden (S)							0.009	0.040	0.020	0.020	0.078	0.076	0.013	0.024	0.027	0.001	0.004			
20	Atlantic menhaden (M)								0.050	0.040	0.020	0.078	0.129		0.010	0.030		0.003			
21	Atlantic menhaden (L)									0.010		0.001	0.099			0.001		0.001			
22	Anchovies			0.014			0.024	0.444	0.253	0.190	0.112	0.232	0.254	0.436	0.463	0.408		0.015			
23	Atlantic mackerel							0.002	0.024	0.020		0.001	0.012				0.086	0.119		0.005	0.019
24	Squid			0.007	0.158	0.010	0.003	0.116	0.177	0.220	0.001	0.016	0.045	0.009	0.020	0.029	0.142	0.122		0.007	0.006
25	Butterfish				0.025			0.266	0.115	0.119		0.021	0.028	0.001	0.009	0.018	0.008	0.020			0.004
26	Small pelagic - other			0.017			0.001	0.035	0.067	0.073	0.113	0.060	0.073	0.066	0.054	0.090	0.028	0.078	0.097	0.157	0.152
27	Bluefish (S)								0.002	0.002		0.001	0.001								0.011
28	Bluefish (M)									0.001			0.001								0.001
29	Bluefish (L)																				
30	Striped bass (S)							0.001	0.001			0.001	0.002					0.001			
31	Striped bass (M)												0.001								
32	Striped bass (L)																				
33	Weakfish (S)							0.001	0.001	0.001	0.002	0.004		0.001	0.003	0.002					
34	Weakfish (M)									0.002						0.023					
35	Weakfish (L)																				
36	Spiny dogfish (S)																	0.001			0.011
37	Spiny dogfish (L)																				0.011
38	Atlantic cod (S)																0.001	0.001			0.008
39	Atlantic cod (M)																				0.006
40	Atlantic cod (L)																				
41	Haddock								0.001	0.006								0.001		0.002	0.016
42	Hake			0.021	0.002			0.056	0.031	0.042	0.025	0.007	0.014	0.006	0.011	0.009	0.062	0.065	0.001	0.068	0.094
43	Atlantic croaker							0.001	0.010	0.007	0.003	0.003	0.010	0.002	0.004	0.002		0.001			
44	Yellowtail flounder (S)								0.001	0.001								0.001			0.003
45	Yellowtail flounder (L)									0.005											0.006
46	Summer flounder (S)								0.002	0.001								0.001			
47	Summer flounder (L)																				
48	Skates				0.001					0.002							0.006	0.013		0.001	0.004
49	Demersal benthivores - other			0.001				0.026	0.081	0.101	0.020	0.046	0.064	0.019	0.035	0.061	0.028	0.075		0.036	0.069
50	Demersal piscivores - other			0.004	0.001				0.009	0.009		0.009		0.001	0.001	0.004	0.001	0.013		0.004	0.011
51	Demersal omnivores - other			0.003				0.006	0.030	0.039	0.014	0.043	0.012	0.002	0.005	0.010	0.040	0.021		0.010	0.023
52	Medium pelagic - other																				
53	Sharks - coastal																				
54	Sharks - pelagic																				
55	Large pelagics (HMS)																				
56	Pinnipeds																				
57	Baleen whales																				
58	Odontocetes																				
59	Seabirds																				
60	Shorebirds - piscivorous																				
61	Detritus	0.163	0.060																		
	Import																				

Table 41. (Continued) Diet composition for Sim2 of the NWACS-FULL model. Columns indicate the predators (labeled by node number) and rows are prey. (Page 3 of 3)

Node	Prey \ predator	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
1	Phytoplankton																				
2	Other primary producers						0.001		0.001	0.001	0.002	0.002									
3	Bacteria																				
4	Microzooplankton																				
5	Small copepods	0.001	0.002	0.001		0.004	0.001		0.001	0.003								0.052			
6	Large copepods														0.025			0.475		0.039	
7	Gelatinous zooplankton	0.002				0.001						0.012	0.001	0.001	0.003	0.020		0.007	0.017		
8	Micronekton	0.138	0.184	0.079	0.134	0.032	0.256	0.032	0.014	0.055	0.035	0.006	0.032	0.036			0.073	0.303	0.031	0.160	
9	Macrobenthos - polychaetes	0.082	0.009	0.308	0.253	0.464	0.001		0.155	0.254	0.022	0.041	0.001								
10	Macrobenthos - crustaceans	0.242	0.222	0.159	0.457	0.333	0.110	0.041	0.176	0.290	0.062	0.063	0.025	0.012	0.010			0.056			0.028
11	Macrobenthos - molluscs	0.048	0.019	0.237	0.005	0.018	0.008	0.003	0.153	0.136	0.059	0.084		0.003				0.011			
12	Macrobenthos - other	0.284		0.006	0.023	0.041			0.005	0.048	0.001	0.013		0.019	0.010			0.021			
13	Megabenthos - filterers	0.006	0.005			0.001			0.003		0.001	0.006		0.003							
14	Megabenthos - other	0.045	0.042	0.083	0.081	0.015	0.059	0.056	0.234	0.129	0.393	0.559		0.019				0.005			0.028
15	Shrimp and Similar Species	0.017	0.044	0.006	0.025	0.003	0.025	0.006	0.016	0.015	0.036	0.013								0.022	
16	Mesopelagics		0.009				0.001				0.001	0.002	0.055		0.005			0.002	0.008		
17	Atlantic herring	0.069	0.057			0.001		0.039	0.019		0.011	0.010	0.009	0.062	0.069	0.152	0.147	0.015	0.073	0.093	
18	Alosines		0.004					0.014	0.004		0.007	0.001	0.027	0.062	0.011		0.051		0.007	0.017	0.088
19	Atlantic menhaden (S)								0.001		0.010	0.022		0.005	0.001	0.030	0.010	0.001	0.010	0.034	0.110
20	Atlantic menhaden (M)								0.001		0.020	0.030		0.020	0.028	0.030	0.029		0.030	0.034	0.165
21	Atlantic menhaden (L)										0.030			0.039	0.009	0.030	0.039		0.051	0.041	0.055
22	Anchovies		0.011	0.064			0.145	0.108	0.018	0.045	0.004	0.004	0.006	0.062	0.021	0.101	0.049	0.001	0.079	0.103	0.276
23	Atlantic mackerel	0.010	0.012					0.060	0.004		0.011			0.062	0.069	0.040	0.146	0.015	0.022	0.117	
24	Squid	0.001	0.130	0.011			0.123	0.210	0.038	0.013	0.040	0.037	0.283	0.126	0.155	0.061		0.006	0.307	0.063	
25	Butterfish	0.001	0.026	0.006			0.003	0.050	0.016		0.017	0.007	0.257	0.062	0.069	0.040	0.146	0.015	0.119	0.117	
26	Small pelagic - other	0.032	0.041	0.006	0.023	0.087	0.008	0.073	0.051		0.020	0.013	0.083	0.062	0.021	0.313	0.049	0.001	0.079	0.103	0.110
27	Bluefish (S)							0.001			0.002	0.002			0.001	0.010					
28	Bluefish (M)													0.020	0.020	0.020	0.010		0.020		
29	Bluefish (L)													0.020	0.020	0.020	0.020		0.010		
30	Striped bass (S)														0.007						0.001
31	Striped bass (M)													0.009	0.009		0.009				
32	Striped bass (L)													0.009	0.009		0.001				
33	Weakfish (S)						0.002	0.002	0.003		0.001	0.001			0.007						0.001
34	Weakfish (M)							0.020							0.007						
35	Weakfish (L)														0.007						
36	Spiny dogfish (S)		0.001					0.001			0.005			0.006	0.007	0.020	0.014		0.007	0.006	
37	Spiny dogfish (L)													0.028	0.028		0.019		0.020		
38	Atlantic cod (S)										0.011			0.004	0.005	0.020	0.010		0.004	0.002	
39	Atlantic cod (M)													0.004	0.005	0.020	0.009		0.004	0.002	
40	Atlantic cod (L)													0.004	0.005		0.009		0.004		
41	Haddock	0.001	0.004				0.002	0.026	0.008		0.008	0.001		0.013	0.010	0.010	0.012				
42	Hake	0.011	0.083				0.121	0.056	0.001		0.024	0.002	0.116	0.013	0.014	0.040	0.014		0.014	0.006	
43	Atlantic croaker						0.013	0.005	0.006	0.001	0.006	0.004		0.013	0.010		0.012				0.006
44	Yellowtail flounder (S)		0.001						0.001		0.001			0.006	0.005		0.012				
45	Yellowtail flounder (L)		0.001								0.001			0.006	0.005						
46	Summer flounder (S)											0.001		0.006	0.007		0.005		0.001	0.002	
47	Summer flounder (L)													0.006	0.007				0.007	0.002	
48	Skates								0.001		0.053	0.005	0.059	0.020	0.019	0.010	0.019				
49	Demersal benthivores - other	0.007	0.060	0.002			0.086	0.139	0.053	0.009	0.053	0.048	0.042	0.013	0.010		0.012				0.011
50	Demersal piscivores - other	0.001	0.026	0.018				0.010	0.004		0.025	0.012		0.013	0.014		0.014		0.014	0.006	0.011
51	Demersal omnivores - other		0.011	0.011			0.035	0.049	0.015		0.028	0.001	0.005	0.062	0.080		0.062		0.060	0.031	0.011
52	Medium pelagic - other														0.021	0.010					
53	Sharks - coastal													0.002	0.008						
54	Sharks - pelagic													0.010	0.019						
55	Large pelagics (HMS)													0.009	0.009						
56	Pinnipeds													0.015	0.015						
57	Baleen whales													0.012	0.010						
58	Odontocetes													0.012	0.020				0.002		
59	Seabirds													0.017	0.020						
60	Shorebirds - piscivorous													0.001							
61	Detritus														0.050			0.013			
	Import																				0.100

Table 42. Summary of the eight NWACS-FULL models fit. Models differed in the diet matrix used, the vulnerability caps (v.cap) that were employed, and the manual adjustments (Man. Adjust) that were made to improve the Atlantic menhaden stock-recruit relationship and the F_{MSY} dynamics for the ERP focal species. Model fits are represented by sum of squares (SS) and Akaike's Information Criteria (AIC).

Sim	Diet	v.cap	Man. Adjust	Fitting Iter.	SS	AIC
1	Base			9	1399	-778
2	**Base**		**X**	**--**	**1764**	**-281**
3	Base	X		--	2218	210
4	Base	X	X	--	2249	240
5	+Menh			12	1448	-704
6	**+Menh**		**X**	**--**	**2013**	**2**
7	+Menh	X		--	2037	28
8	+Menh	X	X	--	2271	261

Table 43. Estimates of Atlantic menhaden F_{MSY} for their three age stanzas based on projections using the base (1982) fishing mortality rates from the NWACS-FULL model. Estimates were made using Sim2 and Sim6 of the NWACS-FULL model by finding an effort multiplier (E_{MULT}) that generates the maximum Atlantic menhaden catch. Atlantic menhaden *F* rates for 2017 are included for comparison.

		Sim 2		Sim 6		
Stanza	F_{1982}	Emult	Fmsy	Emult	Fmsy	F_{2017}
age-0	0.013	2.818	0.038	1.606	0.022	0.000
age-1-2	0.215	3.424	0.735	1.909	0.410	0.038
age-3+	0.368	2.515	0.926	1.303	0.480	0.112

Table 44. Effect of fishing Atlantic menhaden at F_{TARGET} on other species from the NWACS-FULL model. Numerical values (as percentages) are the biomass differences (B_{DIFF}) and catch differences (C_{DIFF}) for species when Atlantic menhaden are fished at their target F levels ("TARG Menh – SQ Others" scenario) relative to the status quo scenario ("SQ Menh – SQ Others"). Calculations were made based on two different model formulations (Sim 2 and Sim 6); see text for calculation of B_{DIFF} and C_{DIFF}. Dashed line separates the ERP focal species from the other groups that were most sensitive (with at least one number greater than 3%).

	Sim 2				Sim 6			
Group	B_{diff} 4 yr	B_{diff} 40 yr	C_{diff} 4 yr	C_{diff} 40 yr	B_{diff} 4 yr	B_{diff} 40 yr	C_{diff} 4 yr	C_{diff} 40 yr
Menhaden	-5	-5	82	82	-8	-7	77	79
Bluefish	0	1	0	1	-2	-11	-3	-11
Striped Bass	-2	-7	-1	-7	-4	-10	-3	-10
Weakfish	0	-2	0	-2	-6	-5	-6	-6
Spiny Dogfish	0	0	0	0	-4	-4	-4	-4
Atlantic Herring	0	2	0	2	0	-2	0	-2
Alosines	0	0	0	0	-5	14	-5	14
Atlantic Cod	0	5	0	5	-1	8	-1	7
Large pelagics (HMS)	-2	-1	-2	-1	-4	-4	-4	-4
Pinnipeds	0	1			0	-4		
Seabirds	-2	-1			-3	-4		
Sharks-coastal	-1	0	-1	0	-1	-4	-1	-4
Demersal Piscivores	-2	-2	-2	-2	-3	-6	-3	-6
Nearshore Pisc. Birds	-5	-9			-9	-14		

Table 45. Effects of different Atlantic menhaden fishing mortality reference points on the equilibrium biomass and catch of different trophic groups from the NWACS-FULL model. Biomass is expressed relative to the equilibrium biomass under the status quo Atlantic menhaden fishing scenario (B/B_{2017}= B/B_{SQ}) while catch is relative to the maximum equilibrium catch across all Atlantic menhaden fishing scenarios (C/C_{MAX}). Non-menhaden species were kept at their target *F* for these projections. Fishing reference points were: no Atlantic menhaden fishing (F=0), status quo fishing (F_{2017}=F_{SQ}), single-species F_{TARGET}, single-species $F_{THRESHOLD}$, EwE F_{MSY} based on Figure 165, and *F* for Atlantic menhaden extinction ($F_{EXTINCTION}$) is included for comparison. The dashed line separates the ERP focal species from other groups experiencing at least a 15% change in B/B_{2017} or C/C_{MAX}. Values differing from 1 by more than 10% are in bold, and groups with biomasses increase at higher Atlantic menhaden *F* indicated with (+).

	F=0		F_{SQ}		F_{Target}		$F_{threshold}$		F_{MSY}		$F_{Extinction}$	
Group	B/B_{SQ}	C/C_{max}	B/B_{SQ}	C/C_{max}	B/B_{SQ}	C/C_{max}	B/B_{SQ}	C/C_{max}	B/B_{SQ}	C/C_{max}	B/B_{SQ}	C/C_{max}
Menhaden	1.06	**0.00**	1.00	**0.17**	0.95	**0.31**	**0.78**	**0.64**	**0.47**	1.00	**0.00**	**0.00**
Striped Bass	1.09	1.00	1.00	0.91	0.92	**0.84**	**0.72**	**0.64**	**0.46**	**0.40**	**0.31**	**0.27**
Bluefish	1.01	1.00	1.00	0.99	0.99	0.98	0.96	0.95	**0.89**	**0.89**	**0.85**	**0.85**
Weakfish	1.01	1.00	1.00	0.99	0.99	0.98	0.98	0.96	0.95	0.93	0.92	0.90
Dogfish	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.99	0.98	1.00	0.99
Herring	1.00	0.96	1.00	0.96	1.00	0.96	0.98	0.96	0.97	0.93	1.04	1.00
Nearshore Birds	1.10		1.00		0.91		**0.68**		**0.39**		**0.23**	
Dem. Pisc.	1.03	1.00	1.00	0.97	0.98	0.95	0.94	0.90	**0.87**	**0.85**	**0.83**	**0.81**
Seabirds	1.03		1.00		0.98		0.92		**0.85**		**0.84**	
Haddock	1.02	1.00	1.00	0.98	0.98	0.96	0.93	0.91	**0.85**	**0.83**	**0.85**	**0.83**
Large Pelagics (HMS)	1.02	1.00	1.00	0.98	0.98	0.96	0.93	0.91	**0.86**	**0.84**	**0.85**	**0.83**
Shark-coastal	1.02	1.00	1.00	0.98	0.98	0.96	0.94	0.92	**0.89**	**0.87**	**0.87**	**0.85**
Med. Pelagics (+)	0.99	**0.84**	1.00	**0.85**	1.01	**0.86**	1.04	**0.88**	1.10	0.93	**1.18**	1.00
Atlantic Cod (+)	0.94	**0.63**	1.00	**0.67**	1.05	**0.71**	**1.19**	**0.80**	**1.39**	0.92	**1.51**	1.00

Table 46. ERP model strengths and weaknesses comparison

	Simulation Tested	Age Structure	Species Complexity	Top-down Predators	Bottom-up Feedback	Fits to Observed Data	Sensitivity	Ability to Incorporate Error	Projections	# of EMOs Addressed	Other Assessment Inputs Needed	Other Assessment Outputs Needed	Type of ERPs	Ability to Assess Stock Status	Other
SPMTVr	Yes	None	Single spp.	No	No	Fits trend, not finer scale variability	Sensitive to start year, mildly sensitive to Binit	CVs on input data; error propagated to output parameters	No	Low	1	0	Umsy (time varying)	Yes	Minimal assumptions /mechanisms
SH	Yes	None	Low	Yes	No	Fits trend, not finer scale variability	Sensitive to start year	No CVs on input data; stochastic projections	Yes	Med	1	1	MUP, consumption	Yes	Proprietary software
MSSCAA	Yes	Full	Med	Yes	No*	Fits indices comparably to single spp	Sensitive to M0 assumptions & diet data	CVs on input data; error propagated to output parameters and stochastic projections	Yes	Med High	5	0	Multispp. MSY, SPR, consumption	Yes	Non-age structured species are problematic
NWACS MICE	No	Stanzas	Med	Yes	Yes	Fits trends for most ERP spp well	Sensitive to pred-prey interaction strengths	CVs incorporated through weighting input data; error not propagated to output parameters; stochastic projections	Yes	High		6	Multispp. Fmsy or Bmsy, consumption	No	
Full NWACS	No	Stanzas	High	Yes	Yes	Fits trends for most ERP spp well, not some other spp	Sensitive to pred-prey interaction strengths & diet data		Yes	High		15	Multispp. Fmsy or Bmsy, consumption	No	Complex data streams (for benchmark); uncertainty from data-poor groups

*Possible with further development

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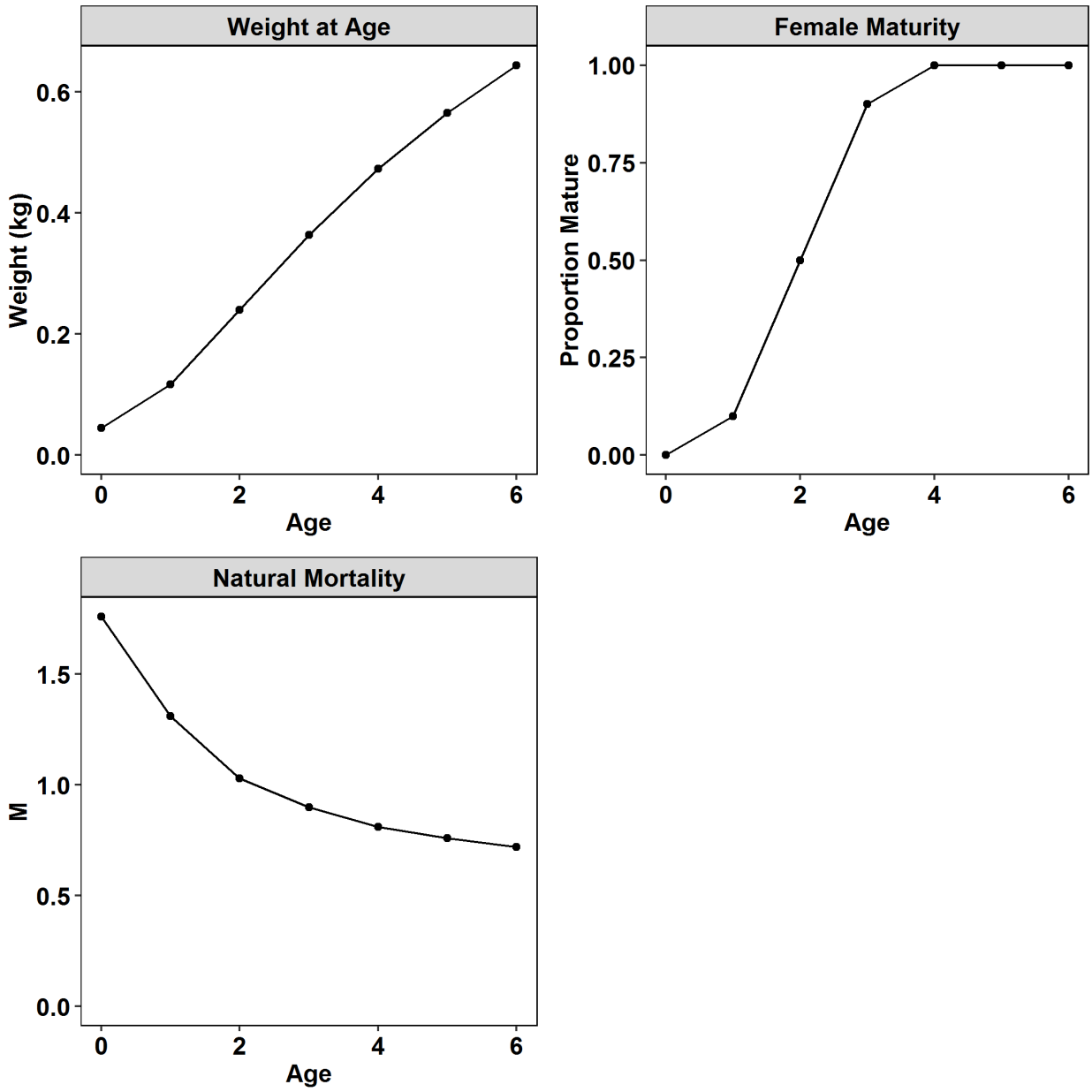


Figure 1. Time-invariant life history parameters for Atlantic menhaden.

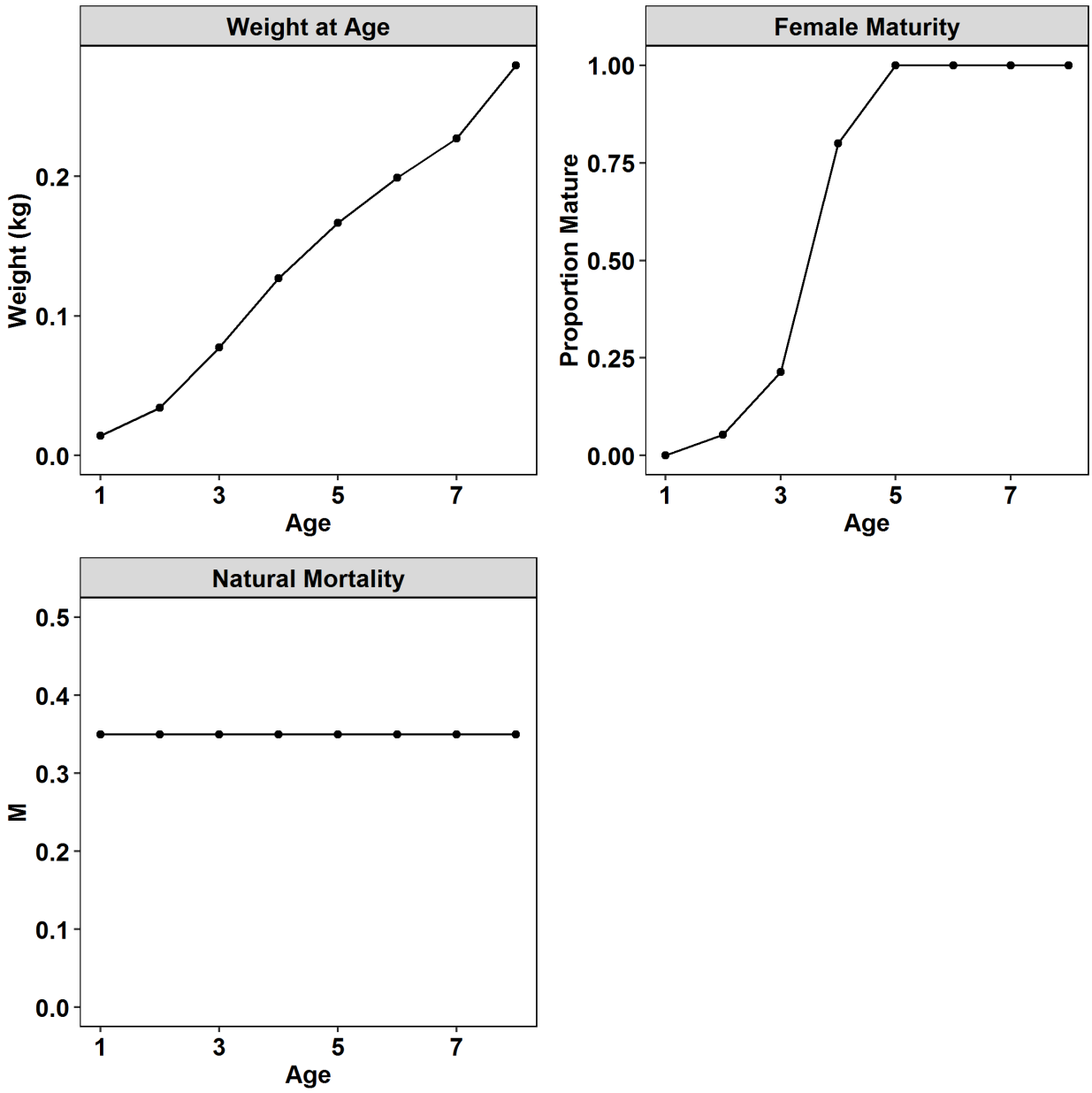


Figure 2. Time-invariant life history parameters for Atlantic herring.

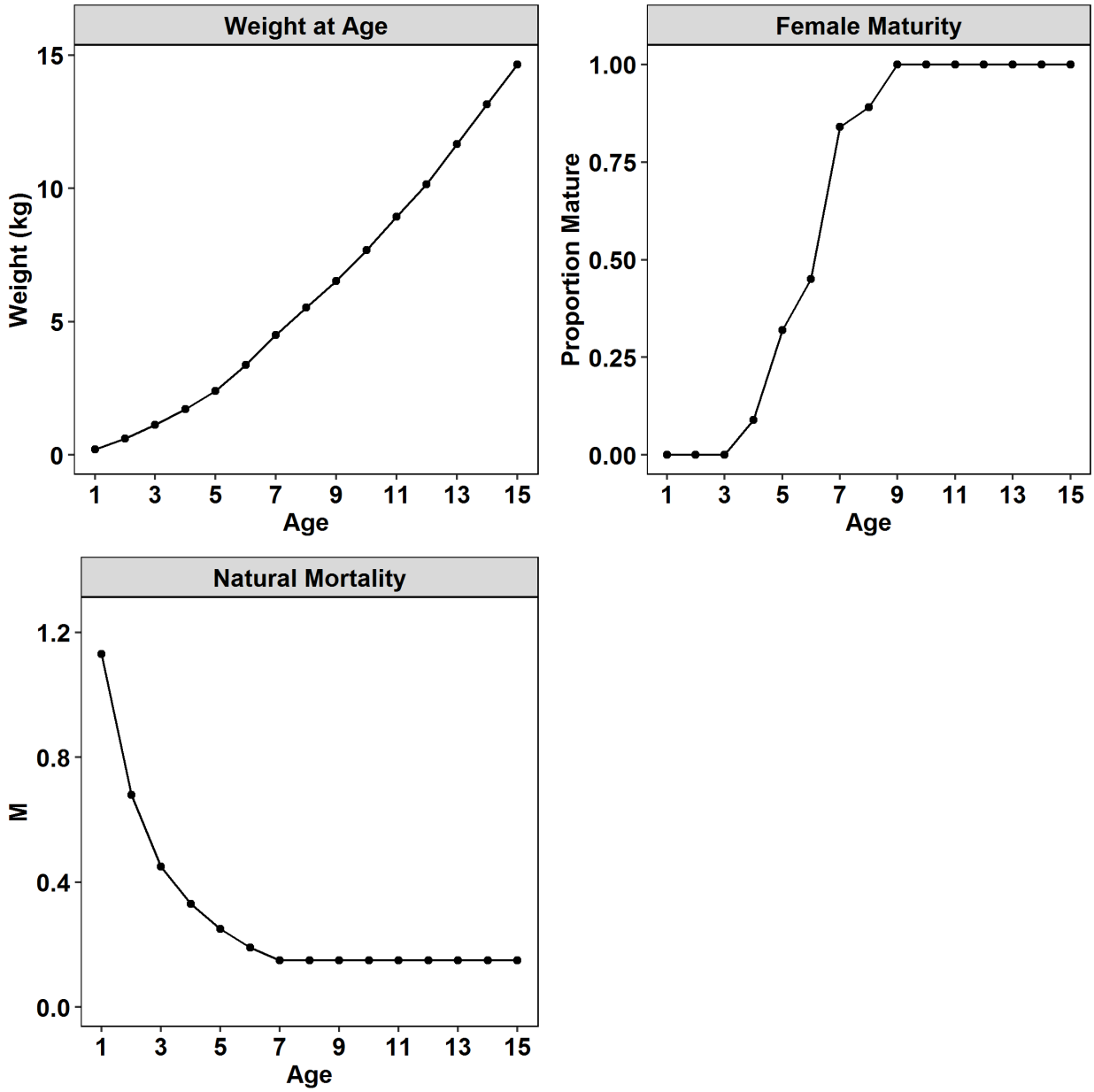


Figure 3. Time-invariant life history parameters for Atlantic striped bass.

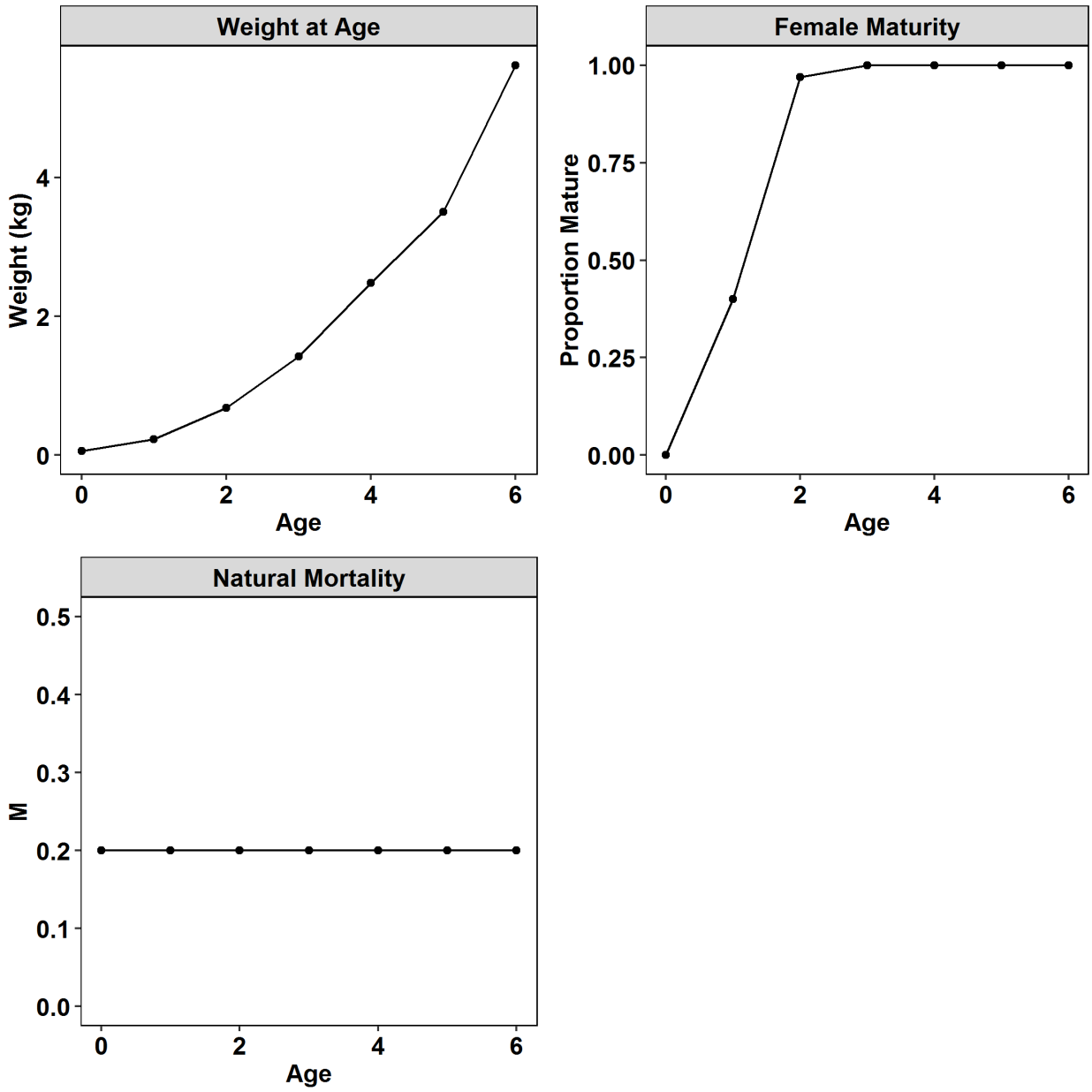


Figure 4. Time-invariant life history parameters for bluefish.

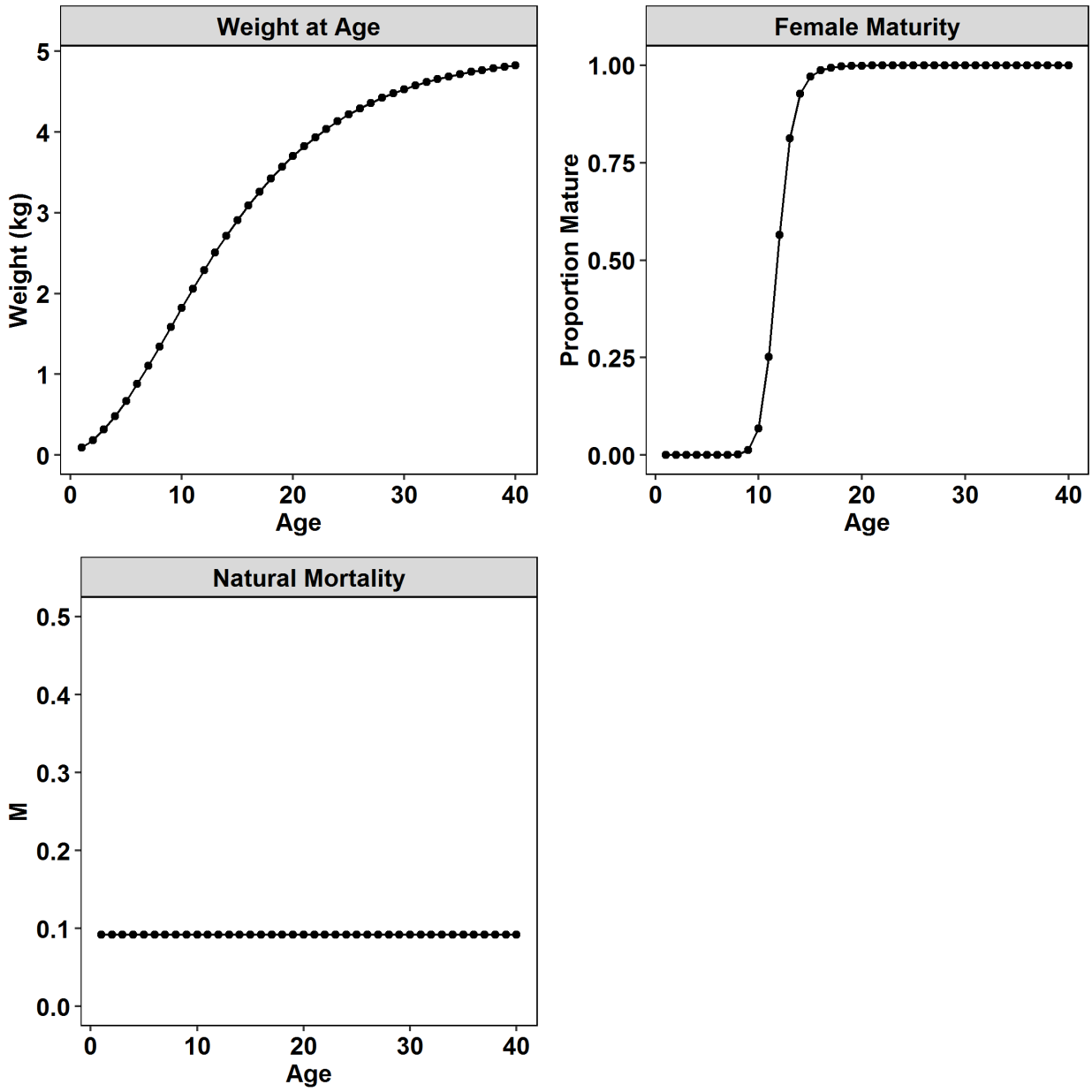


Figure 5. Time-invariant life history parameters for spiny dogfish.

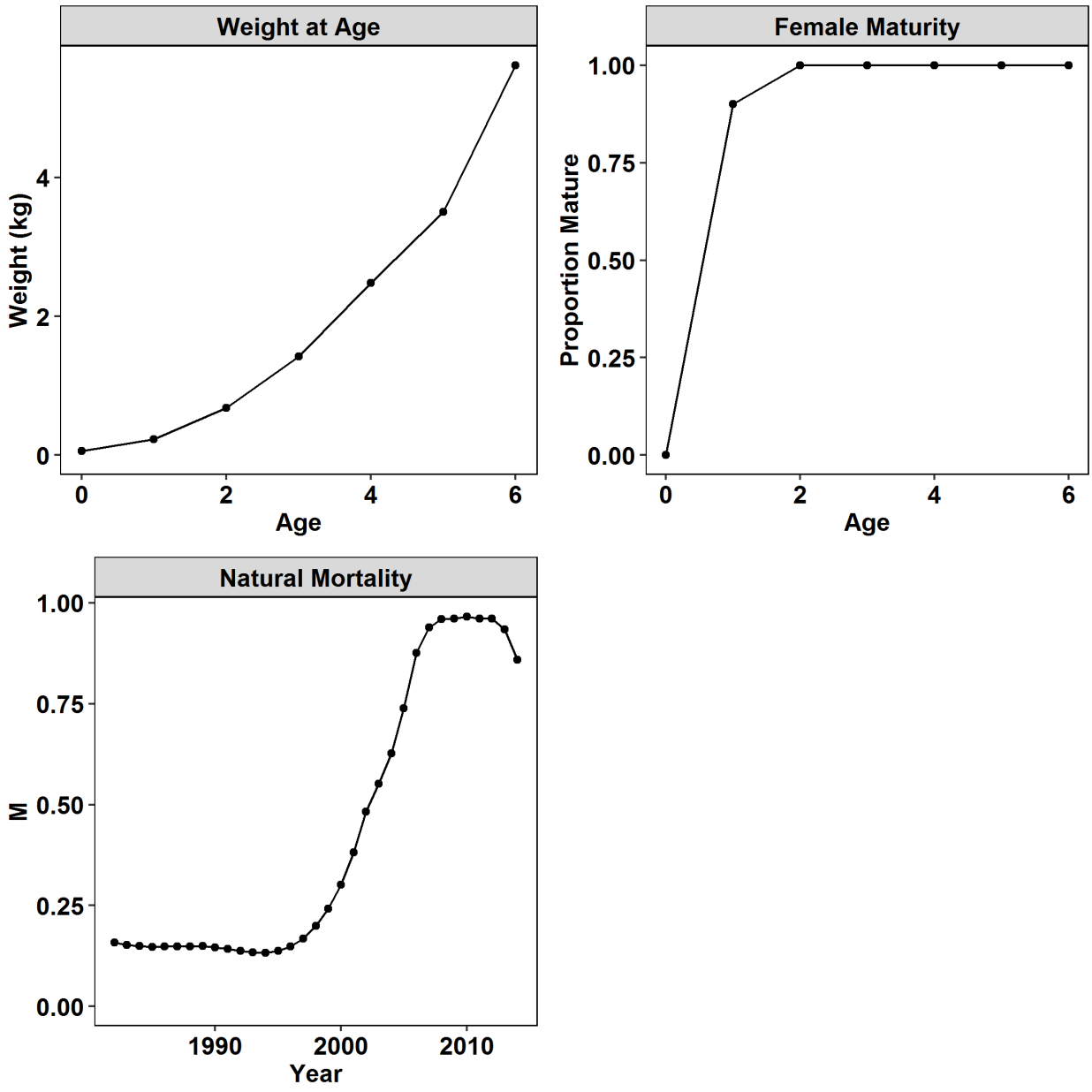


Figure 6. Time-invariant weight at age and maturity at age parameters, and time-varying natural mortality estimates for weakfish.

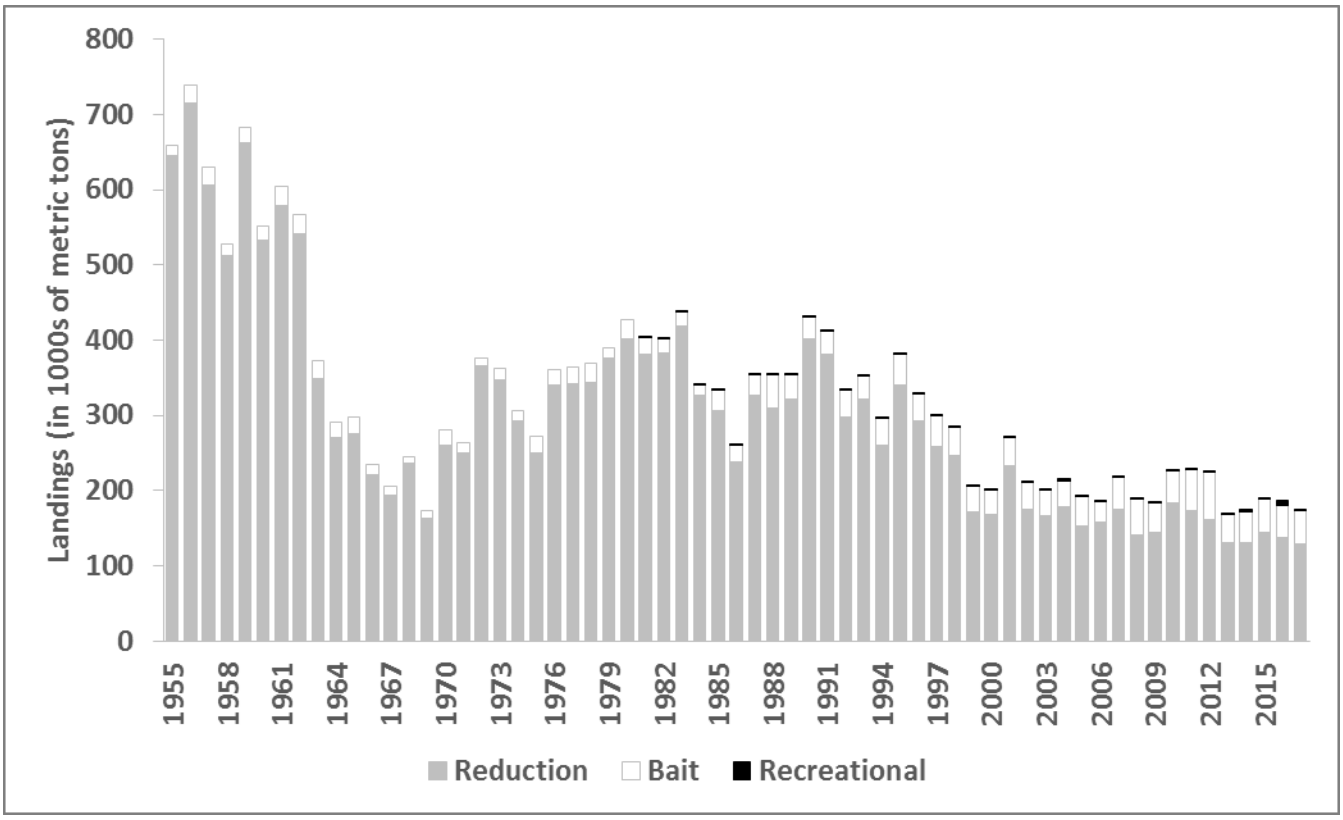


Figure 7. Total removals of Atlantic menhaden by sector.

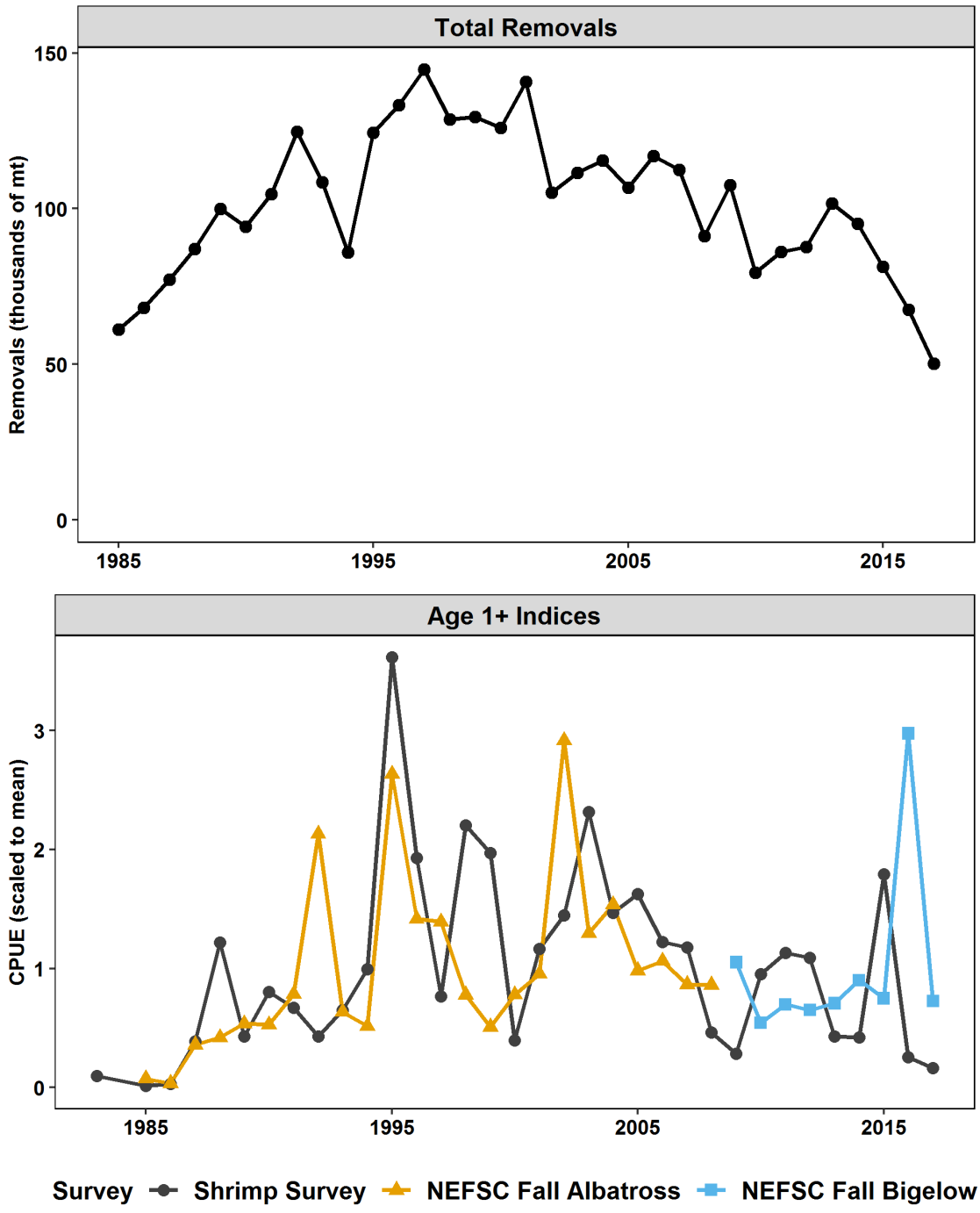


Figure 8. Total removals (top) and indices of abundance (bottom) for Atlantic herring.

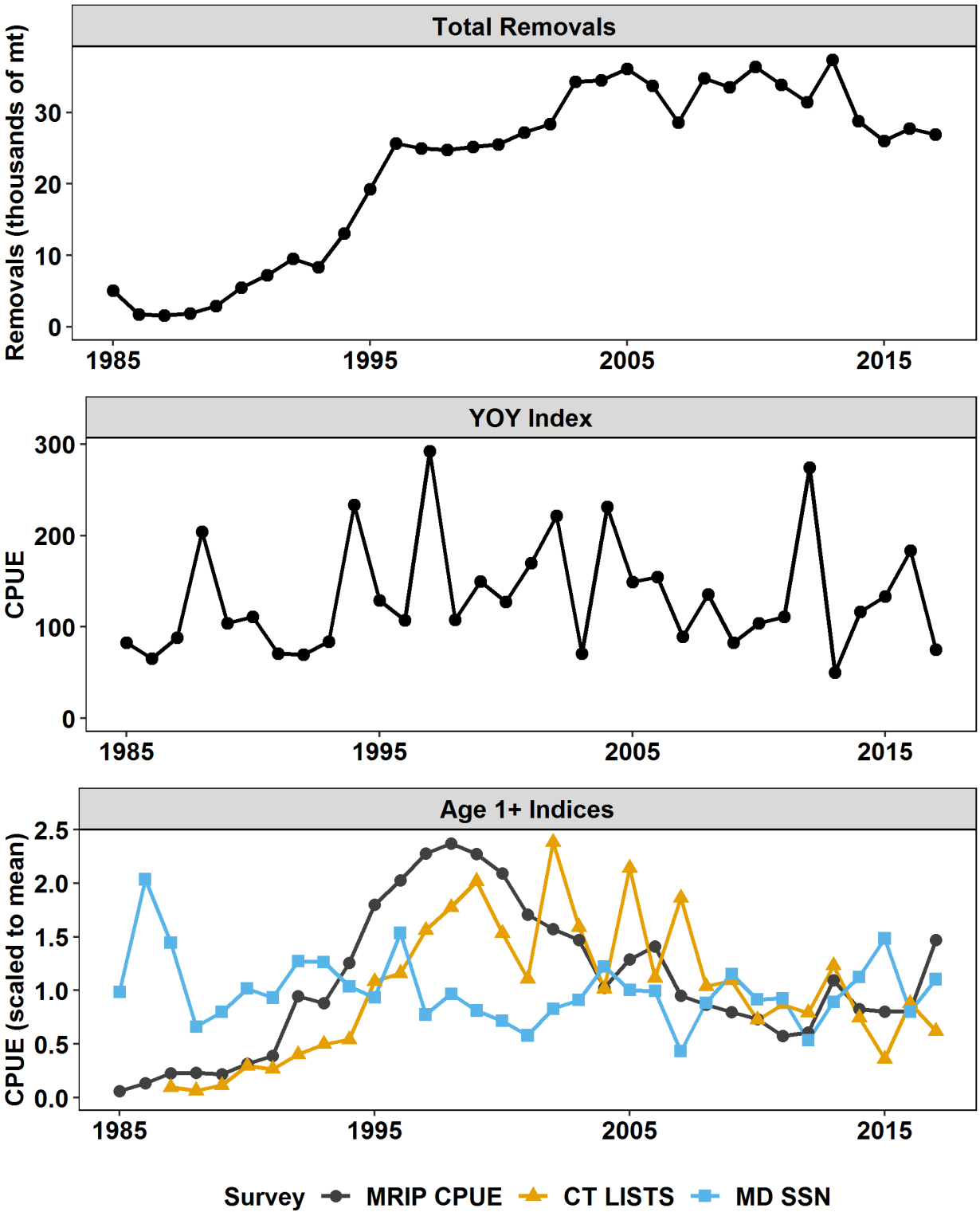


Figure 9. Total removals (top) and indices of recruitment (middle) and age-1+ abundance (bottom) for Atlantic striped bass.

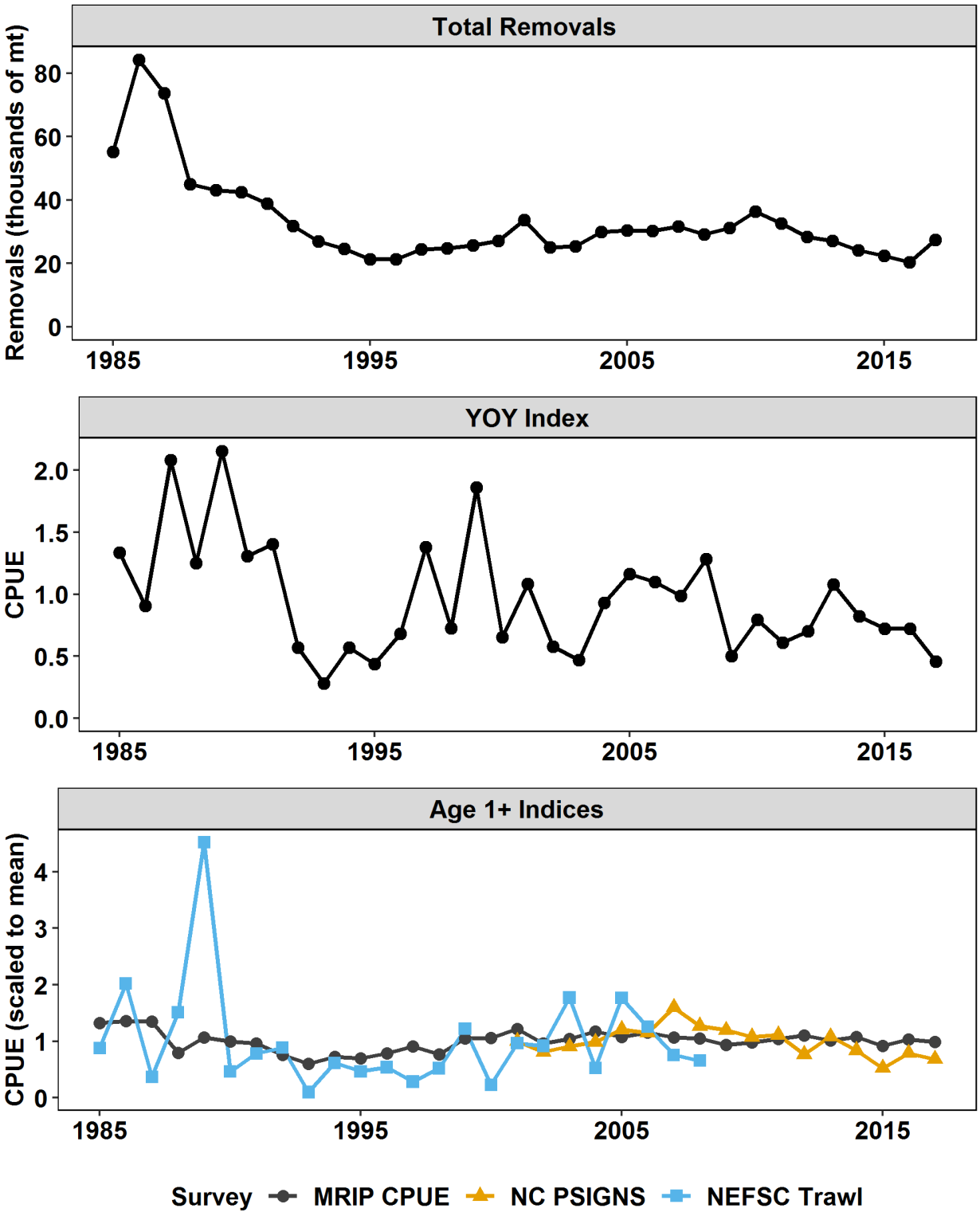


Figure 10. Total removals (top) and indices of recruitment (middle) and age-1+ abundance (bottom) for bluefish.

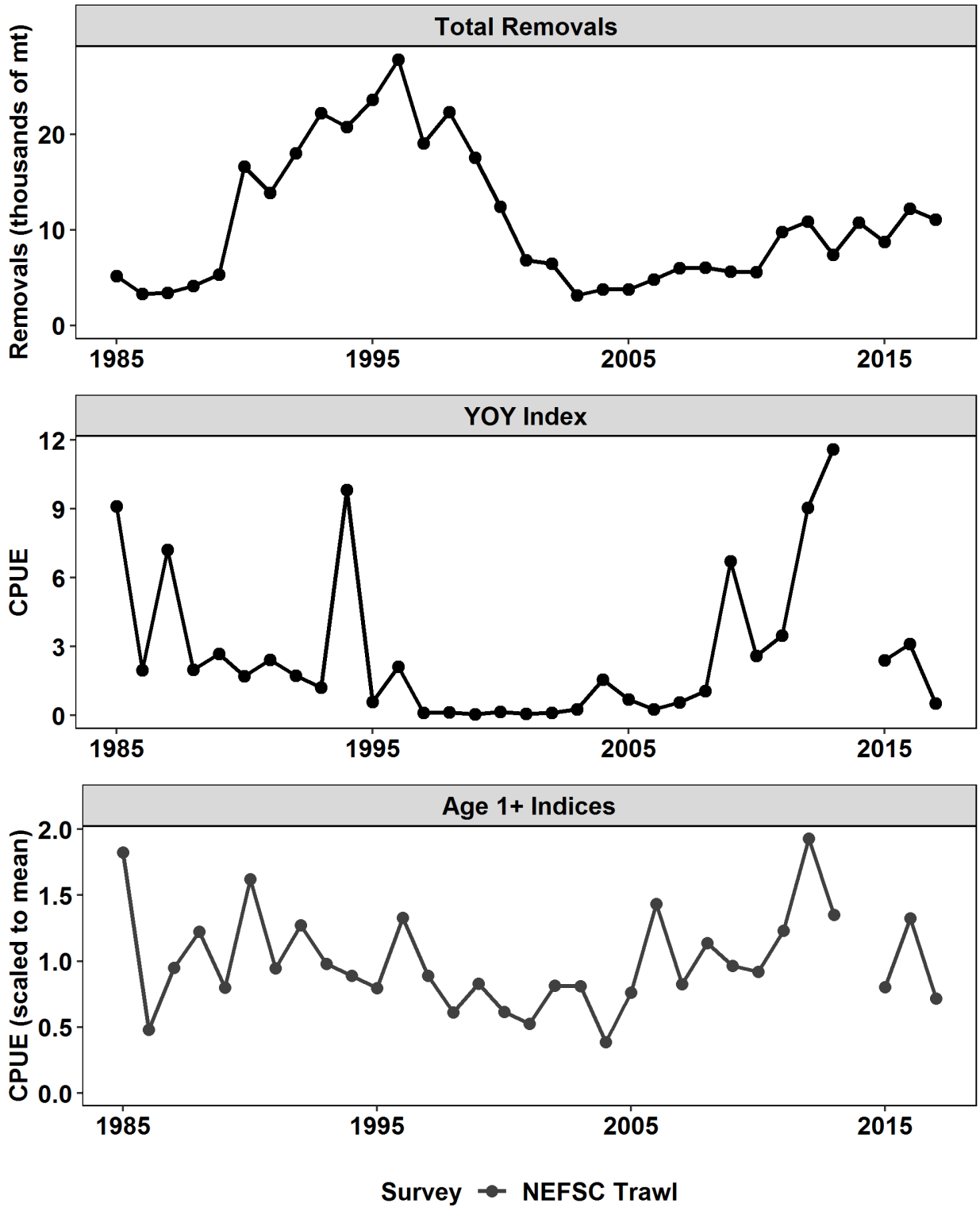


Figure 11. Total removals (top) and indices of recruitment (middle) and age-1+ abundance (bottom) for spiny dogfish.

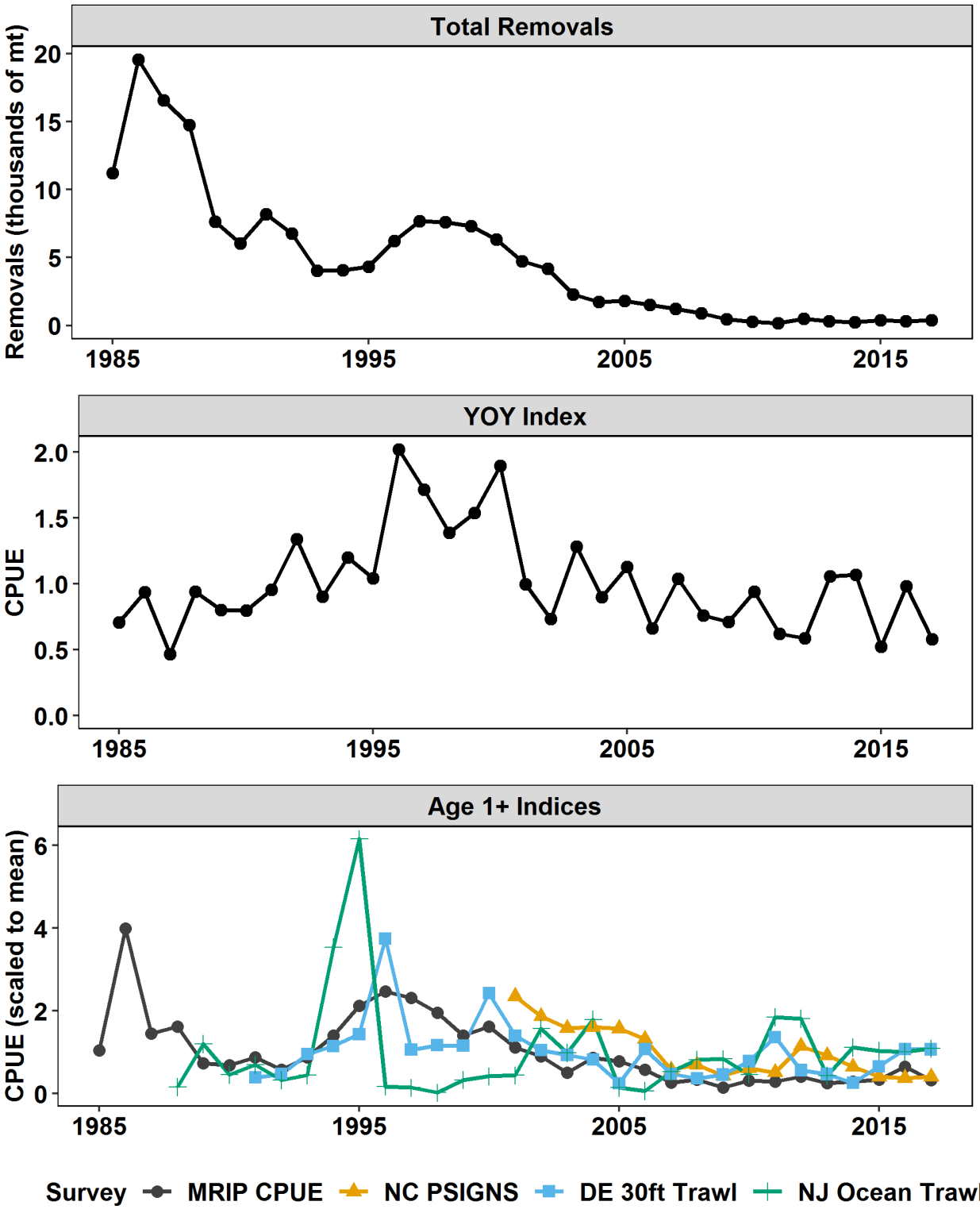


Figure 12. Total removals (top) and indices of recruitment (middle) and age-1+ abundance (bottom) for weakfish.

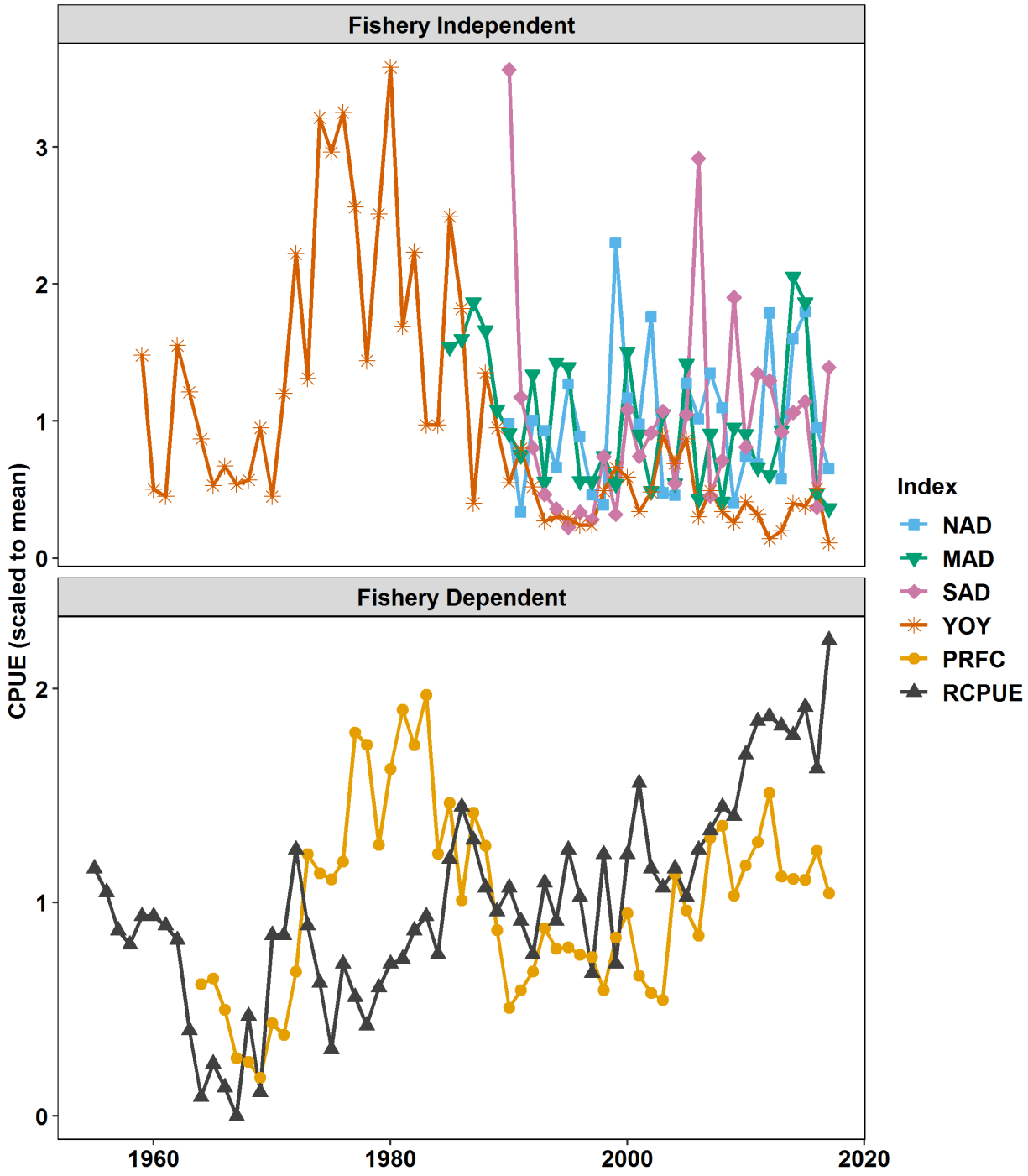


Figure 13. Fishery independent (top) and fishery dependent (bottom) indices of abundance for Atlantic menhaden.

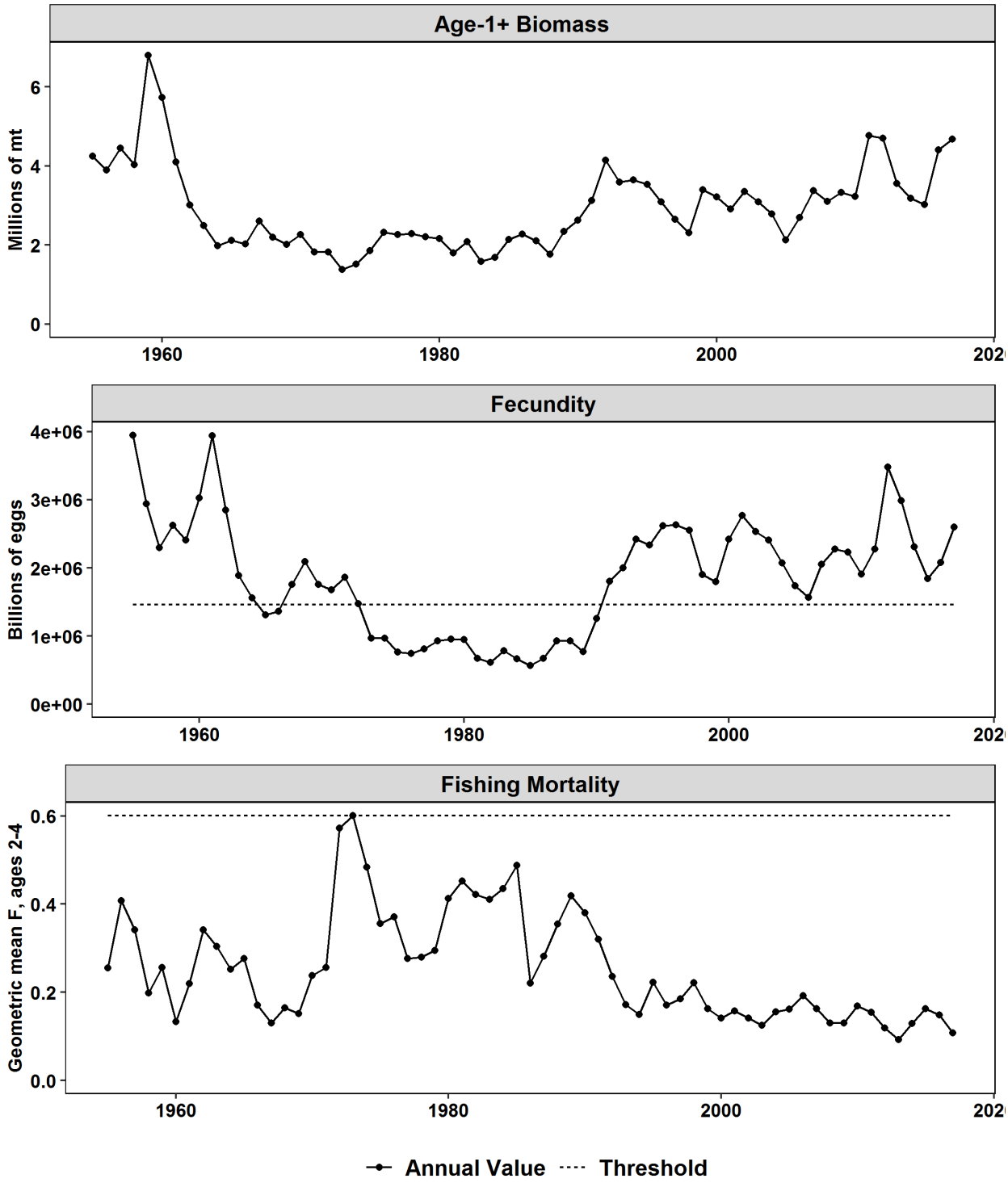


Figure 14. Age-1+ biomass, fecundity, and average *F* for Atlantic menhaden, plotted with their respective thresholds, where defined.

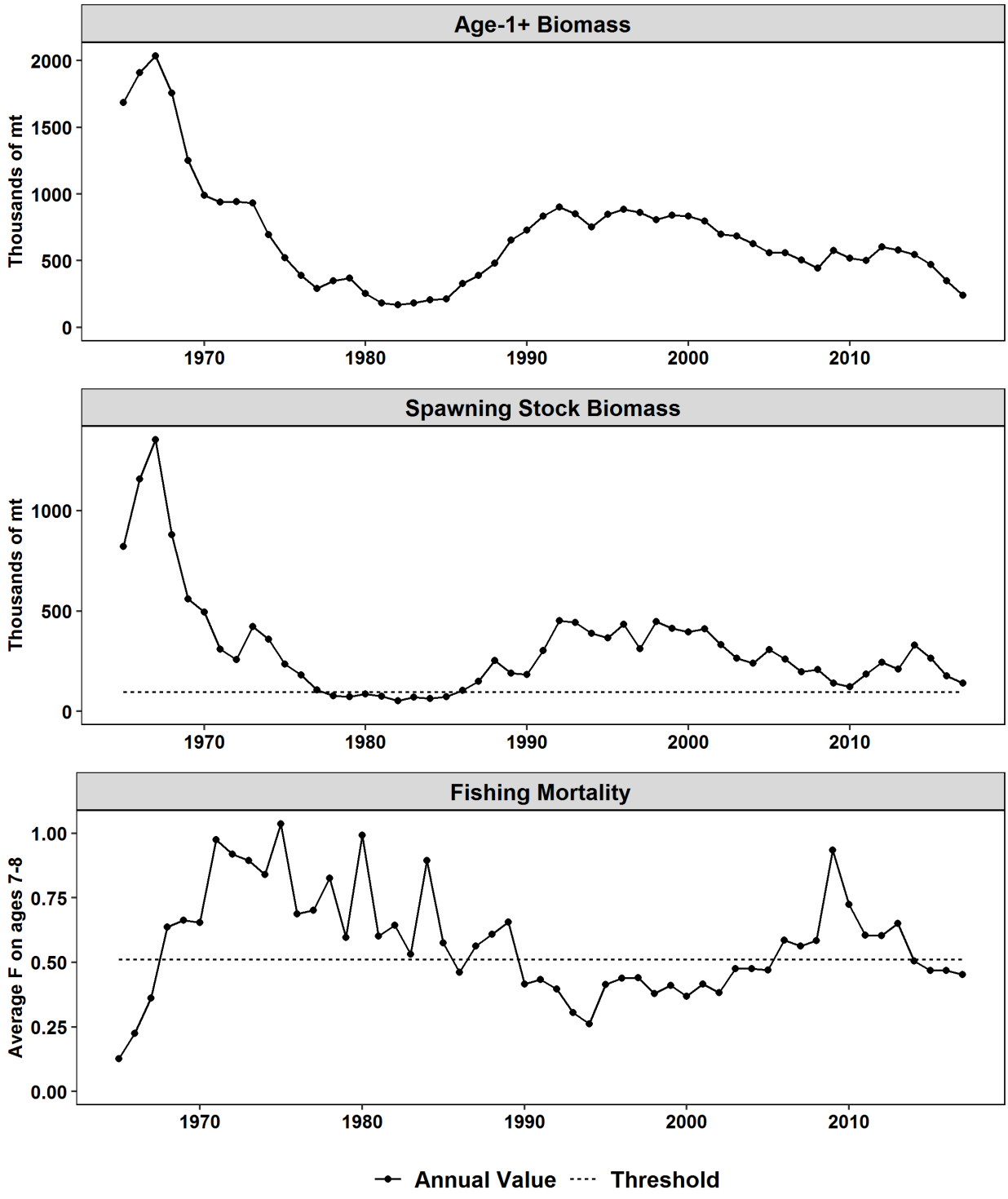


Figure 15. Age-1+ biomass, spawning stock biomass, and average *F* for Atlantic herring, plotted with their respective thresholds, where defined.

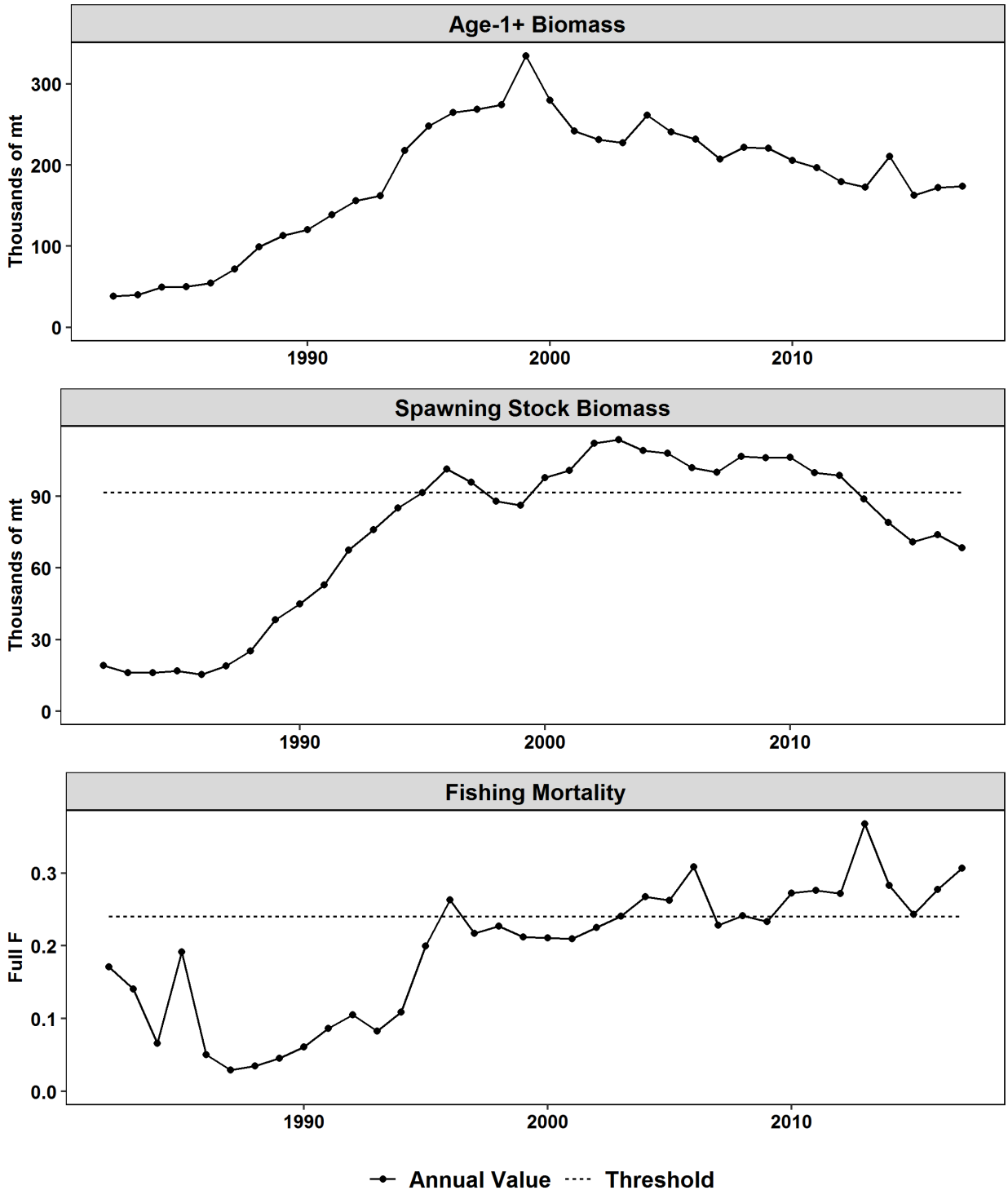


Figure 16. Age-1+ biomass, female spawning stock biomass, and average *F* for Atlantic striped bass, plotted with their respective thresholds, where defined.

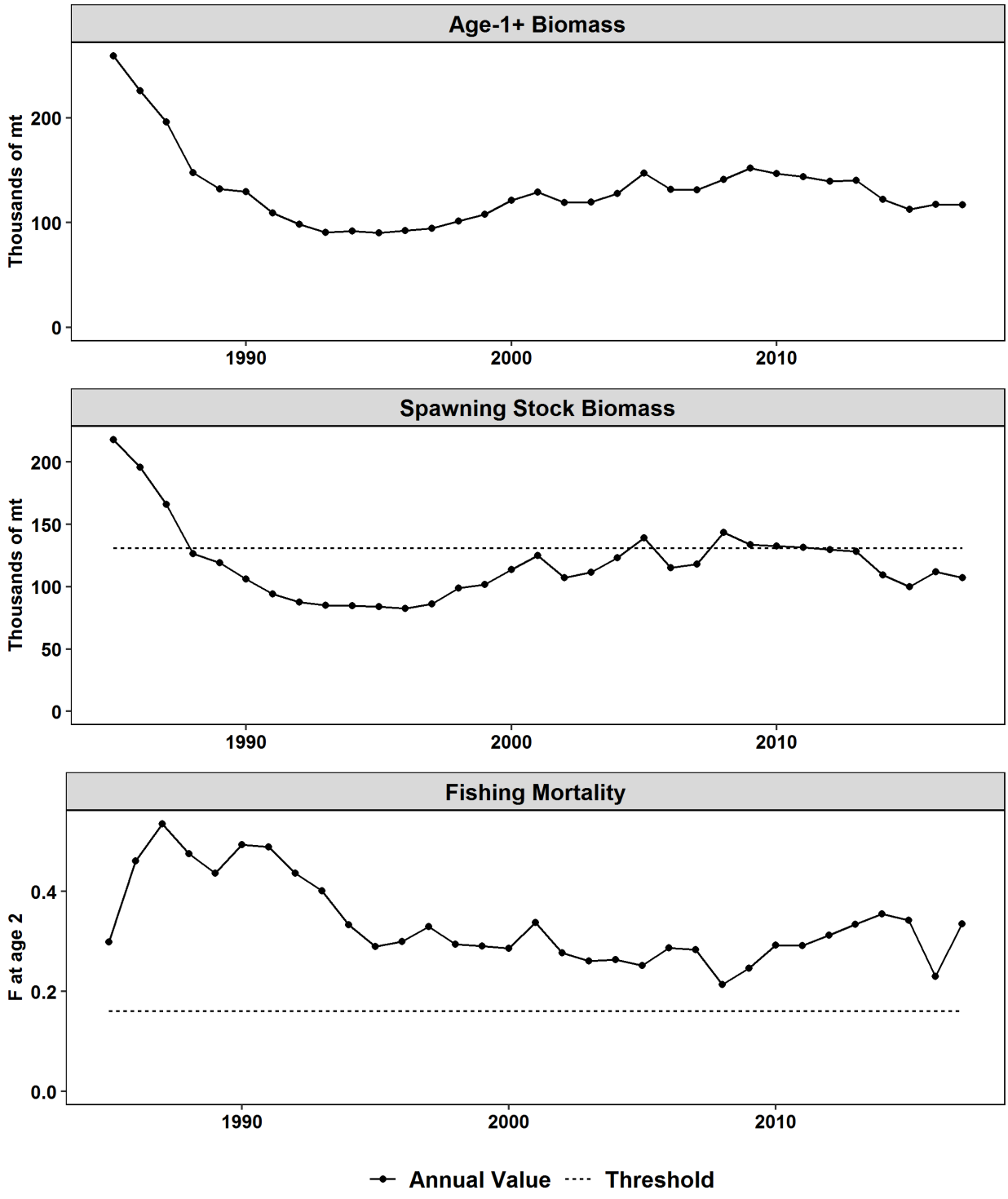


Figure 17. Age-1+ biomass, spawning stock biomass, and full *F* for bluefish, plotted with their respective thresholds, where defined. Estimates are from a preliminary assessment update with data through 2017 and may not match values used for management.

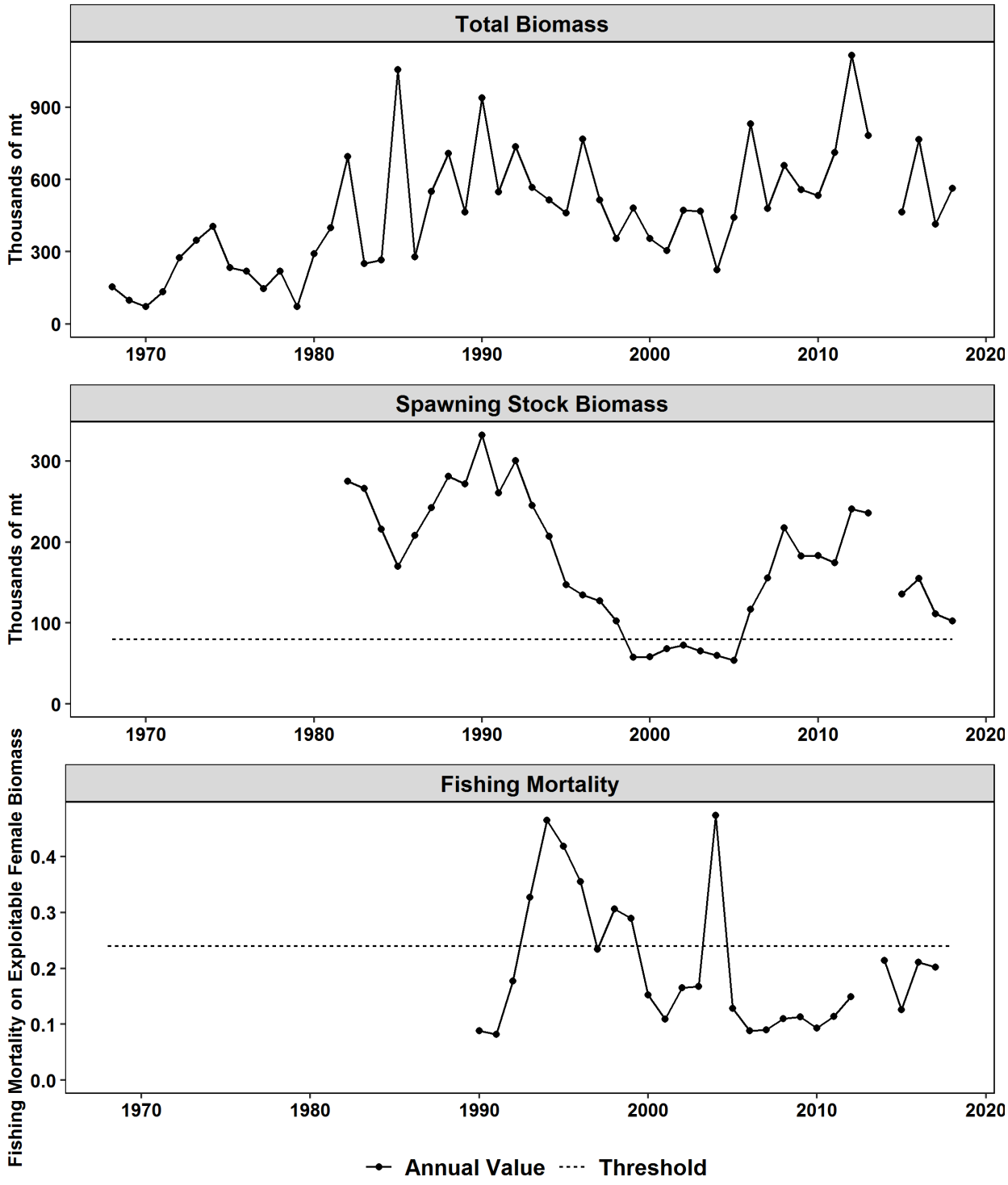


Figure 18. Total biomass, female spawning stock biomass, and *F* for spiny dogfish, plotted with their respective thresholds, where defined.

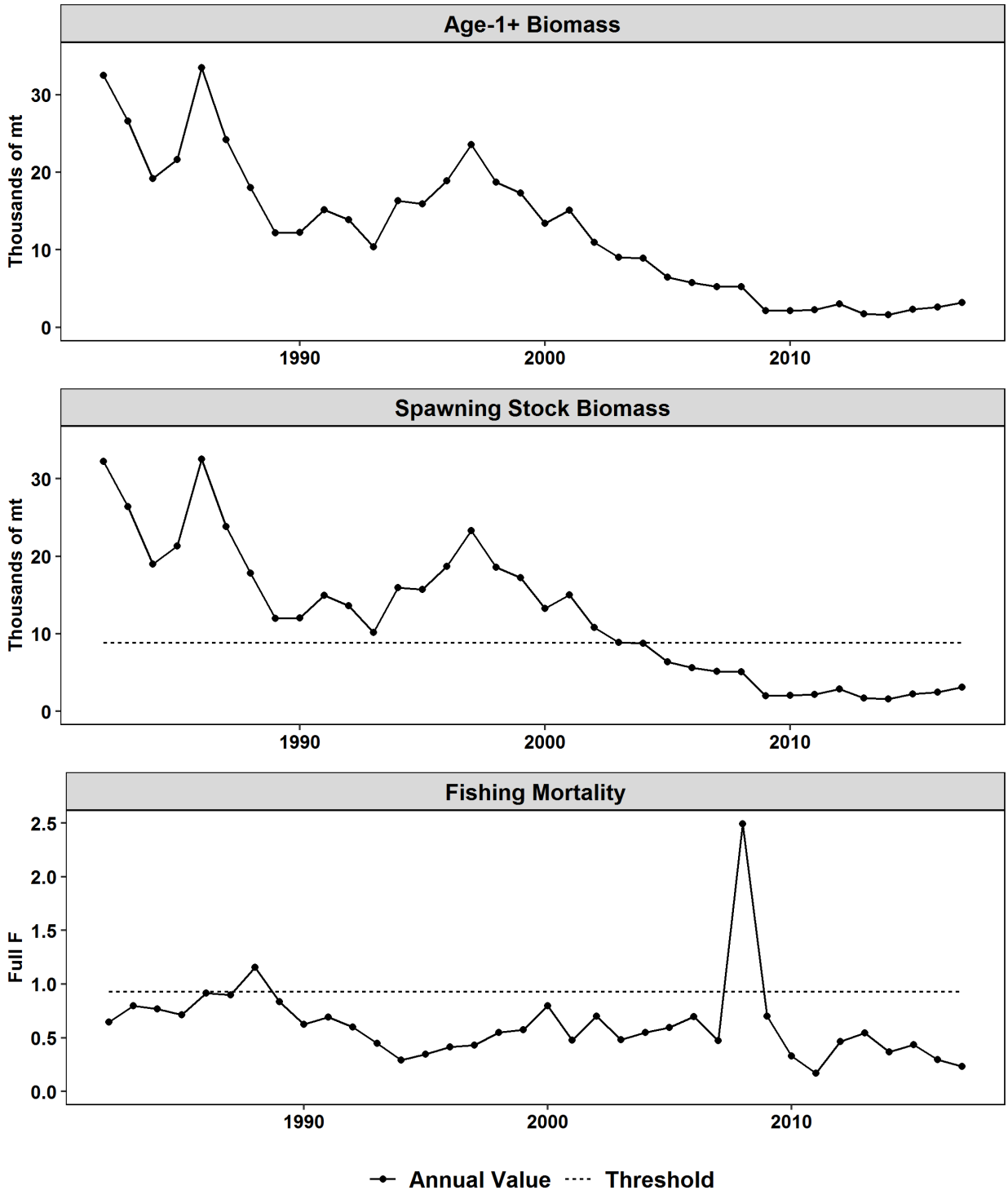


Figure 19. Age-1+ biomass, spawning stock biomass, and full *F* for weakfish, plotted with their respective thresholds, where defined. Estimates are from a preliminary assessment update with data through 2017 and may not match values used for management.

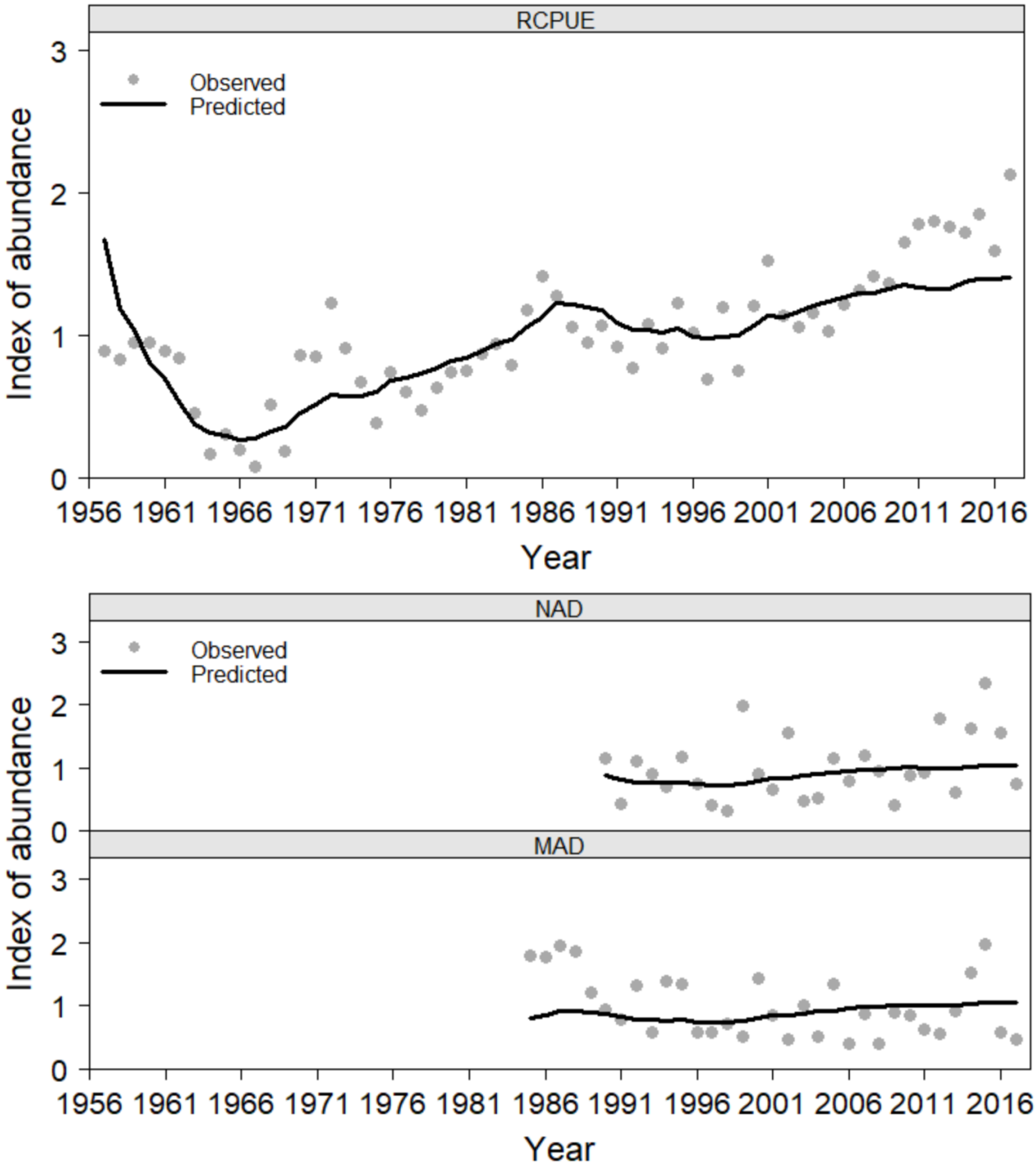


Figure 20. Observed indices of Atlantic menhaden abundance and estimated values predicted by the SPMTVr.

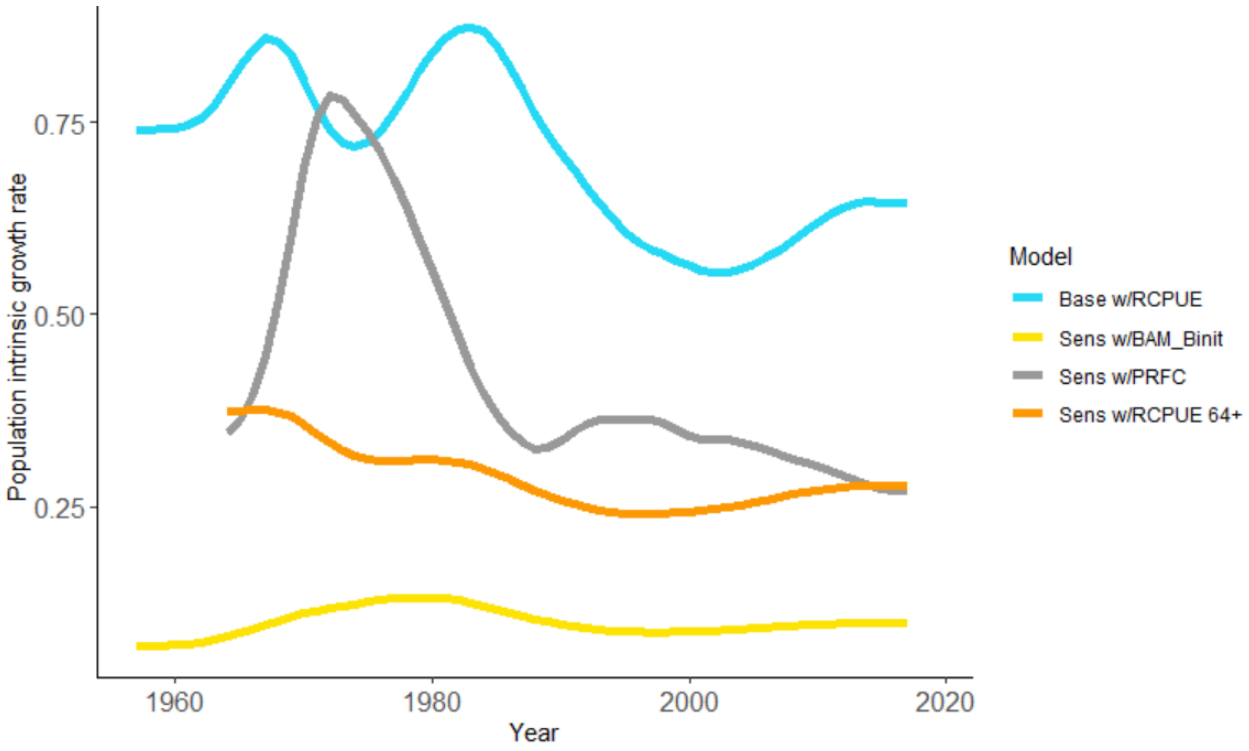


Figure 21. Comparison of estimated trend in population intrinsic growth rate (*r*) for Atlantic menhaden generated by the SPMTVr base model ("Base with RCPUE") with that of sensitivity runs examining alternate model starting year ("Sens w/RCPUE 1964+"), an alternate fishery-dependent abundance index ("Sens w/PRFC"), and an alternate starting value for initial biomass ("Sens w/BAM Binit").

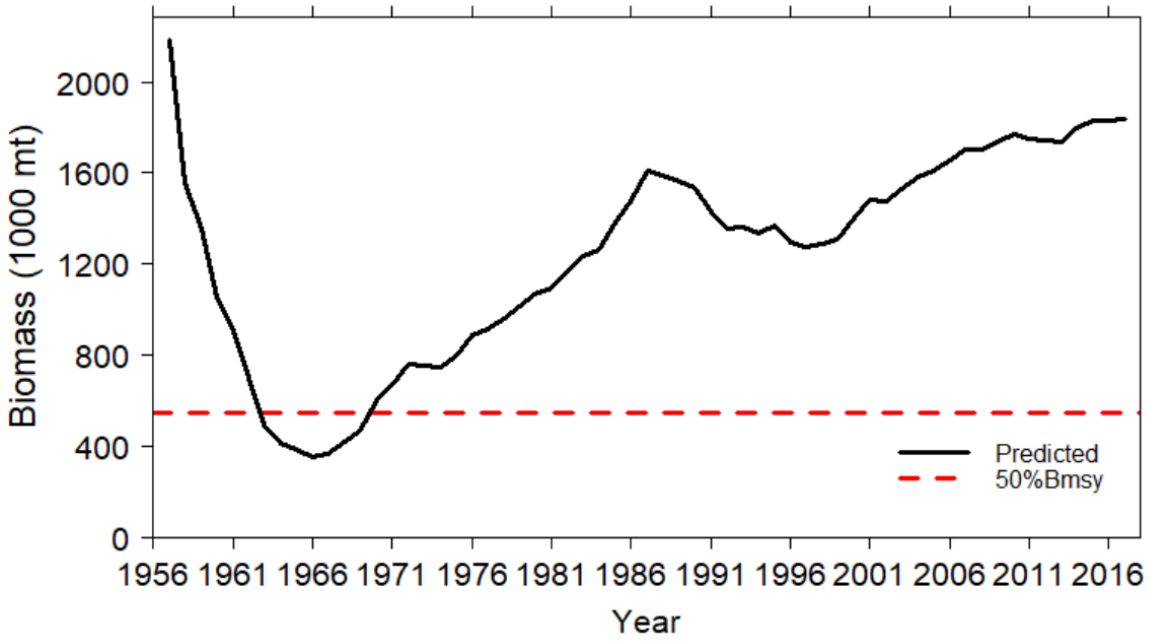


Figure 22. Trend in total biomass estimated by the SPMTVr relative to an overfished threshold of 50% B_{MSY}.

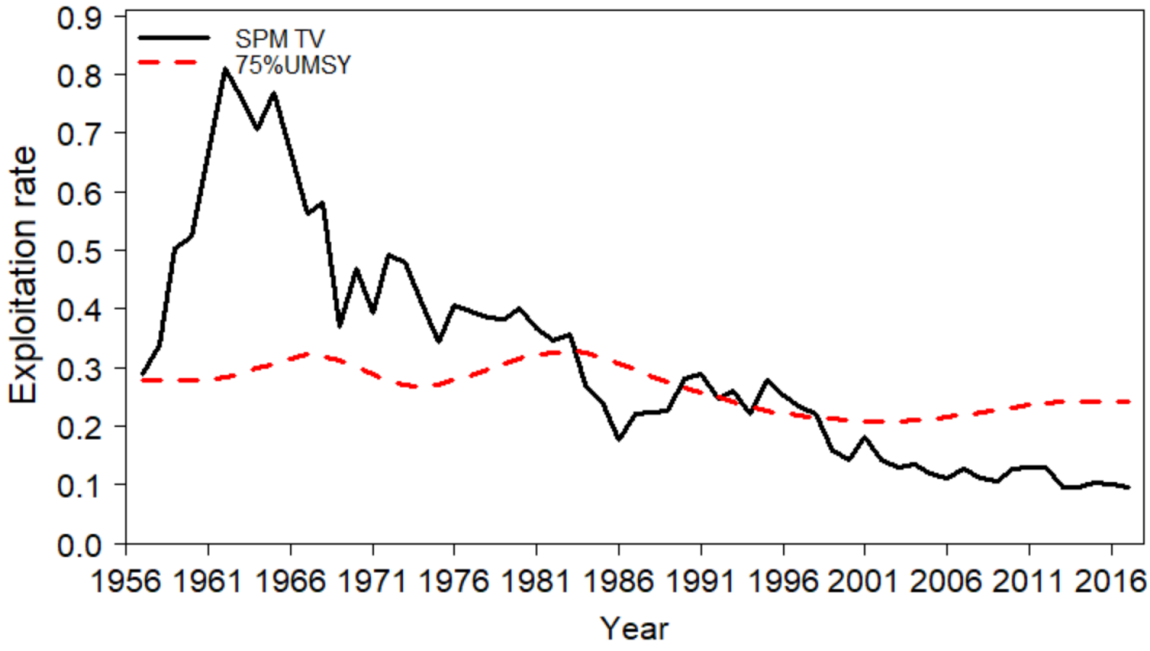


Figure 23. Exploitation rate estimated by the SPMTVr plotted with an overfishing threshold of 75% of the exploitation rate for maximum sustainable yield (U_{MSY}) which varies annually with trends in *r*.

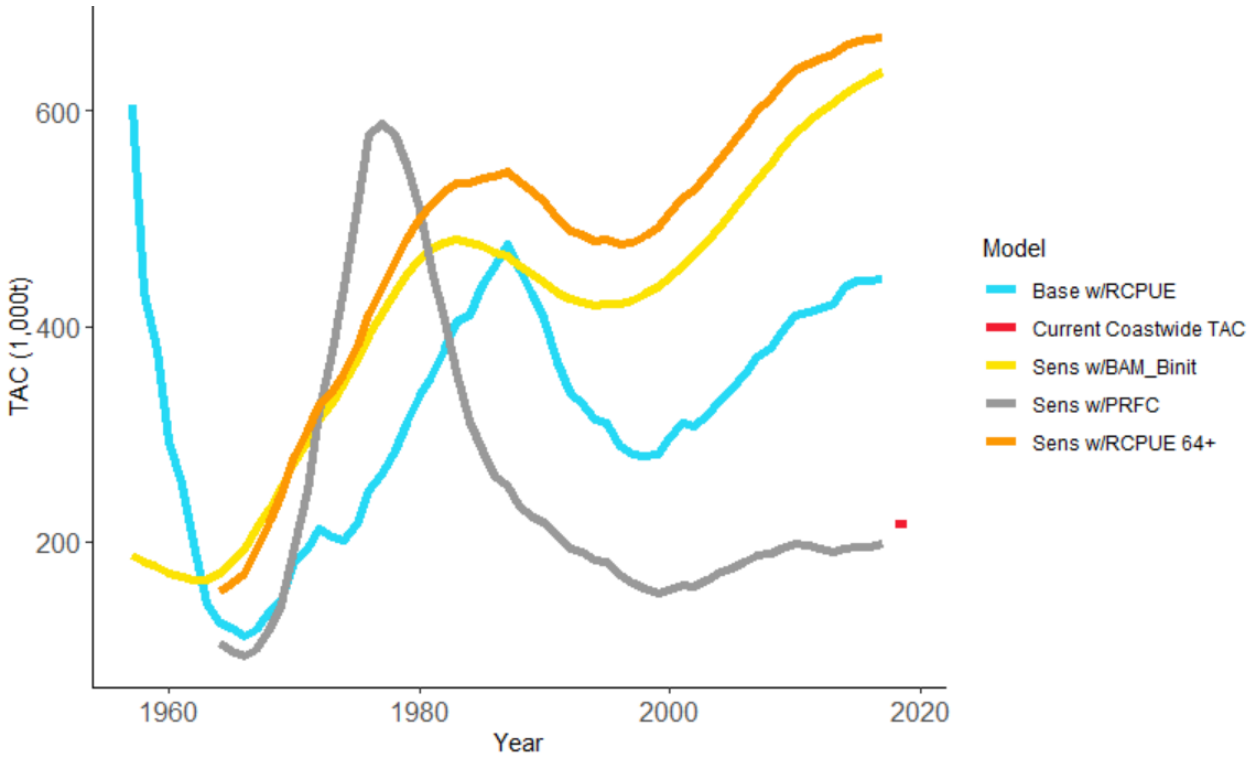


Figure 24. **A comparison of annual TAC estimates produced by the SPMTVr model's base run ("Base with RCPUE") with that of sensitivity runs examining alternate model starting year ("Sens w/RCPUE 1964+"), an alternate fishery-dependent abundance index ("Sens w/PRFC"), and an alternate starting value for initial biomass ("Sens w/BAM Binit").**

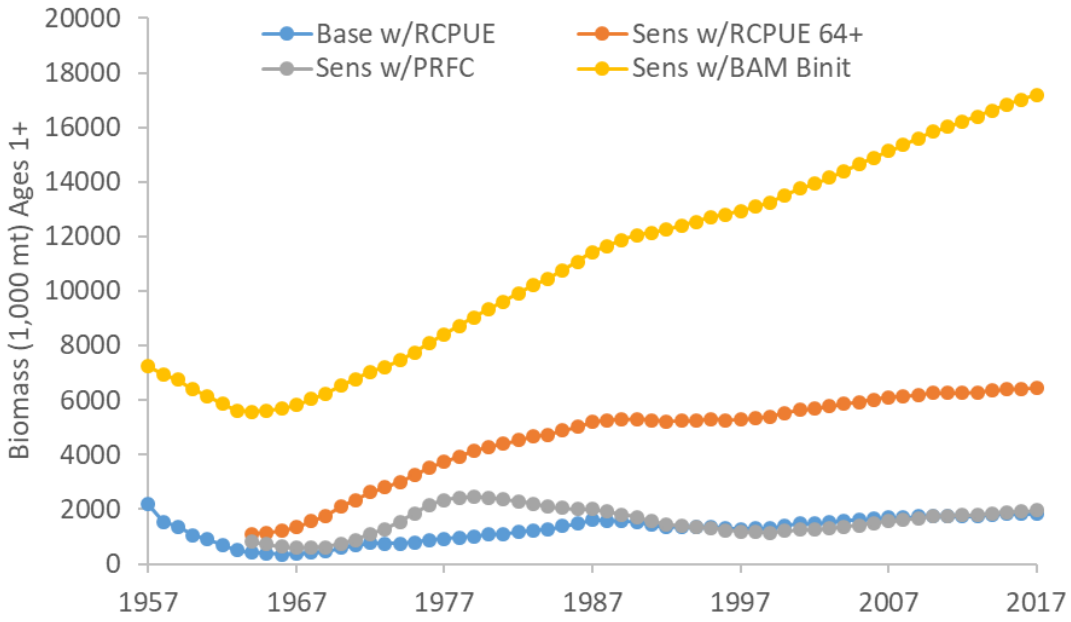


Figure 25. Comparison of base model ("Base with RCPUE") biomass estimates from the SPMTVr model for ages 1+ with that of sensitivity runs examining alternate model starting year ("Sens w/RCPUE 1964+"), an alternate fishery-dependent abundance index ("Sens w/PRFC"), and an alternate starting value for initial biomass ("Sens w/BAM Binit").

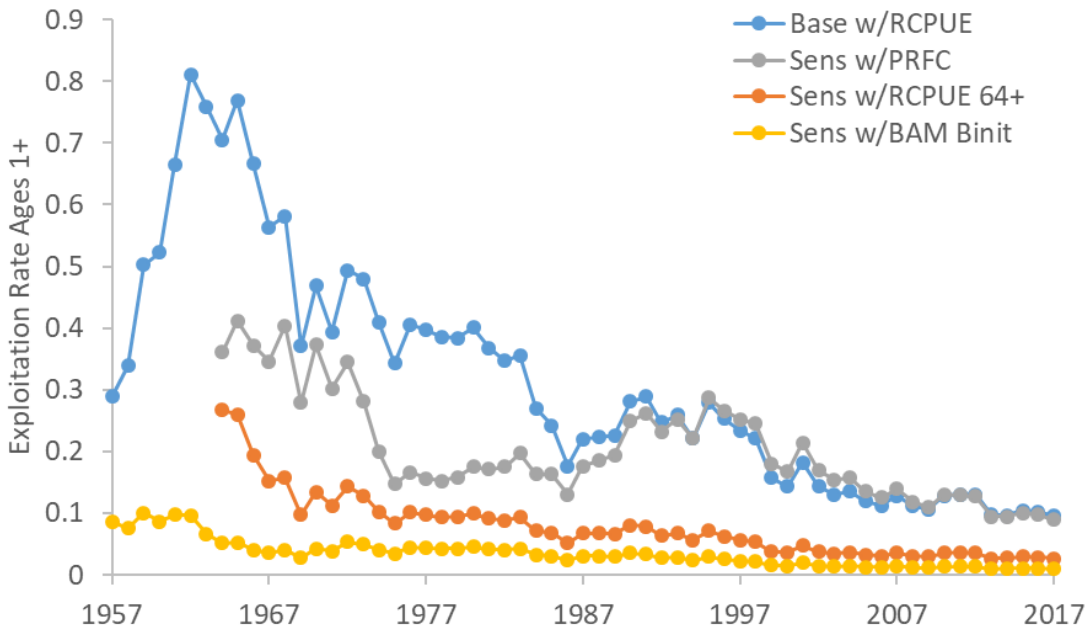


Figure 26. Comparison of base model ("Base with RCPUE") exploitation rate estimates from the SPMTVr model for ages 1+ with that of sensitivity runs examining alternate model starting year ("Sens w/RCPUE 1964+"), an alternate fishery-dependent abundance index ("Sens w/PRFC"), and an alternate starting value for initial biomass ("Sens w/BAM Binit").

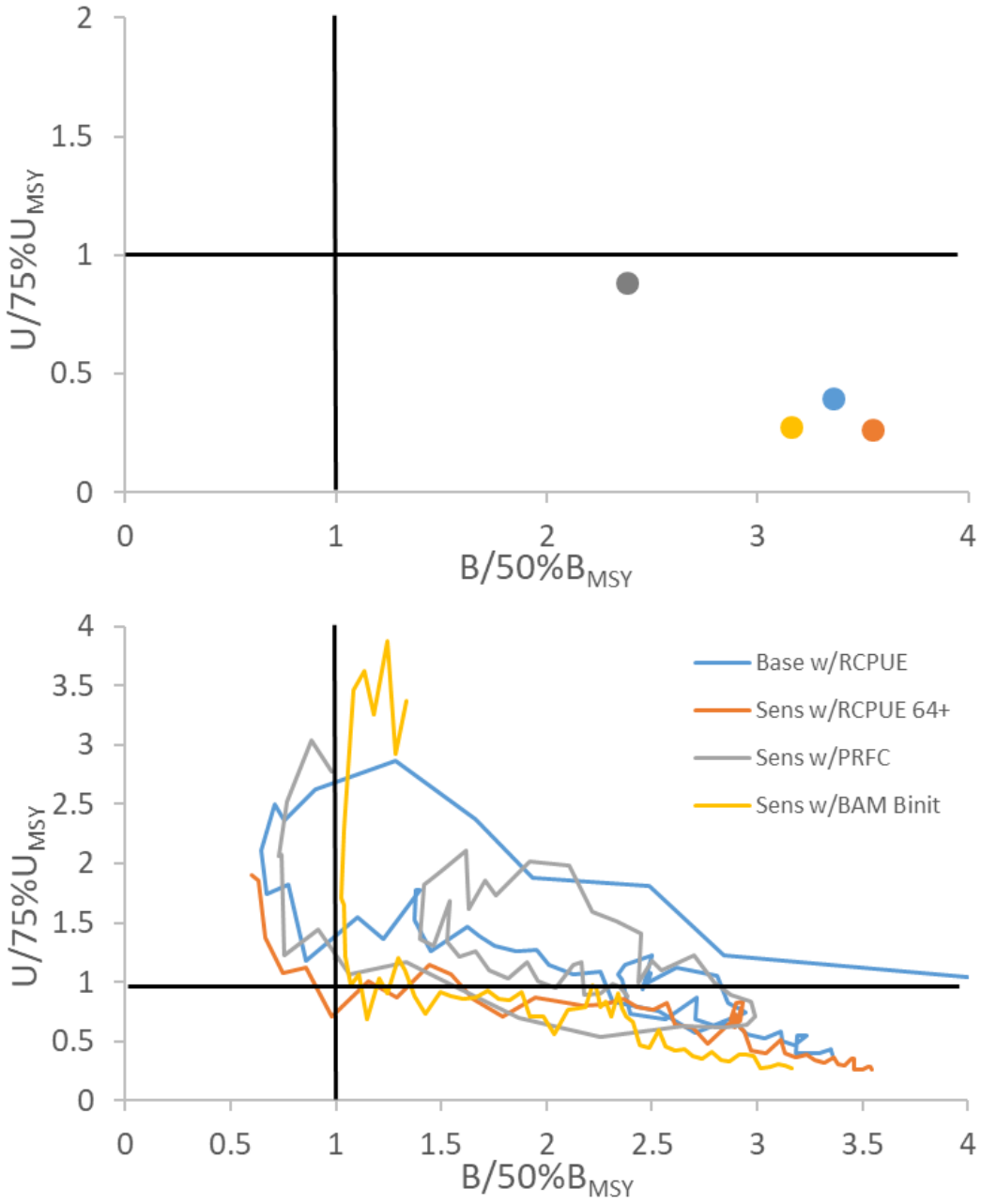


Figure 27. Kobe plots of stock status diagram for the SPMTVr model comparing base model ("Base with RCPUE") stock status estimates with that of sensitivity runs examining alternate model starting year ("Sens w/RCPUE 1964+"), an alternate fishery-dependent abundance index ("Sens w/PRFC"), and an alternate starting value for initial biomass ("Sens w/BAM Binit"). Top panel displays stock status in the terminal year for each model and the bottom panel displays annual stock status relative to time-varying reference points.

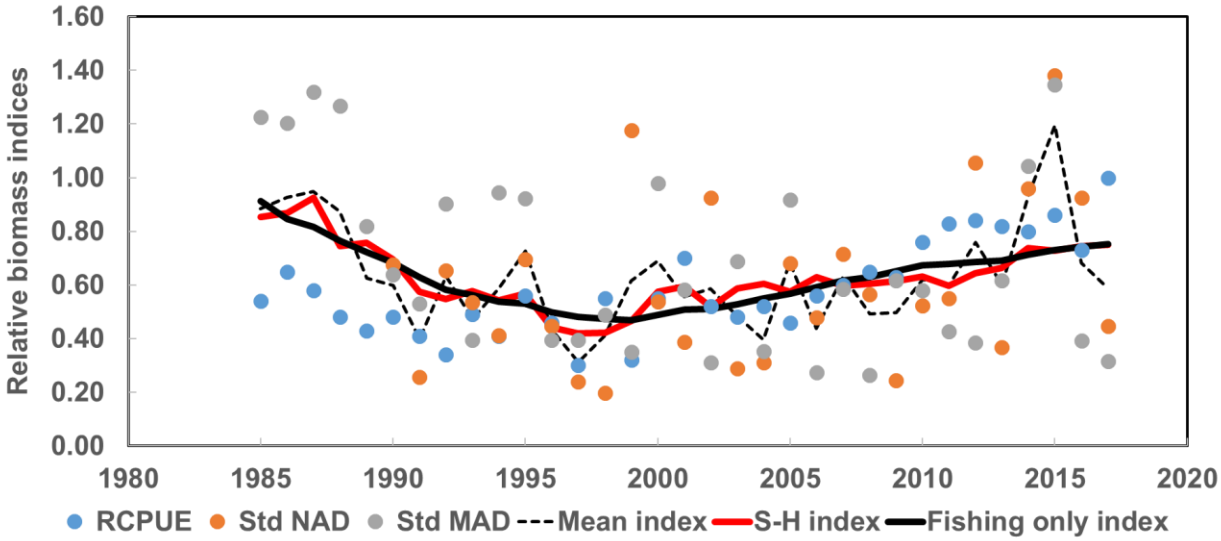


Figure 28. **Time-series of observed age-1+ Atlantic menhaden relative biomass indices, their average, and the values predicted by the fishing-only surplus production model (Fishing only index) and base Steele-Henderson model (S-H index; fishing and striped bass predation). The NAD and MAD indices are standardized into RCPUE units. Mean = average of each year's available indices.**

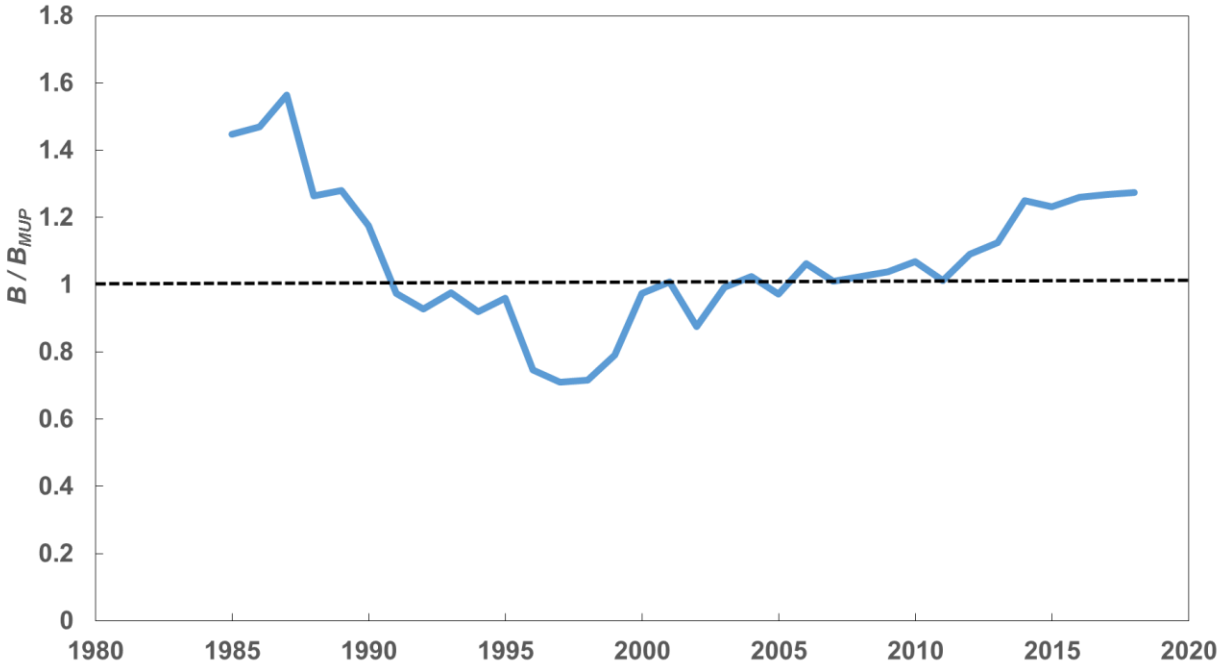


Figure 29. Relative biomass estimates (B/B_{MUP}) from base Steele-Henderson (fishing plus striped bass predation) model. Values less than 1.0 breached the threshold.

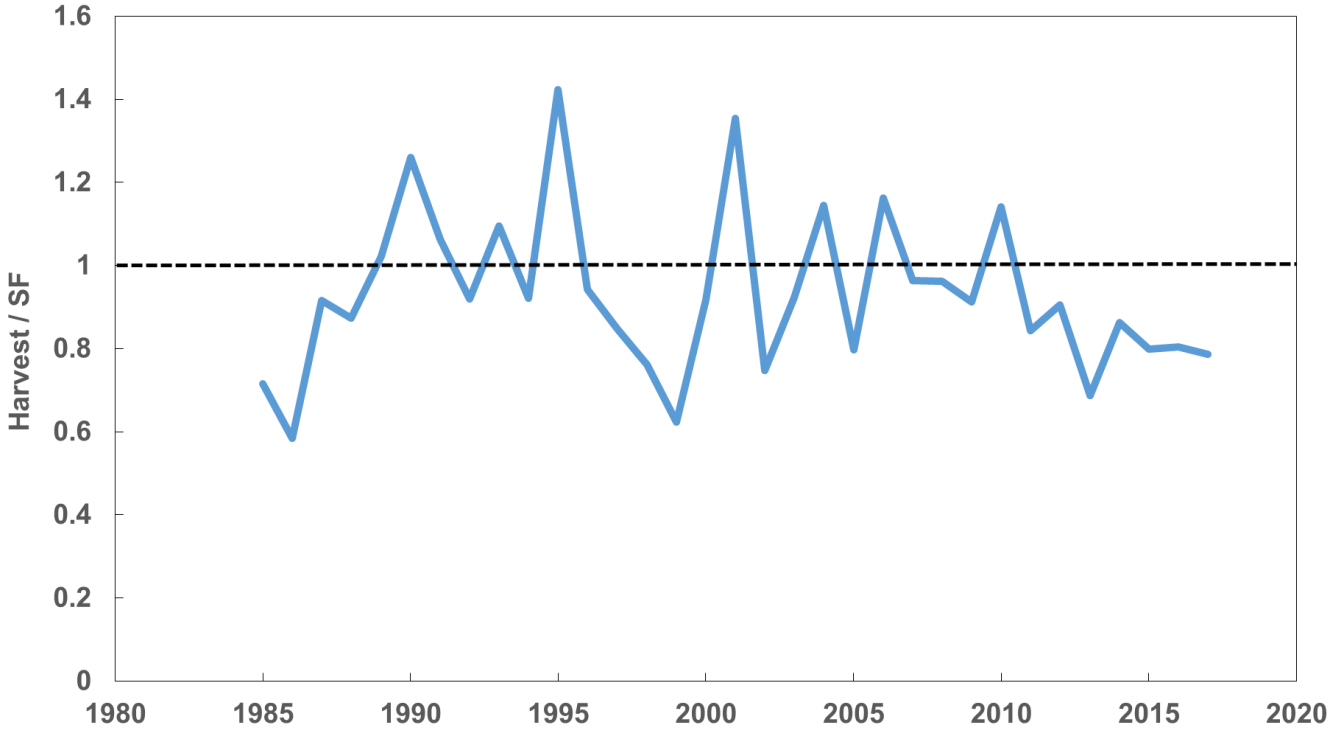


Figure 30. Harvest divided by surplus production available to the fishery after predation losses (SF) from base Steele-Henderson model (fishing plus striped bass predation). Values at 1.0 or more exceeded the threshold.

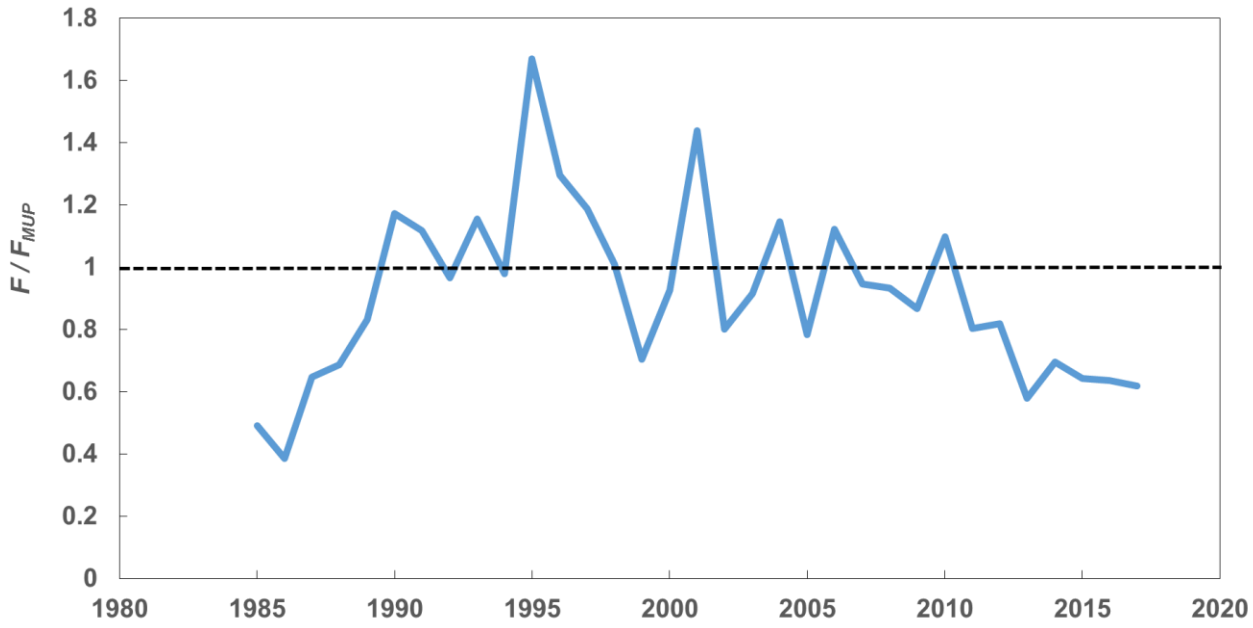


Figure 31. Relative F ($F = F/F_{MUP}$) estimates from base Steele-Henderson model (fishing and Striped Bass predation). Values at 1.0 or more breached the threshold.

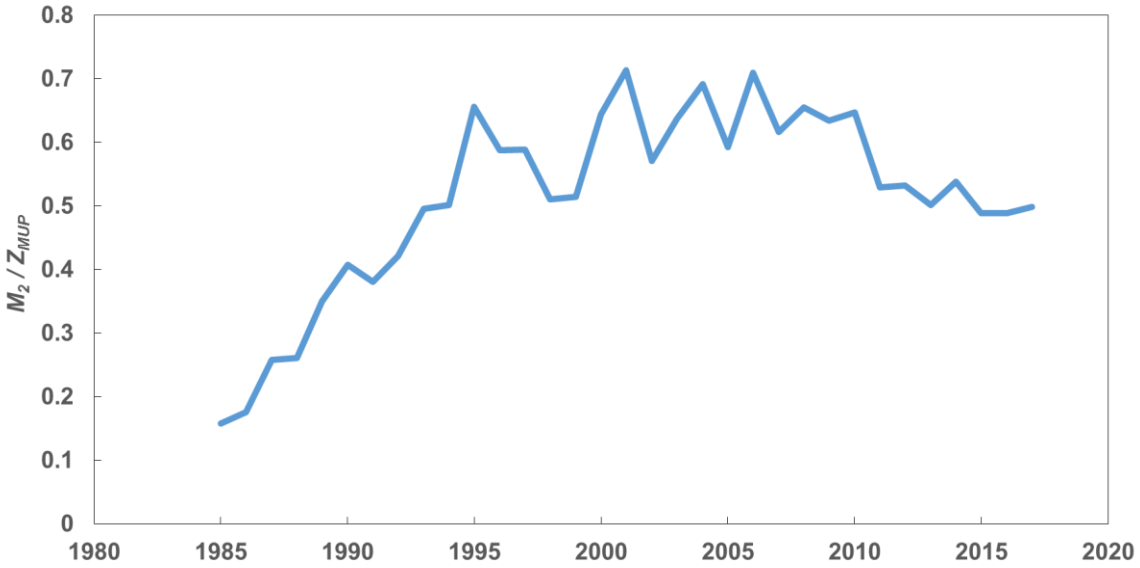


Figure 32. Relative M_2 (M_2 / Z_{MUP}) estimates from base Steele-Henderson models (fishing and striped bass predation).

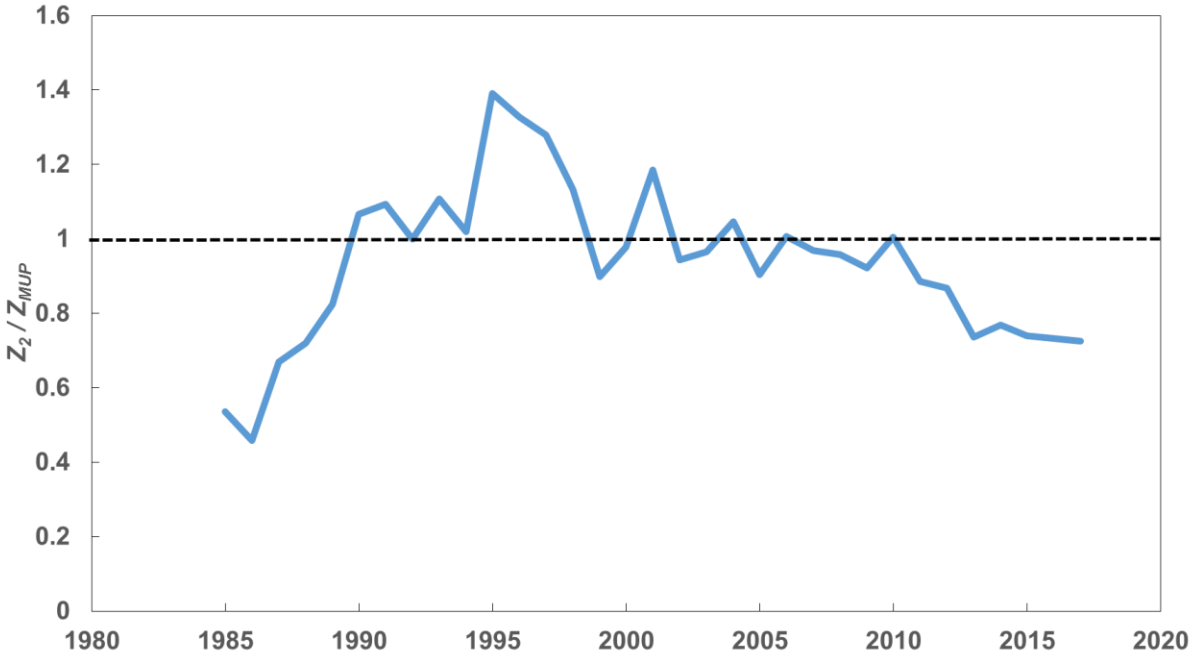


Figure 33. Relative Z_2 estimates from base Steele-Henderson models (fishing and striped bass predation). Relative $Z_2 = Z_2 / Z_{MUP}$ for Steele-Henderson models. Values at 1.0 or more exceeded the threshold.

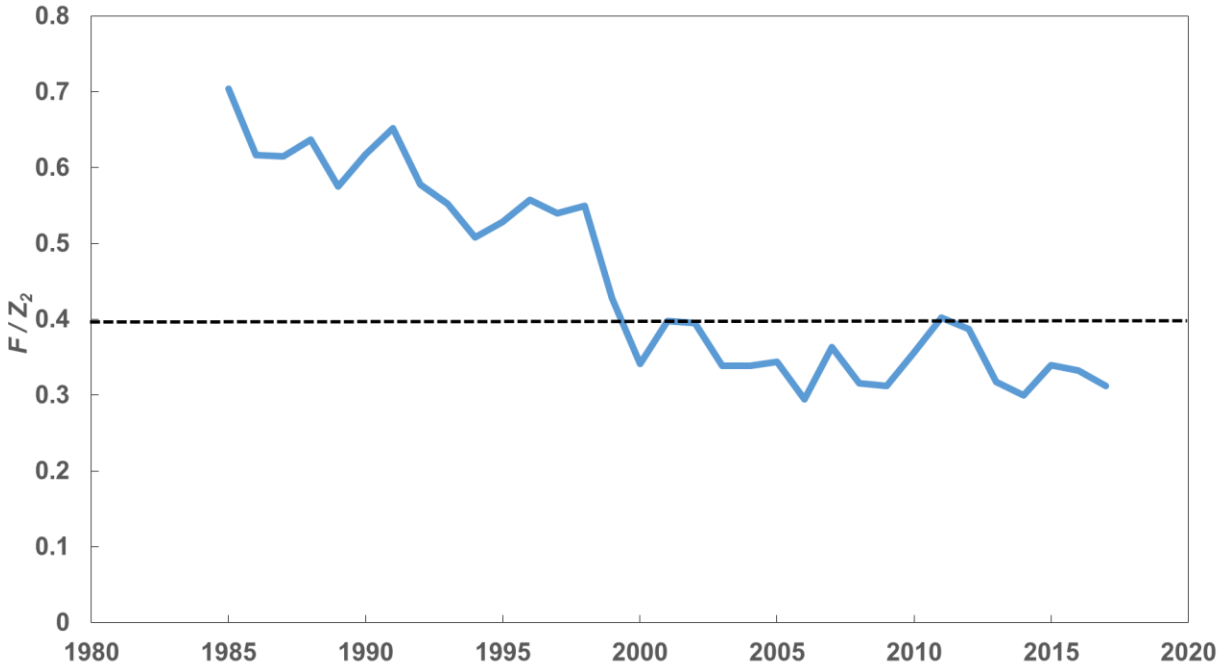


Figure 34. Estimates of F / Z_2 from base Steele-Henderson models (fishing and striped bass predation). Values at 0.4 (dashed line) or more exceeded the threshold.

