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Evaluation of alternative harvest policies for striped bass and their prey, Atlantic menhaden

Samantha Schiano[a], **Geneviève M. Nesslage**[a], **Katie Drew**[b], **Amy M. Schueller**[c], **Ryan J. Woodland**[a], and **Michael J. Wilberg**[a]

[a]University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, Solomons, MD, USA; [b]Atlantic States Marine Fisheries Commission, Arlington, VA, USA; [c]NOAA Fisheries, Southeast Fisheries Science Center, Beaufort, NC, USA

Corresponding author: **Samantha Schiano** (email: samantha.schiano@ecstech.com)

Abstract

Ecosystem approaches to fisheries management are being explored worldwide, but few evaluations of multispecies harvest control rules (HCRs) exist. Our goal was to perform a simulation test of a suite of HCRs using an age-structured predator–prey model to represent the dynamics of a small pelagic fish, Atlantic menhaden (*Brevoortia tyrannus*), and its predator, striped bass (*Morone saxatilis*). We evaluated a suite of static and dynamic single and multispecies HCRs to estimate effects on stock performance metrics. No single HCR achieved ecosystem management objectives for both stocks given their current reference points, but HCRs that involved the "40–10 rule" for striped bass performed well across all predator performance metrics. The most influential factor determining performance of striped bass HCRs was striped bass fishing mortality, and relatively few HCRs achieved target SSB for Atlantic menhaden. Our study indicated that some HCRs recommended for forage fish management may not be effective in systems with generalist predators, and that ecosystem management objectives might be achievable by simultaneously adopting HCRs for both predator and prey stocks that complement one another.

Key words: harvest control rules, ecosystem approach to fisheries management, predator–prey, *Morone saxatilis*, *Brevoortia tyrannus*

Introduction

Ecosystem-based fisheries management (EBFM) is an approach to managing fisheries that extends beyond a single species to incorporate a broader range of resources and aspects of the ecosystem including social, economic, and human interactions (Link and Browman 2014; Dickey-Collas et al. 2022). An ecosystem approach to fisheries management (EAFM), in contrast, focuses on a single or select group of fisheries and specific processes that link them (Patrick and Link 2015). EAFM recognizes the interworking of the ecosystem while remaining similar to traditional fisheries management by focusing on individual stock metrics. Although the concept of EAFM is not new, barriers to implementing EAFM include lack of a multispecies or ecosystem management structure, limited data availability to develop ecosystem models, and competing interests among fisheries (Patrick and Link 2015; Koen-Alonso et al. 2019; Safiq et al. 2021). Despite these challenges, applications of EAFM are growing (Garrison et al. 2010; McGowan et al. 2011; Drew et al. 2021) and have begun to emerge throughout managing bodies across the East Coast of the US (Gaichas et al. 2018; Koen-Alonso et al. 2019; Muffley et al. 2021). In particular, the Atlantic States Marine Fisheries Commission (ASMFC) and the Mid-Atlantic Fisheries Management Council have shifted towards goals and objectives that incorporate ecosystem aspects such as multispecies interactions, including predator–prey dynamics (Anstead et al. 2021). Although single-species management can be highly useful (Hilborn and Ovando 2014), taking an EAFM approach makes it possible to better understand and manage the effects of fishing on ecosystem interactions such as predator–prey relationships (Mace 2001). For example, Multispecies Virtual Population Analysis (MSVPA) has been applied to multiple predator–prey based fisheries in the US and Europe (Gislason and Helgason 1985; Garrison et al. 2010). Studying a limited set of interactions among a small number of species using models of intermediate complexity for the ecosystem (MICE) can make for more robust models to provide management advice for EAFM (Plaganyi et al. 2014).

To achieve either single or multispecies goals and objectives, fishery managers must determine how often and how much harvest to allow. A common tool for setting harvest levels are harvest control rules (HCRs), which are automatic management procedures that are agreed upon in advance and that dictate the rate of fishing that can take place at a given stock size (Deroba and Bence 2008). Fishing mortality (F) is commonly used as a control variable to determine harvest levels in traditional HCRs by setting total allowable catch that is expected to achieve a given F (Punt 2010). HCRs formalize catch limit-setting decisions and help prevent or prepare a response to an overfishing and overfished stock status (Kvamsdal et al. 2016). Dynamic multispecies HCRs (DMSHCRs), in which the target *F* rate of one species depends at least partially on the status of another species, have been proposed (Pikitch et al. 2012). However, Pérez-Rodríguez et al. (2022) demonstrated that it may not be possible to achieve the targets among a three-species predator–prey system simultaneously, demonstrating the difficulty in managing multiple stocks with DMSHCRs.

Despite the potential benefits of EAFM, many predator–prey systems are still managed to achieve single-species objectives. Yet, previous studies have concluded that piscivorous predator conservation should be considered as part of forage fish management (Pikitch et al. 2012; Pikitch et al. 2014). One important predator–prey case study involving piscivorous predator and a small pelagic forage fish is that of striped bass (*Morone saxatilis*) and Atlantic menhaden (*Brevoortia tyrranus*) along the US East Coast for which an EAFM was developed to generate biological reference points for Atlantic menhaden (Chagaris et al. 2020; Anstead et al. 2021). Striped bass supports one of the largest recreational fisheries on the US East Coast and is managed by the ASMFC through a cooperative, interstate fishery management plan (ASMFC 2022). The coastal migratory stock of striped bass is managed using a constant F HCR that is intended to achieve a target SSB (SSB_{TARGET} = 125% of the female SSB estimate from 1995 when the stock was declared recovered from an overfished state). However, striped bass biomass may be highly influenced by the available biomass of key prey species, such as Atlantic menhaden (Chagaris et al. 2020), and that ecosystem perspective is not currently incorporated in the striped bass fishery management plan (ASMFC 2022). In turn, Atlantic menhaden is a key forage fish for many piscivorous predators along the US East Coast, including striped bass (Buchheister et al. 2017), and the Atlantic menhaden stock supports a major directed fishery (SEDAR 2020*a*). Although the Atlantic menhaden stock was neither overfished nor experiencing overfishing relative to single-species reference points (SEDAR 2020*a*), ecosystem-level concerns about the availability of Atlantic menhaden to support striped bass and other predators led the ASMFC to move towards a more holistic management approach that takes into account Atlantic menhaden's role as a forage fish. The ecosystem management objectives for Atlantic menhaden include sustaining biomass to provide for both its fisheries and its predators, minimizing risk of stock collapse, and ensuring an adequate supply of Atlantic menhaden for predators. Atlantic menhaden are now managed with a multispecies focus by selecting an *F* target and threshold for Atlantic menhaden that achieves the biomass target and threshold of their predator, striped bass, while fishing the predator at their target *F* (Chagaris et al. 2020; Anstead et al. 2021).

There is broad interest worldwide among fishery management agencies to incorporate EAFM in their decisions to better account for the impact of fisheries on the ecosystem as a whole. In particular, incorporating predator–prey interactions within ecosystem management objectives can support predator stocks by ensuring adequate prey supply and help evaluate trade-offs that may occur when fishing forage fish stocks (Pikitch et al. 2012). Although the ASMFC has implemented EAFM for Atlantic menhaden by adopting reference points that are linked to the stock status of its most reliant predator, striped bass, the HCRs used to manage Atlantic menhaden and striped bass remain constant F, single-species HCRs. Furthermore, the reference points used to manage Atlantic menhaden include SSB objectives for striped bass, but management of striped bass is conducted without consideration of the consequences for its prey. Thus, the predator–prey relationship of Atlantic menhaden and striped bass in the mid-Atlantic is an excellent candidate for deeper exploration of the relative performance of numerous types of single-species and multispecies HCRs that are either constant or dynamic. For this study, we used the striped bass–Atlantic menhaden-linked predator–prey system as a case study to address the following objectives: (1) compare the relative performance of a broad suite of single and multispecies HCRs in their ability to address ecosystem management objectives and (2) identify and quantify the trade-offs among HCR types.

Methods

We conducted a harvest policy evaluation using a multispecies MICE model that was an updated version of the age-structured, linked predator–prey simulation model from Nesslage and Wilberg (2019) to test a suite of new and existing HCRs on our case study predator and prey stocks of striped bass and Atlantic menhaden. The model simulated the age-structured population dynamics for striped bass ages 1–20+ and Atlantic menhaden ages 0–6+, leveraging two well-established, peer-reviewed, age-structured stock assessments currently used in ASMFC management (NEFSC 2019; SEDAR 2020*a*). The model also included eight static other prey sources that differed in their average weight and abundance to supplement the remainder of the striped bass diet. We parameterized the model using life-history data and abundance estimates from stock assessments for striped bass and Atlantic menhaden (NEFSC 2019; SEDAR 2020*a*). We also utilized information from numerous striped bass diet studies to characterize size-based consumption patterns. The model treated each striped bass age class and each prey age or size class as separate predators and prey, respectively. To model dependence of striped bass on Atlantic menhaden, we used a multi-predator, multi-prey type II functional response relationship (Szalai 2003). Striped bass weight-at-age varied over time based on their achieved consumption. Background natural mortality (M_1, which includes disease and predation by predators other than striped bass) was constant for Atlantic menhaden, but natural mortality due to predation by striped bass (M_2) of Atlantic menhaden varied according to striped bass consumption of Atlantic menhaden. In turn, striped bass M was influenced by its weight-at-age, which was a function of consumption. To compare quasi-equilibrium performance of different HCRs and their ability to achieve long-term ecosystem management objectives for each stock, we ran simulations for 100 years.

We developed a suite of single-species HCRs and DMSHCRs and applied them to the simulated striped bass–Atlantic menhaden predator–prey system. We then evaluated how well each HCR met ecosystem management objectives for each stock. The predator–prey model was developed in AD Model Builder (Fournier et al. 2012) and all other analyses were conducted in R (RStudio team 2020). Parameter and variable definitions are provided in Table 1, model dynamics equations are provided in Table 2, and equations defining the HCRs are provided in Table 3. For each HCR, 100 stochastic simulations were run.

Predator–prey model

The predator–prey model simulated seasonal, age-structured population dynamics for striped bass and Atlantic menhaden based on the predator–prey model of Szalai (2003). The model included seasonal time steps (season 1: January to March, season 2: April to June, season 3: July to September, season 4: October to December). Parameter values were estimated using external analyses (Supplement 1) and recent stock assessments (NEFSC 2019; SEDAR 2020*a*).

Initial abundance-at-age for striped bass and Atlantic menhaden was set to estimated abundance-at-age from the most recent year in their respective stock assessments. Recruits entered the population in the first season of each year following a Beverton–Holt stock-recruitment function. Recruitment of striped bass was calculated based on the spawning stock biomass (SSB) of the previous year (eq. T.2.1), while Atlantic menhaden recruitment did not include a lag (eq. T.2.2). Recruitment included a multiplicative lognormal error that followed a first-order autoregressive process over time (eq. T. 2.3; Atlantic menhaden autocorrelation = 0.31, striped bass autocorrelation = 0.22). Because striped bass and Atlantic menhaden recruitment has historically been out of phase, presumably due to differences in how recruitment is affected by non-predation environmental factors (Wood and Austin 2009), we included a weak negative correlation (−0.11) between the recruitment deviations of striped bass and Atlantic menhaden, which was estimated from the residuals of the stock-recruitment relationships for each species. Stock-recruitment parameters were estimated using SSB and recruitment from the respective stock assessments for each species (Supplement 1). Stock size for the stock-recruitment models was calculated in terms of female SSB. Recruitment represented age-1 for striped bass and age-0 for Atlantic menhaden. After the first age, abundance of a cohort throughout each season declined following the exponential mortality model (eq. T.2.4). Abundance in the first season was calculated using abundance in the previous age and season 4 of the previous year (eq. T.2.5). Abundance of the plus group in the first season was calculated similarly to eq. T.2.5, but the abundance in the last season of the previous age was added to abundance of plus group survivors (eq. T.2.6).

Total instantaneous mortality rates for striped bass and Atlantic menhaden were calculated as the sum of F and all sources of M for a given time step and age (eqs. T.2.7 and T.2.8). The proportion of F in each season was specified based on historical averages of the annual catch in each season. The F in the first year of the simulation was set at the value in the terminal year (2017) from each stock assessment: 0.307 yr^{-1} for striped bass and 0.157 yr^{-1} for Atlantic menhaden. In subsequent years of the simulation, the value for F depended on the HCR applied (Table 4). The background M_1 for each age was constant and divided evenly among the four seasons. M_1 values for striped bass were chosen such that the M in the status quo scenario was approximately equal to the M-at-age vector specified in the stock assessment. In addition to M_1, striped bass was subject to condition-based natural mortality (M_c) such that striped bass M was highest when relative weight was lowest, simulating potential starvation mortality for striped bass that could not consume enough prey (Hoenig et al. 2017). Striped bass standard weight (eq. T. 2.9; Jacobs et al. 2013) was defined as a function of smoothed geometric mean length-at-age (Schiano 2022) and mortality rates estimated by Hoenig et al. (2017) to mimic their reported pattern of increased M for low-condition fish. Standard weight in the previous season was used to calculate striped bass relative weight-at-age in subsequent seasons (eqs. T.2.10 and T.2.11). M_c was calculated such that if an estimated fraction of striped bass at a given age was below a threshold relative weight, the striped bass in that age class experienced higher total M (eq. T. 2.12).

For Atlantic menhaden, total M in a given year and season was the sum of constant, age-specific M_1 background natural mortality (which included disease and predation by predators other than striped bass) and M_2 predation mortality due to consumption-at-age by striped bass that changed over time (eqs. T.2.13 and T.2.14). Predation mortality (M_2) for a given age of Atlantic menhaden was the sum of Atlantic menhaden consumed by each age of striped bass (assuming mid-season abundance) divided by the number of Atlantic menhaden alive at the beginning of the season. Because the Atlantic menhaden assessment total M-at-age vector does not distinguish between M_1 and $M_{2,}$ we iteratively adjusted M_1 in our base model to generate total M-at-age that matched the assessment, on average, under status quo Fs for both species.

Seasonal weight-at-age for Atlantic menhaden was static over time and calculated as the seasonal average of the last 10 years of time-varying weight-at-age from the stock assessment (2008–2017; SEDAR 2020*a*). Striped bass weight-at-age was a function of their maximum potential growth (Gmax) and their consumption (*Cons*) relative to their maximum potential consumption (Cmax) at a given age (eq. T. 2.15). Gmax values were calculated by dividing change in weight at a given age by 0.9, assuming that striped bass achieved 90% of Cmax in 2017 (thereby also achieving 90% of Gmax) (Table S1). Mean striped bass weight-at-age from Schiano (2022) was used to estimate change in weight for each age assuming that growth rates were equal across seasons (Supplement 1). We then calculated *Cmax*-at-age by dividing *Gmax*-at-age by age-specific estimates of conversion efficiency for striped bass reported by Hartman and Brandt (1995) for age-1 and age-2 and Nelson et al. (2006) for age-3 to age-8. We assumed conversion efficiencies for older ages declined to 0 by age-20+.

To model density-dependent consumption of striped bass in an age-structured framework, we used a multi-predator, multi-prey type II functional response (Szalai 2003). A type II relationship assumes predator consumption increases with increasing prey density, then asymptotes due to limitations in the predator's ability to process readily available food (Holling 1959). Although a type III sigmoid-shaped functional

Table 1. Parameter and variable names used in equations for the predator–prey simulation model and consumption dynamics model.

