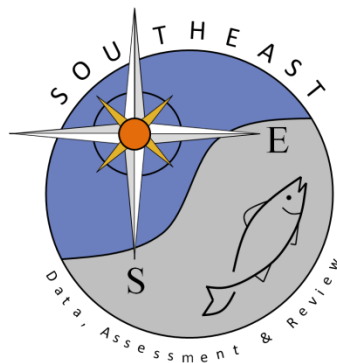# Evaluating the performance of a multispecies statistical catch-at-age model

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ARTICLE

# Evaluating the performance of a multispecies statistical catch-at-age model

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**Abstract:** Predation is a substantial source of mortality that is a function of the abundance of predator and prey species. This source of mortality creates a challenge of incorporating species interactions in statistical catch-at-age models in a way that accounts for the uncertainty in input data, parameters, and results. We developed a statistical, age-structured, multispecies model for three important species in the Georges Bank fish community: Atlantic cod (*Gadus morhua*), silver hake (*Merluccius bilinearis*), and Atlantic herring (*Clupea harengus*). The model was fit to commercial catch, survey, and diet data from 1978 to 2007. The estimated predation rates were high, compared with fishing mortality, and variable with time. The dynamics of the three species can be explained by the interplay between fishing and predation mortality. Monte Carlo simulations were used to evaluate the ability of the model to estimate parameters with known error introduced into each of the data types. The model parameters could be estimated with confidence from input data with error levels similar to those obtained from the model fit to the observed data. This evaluation of model performance should help to move multispecies statistical catch-at-age models from proof of concept to functional tools for ecosystem-based fisheries management.

**Résumé :** La prédation est une importante source de mortalité qui dépend de l'abondance des espèces prédatrices et proies. Cette source de mortalité nécessite l'intégration dans les modèles statistiques de capture à l'âge de l'interaction des espèces d'une manière qui tienne compte de l'incertitude associée aux données d'entrée, aux paramètres et aux résultats. Nous avons élaboré un modèle statistique multispécifique structuré selon l'âge pour trois espèces importantes de la communauté de poissons du banc Georges, à savoir la morue(*Gadus morhua*), le merlu argenté (*Merluccius bilinearis*) et le hareng de l'Atlantique (*Clupea harengus*). Le modèle a été comparé à des données de prises commerciales, de données de campagne pour la période de 1978 à 2007. Les taux de prédation estimés étaient élevés par rapport à la mortalité par pêche et variaient dans le temps. La dynamique des trois espèces peut s'expliquer par l'influence réciproque de la mortalité par pêche et de la mortalité par prédation. Des simulations de Monte Carlo ont été utilisées pour évaluer la capacité du modèle à estimer les paramètres auxquels sont associées des erreurs connues introduites dans chaque type de données. Les paramètres modélisés pouvaient être estimés avec confiance à partir des données d'entrée à des niveaux d'erreur semblables à ceux obtenus en ajustant le modèle aux données d'observation. À la lumière de cette évaluation de leur performance, il est possible d'entrevoir l'utilisation de modèles statistiques multispécifiques de capture à l'âge, toujours au stade de la validation de principe, comme outils fonctionnels de gestion écosystémique des pêches. [Traduit par la Rédaction]

## Introduction

Accounting for trophic interactions among species is an important component of an ecosystem approach to fisheries (Link 2010). Approaches for incorporating species interactions have expanded substantially over the last few decades and range from expanded versions of single-species models to full ecosystem models that incorporate all trophic levels (Plagányi 2007). This spectrum of available models varies in data requirements and model assumptions, exhibiting trade-offs between the ability to incorporate particular species-specific population dynamic processes and the ability to depict the full system (Link 2002). The full array of modeling approaches available to support an ecosystem approach to fisheries has been catalogued elsewhere (Hollowed et al. 2000; Plagányi 2007; Townsend et al. 2008). Here we address those models generally classified as dynamic multispecies models, which are most similar to the age-structured model developed in this study.

Virtual population analysis (VPA), a retrospective method that uses catch-at-age data to estimate population numbers and fishing mortality rates, was extended to multispecies virtual population

analysis (MSVPA) through incorporation of Andersen and Ursin's (1977) seminal work on predator food selection (Helgason and Gislason 1979; Pope 1979; Sparre 1980). MSVPA explicitly models predation mortality among interacting species and therefore more fully describes the age dependence and interannual variability in natural mortality (Sparre 1991; Magnússon 1995). Since its creation, MSVPA and expanded MSVPA-X have been used to estimate the interactions among commercially important fish stocks in several ecosystems, including the North Sea (Gislason and Helgason 1985), Baltic Sea (Sparholt 1994), Bering Sea (Livingston and Jurado-Molina 2000), Georges Bank (Tsou and Collie 2001*a*), northwest Atlantic (Tyrrell et al. 2008), and the western mid-Atlantic (Garrison et al. 2010). MSVPA is a deterministic model that assumes input time series are measured without error (Lewy and Vinther 2004); accordingly, it does not incorporate stochastic variability or uncertainty in the parameter estimates.