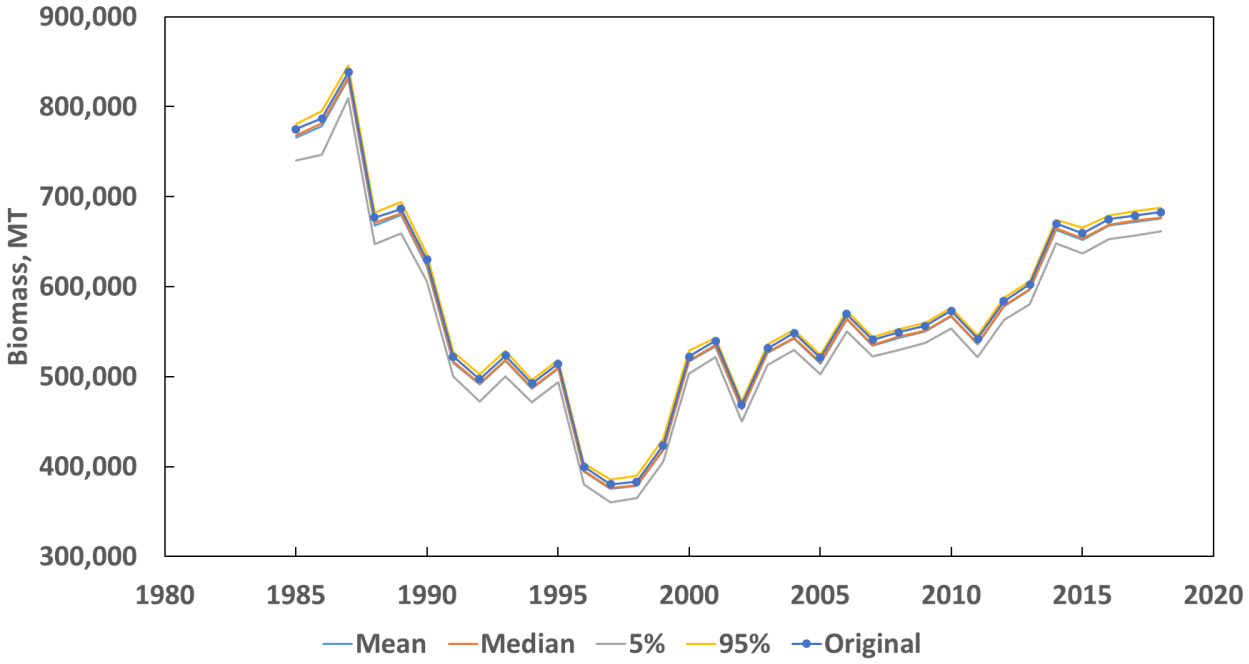


Figure 35. Time-series of age-1+ Atlantic menhaden biomass estimated by the base Steele-Henderson model (fishing and striped bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile). MT = metric tons.

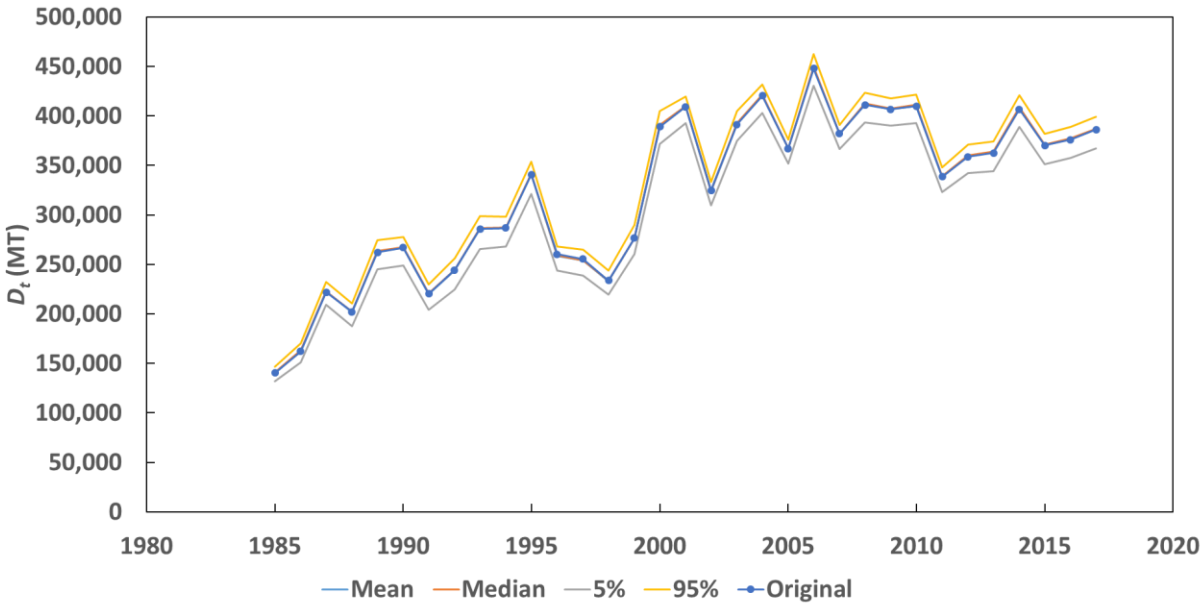


Figure 36. Time-series of age-1+ Atlantic menhaden biomass consumed by striped bass (D_t) estimated by the base Steele-Henderson model (fishing and striped bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile). MT = metric tons.

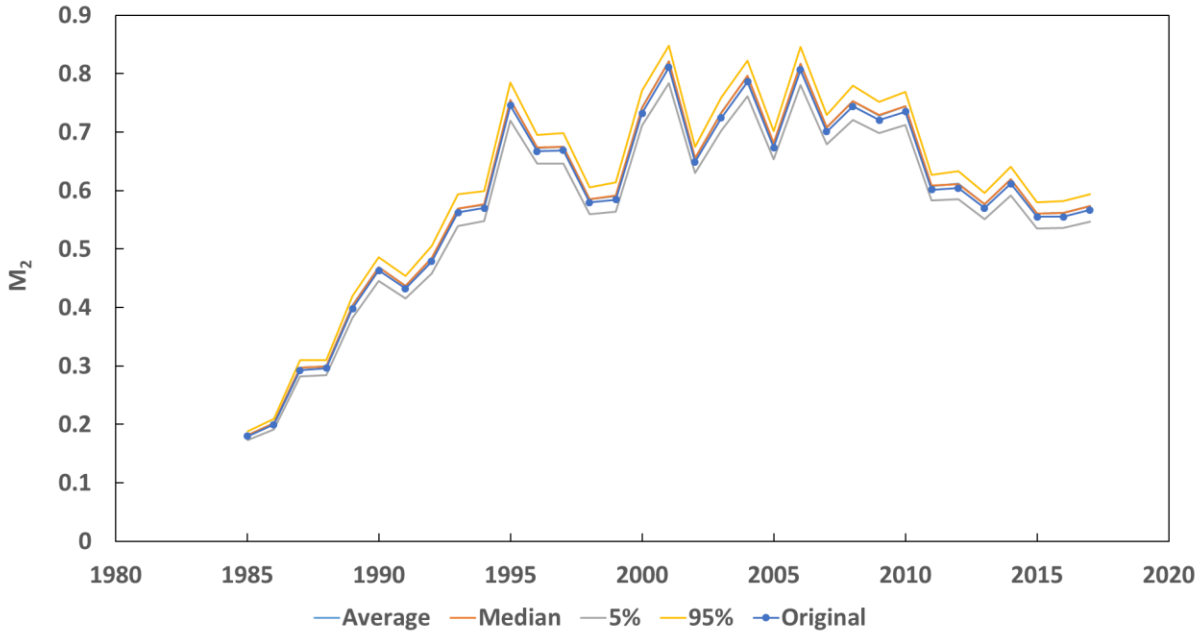


Figure 37. Time-series of age-1+ Atlantic menhaden biomass M_2 estimated by the base Steele-Henderson model (fishing and striped bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile).

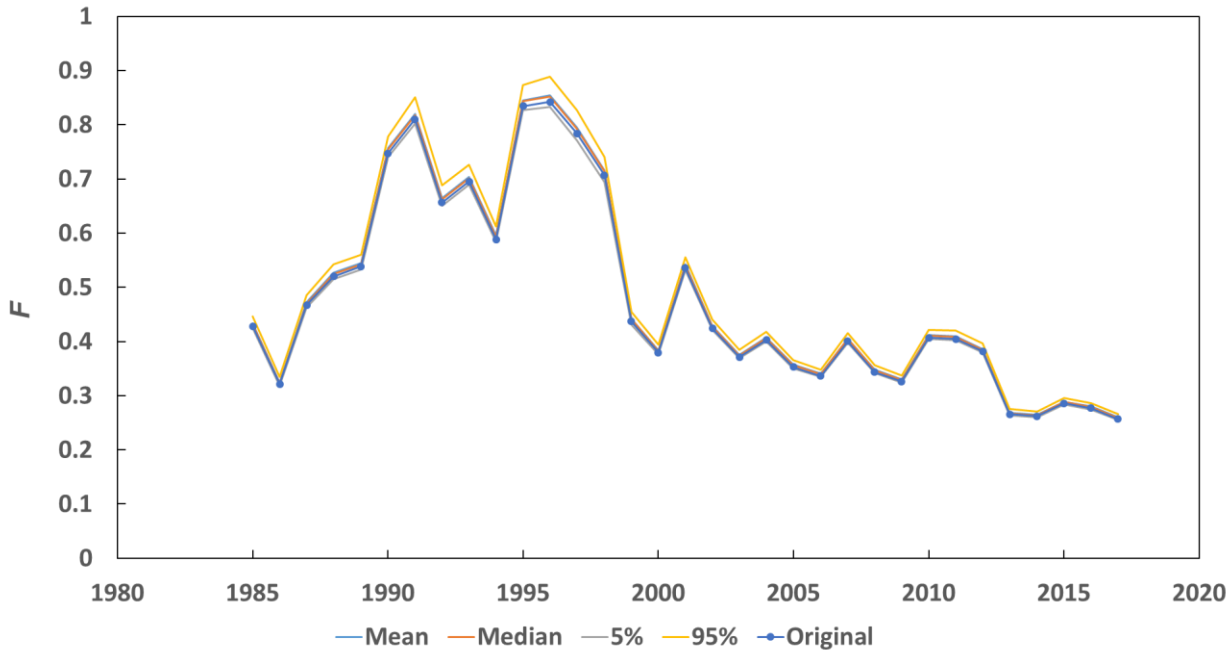


Figure 38. Time-series of ages 1+ Atlantic menhaden biomass *F* estimated by the base Steele-Henderson model (fishing and striped bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile).

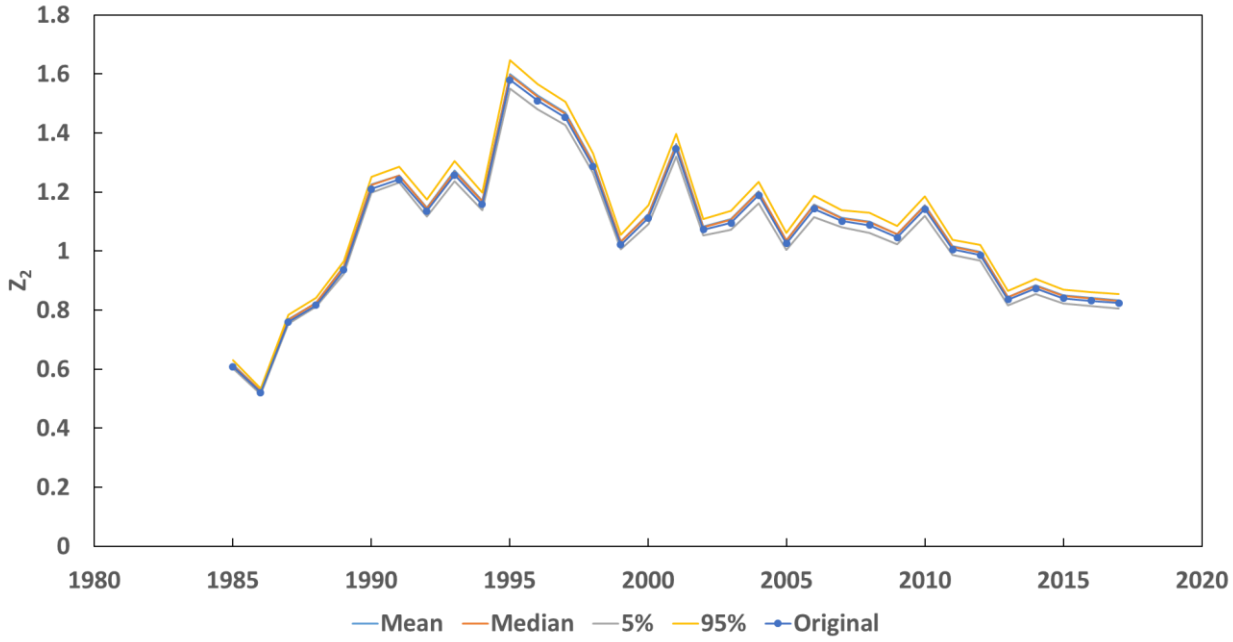


Figure 39. Time-series of age-1+ Atlantic menhaden biomass Z_2 ($F + M_2$) estimated by the base Steele-Henderson model (fishing and striped bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile).

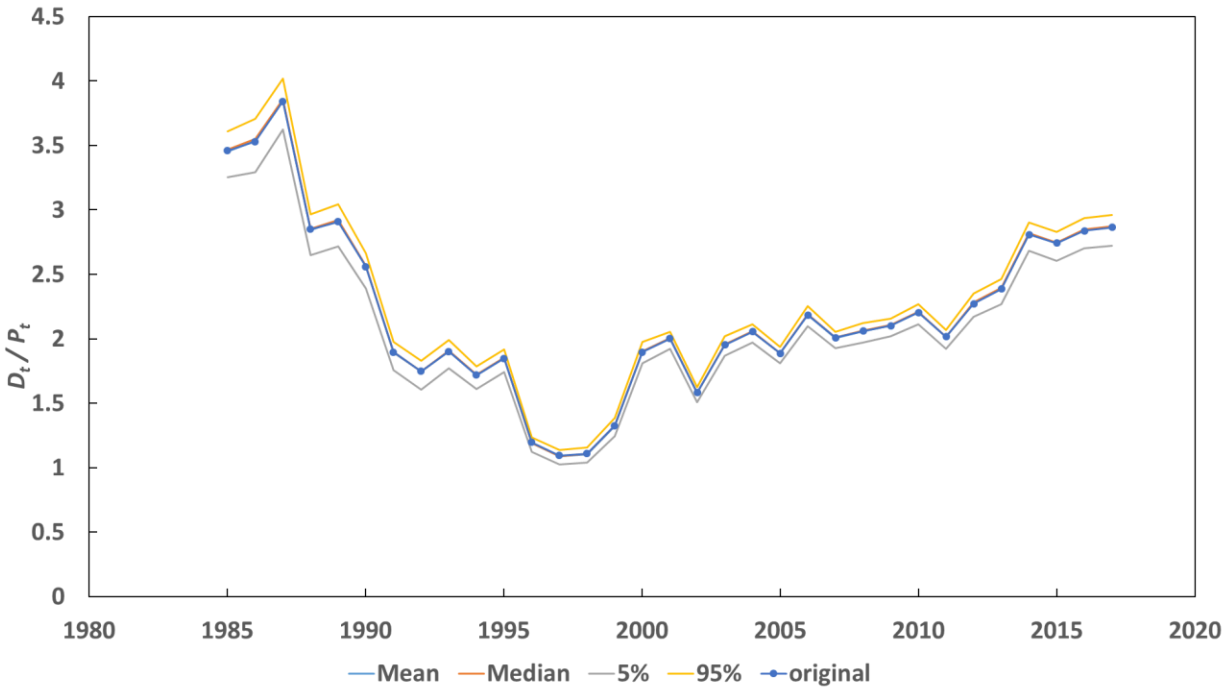


Figure 40. Time-series of annual age-1+ Atlantic menhaden biomass consumed per striped bass biomass (D_t / P_t as MT consumed / MT striped bass) estimated by the base Steele-Henderson model (fishing and striped bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile). MT = metric tons.

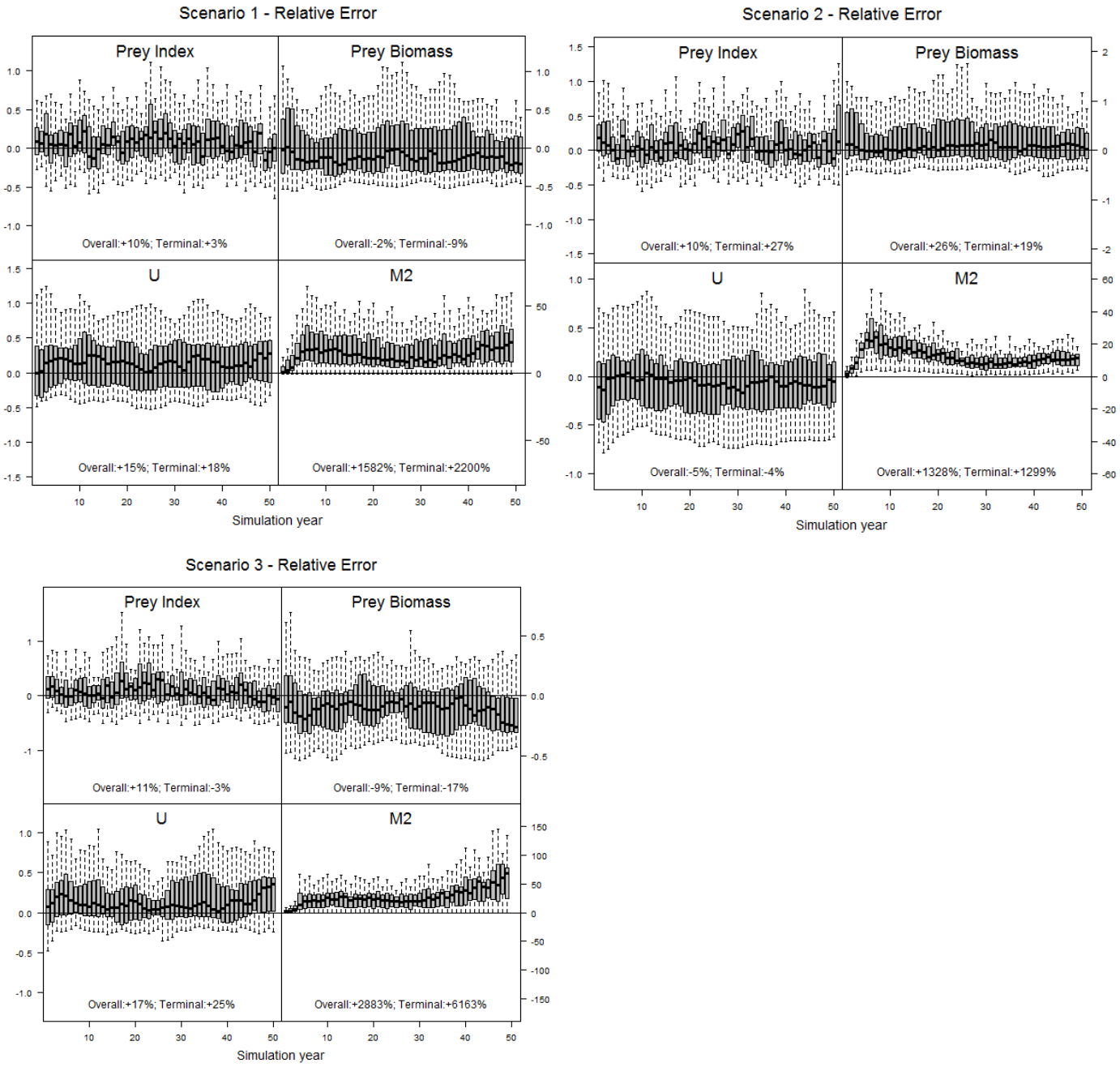


Figure 41. Relative error from Steele-Henderson model results using simulated data. Scenario 1: predator *F* is constant; Scenario 2: predator *F* increasing; Scenario 3: predator *F* decreasing. In all scenarios prey *F* increases and then decreases.

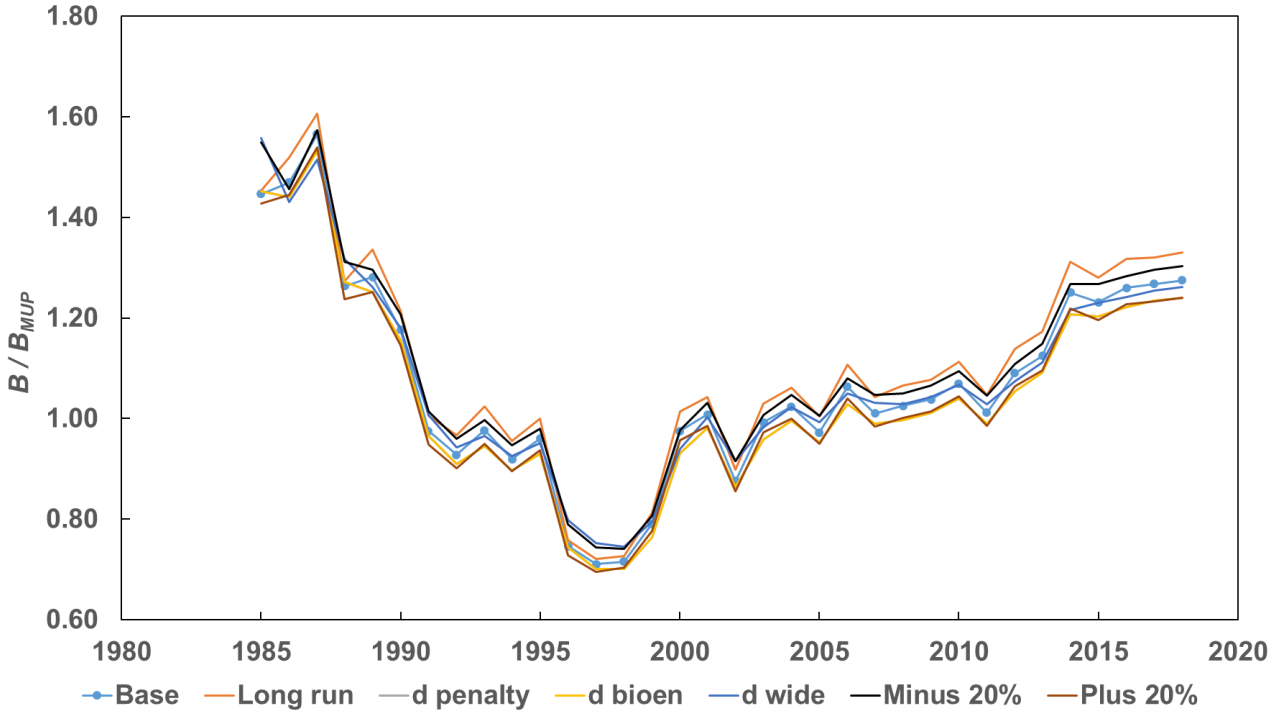


Figure 42. Relative biomass (B / B_{MUP}) estimates from the base Steele-Henderson model (fishing and striped bass predation) and its sensitivity runs. Values at 1.0 or less exceeded the threshold. See Section 11.4 for descriptions of sensitivity runs.

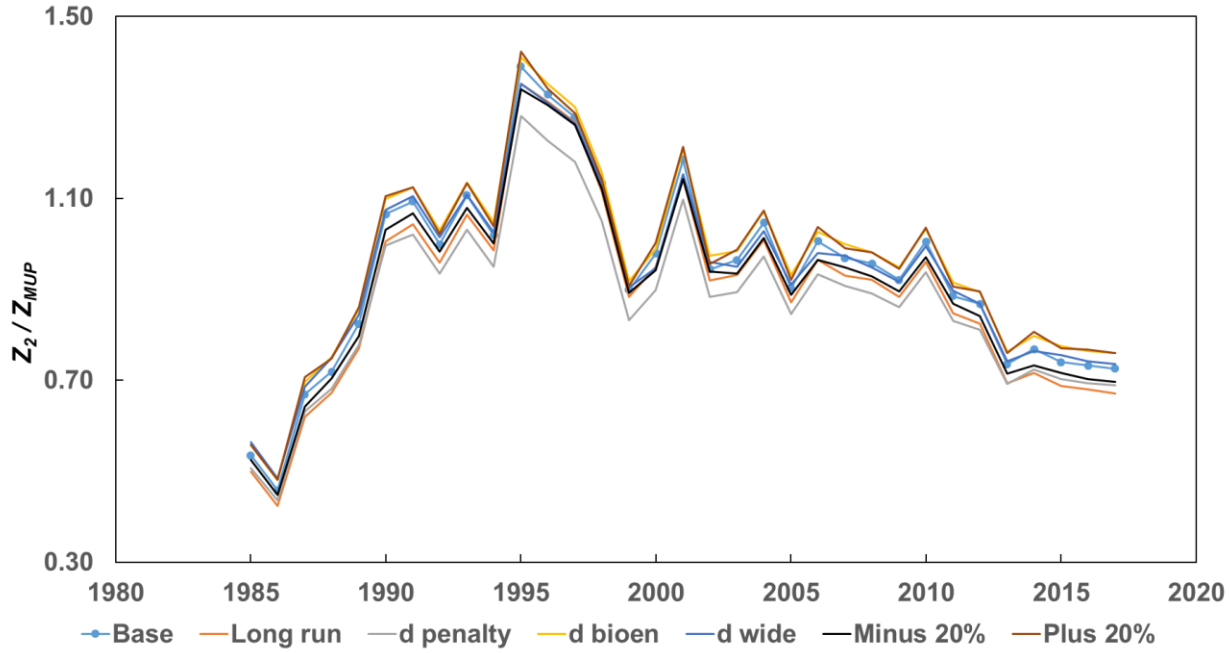


Figure 43. Relative Z_2 (Z_2 / Z_{MUP}) estimates from base Steele-Henderson model (fishing and striped bass predation) sensitivity runs. Values at 1.0 or more exceeded the threshold. See Methods for descriptions of sensitivity runs.

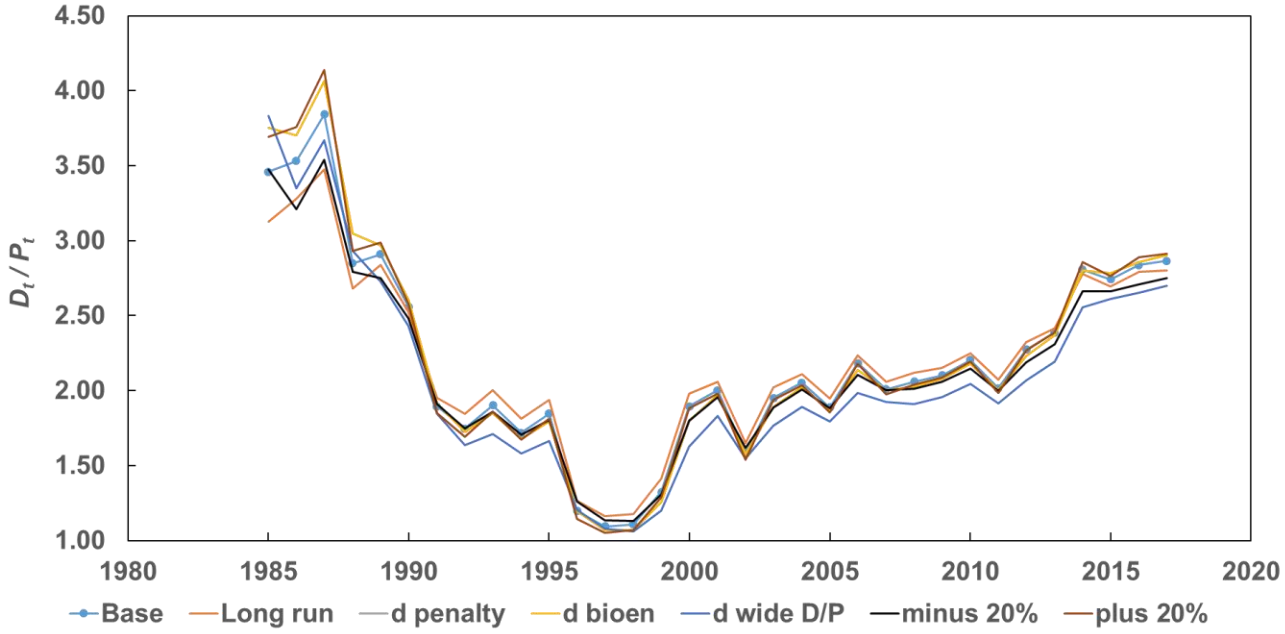


Figure 44. Time-series of annual age-1+ Atlantic menhaden biomass consumed per striped bass biomass from the base Steele-Henderson model and its sensitivity runs (D_t / P_t as mt consumed / mt striped bass).

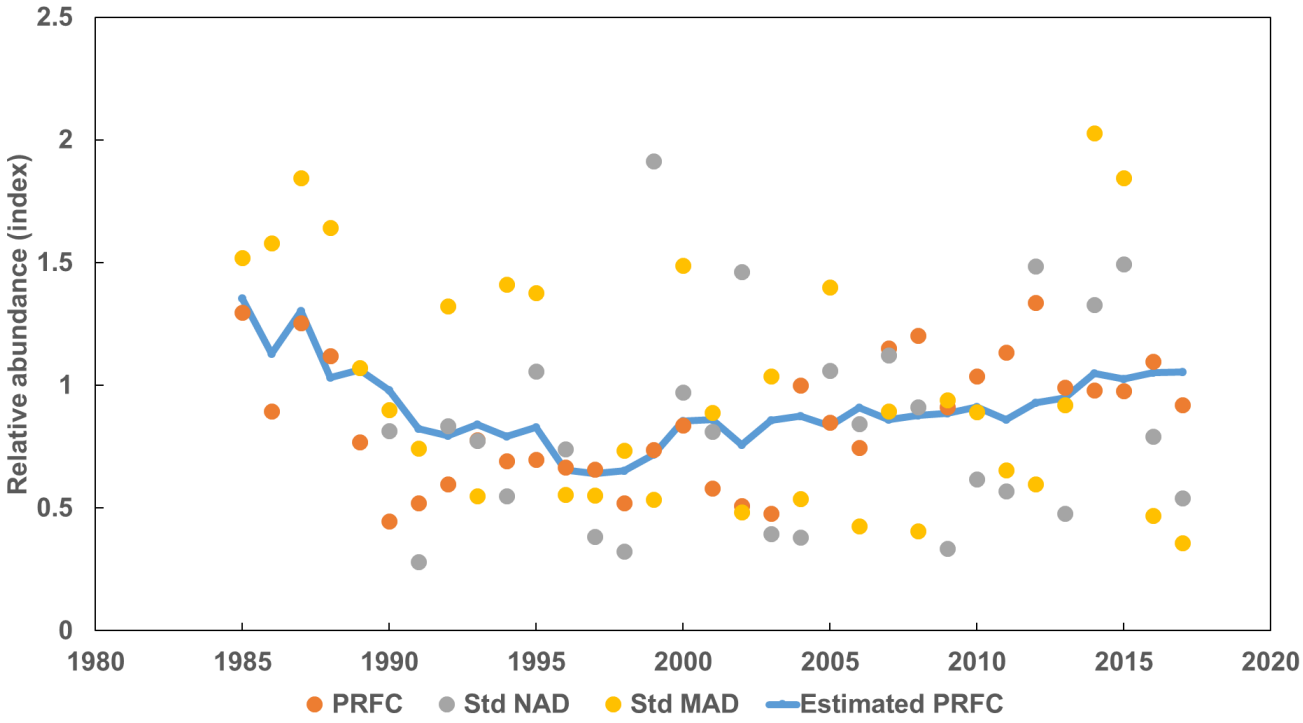


Figure 45. Time-series of observed and predicted age-1+ Atlantic menhaden relative biomass indices from the Steele-Henderson model (fishing and striped bass predation) fit using the PRFC index. NAD and MAD indices are standardized into PRFC units.

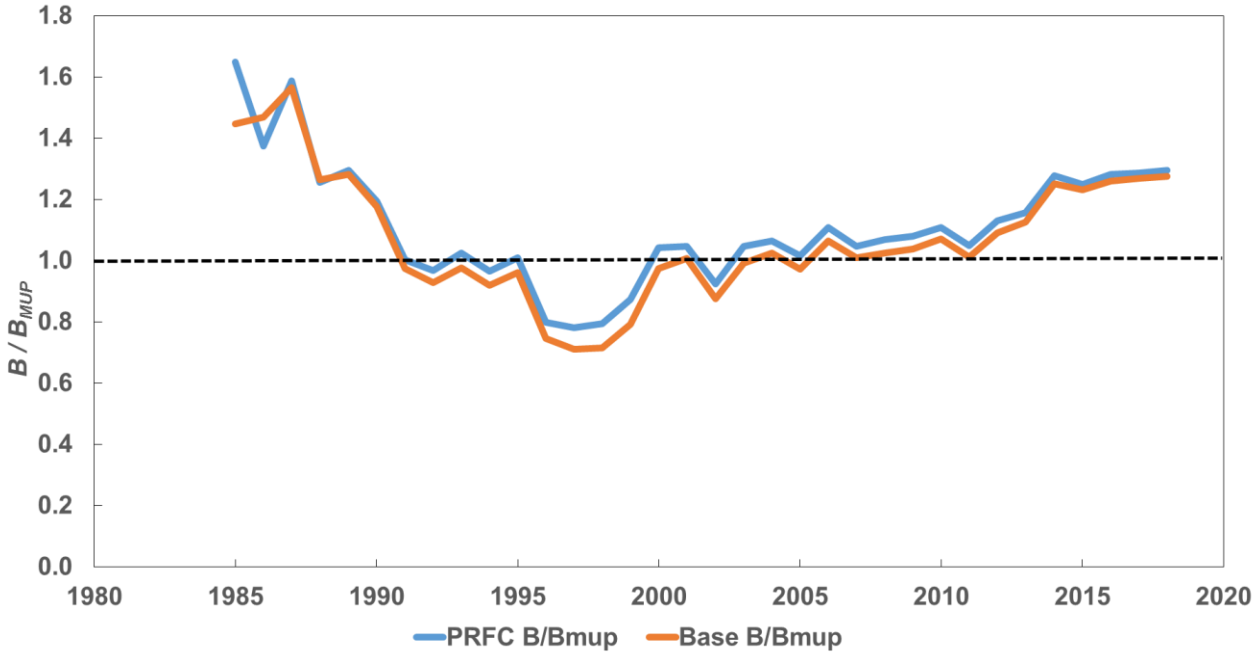


Figure 46. Relative biomass estimates from base and PRFC Steele-Henderson models (fishing and striped bass predation). Relative biomass = B / B_{MUP}. Values at 1.0 or less exceeded the threshold.

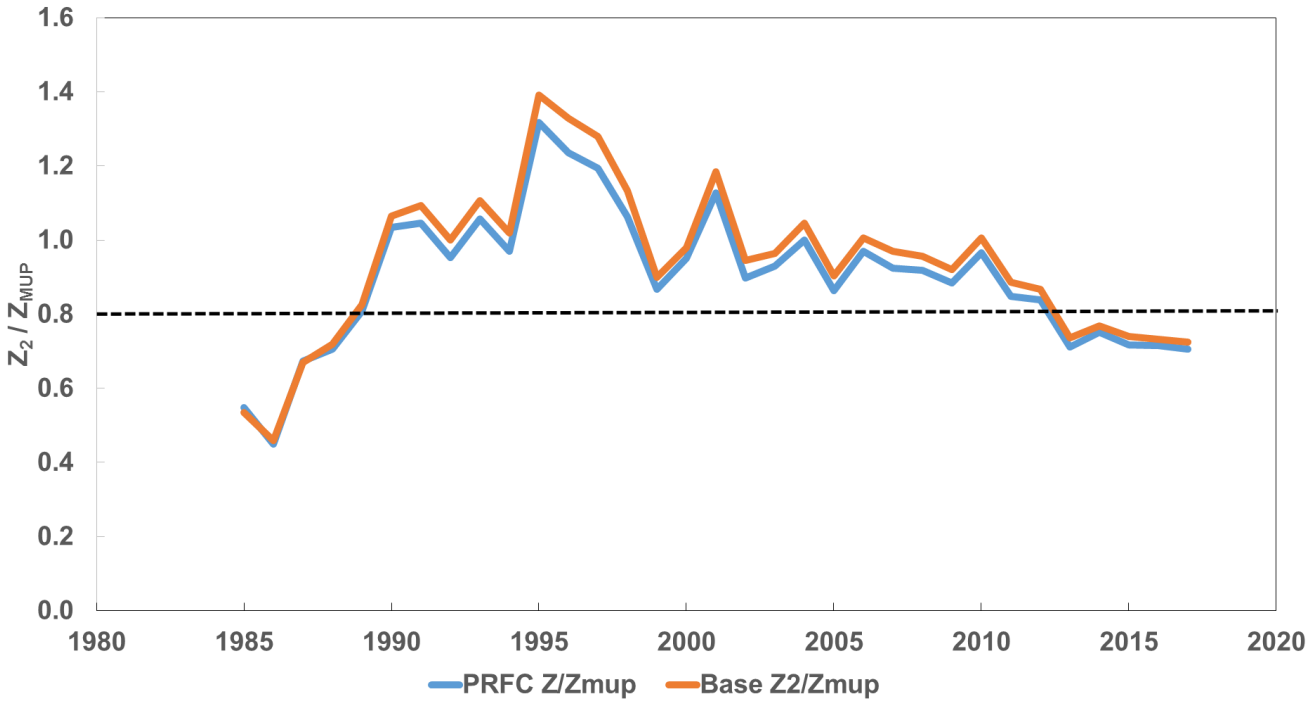


Figure 47. Relative Z_2 estimates from base and PRFC Steele-Henderson models (fishing and striped bass predation). Relative $Z_2 = Z_2 / Z_{MUP}$. Values at 1.0 or more exceeded the threshold.

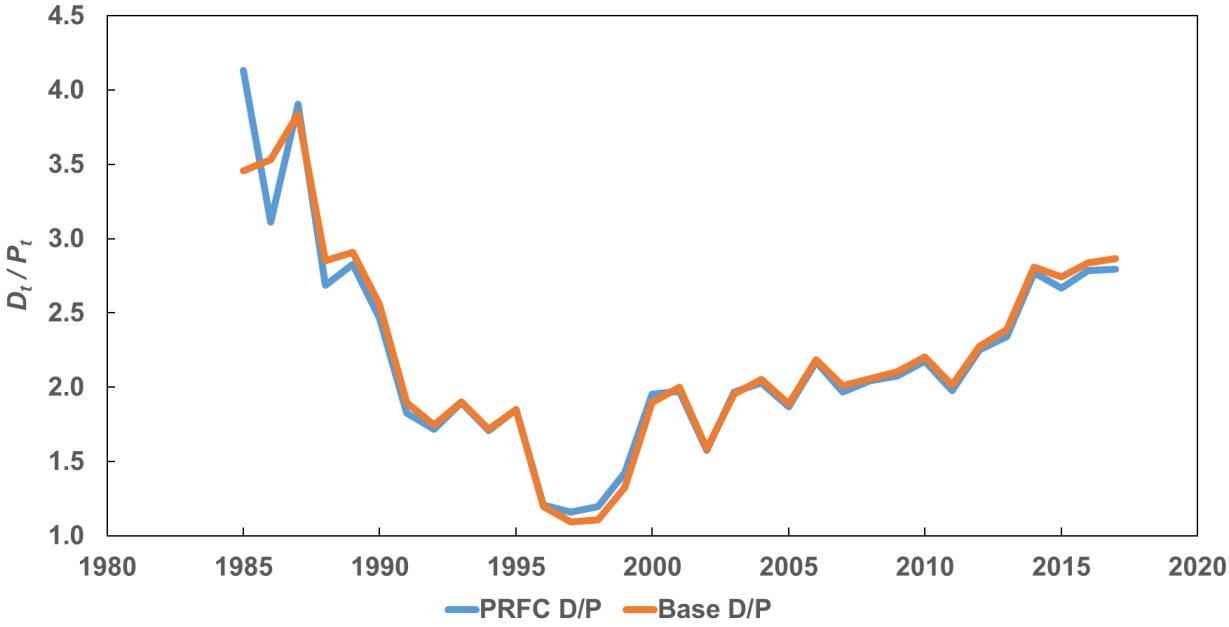


Figure 48. Time-series of annual age-1+ Atlantic menhaden biomass consumed per striped bass biomass estimated by the base and PRFC Steele-Henderson models (D_t / P_t as mt consumed / mt striped bass).

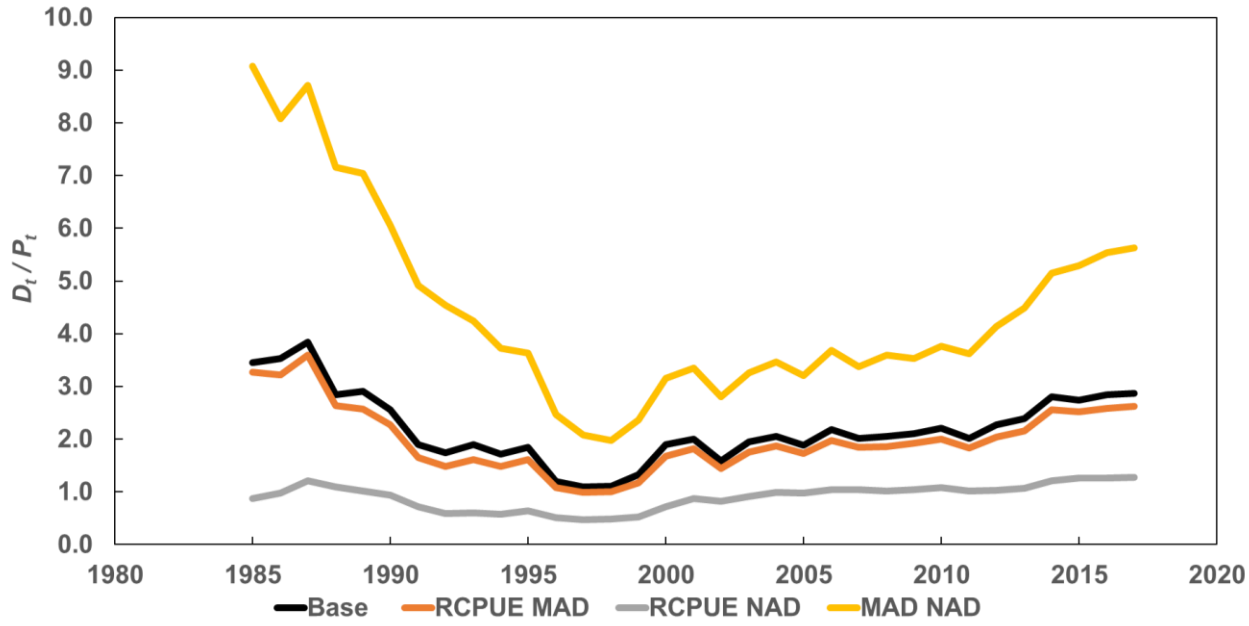


Figure 49. Time-series of annual age-1+ Atlantic menhaden biomass consumed per striped bass biomass estimated by the base Steele-Henderson model and its index removal runs (D_t / P_t as mt consumed / mt striped bass).

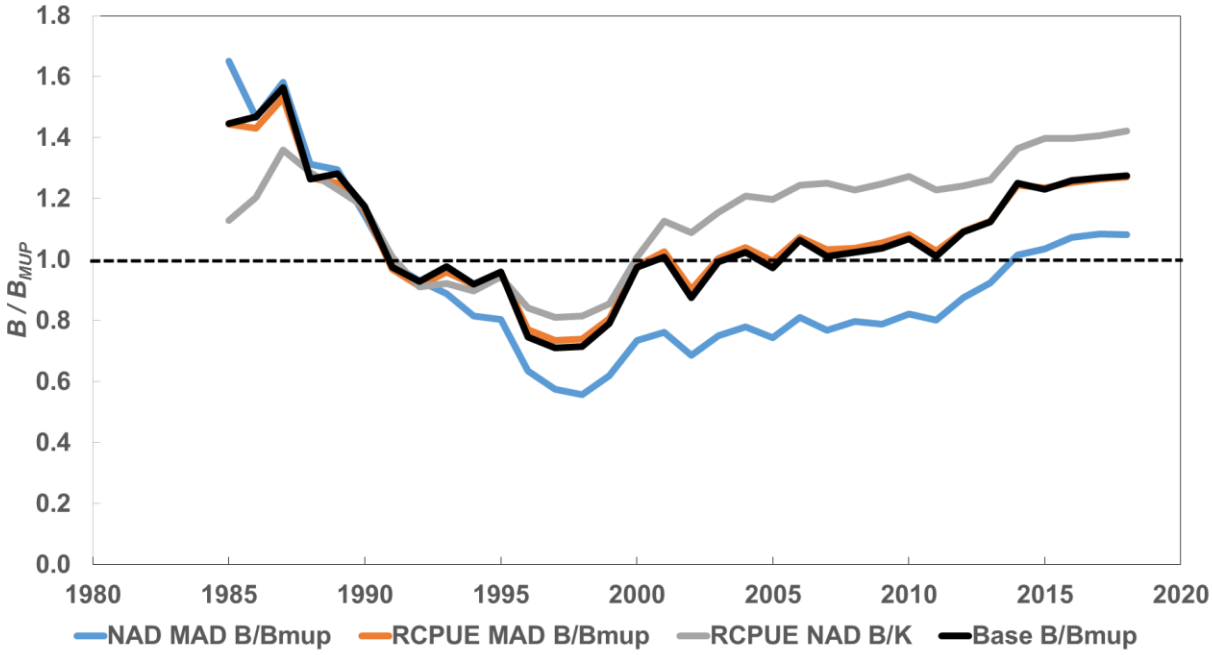


Figure 50. Relative biomass (B / B_{MUP}) estimates from the base Steele-Henderson model (fishing and striped bass predation) and its index removal runs. Values at 1.0 or less were below the threshold.

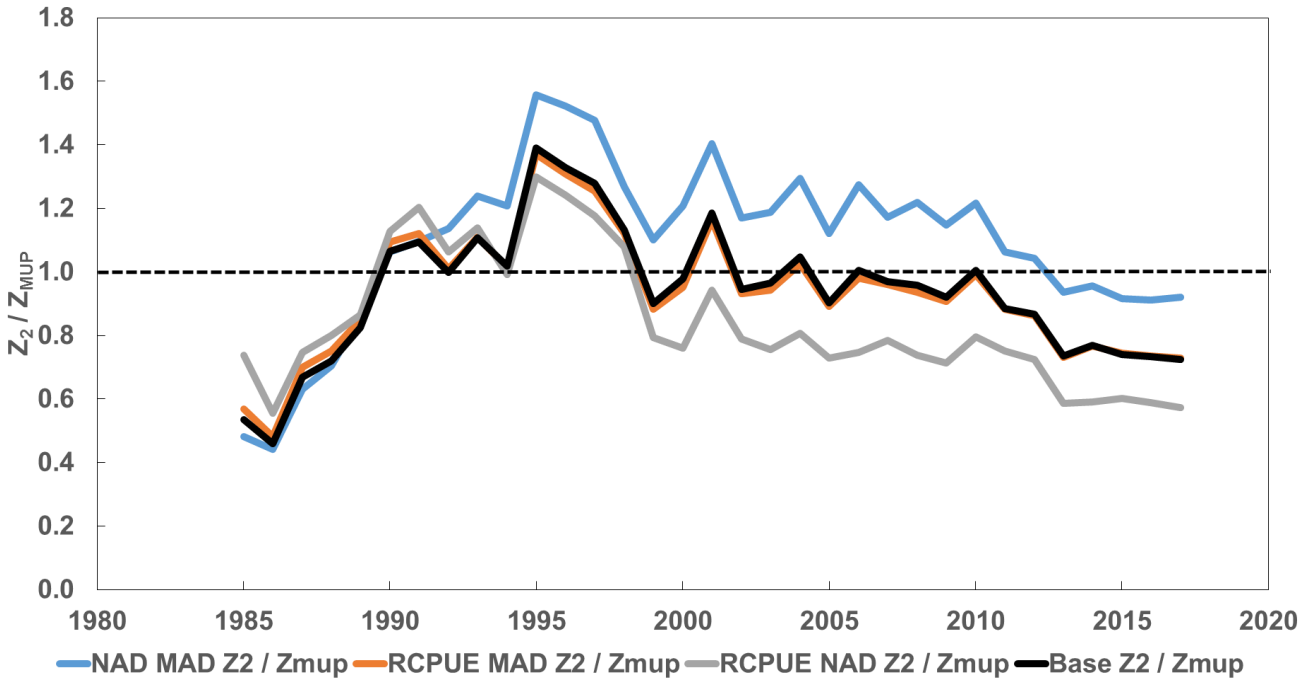


Figure 51. Relative Z_2 (Z_2 / Z_{MUP}) estimates from base Steele-Henderson model (fishing and striped bass predation) index removal runs. Values at 1.0 or more exceeded the threshold.

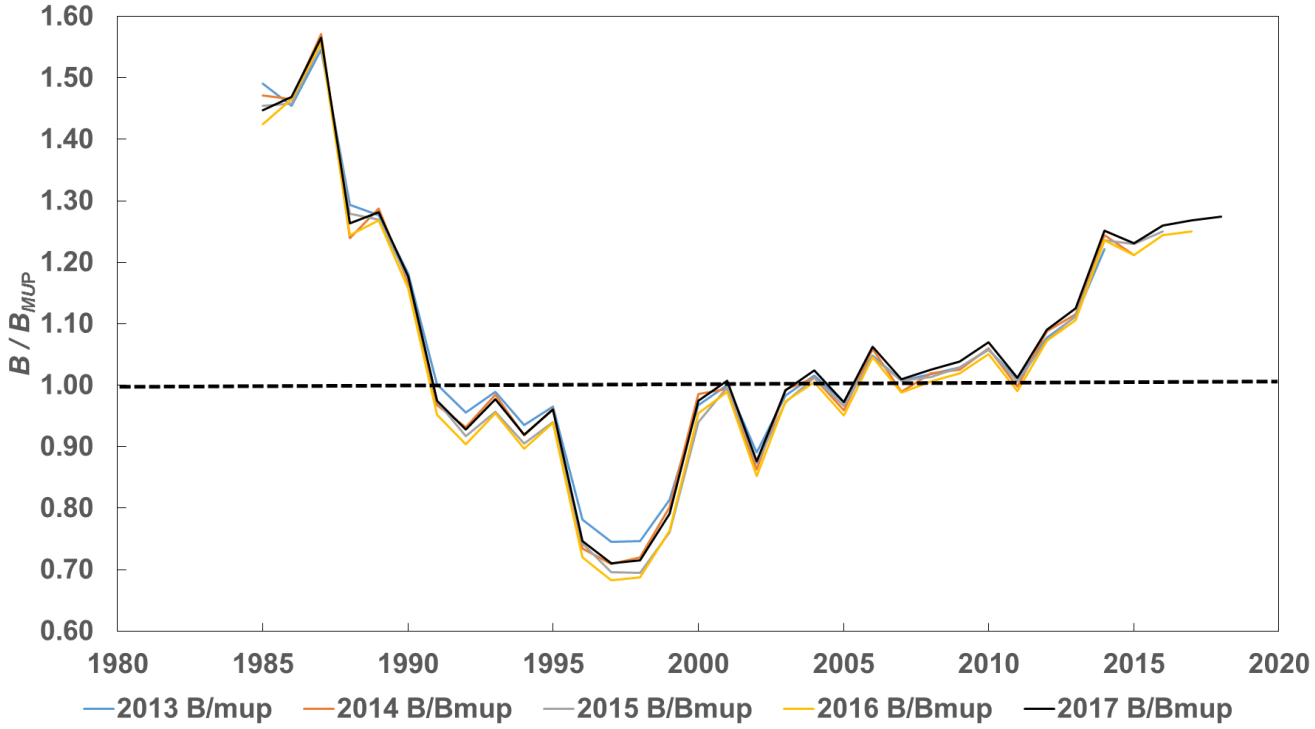


Figure 52. Relative biomass (B / B_{MUP}) estimates from the base Steele-Henderson model (fishing and striped bass predation) and its retrospective runs. Values at 1.0 or less were below the threshold.

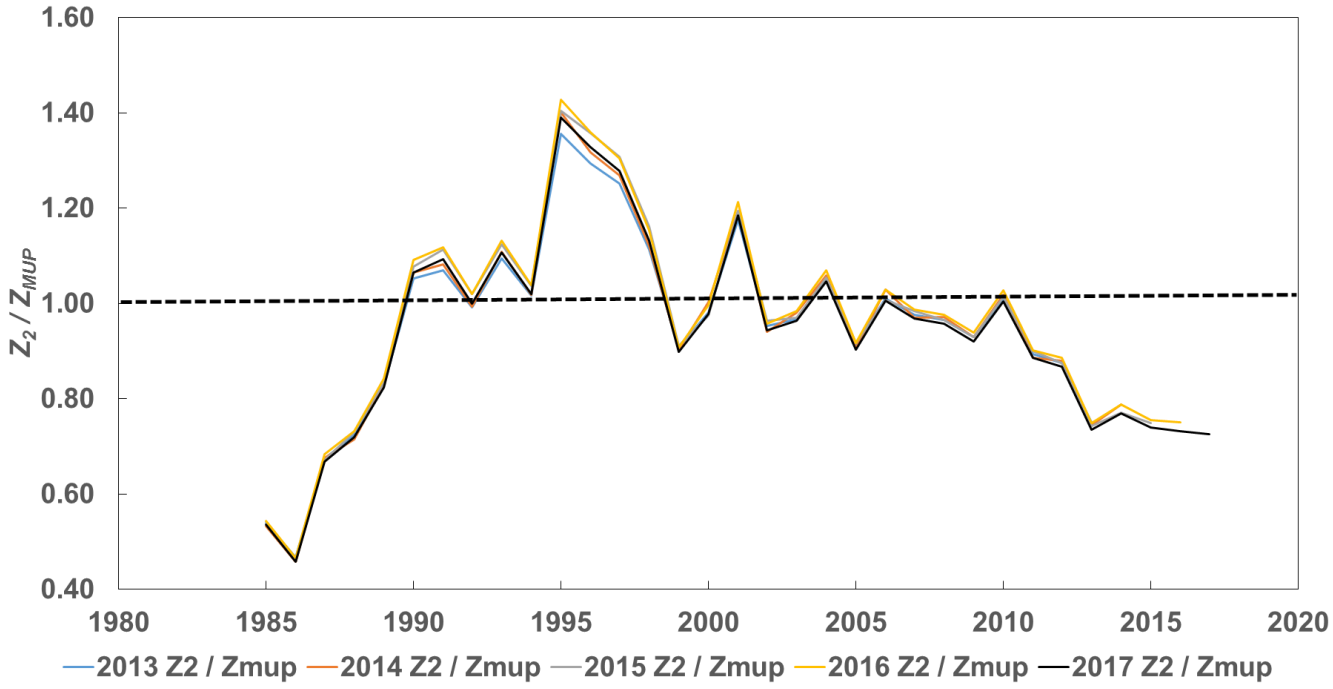


Figure 53. Relative Z_2 (Z_2 / Z_{MUP}) estimates from base Steele-Henderson model (fishing and striped bass predation) retrospective runs. Values at 1.0 or more exceeded the threshold.

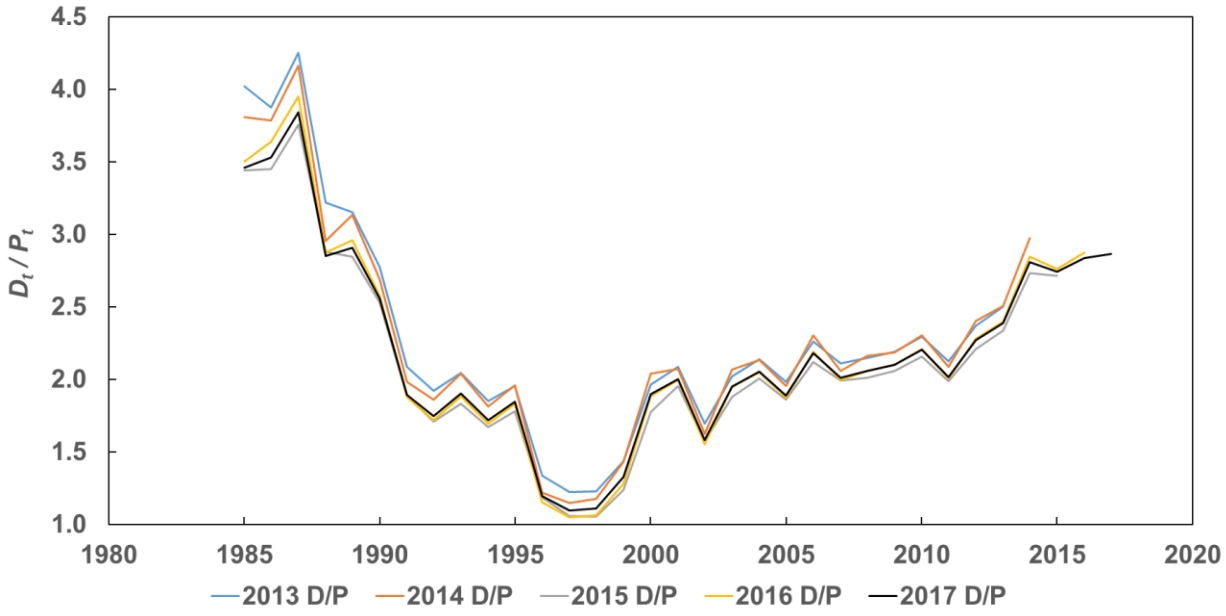


Figure 54. Time-series of annual ages 1+ Atlantic menhaden biomass consumed per striped bass biomass estimated by the base Steele-Henderson model and its retrospective runs (D_t / P_t as mt consumed / mt striped bass).

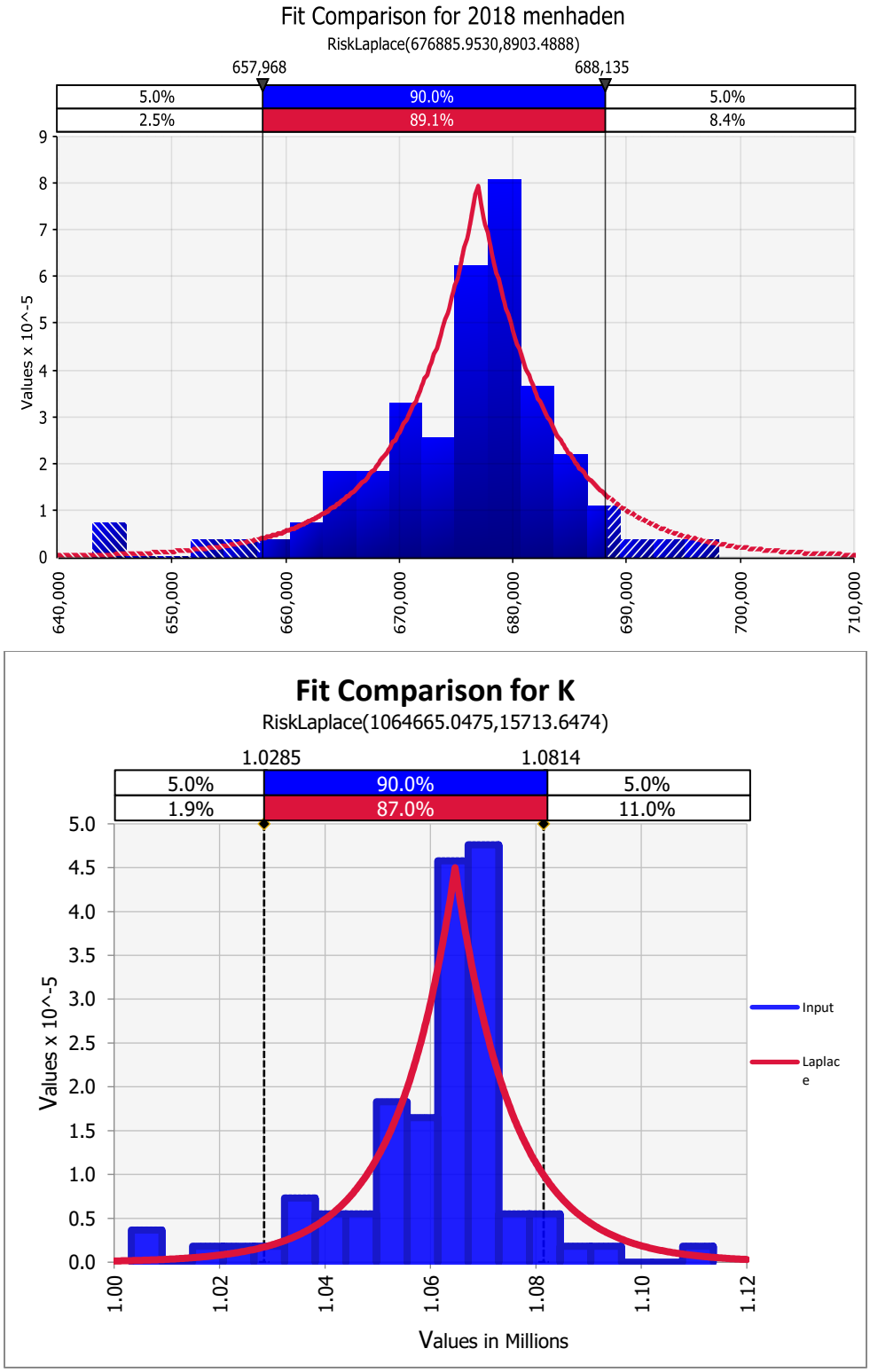


Figure 55. Base Steele-Henderson model jackknifed distributions of January 1, 2018 Atlantic menhaden ages 1+ biomass (MT) and unfished biomass (*K*, MT) and Laplace distributions providing best fit using @Risk's distribution fitting module.

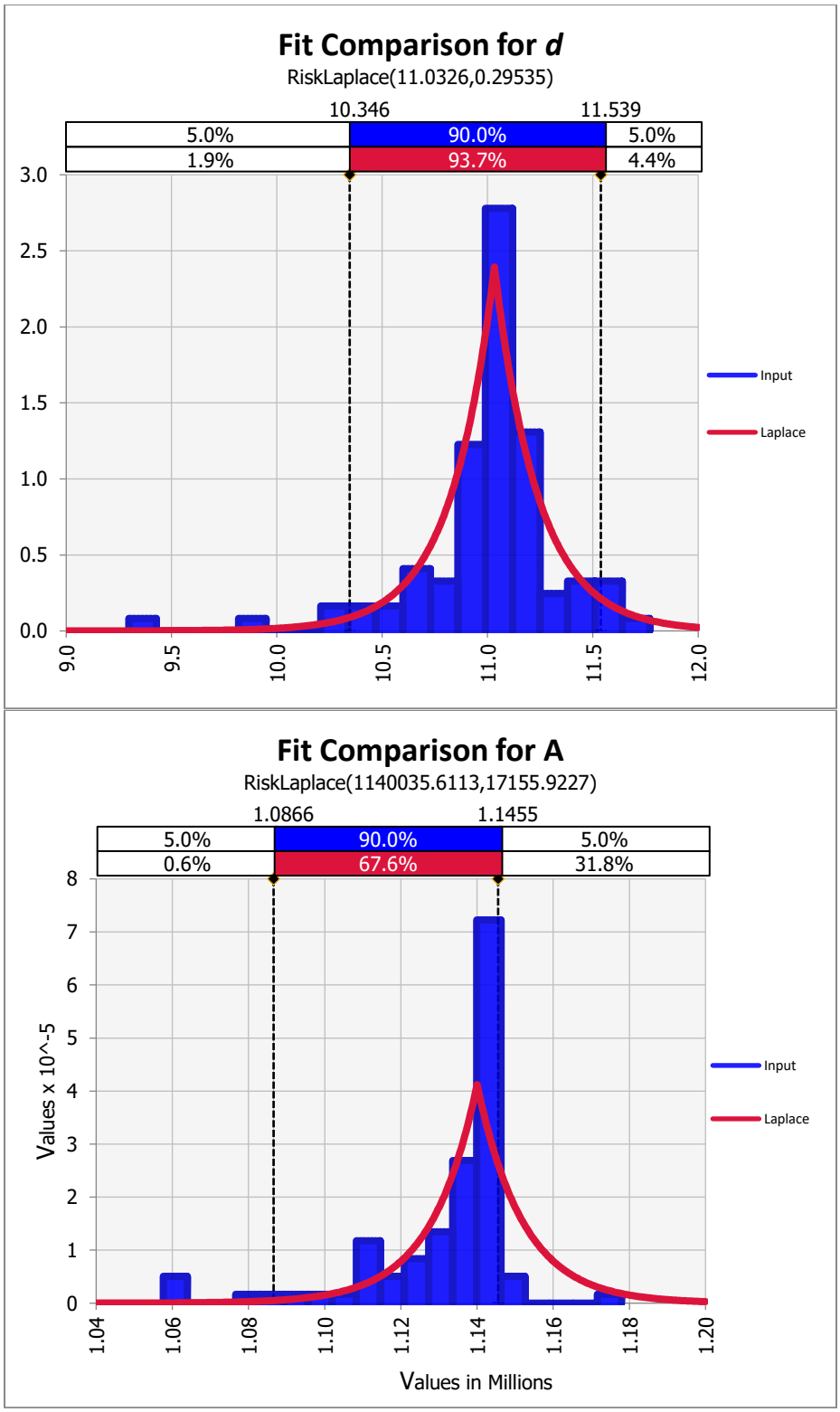


Figure 56. Base Steele-Henderson model jackknifed distributions of parameters *d* and *A* (Atlantic menhaden ages 1+ biomass at striped bass satiation, MT) and Laplace distributions providing best fit using @Risk's distribution fitting module.

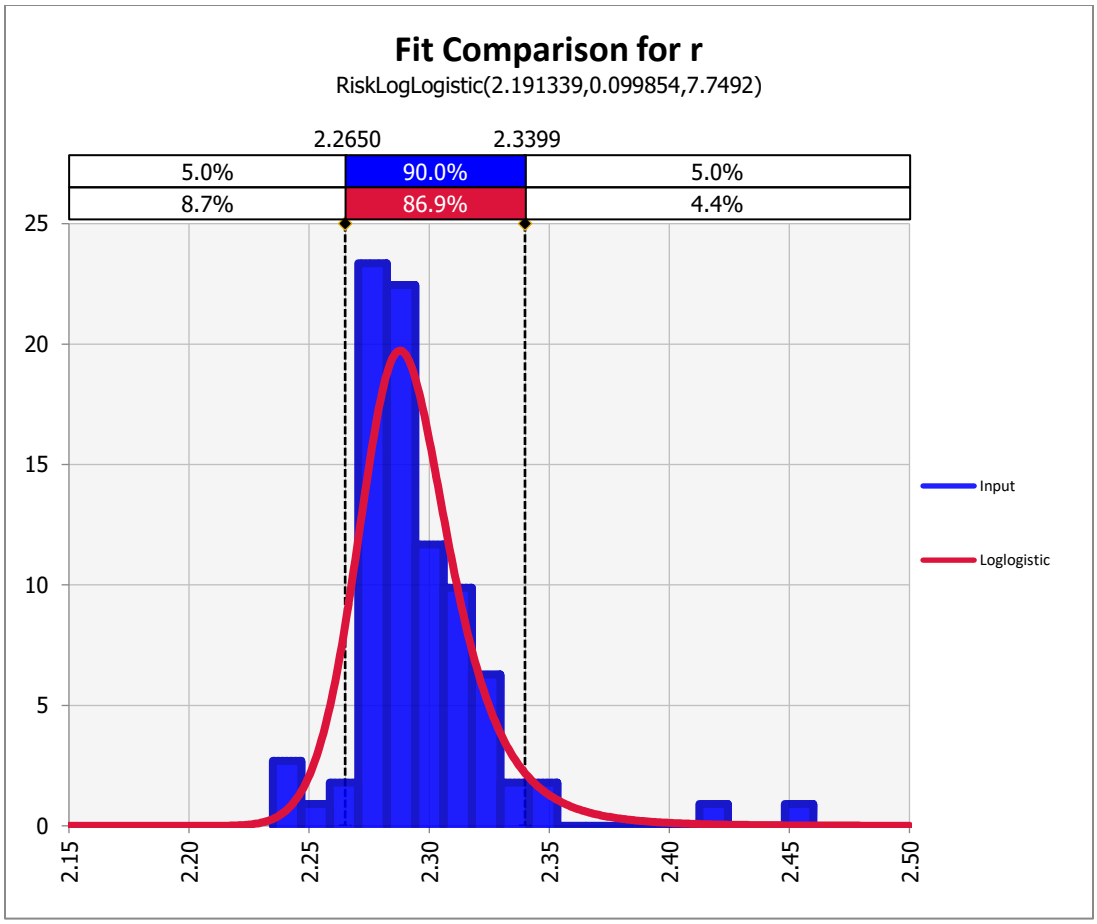


Figure 57. Base Steele-Henderson model jackknifed distribution of intrinsic growth rate, *r*, and the log logistic distribution providing best fit using @Risk's distribution fitting module

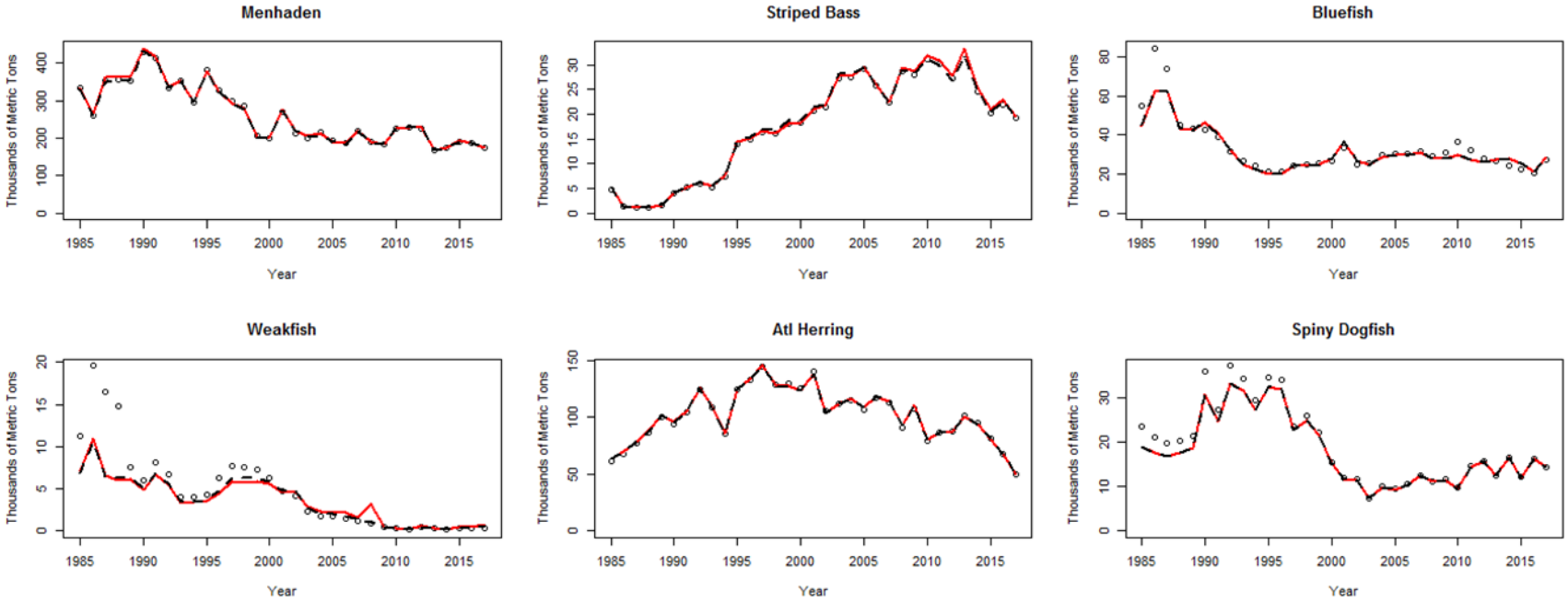


Figure 58. Observed (open circles), predicted with no trophic interactions (dashed black line), and predicted multispecies (solid red line) total annual catch from the VADER model.

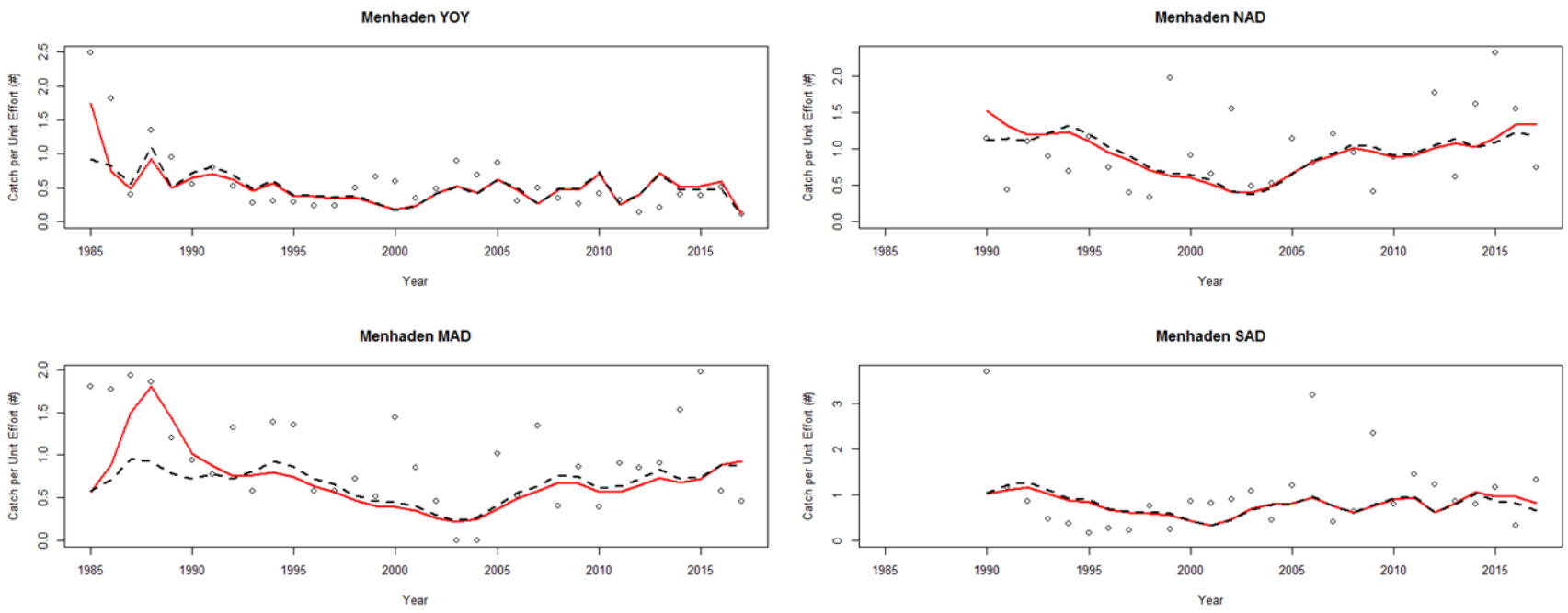


Figure 59. Observed (open circles), predicted with no trophic interactions (dashed black line), and predicted multispecies (solid red line) indices of abundance for Atlantic menhaden from the VADER model.

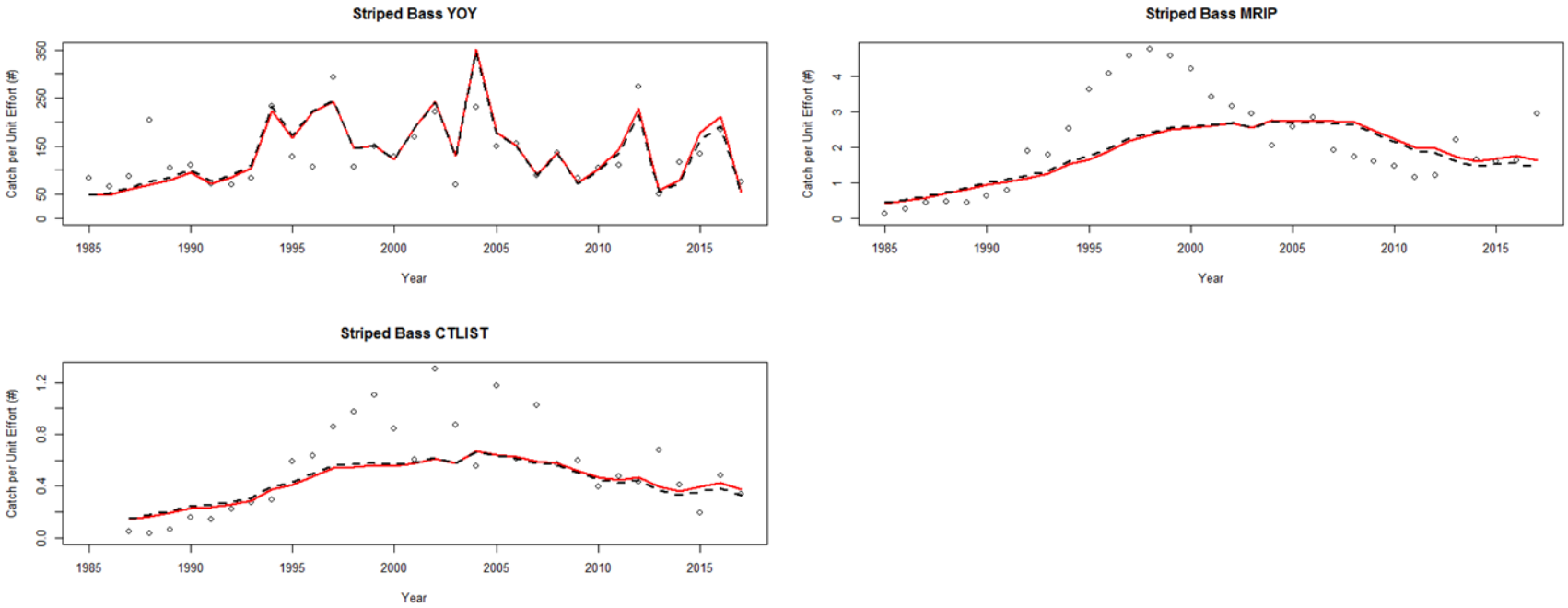


Figure 60. Observed (open circles), predicted with no trophic interactions (dashed black line), and predicted multispecies (solid red line) indices of abundance for striped bass from the VADER model.

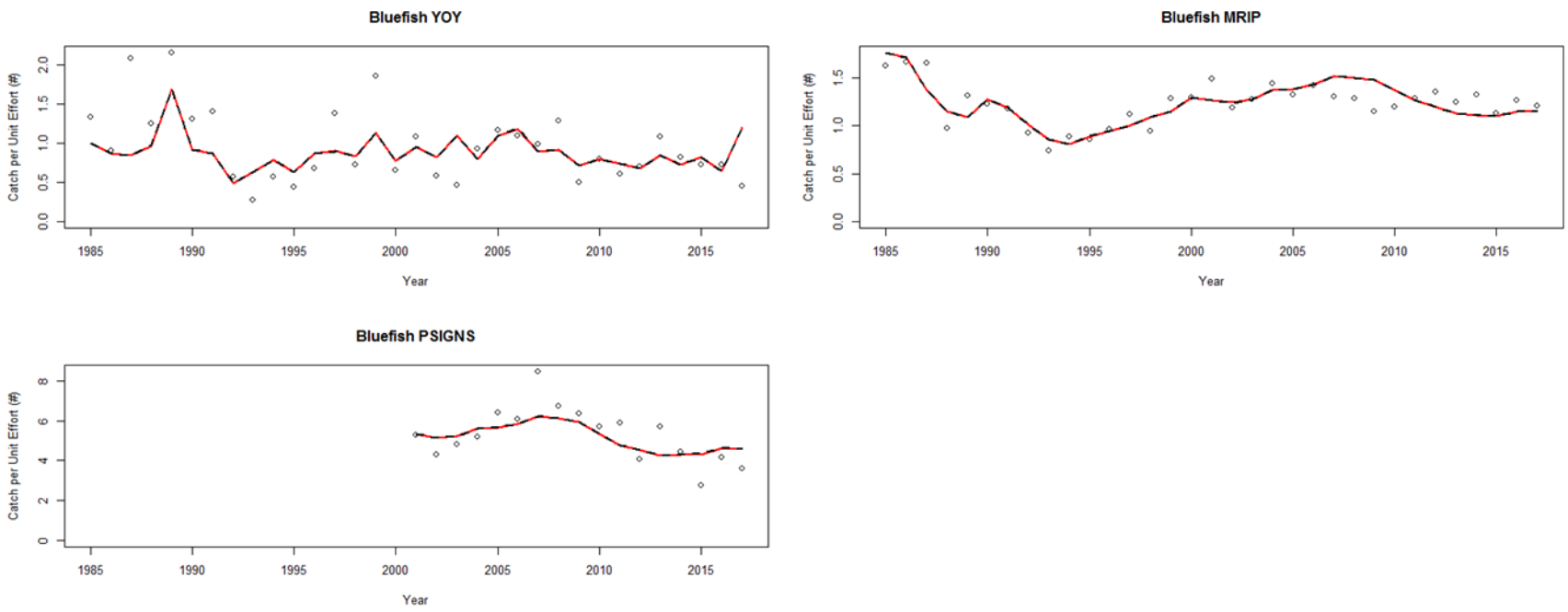


Figure 61. Observed (open circles), predicted with no trophic interactions (dashed black line), and predicted multispecies (solid red line) indices of abundance for bluefish from the VADER model.

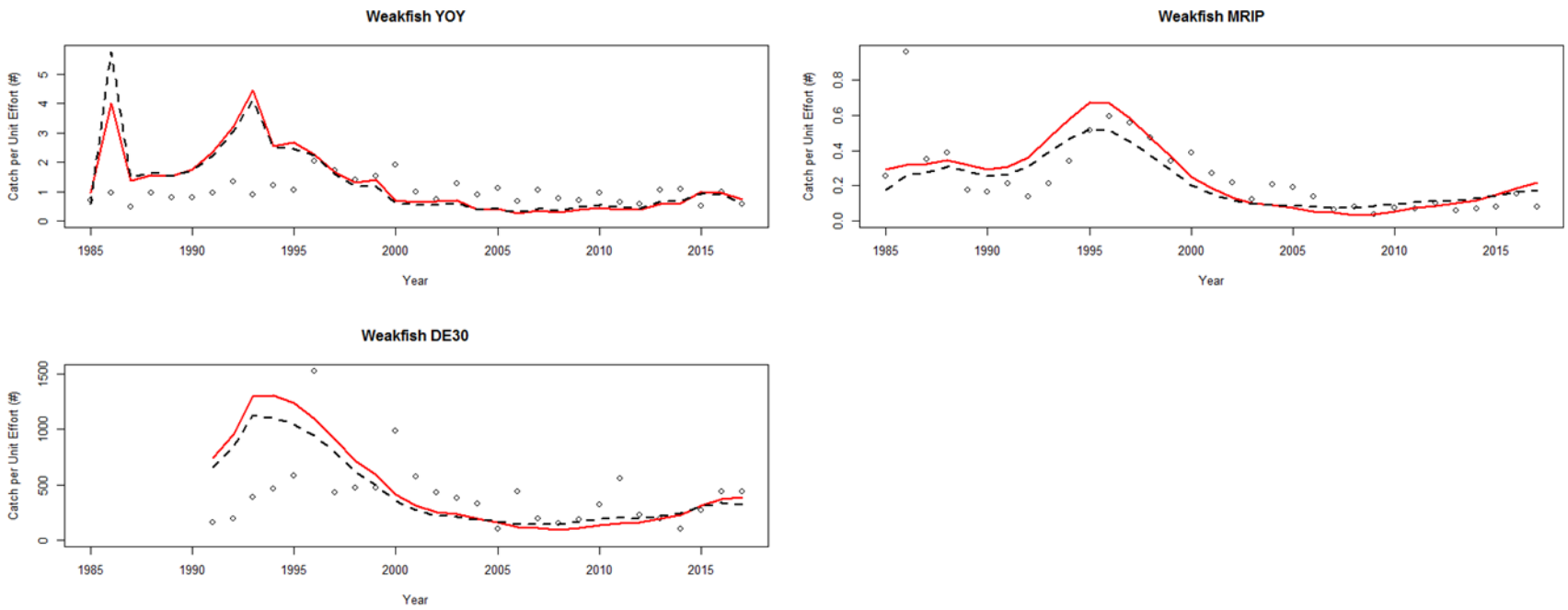


Figure 62. Observed (open circles), predicted with no trophic interactions (dashed black line), and predicted multispecies (solid red line) indices of abundance for weakfish from the VADER model.

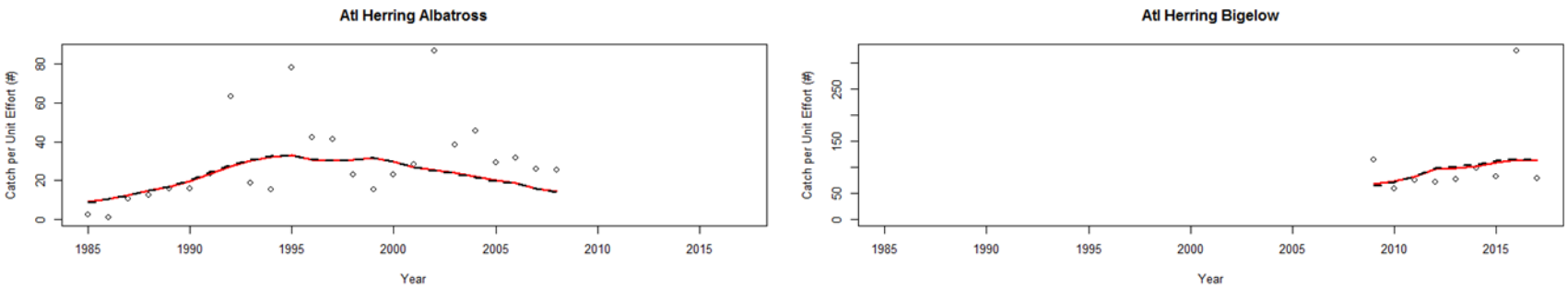


Figure 63. Observed (open circles), predicted with no trophic interactions (dashed black line), and predicted multispecies (solid red line) indices of abundance for Atlantic herring from the VADER model

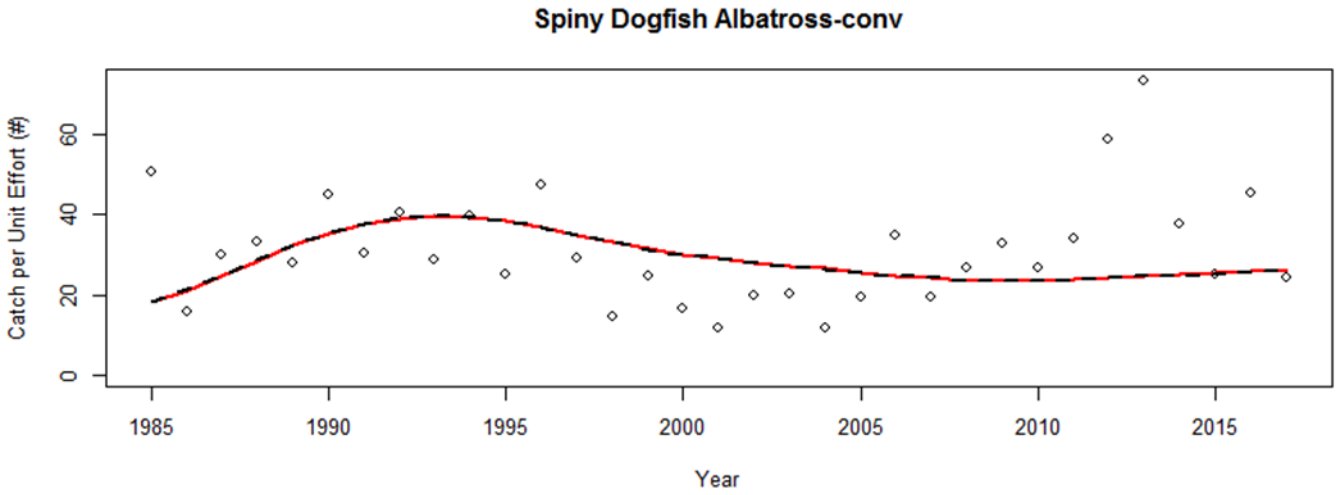


Figure 64. Observed (open circles), predicted with no trophic interactions (dashed black line), and predicted multispecies (solid red line) indices of abundance for spiny dogfish from the VADER model

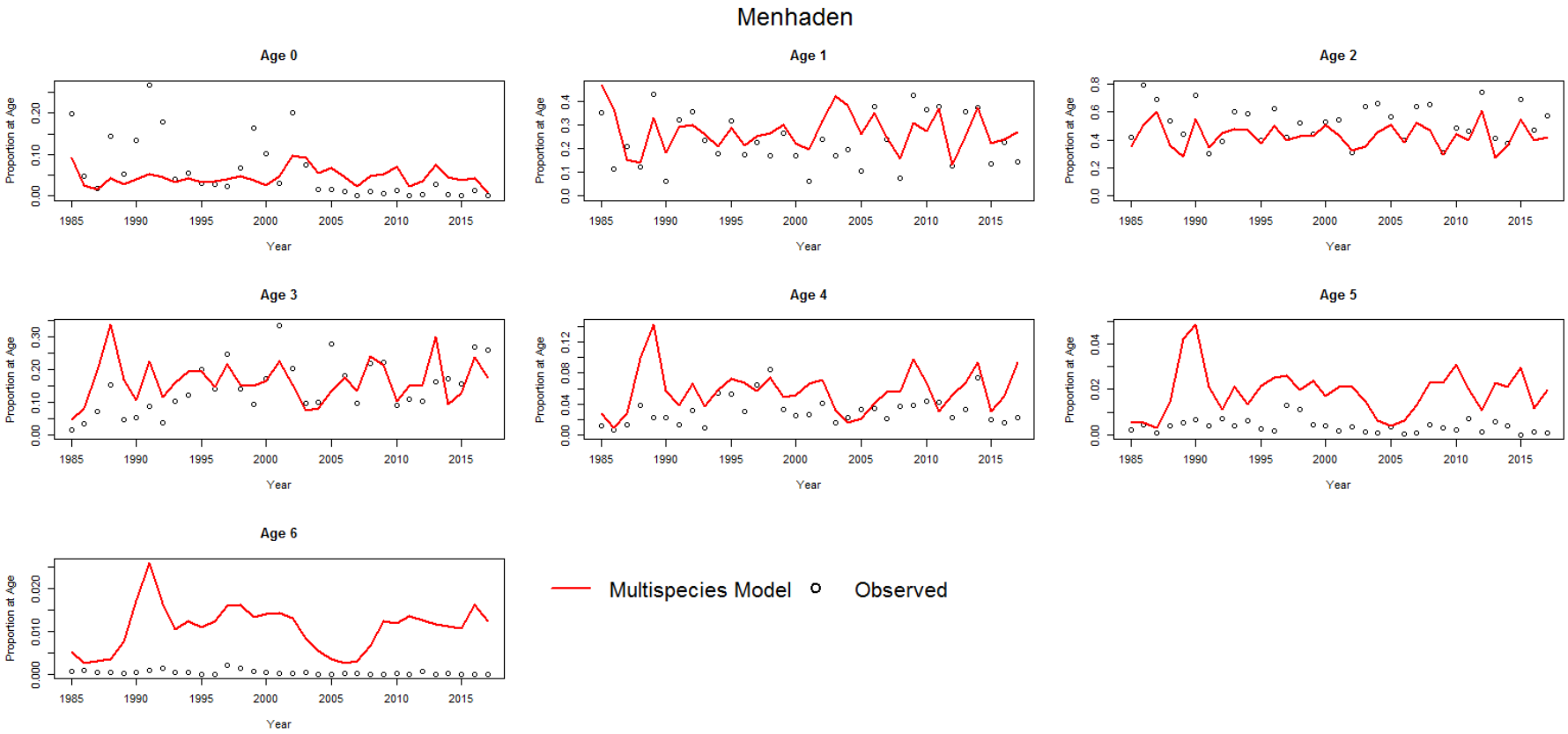


Figure 65. Observed (open circles) and predicted multispecies (solid red line) total catch age proportions for Atlantic menhaden from the VADER model.

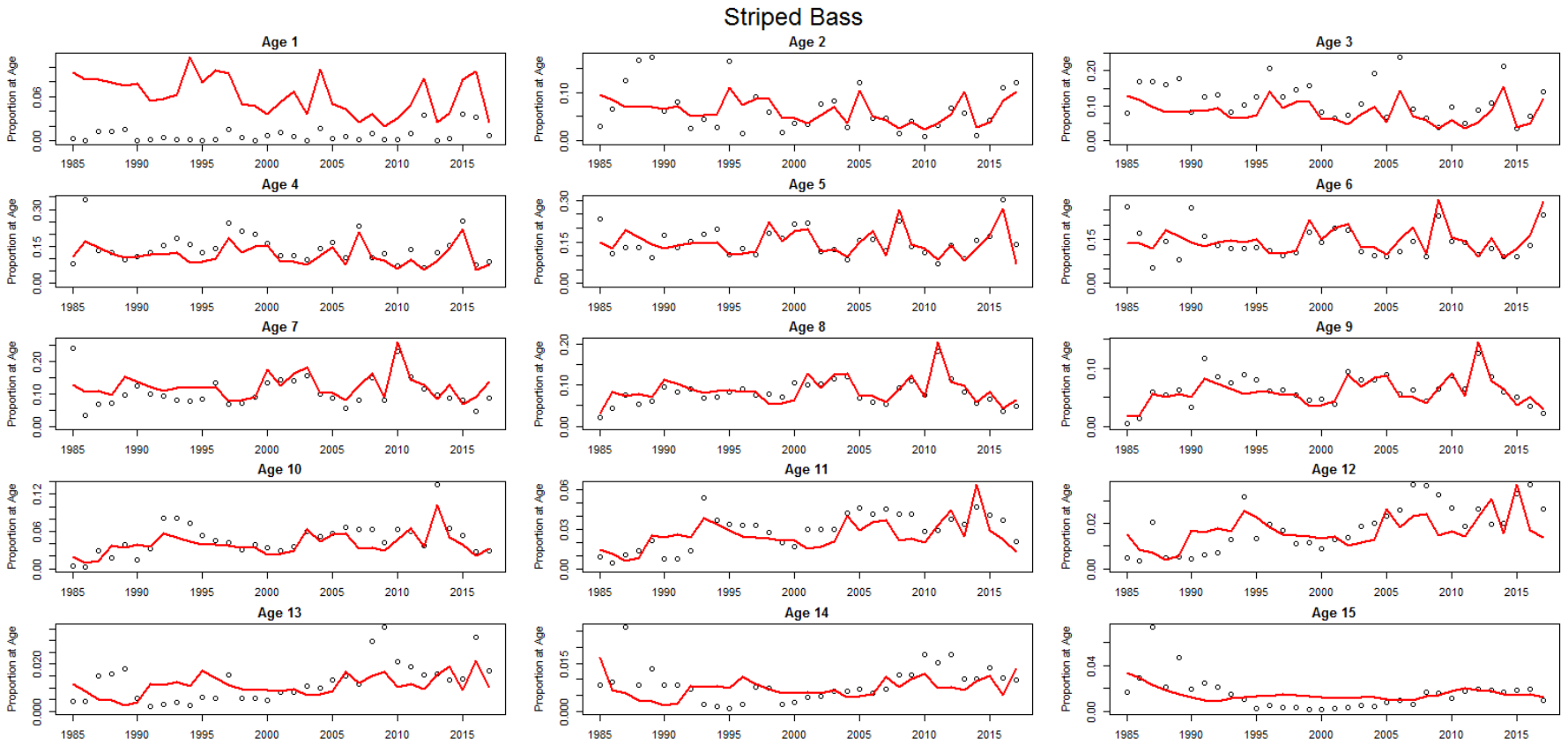


Figure 66. Observed (open circles) and predicted multispecies (solid red line) total catch age proportions for striped bass from the VADER model.

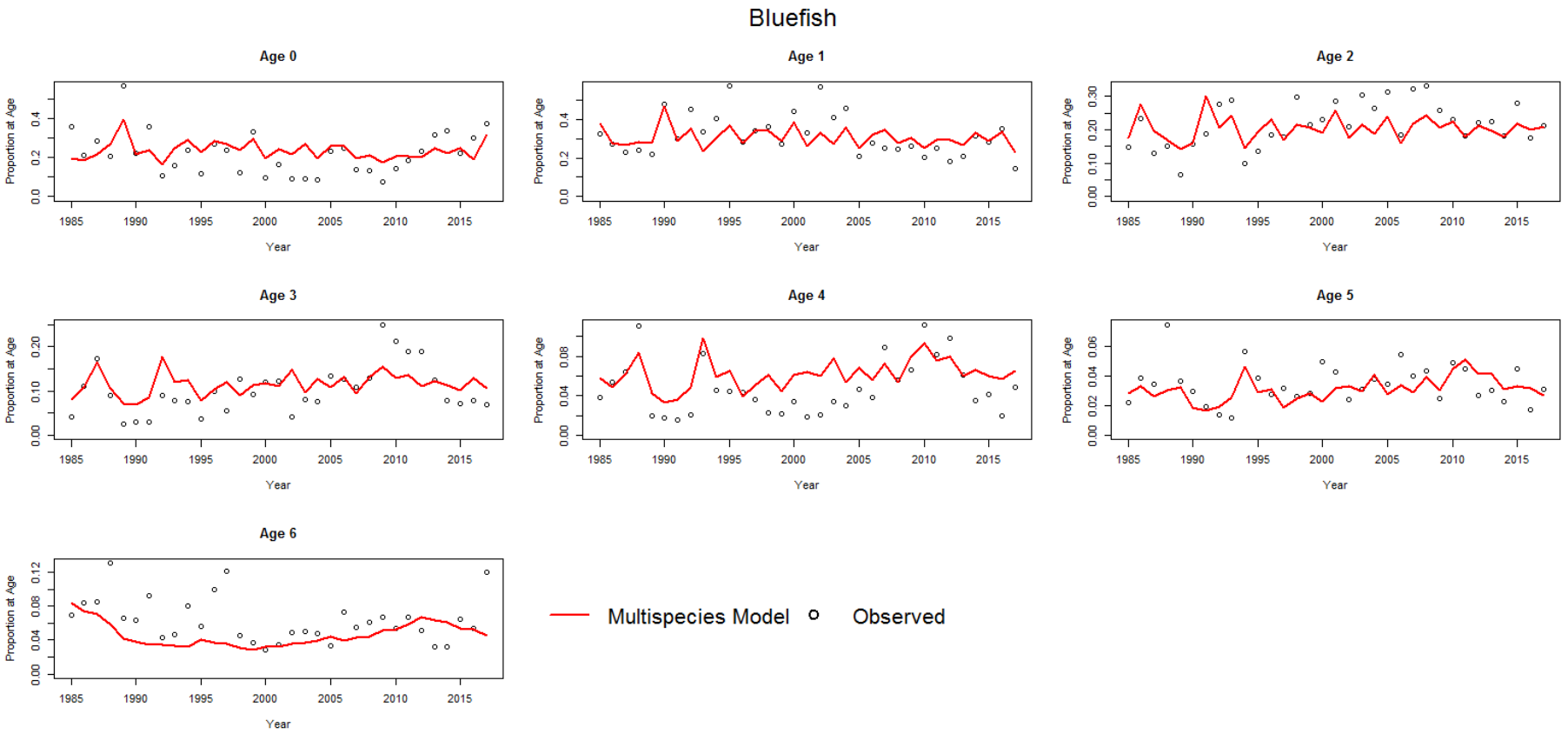


Figure 67. Observed (open circles) and predicted multispecies (solid red line) total catch age proportions for bluefish from the VADER model.

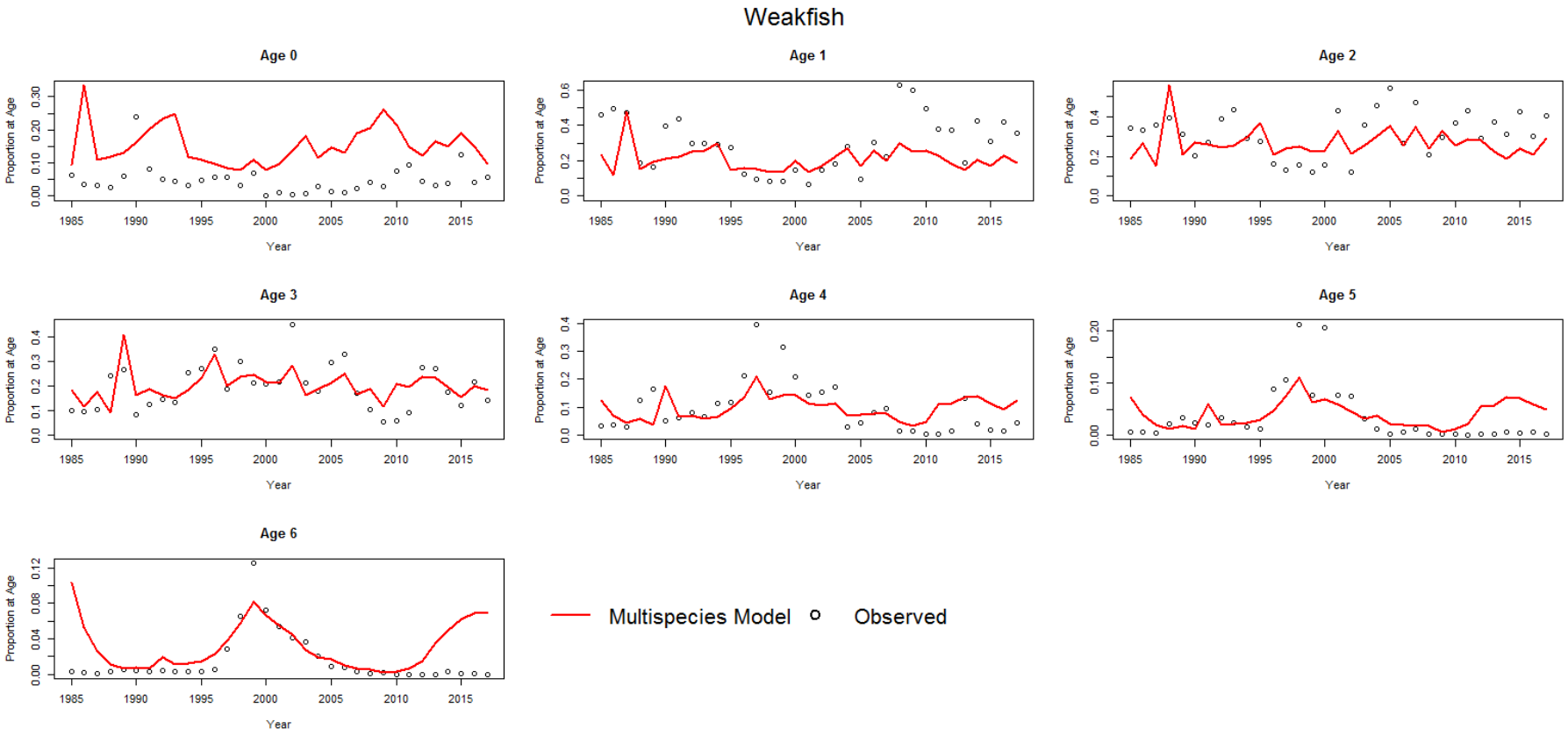


Figure 68. Observed (open circles) and predicted multispecies (solid red line) total catch age proportions for weakfish from the VADER model.

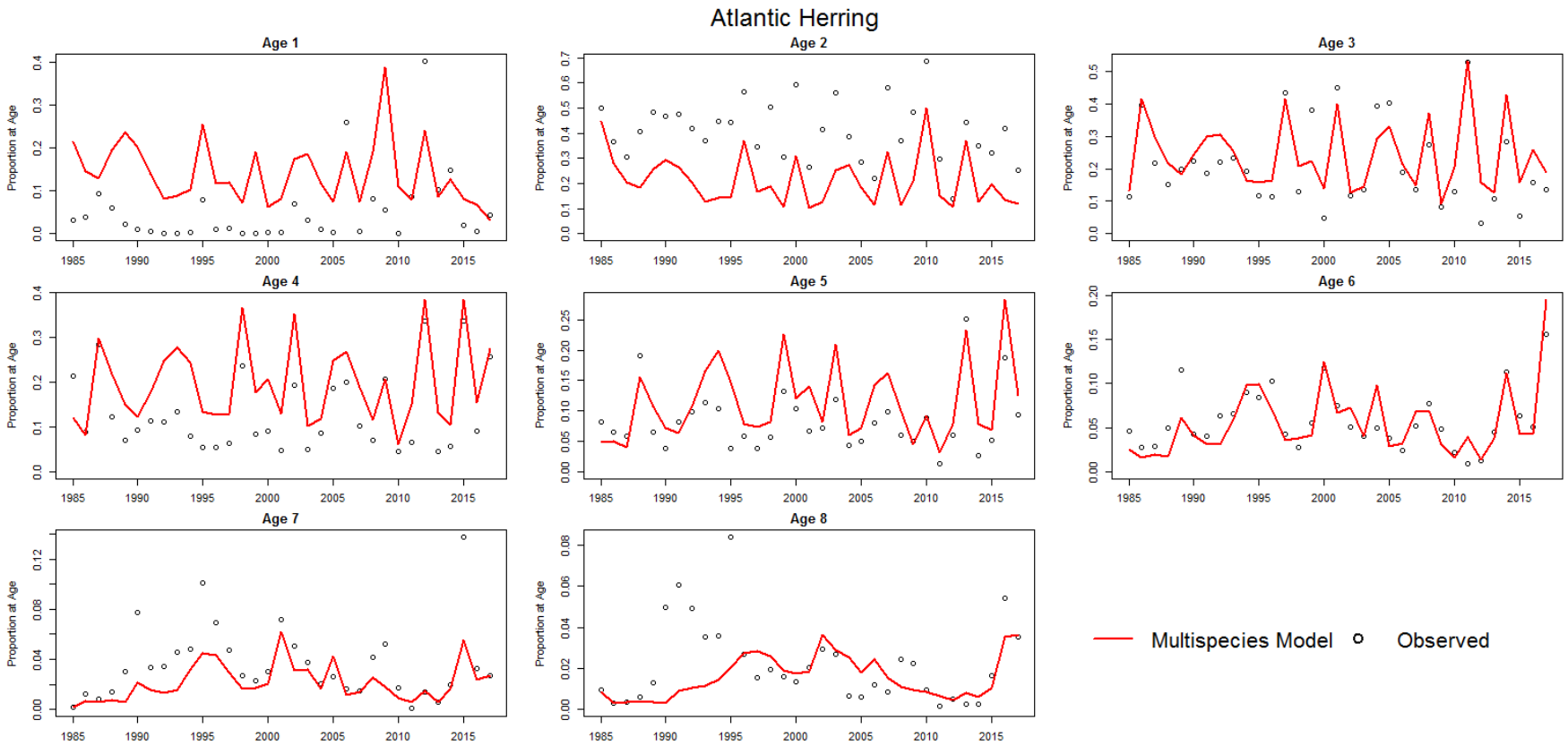


Figure 69. Observed (open circles) and predicted multispecies (solid red line) total catch age proportions for Atlantic herring from the VADER model.

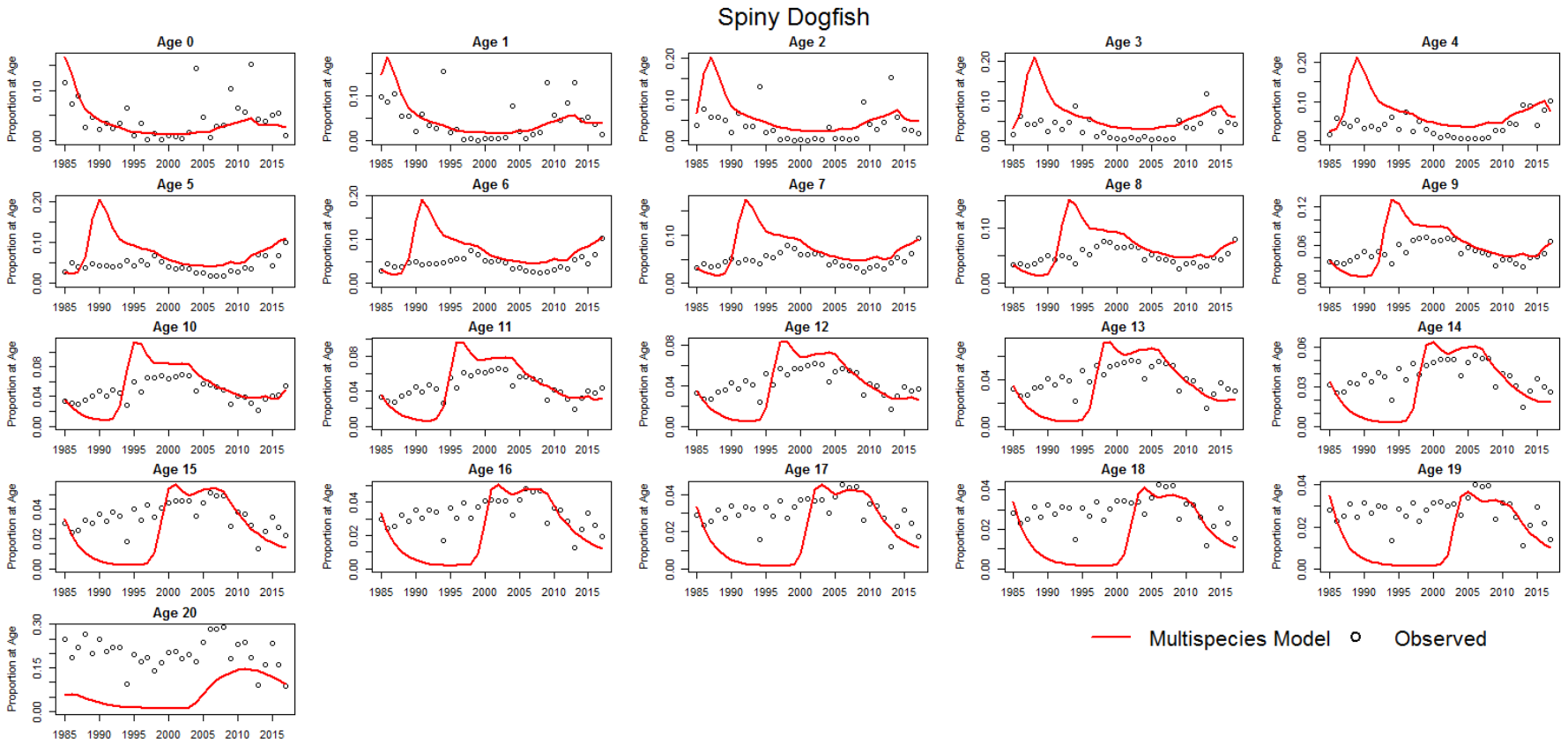


Figure 70. Observed (open circles) and predicted multispecies (solid red line) total catch age proportions for spiny dogfish from the VADER model.

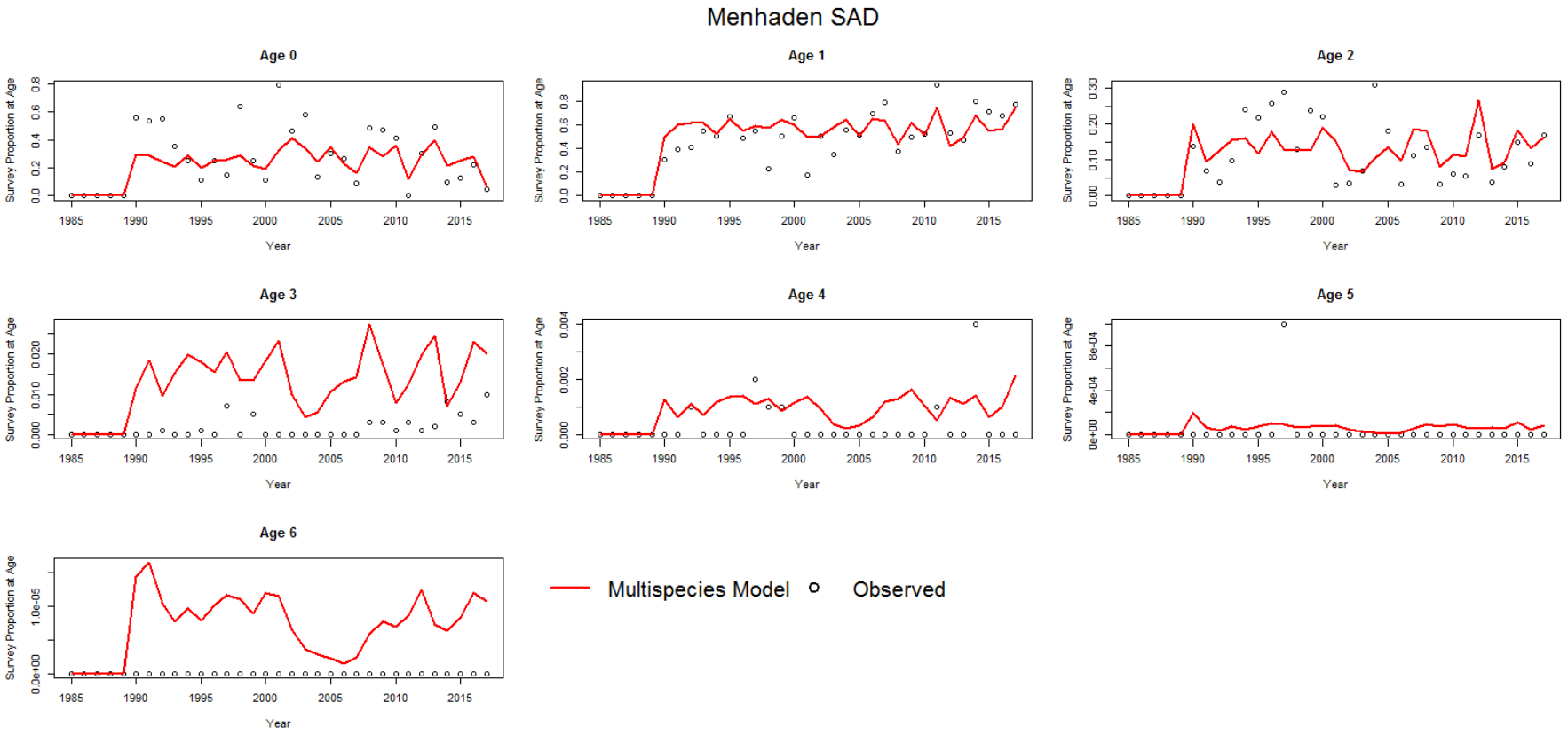


Figure 71. Observed (open circles) and predicted multispecies (solid red line) age proportions for Atlantic menhaden SAD survey from the VADER model.

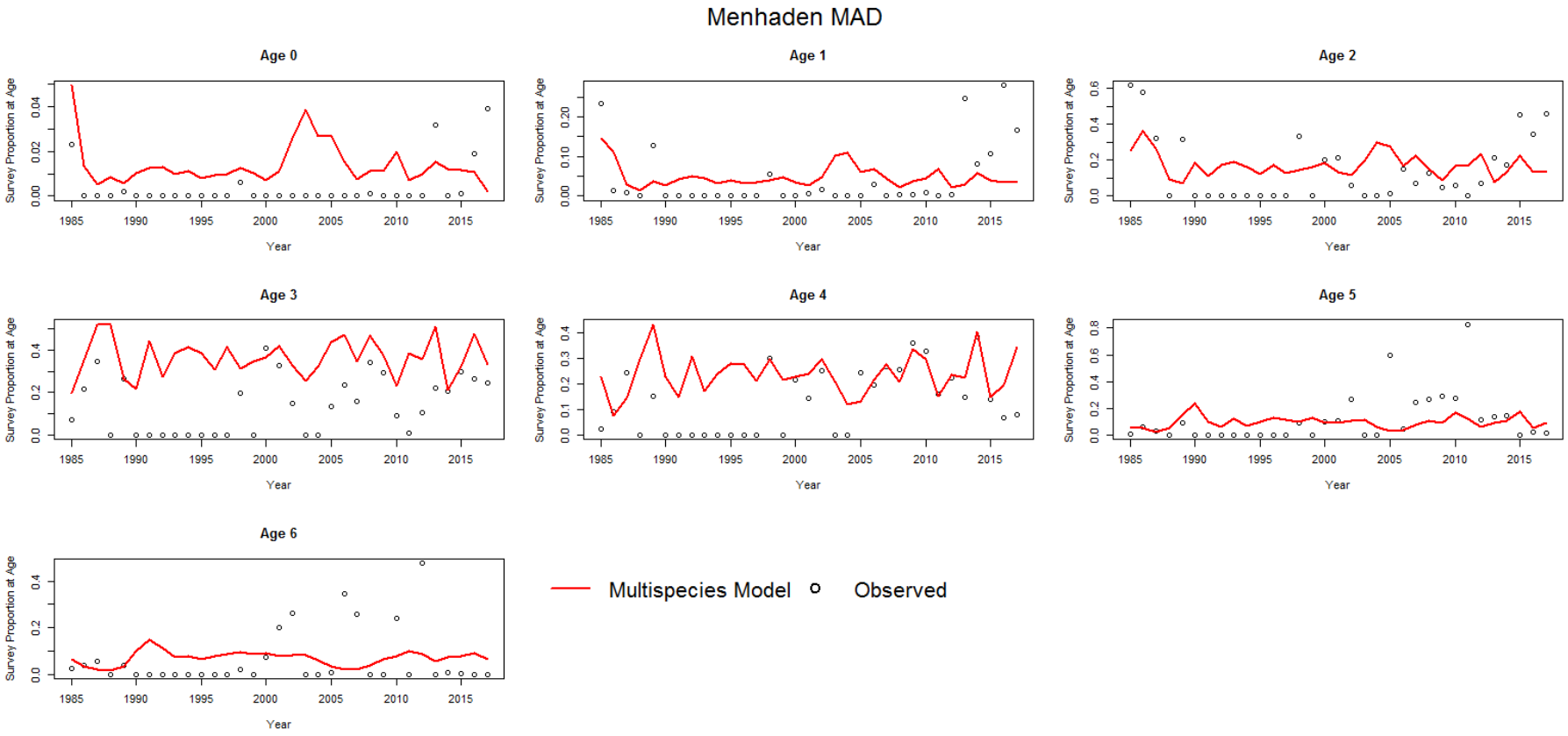


Figure 72. Observed (open circles) and predicted multispecies (solid red line) age proportions for Atlantic menhaden MAD survey from the VADER model.

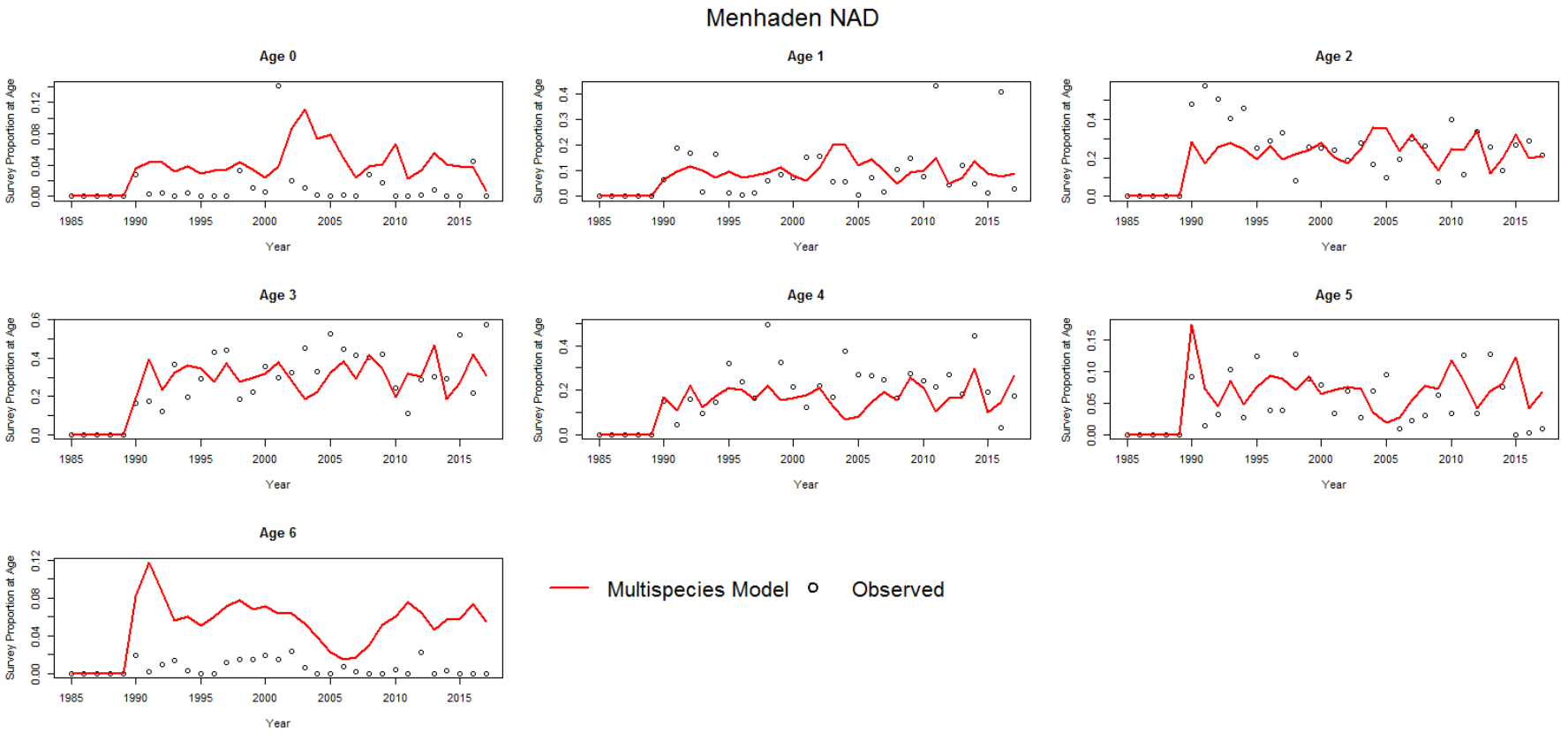


Figure 73. Observed (open circles) and predicted multispecies (solid red line) age proportions for Atlantic menhaden NAD survey from the VADER model.

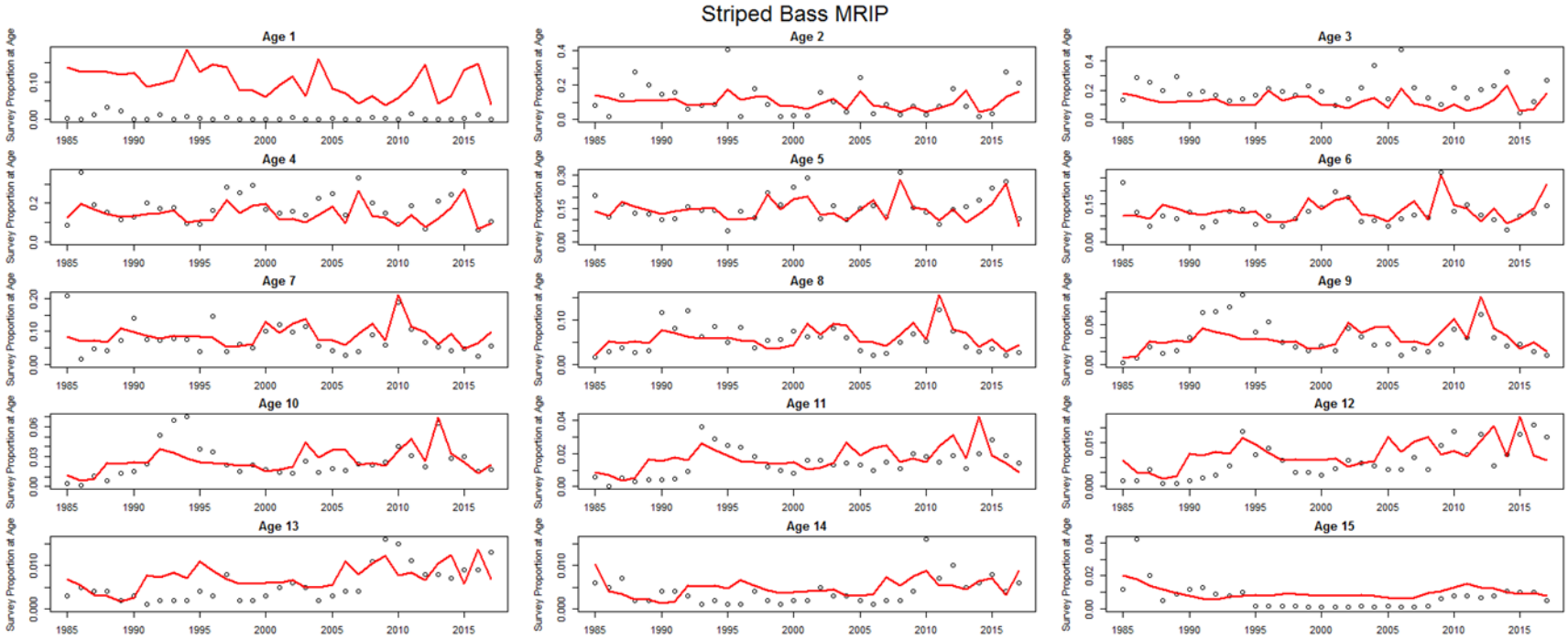


Figure 74. Observed (open circles) and predicted multispecies (solid red line) age proportions for striped bass MRIP CPUE survey from the VADER model.

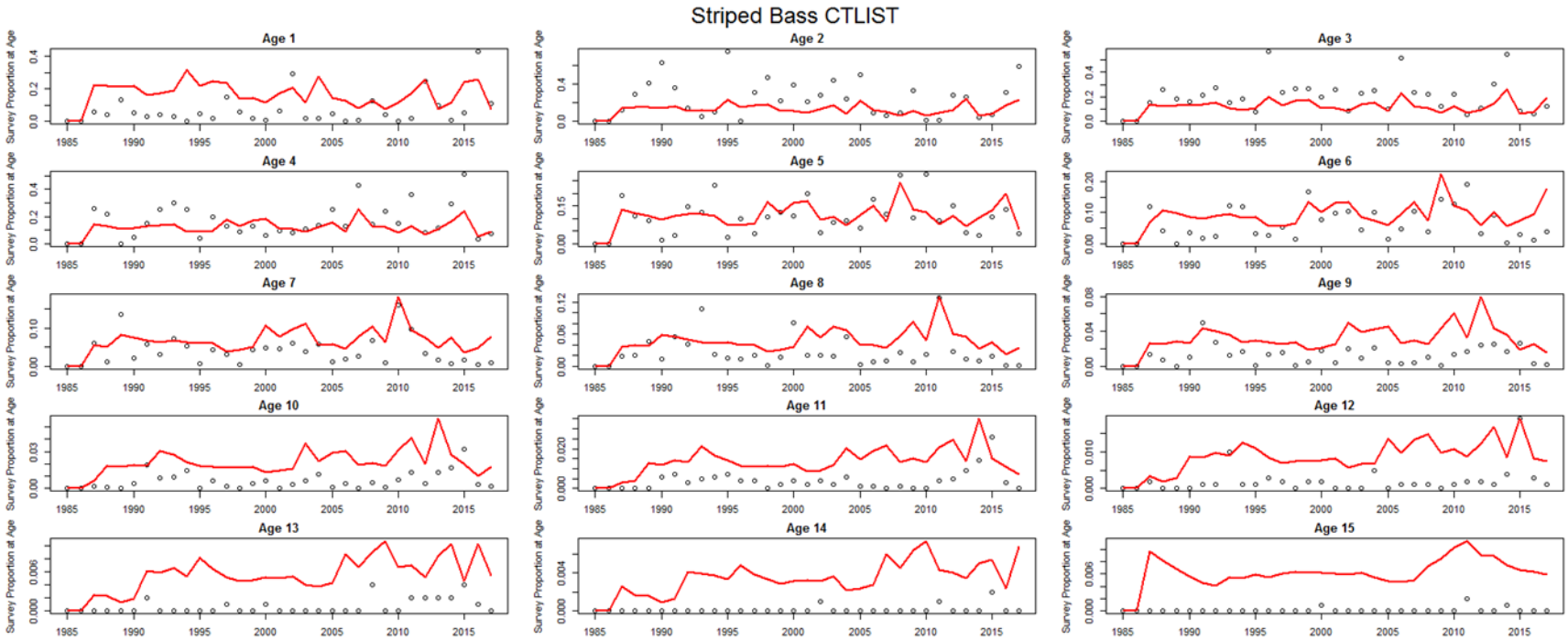


Figure 75. Observed (open circles) and predicted multispecies (solid red line) age proportions for striped bass CT LIST survey from the VADER model.

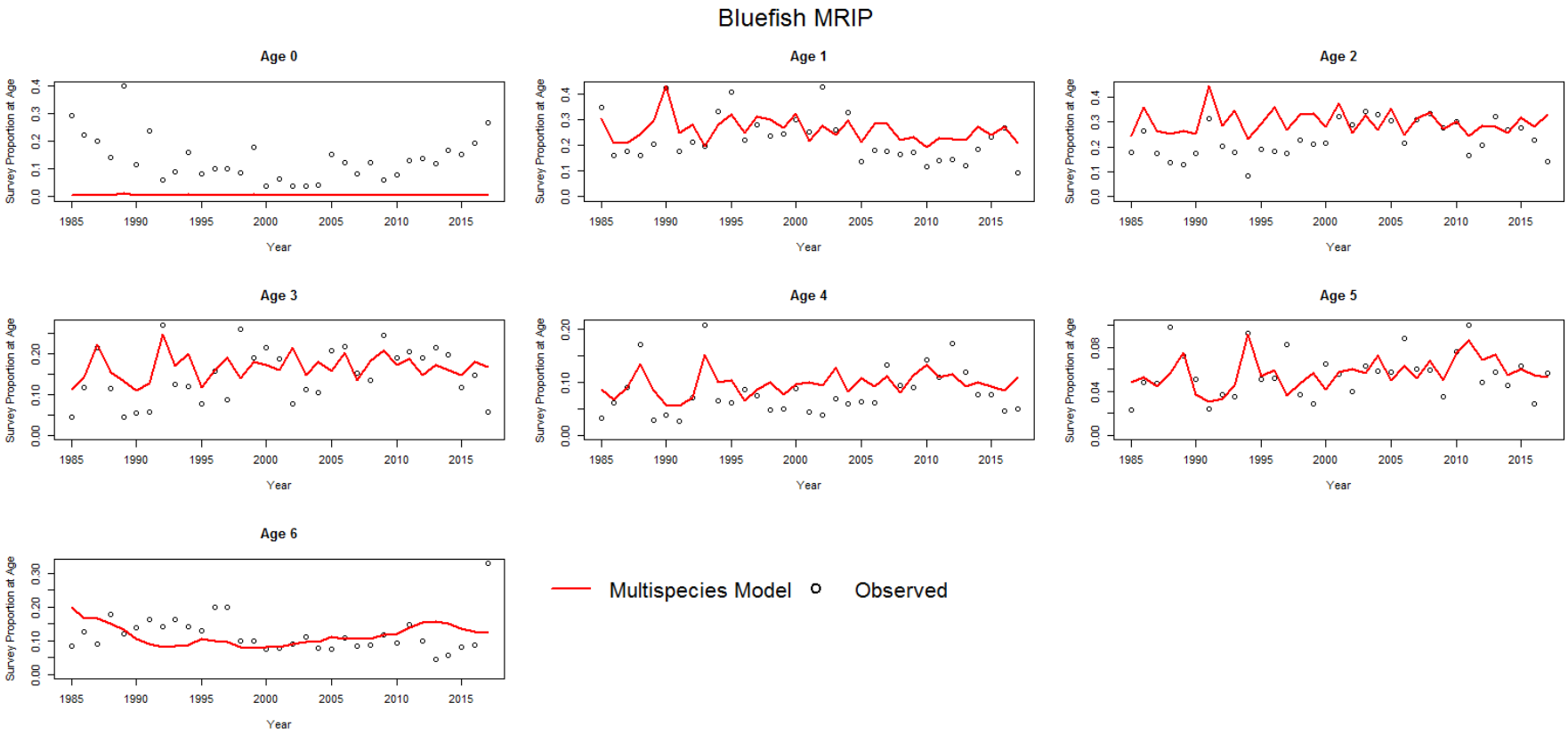


Figure 76. Observed (open circles) and predicted multispecies (solid red line) age proportions for bluefish MRIP CPUE survey from the VADER model.