Symbol	Description (units)
Index variables	
y	Year
t	Season
a	Age
a_1	Minimum age
a_2	Maximum age
j	Predator index
i	Prey index
Parameters	
R	Recruitment
α	Productivity at low stock size
SSB	Spawning stock biomass
δ	Recruitment errors for striped bass
ε	Recruitment errors for Atlantic menhaden
β	Stock-recruitment density dependence term
N	Abundance
Z	Instantaneous total mortality
F	Instantaneous fishing mortality
M	Instantaneous natural mortality
M_1	All other instantaneous natural mortality not due to striped bass predation (Atlantic menhaden) or low relative weight (striped bass)
M_c	Striped bass natural mortality due to low relative weight
Ws	Standard weight
W	Weight
RelW	Relative weight
L	Input length-at-age from Schiano (2022)
Φ	Cumulative density function for a standard normal distribution
ICR	Instantaneous consumption rate
M_2	Instantaneous natural mortality due to predation
PW	Predicted predator weight
Gmax	Maximal potential growth
Cmax	Proportion of maximum consumption achieved by the predator
SP	Size preference of the predator or each prey; length-based
length	Length-at-age of either predator or prey in consumption model
$\text{length}_{\text{opt}}$	Optimum length ratio of prey to predator
ω	Variance of the predator–prey length ratio
TC	Total consumption per predator (in weight)
ρ	Attack rate calculated as a function of the ratio of prey to predator size
W	Weight
γ	Length-based scalar for a predator effective search area
B	Biomass
m_a	Proportion mature-at-age
PF	Proportion of females in a given age class
C	Catch
AAV	Average annual variation of catch
F_l	Lower fishing mortality rate as describes in a HCR
F_u	Upper fishing mortality rate as described in a HCR
SSB_l	Lower spawning stock biomass threshold
SSB_u	Upper spawning stock biomass threshold
int	Intercept parameter for a Type 2 HCR
slope	Slope parameter for a Type 2 HCR
relSSB	Relative SSB using the species SSB target as a reference point
$\text{SSB}_{\text{thresh}}$	Lower SSB threshold for striped bass as applied in a Type 3 Atlantic menhaden HCR

Table 1. (*concluded*).

Symbol	Description (units)
NC30	An alternative predator–prey dynamics operating model that assumes prey consumption at length is normally distributed and up to 30% of striped bass diet is Atlantic menhaden
NC70	An alternative predator–prey dynamics operating model that assumes prey consumption at length is normally distributed and up to 71% of striped bass diet is Atlantic menhaden
LNC30	An alternative predator–prey dynamics operating model that assumes prey consumption at length is normally distributed and up to 30% of striped bass diet is Atlantic menhaden

Table 2. List of equations used in the predator–prey simulation model and consumption dynamics model.

Equation number	Equation	Description
T. 2.1	$R_y = \frac{\alpha SSB_{y-1}}{1+\beta SSB_{y-1}} e^{\delta(y-1)}$	Beverton–Holt stock-recruitment function for striped bass
T. 2.2	$R_y = \frac{\alpha SSB_y}{1+\beta SSB_y} e^{\varepsilon y}$	Beverton–Holt stock-recruitment function for Atlantic menhaden
T. 2.3	$N_{y,\, t\,=\,1,\, a\,=\,a_1} = R_y$	Abundance in the first age and first season
T. 2.4	$N_{y,\, t\,+\,1,\, a} = N_{y,\, t,\, a} e^{-Z_{y,\, t,\, a}}$	Abundance-at-age within the year
T. 2.5	$N_{y\,+\,1,\, t\,=\,1,\, a\,+\,1} = N_{y,\, t\,=\,4,\, a} e^{-Z_{y,\, t\,=\,4,\, a}}$	Abundance-at-age in the first season
T. 2.6	$N_{y\,+\,1,\, t\,=\,1,\, a\,=\,a_2} = N_{y,\, t\,=\,4,\, a\,=\,a_2} e^{-Z_{y,\, t\,=\,4,\, a\,=\,a_2}} + N_{y,\, t\,=\,4,\, a\,=\,a_2\,-\,1} e^{-Z_{y,\, t\,=\,4,\, a\,=\,a_2\,-\,1}}$	Abundance at-age in the plus group in the first season
T. 2.7	$Z_{y,\, t,\, a} = F_{y,\, t,\, a} + M_a + Mc_{y,\, t,\, a}$	Total instantaneous mortality for striped bass
T. 2.8	$Z_{t,\, a} = F_{t,\, a} + M_{t,\, a}$	Total instantaneous mortality for Atlantic menhaden
T. 2.9	$Ws = 0.001 \times 10^{-4.924} \times L_{t,a}^{3.007}$	Standard weight of striped bass (kg)
T. 2.10	$RelW_{t=1,a} = 100 \times \frac{W_{y-1,t=1,a}}{Ws_{t=1,a}}$	Relative weight of striped bass in the first season
T. 2.11	$RelW_{t,a} = 100 \times \frac{W_{y,t-1,a}}{Ws_{t-1,a}}$	Relative weight of striped bass after the first season
T. 2.12	$Mc_{y,t,a} = 3.28 * M_{y,t,a} \Phi\left(\frac{70.52 - RelW_{y,t,a}}{16}\right) + M_{y,t,a}\left(1 - \Phi\left(\frac{70.52 - RelW_{y,t,a}}{16}\right)\right)$	Natural mortality for striped bass with low relative weight
T. 2.13	$M_{2,\mathrm{t},a_i} = \frac{\sum_{a_j=1}^{20}\left(ICR_{t,a_j,a_i} N_{t,a_j,j} e^{\frac{-Z_{t,a_j,j}}{2}}\right)}{N_{t,a_i,i}+0.0001}$	Instantaneous natural mortality rate for Atlantic menhaden due to predation by striped bass
T. 2.14	$M_{a,\, t} = M_{1,\, a} + M_{2,\, t,\, a}$	Instantaneous natural mortality rate for Atlantic menhaden
T. 2.15	$PW_{y,t+1,\mathrm{a}} = PW_{y,t,a} + \frac{Gmax_a TC_{y,t,a}}{Cmax_{\mathrm{a}}}$	Predator weight-at-age as a function of their consumption
T. 2.16	$\mathrm{SP}_{i,j} = e^{\frac{-\left(\frac{\mathrm{length}_i}{\mathrm{length}_j} - \mathrm{length_{opt}}\right)^2}{\omega}}$	Normal size preference of each predator for each prey used in the consumption dynamics for NC30 and NC70
T. 2.17	$\mathrm{TC}_{t,a_j} = \sum_i \mathrm{ICR}_{t,i,a_j} \mathrm{W}_i$	Total consumption in weight per individual for each age striped bass (a_j)
T. 2.18	$\mathrm{ICR}_{i,t,a_j} = \frac{\rho_{a_j} N_{i,t}}{1+\sum_i \frac{\rho_{a_j} N_{i,t} W_i}{Cmax_{a_j}}}$	Consumption rate (in numbers) of each prey type by each age striped bass
T. 2.19	$\rho_a = \mathrm{SP}_{i,\, j} \mathrm{length}_{j,\, a} \gamma_a$	Attack rate of each age predator
T. 2.20	$B_y = \sum_a N_{y,t=1,a} W_{y,t=1,a}$	Biomass at the beginning of each year
T. 2.21	$\mathrm{SSB}_y = \sum_a N_{y,t=4,a} m_a W_{y,t=4,a}$	Spawning stock biomass for Atlantic menhaden
T. 2.22	$SSB_y = \sum_a N_{y,t=4,a} m_a W_{y,t=4,a} PF_a$	Spawning stock biomass for striped bass
T. 2.23	$C_y = \sum_{t \epsilon y} \sum_a \frac{F_{t,a}}{Z_{t,a}} \left(1 - e^{-Zt,a}\right) N_{t,a} W_{t,a}$	Annual catch in biomass
T. 2.24	$C_y = \sum_{t \epsilon y} \sum_a \frac{F_{t,a}}{Z_{t,a}} \left(1 - e^{-Zt,a}\right) N_{t,a}$	Annual catch in numbers
T. 2.25	$AAV_y = \left\lvert \frac{C_y - C_{y-1}}{C_y} \right\rvert$	Average annual variation of catch (in numbers for striped bass and weight for Atlantic menhaden)
T. 2.26	$SP_{i,j} = e^{\frac{-\left(\ln\left(\frac{\mathrm{length}_i}{\mathrm{length}_j}\right) - \ln\left(\mathrm{length_{opt}}\right)\right)^2}{\omega}}$	Lognormal size preference of each predator for each prey used in the consumption dynamics for LNC30

response relationship might better capture prey-switching behavior by predators at low prey density, we chose type II because the available striped bass diet data were not sufficient to parameterize a multispecies type III function, a common limitation (Kalinkat et al. 2023), and because managers of this system are not interested in HCRs that drive prey densities to low levels. We modeled age-specific striped bass consumption of Atlantic menhaden and other prey such that each age class of predator and prey was treated as a distinct predator or prey unit in the multispecies system. Thus, we dy-

Table 3. Equations used to calculate Type 1, Type 2, and Type 3 harvest control rules.

Equation Number	Equation	Description
T. 3.1	$F_y = F_l + \frac{(\mathrm{SSB}_{y-1} - \mathrm{SSB}_l) \times (F_u - F_l)}{\mathrm{SSB}_u - \mathrm{SSB}_l}$	Type 1 HCR when *F* is between the upper and lower SSB thresholds
T. 3.2	$F = \mathrm{int} + \mathrm{slope} \times \mathrm{relSSB}$	Type 2 HCR where *F* of one species is relative to SSB of the other species
T. 3.3	$F_y = \begin{cases} 0 & if \mathrm{SSB} \leq \mathrm{SSB}_{\mathrm{thresh}} \\ F_u & if \mathrm{SSB} > \mathrm{SSB}_{\mathrm{thresh}} \end{cases}$	Type 3 HCRs for Atlantic menhaden only; *F* is only F_u when striped bass SSB is above the designated threshold

namically modeled 20 striped bass predator age classes and seven Atlantic menhaden prey age classes, as well as eight static size-based "other prey" classes. The other prey pools provided striped bass predators an alternative source of prey to Atlantic menhaden. Alternative prey categories 2–8 were assumed to have the same mean length and weight as Atlantic menhaden ages 0–6+. Alternative prey category 1 had a mean length of 59 mm and weight of 0.01 kg to represent prey smaller than an age-0 Atlantic menhaden (e.g., bay anchovy (*Anchoa mitchilli*)).

Striped bass prey preference was modeled using an unscaled normal distribution function of prey length relative to predator length and the optimum ratio of prey-to-predator length from Rudershausen et al. (2005) (eq. T. 2.16). The per capita consumption (eq. T. 2.17) by striped bass was calculated as the product of consumption rate (eq. T. 2.18) and prey weight summed over prey types for each age of striped bass. Consumption rate was a function of prey abundance, prey weight, the instantaneous attack rate (eq. T.2.19), and maximum consumption, while the instantaneous attack rate was the product of prey preference, length, and a length-based scalar for the predator effective search area (γ). We estimated γ-at-length outside the model by minimizing the squared deviations of C/Cmax from the assumed proportion of Cmax consumed for each age in 2017 and 1998. Additional details on the estimation of consumption parameters can be found in Supplement 1.

Harvest control rules

F and SSB reference points for striped bass and Atlantic menhaden were developed by applying a suite of constant F HCRs as in Chagaris et al. (2020). A total of 336 combinations of single species, constant F HCRs were run with *F* ranging from 0 to 1.49 yr^{-1} for Atlantic menhaden (in 0.0075 increments) and 0 to 0.47 yr^{-1} (in 0.0313 increments) for striped bass. We estimated unfished SSB (SSB_0) of striped bass and Atlantic menhaden as the geometric mean of SSB of the respective species when *F* was 0 yr^{-1} for both species. We also estimated the *F* that achieved maximum sustainable yield (F_{MSY}) and the SSB at F_{MSY} ($\mathrm{SSB}_{\mathrm{MSY}}$) for each species when the other was not fished ($F = 0$ yr^{-1}). Lastly, we used these constant F HCRs to compare model performance and predator–prey dynamics with that of the Northwest Atlantic Continental Shelf model of intermediate complexity for ecosystems (NWACS-MICE), an Ecopath with Ecosim (EwE) model used in Atlantic menhaden management (Chagaris et al. 2020).

A suite of 27 HCRs was evaluated to assess relative performance (Table 4). We considered three classes of HCRs: Type 1—traditional single-species HCRs for both striped bass and Atlantic menhaden (Fig. 1); Type 2—HCRs in which *F* on one species was a linear function of relative SSB for the other (Fig. 2); and Type 3—traditional single-species HCRs for striped bass with threshold-based cessation of fishing for Atlantic menhaden when striped bass fall below a relative SSB threshold (Fig. 3). Each HCR determined the annual *F* of either striped bass or Atlantic menhaden in response to relative SSB from the previous year. Relative SSB was calculated by dividing SSB (eqs. T. 2.21–2.22) in the previous year by either the striped bass SSB target (114 million kg; NEFSC 2019) or Atlantic menhaden SSB target (843 million kg; SEDAR 2020*a*). Because the current Atlantic menhaden SSB target is calculated in units of number of eggs, we converted the SSB target into units of weight (millions of kg) by finding the SSB that achieved the target fecundity with a spawning potential ratio model that used age-specific fecundity in SEDAR (2020*a*).

Type 1 HCRs were single-species rules in which the status of the other species was not considered in determining the target *F*. We explored the relative performance of constant F HCRs, threshold-based cessation HCRs, and "hockey stick"-shaped biomass-based HCRs (Deroba and Bence 2008; Pikitch et al. 2012). When the HCR was biomass-based, *F* was calculated using the SSB of the previous year, the SSB upper and lower thresholds, and the lower and higher *F* (eq. T. 3.1; Table 4). The previous year's SSB was used to include a 1-year lag to account for data collection, assessment, and management. Type 2 HCRs were DMSHCRs in which the status of another species guides *F* on the target species. For our model, type 2 HCRs dictated that *F* for striped bass changed in response to SSB of Atlantic menhaden and vice versa (eq. T. 3.2). Type 2 HCRs were created based on Pérez-Rodríguez et al. (2022), which used multispecies "one" or "two-stage" HCRs that take a hockey-stick shape and function in a stepwise manner. Type 3 HCRs involved a threshold-based cessation of fishing for the prey species when predator biomass was below a predetermined level. In these HCRs, if striped bass SSB was under a specified threshold, then *F* was 0 yr^{-1} for Atlantic menhaden. Otherwise, *F* remained at the designated rate (eq. T. 3.3).

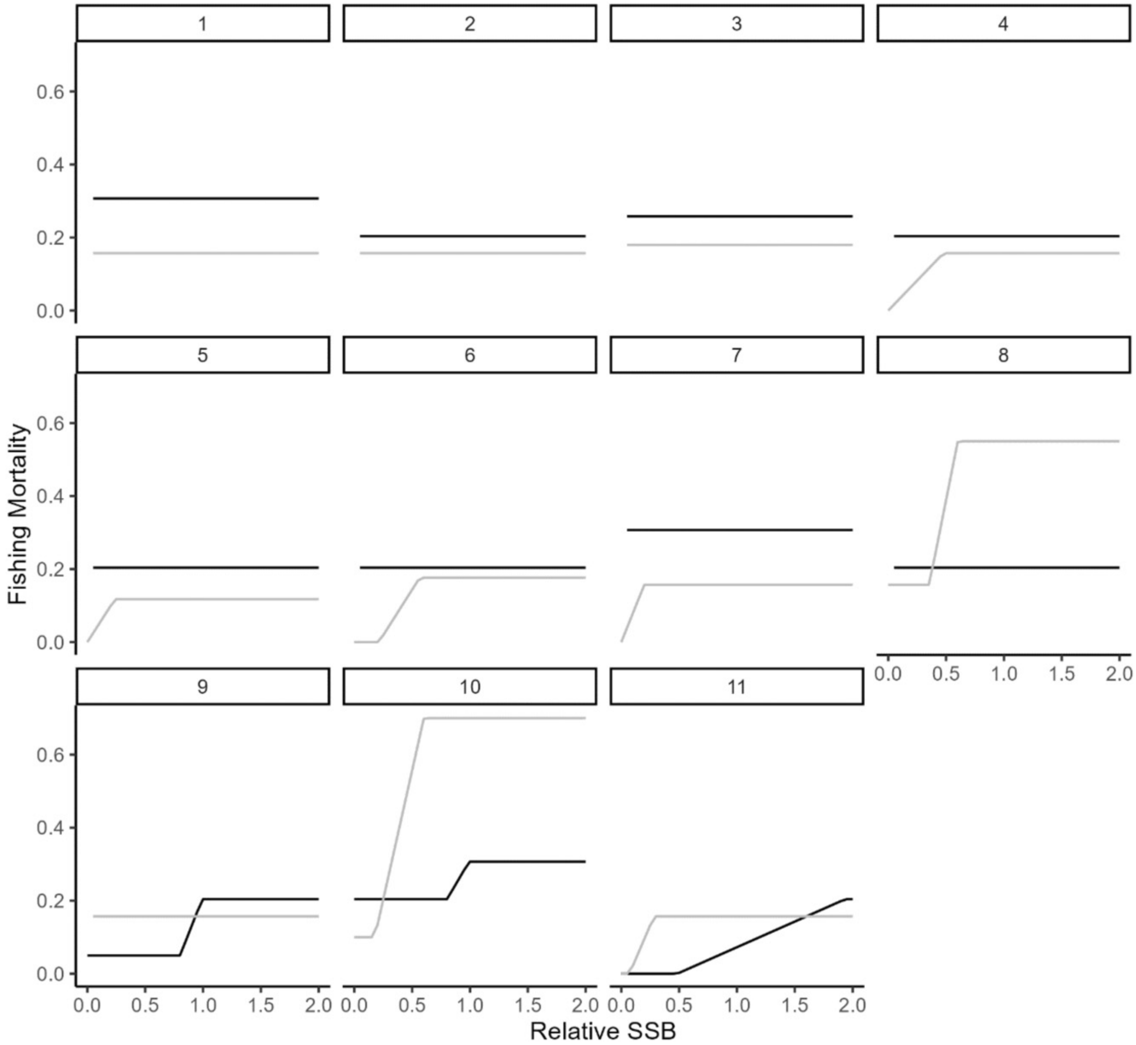
Our suite of HCRs included 11 Type 1, 6 Type 2, and 3 Type 3 HCRs (Table 4). Of the 11 Type 1 HCRs, 3 were constant F HCRs and 8 were biomass-based harvest control rules. HCR 1 implemented constant F rates from the terminal year *F* in each stock assessment (referred to as status quo) and was used as a baseline for comparison. HCR 2 operated under the target *F* rate for striped bass (0.204 yr^{-1}) and status quo for Atlantic menhaden (0.157 yr^{-1}). This scenario was designed to understand the response of the stocks if management was achieving its targets. HCR 3 represented fishing

Table 4. Description of 20 harvest control rules (HCRs) tested.