In contrast with VPA, statistical catch-at-age models account for error in observed catches and other input data through the statistical estimation of model parameters and quantification of uncertainty (Fournier and Archibald 1982; Deriso et al. 1985; Quinn and

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Deriso 1999). Statistical catch-at-age models are one of the preferred methods for single-species stock assessments because the model uncertainty can inform management decisions. These models have been combined with the predation equations from MSVPA to produce multispecies statistical catch-at-age models (Jurado-Molina et al. 2005; Van Kirk et al. 2010).

Several multispecies statistical catch-at-age models have been developed with varying assumptions and applied to several different ecosystems. Some formulations include the estimation of food-selection parameters (Lewy and Vinther 2004; Kinzey and Punt 2009; Van Kirk et al. 2010). Lewy and Vinther's (2004) Stochastic Multi-Species Model for the North Sea is age–length-structured; species abundance, fishing mortality rates, and catch data are age-structured, but both the stomach-content data and the food-selection model are structured by length because predator preference depends on size. Furthermore, the statistical multispecies age-structured model of the Aleutian Shelf (Kinzey and Punt 2009) considered uncertainty regarding the predator functional response. Other variants such as Gadget are also spatially explicit and incorporate additional biological processes such as migration and reproduction (Begley and Howell 2004). To the best of our knowledge, none of these modeling efforts have evaluated model performance with simulated data containing known levels of error.

Here we use Monte Carlo analysis to evaluate the uncertainty in parameter estimation to varying levels of measurement error. Evaluating model performance with simulated data incorporating measurement error will help to elevate these models to the level of statistical rigor expected of fishery population dynamic models.

In the northeast US, a variety of approaches have been applied to incorporate ecological considerations into fisheries models (Townsend et al. 2008). Over the last half century, Georges Bank has exhibited substantial changes in community dynamics. The community once dominated by groundfish and other finfish is now primarily composed of pelagic and elasmobranch species (Fogarty and Murawski 1998; Link and Garrison 2002). Furthermore, several studies have indicated a shift in the dominant piscivores from Atlantic cod (*Gadus morhua*) and silver hake (*Merluccius bilinearis*) to spiny dogfish (*Squalus acanthias*) and winter skate (*Leucoraja ocellata*) (Tsou and Collie 2001*a*; Link and Garrison 2002). Predation mortality on the youngest ages is high, variable (Overholtz et al. 2008; Moustahfid et al. 2009), and may affect the year class strength of commercially important species (Tsou and Collie 2001*b*; Tyrrell et al. 2008, 2011). The overall objective of this study is to develop a multispecies statistical catch-at-age model of the Georges Bank fish community that explicitly quantifies the mortality due to predation; once fully developed, this model can be used as a tool for incorporating ecological considerations into fisheries management.

To test the performance of the multispecies statistical catch-at-age model, we first constructed a submodel of the Georges Bank fish community, including Atlantic cod, silver hake, and Atlantic herring (*Clupea harengus*). These three species were chosen because previous work has demonstrated their importance as predators or prey in the ecosystem (Tsou and Collie 2001*a*; Tyrrell et al. 2008), they are known to exhibit strong interactions via predation (Tsou and Collie 2001*b*; Overholtz and Link 2007), and the required input data are readily available. Accordingly, the specific goals of this manuscript are to (*i*) fit single-species versions of the model to each species to obtain baseline results for the multispecies model, (*ii*) enable species interactions through predation and compare these results with the single-species runs, and (*iii*) measure uncertainty in parameter estimation with Monte Carlo analysis. This three-species model contains important species interactions but is still small enough to permit extensive Monte Carlo simulation.

## Methods

The catch-at-age model comprises Atlantic cod, silver hake, and Atlantic herring. In this submodel, cod is a top predator of both silver hake and herring, silver hake is an intermediate predator only of herring, and herring is a forage species. Cod and silver hake can also exhibit cannibalism.

### Data requirements

Six input data series are required for each species: total commercial catch in weight, aggregate survey index in number-per-tow, age proportions for both commercial catches and survey indices, average individual weight-at-age, and for the multispecies runs, age-specific predator diet.