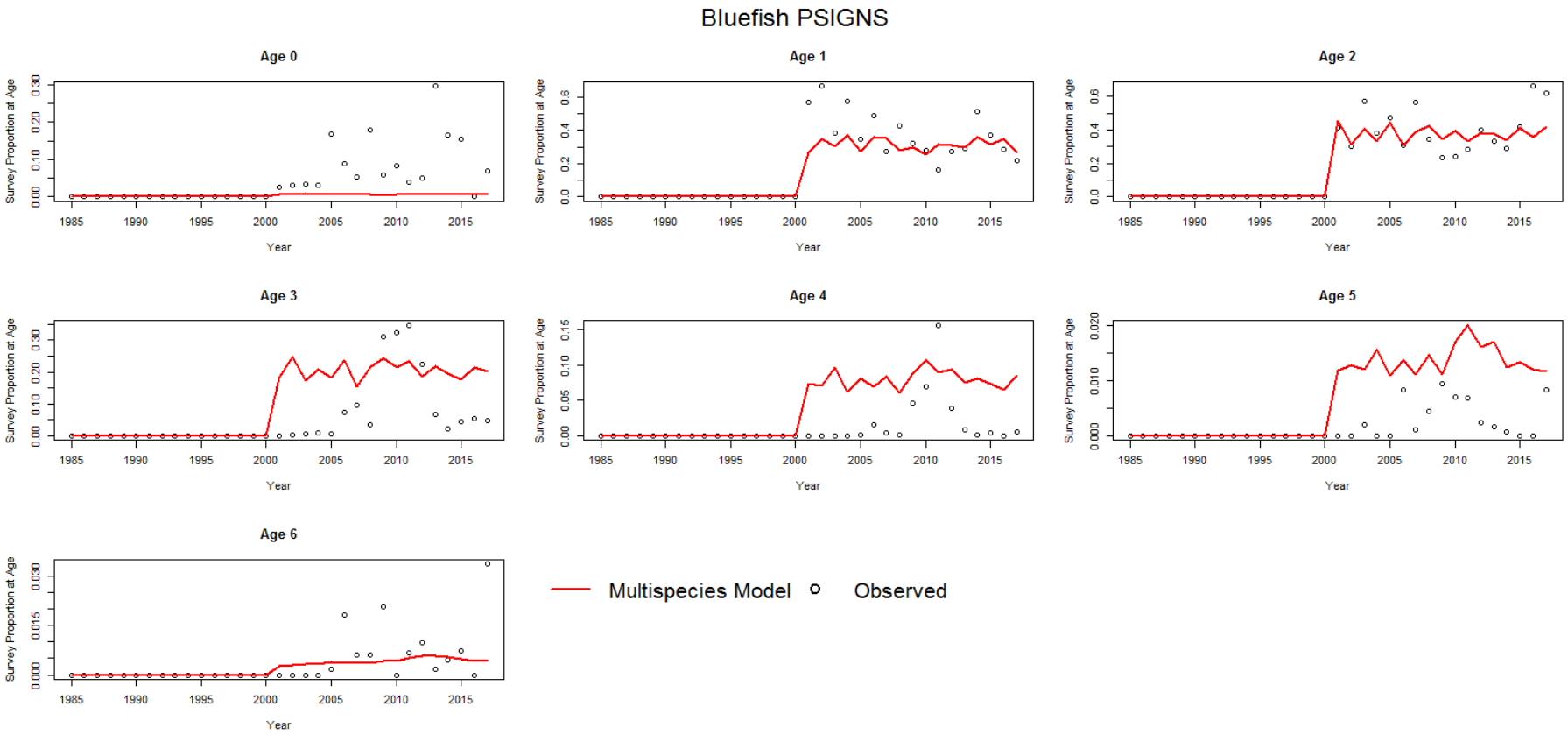


Figure 77. Observed (open circles) and predicted multispecies (solid red line) age proportions for bluefish NC PSIGNS survey from the VADER model.

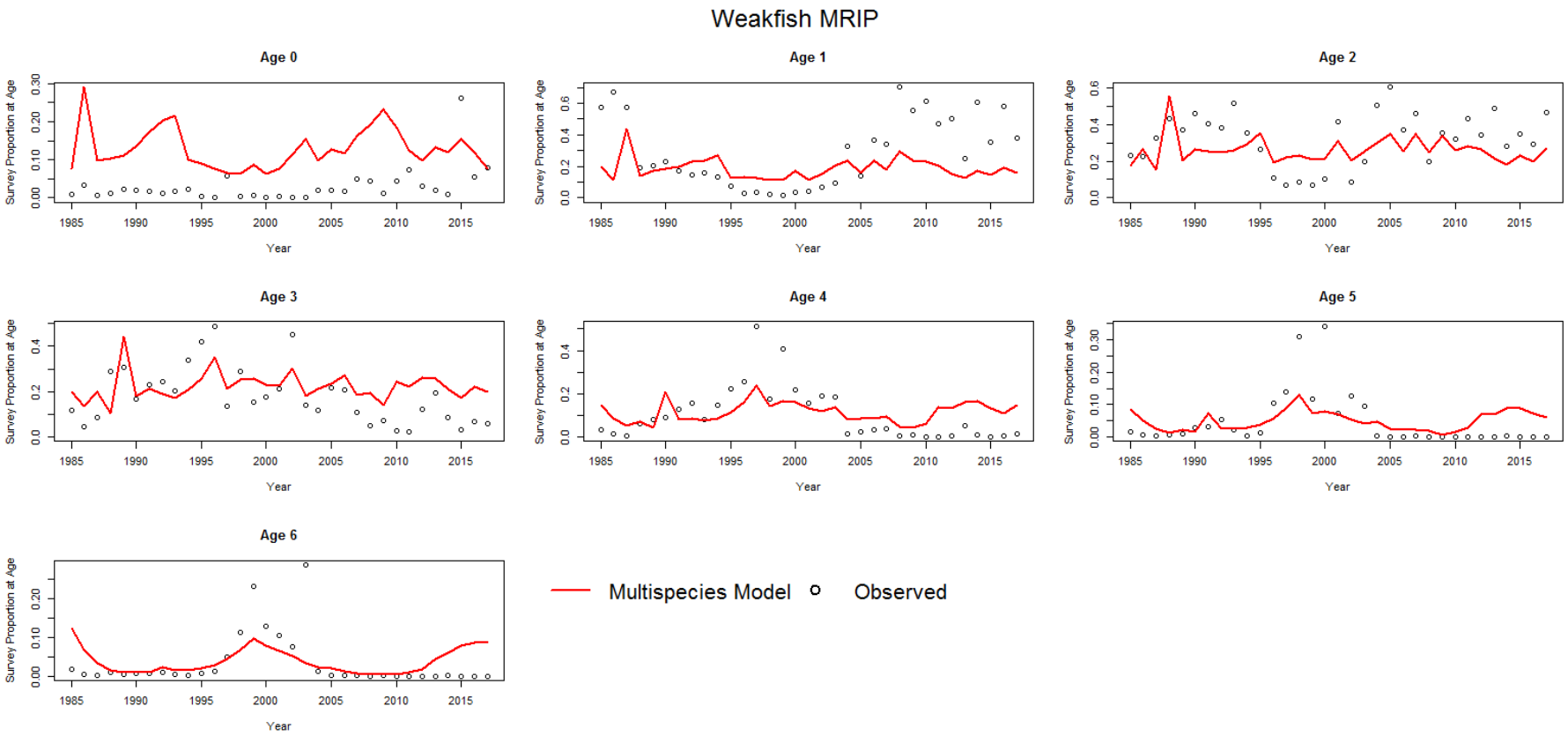


Figure 78. Observed (open circles) and predicted multispecies (solid red line) age proportions for weakfish MRIP CPUE survey from the VADER model.

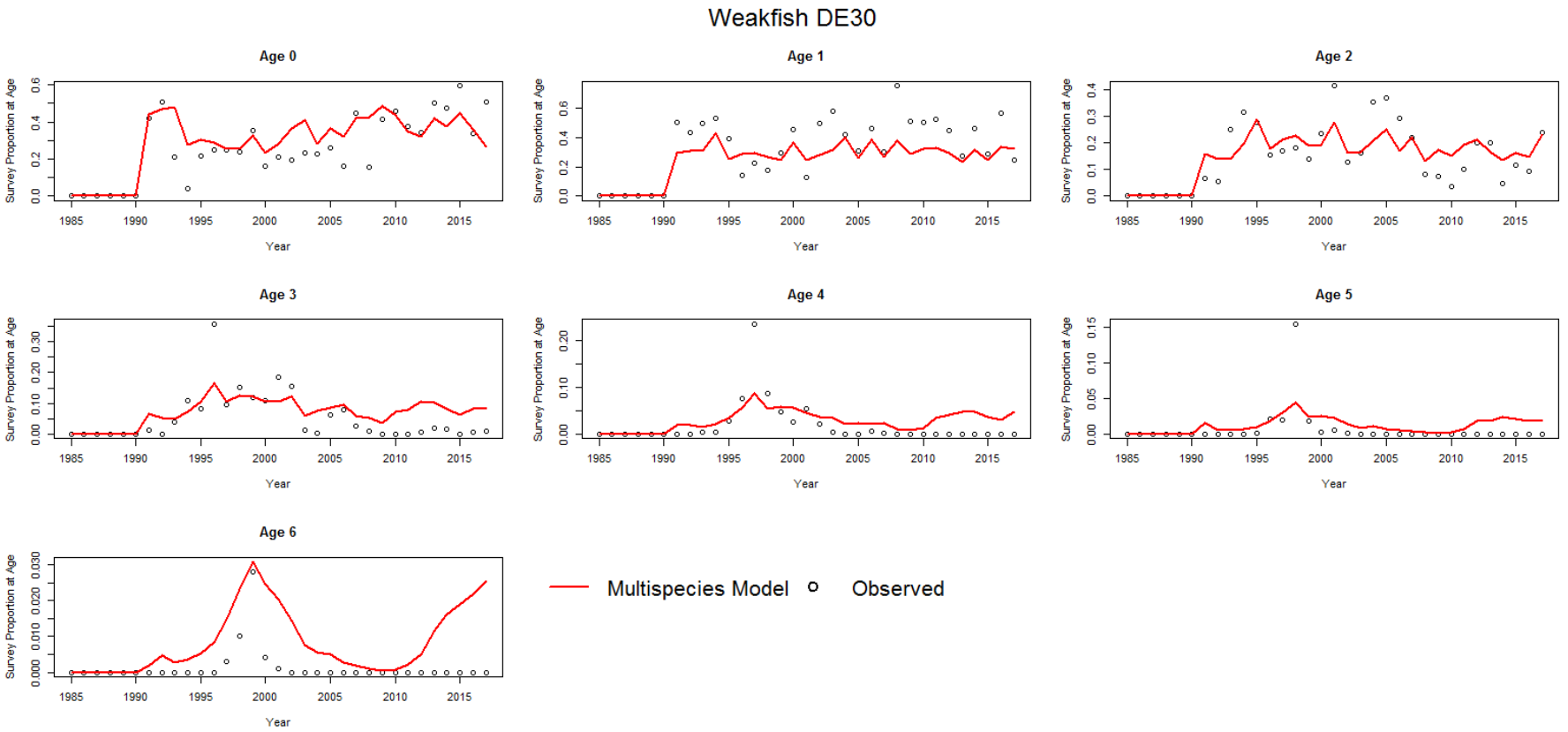


Figure 79. Observed (open circles) and predicted multispecies (solid red line) age proportions for weakfish DE 30' Trawl survey from the VADER model.

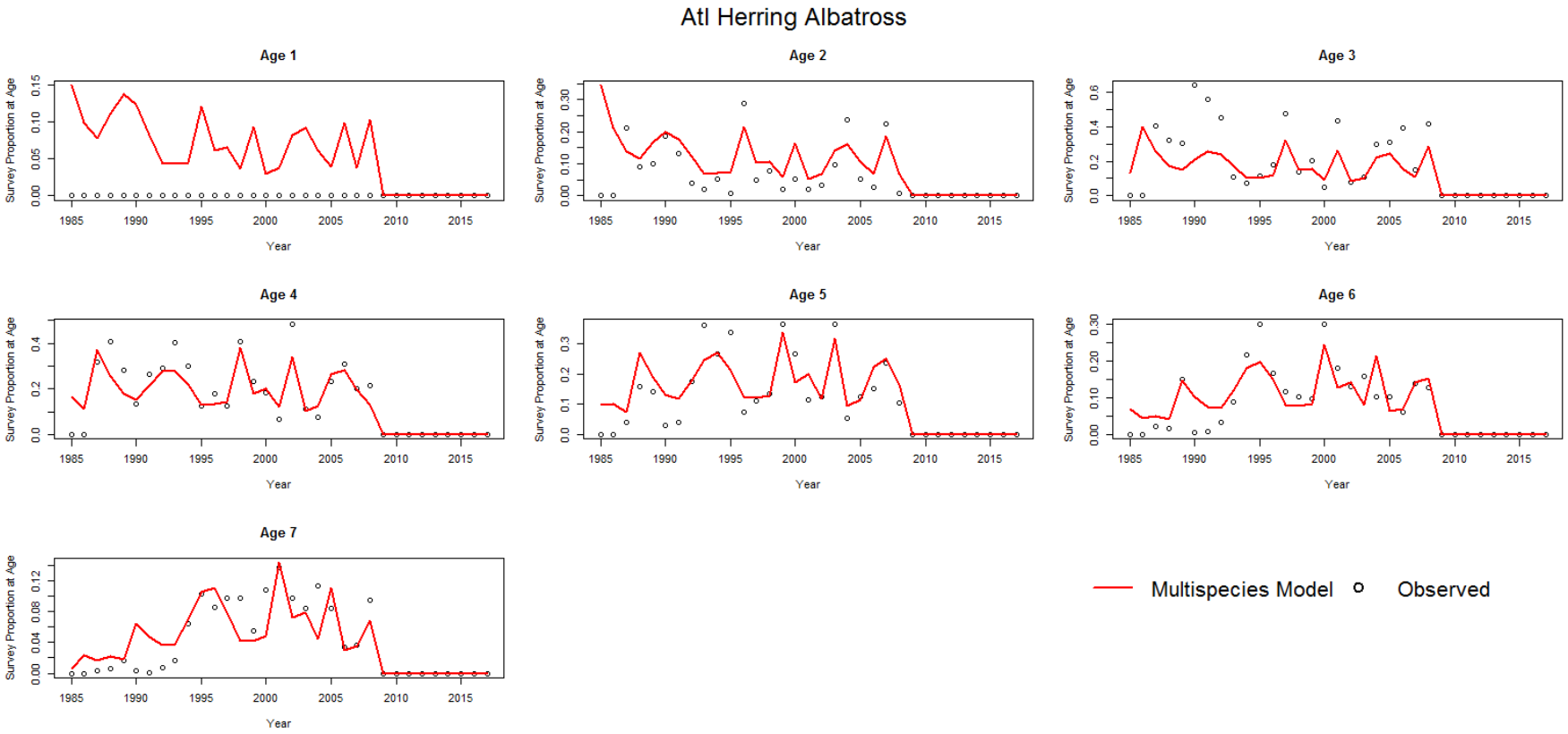


Figure 80. Observed (open circles) and predicted multispecies (solid red line) age proportions for Atlantic herring NEFSC Fall Albatross survey from the VADER model.

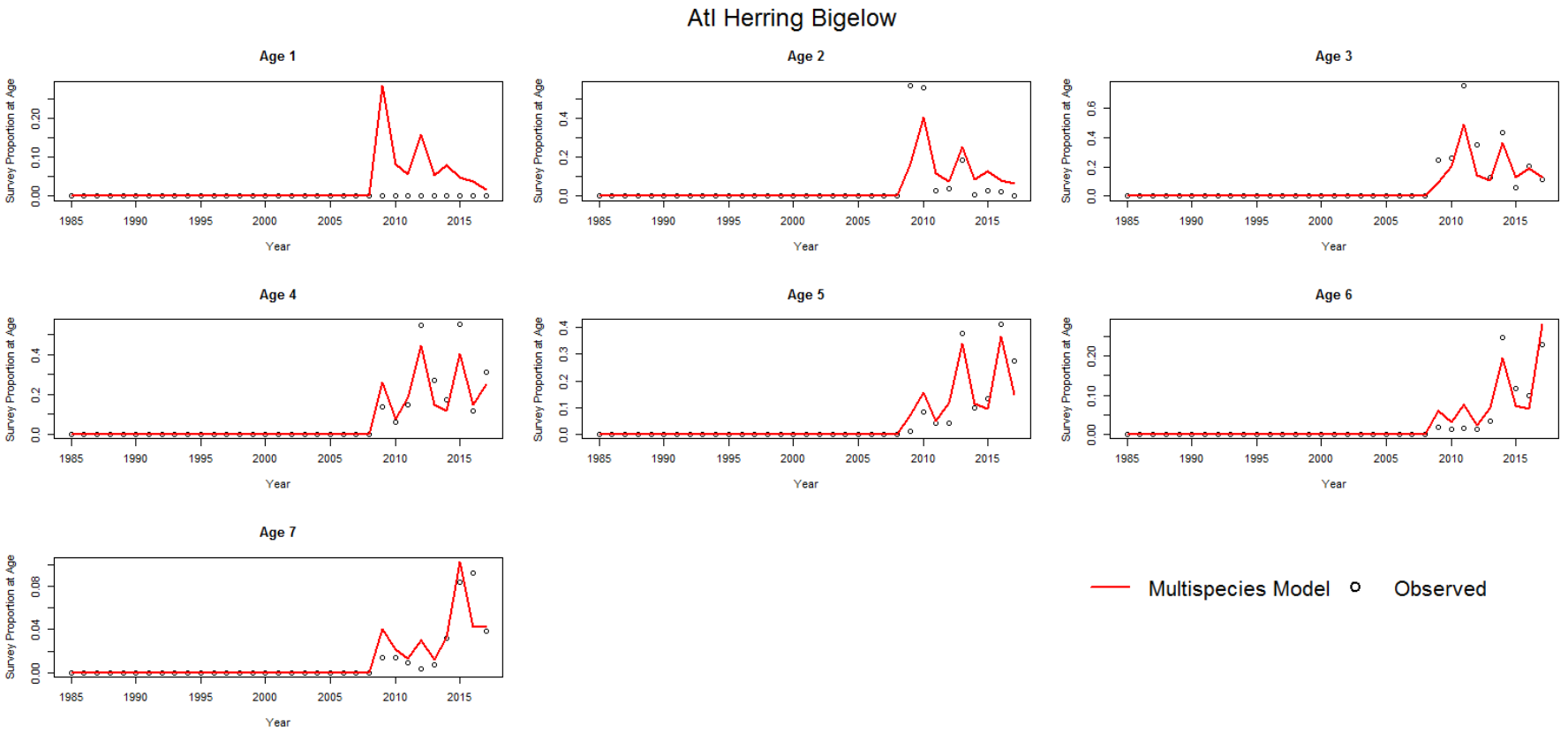


Figure 81. Observed (open circles) and predicted multispecies (solid red line) age proportions for Atlantic herring NEFSC Fall Bigelow survey from the VADER model.

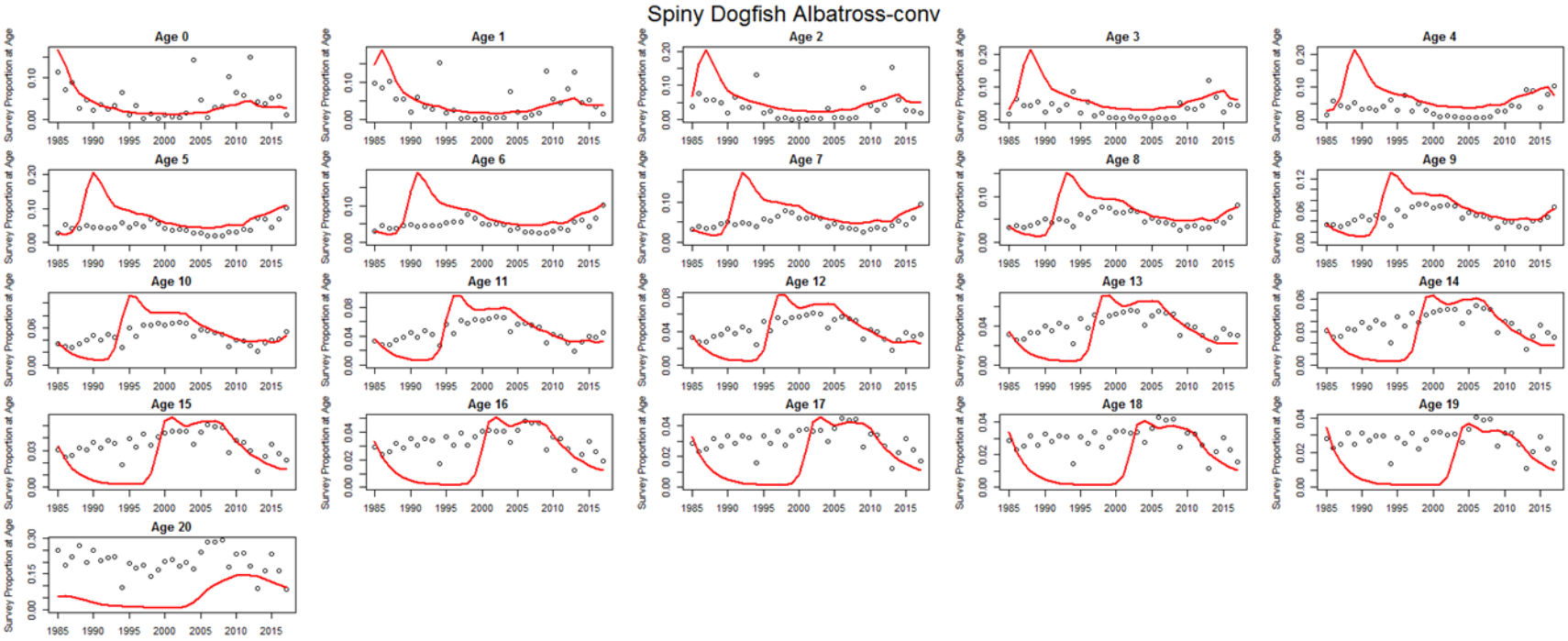


Figure 82. Observed (open circles) and predicted multispecies (solid red line) age proportions for spiny dogfish Albatross survey from the VADER model.

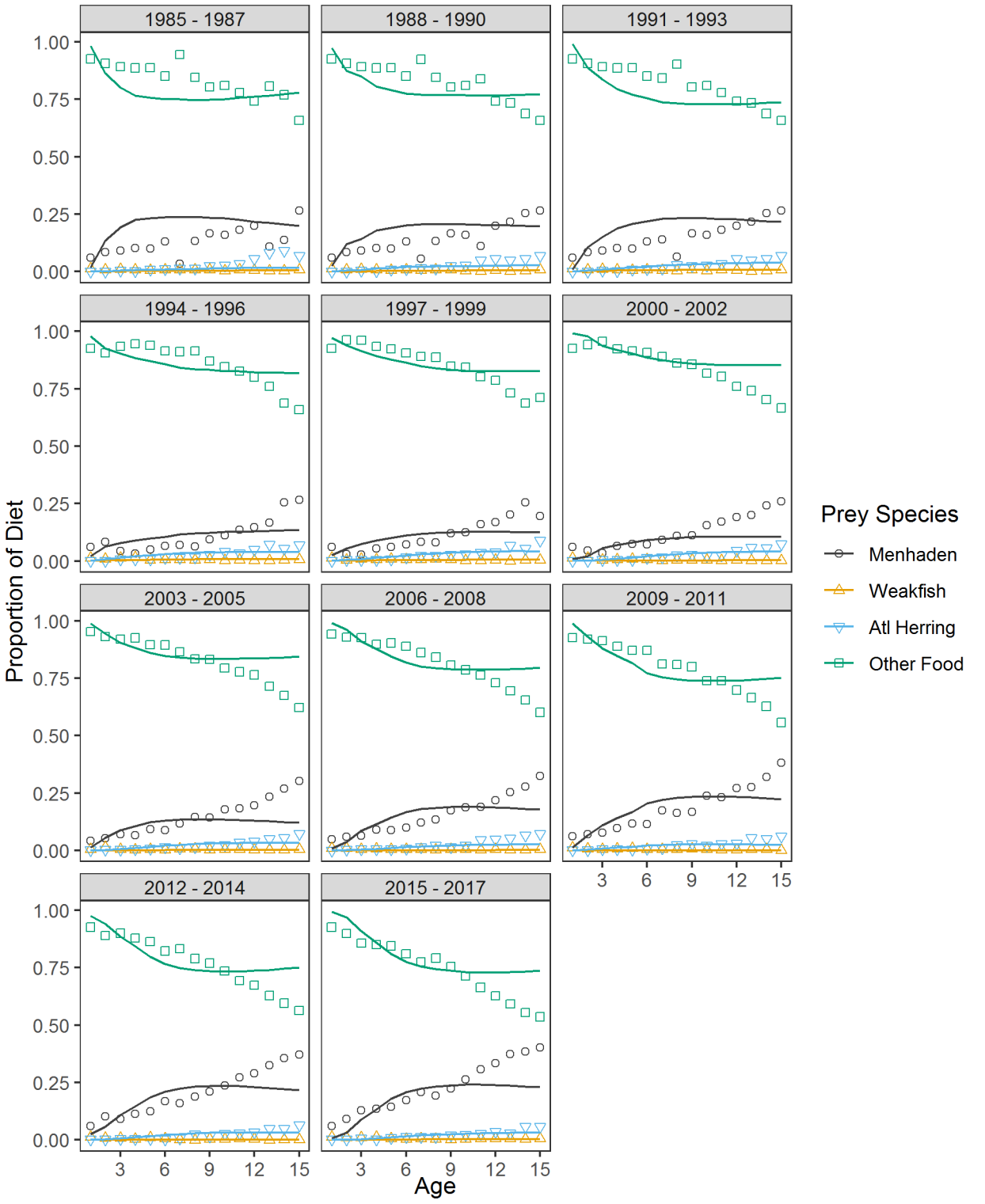


Figure 83. Observed (open points) and predicted (solid lines) diet composition data for striped bass from the VADER model.

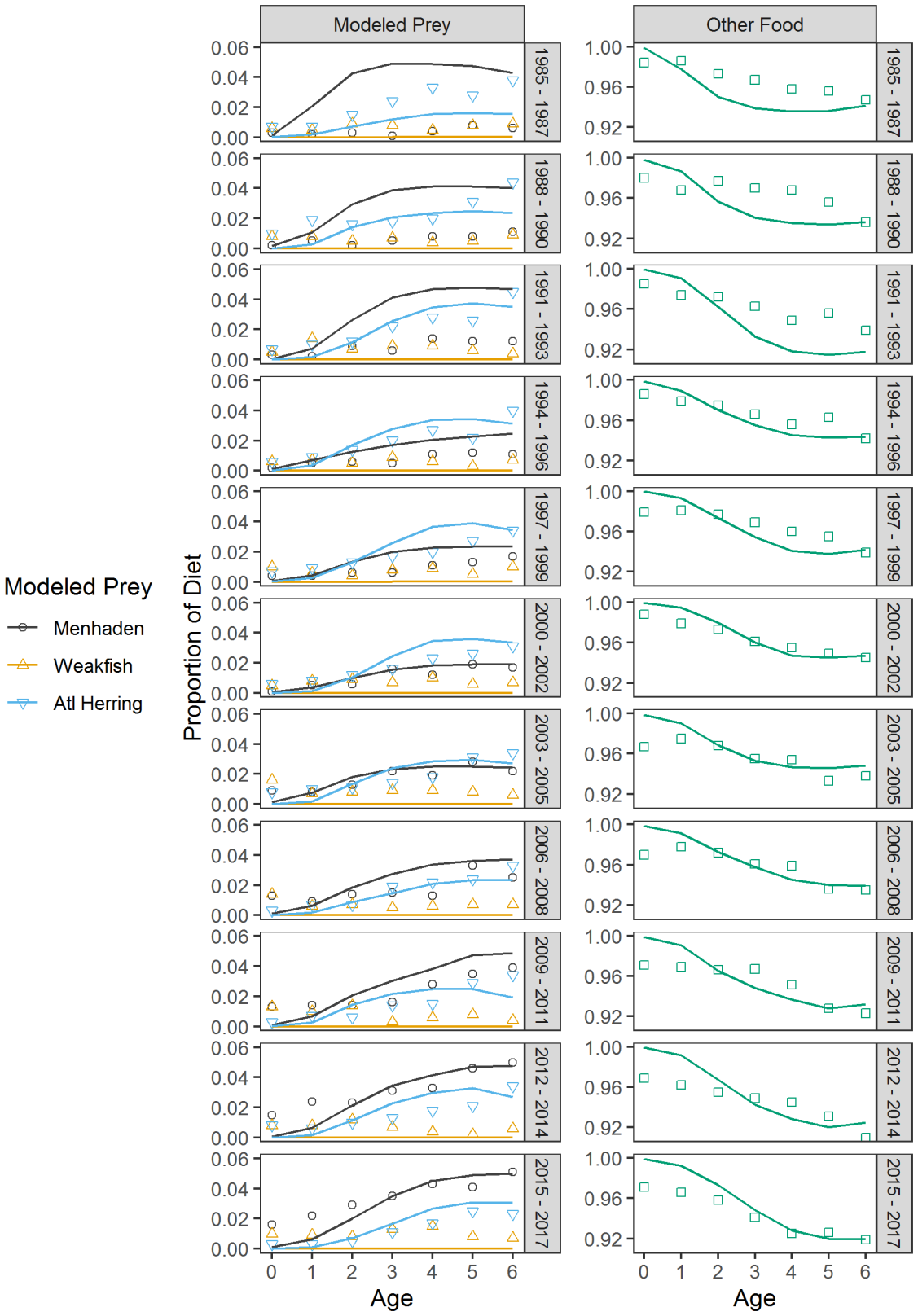


Figure 84. Observed (open points) and predicted (solid lines) diet composition data for bluefish from the VADER model.

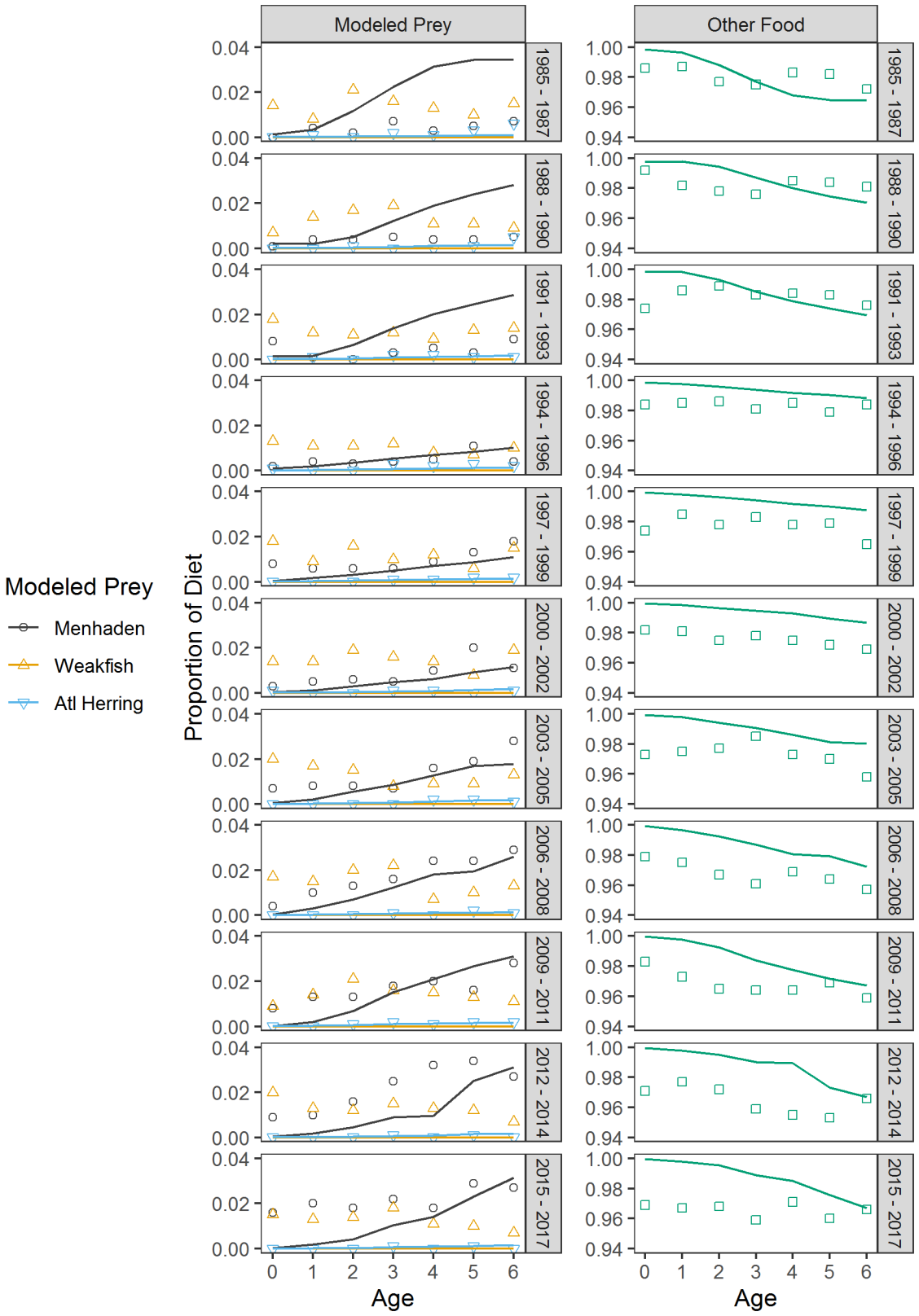


Figure 85. Observed (open points) and predicted (solid lines) diet composition data for weakfish from the VADER model.

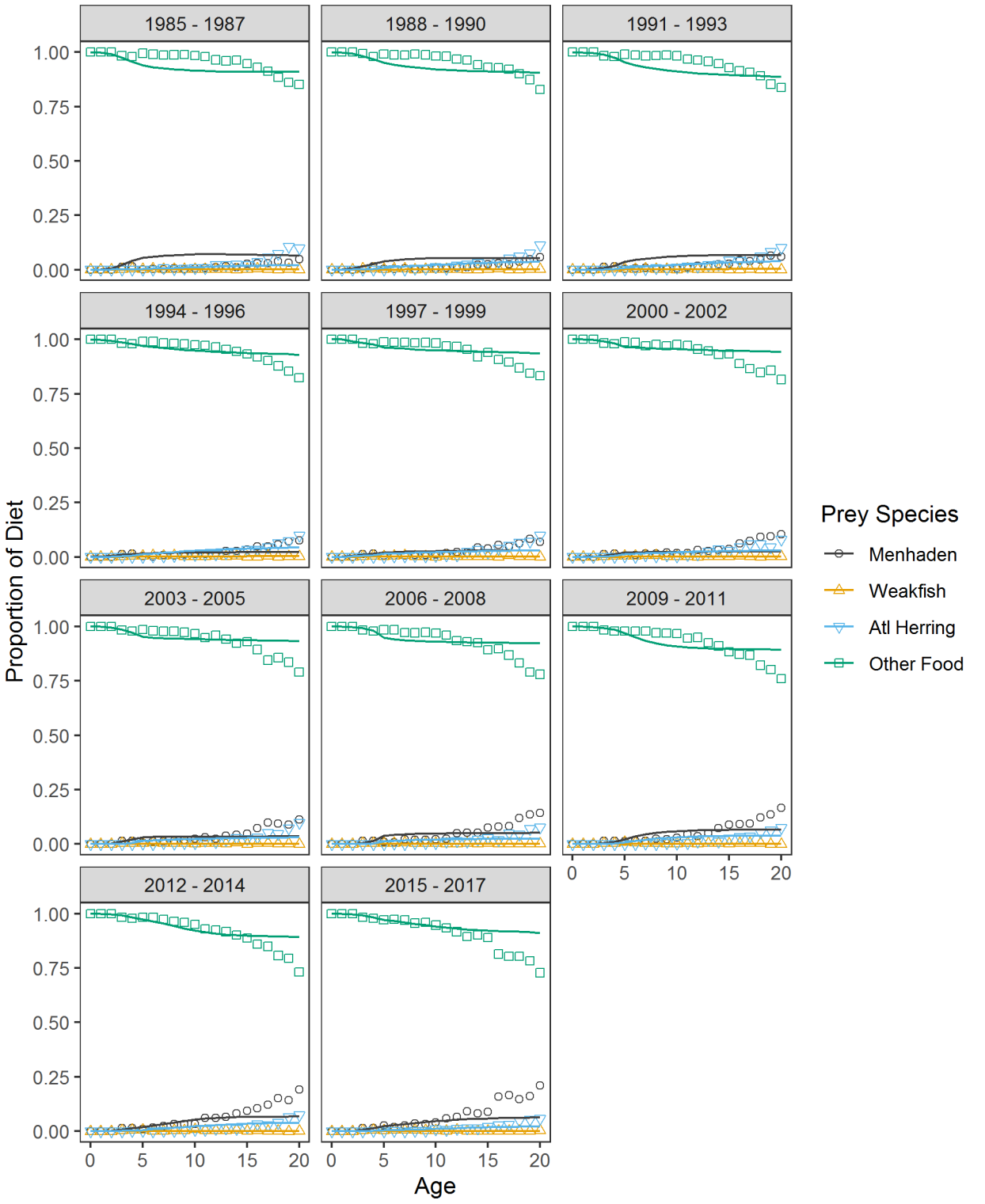


Figure 86. Observed (open points) and predicted (solid lines) diet composition data for spiny dogfish from the VADER model.

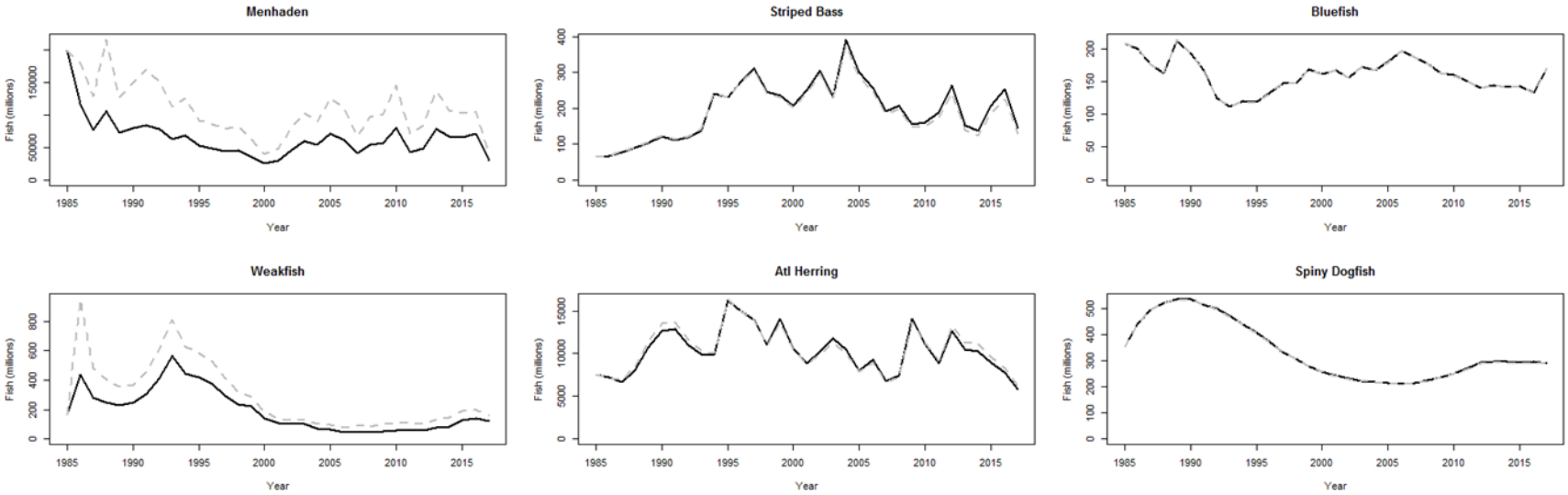


Figure 87. Predicted annual total abundance by species predicted with no trophic interactions (dashed gray line) and multispecies (solid black line) models from the VADER model.

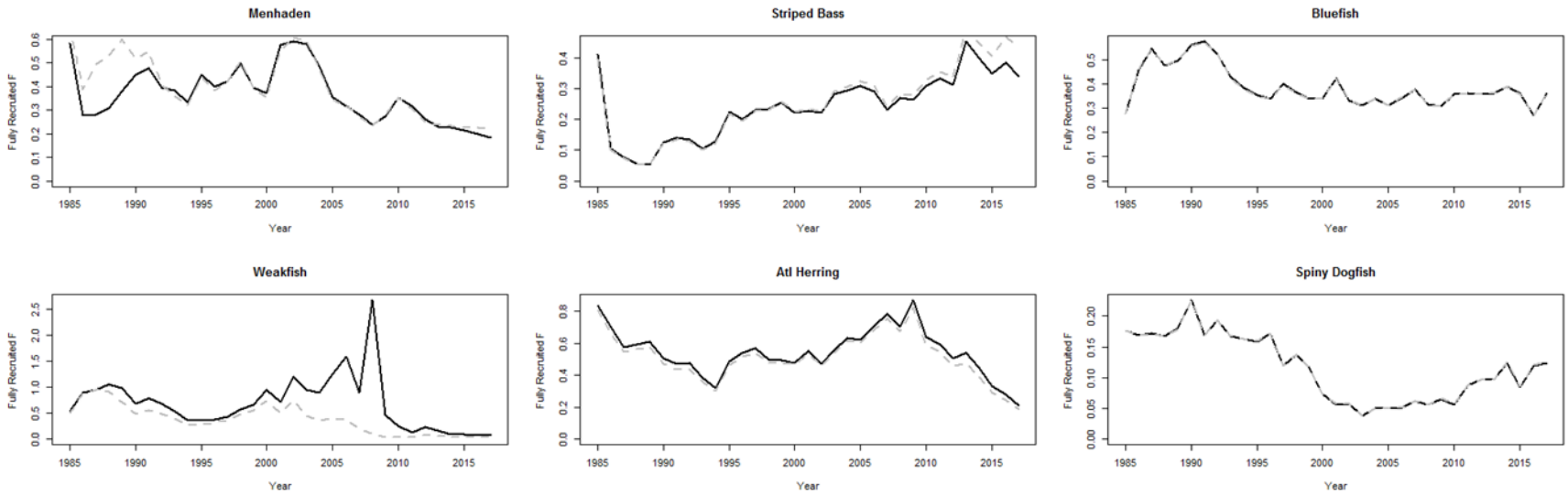


Figure 88. Predicted annual fully recruited fishing mortality (*F*) by species from predicted with no trophic interactions (dashed black line) and multispecies (solid black line) models from the VADER model.

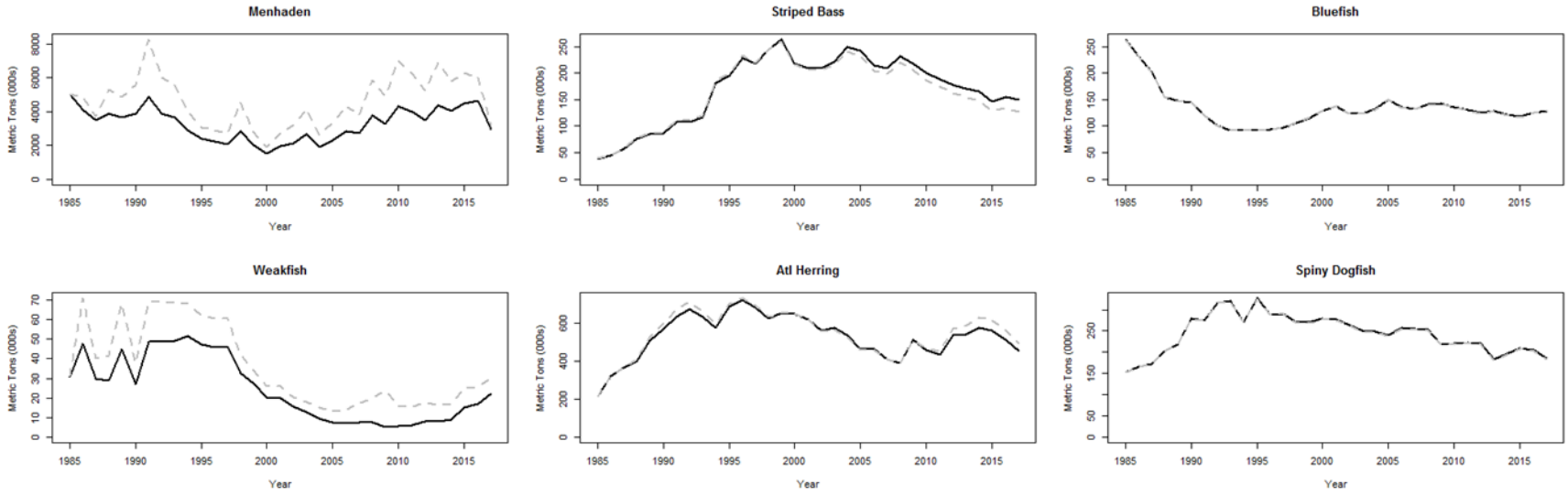


Figure 89. Predicted annual total biomass by species from predicted with no trophic interactions (dashed gray line) and multispecies (solid black line) models from the VADER model.

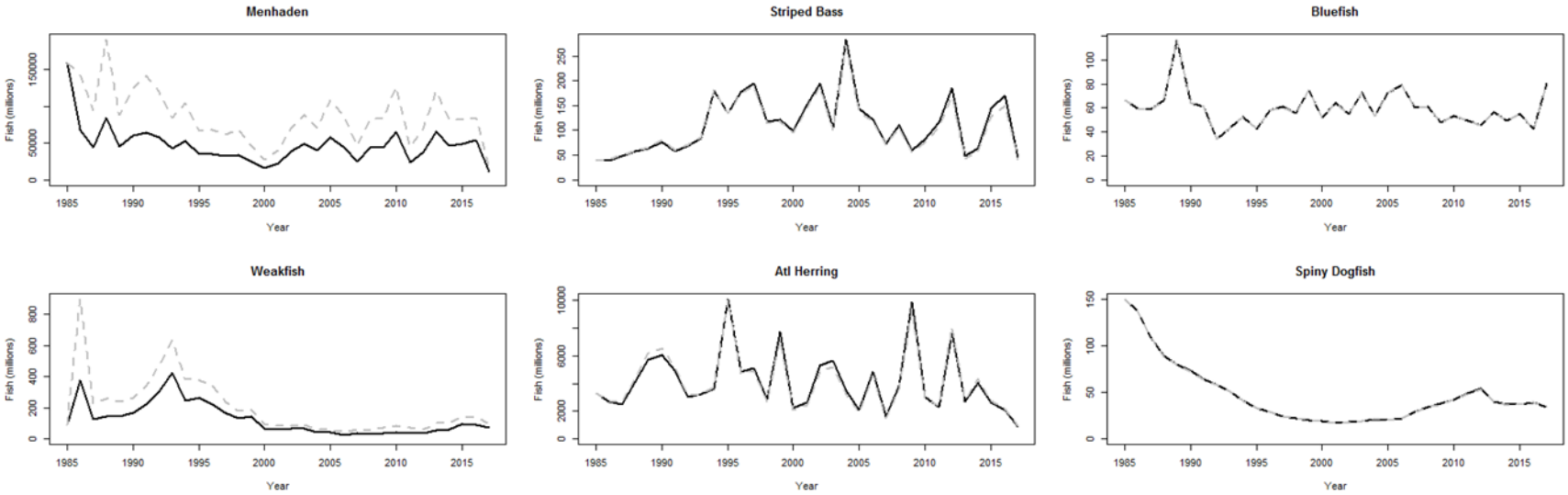


Figure 90. Predicted annual recruitment (first age in the model, species dependent) by species from predicted with no trophic interactions (dashed grey line) and multispecies (solid black line) models from the VADER model

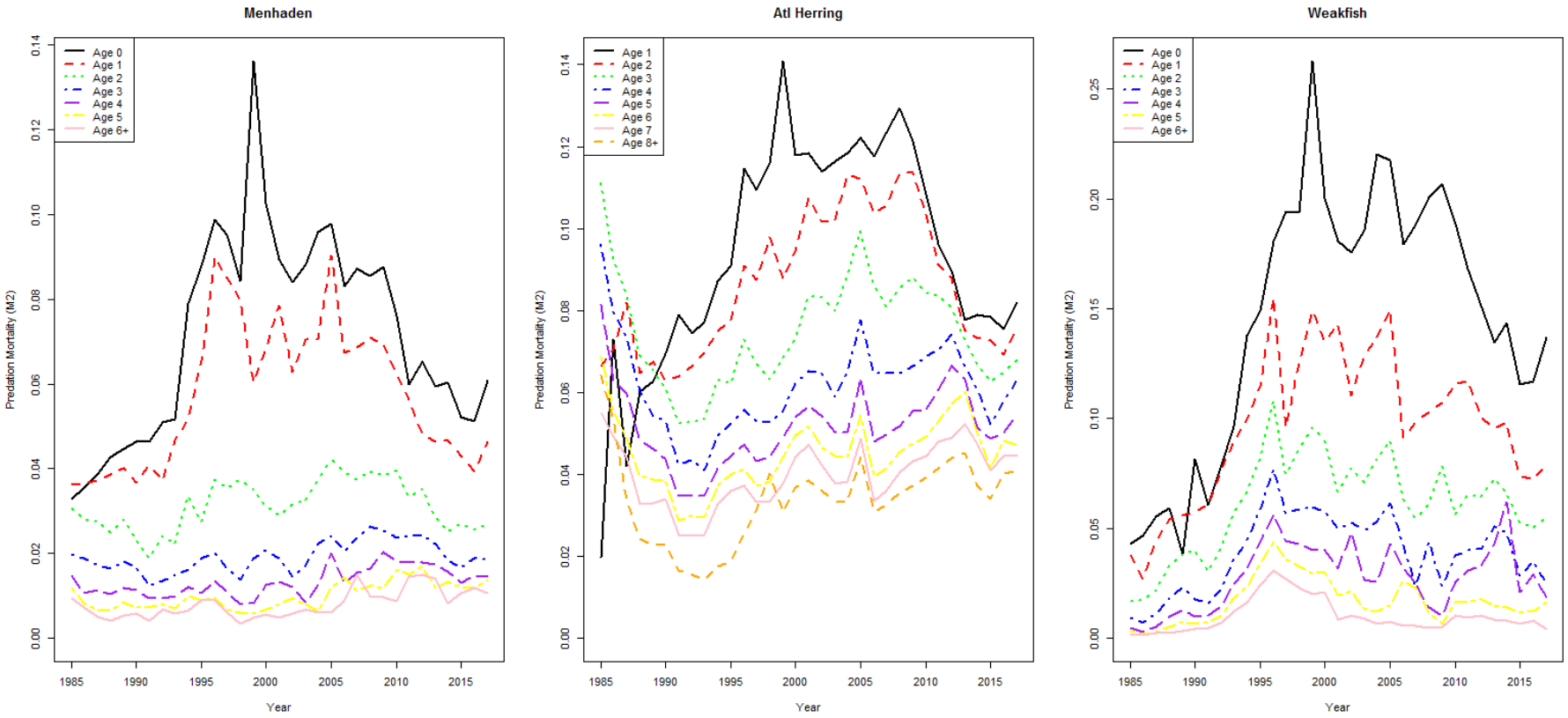


Figure 91. Predicted annual predation mortality-at-age (M_2) for Atlantic menhaden, weakfish, and Atlantic herring from the VADER model.

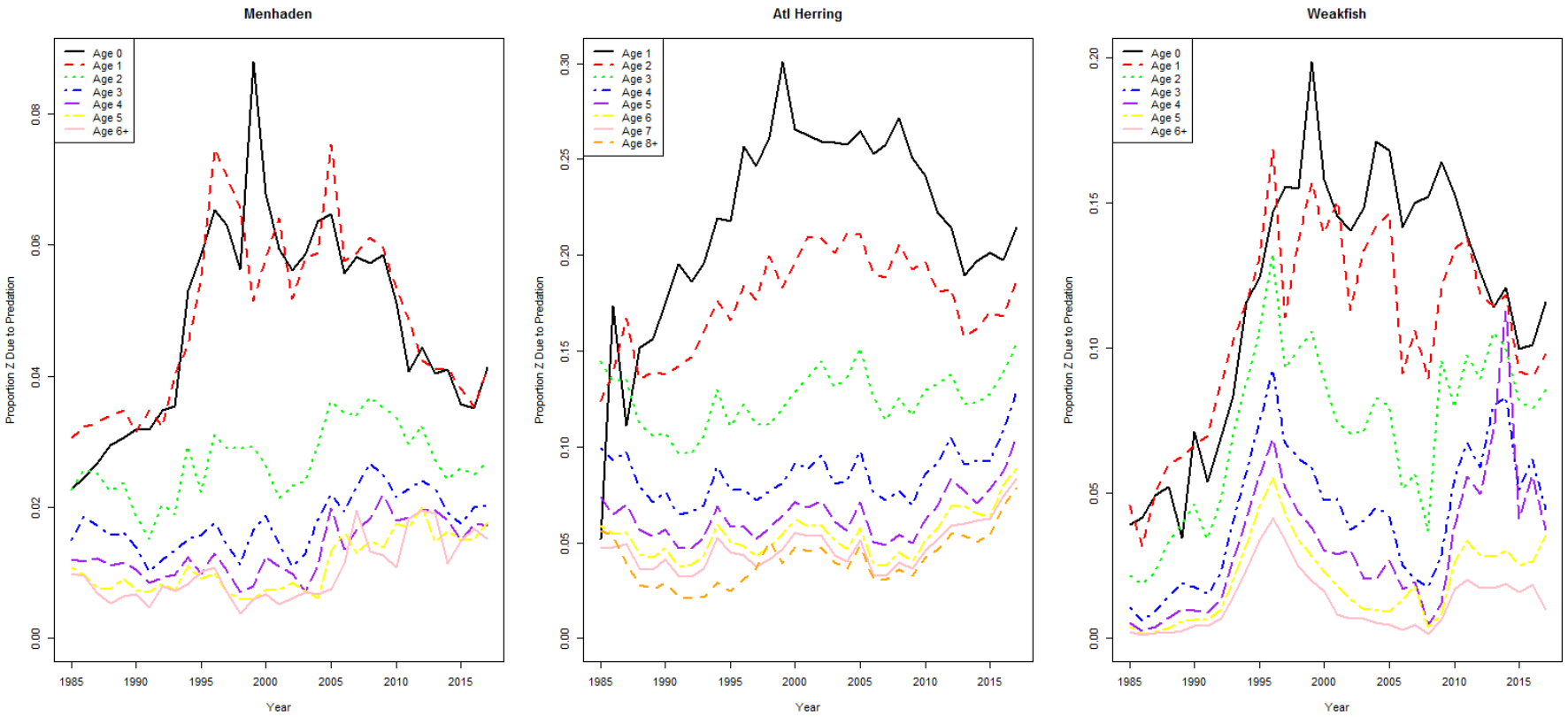


Figure 92. Predicted proportion total mortality (*Z*) at age from predation by species from multispecies models from the VADER model.

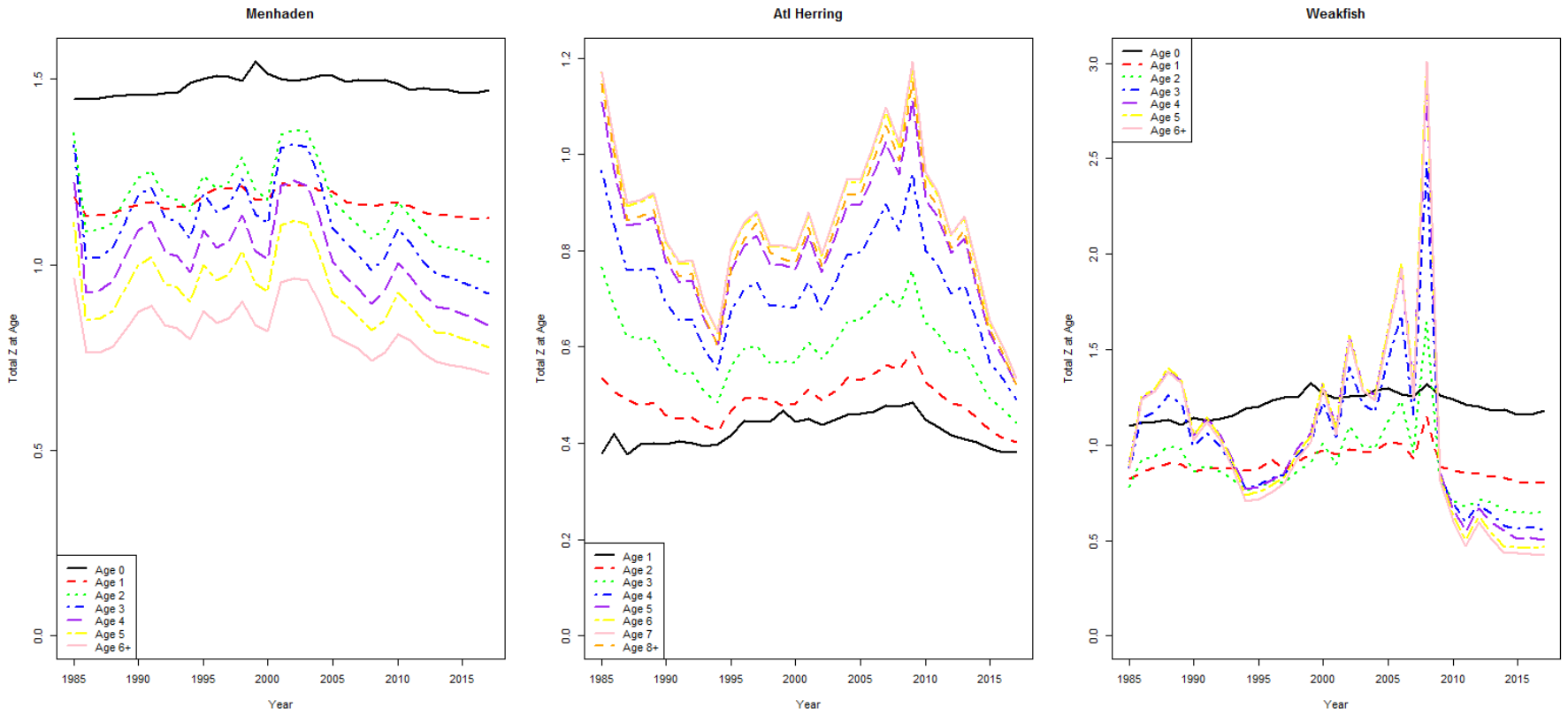


Figure 93. Predicted annual total mortality (*Z*) at age by species from the multispecies run of the VADER model.



Figure 94. Predicted annual consumption in thousands of metric tons by prey for striped bass, bluefish, weakfish, and spiny dogfish from the VADER model.



Figure 95. Predicted annual consumption in thousands of metric tons by predator for Atlantic menhaden, weakfish, and Atlantic herring from the VADER model.

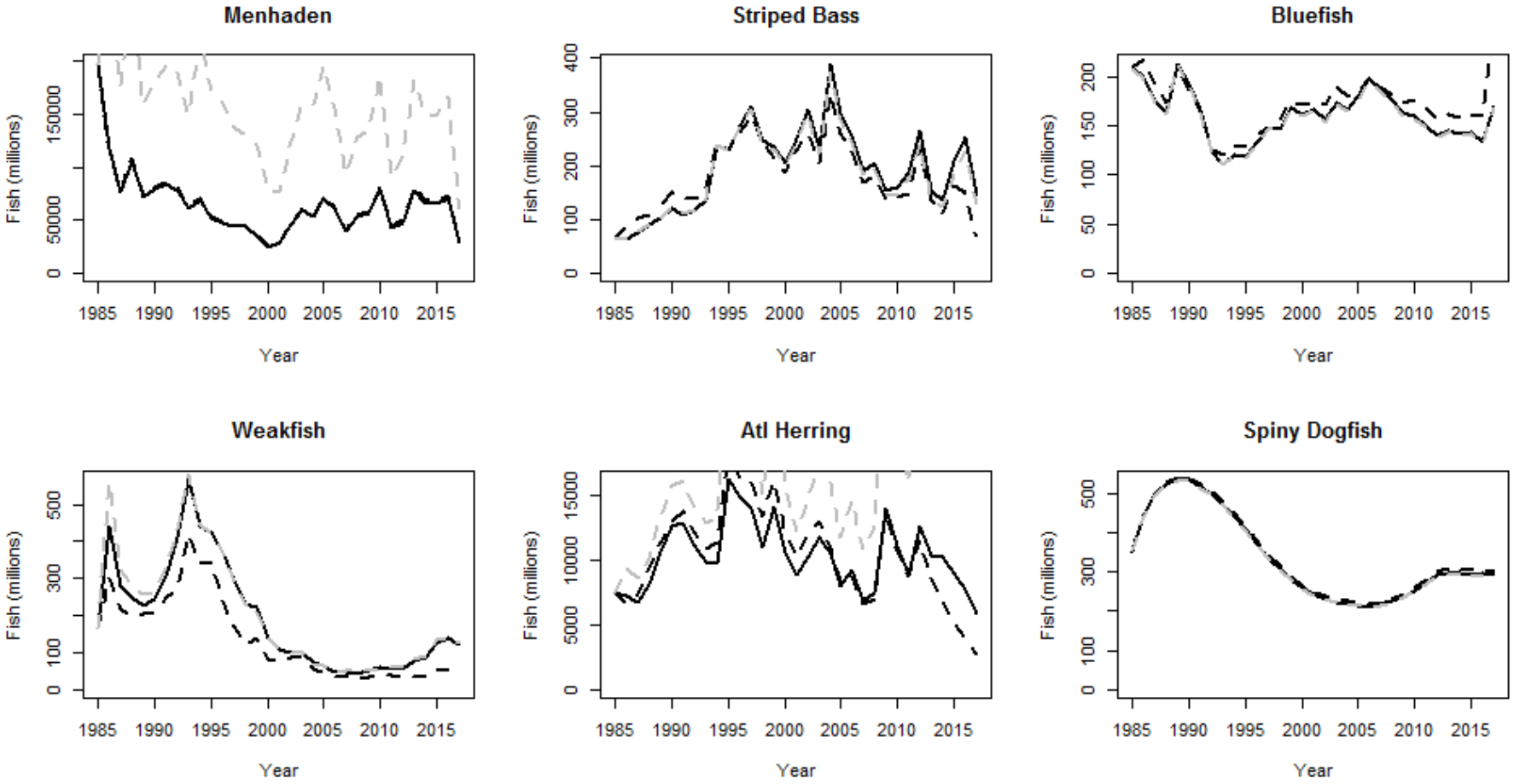


Figure 96. Predicted annual total abundance by species predicted with alternate indices (dashed black line), alternate diet composition (dashed gray line), and multispecies (solid black line) runs from the VADER model.

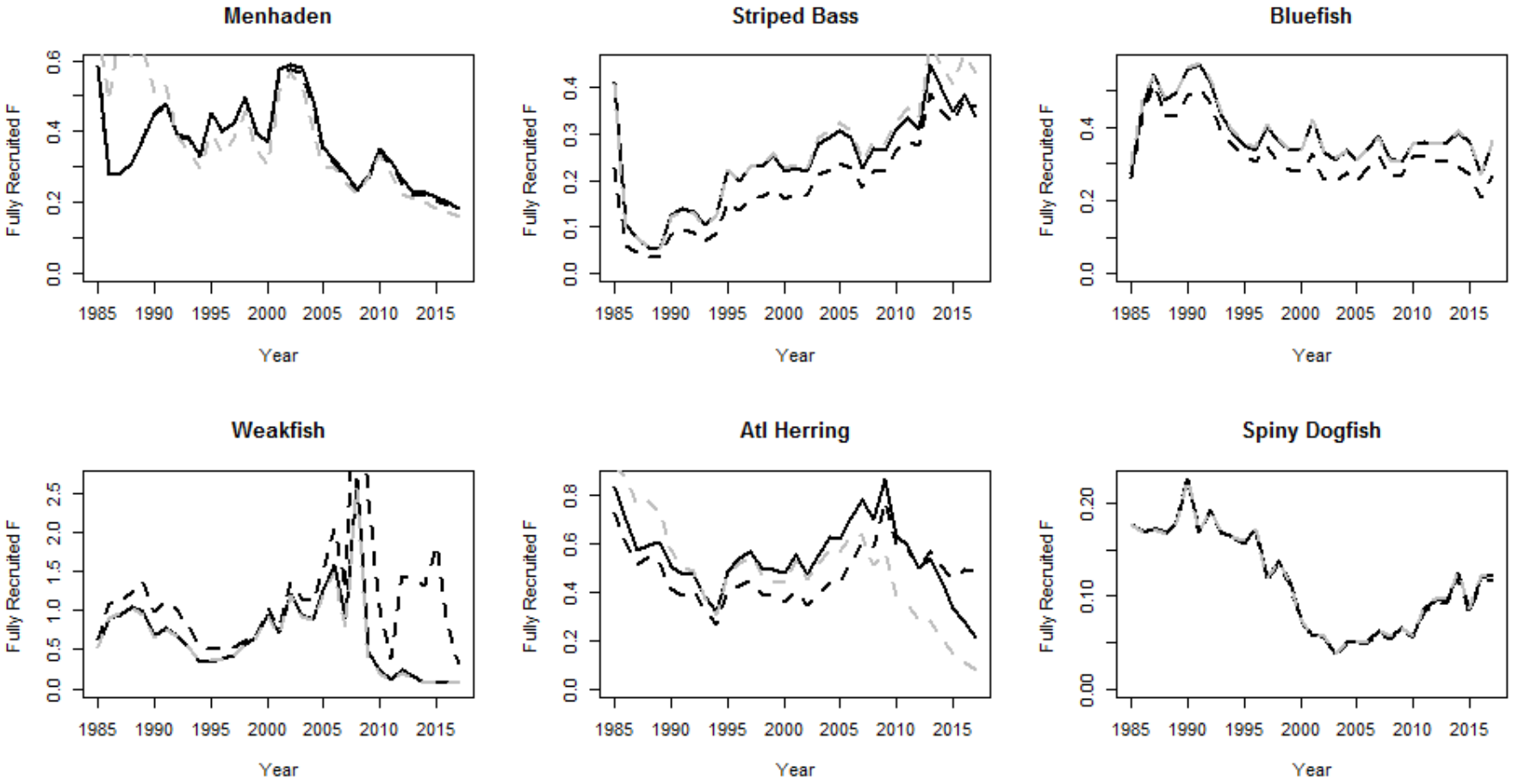


Figure 97. Predicted annual fully recruited fishing mortality (*F*) by species from predicted with alternate indices (dashed black line), alternate diet composition (dashed gray line), and multispecies (solid black line) runs from the VADER model.

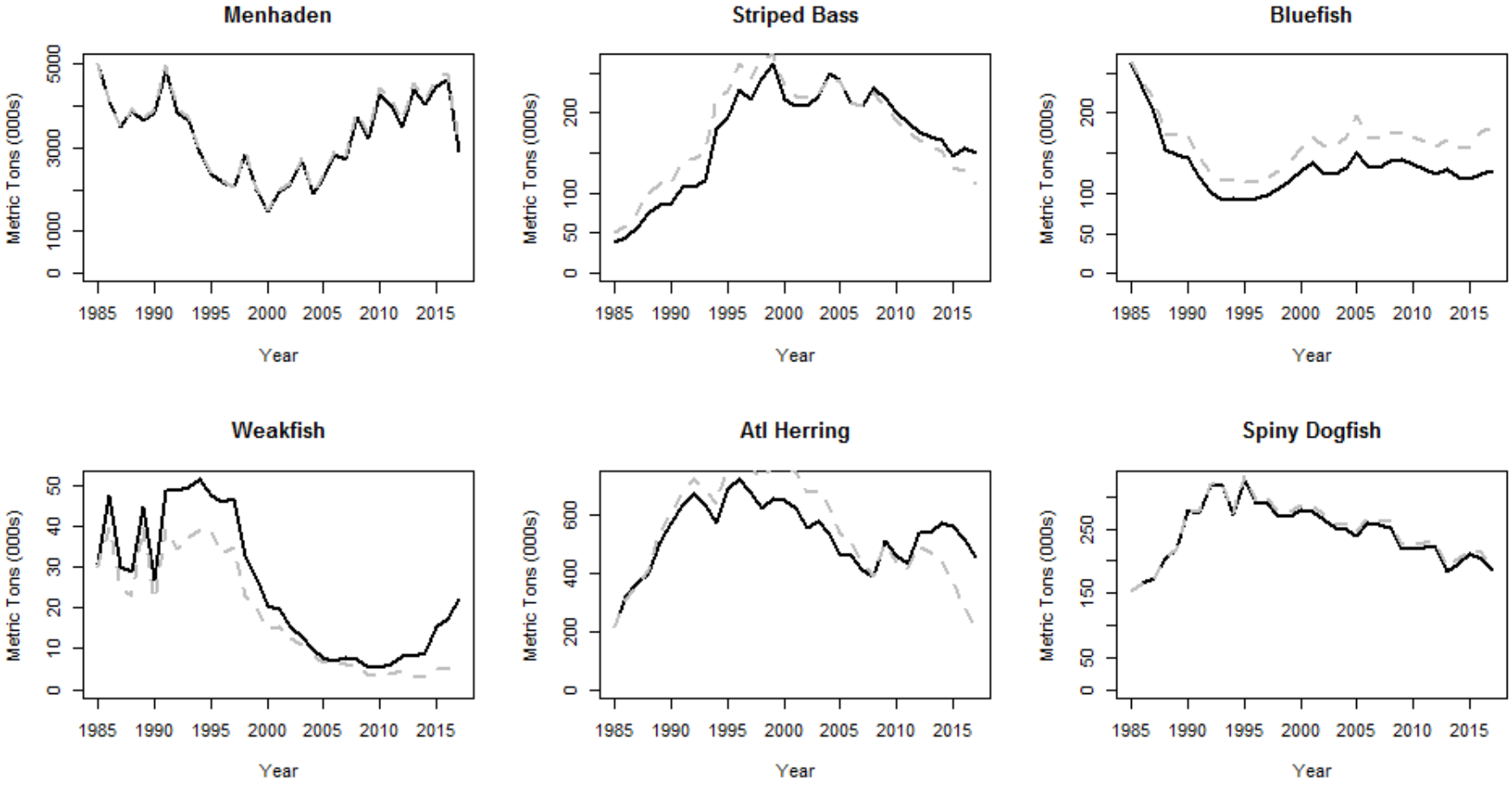


Figure 98. Predicted annual total biomass by species from predicted with alternate indices (dashed black line), alternate diet composition (dashed gray line), and multispecies (solid black line) runs from the VADER model.

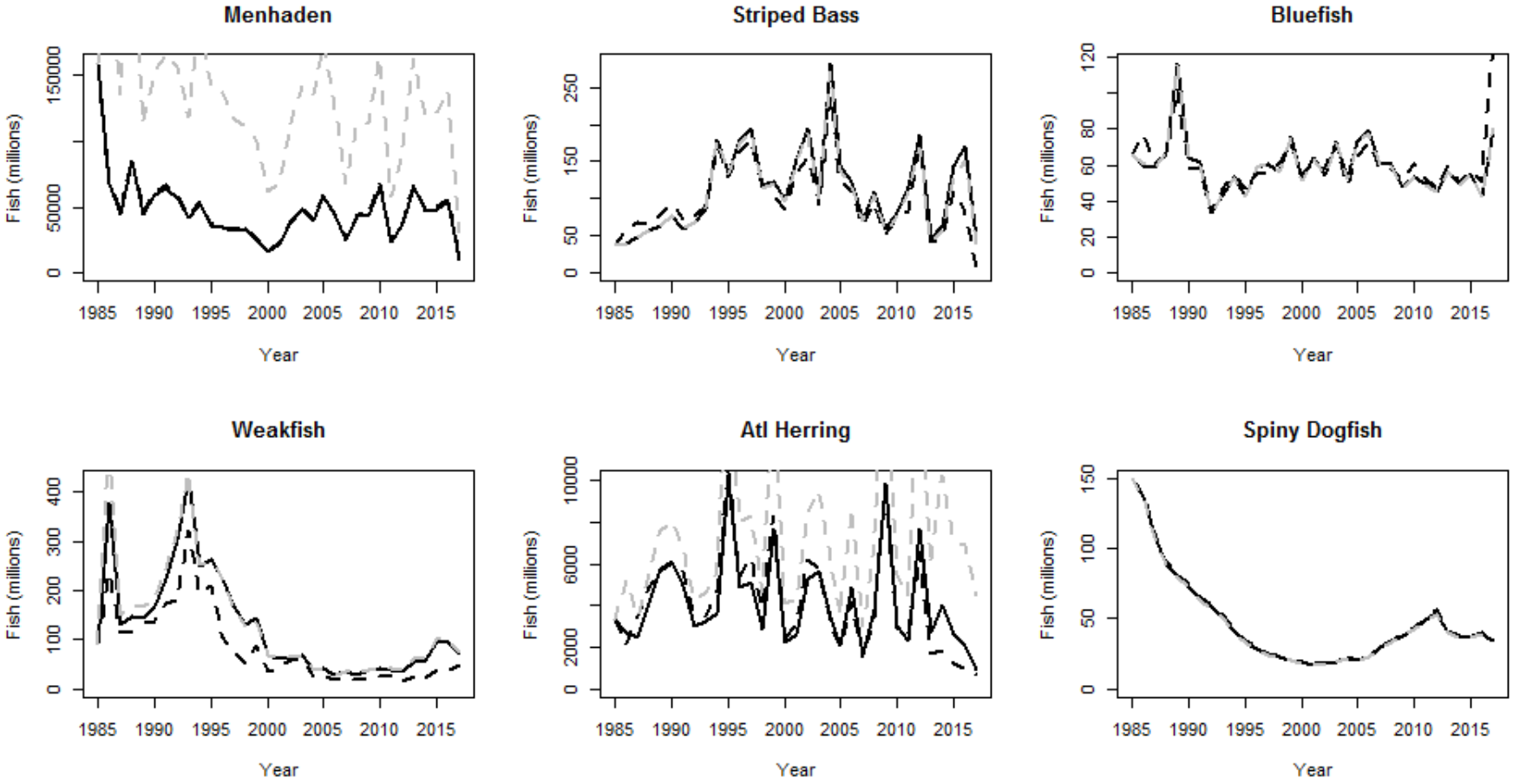


Figure 99. Predicted annual recruitment (first age in the model, species dependent) by species from predicted with alternate indices (dashed black line), alternate diet composition (dashed gray line), and multispecies (solid black line) runs from the VADER model.



Figure 100. Predicted average predation mortality (M_2) for Atlantic menhaden, weakfish, and Atlantic herring from the alternate diet run (dashed gray line) and the base run (solid black line) from the VADER model.

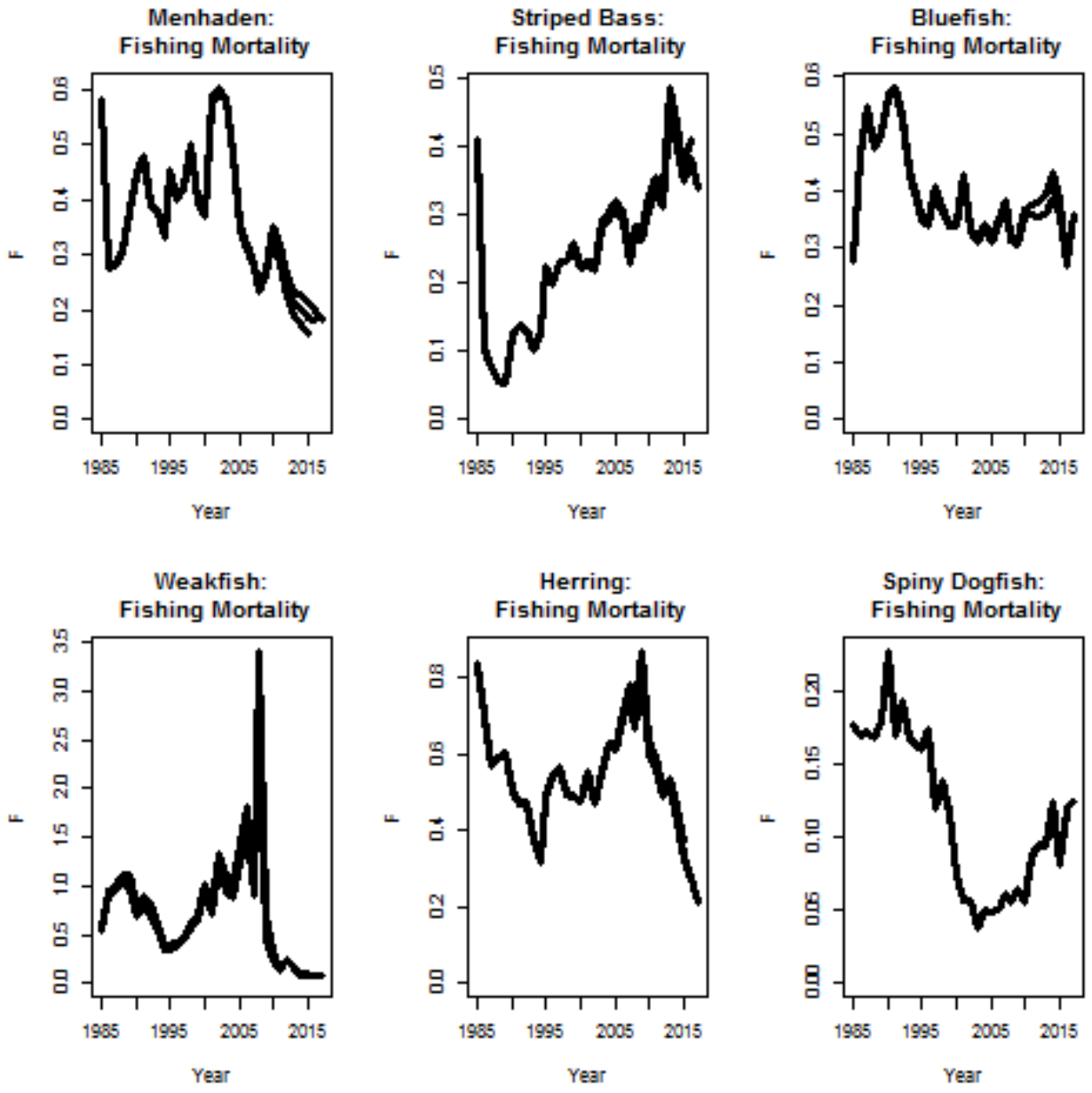


Figure 101. Retrospective analysis for full fishing mortality for all six species from the VADER model.

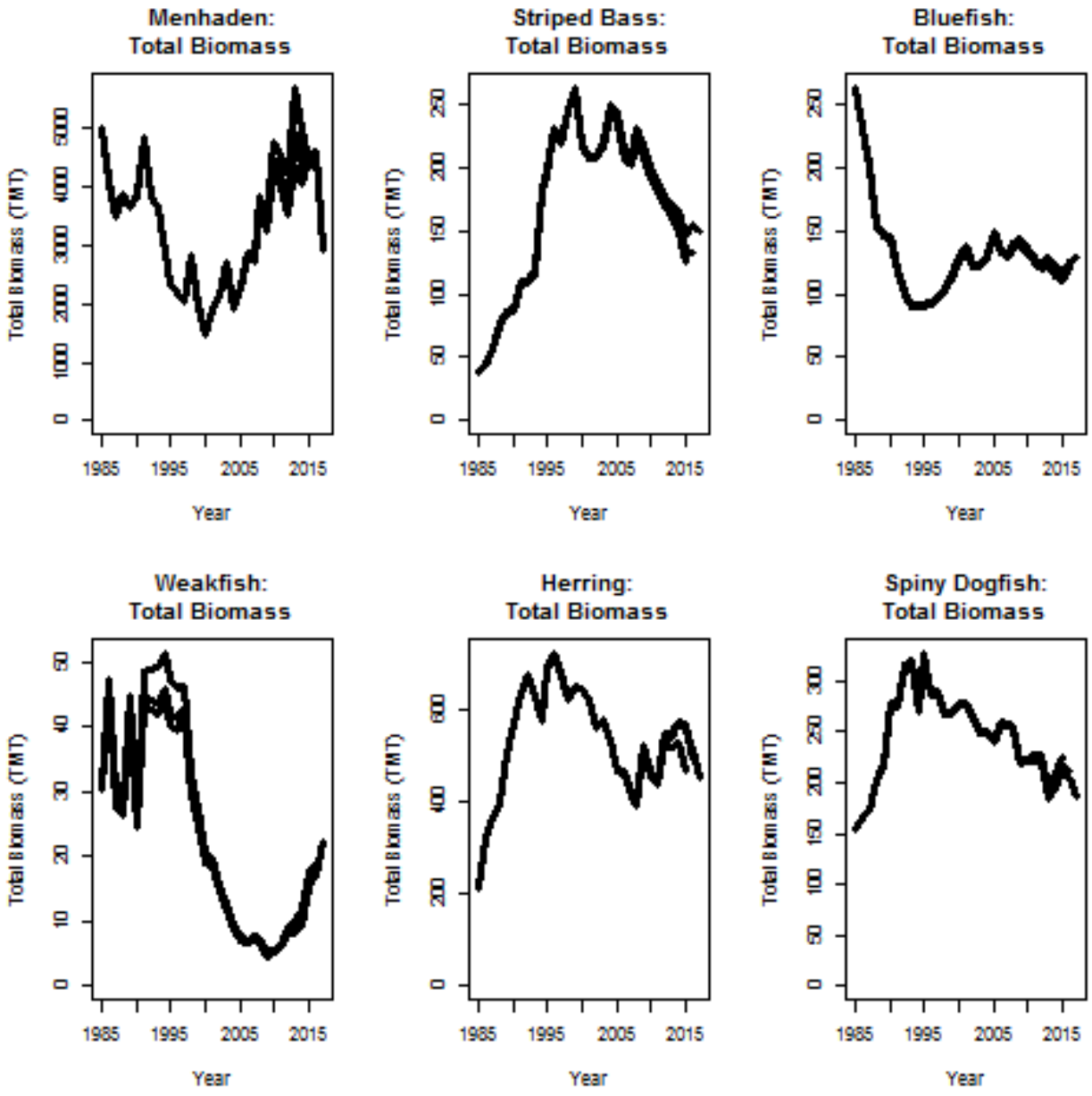


Figure 102. Retrospective analysis for total biomass for all six species from the VADER model.

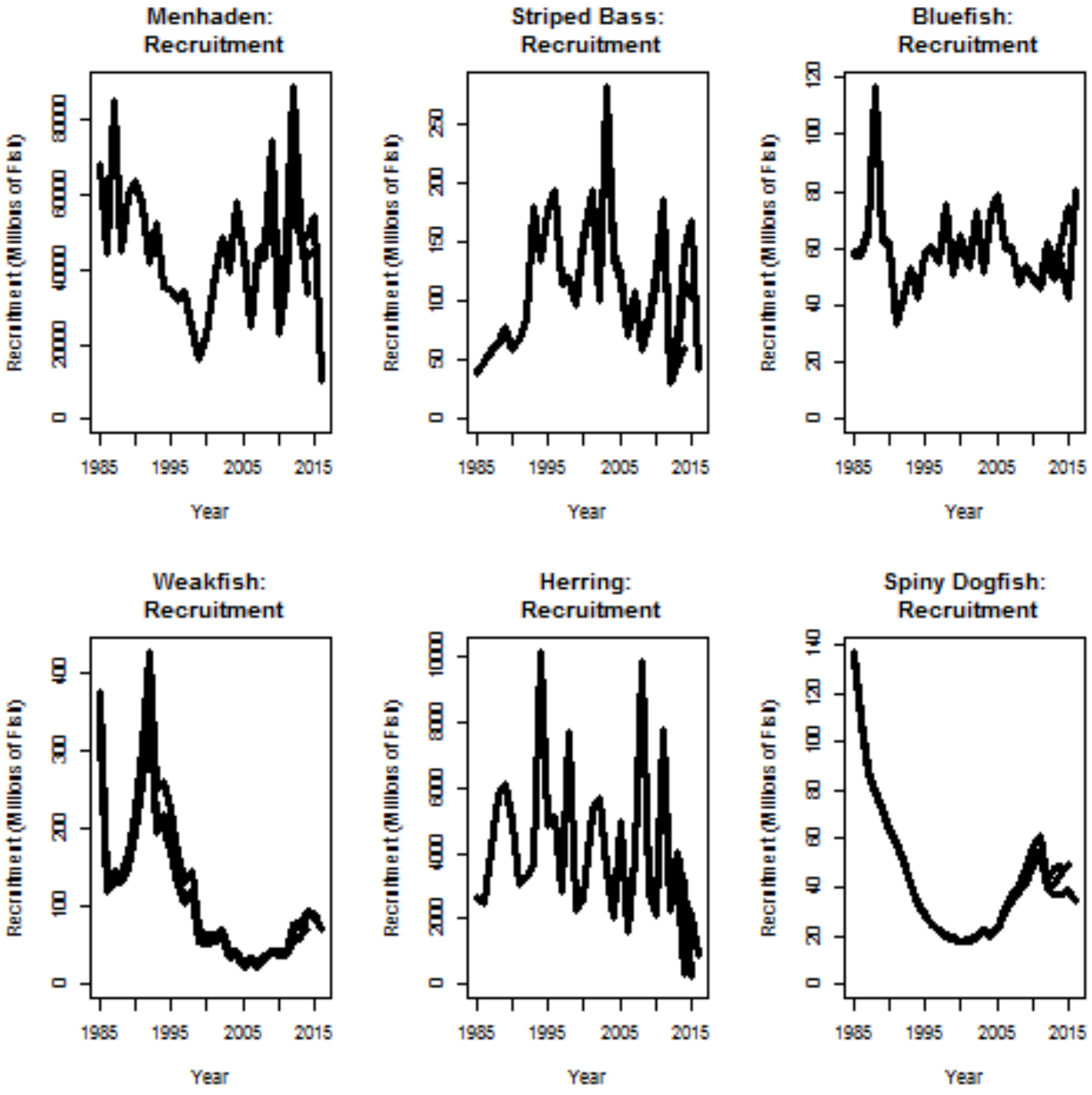


Figure 103. Retrospective analysis for recruitment for all six species from the VADER model.

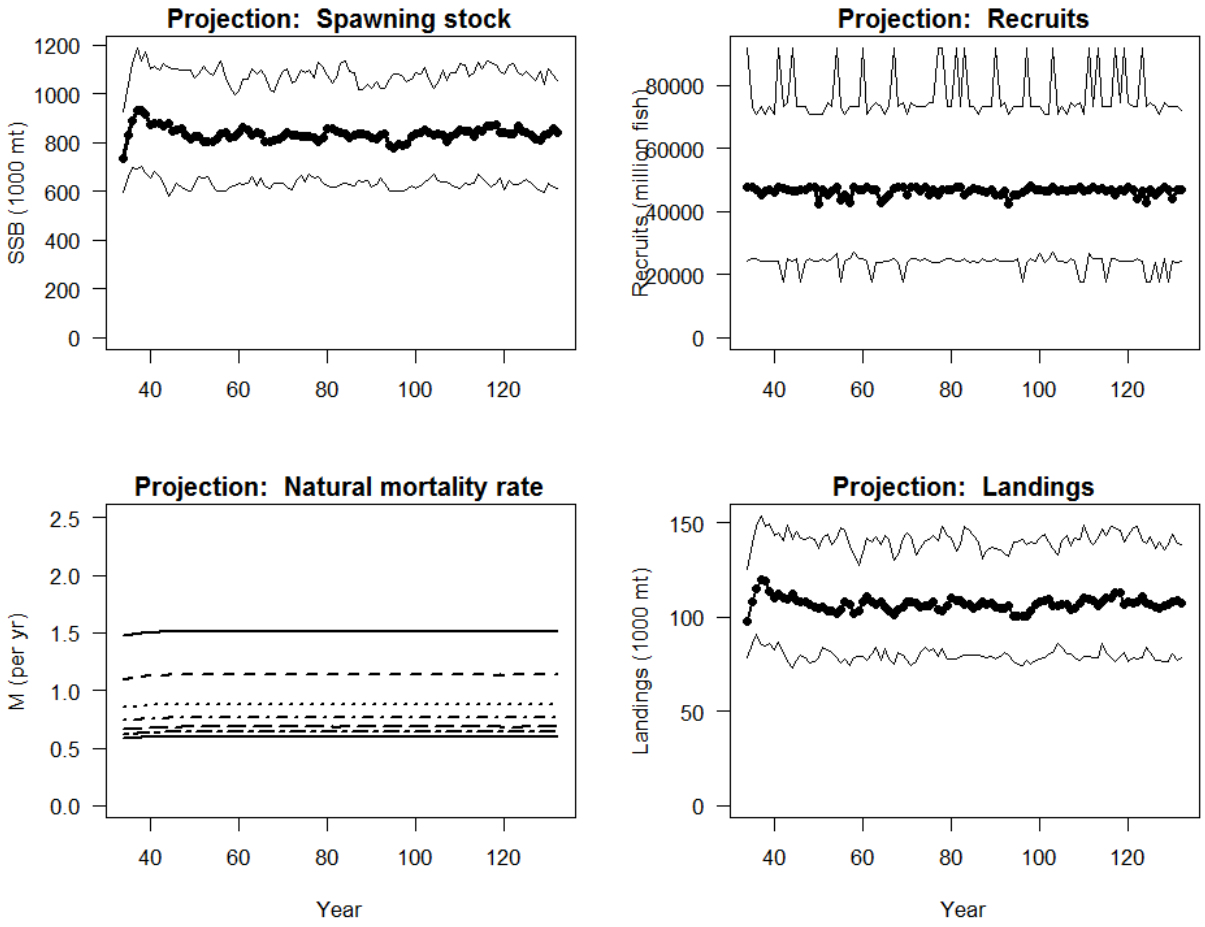


Figure 104. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for Atlantic menhaden under scenario 1 from the VADER model (Atlantic menhaden at status quo *F*, all other species at target *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the M plot, the different lines represent *M*-at-age.

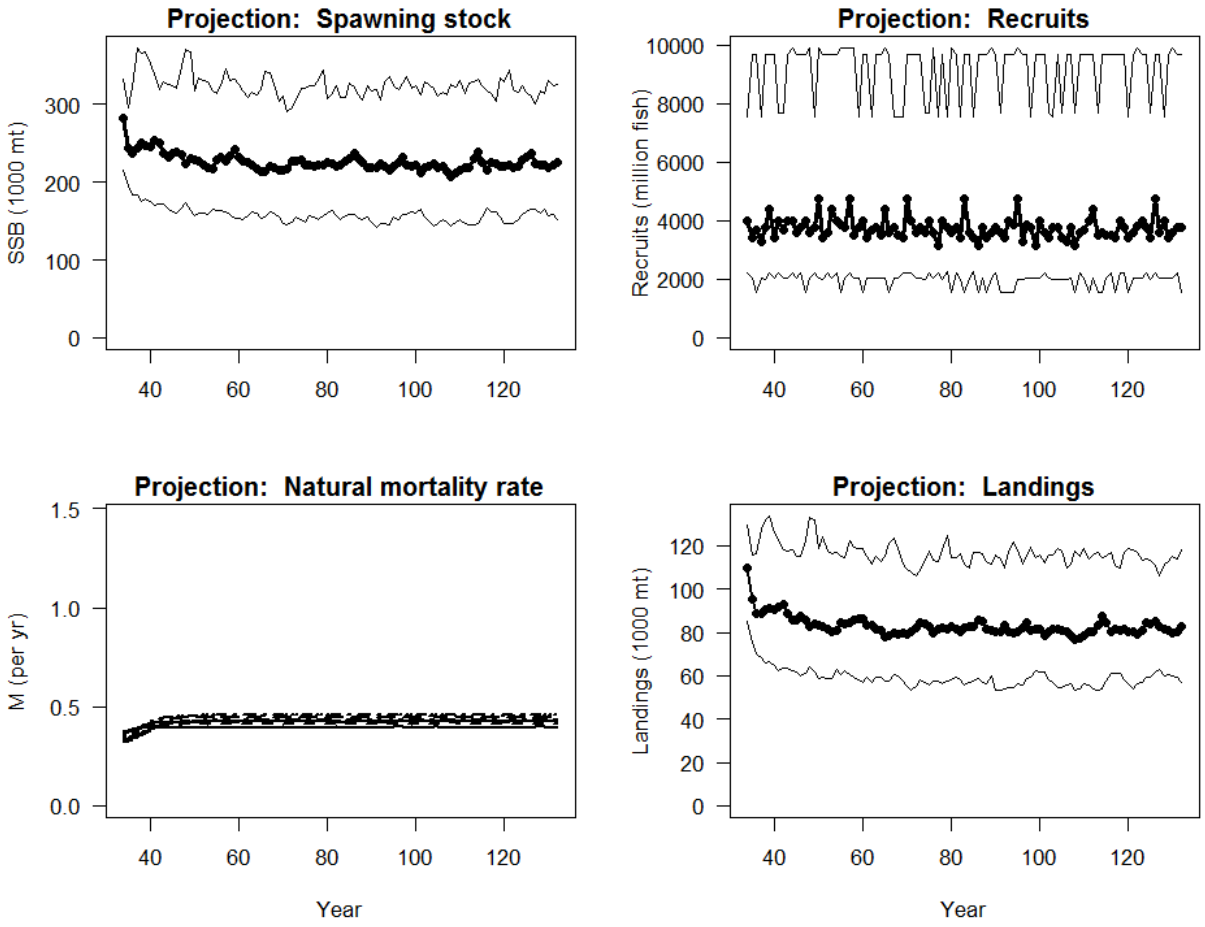


Figure 105. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for Atlantic herring under scenario 1 for the VADER model (Atlantic menhaden at status quo *F*, all other species at target *F*) For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

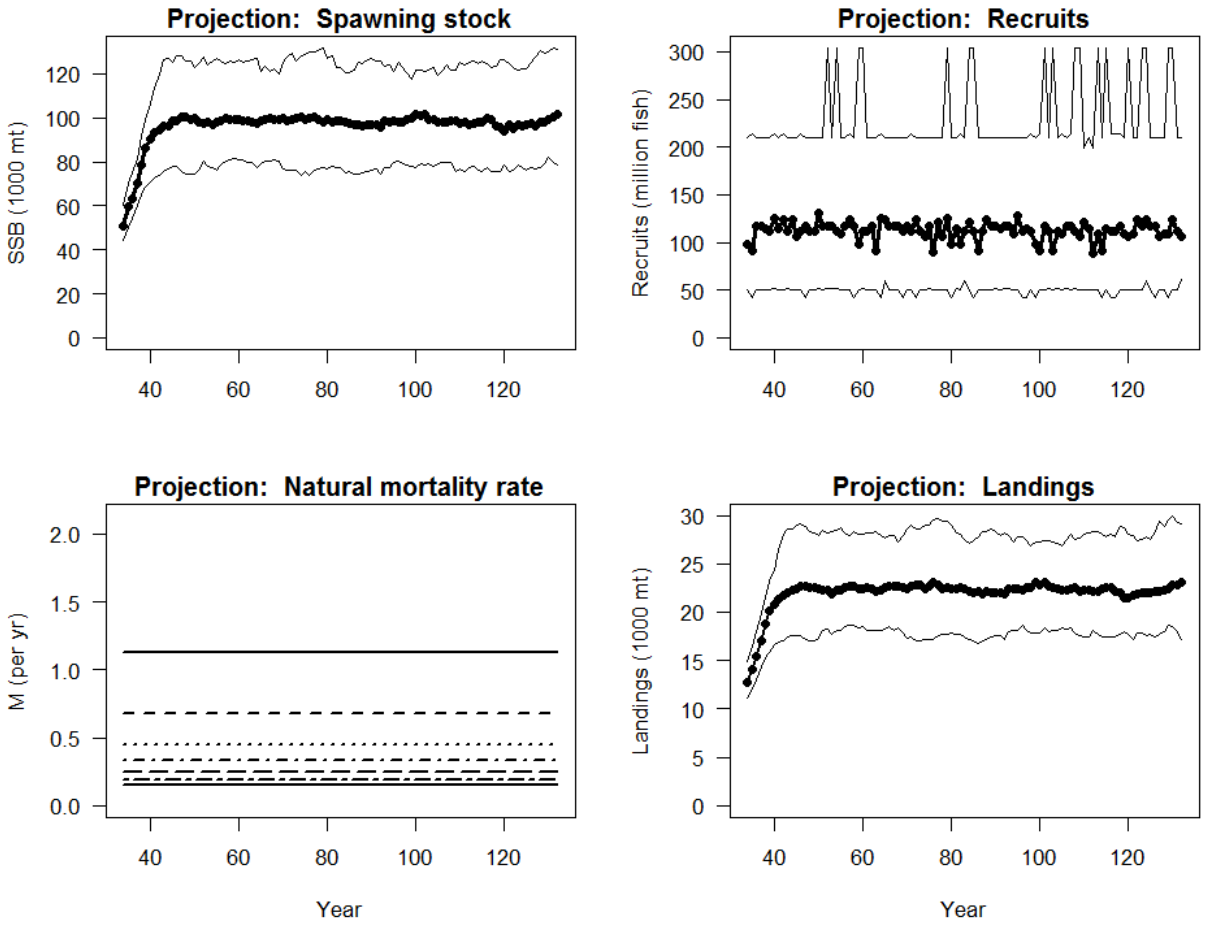


Figure 106. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under scenario 1 for the VADER model (Atlantic menhaden at status quo *F*, all other species at target *F*).For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

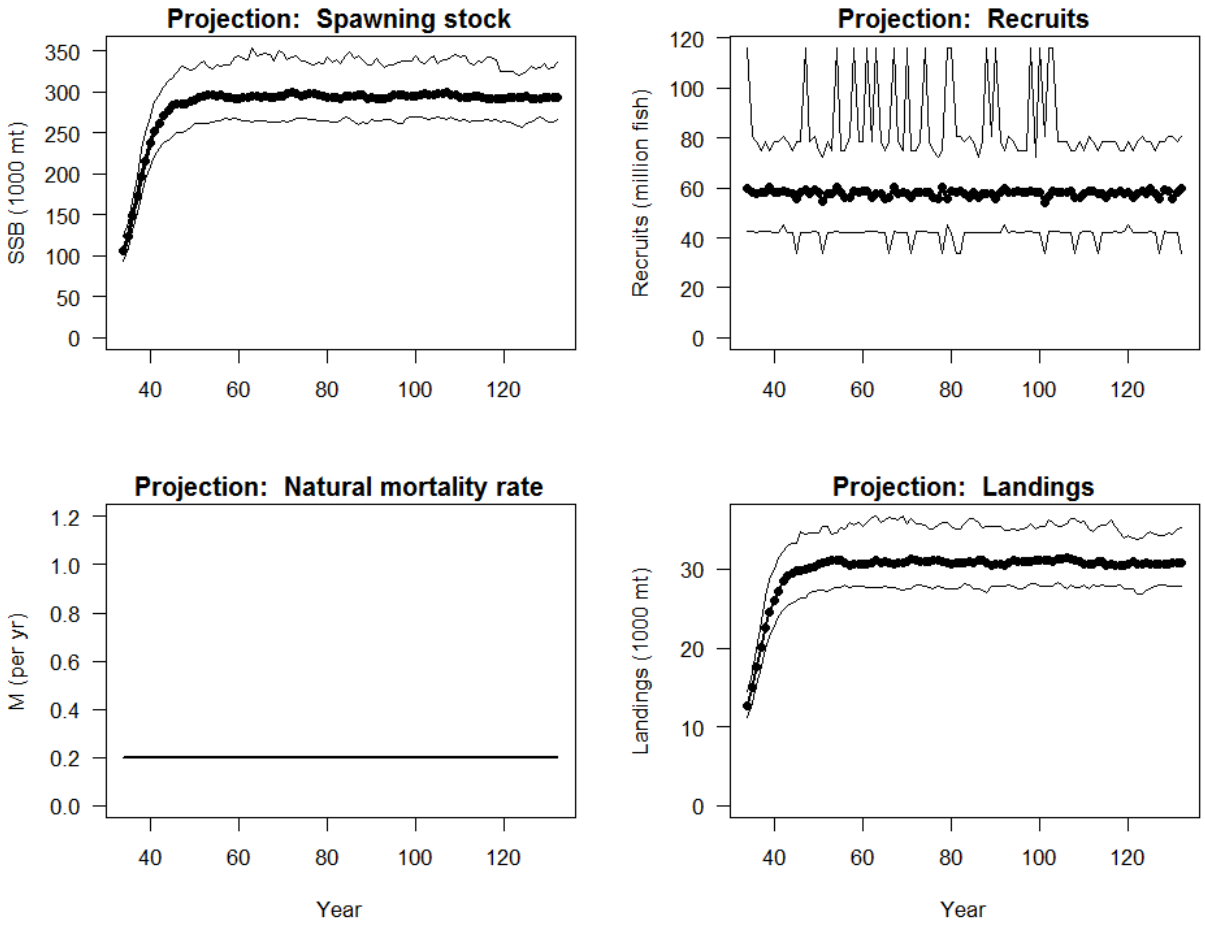


Figure 107. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for bluefish under scenario 1 for the VADER model (Atlantic menhaden at status quo *F*, all other species at target *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

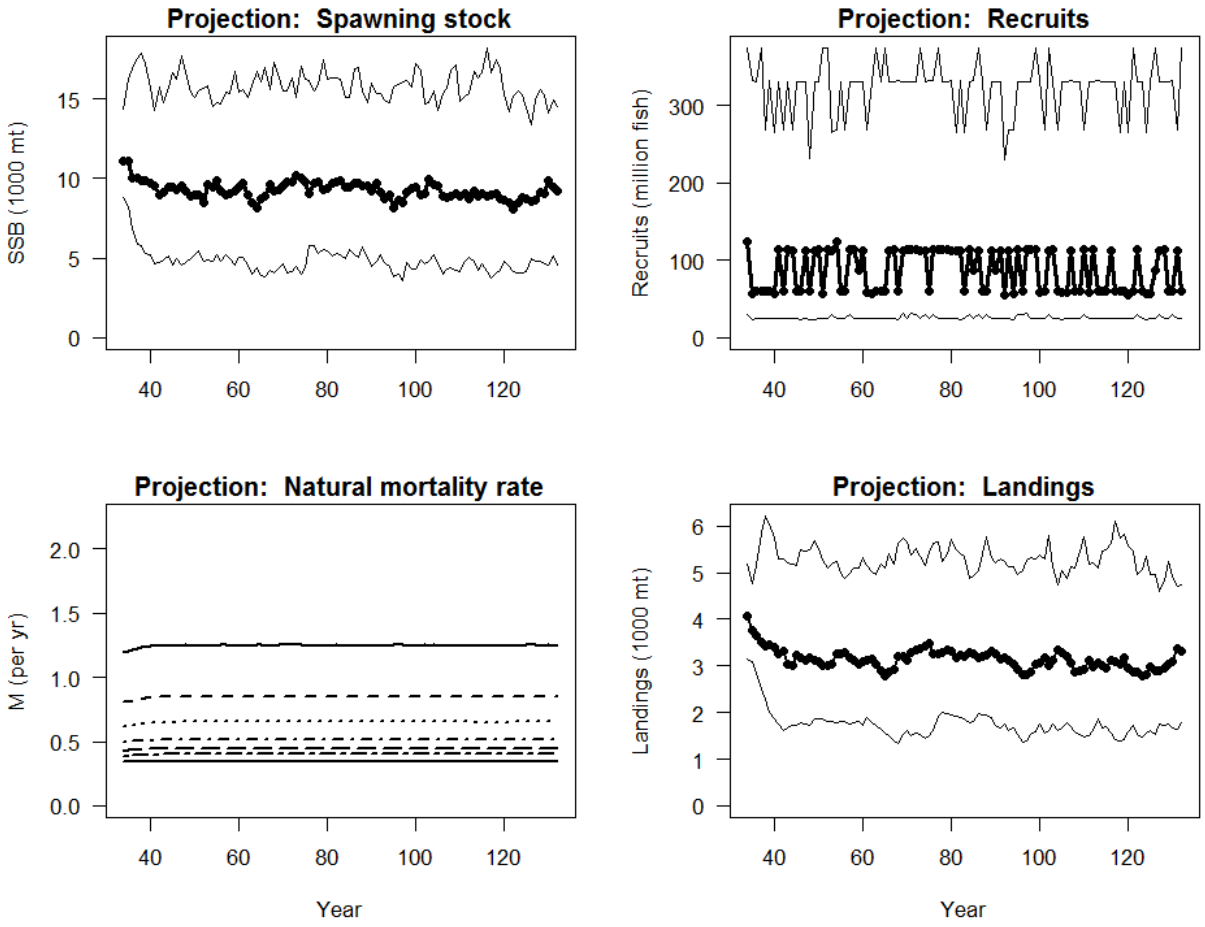


Figure 108. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for weakfish under scenario 1 for the VADER model (Atlantic menhaden at status quo *F*, all other species at target *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

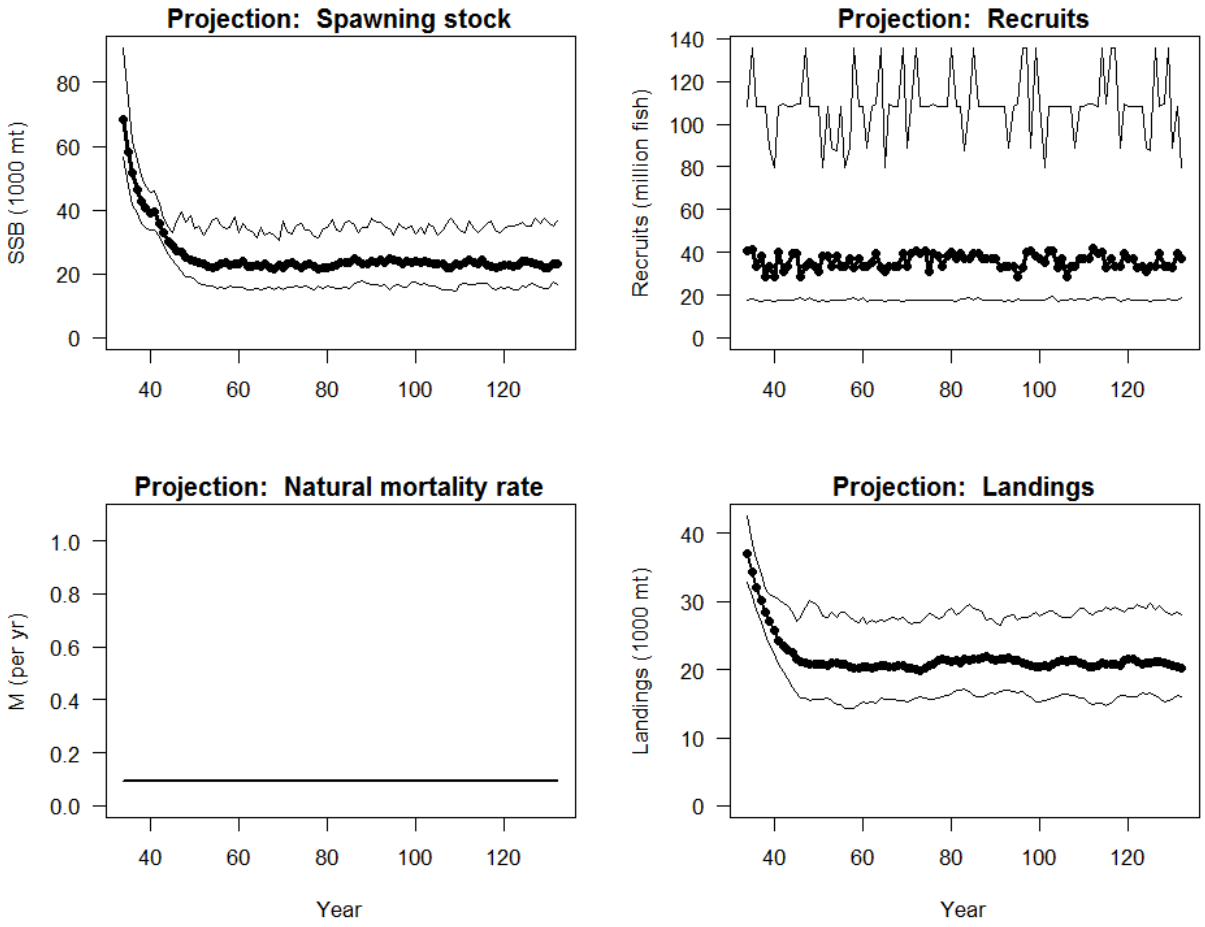


Figure 109. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for spiny dogfish under scenario 1 for the VADER model (Atlantic menhaden at status quo *F*, all other species at target *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

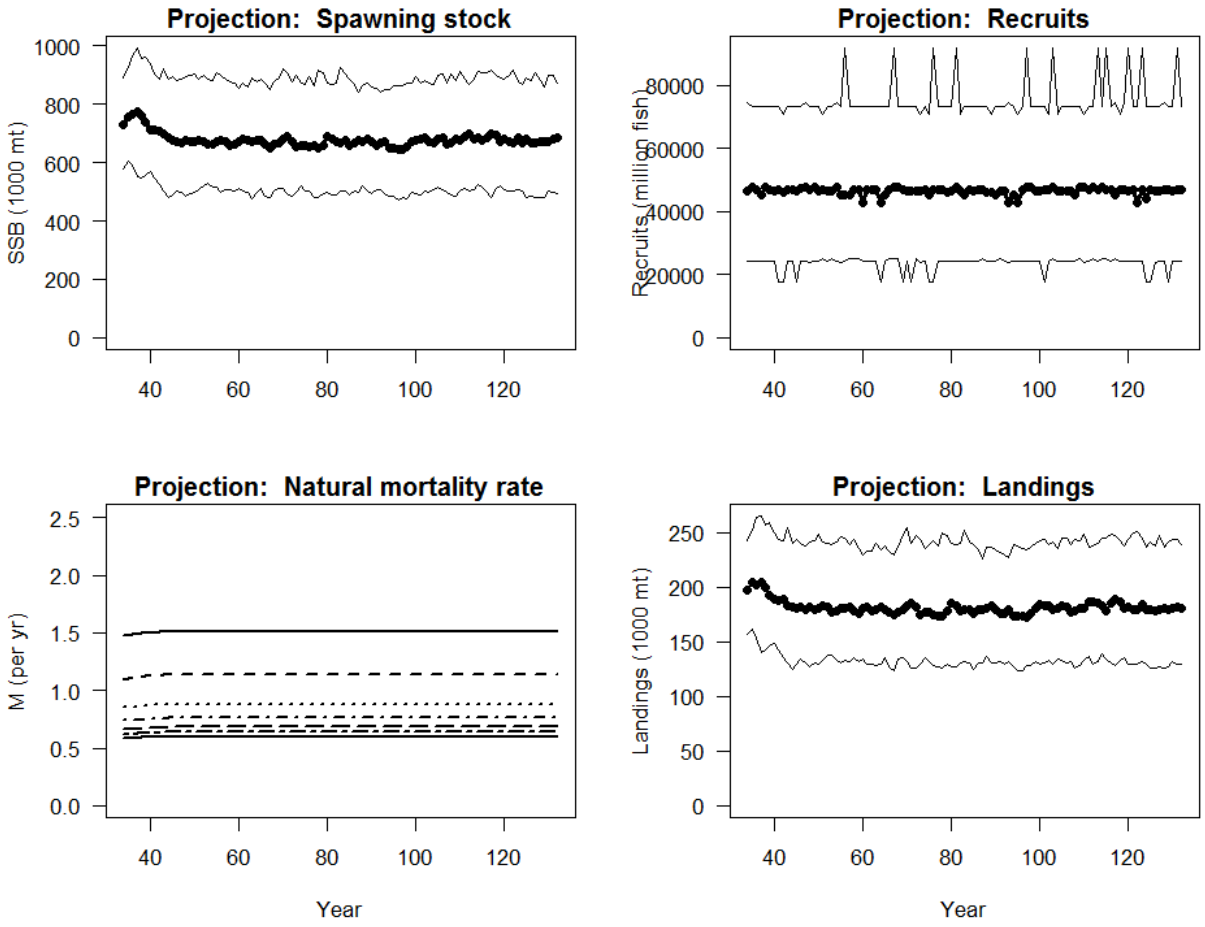


Figure 110. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for Atlantic menhaden under scenario 2 for the VADER model (all species at target *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

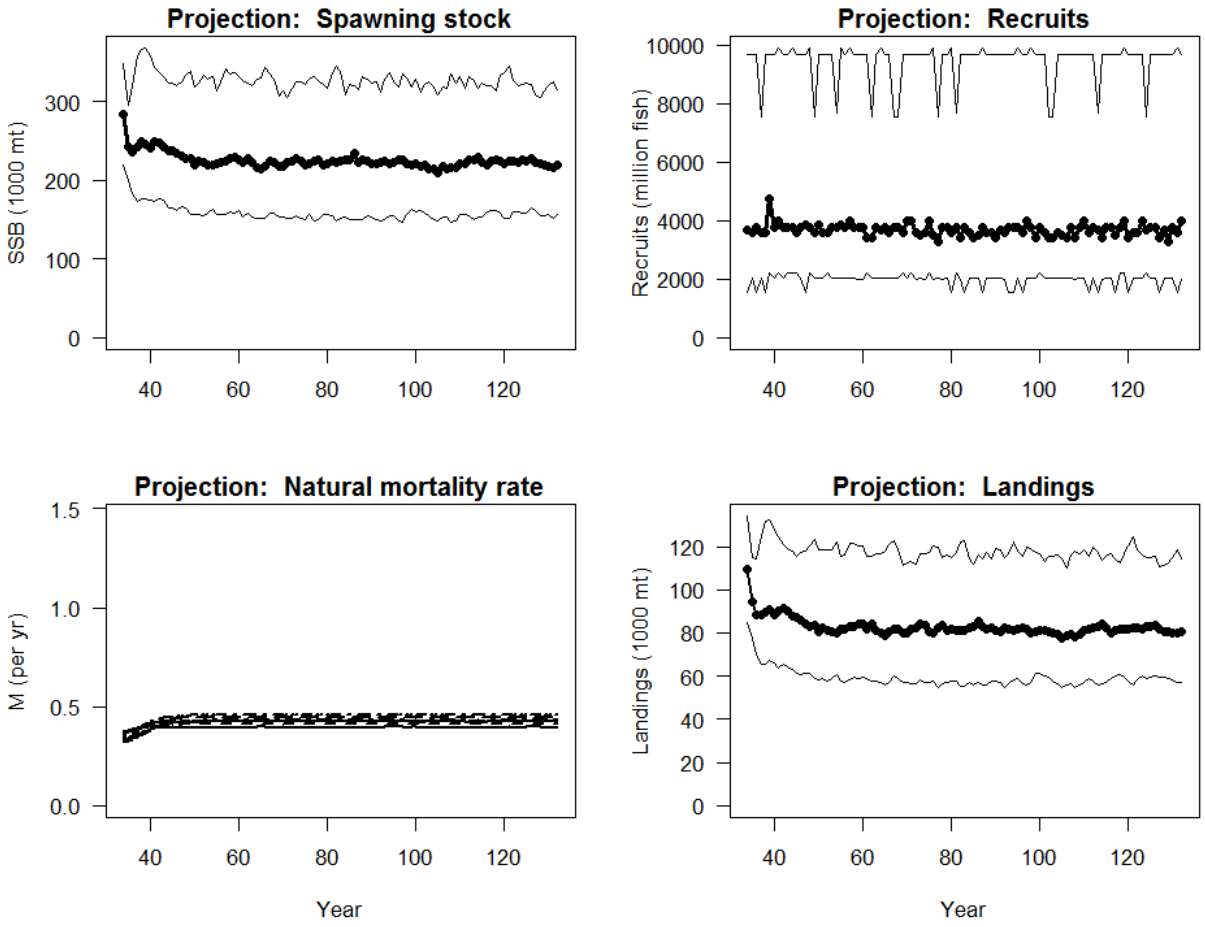


Figure 111. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for Atlantic herring under scenario 2 for the VADER model (all species at target *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

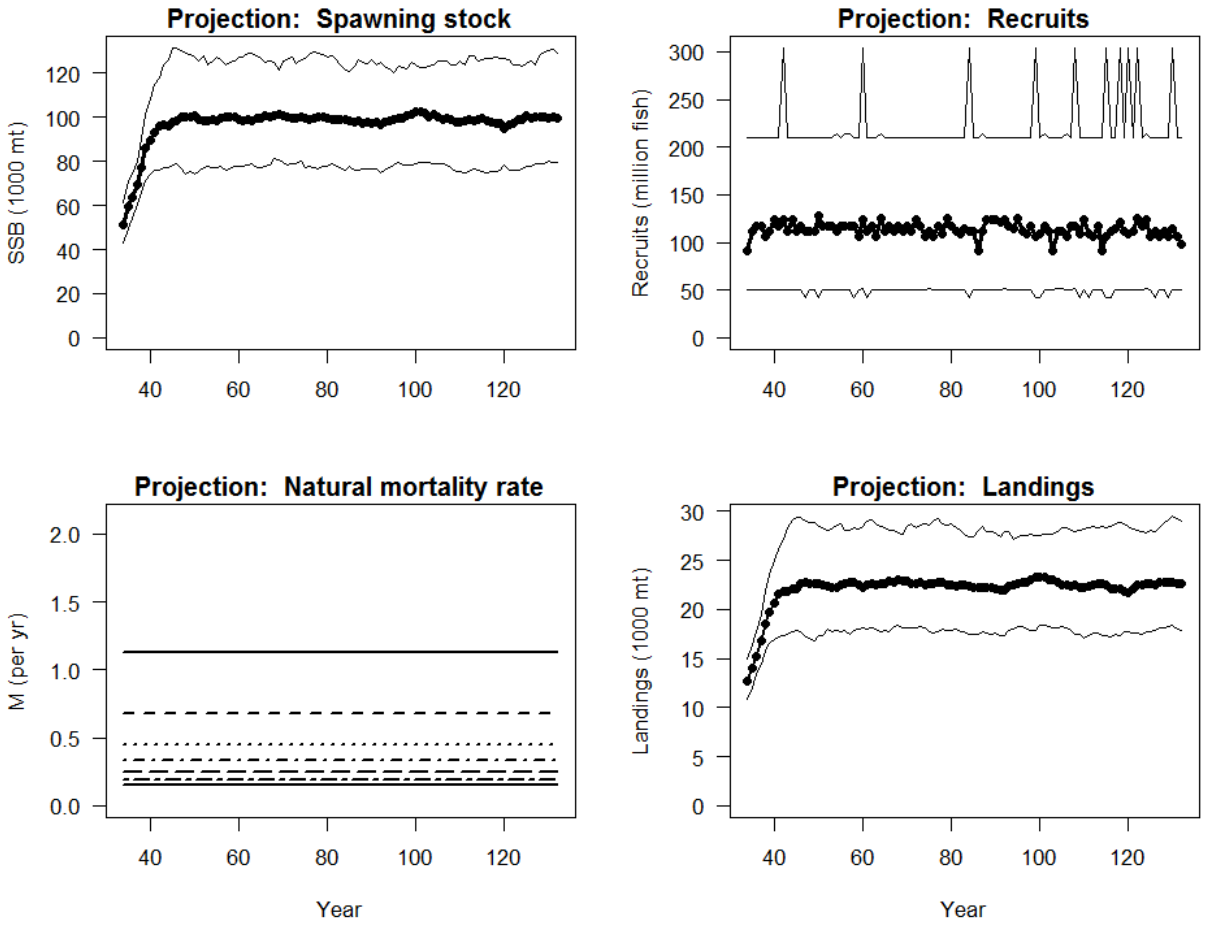


Figure 112. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under scenario 2 for the VADER model (all species at target *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

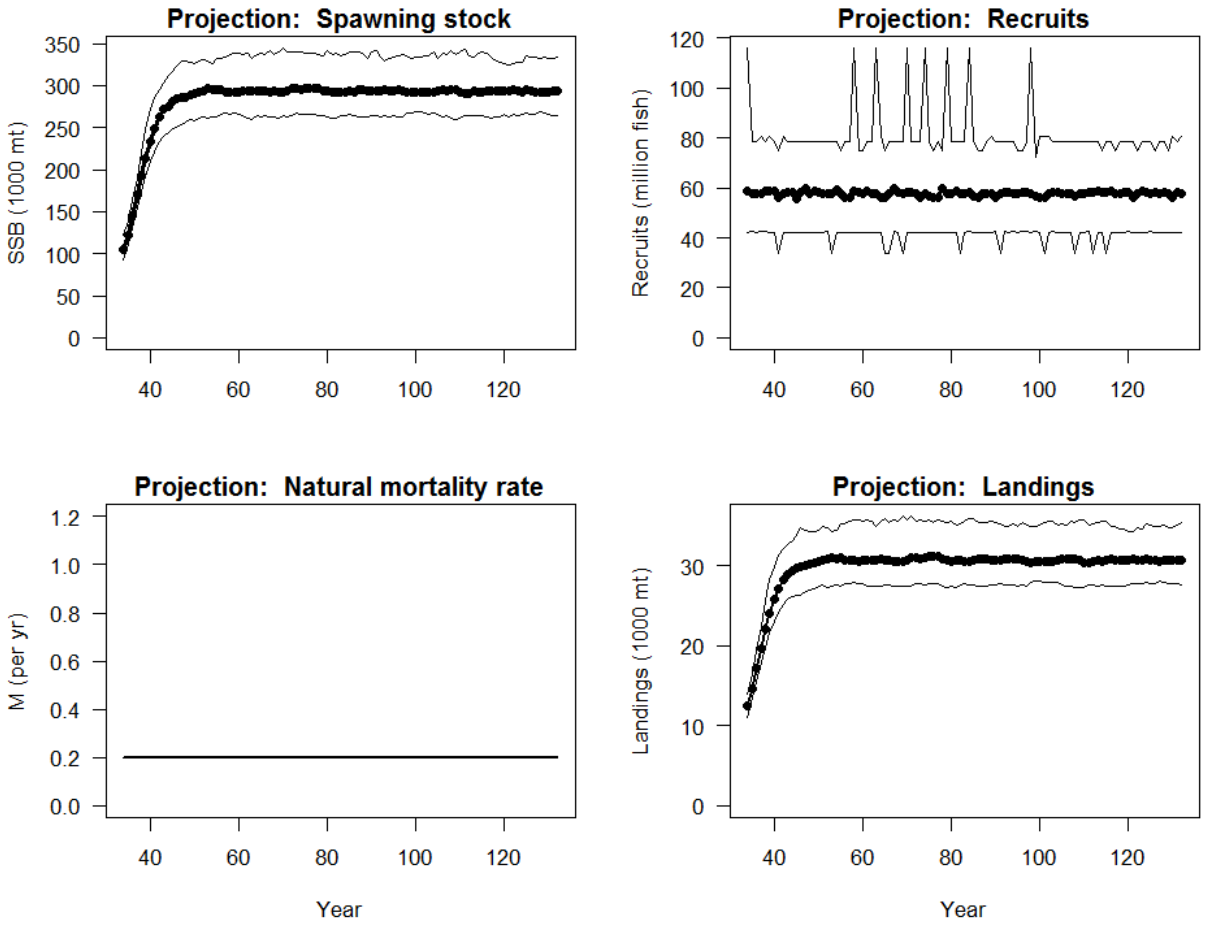


Figure 113. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for bluefish under scenario 2 for the VADER model (all species at target *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

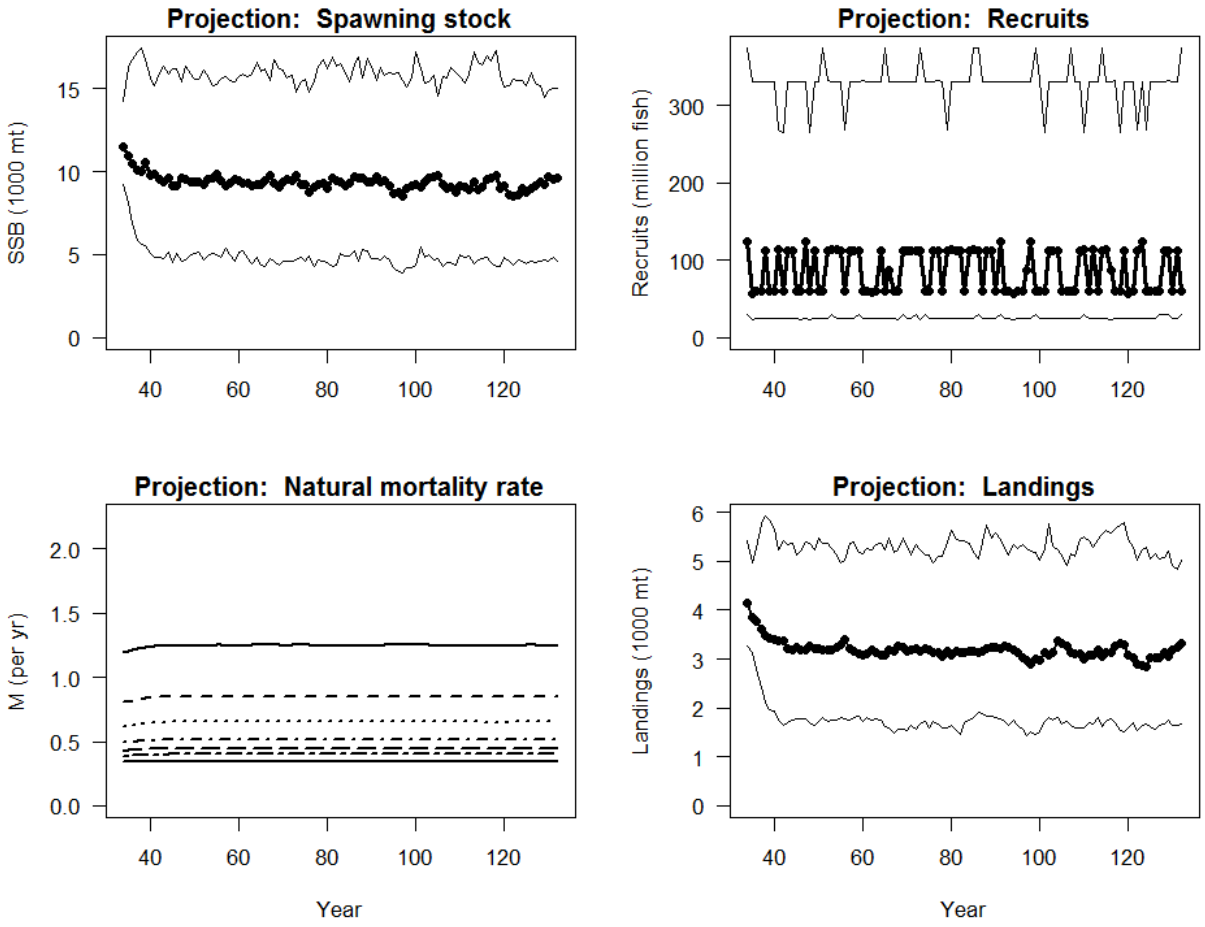


Figure 114. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for weakfish under scenario 2 for the VADER model (all species at target *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

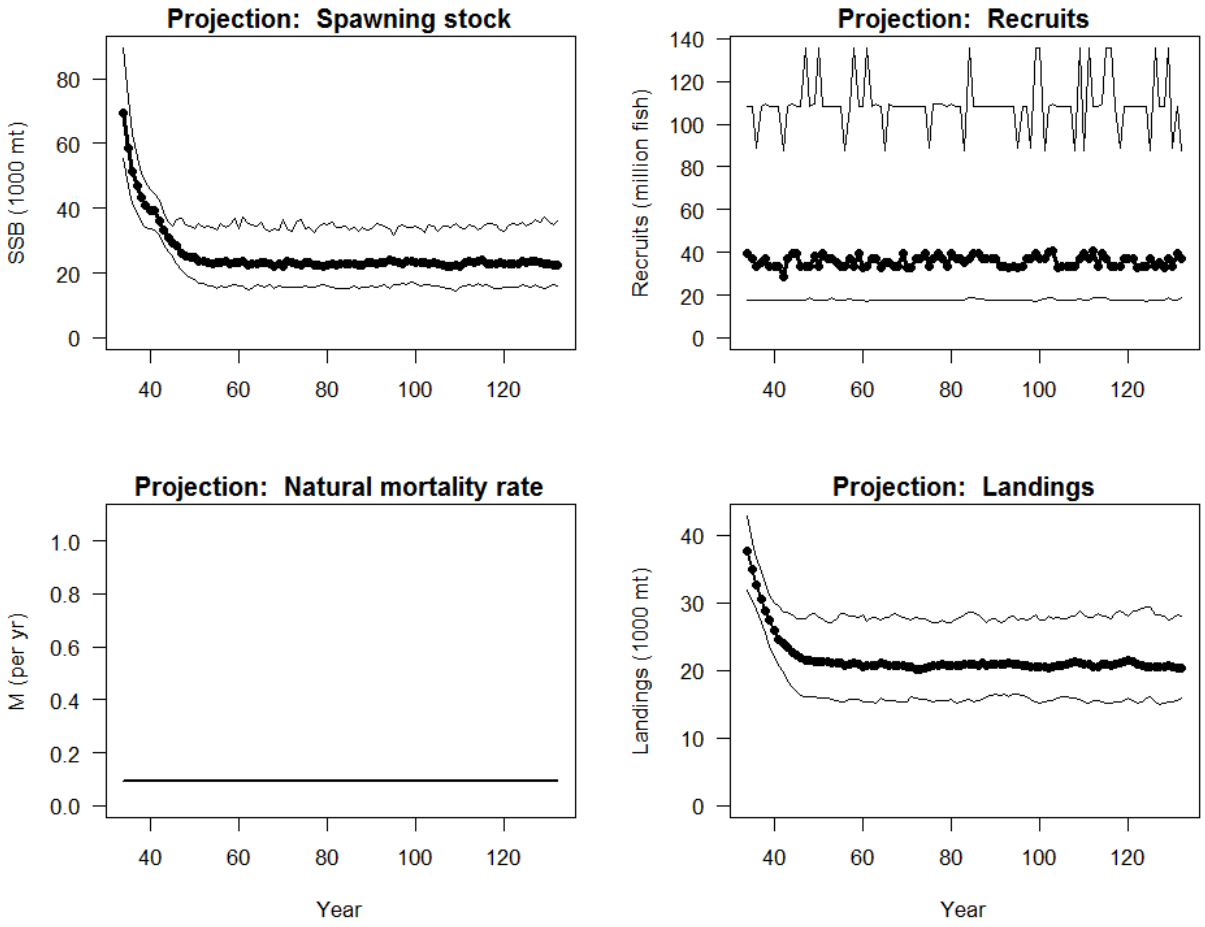


Figure 115. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for spiny dogfish under scenario 2 for the VADER model (all species at target *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