HCR	SS or MS	Type	Description	SB F	AM F
1	SS	1-Constant F	*F* is status quo for both Atlantic menhaden and striped bass.	0 0.307	0 0.157
2	SS	1-Constant F	Atlantic menhaden operates at status quo and striped bass is fished at the target *F*.	0 0.204	0 0.157
3	SS	1-Constant F	*F* for both is the average *F* from 1998 to 2017 for the fully selected age along the selectivity curve. (Age-3 for Atlantic menhaden and age-13 for striped bass).	0 0.258	0 0.18
4	SS	1-AM: Biomass-based, SB: Constant F	Mimics the Lenfest forage fish report low information tier where the Atllantic menhaden stock is not depleted lower than 20% of unfished SSB (Pikitch et al. 2012)	0 0.204	0 0.157
5	SS	1-AM: Biomass-based, SB: Constant F	Mimics the Lenfest forage fish report intermediate information tier where Atlantic menhaden *F* is 50% of F_{MSY} above or equal to 40% unfished SSB (Pikitch et al. 2012)	0 0.204	0 $0.5F_{MSY}$
6	SS	1-AM: Biomass-based, SB: Constant F	Mimics the Lenfest forage fish report high information tier where Atlantic menhaden *F* is 75% of F_{MSY} above 80% of unfished SSB and *F* is 0 under 30% unfished SSB (Pikitch et al. 2012)	0 0.204	0 $0.75F_{MSY}$
7	SS	1-AM: Biomass-based, SB: Constant F	Third for the birds—1/3 of Atlantic menhaden unfished SSB is the lower SSB threshold for the HCR	0 0.307	0 0.157
8	SS	1-AM: Biomass-based, SB: Constant F	An example of Atlantic menhaden operating under a biomass-based HCR while striped bass is under a constant F HCR	0 0.204	0.157 0.55
9	SS	1-AM: Constant F, SB: Biomass-based	Atlantic menhaden is operating under a constant F HCR at status quo, but striped bass is operating under a biomass-based HCR where striped bass is fished at $F = 0.05$ under the lower threshold (202 million lbs) and *F* = striped bass target above the upper threshold (striped bass target of 250 million lbs). Between those two boundaries, *F* operates on a calculated slope.	0.05 0.204	0 0.157
10	SS	1-Biomass-based	General example of both species operating under a biomass-based HCR; Atlantic menhaden lower and upper thresholds are 25% and 85% of SSB0 and striped bass thresholds are the threshold and target, respectively.	0.204 0.307	0.1 0.7
11	SS	1-Biomass-based	Both species are fished at their target above 40% of their unfished SSB and are not fished under 10% SSB	0 0.204	0 0.157
12	MS	2-Dynamic multispecies	Striped bass *F* is determined by Atlantic menhaden biomass levels, both slopes are positive	–	–
13	MS	2-Dynamic multispecies	Example of type 2 dynamics multispecies control rules where both slopes are positive.	–	–
14	MS	2-Dynamic multispecies	Testing dynamics of type 2 HCR with both slopes positive	–	–
15	MS	2-Dynamic multispecies	Testing dynamics of type 2 HCR where Atlantic menhaden have a positive slope and striped bass have a negative slope	–	–
16	MS	2-Dynamic multispecies	Testing dynamics of type 2 HCR where Atllantic menhaden have a negative slope and striped bass have a positive slope	–	–
17	MS	2-Dynamic multispecies	Testing dynamics of type 2 HCR where both species have negative slopes	–	–
18	MS	3-Dynamic multispecies	Atlantic menhaden *F* is at 0.2 when striped bass SSB is above the SSB threshold; striped bass operate under status quo CR	0 0.307	–
19	MS	3-Dynamic multispecies	Atlantic menhaden *F* is at 0.5 when striped bass SSB is above the 75 000 kgs; striped bass operate under status quo CR	0 0.307	–
20	MS	3-Dynamic multispecies	Atllantic menhaden *F* is changed by striped bass SSB; striped bass operate under a biomass-based HCR where the lower threshold is 10% of SSB0 and the upper is at 40% SSB0; reference points for striped bass HCR are generated based on unfished SSB rather than the 1995 reference point used in the stock assessment	0.1 0.307	–

Notes: There were three types of HCRs tested where the number in the column 'Type' represents either Type 1, Type 2, or Type 3 HCRs with a more specific description following. The last 2 columns show the bounding fishing mortality (*F*) for striped bass (SB) or Atlantic menhaden (AM). The top number in each row is the lower *F* bound for the HCR and the second number indicates the upper bound for the HCR. Dynamic multispecies HCRs (DMSHCRs) did not have *F* limits

Fig. 1. Type 1 single-species harvest control rules (HCR) evaluated for striped bass (black) and Atlantic menhaden (grey). Headers indicate the control rule number described in Table 4. Spawning stock biomass (SSB) relative to its target. When SSB of the previous year is at or below the lower SSB threshold (SSB_l), F is at the designated lower F (F_l). When SSB of the previous year is at or above the upper SSB threshold (SSB_u), F is a designated upper F (F_u). In between the SSB references, Type 1 HCRs follow an increasing linear slope using the equation.



at the mean F of striped bass or Atlantic menhaden during 1998–2017 (F of 0.258 yr^{-1} for striped bass and 0.18 yr^{-1} for Atlantic menhaden). This time frame was used to describe recent average fishing pressure of striped bass and Atlantic menhaden.

HCRs 4–6 represented the low, intermediate, and high information tier scenarios of recommended forage fish HCRs from Pikitch et al. (2012). All three scenarios used a Type 1 biomass-based HCR with varying proportions of SSB_0 of Atlantic menhaden as their upper and lower SSB thresholds. HCR 4 and 5 were threshold-based cessation HCRs for Atlantic menhaden. HCR 4 operated at a threshold such that Atlantic menhaden F was 0 yr^{-1} if Atlantic menhaden SSB was less than 0.8 SSB_0. Above this threshold, F was at Atlantic menhaden status quo. In HCR 5, F was 0.5 of F_{MSY} when SSB was above 40% of SSB_0, and F was 0 yr^{-1} if SSB was less than 40% SSB_0. HCR 6 followed a hockey-stick shape in which the lower SSB threshold was 25% of Atlantic menhaden SSB_0 and the upper threshold was at 85% of SSB_0. The lower F for this HCR was 0 yr^{-1} and the upper F was 75% of Atlantic menhaden F_{MSY}. In all three of these HCRs, striped bass operated under a constant F Type 1 HCR with the striped bass target F of 0.204 yr^{-1}. HCR 7, similar to HCRs 4–6, attempted to mimic suggestions for forage fish retention for their predators proposed by Cury et al. (2011) to sustain one-third of Atlantic menhaden unfished biomass to provide for predators (“1/3 for the birds” rule).

HCR 8 tested a constant F HCR on striped bass and a biomass-based HCR for Atlantic menhaden. This HCR was intended to manage striped bass using the current ASMFC target F, but use a higher target F for Atlantic menhaden than the current reference point. HCRs 10 and 11 were used to test dynamics of two biomass-based HCRs. HCR 11 focused on the traditional 40–10 rule (Pacific Fishery Management Council

Fig. 2. Type 2 harvest control rule shapes for striped bass (black) and Atlantic menhaden (grey). Striped bass fishing mortality (*F*) is determined by Atlantic menhaden spawning stock biomass (SSB) relative to its target, and Atlantic menhaden fishing mortality is determined by striped bass relative SSB. Headers indicate the control rule number described in Table 4.

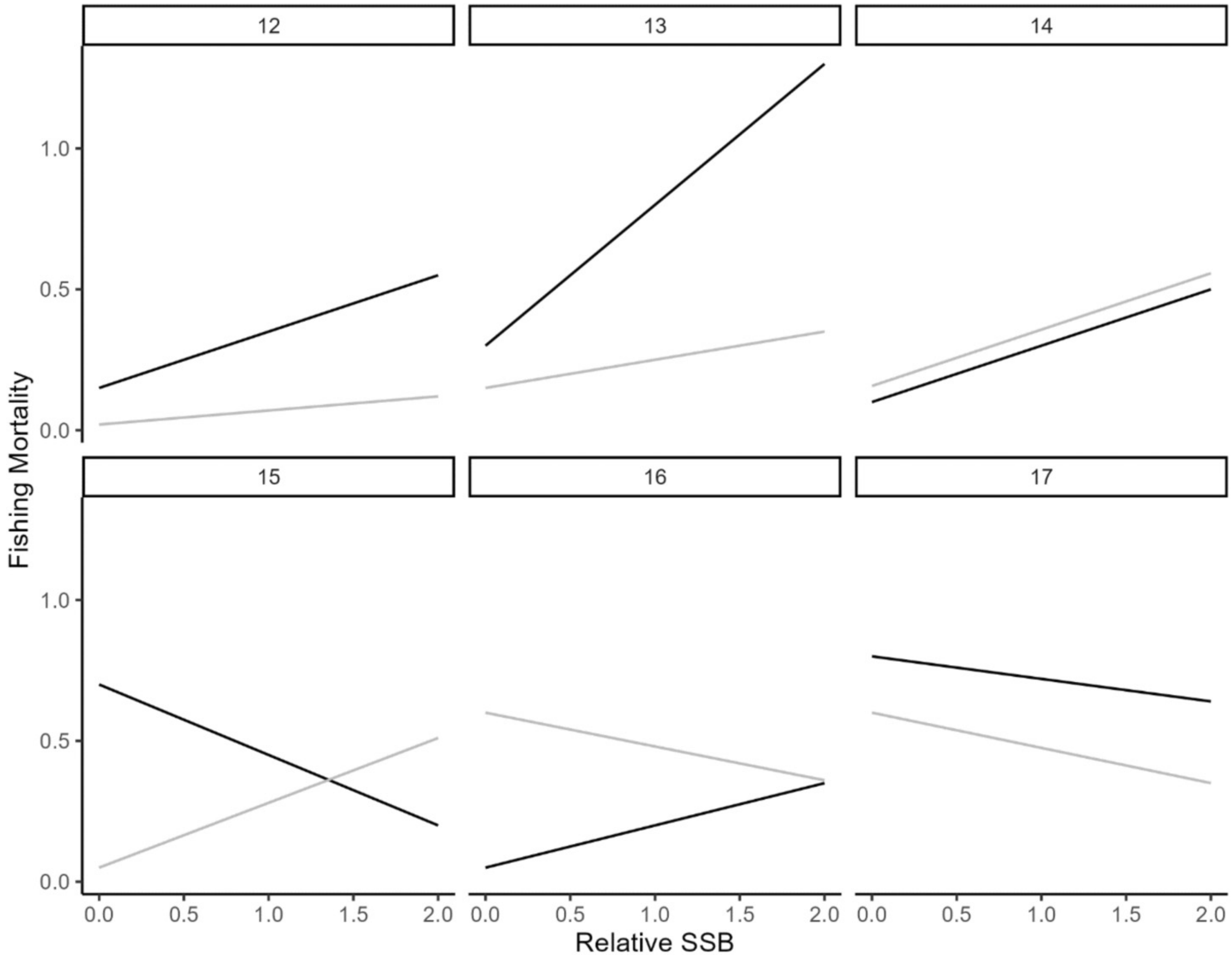


Fig. 3. Multispecies Type 3 harvest control rule (HCR) shapes for striped bass (black) and Atlantic menhaden (grey). Headers indicate the control rule number described in Table 4. Striped bass in a Type 3 HCR operate under a constant fishing mortality HCR (Type 1 single species), while Atlantic menhaden follow a cessation-based HCR when striped bass spawning stock biomass (SSB) relative to its target declines below a specified threshold.

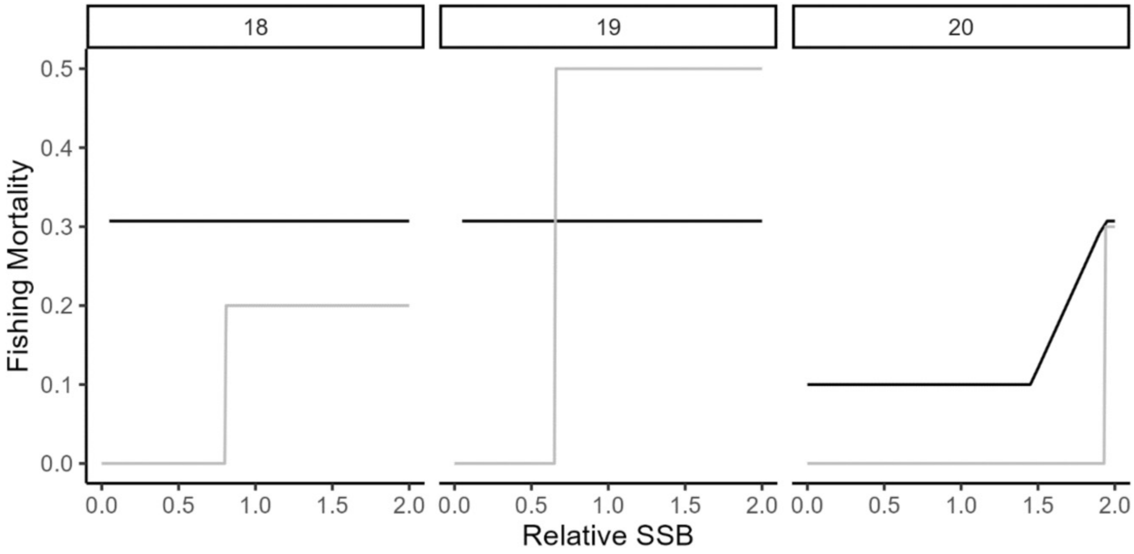


Table 5. Atlantic States Marine Fisheries Commission (ASMFC) ecosystem management objectives used to evaluate harvest control rule performance for both the striped bass and Atlantic menhaden stocks.

ASMFC objectives	ASMFC performance measures	Performance metrics
Manage striped bass using a control rule that manages stock size equal to or greater than target female SSB	Frequency of substantive management action	Average spawning stock biomass is at or above the target SSB set by ASMFC
Provide stability for striped bass fisheries	Variability in yield	% change of catch interannually
Ensure adequate supply of Atlantic menhaden for predators like striped bass	Predators in adequate nutritional state	Average striped bass weight-at-age and natural mortality-at-age
Minimize risk for striped bass stock and fishery collapse		Average and variance of striped bass SSB
Maintain age structure of striped bass stocks to conserve spawning stock biomass		Average and variance of striped bass abundance-at-age
		Average % of years striped bass SSB is above target
Establish an F_{TARGET} that will increase the abundance of age-15+ striped bass in the population		Average abundance of age-15 and older striped bass is above status quo abundance

Note: Performance metrics were designed to aligned with the objectives and quantitatively measure relative performance of each HCR. SSB indicates spawning stock biomass.