Total annual commercial catch was obtained from the most recent published stock assessments (cod: NEFSC 2008; herring: Shepherd et al. 2009) or directly from Northeast Fisheries Science Center (NEFSC) databases (silver hake). For cod and herring, total commercial catches represented landings plus discards; discard estimates were not available for silver hake. Both silver hake and herring stocks are assessed over a wider geographic area than just Georges Bank. Following Collie and Delong (1999), the NEFSC trawl survey was used to calculate the proportion of the species' biomass found on Georges Bank each year from 1978 to 2007. For both species, these proportions did not exhibit a systematic temporal trend. Accordingly, average proportions (silver hake = 0.165, herring = 0.119) were used to determine the commercial catches attributable to Georges Bank in each year.

Time series of annual catch-at-age (millions of fish) were used to calculate age proportions from the commercial catch. For cod, this time series was obtained from the most recent assessment. However, for silver hake and herring, older assessments were used (silver hake: Brodziak et al. 2001; herring: Overholtz et al. 2004) because of limitations in data availability. Herring age proportions in years since the last assessment (2003–2007) were treated as missing data; however, it was necessary to assume average age proportions for silver hake from 1999 through 2007 to avoid confounding between recruitment parameters.

Age-structured seasonal (spring and fall) trawl-survey indices (number-per-tow) were obtained from the most recent assessments for cod and herring. Since herring survey indices represented the Georges Bank – Gulf of Maine stock complex, we assumed that these relative abundances were representative of just Georges Bank as well. For silver hake, average seasonal estimates of number-per-tow for Georges Bank strata were calculated directly from the NEFSC trawl-survey database. Age-structured survey indices were not available in all years. Consequently, trawl-survey indices were split into two components: the aggregate seasonal survey index (summed over age classes) and the age composition of the aggregate index. Average age proportions were assumed for silver hake from 2005 through 2007, calculated using observed age proportions from 1995 through 2004.

Average individual weight-at-age is needed in both the single-species and multispecies versions of the model to convert from numbers to biomass units. Weight-at-age time series were taken from the recent age-structured assessments (cod: NEFSC 2008; herring: Shepherd et al. 2009; silver hake: Brodziak et al. 2001). The silver hake weight-at-age time series extended only through 1999; therefore, average weight-at-age from 1995–1999 was used for 2000–2007.

For multispecies runs, additional data requirements include consumption:biomass (CB) estimates, the biomass of "other food" in the ecosystem, and average predator diet. Age-specific CB ratios were obtained from Grosslein et al. (1980). Following Sparre (1980) as well as the MSVPA application to Georges Bank (Tsou and Collie 2001*a*), we assumed a constant, time-invariant total ecosystem biomass, permitting the biomass of available other food to vary annually. Prior studies have confirmed that the total biomass on

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**Table 1.** Symbols used in model formulations.

| Symbol | Description (units) |
|---|---|
| $i$ | Species or prey species |
| $a$ | Age or prey age (year) |
| $j$ | Predator species |
| $b$ | Predator age (year) |
| $N_{i,a,t}$ | Abundance-at-age in beginning of year ($10^6$ fish) |
| $W_{i,a,t}$ | Average individual weight-at-age (kg) |
| $B_{i,a,t}$ | Biomass-at-age ($10^6$ kg) |
| $Z_{i,a,t}$ | Instantaneous total mortality-at-age (year$^{-1}$) |
| $M_i$ | Instantaneous natural mortality (age- and time-invariant) |
| $M1_i$ | Instantaneous residual natural mortality (age- and time-invariant) |
| $F_{i,a,t}$ | Instantaneous fishing mortality-at-age (year$^{-1}$) |
| $s_{i,a}$ | Fishery selectivity-at-age |
| $M2_{i,a,t}$ | Instantaneous predation mortality-at-age (year$^{-1}$) |
| $C_{i,a,t}$ | Commercial catch-at-age ($10^6$ fish) |
| $SI_{i,a,t}$ | Trawl-survey index (number-per-tow) |
| $r_{i,a}$ | Survey selectivity-at-age |
| $\eta_{i,j}$ | Preferred predator-to-prey weight ratio |
| $\sigma_{i,j}$ | Variance in predator-to-prey weight ratio |
| $g_{i,j,a,b,t}$ | Predator size preference |
| $\rho_{i,j}$ | Prey species preference |
| $v_{i,j,a,b,t}$ | Prey suitability |
| $\emptyset_{i,j,a,b,t}$ | Available prey biomass ($10^6$ kg) |
| TC | Total commercial catch in weight ($10^3$ metric tons) |
| TS | Total survey index (number-per-tow) |
| CP | Commercial catch age proportions |
| SP | Survey index age proportions |
| FH | Food habits proportions (by weight), averaged over 5-year intervals |
| $Yp_i$ | Initial abundance, $N_{i,a,1}$, penalty |
| $Rp_i$ | Recruitment penalty |
| $Bp_i$ | Age-specific biomass penalty |
| $Yr1_{i,a,1}$ | Initial abundances predicted from exponential decay |
| $Rth_i$ | Threshold value for the CV of log recruitment |
| $Bth_i$ | Threshold value for age-specific biomass |