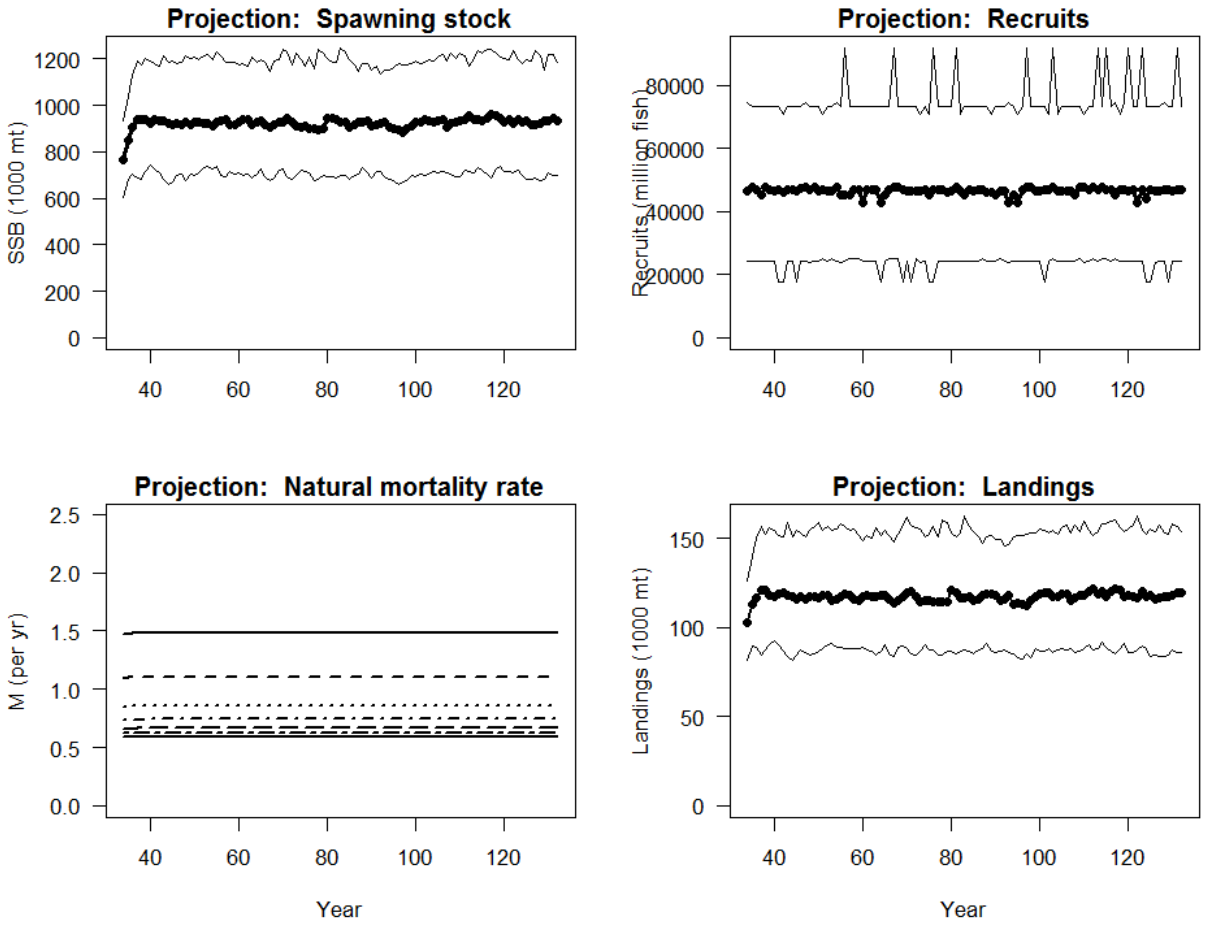


Figure 116. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for Atlantic menhaden under scenario 3 for the VADER model (all species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

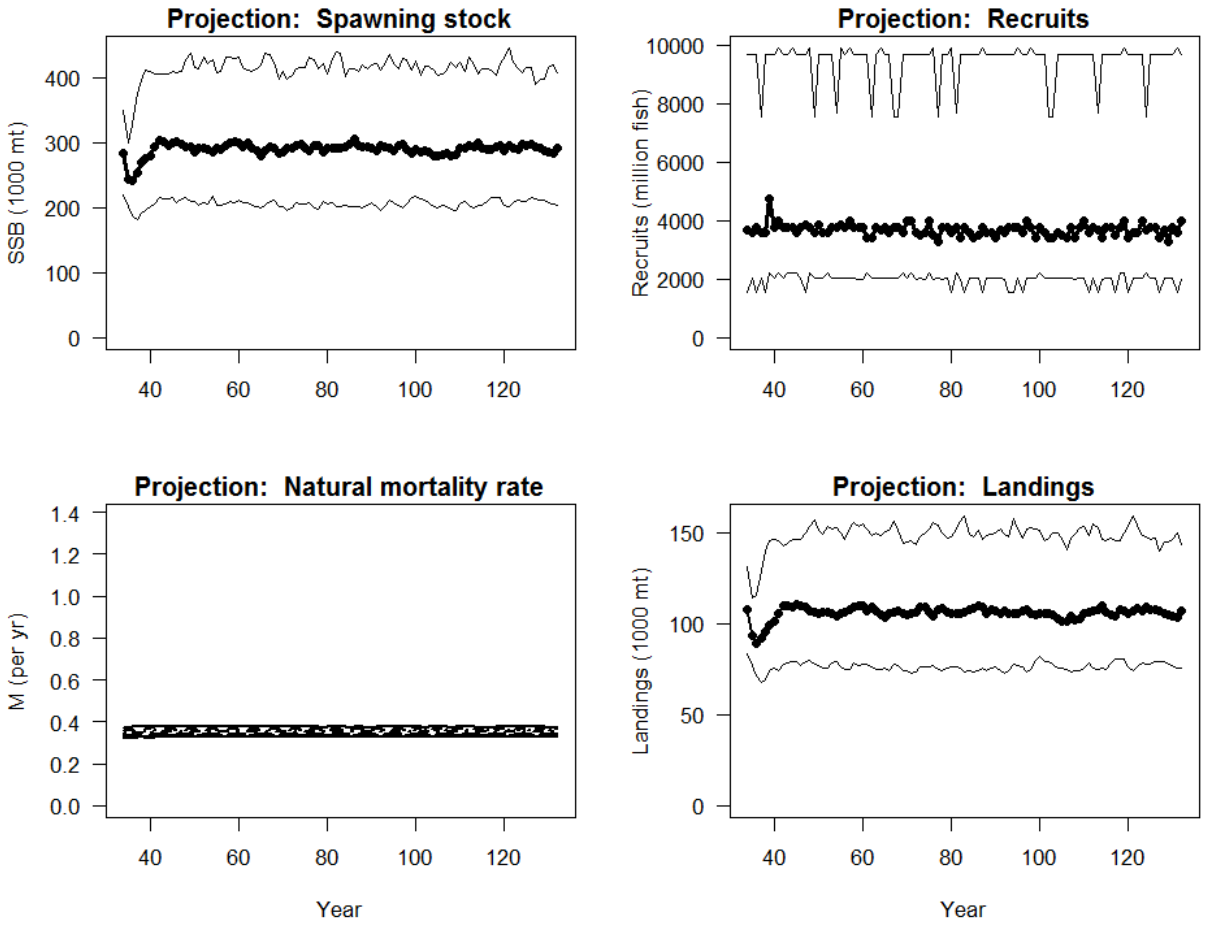


Figure 117. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for Atlantic herring under scenario 3 for the VADER model (all species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

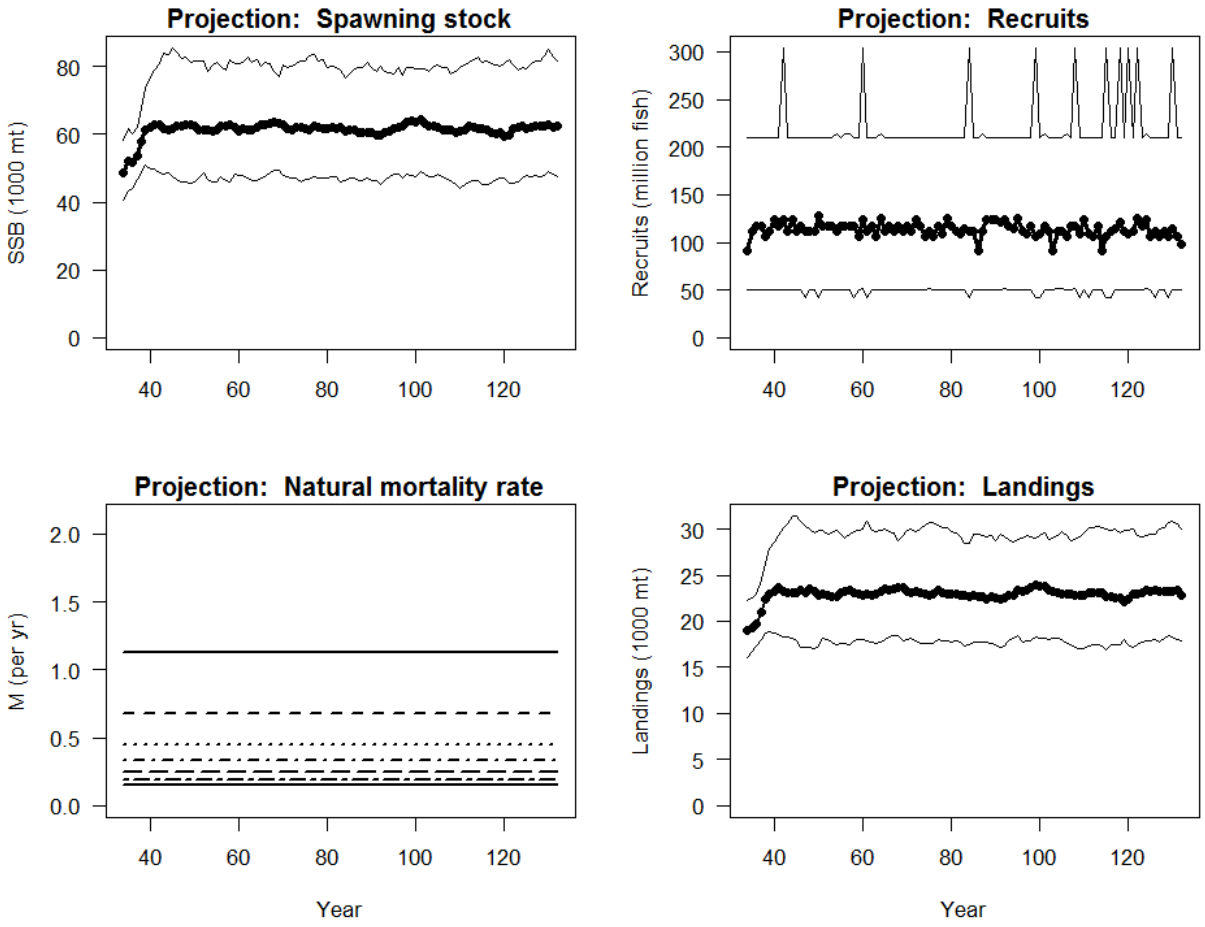


Figure 118. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under scenario 3 for the VADER model (all species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

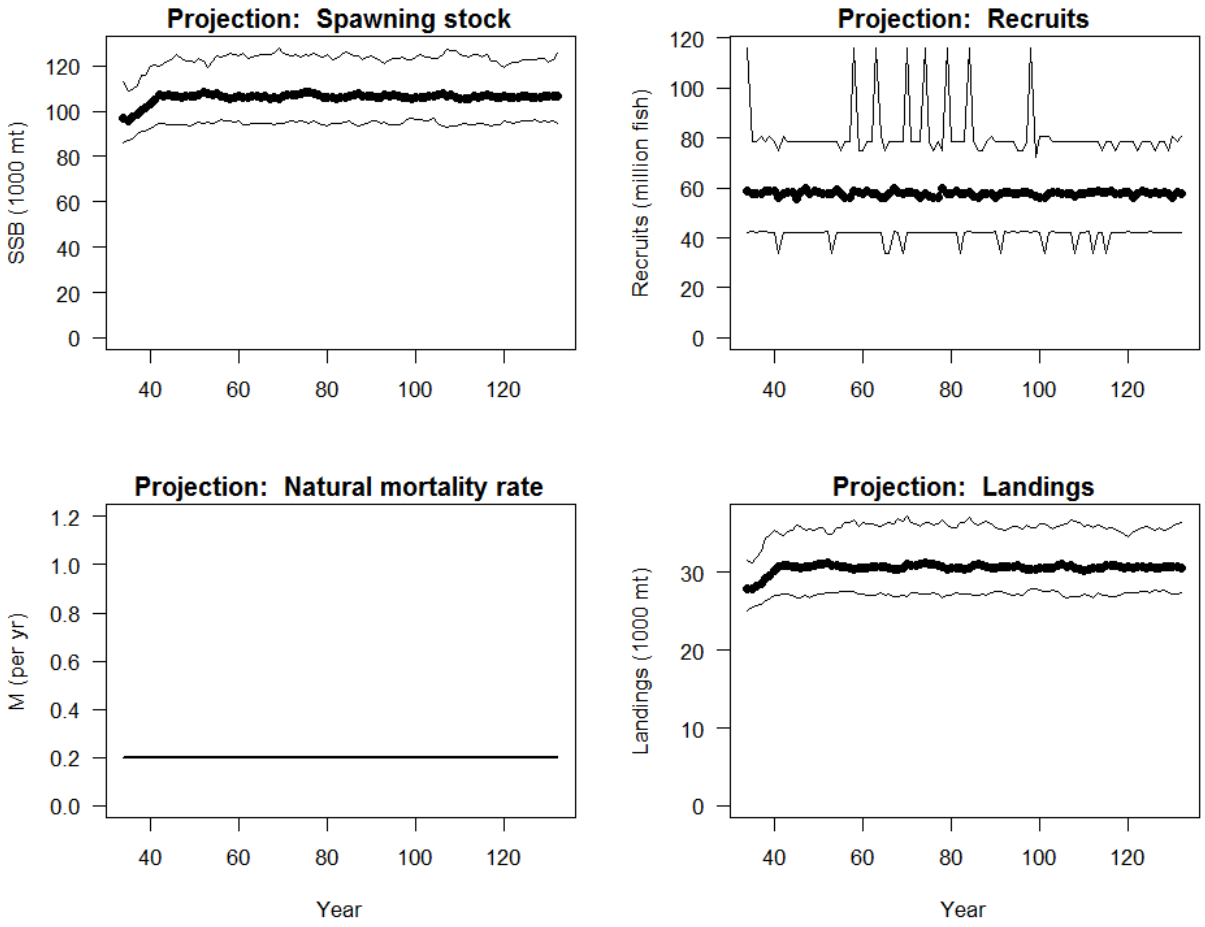


Figure 119. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for bluefish under scenario 3 for the VADER model (all species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

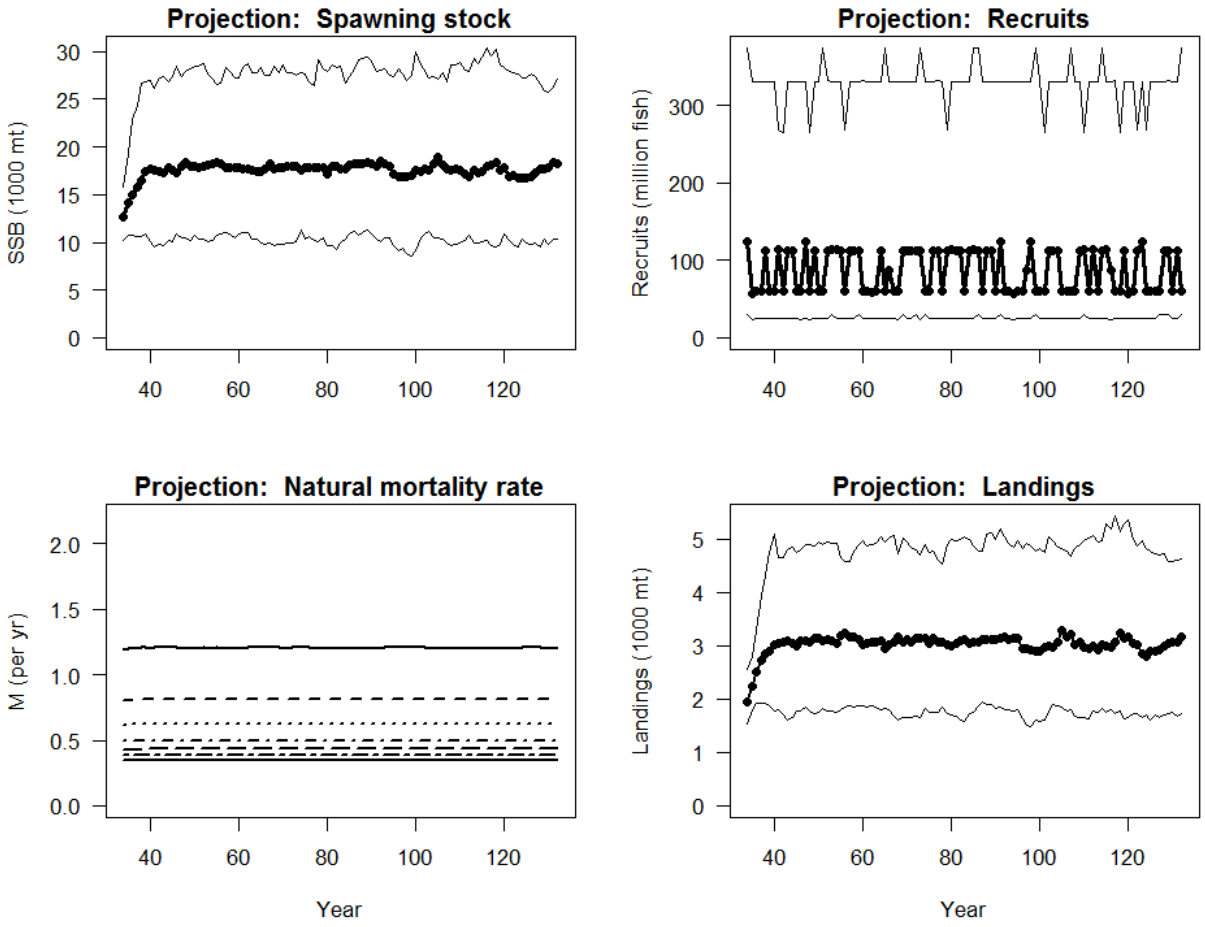


Figure 120. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for weakfish under scenario 3 for the VADER model (all species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

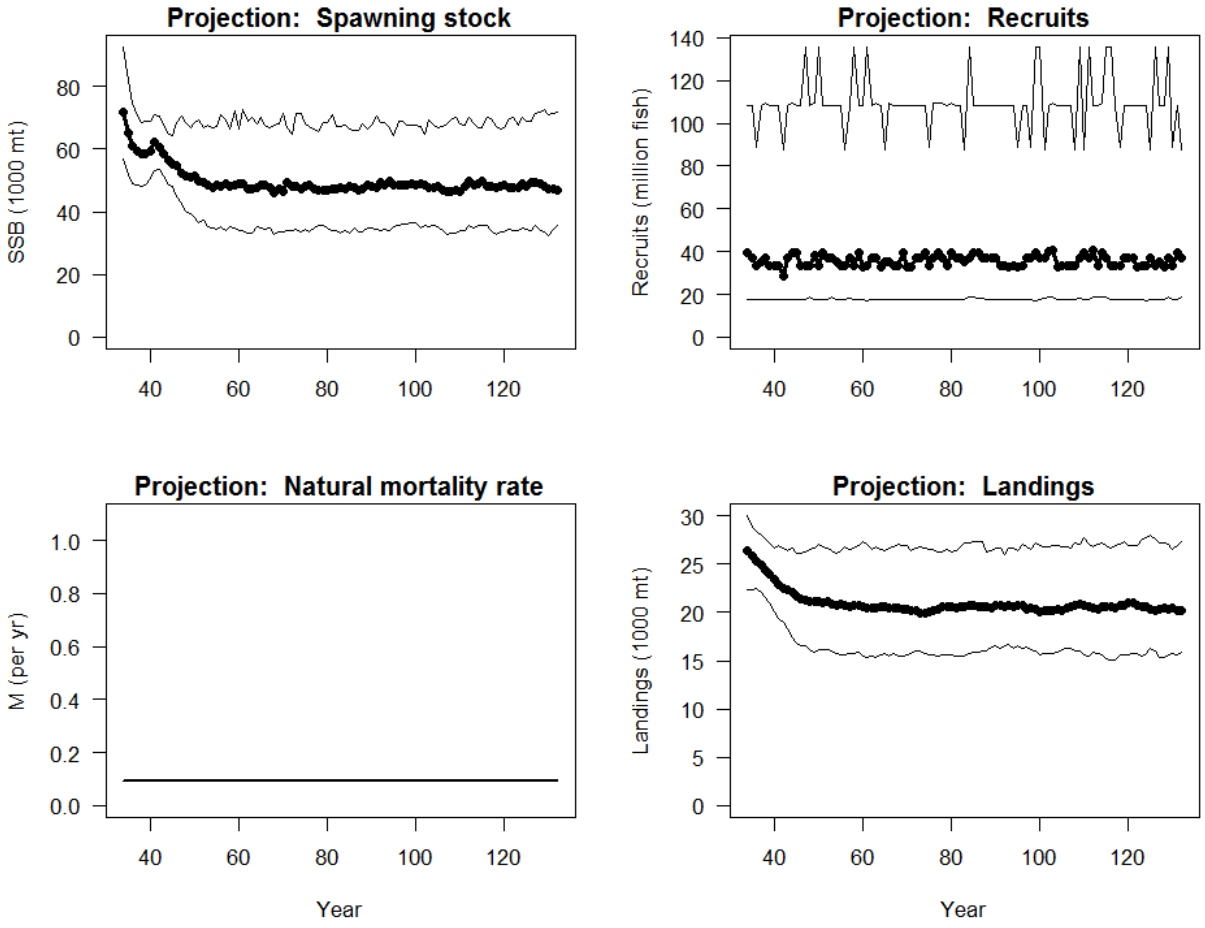


Figure 121. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for spiny dogfish under scenario 3 for the VADER model (all species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

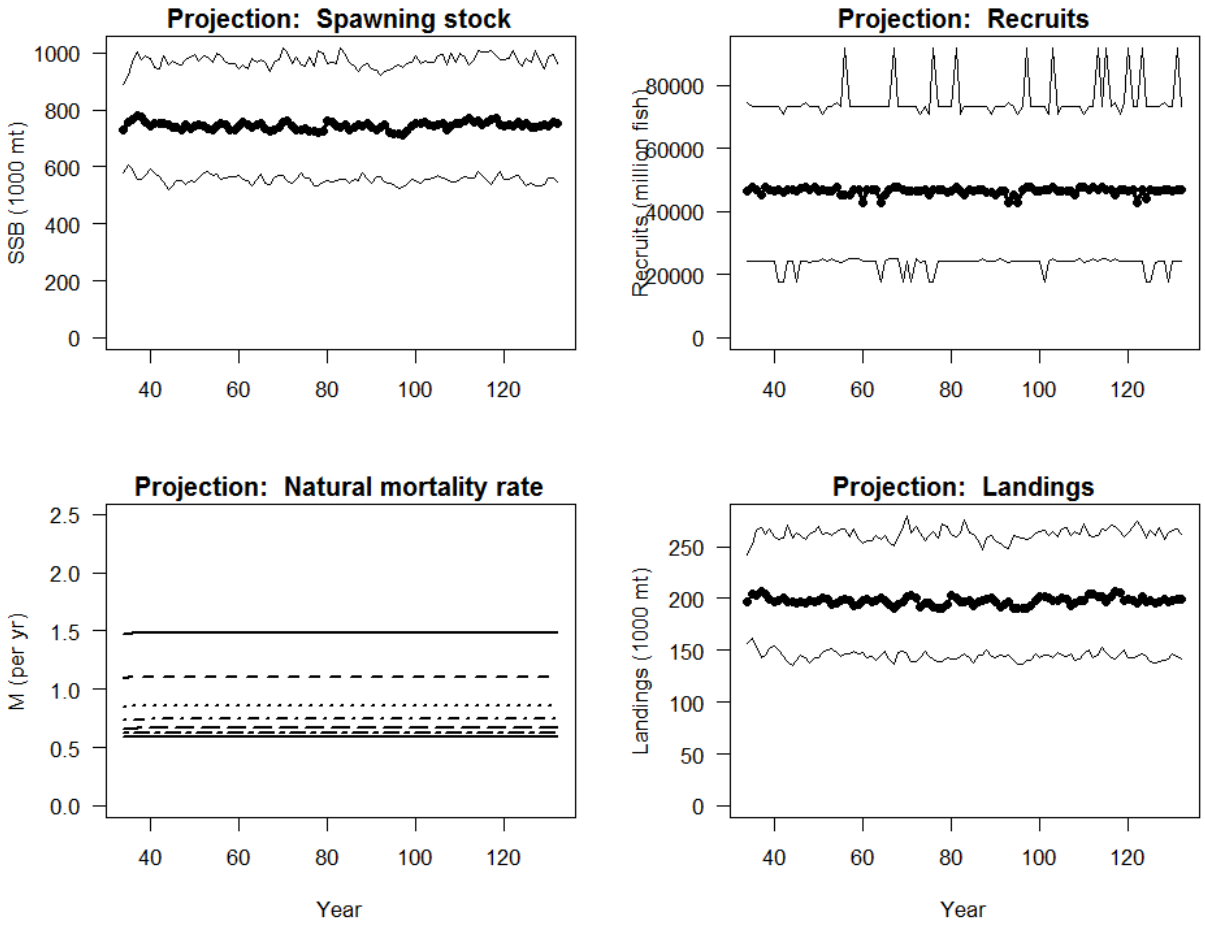


Figure 122. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for Atlantic menhaden under scenario 4 for the VADER model (Atlantic menhaden at target *F,* all other species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

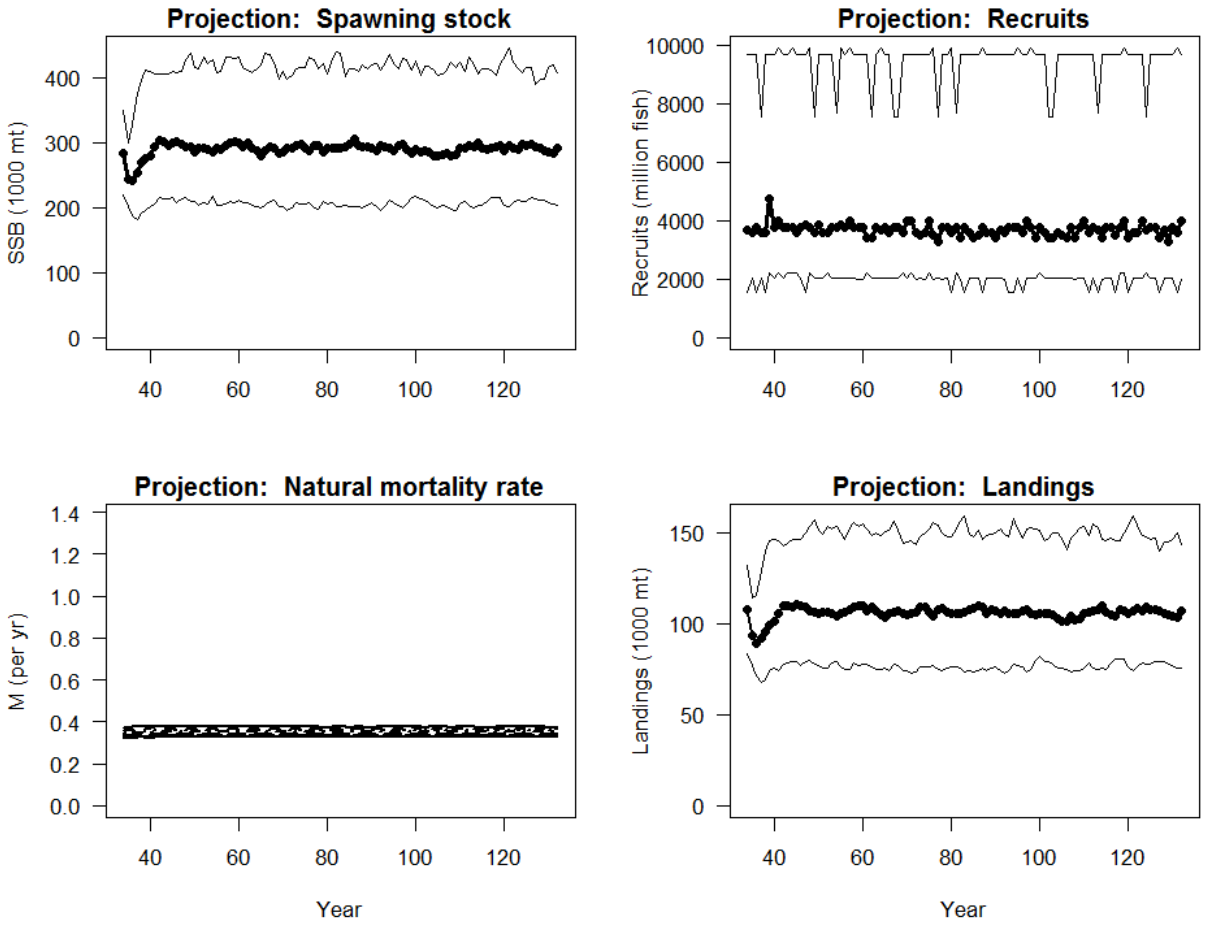


Figure 123. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for Atlantic herring under scenario 4 for the VADER model (Atlantic menhaden at target *F,* all other species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

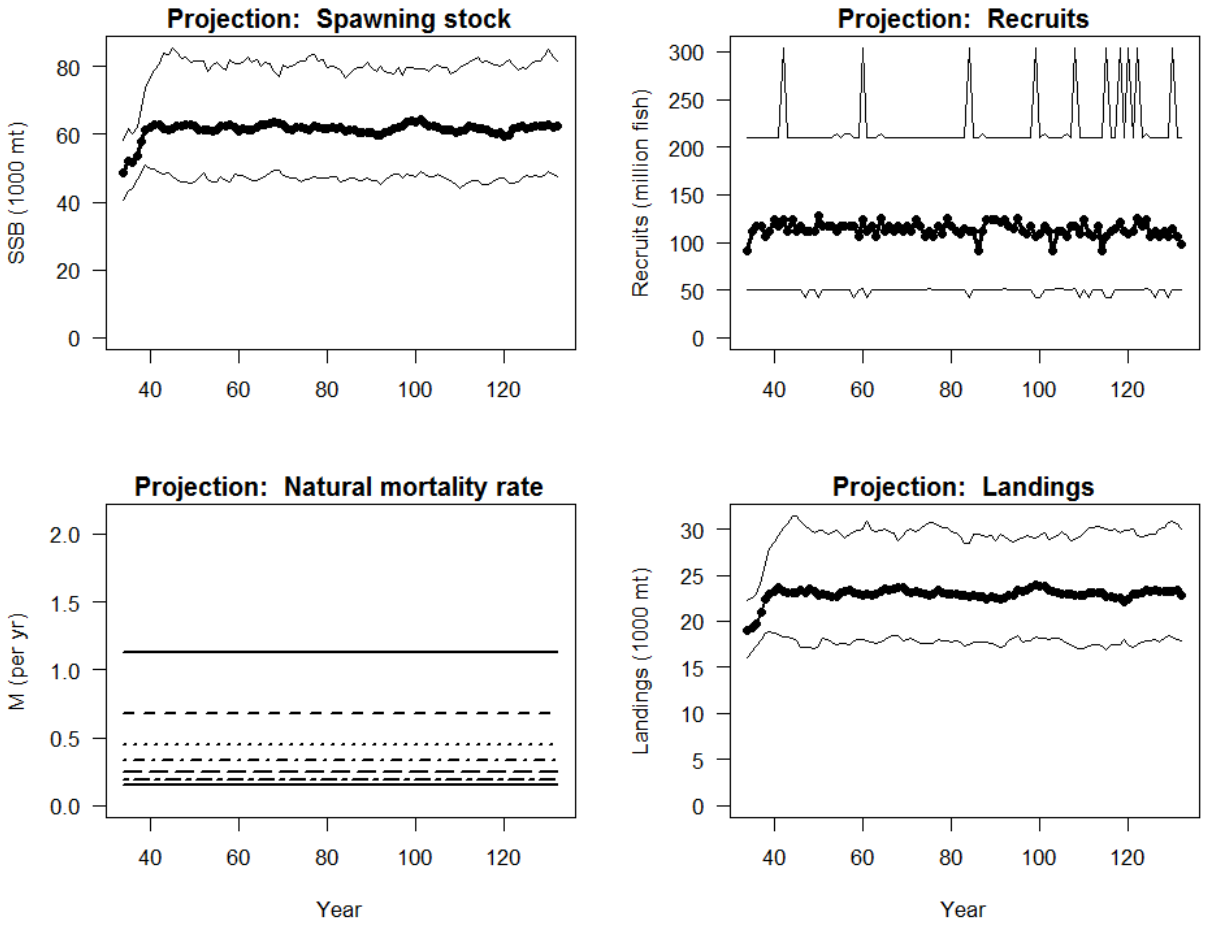


Figure 124. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for striped bass under scenario 4 for the VADER model (Atlantic menhaden at target *F,* all other species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

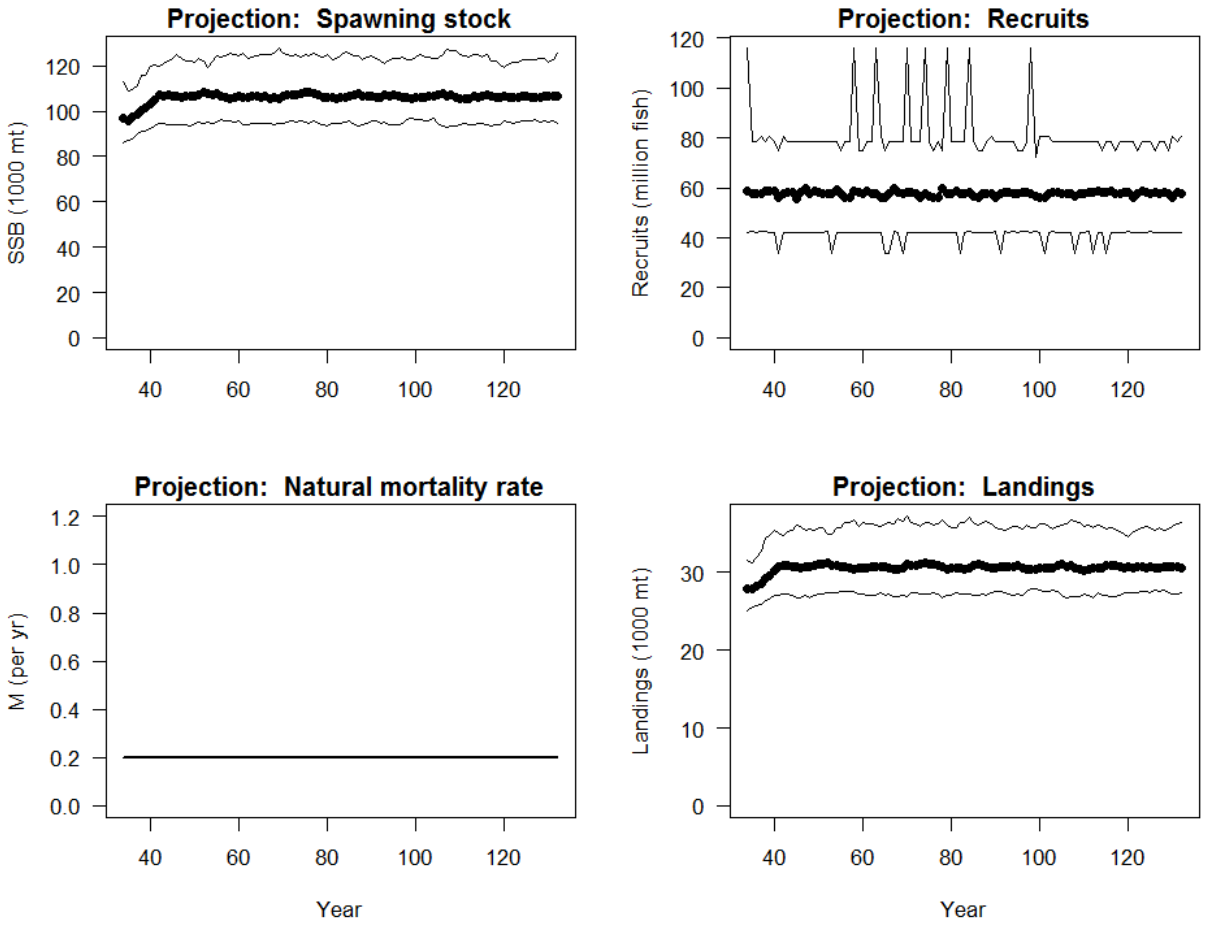


Figure 125. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for bluefish under scenario 4 for the VADER model (Atlantic menhaden at target *F,* all other species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

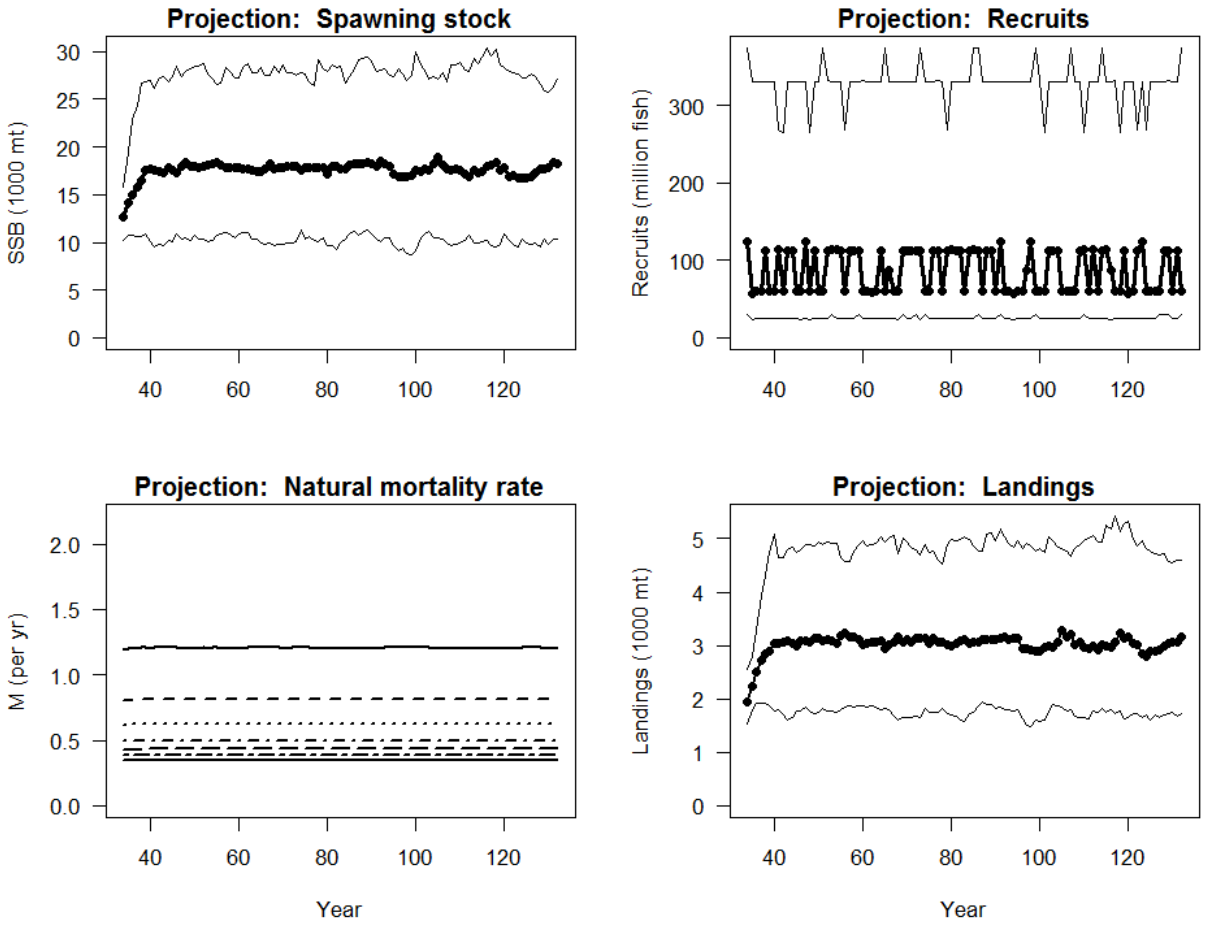


Figure 126. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for weakfish under scenario 4 for the VADER model (Atlantic menhaden at target *F,* all other species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

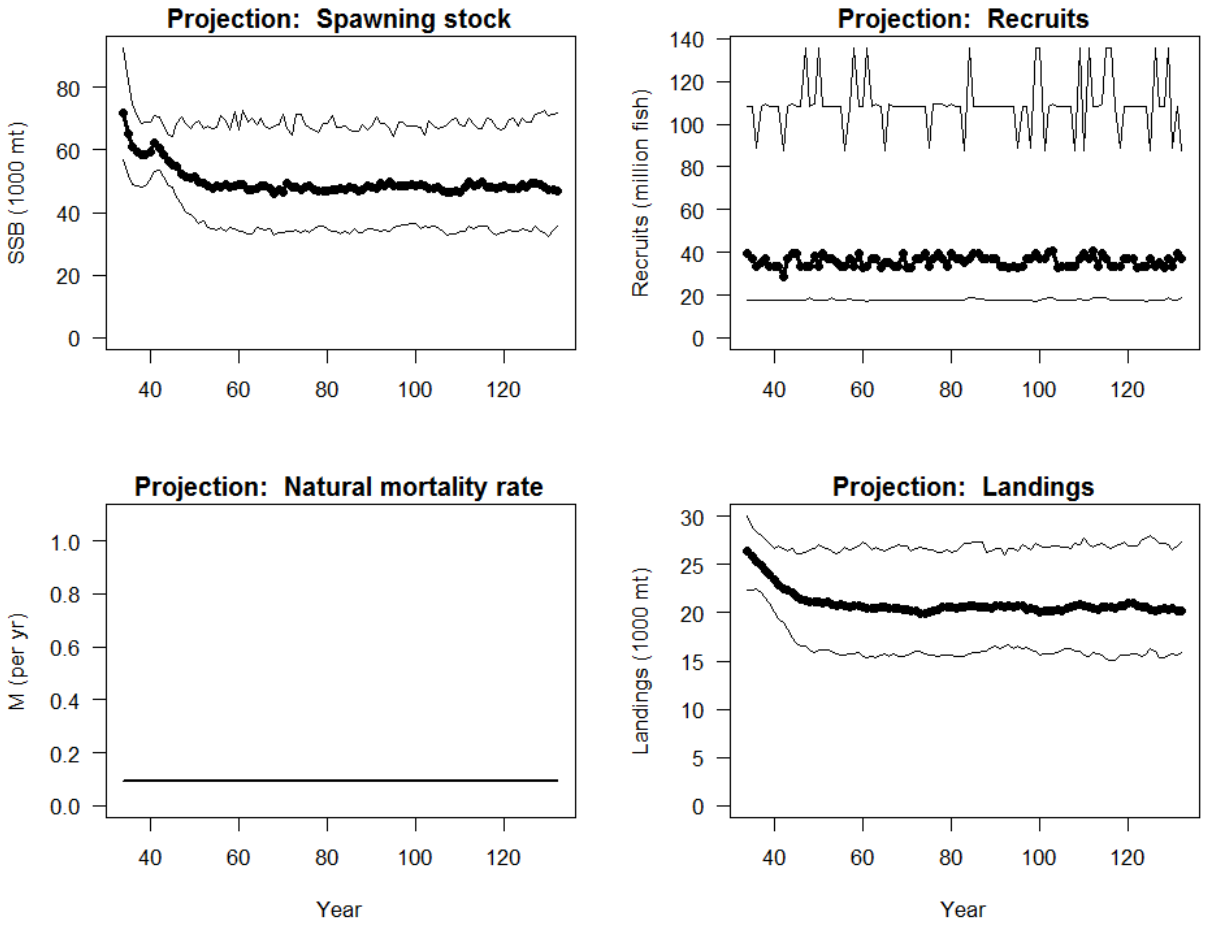


Figure 127. Projected spawning stock biomass, recruitment, natural mortality at-age, and landings for spiny dogfish under scenario 4 for the VADER model (Atlantic menhaden at target *F,* all other species at status quo *F*). For the SSB, recruitment, and landings plots the thin solid lines are the 5th and 95th percentiles, the solid line with circles is the median. For the *M* plot, the different lines represent *M*-at-age.

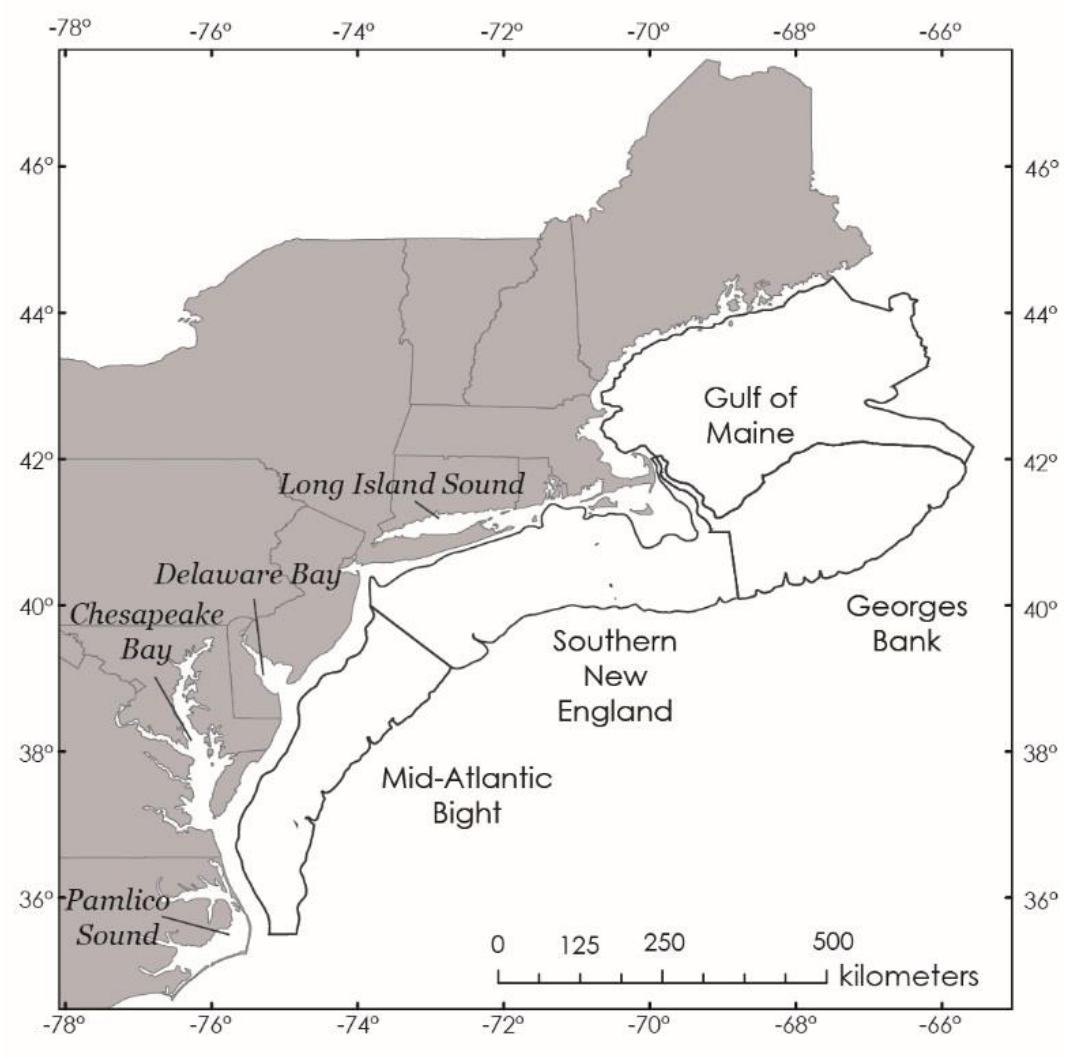


Figure 128. Map of the Northwest Atlantic Continental Shelf (NWACS) system, with major subregions and estuaries labeled. Figure modified from Link et al. (2006).

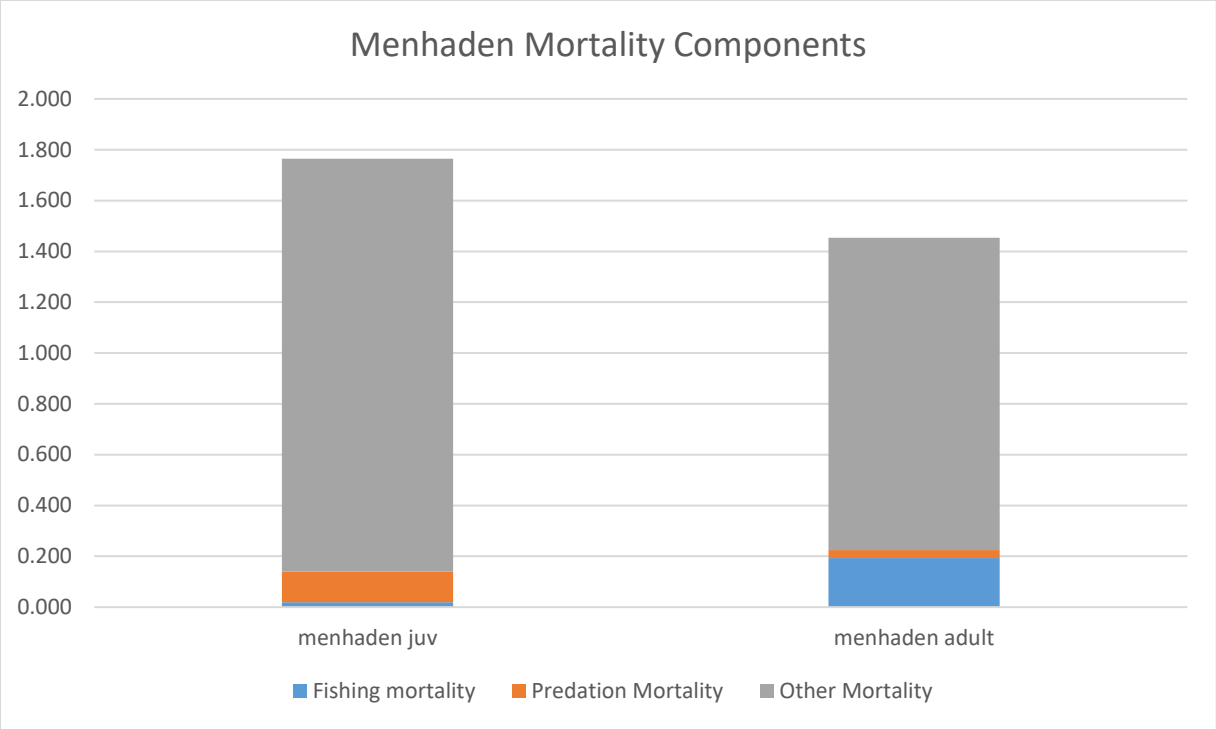


Figure 129. Ecopath Atlantic menhaden mortality components from the NWACS-MICE model.

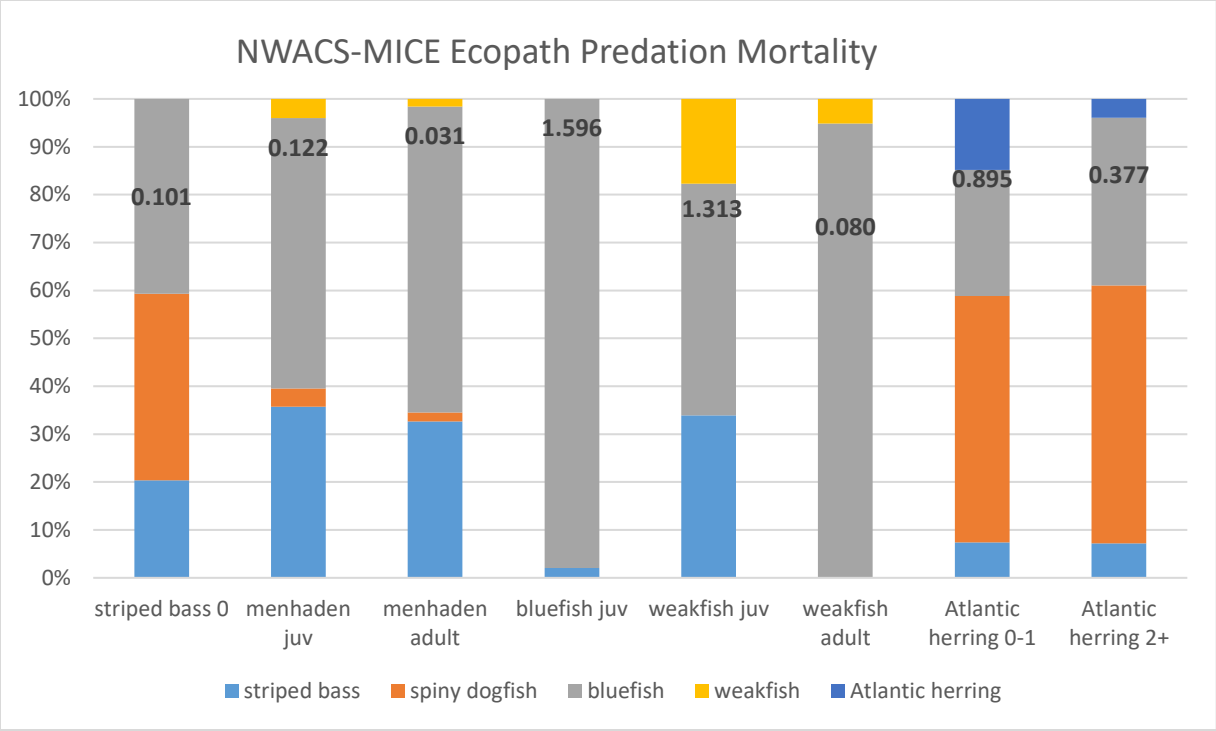


Figure 130. Predation mortality rates by species for the NWACS-MICE model. Each bar represents a prey item and the colors are the contributions by each predator. The values for each bar are the total predation mortality rates.

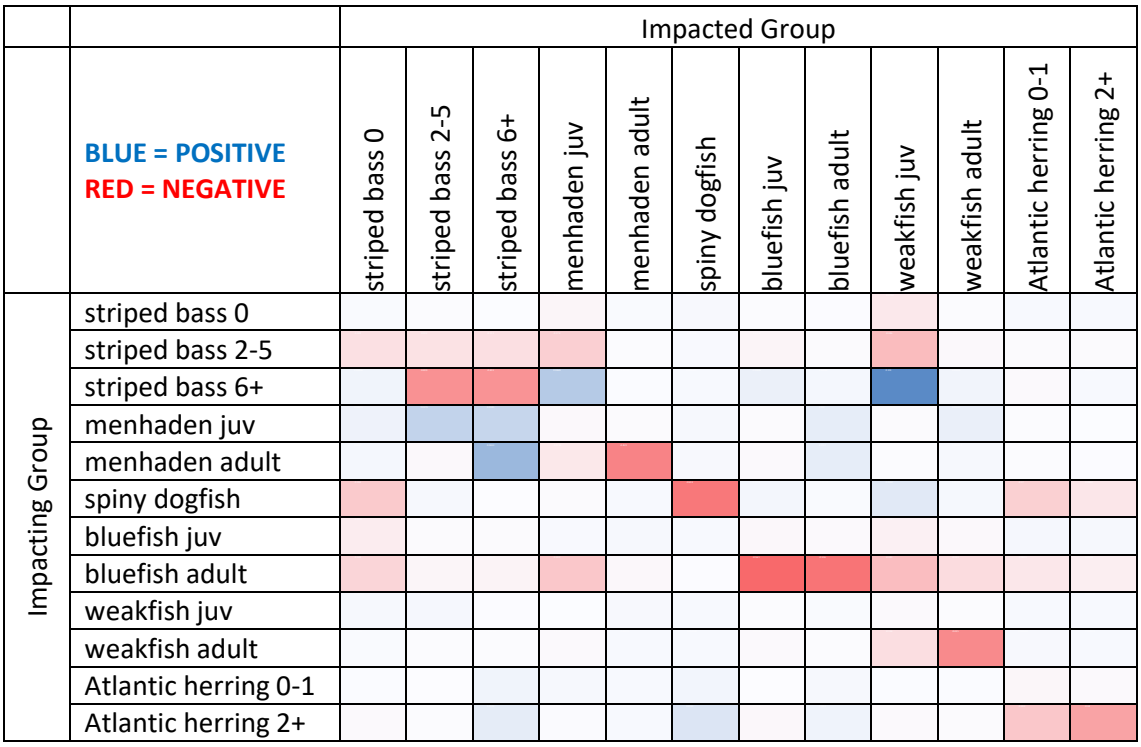


Figure 131. Mixed trophic impacts from the NWACS-MICE model.

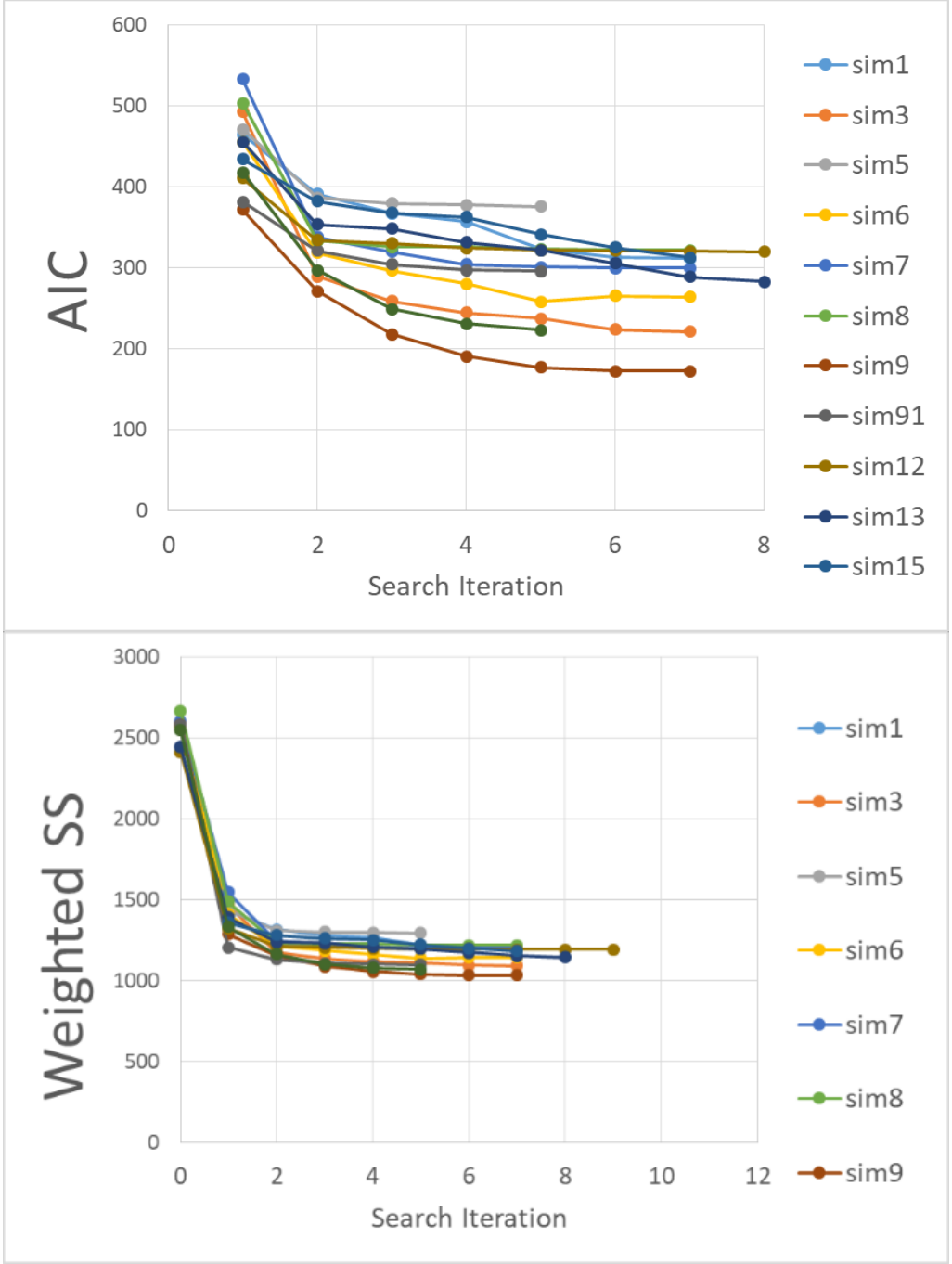


Figure 132. AIC (top) and weighted sums of squares (bottom) by simulation for repeated search iterations from the NWACS-MICE model.

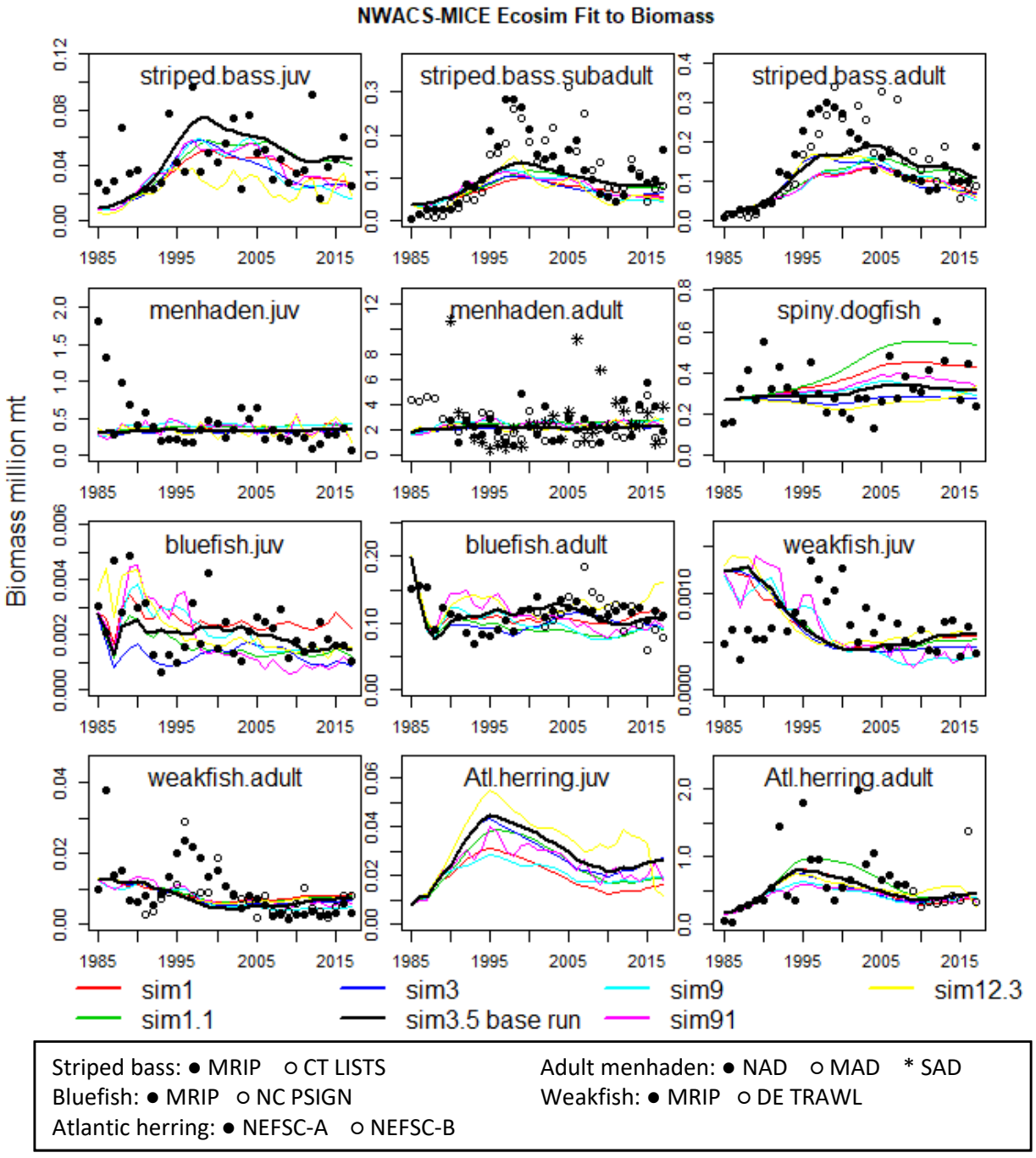


Figure 133. Ecosim fits to biomass from seven alternative runs of the NWACS-MICE model. Observed indices are listed in Table 34.

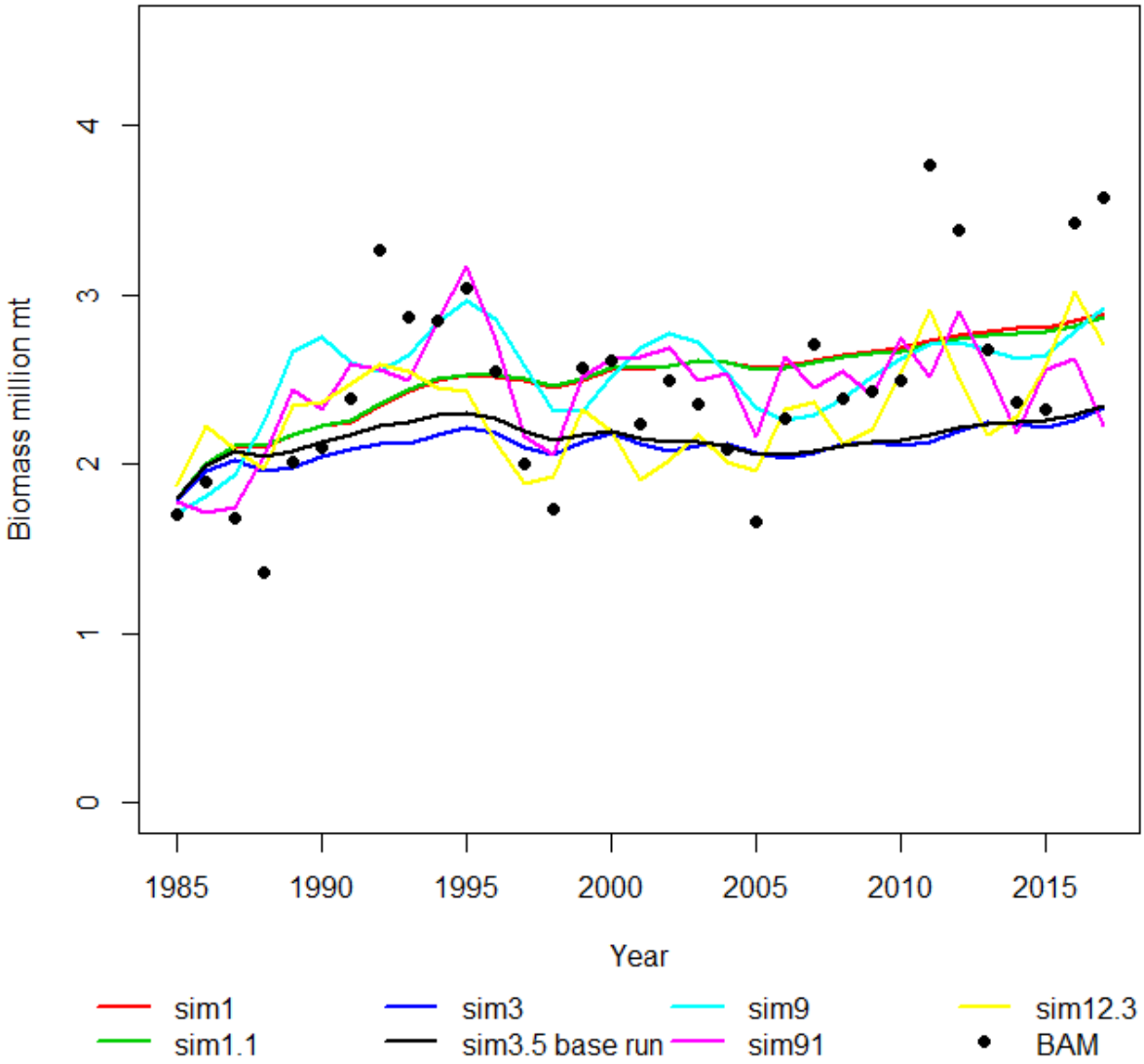


Figure 134. Atlantic menhaden age 1+ biomass predicted by Ecosim from the NWACS-MICE model plotted with age 1+ biomass from the single-species model (BAM).

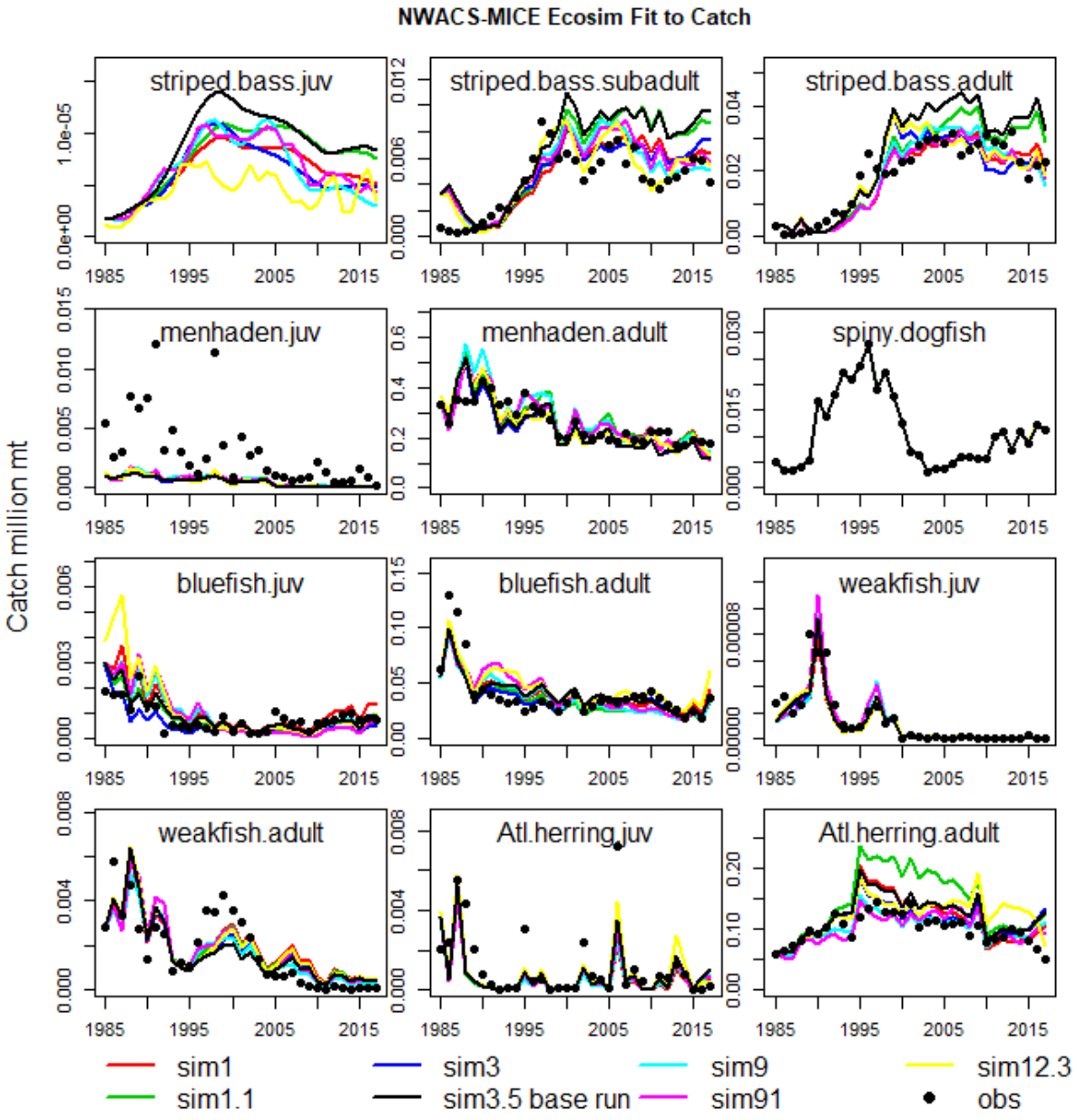


Figure 135. Ecosim fits to observed catch from seven alternative runs of the NWACS-MICE model. Observed catch series are listed in Table 34.

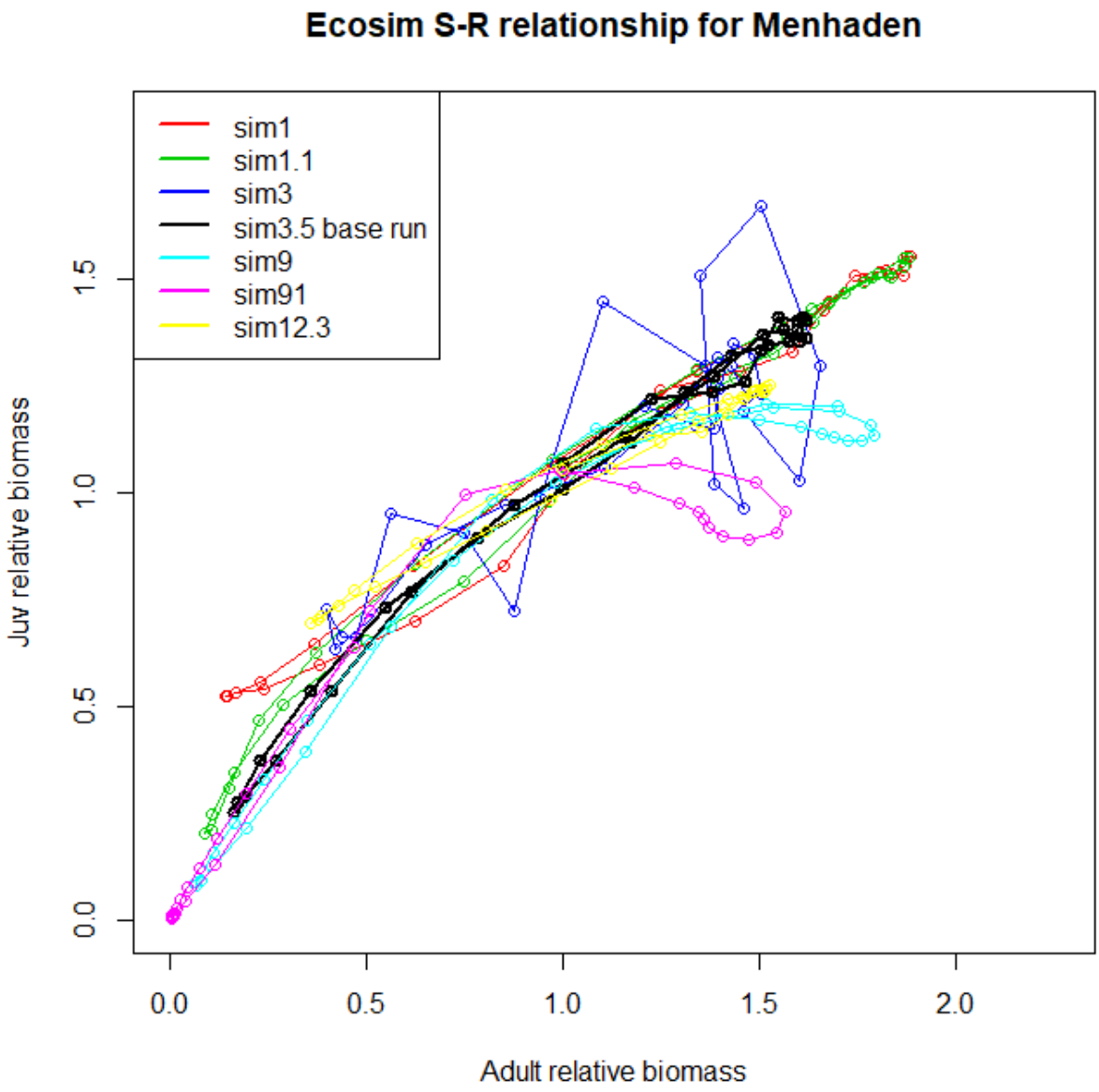


Figure 136. Atlantic menhaden stock-recruit plot from alternative runs of the NWACS-MICE model.

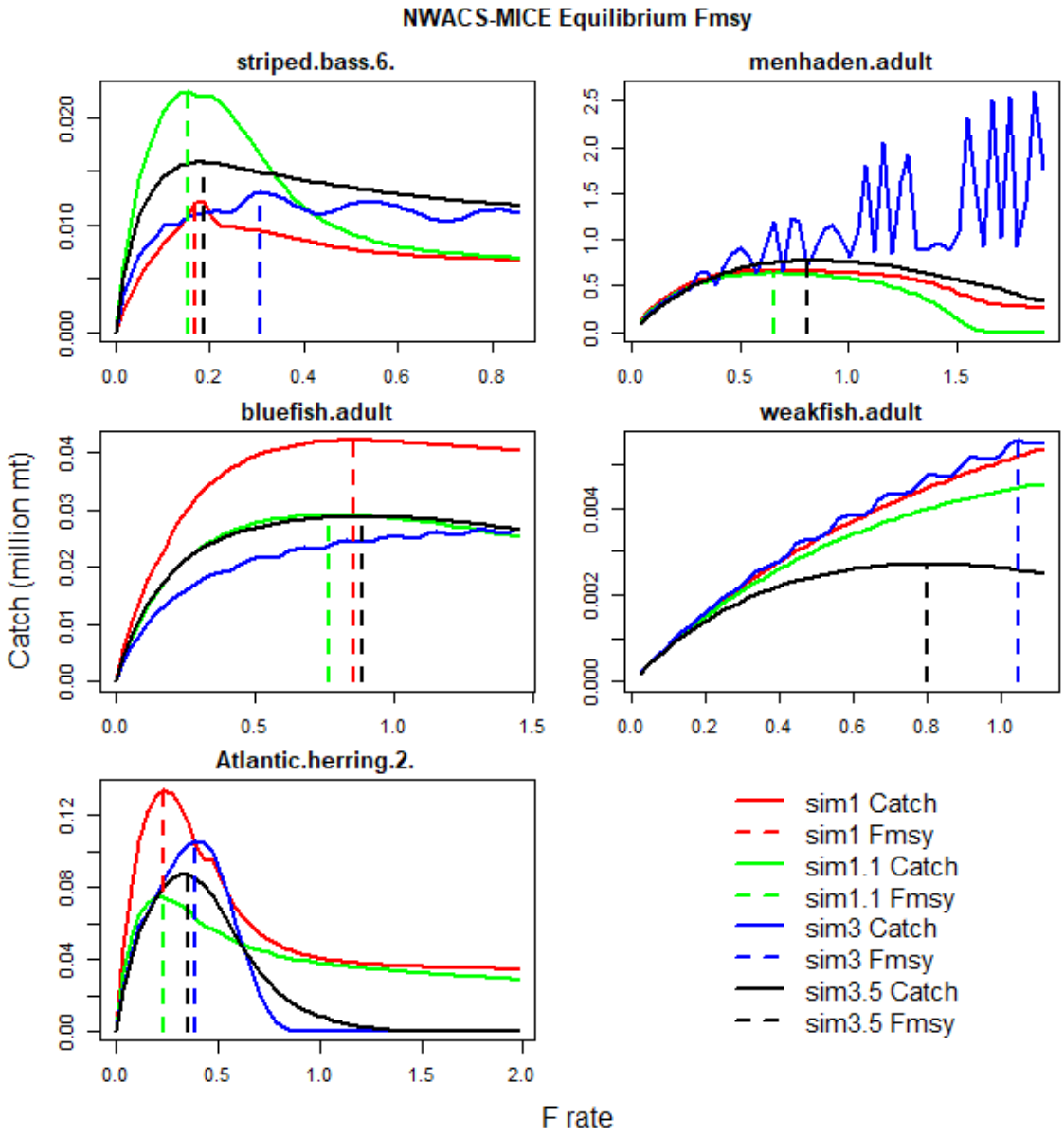


Figure 137. Equilibrium MSY curves from four alternative Ecosim runs (non-stationary system) from the NWACS-MICE model. The solid lines show long term yield over a range of *F*. The dotted lines indicate the *F* at maximum yield, F_{MSY}. Absence of a dotted line indicates that a F_{MSY} value was not found.

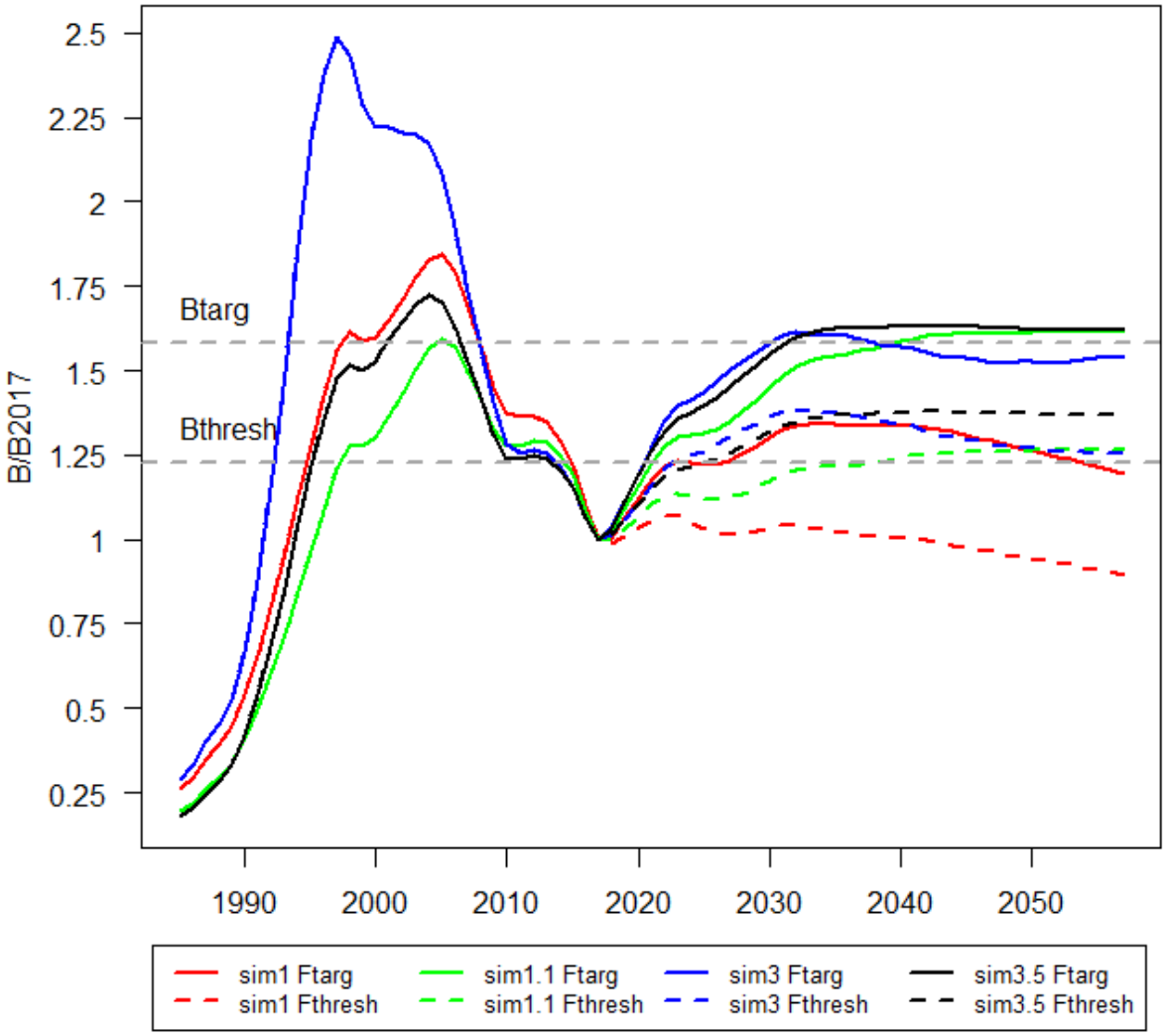


Figure 138. Striped bass age 6+ biomass (scaled to 2017) projected under target and threshold fishing mortality rates from the NWACS-MICE model. All other species were held constant at status quo *F* (F_{2017}).

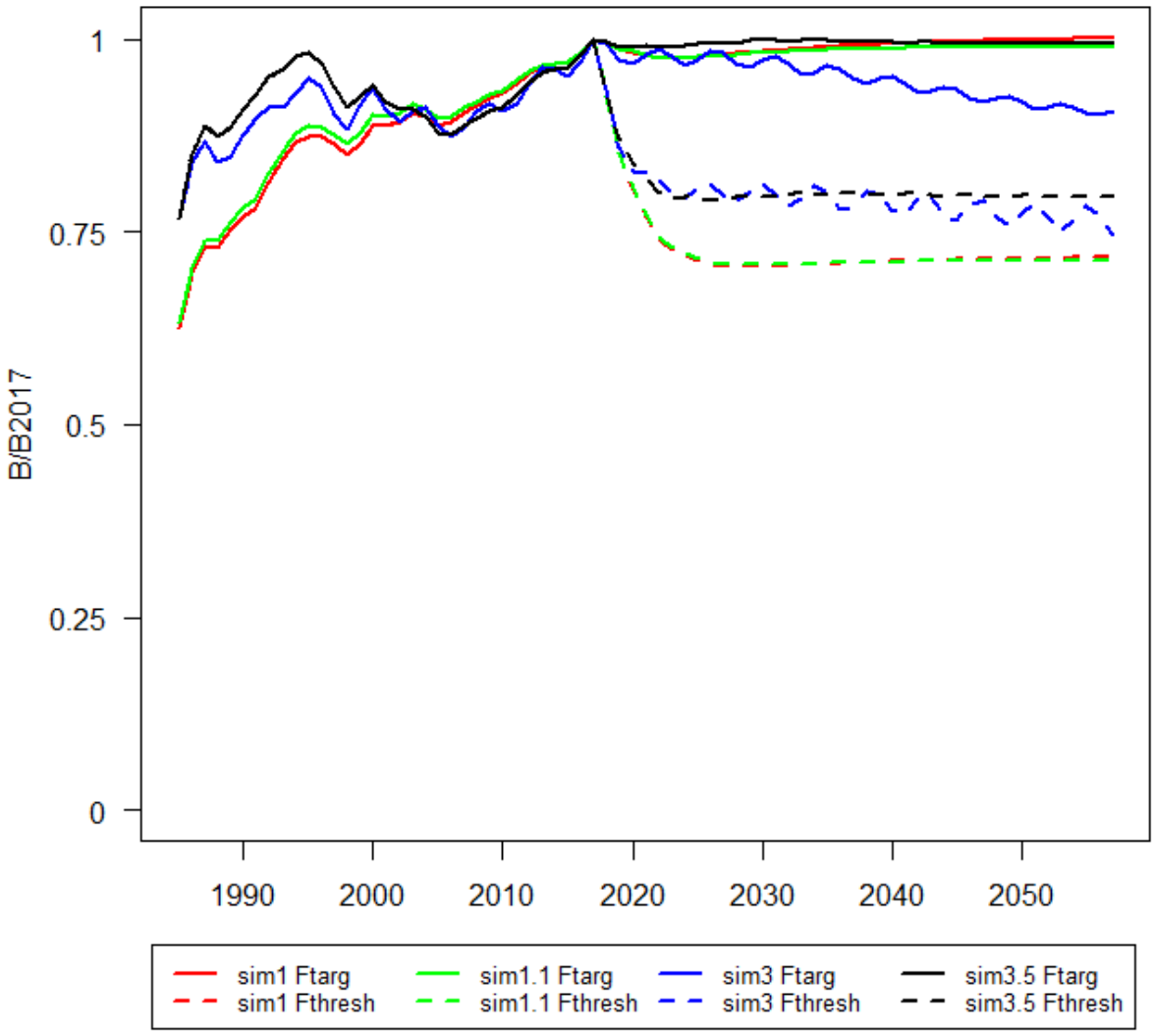


Figure 139. Atlantic menhaden age 1+ biomass projected under target and threshold fishing mortality rates from the NWACS-MICE model. All other species were held constant at status quo *F* (F_{2017}).

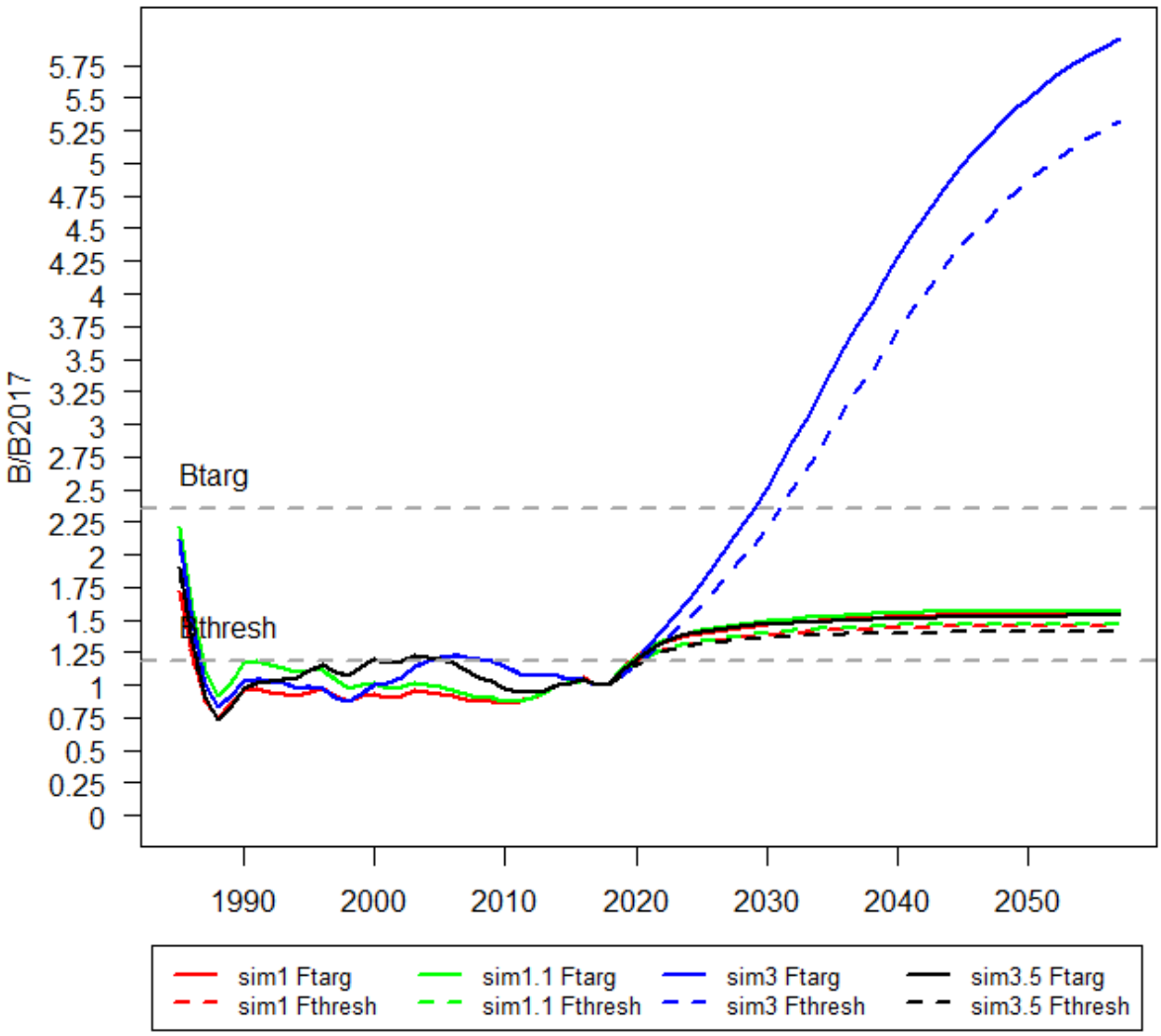


Figure 140. Bluefish age 1+ biomass projected under target and threshold fishing mortality rates from the NWACS-MICE model. All other species were held constant at status quo *F* (F_{2017}).

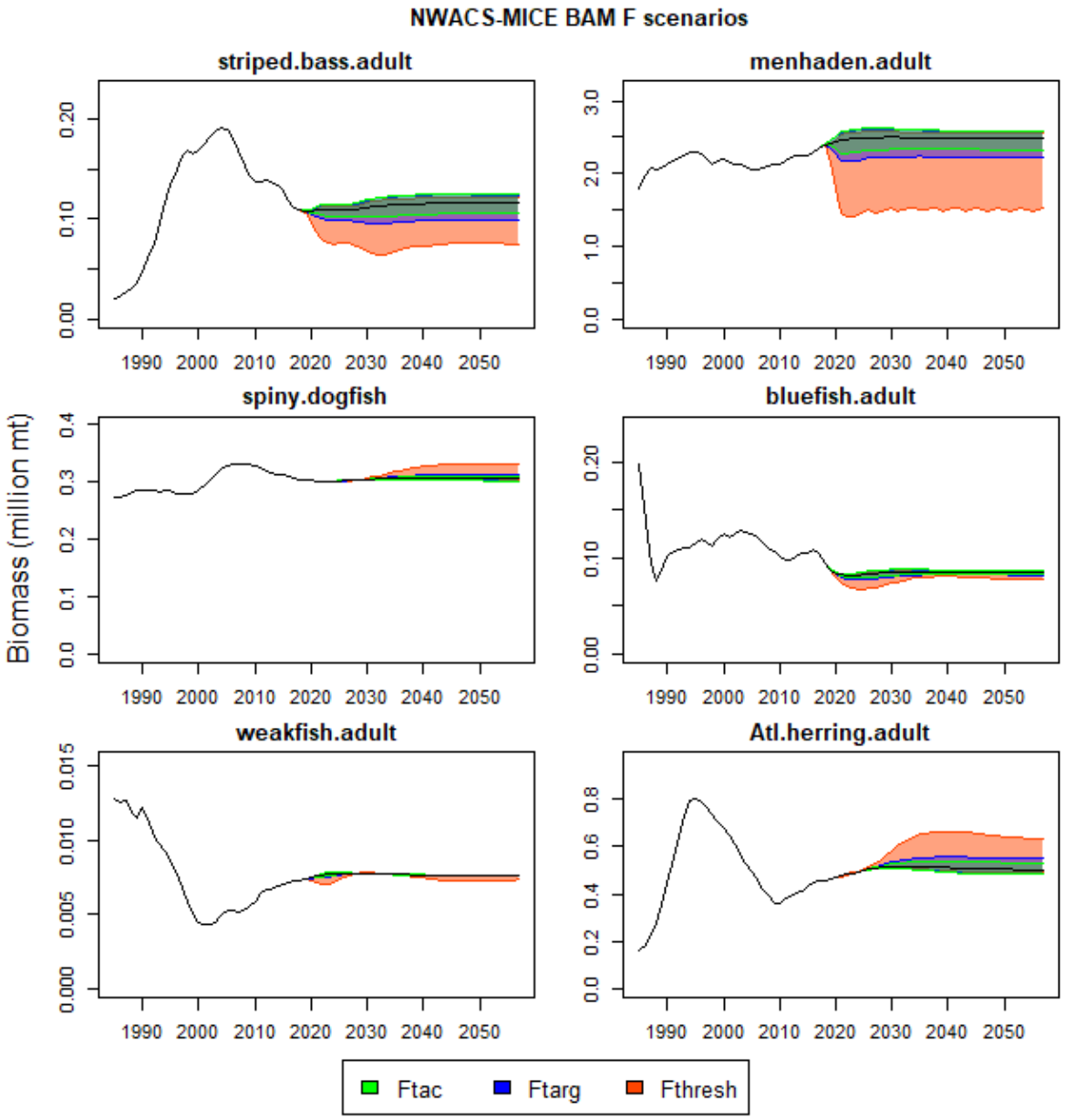


Figure 141. Biomass trajectories from the NWACS-MICE model under the BAM *F* scenarios: Ftac= *F* associated with current TAC; Ftarg = single-species *F* target; Fthresh= single-species *F* threshold. Shaded regions show the full range of biomass predicted under each scenario. In the BAM *F* scenarios, all other species were held constant at their status quo *F* (F_{2017}).

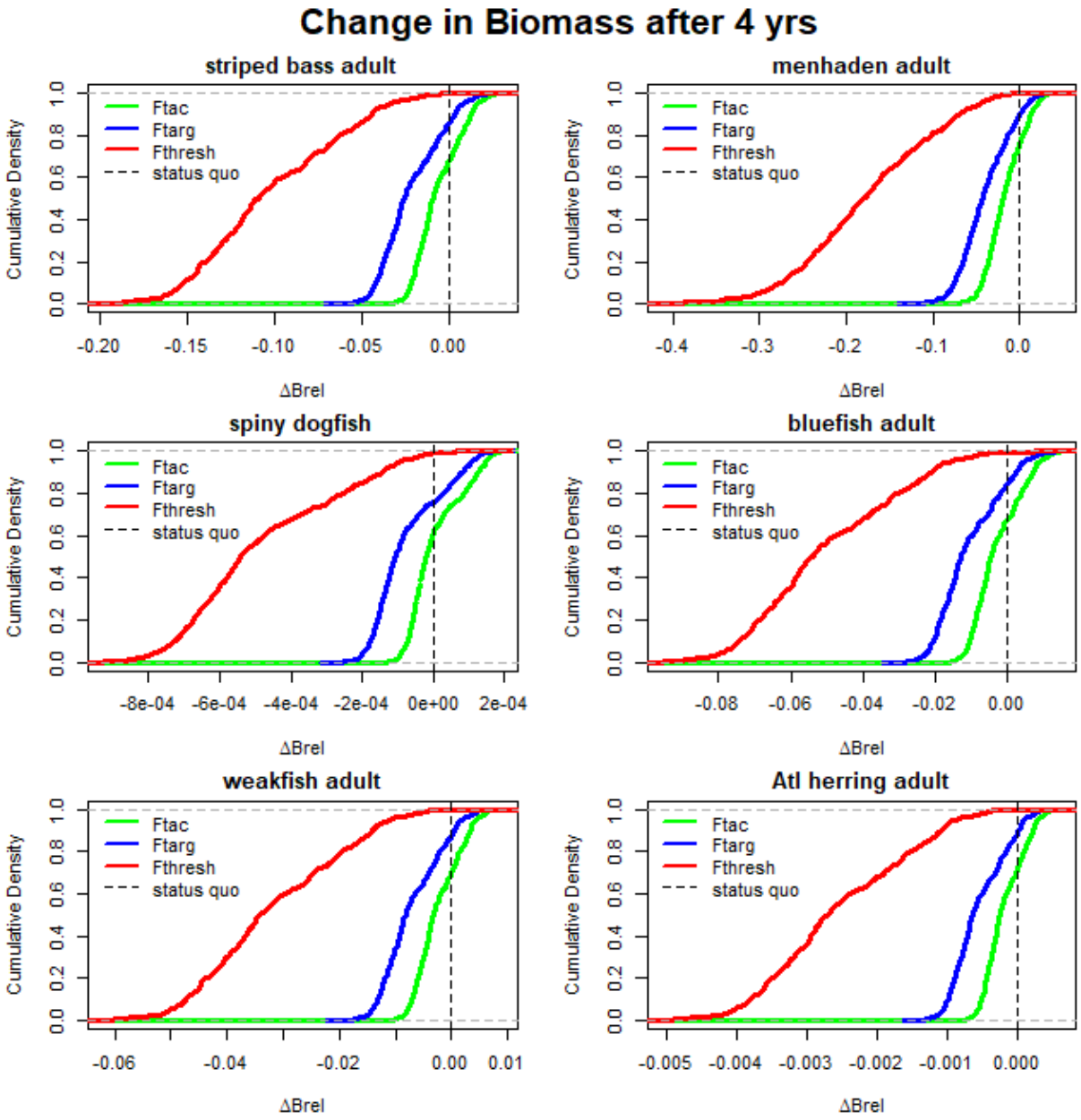


Figure 142. Cumulative density plots of the change in biomass relative to 2017 biomass (ΔB_{REL}) from the NWACS-MICE model for each species after four years of fishing menhaden at current TAC, target, and threshold fishing mortalities (from BAM). Each line shows the proportion of trials (out of 500) that cause biomass to decline below the value on the x-axis. Analysis was conducted using sim3.5.

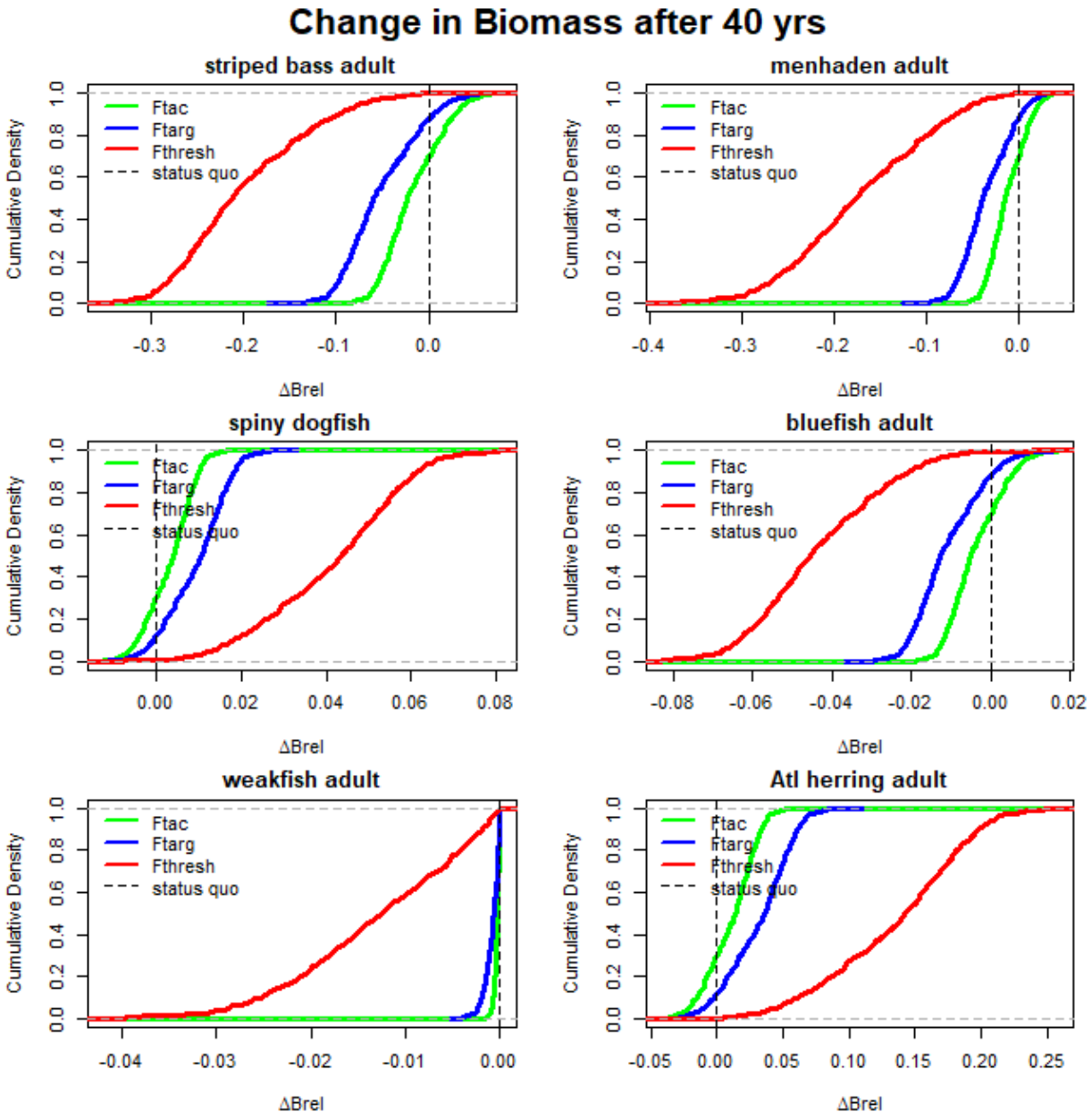


Figure 143. Cumulative density plots of the change in biomass relative to 2017 biomass (ΔB_{REL}) from the NWACS-MICE model for each species after forty years of fishing Atlantic menhaden at current TAC, target, and threshold fishing mortalities (from BAM). Each line shows the proportion of trials (out of 500) that cause biomass to decline below the value on the x-axis. Analysis was conducted using sim3.5.

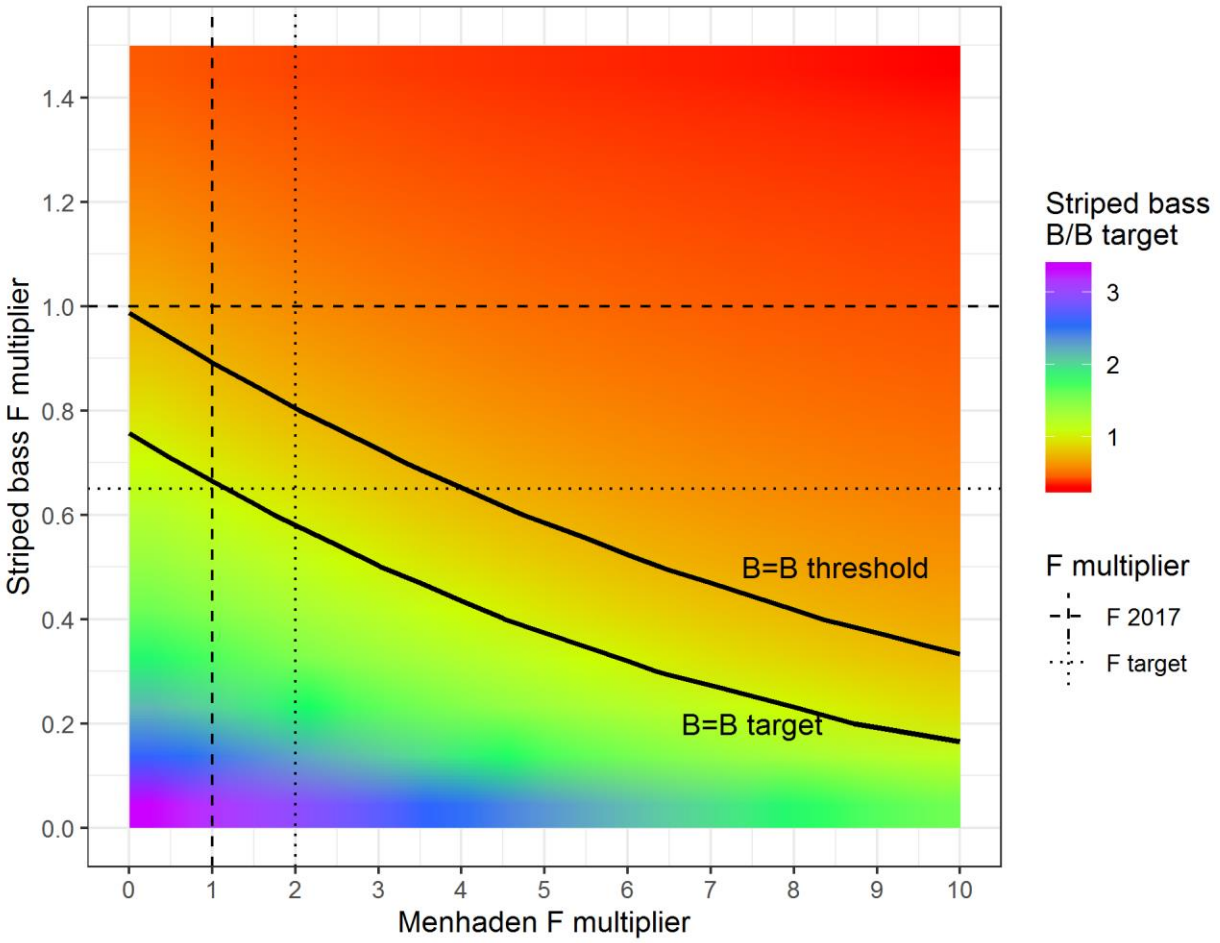


Figure 144. Striped bass age 6+ biomass ratio (B/B_{TARGET}) in the terminal year of the NWACS-MICE projections as a function of fishing mortality on both Atlantic menhaden and striped bass. The solid black lines represent the contours where striped bass $B=B_{THRESHOLD}$ and $B=B_{TARGET}$. The dashed lines highlight specific *F* scenarios where *F* is equivalent to the *F* in 2017 or the single-species *F* target for each species.

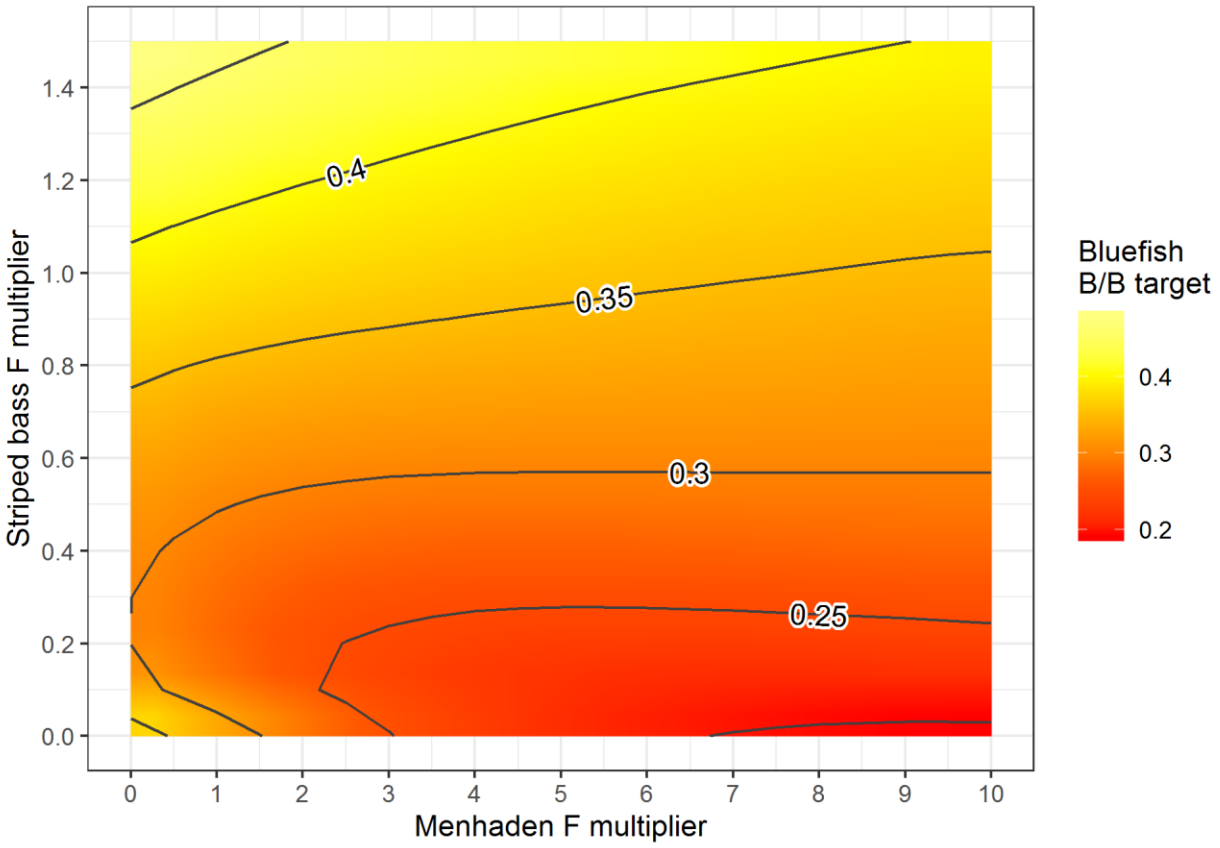


Figure 145. Bluefish age 1+ biomass ratio (B/B_{TARGET}) in the terminal year of the NWACS-MICE projections as a function of fishing mortality on both Atlantic menhaden and striped bass. In these projections, bluefish *F* was held constant at 2017 value.

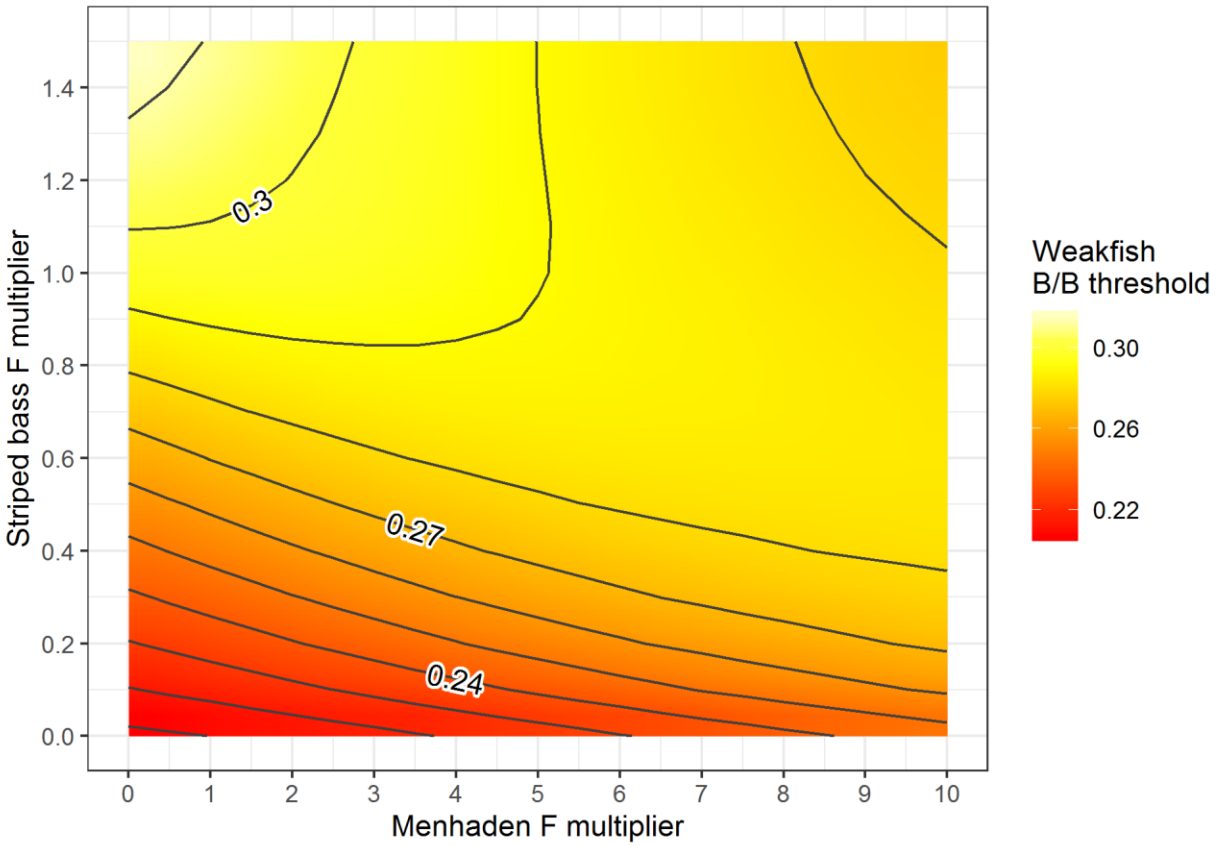


Figure 146. Weakfish age 1+ biomass ratio ($B/B_{THRESHOLD}$) in the terminal year of the NWACS-MICE projections as a function of fishing mortality on both Atlantic menhaden and striped bass. In these projections, weakfish *F* was held constant at the 2017 value.

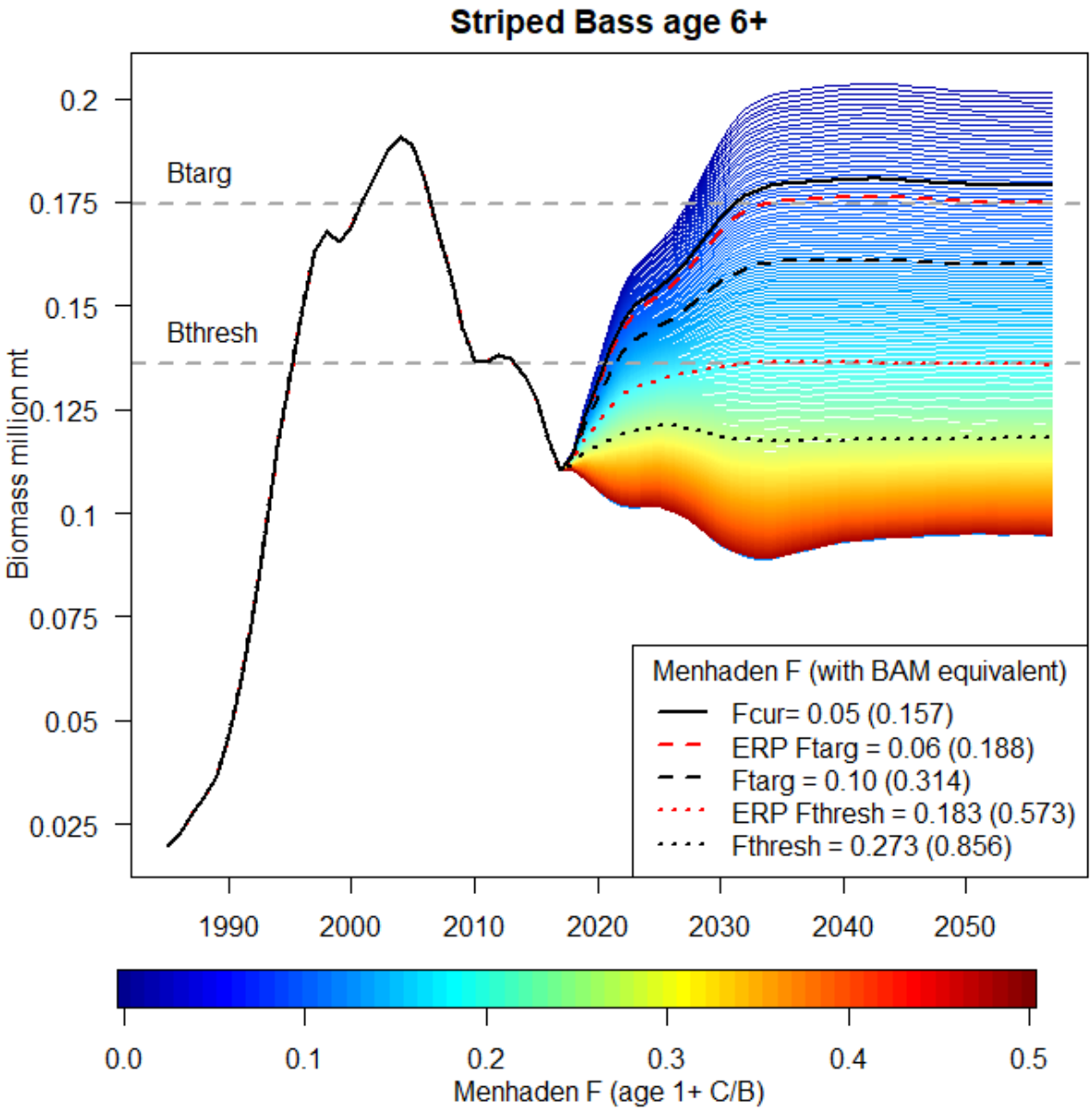


Figure 147. Striped bass age 6+ biomass from the NWACS-MICE model, projected under striped bass *F* = F_{TARGET} from 2018-2057 over a range of Atlantic menhaden *F*. All other species were held constant at their status quo *F*.

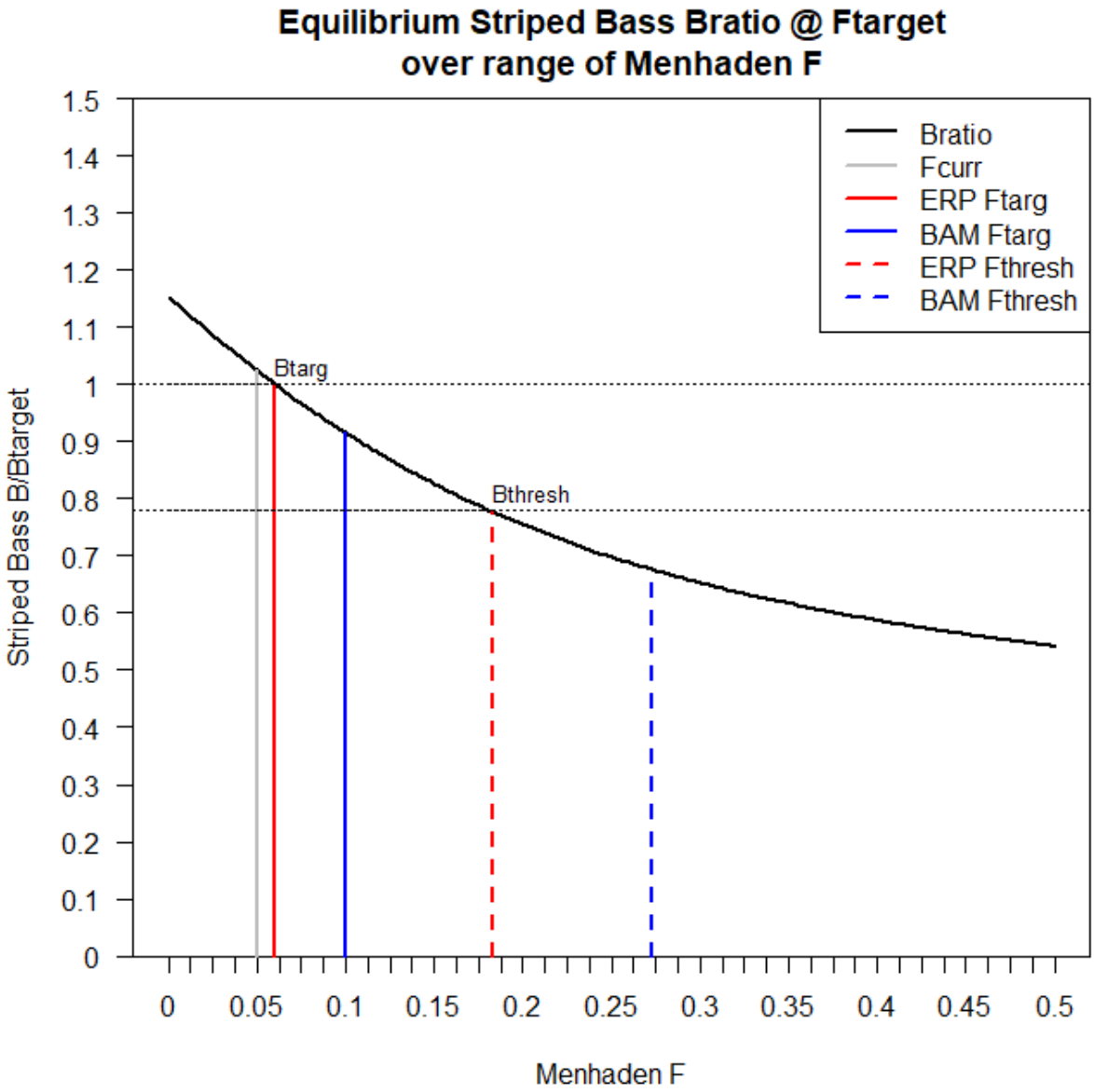


Figure 148. Terminal year biomass ratio (B/B_{TARGET}) from the NWACS-MICE model for age 6+ striped bass over a range of Atlantic menhaden *F* with striped bass fished at their *F* target. Vertical solid and dotted lines indicate the BAM single-species target and threshold *F* as well as the current *F* and the proposed ERP target and threshold *F* for Atlantic menhaden.

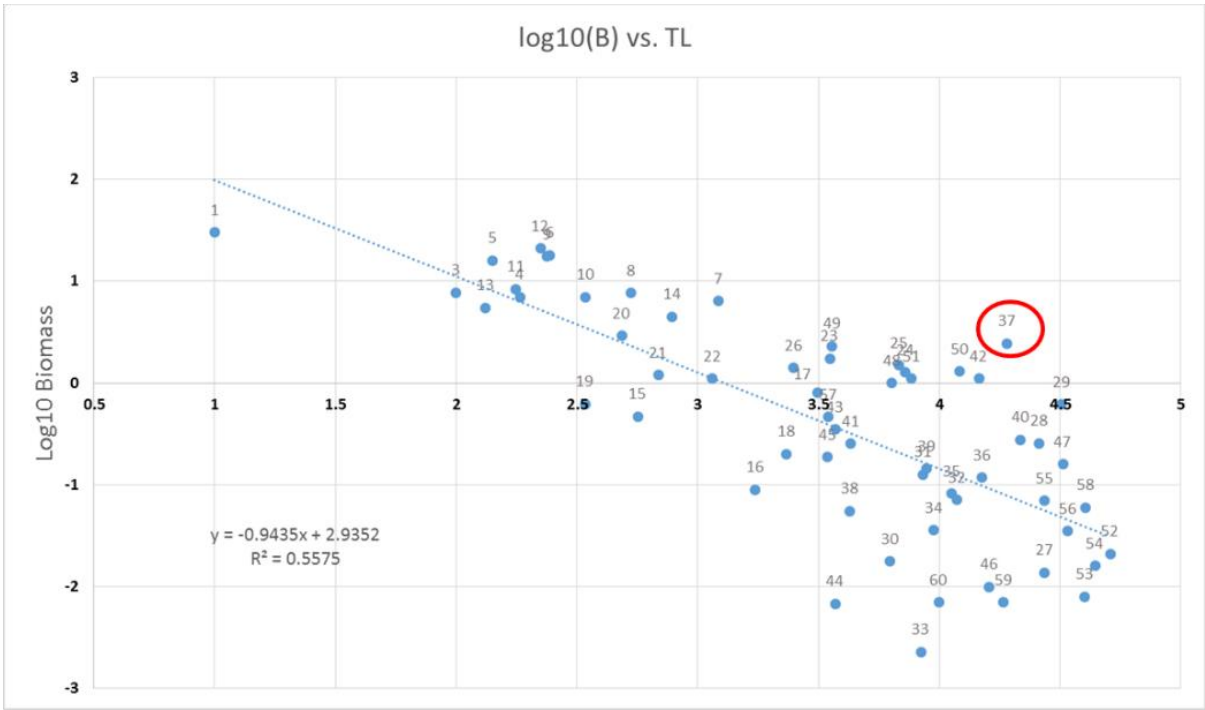


Figure 149. Relationship between log (base 10) biomass and trophic level (TL) for all trophic groups in the NWACS-FULL model before balancing. The decline in biomass is expected (Link 2010), but the red circle highlights large spiny dogfish as an outlier which was used as justification for reducing their biomass in the model.

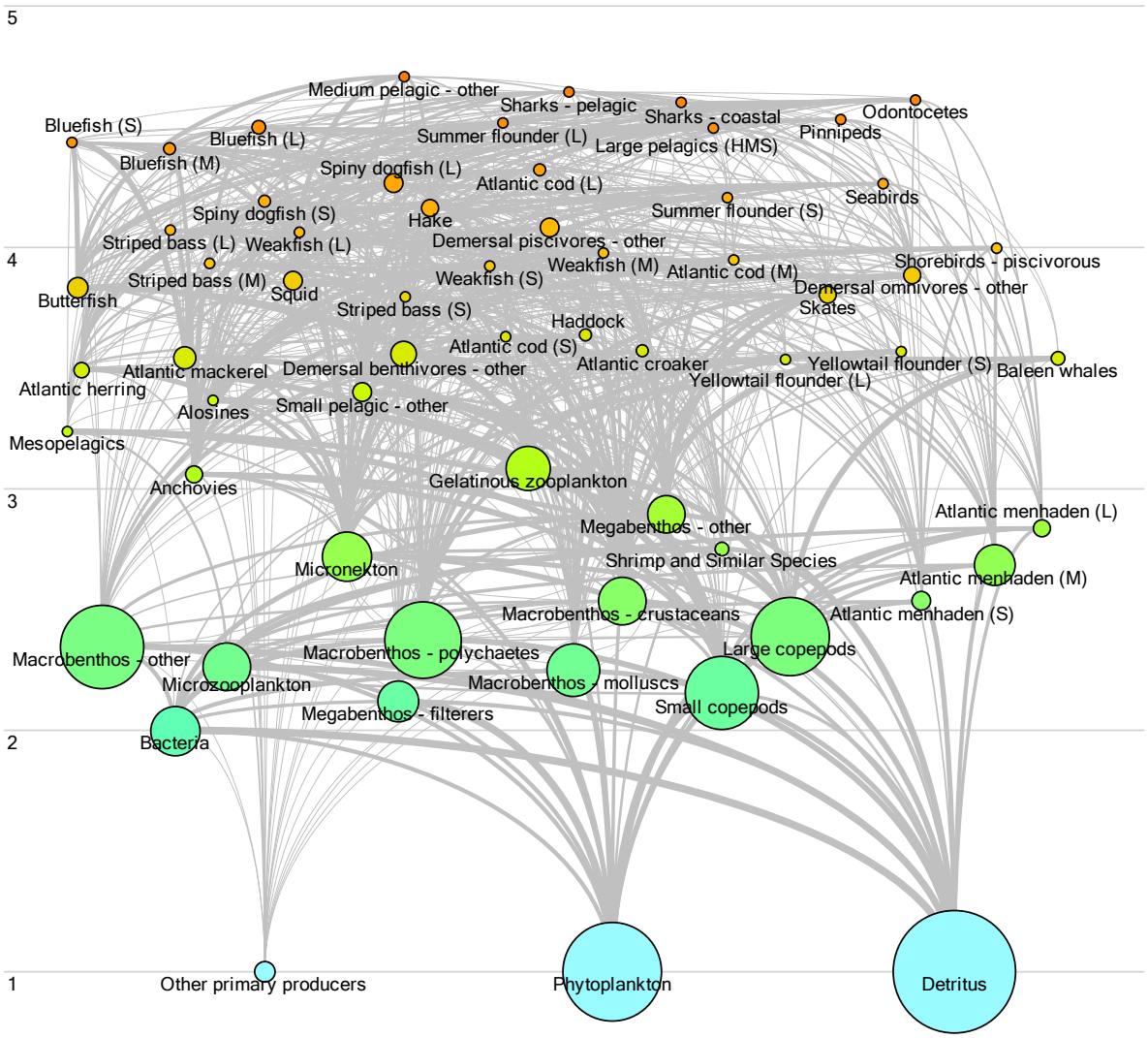


Figure 150. Flow diagram for the NWACS-FULL Model. Nodes represent biomass of modeled trophic groups (scaled to the logarithm of the group's biomass). Lines represent trophic linkages (with a scaled thickness). Colors and horizontal lines denote trophic levels.

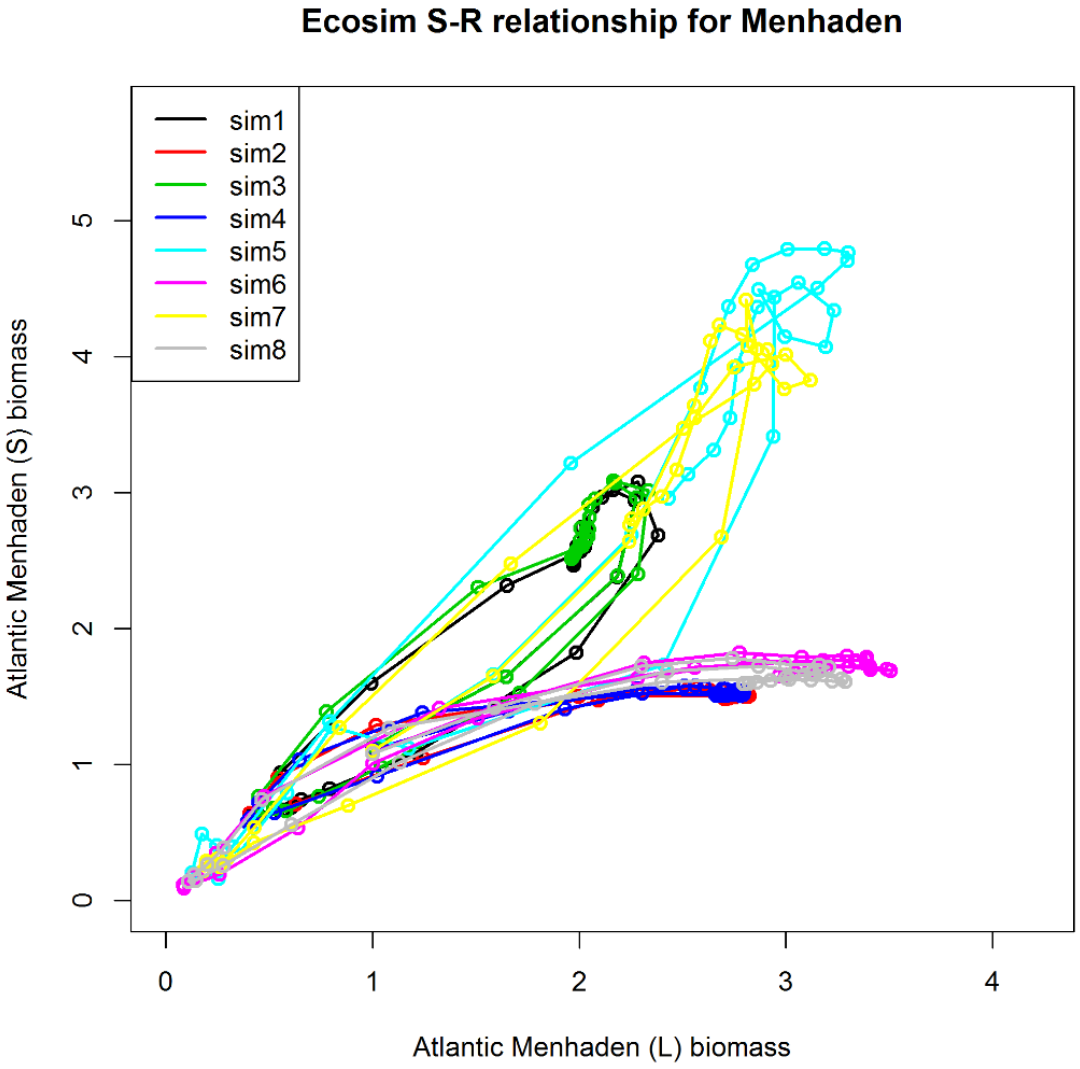


Figure 151. Emergent Atlantic menhaden stock-recruitment relationship from the NWACS-FULL model. Lines depict the relationship between age-3+ (i.e., Large, L) Atlantic menhaden biomass and age-0 (i.e., small, S) biomass for eight different simulations. Some simulations (Sims 2, 4, 6, and 8) had vulnerability parameters manually adjusted to obtain a Beverton-Holt stock-recruitment relationship.