2012) where F is 0 yr^{-1} when a stock is below 10% of SSB_0, F is the stock-specific target when a stock is above 40% of SSB_0, and between the two thresholds F increased linearly between 0 yr^{-1} and the target F.

A smaller number of Type 2 and Type 3 HCRs was tested. HCRs 12–17 were developed to test a suite of Type 2 HCRs. Three of the six Type 2 HCRs had positive slopes of F in relation to SSB for both species, two had one positive and one negative slope, and one HCR had two negative slopes. HCR 18 was developed to maintain striped bass at status quo F while ceasing Atlantic menhaden fishing when striped bass SSB was below its threshold. In HCR 19, Atlantic menhaden fishing ceased when striped bass SSB was lower than the threshold. HCR 20 had striped bass operating under a biomass-based HCR, while Atlantic menhaden were fished at almost double status quo rate (0.3 yr^{-1}) if striped bass SSB was twice the SSB_{TARGET}; otherwise fishing on Atlantic menhaden was 0 yr^{-1}.

Performance metrics

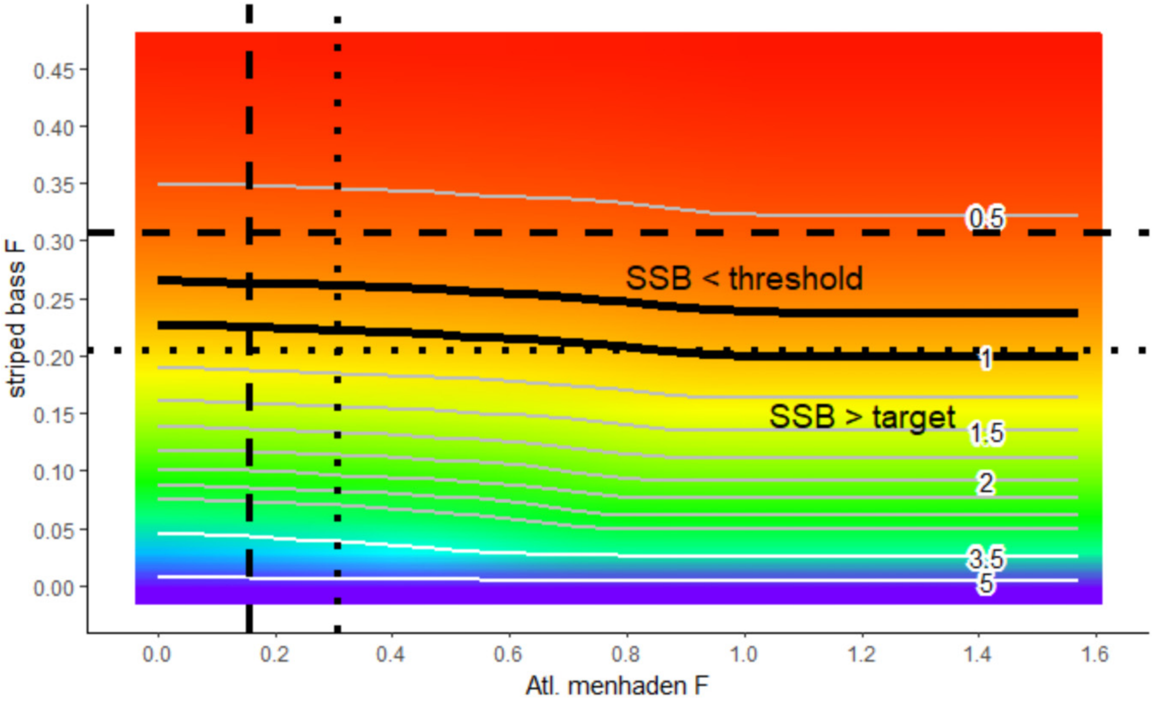
Performance metrics were used to evaluate the ability of the suite of HCRs to achieve the ASMFC's ecosystem management objectives (Table 5) for the striped bass stock and fishery. Four objectives for the striped bass stock were addressed by six performance metrics relating to SSB, catch, or abundance. Metrics were summarized using results from the last 10 years of each simulation to reflect long-term performance of each HCR. Biomass for both striped bass and Atlantic menhaden were calculated as a product of the abundance-at-age and weight-at-age summed over ages in the first season (eq. T. 2.20). Annual SSB for Atlantic menhaden was calculated as the product of abundance-at-age, seasonal weight-at-age, and the maturity-at-age vector from the assessment summed over ages in the first season (eq. T. 2.21). Striped bass SSB was calculated in a similar manner except abundance-at-age multiplied by the proportion female-at-age to calculate female SSB to reflect the management quantity used in striped bass reference points (eq. T. 2.22). Striped bass and Atlantic menhaden catch in weight and numbers were calculated following the Baranov catch equation (eqs. T. 2.23 and T.2.24; Quinn and Deriso 1999). Catch, either in weight or numbers, was then used to calculate the average annual variation (AAV) of catch by calculating the mean of the absolute value of the difference in catch between years (eq. T. 2.25). Higher SSB or catch and lower AAV of catch were considered better performing.

Changes over time in average weight-at-age and natural mortality-at-age from starting conditions were compared to examine the impact of predator–prey dynamics on condition of striped bass and mortality of both species. For brevity, we present results for striped bass age-3, representing the age at which Atlantic menhaden begin to comprise a significant portion of striped bass diets, and age-15, the maximum age in the stock assessment. We also present results for Atlantic menhaden age-1 and age-4, which were selected to represent two age classes that were likely to experience relatively high and low M_2 due to striped bass consumption.

Alternative scenarios

Two main uncertainties for striped bass and Atlantic menhaden are the fraction of Atlantic menhaden in the diet of striped bass and the prey size preference of striped bass. In the base simulation model configuration, the fraction of Atlantic menhaden in the striped bass diet in the first season was 4% for age-1, 15.7% for age-2 through age-5, and 30.4% for ages 6+, and the operating model assumed a symmetric prey size preference function. This meant that older aged striped bass consumed a greater proportion of Atlantic menhaden than younger aged striped bass. Previous studies have estimated that the percentage of Atlantic menhaden in striped bass diets may be as low as 10% and as high as 72% (Hartman and Brandt 1995; Overton et al. 2009). Each of these studies were conducted under relatively short time frames and in relatively small locations within the Atlantic Ocean and the

Fig. 4. Effect of Atlantic menhaden and striped bass fishing mortality rates (*F*) on relative striped bass spawning stock biomass (SSB). A total of 21 Atlantic menhaden Fs were tested, ranging from 0 to 1.49 yr^{-1}, and 16 striped bass Fs were tested, ranging from 0 to 0.47 yr^{-1} following Chagaris et al. (2020). Colors within the plot indicate striped bass SSB relative to the striped bass target SSB. Light grey lines and associated numbers indicate levels of striped bass-relative SSB. Long dashed lines indicate the current status quo F for Atlantic menhaden (vertical) and striped bass (horizontal). Dotted lines indicate the target *F* for Atlantic menhaden (vertical) and striped bass (horizontal).



Chesapeake Bay (Austin and Walter 2001; Griffin and Margraf 2003; Walter et al. 2003; Overton et al. 2008). Additionally, Overton et al. (2009) estimated that large striped bass consumed both more smaller sized prey and a wider range of prey sizes than assumed in the base predator–prey simulation model.

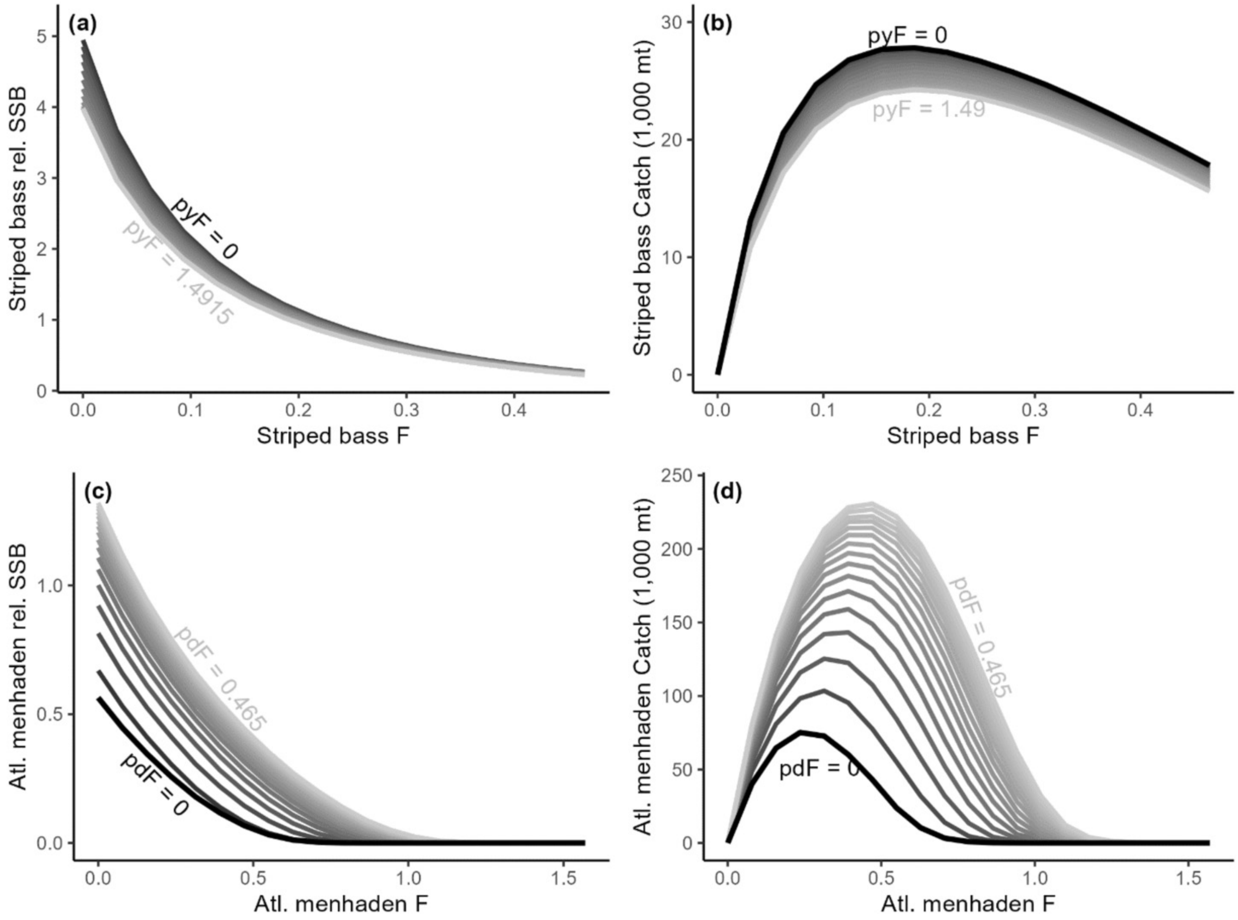
To determine whether these uncertainties affected the relative performance of the HCRs, we developed two alternative operating models that differed from the base predator–prey simulation model (hereafter referred to as NC30) in the consumption dynamics between striped bass and Atlantic menhaden. NC30 assumed that Atlantic menhaden made up 30% of the diet of age-6+ striped bass by weight in the first season (Walter and Austin 2003). The first alternative operating model assumed that striped bass are more reliant on Atlantic menhaden than NC30. Specifically, the alternative operating model (NC70) included modified consumption model parameters that resulted in Atlantic menhaden comprising approximately 70% of striped bass diet by weight in the first season (Hartman and Brandt 1995; Griffin and Margraf 2003), which represents some of the highest published estimates from striped bass diet studies. In NC70, alternative prey abundance is much lower than in NC30 so that Atlantic menhaden comprise up to 70% of striped bass diet. In NC70, consumption of Atlantic menhaden was initially 24% of age-1, 59.2% of age-2, and 71.1% of the age-3 and older striped bass diet. The second alternative scenario (LNC30) used an asymmetric prey size preference function (eq. T. 2.26), namely an unscaled lognormal distribution. The parameters of this prey size preference function were set to match the observed prey sizes of striped bass from Overton et al. (2009). In LNC30, alternative prey abundance was specified such that Atlantic menhaden comprised about 30% of the diet of ages 6 and older striped bass, similarly to NC30.

Results

Predator–prey model

Our model results indicated that the main driver of striped bass SSB was striped bass *F*. Current striped bass SSB was approximately equal to the levels found when fishing at the status quo *F* (HCR 1), but our model indicated that the stock could reach more than quadruple its current SSB in an unfished condition (Fig. 4). In the unfished conditions for both striped bass and Atlantic menhaden, striped bass SSB was 665% higher than status quo SSB and 360% higher than the striped bass SSB target for the NC30 scenario. SSB_0 was estimated to be 553 000 metric tons (mt) for striped bass and 596 000 mt for Atlantic menhaden. Striped bass SSB declined with increasing striped bass *F* (Fig. 5*a*). When fished at the status quo constant F of 0.307 yr^{-1}, striped bass median SSB was below their threshold in all scenarios. There was little effect of a constant F HCR for Atlantic menhaden on striped bass

Fig. 5. Relationship between fishing mortality (*F*) and relative spawning stock biomass (SSB) for striped bass (*a*) and Atlantic menhaden (*b*), and relationship between *F* and striped bass catch (*c*) and Atlantic menhaden catch (*d*) across the range of fishing mortality rates described in Fig. 4. Relative SSB is SSB divided by the stock-specific target. Each line indicates how the relationship changes based on the *F* for the other species (pyF = *F* on Atlantic menhaden and pdF = *F* on striped bass).



SSB (Fig. 5*a*). Fishing at a constant F at or below the striped bass target *F* of 0.204 yr^{-1} resulted in median SSB at or above the target under all Atlantic menhaden constant F HCRs. Increasing Atlantic menhaden *F* resulted in a small decline in striped bass SSB, but the indirect effect of Atlantic menhaden was less than the direct effect of fishing. SSB$_{\mathrm{MSY}}$ for striped bass was estimated to be 139 000 mt when Atlantic menhaden was unfished.

In contrast, Atlantic menhaden SSB was strongly affected by striped bass across the wide range of striped bass *F*s explored (Fig. 5*c*). Atlantic menhaden SSB was at its highest (increase of 20%) when Atlantic menhaden *F* was 0 yr^{-1} and striped bass were heavily fished. Unfished conditions for both species did not result in the highest Atlantic menhaden SSB due to predation pressure from striped bass. Under status quo *F*, Atlantic menhaden was only able to achieve target SSB when striped bass *F* was greater than about 0.35 yr^{-1}. In unfished conditions for striped bass, Atlantic menhaden SSB$_{\mathrm{MSY}}$ was projected to be 257 000 mt, substantially lower than the current SSB target.