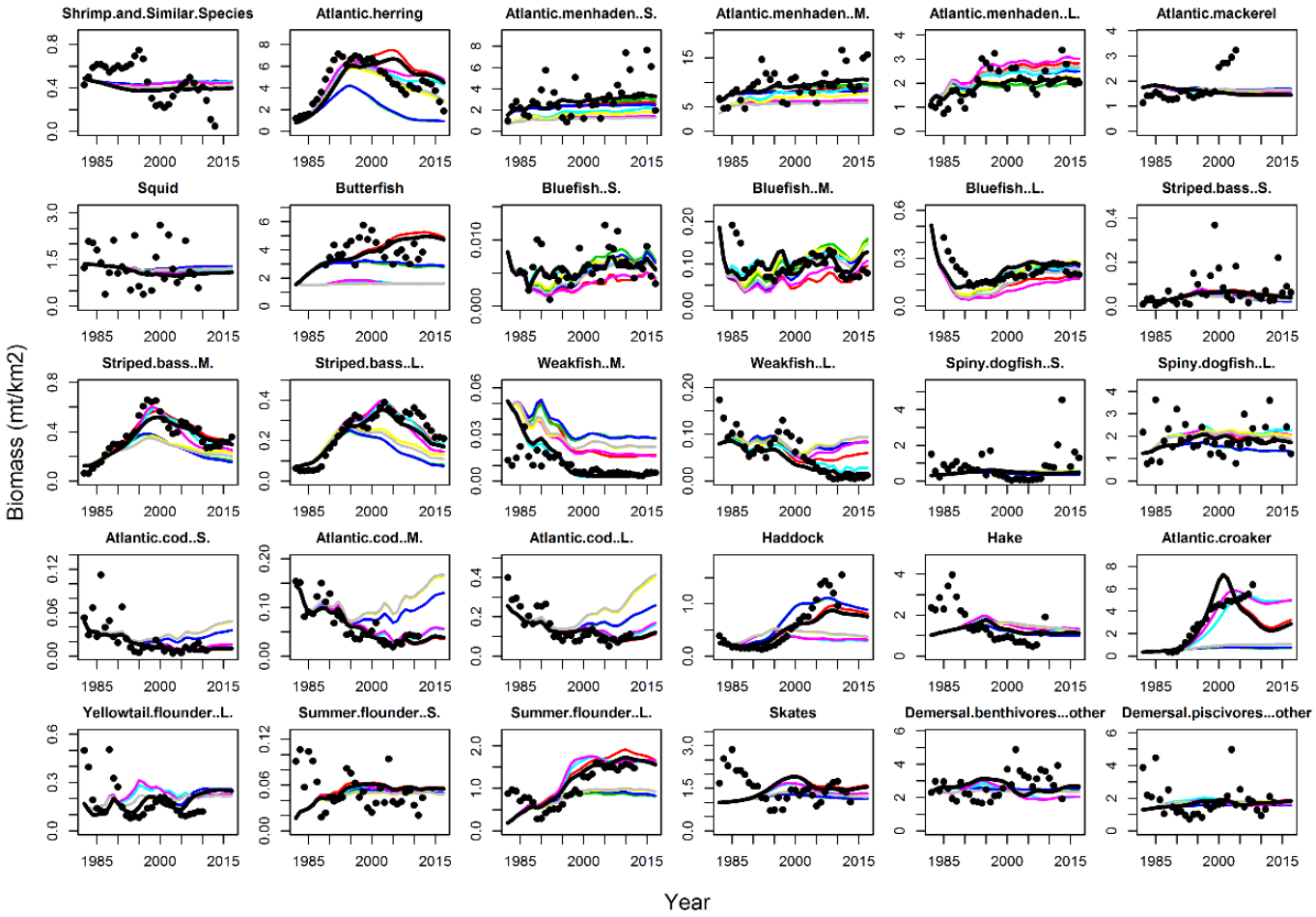


Figure 152. Biomass fits from the NWACS-FULL model. Lines depict predicted biomass estimates by year for different model simulations (sim 1-8: 1-black, 2-red, 3-green, 4-blue, 5-cyan, 6-pink, 7-yellow, 8-gray). Points depict time series of relative biomass from stock assessments and fisheries surveys (magnitude of points is scaled based on sim 1). Panels are labeled by trophic group name and stanza if applicable (S-small, M-medium, L-large). Trophic groups without observed, empirical data are excluded.

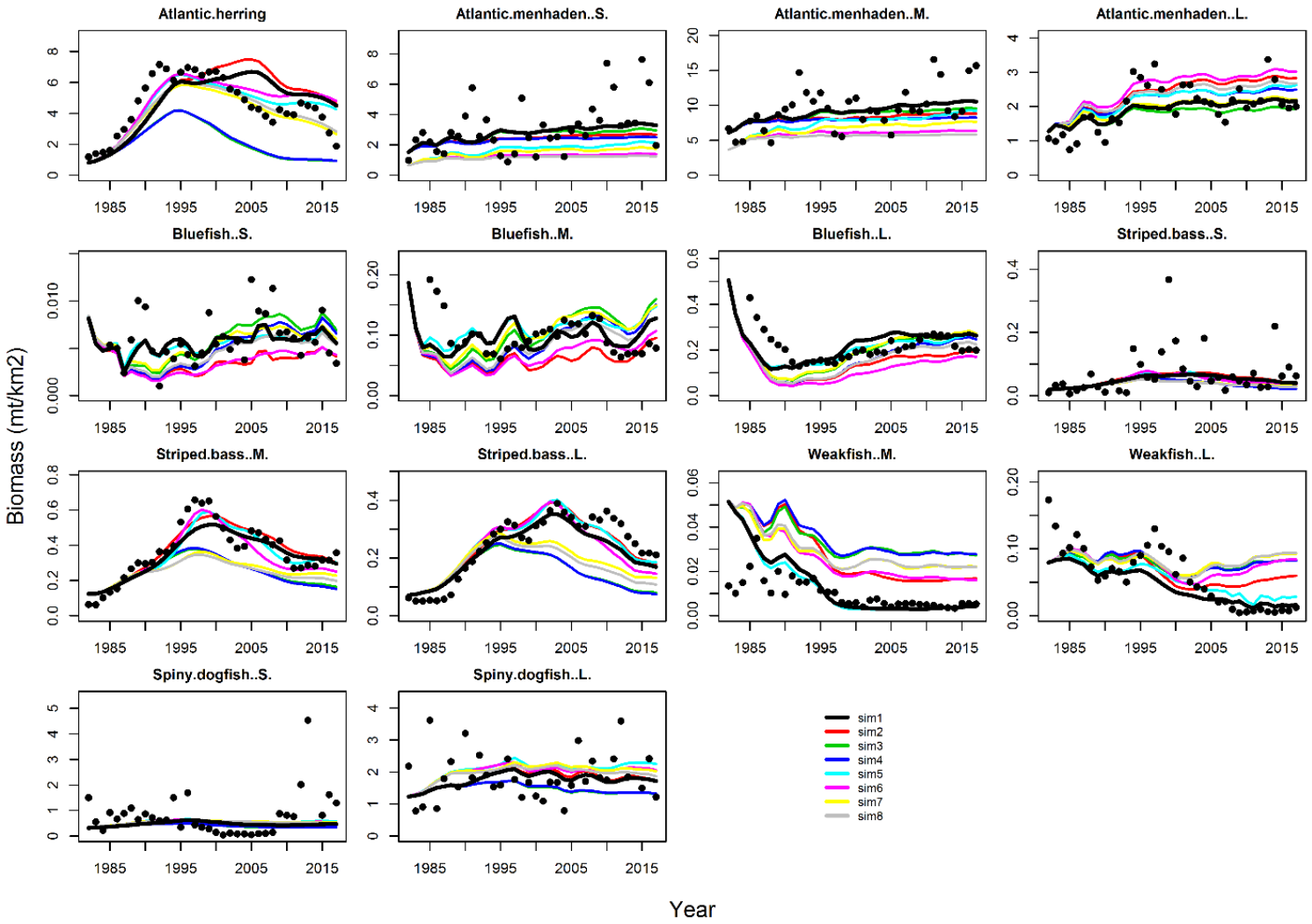


Figure 153. Biomass fits from the NWACS-FULL model for select ERP focal species (Atlantic herring, Atlantic menhaden, bluefish, striped bass, weakfish, and spiny dogfish). See Figure 152 for full description of symbols and lines.

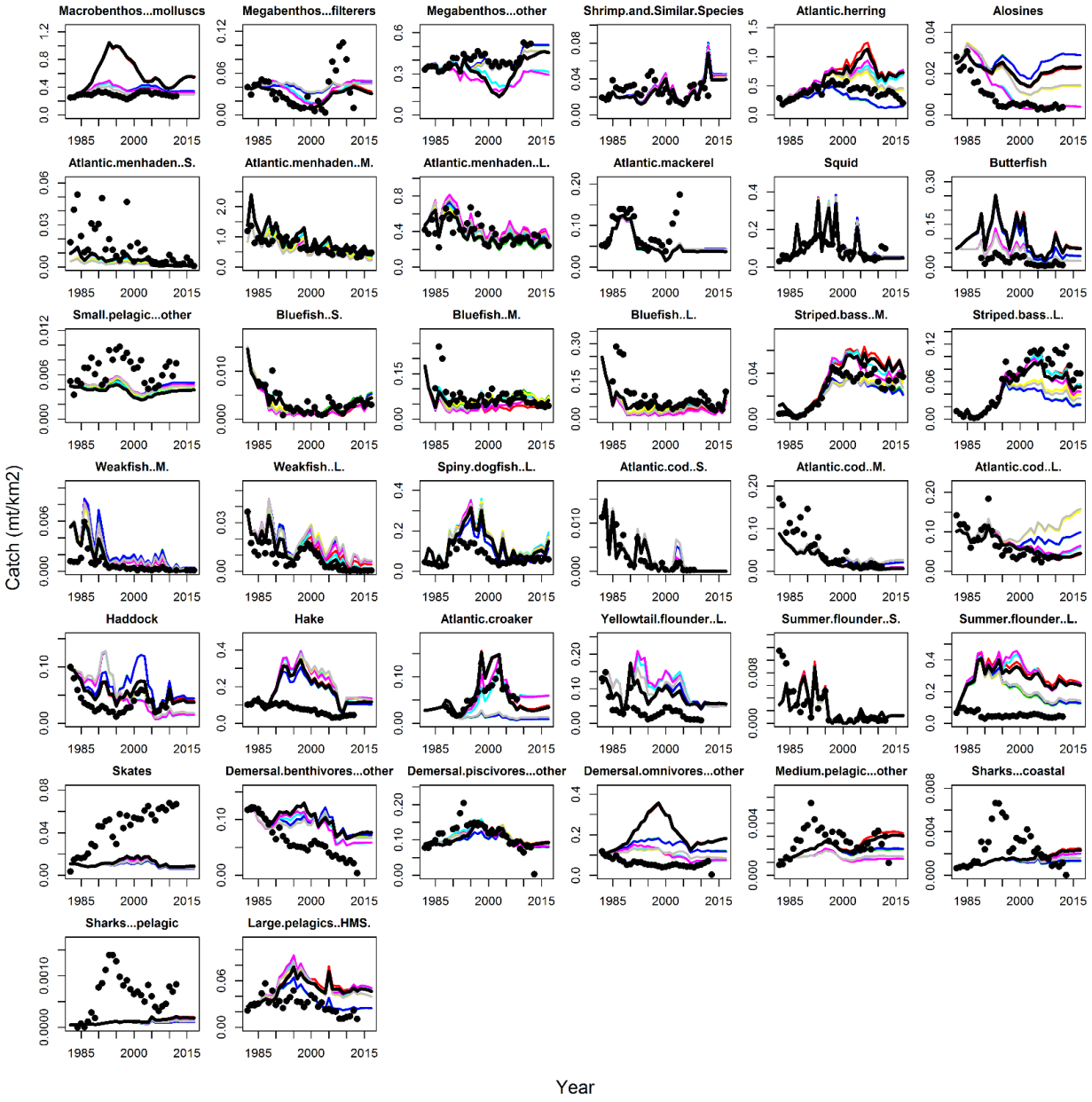


Figure 154. Catch fits from the NWACS-FULL model. Points are the observed catches and lines depict predicted catch by year for different model simulations (sim 1-8: 1-black, 2-red, 3-green, 4-blue, 5-cyan, 6-pink, 7-yellow, 8-gray). Panels are labeled by trophic group and stanza if applicable (S-small, M-medium, L-large). Trophic groups without observed, empirical data are excluded.

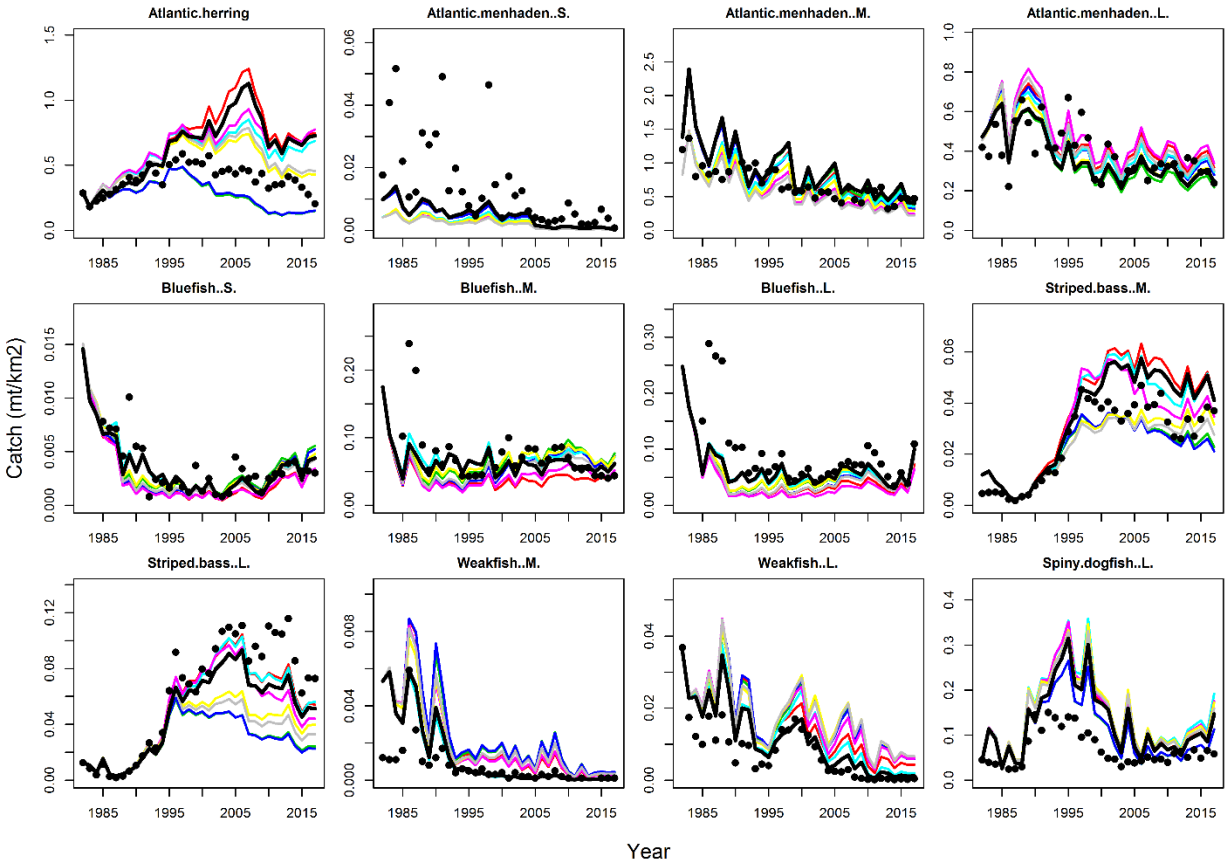


Figure 155. Catch fits for ERP focal species from the NWACS-FULL model. (Atlantic herring, Atlantic menhaden, bluefish, striped bass, weakfish, and spiny dogfish). See Figure 154 for full description.

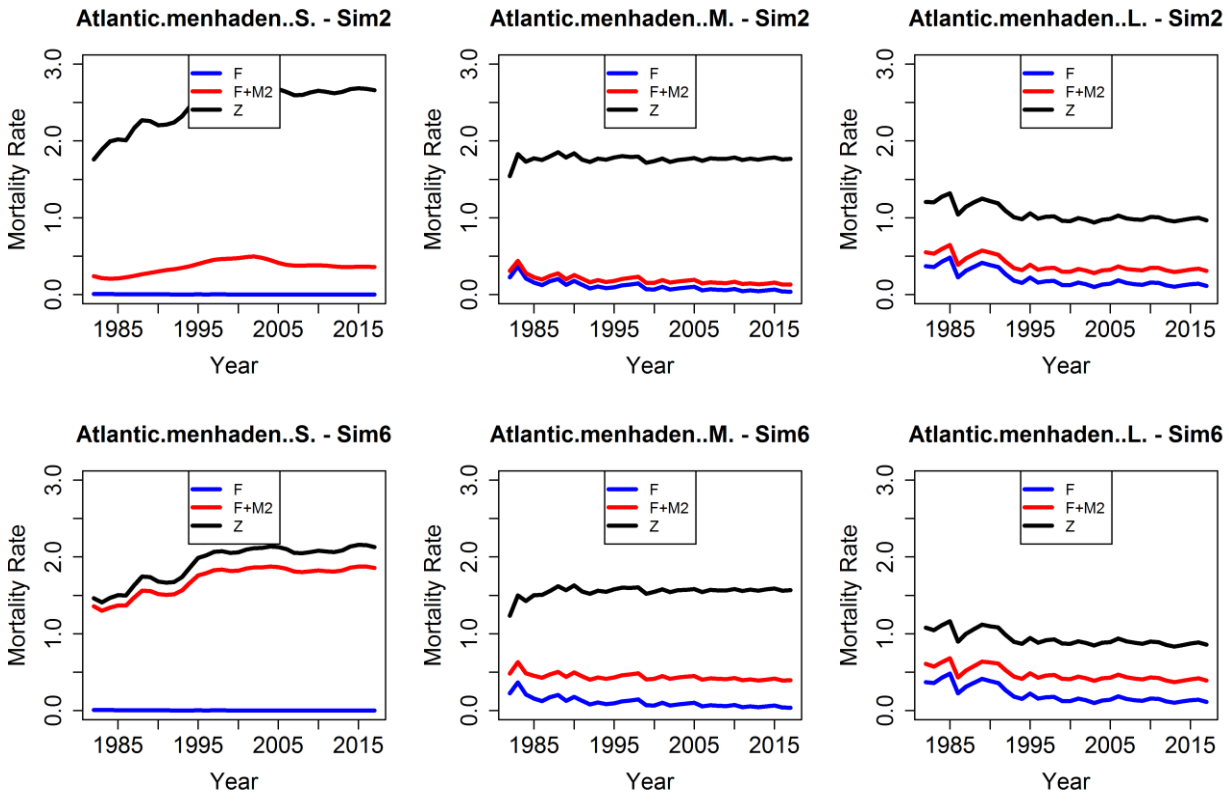


Figure 156. Instantaneous mortality rates for three age-classes of Atlantic menhaden from the NWACS-FULL model (S – age-0, M – age-1-2, L – age3+) based on sim 2 (upper panels) and sim 6 (lower panels)

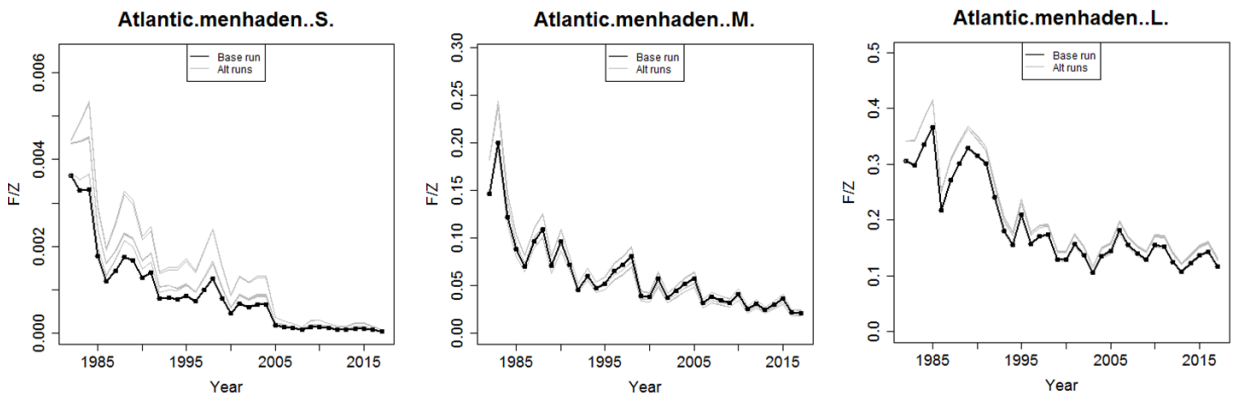


Figure 157. Fishing mortality (*F*) as a proportion of total instantaneous mortality (*Z*) for eight simulations of the NWACS-FULL model

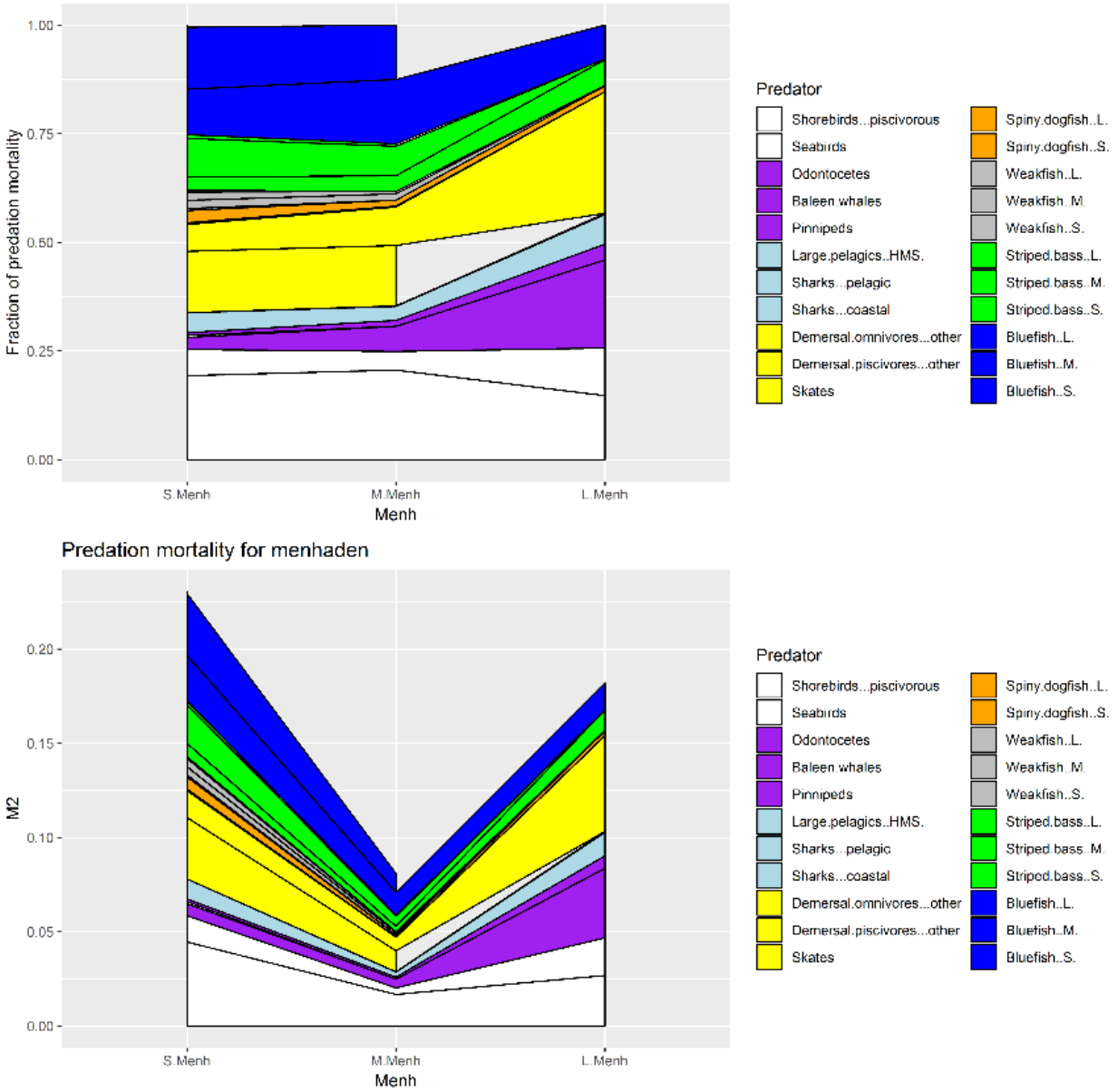


Figure 158. Predator contributions to Atlantic menhaden M_2 (bottom panel) and as fraction of total M_2 (upper panel), based on sim2 of the NWACS-FULL model. Predators and size classes are grouped by color.

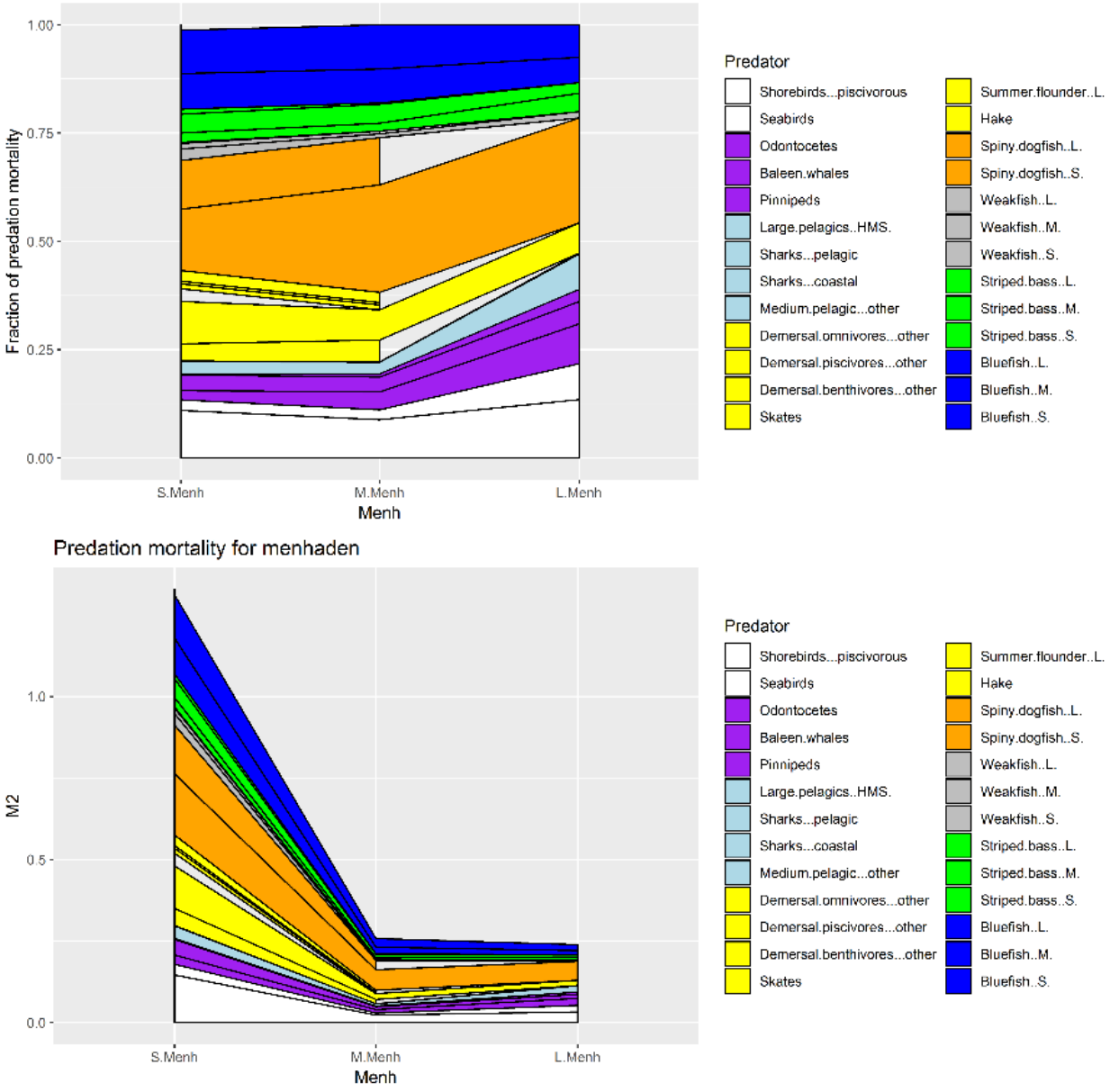


Figure 159. Predator contributions to Atlantic menhaden M_2 (bottom panel) and as fraction of total M_2 (upper panel), based on sim6 of the NWACS-FULL model. Predators and size classes are grouped by color.

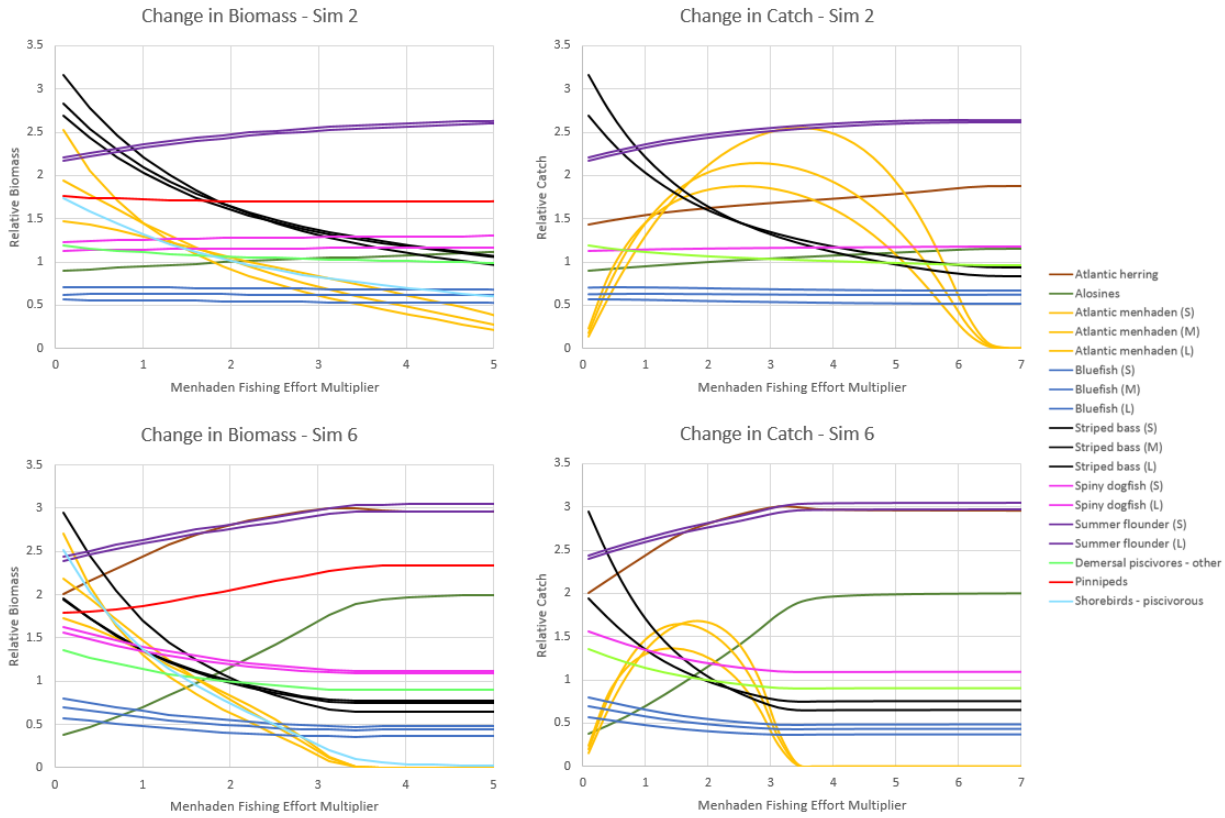


Figure 160. Effect of Atlantic menhaden fishing effort on the relative equilibrium biomass and catch of select trophic groups from the NWACS-FULL model. Non-menhaden species were kept at their Ecopath base (1982) *F* rates while Atlantic menhaden fishing effort was scaled from 0 to 5 times the 1982 values. Results are presented for Sim 2 (upper panels) and Sim 6 (lower panels).

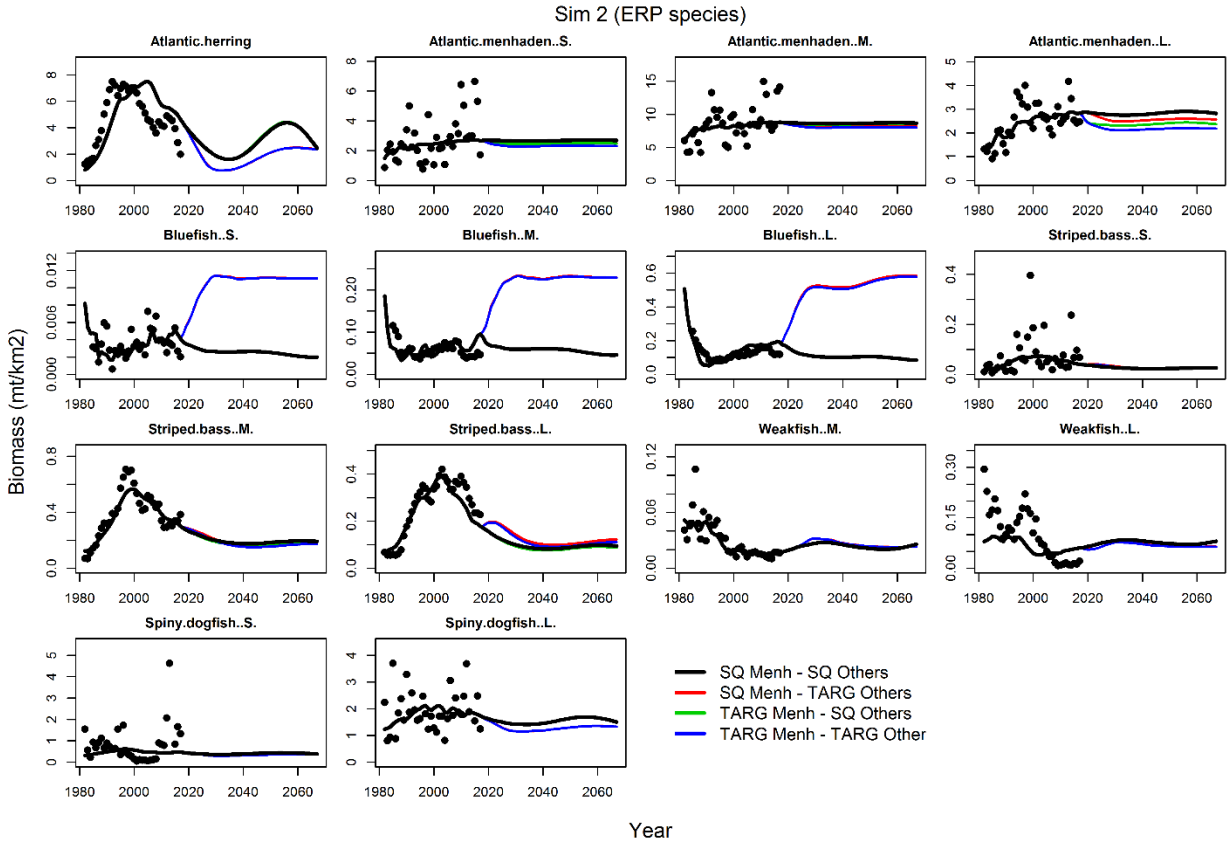


Figure 161. Projected biomass of select species based on Sim 2 of the NWACS-FULL model under four different fishing scenarios. Points are relative observed biomass values and lines are the model predictions when fishing rates are held at 2017 status quo (SQ) levels or target levels (TARG) for Atlantic menhaden (Menh) or focal ERP focal species (Others).

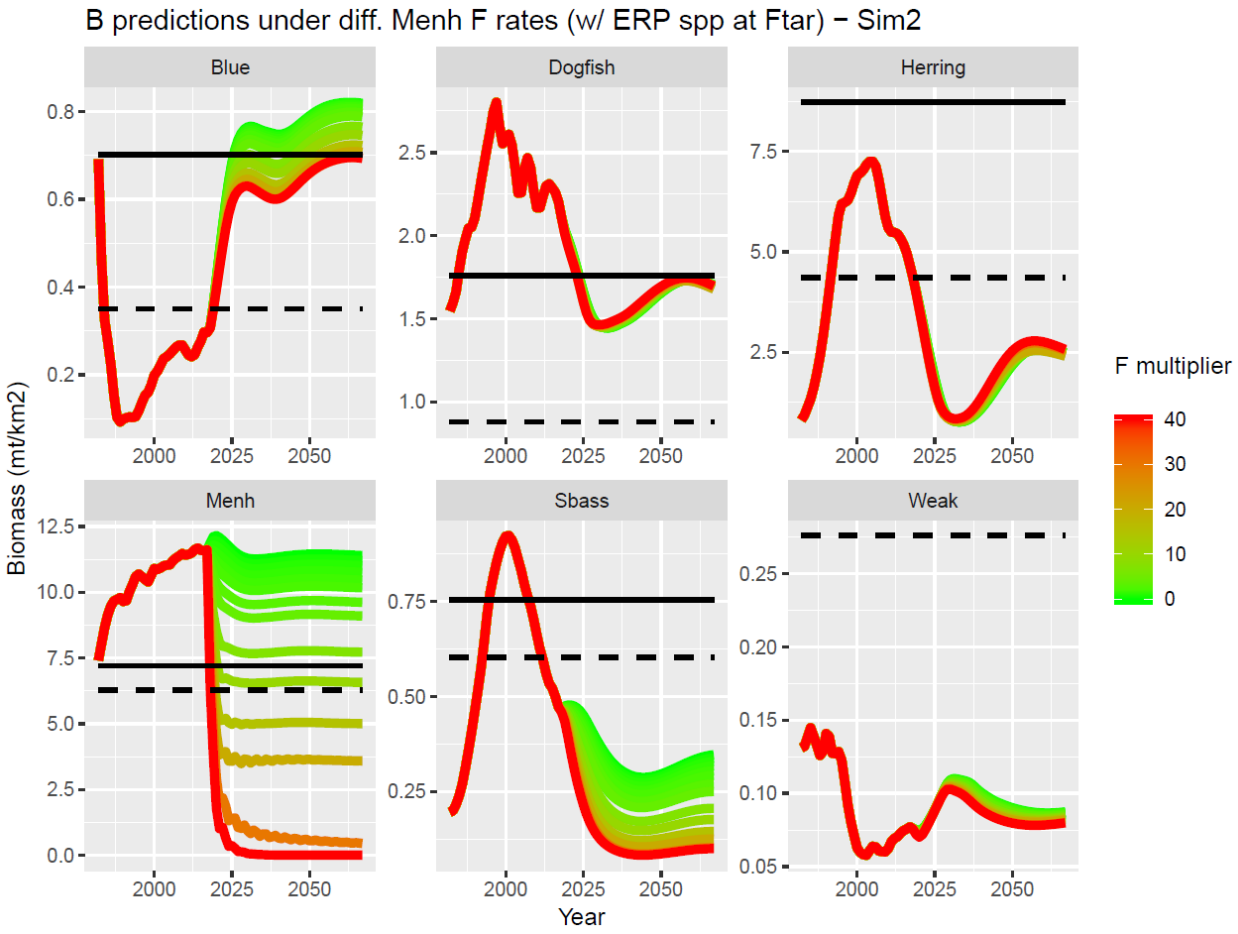


Figure 162. Biomass predictions from the NWACS-FULL model for select species under different Atlantic menhaden *F* rates while fishing the ERP focal species at their respective *F* targets. Atlantic menhaden *F* rates were scaled from F_{2017} using an *F*-multiplier for each simulation. Black horizontal lines denote the Biomass thresholds (dashed) and targets (solid) for each species (as available).

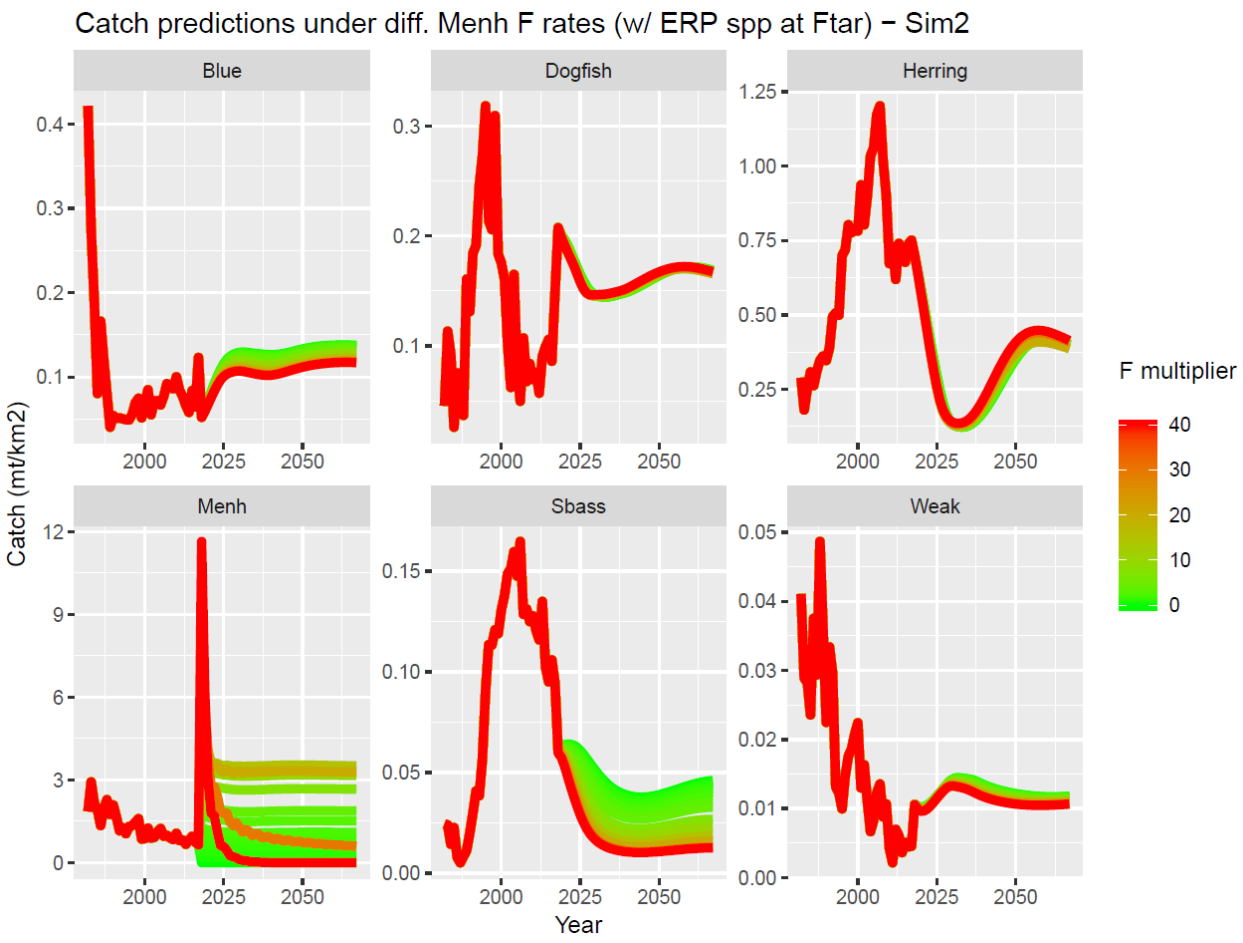


Figure 163. Catch predictions from the NWACS-FULL model for select species under different Atlantic menhaden *F* rates while fishing the ERP focal species at their respective *F* targets. Atlantic menhaden *F* rates were scaled from F_{2017} using an *F*-multiplier for each simulation. Black horizontal lines denote the Biomass thresholds (dashed) and targets (solid) for each species (as available).

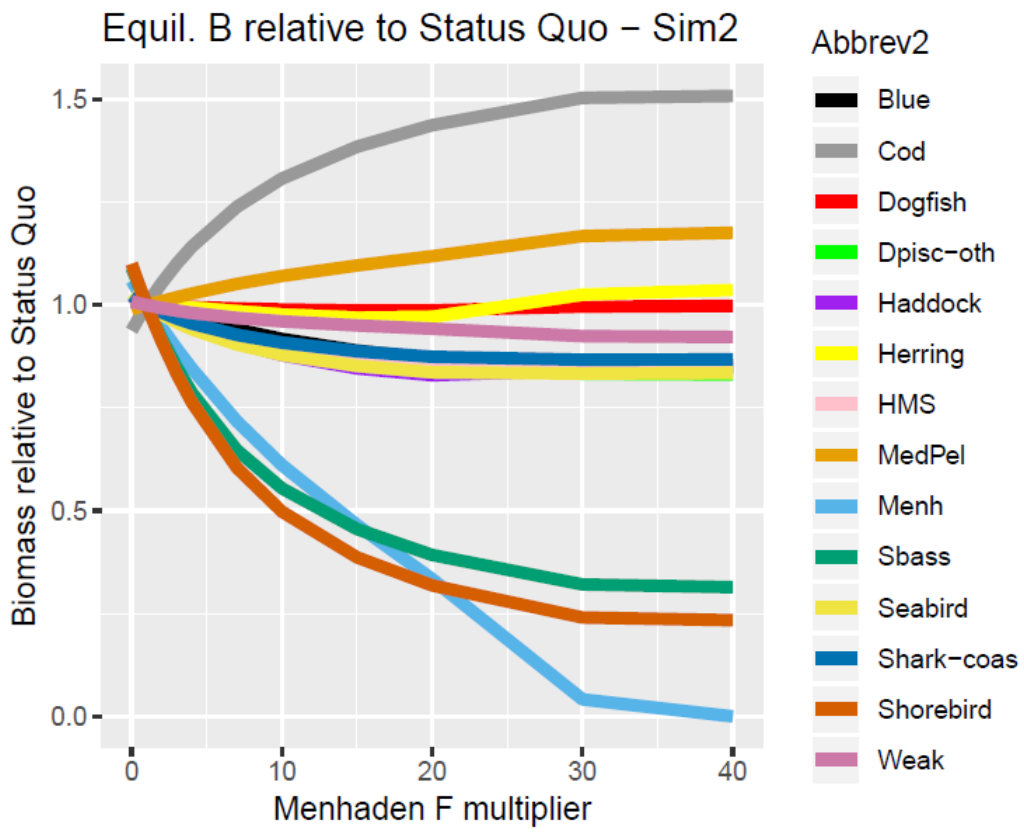


Figure 164. Effect of Atlantic menhaden fishing on equilibrium biomass of select trophic groups (projected for 50 years) relative to their equilibrium biomass under status quo Atlantic menhaden fishing rates from the NWACS-FULL model. ERP focal species were fished at their target *F* while Atlantic menhaden *F* rates were scaled from 0 to 40 times the 2017 values using an F-multiplier. Biomasses for all species were summed across age-stanzas (if applicable). Lines are plotted for all ERP focal species and other trophic groups with non-negligible (>15%) responses.

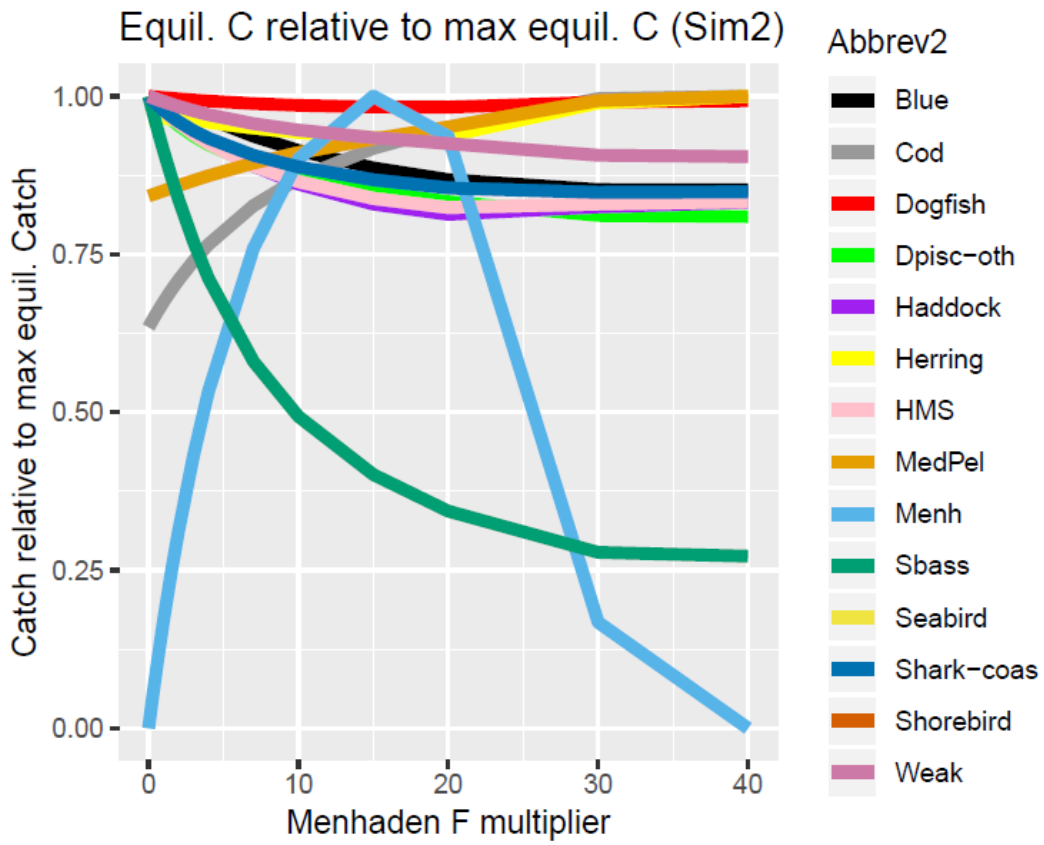


Figure 165. Effect of different Atlantic menhaden fishing mortality projections on the equilibrium (50-year) catch of selected trophic groups relative to the maximum equilibrium catch observed across all fishing scenarios from the NWACS-FULL model. Non-menhaden species were kept at their target *F* while Atlantic menhaden *F* rates were scaled from 0 to 40 times the 2017 values using an F-multiplier. Catches for all species were summed across age-stanzas (if applicable). Lines are plotted for all ERP focal species and other trophic groups with non-negligible (>15%) responses.

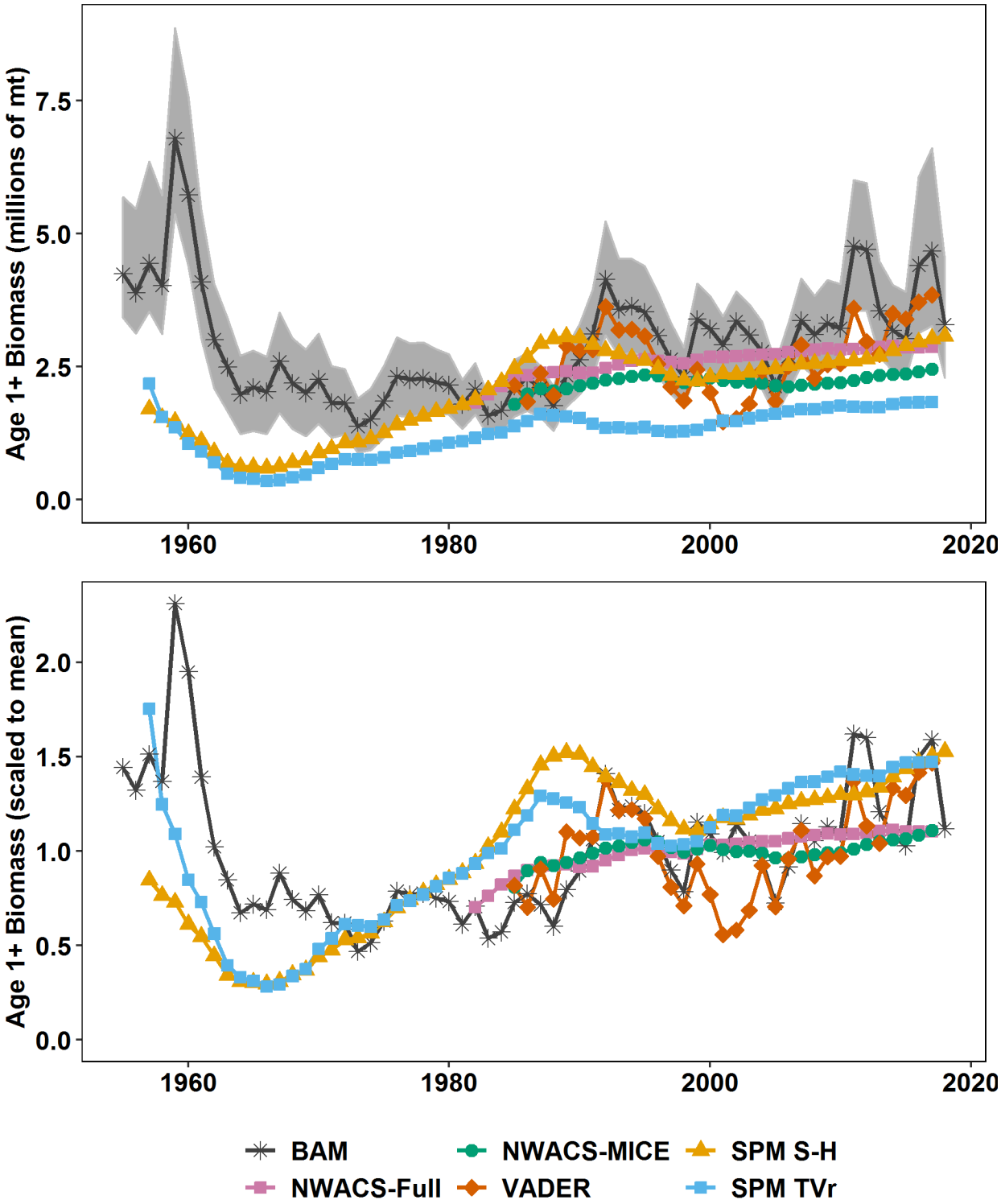


Figure 166. Estimates of age-1+ biomass from the base runs of the ERP models (top) and scaled to their respective time series means (bottom). Shaded area on top plot indicates the MCMC confidence intervals from the single species assessment model.

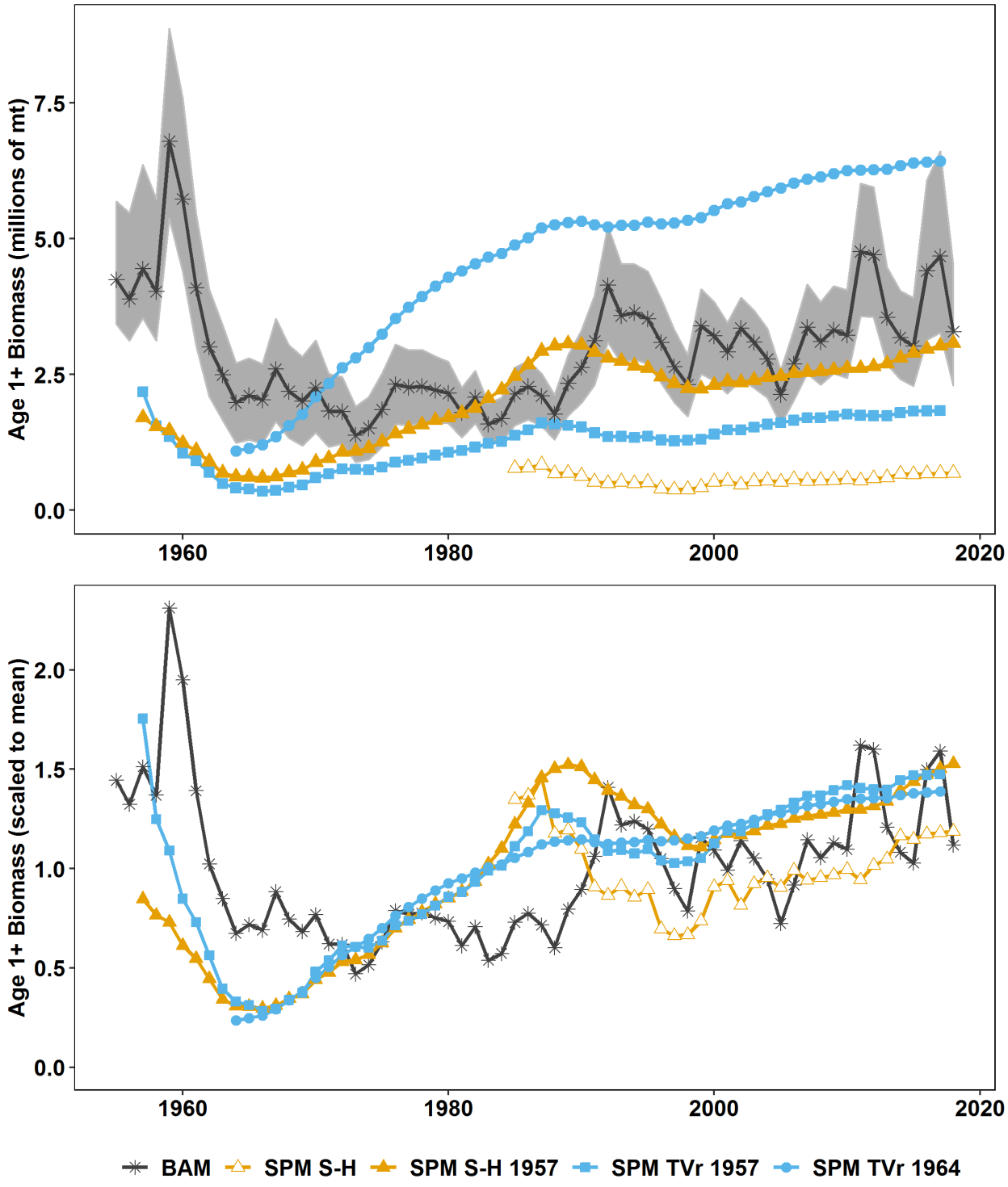


Figure 167. Estimates of age-1+ biomass from the single species (BAM) assessment model plotted with the Steele-Henderson and time-varying *r* surplus production models with different starting years (top) and scaled to their respective time-series means (bottom).Shaded area on top plot indicates the MCMC confidence intervals from the single species assessment model.

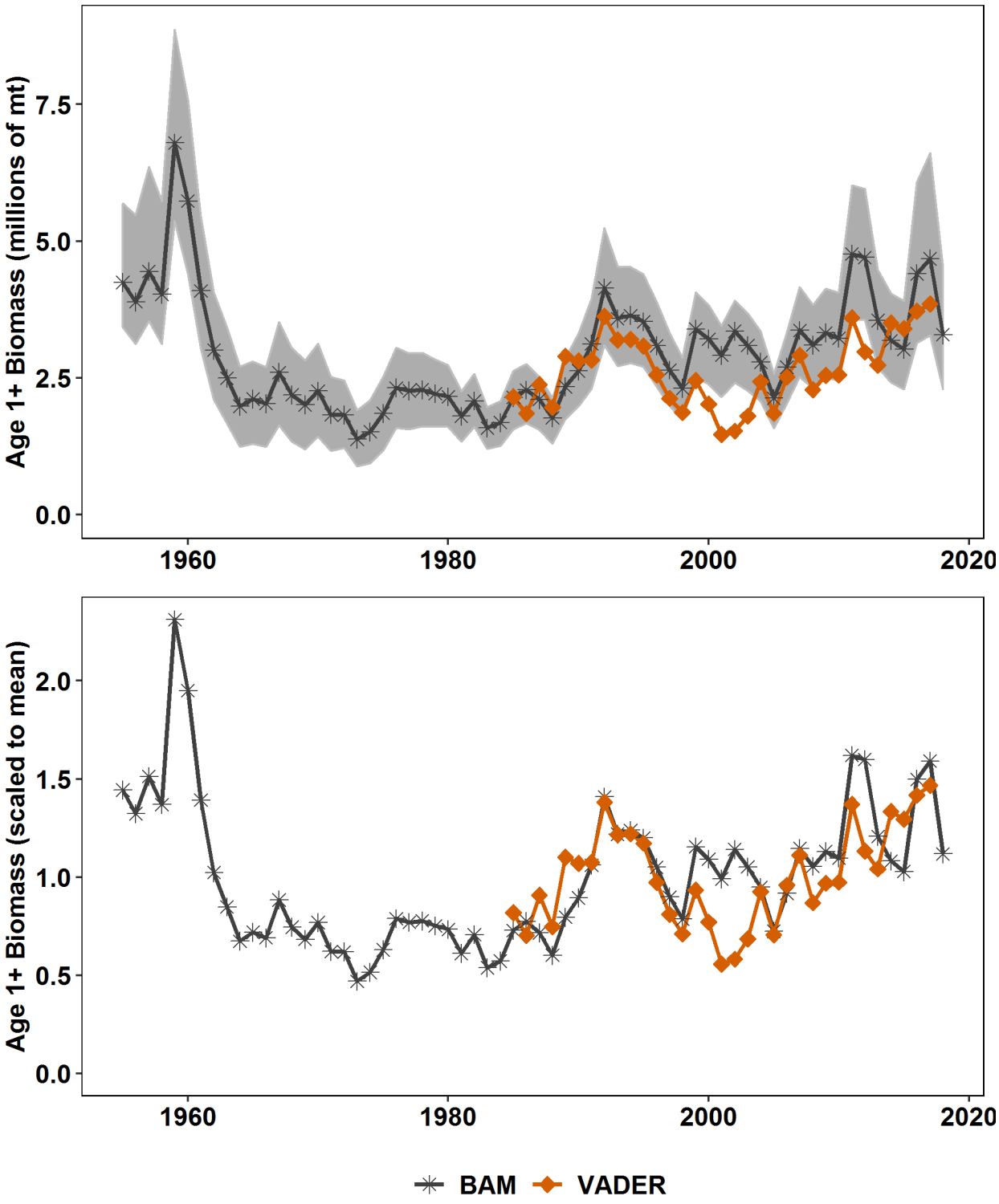


Figure 168. Estimates of age-1+ biomass from the single species (BAM) assessment model plotted with the multispecies statistical catch-at-age (VADER) model (top) and scaled to their respective time-series means (bottom).Shaded area on top plot indicates the MCMC confidence intervals from the single species assessment model.

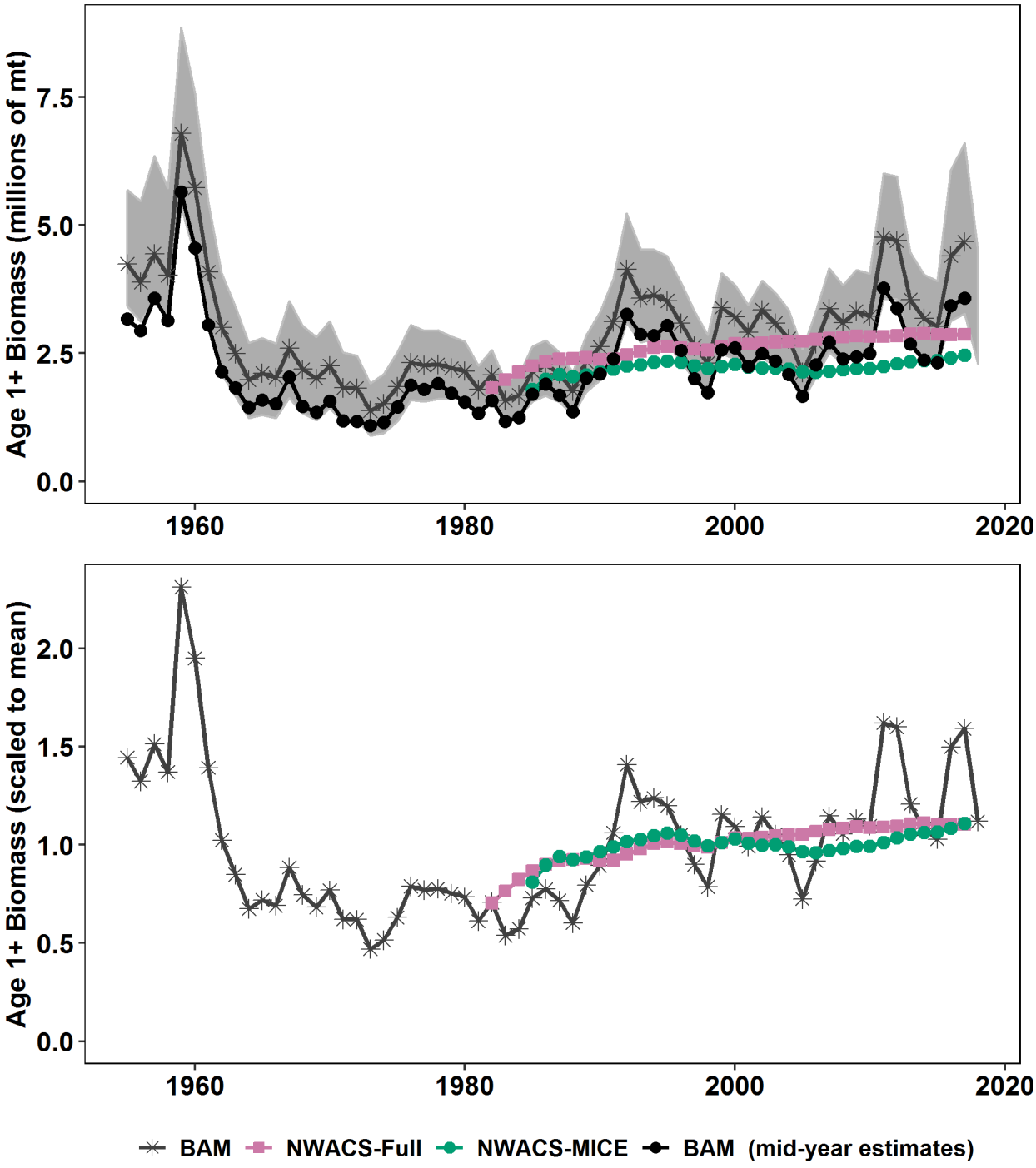


Figure 169. Estimates of age-1+ biomass from the single species assessment model at the start of the year (BAM) and at the middle of the year (BAM mid-year estimates) plotted with the NWACS model estimates (top) and scaled to their respective time series means (bottom). Shaded area on top plot indicates the start of year biomass MCMC confidence intervals from the single species assessment model.

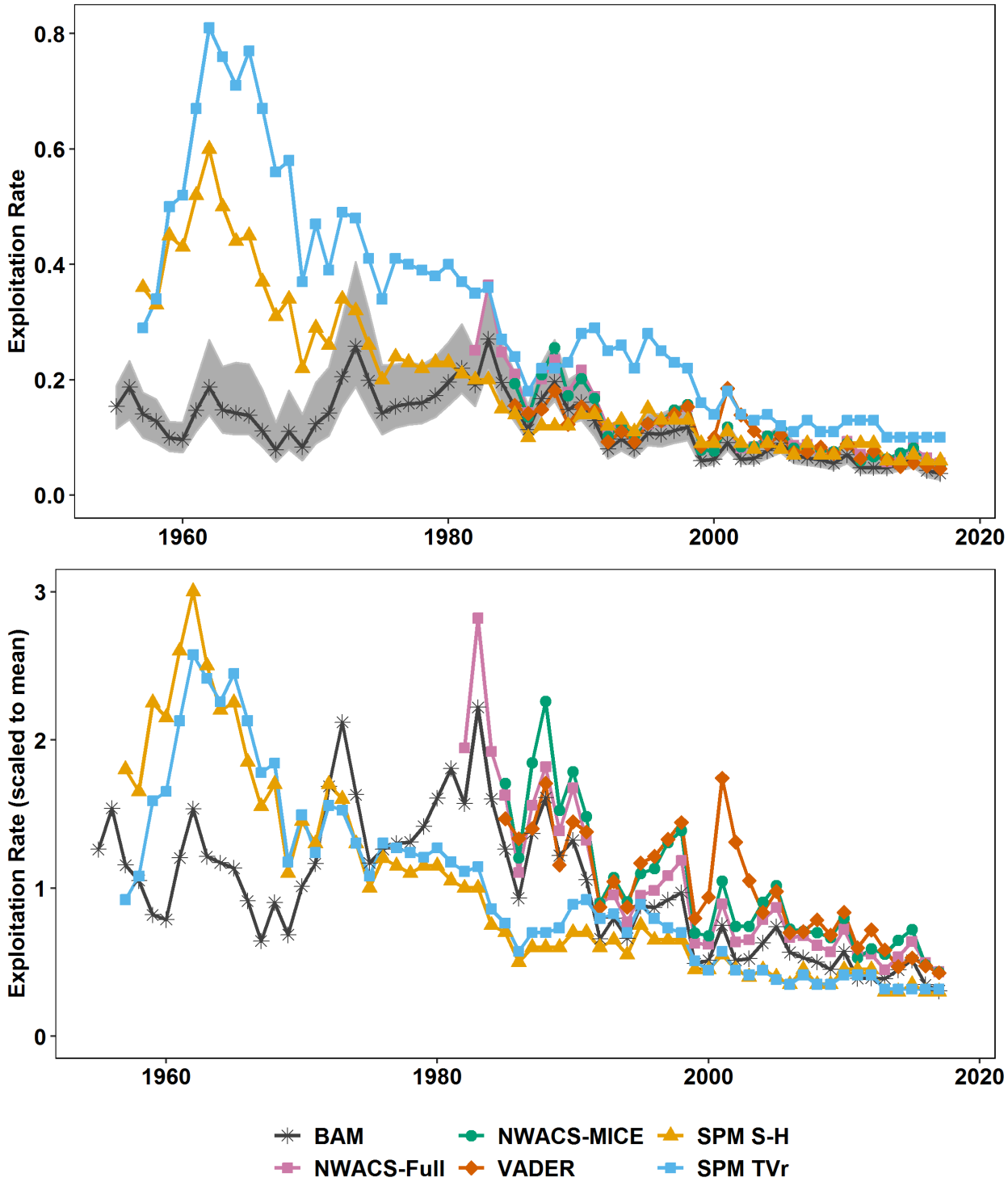


Figure 170. Exploitation rates from the single species assessment model plotted with the exploitation rates from the ERP models (top) and scaled to their respective time series means (bottom).Shaded area on top plot indicates MCMC confidence intervals from the single species assessment model.

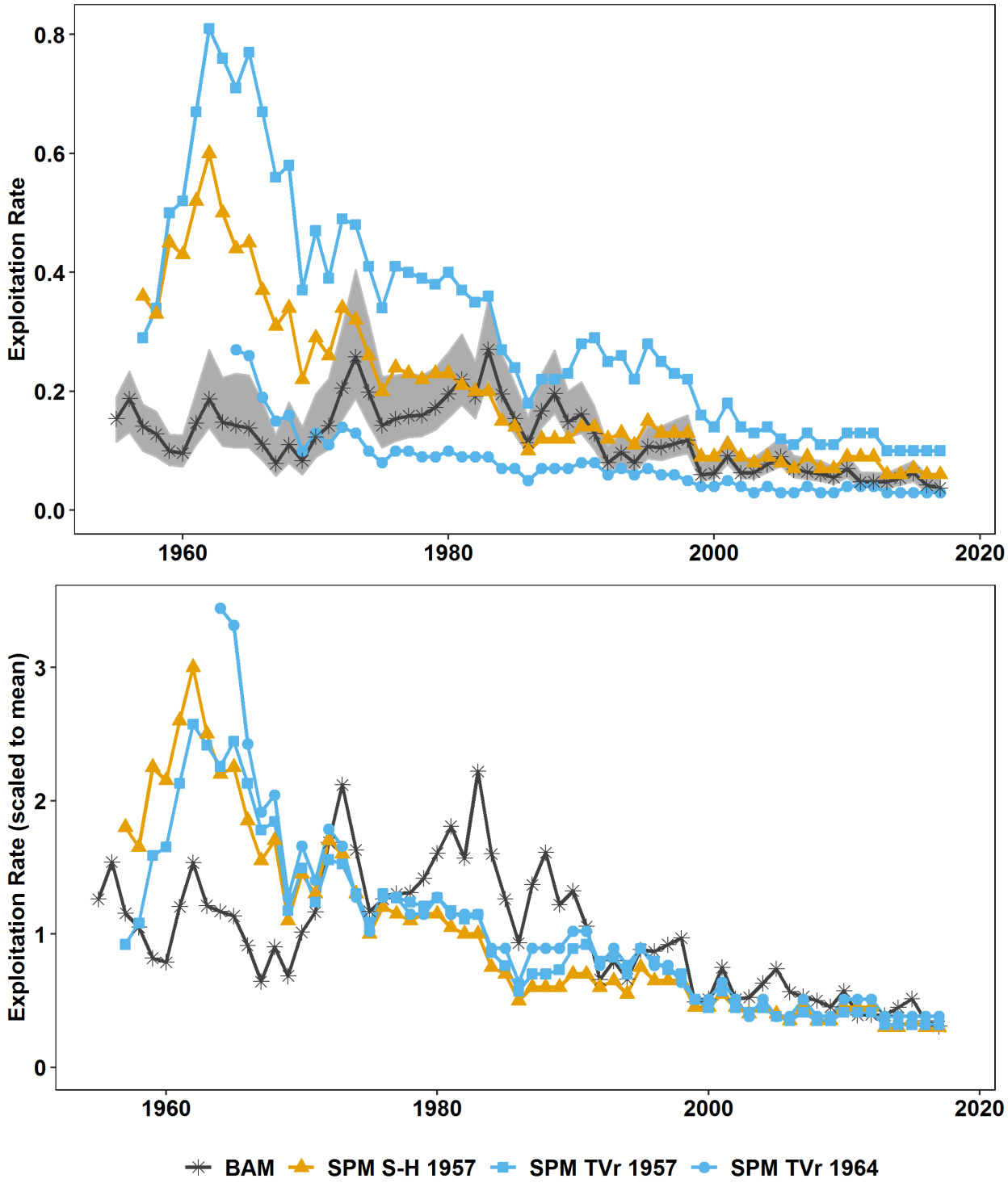


Figure 171. Exploitation rates from the single species model plotted with the exploitation rate estimates from the surplus production models with differing start years. Shaded area on top plot indicates MCMC confidence intervals from the single species assessment model.

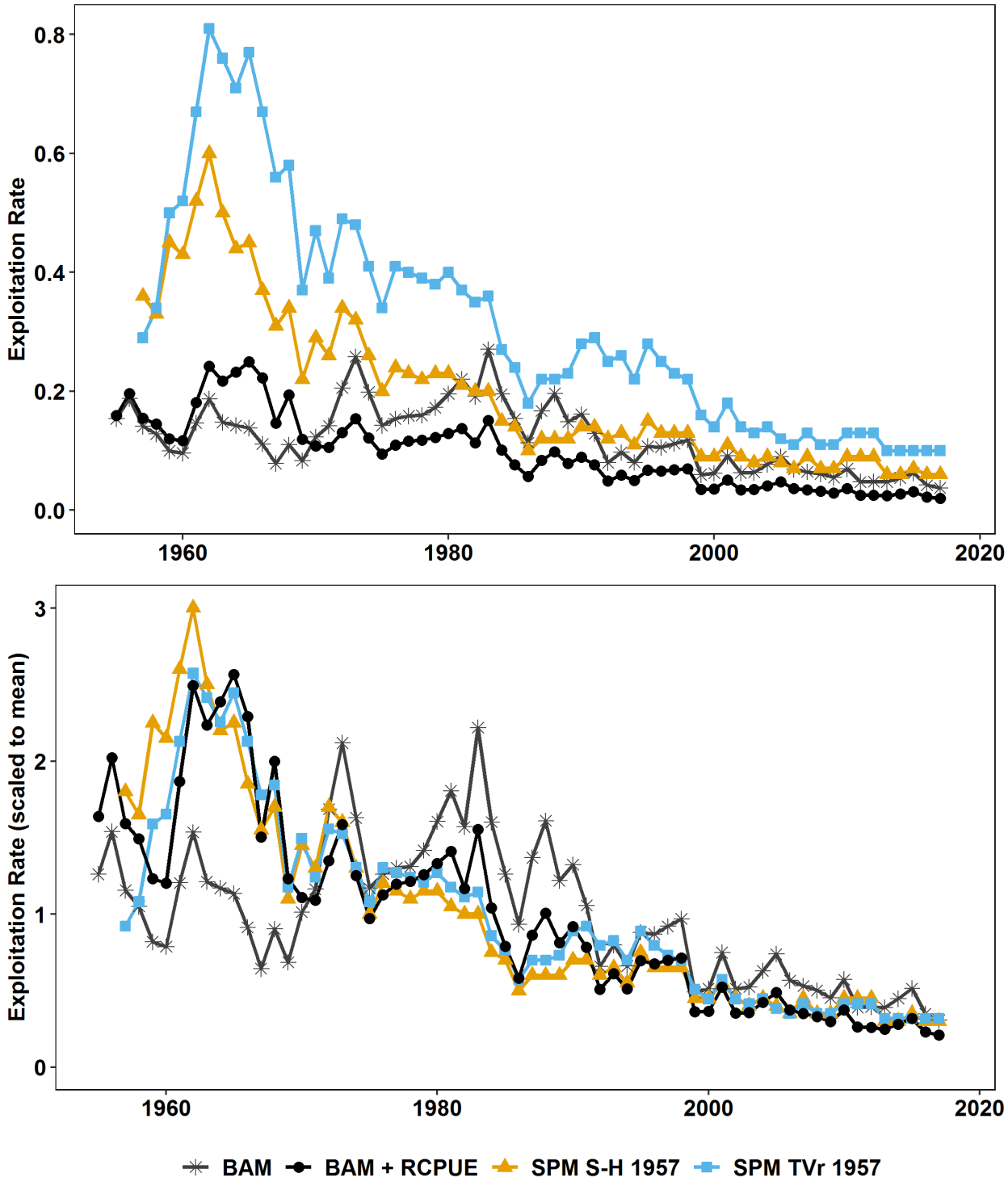


Figure 172. Estimates of exploitation rate from the surplus production models, the base run of the BAM, and a sensitivity run of the BAM that included the RCPUE index.

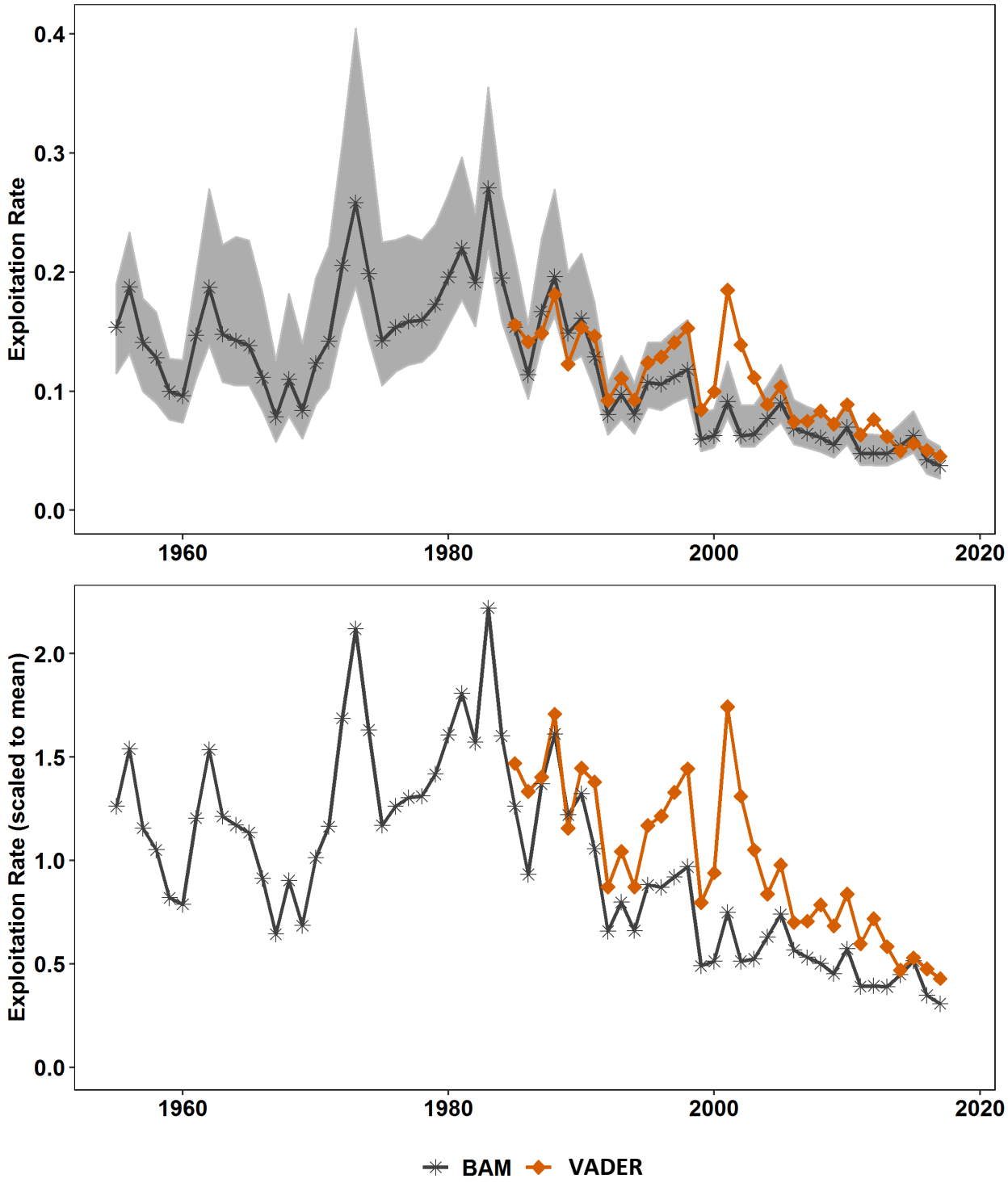


Figure 173. Exploitation rate estimates from the single species assessment model (BAM) plotted with the exploitation rate estimates from the multispecies statistical catch-at-age (VADER) model (top) and scaled to their respective time series means (bottom). Shaded area on top plot indicates MCMC confidence intervals from the single species assessment model.

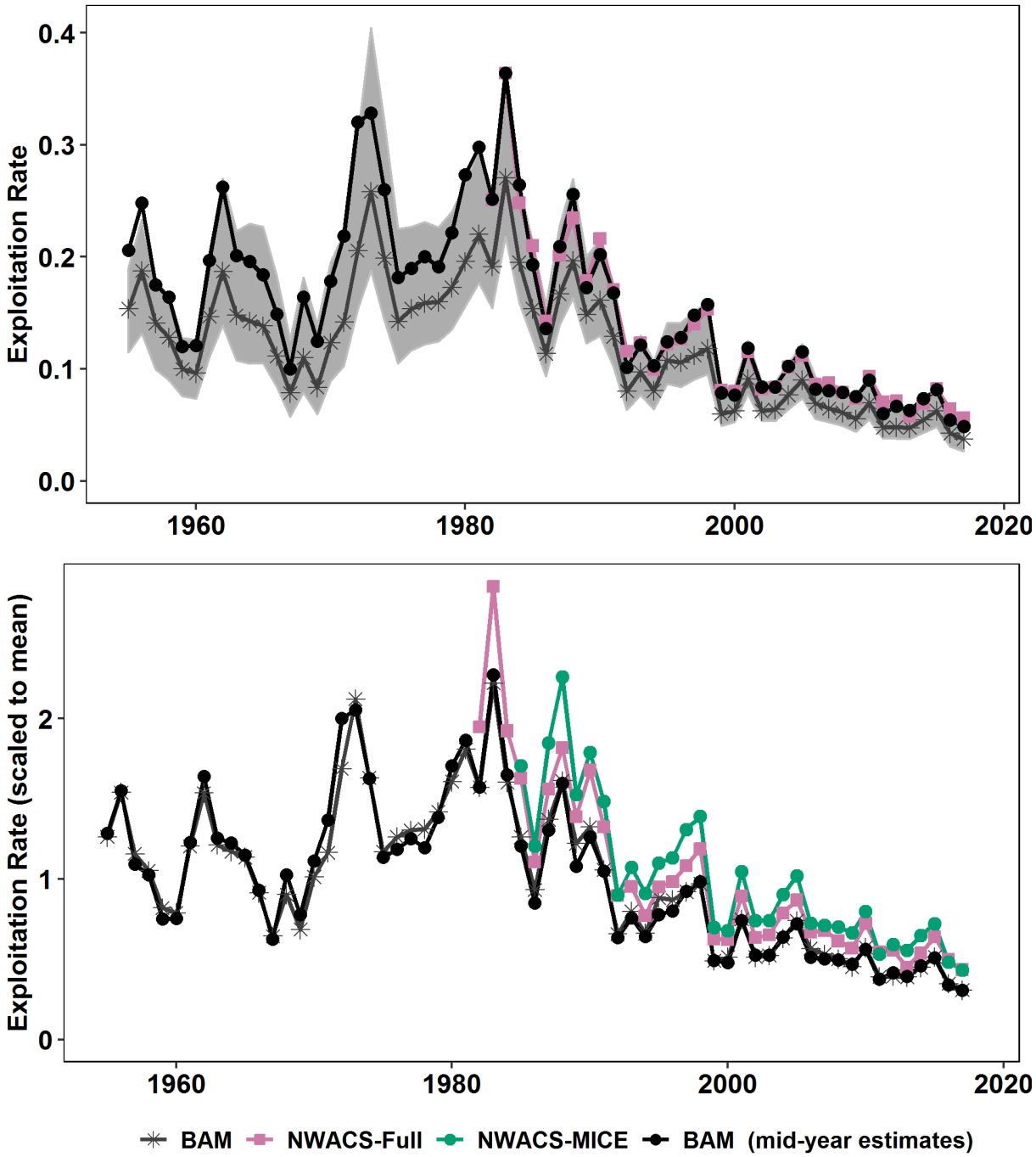


Figure 174. Estimates of exploitation rate from the single species assessment model at the start of the year (BAM) and at the middle of the year (BAM mid-year estimates) plotted with the NWACS model estimates (top) and scaled to their respective time series means (bottom). Shaded area on top plot indicates the start of year biomass MCMC confidence intervals from the single species assessment model.

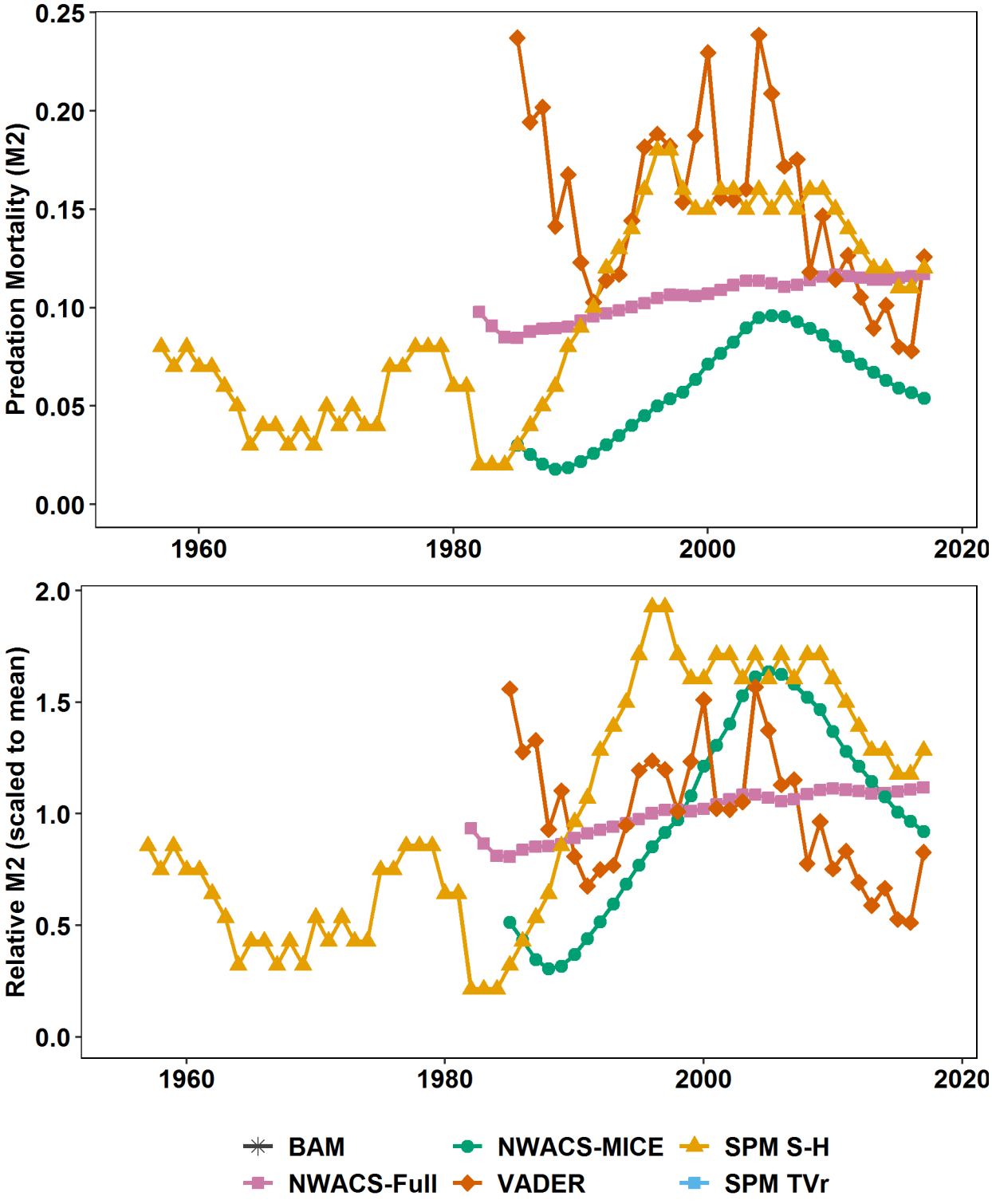


Figure 175. Estimates of modeled predation mortality (M_2) from the ERP models (top) and scaled to their respective time-series means (bottom).

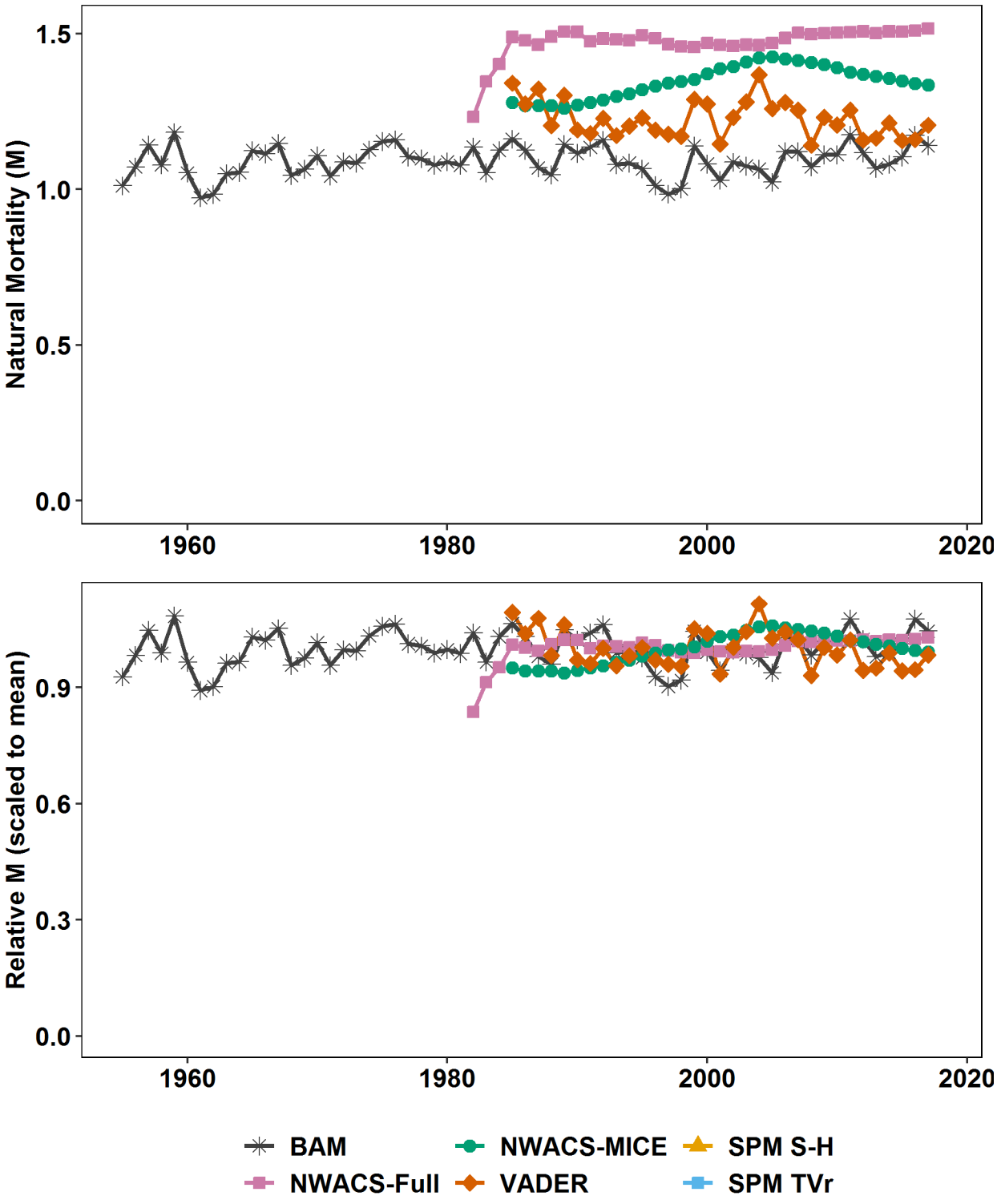


Figure 176. Estimates of total natural mortality (*M*) from the ERP models plotted with the natural mortality estimate from the single-species assessment model.

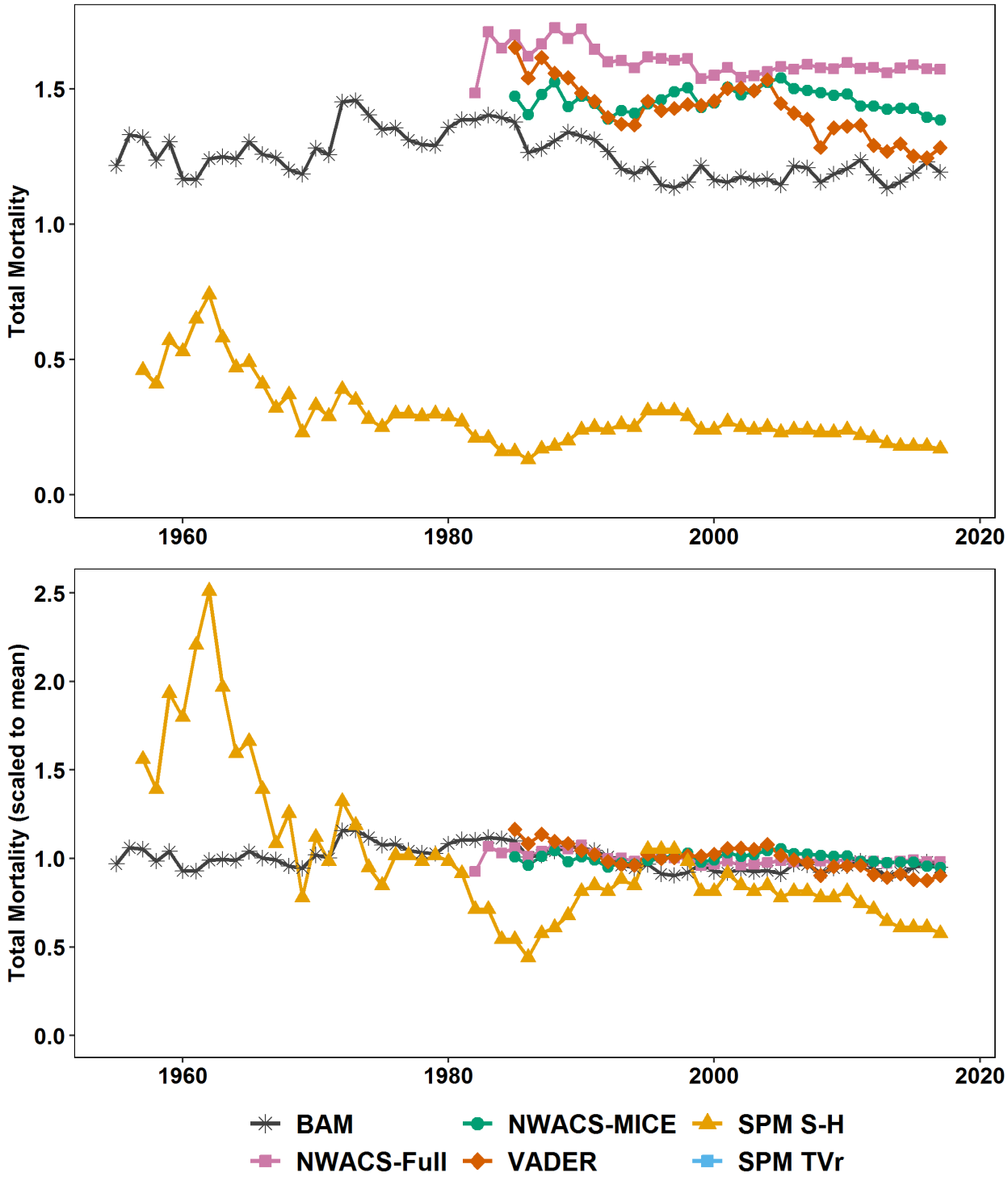


Figure 177. Estimates of total mortality from the single species assessment model (BAM) plotted with the total mortality estimates from the EPR models (top) and scaled to their respective time series means (bottom).

SEDAR

Southeast Data, Assessment, and Review

SEDAR 69

Section III: Review Workshop Report

Atlantic Menhaden

Ecological Reference Point

January 2020

SEDAR
4055 Faber Place Drive, Suite 201 North Charleston, SC 29405

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1. Introduction

1.1 Workshop Time and Place

The SEDAR 69 Review Workshop for Atlantic Menhaden was held November 4-8 , 2019 in Charleston, SC.

1.2 Terms of Reference

1. Evaluate the justification for the inclusion, elimination, or modification of data from the Atlantic menhaden single-species benchmark assessment.

2. Evaluate the thoroughness of data collection and the presentation and treatment of additional fishery-dependent and fishery-independent data sets in the assessment, including but not limited to:
    a. Presentation of data source variance (e.g., standard errors).
    b. Justification for inclusion or elimination of available data sources,
    c. Consideration of data strengths and weaknesses (e.g., temporal and spatial scale, gear selectivities, aging accuracy, sample size),
    d. Calculation and/or standardization of abundance indices.

3. Evaluate the methods and models used to estimate Atlantic menhaden population parameters (e.g., F, biomass, abundance) that take into account Atlantic menhaden's role as a forage fish, including but not limited to:
    a. Evaluate the choice and justification of the recommended model(s). Was the most appropriate model (or model averaging approach) chosen given available data and life history of the species?
    b. If multiple models were considered, evaluate the analysts' explanation of any differences in results.
    c. Evaluate model parameterization and specification as appropriate for each model (e.g., choice of CVs, effective sample sizes, likelihood weighting schemes, calculation/specification of M, stock-recruitment relationship, choice of time-varying parameters, choice of ecological factors).

4. Evaluate the methods used to estimate reference points and total allowable catch.

5. Evaluate the diagnostic analyses performed as appropriate to each model, including but not limited to:
    d. Sensitivity analyses to determine model stability and potential consequences of major model assumptions
    e. Retrospective analysis

6. Evaluate the methods used to characterize uncertainty in estimated parameters. Ensure that the implications of uncertainty in technical conclusions are clearly stated.
7. If a minority report has been filed, review minority opinion and any associated analyses. If possible, make recommendation on current or future use of alternative assessment approach presented in minority report.

8. Recommend best estimates of stock biomass, abundance, exploitation, and stock status of Atlantic menhaden from the assessment for use in management, if possible, or specify alternative estimation methods.

9. Review the research, data collection, and assessment methodology recommendations provided by the TC and make any additional recommendations warranted. Clearly prioritize the activities needed to inform and maintain the current assessment, and provide recommendations to improve the reliability of future assessments.

10. Recommend timing of the next benchmark assessment and updates, if necessary, relative to the life history and current management of the species.

11. Prepare a peer review panel terms of reference and advisory report summarizing the panel's evaluation of the stock assessment and addressing each peer review term of reference. Develop a list of tasks to be completed following the workshop. Complete and submit the report within 4 weeks of workshop conclusion.

1.3 List of Participants

APPOINTEE	FUNCTION	AFFILIATION/LOCATION
Review Panel		
Mike Jones	Review Panel Chair	ASFMC Appointee
Sarah Gaichas	Reviewer	ASMFC Appointee
Kenneth Frank	Reviewer	CIE
Daniel Howell	Reviewer	CIE
Laurence Kell	Reviewer	CIE
Analytical Representatives		
Amy Schueller	Single Species Lead Analyst & Chair	SEFSC – Beaufort, NC
Jason McNamee	Assessment Team	RI DEM – Jamestown, RI
Matt Cieri	ERP Work Group Chair	ME DMR – Boothbay, ME
Katie Drew	Assessment Team	ASMFC – Arlington, VA
Kristen Anstead	Assessment Team	ASMFC – Arlington, VA
Dave Chagaris	ERP Lead Analyst	UF – Gainesville, FL
Ray Mroch	Assessment Team	SEFSC- Beaufort, NC
Staff		
Max Appelman	Atlantic Menhaden Coordinator/Rapporteur	ASMFC – Arlington, VA
Sarah Murray	ERP Coordinator/Rapporteur	ASMFC – Arlington, VA
Patrick Campfield	Science Director	ASMFC – Arlington VA
Ciera Graham	Admin	SAFMC
Kathleen Howington	Coordinator	SEDAR
Observers		
Bob Beal	Observer	ASFMC
Julie Neer	Observer	SEDAR
Joseph Ballenger	Observer	SCDNR
Peter Himchak	Observer	Omega Protein
Genny Nesslage	Observer	UMCES
Chris Dollar	Observer	TRCP
Howard Townsend	Observer	NOAA Fisheries
Jeff Kaelin	Observer	Lunds Fisheries

1.4 List of Background Documents and Review workshop working papers

Document #	Title	Author
SEDAR 69 – SAR1	Assessment of Atlantic Menhaden Single Species Benchmark Report	To be prepared by SEDAR 69
SEDAR 69 – SAR2	Assessment of Atlantic Menhaden Ecological Reference Point Report	To be prepared by SEDAR 69
Supplementary Materials		
SEDAR 69 – RD01	SEDAR 40 Stock Assessment Report Atlantic Menhaden	SEDAR 2015
SEDAR69 – RD02	Hierarchical analysis of multiple noisy abundance Indices	P. Conn 2010
SEDAR 69 – RD03	Estimation of movement and mortality of Atlantic menhaden during 1966–1969 using a Bayesian multi-state mark-recovery model	Liljestrand et.al. 2019
SEDAR 69 – RD04	Trends in Relative Abundance and Early Life Survival of Atlantic Menhaden during 1977–2013 from Long-Term Ichthyoplankton Programs	Simpson et.al. 2016
SEDAR 69 – RD05	Multi-state dead recovery mark-recovery model performance for estimating movement and mortality rates	Liljestranda et. al. 2019
SEDAR 69 – RD06	A MULTISPECIES STATISTICAL CATCH-ATAGE (MSSCAA) MODEL FOR A MIDATLANTIC SPECIES COMPLEX	McNamee, 2018
SEDAR 69 – RD07	Evaluating the performance of a multispecies statistical catch-at-age model	Curti, 2013
SEDAR 69 – RD08	Parameter estimation in Stock Assessment Modelling: Caveats with Gradient-based algorithms	Subbey, 2018
SEDAR 69 – RD09	Reconciling single-species TACs in the North Sea demersal fisheries using the Fcube mixed-fisheries advice framework	Ulrich et.al. 2011
SEDAR 69 – RD10	Working Group on Mixed Fisheries Advice (WGMIXFISH-ADVICE)	ICES Advisory Committee, 2016
SEDAR 69 – RD11	Evaluation of Current and Alternative Harvest Control Rules for Blue Whiting Management using Hindcasting	Kell and Levontin, 2019
SEDAR 69 – RD12	Public comment Forum Submissions	SEDAR, 2019
SEDAR 69 – RD13	Cookbook for Using Model Diagnostics in Integrated Stock Assessments	Carvalho, 2019

2. Review Panel Report

2.1 Executive Summary

The Atlantic States Marine Fisheries Commission (ASMFC) Ecological Reference Points Working Group (ERP WG) provided a comprehensive report, complemented by supplementary materials and a series of presentations at the November 4-8, 2019 SEDAR 69 review workshop, held in Charleston, SC. These materials were reviewed and evaluated by a panel of five fishery experts, three from the Center for Independent Experts and two (including a chair) nominated by the ASMFC. The reports and presentations included thorough and extensive documentation of the data, methods, and results for a series of models intended to reveal aspects of Atlantic menhaden population and fishery dynamics in the context of the broader ecosystem, sensitivity and uncertainty analyses of the models, a comparison of the models, a discussion of potential implications for evaluation of stock status and for determination of ecological reference points, and recommendations for future research and monitoring. Overall the panel was very impressed with the quality and quantity of analyses included in these reports and associated presentations, and acknowledges the novelty of this work. The panel commends the efforts of the ERP WG.

This panel report addresses the Terms of Reference (ToR), which were developed and shared with the panel prior to the workshop. The ToR concerned (1 & 2) the data used in the assessment; (3) methods and models used to account for menhaden's role as a forage fish; (4) methods used to estimate reference points; (5 & 6) treatment of uncertainty; (7) any minority opinions (there were none); (8) conclusions related to stock status; and (9) recommendations for research.

The panel supported the decisions made by the ERP WG regarding datasets, both from the single species menhaden assessment and from other sources, to inform the models they developed. Use of the fishery dependent CPUE index (RCPUE) for the surplus production models was defensible, despite the decision not to use these data for the single species Beaufort Assessment Model (BAM). The panel agreed with the strategy of using data from previously vetted assessments to inform the multi-species models. We concluded that the ERP WG made appropriate use of the available diet data, but acknowledged that these data are not as complete and comprehensive as would be preferred. To that end we encourage future examination of other sources of diet information, including relatively novel methods such as genetic barcoding of stomach samples, at least to provide a basis for evaluating model uncertainty. If the multispecies statistical catch-at-age (VADER) model continues to be used to inform management (see below), the panel recommends a more thorough review of the spiny dogfish data, as this is the one predator species whose inputs are not derived from a previously vetted assessment. Finally, the panel recommended including a "data pedigree" in future documentation of the EwE models.

The ERP WG presented five models, in addition to the BAM, in their report, ranging from a simple surplus production model with time-varying productivity to a full ecosystem trophodynamic model (NWACS-FULL). The panel appreciated the clear summary provided by the ERP WG of the pros and cons of each model in section 15 of their report. They concluded their description and evaluation of these models by recommending use of a combination of the BAM single species assessment model and NWACS-MICE – a reduced complexity Ecopath with Ecosim model. The panel agreed with this conclusion, but also noted that the multi-species statistical catch at age model (VADER) should be retained as a candidate model to inform thinking about menhaden's interaction with other species, with the caveat that this will require addition of prey-dependent dynamics for the predator species in the model. For the NWACS-MICE model, the panel was appreciative of the efforts made by the ERP WG to overcome some of the limitations of the EwE software and arrive at estimates of vulnerability and other parameters that were consistent with the data used to fit the models, yet added ecological realism.

The panel concluded that the methods presented to evaluate trade-offs among reference points and management strategies for menhaden and for their predators were sound and appropriate. The progress that has been made on this since SEDAR 40 (2015) is very impressive. The ERP WG emphasized that the analysis of trade-offs presented in their report are an illustration of how the recommended models could be used to transparently present these trade-offs, rather than a recommendation for a particular set of reference points. The panel supported this position, but concluded that the BAM and NWACS-MICE models are ready to be used to provide management advice. The logical next step will be to start a dialogue with managers to explore trade-offs among management objectives, using these models as an objective basis for elucidating these trade-offs.

The ERG WG focused their examination of model sensitivity and uncertainty on the NWACS-MICE model. This is reasonable, given the recommendation that this model be used going forward. If the VADER model is used to inform management in the future, a more robust sensitivity analysis of the revised model would be appropriate. For the NWACS-MICE model, the panel found the range of sensitivity runs useful and informative; in particular, the additional run that investigated sensitivity to increases in assumed predation mortality for menhaden was extremely useful – it provided evidence that the trade-off analysis the ERP WG reported for striped bass-menhaden management interactions was fairly robust to this uncertainty.

Based on review of both the ERP WG and the single species assessment reports, the panel recommends using the results of the single species assessment to evaluate current abundance and biomass levels, and status relative to reference points. Once managers have discussed the results of the ERP WG analyses and have reached a conclusion about reference points for menhaden that are informed by ecological interactions with other species, specific reference point values can be developed. These new reference points should include consideration of outputs from other models, such as those presented for the NWACS-MICE model, in addition to the single species assessment. Stock status would then be evaluated on the basis of the new reference points.

Finally, the panel generally supported the recommendations of the ERP WG for future research, data collection, and assessment methodology, and provided a number of additional specific suggestions throughout the discussion of ToRs 1-6. As noted in the single species review, the panel supports the recommendation of moving forward with a Management Strategy Evaluation, but urges a cautious, pragmatic approach that is more likely to produce timely outputs for managers.

2.2 Statements addressing each TOR

ToR 1. Evaluate the justification for the inclusion, elimination, or modification of data from the Atlantic menhaden single-species benchmark assessment.

Two long-term fishery-dependent indices of abundance for Atlantic menhaden were considered for inclusion in the ERP assessment (specifically for the two production models): a commercial reduction fishery CPUE index (RCPUE index) and the Potomac River Fisheries Commission index (PRFC) derived from the commercial bait fishery. Neither of these indices was used in the single-species assessment for a variety of well understood reasons. However surplus production models require relatively long CPUE time series for model tuning.

The ERP WG decided to use the RCPUE index rather than the PRFC for ERP model base runs because of its larger spatial coverage, consistently recorded unit of effort, known variance structure, support from supplemental analyses that showed relatively strong correlations with other sources of data, and the

ability to standardize the data through explanatory covariates (week, factory, vessel size), among other factors. The panel agreed with the choice of the inclusion of the RCPUE and exclusion of PRFC.

The panel also agreed with the use of BAM model outputs for tuning the EwE models, and the data used in the menhaden single species assessment for the multi-species statistical catch-at-age (VADER) model. Finally, the panel encouraged the ERP WG to consider the pros and cons of directly inputting single species model outputs into the ecosystem models versus allowing the ecosystem models to estimate biomass, F, and other quantities of interest where possible.

ToR 2: Evaluate the thoroughness of data collection and the presentation and treatment of additional fishery-dependent and fishery-independent data sets in the assessment, including but not limited to:

a. Presentation of data source variance (e.g., standard errors).
b. Justification for inclusion or elimination of available data sources,
c. Consideration of data strengths and weaknesses (e.g., temporal and spatial scale, gear selectivities, aging accuracy, sample size),
d. Calculation and/or standardization of abundance indices.

The panel generally considered data collection, presentation and treatment of additional fishery-dependent and fishery-independent data sets across all five presented ERP models thorough and appropriate. The panel was impressed by the amount of work and extent of data collation and treatment represented in the report. That said, with five models at different levels of complexity including representations of multispecies and full food web dynamics, there are always data gaps to be filled or alternative treatments of data that might be considered, which we propose as research recommendations for future work.

Overall, the panel agreed with the strategy of using input datasets (fishery-independent indices, total catch, and both fishery-dependent and -independent age and length data) directly from previously vetted and approved stock assessments for modeled predator species. This streamlines the process for multispecies and ecosystem modeling greatly by relying on existing processes to review input data. The review panel did not need to review already vetted assessment inputs again for this process, and trusts that previous review processes evaluated variance in data sources, calculation and/or standardization of indices, and considered data strengths and weaknesses. However, the panel noted that none of the data sources for ERP models were shown with standard errors or other depictions of variance. In future reporting, it would be helpful to include a presentation of the variance even if data are previously vetted to ensure that future review panels can address specific requests such as ToR 2a.

The review panel therefore primarily considered whether the process for inclusion/elimination of available predator stock assessment input data sources was appropriate, and applied all considerations above to data sources that had not been previously reviewed (i.e. diet data, dogfish inputs for the VADER model, and additional EwE inputs). Here we did not consider stock assessment model outputs (F, SSB, recruitment, or other model-estimated quantities) to be "data" even if they were inputs to ERP models; we consider these to be previously reviewed information. However, we comment on when it is appropriate to use stock assessment model outputs as inputs to ERP models and when it may not be.

Selecting stock assessment fishery independent indices

To streamline the amount of input data for ERP models, a subset of assessment inputs (fishery-independent indices) were selected. The panel agreed that ERP models do not need to use all index datasets that single species assessment models do, as long as the most influential assessment indices are retained for ERP models. This was achieved by asking relevant Technical Committees for each species to advise on the top three most influential indices plus alternate indices for use in sensitivity runs. The panel

agreed with this approach, which efficiently uses knowledge gained from existing assessment development and review processes in ERP modeling.

Diet data

ERP models were developed based on diet data from NEFSC, NEAMAP, and ChesMMAP bottom trawl surveys, as well as other "snapshot" sources. The panel agreed that these sources taken together represent a good basis for diet composition inputs across the spatial range of menhaden and key modeled fish predators. The time series of diet composition is longest from the NEFSC bottom trawl survey, but the panel noted that the BAM model does not use this survey as an index due to the low number menhaden catch records. While the NEFSC trawl survey catches key menhaden predators more often than menhaden, the low catch rate of menhaden may be related to the generally low numbers of menhaden in predator stomachs in this survey. The panel agreed that including the NEFSC trawl survey diet data is useful, but strongly supports the inclusion of additional diet data from NEAMAP and ChesMMAP as well. The panel suggested including other sources of diet data as possible from additional surveys encountering menhaden and their predators to reduce uncertainty in the predator-prey relationships considered in ERP models.

Both ERP models identified as candidates for future work would benefit from additional sources of diet data as part of further development. The VADER model has the most stringent diet data requirements for time series of diet by age, while the EwE models require a snapshot diet composition input which more flexibly accommodates diet data from single studies to supplement survey-collected stomachs (but which requires diet information from seabirds, marine mammals, and other species not sampled by fish trawl surveys for full EwE). ERP modelers suggested that the Bayesian approach for allocating diet information to appropriate model age and year bins could be adjusted to use additional diet data "snapshots" from single studies as priors; the panel supported this suggestion. In addition, other methods to estimate diets from genetic barcoding or stable isotopes could be explored, possibly using short-term research projects to identify promising datasets and methods. The panel also recommended further sensitivity analysis to evaluate impacts of different diet inputs to models (see below).

Spiny dogfish data inputs to VADER

The only exception to the direct use of previously vetted assessment data inputs was for spiny dogfish in the VADER model. The spiny dogfish assessment is a female-only index-based assessment because there is no catch-at-age data from the fishery (which catches 95% females). ERP modelers reconstructed male and female indices from NEFSC bottom trawl survey data, and also extrapolated fishery catch-at-age for spiny dogfish from length-at-age in surveys combined with an age-length key to create a combined-sex age structured population dynamics model. Clearly the assumption that fishery catch-at-age is similar to survey catch-at-age is critical to use the data in this way; however, this assumption was not examined in depth during this review, nor were sensitivities conducted to evaluate the effects of alternative assumptions. While the methods as outlined in the assessment report seem reasonable to get the VADER model up and running, the panel noted that more rigorous review of these methods is required if the VADER model will be used as a primary ERP model or as an MSE operating model in the future. In particular, the panel recommended that ERP modelers work with spiny dogfish assessment scientists to evaluate the most appropriate data to support future multispecies modeling.

Ecopath biomass inputs

While stock assessment model output is not "data", assessment model-estimated biomass is used as input to the Ecopath portion of both EwE models. This is considered appropriate by the panel given that the EwE models are intended to integrate what is currently considered the "best available information" across assessed species and to reconcile reference points at the scales currently used in management by incorporating predator-prey dynamics. This acknowledges that EwE software is not well suited to statistical estimation of the observation processes required to convert survey index data into the snapshot

of total biomass required to initialize the dynamic food web model. However, the panel noted that any potential (currently undetected) bias in stock assessment estimated biomass is passed along to EwE when using this as input, and remains an issue for any subsequent ERP analysis.

The panel noted that the EwE MICE model was fit to index data (as described above for the VADER model), rather than stock assessment model output. The use of stock assessment output in the initial mass balance sets up the scale of the food web model while the dynamic predator prey interactions are estimated from the combination of index trends across all species/groups in the EwE MICE model. This approach "lets the data speak" to some extent in estimating key dynamic predator-prey parameters used for ERP development.

In contrast, the full EwE model is fit to stock assessment estimated biomass trends rather than index data. This approach relies on a stronger assumption of the accuracy of stock assessment estimated trends across all modeled species in estimating dynamic predator-prey parameters. The panel was unable to fully evaluate the differences between these approaches.

The panel suggested that uncertainty information in the form of a "data pedigree" be included with future documentation of both EwE models. This information exists for the datasets used and could be summarized in the common format for these food web models and then carried forward in sensitivity and/or uncertainty analyses.

Environmental data (discussed but not implemented at present)

While there are stated objectives to ensure menhaden sustainability in the face of a changing environment, most of the ERP models presented do not yet include environmental data because they were developed to address predator prey interactions as a first priority. The panel agreed with this prioritization for developing ERPs, and suggests that environmental drivers can be evaluated and incorporated as appropriate in the future.

The VADER model has the capacity to include a temperature time series which affects consumption rates; however, this was not implemented in ERP model runs reviewed by the panel. Nevertheless, the description of the temperature data product in the report is an appropriate starting point for incorporating environmental data into the VADER model.

There are many resources for environmental and oceanographic data that can be applied at multiple spatial and temporal scales for the region addressed by ERP models. The panel suggested that future work could first identify any broad environmental drivers likely to affect all species in the VADER and EwE-MICE models and then investigate which datasets best represent these drivers. In addition, the panel agreed with ERP modelers that converting spatially-explicit environmental information into time series for input into spatially aggregated models is challenging, and research into appropriate methods for handling environmental data is appropriate.

ToR 3. Evaluate the methods and models used to estimate Atlantic menhaden population parameters (e.g., F, biomass, abundance) that take into account Atlantic menhaden's role as a forage fish, including but not limited to:

a. Evaluate the choice and justification of the recommended model(s). Was the most appropriate model (or model averaging approach) chosen given available data and life history of the species?
b. If multiple models were considered, evaluate the analysts' explanation of any differences in results.
c. Evaluate model parameterization and specification as appropriate for each model (e.g., choice of CVs, effective sample sizes, likelihood weighting schemes, calculation/specification of M, stock-recruitment relationship, choice of time-varying parameters, choice of ecological factors).

In addition to the existing stock assessment model (BAM), the ERP report presented five models to estimate menhaden population parameters that account for menhaden's role as forage. The models ranged in structural complexity from a simple surplus production model with time-varying menhaden production (SPM-TVr) to a full food web model for the Northwest Atlantic continental shelf (NWACS-FULL). Intermediate models included a surplus production model that explicitly accounted for menhaden removals due to predation (Steele-Henderson), a multispecies statistical catch at age model with menhaden and five other species (VADER), and a scaled down food web model focused on menhaden and a subset of key predator and prey species (NWACS-MICE). (The panel interpreted this ToR to mean that we are not evaluating predator stock assessments that provided inputs to ERP models, but rather the ERP models presented that are used to develop a tool to estimate reference points.)

The ERP report recommended a combination of the BAM model and the NWACS-MICE model to estimate Atlantic menhaden population parameters that take into account Atlantic menhaden's role as a forage fish. The ERP report further recommended this combination as a tool for managers to use in achieving multispecies objectives, rather than recommending a specific F or catch level for menhaden at this time. The panel agreed with these recommendations, and details justifications and caveats for methods and models below.

The ERP working group provided strong justification for choosing the BAM and NWACS-MICE models based on their ability to provide information relevant to ecosystem management objectives specified in a 2015 stakeholder workshop as well as their technical merits. Objectives and performance metrics from the 2015 workshop related to sustaining menhaden to provide for menhaden fisheries and predators, to provide fishery stability, and to minimize risk due to changing environmental conditions. While all presented models could address sustainability for menhaden fisheries, only VADER, NWACS-MICE, and NWACS-FULL could address menhaden predators or their fisheries (and no models are currently set up to address changing environmental conditions). Further, only the NWACS models directly model menhaden effects on predators as well as predator impacts on prey, and the NWACS-FULL model was difficult to update within required management time frames. The panel thus agreed with the conclusion that NWACS-MICE is best able to address the full suite of management objectives when combined with BAM, which best captured menhaden population dynamics.

The panel noted that the VADER model may also be useful in the future for addressing the specified ecosystem management objectives if prey-dependent dynamics can be incorporated for modeled predators. However, the panel recognized that this may be difficult, and that there is a lack of published examples where this has been done within multispecies statistical catch-at-age models.

The ERP report retained analysis of all models and compared results across them (including BAM) in section 15. This panel appreciated the clear summary with the pros and cons of each model listed in this section. The panel agreed that all models showed generally similar recent trends and scale in comparable outputs (age 1+ biomass, exploitation rate). This approach increases confidence that input data rather than model structure is largely driving model results, and argues for continuing to maintain a suite of supporting models with a range of complexity. Differences between the results were mainly attributable to structural assumptions: for example, surplus production/biomass dynamics models are not designed to track short term biomass changes that arise from inter-annual recruitment variability. Further useful comparisons explaining differences between the NWACS-MICE and -FULL models were made in the report and in presentations during the meeting.

In sections below, we present the panel's evaluation of model parameterization and specification for each ERP model. Note that our suggestions for further model development and evaluation should be interpreted as constructive advice for future work, not additional work that is required before the two recommended models (BAM and NWACS-MICE) can be used to guide future management.

NWACS-MICE (selected model)

The panel found the overall specification of NWACS-MICE to be reasonable, given the different requirements of the EwE modeling framework from those of BAM or other statistical catch-at-age frameworks. There are two components to the specification: the static (Ecopath) model and the dynamic (Ecosim) model. The static model initializes the dynamic model, which is then calibrated using sum of squares fits to time series of biomass and catch for multiple species.

The NWACS-MICE static (Ecopath) model parameterization used information from regional databases and stock assessments as available; this is appropriate and is discussed in detail under ERP ToR 2. In particular, the panel supported the decision to use biomass accumulation terms, which does not force the food web model to start in equilibrium. Some parameters were used directly or aggregated from NWACS-FULL (such as diet imports for predators); therefore, these models should continue to be reviewed and updated together. The main issue noted with the static model parameterization related to low estimates of ecotrophic efficiency (EE) for menhaden age groups resulting from B and P/B inputs from the BAM for menhaden combined with diet and other inputs for predators, even when considering that only a subset of predators was included in the model. This was addressed in a sensitivity run (see ToR 5).

The panel had suggestions for future work on the static model parameterization; some can be addressed by sensitivities and some can contribute to uncertainty characterization (see ToRs 5 and 6). First, biomass (B) parameters based on stock assessments may change substantially between assessments; therefore, sensitivity of the static model to changes in these inputs over a historical range of assessments for key species should be evaluated. Second, there are multiple methods for estimating P/B and Q/B ratios based on empirical information that should be explored. The assumption here that stock assessment $M + F = Z = P/B$ is a reasonable starting point, but potentially builds in resilience of stock productivity to F that may not exist in reality. This is particularly concerning if the model is parameterized at a time when a stock was subject to overfishing. Third, the reduction from NWACS-FULL to NWACS-MICE results in simplification of food web network topology; while general results from the two models were similar, impacts of this simplification on dynamic model behavior could be evaluated in more detail as management for more interacting species is considered. Finally, uncertainty in input parameters can be characterized in an EwE "data pedigree" which ranks quality and relevance of B, P/B, Q/B, and diet composition (DC) information sources. Including this information on all static parameter sources (for NWACS-FULL and NWACS-MICE) will be useful in future reviews.

For the dynamic (Ecosim) parameterization, the panel expressed concern about the inherent software constraints in EwE that limit a modeler's ability to fully explore interactions between the model and input data, or to conduct sensitivities on combinations of dynamic parameters that must be altered by hand in a GUI framework that limits reproducibility. However, several approaches were taken to compensate for inflexibility in the software, which gave the panel more confidence in the results. First, estimation of vulnerability parameters was done in stages to ensure that the model had fully converged. Second, an "ecological realism" constraint was placed on estimated vulnerability parameters to limit predation mortality by a single predator to 75-100% of total natural mortality for the prey. This constraint was applied manually after the EwE automated fitting procedure. Third, multiple parameterizations were presented with combinations of other manually set dynamic parameters (prey switching, foraging time adjustment, etc.) to bound the behavior of the model. Future work is recommended to either formally incorporate more flexibility in the software or to move the NWACS models into a more flexible and modifiable framework; alternative implementations of EwE exist in C, R, Matlab, and other languages. The panel also suggested that future work could investigate using an ensemble of dynamic model parameterizations to provide advice, rather than selecting a single model.

The panel noted that simulation testing similar to that performed for other ERP models could be useful for the NWACS-MICE model in the future.

The panel found the parameterizations and specification of supporting models to be reasonable, and made only brief comments for consideration in the future.

Surplus production with time varying r (supporting model)

The panel agreed with the use of this model as a supporting model rather than as a primary model for ERP advice, and further agreed with the choice of RCPUE time series as the primary input. This simple model could be used to evaluate correlations between r and predator metrics, and could potentially contribute to a powerful predictive analysis to evaluate time series of menhaden r and effects on striped bass. For exploring model sensitivities in the future, evaluating impacts of starting the model in specific years (rather than just early or late in the full time series) would be useful. The panel found the simulation testing approach and results useful, and suggests that all ERP models should attempt similar testing.

Steele-Henderson surplus production (supporting model)

The panel agreed with the use of this model as a supporting model rather than as a primary model for ERP advice. One suggestion was to consider all consumption by all predators together as a functional group rather than just striped bass to see if explanatory power improved. The panel also suggests that other wide-area search algorithms could be applied to free the model from its current implementation in proprietary software.

VADER statistical catch at age (supporting model)

The panel agreed with the use of this model as a supporting model rather than as a primary model for ERP advice at this time. There was interest from the panel in exploring the assumption of constant ecosystem carrying capacity but variable "other food" versus the more common assumption of fixed "other food". Further, the interaction of "other food" with assumptions about unexplained mortality (M0) for each species should be explored to determine which factors influence the intensity of species interactions within the model. Conversions from length to age to weight for parameterizing the consumption equations may lose information content in the data relative to re-parameterizing some equations to be length-based.

The panel noted that this is a promising approach that has advantages over EwE in its ability to estimate F and other management–relevant quantities directly from data. Using both models together in the future would give managers information that incorporates structural uncertainty. For future work, the panel recommends conducting a jitter analysis similar to that applied to BAM to ensure that optimization is working as expected, in addition to exploring more ecologically direct length-based predator prey dynamics, and conducting simulation testing.

NWACS-FULL (supporting model)

The panel agreed with the use of this model as a supporting model rather than as a primary model for ERP advice. The panel agreed that updating this model is more time-consuming than NWACS-MICE. However, it would be useful in future iterations to apply the same parameter estimation techniques as used for NWACS-MICE (see above), which alleviate some concerns that arise from EwE software constraints. In addition, alternative specifications that fit NWACS-FULL to index time series instead of assessments would be useful for comparison with NWACS-MICE. Further exploration of incorporating habitat drivers into NWACS-FULL would also be useful to address the management objectives to minimize risks due to shifting environmental drivers.

ToR 4. Evaluate the methods used to estimate reference points and total allowable catch.

The methods used to estimate ecosystem reference points were reviewed. The panel agreed that the methods presented were sound. Compared to SEDAR 40 in 2014, extraordinary progress has been made, and the value of the Ecosystem Management Objectives Workshop in providing ecosystem objectives was recognized. The models presented provide a transparent approach that allows the trade-offs between menhaden and their predators to be evaluated within a multispecies context. For example, NWACS-MICE and BAM could be used to develop a scientific management framework to both set single species TACs and evaluate their impact on predator species. The panel concluded that the approach illustrated in

the ERP report seems appropriate and is ready for presentation to managers to initiate discussions about trade-offs among potentially competing fishery objectives.

The example trade-off analysis (e.g. Figure 144), illustrated why estimation of reference points for menhaden needs to be integrated with discussion of reference points for predator stocks. Striped bass are currently above their F target and the future status of this population will influence the outcome for a range of menhaden reference points. More generally, ecosystem models such as NWACS-MICE provide a valuable tool for exploring scenarios corresponding to alternative stock levels and exploitation rates for the species included in the models. It will be important to explore a variety of scenarios and to communicate that ERPs are inter-dependent since changes in one stock will affect the levels of other species.

The panel believes that the models are ready to be used to provide management advice. The models are able to provide a quantitative representation of system and predator-prey dynamics. The next step is to start a dialogue with managers and to evaluate trade-offs between management objectives. This will support the selection of targets, limits and thresholds to balance overall management objectives for the resource.

ToR 5. Evaluate the diagnostic analyses performed as appropriate to each model, including but not limited to:

d. Sensitivity analyses to determine model stability and potential consequences of major model assumptions

The different classes of models evaluated here have different structures, and therefore used different sensitivity tests. Because the NWACS-MICE model is the one currently proposed for use in management this section focusses on that model; however, the other models are summarized first.

For the surplus production models, a sensitivity to the choice of two potential CPUE indices (RCPUE and PRFC) was conducted, and indicated significant differences in trend between 1970 and 1990, although a much closer agreement since 1990. The rationale presented to use the RCPUE as the base case and the PRFC as the sensitivity was clearly presented, and the panel concurred with the conclusion. Sensitivity tests for the production models also included a brief analysis of the impact of the start date of the model, this is addressed under the retrospective analysis below.

For the VADER model the sensitivity run comparing the model with and without trophic interactions produced counter-intuitive results. This could point at problems with the proportion of total mortality (Z) allocated to predation, and a research recommendation is to investigate this through a more detailed sensitivity analysis. The modelled sensitivity to alternate tuning indices and prey composition was also presented.

The review panel would recommend a sensitivity test of the choice to fix overall food biomass (other food plus modelled prey) against the alternate hypothesis of fixing other food and allowing total biomass to vary.

The panel concluded that the suite of sensitivity tests performed on the VADER model and the two surplus production models was adequate at this time, given that these are not being currently proposed for direct use in management. Should the VADER model be used to inform management in the future, the additional sensitivity tests noted above would be recommended.

For the NWACS-MICE and NWACS-FULL model a suite of sensitivity runs was conducted with alternative dynamic (Ecosim) parameterizations using iterative vulnerability estimation as described above under ToR 3. NWACS-FULL sensitivities explored model behavior with and without vulnerability caps, with and without manual adjustments to selected parameters, and with observed and increased diet

proportions of menhaden for predators (in the static Ecopath model). NWACS-MICE sensitivities explored similar parameterizations to NWACS-FULL as well as the effect of EwE-estimated "primary production anomalies." A final sensitivity examined impacts of fitting to recruitment deviations as well as increasing the prey-switching exponent to 1.5 (increasing tendency of predators to abandon menhaden as prey as menhaden biomass decreased).

The panel found the range of sensitivity runs useful and informative. Exploration of sensitivity to Ecosim dynamic parameters is especially valuable because there are so few examples in the literature, and model results tend to be highly sensitive to these parameter settings. In general, sensitivity runs for NWACS-FULL suggested that manual tuning of parameters was necessary to balance model fits to biomass with reasonable stock-recruitment dynamics. For NWACS-MICE (fitting to indices rather than stock assessment outputs), sensitivity runs demonstrated that vulnerability caps reduced or eliminated model instabilities in projections, which is desirable.

One additional sensitivity test was performed for the NWACS-MICE model during the meeting, at the request of the review panel. This investigated the sensitivity of the results to increases in predation mortality for menhaden. The EE parameter represents the fraction of species production that is used within the ecosystem, so a low EE suggests that the model is not accounting for much mortality (or other loss from the system) explicitly. For forage species, food web models usually account for a substantial proportion of production as predation mortality, with EE often approaching 1. The panel noted that predation mortality on menhaden estimated by the model was quite low, and the proportion caused by any given predator even lower (for 0 group menhaden around 4% of overall mortality came from striped bass, while for age 1+ menhaden predation this value was around 1%). Given the available data, it is difficult to say if this is correct or not, but it does give rise to a situation where small changes in the absolute value might have significant impacts on model outputs.

A single sensitivity run was conducted, which indicated that increasing the EE to a higher (but reasonable) value by increasing predator diet proportions of menhaden increased the slope of the curve relating B/B_{target} for striped bass to F in menhaden (Figure 148 in the ERP report). This resulted in very little change in the results for small changes around current menhaden F. However, the distance between B_{target} and $B_{threshold}$ decreased as the slope increased, indicating that the results from larger changes in menhaden F could be sensitive to the choice of EE parameters.

This sensitivity test was welcomed by the panel, and indicated that the overall NWACS-MICE result was robust to both reasonable increases in predator consumption of menhaden from those currently observed in food habits data and to small changes from current management. The panel therefore recommends that a further suite of sensitivity tests to examine how robust the results are for greater deviations from current management. The results of the sensitivity tests on all of the key outputs for management (ERP Report, Figures 144-148) should be investigated.

These tests should cover:

- A more thorough investigation of reasonable bounds on predation mortality to evaluate the effect of low observed predation mortality on low EE
- Runs with menhaden B and P/B at different values (using bounds from BAM sensitivity runs), to evaluate the effect of high production on low EE
- Runs including a range of values for other predators in the ecosystem (current runs looked at only status quo F, while one could use target, threshold, or specified F based on catch limits on the books for future years)

In addition, the panel recommends testing of key ERP results to the static (Ecopath) model input parameters (B, P/B, Q/B) for predators of menhaden and other key groups. As noted under ToR 3, biomass (B) parameters based on stock assessments may change substantially between assessments;

therefore sensitivity of the Ecosim results to changes in these inputs over a historical range of assessments for key species should be evaluated. Second, alternative values for P/B and Q/B ratios based on empirical information or other methods should be evaluated to determine Ecosim sensitivity to these assumptions. Finally, uncertainty in input parameters can be characterized in an EwE "data pedigree" which ranks quality and relevance of B, P/B, Q/B, and diet composition (DC) information sources. Including this information on all static parameter sources (for NWACS-FULL and NWACS-MICE) will be useful in future reviews and for uncertainty analysis using multiple potential approaches (e.g., Chaalali *et al.*, 2015; Gaichas *et al.*, 2015; Guesnet *et al.*, 2015; Bentley *et al.*, 2019).

As noted earlier (ToR 4), notwithstanding this request for further analysis of the range over which the NWACS-MICE model can be considered robust and the caveat that the model is most suitable for examining small changes from status quo fisheries and stock sizes, the panel concludes that the NWACS-MICE model is suitable for use in exploring trade-offs in a management context.

e. Retrospective analysis

Retrospective analysis is most relevant is the multispecies SCAA model VADER, and a retrospective analysis was presented for this model. The retrospective was short, only a three-year peel. This was limited by the three-year block used for averaging the prey preferences over a three-year period. This would not prevent a longer peel, but one would expect a discontinuity every three years as the peel extended to a different three-year block of diet preferences. Within the three-year period, the model was stable,

Some retrospective analyses were also conducted for the production models. Here removal of up to four years of data from the end of the time series had little effect on model performance. This is as expected, since there is little contrast in the CPUE data at the end of the time series. In contrast, the outputs of the surplus production models were strongly influenced by the start time of the model. Again, this is not surprising given that the greatest contrast is in the early years. A research recommendation would be to conduct a retrospective-style analysis at the start of the surplus production models to identify which years had the greatest impact on model performance.

Bentley, J. W., Hines, D., Borrett, S., Serpetti, N., Fox, C., Reid, D. G., and Heymans, J. J. 2019. Diet uncertainty analysis strengthens model-derived indicators of food web structure and function. Ecological Indicators, 98: 239–250.

Chaalali, A., Saint-Béat, B., Lassalle, G., Le Loc'h, F., Tecchio, S., Safi, G., Savenkoff, C., *et al.* 2015. A new modeling approach to define marine ecosystems food-web status with uncertainty assessment. Progress in Oceanography, 135: 37–47.

Gaichas, S., Aydin, K., and Francis, R. C. 2015. Wasp waist or beer belly? Modeling food web structure and energetic control in Alaskan marine ecosystems, with implications for fishing and environmental forcing. Progress in Oceanography, 138, Part A: 1–17.

Guesnet, V., Lassalle, G., Chaalali, A., Kearney, K., Saint-Béat, B., Karimi, B., Grami, B., Tecchio, S., Niquil, N., Lobry, J., 2015. Incorporating food-web parameter uncertainty into Ecopath-derived ecological network indicators. Ecol. Model. 313 (29–40), 03043800. https://doi.org/10.1016/j.ecolmodel.2015.05.036.

ToR 6. Evaluate the methods used to characterize uncertainty in estimated parameters. Ensure that the implications of uncertainty in technical conclusions are clearly stated.

For the ERP models, less formal attention was given to characterizing uncertainty in estimated parameters. In a sense, the consideration of multiple models constitutes an approach to accounting for structural (model) uncertainty. The model comparisons presented in the ERP report generally suggested qualitative alignment among comparable simulations across models, particularly when the models were adjusted for scaling differences in relevant parameters. However, as noted in the ERP report, this alignment is not surprising given the common datasets used to inform the various models. When alternative time series (e.g., PRFC index) were used to inform the models the outcomes were quite different, but the panel interpreted this is evidence of the unsuitability of this local index for informing a regional model.

Other aspects of uncertainty were addressed in sensitivity analyses, and are discussed elsewhere in this report (e.g, impacts of alternative vulnerability parameters in the NWACS MICE model). Overall the panel felt the level of uncertainty analysis was appropriate for this stage of ERP model development and application. However, we offer a couple of recommendations for future uncertainty analyses:

- If development of the VADER model continues and is considered informative for management advice, examination of the uncertainty/sensitivity related to the magnitude of M0 and its potential interaction with assumptions about the "other food" biomass pool (fixed versus variable, relative to size of explicit prey pools) would be desirable
- Examination of the influence of uncertainty about the distributions of base parameters for the NWACS-MICE model would increase confidence in the results of trade-off analyses among species reference points and management strategies

ToR 7. Minority report.

There was no minority report.

ToR 8. Recommend best estimates of stock biomass, abundance, exploitation, and stock status of Atlantic menhaden from the assessment for use in management, if possible, or specify alternative estimation methods.

At this stage in the development of multispecies models, the panel recommends using the stock biomass, abundance, exploitation and stock status estimates from the base run of the BAM model for use in management, as per ToR 6 for the single species review.

ToR 9. Review the research, data collection, and assessment methodology recommendations provided by the TC and make any additional recommendations warranted. Clearly prioritize the activities needed to inform and maintain the current assessment, and provide recommendations to improve the reliability of future assessments.

The report included a number of recommendations for future research, data collection, modelling and management, for both the short and long term. These included expanding collection of diet and condition data, to include non-finfish predators and data-poor prey species, to conduct management-strategy evaluation (MSE) to identify harvest strategies that will meet ecosystem management objectives, and to continue the development of the NWACS-MICE, NWACS-FULL and VADER models.

The panel fully supported these recommendations. A number of additional specific recommendations for research on the ERP models and assessment methods to inform these models are presented earlier in this report in the context of other ToRs.

We recognized the potential strategic importance of conducting an MSE and noted the benefit of having already completed an Ecosystem Management Objectives Workshop to identify fundamental ecosystem management objectives for Atlantic menhaden. An MSE could be used to examine alternative scenarios to ensure the management advice is robust and to fully explore tradeoffs among alternative management strategies. However, as noted under ToR 8 for the single species review, it will be important to plan an MSE process carefully, to avoid progress on management being impeded by a process that could take several years and require a large commitment of resources.

ToR 9. Recommend timing of the next benchmark assessment and updates, if necessary, relative to the life history and current management of the species.

The SAS recommended continuing the timing of benchmark assessments and updates for the single species assessment, with an update in 3 years and the next benchmark in 6 years. The panel supports this recommendation. The single species assessment model is "mature" and does not appear to require any substantial modifications that would warrant a benchmark sooner than 2025. Given the relatively short lifespan of Atlantic menhaden, and the unpredictability of future recruitment trends, it does not seem appropriate to extend the time between benchmarks beyond 6 years. Even if recommendations from this review regarding fishery-independent assessment of larger, older menhaden are successfully addressed soon, it will take several years for a new index time series to be highly informative in the assessment model.

The panel notes, however, that with movement towards ecosystem-based reference points for Atlantic menhaden and consequently linkages between management strategies for several species of ASMFC concern, there will be large benefits in the future for synchronization of assessment updates and benchmarks among the key species in the models that inform ecosystem-based reference points. This may have implications for the timing of future Atlantic menhaden assessment updates.

2.3 Summary Results of Analytical Requests

During the ERP assessment review, the panel requested an additional sensitivity run for the NWACS MICE model, which was completed and reviewed during the workshop (see ToR 5):

- Adjust the diet proportions for predators on menhaden to increase EE values, but only to plausible levels given the limited suite of predators included in this reduced model
- Then run simulations to reproduce the plots of striped bass biomass levels associated with different combinations of harvest policies for striped bass and menhaden, and compare these to the base run plots.

2.4 Public Comments

The panel reviewed comments provided by the public and considered them during their deliberations. The panel appreciated the public interest and transparency in the process.

Appendices to the 2019 Atlantic Menhaden Ecological Reference Point Stock Assessment Report

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Appendix 1: Surplus Production Model with Time-Varying *r* (SPMTVr) Working Paper

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ARTICLE

A performance evaluation of surplus production models with time-varying intrinsic growth in dynamic ecosystems

Geneviève M. Nesslage and Michael J. Wilberg

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Abstract: We conducted a simulation study to evaluate performance of surplus production models (SPMs) with a time-varying intrinsic growth rate (SPMTVr) for stocks with predation-driven changes in productivity. Data sets were simulated using an age-structured, linked, predator–prey model of Atlantic menhaden (*Brevoortia tyrannus*), a forage fish native to the Northwest Atlantic, and Atlantic striped bass (*Morone saxatilis*), its primary predator, with differing time series of fishing mortality on both predator and prey. Simulations generated test data sets for Atlantic menhaden SPMs that included either a static or time-varying intrinsic growth rate parameter. The SPMTVr largely produced more accurate, less variable estimates of exploitation rate and biomass than models with static intrinsic growth. We also applied SPMTVr to empirical Atlantic menhaden catch and survey data for 1964–2016. The SPMTVr fit the survey data well, estimated an intrinsic growth rate time series that mirrored long-term juvenile survey trends, and produced biomass and exploitation rate trends that mirrored a statistical catch-at-age model. The SPMTVr estimated dynamic, maximum sustainable yield (MSY)-based reference points that reflected changing stock productivity.

Résumé : Nous avons effectué une étude de simulation afin d'évaluer la performance de modèles de production excédentaire (SPM) intégrant un taux de croissance intrinsèque variable dans le temps (SPMTVr) pour des stocks présentant des changements de la production modulés par la prédation. Des ensembles de données ont été simulés en utilisant un modèle de prédateur-proie relié structuré par âge de l'alose tyran (*Brevoortia tyrannus*), un poisson-fourrage natif de l'Atlantique Nord-Ouest, et du bar d'Amérique (*Morone saxatilis*), son principal prédateur, avec différentes séries chronologiques de mortalité par pêche tant pour le prédateur que pour la proie. Les simulations ont produit des ensembles de données expérimentaux pour des SPM pour l'alose tyran qui comprenaient un paramètre de taux de croissance intrinsèque soit statique ou variable dans le temps. Les SPMTVr produisent généralement des estimations plus exactes et moins variables des taux d'exploitation et de la biomasse que les modèles à croissance intrinsèque statique. Nous avons aussi appliqué des SPMTVr à des données empiriques de prises et d'évaluation pour l'alose tyran pour la période de 1964 à 2016. Les SPMTVr collent bien aux données d'évaluation, permettent d'estimer une série chronologique de croissance intrinsèque qui concorde avec les tendances à long terme pour les juvéniles découlant d'évaluations et produisent des tendances de la biomasse et des taux d'exploitation qui concordent avec un modèle statistique des prises selon l'âge. Les SPMTVr estiment des points de référence dynamiques basés sur le rendement équilibré maximal (RSM) qui reflètent l'évolution de la productivité des stocks. [Traduit par la Rédaction]

Introduction

The dynamic nature of complex ecosystems provides serious challenges to fisheries stock assessment and management (Thorson et al. 2015; Collie et al. 2016; Tommasi et al. 2017*a*). Shifts in stock productivity driven by environmental fluctuations, climate change, and fishing have been observed for many fish stocks (Hollowed et al. 2013; Petitgas et al. 2013; Hare et al. 2016; Tommasi et al. 2017*a*). In some circumstances, incorporation of well-characterized ecosystem processes into assessment models can improve hindcasts and forecasts as well as the estimation of biomass reference points and selection of appropriate harvest control rules (Maunder and Watters 2003; Haltuch et al. 2009; Haltuch and Punt 2011; Lee et al. 2018; Tommasi et al. 2017*b*). However, accuracy of assessments and resulting management advice can be greatly reduced if the relationship between ecosystem drivers and population processes is incorrectly specified, changes unexpectedly over time, or coincides with fishery-driven stock trends (De Oliveira et al. 2005; Haltuch and Punt 2011; Deroba and Schueller 2013; Punt et al. 2014; Lee et al. 2018). Also, data available for most stocks are inadequate to parameterize models that explicitly incorporate ecosystem drivers (Punt et al. 2016). Reliable models of intermediate complexity that account for ecosystem effects without requiring extensive data collection or complicated model building are needed (Plagányi et al. 2014; Angelini et al. 2016; Punt et al. 2016; Tulloch et al. 2018).

An alternative to explicit incorporation of ecosystem processes in stock assessments is the use of single-species models that implicitly estimate changes with time-varying parameters. Age- and length-structured stock assessments often implicitly account for anthropogenic and environmental effects on stock dynamics through the estimation of time-varying parameters such as natural mortality, growth, selectivity, and catchability (Fu and Quinn 2000; Wilberg et al. 2009, 2011; Methot and Wetzel 2013; Nielsen and Berg 2014; Xu et al. 2019). In situations with less data, the use of surplus production models (SPMs) with time-varying parameters may provide an alternative to explicit modeling of ecosystem drivers (Nesslage and Wilberg 2012). Using only a time series of

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catch and at least one index of abundance, SPMs estimate stock biomass, carrying capacity, and the population's intrinsic growth rate (Prager 1994). The intrinsic growth rate of the population encompasses the growth response of the stock to its surrounding ecosystem, including mortality processes such as predation and recruitment processes affected by environmental conditions. If allowed to vary over time, SPM parameters may implicitly capture the effects of shifting drivers on fish stocks without having to explicitly model the underlying mechanisms, especially when time series are of sufficient length to cover periods of major anthropogenic or environmental change are available. However, the use of time-varying parameters in surplus production models has not been tested in single-species situations where stock dynamics are driven by predation that results in complex age-structured dynamics.

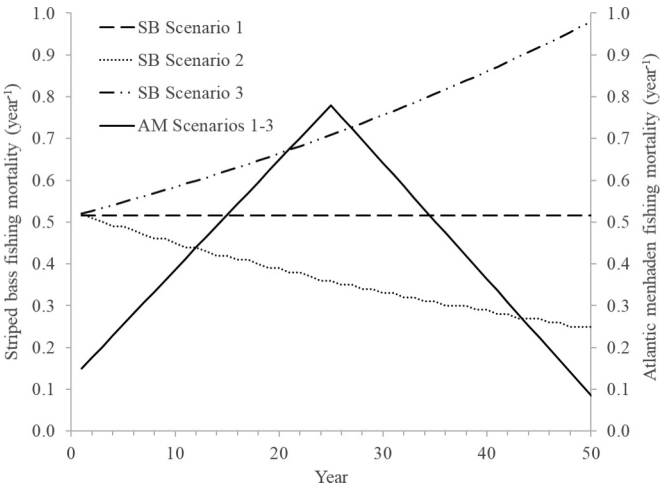
The goal of our study was to evaluate the performance of SPMs with time-varying intrinsic growth in situations where recruitment, fishing mortality, and age-structured predation mortality on a stock were dynamic. Our objectives were to (*i*) test the ability of age-aggregated SPMs to accurately characterize stock dynamics using data generated by an age-structured, linked predator–prey simulation model; (*ii*) examine the relative performance of SPMs with and without a time-varying intrinsic growth parameter in their ability to estimate metrics critical for fisheries management, namely fishery exploitation rate and biomass; and (*iii*) implement a case study in which an SPM with time-varying intrinsic growth is applied to a real fish stock and status is determined using dynamic maximum sustainable yield (MSY)-based reference points.

For our case study, we chose Atlantic menhaden (*Brevoortia tyrannus*), a forage fish native to the Northwest Atlantic that supports the largest US east coast fishery by weight and that has exhibited wide fluctuations in stock dynamics across six decades of population monitoring (SEDAR 2015; ASMFC 2017). Atlantic menhaden are a good candidate for testing the performance of SPMs with time-varying parameters given the stock exhibits complicated age-structured population dynamics (Schueller and Williams 2017), fluctuations in recruitment success linked to climate drivers (Buchheister et al. 2016), and top-down, age-specific predation mortality that has changed over time in response to predator trends and predator field composition (Garrison et al. 2010). Our performance evaluation outlines the potential implications to assessment and management of modeling complex stock dynamics using SPMs with and without time-varying parameters.

Methods

We conducted a simulation study to evaluate the performance of SPMs in complex, dynamic ecosystems. The age-structured, linked, predator–prey dynamics of Atlantic menhaden and Atlantic striped bass (*Morone saxatilis*) were simulated over 50 years for three scenarios that differed in time series of age-specific fishing mortality on both predator and prey. Simulations were used to generate input data sets for SPM estimation models that included either a static or a time-varying intrinsic growth rate parameter. Estimation model accuracy and relative performance were evaluated using quantities important for Atlantic menhaden management, namely biomass of Atlantic menhaden and exploitation rates of the Atlantic menhaden fishery. We concluded with a case study in which an SPM with time-varying intrinsic growth was applied to Atlantic menhaden data. All modeling was conducted in AD Model Builder (Fournier et al. 2012).

Fig. 1. Trends in striped bass (SB) and Atlantic menhaden (AM) fishing mortality used to simulate SB and AM dynamics for Scenarios 1–3.



Simulation study

Simulation model

We generated complex, age-structured predator–prey dynamics for ages 0–6+ Atlantic menhaden and ages 1–13+ striped bass using life history and fishery parameters that mirrored recent stock assessment inputs (NEFSC 2013; SEDAR 2017) and relevant diet literature as closely as possible. Both predator and prey dynamics were driven by stochastic Beverton–Holt stock–recruitment processes and trends in age-specific fishing mortality. Additionally, striped bass weight-at-age was influenced by size-specific availability of Atlantic menhaden and other prey that varied over time. Atlantic menhaden dynamics were influenced by age-specific predation mortality that varied over time in response to age-specific consumption by striped bass. A detailed description of the simulation model can be found in the online Supplementary material[1].

Three scenarios with differing trends in striped bass fishing mortality were used to generate complex predator–prey dynamics (Fig. 1). In Scenario 1, striped bass fishing mortality was held constant over time. In Scenario 2, striped bass fishing mortality decreased linearly across the time series, whereas striped bass fishing mortality increased linearly across the time series in Scenario 3. In all 3 scenarios, a trend in fishing mortality on Atlantic menhaden was assumed to guarantee some contrast in Atlantic menhaden biomass and help avoid the generation of unidirectional trends in biomass (i.e., one-way trips) that would prevent independent estimation of intrinsic growth rate and carrying capacity parameters (Hilborn and Walters 1992). In all scenarios, fishing mortality on Atlantic menhaden increased across the first half of the time series, then declined across the second half of the time series. For each of the three scenarios, 1000 simulated data sets were generated to test the performance evaluation of SPMs. Data sets included (*i*) simulated time series of total annual Atlantic menhaden biomass and annual fishery exploitation rate, (*ii*) simulated total annual catch of Atlantic menhaden by the fishery, and (*iii*) an annual (50-year) index of biomass (I) generated from each simulated trend in Atlantic menhaden biomass such that

$$I_t = (qB_t)e^{\varepsilon_t} \quad (1)$$

where q was the survey catchability, and ε_t were observation errors drawn from a normal distribution with a mean of zero and a

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0292.

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standard deviation (SD) of 0.4. Additional simulations with smaller (SD = 0.2) and larger (SD = 0.8) observation errors were conducted to explore the effect of observation error variance on model performance. A time-invariant value of q = 0.005 was assumed across all simulations.

Estimation models

SPMs with and without time-varying intrinsic growth rates (SPMTVr) were fitted to simulated Atlantic menhaden catch and an index of Atlantic menhaden biomass to generate annual estimates of fishery exploitation rate and total Atlantic menhaden biomass. A common form of surplus production model (hereinafter referred to as a "simple SPM") uses a Schaefer SPM with observation error (Polacheck et al. 1993; Quinn and Deriso 1999), which follows a logistic population growth process:

$$\hat{B}_{t+1} = \hat{B}_t + \hat{r}\hat{B}_t\left(1 - \frac{\hat{B}_t}{\hat{K}}\right) - C_t \quad (2)$$

such that $\hat{B}_t$ is estimated Atlantic menhaden biomass at time t, $\hat{r}$ is intrinsic population growth rate, $\hat{K}$ is carrying capacity, and C_t is catch at time t. Our simple SPMs assumed no change in intrinsic population growth over time and estimated one growth rate parameter, $\hat{r}$, across the time series. The SPMTVr used eq. 2 with one modification; the intrinsic growth $\hat{r}_t$ was estimated annually according to a random walk on the log scale:

$$\log_e \hat{r}_{t+1} = \log_e \hat{r}_t + \omega_t \quad (3)$$

with annual deviations, ω_t, from a normal distribution with a mean of zero and an SD of 0.15. A random walk was selected to generate annual deviations in r because random walk estimation processes have been shown to perform well under a variety of circumstances with trends over time, whereas other forms of annual deviations such as white noise are limited in their application (Wilberg and Bence 2006). An SD of 0.15 was chosen based on previous research in the use of random walk processes (Wilberg and Bence 2006; Nesslage and Wilberg 2012); however, model performance with random walk SDs of 0.05 and 0.25 were explored as well.

For both models, the estimated index of biomass, $\hat{I}_t$, was the product of catchability and biomass:

$$\hat{I}_t = \hat{q}\hat{B}_t \quad (4)$$

where $\hat{q}$ was survey catchability. Total catch was assumed known without error. We obtained parameter estimates by minimizing the concentrated negative log likelihood function:

$$-\mathrm{LL}_1 = \frac{n}{2}\log_e\left\{\sum\left[\log_e(I_t) - \log_e(\hat{I}_t)\right]^2\right\} \quad (5)$$

Multiplicative lognormal observation errors were assumed for the index of biomass. A normal (on the $\log_e$ scale) prior, $-\mathrm{LL}_2$, was included:

$$-\mathrm{LL}_2 = 0.5\left[\frac{\log_e(B_{t=1}) - \log_e(\mathrm{prior})}{\mathrm{SD}}\right]^2 \quad (6)$$

such that $\hat{B}_{t=1}$ was the estimated biomass in the first year, prior was the prior point estimate, and SD was the standard deviation of the lognormal prior distribution. The SPMTVr included an additional term, $-\mathrm{LL}_3$:

$$-\mathrm{LL}_3 = \frac{1}{2\sigma^2}\sum \omega_t^2 \quad (7)$$

to account for the annual random walk deviations, such that annual deviations were normally distributed with a mean of zero and a known variance.

The large number of simulations conducted prevented us from closely examining the diagnostics of each model individually. Therefore, we provided each SPM with some information about the appropriate starting values as described below, but allowed estimates to deviate from those values as the estimation procedure progressed within wide bounds. The starting value for parameter $\hat{K}$ was set at approximately ten times the maximum simulated catch, and the starting value for catchability was set equal to the simulated value of 0.005. The starting value for the intrinsic growth rate was set to 0.4. Biomass in the first year was estimated assuming a prior with mean equal to the logarithm of the simulated initial biomass and an SD of 0.15.

Performance of each estimation model was evaluated using quantities important to management, namely annual estimates of exploitation rate ($\hat{U}$) and total biomass ($\hat{B}$). These two quantities were deemed important because $\hat{U}$ relative to $\widehat{U_{\mathrm{MSY}}}$ determines the overfishing status and $\hat{B}$ relative to $\widehat{B_{\mathrm{MSY}}}$ determines overfished status when SPMs are used to provide fishery management advice in many fisheries. We quantified estimation model performance by calculating the percent relative error of estimates for each year:

$$\mathrm{RE}_t = \frac{\mathrm{estimated}_t - \mathrm{true}_t}{\mathrm{true}_t} \times 100 \quad (8)$$

in both exploitation rate and total biomass. The number of estimation model runs for each model that did not converge (maximum gradient component ≥ 0.0001) were counted, but the results from these runs were not included in relative error calculations. Root mean square relative errors (RMSRE) in terminal year estimates of biomass and exploitation rate

$$\mathrm{RMSRE}_i = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(\frac{\mathrm{estimated}_i - \mathrm{simulated}_i}{\mathrm{simulated}_i}\right)^2} \quad (9)$$

were calculated such that n was the total number of i estimates of either biomass or exploitation rate for all converged model runs. RMSRE allows for comparison of the magnitude of errors across simulations and between biomass and exploitation rate estimates. We also calculated mean relative error

$$\mathrm{MRE}_i = \frac{1}{n}\sum_{i=1}^{n}\frac{\mathrm{estimated}_i - \mathrm{simulated}_i}{\mathrm{simulated}_i} \quad (10)$$

to assess bias; MRE = 0 indicated estimation model results were unbiased relative to simulated data.

Case study — Atlantic menhaden

We constructed both a simple SPM and an SPMTVr for Atlantic menhaden using data available from the most recent assessments (SEDAR 2015; ASMFC 2017). Data inputs included total landings from three fleets (×1000 t) during 1964–2016 (Fig. 2) and three adult indices of abundance: (*i*) a fishery-dependent catch per unit effort index generated from Potomac River Fisheries Commission data collected near the center of species' range and spanning 1964–2012 (PRFC; SEDAR 2015); (*ii*) a composite adult index of multiple surveys from the northern portion of the range spanning 1980–

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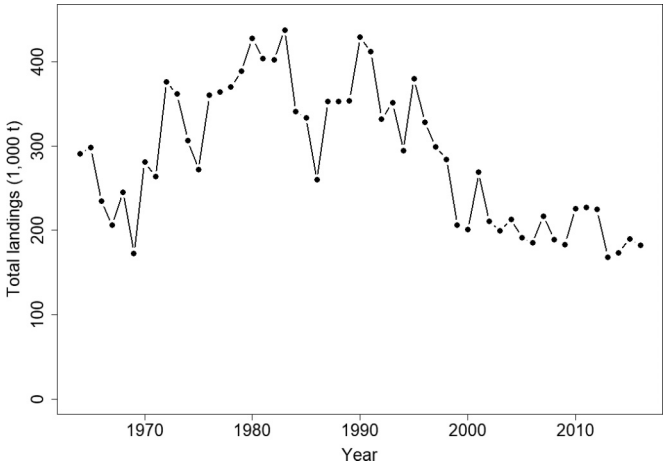
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Table 1. Estimated parameters, starting values, bounds, parameter estimates, and coefficient of variation (CV) for the case study implementation of a surplus production model with a time-varying intrinsic growth rate parameter (SPMTVr) and a simple surplus production model (SPM) for Atlantic menhaden.

Parameter	Description	Starting value	Lower, upper bounds	SPMTVr estimate	SPMTVr CV	SPM estimate	SPM CV
r_{1964}	Intrinsic growth rate (1964)	0.4	0.0001, 1.1	0.36	0.17	0.36	0.15
K	Carrying capacity (1000 t)	4378	1000, 10 000	3095	0.03	4344	0.02
B_{1964}	Initial biomass (1000 t)	1118	200, 3000	775	0.02	1112	0.02
q_{PRFC}	Catchability (PRFC index)	0.001	1×10e^{-8}, 0.005	0.0013	0.03	0.0009	0.03
q_{NAD}	Catchability (NAD index)	0.001	1×10e^{-8}, 0.005	0.0005	0.03	0.0009	0.03
q_{SAD}	Catchability (SAD index)	0.001	1×10e^{-8}, 0.005	0.0005	0.03	0.0009	0.03

Note: PRFC, Potomac River Fisheries Commission; NAD, northern adult fishery-independent; SAD, southern adult fishery-independent.

Fig. 2. Total landings of Atlantic menhaden (×1000 t), 1964–2016.



2016 (NAD; ASMFC 2017); and (*iii*) a composite adult index of multiple surveys from the southern portion of the range spanning 1990–2016 (SAD; ASMFC 2017).

We estimated intrinsic population growth rate in 1964 and annual deviations from that rate in each subsequent year. Other estimated parameters included catchability of each of the three indices of abundance, initial biomass, and carrying capacity. All estimated parameters were bounded (Table 1). Estimates of mean fishing mortality across the species' range (F = 0.55year^{-1}) and natural mortality (M = 1.18year^{-1}) generated from an historical tagging study conducted in the late 1960s (Liljestrand et al. 2019) were used along with a reported catch of 290 700 t in 1964 (ASMFC 2017) to estimate a starting value for initial biomass of 1 118 000 t. In addition, we placed a normal prior on the logarithm of initial biomass with a mean equal to our estimate of biomass in 1964 and a SD of 0.15. The starting value for the PRFC index coefficient of variation (CV) was assumed to be 0.5. For fishery-independent indices, CVs were assumed to be the time series average CV for the NAD (CV = 0.43) and SAD (CV = 0.52). Log-scale SDs for each index were adjusted iteratively to determine the final weights applied to each index (Francis 2011).

To demonstrate the potential use of SPMs with time-varying reference points in management, we generated example MSY-based reference points. For both the SPM and SPMTVr, we defined biomass at 50% of B_{MSY} (calculated as $K/2$) as a potential overfished threshold for Atlantic menhaden given its common use in US federal fisheries management. The exploitation rate reference point generated by the simple SPM was calculated as 75% of the terminal year U_{MSY} estimate (calculated as $r_{2016}/2$). We selected 75% of U_{MSY} given it has been suggested as a general overfishing limit for forage species (Pikitch et al. 2012). For the SPMTVr, a dynamic overfishing threshold was produced by calculating 75% of annual U_{MSY} estimates (calculated as $r_t/2$). Use of 75% of U_{MSY} in the terminal year as a reference point for management assumes that the r in the terminal year will continue.

Results

Simulation study

A complete set of model diagnostics are provided for the "base run" simulations in which SD of the distribution used to generate observation error around the index of abundance was 0.4 (Table 2; Figs. 3–5); RMSRE and MRE are reported for simulations with observation error SDs of 0.2 and 0.8 as well (Table 2). In general, SPMTVr converged less often than SPM. For example, estimation models confronted with base run simulations (Figs. 3–5) converged less often for SPMTVr (891, 865, 861 runs for Scenarios 1–3, respectively) compared with the simple SPM (975, 995, 969 runs for Scenarios 1–3, respectively).

SPMs with time-varying intrinsic growth rate (SPMTVr) outperformed simple SPMs under most conditions of dynamic, age-structured fishing and predation pressure. When presented with base run and more optimistic simulations (observation error SDs of 0.4 and 0.2), SPMTVr produced more accurate (i.e., lower RMSRE) and less biased (i.e., lower MRE) estimates of biomass and exploitation rate in the terminal year (Table 2) and across most of the time series (Figs. 3–5). When the observation error of the index of abundance was higher (SD = 0.8), relative performance of the two models depended on the scenario and the performance metric (Table 2). Neither model performed well, but SPMTVr generally outperformed the simple SPM, with the exception of slightly higher RMSRE for Scenario 1 estimates of exploitation rate and Scenario 3 estimates of exploitation rate; for Scenario 3, the magnitude of bias (MRE) in biomass estimates from the SPMTVr was also greater than the simple SPM.

Both models had difficulty estimating biomass and exploitation rate in the first 3–5 years as the age distribution changed rapidly from initial conditions in response to simulated fishing mortality. However, when presented with base run simulations, the SPMTVr tended to outperform the SPM across the remainder of the time series for all three scenarios. For Scenario 1, in which striped bass fishing mortality remained constant across the time series, the SPMTVr exhibited lower variability and less patterning in bias for estimates of both Atlantic menhaden biomass and exploitation rate than the simple SPM (Table 2; Fig. 3). Both SPMs tended to underestimate biomass and overestimate exploitation rate except the simple SPM during the middle of the time series when fishing mortality on Atlantic menhaden was transitioning from an increase to a decline (Fig. 1) during which the direction of bias switched. Despite the fact that predation mortality did not vary as much in this scenario as the other scenarios, variability in recruitment added some degree of nonstationarity that was accounted for better by SPMTVr than the by the simple SPM in terminal year estimates (Table 2). For Scenario 2 in which striped bass fishing mortality declined across the time series, the simple SPM exhibited high variability and substantial bias such that Atlantic menhaden biomass was overestimated and exploitation rate underestimated across most of the time series (Fig. 4). The SPMTVr was also biased

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Table 2. Root mean square relative error (RMSRE) and mean relative error (MRE) in terminal year biomass and exploitation rates produced by a traditional surplus production model (SPM) and an SPM with a time-varying intrinsic growth rate (SPMTVr) when presented with data sets simulated by an age-structured predator–prey model with constant (Scenario 1), decreasing (Scenario 2), and increasing (Scenario 3) fishing mortality on the predator.

		Exploitation rate				Biomass			
		RMSRE		MRE		RMSRE		MRE	
CV	Scenario	SPMTVr	SPM	SPMTVr	SPM	SPMTVr	SPM	SPMTVr	SPM
0.2	1	0.15	0.21	0.01	0.06	0.15	0.18	0.01	−0.03
	2	0.18	0.39	−0.09	−0.22	0.24	0.63	0.13	0.44
	3	0.17	0.31	0.08	0.22	0.14	0.23	−0.06	−0.15
0.4	1	0.22	0.24	0.04	0.06	0.21	0.23	0.003	−0.003
	2	0.25	0.36	−0.09	−0.27	0.35	0.67	0.18	0.50
	3	0.28	0.35	0.15	0.20	0.20	0.26	−0.09	−0.12
0.8	1	0.38	0.36	0.07	0.04	0.38	0.44	0.05	0.10
	2	0.36	0.41	−0.08	−0.28	0.54	0.87	0.24	0.60
	3	0.45	0.44	0.20	0.13	0.33	0.43	−0.08	0.03

Note: Simulations differed in the amount of error (CV) used to generate an index of abundance from simulated biomass.

in the same direction for both estimates across most of the time series but to a much lesser extent and with substantially lower variability. For Scenario 3 in which striped bass fishing mortality increased across the time series, the simple SPM exhibited greater variability and bias than SPMTVr (Fig. 5). After the first few years, SPM demonstrated an alternating pattern of overestimation followed by underestimation of Atlantic menhaden biomass and the reverse for exploitation rate. In contrast, the SPMTVr underestimated Atlantic menhaden biomass and overestimated exploitation rate across most of the time series but to a lesser extent than the simple SPM.

Case study — Atlantic menhaden

Given a time series of total landings and three indices of abundance (Fig. 6), both the SPMTVr and simple SPM converged on a stable solution and parameter estimates did not approach bounds (Table 1). However, the simple SPM did not deviate much from initial starting values and could not fit the indices of abundance well (Fig. 6). In contrast, the long-term PRFC fishery-dependent index of abundance was fit well by the SPMTVr (Fig. 6). Overall trends in the NAD and SAD fishery-independent indices of abundance were better fit by the SPMTVr than by the simple SPM, which overestimated most years in the time series. Final log-scale SDs for each index after iterative reweighting were 0.45 and 0.26 (PRFC), 0.65 and 0.62 (NAD), and 0.77 and 0.72 (SAD) for the simple SPM and SPMTVr, respectively.

The simple SPM produced a population intrinsic growth rate estimate of 0.36. The SPMTVr estimated a trend in the population intrinsic growth rate that ranged from 0.36 at the beginning of the time series to a peak of 0.82 in 1972 before returning to values in the range of 0.44 (Fig. 7). In both the simple SPM and SPMTVr models, estimated biomass increased in the 1960s, reached a peak in the late 1970s, remained stable (simple SPM) or declined (SPMTVr) through the late 1990s, then increased again through the end of the time series (Fig. 8). The simple SPM predicted relatively constant exploitation rate through the early 1990s, followed by a decline across the remainder of the time series (Fig. 9). In contrast, the SPMTVr estimated a decline in exploitation rate through the 1970s followed by a rise to a new peak in the mid-1990s and a subsequent decline.

Across most of the time series, production model estimates of Atlantic menhaden biomass and fishery exploitation rate were on the same scale as estimates produced by the statistical catch-at-age (SCAA) model used in management (Figs. 8–9; ASMFC 2017). SCAA biomass estimates were more closely correlated with that of the SPMTVr ($r_{[51]} = 0.69$, $p < 0.001$) than the simple SPM ($r_{[51]} = 0.38$, $p = 0.005$), largely because the simple SPM estimated consistently larger biomass across the time series and resulted in much higher terminal biomass than the SPMTVr or SCAA. With the exception of the decline in exploitation rate predicted by the SPMTVr in the 1970s and 1980s, all three models produced overall similar trends in exploitation rate (Fig. 9). SCAA biomass estimates were more closely correlated with that of the simple SPM ($r_{[51]} = 0.73$, $p < 0.001$) than the SPMTVr ($r_{[51]} = 0.58$, $p < 0.001$).

The simple SPM produced static biomass (50% of B_{MSY} = 1 061 000 t) and exploitation rate reference points (75% of U_{MSY} = 0.18year^{-1}). The SPMTVr produced a static biomass reference point (50% of B_{MSY} = 774 000 t) and a dynamic exploitation rate reference point (75% of annual U_{MSY}) that ranged from 0.13 to 0.31year^{-1}. The simple SPM results suggested that Atlantic menhaden have approached the biomass threshold but never exceeded it (Fig. 8). In contrast, the SPMTVr results suggested that Atlantic menhaden were overfished prior to 1971, but have remained above that reference point for the remainder of the time series; only in the late 1990s did biomass approach the threshold. The simple SPM results also suggested that the exploitation rate regularly exceeded 75% U_{MSY} prior to 1999 (Fig. 9). In contrast, the SPMTVr suggested the stock was not experiencing overfishing in the late 1970s during the period of higher estimated productivity (Figs. 7 and 9); in addition, the SPMTVr suggested that the stock has not experienced overfishing since 1998.

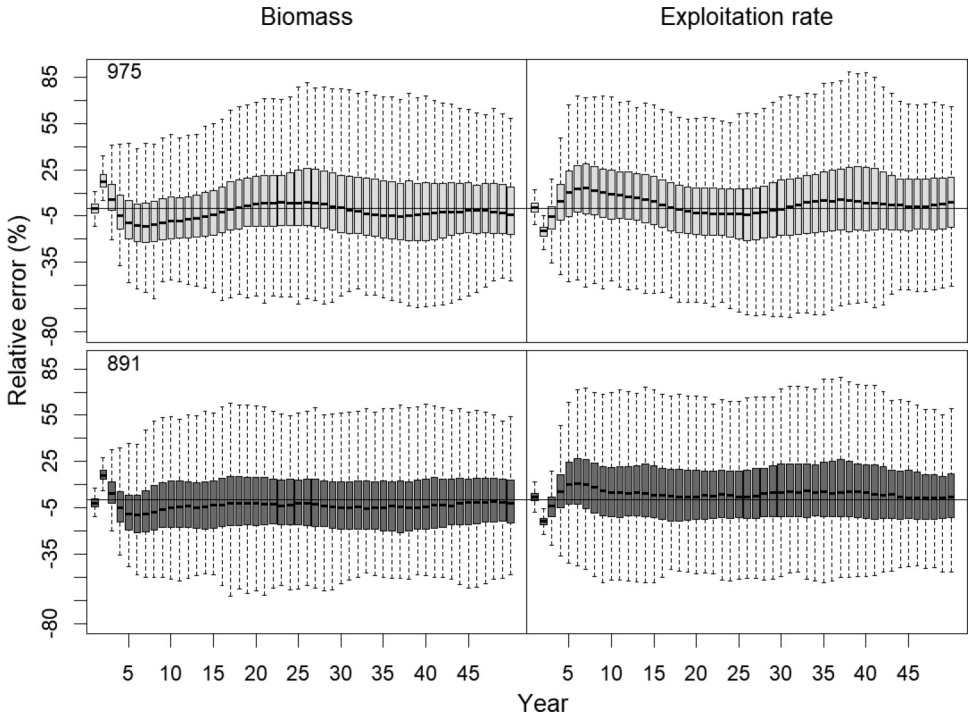
Discussion

Overall, SPMTVr performed well when presented with data generated by an age-structured predator–prey model in which both fishing and predation mortality changed over time, indicating that flexible production models can provide useful information about age-structured stocks that exhibit complex dynamics. Simple SPMs that assumed r did not vary over time generally produced less accurate estimates of biomass and exploitation rate and exhibited far more variability in those estimates than the SPMTVr. The SPMTVr approach allowed for estimation of biomass and exploitation rates under conditions of time-varying predation mortality without the need to explicitly incorporate predator trends and diet information. When applied to empirical data for Atlantic menhaden, the SPMTVr produced estimates on the same scale as an SCAA and estimated fluctuations in Atlantic menhaden productivity as the stock responded to anthropogenic and ecosystem change. In addition, the SPMTVr approach allowed for estimation of dynamic, MSY-based reference points that implicitly incorporated the stock's response to ecosystem change.

Simulation study

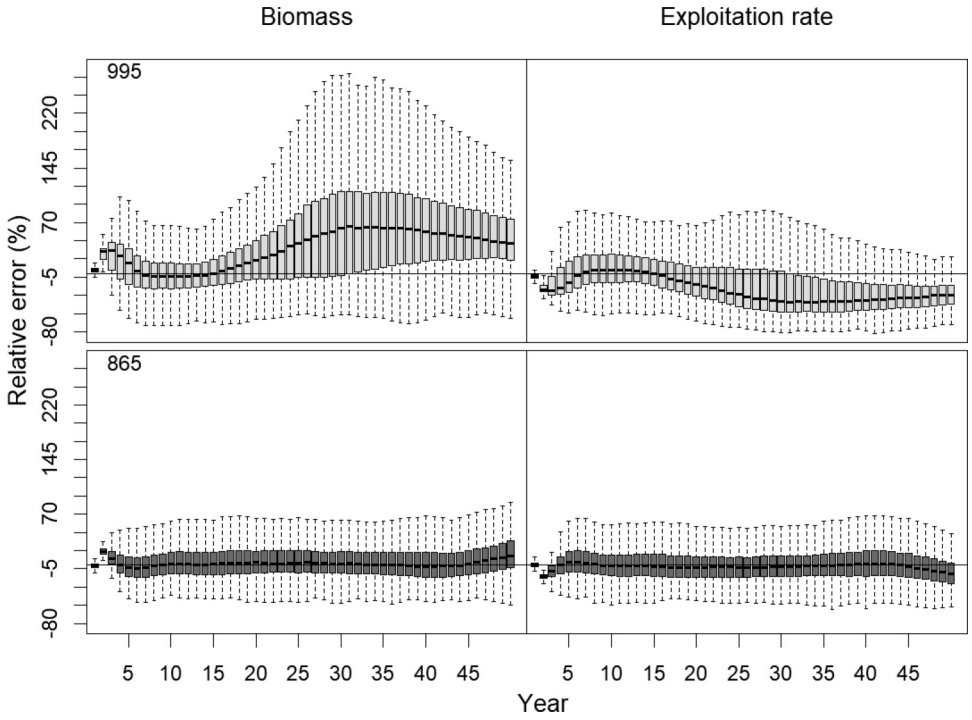
In most situations, the SPMTVr outperformed a simple SPM when presented with test data sets generated from a simulated population with complex, age-structured dynamics. SPM performance is

Fig. 3. Annual relative error in Atlantic menhaden biomass (left panels) and fishery exploitation rate (right panels) for a traditional surplus production model (SPM; top panels, light gray bars) and an SPM with time-varying intrinsic growth rate (bottom panels, dark gray bars) using data generated by simulation Scenario 1 (constant fishing mortality on the predator) and observation errors drawn from a normal distribution with a mean of zero and a standard deviation (SD) of 0.4. Boxes denote first and third quartiles, dark horizontal lines denote the median, and whiskers denote 1.5 times the interquartile range. Positive values of relative error indicate overestimation, and negative values indicate underestimation. Numbers in the upper left corner of left panels represent the number of runs (out of 1000 per scenario per model) that met the convergence criteria and were included in relative error calculations.



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Fig. 4. Annual relative error in Atlantic menhaden biomass (left panels) and fishery exploitation rate (right panels) for a traditional surplus production model (SPM; top panels, light gray bars) and an SPM with time-varying intrinsic growth rate (bottom panels, dark gray bars) using data generated by simulation Scenario 2 (decreasing fishing mortality on the predator) and observation errors drawn from a normal distribution with a mean of zero and an SD of 0.4. Boxplot interpretation as in Fig. 3.



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Fig. 5. Annual relative error in Atlantic menhaden biomass (left panels) and fishery exploitation rate (right panels) for a traditional surplus production model (SPM; top panels, light gray bars) and an SPM with time-varying intrinsic growth rate (bottom panels, dark gray bars) using data generated by simulation Scenario 3 (increasing fishing mortality rate on the predator) and observation errors drawn from a normal distribution with a mean of zero and an SD of 0.4. Boxplot interpretation as in Fig. 3.

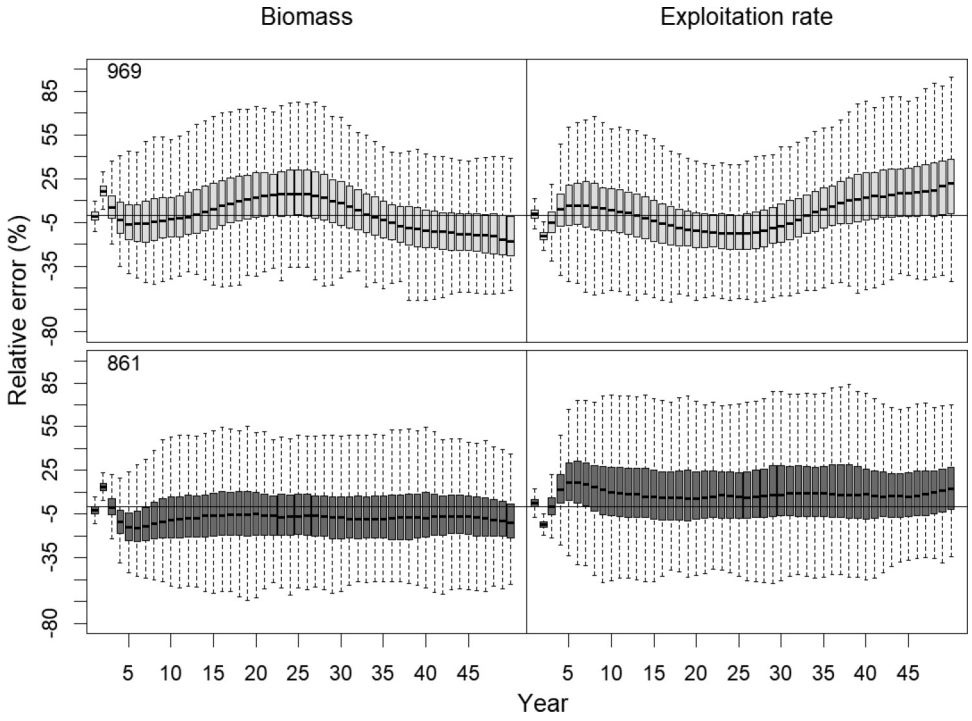
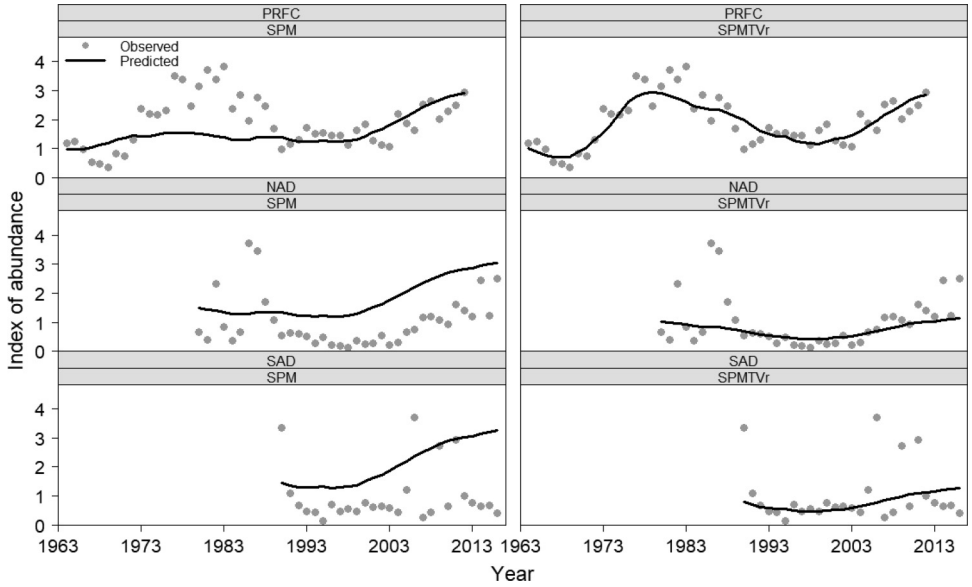


Fig. 6. Observed and predicted indices of abundance for Atlantic menhaden case study application of a simple surplus production model (SPM) and a surplus production model with a time-varying intrinsic growth rate (SPMTVr). PRFC is the index generated by Potomac River Fisheries Commission catch per unit effort data, NAD is the northern adult fishery-independent index, and SAD is the southern adult fishery-independent index.



often tested using data generated from a logistic growth model to match the underlying assumption of the SPM estimation model (Mohn 1980; Uhler 1980; Cadrin 2000; Nesslage and Wilberg 2012; Nakayama et al. 2017); however, several studies have tested SPM performance using age-structured, single-species simulation models and found that simple SPMs can reliably quantify age-structured stock dynamics in many circumstances if there is sufficient contrast in the data, little systematic error in catch and index data, and processes affecting catchability are not time-varying (Hilborn 1979; Punt 1988; Prager et al. 1996; Breen and Kendrick 1998; Prager and Goodyear 2001). Our performance evaluation demonstrated that when catch is known and observation error in indices of abundance are moderate and unbiased, SPMTVr can estimate biomass and exploitation rate reasonably well even if the underlying age-structured population dynamics are influenced by trends in predator-driven natural mortality.

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Fig. 7. Estimated trend in population intrinsic growth rate (*r*) for Atlantic menhaden generated by a surplus production model with a time-varying intrinsic growth rate.

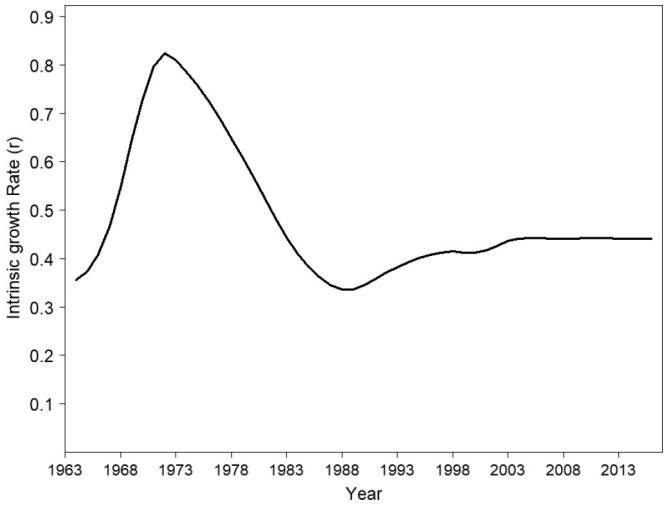
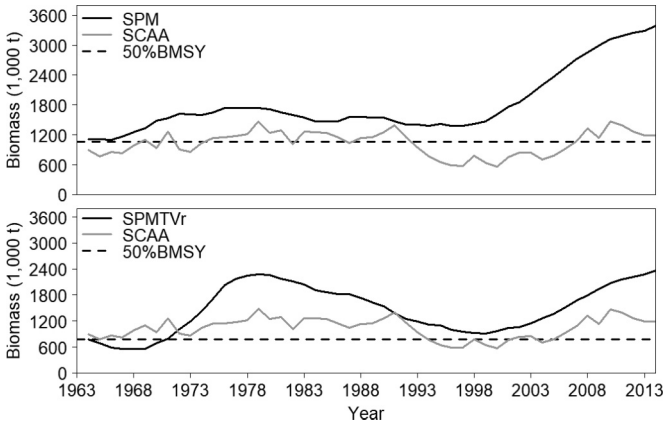
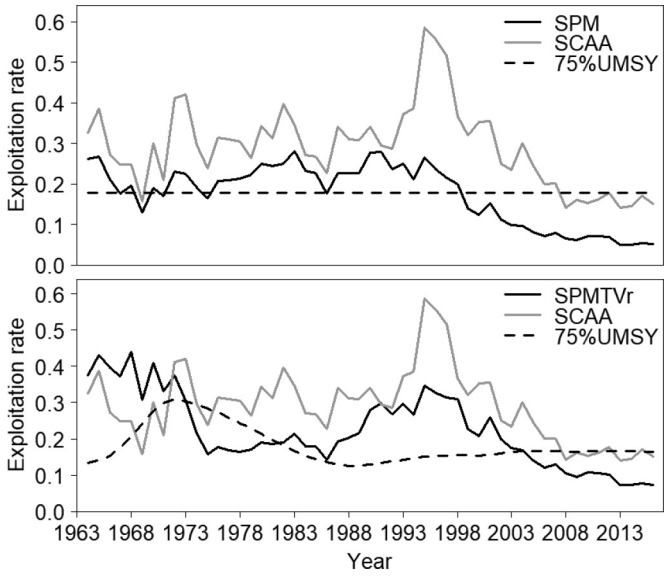


Fig. 8. Trend in total biomass estimated by a simple surplus production model (SPM), a surplus production model with a time-varying intrinsic growth rate (SPMTVr), and the statistical catch-at-age model used in Atlantic menhaden management (SCAA) relative to an overfished threshold of 50%B_{MSY} generated from each production model.



A strength of the SPMTVr approach is implicit estimation of unknown or poorly characterized drivers of stock productivity. Although improved SPM fit can be achieved with explicit incorporation of environmental drivers (Wang et al. 2016, 2018), model performance relative to true conditions is unknown. Even when the mechanism underlying environmental drivers of certain aspects of stock dynamics (e.g., recruitment, natural mortality) are well described, the overall combined effects of these drivers may be confounded with trends in fishing mortality. For example, explicit incorporation of low frequency recruitment drivers has been shown to result in less accurate stock assessments when fishery-driven stock declines happen to coincide with environmentally driven declines in recruitment (Haltuch et al. 2009; Haltuch and Punt 2011). In our study, we implicitly estimated the impact of unspecified environmental drivers by assuming a small SD in annual *r* deviations, which allowed intrinsic growth rate of the population to vary gradually over time in response to gradual shifts in predation pressure. Our approach is similar to a state-space modeling approach (Montenegro and Branco 2016; Miller and Hyun 2018; Pedersen and Berg 2017; Thorson and Cope 2017; Winker et al. 2017*a*, 2017*b*) except that the intrinsic rate of increase parameters are not treated as random effects. Previous authors have demonstrated how implicit incorporation of time-varying processes or state-space approaches in SPMs can improve model performance (Fréon 1988; Prager 1994; Punt 2003). For example, Nakayama et al. (2017) used a modified SPM with an annually time-varying parameter for accessibility that allowed the proportion of the population observed to vary over time and found the model generated nearly unbiased reference point estimates when a sufficiently long time series of data was available. Our study adds to this body of research by demonstrating how allowing the intrinsic growth parameter to vary over time in an SPM can capture the dynamics of a stock that is subject to complex, age-structured trends in fishing and natural mortality.

Fig. 9. Trend in fishery exploitation rate estimated by a simple surplus production model (SPM), a surplus production model with a time-varying intrinsic growth rate (SPMTVr), and the statistical catch-at-age model used in Atlantic menhaden management (SCAA) relative to an overfishing threshold of 75% of the exploitation rate for maximum sustainable yield (U_{MSY}) generated from each production model.



The incorporation of time-varying parameters in an SPM can be a powerful tool, but the decision of when and how to allow model parameters to vary over time should be thoughtful and justified. Szuwalski et al. (2018) simulated time-varying processes such as selectivity, natural mortality, and growth in an age- and length-structured population model and then tested the impact of allowing different parameters to vary over time. Although the incorporation of time-varying parameters generally decreased the magnitude of the retrospective pattern, resulting reference points sometimes produced highly erroneous values when a process other than the true time-varying process was allowed to vary. In our simulation study, age-aggregated SPMs with time-varying parameters generally outperformed models without time-varying parameters in the estimation of biomass and mortality when true fishing and natural mortality varied over time. However, we could not evaluate the ability of the SPMTVr to produce accurate reference points because our simulations were age-structured and numerous process varied over time such that the "true" values of *r* and *K* (and thus MSY and B_{MSY}) were not tractable. Given this uncertainty in model performance, analysts faced with a data-poor situation must ultimately make an expert judgement call as to whether the potential error induced by ignoring ecosystem change outweighs the potential benefits of improved mortality and biomass estimation. Our simulation study indicates SPMTVr may perform similarly to a simple SPM in some situations, but will

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outperform a simple SPM in others (e.g., Scenario 2; Table 2; Figs. 3–5). Thus, an analyst is likely to produce (at worst) largely similar and (at best) far more accurate estimates of biomass and exploitation rate by choosing to allow the *r* parameter to vary over time. In general, though, a precautionary management approach is more likely to ensure successful management than explicit incorporation of uncertain environmental drivers (De Oliveira et al. 2005; Punt et al. 2014).

When models with time-varying parameters are used, analysts are faced with the decision of how much flexibility to allow in the estimation of those parameters. In general, the SD for random walks in nonlinear assessment models is not estimable without employing Bayesian approaches with informative priors. In a previous study (Nesslage and Wilberg 2012), we found production models with time-varying parameters would not converge to unique solutions if the random walk was allowed too much flexibility (SD > 0.2). In this simulation study, we estimated time-varying *r* assuming a random walk process with annual deviations drawn from a normal distribution with a mean of zero and an SD of 0.15 (eq. 3). An SD of 0.15 appeared to be a reasonable compromise between flexibility and oversimplification after comparing alternative results with SDs of 0.05 and 0.25 (Table S1[1]); however, the decision of exactly how much flexibility to allow is likely situation-dependent such that analysts will need to explore sensitivity to this assumption before determining the most reasonable random walk SD for a specific situation.

To facilitate exploration of a large number of simulations, we provided our models with more information about the true population than might be the case in a real assessment. We placed a prior on initial biomass to provide the model with some information on the magnitude of stock size and provided appropriate starting values for all parameters; we also simulated observation error in our indices, but did not explore systematic bias across the time series. Despite the additional information provided, the SPMTVr failed to converge more often than simple SPMs, indicating that time-varying parameters may not be estimable in some cases, especially if real life situations are less informative or more complex than those we simulated. For example, we explored alternate simulation configurations and found that convergence rates declined with increasing Atlantic menhaden recruitment variability. However, the SPMTVr runs that did converge still produced more accurate results than a simple SPM for the scenarios we simulated, suggesting the use of an SPMTVr would produce more reliable results than a simple SPM if the data are sufficiently informative. Both the simple SPM and the SPMTVr tended to exhibit higher bias in estimates of exploitation rate and biomass when the starting value and mean of the prior on initial biomass were reduced by 2/3 or increased by 3/2 (Table S2[1]). As is typical of most production models (Prager 1994), both the simple SPM and SPMTVr had difficulty estimating the initial biomass of the population without being provided additional information such as informative constraints on initial biomass. SPMs applied to data-poor stocks with little prior information about the magnitude of initial biomass (either alone or relative to *K*) are unlikely to provide accurate biomass estimates or management advice and should be used with extreme caution.

Another limitation of SPMTVr as implemented in this study is that the abundance index time series must span all years in which *r* is estimated. SPMs often require the use of abundance indices with long time series to help ensure adequate contrast and successful independent estimation of *r* and *K* parameters (Hilborn and Walters 1992). Thus, SPMs in general, including SPMTVr, are likely not appropriate for stocks that have indices spanning short periods of time. If survey time series were limited but informative, the SPMTVr could be modified to estimate constant *r* in periods with only a catch time series and time-varying *r* in periods with index values.

An SPMTVr approach could have broad application given many assessments use SPMs due to the lack of age-specific catch and diet or tagging data required to support estimation of time-varying natural mortality or environmentally linked, age-structured, or ecosystem models (Garrison et al. 2010; Buchheister et al. 2017; McNamee 2018). By allowing *r* to vary over time, SPMTVr implicitly accounts for the (sometimes combined) effects of fluctuations in recruitment and predation mortality without having to specify the exact drivers of changes in productivity or how primary drivers may have changed over time. In data-poor situations where diet data or recruitment are not adequately monitored, SPMTVr may provide a reasonable alternative to ignoring ecosystem change entirely. The RAM Legacy Stock Assessment Database Version 3.0 (ramlegacy.org) reports that approximately 16% of assessments worldwide use production models, although that estimate is likely biased low due to the absence of assessments for tropical species (Ricard et al. 2012), which often lack age-structured data and thus would be potential candidates for SPM-based assessments. SPMTVr provides a new approach for exploring the potential effects of ecosystem change on a wide range of data-limited stocks.

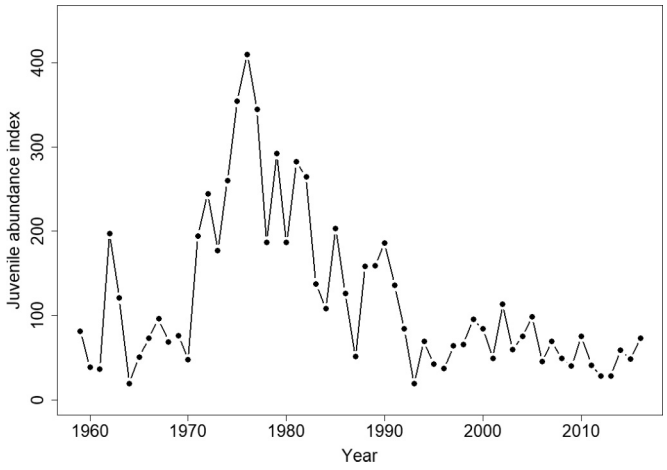
Although we did not explore the performance of SPM models in which *K* varied over time, our simulated data included changes in both *r* and *K* in the form of stochastic recruitment and dynamic predation pressure. Thus, favorable performance of SPMTVr in most scenarios indicated that this approach is robust to changes in both *r* and *K*. However, we did not explore model performance in light of changing index catchability, which, if modeled erroneously as TVr, would likely provide inaccurate results and poor management advice. As length of time series considered in stock assessments increases, time-varying *r*, *K*, and *q* will become a growing problem for data-poor stocks. Given some knowledge about the nature of the dynamic processes affecting a stock, SPMTV offers a potentially viable alternative to ignoring long-term ecosystem impacts on stock dynamics.

Case study — Atlantic menhaden

Application of the SPMTVr to our case study of Atlantic menhaden demonstrated the model's ability to capture the dynamics of a complex age-structured process, to estimate exploitation rate and biomass on the same scale as the SCAA used in management, and to estimate dynamic, MSY-based reference points for management. The simple SPM was unable to fit indices of abundance with high contrast (Fig. 6). Although the SPMTVr produced more comparable biomass estimates to the SCAA than the simple SPM (Fig. 9), it deviated from the other models in its estimation of stock productivity (Fig. 7) and resulting exploitation rates during the 1970s and 1980s (Fig. 9). Unlike a simple SPM, SPMTVr was able to incorporate information from the highly dynamic PRFC index of abundance and estimate a change in productivity of the stock that peaked in 1972; this peak corresponds with a large spike in juvenile fish production observed in fishery-independent surveys during the same time period (Fig. 10). Without explicit incorporation of juvenile abundance data, the SPMTVr was flexible enough to estimate fluctuations in productivity (*r*) over time (Fig. 7), as the stock responded to ecosystem change in a way that the simple SPM could not. Although the SCAA model uses the juvenile abundance index as a data source, it cannot fit the index adequately without estimating separate catchability parameters in each period of high (1959–1986) and low (1987–2013) productivity (SEDAR 2015). Thus, the SPMTVr differs from the SCAA and simple SPM in its ability to characterize this period of high productivity and thus deviates from these models in its estimates of exploitation rate. We will never know whether the magnitude of productivity reflected in the PRFC index and juvenile abundance index is correct; however, our SPMTVr modeling approach provides an opportunity to explore the consequences of such changes in productivity over time without having to explicitly model ecosystem dynam-

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Fig. 10. Juvenile abundance index for Atlantic menhaden, 1959–2016 (ASMFC 2017).



ics. Our approach shows how understanding of long-term trends in highly dynamic fish stocks such as Atlantic menhaden may be enhanced by using SPMs with time-varying parameters.

Another advantage of the SPMTVr approach is its ability to estimate dynamic, MSY-based reference points for Atlantic menhaden that implicitly incorporated the stock's response to ecosystem change. Dynamic reference points encourage the consideration of MSY goals relative to changing productivity of the stock. If the stock has experienced large shifts in productivity over time as a result of ecosystem change (e.g., predation pressure or climate-induced effects on recruitment), dynamic MSY reference points may be more suitable for management than static reference points, regardless of what the mechanism of ecosystem change might be or how it has changed over time. For instance, an exploitation rate of 0.25 in the mid-1970s would not be considered overfishing due to higher productivity of the stock at that time; however, the same rate would be considered overfishing during periods of low productivity in the 1990s (Fig. 9; Fig. S5[1]). Dynamic MSY-based reference points could allow managers to maintain sustainable fisheries without needing to invest in the collection and analysis of spatially and temporally extensive predator, climate, and diet data necessary for most multispecies and ecosystem models (Garrison et al. 2010; Buchheister et al. 2017). However, this dynamic MSY-based exploitation rate reference point likely does not maximize catch across the entire time series. Further simulation testing will be required to determine the optimal set of MSY-based reference points and associated harvest policies that would achieve Atlantic menhaden fishery objectives.

The Atlantic States Marine Fisheries Commission (ASMFC) has set an explicit goal of adopting "Ecological Reference Points" that will help "manage Atlantic menhaden at sustainable levels to support fisheries and meet predator demands" (ASMFC 2012). Although multispecies models are being constructed that will be able to quantify explicit biomass targets that would meet specific predator demands (Buchheister et al. 2017; McNamee 2018), the SPMTVr may be able to implicitly capture the stock's response to changing predation pressure and provide reference points that reflect sustainable harvest goals in light of ecosystem change, thus providing a model of intermediate complexity for addressing ecosystem considerations in a single-species stock assessment framework. Our approach may also be applicable to other highly dynamic stocks with long-term trends in catch and relative abundance that reflect unknown or uncertain fluctuations in response to ecosystem change.

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Appendix 2: Steele-Henderson Surplus Production (S-H) Model Working Paper

Steele-Henderson and Biomass Dynamic Models

Jim Uphoff, Maryland Department of Natural Resources

Introduction

Steele-Henderson (S-H) models are biomass dynamic models with additional sigmoidal type III predation functions that estimate predation losses from one or more predators (Collie and Spencer 1993). They quantify the extent that modeled predators and fishing influence a prey species. When applied generally, the S-H model reproduced rapid shifts in productivity exhibited by marine populations (regime shifts; Steele and Henderson 1984; Spencer 1997). S-H models have been used to explore the role of predation on management of Haddock (Spencer and Collie 1997), weakfish (ASMFC 2009), and Atlantic menhaden (Crecco 2010; Uphoff and Sharov 2018). Increased *M* of weakfish detected by S-H models in ASMFC (2009) was confirmed by an age-structured model of weakfish with time varying *M* (ASMFC 2016).

Biomass dynamic models are the simplest single-species stock assessment method; the stock is considered undifferentiated biomass that changes with harvest under stable ecological conditions (Hilborn and Walters 1992; Spencer and Collie 1997; Haddon 2001). Aggregate changes in biomass due to growth, recruitment, and natural mortality (incorporated in a single intrinsic rate of increase) are modulated by closeness of biomass to unfished biomass (Hilborn and Walters 1992). Age, size, and sex structure are ignored (Hilborn and Walters 1992; Haddon 2001). Biomass dynamic model data needs are small - an index of relative biomass and landings (Hilborn and Walters 1992; Prager 1994; Haddon 2001). They come closer than age-structured stock assessment models to the principal of parsimony applied in modern statistics (Rothschild et al. 2013). Biomass dynamic models represent a fundamentally different approach to stock assessment than age-structured models and understanding differences in results that arise between the two approaches may be as useful as concurrence of results (Hilborn and Walters 1992).

Biomass dynamic models estimate maximum sustained yield (MSY) reference points and can provide stock projections (Prager 1994; Rothschild and Jiao 2013). Moustahfid et al. (2009a) explored the use of biomass dynamic models that included predation losses (estimated by a different process than a S-H model) and treated them as an additional "fleet" along with harvest to estimate reference points for Longfin Squid; the concept of MSY changed to maximum useable production (MUP) - surplus production available to modeled predators and the fishery. MUP reference points have been proposed for Atlantic herring and Atlantic Mackerel as well (Overholtz et al. 2008; Moustahfid et al. 2009b)**.** MUP reference points can be generated from S-H models.

The S-H modeling approach has theoretical appeal since it incorporates compensatory stock dynamics of exploited prey with harvest plus a foraging response by one or more candidate predators (Spencer and Collie 1997). A S-H model has the same data requirements as a biomass dynamic model, plus it needs predator biomass estimates or indices to generate estimates of predation losses through a type III functional response (Collie and Spencer 1993; Crecco 2010). Parameters of the predation terms may be good candidates for fitting exercises since predation is a large scale process difficult to measure directly in the field (Walters and Martell 2004).

A S-H model could be considered a "minimal realistic model" and the key feature of this approach is that only predators likely to have important impacts on the prey of interest are considered (Punt and Butterworth 1995; Yodzis 2001). Virtues of a minimum-realistic approach such as the S-H model are tractability in analyzing and parameterizing, but there is no way to know how much complexity is the minimum needed (Yodzis 2001). Important trophic interactions may get omitted and invalid inferences could be drawn by ignoring species, but adding more predators does not guarantee more robust results because of greater demands on data (Kinzey and Punt 2009) and increased risk of overparameterization (Babyak 2004; Walters and Martell 2004; Fogarty 2014; Collie et al. 2016).

The S-H model approach was fundamentally different from biomass dynamic or other age-structured multispecies models employed by Hollowed et al. (2000), Overholtz et al. (2008), Moustahfid et al. (2009a; 2009b), Garrison et al. (2010), Curti et al. (2013) that required some combination of estimates of annual consumption rates or consumption by age, size and prey type preference parameters, evacuation rates, biomass of “other food” not explicitly modeled, and annual or semi-annual diet (Hollowed et al. 2000; Overholtz et al. 2008; Moustahfid et al. 2009a; 2009b; Garrison et al. 2010; Curti et al. 2013). Prey consumption by S-H model predators could only come from the aggregated prey biomass, but this does not mean that a specific prey outside of age or size bounds considered or other prey were not eaten, since the Type III predator-prey function allows for prey switching (van Leeuwen et al. 2013).

S-H models provide estimates of *F* and time-varying natural mortality from modeled predators (M_2) that quantify the extent that predation and fishing could be influencing a prey species. An important, practical question for management of Atlantic menhaden as forage is whether the current single-species assessment captures enough predator-prey dynamics to serve as the basis for management or whether other approaches are needed (SEDAR 2015). Applying similarly structured assessment models with and without predation could help address predation’s impact on Atlantic menhaden. Biomass, M_2, and *F* (in biomass units) from a S-H model can be contrasted with estimates of biomass and *F* from a fishing-only biomass dynamic model based on the same indices and harvest to judge whether predation was important for management of Atlantic menhaden. Kinzey and Punt (2009) compared results from similar age-structured single-species and multispecies models for three commercially harvested fish on the Aleutian Shelf, Alaska, and found differences with important management implications.

The S-H model does not model feedback of prey consumption by predators on the dynamics of the predators. However, estimates of average annual biomass of Atlantic menhaden consumed per biomass by predators (per biomass consumption) from the S-H model can be compared to empirical indicators of well-being, such as condition indices, weight-at-age, and time-varying *M*. Uphoff and Sharov (2018) found associations of per biomass consumption of Atlantic menhaden to tag-based estimates of *M* of Chesapeake Bay striped bass and weights-at-age of striped bass along the Atlantic Coast during 1985-2010.

Methods

Base Model Inputs

The base S-H model excluded age 0 Atlantic menhaden since they undergo very limited harvest; ages 1+ were important to the fishery. Candidate predators that were thought to be abundant enough to potentially consume enough ages 1+ Atlantic menhaden to affect their biomass dynamics were striped bass, bluefish, and spiny dogfish. Candidate predators were screened for inclusion as a major predator (a predator impacting Atlantic menhaden biomass dynamics) in the base S-H model. The period 1985-2017 was the common timeframe among the predator-prey models being considered in this assessment. Bluefish and striped bass have large recreational catches that influence their stock assessments and 1985-2017 reflected when recreational catches were believed to be well estimated.

Base biomass dynamic and S-H Models were developed from the same set of ages 1+ Atlantic menhaden biomass indices: fishery-dependent RCPUE (1985-2017), and fishery-independent MAD (1985-2017) and NAD (1990-2017). The SAD index was excluded because of high representation of age-0 Atlantic menhaden. The fishery-dependent RCPUE index, chosen as the preferred long-term biomass index was the basis for the Time Varying *r* (TVr) model, provided for development of long-term exploratory S-H models (back to 1957) . The other long-term fishery-dependent index (PRFC; 1964-2017) was included in sensitivity and exploratory analyses. The RCPUE index was positively correlated with the PRFC index during 1985-2017 (ρ = 0.43, P = 0.01; correlation coefficients are abbreviated as ρ to avoid confusion with the intrinsic rate parameter, *r*, of biomass dynamic and S-H models) and trends were very similar until the last five years (RCPUE ascends while the PRFC levels off). These two fishery-dependent indices were not well correlated in the long-term (1964-2017; ρ = 0.19, P = 0.016). The MAD and NAD indices were scaled into RCPUE units using a ratio of averages approach based on years in common (1990-2017). Base S-H and fishing only biomass dynamic models (based on indices) were contrasted with counterpart models based on BAM estimates of ages 1+ Atlantic menhaden biomass (i.e., known-biomass biomass dynamic models; MacCall 2002).

Steele Henderson Predator-Prey and Fishing Only Biomass Dynamic Models

The Haddon (2001) spreadsheet version of a Schaefer biomass dynamic model was adapted to the S-H model formulation. An observation error model was used that assumed all residual errors were in the index observations and the equation used to describe the time-series was deterministic and without error (Haddon 2001). Biomass dynamics of Atlantic menhaden with losses from harvest and major predators were described by the following discrete time-step equation:

$$(1)\ B_t = B_{t-1} + rB_{t-1}(1-(B_{t-1}/K)) - H_{t-1} - (\sum D_{t-1}) + \varepsilon;$$

where B_t was estimated ages 1+ Atlantic menhaden biomass in year t; B_{t-1} = estimated biomass the previous year, r = intrinsic rate of population increase; K = carrying capacity (unfished biomass); H_{t-1} = harvest in the previous year; $\sum D_{t-1}$ = the sum of estimated predation losses from predators in the previous year (estimated for each predator by equation 2, below); and ε = observation error (Collie and Spencer 1993; Spencer and Collie 1995). Biomass was estimated directly for 1985 as a separate parameter (B_{1985}) and then projected forward by the S-H model. A fishing-only Schaefer biomass dynamic model was estimated by equation 1 by excluding predation loss terms ($\sum D_{t-1}$).

Annual consumption of Atlantic menhaden biomass (D_{t-1}) by candidate predators in the S-H model was estimated by a type III predation function as

$$(2)\quad D_{t-1} = [(dP_{t-1}(B_{t-1})^2) / (A^2 + (B_{t-1})^2)];$$

where d was estimated maximum per biomass consumption by each predator; P_{t-1} was predator biomass; A was estimated Atlantic menhaden biomass where predator satiation begins for each species (Collie and Spencer 1993; Spencer and Collie 1995) and B_{t-1} represented estimated ages 1+ Atlantic menhaden biomass. Predator biomass was an input and the remaining three terms were model estimates. Evaluation and selection of candidate predators will be described later.

The Haddon (2001) spreadsheet version of a biomass dynamic model was easy to adapt to S-H model formulation because it estimated Atlantic menhaden biomass as a first step and then estimated an annual scalar (q_t) as B_t / I_t; where I_t is an observed index for year t (Haddon 2001). Estimating Atlantic menhaden biomass first allowed predator biomass estimates to be used directly rather than as index equivalents. The mean of annual estimates of q_t was used to predict I_t as (mean q_t) • B_t.

A genetic algorithm super solver (Evolver; Palisade Corporation 2010) was used to estimate S-H and fishing model parameters that minimized $\sum$(observed $\log_e I_t$ - predicted $\log_e I_t$)^2 (Haddon 2001). Genetic algorithms, unlike traditional hill climbers, do not evaluate and improve a single solution, they evaluate a set of solutions (a "population"; Meyer-Baese and Schmid 2014). A genetic algorithm produces successor solutions by mutation and recombination of the best currently known solutions at each iteration. A genetic algorithm's most important property is robustness and this means that it is possible to find a solution even if the input data are messy (Meyer-Baese and Schmid 2014).

Model runs had an initial time budget of 3 minutes. If the progress optimization summary graph indicated the sums of squares converged on an asymptote, the run was used. If the graph indicated it was not reached, then another run of 3-min was made. It was not necessary to make runs longer than 6-min. The spreadsheet version of the model combined with the genetic algorithm provided a great deal of flexibility for trying different model variations.

Akaike information criteria for small sample sizes (AIC_c) were used to evaluate biomass dynamic and S-H models that related changes in Atlantic menhaden biomass to fishing alone or to fishing and predation (Burnham and Anderson 2001):

$$(10)\quad AIC_c = -2(\text{log-likelihood}) + 2J + [(2J(J+1)) / (n-J-1)];$$

where n is sample size and J is the number of model parameters. Lognormal likelihoods were used (Haddon 2001). AIC_c values were rescaled to Δ_i, ($AIC_{c\,i}$ – minimum AIC_c) where i is an individual model. The Δ_i values provide a quick "strength of evidence" comparison and ranking of models and hypotheses. Values of $\Delta_i \leq 2$ have substantial support, while those > 10 have essentially no support. Δ_i was used to calculate Akaike weights that approximated the probability that model i constituted the best model of the hypothesis given the data (Burnham and Anderson 2001) when disparities were close enough to merit consideration of both models.

Jackknifing was used to examine precision and bias (Efron and Gong 1983). Each index was removed sequentially, the mid-range parameter values were re-established, and the model was run. Parameters were outputted and the various time-series (*B, F, M_2*, etc) were recreated. None of these required an extra time limit during the fitting routine. Jackknifing was not pursued for the base fishing only model. This model's purpose was to contrast with the base S-H model and not serve as a stand-alone single-species assessment.

Due to high variability of individual indices, a mean of each year's standardized index was estimated and an r^2 (coefficient of determination) was estimated by regressing the mean of observed indices with the predicted index to aid interpretation of fit; the mean index was not included in the SSQ. Residuals of each model were examined for serial trends and normality.

Evolver required a starting range for each parameter (Palisade Corporation 2016) and the ranges used were broad. Parameter *r* varied from 0.1 (very low) to 3.0 (a value associated with chaotic behavior of populations described by logistic equations; May 1974). The range of *K* fell between 100,000 and 10,000,000 MT, a range that fell below lowest observed landings to about 23-times the highest landings. Initial biomass ranged from 50,000 to 2,500,000 MT. The same ranges of estimates of *d* (0 – 17-times predator weight) for striped bass and bluefish estimated by Uphoff and Sharov (2018) were used for the three candidate predators. The range in parameter *A* was set equal to the range for *K*. Mid-range values were used as starting values for all models, excluding sensitivity analyses (described below).

Estimates of *ad libitum* consumption of prey at optimal temperature as g prey per g of striped bass per day derived from Hartman and Brandt (1995a; 1995b) bioenergetics models (C_{MAX}) provided a means to judge a maximum value for parameter *d* for striped bass in the initial parameterization of the S-H model. A striped bass-specific estimate of parameter *d* was compared with bioenergetics-based annual C_{MAX} estimates derived by Uphoff and Sharov (2018); annual C_{MAX} for striped bass ranged from 12.7 to 15.6-times striped bass body weight and the median equaled 14.6. Buckel et al. (1999) estimated annual C_{MAX} for bluefish (17.8). Similar information was for spiny dogfish was not available and the range for the other two species was used.

Estimates of annual instantaneous fishing mortality (*F*) in year *t* for both the MSVPA-X and S-H models were calculated by rearranging equation 1.40 in Ricker (1975) to

$$(4)\quad H_{t-1} / [(B_t + B_{t-1}) / 2].$$

An equivalent M_2 from predators was estimated for both models by rearranging equation 1.41 in Ricker (1975) to

$$(5)\ D_{t-1} / [(B_t + B_{t-1}) / 2].$$

Background predation mortality (M_1) by species other than those included in the S-H model would be accounted for by the interplay of *r* and *K* (Collie and DeLong 1999).

Average annual consumption of age 1+ Atlantic menhaden biomass per predator biomass (per biomass consumption) from both models was estimated as

(6) D_t / P_t (Uphoff and Sharov 2018).

This estimate was compared to estimates of consumption (generated by bioenergetics or feeding experiments) to check plausibility of the S-H model's estimate (Uphoff and Sharov 2018).

Predator Selection

Uphoff and Sharov (2018) examined published fish prey length versus striped bass and bluefish length plots of to select minimum size classes (converted to approximate age) of each predator capable of eating age-1 Atlantic menhaden, i.e., prey fish in the plots were the same length or larger than age-1 Atlantic menhaden (minimum TL ~ 150 mm). Atlantic menhaden were identified a diet items for these predators (Uphoff and Sharov 2018). Three year-old striped bass were the first age-class capable of consuming age-1 Atlantic menhaden and all size groups of bluefish were capable of consuming age-1 Atlantic menhaden. These groupings were used to estimate biomass of these candidate predators.

Link and Almeida (2000), Link et al. (2002), and Bangley and Rulifson (2014) described spiny dogfish along the North and Mid-Atlantic region as highly piscivorous. Pelagic Clupeids ranked second (likely to have been mostly Atlantic herring to the north) among all prey groups summarized in these studies. Atlantic menhaden become more important to spiny dogfish in the southern extent of their range (Bangley and Rulifson 2014). Atlantic menhaden have accounted for 7.5% of all diet items in all sizes of spiny dogfish, by weight, captured in spring and fall since NEAMAP surveys of nearshore waters between Cape Cod, MA, and Cape Hatteras, NC (Virginia Institute of Marine Science 2016). This percentage was second of all items identifiable to species (Longfin Squid were first at 11.4%; Virginia Institute of Marine Science 2016). Atlantic menhaden comprised nearly 60% of mature female spiny dogfish diet, by weight, in winter trawl samples off North Carolina during 2008-2010 (Bangley and Rulifson 2014).

Overholtz and Link (2006) reported that spiny dogfish 39 cm and larger consumed fish, while Scharf et al. (2000) indicated that feeding on fish began at about 28 cm. Fish prey 150 mm and larger appeared in diets of spiny dogfish at approximately 40 cm (Scharf et al. 2000). These sizes do not correspond directly with size categories of biomass estimates ($\leq$ 35 cm, 36-79 cm, and $\geq$ 80 cm) used in the spiny dogfish assessment, but the fraction of biomass represented by the smallest size category that did not feed on fish appeared very small and unlikely to induce substantial bias. Biomass of spiny dogfish that were capable of feeding on ages 1+ Atlantic menhaden were estimated as the sum of the biomass estimates of 36-79 cm, and $\geq$ 80 cm length categories in the spiny dogfish stock assessment.

Striped bass, bluefish, and spiny dogfish were screened for consideration as major predators of using correlation analyses of Atlantic menhaden indices (RCPUE, MAD, and NAD) and predator biomass estimates from single-species assessments. Positive correlations could indicate

predation proportional to prey biomass, while negative correlations suggest predators capable of generating disproportionately higher M (Ulltang 1996).

S-H models featuring each candidate predator as the lone Atlantic menhaden predator were used to screen candidate predators as well. The r^2 of each estimated and observed index time-series (fishing-only and each candidate predator) and AIC_c were used to separate major predators from the candidates (Burnham and Anderson 2001). S-H models of candidate predator and Atlantic menhaden could be judged by Δ_i comparisons with fishing only biomass dynamic models, the potential contribution of ages 1+ Atlantic menhaden to their diet (see below), and by the magnitude of M_2 from the S-H model. S-H models that were unlikely to be reasonable descriptions of dynamics when compared to a fishing only model ($\Delta_i > 4$) would be rejected as would S-H models that produced M_2 estimates of 0. If more than one candidate predator was possible, a multiple predator S-H model was developed. Fit, AIC_c, and M_2 estimates from multiple predator models were compared to single predator S-H models using the steps outlined above to further evaluate how many should be considered major predators.

Candidate and major predator estimates of D_t / P_t were compared to minimum, maximum, and median (if available) estimates of annual per biomass consumption of all prey from bioenergetics models or feeding experiments (C_t; Uphoff and Sharov 2018). These estimates provided plausibility boundaries for D_t / P_t; estimated consumption of age 1+ Atlantic menhaden should, at the least, fall below maximum C_t and ideally fall below the minimum (i.e., ages 1+ Atlantic menhaden would not make up the entire potential diet). A S-H model with D_t / P_t estimates above maximum C_t would be rejected and estimates between the maximum and minimum would be viewed skeptically.

Striped bass D_t / P_t could be compared to estimates of C_t derived in Uphoff and Sharov (2018) from published bioenergetics analyses. Estimates of annual C_t for all prey in Chesapeake Bay ranged between 4.2- and 6.3- times striped bass body weight and the median among ages and studies (Hartman and Brandt 1995a; 1995b; Griffin 2001; Overton 2003; Nelson et al. 2006) was 5.5-times (Uphoff and Sharov 2018). Buckel et al. (1999) estimated that bluefish along the Atlantic Coast (all ages) consumed 7.7–10.8 kg of prey per kg of bluefish during 1995. Spiny dogfish were estimated to consume 0.95 to 3.0-times their body weight in prey per year in feeding experiments summarized in Spencer and Collie (1995), and Bangley and Rulifson (2014).

Forage Reference Points and Stock Status

Forage reference points (FRPs), benchmarks that allow Atlantic menhaden to maintain its forage role, were estimated for S-H models, while standard MSY reference points were estimated for fishing only models. Prager (1994) and Moustahfid et al. (2009a) warned that absolute levels of stock biomass (and related quantities) are usually estimated with less precision by biomass dynamic models. Prager (1994) suggested presenting relative mortality and relative biomass trends, which are year-specific estimates of B standardized by B_{MSY} and F standardized by F_{MSY} for fishing only biomass dynamic models. For an S-H model, B, Z_2, and F would be standardized by B_{MUP}, Z_{MUP}, and F_{MUP} (described below), respectively (Moustahfid et al. 2009a). Ratios of 1.0 were set as a thresholds for mortality and biomass. Maintaining total

mortality below a threshold level is a guiding principle for managing prey populations (Collie and Gislason 2001). Since S-H models do not contain all predators, using 1.0 as a threshold would provide some (but unknown) buffering against a possibility of additional important predation by an excluded predator or predators. Estimates of Z_2 / Z_{MUP} and F / F_{MUP} would need to be 1.0 or more to meet threshold conditions while B / B_{MUP} needed a ratio of *1.0* or less.

Biomass at MUP was estimated as

(7) $B_{MUP} = K / 2$ (Moustahfid et al. 2009a).

Total instantaneous mortality from the fishery and modeled predators at MUP was estimated as F_{MSY} would with a Schaefer model (Haddon 2001; Moustahfid et al. 2009a**),**

(8) $Z_{MUP} = r / 2$.

Schaefer model reference points were estimated for fishing-only models as

(9) $F_{MSY} = r / 2$ and (10) $B_{MSY} = K / 2$ (Prager 1994).

Estimates of MUP for S-H models and MSY for the fishing only biomass dynamic models were estimated as

(11) $(r \cdot K) / 4$

(Prager 1994; Moustahfid et al. 2009a). To partition MUP into a portion available to the fishery, the approach described in Overholtz et al. (2008) as ''recent proportion'' was followed. The surplus for the fishery (*SF*) was estimated as

(12) $SF = MUP - D$.

Instantaneous annual fishing mortality at MUP (F_{MUP}) was estimated as

(13) $F_{MUP} = SF / B_{MUP}$ (Moustahfid et al. 2009a).

Interpretation of F / F_{MSY} was straightforward for fishing-only scenarios, but Z_2 / Z_{MUP} needed an additional metric to interpret the contribution of *F* and M_2. An indicator of management leverage was developed:

(14) F / Z_2.

F / Z_2 in excess of 0.5 would indicate that fishing was an increasing driver of dynamics and less than 0.5 would indicate that fishing was a lesser driver of dynamics (Crecco 2010). Patterson (1992) used linear regression to establish a general relationship of biomass of exploited small pelagic fishes (11 species and 28 stocks of Herring, Sardines, Mackerel, Scad, and Gaddoids) to F / Z and proposed that F / Z higher than 0.4 would lead to declines in stock size. The analysis of Patterson (1992) was based on single species assessments of numeric *F* at constant *M* rather than biomass, but 0.4 was used as a starting point for evaluation of F / Z_2 as a threshold.

Predator Consumption Threshold

Direct feedback from prey to predator is not a feature of an S-H model and an empirical approach was employed to develop a threshold based on major predator condition. Indicators of condition were not routinely estimated for major predators and annual weights-at-age were used as a condition metric for major predators assessed by catch-at-age models (potentially bluefish and striped bass). Changes in striped bass weight-at-age may have been a coarse indicator of condition since fasting replace lipids (the energy currency in marine fish; Rose and O'Driscoll 2002) with water in a linear fashion (Jacobs et al. 2013).

Correlation analysis (Pearson correlation coefficients, ρ; $P \leq 0.05$) was used to estimate strength of associations of D_t / P_t estimated by the base S-H model with weight-at-age in the same year, and one, two, and three years before (an immediate response in weight to feeding and lagged responses). Dutil and Lambert (2000) found that the response Atlantic Cod to unfavorable feeding conditions could be delayed. Some stocks of Atlantic Cod experienced forage fish declines, followed by declining body condition and increased M; starvation caused declines in energy reserves, physiological condition, and enzyme activity (Lilly 1994; Lambert and Dutil 1997; Dutil and Lambert 2000; Shelton and Lilly 2000; Rose and O'Driscoll 2002). Correlations with weight-at-age were considered biologically significant if they occurred over continuous blocks of ages rather than sporadically.

If a major predator had a block of ages with D_t / P_t correlated with weights-at-age, the series of weights for a given age within the block were standardized to their age-specific time-series mean. Then a linear regression of D_t / P_t from the base S-H model and standardized weight-at-age for all ages within the time block was used to predict the point where D_t / P_t result in average weight (standardized weight-age-age = 1.0). This point was considered a threshold consumption for predator condition. Data were further examined to determine the risk that below average weight would occur when D_t / P_t was at or below the threshold and to see if a potential D_t / P_t target was suggested where the chance of a predator being below average in weight was substantially less.

Sensitivity Analyses

A series of sensitivity analyses were run for the base model. Presentation of results will be limited to parameter estimates, B / B_{MUP}, Z / Z_{MUP}, and D_t / P_t.

Since the genetic algorithm did not provide a defined endpoint for convergence, the base S-H model was run for one hour to look at run time sensitivity. Three runs were made with different limits on S-H model parameter *d*: *d* was confined to a range estimated from bioenergetics; d was allowed a higher maximum (starting range for *d* was 0-20.0); and the default penalty function in Evolver was imposed for *d* if estimates exceeded the maximum (17.0). These three runs were prompted by concerns about parameter *d* being at its maximum constraint for one of the predators in Uphoff and Sharov (2018). Runs were made with initial values 20% higher or lower than the midpoints used as the common starting value. The PRFC index was substituted for the RCPUE index (MAD and NAD indices were standardized to PRFC index units using the same approach used for RCPUE). Retrospective bias of the base run was investigated by sequentially removing up to the last four years (2014-2017) from analysis. Additional runs were made that removed one of the indices from analysis to investigate an individual index's influence. Index pairs considered were RCPUE and NAD, RCPUE and MAD, and NAD and MAD.

Projections

Projections using the base S-H model were made for 2018-2041. They explored four scenarios: (1) continuation of 2017 harvest with major predators at 2017 levels (status quo projection), (2) major predator biomass increases to recovered status and Atlantic menhaden are fished at one half their target *F* (major predator recovery, half-target *F* projection); (3) major predator biomass increases to recovered status and Atlantic menhaden are fished at their target *F* (major predator recovery, target *F* projection); and (4) predator biomass increases to a point where a proposed consumption threshold is met and Atlantic menhaden are fished at their current harvest (predator consumption threshold, current harvest projection). For S-H model projections featuring predator recovery, a ten-year period was arbitrarily chosen for recovery and then predator biomass was held steady for another ten years. Terminal estimates represented "equilibrium" conditions for each projection.

Atlantic menhaden target *F* was in numeric currency while the S-H model *F* was biomass based. Numeric *F* in 2017 was at half its target and the S-H model estimate of *F* for 2017 was used as a proxy for *F* at half its target, while target *F* was twice the estimate for 2017.

Off-the-shelf Monte Carlo simulation software (@Risk; Palisade Corporation 2010) interfaced with an Excel spreadsheet was used to add uncertainty to the four projections. This software combination was used by Overholtz and Link (2006) to estimate uncertainty of Atlantic herring consumption by predators in the Gulf of Maine – Georges Bank complex. A version of Monte Carlo simulation, Latin Hypercube sampling, was used. Latin Hypercube sampling recreates input distributions by stratifying their cumulative curves into equal intervals and then samples each interval without replacement (Palisade Corporation 2016). Latin Hypercube sampling uses fewer iterations compared to random sampling employed by Monte Carlo simulations and is more effective when low probability outcomes are present (Palisade Corporation 2016). Each simulation consisted of 5,000 iterations.

Distribution functions of S-H model parameters r, K, d, and A were determined from their jackknifed distributions using @Risk's distribution fitting function (minimum AIC was the basis for selection of a distribution used to represent a parameter). Correlations among these parameters were included in the simulations. The distribution of ages 1+ Atlantic menhaden biomass in January 1, 2018, was used to initiate the projection, as was the latest major predator or predators biomass. Coefficients of variation of major predator biomass from stock assessments were used to assign uncertainty to these estimates. Uncertainty of catch (and its management) were represented by a triangular distribution, with the peak representing a specified catch or catch associated with a level of F, the portion where catch was less than the peak ended at 90% of the quota and the portion where catch was more than the peak was 102% of the quota.

Ninety percent intervals of the terminal year's estimates of B / B_{MUP}, Z / Z_{MUP}, and D_t / P_t were constructed for comparisons among models; it was possible to include more metrics, but these three were selected to keep comparisons tractable. Risk for each of the three parameters was estimated as the portion of the cumulative distribution that breached the proposed thresholds.

Risk was rounded to the nearest 5%, but it was possible to set up the simulation to provide an exact estimate.

Caddy and McGarvey (1996) outlined how target and limit biological reference points (BRPs) could be used synchronously to reduce risk of overfishing in single-species management. A limit biological reference point sets a "safe" upper limit of fishery exploitation and a target BRP sets a lower level of exploitation toward which management strives. Requirements are a preset limit (threshold) BRP, an estimation of current exploitation rate and its variance, and agreement on the acceptable risk of exceeding the limit. Risk of overfishing is a pre-agreed upon probability that is quantified as the probability corresponding to the right tail of the distribution of current fishing mortality estimates lying beyond the limit BRP. The target BRP is a level of "safe" *F* that is below the limit BRP that provides a margin of error for an overshoot (Caddy and McGarvey 1996).

The target-limit approach to FRPs requires selection of a probability of an overshoot of a threshold where collapse of a species forage role is unacceptable and target FRPs representing an agreed upon trade-off of yield and predator consumption. The former were focused on because they represented a more technical challenge than the trade-offs that will need to be considered by managers if they choose to set target FRPs.

Applying the Francis and Shotton (1997) description of risk in a single species context to FRPs, exceeding a FRP threshold (limit) does not mean a forage role collapse, only that the chance of collapse is thought to be significant. The choice of a FRP requires balancing between a FRP so low that yield will be sacrificed and one that is too high and carries a considerable risk of forage role collapse. Caddy and McGarvey (1996) described somewhat contradictory guidelines for selecting standard overfishing reference points; they recommended setting the risk of breaching an overfishing threshold above 5% to avoid unnecessarily sacrificing yield, but described a risk between 10-30% as relatively high (Caddy and McGarvey 1996). A risk of 10% might be a "best" choice in because it lies above the level where yield is sacrificed unnecessarily and it is the most conservative of the "risky" choices. A 10% risk of breaching a FRP threshold was used to delineate low and high risk in the four projections. However, choice of risk may be different for different stakeholders and fishery managers, depending on how they perceive the trade-off between risk of forage collapse and curtailment of fishing.

Results

Model inputs

The RCPUE, MAD, and NAD indices (latter two standardized to RCPUE) exhibited variability in relative biomass within and among years during 1985-2017 (Table 1; Figure 1). It was not common for the indices to fall in the same status realm in a given year (i.e., all high, low, or in-between). The mean of the indices (mean index) was highest during 1985-1988 (above 0.85). The mean index fell sharply by about half by 1991 (to 0.41) and varied from about 0.30 to 0.60 through 2009. After 2009, the mean index increased and was steadily above 0.60. The mean index was particularly high during 2014 (0.93) and 2015 (1.20), but declined to 0.68 and 0.59 in

2016 and 2017, respectively (Table 1; Figure 1). The three biomass indices were not well correlated with each other (ρ between -0.02 and 0.29) and none of their associations were significant at $P < 0.05$ (Table 2). The two fishery-independent indices were similarly and strongly correlated with the mean index ($\rho = 0.80$, $P < 0.0001$), while the correlation of RCPUE was not as strong ($\rho = 0.39$, $P = 0.03$; Table 2).

Highest harvest of ages 1+ Atlantic menhaden during 1985-2017 (429,716 MT) was 2.5 times greater than the lowest (168,934 MT; Figure 2). Landings were usually in excess of 260,000 mt during 1985-1998 and averaged about 340,000 mt. Landings after 1998 were lower, averaging 203,000 mt. Landings were less than 200,000 mt after 2012 (Figure 2). Annual harvest caps in Chesapeake Bay were imposed after 2005 and a total allowable catch (TAC) for the Atlantic coast was put in place in 2013 (SEDAR 2015).

Candidate Predators

Striped bass ages 3+ biomass was estimated to have been between 40,000 and 233,000 mt during 1985-2017 (Figure 3). Biomass rose from its minimum to its maximum during 1985-1997. Striped bass biomass fell gradually to 193,000 mt in 2009. The decline steepened afterward and biomass reached its nadir of 133,000-134,000 mt during 2016 and 2017, respectively. Bluefish biomass estimates ranged between 93,000 and 262,000 mt during 1985-2017. Biomass peaked in 1985, then underwent a prolonged decline before bottoming at 93,000-95,000 mt during 1993-1996. Bluefish biomass rose between 1997 and 2000 and plateaued between 120,000-155,000 mt during 2001-2017. Spiny dogfish biomass was usually above 500,000 mt during 1985-2017; 1998-2005 were exceptions and biomass estimates fell as low as 378,000 mt (Figure 3).

Correlation analysis provided weak evidence of potential predator-prey interactions. Striped bass was the only candidate predator whose biomass was negatively correlated with ages 1+ Atlantic menhaden biomass indices; only the correlation with the MAD index was significant (Table 3). Bluefish and spiny dogfish biomasses were positively correlated with Atlantic menhaden biomass indices. Only the correlation of bluefish biomass with the MAD index was significant (Table 3).

Comparison of Fishing and Fishing plus Predation Models

Striped bass was considered the sole major predator for the base S-H model for the RCPUE, NAD, and MAD indices. Based on AIC_c, a fishing biomass dynamic model and a S-H model featuring striped bass were equally likely the best models given the data; both models had an AIC_c of -156 (Table 4). The closeness of AIC_c scores indicated that ignoring predation from striped bass would be risky for management. A S-H model featuring spiny dogfish had AIC_c of -154, but parameter *d* equaled 0, so M_2 losses were not generated; it duplicated the fishing only model. An S-H model with bluefish had an AIC_c of -149 (Δ_I of 5), indicating is was not likely to be the best model. However, it did generate M_2 estimates, so a combined striped bass and bluefish S-H model was attempted. This combined model had an AIC_c of -149 as well; parameter *r* was at its maximum constraint and parameter *d* was 0 for bluefish (Table 4). This two predator model was rejected.

Estimates of *r* and *K* were quite different between the base fishing-only and the striped bass S-H models (Table 4). All estimated parameters were within bounds for both models. The estimate of *r* was higher for the S-H model (2.27) than the fishing only model (0.32) and *K* was about 3-times lower for the S-H model (Table 4). Adding striped bass predation to harvest resulted in a general shift in depiction from a stock with low productivity and high biomass to one with high productivity and low biomass. The estimate of MSY from the fishing only model was 273,184 mt, while the estimate of MUP from the S-H model was 608,517 mt. It is not uncommon with biomass dynamic models that data can be well explained as coming from a small, productive stock or a large, unproductive one since estimates of *r* and *K* are often highly negatively correlated (Walters and Martell 2004).

Base Steele-Henderson Model: Fit and Precision

Neither the base fishing only model nor the base striped bass S-H model (base S-H model) fit the individual indices well. The r^2 for the fishing only model was 0.21 for the fit of the estimated and observed RCPUE indices, 0.10 for NAD, 0.25 for MAD, and 0.42 for the mean index (not used in the SSQ). The r^2 for the striped bass S-H model was 0.18 for the fit of the observed and estimated RCPUE indices, 0.12 for NAD, 0.33 for MAD, and 0.49 for the mean index. Residuals appeared normally distributed with a mean near zero and serial patterning was not evident. Trends in estimated indices were similar between the fishing only and striped bass S-H models, but the fishing only model trend was smoother (Figure 4). The S-H model was able to account for some year-to-year variability (Figure 4).

Parameters *r*, *K*, B_{1985}, Type III predation function terms *d* and *A*, and MUP of the original run of the base S-H model fell within jackknifed 90% intervals, and within 1% of their jackknifed means

and medians (Table 5). Bounds of the 90% intervals of *r, K,* B_{1985}*, A*, and MUP were within 5%, while *d* was less precise (9%). High precision of model parameters lead to precise estimates of ages 1+ Atlantic menhaden biomass (Figure 5), *D* (total biomass consumed by striped bass; Figure 6), M_2 (Figure 7), *F* (Figure 8), Z_2 (Figure 9), and D_t / P_t (Figure 10).

Models Based on BAM Biomass

Fishing only biomass dynamic models and S-H models using BAM ages 1+ Atlantic menhaden biomass estimates had the same AIC_c (-97), but the S-H model explained more of the observed variation in BAM biomass (r^2 = 0.47 versus 0.27 for the fishing only model; Table 6; Figure 11). Estimates of *r* and *K* from both models depicted a stock with modest productivity and high biomass (relative to the base S-H model). All estimated parameters were within bounds for both models using BAM biomass. The estimate of *r* was lower for the BAM S-H model (0.46) than the BAM fishing only model (0.59) and *K* was about 1.7-times higher for the BAM S-H model (Table 6; Figure 11). The estimate of MSY from the BAM fishing only model was 560,085 mt and MUP was estimated as 741,649 mt with the BAM S-H model. Maximum sustained yield is not used to manage Atlantic menhaden, but it is useful for comparisons with MUP from the S-H model.

Stock Status from the Base and BAM Based Steele-Henderson and Fishing Only Models

Relative biomass estimates from base and Ages 1+ BAM biomass based models depicted quite different status in the early part of the time-series and then converged in the early 1990s (Figure 12). The base S-H model indicated that biomass was initially high (B / B_{MUP} ~ 1.5), then declined steadily into the late 1990s (B / B_{MUP} ~ 0.7), increased sharply to near 1.0 by 2000, and finally increased to about 1.25 in 2014 and remained there through January 1, 2018. Biomass was below its threshold during 1990-2001. Estimated B / B_{MSY} from the base fishing only model followed a similar trajectory, but was 14% higher overall than indicated by the base S-H model. Relative biomass was a good deal higher (averaging 70% higher) for the fishing only model based on BAM biomass. The BAM fishing only biomass dynamic model (hereafter BAM fishing model) depicted a sharp rise in B / B_{MSY} between 1985 and 1990 (from 1.0 to 1.6), followed by a slow rise toward an asymptote of about 1.8 that was reached in 2001. The BAM S-H model B / B_{MUP} estimates indicated very low status in 1985 (B / B_{MUP} ~ 0.5), rising quickly to 0.9 by 1990, followed by a slight dip in the mid-to-late 1990s, and then a more-or-less steadily increased to 1.25 by 2018. The BAM S-H model estimated that biomass was below its threshold during 1985-2006 (Figure 12).

Base S-H model estimates of landings as a proportion of annual *SF* (H_t / SF_t) indicated that the ratio exceeded 1.0 seven times between 1990 and 2010; it has been between 0.69 and 0.86

since 2013 (Figure 13). The BAM S-H model indicated only a sustained period of H_t / SF_t above 1.0 during 1995-1998 and it has been at or below 0.60 since 2013 (Figure 13). An estimate of annual *SF* was needed to calculate F_{MUP} to estimate relative *F* for the S-H models.

Trends and magnitude of relative *F* (F / F_{MUP} for S-H models and F / F_{MSY} for fishing only models) were similar for the two base models and the BAM S-H model (Figure 14), although the span of years where relative *F* exceeded the threshold varied. Relative *F* was above the threshold intermittently during 1990-2010 with the base S-H model, during 1995-2001 with the BAM S-H model, and during 1990-1998 with the fishing only base model. All three of these models identified 1995-1998 as the period of highest *F*. The BAM fishing model indicated that relative *F* was well below the threshold during 1985-2017 and never exceeded 0.60 (Figure 14).

Trends and magnitude of relative M_2 (M_2 / Z_{MUP}) were similar for the base and BAM S-H models (Figure 15). Relative M_2 rose from less than 0.20 in 1985 to a plateau of 0.60-0.70 that was maintained from the mid-1990s to 2010. It then dropped to approximately 0.50 by 2013 and remained there through 2017 (Figure 15). Given that BAM assumed constant *M* over time, either S-H models found M_2 associated with the striped bass biomass trend that was not present or M_2 mortality was confounded by fishing-related parameters estimated in the age structured BAM and its assumption or age varying, constant *M* over time.

Relative Z_2 (Z_2 / Z_{MUP}) trends were similar for the base and BAM S-H models (Figure 16). This is not surprising, given similarities in relative *F* and relative M_2. Relative Z_2 was below the threshold during 1985-1989. Relative Z_2 estimated by the base S-H model consistently breached the threshold from 1990 to 1997 and intermittently through 2010. The BAM S-H model estimates breached the threshold during 1995-1999 and intermittently through 2004. Both fell below the threshold and remained at about 0.80 after 2012 (Figure 16).

Estimates of F / Z_2 indicated that *F* was the major influence on the stock until the early 1990s (BAM S-H model) to late 1990s (base S-H model; Figure 17). Estimates of F / Z_2 from the base S-H model were generally below the threshold after 1998, but were at or near it during 2001-2002 and 2011-2012. Estimates of F / Z_2 from the BAM S-H model fell below the threshold (0.4) and remained there after 1995. Base S-H model estimates of F / Z_2 were consistently higher than BAM S-H model estimates after 1990 (Figure 17).

Ranges of D_t / P_t of the two S-H models were similar: 1.1 – 3.8 for the base S-H model and 1.0 – 3.3 for the BAM S-H model (Figure 18), but dissimilar in trend until after 2000. Estimates from the base S-H model started high during 1985-1987 (3.5-3.8), fell to a nadir (1.1) during 1997-

1998, quickly rose to near 2.0 by 2001, dipped to 1.6 in 2002, rose again, remained near 2.0 during 2003-2011, climbed to about 2.8 in 2014, and remained there through 2017. Estimates of D_t / P_t from the BAM S-H model started at the lowest of the time-series (1.0 in 1985), rose rapidly to 2.0 by 1990, continued to rise to 2.5 in 1995, fell to 2.2 in 1998 and then rose steadily to 3.3 by 2017 (Figure 18). Both sets of D_t / P_t estimates fell below the minimum C_t estimates derived from bioenergetics models and were not obviously excessive. They were considered plausible. Highest estimates of D_t / P_t indicated that Ages 1+ Atlantic menhaden could comprise a large portion of Age 3+ striped bass diets.

Base Steele-Henderson Model Sensitivity Analyses

Sensitivity runs resulted in a "population" of base S-H models with well correlated parameters that produced the same general depiction of Atlantic menhaden (high *r* and low *K*) as the base S-H model (Table 6). Estimates of *r* ranged from 1.66 to 2.56; *K*, $9.7 \cdot 10^5 – 1.4 \cdot 10^6$ mt, B_{1985}, $7.1 \cdot 10^5 – 1.1 \cdot 10^6$ mt; *d*, 7.8 – 17.0 (two were at maximum constraint) and *A*, $7.8 \cdot 10^5 – 2.0 \cdot 10^6$ mt (Table 6). Correlations among S-H model parameters of the base S-H model and six sensitivity runs were high for *r*, *K*, B_{1985}, and *A*, and for *d* and *A* ($\rho \geq 0.90$ or ≤ -0.91; $P \leq 0.0064$; Table 7). Parameter *d* was modestly correlated with *r* ($\rho = 0.67$, $P = 0.10$) and *K* ($\rho = 0.63$, $P = 0.15$); inspection of scatter plots (not shown) did not indicate that estimates of *d* that fell at their maximum constraint were the sole source of scatter in these associations. High correlation of *r* and *K* led to estimates of MUP among the seven runs with a maximum difference of 4% from the base run (Table 6).

Base S-H model estimates of B / B_{MUP} (Figure 19), Z_2 / Z_{MUP} (Figure 20), and D_t / P_t during 1985-2017 (Figure 21) were closely bracketed by their counterparts in sensitivity runs. Substantially different conclusions about status were unlikely among the S-H model runs. Large differences among annual estimates of B / B_{MUP}, Z_2 / Z_{MUP}, and D_t / P_t were not present. Estimated percent differences of B / B_{MUP} from all sensitivity runs and the base run during 1985-2017 ranged from -7.7% to 4.5%, with a 90% interval of -4.4% to 3.3%, and averaged 0% (Table 8). Percent differences of Z_2 / Z_{MUP} from the all sensitivity runs and the base run ranged from -5.7% to 8.2%, with a 90% interval of -4.4% to 7.3%, and averaged 1.2%. Percent differences of D_t / P_t from the all sensitivity runs and the base run ranged from –10.8% to 14.2%, with a 90% interval of -6.1% to 8.0%, and an average difference of 1.0% (Table 8).

A striped bass S-H model using the PRFC index and NAD and MAD indices standardized to the PRFC index (PRFC S-H model) fit the data similarly to how RCPUE and NAD and MAD indices standardized to RCPUE fit the base model (Figure 22). The r^2 for the PRFC S-H model was 0.35 for the observed and estimated PRFC indices, 0.01 for NAD, 0.25 for MAD, and 0.40 for the

mean index (not included in the SSQ). Residuals appeared normally distributed and serial patterning was not evident.

Different conclusions about stock status were not likely if the PRFC index was substituted for the RCPUE index during 1985-2017. Trends in B / B_{MUP}, Z_2 / Z_{MUP}, and D_t / P_t during were very similar between the base run and the PRFC S-H model. Estimates of B / B_{MUP} from the PRFC S-H model were generally higher than for the base run (Figure 23); differences of the PRFC S-H model B / B_{MUP} and estimates of the base model ranged between -7% and 14%, with a 90% interval between 0% and 11%, and an average difference of 4%. Largest differences in B / B_{MUP} were found at the first two years of the time-series and during 1997-1999 (Figure 23). Estimates of Z / Z_{MUP} from the PRFC S-H model were generally lower than for the base run (Figure 24); differences of the PRFC S-H model Z / Z_{MUP} and estimates of the base model ranged between -7% and 2%, with a 90% interval between -6 % and -1%, and an average difference of -4%. Largest differences in Z / Z_{MUP} were during 1997-1999 (Figure 24). Estimates of D_t / P_t were similar (Figure 25); differences of the PRFC and the base model ranged between -12% and 20%, with a 90% interval between -5 % and 8%, and an average difference of 0%. Largest differences in D_t / P_t were located at the first two years of the time-series and during 1997-1999 (Figure 25).

Removal of up to four years from the end of the time-series in retrospective runs had minimal impact. Variability (SSQ / N) remained close to that of the base run (Table 9). Most parameters estimated were well correlated ($\rho > 0.90$ or < -0.90 for r, K, and B_{1985}, K and A, and A and d) among the retrospective runs. All combinations resulted in parameters that would generalize Atlantic menhaden as a small, productive stock (Table 9). Retrospective bias was not apparent in B / B_{MUP} (Figure 26), Z_2 / Z_{MUP} (Figure 27), and D_t / P_t (Figure 28) when up to four years were removed from the end of the 1985-2017 time series.

Removal of a single index from the time-series increased variability (SSQ / N) by about a third over the base run for the two pairings that included RCPUE and the variability of the run featuring only fishery-independent indices was nearly double that of the base run (Table 9). Few parameters were well correlated ($\rho > 0.90$ or < -0.90 for r and B_{1985} and B_{1985} and K; B_{1985} is more of a nuisance parameter than essential). Pairing RCPUE and MAD generally reproduced the parameters and metrics of the base run. All pairing combinations resulted in parameters that would generalize Atlantic menhaden as a highly productive stock. If the MAD index was included in the time-series, r ranged between 2.01 and 2.27; r equaled 1.26 for the run without the MAD index (RCPUE and NAD; Table 9). Estimates of K were similar for runs that included RCPUE (~1.1 to $1.4 \cdot 10^6$ mt) and higher (~$1.8 \cdot 10^6$ mt) for the run with only fishery-independent indices (Table 9).

Removal of the RCPUE index (i.e., fishery-independent indices remained) resulted in D_t / P_t estimates that exceeded the maximum estimated for striped bass from bioenergetics models during 1985-1989 and fell between the minimum and maximum during 1990-1993 and 2013-2017 (Figure 29). These estimates were considered unlikely and assessment based on the two fishery-independent indices alone would be biased. Remaining runs fell below the bioenergetics based criteria and estimates of D_t / P_t from these three runs with RCPUE were considered plausible. The RCPUE and NAD run indicated that ages 1+ Atlantic menhaden were a lesser component of Ages 3+ striped bass (low D_t / P_t), while the base run and run with RCPUE and MAD were similar and D_t / P_t was about 2-3 times that of the RCPUE and NAD run (Figure 29).

The RCPUE and MAD S-H model estimates of B / B_{MUP} were very close to the base run (Figure 30). All four runs indicated that B / B_{MUP} was above the threshold during 1985-1990. The base run, RCPUE and MAD run, and the RCPUE and NAD run fell below (breached) the B / B_{MUP} threshold during the 1990s. The base and two-index runs that included RCPUE remained near the threshold through 2011 and then climbed above 1.20 and remained there. The RCPUE and NAD run diverged from the base run in the early 1990s and for the remainder of the time-series provided a more optimistic view of B / B_{MUP} that was an additional 0.10 - 0.20 greater than the base run. Estimates of B / B_{MUP} from the MAD and NAD run reflected the unrealistically high estimates of consumption and were 0.15 to 0.25 lower than the base run after striped bass recovered in 1995 (Figure 30). Trends in Z_2 / Z_{MUP} were the converse of those described for B / B_{MUP} (Figure 31).

Base Steele-Henderson Model Predator Consumption Threshold

Striped Bass weights-at-age and D_t / P_t (base model only) at the four lags considered are presented in Table 10. Correlations of Striped Bass weight-at-age at ages 6-14 (except for 9 year-olds) and D_t / P_t with a two year lag were most consistent (ρ ranged between 0.43 and 0.59, $P \leq 0.05$; Table 11) and this lag was used in the linear regression to derive a threshold for consumption below which average weight was less likely to be maintained. These ages correspond to the coastal component of the Striped Bass stock and to sizes capable of eating ages 1+ Atlantic menhaden consistently (Uphoff and Sharov 2018).

The linear regression of standardized weight-at-age (weight-at-age of each year and age divided by the time-series weight for that age) of 6 to 14 year-old Striped Bass (it includes age 9) against D_t / P_t was significant ($r^2 = 0.22$, $P < 0.001$; Figure 32). The equation describing the relationship of standardized weight (SW) to average per Striped Bass consumption (D_t / P_t) two years earlier was

$$(15)\ SW = (0.074 \cdot D_t / P_t) + 0.86;$$

SE equaled 0.01 for the slope and 0.02 for the intercept. Average weight was predicted to occur when D_t / P_t was 2.0. Based on data used in the regression (Figure 32), there was a 63% chance that weight would be average to below average when D_t / P_t was 2.0 or less. This chance shrank to 18% when D_t / P_t was 2.2 or above and this value represented a potential target. A scatter plot of D_t / P_t and Z_2 / Z_{MUP} indicated that the thresholds corresponded to one another (i.e., D_t / P_t was 2.0 at $Z_2 / Z_{MUP} \sim 1.0$; Figure 33), although D_t / P_t associated with below average weights was predominate out to $Z_2 / Z_{MUP} \sim 0.90$. The potential target for D_t / P_t (2.2) was consistently met or exceeded once Z_2 / Z_{MUP} fell below 0.87 (Figure 33).

Forage Status of Ages 1+ Atlantic Menhaden for Striped Bass in 2017

Based on the base S-H model, ages 1+ Atlantic menhaden were at low risk of not maintaining their forage role for Striped Bass in 2017. Atlantic menhaden harvest was low relative to historic levels and estimated Striped Bass biomass was at its lowest since recovery in 2017. This combination led to relatively low demand. None of the proposed indicators (B / B_{MUP}, Z_2 / Z_{MUP}, D_t / P_t, F / Z_2, F / F_{MUP}, and H_t / SF) breached threshold conditions in 2017 and the risk that they did (based on jackknifed distributions for 2017) was estimated as 0% (Table 12). None of the 90% intervals overlapped a threshold. If the suggested target conditions ($D_t / P_t \geq 2.2$ and $Z_2 / Z_{MUP} < 0.87$) in the previous section are considered, then the risk of not meeting these targets was also zero. The base S-H model cannot address forage demand by other components of the ecosystem; these would be addressed through the MICE EWE model, the updated NWACS EWE model, and the multispecies catch-at-age model.

Base Steele-Henderson Model Projections

Two distributions provided the best depiction of jackknifed base S-H model parameters. A Laplace distribution (also known as a double exponential distribution) fit *K, d, A*, and Atlantic menhaden ages 1+ biomass on January 1, 2018, best. The distribution of *r* was best described by a log logistic distribution. Jackknifed estimates of the four S-H parameters needed for projections (*r, K, d*, and *A*) were weakly to moderately correlated (Table 13). Graphs of distributions are presented in Figures 34 - 36. Table 14 provides a summary of location, scale, and shape values assigned to distribution functions for each simulated parameter. The triangular distribution assigned to landings was described in Methods.

The Laplace distribution is a two parameter, symmetric, sharply peaked distribution (resembling a pointy witch's hat). This sharply peaked distribution reflected low variation in

jackknifed distributions. The probability density function describing the Laplace distribution in @Risk was

$$(15)\quad (1 / (\sqrt{2} \cdot \sigma)) \cdot e^{(-\sqrt{2} \cdot | x - u / \sigma |)};$$

where σ is a continuous scale parameter, x is a value in the distribution, and u is a location parameter (Palisade Corporation 2016).

The log-logistic distribution is the probability distribution of a variable whose logarithm has a logistic distribution. The distribution of *r* was asymmetric and skewed slightly towards smaller values. The probability density function describing the log logistic distribution in @Risk was

$$(16)\quad (\alpha \cdot t^{\alpha - 1}) / (\beta \cdot (1 + t^{\alpha})^{2});$$

where α is a continuous shape parameter (> 0), β is a continuous scale parameter (> 0), and t = (x – γ) / β with x equaling a value in the distribution and γ is a location parameter (Palisade Corporation 2016).

Biomass of ages 3+ Striped Bass in 2018 was set at the estimate for 2017 (134,796 mt). Striped Bass biomasses for 2018 and subsequent years were assumed to be normally distributed and were assigned a CV of 6% based on variation of biomass estimates in the recent assessment. Striped Bass recovery is based on an SSB target. Target ages 1+ Striped Bass biomass at target SSB for projections was estimated for ages 1+ (K. Drew, ASMFC, personal communication), but ages 3+ target biomass was needed for the S-H model. The median proportion of ages 1+ Striped Bass biomass that was comprised of ages 3+ (0.84) during the period the stock has been considered recovered (1995-2017) was multiplied by the target estimate for ages 1+ to approximate target biomass of ages 3+ Striped Bass (260,685 mt) capable of eating ages 1+ Atlantic menhaden at target SSB.

The status quo projection indicated very low risk that ages 1+ Atlantic menhaden's forage role would not be maintained (Table 15). At "equilibrium", the 90% CI's of B / B_{MUP}, Z_2 / Z_{MUP}, and D_t / P_t did not overlap their proposed thresholds and estimated risk of breaching these thresholds was 0%. Projected D_t / P_t averaged 2.89 (45% higher than the threshold), a value associated with higher than average weights (i.e., better condition) of ages 6+ Striped Bass (Table 15). Maintaining the forage role of ages 1+ Atlantic menhaden for Striped Bass was likely.

The projection where Striped Bass biomass increased to recovered status (ages 3+ biomass nearly doubles) and Atlantic menhaden are fished at one-half their target *F* represented a high risk strategy (Table 15). Substantial portions of 90% intervals of all three metrics overlapped their thresholds. Risk of breaching the B / B_{MUP} threshold was 80%; risk of breaching the Z_2 / Z_{MUP} threshold, 55%; and the risk of breaching the D_t / P_t threshold, 85%. Average yield would

be 26% less than in 2017 and average D_t / P_t was 10% less than the threshold (Table 15). Maintaining the forage role of ages 1+ Atlantic menhaden for Striped Bass was unlikely with this strategy.

The projection where Striped Bass biomass increased to recovered status and Atlantic menhaden were fished at their target *F* had the highest risk (Table 15). Ninety percent intervals of all three metrics came close to completely overlapping their thresholds. Risk of breaching the B / B_{MUP} threshold was 100%; breaching the Z_2 / Z_{MUP} threshold, 95%; and the risk of breaching the D_t / P_t threshold was 100%. Yield was 26% greater than in 2017 and average D_t / P_t was 30% less than the threshold (Table 15). Maintaining the forage role of ages 1+ Atlantic menhaden for Striped Bass was unlikely.

The projection with predator biomass increasing to a point where their consumption threshold is met and Atlantic menhaden harvested at their current level represented a high-risk option, but not as risky as the previous two (Table 15). Ninety percent intervals of all three metrics overlapped their thresholds near the interval midpoint. Risk of breaching the B / B_{MUP} threshold was 45%; risk of breaching the Z_2 / Z_{MUP} threshold, 60%; and the risk of breaching the D_t / P_t threshold was 50%. Striped Bass biomass was 83% of the target to maintain D_t / P_t at its threshold (Table 15). Risk that the forage role of ages 1+ Atlantic menhaden for Striped Bass would not be met was high. Atlantic menhaden harvest in this projection would be considered low by historical standards and Striped Bass biomass had to be below its current target in order to meet threshold (not target) D_t / P_t. Trade-offs between Striped Bass biomass and Atlantic menhaden yield will have to be considered if feeding success and condition of Striped Bass becomes a management consideration.

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Tables

Table 1. Biomass indices for the base Steele-Henderson and fishing only biomass dynamic models. NAD, and MAD indices are scaled into common RCPUE units. Mean index = average of each year's available indices.

YEAR	RCPUE	NAD	MAD	Mean index
1985	0.54		1.23	0.88
1986	0.65		1.20	0.93
1987	0.58		1.32	0.95
1988	0.48		1.27	0.87
1989	0.43		0.82	0.62
1990	0.48	0.68	0.64	0.60
1991	0.41	0.26	0.53	0.40
1992	0.34	0.65	0.90	0.63
1993	0.49	0.54	0.40	0.47
1994	0.41	0.41	0.94	0.59
1995	0.56	0.70	0.92	0.73
1996	0.46	0.45	0.40	0.43
1997	0.30	0.24	0.39	0.31
1998	0.55	0.20	0.49	0.41
1999	0.32	1.18	0.35	0.62
2000	0.55	0.54	0.98	0.69
2001	0.70	0.39	0.58	0.56
2002	0.52	0.93	0.31	0.59
2003	0.48	0.29	0.69	0.49
2004	0.52	0.31	0.35	0.40
2005	0.46	0.68	0.92	0.69
2006	0.56	0.48	0.27	0.44
2007	0.60	0.71	0.58	0.63
2008	0.65	0.57	0.26	0.49
2009	0.63	0.24	0.62	0.50
2010	0.76	0.52	0.58	0.62
2011	0.83	0.55	0.43	0.60
2012	0.84	1.05	0.38	0.76
2013	0.82	0.37	0.62	0.60
2014	0.80	0.96	1.04	0.93
2015	0.86	1.38	1.35	1.20
2016	0.73	0.93	0.39	0.68
2017	1.00	0.45	0.32	0.59

Table 2. Correlations among biomass indices and with the mean index (average of each year's available indices). ρ = correlation coefficient.

Index	Statistic	RCPUE	NAD	MAD
	ρ	0.24		
NAD	*P*	0.22		
	N	28		
	ρ	-0.02	0.29	
MAD	*P*	0.893	0.137	
	N	33	28	
	ρ	0.39	0.80	0.80
Mean index	*P*	0.03	<.0001	<.0001
	N	33	28	33

Table 3. Correlations of candidate predator biomasses and Atlantic menhaden ages 1+ biomass indices. ρ = correlation coefficient.

Predator	Statistic	RCPUE	NAD	MAD
	ρ	-0.12	-0.29	-0.63
Striped Bass	P	0.51	0.13	<.0001
	N	33	28	33
	ρ	0.21	0.04	0.45
Bluefish	P	0.25	0.86	0.008
	N	33	28	33
	ρ	0.31	0.16	0.05
Spiny Dogfish	P	0.08	0.42	0.79
	N	33	28	33

Table 4. Summary of results for index based fishing only biomass dynamic models and Steele-Henderson predator-prey models with candidate predators. Shaded cells indicate parameters at constraint. Parameter *r* is the intrinsic rate of increase; *K* is maximum biomass of ages 1+ Atlantic menhaden; B_{1985} is the initial biomass in 1985 of ages 1+ Atlantic menhaden; *d* is maximum Atlantic menhaden biomass consumption per predator biomass; *A* of ages 1+ Atlantic menhaden where predator satiation begins; and MT = metric tons. Estimates with parameter *d* = 0 do not produce M_2.

Model Predator 1 Predator 2	Fishing	Fishing Bass	Fishing Bluefish	Fishing Dogfish	Fishing Bass Bluefish
AIC_c	-156	-156	-149	-154	-149

SSQ / N	0.170	0.161	0.170	0.170	0.170
			Parameters		
r	0.32	2.27	0.30	0.32	3.00
K (MT)	3,430,522	1,071,224	4,998,378	3,433,550	4,456,472
B_{1985} (MT)	3,022,384	775,014	2,977,523	3,022,199	3967296.312
q	0.00000030	0.00000110	0.00000032	0.00000030	0.00000019
Predator 1 d		11.0	5.1	0	14.0
Predator 1 A (MT)		1,143,513	4,933,403	10,000,000	507,280
Predator 2 d					0
Predator 2 A (MT)					10,000,000

Table 5. Summarized distributions of jackknifed Steele-Henderson model parameters. Parameter *r* is the intrinsic rate of increase; *K* is maximum biomass of ages 1+ Atlantic menhaden; B_{1985} is the initial biomass in 1985 of ages 1+ Atlantic menhaden; *d* is maximum Atlantic menhaden biomass consumption per predator biomass; *A* of ages 1+ Atlantic menhaden where predator satiation begins; and MT = metric tons.

Parameter	Mean	Median	5%	95%	Minimum	Maximum	Original
r	2.30	2.29	2.27	2.33	2.23	2.46	2.27
K (MT)	1,060,962	1,064,665	1,032,321	1,079,744	1,003,265	1,113,646	1,071,224
B_{1985} (MT)	765,746	768,435	740,549	780,936	576,377	889,510	775,014
Striped Bass *d*	11.0	11.0	10.4	11.5	9.3	11.8	11.0
Striped Bass *A* (MT)	1,131,812	1,140,036	1,092,129	1,144,456	1,057,633	1,177,933	1,143,513
MUP (MT)	608,731	609,302	591,877	619,413	577,080	637,223	608,517

Table 6. Summary of results for the BAM fishing only biomass dynamic model and BAM Steele-Henderson Striped Bass model. Parameter *r* is the intrinsic rate of increase; *K* is maximum biomass of ages 1+ Atlantic menhaden; B_{1985} is the initial biomass in 1985 of ages 1+ Atlantic menhaden; *d* is maximum Atlantic menhaden biomass consumption per predator biomass; *A* of ages 1+ Atlantic menhaden where predator satiation begins; and MT = metric tons.

Model	Fishing	S-H
	Statistics	
AIC_c	-97	-97
SSQ / N	0.040	0.031
r^2	0.27	0.47
	Parameters	
r	0.59	0.46
K (MT)	3,810,717	6,491,268
B_{1985} (MT)	1,832,533	1,768,486
d		7.5
A (MT)		4,500,949

Table 6. Model parameters for base and sensitivity runs. Grey shading indicates parameter is at maximum constraint. See Methods for descriptions of sensitivity runs. Parameter *r* is the intrinsic rate of increase; *K* is maximum biomass of ages 1+ Atlantic menhaden; B_{1985} is the initial biomass in 1985 of ages 1+ Atlantic menhaden; *d* is maximum Atlantic menhaden biomass consumption per predator biomass; *A* of ages 1+ Atlantic menhaden where predator satiation begins; MUP = maximum usable production, and MT = metric tons.

	Parameter					
Model run	*r*	*K* (MT)	B_{1985} (MT)	*d*	*A* (MT)	MUP (MT)
Base	2.27	1,071,224	775,014	11.0	1,143,513	608,517
Long	2.56	971,189	706,019	7.0	783,581	621,302
d bio	2.01	1,200,251	871,548	15.6	1,548,475	602,859
d wider	1.66	1,402,670	1,092,780	17.0	2,025,389	582,062
d constraint	2.21	1,093,466	787,412	12.6	1,263,289	605,021
minus 20%	2.05	1,175,749	910,940	9.0	1,151,076	602,375
plus 20%	2.22	1,089,415	777,844	17.0	1,477,231	604,163

Table 7. Correlations among model parameters for base and sensitivity runs. *n* = 7.