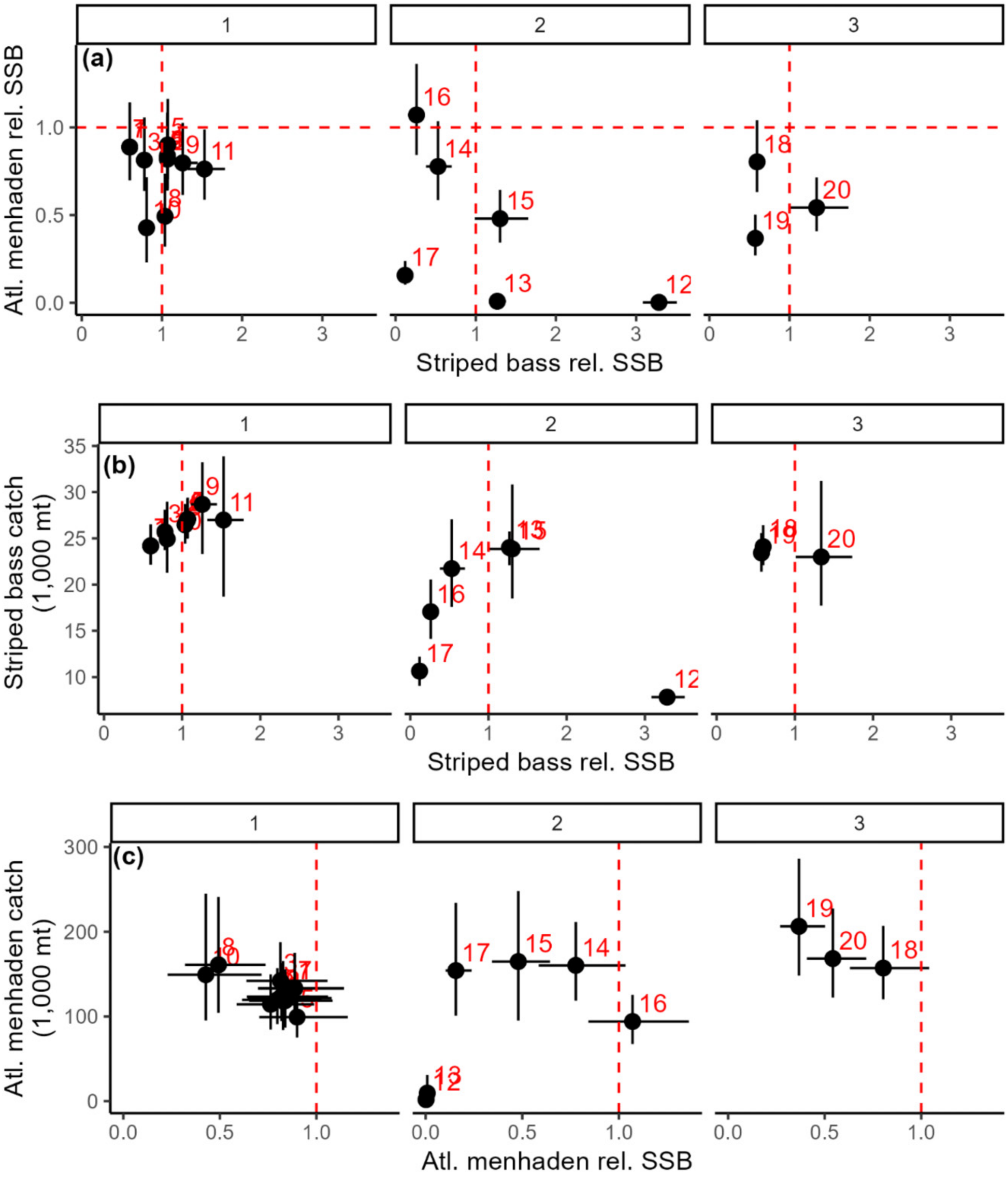
Median striped bass catch varied by less than 20% across Atlantic menhaden *F*s (Fig. 5*b*). F_{MSY} for striped bass when *F* was 0 yr^{-1} for Atlantic menhaden was 0.186 yr^{-1}. Under status quo *F* (0.307 yr^{-1}), median striped bass catch was lower than at the target *F* (0.204 yr^{-1}) and at F_{MSY}. Atlantic menhaden median catch also showed a dome-shaped response to fishing mortality in which median catch eventually reached 0 at *F*s above approximately 1.0 yr^{-1} (Fig. 5*d*). F_{MSY} for Atlantic menhaden when striped bass *F* was 0 yr^{-1} was 0.236 yr^{-1}. Additionally, the median Atlantic menhaden catch varied in response to indirect effects of the striped bass *F* by as much as 430%.

All three consumption scenarios, NC30 (Figs. S1–S8), NC70 (Figs. S9–S23), and LNC30 (S24–S39), produced similar results. The main difference among scenarios was that NC70 and LNC30 had wider ranges of median catch and SSB for striped bass than NC30 under the range of Atlantic menhaden *F*s evaluated. Therefore, this result section focuses on the NC30 scenario, and results for the other two scenarios can be found in Supplement 2.

Harvest control rules

None of the HCRs we explored resulted in median SSB above the targets for both striped bass and Atlantic men-

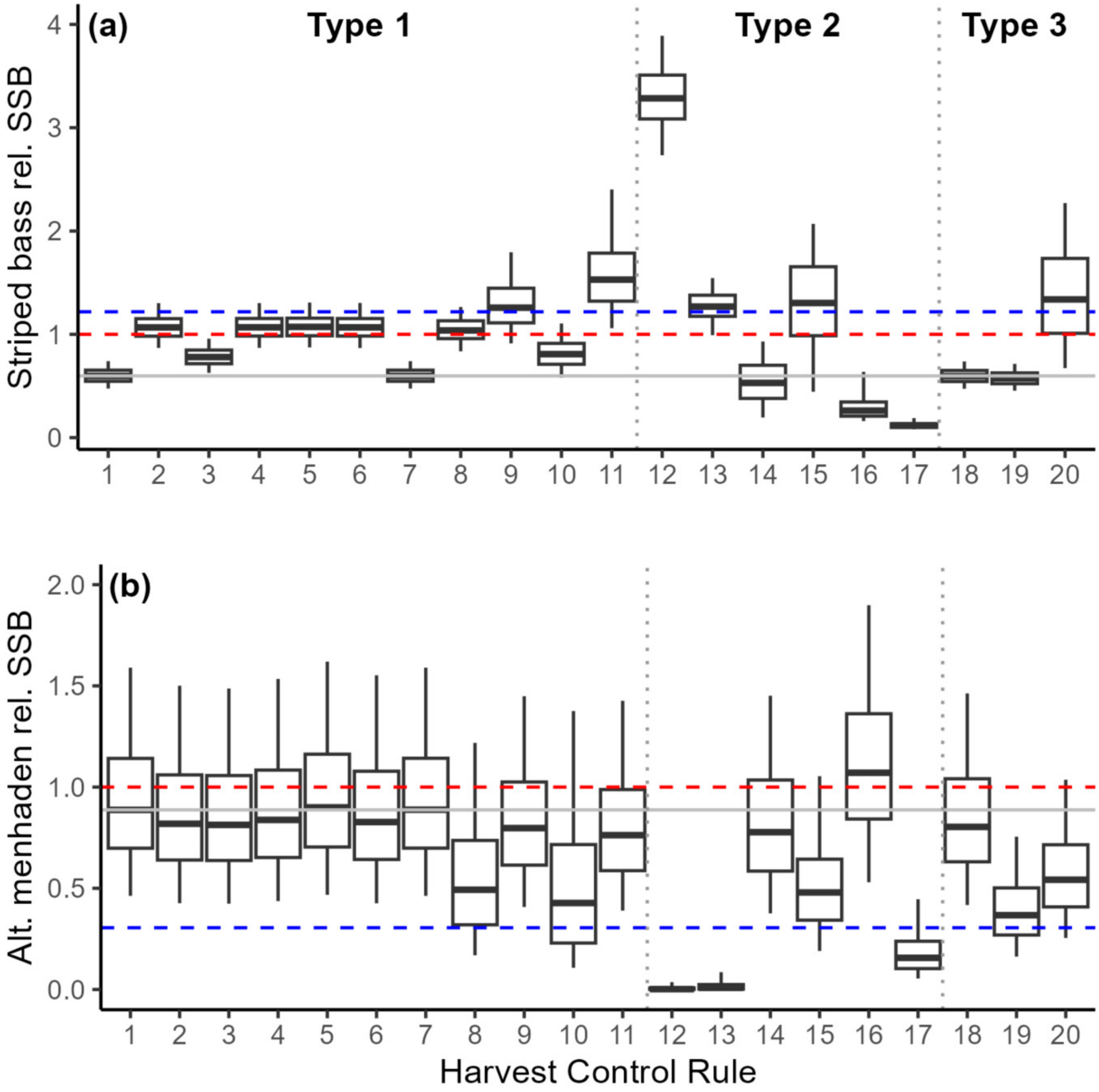
Fig. 6. Trade-offs between (*a*) striped bass and Atlantic menhaden spawning stock biomass relative to its target (striped bass relative SSB; Atlantic menhaden SSB), striped bass relative SSB and catch in metric tons (*b*) and Atlantic menhaden relative SSB and catch in metric tons (*c*) for 20 harvest control rules (HCR; numbers defined in Table 4). Red dashed lines indicate the relative SSB targets for each species. Points indicate the median SSB and lines show the interquartile range for striped bass (horizontal) and Atlantic menhaden (vertical). HCR types are designated by shapes of the point for Type 1 (circle), Type 2, (triangle), and Type 3 (square).



haden simultaneously (Fig. 6*a*). HCRs that resulted in a high median SSB for Atlantic menhaden often resulted in a low median SSB for striped bass, particularly for Types 2 and 3 (Fig. 7). Similarly, no single HCR resulted in high catches for both striped bass and Atlantic menhaden (Figs. 6*b*–6*c* and 8). In general, most Type 1 single-species HCRs resulted in median striped bass catch above status quo (Fig. 8*a*) and relatively low AAV of catch (Fig. 9*a*). In contrast, most of the highest Atlantic menhaden catches were achieved with Types 2 and 3 HCRs (Figs. 8*b*) at the expense of higher AAV of Atlantic menhaden catch (for Type 2 HCRs) and relatively low predator SSB (Fig. 9*b*).

Although no single HCR achieved both predator and prey SSB targets, some HCRs achieved multiple ecosystem management objectives for both species. Two Type 1 single-species HCRs that involved biomass-based management of the preda-

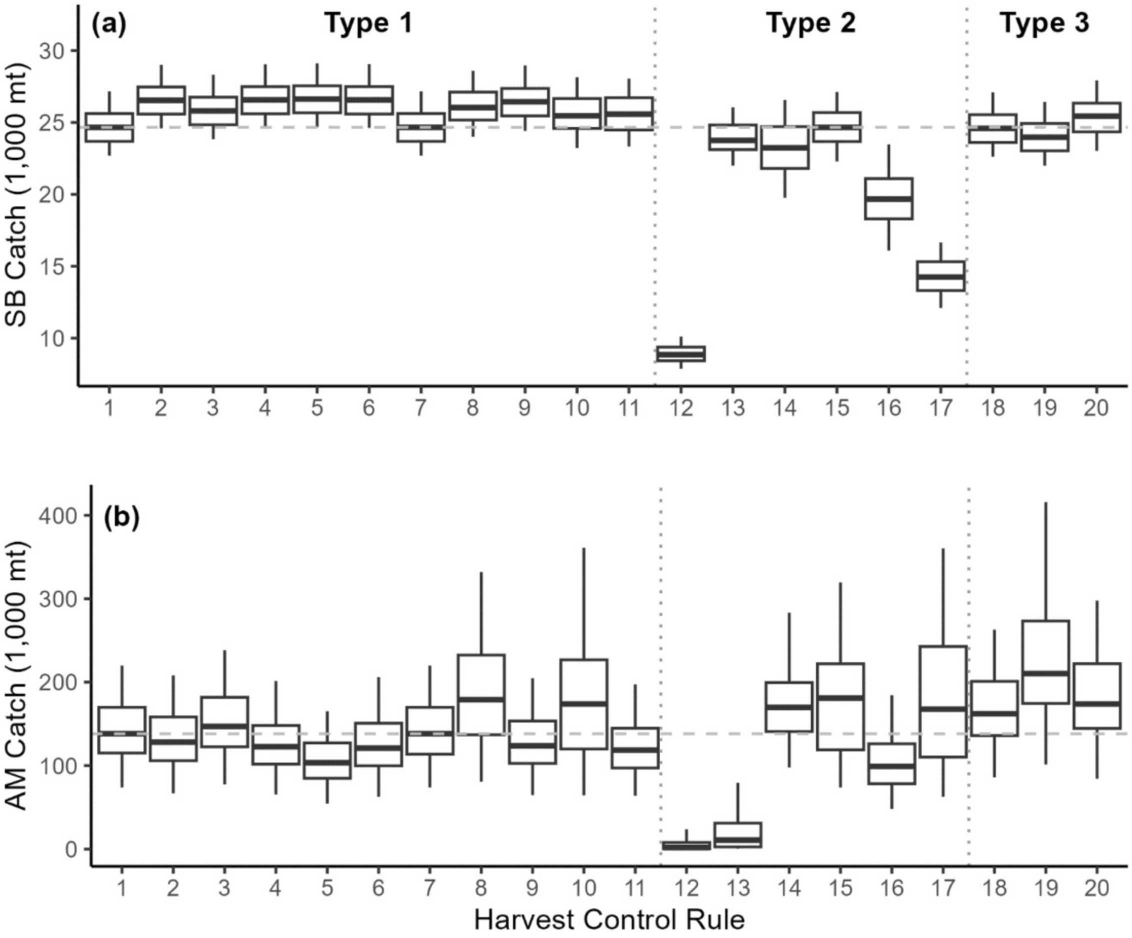
Fig. 7. Box plots of spawning stock biomass (SSB) for striped bass (*a*) and Atlantic menhaden (*b*) relative to their targets. Harvest control rules are defined in Table 4. The red dashed line indicates the target SSB, the solid grey line indicates SSB at status quo, and the blue dashed line indicates SSB for maximum sustainable yield. The vertical dashed lines separate the control rules into categories by type, where HCRs 1–11 are Type 1, 12–17 are Type 2, and 18–20 are Type 3 HCRs. The solid lines indicate the medians, the boxes represent the 25th and 75th percentiles, and the whiskers indicate the 5th and 95th percentiles.



tor (9 and 11) resulted in median SSBs above the target for striped bass while maintaining Atlantic menhaden SSB just below status quo (Fig. 7). One Type 3 DMSHCRs (20) resulted in striped bass SSB above the target with relatively high median catches of both species at the expense of median Atlantic menhaden SSB lower than the target. Also, four Type 1 single-species HCRs (4, 5, 9, and 11) resulted in median striped bass SSBs above the target while maintaining both striped bass and Atlantic menhaden *F* below their targets (Fig. 7, Figs. S1 and S2).

The main driver of striped bass SSB in our study was striped bass F (Fig. 5*a* and Fig. S1). Thus, relative performance of HCR Types based on median SSB varied based primarily on the resulting striped bass *F*, with some HCRs reaching or exceeding $\mathrm{SSB}_{\mathrm{MSY}}$, and others reaching or exceeding the $\mathrm{SSB}_{\mathrm{TARGET}}$ (Figs. 6*a* and 7*a*). For Atlantic menhaden, only one Type 2 DMSHCR (16) achieved Atlantic menhaden median SSBs at or above their target, but this HCR also resulted in striped bass below its target and status quo SSB (Fig. 7). In contrast, two Type 2 DMSHCRs (12 and 13) resulted in the lowest median SSBs for Atlantic menhaden. Most HCRs achieved median SSB of 40%–90% of the target (Fig. 7*b*). Type 1 single-species HCRs 4–6 that were designed to represent the Lenfest Ocean Program's recommendations for managing forage fish for the benefit of predators (Pikitch et al. 2012) were able to achieve all ASMFC objectives for striped bass but resulted in Atlantic menhaden SSB below the target by 8%–15%. The "third for the birds" approach also proposed for ecosystem-based forage fish man-

Fig. 8. Box plots of average catches in biomass in the last 10 years of the simulation for striped bass (SB; *a*) and Atlantic menhaden (AM; *b*) Harvest control rules (HCRs; defined in Table 4). The horizontal dashed grey line indicates catch at status quo. The vertical dashed lines separate the control rules into categories by type, where HCRs 1–11 are Type 1, 12–17 are Type 2, and 18–20 are Type 3 HCRs. The solid lines indicate the medians, the boxes represent the 25th and 75th percentiles, and the whiskers indicate the 5th and 95th percentiles.



agement (HCR 7), resulted in status quo Atlantic menhaden and striped bass SSB (Fig. 7).