Parameter	Statistic	r	K	1985 biomass	Bass d
K	ρ	-0.99			
	P	<.0001			
1985 biomass	ρ	-0.96	0.99		
	P	0.0004	<.0001		
d	ρ	-0.67	0.63	0.50	
	P	0.1018	0.1315	0.2522	
A	ρ	-0.91	0.90	0.83	0.90
	P	0.0044	0.0053	0.0217	0.0064

Table 8. Summarized percentage differences between S-H model base run and sensitivity analyses estimates of B / B_{MUP}, Z / Z_{MUP}, and D_t / P_t estimates for 1985-2017.

Sensitivity run	Base	Long run	d penalty	d bioen	d wide	minus 20%	plus 20%
				B / B_{MUP}			
Maximum	4.5%	-0.5%	4.5%	4.5%	3.6%	0.9%	2.9%
Minimum	-7.7%	-4.8%	-0.6%	-0.6%	-7.0%	-5.7%	1.7%
5th %	-4.4%	-4.6%	0.1%	0.1%	-6.2%	-5.0%	1.7%
95th %	3.3%	-1.3%	3.4%	3.4%	3.0%	-0.4%	2.8%
Median	1.2%	-3.7%	2.6%	2.6%	0.1%	-2.3%	2.4%
Average	0.0%	-3.4%	2.3%	2.3%	-0.6%	-2.6%	2.3%
				Z / Z_{MUP}			
Maximum	8.2%	7.5%	8.2%	-1.1%	3.3%	4.7%	-0.7%
Minimum	-5.7%	0.8%	4.7%	-5.0%	-5.6%	0.6%	-5.7%
5th %	-4.4%	1.4%	4.9%	-4.7%	-4.6%	0.8%	-4.9%
95th %	7.3%	7.4%	7.7%	-1.6%	2.7%	4.0%	-0.9%
Median	1.5%	4.1%	6.5%	-3.0%	-0.6%	2.9%	-2.5%
Average	1.2%	4.5%	6.5%	-3.0%	-0.5%	2.7%	-2.9%
				D_t / P_t			
Maximum	14.2%	9.5%	5.2%	5.2%	14.2%	9.1%	4.5%
Minimum	-10.8%	-6.5%	-8.5%	-8.5%	-10.8%	-5.3%	-7.8%
5th %	-6.1%	-6.1%	-6.3%	-6.3%	-1.6%	-2.8%	-6.5%
95th %	8.0%	8.1%	4.2%	4.2%	9.9%	6.5%	3.7%
Median	1.2%	-2.6%	1.0%	1.0%	6.3%	2.3%	0.8%
Average	1.0%	1.0%	1.3%	1.5%	2.7%	1.2%	0.2%

Table 9. Model parameters for base (1985-2017) and retrospective runs. Parameter *r* is the intrinsic rate of increase; *K* is maximum biomass of ages 1+ Atlantic menhaden; B_{1985} is the initial biomass in 1985 of ages 1+ Atlantic menhaden; *d* is maximum Atlantic menhaden biomass consumption per predator biomass; *A* of ages 1+ Atlantic menhaden where predator satiation begins; MUP = maximum usable production, and MT = metric tons.

	Parameters					
	r	*K*	B_{1985} (MT)	*d*	*A* (MT)	SSQ / N
Base run	2.27	1,071,224	775,014	11.0	1,143,513	0.16
End year			Retrospective			
2013	1.98	1,267,432	944,767	16.9	1,692,663	0.15
2014	2.40	1,042,689	767,328	12.8	1,178,648	0.15
2015	2.13	1,128,231	820,564	10.4	1,169,501	0.16
2016	2.33	1,042,940	742,861	11.6	1,132,136	0.16
Index pairs			Index removal			
RCPUE MAD	2.01	1,140,899	824,306	17.0	1,688,439	0.21
RCPUE NAD	1.26	1,360,902	767,694	7.7	2,138,622	0.22
NAD MAD	2.12	1,769,138	1,459,544	17.0	1,363,111	0.31

Table 10. Per bass biomass consumption of ages 1+ Atlantic menhaden biomass estimated by the base Steele-Henderson Model (and D_t / P_t) at four lags and Striped Bass weight-at-age estimates (kg on January 1) from the 2018 stock assessment used in correlation analyses. Age = age of Striped Bass that mean weight was estimated.

	D_t / P_t lag (years)				Age (years)											
Year	0	1	2	3	3	4	5	6	7	8	9	10	11	12	13	14
1995	1.85				1.35	2.18	2.77	3.65	5.38	6.16	7.27	8.86	7.57	9.73	10.96	12.08
1996	1.20	1.85			1.47	2.32	3.23	4.52	6.39	7.11	7.81	9.20	9.31	10.10	11.88	13.03
1997	1.09	1.20	1.85		1.18	2.46	2.81	3.64	4.51	5.07	6.73	9.17	9.94	10.24	12.29	13.80
1998	1.11	1.09	1.20	1.85	1.20	1.62	2.25	2.95	4.69	5.66	6.82	7.03	7.76	9.87	10.82	12.10
1999	1.33	1.11	1.09	1.20	1.11	1.44	1.91	2.51	3.36	5.03	6.56	7.85	8.69	9.76	11.67	13.33
2000	1.90	1.33	1.11	1.09	1.10	1.45	1.96	2.79	3.89	5.09	7.11	7.37	9.70	10.70	12.68	14.56
2001	2.00	1.90	1.33	1.11	1.12	1.75	2.21	3.25	4.12	5.02	6.36	7.79	8.65	8.29	10.42	11.64
2002	1.58	2.00	1.90	1.33	1.06	1.51	2.18	3.17	4.19	5.48	6.03	7.56	9.09	9.75	11.53	13.05
2003	1.95	1.58	2.00	1.90	1.00	1.40	2.20	3.20	4.10	5.20	6.10	7.20	8.50	9.40	10.94	12.33
2004	2.05	1.95	1.58	2.00	0.84	1.40	2.43	3.11	4.14	5.17	6.07	7.12	8.18	9.03	10.55	11.85
2005	1.89	2.05	1.95	1.58	1.14	1.64	2.22	3.23	4.18	5.64	6.38	7.21	8.51	10.00	11.30	12.74
2006	2.18	1.89	2.05	1.95	0.81	1.35	1.96	2.80	3.84	5.35	6.70	7.41	8.58	9.40	11.29	12.81
2007	2.01	2.18	1.89	2.05	0.94	1.30	2.10	3.07	4.31	5.32	6.89	7.84	9.39	10.12	12.16	13.82
2008	2.06	2.01	2.18	1.89	1.04	1.43	2.14	3.47	5.05	5.51	6.69	8.26	9.19	9.82	11.77	13.24
2009	2.10	2.06	2.01	2.18	1.03	1.41	1.92	3.29	4.49	5.74	6.87	7.73	8.81	9.47	11.35	12.76
2010	2.20	2.10	2.06	2.01	1.11	1.41	1.99	3.34	4.27	5.21	6.27	7.65	8.97	9.15	11.09	12.49
2011	2.02	2.20	2.10	2.06	1.04	1.55	2.00	3.08	4.10	5.13	6.41	7.54	8.20	9.98	11.34	12.85
2012	2.27	2.02	2.20	2.10	1.01	1.67	2.30	3.25	4.44	5.88	6.57	8.31	9.05	10.41	12.12	13.69
2013	2.39	2.27	2.02	2.20	0.96	1.39	2.27	3.38	4.14	5.30	6.69	7.55	9.26	10.44	12.12	13.78
2014	2.81	2.39	2.27	2.02	0.89	1.27	2.15	3.07	4.28	5.30	6.99	8.43	9.17	11.91	13.50	15.55
2015	2.74	2.81	2.39	2.27	0.92	1.59	2.50	3.75	4.56	5.69	6.97	7.69	8.95	10.54	11.96	13.48
2016	2.84	2.74	2.81	2.39	0.78	1.25	2.17	3.40	4.75	6.05	7.06	8.92	10.03	11.23	13.42	15.31
2017	2.86	2.84	2.74	2.81	1.06	1.59	2.49	3.28	4.46	5.31	6.38	8.57	9.78	10.81	13.06	14.85

Table 11. Results of correlation analysis of Striped Bass weight-at-age and estimates of consumption of age-1+ Atlantic menhaden per Striped Bass from the base Steele-Henderson model. Age = age of Striped Bass that mean weight was estimated; ρ = Pearson correlation.

		Age											
Lag (years)	Statistic	3	4	5	6	7	8	9	10	11	12	13	14
0	ρ	-0.67	-0.56	-0.26	-0.05	-0.16	-0.10	-0.08	0.03	0.28	0.42	0.47	0.50
	P	0.0005	0.0055	0.226	0.8236	0.4766	0.637	0.7071	0.8751	0.1991	0.048	0.0247	0.0162
	N	23	23	23	23	23	23	23	23	23	23	23	23
1	ρ	-0.47	-0.33	0.04	0.31	0.18	0.21	0.02	0.22	0.30	0.37	0.41	0.40
	P	0.0258	0.1297	0.8591	0.1644	0.423	0.3546	0.9249	0.3275	0.1734	0.0913	0.0599	0.0652
	N	22	22	22	22	22	22	22	22	22	22	22	22
2	ρ	-0.51	-0.16	0.24	0.59	0.52	0.51	0.08	0.52	0.43	0.47	0.52	0.49
	P	0.0191	0.4837	0.29	0.0047	0.0154	0.0181	0.7303	0.0165	0.0514	0.0302	0.0169	0.0246
	N	21	21	21	21	21	21	21	21	21	21	21	21
3	ρ	-0.47	-0.24	0.44	0.52	0.53	0.44	0.15	0.42	0.25	0.40	0.38	0.35
	P	0.0354	0.3076	0.0553	0.0177	0.0153	0.0543	0.5227	0.0627	0.2963	0.083	0.099	0.1327
	N	20	20	20	20	20	20	20	20	20	20	20	20

Table 12. Summary of metrics, conditions for breaching their thresholds, estimated risk of breaching their thresholds, and mean and 5th and 95th percentiles in 2017.

			Statistic		
Metric	Threshold	Risk (%)	Mean	5th %	95th %
B / B_{MUP}	≤ 1.0	0	1.27	1.26	1.29
Z_2 / Z_{MUP}	≥ 1.0	0	0.73	0.71	0.74
D_t / P_t	≤ 2.0	0	2.87	2.72	2.96
F / Z_2	≤ 0.4	0	0.31	0.30	0.32
F / F_{MUP}	≥ 1.0	0	0.62	0.60	0.64

Table 13. Correlations of Steele-Henderson model parameters used in projections. Parameter *r* is the intrinsic rate of increase; *K* is maximum biomass of ages 1+ Atlantic menhaden; *d* is maximum Atlantic menhaden biomass consumption per predator biomass; *A* of ages 1+ Atlantic menhaden where predator satiation begins; MUP = maximum usable production, and MT = metric tons.

Parameter	r	K	d
K	-0.50		
d	0.11	0.39	
A	-0.59	0.44	0.55

Table 14. Summary of parameters, their distribution, and shape, scale, and location values for their probability density functions used in Monte Carlo simulations of four management scenarios.

Parameter	Species	Distribution	Shape	Scale	Location
r	Menhaden	Log logistic	$\alpha = 0.10$	$\beta = 7.75$	$\gamma = 2.19$
K	Menhaden	Laplace		$\sigma = 15{,}713$	$u = 1{,}064{,}665$
d	Bass	Laplace		$\sigma = 0.30$	$u = 11.0$
A	Bass	Laplace		$\sigma = 17{,}155$	$u = 1{,}140{,}035$
2018 biomass	Menhaden	Laplace		$\sigma = 8{,}903$	$u = 676{,}885$
2018 biomass	Bass	Normal		CV = 0.06	$u = 134{,}796$

Table 15. Summary of projection results. Bass = Ages 3+ Striped Bass. Atlantic menhaden = Ages 1+ Atlantic menhaden. All parameters reported are for terminal year estimates that were considered "equilibrium" estimates for a strategy. 5% and 95% = bounds of the 90% percentile interval for simulated results. MT = metric tons.

Species	Parameter	Mean	5%	95%	Threshold breach risk
Strategy		Status Quo			
Bass	Biomass (MT)	134,000			
Menhaden	Harvest (MT)	175,000			
Menhaden	B / B_{MUP}	1.28	1.22	1.33	0%
Menhaden	Z / Z_{MUP}	0.72	0.67	0.78	0%
Bass	D_t / P_t	2.89	2.7	3.09	0%
Strategy		1/2 Menhaden target F, bass recover			
Bass	Biomass (MT)	260,000			
Menhaden	Harvest (MT)	132,000			
Menhaden	B / B_{MUP}	0.95	0.85	1.05	< 80%
Menhaden	Z / Z_{MUP}	1.05	0.81	1.34	< 55%
Bass	D_t / P_t	1.83	1.49	2.13	< 85%
Strategy		Menhaden target F, bass recover			
Bass	Biomass (MT)	260,000			
Menhaden	Harvest (MT)	226,000			
Menhaden	B / B_{MUP}	0.82	0.74	0.89	100%
Menhaden	Z / Z_{MUP}	1.19	1.00	1.42	< 95%
Bass	D_t / P_t	1.40	1.18	1.61	100%
Strategy		Menhaden at current harvest, bass Dt / Pt at threshold			
Bass	Biomass (MT)	215,000			
Menhaden	Harvest (MT)	175,000			
Menhaden	B / B_{MUP}	1.01	0.92	1.10	< 45%
Menhaden	Z / Z_{MUP}	0.99	1.10	1.21	< 60%
Bass	D_t / P_t	2.01	2.23	2.23	< 50%

Figures

Figure 1. Time-series (1985-2017) of ages 1+ Atlantic menhaden relative biomass indices. NAD and MAD indices are standardized into RCPUE units. Mean = average of each year's available indices.

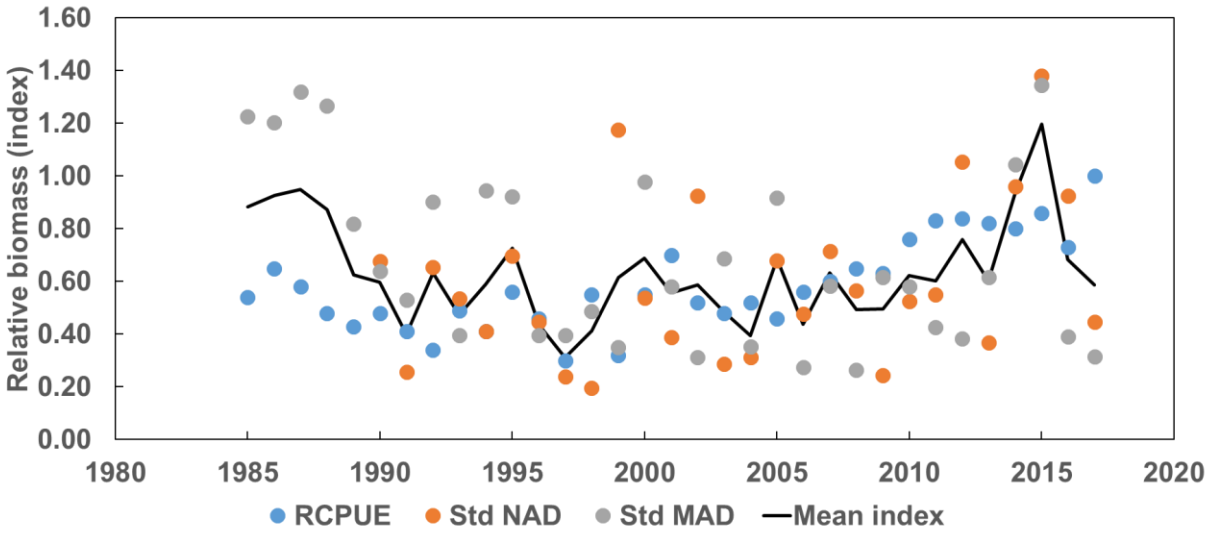


Figure 2. Metric tons (MT) of ages 1+ Atlantic menhaden harvested.

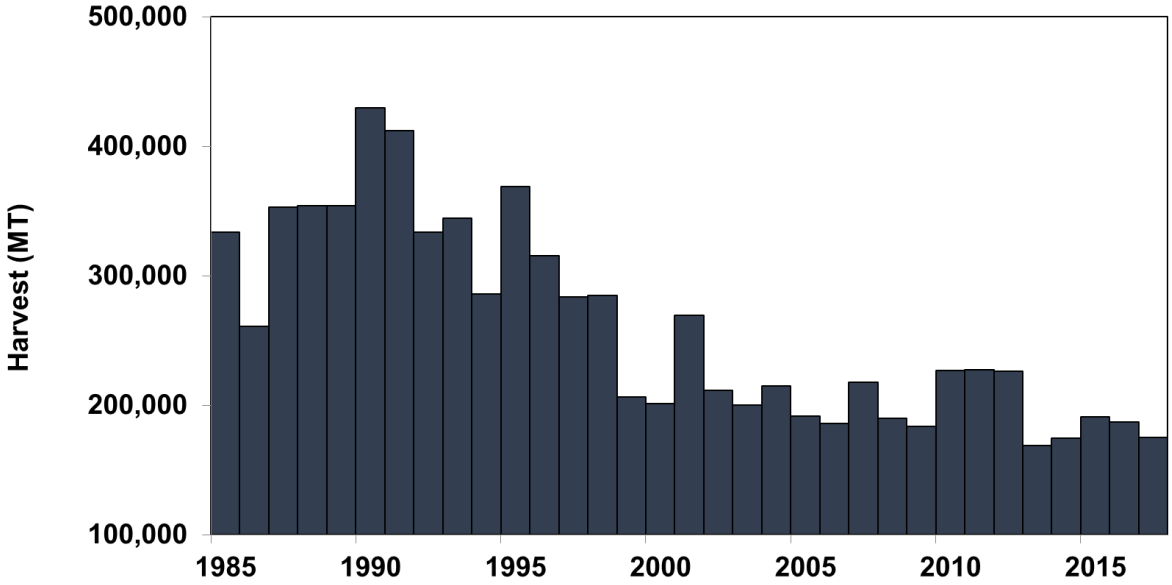


Figure 3. Biomass (metric tons, MT) of candidate predators capable of feeding on ages 1+ Atlantic menhaden.

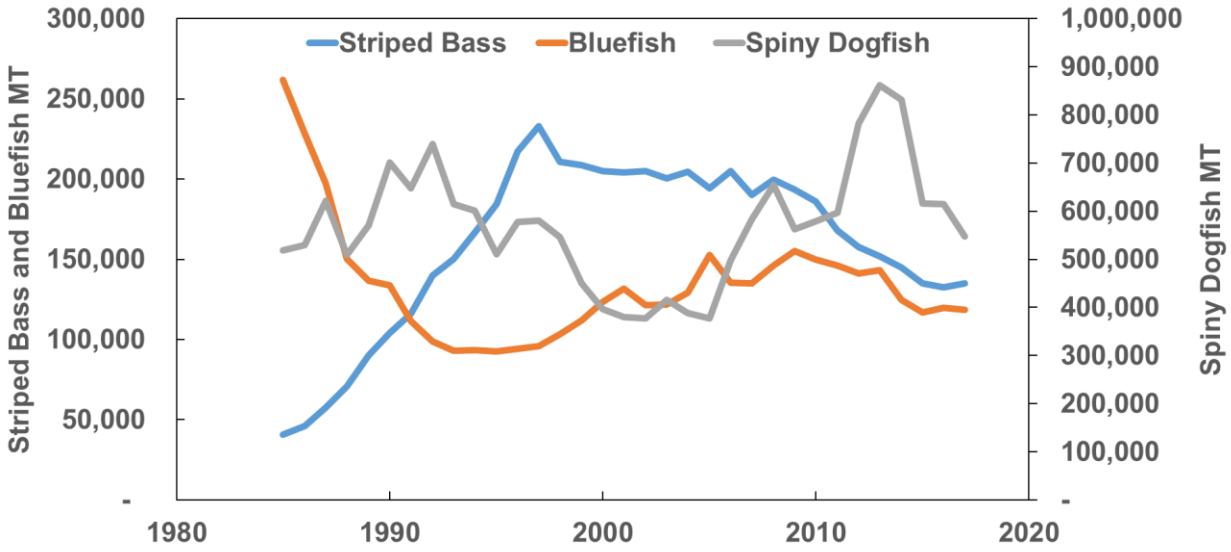


Figure 4.Time-series (1985-2017) of ages 1+ Atlantic menhaden RCPUE, NAD, and MAD relative biomass indices, their average, and time-series estimated by base fishing only and Steele-Henderson (S-H) models (fishing and Striped Bass predation). NAD and MAD indices are standardized into RCPUE units. Mean = average of each year's available indices.

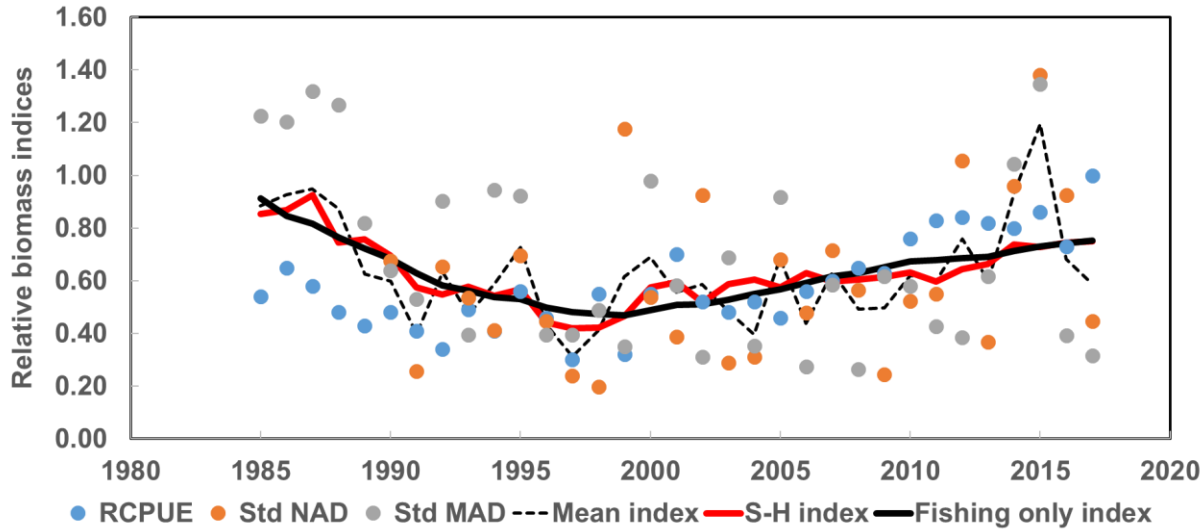


Figure 5. Time-series of ages 1+ Atlantic menhaden biomass estimated by the base Steele-Henderson model (fishing and Striped Bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile). MT = metric tons.

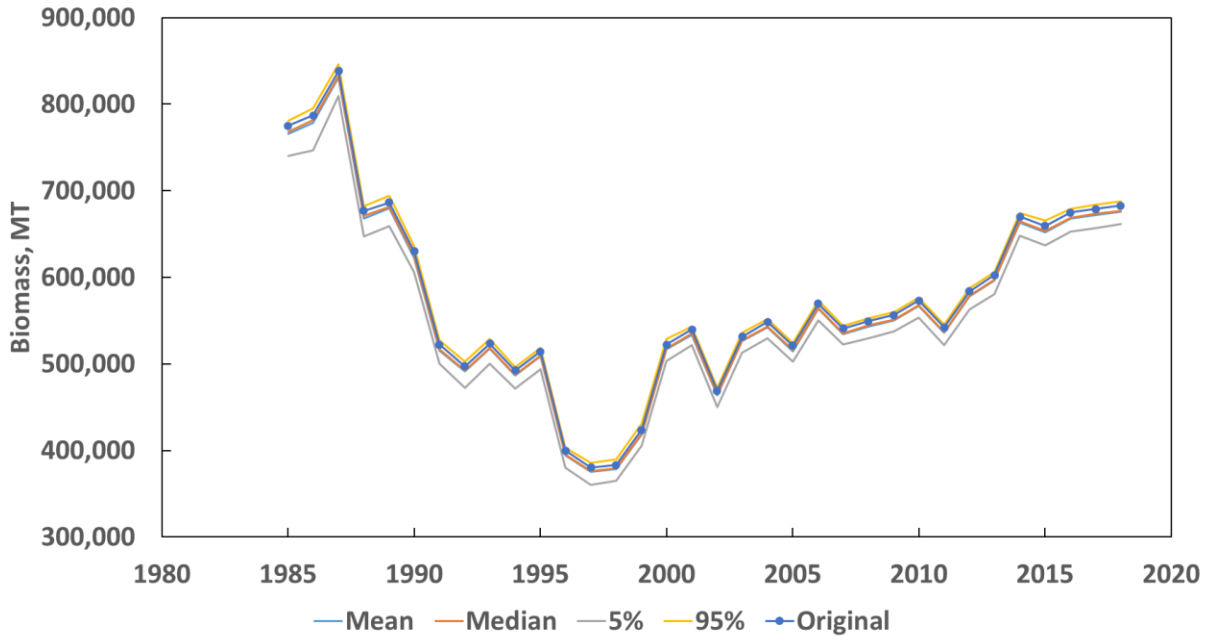


Figure 6. Time-series of ages 1+ Atlantic menhaden biomass consumed by Striped Bass (D_t) estimated by the base Steele-Henderson model (fishing and Striped Bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile). MT = metric tons.

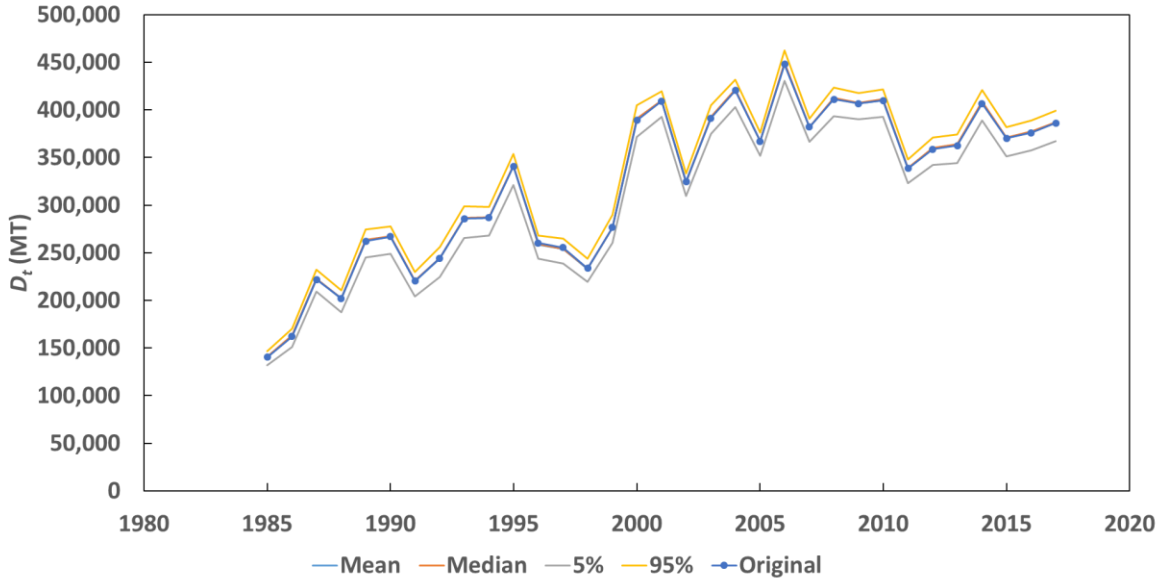


Figure 7. Time-series of ages 1+ Atlantic menhaden biomass M_2 estimated by the base Steele-Henderson model (fishing and Striped Bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile).

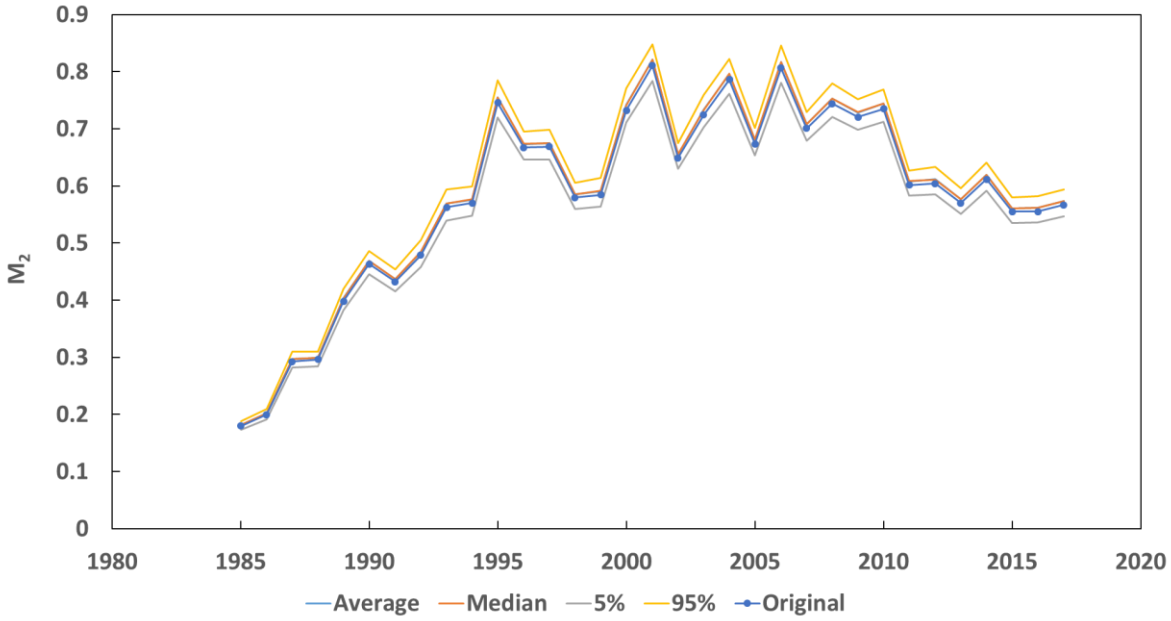


Figure 8. Time-series of ages 1+ Atlantic menhaden biomass *F* estimated by the base Steele-Henderson model (fishing and Striped Bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile).

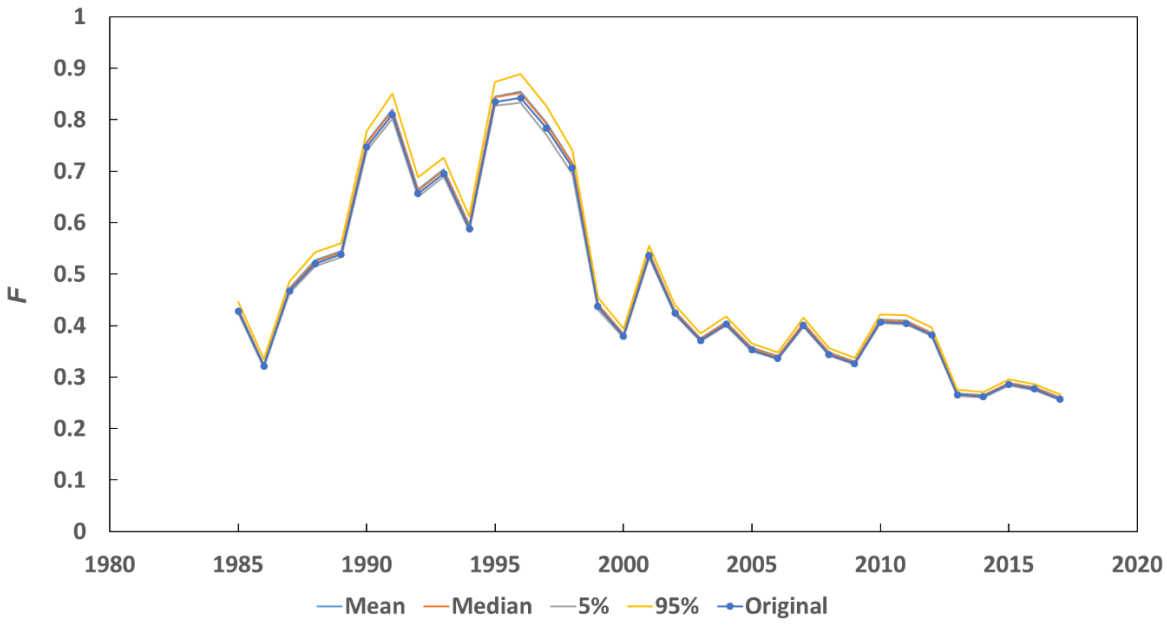


Figure 9. Time-series of ages 1+ Atlantic menhaden biomass Z_2 ($F + M_2$) estimated by the base Steele-Henderson model (fishing and Striped Bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile).

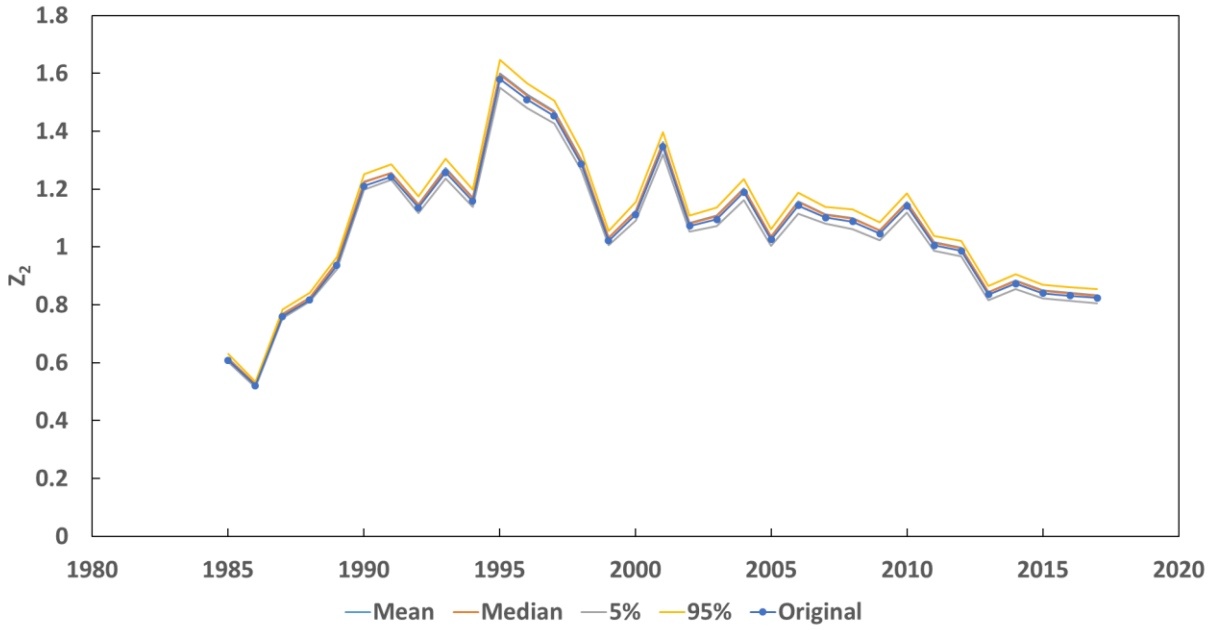


Figure 10. Time-series of annual ages 1+ Atlantic menhaden biomass consumed per Striped Bass biomass (D_t / P_t as MT consumed / MT Striped Bass) estimated by the base Steele-Henderson model (fishing and Striped Bass predation), and distribution of its jackknifed estimates (mean, median, 5th percentile, and 95th percentile). MT = metric tons.

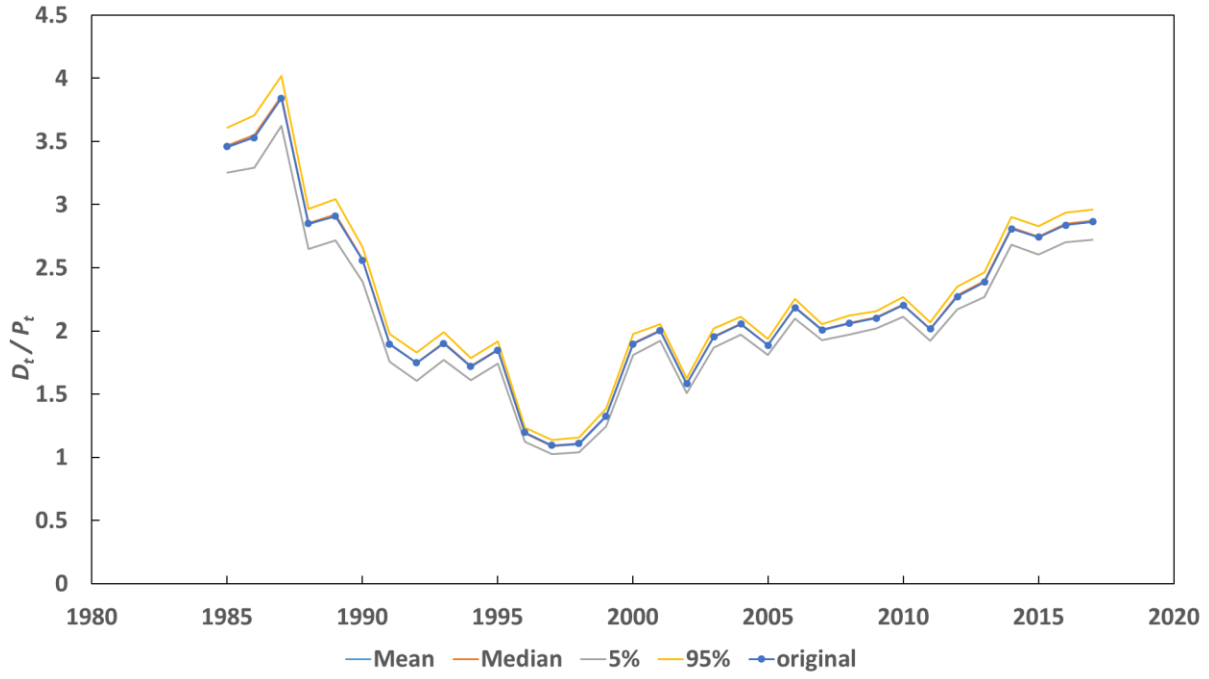


Figure 11. Time-series (1985-2017) of ages 1+ Atlantic menhaden biomass estimated by BAM, and time-series of ages 1+ Atlantic menhaden biomass estimated by a fishing only biomass dynamic model and a Steele-Henderson model (fishing and Striped Bass predation) fit to BAM biomass estimates.

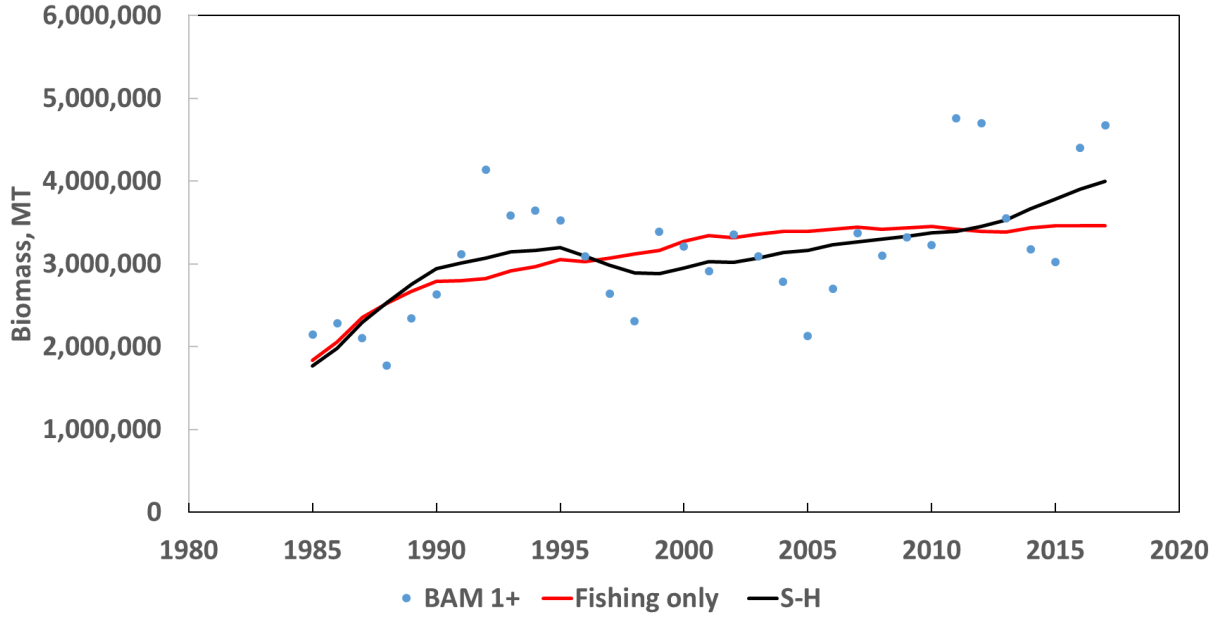


Figure 12. Relative biomass estimates from base and BAM Steele-Henderson (S-H) models (fishing and Striped Bass predation) and fishing only biomass dynamic models. Relative biomass = B / B_{MUP} for S-H models and B / B_{MSY} for fishing only models. Values at 1.0 or less breached the threshold.

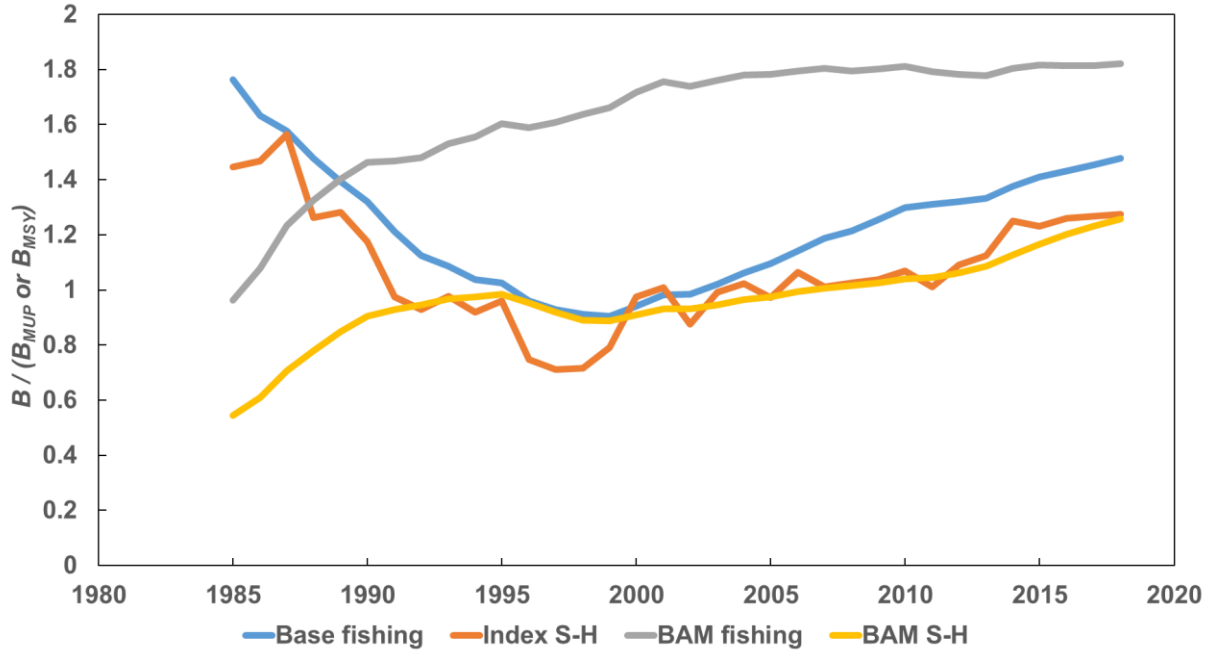


Figure 13. Harvest / SF (SF = surplus production available to the fishery after predation losses) from base and BAM Steele-Henderson (S-H) models (fishing and Striped Bass predation). Values at 1.0 or more breached the threshold.

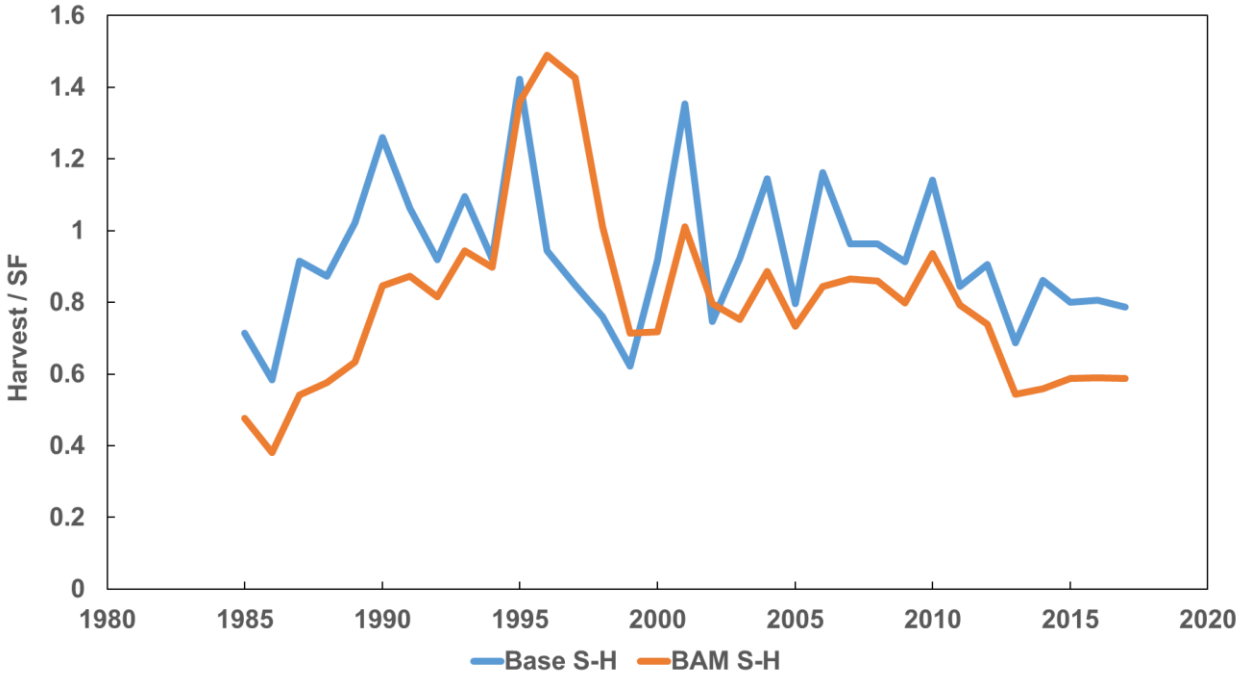


Figure 14. Relative *F* estimates from base and BAM Steele-Henderson (S-H) models (fishing and Striped Bass predation) and fishing only biomass dynamic models. Relative $F = F / F_{MUP}$ for S-H models and F / F_{MSY} for fishing only models. Values at 1.0 or more breached the threshold.

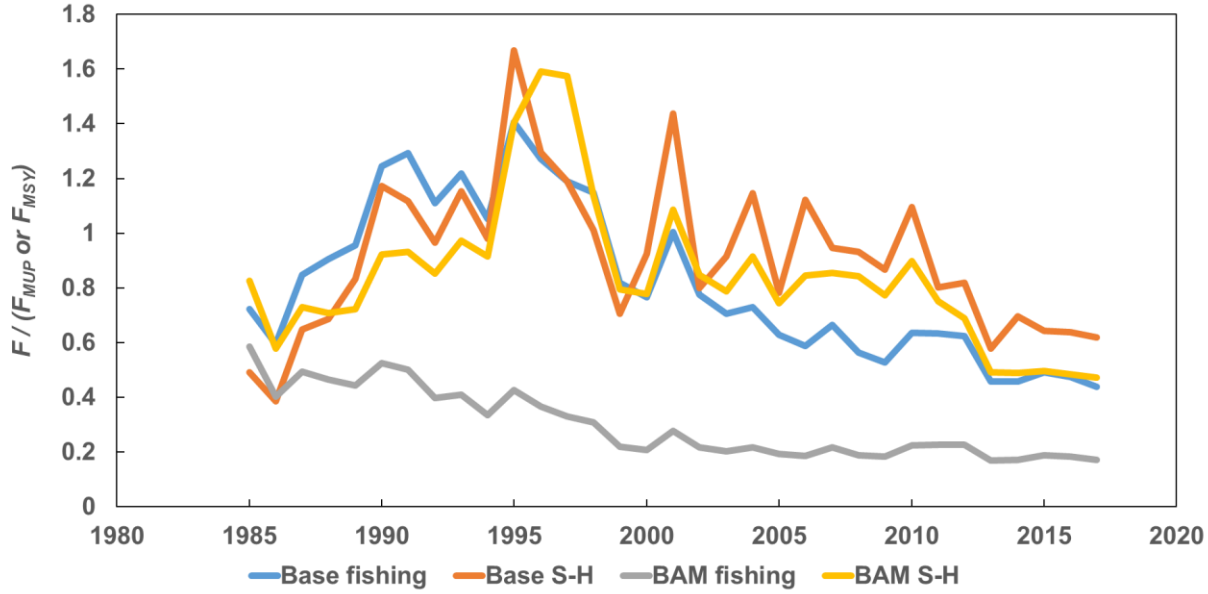


Figure 15. Relative M_2 (M_2 / Z_{MUP}) estimates from base and BAM Steele-Henderson (S-H) models (fishing and Striped Bass predation).

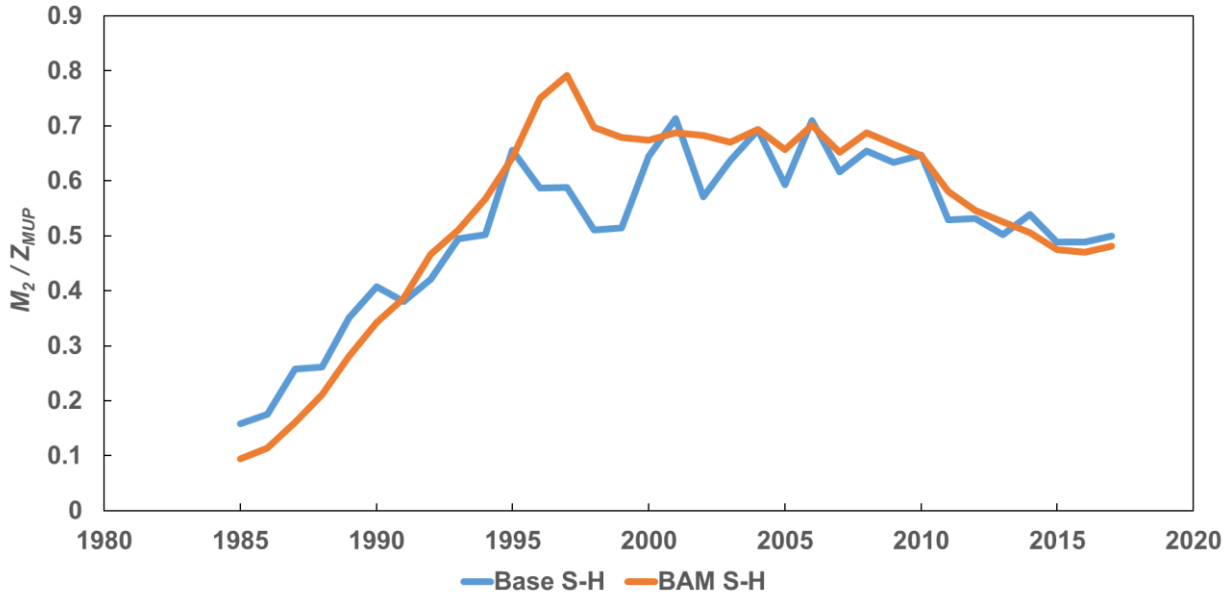


Figure 16. Relative Z_2 estimates from base and BAM Steele-Henderson (S-H) models (fishing and Striped Bass predation). Relative $Z_2 = Z_2 / Z_{MUP}$ for S-H models. Values at 1.0 or more breached the threshold.

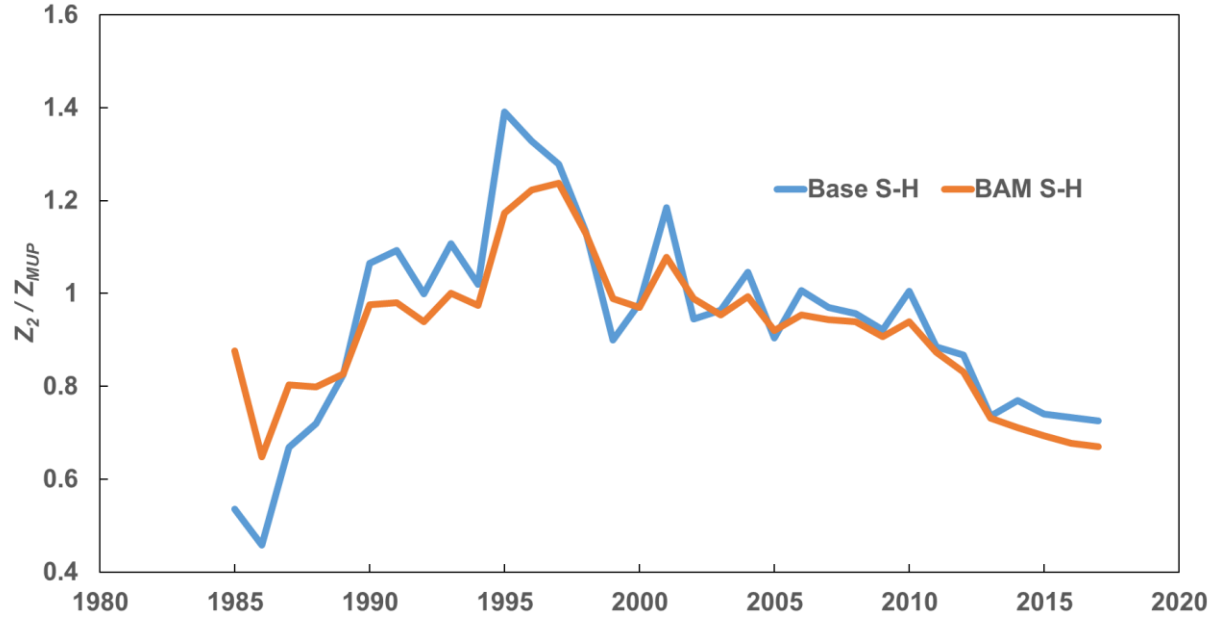


Figure 17. Estimates of F / Z_2 from base and BAM Steele-Henderson (S-H) models (fishing and Striped Bass predation). Values at 0.4 (horizontal line) or more breached the threshold.

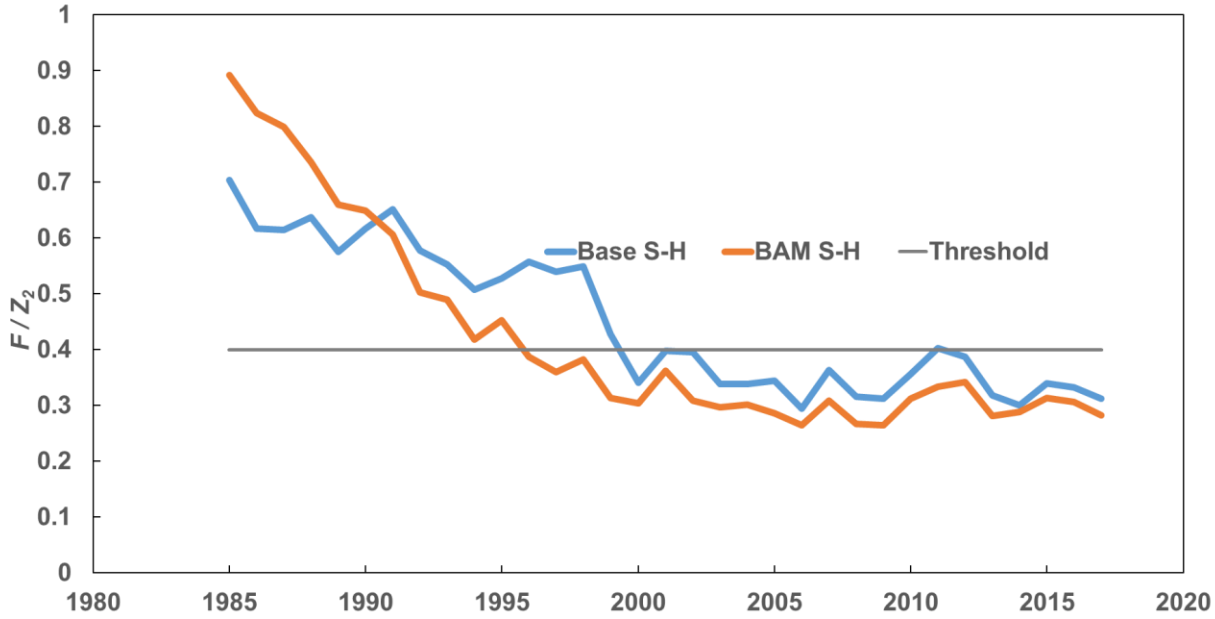


Figure 18. Time-series of annual ages 1+ Atlantic menhaden biomass consumed per Striped Bass biomass (D_t / P_t as MT consumed / MT Striped Bass) estimated by the base and BAM Steele-Henderson models.

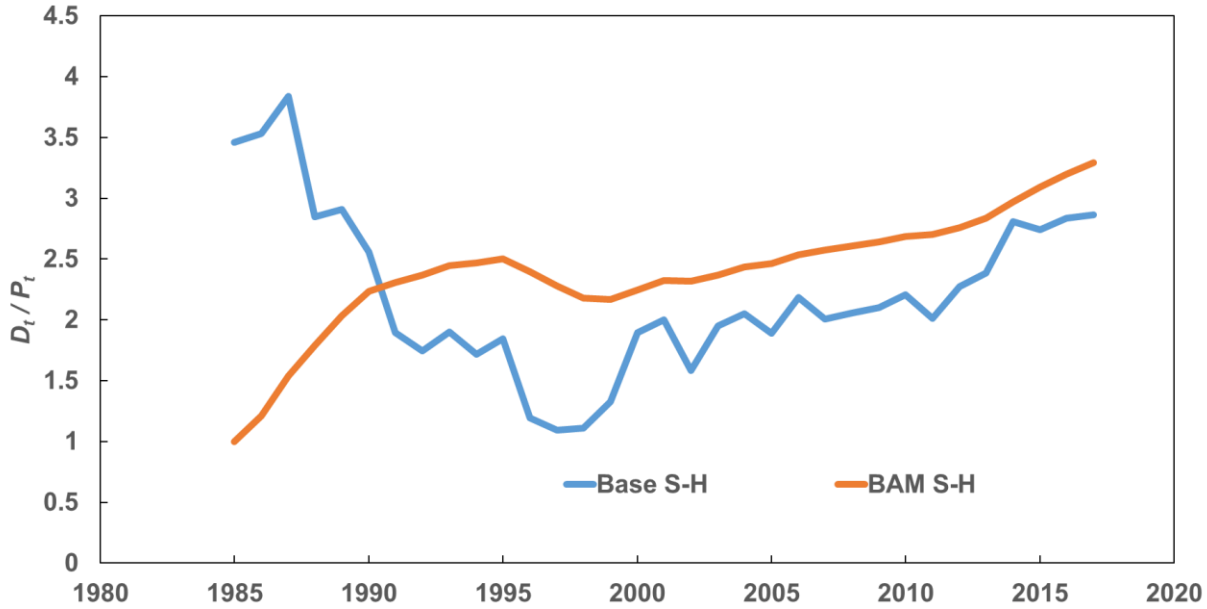


Figure 19. Relative biomass (B / B_{MUP}) estimates from the base Steele-Henderson (S-H) model (fishing and Striped Bass predation) and its sensitivity runs. Values at 1.0 or less breached the threshold. See Methods for descriptions of sensitivity runs.

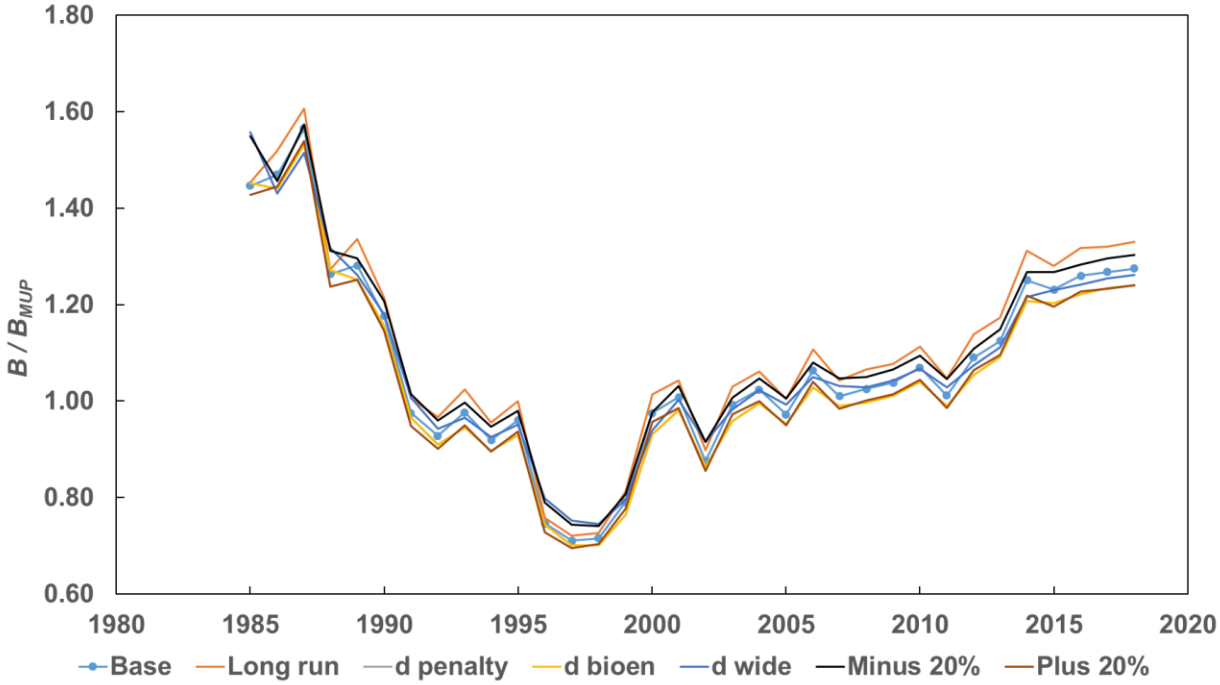


Figure 20. Relative Z_2 (Z_2 / Z_{MUP}) estimates from base Steele-Henderson (S-H) model (fishing and Striped Bass predation) sensitivity runs. Values at 1.0 or more breached the threshold. See Methods for descriptions of sensitivity runs.

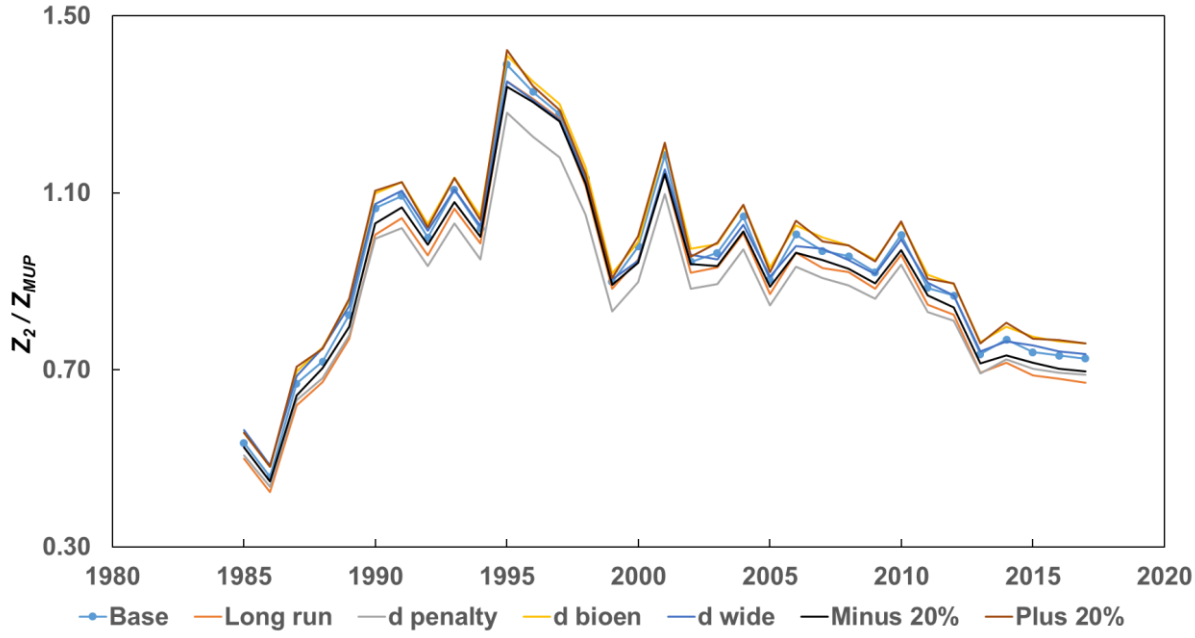


Figure 21. Time-series of annual ages 1+ Atlantic menhaden biomass consumed per Striped Bass biomass (D_t / P_t as MT consumed / MT Striped Bass) estimated by the base Steele-Henderson model and its sensitivity runs.

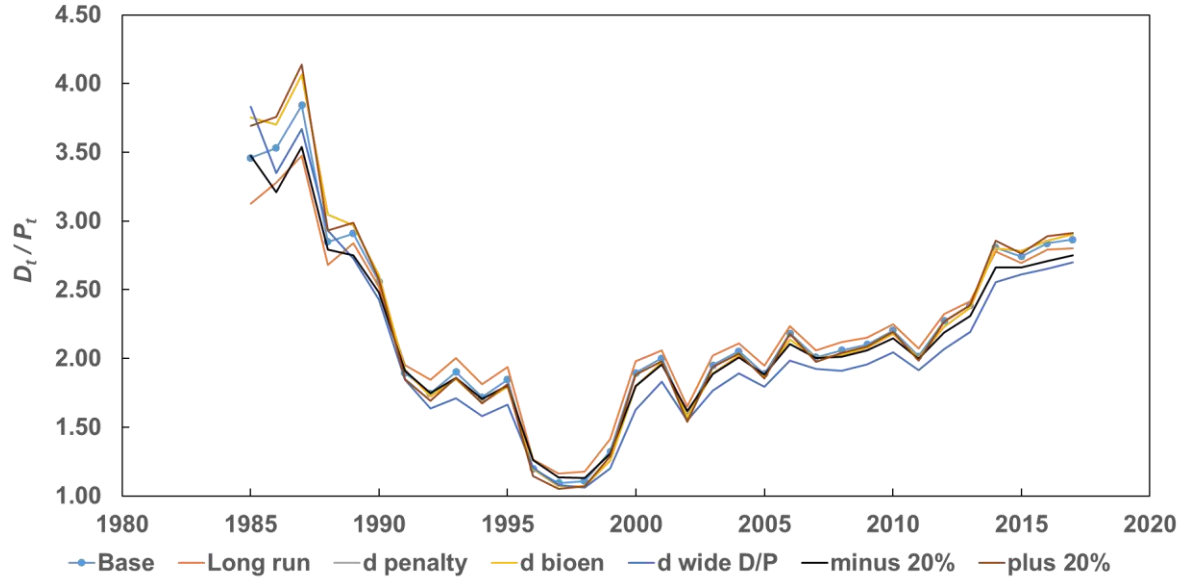


Figure 22. Time-series (1985-2017) of ages 1+ Atlantic menhaden PRFC, NAD, and MAD relative biomass indices and time-series estimated by a Steele-Henderson model (fishing and Striped Bass predation). NAD and MAD indices are standardized into PRFC units.

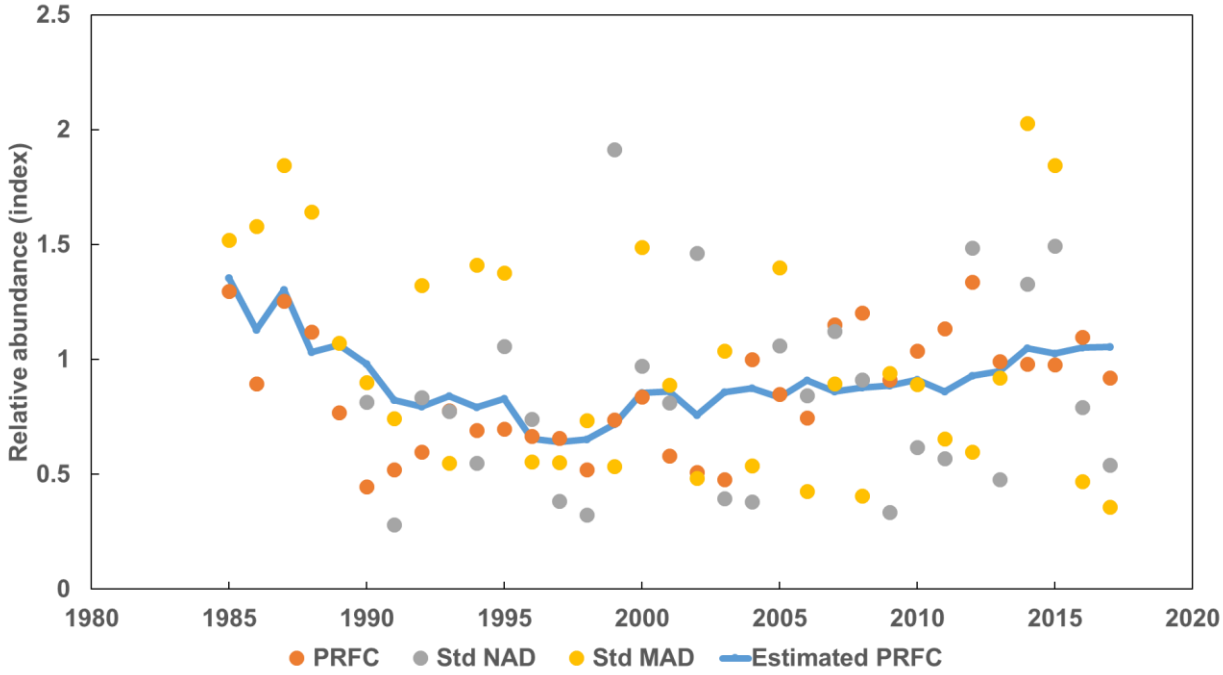


Figure 23. Relative biomass estimates from base and PRFC Steele-Henderson (S-H) models (fishing and Striped Bass predation). Relative biomass = B / B_{MUP}. Values at 1.0 or less breached the threshold.

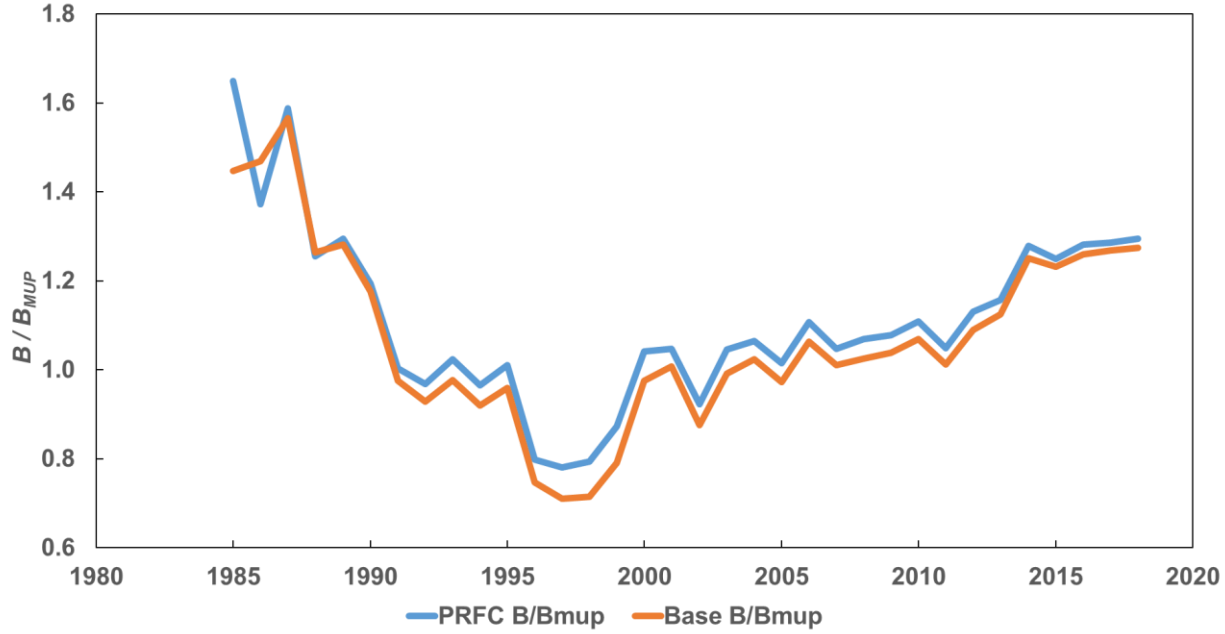


Figure 24. Relative Z_2 estimates from base and PRFC Steele-Henderson (S-H) models (fishing and Striped Bass predation). Relative $Z_2 = Z_2 / Z_{MUP}$. Values at 1.0 or more breached the threshold.

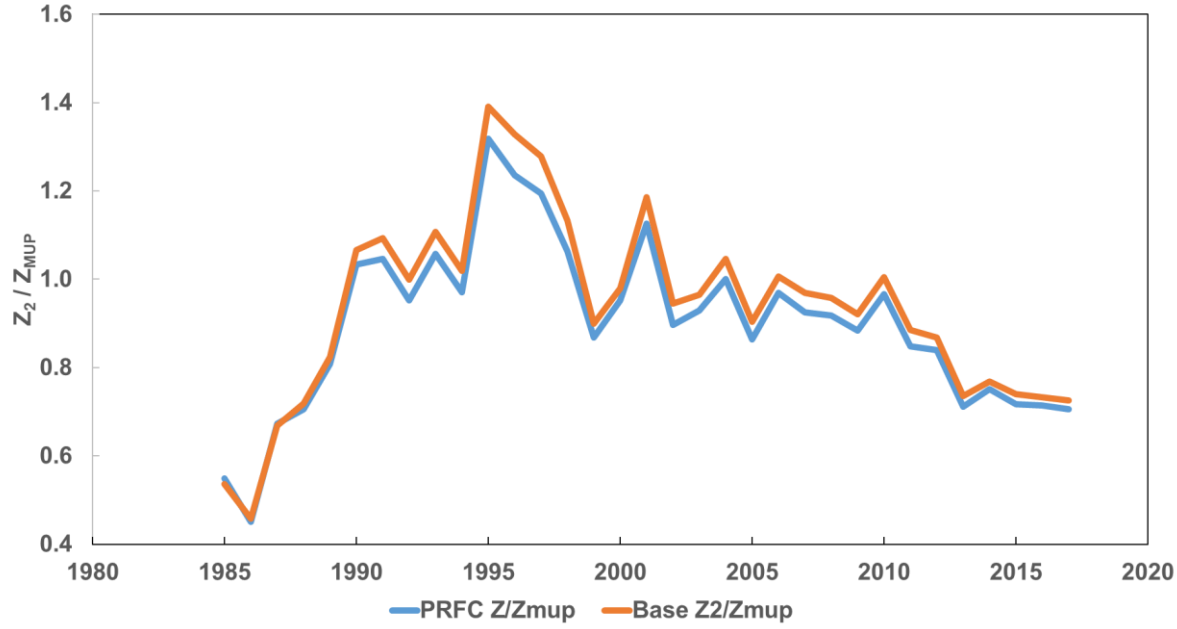


Figure 25. Time-series of annual ages 1+ Atlantic menhaden biomass consumed per Striped Bass biomass (D_t / P_t as MT consumed / MT Striped Bass) estimated by the base and PRFC Steele-Henderson models.

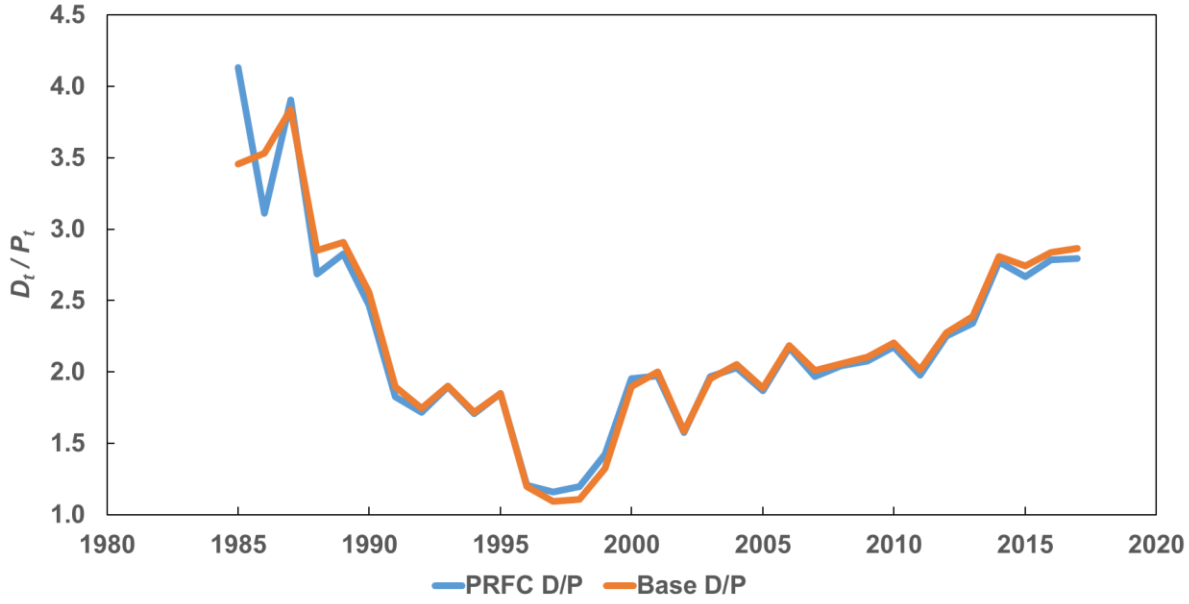


Figure 26. Relative biomass (B / B_{MUP}) estimates from the base Steele-Henderson (S-H) model (fishing and Striped Bass predation) and its retrospective runs. Values at 1.0 or less breached the threshold.

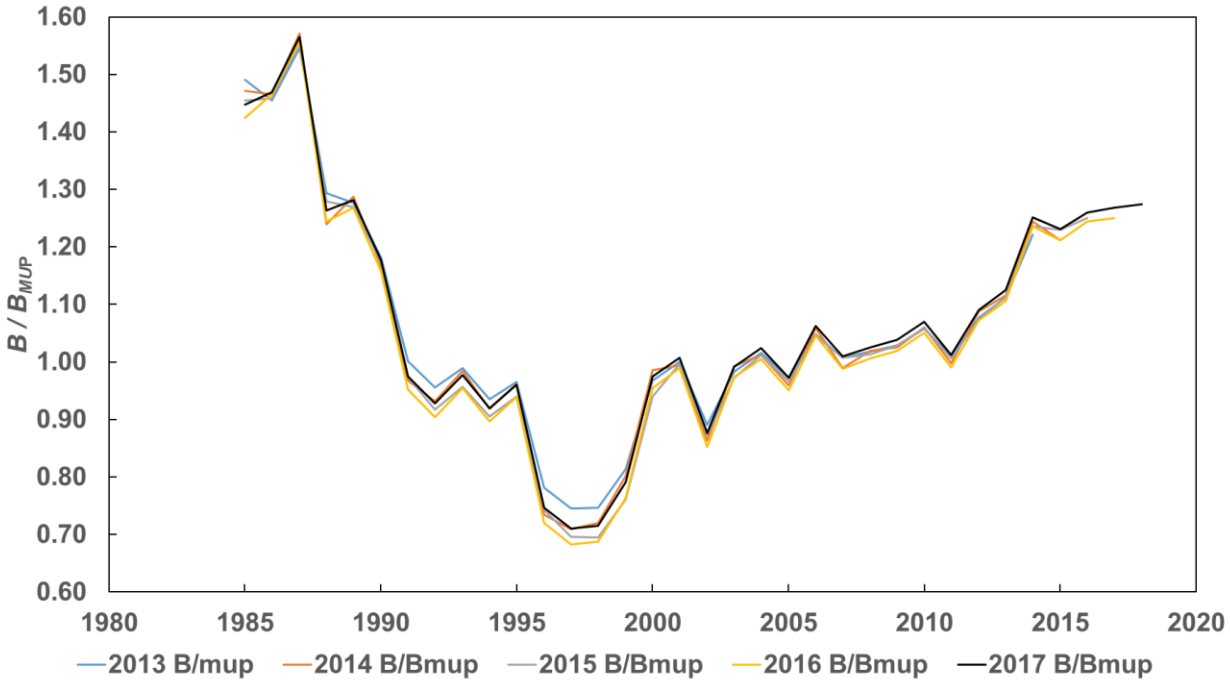


Figure 27. Relative Z_2 (Z_2 / Z_{MUP}) estimates from base Steele-Henderson (S-H) model (fishing and Striped Bass predation) retrospective runs. Values at 1.0 or more breached the threshold.

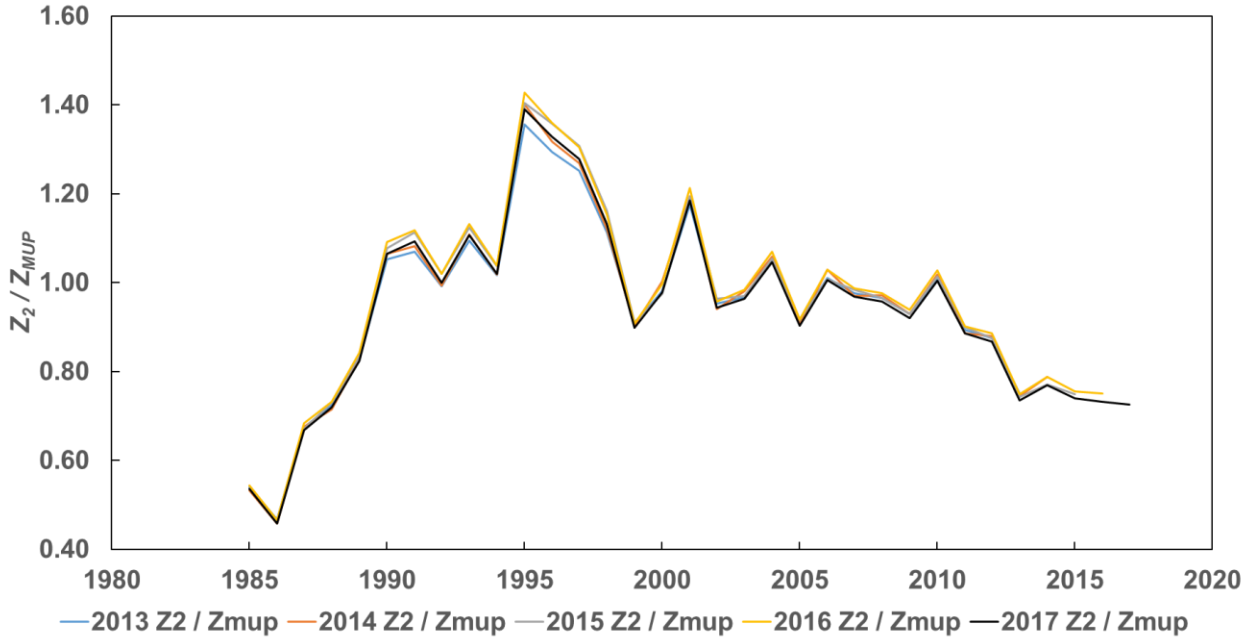


Figure 28. Time-series of annual ages 1+ Atlantic menhaden biomass consumed per Striped Bass biomass (D_t / P_t as MT consumed / MT Striped Bass) estimated by the base Steele-Henderson model and its retrospective runs.

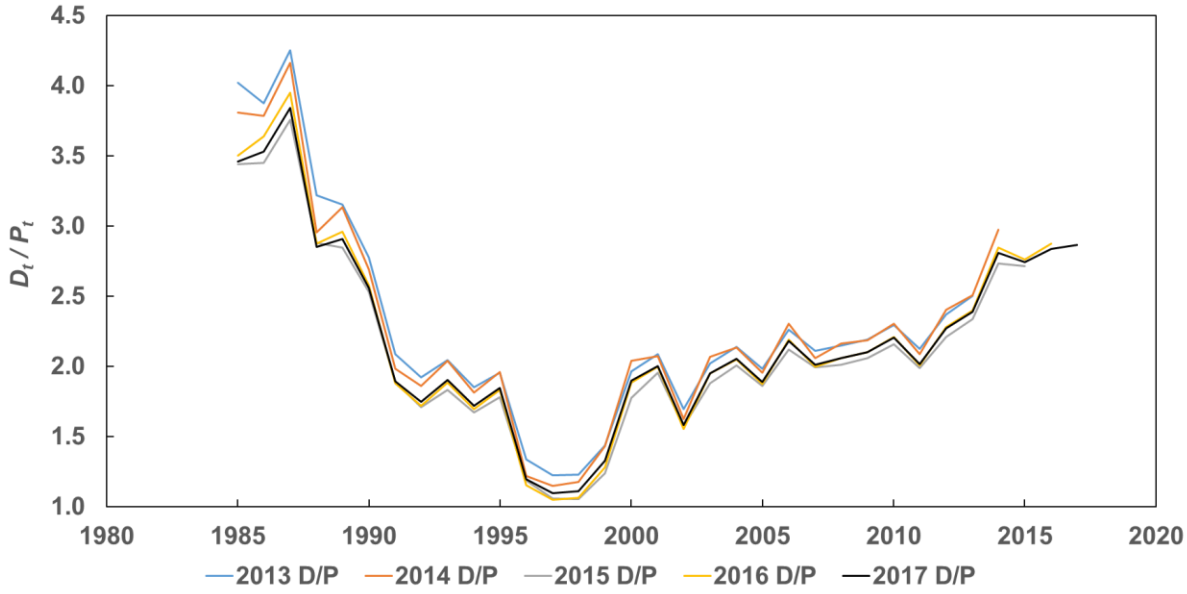


Figure 29. Relative biomass (B / B_{MUP}) estimates from the base Steele-Henderson (S-H) model (fishing and Striped Bass predation) and its index removal runs. Values at 1.0 or less breached the threshold.

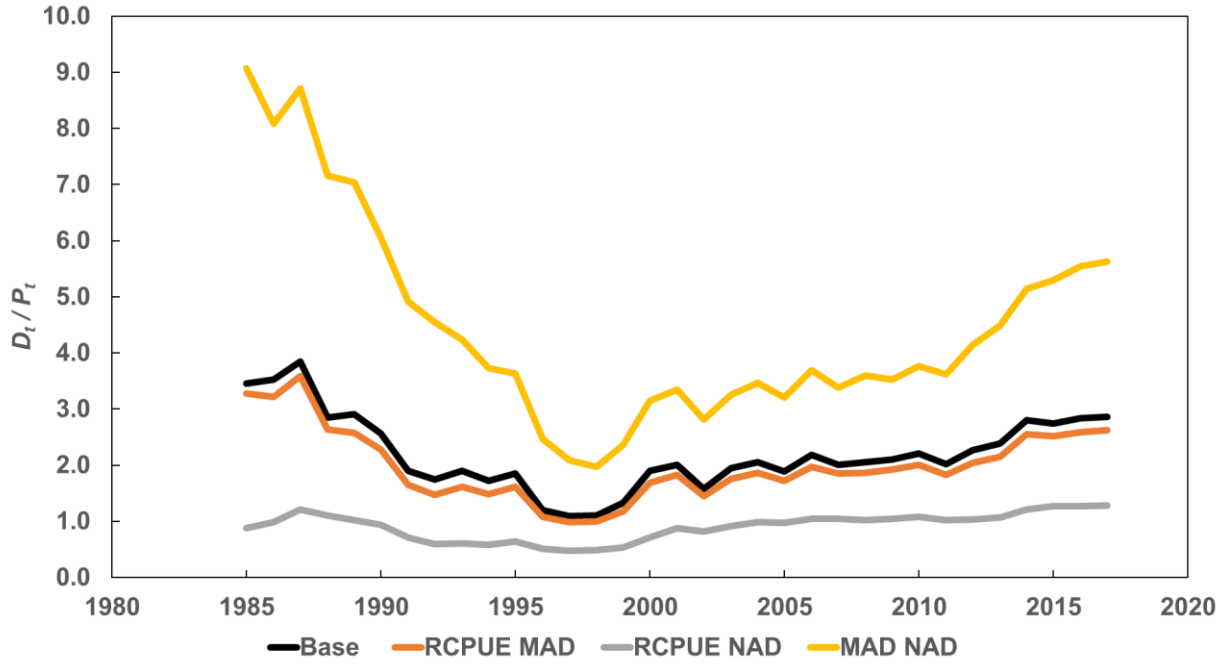


Figure 30. Relative Z_2 (Z_2 / Z_{MUP}) estimates from base Steele-Henderson (S-H) model (fishing and Striped Bass predation) index removal runs. Values at 1.0 or more breached the threshold.

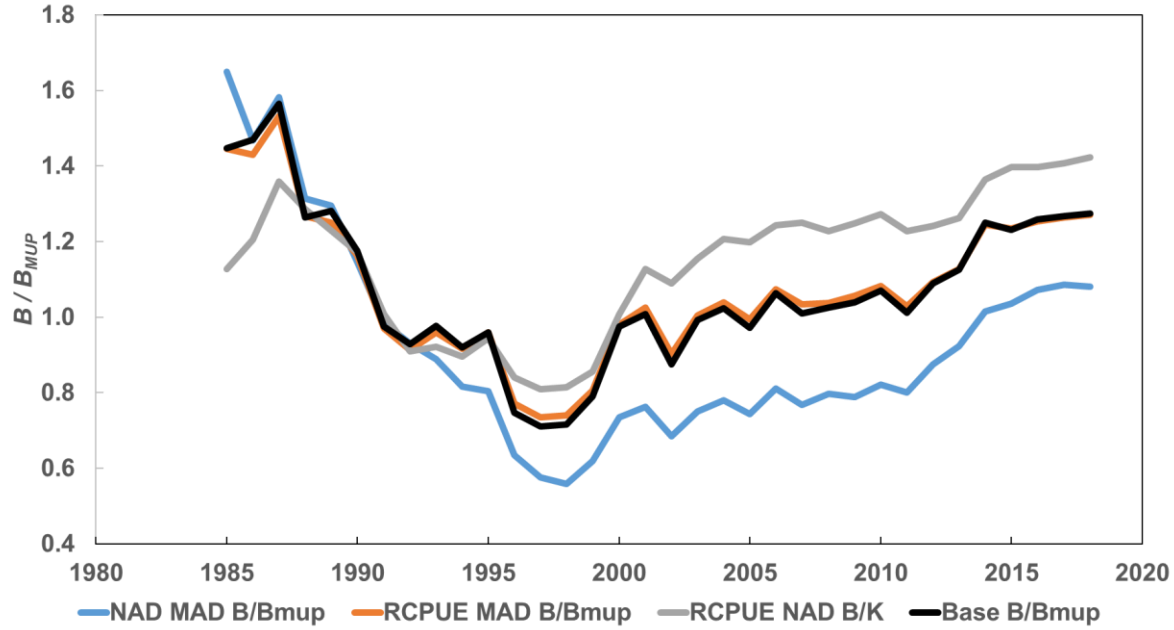


Figure 31. Time-series of annual ages 1+ Atlantic menhaden biomass consumed per Striped Bass biomass (D_t / P_t as MT consumed / MT Striped Bass) estimated by the base Steele-Henderson model and its index removal runs.

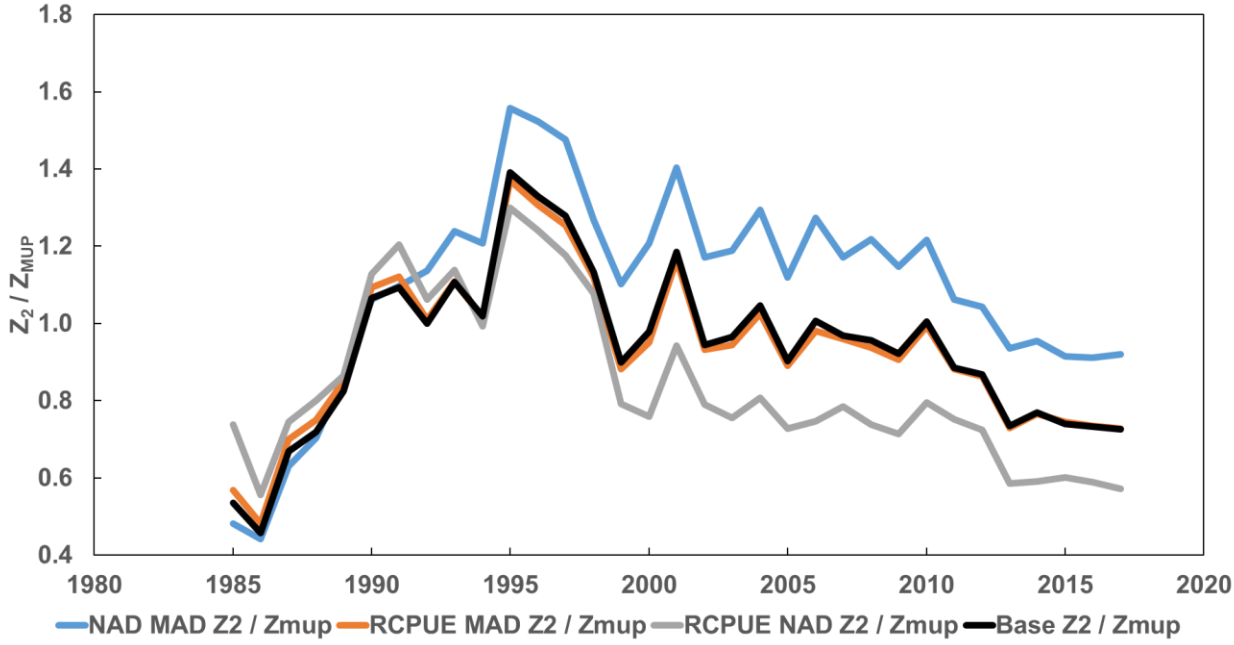


Figure 32. The linear relationship of standardized weight-at-age (weight-at-age of each year and age divided by the time-series weight for that age) of 6 to 14 year-old Striped Bass and D_t / P_t (annual ages 1+ Atlantic menhaden biomass consumed per Striped Bass biomass as MT consumed / MT Striped Bass).

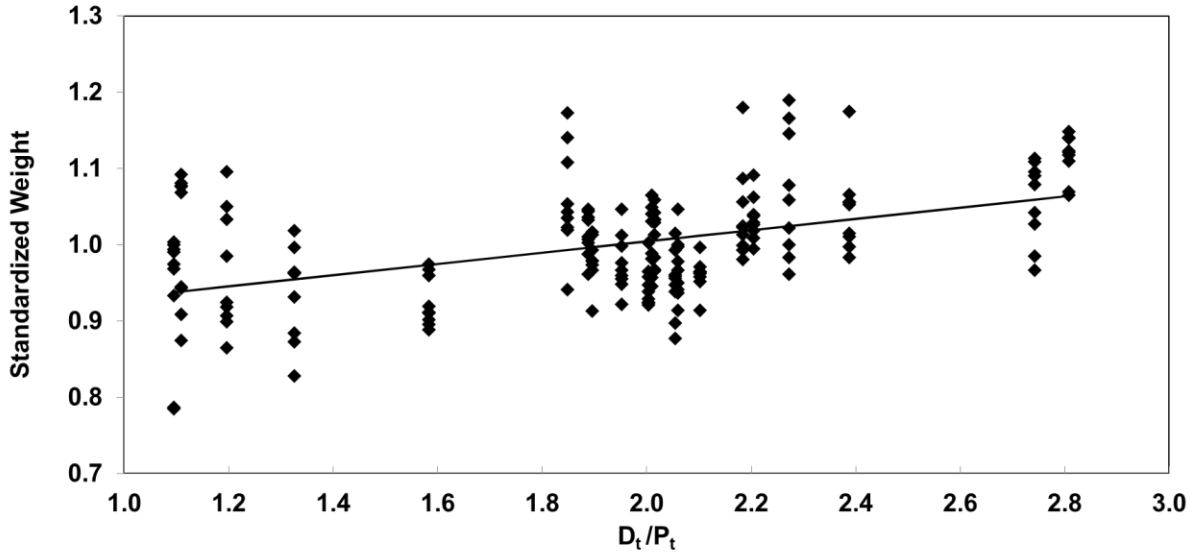


Figure 33. Plot of relative total mortality (Z_2 / Z_{MUP}) against annual ages 1+ Atlantic menhaden biomass consumed per Striped Bass biomass as MT consumed / MT Striped Bass (D_t / P_t). Horizontal line indicates D_t / P_t threshold.

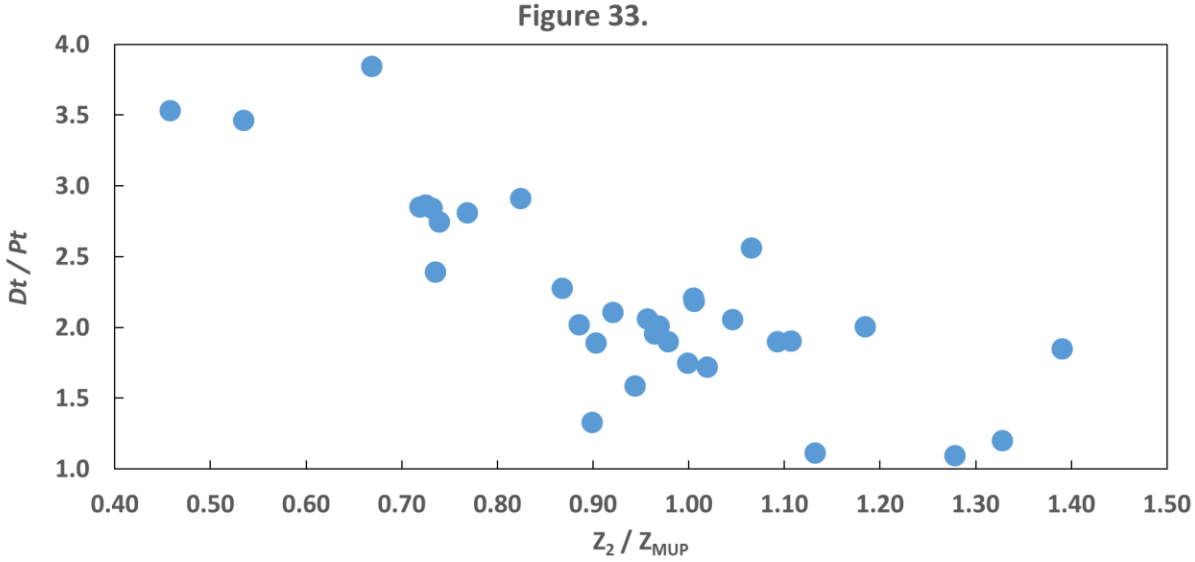


Figure 34. Base Steele-Henderson model jackknifed distributions of January 1, 2018 Atlantic menhaden ages 1+ biomass (MT) and unfished biomass (*K,* MT) and Laplace distributions providing best fit using @Risk's distribution fitting module.

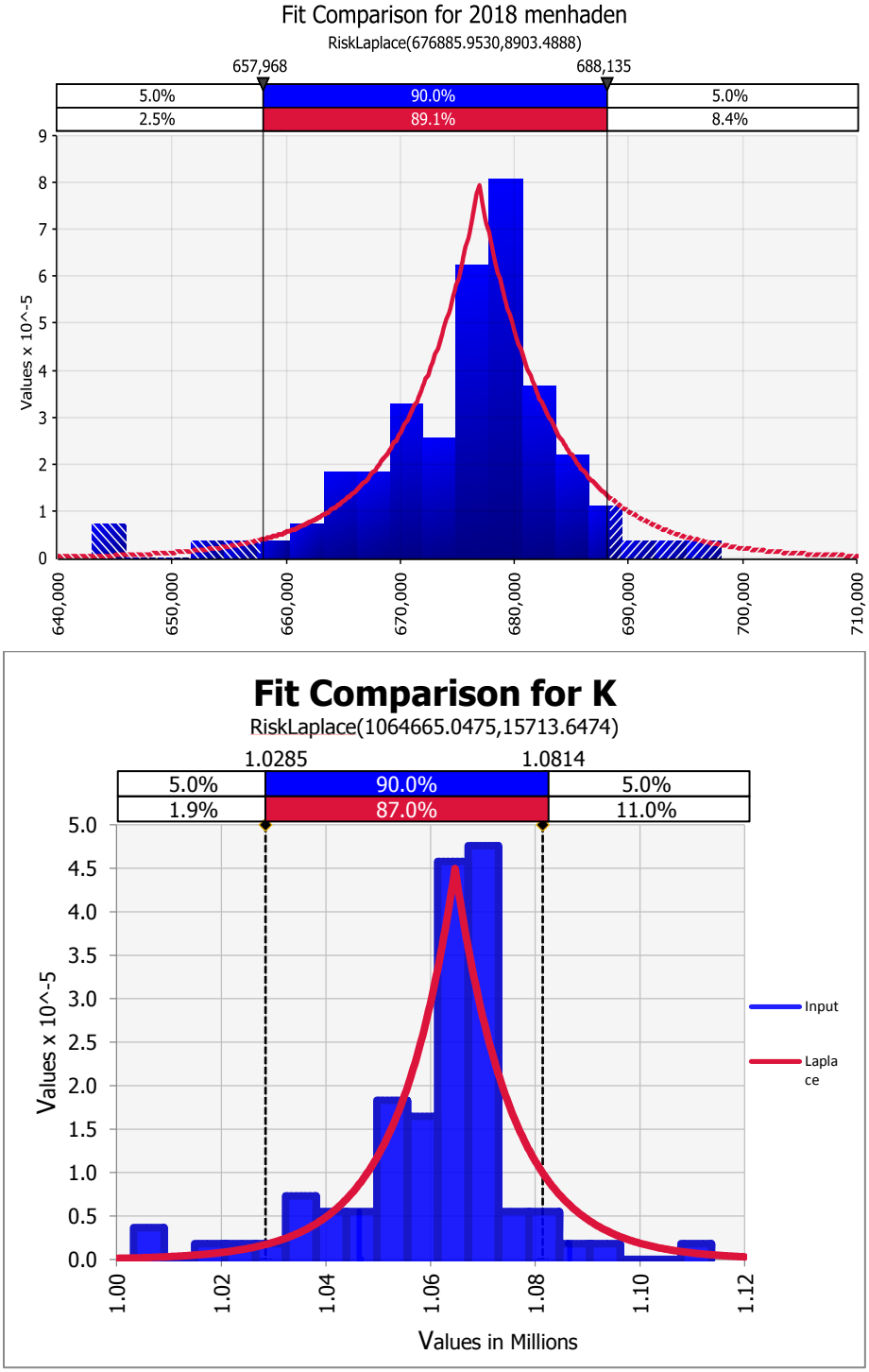


Figure 35. Base Steele-Henderson model jackknifed distributions of parameters *d* and *A* (Atlantic menhaden ages 1+ biomass at Striped Bass satiation, MT) and Laplace distributions providing best fit using @Risk's distribution fitting module.

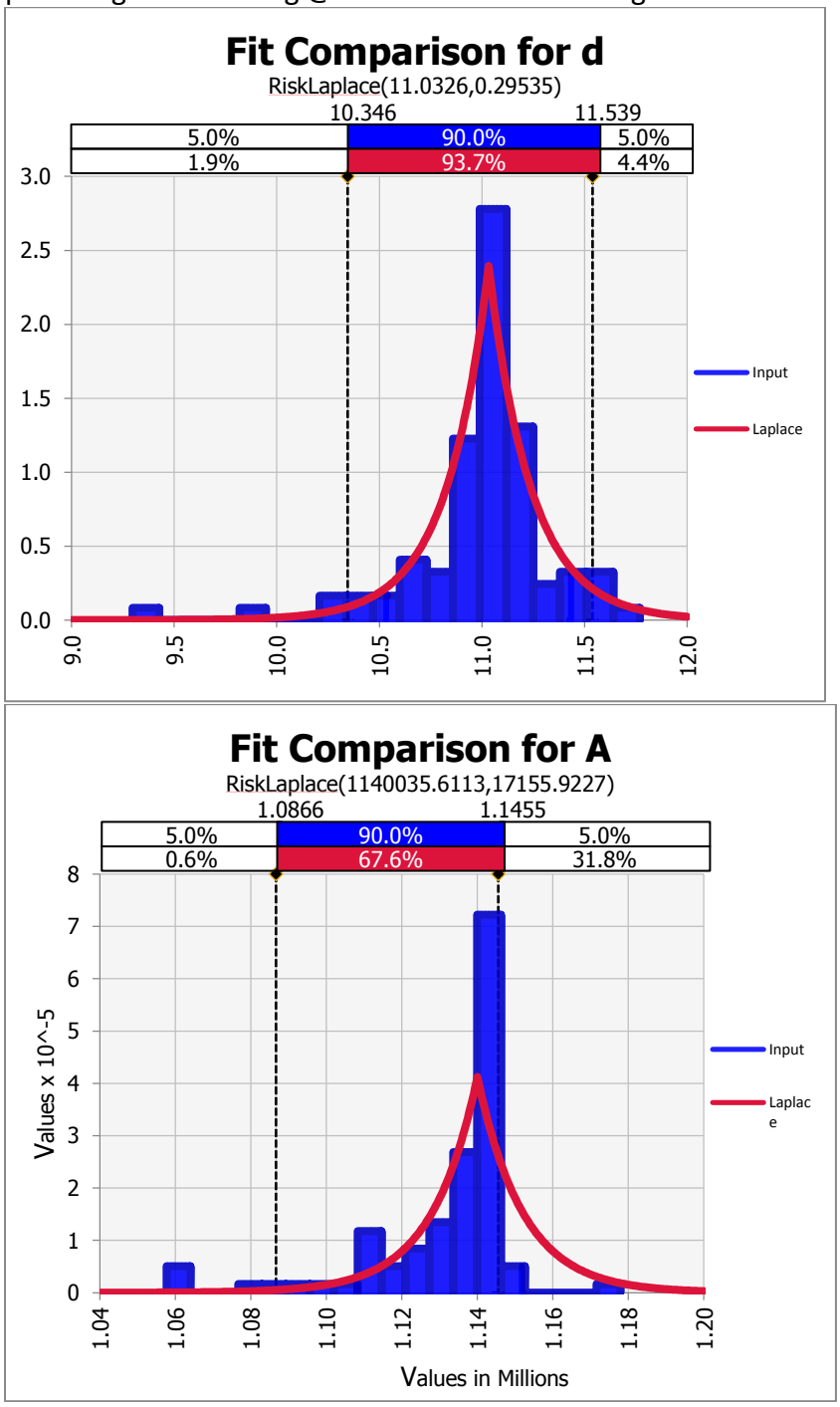
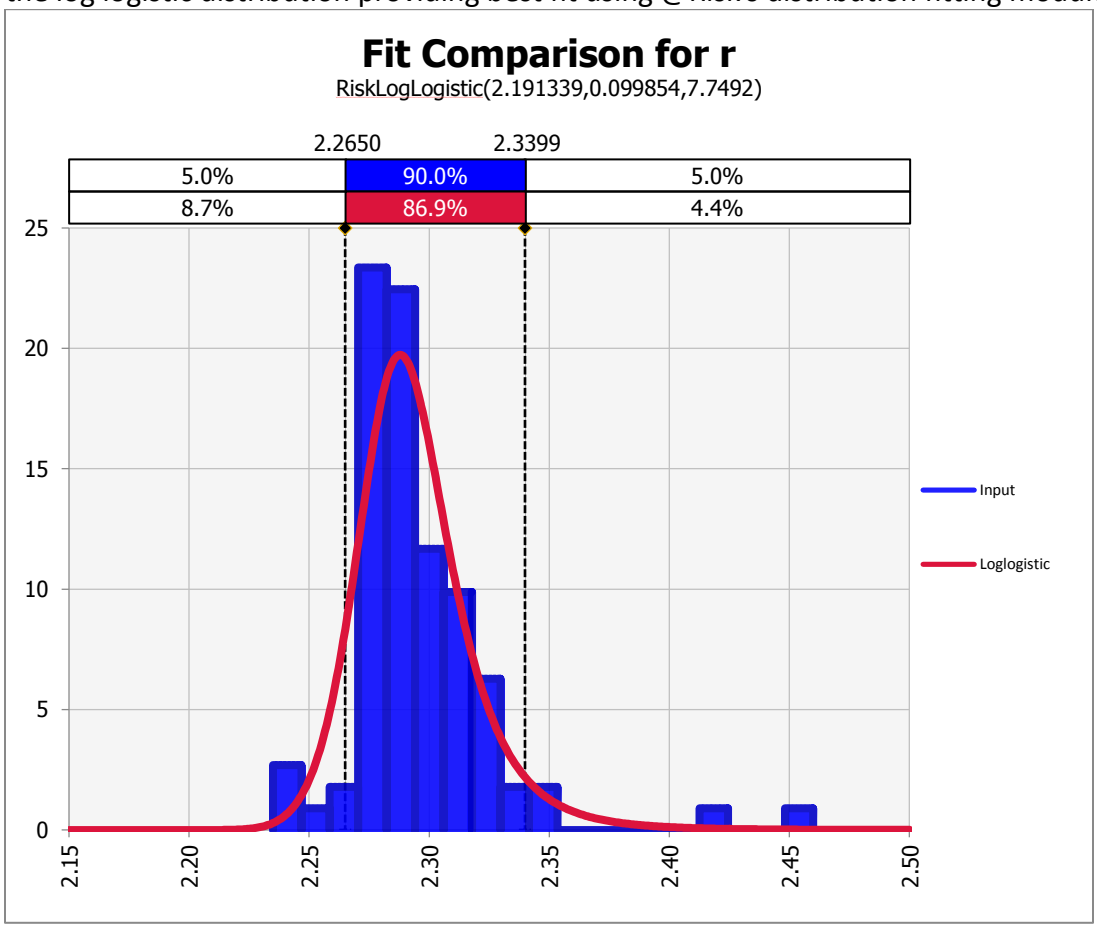


Figure 36. Base Steele-Henderson model jackknifed distribution of intrinsic growth rate, *r*, and the log logistic distribution providing best fit using @Risk's distribution fitting module



Appendix 3: Northwest Atlantic Continental Shelf (NWACS) Model Working Paper

Ref. No. [UMCES]CBL 2017-021

Report: TS-694-17

TECHNICAL DOCUMENTATION OF THE NORTHWEST ATLANTIC CONTINENTAL SHELF (NWACS) ECOSYSTEM MODEL

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http://hjort.cbl.umces.edu/NWACS/TS_694_17_NWACS_Model_Documentation.pdf

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1. Abstract

This report describes and presents an ecosystem model of the marine and estuarine waters of the Northwest Atlantic Continental Shelf (NWACS). Although built to support ecosystem based fisheries management efforts generally, the primary motivation for the NWACS model was to inform the development and evaluation of ecological reference points for the management of Atlantic menhaden by explicitly accounting for food web interactions and tradeoffs. The NWACS model, built using the Ecopath with Ecosim software, relied on information from fisheries stock assessments, research surveys, and primary and secondary literature; it also leveraged existing ecosystem models from the region. This technical document describes the methodology, data sources, balancing, and parameterization of the NWACS model for the years 1982-2013.

2. Introduction

As fisheries management continues to incorporate ecosystem considerations and multi-species interactions into the management arena, the focus of management has been shifting from single species approaches to an ecosystem approach to fisheries management (EAFM) or to ecosystem based fisheries management (EBFM). EAFM maintains a primary focus on individual species but accounts for broader ecosystem considerations, whereas EBFM is a place-based management approach that focuses on an entire system and all of the fisheries therein (Fogarty 2014). Efforts in facilitating and promoting these transitions to EAFM and EBFM (Whipple et al. 2000) are evidenced by the multi-species models that account for predation mortality (Whipple et al. 2000; Garrison et al. 2010), restrictions by the Pacific and Mid-Atlantic Fishery Management Councils on opening new fisheries for forage species as a precautionary measure to avoid reductions in the forage base (Federal Register 2016; MAFMC 2016), and development of ecosystem indicators (Levin et al. 2009; Shin and Shannon 2010; Fay et al. 2013). Numerous modeling tools have become available of varying complexity ranging from relatively simple multispecies production models (e.g., Collie and DeLong, 1999) to end-to-end ecosystem models that model everything from nutrients to fisheries and economics (e.g., Fulton *et al.*, 2011; Rose *et al.*, 2010). Despite these advances in EAFM and EBFM, there remain several challenges in institutionalizing and implementing any new approaches. One approach has been an evolutionary transition away from single species methods by accounting for multi-species and ecosystem considerations, but even these transitions can be challenging.

The management of Atlantic menhaden (*Brevoortia tyrannus,* hereafter menhaden) is one case where these challenges are evident. Menhaden is an important forage fish species found along the eastern USA from Florida to Maine. Menhaden filter phytoplankton from the water column as juveniles, and are thus important primary consumers. Menhaden are consumed by diverse predators including fishes, marine mammals, and birds (MDSG, 2009); several of these predators, such as striped bass, bluefish, and weakfish, are themselves commercially- and recreationally-important fished species (MDSG, 2009). Menhaden also supports the largest directed fishery on the east coast, with harvested fish used for fish meal and fish oil and for bait in other fisheries (MDSG, 2009; SEDAR, 2015). Thus, menhaden provides important ecosystem services, including 1) supporting predators (and their fisheries) as a food resource,

2) supporting a large directed fishery, and 3) filtering phytoplankton and associated nutrients from the water column as juveniles. Conflicts arise among stakeholders given these multiple ecosystem services, and tradeoffs in management exist based on the specific management objectives desired.

Menhaden fisheries are managed by the Atlantic States Marine Fisheries Commission (ASMFC). The current goal of the Fishery Management Plan (FMP) is to manage the fishery "in a manner that is biologically, economically, socially and ecologically sound, while protecting the resource and those who benefit from it" (ASMFC 2012). Of the 13 stated FMP objectives to achieve this broad goal, two objectives in particular pertain to the role of menhaden as a forage species: 1) "Protect and maintain the Atlantic menhaden stock at levels to maintain viable fisheries and the forage base with sufficient spawning stock biomass to prevent stock depletion and guard against recruitment failure", and; 2) "Protect and maintain the important ecological role Atlantic menhaden play along the coast" (ASMFC 2012).

Historically and currently, menhaden is managed in a single species (SS) context using SS reference points (MDSG, 2009). Presently, these SS reference points are intended to be interim values until ecological reference points (ERPs) can be developed (ASMFC 2012; SEDAR 2015). ERPs would more explicitly account for the other services that menhaden perform within the ecosystem (e.g., supplying food for predators). Development of ERPs is being undertaken by the ASMFC's Biological Ecological Reference Point Working Group (BERP). For the 2015 stock assessment (SEDAR 2015), the BERP developed a report highlighting various approaches that could be used to develop ERPs for menhaden. Of the options put forward, only an ecosystem model fully accounts for effects of menhaden on their predators (and the broader ecosystem) by including a dynamic feedback among predator and prey groups.

Ecopath with Ecosim (EwE) is an ecosystem modeling framework that has become a common modeling approach for exploring and evaluating potential ecosystem consequences of different fisheries management strategies (Christensen and Walters 2004; Coll et al. 2009; Link 2010a). Once an EwE model is developed and calibrated to time-series of empirical data, it can be used to simulate ecosystem changes under alternative fisheries management scenarios. Thus, model simulations can be used to identify potential reference points for fishing mortality and biomass that best achieve specific management objectives.

We developed an EwE model of the Northwest Atlantic Continental Shelf (NWACS) as a tool to inform decisions on management of menhaden fisheries in an ecosystem context, by explicitly accounting for effects that the menhaden fishery has on other components of the ecosystem. The primary objectives of our research were to: 1) develop an ecosystem model that can be used as a tool to inform strategic decisions for EAFM of menhaden fisheries, 2) evaluate the ecosystem impacts of a range of different menhaden fishing mortality rates, and 3) compare the performance of some potential reference points proposed for menhaden management. The NWACS model that we developed leveraged a large body of earlier research by the Northeast Fisheries Science Center (NEFSC) in developing four Ecopath models within the region for the Energy Modeling and Analysis eXercise (EMAX) project (Link et al. 2006, 2008).

The NWACS EwE model extends the earlier research by making the model time-dynamic and by increasing the taxonomic resolution of many important fished species. The model was developed for applications to EAFM of menhaden and it can contribute to assessment modeling being used (and explored) by the ASMFC. More generally, the NWACS model can be used to support development of EAFM for other managed species in the Northwest Atlantic or for broader ecosystem-based EBFM.

This report documents the methodology, data sources, and parameterization of our NWACS EwE model. Appendix 1 describes the parameterization of each trophic group in the model and Appendix 2 tabulates all parameters of the balanced NWACS model.

3. Methods

3.1. Modeling Framework

The NWACS model (v. 2.8.2) was developed using the Ecopath with Ecosim (v. 6.4.3) software package. The Ecopath module is used to develop a mass-balanced description of the food web at a single point in time. The Ecosim module is used for a time-dynamic representation of the system that examines the changes in the food web over time. Full details of the underlying theory, assumptions, and model mechanics are described elsewhere (Walters et al. 1997; Christensen and Walters 2004; Christensen et al. 2008), and are only summarized here.

3.1.1. Ecopath

The mass-balanced Ecopath model relies on two underlying "master" equations. One equation describes the production of each group, while the second describes the energy balance for each group (Christensen and Walters 2004). The first equation divides the total production rate (P_i) for each group *i* among various components for a given time period (typically 1 year) (Christensen and Walters 2004):

$$P_i = Y_i + M2_i \times B_i + E_i + BA_i + P_i(1 - EE_i) \quad \text{(Eq. 1)}$$

Where Y_i is the total fishery catch rate for group *i*, $M2_i$ is the instantaneous predation rate for *i*, B_i is the biomass of group i, E_i is the net migration rate (emigration – immigration) for *i*, BA_i is the biomass accumulation rate for *i*, and EE_i is the "ecotrophic efficiency" of *i* such that $P_i(1\text{-}EE_i)$ represents all the other (non-predation) mortality that is not modeled explicitly. Ecotrophic efficiency (EE_i) is the proportion of the production that is utilized in the ecosystem and accounted for by fishing, predation, migration, and biomass accumulation.

The first Ecopath master equation (Eq. 1) can also be written (Christensen et al. 2008) as:

$$B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i - Y_i - E_i - BA_i - \sum_{j=1}^{n} B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} = 0 \quad \text{(Eq. 2)}$$

Where $(P/B)_i$ is the production to biomass ratio for *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 average diet composition of predator *j*. Equation 2 defines a system with as many linear equations as there are groups in the system. The model requires three of the following four parameters to be

parameterized for each group, solving for the fourth: biomass, production/biomass ratio, consumption/biomass ratio, and ecotrophic efficiency. Additionally, all groups require data on catch rate, net migration rate, biomass accumulation rate, and diet composition.

The second master equation describes the energy balance within each group, based on the principle of conservation of mass:

Consumption = *production* + *respiration* + *unassimilated food* (Eq. 3)

Here, the consumption of biomass by each trophic group is allocated to growth of somatic tissue (production), to metabolic costs (respiration), and to waste products that are egested (unassimilated food). This energy balance equation (Eq. 3) is used to estimate respiration from inputs of the other quantities because respiration rates are not readily available for most groups.

EwE models have the ability to account for different life history stages or stanzas of individual species based on age. Multiple stanzas can be used to account for ontogenetic changes in feeding and mortality, with these processes assumed to be similar for individuals within each stanza (Christensen and Walters 2004). For multistanza groups, additional inputs are needed, specifically stanza-specific total instantaneous mortality rates (Z), the von Bertalanffy growth parameter K, and the ratio of the average weight at maturity to the asymptotic weight. Biomass and Q/B for a "leading" stanza are entered, and values for other stanzas are estimated based on the assumption that growth follows the von Bertalanffy model with weight proportional to cube of the length. It also is assumed that the population has a stable age-size distribution, and that feeding rates vary with age as the 2/3 power of body weight (Christensen and Walters 2004).

3.1.2. Ecosim

Ecosim is the time dynamic module that extends the static Ecopath model to simulate changes in the ecosystem over time. For Ecosim, the system of linear equations defined by Eq. 2 is re-expressed as a system of coupled differential equations (Christensen and Walters 2004), defined as:

$$\frac{dB_i}{dt} = g_i \sum_{j=1}^{n} Q_{ji} - \sum_{j=1}^{n} Q_{ij} + I_i - (M0_i + F_i + e_i)B_i \quad \text{(Eq. 4)}$$

Where dB_i/dt_i 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. The summation of Q_{ji} is the total consumption by group i, whereas the second summation of Q_{ij} is the consumption of group i by all of its predators. Consumption rates (Q_{ji}) are calculated based on the "foraging arena" concept, whereby the rate of effective prey searching by predators is influenced by the transition of prey between vulnerable and invulnerable states (Walters et al. 1997; Christensen and Walters 2004). The transfer rate between these states, termed a vulnerability parameter, replaces functional response curves used in many other multi-

species models and ultimately determines the degree to which groups are controlled by top-down or bottom-up forcing (Walters et al. 1997; Christensen and Walters 2004).

Forcing functions of external environmental factors (e.g., temperature, dissolved oxygen) can be incorporated to drive changes in production, mortality, or consumption for predator and prey groups. Ecosim parameters are calibrated using available time series of relative biomass, fisheries landings, fishing effort, and fishing mortality, typically obtained from monitoring surveys and stock assessments. Fishing mortalities, fishing effort, or landings are typically used to "drive" the model by representing observed perturbations to the historical system.

3.2. NWACS model structure

Spatial structure. The spatial domain for the model is the Northwest Atlantic Continental Shelf ecosystem, which spans the continental shelf of the Northwest Atlantic Ocean from North Carolina to Maine (Figure 1). The model domain includes four continental shelf subregions, following the regional strata of the NEFSC trawl survey: Mid-Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB), and Gulf of Maine (GOM). Our model also represents the estuaries along the coastline, such as the Chesapeake Bay, Delaware Bay, and Long Island Sound (Figure 1). Although the domain does not encompass the entire distributional range of Atlantic menhaden (from Florida to Nova Scotia), it is similar to the range in the Multispecies Virtual Population Analysis (MSVPA) developed for Atlantic menhaden (Garrison et al. 2010) and to existing Ecopath models for the region (Link et al. 2008). This domain relies on the natural faunal and oceanographic break in NC (Longhurst 1998), while also including the bulk of historical menhaden fishing effort concentrated in Chesapeake Bay and the Mid-Atlantic (SEDAR 2015).

Temporal structure. The model was parameterized using available data for the ecosystem from 1982 to 2013. The initial year 1982 was chosen because this is the first year of available catch data for many of the single species stock assessments.

Trophic structure. The trophic structure of the model represents the principal groups in the ecosystem from detritus and phytoplankton to marine mammals and seabirds using 61 different groups (Table 1). Groups are aggregated taxa based on similar functional or taxonomic characteristics, with a higher degree of aggregation for lower trophic levels (e.g., phytoplankton, zooplankton, and benthic invertebrates) and highest trophic levels (e.g., sharks, marine mammals, seabirds). The degree of taxonomic resolution at lower and higher trophic levels largely followed the structure used for the EMAX models (Link et al. 2006, 2008). Given that the initial application of our NWACS model was for menhaden, important menhaden predators (e.g., striped bass, bluefish, weakfish) are represented as individual species, as are alternative prey for those predators (e.g., Atlantic herring *Clupea harengus*, Atlantic mackerel *Scomber scombrus*, anchovies *Anchoa spp.*). Other fish species (e.g., Atlantic cod *Gadus morhua*, summer flounder *Paralichthys dentatus*, spiny dogfish *Squalis acanthias*) that are of particular management concern or ecological significance also were retained explicitly in the model. Several fishes were partitioned into multiple age stanzas to account for documented ontogenetic differences in diets (e.g., Buchheister and Latour, 2015; Garrison and Link, 2000; Smith and Link, 2010) or changes in habitat or migration behaviors (Table 1). Stanzas were defined based on age, but

associated length cutoffs were also assigned to allow length-based data to be partitioned appropriately among stanzas (e.g., trawl survey catches and diets based on predator length). Length cutoffs for each age were approximated using length-at-age relationships from trawl surveys (NEFSC, NEAMAP, and ChesMMAP) or from literature studies. For simplicity and consistency in naming of multi-stanza groups, stanzas were labeled as either small (S), medium (M), or large (L), although they represent specific ages and lengths for each species (Table 1).

Fishing Fleets. Multiple fishing fleets were modelled to account for the dynamics of fishing operations in the region. Modelled fleets were defined based on predominant fishing gears used within the model domain, based on landings data from NOAA (see Section 3.3.2.4). The eight modeled fishing fleets were labeled as dredge, trawl, trap, gill net, purse seine, recreational, longline, and other.

3.3. ECOPATH Model parameterization - General methods

This section describes the general approaches and sources of data used to parameterize the NWACS model because there were many similarities across groups. Any deviations from the methods (or important additional details) are provided in the group-specific sections of Appendix 1. The model was developed using several data sources, including fishery-independent surveys, single species stock assessments, primary and gray literature, and existing ecosystem models from the Northwest Atlantic shelf and its estuaries. Given that our model adopted many parameters of the EMAX Ecopath models (particularly at the lower and higher trophic levels), we begin with a summary of methods for parameterizing the lower and higher trophic levels groups. Then we document general methods for parameterization of the other trophic groups (mostly fishes).

3.3.1. Parameters for lower and higher trophic levels that leverage the EMAX models

We relied heavily on ecosystem models developed by the NEFSC for the Energy Modeling and Analysis eXercise (EMAX) project (Link et al. 2006, 2008). For EMAX, scientists from varied disciplines (covering physics, biology, and social sciences) contributed to the development of four Ecopath models of the Mid-Atlantic Bight, Southern New England, Georges Bank, and Gulf of Maine regions (Figure 1). These models were parameterized for 1996-2000 using a coarse taxonomic resolution, with 36 trophic groups. Our NWACS model has greater taxonomic resolution for several fish groups, but we largely retained a trophic structure similar to the EMAX models at lower and higher trophic levels to leverage their extensive efforts in estimating parameters for these groups that are relatively data-poor.

Ecopath parameters (B, P/B, Q/B, and diets) from the four regional EMAX models were combined using weighted averages of the parameters from each region. The total biomass estimates (mt) were calculated from the biomass densities and the region areas, and then divided by the total area (246,662 km^2). For each trophic group, P/B values were averaged across the four EMAX models, weighted by the respective regional biomasses. Q/B and unassimilated consumption were typically consistent across EMAX models, but in situations where this was not the case, values were averaged and weighted using the total biomass from each region. Diets for each group were averaged among regional models, but they were not biomass-weighted because the EMAX diets were based on general literature values that did not differ by substantial amounts across regions. All calculations were conducted for both the original EMAX input values as well as the final, balanced values of the EMAX models. We preferentially

used the original EMAX input values as our starting point, but some values were changed during the model balancing process. In the absence of more information for the lower and higher trophic level groups, EMAX values for 1996-2000 were assumed to adequately represent values for our 1982-2013 Ecopath model; however, we note that several of the original EMAX values themselves were derived from different time periods due to the lack of information for some groups (Link et al. 2006).

3.3.2. Parameters for mid-trophic level groups (most fish groups)

The NWACS model has a greater taxonomic resolution for the fish groups (typically in the middle to high trophic levels) than do the EMAX models. We used stock assessment and fisheries independent survey data to parameterize these groups, when possible. Given the interannual variability in biomass estimates and catches, we generally calculated mean values across a 3-5 year period (e.g., 1981-1985), depending on data availability. In Appendix 1, these multi-year averages are referred to as being estimates for the "1982 year block".

3.3.2.1. Biomass

When available, biomass estimates for fished groups were obtained from the most recent stock assessment for a given group. Data from multiple assessments were combined in cases where there were multiple stocks within the modeled domain (e.g., GOM and GB Atlantic cod). In the situations with multiple stocks, absolute biomasses (in mt) were summed, whereas P/B and Z were calculated as biomass-weighted averages. In cases where a stock's distribution extends beyond the modelled domain (e.g., some species inhabit the South Atlantic Bight (SAB) in addition to the MAB), biomass was apportioned into our model domain based on regional catch or biomass proportions (if available). However, in most of these instances (e.g., Atlantic croaker *Micropogonias undulatus*), the entire stock biomass was used for our model because the contribution of the SAB catch (or biomass) was negligible and would not have a substantial impact. All absolute biomasses were divided by the model area (246,662 km^2) to obtain the biomass density in mt/km^2.

Fisheries-independent trawl survey data were obtained from the Northeast Fisheries Science Center (NEFSC) to parameterize the biomasses of non-assessed species. The NEFSC trawl survey is a longstanding fisheries independent monitoring program that has been conducted from 1963 – present, and samples depths from 27-366 m on the continental shelf (Azarovitz 1981). All species captured by the NEFSC trawl were re-classified into the NWACS group definitions, and catchability-corrected biomass estimates were generated following Link et al. (2006). Catchability coefficients (q) were assumed to be constant and were estimated using a Bayesian approach that incorporates information on catchability from previous studies. Details on the estimation of catchability coefficients are available in Link et al. (2006). For multispecies groups (e.g., Demersal benthivores-other) that are composed of multiple individual species with different q values, the median q was used.

3.3.2.2. Multi-stanza group treatment

Eight species were modeled using multiple stanzas (Table 1). With the exception of spiny dogfish, data for these groups came primarily from stock assessments. Generally, age-specific biomass estimates were available and summed based on the defined age classes. In the absence of age-specific biomasses, these were calculated from abundance-at-age and weight-at-age data, if possible. Fishing mortality rates

(F) were calculated as C/B using time series from stock assessments (Christensen and Walters 2004). Instantaneous total mortality rate estimates (Z) for each age class were calculated as the sum of F and natural mortality (M) estimates from the stock assessments. Often M was assumed to be constant in the assessments, but if age-specific M values were available, we calculated an average for each of our age stanzas.

Additional parameters are required for modeling multi-stanza groups, including the von Bertalanffy curvature parameter K, weight at maturity relative to the weight at infinity (W_{mat}/W_{inf}), and a recruitment parameter (termed the recruitment power). The recruitment parameter sets the degree of density dependence in juvenile survival for juveniles that might be reared outside the system, but this was not a concern for our groups because the juveniles are reared in the system, and the parameter was kept at its default value of 1 for all groups (Christensen et al. 2008). Values and sources for the other parameters were obtained from stock assessments, literature, and other models, as detailed for each trophic group (Appendix 1).

3.3.2.3. BA/B rates

Biomass accumulation rates (BA_i/B) were calculated for all assessed species. BA rates describe the instantaneous rate of change of a functional group's biomass, and they account for groups that are not in equilibrium with their sources of mortality. Negative values indicate a declining biomass and positive values indicate an increasing biomass within the Ecopath model. Biomass accumulation rates were calculated as the rate of change in biomass per year from 1982-1983 [$(B_{1983}- B_{1982})/ B_{1983}$], based on data availability. BA rates were entered as relative rates (yr^{-1}) for all trophic groups, but they can also be expressed in absolute terms (with units in mt km^{-1} yr^{-1}).

3.3.2.4. Catches

Catch data were obtained from National Oceanic and Atmospheric Administration (NOAA) online databases and stock assessments. Commercial landings data by weight were downloaded for the entire east coast of the USA by year, species, state, and gear type (NOAA 2014a, http://www.st.nmfs.noaa.gov/commercial-fisheries/index). State-specific landings from North Carolina to Maine were summed to obtain landings for the NWACS model domain. The 127 unique gear types in the database were classified into seven gear types that were used as fishing fleets in the NWACS model (dredge, trawl, trap, gill net, purse seine, longline, and other). An eighth fleet, representing recreational fisheries, was also included using recreational landings data obtained from NOAA by state, year, and species (NOAA 2014b, http://www.st.nmfs.noaa.gov/recreational-fisheries/index). Recreational data included estimates of catch that was brought back to the dock and could be identified by trained interviewer (Type A) and catch that was used for bait, released dead, or filleted as identified by anglers (Type B1).

For assessed species, we preferentially used the landings data from the assessment reports, as these were more detailed and tended to be larger, and we presumed them to be more accurate. Landings data from assessments included dead discards for a more complete estimate of biomass removal. Total catch for each group was apportioned among the eight fishing fleets based on the fractional catches

obtained from the NOAA databases. For all multi-stanza groups (except spiny dogfish), catch-at-age matrices from the stock assessment were used to partition catch among stanzas.

3.3.2.5. Unassimilated material

The ratio of unassimilated material to consumed biomass (UA/Q) represents the fraction of consumed biomass that is egested and not used for production or respiration. The assimilation efficiency (AE) is 1 – UA/Q. We assumed a UA/Q value of 0.2 for carnivorous fishes and higher trophic levels (Christensen et al. 2008). For lower trophic levels, we relied on estimates of UA/Q from the EMAX models, although several of these were increased during the balancing process to balance the detritus group.

3.3.2.6. Diets

Diets for trophic groups were obtained from the previous EMAX models, fisheries survey data, and the literature. Diets from the EMAX models were used in our NWACS model for any groups that were identical in the respective models, which were the lower trophic level groups (nodes 3-16; Table 1) and higher trophic level groups (nodes 53-59; Table 1). These groups are not typically captured in fisheries surveys. Diets for these groups were averaged across the four regional EMAX models. For each of the lower trophic level groups (nodes 3-16), the majority of the diets (94-100%) was comprised of a variety of the same lower trophic level prey and detritus, and thus no major adjustments to the EMAX diet matrix was needed. However, for the higher trophic level groups, the higher taxonomic resolution of our NWACS model necessitated additional mapping of prey groups. Diets of any EMAX trophic groups that did not exist in the NWACS model were apportioned equally across the NWACS groups that comprised the EMAX group. For example, if a predator consumed 9% of the "Small Pelagics – Commercial" EMAX group, that diet was divided equally among the appropriate NWACS groups (Atlantic herring, Atlantic mackerel, and butterfish *Peprilus triacanthus*) based on the EMAX group definitions. Some of these values were later adjusted in the model balancing process, for example to account for the different relative biomasses of the different prey groups.

Diets for nodes 17-52 (Table 1) were obtained primarily from the NEFSC and the Northeast Area Monitoring and Assessment Program (NEAMAP) trawl surveys that conduct extensive diet sampling within the model domain. Summaries of the sampling protocols and estimation methods for the NEFSC and NEAMAP surveys are described by Link and Almeida (2000) and Bonzek et al. (2015), respectively. Briefly, the NEFSC survey has sampled diets from the continental shelf (27-366 m) from 1963-present, whereas the NEAMAP survey samples shallower coastal waters (typically 6-18 m; but up to 37 m in some strata) from 2007-present. Diet summaries, pooled across years, were obtained from data managers of each survey (NEFSC – Sean Lucey; NEAMAP – Chris Bonzek). The summaries were provided for predators and prey defined using the NWACS taxonomic groupings. For multi-stanza groups, predators were defined based on the size-cutoffs for each age class, but prey were not classified by age or size because that information was not available in the databases. Note that each survey uses a slightly different statistical estimator for the mean diet; NEFSC generated stratum-specific diets, weighted by the number of tows (Link and Almeida 2000), whereas NEAMAP uses a cluster sampling estimator that weights station level diet data by the number of predators captured (Bonzek et al. 2015). Any unidentified material was divided among identified prey based on their relative proportions, for each unidentified

group. For example, unidentified fish were apportioned among identified fishes, then unidentified material was apportioned among all identified prey.

Given the central objectives pertaining to menhaden, diet estimates for menhaden and three dominant predators (striped bass *Morone saxatilis*, weakfish *Cynoscion regalis*, and bluefish *Pomatomus saltatrix*) were augmented with literature studies. A diet database for the three predators had been generated to parameterize a MSVPA model that was developed to complement the menhaden stock assessment (Garrison et al. 2010; SEDAR 2015). In addition to data from 21 literature studies, the database includes the diet data from the NEFSC and NEAMAP surveys (mentioned previously), as well as the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) survey (Bonzek et al. 2008). For the MSVPA, age-, region-, and season-specific diets are calculated as an average from these multiple sources weighted by sample sizes, study area, and number of years (SEDAR 2015). For use in the NWACS model, size classes (representative of age) for the predators were matched to the NWACS definitions, and diets were calculated for the full year. The outputted MSVPA diets were region-specific for the MSVPA regions (GOM, SNE, MAB, Chesapeake Bay, and North Carolina). These regional diets were averaged using region-specific biomasses of each predator species as determined from the NEFSC trawl survey. Given differences in regional definitions, we assumed that the MSVPA regions identified as Chesapeake Bay, North Carolina, and MAB were equally representative of the NWACS MAB region.

3.3.2.7. Diet – Size selectivity

Predator diets were modified to apportion the contribution of any multi-stanza prey groups across age-classes. For example, a 13% contribution of menhaden to the diet of medium striped bass was allocated among the three menhaden age-classes. These allocations were based on size selectivity information for the predators (when available) and on general guidelines. The general guidelines included the following: 1) Smaller-sized, single-stanza predators with low consumption of multi-stanza prey were assumed to only consume the small prey stanza; 2) All consumption by small size-class predators was assumed to come from small prey classes; and 3) allocations for some groups (e.g., sharks, highly migratory species, marine mammals, birds) were made on a case by case basis, but typically involved an equal partitioning among prey stanzas.

For larger predators that consumed higher amounts of multi-stanza prey, size selectivity information was obtained to partition the diets. The general approach was to use prey:predator length ratios to estimate the cumulative probabilities of a prey stanza being consumed by the predator, and using this information to calculate the proportion of consumption coming from each prey size class (i.e., using the difference of the cumulative probability cutoff values for each size class). For predator stanzas, length was based on the midpoint of the stanza lengths (with the upper threshold for Large predators obtained from FishBase), and for prey stanzas we used the length threshold to obtain cumulative probabilities (see Table 1 for stanza length ranges). Size selectivity information was obtained from two sources. First, for the MSVPA predators (striped bass, weakfish, and bluefish), we relied on the predator-specific size selectivity equations used for the MSVPA (Table 2 in Appendix A of SEDAR, 2015). Second, for other predators with multiple size classes (cod, spiny dogfish, summer flounder), size-selectivity information was obtained from Figure 4 in Scharf et al. (2000), and a similar approach was used based on the

cumulative frequency of prey:predator length ratios in the stomachs. Diet allocations for weakfish and bluefish were calculated separately from data in both sources (Scharf et al. 2000; SEDAR 2015), and differences between sources were small (typically <4%), indicating that both methods were comparable.

3.4. Description of Ecopath balancing procedure

The process of balancing the NWACS Ecopath model was iterative and relied on diverse changes to the initial parameterization. Following some general diagnostic analyses, our approach was to iteratively focus on groups with the highest ecotrophic efficiencies (those that were most out of balance) and adjust parameters using a variety of pieces of information. First, we conducted a series of pre-balance (PREBAL) diagnostics as recommended by Link (2010b). The PREBAL diagnostics evaluate biomasses, biomass ratios, vital rates, vital rate ratios, and other system characteristics, and can identify anomalous groups or parameters (e.g., biomass, P/B, Q/B) that deviate from expected patterns based on general ecological and fishery principles (Link 2010b). Second, we checked that most of the gross efficiency (GE) estimates (GE=P/Q) were realistic with values between 0.1-0.3 for most groups (Christensen et al. 2008). Third, the accuracy and quality of the parameters were evaluated, and we preferentially made changes to parameters that were less reliable, based on the quality of the data sources. Fourth, we checked the predation mortalities to determine if an unusually large amount of predation was caused by a single (or few) predators, and the diet matrix was adjusted as needed. Particular attention was paid to predation cycles (i.e., groups that feed on each other) and cannibalism, both of which can impede the balancing process. Given the large model domain, the majority of mortality should be accounted for in the model for most groups. Therefore, we also examined groups that had low EE values, and we attempted to make appropriate adjustments to increase EEs closer to 1.0. Justifications for parameter changes often varied; changes could be based on information from the literature, stock assessments, fishery independent surveys, or other ecosystem models, but the changes were also justified based on general ecological principles and hypotheses about how the system operated to ensure maintenance of the mass balance constraint of the food web model.

A detailed list of model changes was maintained in a text file, and numerous intermediary model versions were archived during the balancing procedure. Rather than documenting the exhaustive list of changes, we document here some major changes or general issues.

Initially, 31 of the 61 trophic groups had an EE>1. The small stanza for many of the multi-stanza groups had very high EEs, indicative of insufficient production to meet consumptive demand. Aside from adjusting the diet matrix, many of the Z estimates for these small stanzas had to be increased, particularly given that many of the initial Z estimates for these groups were based on the natural mortality rate from assessments that were assumed to be constant across ages (which is unlikely). Based on PREBAL diagnostics and high EE values, some groups (e.g., mesopelagics, anchovies, small pelagics, and demersal omnivores), were deemed to have greatly underestimated biomasses due to poor sampling (and inaccurate catchability estimates) by the NEFSC trawl survey gear. Link et al (2006) had recognized that the EMAX model values for unassimilated fractions were low for several low-trophic-level groups (e.g., bacteria, microzooplankton, copepods, and micronekton); therefore, we increased the

unassimilated fractions for those groups to balance the detritus group and to bring the values more in line with general recommendations (Link et al. 2006; Christensen et al. 2008).

3.5. General methods for ECOSIM parameterization

3.5.1. Time series

The input data needed for the time-dynamic Ecosim model included time series of relative biomass, catch, fishing mortality, and fishing effort. We used time series of catch and relative biomass as reference time series, whereas fishing mortality (for all groups with stock assessments) and fishing effort (for groups that are not assessed) were used to drive or force the model. Relative biomass time series were obtained from stock assessment reports (for assessed species), or from the NEFSC trawl survey for all other fish groups (see section 3.3.2.1). For assessed species, data from stock assessment reports were used to obtain catch (see section 3.3.2.4) and fishing mortality time series. Data from NOAA landings databases (see section 3.3.2.4 for description) were used to obtain catch time series for non-assessed fishes and non-assessed, commercially-harvested invertebrate species. Fishing effort by fleet was assumed to be proportional to changes in fleet-specific catch through time, and it was used to drive non-assessed trophic groups. Fishing mortality was used to drive changes in groups with stock assessment data, which included the groups of greatest commercial importance and of greatest relevance to our research objectives. For multi-stanza groups that had assessments, fishing mortality rates for each stanza were calculated as catch divided by biomass (F=C/B) (unless noted in Appendix 1). For any fishing mortality time series that did not extend for the full 1982-2013 time period, we used a 3-4 year mean of the nearest assessed years to extrapolate any missing values, but this was typically only needed for <5 years; however, Atlantic mackerel, butterfish, spiny dogfish, and Atlantic croaker had longer segments of missing Fs, with 6-9 years missing at either the beginning or end of the time series.

3.5.2. Parameterization and calibration

We followed the general process for Ecosim parameterization outlined by Christensen et al. (2008). We first set up the Ecosim model and the reference time series. Second, we examined simulated and observed patterns of response indices, and looked for groups with large discrepancies. We focused predominantly on groups that were central to our research objectives. Third, we explored alternative hypotheses that could have caused the poor fit for each group, including bad trend data, incomplete forcing data, inappropriate vulnerabilities, or inappropriate Ecopath parameters. During the calibration process, we made some modifications to the time series and to the Ecopath base parameterization to improve the fits for certain key groups (see below). As with all ecosystem models, there is no single, objective method for arriving at a calibrated model. Instead, modelers are required to make the best decisions they can throughout the process based on available data and literature, expert opinion, and their best judgement. Acknowledging that alternative model parameterizations can lead to different model behavior (e.g., Mackinson, 2014), we conducted Monte Carlo simulations to evaluate the sensitivity of model results to parameters as is considered best practice for such models (Heymans et al. 2016).

Ecosim models are sensitive to the choice of vulnerability exchange rate parameters that influence the relative importance of bottom-up and top-down processes on each group (Christensen et al. 2008). EwE

has a tool for minimizing the model sum of squared deviations (SSQ) between predicted and observed time series data by adjusting vulnerability parameters that are selected by the modeler. Starting with default vulnerabilities of v=2, we used the "Vulnerability Search" in the "Fit to time series" tool to identify and select the 100 predator-prey vulnerability parameters that were most influential in determining the model SSQ. In addition to these 100 vulnerability parameters, we also selected any other remaining vulnerability parameters (by predator) for a total of ten different stanzas of menhaden and three of their focal predators (striped bass, weakfish, and bluefish). These sets of vulnerability values for the ten stanzas were selected because they are of particular management concern for menhaden managers. An automated search was conducted to minimize the SSQ for the model based on the selected vulnerability parameters (100 predator-prey vulnerabilities and 10 remaining sets of vulnerabilities by predator stanza). We set a minimum value of 1.01 (instead of v=1) for all vulnerability values to allow at least some miniscule amount of top-down effect. Manual modifications were also made to correct any situations deemed to be unrealistic, such as large biomass oscillations or complete extinction of groups when projected into the future under different fishing scenarios.

Detailed notes were taken on adjustments made to time-series, vulnerabilities, and Ecopath parameters. Here we summarize some of the major adjustments and observations. Some additional comments are noted in Appendix 1.

1) Initially, all time-series of catch were obtained from the NOAA landings databases, but catch data from stock assessment reports for assessed species were shown to be different in several cases (with catches typically greater in the stock assessments). Therefore, we updated the catch time series for all assessed species assuming the catch data from the stock assessment reports were more accurate than the data from the NOAA landings databases alone.

2) Generally, model diagnostics were improved when diets of apex predators were adjusted to have greater consumption of larger stanzas of some species like bluefish and striped bass (e.g., shifting the diet away from smaller and medium stanzas). This change equated to revisiting the assumptions made for prey allocations described in Section 3.3.2.7.

3) Originally the diet of spiny dogfish had initially been mistakenly determined only using NEAMAP survey data (without the NEFSC estimates), yielding counterintuitive Ecosim results. Dogfish diets were updated and based on the NEFSC data because the NEFSC dataset had a much larger sample size.

4) Ecopath parameterizations were changed for several groups to increase their EE and improve the fits to the time series. Given the large spatial domain of the model, most of the EEs should be relatively high.

5) Fitting both the biomass and the catch time series simultaneously for striped bass stanzas was a challenge. Changes to improve the fit to one of the time series typically resulted in poorer fits to the other. We were unable to achieve good fits for both biomass and catch time series despite exploring numerous alternative hypotheses for the discrepancy (e.g., adjusting vulnerability parameters, increasing the weights of striped bass time series for the automated fitting procedure, adding a striped bass fishing fleet, adjusting the scale of F time series, changing the

scale of biomass, modifying degree of density dependence, and modifying different combinations of Ecopath and Ecosim parameters). Given these challenges, we chose a parameterization that prioritized a more accurate fit to the biomass reference time series (instead of the catch time series), because the biomass trend was more biologically meaningful for the objectives of our study. During this process, we did increase the landings of medium striped bass in the Ecopath model from 0.0037 to 0.0047 mt/km^2 (which was 9% greater than the 3-yr mean catch of 0.0043). This was done to achieve a better fit to the catch time series (especially catch of large striped bass). The change can be partly justified by the uncertainty in the release mortality for M striped bass; the assessment used an estimate of 9% mortality but some studies suggest mortality up to 26% (see section B6.6.5 in NEFSC (2013)).

6) For the multistanza groups, the estimated biomasses for the non-leading stanzas could diverge from the assessment data, contributing to some of the differences in fit. Often, the Ecopath biomasses for small stanzas were lower than the assessment predictions (e.g., menhaden), thus contributing to the underestimated C for such groups. This discrepancy is likely associated with the assumption of a stable age distribution in the EwE formulation for multi-stanza groups, and reflects one of the potential limitations of the Ecopath modeling framework.

7) Exploration of alternative parameterizations of the model revealed a particular sensitivity of model results to the estimate of the von Bertalanffy parameter, K, for menhaden and bluefish. When K deviated from the value used in the final base model (K= 0.304 for menhaden and K=0.262 for bluefish), the model demonstrated large oscillations in the biomasses of both striped bass and menhaden.

8) We modified the approach we used to obtain F estimates for assessed stocks. Initial versions of the NWACS model relied on F estimates obtained directly from stock assessments for different species, but many of these F rates were calculated based on abundances. To standardize the methodology for obtaining F and to express F rates in terms of biomass, we chose to calculate time series of F as F=catch/biomass for each year using stock assessment data. This change in methodology had little impact on model performance and conclusions, but is consistent with the approaches used in many other models (Christensen and Walters 2004; Chagaris et al. 2015; Heymans et al. 2016).

9) Maximum vulnerabilities for striped bass, weakfish, and bluefish were adjusted to improve the fits for some groups or to avoid qualitatively and quantitatively unrealistic model results. We constrained the vulnerabilities of the focal menhaden predators (striped bass, weakfish, bluefish) to be v $\leq$100; this was done to prevent dynamics that were excessively top-down. The vulnerabilities can be interpreted as the maximum predation mortality (M2) a predator may exert on a prey divided by the baseline M2 from the Ecopath model (Christensen and Walters 2004). Based on this definition and the baseline Ecopath M2 values, the originally estimated vulnerabilities of $1*10^{10}$ were deemed too large. Setting v $\leq$100 for these three predators only changed the model SSQ by 0.2%.

10) Vulnerabilities for menhaden were adjusted to ensure v $\geq$1.5 instead of v=1.01. This was done to prevent dynamics that were excessively bottom up. Lower vulnerability implies high productivity at low biomass because the group would be less available to predators.

Consequently, lower v's typically result in higher estimates of F_{MSY} (Heymans et al. 2016). The menhaden stock assessment does not produce F_{MSY} estimates and so we could not use the F_{MSY} estimates as a means to calibrate the vulnerability value, as recommended by Heymans et al. (2016). The adjustment to the minimum menhaden v had a negligible effect (0.2%) on the model SSQ.

4. Results

The balanced and calibrated base NWACS Ecopath model output represents the biomass, consumption, mortality, and diet of 61 trophic groups (from phytoplankton to top predators) along the Northeast USA). A food web diagram of the balanced NWACS Ecopath model demonstrates the complexity and interconnectedness of the 61 modeled trophic groups in the system (Figure 2). Such complexity is common for open marine systems (Link 2002). For example, menhaden supported a total of 22 predator groups (36% of the modeled trophic groups) and they contributed up to 33% to the diets of some predators, notably 30% for large striped bass and 33% for nearshore piscivorous birds (Figure 3). The biomass of modeled taxa and trophic groups spanned a total of four orders of magnitude and generally declined with trophic level (TL), but variability was high for a given TL due in part to the different levels of taxonomic aggregation of each group (Figure 4).

Output of our calibrated EwE model corresponded well to historical trends in biomass and catch time series for numerous species groups. Model fits to reference biomass time series captured the pattern and scale for a majority of groups (Figure 5). Examples of good fits include those for shrimp, Atlantic herring, menhaden (S, M, and L), striped bass, weakfish, hake and L summer flounder (Figure 5). For some groups (e.g., squid *Illex illecebrosus* and *Doryteuthis pealeii*, butterfish, S bluefish, S summer flounder, demersal piscivores), there was not much contrast (or high interannual variability) in the observed time series and thus the predictions were relatively flat. In other cases, the model did not predict the observed, steep biomass changes at the bounds of the time series (e.g., Atlantic mackerel, L bluefish, haddock, hake, S spiny dogfish). In the case of Atlantic mackerel, the time series from the assessment is short, necessitating extrapolation of fishing mortalities. For S spiny dogfish, the biomass time series from the NEFSC survey may not be a good representation of biomass due to change in catchability or availability of the stock (Rago and Sosebee 2009, 2013); it is unlikely that dogfish would experience a >20-fold increase in biomass in the most recent 6 years, given their life history.

There was a greater diversity in model fits to the catch time series (Figure 6). Catches for several groups were predicted well (e.g., Macrobenthos molluscs, megabenthos-other, , S and L bluefish, L striped bass, M weakfish, S cod, demersal benthivores, demersal piscivores). In some cases model output matched the pattern in the observed catch data, but the scale was off to varying degrees (e.g., shrimp, butterfish, M striped bass, L weakfish, haddock *Melanogrammus aeglefinus*, yellowtail flounder *Limanda ferruginea*), whereas in other situations the modeled catches depict the scale but not the pattern (Figure 6). For some groups (e.g., Atlantic mackerel, skates, coastal and pelagic sharks), both the scale and pattern of predictions deviate from the observed catches (Figure 6). In many of these cases of poor model fit, the lack of fit is partly attributable to absence of detailed information on fishing mortality for these groups; for most of the groups with poor fit, fishing pressure was forced based on fishing effort

rather than fishing mortality. However, we represent a large diversity of fishing methods and gears using eight general fishing fleets (based on gear type). Thus, the specific dynamics of effort through time for these groups are not well represented by the coarser resolution we applied in our fleet definitions. We chose to maintain a more general and parsimonious description of fishing fleets, because we do not anticipate that the added complexity would generate a greater understanding of system processes. For example, the addition of the longline fleet was intended to improve the C fits for the shark groups, but there was little effect.

The calibrated model fit represents a compromise in applying available information and considering probable ecological processes that affect outcomes in the ecosystem. It is also important to note that data included as "observed" or "reference" data are themselves typically the products of statistical or population models with their own inherent errors. For example, biomass estimates from single species stock assessments are influenced by model assumptions, process error, and measurement error. Despite the complexity and uncertainties of our NWACS model, the model synthesized available data and is a fair representation of the complex dynamics of the NWACS ecosystem.

5. Conclusion

As with all models, ecosystem models are influenced by various sources of uncertainty (Link et al. 2012). From a technical aspect, the main sources of uncertainty include natural variability in the ecosystem (e.g., spatial and temporal variation in ecological conditions), structural complexity of the model (e.g., number of groups, temporal scale, spatial dynamics), and observation error (Link et al. 2012). Results from Monte Carlo sensitivity analyses (conducted for evaluation of menhaden ecological reference points; Buchheister, unpublished) suggests that conclusions are not sensitive to deviations from the base Ecopath parameterization despite the complexity of the NWACS model. In the future, multi-model inference and comparison will be an important method for evaluating uncertainty related to the structural complexity of our model. For example, comparisons with other ecosystem, multi-species, or even single species models (that each have different underlying assumptions and functional forms) can address the robustness of model conclusions.

The NWACS ecosystem model can serve as a tool for managers, stakeholders, and scientists to explore the ecosystem consequences and tradeoffs of different management approaches for menhaden or other modeled groups. In so doing, the NWACS model can inform the development of strategic, long-term management decisions that account for predator-prey interactions and ecosystem interactions. Given that experimentation at an ecosystem-scale is not possible, simulation models such as NWACS are required for making predictions of possible ecosystem impacts resulting from fishing and other perturbations. It is important to note that the NWACS model is not intended to provide short-term tactical management advice, and thus will not fully replace any single or multi-species model, but rather could be used with other modeling approaches to strategically inform fisheries management (Christensen and Walters 2011).

For application to menhaden management specifically, the NWACS model can explicitly address predator-prey feedbacks to evaluate potential consequences of menhaden fishing on its predators and

the broader ecosystem. Thus, the NWACS model can serve to evaluate the tradeoffs associated with the main ecosystem services menhaden provides as forage and as the target of a directed fishery. Analyses addressing these aspects have been submitted for publication (Buchheister et al., submitted). Tradeoffs are at the core of the management concerns for menhaden and other forage species. The NWACS model can serve as an important platform for comparing outcomes of different management strategies and different ERPs, ultimately facilitating a transition to EAFM for menhaden.

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7. References

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8. Tables

Table 1. Ecosystem model trophic groups. Trophic groups are arranged by node number and arranged into broader categories. Eight species were modeled using multi-stanza groups that were identified as small (S), medium (M), or large (L), and the defining ages (in years) and fork lengths (cm) for each of the eight species is listed.

		Small		Medium		Large	
Node	Node Name	age	size	age	size	age	size
Primary Producers							
1	Phytoplankton						
2	Other primary producers						
Bacteria							
3	Bacteria						
Zooplankton							
4	Microzooplankton						
5	Small copepods						
6	Large copepods						
7	Gelatinous zooplankton						
8	Micronekton						
Benthic Invertebrates							
9	Macrobenthos - polychaetes						
10	Macrobenthos - crustaceans						
11	Macrobenthos - molluscs						
12	Macrobenthos - other						
13	Megabenthos - Filterers						
14	Megabenthos - other						
15	Shrimp and Similar Species						
Forage Fishes							
16	Mesopelagics						
17	Atlantic herring						
18	Alosines						
19-21	Atlantic menhaden	0	<14	1-2	14-24	3+	>24
22	Anchovies						
23	Atlantic mackerel						
24	Squid						
25	Butterfish						
26	small pelagic - other						
Fishes							
27-29	Bluefish	0	<30	1-3	30-60	4+	>60
30-32	Striped bass	0-1	<25	2-6	25-70	7+	>70
33-35	Weakfish	0	<20	1-2	20-40	3+	>40
36-37	Spiny dogfish	0-5	<60			6+	>60
38-40	Cod	0-1	<20	2-3	20-50	4+	>50
41	Haddock						
42	Hakes						
43	Atlantic croaker						
44-45	Yellowtail flounder	0	<20			1+	>20
46-47	Summer flounder	0	<25			1+	>25
48	Skates						
49	Demersal benthivores - other						
50	Demersal piscivores - other						
51	Demersal omnivores - other						
52	Medium pelagic - other						
Apex Predators							
53	Sharks - coastal						
54	Sharks - pelagic						
55	Large pelagics (HMS)						
56	Pinnipeds						
57	Baleen whales						
58	Odontocetes						
59	Seabirds						
60	Shorebirds - piscivorous						
Detritus							
61	Detritus						

9. Figures

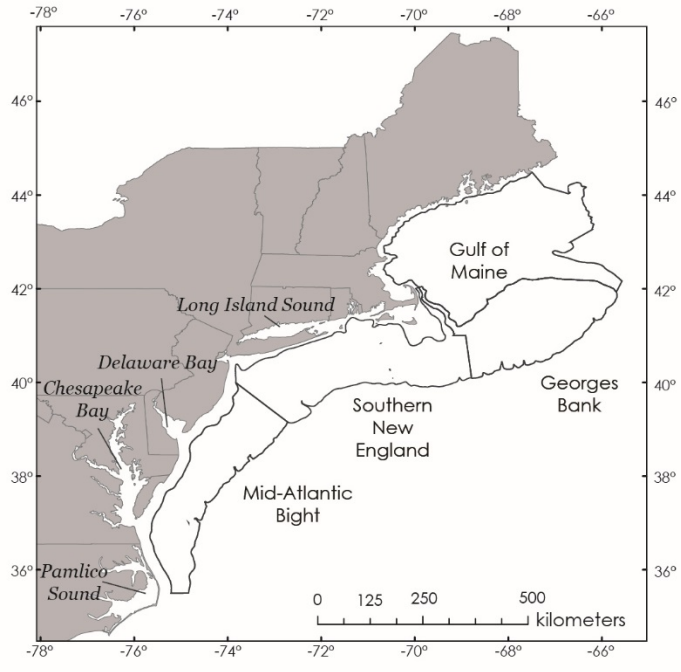


Figure 1. Map of the Northwest Atlantic Continental Shelf (NWACS) system, with major subregions and estuaries labeled. Figure modified from Link et al. 2006.

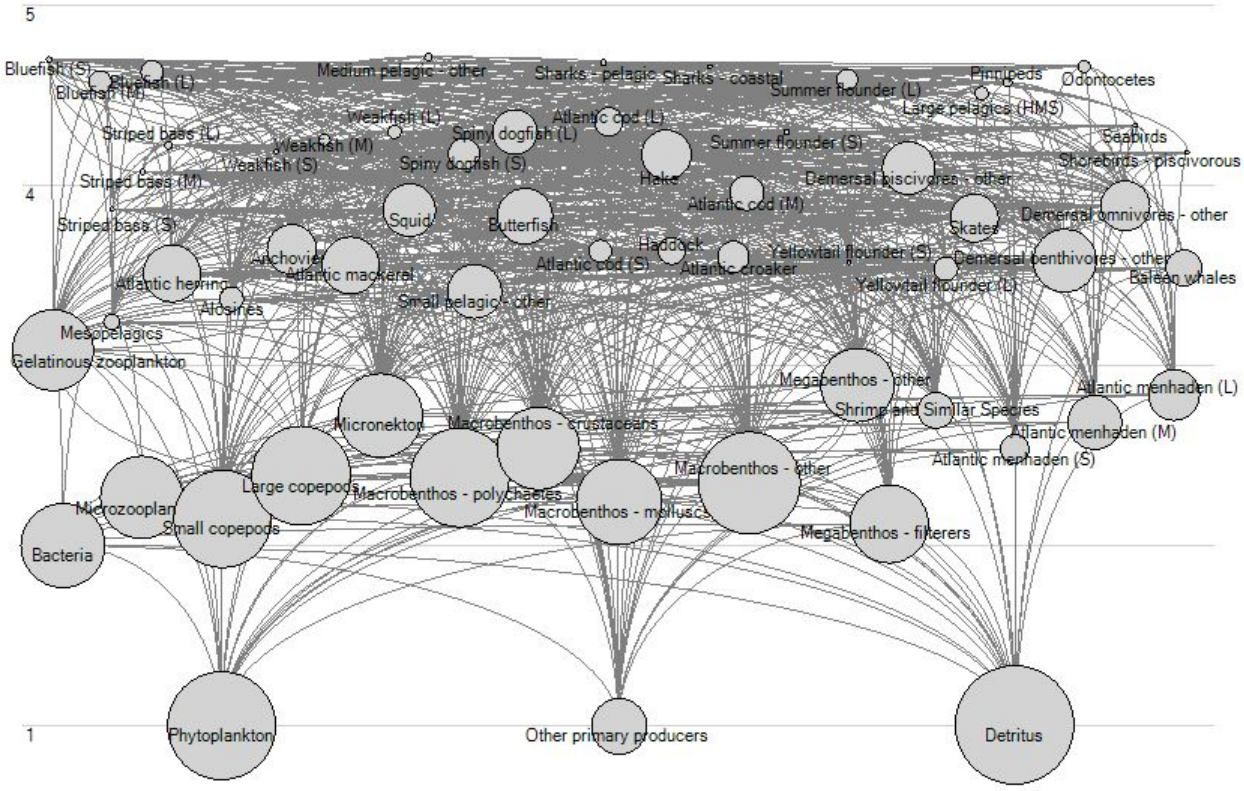


Figure 2. Food web diagram of the NWACS ecosystem model. Nodes represent modeled trophic groups (as labeled) with the size of the circle proportional to biomass, and lines represent trophic linkages among groups. Groups with multiple age classes are labeled generically as small (S), medium (M), and large (L). Numbers on the left demark trophic level.

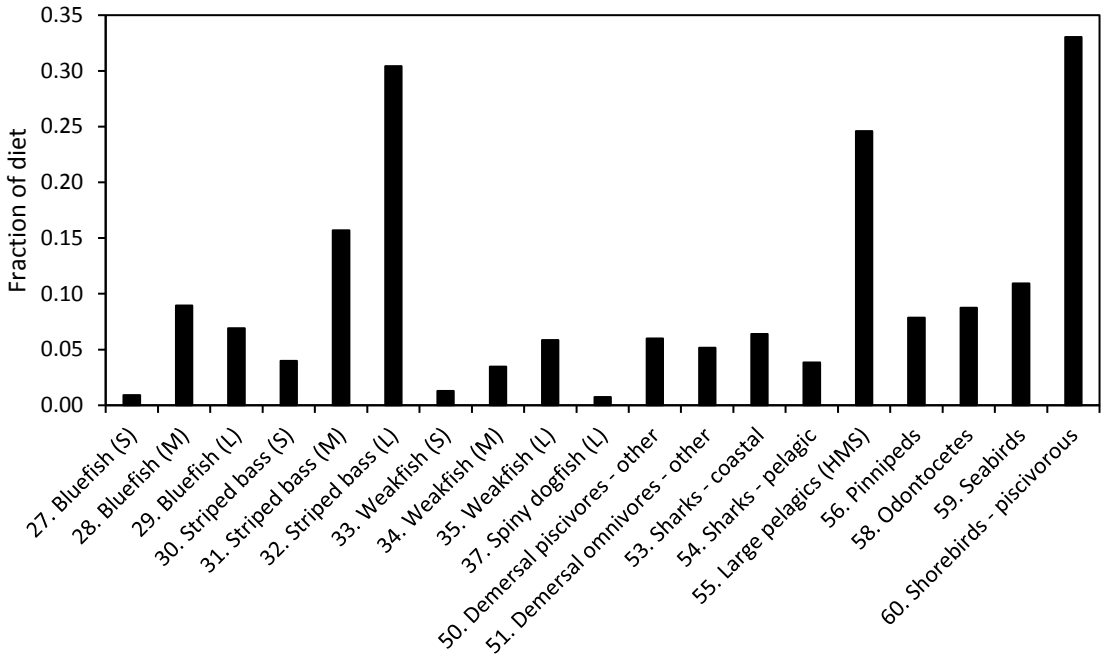


Figure 3. Contributions of menhaden to the diets of predators in the balanced NWACS Ecopath model.

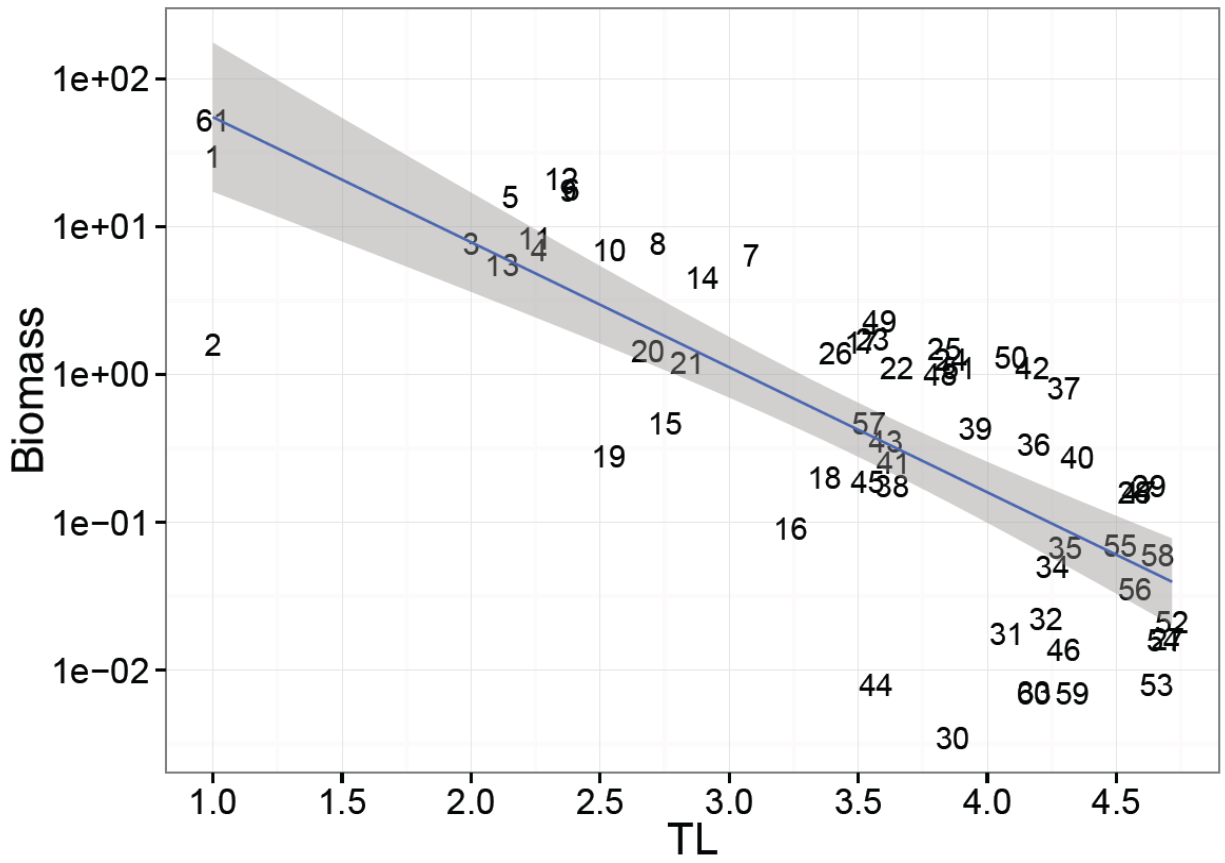


Figure 4. Biomass for each trophic group by trophic level (TL) with a fitted linear regression (with shading for 95% confidence interval), based on the balanced NWACS Ecopath model. Trophic groups are labeled by node number (see Table 1).

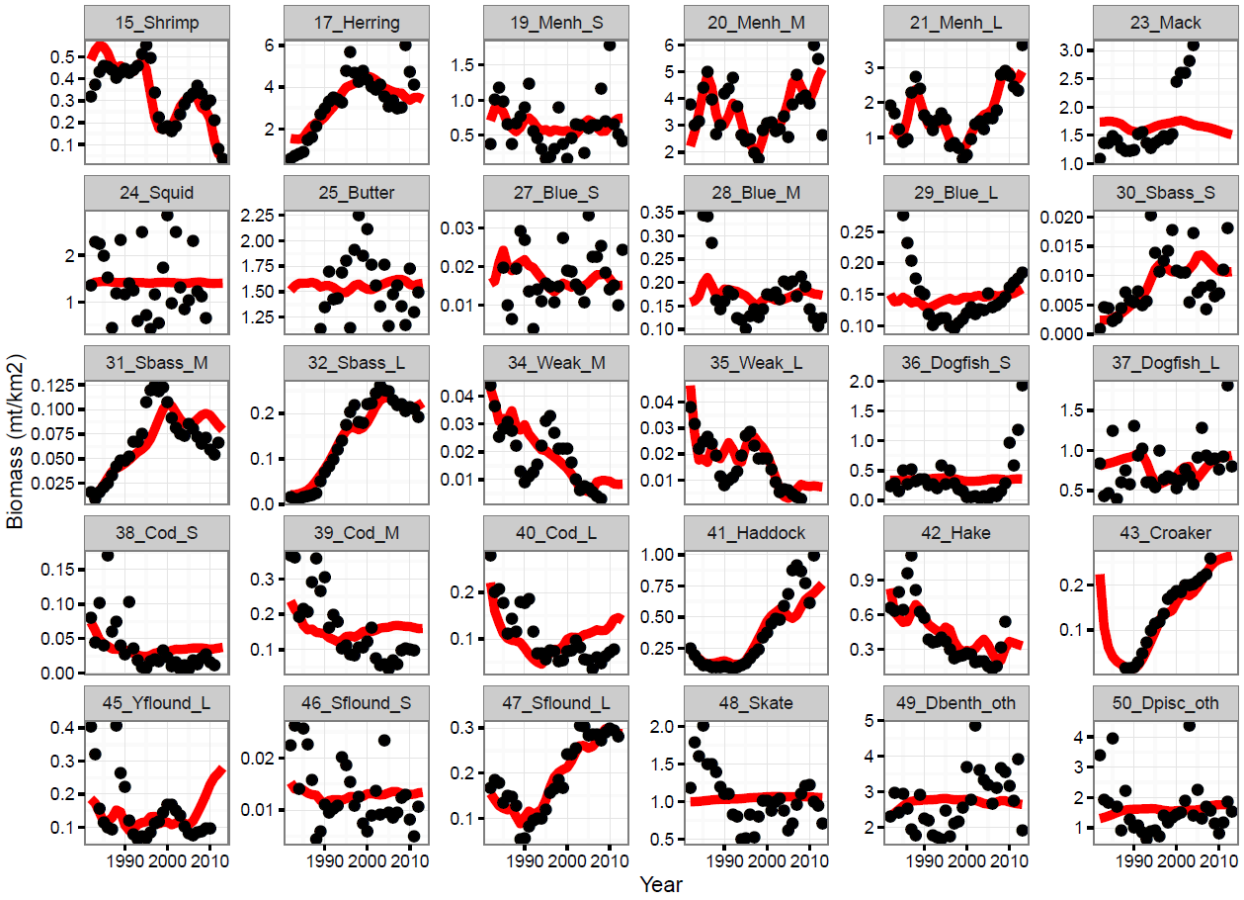


Figure 5. Biomass fits for the Ecosim model. Observed (points) and predicted (lines) biomass estimates by year for the ecosystem model of the Northwest Atlantic Continental Shelf. Panels are labeled by trophic group number, abbreviation, and stanza if applicable (S-small, M-medium, L-large). Trophic groups without observed, empirical data are excluded.

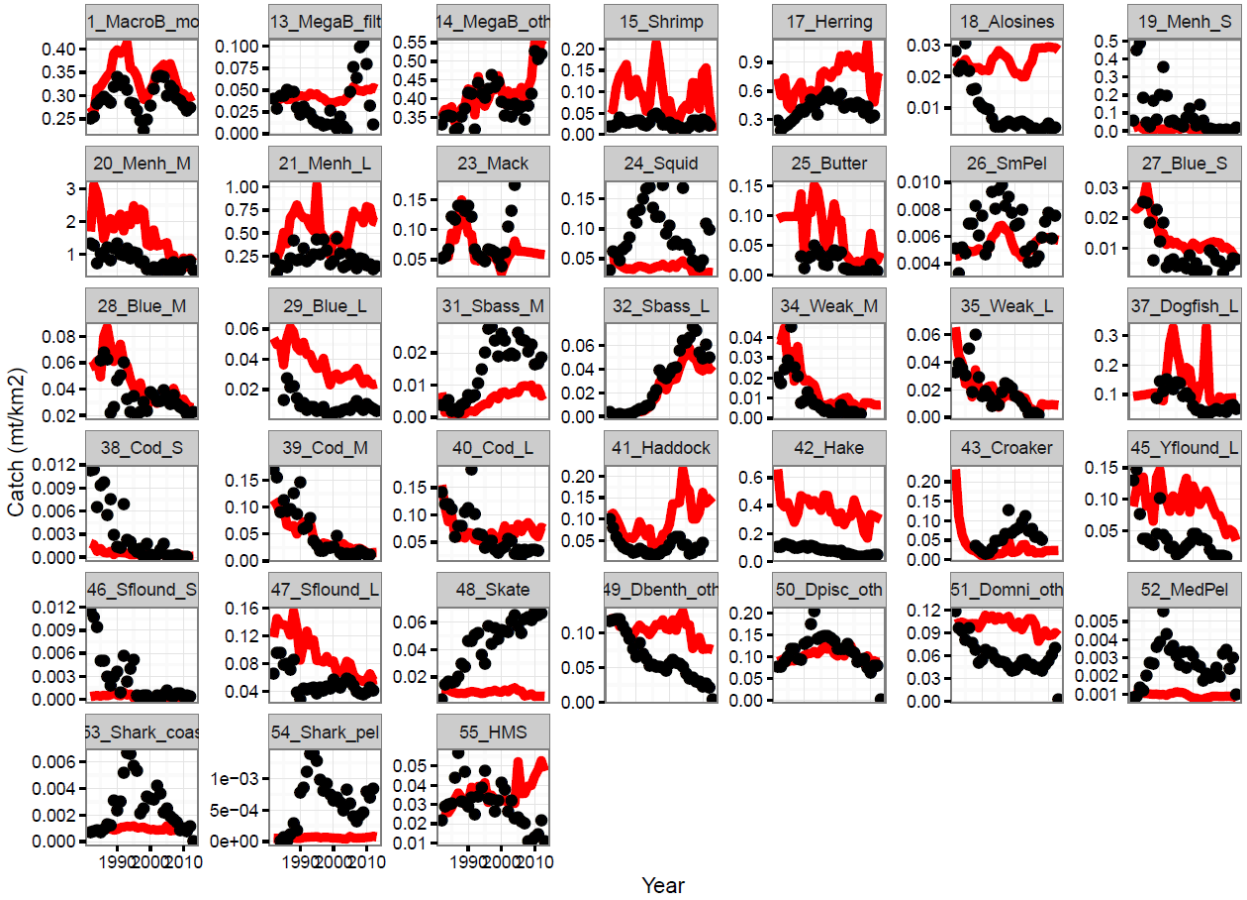


Figure 6. Catch fits for the Ecosim model. Observed (points) and predicted (lines) catch estimates by year for the ecosystem model of the Northwest Atlantic Continental Shelf. Panels are labeled by trophic group number, abbreviation, and stanza if applicable (S-small, M-medium, L-large). Trophic groups without observed, empirical data are excluded.

Appendix 1 – Parameterization of trophic groups in the NWACS ecosystem model

Group 1. Phytoplankton

Phytoplankton represented the dominant group of primary producers in the model. Phytoplankton parameters were obtained from the EMAX models, following the methods described in section 3.3.1. Biomass was estimated to be 20.13 mt/km^2, based on calculations from vertically integrated profiles of chlorophyll a and remotely sensed near-surface chlorophyll from the SeaWiFS satellite (Link et al. 2006). P/B was estimated as 180.7, using a vertically generalized productivity model (Link et al. 2006).

Group 2. Other primary producers

The other primary producer (PP) group accounts for additional primary production sources aside from pelagic phytoplankton. This lower trophic level group was not included in the original EMAX models, but it can be an important source of production, particularly in nearshore waters, but also throughout the continental shelf (Cahoon et al. 1994). Other PP includes microphytobenthos, submerged aquatic vegetation in shallow habitats, and macroalgae.

Reliable estimates of microphytobenthos and SAV biomass and production are not available for the spatial extent of our model. Therefore, we assumed an EE value of 0.90 and a used a P/B value of 55.57 (Okey 2001). B was estimated using the Ecopath model.

There are no reliable diet data for consumption of microphytobenthos and other primary production, particularly at the large scales of our model domain that spans shallow water habitats with shelf habitats. For bacteria, megabenthos filterers, and all macrobenthic groups, we assumed that a small amount (3%) of the detritus consumed was comprised of other primary production, specifically microphytobenthos, which is typically consumed by detritivores or by suspension feeders that consume re-suspended detritus (Miller et al. 1996).

Group 3. Bacteria

Bacteria are an important component of the microbial loop within aquatic systems. Bacteria convert labile and refractory dissolved organic matter into biomass that can be utilized by higher trophic levels, but the microbial loop in general may largely act as a carbon sink (Ducklow and Carlson 1992). Estimates of bacterial B (3.827 mt/km^2), P/B (91.25 yr^{-1}), Q/B (380.2 yr^{-1}), and diet were obtained from the EMAX models, following the methods described in section 3.3.1.

Group 4. Microzooplankton

Microzooplankton represents a diverse assemblage of organisms including protozoa, ciliates, flagellates, copepod nauplii, and larval stages of benthic invertebrates (e.g., trochophores, veligers, etc.). Estimates of B (3.161 mt/km^2), P/B (72.00 yr^{-1}), Q/B (242.4 yr^{-1}), and diet were obtained from the EMAX models, following the methods described in section 3.3.1.

Groups 5-6. Small and Large copepods

Small and large copepods were defined based on body size of species and copepodite stages. Large copepods included stages V and VI of *Calanus finmarchicus*, *Metridia lucens*, and *Centropages typicus*. Small copepods included copepodite stages I-IV of the large copepod species and all stages of *Centropages hamatus*, *Pseudocalanus spp.*, *Temora longicornis*, *Paracalanus parvus*, *Nannocalanus minor*, and *Clausocalanus arcuicornis*. All model parameters were obtained from the EMAX models, following the methods described in section 3.3.1. For small copepods, we used the following estimates: B – 7.809 mt/km^2, P/B – 41.114 yr^{-1}, and Q/B – 127.75 yr^{-1}. For large copepods, we used these estimates: B – 17.966 mt/km^2, P/B – 48.523 yr^{-1}, and Q/B – 109.5 yr^{-1}.

Group 7. Gelatinous zooplankton

Gelatinous zooplankton included Cnidarians (medusae and hydrozoans), Ctenophores, colonial Siphonophores, and colonial Salpidae. Estimates of B (6.349 mt/km^2), P/B (40.00 yr-1), Q/B (145.3 yr^{-1}), and diet were obtained from the EMAX models, following the methods described in section 3.3.1.

Group 8. Micronekton

Micronekton were defined as the largest animals captured in plankton nets with body lengths usually 5-10 mm or greater (Link et al. 2006). This group included amphipoda, euphausiacea, mysidacea, other similar decapods, and chaetognatha. Estimates of B (7.654 mt/km^2), P/B (14.25 yr^{-1}), Q/B (85.50 yr^{-1}), and diet were obtained from the EMAX models, following the methods described in section 3.3.1.

Groups 9-12. Macrobenthos (polychaetes, crustaceans, molluscs, other)

Macrobenthos was defined as the invertebrate infauna and epifauna that can be sampled quantitatively by a Smith McIntyre grab and be retained on a 1.0 mm or 0.5 mm sieve (Link et al. 2006). Macrobenthos was divided taxonomically into a polychaete, crustacean, mollusk, and other group. The “other” group includes echinoderms, nemerteans, tunicates, and coelenterates. Each group is highly speciose, but Table 2 identifies some of the dominant taxa based on biomass. Parameters and diets for the macrobenthic groups were estimated from the EMAX models, following the methods in section 3.3.1. Biomasses were estimated as 17.452, 5.896, 8.34, and 70.738 mt/km^2 for the polychaete, crustacean, mollusc, and other groups respectively, based on benthic survey data (Link et al. 2006). P/B ratios were calculated using production estimates from the literature for dominant species and the estimated biomasses, yielding values of 2.5, 3, 1.737, and 2 for each of the four groups respectively. Q/B values, from the EMAX models were 17.50, 21.00, 13.95, and 16.06 yr^{-1} for the polychaete, crustacean, mollusc, and other groups respectively.

Table 2. List of taxa included in the four Macrobenthos trophic groups (crustaceans, molluscs, polychaetes, and other).

Macrobenthos			
Crustaceans	**Molluscs**	**Polychaetes**	**Other**
Ampelisca agassizi	*Anomia aculeata*	*Aglaophamus circinata*	*Actinauge verrilli*
Ampelisca vadorum	*Aporrhais occidentalis*	*Ampharete arctica*	*Actiniaria unident.*
Amphipoda unident.	*Astarte crenata*	*Anobothrus gracilis*	*Amphioplus abditus*
Byblis serrata	*Astarte undata*	*Aphrodita hastata*	*Anthozoa*
Cirolana polita	*Bivalvia unident.*	*Aphrodita sp.*	*Arachnida*
Cirolana sp.	*Buccinum sp.*	*Asabellides oculata*	*Arbacia punctulata*
Corophium crassicorne	*Buccinum undatum*	*Capitellidae*	*Ascidiacea*
Crangon septemspinosa	*Busycon canaliculatum*	*Chone infundibuliformis*	*Asteroidea*
Diastylis quadrispinosa	*Busycon carica*	*Filograna implexa*	*Brisaster fragilis*
Edotea acuta	*Busycotypus canaliculatus*	*Glycera dibranchiata*	*Ceriantheopsis americanus*
Gammarus annulatus	*Colus pubescens*	*Harmothoe oerstedi*	*Cerianthus sp.*
Isopoda unident.	*Colus pygmaeus*	*Lumbrineris acicularum*	*Craniella*
Leptocheirus pinguis	*Colus stimpsoni*	*Lumbrineris hebes*	*Cucumariidae unident.*
Meganyctiphanes sp.	*Crepidula*	*Lumbrineris magalhaensis*	*Echinarachnius parma*
Pagurus acadianus	*Cyclocardia borealis*	*Lumbrineris sp.*	*Edwardsia elegans*
Pagurus longicarpus	*Ensis directus*	*Maldane sarsi*	*Encope emarginata*
Pagurus pollicaris	*Euspira heros*	*Nephtys bucera*	*Havelockia scabra*
Pagurus pubescens	*Gastropoda unident.*	*Nephtys incisa*	*Hydrozoa*
Pagurus sp.	*Lunatia triseriata*	*Nephtys picta*	*Mellita quinquiesperforata*
Palaemonetes	*Modiolus modiolus*	*Nephtys sp.*	*Molgula arenata*
Politolana concharum	*Mytilus edulis*	*Ninoe nigripes*	*Molpadia oolitica*
Politolana impressa	*Nassarius trivittatus*	*Onuphis opalina*	*Ophiura sarsi*
Politolana polita	*Neverita duplicata*	*Pherusa affinis*	*Ophiuroidea unident.*
Pseudunciola obliqua	*Nucula proxima*	*Polychaeta unident.*	*Paranthus rapiformis*
Rhepoxynius hudsoni	*Nucula sp.*	*Scalibregma inflatum*	*Pennatula aculeata*
Unciola inermis	*Pitar morrhuanus*	*Spio filicornis*	*Porifera*
Unciola irrorata	*Pleurobranchaea sp.*	*Spio setosa*	*Rhynchocoela*
Unciola sp.	*Pleurobranchaea tarda*	*Spiophanes bombyx*	*Schizaster sp.*
	Polinices duplicatus	*Sternaspis fossor*	*Sclerodactyla briareus*
	Polinices heros	*Sternaspis scutata*	*Steroderma unisemita*
		Streblosoma sp.	*Strongylocentrotus droebachiensis*

Groups 13-14. Megabenthos (filterers, other)

Megabenthos is a term used to refer to larger benthic invertebrates, although the group is not strictly defined in terms of size. Megabenthos filterers included larger, exploited bivalve species, including the ocean quahog (*Arctica islandica*), Atlantic surf clam (*Spisula solidissima*), sea scallop (*Placopecten magellanicus*), hard clam (*Mercenaria mercenaria*), and soft shell clam (*Mya arenia*). All other bivalves are included in the macrobenthic mollusc group. Following Link et al. (2006), the "other" megabenthos group was comprised of large arthropods (e.g., Brachyuran and Anomuran crabs, lobsters, octopods, and mantis shrimp) and asteroid echinoderms. Table 3 lists some of the abundant and commonly occurring species in these groups.

Parameters and diets for the megabenthic groups were estimated from the EMAX models, following the methods in section 3.3.1. Biomasses were estimated as 2.997 and 4.498 mt/km^2 for the filterers and other group respectively, based on fisheries independent survey data from the NEFSC Bottom Trawl, Clam, and Scallop Surveys (Link et al. 2006). P/B ratios were calculated from the EMAX models as 7.711 and 1.855 yr^{-1}, and Q/B values were 16.51 and 15.53 yr^{-1} for the filterers and other group respectively.

Table 3. List of taxa included in the Megabenthos – Other trophic group.

Megabenthos - Other			
Asterias forbesii	*Carcinus maenas*	*Libinia emarginata*	*Portunus gibbesii*
Asterias vulgaris	*Chionoecetes opilio*	*Limulus polyphemus*	*Scyllarides aequinoctialis*
Astropecten spp.	*Ctenodiscus crispatus*	*Lithodes maja*	*Scyllarides nodifer*
Calappa flammea	*Galatheidae*	*Majidae*	*Solaster sp.*
Calappa sulcata	*Galatheidae Galatheids,*	*Octopus vulgaris*	*Squilla*
Calappidae	*Geryon affinis*	*Ovalipes ocellatus*	*Stomatopoda*
Callinectes	*Geryon fenneri*	*Ovalipes sp*	
Callinectes sapidus	*Geryon quinquedens*	*Ovalipes stephensoni*	
Callinectes similis	*Hepatus epheliticus*	*Paguristes erythrops*	
Cancer	*Homarus americanus*	*Paguroidea*	
Cancer borealis	*Leptasterias sp.*	*Pagurus*	
Cancer irroratus	*Libinia*	*Panulirus argus*	
Cancridae	*Libinia dubia*	*Portunidae*	

Group 15. Shrimps

The shrimp group includes several species, including bristlebeaked shrimp (*Dichelopandalus leptocerus*), brown shrimp (*Farfantepenaeus aztecus*), glass shrimp (*Pasiphaea multidentata*), northern pink shrimp (*Farfantepenaeus duorarum*), northern red shrimp (*Pandalus borealis*), northern white shrimp (*Litopenaeus setiferus*), other northern shrimps (*Pandalus spp*.), and roughneck shrimp (*Rimapenaeus constrictus*). Shrimp in the Crangonidae family can also be abundant, but these were included in the Macrobenthic crusteacean group because they are smaller and captured with benthic grabs (Link et al. 2006). Parameters and diets for this group were obtained from the EMAX models, as described in section 3.3.1. Biomass was calculated to be 0.087 mt/km^2, P/B was assumed to be 1.000 yr^{-1}and Q/B was set at 5.000 yr^{-1}.

Group 16. Mesopelagics

The mesopelagic group included *Myctophidae* and *Maurolicus sp.* and represents the small bodied, vertically migrating fishes that are more abundant in the deeper, mesopelagic waters off of the continental shelf.

Parameters for this group were obtained from the NEFSC survey and the EMAX models. The q-corrected biomass was 0.004 mt/km^2 based on the NEFSC survey. Based on the EMAX model, P/B was assumed to be 0.95 yr-1 and Q/B was set at 1.825 yr^{-1}. Diets for mesopelagics were also obtained from the EMAX models, following the methods described in section 3.3.1.

Group 17. Atlantic herring

Atlantic herring (*Clupea harengus*) is an abundant forage fish that supports one of the largest fisheries on the US east coast. Parameters for this group were obtained from the Atlantic herring stock assessment (NEFSC 2012a). Biomass for the 1982 year block (1981-1985) was estimated to be 0.908 mt/km^2. P/B was estimated as 0.621 yr^{-1}, based on an F of 0.421 yr^{-1} for the 1982 year block and an assumed M of 0.2 yr^{-1}. Based on the EMAX model, Q/B was set at 1.978 yr^{-1}. Diet

compositions were calculated from the NEFSC trawl survey's food habits program. Time series of B, C, and F were obtained from the stock assessment (NEFSC 2012a).

Group 18. Alosines

The Alosine group includes the anadromous clupeids in the Alosinae subfamily, including blueback herring (*Alosa aestivalis*), hickory shad (*A. mediocris*), alewife (*A. pseudoharengus*), and American shad (*A. sapidissima*). In the EMAX models, this group was named the "small pelagic – anadromous" group. Parameters for the Alosine group were obtained from the NEFSC survey and the EMAX models. The q-corrected biomass was 0.069 mt/km^2 based on the NEFSC survey for the 1982 year block. Based on the EMAX model, P/B was assumed to be 0.42 yr^{-1}and Q/B was set at 2 yr^{-1}. Diets for Alosines were calculated as an average of the diet compositions from the NEFSC and NEAMAP surveys.

Groups 19-21. Atlantic menhaden (age-0, age-1-2, age-3+)

Atlantic menhaden (*Brevoortia tyrannus*) is an important clupeid forage fish in the system. Menhaden were divided into three age stanzas (S=age-0, M=ages 1-2, and L=age 3+). These stanzas were chosen to 1) capture their dietary shift from feeding on phytoplankton to zooplankton after age-0 (MDSG 2009; Lynch et al. 2010), 2) capture fishery dynamics that largely target ages 1-3, and 3) facilitate potential future modeling of spatial patterns in distribution given that older menhaden migrate farther north (Nicholson 1978).

Biomass

Biomass values were obtained from the menhaden stock assessment (SEDAR 2015), following the methods described in section 3.3.2.1. The large size class was used as the leading stanza, with a Biomass of 1.2 mt/km^2. Biomasses for the other stanzas were estimated to be 0.658 mt/km^2 (small stanza) and 3.292 mt/km^2 (medium stanza) based on the multistanza growth and mortality parameters. The Von Bertalanffy growth parameter K was initially set at 0.424 from the CBFEM (Christensen et al. 2009) but was updated to 0.304 during the balancing process based on the stock assessment (SEDAR 2015). Wmat/Winf was set at 0.24 using the value from the CBFEM (Christensen et al. 2009).

Z

Total mortality was obtained from the stock assessment based on estimates of M and F. Age-specific Lorenzen (1996) M values were averaged for each age class yielding values of 1.231, 0.805, and 0.596 yr^{-1} for the S, M, and L size classes. F values for each age class in 1982 were calculated as F=C/B from the assessment data, with values of 0.065, 0.504, 0.160 yr^{-1} for the S, M, and L stanzas. Thus, the Z estimates were 1.296, 1.308, 0.756 yr^{-1} respectively.

Q/B

Q/B was set at 2.0 for the L stanza (the leading stanza), based on values from the EMAX models.

Diet

Various studies indicate that Atlantic menhaden shift from particulate zooplanktivory as larvae (June and Carlson 1971; Kjelson et al. 1975) to obligate filter feeders that consume phytoplankton, zooplankton and detritus as juveniles and adults (June and Carlson 1971; Edgar and Hoff 1976; Peters and Schaaf 1981; Lewis and Peters 1984, 1994; Brush et al. 2009). However, for juveniles and adults the relative importance of these different nutrient sources remains unclear. The importance of each of these food sources varies spatially, temporally, and ontogenetically, and precise quantitative estimates are confounded by a large degree of unidentifiable, amorphous matter. Brush et al. (2009) used stable isotope analysis to estimate the time-integrated contribution of zooplankton and particulate organic matter (POM; primarily phytoplankton and detritus) to juvenile and adult menhaden in Chesapeake Bay. We used an average of their estimates for juvenile and adult menhaden as an initial representation of POM and zooplankton consumption for small menhaden (58% POM, 42% zooplankton) and for large menhaden (34% POM, 66% zooplankton) respectively. These values from Brush et al. 2009 lay within the range of values in other published studies (cited above), and were deemed to suitably measure central tendency. For each menhaden group, the zooplankton diet fraction was divided equally among microzooplankton, small copepods, and large copepods. The POM diet fraction was assumed to be comprised of phytoplankton (48%), detritus (48%), and other primary producers (4%). The small amount of other primary production represents consumption of benthic algae, which can be an important dietary component in some locations (Edgar and Hoff 1976). For medium menhaden, the diet matrix was filled using the average of dietary values for the small and large menhaden.

Catch

Menhaden catch was calculated for each group following the methods described in section 3.3.2.4. Due to interannual variability, we used the average catch from 1981-1985, with values of 0.321, 1.071, and 0.165 mt/km^2 for the S, M, and L stanzas.

Group 22. Anchovies

Anchovies, an abundant forage group, included bay anchovy (*Anchoa mitchilli*), striped anchovy (*Anchoa hepsetus*), and silver anchovy (*Engraulis eurystole*). Parameters for this group were obtained from the NEFSC survey and the EMAX models, following the methods described in sections 3.3.2.1 and 3.3.1. The q-corrected biomass was 0.439 mt/km^2 based on the NEFSC survey. Based on the EMAX model, P/B was assumed to be 0.849 yr^{-1} and Q/B was set at 1.978 yr^{-1}. Diets were estimated from NEFSC survey food habits data.

Group 23. Atlantic mackerel

Atlantic mackerel (*Scomber scombrus*) is a pelagic, schooling species that supports diverse predators and a commercial fishery. Parameters for this group were obtained from the NEFSC survey and the EMAX models, following the methods described in sections 3.3.2.1 and 3.3.1. The q-corrected biomass was 0.358 mt/km^2 based on the NEFSC survey. Based on the "small pelagic-

commercial" group in the EMAX models, P/B was assumed to be 0.45 yr^{-1} and Q/B was set at 1.978 yr^{-1}. Diets were estimated from NEFSC survey food habits data.

Group 24. Squid

The squid group included the northern shortfin squid (*Illex illecebrosus*), the longfin inshore squid (*Doryteuthis pealeii*), and other related cephalopods. Estimates of B (1.267 mt/km^2), P/B (0.969 yr^{-1}), Q/B (2.703 yr^{-1}), and diet were obtained from the EMAX models, following the methods described in section 3.3.1. During the balancing process, P/B was increased to 5.72 yr^{-1} based on the M estimated for nonspawning *Doryteuthis pealeii* in the stock assessment (NEFSC 2011); this value is more consistent with the short life span of squids.

Group 25. Butterfish

Butterfish (*Peprilus triacanthus*) is an abundant and commercially important forage species. Biomass was set at 1.488 mt/km^2 based on q-corrected swept-area estimates from the NEFSC trawl survey. The natural mortality estimate of 1.27 yr^{-1} from the stock assessment (NEFSC 2014a) was used for P/B, given that fishing mortality estimates averaged only 3% of M, and the earliest estimates for F were from 1989. Q/B was assumed to be 1.978 based on the average EMAX values for small pelagic fishes (Link et al. 2006). Butterfish diets were calculated from NEFSC food habits data.

Group 26. Small pelagic - other

The other small pelagic group represents all relatively smaller bodied pelagic fishes (from both estuarine and marine habitats) that are not included in any other groups. It includes fishes in various families such as Ammodytidae, Atherinopsidae, Carangidae, Clupeidae, Mugilidae, and Scombridae (Table 4). Estimates of B (0.365 mt/km^2), P/B (0.849 yr^{-1}), Q/B (2.000 yr^{-1}), and diet were obtained from the EMAX models, following the methods described in section 3.3.1.

Table 4. List of taxa included in the Small Pelagic-Other trophic group.

small pelagic - other	
Ablennes hians	*Opisthonema oglinum*
Ammodytes	*Osmerus mordax*
Ammodytes americanus	*Peprilus alepidotus*
Ammodytes dubius	*Sardinella aurita*
Argentina silus	*Scomber japonicus*
Ariomma bondi	*Scomberesox saurus*
Decapterus macarellus	*Scomberomorus cavalla*
Decapterus punctatus	*Scomberomorus maculatus*
Etrumeus teres	*Selar crumenophthalmus*
Menidia menidia	*Selene setapinnis*
Mugil cephalus	*Trachurus lathami*
Mugil curema	

Groups 27-29. Bluefish (age-0, age-1-3, age-4+)

Bluefish (*Pomatomus saltatrix*) was divided into three stanzas. The small (S), medium (M), and large (L) stanzas were defined as: S = age 0 (<=30cm), M = ages 1-3 (30-60cm), and L = age 4+ (>60cm). These stanzas were chosen to capture changes in feeding with size (Buchheister and Latour 2015; SEDAR 2015). Biomass values were originally obtained from the 2012 update of the bluefish stock assessment (NEFSC 2012b), but a more recent and reliable assessment was completed in 2015 (NEFSC 2015), and the NWACS model was updated with this information as part of the calibration and balancing process.

Biomass

Biomass values obtained from the most recent bluefish stock assessment (NEFSC 2015) followed the methods described in section 3.3.2.1. The medium stanza was used as the leading stanza, with B=0.205 mt/km^2 using the average of first 3 years (1985-1987) of available estimates. Biomasses for the other stanzas were estimated to be 0.0075 mt/km^2 (small stanza) and 0.336 mt/km^2 (large stanza) based on the multistanza growth and mortality parameters. Von Bertalanffy K was set at 0.26 (Salerno et al. 2001), and Wmat/Winf was assumed to be 0.2 based on the CBFEM (Christensen et al. 2009).

Z

Total mortality was obtained from the stock assessment based on estimates of M and F. Age-specific M values were calculated using empirical size-based relationships (Lorenzen 1996) and then averaged across the ages comprising each stanza (0.94, 0.51, and 0.27 yr^{-1} for the S, M, and L stanzas respectively). F estimates were calculated as C/B with values of 0.29 and 0.04 yr^{-1} for the M and L stanzas (there was no recorded catch for S stanza fish). The resulting Z estimates for the three stanzas were 0.94, 0.80, and 0.31 yr^{-1}, respectively.

Q/B

Q/B was assumed to be 18.11 yr^{-1} for the S stanza (the leading stanza for the Q/B estimates), based on the value used by Christensen et al. (2009).

Diet

Bluefish diets for each stanza were estimated using a diet database compiled for use in the MSVPA for Atlantic menhaden (SEDAR 2015), as described in section 3.3.2.6. The diet estimates included information from three fisheries independent surveys and numerous literature studies.

Catch

Bluefish catches were calculated from the old stock assessment for the earliest years of the available time series (1985-1987), following the methods described in section 3.3.2.4. The catch values were 0.03, 0.072, and 0.024 mt/km^2 for the S, M, and L stanzas, respectively. During the balancing process, these catch values were updated using information from the new stock assessment (NEFSC 2015), and catches were extrapolated back to 1982 using the catch trends

from the NOAA commercial and recreational landings databases scaled to the stock assessment values. These revised catch rates were 0.025, 0.062, and 0.013 mt/km^2 for the S, M, and L stanzas, respectively.

Groups 30-32. Striped bass (ages-0-1, ages-2-6, age-7+)

Striped bass is an important, commercially and recreationally valuable predator in the system. Striped bass was divided into three stanzas. The small (S), medium (M), and large (L) stanzas were defined as: S = ages 0-1 (<=25cm), M = ages 2-6 (26-70cm), and L = age 7+ (>70cm). These stanzas were chosen to capture a diet transition to greater piscivory from ages 0-1 and age 2+ (SEDAR 2015), and to capture migratory changes in striped bass populations, in which fish <7 years old tend to be more resident in estuaries such as Chesapeake Bay (Dorazio et al. 1994). Striped bass is a species that exhibited a drastic change in biomass during the modeled time period, recovering from very low values in the early 1980s.

Biomass

Biomass values were obtained from the striped bass stock assessment (NEFSC 2013a), following the methods described in section 3.3.2.1. The large size class was used as the leading stanza, with B=0.022 mt/km^2 in 1982. Biomasses for the other stanzas were estimated in Ecopath to be 0.0034 mt/km^2 (small stanza) and 0.0176 mt/km^2 (medium stanza) based on the multi-stanza growth and mortality parameters. Von Bertalanffy K was set at 0.110 based on the average of FishBase values (Christensen et al. 2009), and W_{mat}/W_{inf} was set at 0.1 using the value from the CBFEM (Christensen et al. 2009).

Z

Total mortality was obtained from stock assessment data based on estimates of M and F. Age-specific M values were approximated to be 1.15, 0.45, and 0.16 yr^{-1} for S, M, and L stanzas, respectively, based on relationships presented using various methods [Fig. 2 of Appendix B5 in (NEFSC 2013a)]. Thus, the Z estimates were calculated to be 1.152, 0.640, and 0.293 yr^{-1} respectively. F estimates were calculated as C/B with 1982 values of 0.076 and 0.157 yr^{-1} for the M and L stanzas (there was no recorded catch for S stanza fish). The resulting Z estimates for the three stanzas were 1.150, 0.526, and 0.317 yr^{-1}, respectively.

Q/B

Q/B was calculated as 1.82 yr^{-1} for the L stanza (the leading stanza), using an empirical equation for Q/B (Palomares and Pauly 1998), based on a water temp of 8°C, W_{inf} of 13 kg, and caudal fin aspect ratio of 1.5.

Diet

Striped bass diets for each stanza were estimated using a diet database compiled for use in the MSVPA for Atlantic menhaden (SEDAR 2015), as described in section 3.3.2.6. The diet estimates included information from three fisheries independent surveys and numerous literature studies.

Catch

Striped bass catch was calculated for each stanza following the methods described in section 3.3.2.4. The catch values for 1982 were 0, 0.0037, and 0.0035 mt/km^2 for the S, M, and L stanzas, respectively. During the balancing and calibration process, catch value for the M stanza was modified slightly to improve Ecosim fits (see section 3.5.2).

Groups 33-35. Weakfish (age-0, age1-2, age-3+)

Weakfish (*Cynoscion regalis*) were represented by three stanzas. The small (S), medium (M), and large (L) stanzas were defined as: S = age-0 (<=20cm), M = ages 1-2 (21-40cm), and L = age 3+ (>40cm). These stanzas were chosen to capture a diet transition to greater piscivory (Buchheister and Latour 2015; SEDAR 2015), and to provide greater resolution of predator-prey dynamics with menhaden which are an important prey component in the diet.

Biomass

Age 1+ biomass information was obtained from the weakfish stock assessment (ASMFC, 2016). Because age-specific B estimates were not provided, they were calculated from abundance and weight at age. The calculated biomass for the L (age-3+) stanza was 0.036 mt/km^2, and this was used as the leading stanza. The weakfish stock spans from FL to MA, but given that >94% of the commercial and recreational weakfish landings come the NWACS model domain with the remainder coming from the South Atlantic Bight (NEFSC 2009), we assumed the entire biomass estimate from the assessment pertained to our model domain. Biomasses for the other stanzas were estimated in Ecopath to be 0.00576 mt/km^2 (small stanza) and 0.0379 mt/km2 (medium stanza) based on the multi-stanza growth and mortality parameters in the balanced model. Von Bertalanffy K was set at 0.26 based on FishBase values (Christensen et al. 2009), and W_{mat}/W_{inf} was set at 0.1 using the value from the CBFEM (Christensen et al. 2009).

Z

Total mortality was calculated from the stock assessment data using Z=M+F. Natural mortality in 1982 was estimated to be M=0.17 (ASMFC 2016). Based on the equation F=C/B, we calculated the F rates in 1982 to be 0.00, 0.60, and 0.65 yr^{-1} for the S, M, and L stanzas, respectively. Thus, the initial Z estimates for the S, M, and L stanzas were 0.17, 0.77, and 0.82 yr^{-1}.

Q/B

Q/B was assumed to be as 13.52 yr^{-1} for the S stanza (the leading stanza for the Q/B estimates), based on the value used by Christensen et al. (2009).

Diet

Weakfish diets for each stanza were estimated using a diet database compiled for use in the MSVPA for Atlantic menhaden (SEDAR 2015), as described in section 3.3.2.6. The diet estimates included information from three fisheries independent surveys and numerous literature studies.

Catch

Weakfish catch was calculated for each stanza using stock assessment data (NEFSC 2009), following the methods described in section 3.3.2.4. The catch-at-age matrix in numbers (for commercial and recreational fisheries combined) was converted to biomass using the weight-at-age matrix and aggregated based on the age definitions of each stanza. The average catch values for 1982-1985 were 0, 0.023, and 0.034 mt/km^2 for the S, M, and L stanzas, respectively (NEFSC 2009).

Groups 36-37. Spiny dogfish (age-0-5, age-6+)

Spiny dogfish (*Squalus acanthias*) is a shark species that can be captured in large quantities in the NWACS area. Spiny dogfish were represented by two stanzas. The small (S) and large (L) stanzas were defined as: S = ages 0-5 (<=60cm) and L = age 6+ (>60cm). Stanzas were chosen to capture diet transitions (Garrison and Link 2000a, 2000b) and fishery dynamics which tend to target larger females.

Biomass

Biomass information was initially obtained from the NEFSC survey. The q-corrected area-swept biomass estimate for L spiny dogfish (the leading stanza) was very high (14.5 t/km^2) and a large outlier based on PREBAL diagnostics. This divergence was likely due to the schooling behavior of spiny dogfish and an inaccurate catchability estimate that had been derived for a broader suite of fishes. This value was reduced during the balancing process to 0.8 t/km^2 to yield a total spiny dogfish biomass of 1.137 t/km^2 which was comparable to the biomass estimates from the stock assessment, which ranged from 1.01-2.82 t/km^2 from 1982-1983 (Rago and Sosebee 2013). Von Bertalanffy K was set at 0.11 (Bubley et al. 2012), and Wmat/Winf was set at 0.29 (Araújo and Bundy 2011).

Z

Total mortality was estimated based on assumed values of M and F. The stock assessment estimated F for males and females separately from 1990-2008 only. F was assumed to be the average across sex and year yielding a value of F=0.121 yr^{-1}. M was assumed to be 0.2 yr^{-1}. During the balancing process, we found additional catch information (Rago and Sosebee 2014) that indicated that the majority of the catch was predominantly large females and fish >60 cm, therefore we assumed F=0 for the small stanza, and we assumed fishing only targeted the large stanza. The time series for F was derived from the F time series for females (1990-2008) from the stock assessment. To expand the time series for the full time period of the model, F for 1982-1989 and F for 2009-2013 were assumed to be the 3-year average of F values from the beginning and end of the stock assessment F values.

Q/B

Q/B was assumed to be 1.81 yr^{-1} for the L stanza (the leading stanza for the Q/B estimates), based on gastric evacuation models conducted for Ecopath models in neighboring Canadian Shelf waters (Araújo and Bundy 2011).

Diet

Diets for each stanza were obtained from the NEFSC trawl survey, as described in section 3.3.2.6.

Catch

Total spiny dogfish catch from the NOAA landings database (0.0045 mt/km^2) was not partitioned by size or age. Initially, we assumed that the L stanza comprised 75% of the total catch. During the balancing process, we found additional catch information (Rago and Sosebee 2014) that indicated that the majority of the catch was predominantly large females and fish >60 cm, therefore we modified the catch to be composed 100% of the L stanza. During the calibration process we also chose to use the stock assessment time series of catch (with dead discards), instead of using the NOAA landings database. The Ecopath catch value (0.114 mt/km^2) was set as the 3 year average from the beginning of the assessment time series (1989-1991).

Groups 38-40. Atlantic Cod (age-0-1, age-2-3, age-4+)

Atlantic cod (*Gadus morhua*) was divided into three stanzas. The small (S), medium (M), and large (L) stanzas were defined as: S = ages 0-1 (<=20cm), M = ages 2-3 (21-50cm), and L = age 4+ (>50cm). These stanzas were chosen to capture dietary shifts (Garrison and Link 2000a, 2000b) and provide greater resolution for fishery dynamics.

Biomass

Biomass values were calculated using information from the assessments of both the Georges Bank and the Gulf of Maine cod stocks (NEFSC 2013b). Stock biomasses were added for each stanza yielding the total biomass. Stock assessments are conducted for GOM and GB separately. For the GOM stock, biomass was determined based on the average of two assessment models because no consensus was reached regarding which of the two models was preferred (NEFSC, 2013b, p. 76). The large size class was used as the leading stanza, with B=0.277 mt/km^2 based on the 1982-1985 average. Biomasses for the other stanzas were estimated in Ecopath to be 0.177 mt/km^2 (small stanza) and 0.433 mt/km^2 (medium stanza) based on the multi-stanza growth and mortality parameters. Von Bertalanffy K was set at 0.170 and Wmat/Winf was set at 0.04 based on Ecopath models from neighboring Canadian waters (Araújo and Bundy 2011).

Z

Total mortality was calculated using estimates of M and F. M estimates for each stanza were the average of Lorenzen-based (Lorenzen 1996) age-specific M estimates reported for the GOM stock, with values of 0.86, 0.52, and 0.25 yr^{-1} for the S, M, and L stanzas respectively (Table A.71 of (NEFSC 2013b)). F estimates were calculated as C/B with 1982 values of 0.227, 0.605, and 0.394 yr^{-}

[1] for the S, M, and L stanzas. The resulting Z estimates (Z=M+F) for the three stanzas were 1.087, 1.125, and 0.644 yr^{-1}, respectively.

Q/B

Q/B was assumed to be 1.5 yr^{-1} for the L stanza (the leading stanza), based on Araujo and Bundy (2011) who estimated Q/B for use in their Ecopath from a gastric evacuation model using stomach content data. Q/B for the other stanzas were estimated in Ecopath to be 4.461 yr^{-1} (small stanza) and 2.309 yr^{-1} (medium stanza).

Diet

Cod diets for each stanza were obtained from the NEFSC survey, as described in section 3.3.2.6.

Catch

Cod catches were calculated for each stanza following the methods described in section 3.3.2.4, and then added across the two stocks. The catch values for the 1982 year block were 0.010, 0.132, and 0.122 mt/km^2 for the S, M, and L stanzas, respectively.

Group 41. Haddock

Haddock (*Melanogrammus aeglefinus*) was modeled as a separate group because it supports a commercial fishery. Two stocks are recognized in the US EEZ, in the Gulf of Maine (GOM) and Georges Bank (GB). Parameters for haddock were derived from information from the stock assessments of the GOM (NEFSC 2014b) and GB stocks (NEFSC 2012c). Biomass was set at 0.254 mt/km^2, calculated as the combined biomass estimates for the two stocks divided by the total model domain area. Fishing mortality for the 1982 year block was calculated as the biomass-weighted annual average F from the 2 stock assessments, yielding an F of 0.56. Following the GOM haddock assessment (NEFSC 2014b), we assumed M=0.2, for a total P/B of 0.76. Q/B was initially assumed to be 0.905 based on the average EMAX values for demersal benthivores (Link et al. 2006). Catch was initially set at 0.063 mt/km^2, based on the landings data from the NOAA databases, but the value was later updated based on the information from the stock assessments (to 0.082 mt/km^2). Haddock diets were calculated from NEFSC food habits data. Time series of B, F, and C were obtained from the stock assessment reports, and calculated as sums across the two stocks (for B and C), or as biomass-weighted averages (for F).

Group 42. Hakes

Hakes included gadid fishes in the genera *Merluccius* and *Urophycis*, specifically silver hake (*Merluccius bilinearis*), offshore hake (*M. albidus*), red hake (*Urophycis chuss*), spotted hake (*U. regia*), and white hake (*U. tenuis*). Of these species, silver hake and white hake account for >95% of the total hake landings, with silver hake being the most important (~80% of the total hake catch) based on the NOAA landings database.

Biomass was set at 0.669 mt/km^2 based on q-corrected swept-area estimates from the NEFSC trawl survey. The P/B value for hake (P/B=1.115 yr^{-1}) was estimated using an average of the age-specific F and M estimates for silver hake for the 1982 year block. Q/B was set at 3.85 based on Pauly (1989). Hake catch for the 1982 year block was 0.109 mt/km^2, based on the NOAA landings database. Hake diets were calculated from NEFSC food habits data.

Time series of F and relative B were obtained from the stock assessment report for silver hake (NEFSC 2011) and assumed to be representative of the entire group, given its biomass dominance and higher catches within the hake group. White hake are the second most important species, and they showed similar temporal trends in relative B (NEFSC 2013c), so use of the relative silver hake B trends in Ecosim was deemed appropriate for the group. Catch time series were obtained from the NOAA landings database.

Group 43. Atlantic Croaker

Atlantic croaker (*Micropogonias undulatus*) was modeled as a separate group because it supports a fishery and can be a biomass dominant component of the demersal community in the mid-Atlantic bight and its estuaries (e.g., Buchheister et al. 2013). Biomass was set at 0.669 mt/km^2 based on q-corrected swept-area estimates from the NEFSC trawl survey. Stock assessment biomass for croaker was not used because 1) the estimate was sensitive to assumptions made regarding croaker bycatch mortality in the shrimp fishery (ASMFC 2010) and 2) it is uncertain what fraction of the total stock, which resides from Massachussetts to Florida, should be attributed to the NWACS spatial domain. P/B was estimated to be 0.994 yr^{-1} using stock assessment data (ASMFC 2010), based on a natural mortality estimate of 0.27 yr^{-1} and a fishing mortality estimate of 0.724 (for the earliest assessed years, 1988-1992). Q/B was assumed to be 0.905 based on the average EMAX values for demersal benthivores (Link et al. 2006). Croaker diets were averaged from NEAMAP and NEFSC food habits data.

Groups 44-45. Yellowtail Flounder (age-0, age-1+)

Yellowtail flounder (*Limanda ferruginea*) was represented by two stanzas. The small (S) and large (L) stanzas were defined as: S = age-0 (<=20cm) and L = age 1+ (>20cm), and they were chosen to capture ontogenetic dietary changes (Garrison and Link 2000a). Yellowtail flounder are managed as three separate stocks in GOM, GB, and SNE (NEFSC 2012d; TRAC 2014).

Biomass

Originally, biomass (B=0.111 mt/km^2) was based on q-corrected swept-area estimates from the NEFSC trawl survey, using the L stanza as the leading stanza. In the balancing process, biomass values were updated to those obtained from the yellowtail flounder stock assessments (NEFSC 2012d), following the methods described in section 3.3.2.1, with a value of 0.187 mt/km^2. Von Bertalanffy K was set at 0.901 based on values presented in the SNE stock assessment (NEFSC 2012d), but during the balancing process, this was changed to 0.16 following Dwyer *et al.* (2003).

W_{mat}/W_{inf} was originally calculated as 0.32 using growth parameters from the SNE assessment, but this was updated to 0.1 using the revised growth parameters (Dwyer et al. 2003).

Z

For the L stanza, 1982 F was calculated as C/B with a value of 0.447 yr^{-1} (there was no recorded catch for S stanza fish). M was assumed to be 0.2 yr^{-1} for a total Z estimate of 0.647yr^{-1}.

Q/B

Q/B for the L, leading stanza was assumed to be the same as for summer flounder with a value of Q/B=2.9 yr^{-1}.

Diet

Yellowtail flounder diets for each stanza were calculated using data from the NEFSC trawl surveys food habits program.

Catch

Total yellowtail flounder catch was 0.085 mt/km^2 based on the NOAA landings database. This catch was attributed to the large stanza because age-0 yellowtail flounder are not captured in the fishery (NEFSC 2012d). The catch time series was calculated as the sum of the catches for the three yellowtail flounder stocks.

Groups 46-47. Summer flounder (age-0, age-1+)

Summer flounder (*Paralichthys dentatus*) was represented by two stanzas. The small (S) and large (L) stanzas were defined as: S = age-0 (<=25cm) and L = age 1+ (>25cm). These stanzas were chosen to capture diet transitions to greater consumption of fishes and squid (Garrison and Link 2000a; Buchheister and Latour 2015).

Biomass

Biomass values were obtained from the summer flounder stock assessment (NEFSC 2013d), following the methods described in section 3.3.2.1. The L stanza was used as the leading stanza, with average B=0.159 mt/km^2 from 1982-1985. B for the small stanza were estimated by Ecopath to be .009 mt/km^2, based on growth and mortality parameters. Von Bertalanffy K was estimated as 0.299 using data from the ChesMMAP trawl survey (A. Buchheister, unpublished data) and W_{mat}/W_{inf} was calculated as 0.053 using the growth data from the assessment.

Z

Total mortality was obtained from the stock assessment based on estimates of M and F. M was estimated to be 0.26 for age-0 fish and used for the S stanza, and the overall mean M of 0.25 was used for the L stanza (NEFSC 2013d). F estimates were calculated for 1982 as F=C/B with values of 0.178 and 0.405 yr^{-1} for the S and L stanzas. The resulting Z estimates for the two stanzas were 0.438 and 0.655 yr^{-1}, respectively.

Q/B

Q/B was set as 2.9 for the L stanza (the leading stanza) following Christensen et al. (2009).

Diet

Summer flounder diets for each stanza were calculated as an average of the diet compositions from the NEFSC and NEAMAP trawl surveys.

Catch

Using the available data from the assessment (NEFSC 2013d), summer flounder catch was calculated using the relative catch-at-age (in numbers) to apportion the reported total catch (in weight) to each of the two stanzas. The average catch values from 1982-1985 were 0.009, and 0.084 mt/km^2 for the S and L stanzas, respectively.

Group 48. Skates

Skates are a biomass dominant component of the demersal fish fauna in the NWACS system. Skates include various species in the family Rajidae, particularly *Amblyraja radiate*, *Dipturus laevis*, *Leucoraja erinacea*, *Leucoraja garmani*, *Leucoraja ocellata*, and *Raja eglanteria*. Parameters for this group were obtained from the NEFSC survey and the EMAX models. The q-corrected biomass was 2.956 mt/km^2 based on the NEFSC survey. P/B was assumed to be 0.45 yr^{-1} and Q/B was set at 0.905 yr^{-1}, based on values from the EMAX model. Diets for skates were calculated as an average of diet compositions from the NEFSC and NEAMAP surveys.

Groups 49-52. Other demersal fishes (benthivores, piscivores, omnivores) and medium pelagics

The three other demersal fishes groups were defined based on feeding preferences. These three speciose groups represent the many other bottom-associated species that were not modeled in any of the other groups (Tables 7, 8, 9). The medium pelagics group included *Sarda sarda*, *Scomberomorus regalis*, and *Rachycentron canadum*.

Estimates of q-corrected swept area biomasses were obtained for each group from the NEFSC trawl survey. Estimates of B were 1.988 mt/km2 (benthivores), 1.312 mt/km2 (piscivores), 0.013 mt/km^2 (omnivores), and 0.021 mt/km^2 (medium pelagics). Note that the biomass of demersal omnivores was greatly increased in the balancing process; the NEFSC estimate for this group was deemed inaccurate given sampling considerations and the fact that the estimated B was an order of magnitude lower than the landings. P/B was assumed to be 0.45 and Q/B was set at 0.905 (benthivores), 1.213 (piscivores), 0.814 (omnivores), and 1.838 (medium pelagics) based on the EMAX models and the methods described in section 3.3.1. Diets for these groups were calculated as averages of diet compositions for the NEAMAP and NEFSC surveys, as described in section 3.3.1. Catches of each group were obtained from the NOAA commercial and recreational landings databases (see Section 3.3.2.4) and calculated to be 0.119 mt/km^2 (benthivores), 0.089 mt/km^2 (piscivores), 0.101 mt/km2 (omnivores), and 0.001 mt/km^2 (medium pelagics).

Table 5. List of taxa included in the Demersal Benthivore – Other trophic group.

Demersal Benthivores - Other			
Acipenser oxyrinchus	*Enchelyopus cimbrius*	*Lycenchelys verrillii*	*Poecilopsetta beani*
Alectis ciliaris	*Epigonus pandionis*	*Lycodes reticulatus*	*Pogonias cromis*
Anarhichas lupus	*Etmopterus princeps*	*Macrorhamphosus scolopax*	*Polymetme thaeocoryla*
Ancylopsetta ommata	*Etropus*	*Macrouridae*	*Polymixia lowei*
Antigonia capros	*Etropus crossotus*	*Macrourus berglax*	*Polymixia nobilis*
Antimora rostrata	*Etropus microstomus*	*Macrozoarces americanus*	*Pontinus longispinis*
Archosargus probatocephalus	*Eucinostomus argenteus*	*Malacocephalus occidentalis*	*Porichthys plectrodon*
Artediellus sp.	*Eumicrotremus spinosus*	*Malacoraja senta*	*Prionotus carolinus*
Aspidophoroides monopterygius	*Gaidropsarus ensis*	*Menticirrhus*	*Prionotus evolans*
Astroscopus guttatus	*Gephyroberyx darwini*	*Menticirrhus saxatilis*	*Prionotus paralatus*
Bagre marinus	*Glyptocephalus cynoglossus*	*Monolene sessilicauda*	*Pseudopleuronectes americanus*
Bairdiella chrysoura	*Gobiosoma bosc*	*Morone americana*	*Rhinoptera bonasus*
Balistes	*Gonostoma atlanticum*	*Mullus auratus*	*Saurida brasiliensis*
Balistes capriscus	*Gonostoma bathyphilum*	*Mustelus canis*	*Scophthalmus aquosus*
Bothus ocellatus	*Gonostoma elongatum*	*Myliobatis freminvillei*	*Sebastes fasciatus*
Brosme brosme	*Gymnachirus melas*	*Myliobatis freminvillii*	*Selene vomer*
Caranx hippos	*Helicolenus dactylopterus*	*Myoxocephalus aenaeus*	*Sphoeroides maculatus*
Careproctus ranula	*Helicolenus maderensis*	*Myoxocephalus octodecemspinosus*	*Stenotomus chrysops*
Chauliodus danae	*Hemitripterus americanus*	*Myoxocephalus scorpius*	*Synagrops bellus*
Chilomycterus schoepfii	*Hippoglossina oblonga*	*Nesiarchus nasutus*	*Synagrops spinosus*
Chlorophthalmus agassizi	*Hippoglossoides platessoides*	*Nezumia bairdi*	*Tautoga onitis*
Chlorophthalmus sp.	*Hoplostethus occidentalis*	*Ogcocephalus corniger*	*Tautogolabrus adspersus*
Chloroscombrus chrysurus	*Howella sherborni*	*Ophidion grayi*	*Torpedo nobiliana*
Citharichthys arctifrons	*Lagodon rhomboides*	*Ophidion marginatum*	*Trachinotus carolinus*
Coelorhynchus carminatus	*Larimus fasciatus*	*Ophidion welshi*	*Trachinotus falcatus*
Cottidae	*Leiostomus xanthurus*	*Opsanus pardus*	*Triglidae*
Cryptacanthodes maculatus	*Lepophidium profundorum*	*Opsanus tau*	*Triglops murrayi*
Dasyatis americana	*Liparis inquilinus*	*Orthopristis chrysoptera*	*Trinectes maculatus*
Dasyatis centroura	*Lopholatilus chamaeleonticeps*	*Otophidium omostigmum*	*Ulvaria subbifurcata*
Dasyatis sabina	*Lumpenus lumpretaeformis*	*Paralichthys oblongus*	*Vinciguerria sp.*
Dasyatis say	*Lumpenus maculatus*	*Parasudis truculenta*	*Xenodermichthys copei*
Dibranchus atlanticus	*Lycenchelys verrilli*	*Peristedion miniatum*	*Zoarces americanus*

Table 6. List of taxa included in the Demersal Piscivore – Other trophic group.

Demersal piscivores - other			
Centroscyllium fabricii	*Lutjanidae*	*Lutjanus vivanus*	*Trichiurus lepturus*
Conger oceanicus	*Lutjanus analis*	*Myxine glutinosa*	*Urophycis chesteri*
Gadidae	*Lutjanus apodus*	*Pollachius virens*	
Gymnura altavela	*Lutjanus buccanella*	*Reinhardtius hippoglossoides*	
Gymnura micrura	*Lutjanus campechanus*	*Scyliorhinus retifer*	
Hippoglossus hippoglossus	*Lutjanus griseus*	*Squatina dumeril*	
Lophius americanus	*Lutjanus jocu*	*Synodus foetens*	

Table 7. List of taxa included in the Demersal Omnivore – Other trophic group.

Demersal omnivores - other			
Abudefduf saxatilis	*Citharichthys cornutus*	*Holacanthus ciliaris*	*Prionotus tribulus*
Acanthurus bahianus	*Citharichthys gymnorhinus*	*Holacanthus tricolor*	*Pristigenys alta*
Acanthurus chirurgus	*Citharichthys macrops*	*Holanthias martinicensis*	*Pristipomoides aquilonaris*
Acanthurus coeruleus	*Citharichthys sp.*	*Hyperoglyphe perciformis*	*Pseudupeneus maculatus*
Aluterus heudelotii	*Citharichthys spilopterus*	*Hypleurochilus geminatus*	*Raja ackleyi*
Aluterus monoceros	*Clepticus parrae*	*Hypsoblennius hentz*	*Raja texana*
Aluterus schoepfi	*Clinidae*	*Hypsoblennius ionthas*	*Rhomboplites aurorubens*
Aluterus scriptus	*Cookeolus japonicus*	*Isurus paucus*	*Ruvettus pretiosus*
Anchoa lyolepis	*Cryptotomus roseus*	*Kathetostoma albigutta*	*Rypticus bistrispinus*
Ancylopsetta dilecta	*Cubiceps pauciradiatus*	*Kyphosus sectatrix*	*Rypticus subbifrenatus*
Ancylopsetta quadrocellata	*Cyclopsetta fimbriata*	*Labridae*	*Scaridae*
Anguilla rostrata	*Cynoscion arenarius*	*Lachnolaimus maximus*	*Scarus coeruleus*
Anisotremus virginicus	*Cynoscion nebulosus*	*Lactophrys bicaudalis*	*Schultzea beta*
Apogon aurolineatus	*Cynoscion nothus*	*Lactophrys polygonia*	*Sciaenidae*
Apogon maculatus	*Dactylopterus volitans*	*Lactophrys quadricornis*	*Sciaenops ocellatus*
Apogon pseudomaculatus	*Dasyatis violacea*	*Lactophrys trigonus*	*Scombridae*
Argentina striata	*Decodon puellaris*	*Lactophrys triqueter*	*Scorpaena agassizi*
Ariomma melanum	*Diodon holocanthus*	*Laemonema barbatulum*	*Scorpaena brasiliensis*
Ariomma regulus	*Diodon hystrix*	*Lepidocybium flavobrunneum*	*Scorpaena calcarata*
Astroscopus y-graecum	*Diplectrum bivittatum*	*Lobotes surinamensis*	*Scorpaena dispar*
Balistes vetula	*Diplectrum formosum*	*Lutjanus synagris*	*Scorpaena grandicornis*
Balistidae	*Diplodus argenteus*	*Macroramphosus scolopax*	*Scorpaena plumieri*
Bathygobius soporator	*Diplodus holbrooki*	*Malacanthus plumieri*	*Scorpaenidae*
Bathyraja spinicauda	*Dipturus olseni*	*Menticirrhus americanus*	*Seriola fasciata*
Bellator brachychir	*Dormitator maculatus*	*Menticirrhus littoralis*	*Seriola zonata*
Bellator egretta	*Echeneis naucrates*	*Monacanthus ciliatus*	*Serraniculus pumilio*
Bellator militaris	*Echiophis punctifer*	*Mugil gyrans*	*Serranidae*
Bembrops gobioides	*Engraulidae*	*Mugil liza*	*Serranus annularis*
Blenniidae	*Engyophrys senta*	*Mustelus norrisi*	*Serranus atrobranchus*
Bodianus pulchellus	*Epinephelus*	*Mycteroperca bonaci*	*Serranus baldwini*
Bothidae	*Epinephelus adscensionis*	*Mycteroperca interstitialis*	*Serranus notospilus*
Bothus lunatus	*Epinephelus drummondhayi*	*Mycteroperca microlepis*	*Serranus phoebe*
Bothus robinsi	*Epinephelus flavolimbatus*	*Mycteroperca phenax*	*Serranus subligarius*
Brama brama	*Epinephelus guttatus*	*Mycteroperca venenosa*	*Sparidae*
Breviraja plutonia	*Epinephelus inermis*	*Myliobatis goodei*	*Sparisoma radians*
Calamus bajonado	*Epinephelus morio*	*Myoxocephalus quadricornis*	*Sphoeroides dorsalis*
Calamus calamus	*Epinephelus mystacinus*	*Narcine brasiliensis*	*Sphoeroides nephelus*
Calamus leucosteus	*Epinephelus nigritus*	*Neomerinthe hemingwayi*	*Sphoeroides pachygaster*
Calamus nodosus	*Epinephelus niveatus*	*Nicholsina usta*	*Sphoeroides spengleri*
Calamus penna	*Epinephelus striatus*	*Ocyurus chrysurus*	*Sphoeroides testudineus*
Calamus proridens	*Equetus acuminatus*	*Ogcocephalus radiatus*	*Sphyraena barracuda*
Canthidermis sufflamen	*Equetus lanceolatus*	*Ophidion*	*Sphyraena borealis*
Canthigaster rostrata	*Equetus punctatus*	*Ophidion beani*	*Sphyraena guachancho*
Caranx crysos	*Equetus umbrosus*	*Ophidion selenops*	*Sphyrna media*
Carcharhinus altimus	*Etheostoma nigrum*	*Opistognathus lonchurus*	*Squalidae*
Carcharhinus isodon	*Etmopterus gracilispinis*	*Opistognathus maxillosus*	*Stellifer lanceolatus*
Carcharhinus longimanus	*Etmopterus hillianus*	*Pagrus sedecim*	*Stenotomus caprinus*
Carcharhinus perezii	*Etropus rimosus*	*Parablennius marmoreus*	*Stromateidae*
Carcharhinus porosus	*Etropus sp*	*Parahollardia lineata*	*Syacium gunteri*
Carcharhinus signatus	*Eucinostomus gula*	*Paralepidae*	*Syacium micrurum*
Caulolatilus chrysops	*Fistularia tabacaria*	*Paralichthys albigutta*	*Syacium papillosum*
Caulolatilus cyanops	*Foetorepus agassizi*	*Paralichthys lethostigma*	*Symphurus civitatus*
Caulolatilus intermedius	*Gastropsetta frontalis*	*Paralichthys sp.*	*Symphurus diomedianus*
Caulolatilus microps	*Gempylus serpens*	*Paralichthys squamilentus*	*Symphurus marginatus*
Centropristis ocyurus	*Gerreidae*	*Paranthias furcifer*	*Symphurus minor*
Centropristis philadelphica	*Gobiesox strumosus*	*Perciformes*	*Symphurus plagiusa*
Centropristis striata	*Gobiidae*	*Peristedion gracile*	*Symphurus pusillus*
Centroscymnus coelolepis	*Gymnothorax saxicola*	*Pholis fasciata*	*Symphurus urospilus*
Chaetodipterus faber	*Haemulidae*	*Pleuronectidae*	*Syngnathus fuscus*
Chaetodon aculeatus	*Haemulon aurolineatum*	*Pleuronectiformes*	*Synodontidae*
Chaetodon aya	*Haemulon carbonarium*	*Polydactylus octonemus*	*Tetraodontidae*
Chaetodon capistratus	*Haemulon plumieri*	*Pomacanthus arcuatus*	*Trachyscorpia cristulata*
Chaetodon ocellatus	*Haemulon striatum*	*Pomacentrus leucostictus*	*Triakis semifasciata*
Chaetodon sedentarius	*Halichoeres bathyphilus*	*Pomacentrus variabilis*	*Trichiuridae*
Chaetodon striatus	*Halichoeres bivittatus*	*Pontinus rathbuni*	*Upeneus parvus*
Chaetodontidae	*Halichoeres caudalis*	*Priacanthus arenatus*	*Uranoscopidae*
Chascanopsetta lugubris	*Halichoeres poeyi*	*Priacanthus cruentatus*	*Uraspis secunda*
Chasmodes bosquianus	*Halichoeres radiatus*	*Prionotus alatus*	*Urolophus jamaicensis*
Chaunax stigmaeus	*Harengula jaguana*	*Prionotus longispinosus*	*Urophycis*
Chilomycterus antillarum	*Hemanthias aureorubens*	*Prionotus ophryas*	*Xenocephalus egregius*
Chilomycterus atinga	*Hemanthias vivanus*	*Prionotus roseus*	*Xenolepidichthys dalgleishi*
Chromis enchrysurus	*Hemipteronotus novacula*	*Prionotus rubio*	
Chromis insolata	*Hippocampus erectus*	*Prionotus scitulus*	
Citharichthys arenaceus	*Holacanthus bermudensis*	*Prionotus stearnsi*	

Groups 53-54. Sharks (coastal, pelagic)

Large sharks were divided into two groups based on habitat. Coastal sharks included the Atlantic sharpnose shark *(Rhizoprionodon terraenovae*), dusky shark (*Carcharhinus obscurus*), sand tiger shark (*Carcharias Taurus*), sandbar shark (*Carcharhinus plumbeus*), and spinner shark (*Carcharhinus brevipinna*). Pelagic sharks included the blue shark (*Prionace glauca*), great white shark (*Carcharodon carcharias*), hammerheads (*Sphyrna spp*.), mako sharks (*Isurus spp*.), porbeagle (*Lamna nasus*), and thresher shark (*Alopias vulpinus*).

Parameters for these groups were obtained from the EMAX models, following the methods described in section 3.3.1. Biomasses were estimated to be 0.008 and 0.016 mt/km^2 for the coastal and pelagic sharks, respectively. P/B was estimated to be 0.100 and 0.113 yr^{-1}, and Q/B was set at 1.247 and 0.690 yr^{-1} for the coastal and pelagic sharks respectively. Diets from the EMAX models were modified to account for the higher resolution of trophic groups in this model (see section 3.3.2.7).

Group 55. Highly Migratory Species (HMS)

The highly migratory species (HMS) group represents the large, pelagic, non-shark species in the system. The HMS group includes tunas (*Thunnus thynnus*, *Thunnus alalunga*, *Thunnus obesus*), billfish (Istiophoridae), and swordfish (*Xiphias gladius*).

Parameters for this group were obtained from the EMAX models, following the methods described in section 3.3.1. Biomasses were estimated to be 0.017 mt/km^2, P/B was estimated to be 0.579 yr^{-1}, and Q/B was set at 6.794 yr^{-1}. Diets from the EMAX models were modified to account for the higher resolution of trophic groups in this model (see section 3.3.2.7), but values were also modified to include greater predation of larger bony fishes based on data from the primary literature (Chase 2002; Estrada et al. 2005; Butler et al. 2010).

Groups 56-58. Marine mammals (Pinnipeds, Baleen whales, Odontocetes)

Marine mammals were modeled as three distinct trophic groups, following the EMAX models (Link et al. 2006). Pinnipeds included the harbor seal (*Phoca vitulina*), gray seal (*Halichoerus grypus*), harp seal (*Pagophilus groenlandicus*), and hooded seal (*Cystophora cristata*). Baleen whales included fin whales (*Balaenoptera physalus*), sei whales (*B. borealis*), minke whales (*B. acutorostrata*), humpback whales (*Megaptera novaeangliae*), and right whales (*Eubalaena glacialis*). Lastly, the toothed whales (Odontocetes) included: bottlenose dolphins (*Tursiops truncatus*), common dolphins (*Delphinus delphis*), beaked whales (*Ziphius* or *Mesoplodon spp*.), Risso's dolphins (*Grampus griseus*), harbor porpoise (*Phocena phocena*), dwarf sperm or pygmy sperm whale (*Kogia spp*.), long-fin and short-fin pilot whales (*Globicephala spp*.), sperm whales (*Physeter macrocephalus*), spotted dolphins (*Stenella frontalis*), striped dolphins (*S. coeruleoalba*), and white-sided dolphins (*Lagenorhynchus acutus*).

Parameters for these groups were obtained from the EMAX models, following the methods described in section 3.3.1. Biomasses were estimated from shipboard and aerial sighting surveys

conducted by the NEFSC during 1998 and 1999. Biomasses were estimated to be 0.35, 0.464, and 0.060 mt/km^2 for pinnipeds, baleen whales, and odontocetes respectively. P/B was estimated to be 0.075, 0.040, and 0.040 yr^{-1}, and Q/B was set at 5.581, 3.217, and 14.30 yr^{-1}for pinnipeds, baleen whales, and odontocetes respectively. Diets from the EMAX models were modified to account for the higher resolution of trophic groups in this model (see section 3.3.2.7).

Group 59. Seabirds

Marine sea birds represent avian predators that can feed in continental shelf waters hundreds of miles from shore. This group included Black-legged kittiwake (*Rissa triactyla*), Cory's shearwater (*Calonectris diomedae*), Sooty shearwater (*Puffinus griseus*), Greater shearwater (*Puffinus gravis*), Great black-backed gull (*Larus marinus*), Herring gull (*Larus argentatus*), Laughing gull (*Larus philadelphia*), Northern fulmar (*Fulmarus glacialis*), Northern gannet (*Sula bassanus*), Red phalarope (*Phalaropus fulicarius*), Wilson's storm petrel (*Oceanites oceanicus*). These 11 species accounted for >97% of total seabird density in an offshore survey (Powers 1983).

Parameters for this groups were obtained from the EMAX models, following the methods described in section 3.3.1. Biomass was estimated to be 0.007 mt/km^2, P/B was estimated to be 0.279 yr^{-1}, and Q/B was set at 9.318 yr^{-1}. During the balancing process, the Q/B was changed to 80 yr^{-1}, as the original EMAX estimate (9.318 yr^{-1}) was substantially lower than expected for endotherms with high metabolisms. We used a Q/B of 80 yr^{-1} because it was in the range of values of other ecosystem models of the Northwest Atlantic [87.6 yr^{-1}, (Araújo and Bundy 2011); 76-80 yr^{-1}, (Okey 2001)], and comparable to estimates for some individual bird species [great blue heron, 22-80 yr-1, (Pitt et al. 1998); double crested cormorant, ~91 yr^{-1}, (Johnson et al. 2002)]. Diets were taken from the EMAX models but modified to account for the higher resolution of trophic groups in the NWACS model (see section 3.3.2.7).

Group 60. Nearshore piscivorous birds

The coastal water birds group distinguishes piscivorous birds that tend to be more coastal in their habitat (relative to the seabirds). This group was included to includes the bald eagle (*Haliaeetus leucocephalus*), blue heron (*Ardea herodias*), brown pelican (*Pelecanus occidentalis*), cormorants (*Phalacrocorax spp*.), and osprey (*Pandion haliaetus*).

As with several of the other higher trophic level predators, quantitative information to parameterize this group was very limited. We assumed the biomass and P/B of this group was equivalent to the seabird group (0.007 mt/km^2 and 0.279 yr^{-1}, respectively). Diets were based on literature studies for multiple species (Quinney 1982; Hingtgen et al. 1985; Blackwell et al. 1995; Johnson et al. 2002; Glass and Watts 2009). Coastal, piscivorous water birds were assumed to consume primarily fishes (90%), with diets supplemented by crustaceans (2.5% each of MacroB-crus and MegaB-oth) and 5% imported (to account for mammals and amphibians). 75% of total diet was partitioned among forage and small pelagic fishes (alosines, menhaden, anchovies, and other small pelagics), and 15% was partitioned among other demersal and benthic fishes

(primarily small size classes of striped bass, weakfish, summer flounder, along with croaker, demersal benthivores, demersal omnivores, and demersal piscivores).

Group 61. Detritus

Detritus represented both dissolved organic carbon (DOC) and particulate organic carbon (POC), which is a major source of carbon for the microbial food web. Parameters for detritus were obtained from the EMAX models, as described in section 3.3.1. Biomass was calculated as 52.60 mt/km^2, based on estimates derived from first generating a generalized vertical profile of DOC, then integrating the profile from surface to bottom using bathymetry data (Link et al. 2006). A specific DOC:POC ratio was assumed based on literature values, but typically, the standing stock of DOC is an order of magnitude greater than POC (Link et al. 2006). P/B, Q/B, and diet parameters were not needed for the detritus group.

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Appendix 2 – Parameters for the balanced NWACS ecosystem model

Table 8. Parameters for the balanced NWACS Ecopath model. Ecopath-estimated values in bold.

Node	Group name	TL	B (t/km^2)	Z (yr^{-1})	P/B (yr^{-1})	Q/B (yr^{-1})	EE	P/Q	BA ($t/km^2/yr$)	BA rate (/yr)	Unassimil. Consump.	Landings (t/km^2)
1	Phytoplankton	1.00	30.000		180.700	0.000	**0.941**		0.000	0.000	0.00	0.000
2	Other primary producers	1.00	**1.605**		55.570	0.000	0.900		0.000	0.000	0.00	0.009
3	Bacteria	2.00	7.700		91.250	380.208	**0.941**	0.240	0.000	0.000	0.40	0.000
4	Microzooplankton	2.26	7.000		85.000	283.400	**0.922**	0.300	0.000	0.000	0.30	0.000
5	Small copepods	2.15	16.000		46.000	140.000	**0.984**	0.329	0.000	0.000	0.30	0.000
6	Large copepods	2.39	17.966		46.000	150.000	**0.970**	0.307	0.000	0.000	0.30	0.000
7	Gelatinous zooplankton	3.08	6.349		40.000	145.326	**0.590**	0.275	0.000	0.000	0.35	0.000
8	Micronekton	2.72	7.654		14.250	85.497	**0.681**	0.167	0.000	0.000	0.30	0.000
9	Macrobenthos - polychaetes	2.38	17.452		2.500	17.500	**0.798**	0.143	0.000	0.000	0.50	0.002
10	Macrobenthos - crustaceans	2.54	7.000		3.600	21.000	**0.766**	0.171	0.000	0.000	0.50	0.000
11	Macrobenthos - molluscs	2.25	8.340		2.200	13.949	**0.830**	0.158	0.000	0.000	0.60	0.275
12	Macrobenthos - other	2.35	21.000		2.000	16.059	**0.865**	0.125	0.000	0.000	0.50	0.000
13	Megabenthos - filterers	2.12	5.500		1.200	6.660	**0.857**	0.180	0.000	0.000	0.70	0.041
14	Megabenthos - other	2.89	4.498		2.300	15.533	**0.731**	0.148	0.000	0.000	0.30	0.350
15	Shrimp and Similar Species	2.75	0.470		2.000	6.660	**0.893**	0.300	0.068	0.144	0.30	0.021
16	Mesopelagics	3.24	0.090		1.100	3.700	**0.957**	0.297	0.000	0.000	0.20	0.000
17	Atlantic herring	3.50	1.650		1.100	3.700	**0.886**	0.297	0.276	0.167	0.20	0.230
18	Alosines	3.37	0.200		1.300	4.400	**0.775**	0.295	0.000	0.000	0.20	0.025
19	Atlantic menhaden (S)	2.53	0.371	1.900		15.860	**0.830**	0.120	0.046	0.124	0.20	0.321
20	Atlantic menhaden (M)	2.68	2.048	1.309		6.643	**0.557**	0.197	0.254	0.124	0.20	1.071
21	Atlantic menhaden (L)	2.84	1.200	0.756		3.785	**0.451**	0.200	0.149	0.124	0.20	0.165
22	Anchovies	3.06	1.100		2.200	7.333	**0.834**	0.300	0.000	0.000	0.20	0.000
23	Atlantic mackerel	3.55	1.740		0.550	2.170	**0.675**	0.253	0.000	0.000	0.20	0.052
24	Squid	3.86	1.267		5.720	19.000	**0.926**	0.301	0.516	0.407	0.20	0.042
25	Butterfish	3.83	1.488		1.312	4.230	**0.833**	0.310	0.030	0.020	0.20	0.024
26	Small pelagic - other	3.40	1.400		1.200	4.000	**0.772**	0.300	0.000	0.000	0.20	0.004
27	Bluefish (S)	4.44	0.017	3.900		20.935	**0.938**	0.186	-0.002	-0.097	0.20	0.025
28	Bluefish (M)	4.41	0.160	0.900		6.093	**0.708**	0.148	-0.016	-0.097	0.20	0.062
29	Bluefish (L)	4.51	0.509	0.310		3.139	**0.339**	0.099	-0.049	-0.097	0.20	0.013
30	Striped bass (S)	3.80	0.003	1.500		10.265	**0.984**	0.146	0.000	0.000	0.20	0.000
31	Striped bass (M)	3.93	0.022	0.526		3.429	**0.580**	0.153	0.000	0.000	0.20	0.005
32	Striped bass (L)	4.07	0.022	0.317		1.820	**0.557**	0.174	0.000	0.000	0.20	0.003
33	Weakfish (S)	3.92	0.006	3.300		13.520	**0.897**	0.244	0.000	0.000	0.20	0.000
34	Weakfish (M)	3.98	0.038	0.900		4.689	**0.822**	0.192	0.000	0.000	0.20	0.023
35	Weakfish (L)	4.05	0.036	1.000		2.803	**0.959**	0.357	0.000	0.000	0.20	0.034
36	Spiny dogfish (S)	4.18	0.337	0.321		3.519	**0.481**	0.091	0.000	0.000	0.20	0.000
37	Spiny dogfish (L)	4.28	0.800	0.321		1.810	**0.594**	0.177	0.000	0.000	0.20	0.114
38	Atlantic cod (S)	3.63	0.055	1.087		5.059	**0.725**	0.215	-0.013	-0.228	0.20	0.010
39	Atlantic cod (M)	3.95	0.144	1.125		2.603	**0.931**	0.432	-0.033	-0.228	0.20	0.132
40	Atlantic cod (L)	4.34	0.277	0.700		1.500	**0.706**	0.467	-0.063	-0.228	0.20	0.122
41	Haddock	3.63	0.254		0.700	3.000	**0.906**	0.233	0.000	0.000	0.20	0.082
42	Hake	4.16	1.100		1.296	3.850	**0.741**	0.337	0.000	0.000	0.20	0.109
43	Atlantic croaker	3.57	0.350		0.994	3.550	**0.263**	0.280	0.000	0.000	0.20	0.027
44	Yellowtail flounder (S)	3.57	0.007	2.700		12.168	**0.879**	0.222	0.000	0.000	0.20	0.000
45	Yellowtail flounder (L)	3.54	0.187	0.850		2.900	**0.648**	0.293	0.000	0.000	0.20	0.085
46	Summer flounder (S)	4.21	0.010	2.200		10.283	**0.922**	0.214	0.001	0.106	0.20	0.009
47	Summer flounder (L)	4.51	0.159	1.050		2.900	**0.541**	0.362	0.017	0.106	0.20	0.084
48	Skates	3.80	1.000		0.250	0.900	**0.761**	0.278	0.000	0.000	0.20	0.011
49	Demersal benthivores - other	3.56	2.300		0.550	1.833	**0.946**	0.300	0.000	0.000	0.20	0.119
50	Demersal piscivores - other	4.08	1.300		0.450	1.500	**0.728**	0.300	0.000	0.000	0.20	0.089
51	Demersal omnivores - other	3.89	1.100		0.550	1.833	**0.896**	0.300	0.000	0.000	0.20	0.101
52	Medium pelagic - other	4.71	0.021		0.450	1.838	**0.643**	0.245	0.000	0.000	0.20	0.001
53	Sharks - coastal	4.60	0.008		0.200	1.247	**0.564**	0.160	0.000	0.000	0.20	0.001
54	Sharks - pelagic	4.64	0.016		0.113	0.690	**0.194**	0.164	0.000	0.000	0.20	0.000
55	Large pelagics (HMS)	4.43	0.070		0.579	6.794	**0.671**	0.085	0.000	0.000	0.20	0.027
56	Pinnipeds	4.53	0.035		0.075	5.581	**0.118**	0.013	0.000	0.000	0.20	0.000
57	Baleen whales	3.54	0.464		0.040	3.217	**0.012**	0.012	0.000	0.000	0.20	0.000
58	Odontocetes	4.61	0.060		0.040	14.301	**0.888**	0.003	0.000	0.000	0.20	0.000
59	Seabirds	4.26	0.007		0.279	80.000	**0.373**	0.003	0.000	0.000	0.20	0.000
60	Nearshore pisc. birds	4.00	0.007		0.279	80.000	**0.005**	0.003	0.000	0.000	0.20	0.000
61	Detritus	1.00	52.600				**0.867**		0.000	0.000	0.00	0.000

Table 9. Diet compositions for NWACS model trophic groups.

Node	Prey \ predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	Phytoplankton	0.2428	0.2247	0.7442	0.6678	0.1066	0.2330	0.1307	0.1770	0.4235	0.2360	0.6923		0.0672	0.0263			0.2783	0.2210	0.1630	0.1300							
2	Other primary producers	0.0230						0.0154	0.0117	0.0101	0.0134	0.0060						0.0230	0.0180	0.0140	0.0250						0.0022	0.0011
3	Bacteria		0.1957			0.0248		0.3128	0.1664	0.2006	0.2438	0.1199	0.2702	0.3966	0.0152													
4	Microzooplankton		0.0537	0.1105	0.0600	0.0310									0.0747			0.1401	0.1800	0.2200								
5	Small copepods			0.0105	0.1139	0.3032	0.1487		0.0148						0.4394	0.3985	0.6008	0.1401	0.1800	0.2200	0.3000	0.3995		0.0281	0.4539			
6	Large copepods				0.0649	0.4315	0.3234		0.0329						0.4293			0.1401	0.1800	0.2200	0.3000		0.1516		0.1723			
7	Gelatinous zooplankton				0.0421	0.0347										0.0207	0.0020					0.0232	0.0083	0.5073	0.0180	0.0020	0.0045	0.0056
8	Micronekton						0.0595	0.0154	0.0138	0.0091	0.0189			0.1343	0.0131	0.3648	0.2267				0.0840	0.3653	0.5087	0.1122	0.1864	0.0091	0.0089	
9	Macrobenthos - polychaetes							0.0051	0.0986		0.0210		0.1328			0.0011	0.0020				0.0100	0.0022		0.0191	0.0010	0.0010	0.0022	0.0011
10	Macrobenthos - crustaceans				0.0011			0.0031	0.0010		0.0011		0.0462	0.0256		0.1394	0.1344				0.0910	0.1280	0.1177	0.3143	0.1353	0.0161	0.0167	0.0124
11	Macrobenthos - molluscs							0.0010	0.0103	0.0010	0.0105		0.1103			0.0022							0.0022					0.0011
12	Macrobenthos - other				0.0011			0.0144	0.0837	0.0111	0.0110		0.1460	0.0608		0.0011	0.0050						0.0208	0.0056	0.0040	0.0010		
13	Megabenthos - filterers							0.0031	0.0138	0.0101	0.0011		0.0125															
14	Megabenthos - other							0.0010	0.0021	0.0010	0.0067		0.0119			0.0033	0.0020						0.0042			0.0050	0.0145	0.0147
15	Shrimp and Similar Species													0.0011		0.0302	0.0050					0.0107	0.0010	0.0011	0.0010	0.0010	0.0011	0.0011
16	Mesopelagics																						0.0010			0.0010	0.0033	0.0034
17	Atlantic herring															0.0051						0.0033					0.0311	0.0314
18	Alosines																										0.0190	0.0158
19	Atlantic menhaden (S)																									0.0091	0.0398	0.0197
20	Atlantic menhaden (M)																										0.0497	0.0394
21	Atlantic menhaden (L)																											0.0099
22	Anchovies															0.0272	0.0030					0.0143			0.0240	0.4436	0.2511	0.1885
23	Atlantic mackerel																									0.0020	0.0234	0.0203
24	Squid					0.0001																0.0066	0.1580	0.0101	0.0030	0.1159	0.1752	0.2178
25	Butterfish																						0.0249			0.2661	0.1138	0.1185
26	Small pelagic - other															0.0044	0.0191					0.0166			0.0010	0.0353	0.0662	0.0724
27	Bluefish (S)																										0.0099	0.0098
28	Bluefish (M)																											0.0011
29	Bluefish (L)																											
30	Striped bass (S)																									0.0010	0.0011	
31	Striped bass (M)																											
32	Striped bass (L)																											
33	Weakfish (S)																									0.0010	0.0010	0.0010
34	Weakfish (M)																											0.0023
35	Weakfish (L)																											
36	Spiny dogfish (S)																											
37	Spiny dogfish (L)																											
38	Atlantic cod (S)																											
39	Atlantic cod (M)																											
40	Atlantic cod (L)																											
41	Haddock																										0.0011	0.0056
42	Hake															0.0010						0.0214	0.0018			0.0565	0.0311	0.0414
43	Atlantic croaker																									0.0010	0.0100	0.0068
44	Yellowtail flounder (S)																										0.0011	0.0011
45	Yellowtail flounder (L)																											0.0052
46	Summer flounder (S)																										0.0022	0.0011
47	Summer flounder (L)																											
48	Skates																						0.0010					0.0023
49	Demersal benthivores - other																					0.0011				0.0262	0.0804	0.1005
50	Demersal piscivores - other															0.0011						0.0044	0.0010				0.0089	0.0090
51	Demersal omnivores - other																					0.0033				0.0060	0.0301	0.0384
52	Medium pelagic - other																											
53	Sharks - coastal																											
54	Sharks - pelagic																											
55	Large pelagics (HMS)																											
56	Pinnipeds																											
57	Baleen whales																											
58	Odontocetes																											
59	Seabirds														0.0010													
60	Nearshore pisc. birds																											
61	Detritus	0.7343	0.5258	0.1347	0.0490	0.0681	0.2354	0.4980	0.3741	0.3333	0.4364	0.1818	0.2702	0.3145	0.0010			0.2783	0.2210	0.1630	0.0600							
62	Import																											
63	Sum	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
64	(1 - Sum)																											

Node	Prey \ predator	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
1	Phytoplankton																															
2	Other primary producers		0.0010	0.0030	0.0012		0.0010											0.0010		0.0013	0.0012	0.0024	0.0020									
3	Bacteria																															
4	Microzooplankton																															
5	Small copepods	0.0268			0.0047	0.0021	0.0010			0.0021			0.0010	0.0018	0.0011		0.0040	0.0010		0.0013	0.0035								0.0521			
6	Large copepods	0.0268			0.0047	0.0021	0.0010			0.0021																0.0251			0.4755		0.0389	
7	Gelatinous zooplankton					0.0011	0.0020	0.2282	0.1391				0.0020				0.0010						0.0119	0.0010	0.0010	0.0028	0.0392		0.0070	0.0167		
8	Micronekton	0.0924	0.0156	0.0020	0.2285	0.1744	0.1321	0.0993	0.0183	0.1496	0.0243	0.0023	0.1385	0.1838	0.0791	0.1339	0.0321	0.2560	0.0327	0.0138	0.0547	0.0346	0.0060	0.0317	0.0362			0.0729	0.3033	0.0292	0.1604	
9	Macrobenthos - polychaetes	0.0189	0.0342	0.0278	0.0094	0.0096	0.0050	0.0201	0.0049	0.0753	0.0243	0.0146	0.0825	0.0088	0.3080	0.2527	0.4639	0.0010		0.1547	0.2536	0.0215	0.0408	0.0010								
10	Macrobenthos - crustaceans	0.4613	0.2286	0.0328	0.1390	0.1244	0.1079	0.0443	0.0171	0.4731	0.1468	0.0259	0.2424	0.2223	0.1594	0.4565	0.3327	0.1100	0.0409	0.1756	0.2903	0.0621	0.0626	0.0248	0.0117	0.0102			0.0561			0.0276
11	Macrobenthos - molluscs	0.0050	0.0410	0.0159	0.0012	0.0021		0.1168	0.0684	0.0159	0.0607	0.0496	0.0479	0.0193	0.2374	0.0050	0.0180	0.0080	0.0031	0.1534	0.1361	0.0585	0.0845		0.0029				0.0110			
12	Macrobenthos - other	0.0050	0.0020	0.0030			0.0010	0.0040	0.0037	0.0870	0.0959	0.0124	0.2841		0.0064	0.0230	0.0411			0.0050	0.0477	0.0012	0.0129		0.0186	0.0102			0.0210			
13	Megabenthos - filterers		0.0078	0.0010				0.0255	0.0818	0.0149	0.0437	0.0327	0.0061	0.0053			0.0010			0.0025		0.0012	0.0060		0.0029							
14	Megabenthos - other	0.0189	0.0381	0.0208	0.0153	0.0170	0.0282	0.0148	0.0195	0.0297	0.1844	0.1296	0.0448	0.0420	0.0834	0.0809	0.0150	0.0590	0.0562	0.2339	0.1291	0.3906	0.5586		0.0186				0.0050			0.0276
15	Shrimp and Similar Species	0.0050	0.0010		0.0389	0.0266	0.0091	0.0121	0.0061	0.0528	0.0606	0.0169	0.0173	0.0436	0.0064	0.0250	0.0030	0.0250	0.0061	0.0157	0.0151	0.0358	0.0129								0.0224	
16	Mesopelagics							0.0040	0.0012					0.0088				0.0010				0.0012	0.0020	0.0546		0.0046			0.0020	0.0073		
17	Atlantic herring		0.0234	0.0615				0.0107	0.1178		0.0667	0.3009	0.0692	0.0566			0.0010		0.0389	0.0189		0.0106	0.0099	0.0089	0.0616	0.0688	0.1469	0.1458	0.0150	0.1137	0.0930	
18	Alosines	0.0099	0.0078	0.0119		0.0011	0.0020		0.0073		0.0024	0.0079		0.0035					0.0143	0.0038		0.0072	0.0010	0.0268	0.0616	0.0112		0.0513		0.0063	0.0165	0.0882
19	Atlantic menhaden (S)	0.0199	0.0780	0.0763	0.0130	0.0245	0.0272	0.0013	0.0037											0.0013		0.0100	0.0219		0.0047	0.0009	0.0197	0.0098	0.0010	0.0097	0.0342	0.1101
20	Atlantic menhaden (M)	0.0199	0.0780	0.1288		0.0102	0.0302		0.0024											0.0010		0.0200	0.0298		0.0197	0.0280	0.0984	0.0295		0.0291	0.0342	0.1651
21	Atlantic menhaden (L)		0.0010	0.0991			0.0010		0.0012													0.0300			0.0394	0.0093	0.1278	0.0393		0.0486	0.0410	0.0551
22	Anchovies	0.1123	0.2315	0.2541	0.4359	0.4626	0.4130		0.0134					0.0105	0.0642			0.1450	0.1094	0.0176	0.0454	0.0036	0.0040	0.0060	0.0616	0.0214	0.0979	0.0486	0.0010	0.0751	0.1026	0.2755
23	Atlantic mackerel		0.0010	0.0119				0.0890	0.1101		0.0049	0.0169	0.0102	0.0116					0.0603	0.0038		0.0107			0.0616	0.0688	0.0392	0.1458	0.0150	0.0209	0.1168	
24	Squid	0.0010	0.0156	0.0447	0.0094	0.0202	0.0292	0.1476	0.1123		0.0073	0.0056	0.0010	0.1296	0.0107			0.1230	0.2117	0.0377	0.0128	0.0394	0.0368	0.2828	0.1261	0.1552	0.0392		0.0060	0.2941	0.0625	
25	Butterfish		0.0215	0.0278	0.0012	0.0085	0.0182	0.0081	0.0183			0.0034	0.0010	0.0263	0.0064			0.0030	0.0501	0.0163		0.0167	0.0070	0.2570	0.0616	0.0688	0.0196	0.1458	0.0150	0.1137	0.1168	
26	Small pelagic - other	0.1133	0.0596	0.0735	0.0660	0.0542	0.0908	0.0295	0.0720	0.0965	0.1568	0.1364	0.0316	0.0406	0.0064	0.0230	0.0872	0.0080	0.0736	0.0509		0.0203	0.0129	0.0833	0.0616	0.0214	0.1567	0.0486	0.0010	0.0751	0.1026	0.1102
27	Bluefish (S)		0.0010	0.0010								0.0097							0.0010			0.0020	0.0020			0.0009						
28	Bluefish (M)			0.0010								0.0011													0.0196	0.0196	0.0392	0.0098		0.0194			
29	Bluefish (L)																								0.0196	0.0196	0.0588	0.0196		0.0097			
30	Striped bass (S)		0.0010	0.0020					0.0012																	0.0074						0.0011
31	Striped bass (M)			0.0010																					0.0093	0.0093		0.0090				
32	Striped bass (L)																								0.0093	0.0093		0.0010				
33	Weakfish (S)	0.0020	0.0039		0.0010	0.0031	0.0102											0.0020	0.0102	0.0025		0.0011	0.0010			0.0074						0.0011
34	Weakfish (M)						0.0030												0.0031							0.0074						
35	Weakfish (L)																									0.0074						
36	Spiny dogfish (S)								0.0012			0.0098		0.0012					0.0010			0.0101			0.0059	0.0074	0.0196	0.0144		0.0063	0.0059	
37	Spiny dogfish (L)											0.0098													0.0284	0.0280	0.0295	0.0190		0.0190		
38	Atlantic cod (S)							0.0013	0.0012			0.0068										0.0108			0.0039	0.0046		0.0099		0.0042	0.0024	
39	Atlantic cod (M)											0.0056													0.0039	0.0046	0.0196	0.0090		0.0042	0.0024	
40	Atlantic cod (L)																								0.0039	0.0046	0.0196	0.0090		0.0042		
41	Haddock								0.0012		0.0024	0.0146	0.0010	0.0035				0.0020	0.0266	0.0075		0.0084	0.0010		0.0127	0.0102	0.0098	0.0117				
42	Hake	0.0249	0.0068	0.0139	0.0059	0.0106	0.0091	0.0644	0.0598	0.0011	0.0679	0.0845	0.0112	0.0826				0.1210	0.0562	0.0012		0.0237	0.0020	0.1161	0.0127	0.0139		0.0144		0.0136	0.0059	
43	Atlantic croaker	0.0030	0.0029	0.0099	0.0024	0.0043	0.0020		0.0012									0.0130	0.0051	0.0063	0.0012	0.0060	0.0040		0.0127	0.0102		0.0117				0.0055
44	Yellowtail flounder (S)								0.0012			0.0023		0.0012						0.0010		0.0012			0.0059	0.0046		0.0117				
45	Yellowtail flounder (L)											0.0050		0.0012								0.0010			0.0059	0.0046						
46	Summer flounder (S)								0.0012														0.0010		0.0059	0.0074		0.0049		0.0010	0.0024	
47	Summer flounder (L)																								0.0059	0.0074				0.0063	0.0024	
48	Skates							0.0064	0.0117		0.0012	0.0034								0.0013		0.0525	0.0050	0.0594	0.0196	0.0194	0.0098	0.0195				
49	Demersal benthivores - other	0.0199	0.0459	0.0635	0.0188	0.0351	0.0615	0.0295	0.0696		0.0364	0.0620	0.0071	0.0595	0.0021			0.0860	0.1401	0.0528	0.0093	0.0529	0.0477	0.0417	0.0127	0.0102		0.0117				0.0110
50	Demersal piscivores - other		0.0088		0.0012	0.0011	0.0040	0.0013	0.0122		0.0036	0.0101	0.0010	0.0263	0.0182				0.0102	0.0038		0.0251	0.0119		0.0127	0.0139		0.0144		0.0136	0.0059	0.0110
51	Demersal omnivores - other	0.0139	0.0430	0.0119	0.0024	0.0053	0.0101	0.0416	0.0195		0.0097	0.0203		0.0105	0.0107			0.0350	0.0491	0.0151		0.0275	0.0010	0.0050	0.0616	0.0799		0.0621		0.0574	0.0310	0.0110
52	Medium pelagic - other																									0.0214	0.0098					
53	Sharks - coastal																								0.0020	0.0084						
54	Sharks - pelagic																								0.0098	0.0186						
55	Large pelagics (HMS)																								0.0091	0.0091						
56	Pinnipeds																								0.0147	0.0149						
57	Baleen whales																								0.0117	0.0102						
58	Odontocetes																								0.0117	0.0204				0.0021		
59	Seabirds																								0.0166	0.0204						
60	Nearshore pisc. birds																								0.0010							
61	Detritus																									0.0502			0.0130			
62	Import																															0.1000
63	Sum	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
64	(1 - Sum)																															