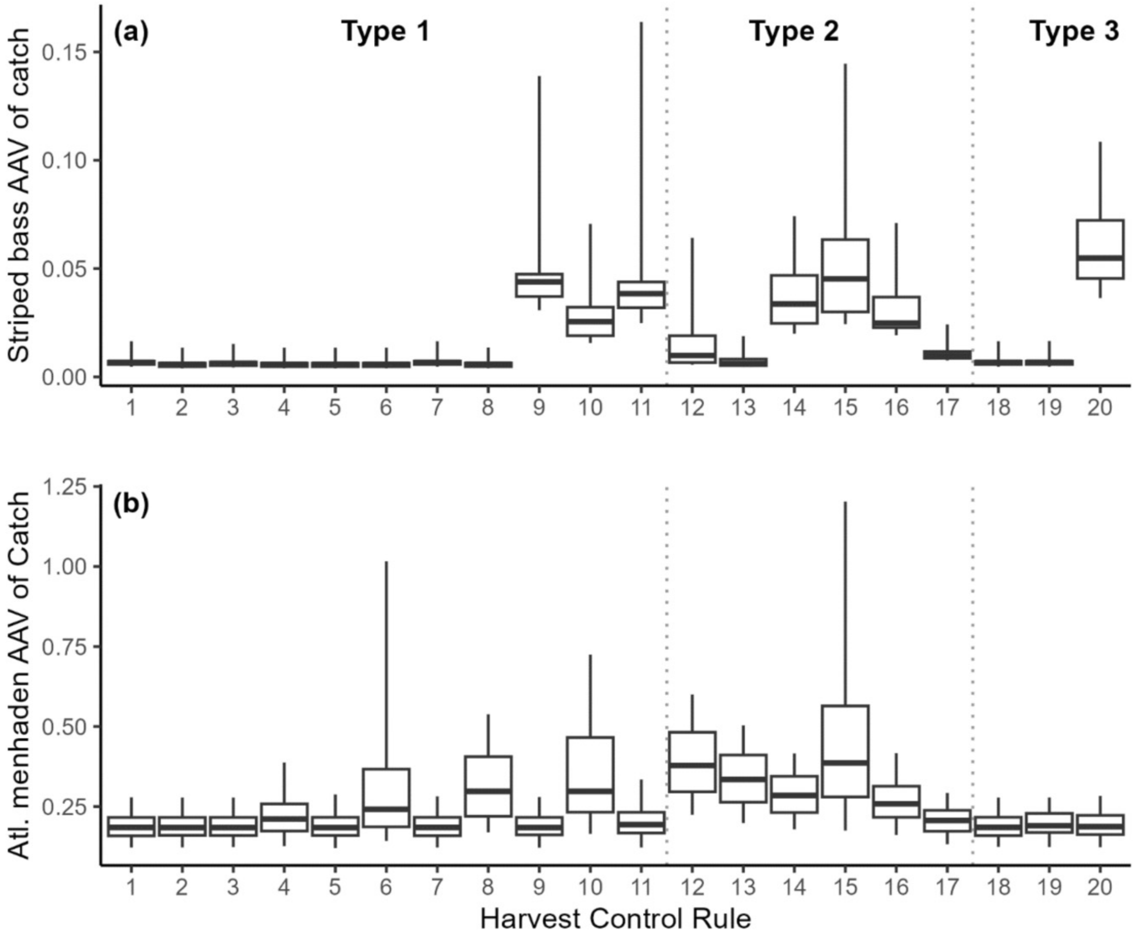
DMSHCRs HCRs resulted in the widest range of median SSB for striped bass; in particular, Type 2 HCRs 12 and 13 resulted in some of the highest striped bass SSB, but Atlantic menhaden SSB declined to near zero. Type 2 HCRs were also among those with the highest variation in catch. The most successful Type 2 HCRs typically had low absolute values of the slope parameters, with either positive slopes for both species or one positive and one negative slope in the HCR pair, which are close to constant F HCRs. Type 3 HCRs explored in this study performed moderately well for Atlantic menhaden in that SSB for HCRs 18–20 was also below the $\mathrm{SSB}_{\mathrm{TARGET}}$, but above $\mathrm{SSB}_{\mathrm{MSY}}$, it had catches above status quo, and had AAVs similar to that of single-species HCRs.

Consumption of Atlantic menhaden (Fig. 10), striped bass weight (Figs. 11*b* and 1*d*), and M (Figs. 11*a* and 1*c* and 12) differed among HCRs. Under most Type 1 HCRs, age-3 striped bass consumption of Atlantic menhaden was similar to HCR 1 (status quo), but most Type 2 and 3 DMSHCRs resulted in lower consumption (Fig. 10), usually due to lower Atlantic menhaden SSB (Fig. 7). Age-15 striped bass displayed similar relative patterns of consumption across HCRs to that of age-3 striped bass. Given striped bass weight-at-age was a function of consumption, striped bass also displayed low variability in median weight-at-age among HCRs with the exception of HCRs 12 and 13 (Fig. 11*b*). In contrast, median striped bass M-at-age varied across HCRs with Type 1 single-species HCRs displaying the lowest change in *M*; however, Type 2, Type 3, and biomass-based Type 1 HCRs resulted in larger % changes in M-at-age. Median Atlantic menhaden M at age-1 also varied among HCRs (Fig. 12). Similar to striped bass, the highest and lowest % change in M-at-age resulted from Type 2 HCRs.

HCR performance across operating models

We evaluated the robustness of each HCR to consumption model assumptions by comparing their performance among three alternative operating model scenarios: NC30, NC70, and LNC30 (Supplement 2). Most HCRs demonstrated similar

Fig. 9. Box plots of average annual variation (AAV) in striped bass catch in numbers (*a*) and Atlantic menhaden catch in biomass (*b*). Harvest control rules are defined in Table 4. The vertical dashed lines separate the control rules into categories by type, HCRs 1–11 are Type 1, 12–17 are Type 2, and 18–20 are Type 3 HCRs. The solid lines indicate the medians, the boxes represent the 25th and 75th percentiles, and the whiskers indicate the 5th and 95th percentiles.



relative performance across scenarios and were thus robust to assumptions about striped bass diet. The best-performing HCRs for striped bass across operating models were those that incorporated the "40–10 rule" (HCRs 11 and 20). In these two HCRs, striped bass SSB was maintained above its target and Atlantic menhaden SSB was maintained below the target, but above the estimated SSB_{MSY}. Also, Atlantic menhaden median SSB was lower for LNC30 across all HCRs compared, and more HCRs in LNC30 performed worse compared to targets for each species than in the other two scenarios.

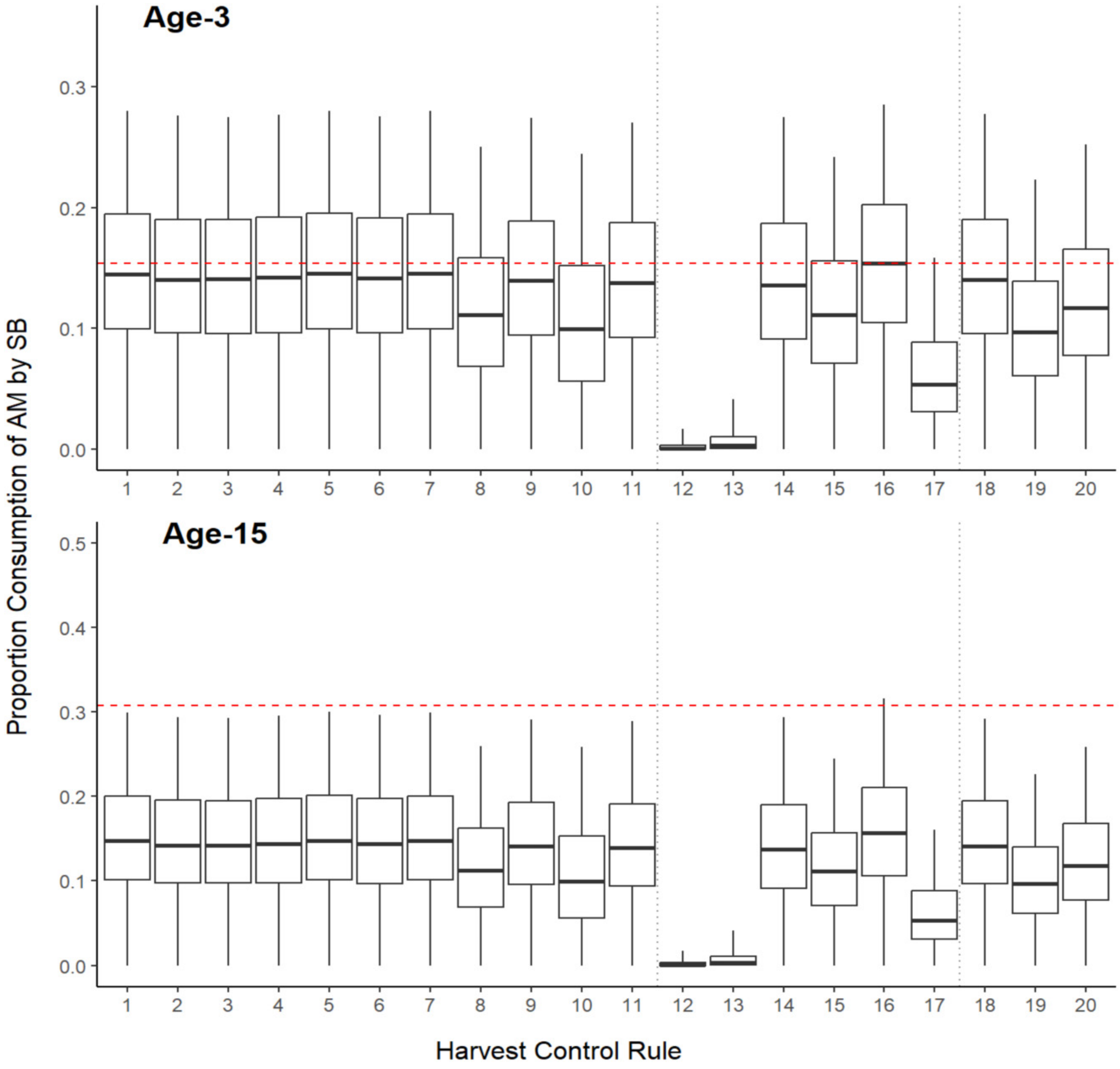
Not surprisingly, the largest differences among operating models in HCR performance were for metrics associated with striped bass consumption such as maximum proportion consumption of Atlantic menhaden, striped bass weight-at-age, and M for both species. In particular, a 71% proportion of Atlantic menhaden in the striped bass diet was difficult to achieve at all ages. For LNC30, the proportion consumption of Atlantic menhaden was consistent with model expectations except at younger ages where proportion consumption was on average 30% rather than 15.7%. The variability and change in weight-at-age among HCRs in NC70 was wider than what was found in NC30 and LNC30 for striped bass older than age-9. Weight at ages 1–9 for striped bass was relatively consistent among HCRs and operating models.

Discussion

Predator–prey model

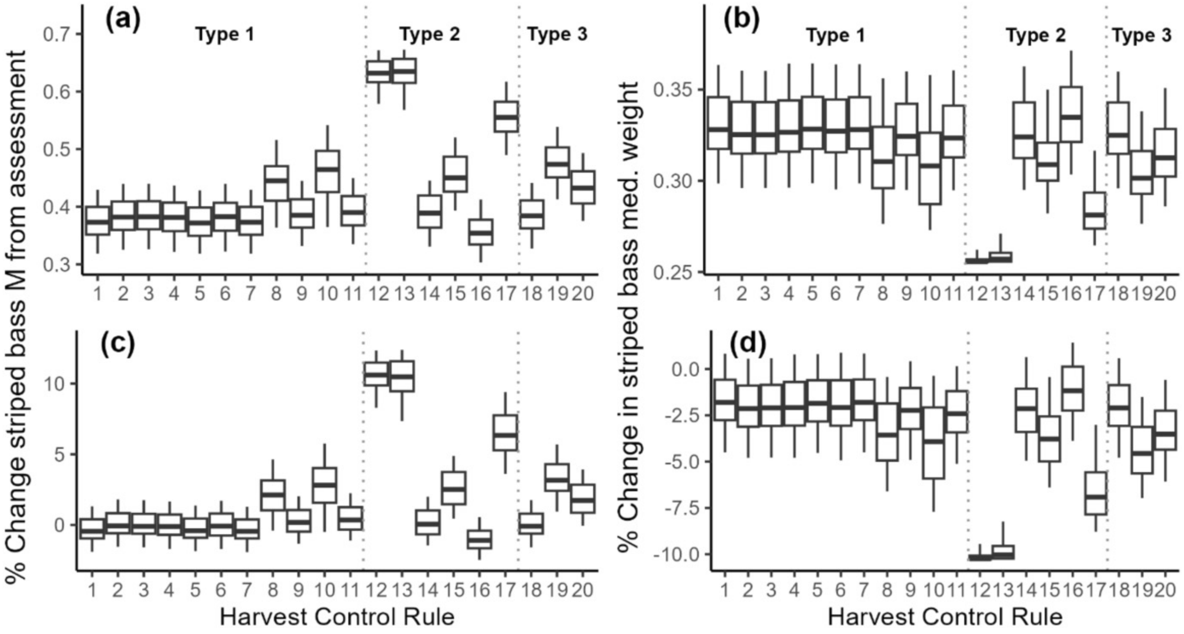
Our age-structured, linked, predator–prey model of striped bass and Atlantic menhaden dynamics allowed us to examine trade-offs among a suite of HCRs in their ability to attain EAFM objectives. The model captured the range of observed %Atlantic menhaden in striped bass diet reported in the literature (30%–70%; Hartman and Brandt 1995; Walter et al. 2003). Atlantic menhaden were sensitive to both directed fishing mortality and predation by striped bass when an HCR (11, 12, 15, and 20) resulted in high striped bass SSB, indicating that Atlantic menhaden were responsive to both fishing mortality and predation. However, striped bass were not as highly influenced by Atlantic menhaden, and the main driver affecting the striped bass stock was fishing. Atlantic menhaden had a bottom-up effect on striped bass weight- and M-at-age (Fig. 11), but not enough to strongly affect overall

Fig. 10. Box plots of the proportion consumption of Atlantic menhaden (AM) by age-3 (top) and age-15 (bottom) striped bass (SB) for 20 harvest control rules (HCRs; defined in Table 3). Atlantic menhaden at these ages comprise approximately 15.4% and 30.7%, respectively, of striped bass diets according to Chagaris et al. (2020) (red dashed line). The vertical dashed lines separate the control rules into categories by type, where HCRs 1–11 are Type 1, 12–17 are Type 2, and 18–20 are Type 3 HCRs. The solid lines indicate the medians, the boxes represent the 25th and 75th percentiles, and the whiskers indicate the 5th and 95th percentiles.



dynamics (Fig. 6), because striped bass are generalist predators and we employed a static other prey category, which ensured that a minimum amount of prey would be available for striped bass consumption (Fig. 4). Also, HCRs 1–20 were designed to achieve fishery objectives centered around status quo or target SSB, which is based on an ad hoc value of striped bass SSB from 1995 and is not reflective of the maximum potential of the stock. Thus, for HCRs 1–20, menhaden generally did not experience as intense predation pressure as they might if striped bass were allowed to increase above their target SSB. In contrast, simulations conducted across a wide range of constant F HCRs (Fig. 4, and Fig. 5, as in the 2020 Atlantic menhaden stock assessment) explored the potential effects of striped bass *F* rates lower than historically observed in the striped bass stock assessment. These simulations resulted in much higher top–down effects of striped bass on Atlantic menhaden (Fig. 5) than HCRs 1–20 (Figs. 6 and 12) because many of these constant F HCRs allowed striped bass SSB to increase up to five times the current target SSB. Our results are similar to ecosystem-based modeling approaches applied to this predator–prey system, which resulted in striped bass SSB increases of up to three times the current target SSB (Chagaris et al. 2020). Our simulations and that of Chagaris et al. (2020) both indicate that the data, model structure, and assumptions inherent in the current striped bass stock assessment imply the stock has much greater biological potential than recognized by the current ad hoc SSB target. If the striped bass stock increased three to five times its current biomass, our model results suggest that natural mortality rates of Atlantic menhaden by striped bass would increase

Fig. 11. Box plots of the % change of age-3 striped bass natural mortality (*a*) and weight (*b*) and age-15 natural mortality (*c*) and weight (*d*) from the stock assessment for 20 harvest control rules (HCRs; defined in Table 3). The vertical dashed lines separate the control rules into categories by type, where HCRs 1–11 are Type 1, 12–17 are Type 2, and 18–20 are Type 3 HCRs. The solid lines indicate the medians, the boxes represent the 25th and 75th percentiles, and the whiskers indicate the 5th and 95th percentiles.



considerably and cause a reduction of Atlantic menhaden biomass. This result is difficult to put into historical context because estimates of striped bass fishing mortality rates and biomass are not available prior to the early 1980s, a point at which the striped bass stock was severely depleted (NEFSC 2019).

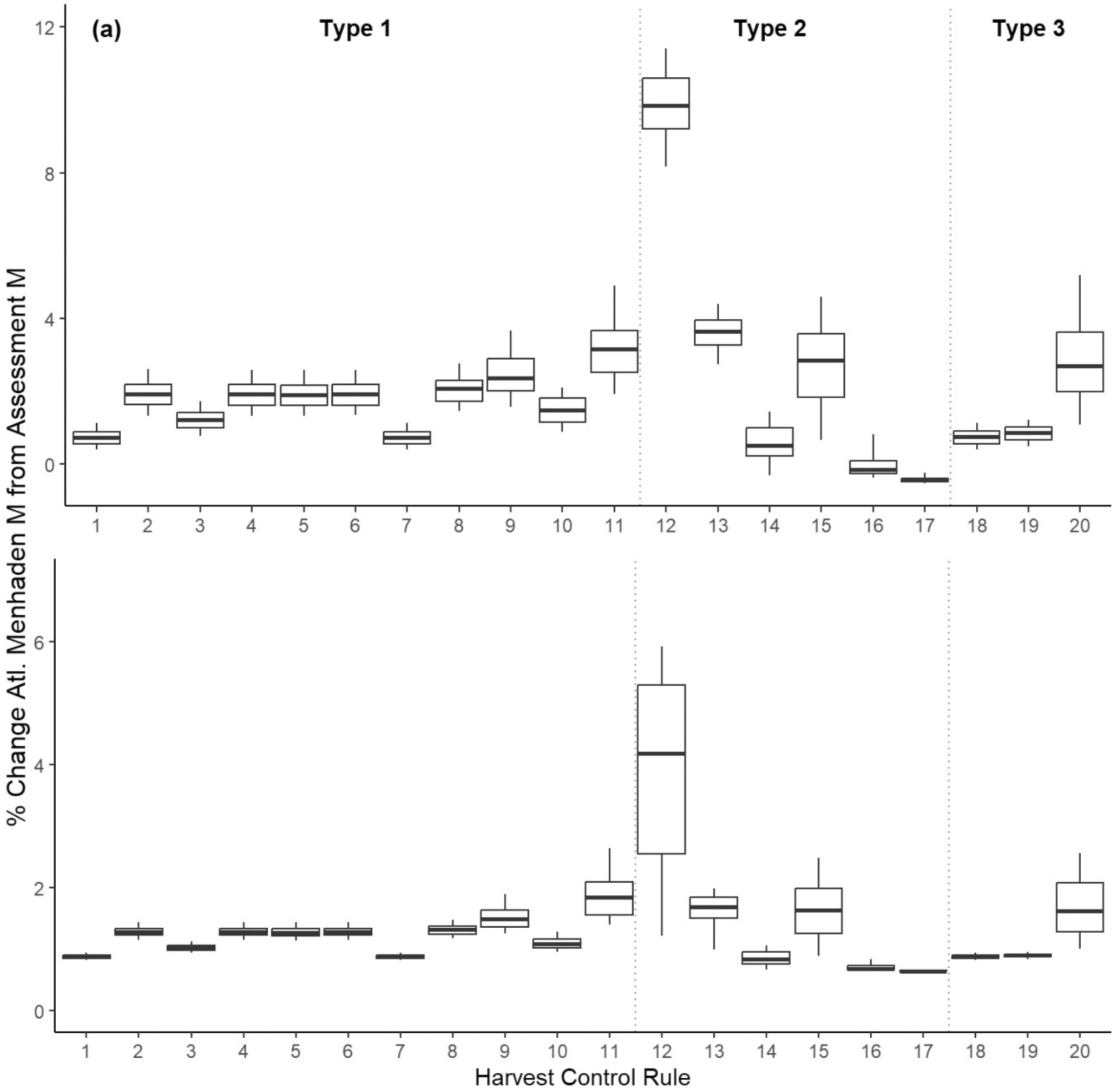
The results of our predator–prey model simulations also suggested that the current single-species target reference points used in the management of striped bass and Atlantic menhaden may not align with management objectives (Table 5). The striped bass inputs and reference points used in this study were based on the 2019 assessment, which estimated an F target of 0.204 yr^{-1}, while our simulations of striped bass dynamics were based on the 2019 assessment assuming an Atlantic menhaden $F = 0\ \text{yr}^{-1}$ across a range of striped bass Fs resulted in an estimate of striped bass $F_{\text{MSY}} = 0.186\ \text{yr}^{-1}$ (Fig. 5*b*). This implies that a lower target F would result in enhanced fishery benefits, e.g., higher yield and greater catch per trip. Also, our model suggested that the current Atlantic menhaden target SSB would be difficult to achieve because only one HCR (16) achieved median SSB above the target. Thus, our model indicates that the SSB reference point for Atlantic menhaden may not be attainable if ecosystem management objectives are achieved and striped bass SSB increases.

Harvest control rules

In our study, none of the HCRs we tested met all ecosystem management objectives for striped bass and Atlantic menhaden (Table 5). No single HCR performed well for both stocks, which follows similar conclusions from other studies investigating performance of HCRs for predator–prey systems that reported difficulties in achieving objectives for multiple species simultaneously (Kaplan et al. 2020; Pérez-Rodríguez et al. 2022). Our model indicated that it would be difficult to achieve the Atlantic menhaden SSB target due to the effects of top–down predation pressure by striped bass at or above their target SSB (Figs. 6*a* and 7). Balancing HCRs among multiple species in an ecosystem is challenging, and both scientists and managers should recognize that, in some situations, it may not be possible for both predator and prey stocks to be maintained at their targets (Pérez-Rodríguez et al. 2022).

Although there was no one HCR that stood out from the rest, several performed well across multiple metrics. Similar to Kaplan et al. (2020), we found biomass-based HCRs (referenced as “threshold HCRs” in their study) resulted in higher variability of catch compared with constant F HCRs, but generally outperformed constant F HCRs when applied to both predator and prey (Fig. 6*a*). Our single-species biomass-based HCR that involved the “40–10 rule” for striped bass (HCR 11) performed well for striped bass SSB and catch performance metrics without driving Atlantic menhaden to low SSB, indicating it may be a good candidate for further testing and potential use in EAFM. The performance of other Type 1 HCRs, specifically traditional single-species constant F HCRs such as are currently used in striped bass management, were more variable as has been shown in other studies of single-species HCR performance (Deroba and Bence 2008).

Fig. 12. Box plots of the %change of age-1 (a) and age-4 (b) Atlantic menhaden M from the stock assessment M. The vertical dashed lines separate the harvest control rules into categories by type, where HCRs 1–11 are Type 1, 12–17 are Type 2, and 18–20 are Type 3 HCRs. The solid lines indicate the medians, the boxes represent the 25th and 75th percentiles, and the whiskers indicate the 5th and 95th percentiles.



In this study, the DMSHCRs we explored were highly variable in their performance. Type 2 DMSHCRs, in which the *F* for one species depended on the SSB of the other, generally did not perform well and should be critically evaluated before being applied for use in management. For these DMSHCRs, the predator or prey SSB was used to determine *F* on the other species, making it difficult to balance the effects of fishing with the effects of predation. Type 3 HCRs performed similarly to single-species HCRs, which indicated little benefit of cessation of fishing on Atlantic menhaden to help recover striped bass. Although cessation-based HCRs have been explored in the literature, our Type 3 HCRs are novel. Kaplan et al. (2020) investigated the impacts of forage fish productivity on predator fish stocks by implementing threshold HCRs that increased or decreased predator *F* when prey productivity was high or low, which is different than our Type 3 HCRs that based prey *F* on predator SSB. Our Type 3 HCRs 18 and 19 were designed to conserve prey SSB to meet the needs of the predator, but did not perform well for striped bass because reducing fishing on Atlantic menhaden was not sufficient to allow striped bass to recover when striped bass *F* was above the *F* threshold.

Other studies have proposed HCRs for ecosystem-based management of forage fishes such as Atlantic menhaden, including Pikitch et al. (2012) and Cury et al. (2011). HCRs 4–6 were designed to implement the recommendations of Pikitch et al. (2012) such that prey F differed depending on the levels of information available about forage fish and their predators in an ecosystem. These HCRs performed reasonably well for Atlantic menhaden, but they did not result in improvements in performance for striped bass because the striped bass target *F* exceeded F_{MSY} in our operating models, highlighting the need for appropriate single-species reference points to support multispecies management efforts. The single-species HCR modeled after Cury et al. (2011) with the goal of conserving at least one-third of unfished biomass for avian predators (HCR 7) also did not result in increased striped bass SSB. A similar result was found in Hilborn et al. (2017) in which forage fish fishing had little effect on the forage fish's predator, particularly in the case of Atlantic menhaden and striped bass. Both the Pikitch et al. (2012) and Cury et al. (2011) approaches were developed for ecosystems in which predators only had one dominant prey species. Given striped bass are generalist predators (Hartman and Brandt 1995; Walter and Austin 2003; Overton et al. 2009), Atlantic menhaden-centric HCRs like the ones explored in this study may not be the most-efficient approach to meet ecosystem management objectives (Table 5).

Model comparisons

Consideration of multiple alternative models that differ in structure when developing EAFM approaches should lead to more robust fishery management decisions. Our study examined a wider range of HCRs than had been explored previously for the striped bass–Atlantic menhaden predator–prey system. Prior work focused solely on developing constant F, single-species HCRs (Chagaris et al. 2020; Drew et al. 2021), whereas we compared the relative performance of these types of HCRs with a suite of true multispecies HCRs, including both constant and dynamic *F* options (Table 4). Thus, direct comparison among HCR performance is relevant only for constant F HCRs (Fig. 4).

Our model differed in structure from that of other models developed for this system to date (Drew et al. 2021; SEDAR 2020*b*) in that it is an age-structured predator–prey model with stochastic recruitment that is capable of simulating both top–down and bottom–up effects. We focused on capturing the detailed structure of predator–prey interactions for two species of interest to the ASMFC. In contrast, the NWACS-MICE used currently to inform Atlantic menhaden management focuses on capturing the details of the broader ecosystem in which Atlantic menhaden and striped bass operate. Our approach is most similar to the multispecies statistical catch-at-age model developed during the 2020 Atlantic menhaden stock assessment (SEDAR 2020*b*), but that model was not put forward for management consideration because it lacked bottom–up effects of prey on predators. Our operating models differed in that it was not formally conditioned by fitting to historical data; rather, we used historical data and stock assessment estimates to simulate the potential impact of harvest policies. Thus, our operating models produced predator–prey dynamics that likely differ in some ways from the NWACS-MICE Ecopath with Ecosym and statistically fitted models of the same system (Drew et al. 2021). Differences in outcomes among models of the same system allow us to begin to explore the potential impacts of model assumptions and a more holistic evaluation of model structure uncertainty for robust fishery management advice.

There are several similarities between our model and that of the NWACS-MICE approach used to generate ecosystem-based reference points for Atlantic menhaden (Chagaris et al. 2020). Our models are similar in that both approaches rely on accurate time series estimates of stock size (biomass) and catch by age class or stanza for the modeled predator and prey species. Our model and the NWACS-MICE model also assume that an alternative prey of the same size as a menhaden would be equally preferred by striped bass and that all prey have equal nutritional value. If striped bass supplement their diet with alternative prey that have a higher nutritional value, model estimates of consumption and prey M_2 in both models would be affected.

Our model differed from that of the NWACS-MICE model in several key ways. First, our predator–prey model was age structured (ages 1–20+ for striped bass and ages 0–6+ for Atlantic menhaden), whereas the NWACS-MICE model used more coarsely grouped age categories for striped bass (age 0–1, 2–5, and 6+) and Atlantic menhaden (age 0 and 1+). Another difference between these two models was that our model incorporated a type II functional response, which differs from the NWACS-MICE model's foraging arena predator–prey dynamics (similar to a type-III functional response). Also, the NWACS-MICE model includes time-varying predation pressure from multiple predators, whereas our model includes a single predator and assumes that all other predation impacts are captured in our static M_1 parameter. Finally, the NWACS-MICE models use a dynamic other prey pool, which allows prey resources to be driven quite low by predators; in contrast, we adopted the use of a static other prey pool.

Differences in structure among our models likely led to differences in predator–prey dynamics such that striped bass was less responsive to decreases in Atlantic menhaden biomass in our model than in the NWACS-MICE. We suspect this is primarily due to the way in which we modeled our eight other (non-menhaden) prey categories. Unlike Atlantic menhaden, which were dynamically modeled, our other prey categories were static over time; this established a floor to the amount striped bass could consume in our model, given that they are always able to consume a minimum amount of other prey biomass. We chose our levels of other prey biomass by selecting values that allowed us to match the proportion of Atlantic menhaden in the diet of striped bass and the observed range of striped bass growth (Schiano 2022). In contrast, Chagaris et al. (2020) developed time-varying estimates of alternative prey by mass balancing an Ecopath model. The impact of our static other prey categories is apparent in Fig. 4 such that the striped bass SSB target and SSB threshold lines flatten around an Atlantic menhaden *F* of 1 yr^{-1}. At this point, striped bass are primarily consuming other prey, and striped bass SSB remains relatively constant because the other prey biomass is constant. An improved understanding of the dynamics of alternative prey species for striped bass would advance multispecies model development and the development of multispecies HCRs.

Despite this difference, our model results were similar to that of the NWACS-MICE and other models of the striped bass–Atlantic menhaden predator–prey system in several ways. Both our model and the NWACS-MICE indicated that striped bass *F* was an important driver of striped bass biomass, and that even reducing Atlantic menhaden F to 0 yr^{-1} would not rebuild striped bass to its SSB target without a reduction in striped bass F as well. Also, our simulated total M for Atlantic menhaden ranged in our model from 0.77 to 1.78 (age-6+–age-0) with an average of 1.04, making it comparable to that of the suite of multispecies models explored during the last benchmark assessment (SEDAR 2020*b*; fig. 176). Across the 27 HCR simulations, our estimates of Atlantic menhaden M_2 ranged from 0 to 0.072 for age-0 (mean = 0.017) and from 0 to 0.011 (mean = 0.001) for age-6+. Compared with other models used to estimate M_2 for this predator–prey system (SEDAR 2020*b*), our estimates were most similar to that of the multispecies age-structured statistical catch-at-age model (0.06 for age-0 and ~0.01 for age-6+ in the terminal year). Alternative models with greater structural differences resulted in larger differences in outcomes. For example, our estimates of M_2 were much lower than that of the MICE EwE model (0.12 for juveniles and 0.031 for adults) and the MSVPA (~0.2 for age-1, ~1 for age-0, ~0 for age-2+), both of which included multiple predators on menhaden, as well as that of the surplus production-based Steele–Henderson model (0.2–0.7). In our model, effects of other predators on Atlantic menhaden were part of M_1.

Conclusions

Our study was designed to help fishery managers proactively examine the potential pros and cons of a suite of alternative HCRs and any unexpected consequences of implementing them. The ASMFC has already taken an important first step in EAFM by adopting targets and thresholds for Atlantic menhaden that consider their role as forage fish (Anstead et al. 2021). However, management of Atlantic menhaden and striped bass continue to use constant F, single-species reference points applied independently within two distinct single-species management frameworks. Our study suggests that the ASMFC's ecosystem management objectives (Table 5) might be achievable by simultaneously adopting HCRs for both striped bass and Atlantic menhaden stocks that complement one another. Our results can be used to enhance the ASMFC's EAFM efforts by expanding the range of management options explored during future benchmarks. Although our inputs differ from that of the most recent stock assessment updates and stock status of striped bass has changed in recent years (no longer overfishing), the structure of both assessment models has not changed appreciably and thus the overarching conclusions of our study regarding relative performance of HCRs should still be applicable. However, our model would need to be updated with the most recent assessment information for both species before being used to operationally inform HCR selection or new reference points for these species. We also caution that HCRs in our study were implemented using a 1-year time lag between assessment and management. Future studies should include examination of the potential impacts of data frequency and management implementation on multispecies HCR performance as has been done for single-species HCRs (Hutniczak et al. 2019).

Our study should also help inform the consideration of HCR types for use in EAFM for other predator–prey systems worldwide. In particular, our conclusions regarding efficacy of HCRs designed for use in forage fish management (Cury et al. 2011; Pikitch et al. 2012) may help to identify situations in which these approaches will be highly effective (e.g., tightly linked predator–prey systems) versus less effective (e.g., generalist predators). Further exploration of forage fish HCRs is needed given the variability in these populations and their potential drivers, both biotic and abiotic (Hilborn et al. 2017).

More broadly, our modeling approach can be adapted for use in other predator–prey systems. In particular, our predator–prey model structure may be especially useful in the common situation in which type III functional response relationships are not estimable (Kalinkat et al. 2023). We used the multi-predator multi-prey type II functional response modeling approach used by Szalai (2003) to estimate dynamics of alewife (*Alosa pseudoharengus*) prey and their Chinook salmon (*Oncorhynchus tshawytscha*) predator in Lake Michigan. We hope our study draws attention to her approach, which may be a tractable modeling option for scientists attempting to characterize complex, age-structured predator–prey relationships without adequate diet information. Note, though, that adopting a type II functional response relationship may not work well if HCRs that drive prey to low densities are to be explored. We also acknowledge that our model relied on the use of two, well-established age-structured stock assessments, several predator diet studies, and regional diet monitoring programs. In the absence of this level of information, more scenarios about prey preference and diet importance may need to be considered or a less detailed modeling approach may need to be explored, such as multispecies surplus production models (Collie and Delong 1999; Mueter and Megrey 2006; Gamble and Link 2009).

Regardless of the model structure used, all models used to inform EAFM should explore the robustness of their advice to key ecosystem assumptions in the face of uncertainty. Given a wide range of values have been reported for the importance of Atlantic menhaden in the striped bass diet, we developed alternative operating models that encompassed the range of Atlantic menhaden in the diets of older striped bass: 21% (Overton et al. 1999), 44% (Walter and Austin 2001, 2003), 50% (Overton et al. 2008), and 70% (Hartman and Brandt 1995). Uncertainty regarding the importance of Atlantic menhaden in striped bass diets creates a significant challenge for modeling predator–prey dynamics. Our study addressed this challenge by exploring multiple operating models and demonstrating that HCR performance was similar across a range of predator diet assumptions.

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Data availability

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Author information

Author ORCIDs

Samantha Schiano https://orcid.org/0009-0003-3744-6428
Geneviève M. Nesslage https://orcid.org/0000-0003-1770-6803

Author notes

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Author contributions

Conceptualization: GMN, KD, AMS, MJW
Data curation: SS, MJW
Formal analysis: SS, GMN, MJW
Funding acquisition: GMN, KD, AMS, MJW
Methodology: GMN, KD, AMS, RJW, MJW
Project administration: GMN, MJW
Software: SS, MJW
Visualization: SS
Writing – original draft: SS
Writing – review & editing: GMN, KD, AMS, RJW, MJW

Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2023-0089.

References

Anstead, K.A., Drew, K., Chagaris, D., Schueller, A.M., McNamee, J.E., Buchheister, A., et al. 2021. The path to an ecosystem approach for forage fish management: a case study of Atlantic menhaden. Front. Mar. Sci. **8**(May). doi:10.3389/fmars.2021.607657.

ASMFC. 2022. Draft Amendment 7 to the Interstate Fishery Management Plan for Atlantic Striped Bass For Public Comment Draft Document for Public Comment. Available from http://www.asmfc.org/uploads/file/61fd9572AtlStripedBassDraftAm7forPublicComment_Feb2022.pdf [accessed February].

Austin, H.M., and Walter, J.F. 2001. Food habits of large striped bass in the lower Chesapeake Bay and its tributaries March 1997–May 1998. Virginia Marine Resource Report No. 2001-7. Virginia Institute of Marine Science, William & Mary. doi:10.21220/V5JB2J.

Buchheister, A., Miller, T.J., and Houde, E.D. 2017. Evaluating ecosystem-based reference points for Atlantic Menhaden. Mar. Coast. Fish. **9**(1): 457–478. doi:10.1080/19425120.2017.1360420.

Chagaris, D., Drew, K., Schueller, A., Cieri, M., Brito, J., and Buchheister, A. 2020. Ecological reference points for Atlantic menhaden established using an ecosystem model of intermediate complexity. Front. Mar. Sci. **7**(November): 1–17. doi:10.3389/fmars.2020.606417. PMID: 32802822.

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

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., et al. 2011. Global seabird response to forage fish depletion—one-third for the birds. Science, **334**(December): 1703–1706. doi:10.1126/science.1212928. PMID: 22194577.

Deroba, J.J., and Bence, J.R. 2008. A review of harvest policies: understanding relative performance of control rules. Fish. Res. **94**(3): 210–223. doi:10.1016/j.fishres.2008.01.003.

Dickey-Collas, M., Link, J.S., Snelgrove, P., Anderson, M.R., Kenchington, E., Roberts, J.M., et al. 2022. Exploring ecosystem-based management in the North Atlantic. J. Fish Biol. **101**(2): 342–350. doi:10.1111/jfb.15168. PMID: 35841280.

Drew, K., Cieri, M., Schueller, A.M., Buchheister, A., Chagaris, D., Nesslage, G., et al. 2021. Balancing model complexity, data requirements, and management objectives in developing ecological reference points for Atlantic menhaden. Front. Mar. Sci. **8**(February): 1–17. doi:10.3389/fmars.2021.608059.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., et al. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Softw. **27**(2): 233–249. doi:10.1080/10556788.2011.597854.

Gaichas, S.K., DePiper, G.S., Seagraves, R.J., Muffley, B.W., Sabo, M.G., Colburn, L.L., and Loftus, A.J. 2018. Implementing ecosystem approaches to fishery management: risk assessment in the US Mid-Atlantic. Front. Mar. Sci. **5**(NOV): 1–25. doi:10.3389/fmars.2018.00442. PMID: 29552559.

Gamble, R.J., and Link, J.S. 2009. Analyzing the tradeoffs among ecological and fishing effects on an example fish community: a multispecies (fisheries) production model. Ecol. Model. **220**(19): 2570–2582. doi:10.1016/j.ecolmodel.2009.06.022

Garrison, L.P., Link, J.S., Kilduff, D.P., Cieri, M.D., Muffley, B., Vaughan, D.S., et al. 2010. An expansion of the MSVPA approach for quantifying predator–prey interactions in exploited fish communities. ICES J. Mar. Sci. **67**(5): 856–870. doi:10.1093/icesjms/fsq005.

Gislason, H., and Helgason, T. 1985. Species interaction in assessment of fish stocks with special application to the North Sea. Dana, **5**: 1–44.

Griffin, J.C., and Margraf, F.J. 2003. The diet of Chesapeake Bay striped bass in the late 1950s. Fish. Manag. Ecol. **10**(5): 323–328. doi:10.1046/j.1365-2400.2003.00367.x.

Hartman, K.J., and Brandt, S.B. 1995. Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: applications of bioenergetics models. Can. J. Fish. Aquat. Sci. **52**(8): 1667–1687. doi:10.1139/f95-760.

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

Hilborn, R., and Ovando, D. 2014. Reflections on the success of traditional fisheries management. ICES J. Mar. Sci. **71**(5): 1040–1046. doi:10.1093/icesjms/fsu034.

Hoenig, J.M., Groner, M.L., Smith, M.W., Vogelbein, W.K., Taylor, D.M., Landers, D.F., et al. 2017. Impact of disease on the survival of three commercially fished species. Ecol. Appl. **27**(7): 2116–2127. doi:10.1002/eap.1595 . PMID: 28675580.

Holling, C. 1959. The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly. Can. Entomol. **91**(5): 293–320. doi:10.4039/Ent91293-5.

Hutniczak, B., Lipton, D., Wiedenmann, J., and Wilberg, M. 2019. Valuing changes in frequency of fish stock assessments. Can. J. Fish. Aquat. Sci. **76**(9): 1640–1652. doi:10.1002/eap.1595.

Jacobs, J.M., Harrell, R.M., Uphoff, J., Townsend, H., and Hartman, K. 2013. Biological reference points for the nutritional status of Chesapeake Bay striped bass. N. Am. J. Fish. Manag. **33**(3): 468–481. doi:10.1080/02755947.2013.763876.

Kalinkat, G., Rall, B.C., Uiterwaal, S.F., and Uszko, W. 2023. Empirical evidence of type III functional responses and why it remains rare. Front. Ecol. Evol. **11**: 1033818. doi:10.3389/fevo.2023.1033818.

Kaplan, I.C., Hansen, C., Morzaria-Luna, H.N., Girardin, R., and Marshall, K.N. 2020. Ecosystem-based harvest control rules for Norwegian and US ecosystems. Front. Mar. Sci. **7**(August): 1–15. doi:10.3389/fmars.2020.00652. PMID: 32802822.

Koen-Alonso, M., Pepin, P., Fogarty, M.J., Kenny, A., and Kenchington, E. 2019. The Northwest Atlantic Fisheries Organization roadmap for the development and implementation of an ecosystem approach to fisheries: structure, state of development, and challenges. Mar. Pol. **100**(November 2018): 342–352. doi:10.1016/j.marpol.2018.11.025.

Kvamsdal, S.F., Eide, A., Ekerhovd, N.A., Enberg, K., Gudmundsdottir, A., Hoel, A.H., et al. 2016. Harvest control rules in modern fisheries managementharvest control rules in modern fisheries management. Elementa, **2016**: 1–22. doi:10.12952/journal.elementa.000114.

Link, J.S., and Browman, H.I. 2014. Integrating what? Levels of marine ecosystem-based assessment and management. ICES J. Mar. Sci. **71**(5): 1170–1173. doi:10.1093/icesjms/fsu026 Contribution.

Mace, P.M. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. Fish Fish. **2**(1): 2–32. doi:10.1046/j.1467-2979.2001.00033.x.

McGowan, C.P., Smith, D.R., Sweka, J.A., Martin, J., Nichols, J.D., Wong, R., et al. 2011. Multispecies modeling for adaptive management of horseshoe crabs and red knots in the delaware bay. Nat. Resour. Model. **24**(1): 117–156. doi:10.1111/j.1939-7445.2010.00085.x.

Mueter, F.J., and Megrey, B.A. 2006. Using multispecies surplus production models to estimate ecosystem-level maximum sustainable yields. Fish. Res. **81**(2-3): 189–201. doi:10.1016/j.fishres.2006.07.010.

Muffley, B., Gaichas, S., DePiper, G., Seagraves, R., and Lucey, S. 2021. There Is no I in EAFM adapting integrated ecosystem assessment for Mid-Atlantic fisheries management. Coastal Manage. **49**(1): 90–106. doi:10.1080/08920753.2021.1846156.

NEFSC. 2019. 66th Northeast Regional Stock Assessment Workshop (66th SAW) Assessment Report. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 19-08; 1170 p. Available from http://www.nefsc.noaa.gov/publications/ [accessed November 2020].

Nelson, G.A., Chase, B.C., and Stockwell, J.D. 2006. Population consumption of fish and invertebrate prey by striped bass (Morone saxatilis) from coastal waters of Northern Massachusetts, USA. J. Northwest Atl. Fish. Sci. **36**: 111–126. doi:10.2960/J.v36.m576.

Nesslage, G.M., and Wilberg, M.J. 2019. A performance evaluation of surplus production models with time-varying intrinsic growth in dynamic ecosystems. Can. J. Fish. Aquat. Sci. **76**(12): 2245–2255. doi:10.1139/cjfas-2018-0292.

Overton, A.S., Griffin, J., and Margraf, F.J. 1999. A bioenergetics approach for determining the effect of increased striped bass population on its prey in the Chesapeake Bay. Final Report to MDDNR, **44**.

Overton, A.S., Manooch, C.S., Smith, J.W., and Brennan, K. 2008. Interactions between adult migratory striped bass (*Morone saxatilis*) and their prey during winter off the Virginia and North Carolina Atlantic coast from 1994 through 2007. Fish. Bull. **106**(2): 174–182.

Overton, A.S., Margraf, F.J., and May, E.B. 2009. Spatial and temporal patterns in the diet of striped bass in Chesapeake Bay. Trans. Am. Fish. Soc., **138**(4): 915–926. doi:10.1577/t07-261.1.

Pacific Fishery Management Council. 2012. Terms of reference for the groundfish and coastal pelagic species stock assessment and review process for 2013–2014. Available from https://www.pcouncil.org/documents/2013/03/terms-of-reference-for-the-groundfish-and-coastal-pelagic-species-stock-assessment-and-review-process-for-2013-2014.pdf/ [accessed November 2022].

Patrick, W.S., and Link, J.S. 2015. Myths that continue to impede progress in ecosystem-based fisheries management. Fisheries, **40**(4): 155–160. doi:10.1080/03632415.2015.1024308.

Pérez-Rodríguez, A., Umar, I., Goto, D., Howell, D., Mosqueira, I., and González-Troncoso, D. 2022. Evaluation of harvest control rules for a group of interacting commercial stocks using a multispecies MSE framework. Can. J. Fish. Aquat. Sci. **1320**(January): 1–19. doi:10.1139/cjfas-2021-0069.

Pikitch, E., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Essington, T., et al. 2012. Little fish, big impact: managing a crucial link in ocean food webs. Lenfest Ocean Program. Available from https://www.researchgate.net/publication/281570668_Little_Fish_Big_Impact_Managing_a_Crucial_Link_in_Ocean_Food_Webs [accessed September 2020].

Pikitch, E.K., Rountos, K.J., Essington, T.E., Santora, C., Pauly, D., Watson, R., et al. 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish Fish. **15**(1): 43–64. doi:10.1111/faf.12004.

Plagányi, É.E., Punt, A.E., Hillary, R., Morello, E.B., Thébaud, O., HutI, T., et al. 2014. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. Fish Fish. **15**(1): 1–22. doi:10.1111/j.1467-2979.2012.00488.x.

Punt, A.E. 2010. Harvest control rules and fisheries management. Handbook of marine fisheries conservation and management, Oxford University Press, New York. pp. 582–594.

Quinn, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics. New York, Oxford University Press.

RStudio Team 2020. RStudio: integrated development for R. RStudio, PBC, Boston, MA. Available from http://www.rstudio.com/.

Rudershausen, R.J. Tuomikoski, J.E. Buckel, J. A., and Hightower, J. E. 2005. Prey Selectivity and Diet of Striped Bass in Western Albemarle Sound, North Carolina. Trans. Am. Fish. Soc., **134(5)**: 1059–1074. doi:10.1577/t04-115.1.

Safiq, A., Free, C.M., Caracappa, J., Valenti, J.L., and Jensen, O. 2021. Perceptions of ecosystem-based fisheries management among State Natural Resource Agency scientists in the Northeastern United States. Fisheries, **46**(2): 66–75. doi:10.1002/fsh.10527.

Schiano, S.E. 2022. Evaluating the consequences of alternative Atlantic striped bass harvest control rules on their prey, Atlantic Menhaden. Masters thesis, University of Maryland, College Park, MD.

SEDAR. 2020a. SEDAR 69 – Atlantic Menhaden Benchmark Stock Assessment Report. SEDAR, North Charleston SC. 691pp. Available from http://sedarweb.org/sedar-69 [accessed August 2020].

SEDAR. 2020b. SEDAR 69 – Atlantic Menhaden Ecological Reference Points Stock Assessment Report. SEDAR, North Charleston SC. 560pp. Available from http://sedarweb.org/sedar-69 [accessed August 2020].

Szalai, E. 2003. Uncertainty in the population dynamics of alewife (Alosa pseudoharengus) and bloater (Coregonus hoyi) and its effects on salmonine stocking strategies in Lake Michigan. Dissertation. Michigan State University, East Lansing, MI.

Walter III, J.F., and Austin, H.M. 2001. Diet composition of large striped bass (*Morone saxatilis*) in Chesapeake Bay. Fish. Bull. **101**(2): 414–423.

Walter, J.F., and Austin, H.M. 2003. Diet composition of large striped bass (*Morone saxatilis*) in Chesapeake Bay. Fish. Bull. **101**(2): 414–423.

Walter, J.F., Overton, A.S., Ferry, K.H., and Mather, M.E. 2003. Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology. Fish. Manage. Ecol. **10**(5): 349–360. doi:10.1046/j.1365-2400.2003.00373.x.

Wood, R.J., and Austin, H.M. 2009. Synchronous multidecadal fish recruitment patterns in Chesapeake Bay, USA. Can. J. Fish. Aquat. Sci. **66**(3): 496–508. doi:10.1139/F09-013.