**Table 2.** Single-species equations from Quinn and Deriso (1999).

| Equation | Description |
|---|---|
| $N_{i,a+1,t+1} = N_{i,a,t} \cdot e^{-Z_{i,a,t}}$ | Abundance-at-age: $2 \leq a < \max(a)$ |
| $N_{i,a,t+1} = N_{i,a-1,t} \cdot e^{-Z_{i,a-1,t}} + N_{i,a,t} \cdot e^{-Z_{i,a,t}}$ | Abundance-at-age: $a = \max(a)$ |
| $C_{i,a,t} = \dfrac{F_{i,a,t}}{Z_{i,a,t}} N_{i,a,t}(1 - e^{-Z_{i,a,t}})$ | Catch-at-age |
| $F_{i,a,t} = s_{i,a} F_{i,t}$ | Fishing mortality-at-age |

**Note:** Symbols are defined in Table 1.

1999). All symbols are defined in Table 1, and single-species equations are listed in Table 2.

In single-species runs, total mortality in year $t$ comprised an age- and time-invariant instantaneous natural mortality ($M$) rate and an age- and year-specific instantaneous fishing mortality rate:

$$(1) \qquad Z_{i,a,t} = F_{i,a,t} + M_i$$

Total natural mortality ($M$) was set to 0.2 for all three species based on values used in recent stock assessments or species' life histories (Hoenig 1983; NEFSC 2008; Shepherd et al. 2009).

A fishery-independent trawl-survey index ($SI_{i,a,t}$) was related to age-specific abundances, assuming age-invariant catchability $q_i$ and age-specific selectivity $r_{i,a}$ coefficients, as

$$(2) \qquad SI_{i,a,t} = q_i r_{i,a} N_{i,a,t}\, e^{-\frac{m}{12} Z_{i,a,t}}$$

where $m$ represents the month in which the trawl survey was conducted. Relative abundance estimates from both the spring and fall surveys were initially used for each species; the season providing the most consistent abundance estimates and the best diagnostics was included in the final model. Fall time series were used for cod and silver hake; the spring time series was used for herring. Species-specific catchabilities ($q_i$) were calculated from deviations between predicted absolute abundance ($N_{i,a,t}$) and predicted relative abundance ($SI_{i,a,t}$), as in Walters and Ludwig (1994). Age-specific fishery and survey selectivity coefficients were estimated for each species from age-1 to the assumed age of full recruitment. The ages of full recruitment to the fishery and survey were both selected iteratively. Ages corresponding to selectivities whose estimates were approximately 1.0 in initial runs were assumed to be fully recruited in subsequent iterations. Furthermore, dome-shaped selectivity ogives were not permitted; once full selectivity was reached, all selectivity parameters for older age classes were fixed at one. For the fishery, the age of full recruitment in the final run was set to age-4 for cod and age-3 for both silver hake and herring. Likewise, the age of full recruitment to the survey was set to age-3 for cod and age-2 for silver hake and herring.

## Multispecies formulations

The formulation of the multispecies model generally follows that of MSVPA and the multispecies age-structured assessment of Van Kirk et al. (2010). In multispecies runs, natural mortality was partitioned into two components: the mortality due to predation ($M2$) and the residual natural mortality ($M1$) (Helgason and Gislason 1979), such that

$$(3) \qquad M_{i,a,t} = M1_i + M2_{i,a,t}$$

In these runs, the species-specific residual natural mortality was chosen such that the total natural mortality rate ($M_{i,a,t}$) for the oldest age classes was as similar as possible to the 0.2 value assumed in the single-species runs. Accordingly, residual natural

Georges Bank has remained relatively stationary (Link et al. 2008; Auster and Link 2009). During the development of the Georges Bank MSVPA, the total ecosystem biomass of fish and their prey on Georges Bank was estimated to be 15 million metric tons (Tsou and Collie 2001a). More recent work estimated the total Georges Bank ecosystem biomass as 7.34 million metric tons (Rochet et al. 2011). While Tsou and Collie's (2001a) estimate was used in this study, the impact of assuming Rochet et al.'s (2011) estimate on estimated predation rates was explored in a sensitivity run.

Georges Bank stomach-content data were obtained from the NEFSC Food Web Dynamics Program, which has systematically sampled predator food habits since 1973 (Link and Almeida 2000). These food-habits data are structured by predator species and length, but primarily only by prey species because prey lengths and ages are not routinely measured. A subset of the database is structured by both predator and prey lengths; it contains over 1900 predator and prey length measurements for the species interactions modeled here and collected though the time series. Average length-at-age estimates (Penttila et al. 1989) were used to convert predator and prey lengths to ages. Age-specific predator diet, represented as proportion by weight, was averaged over 5-year periods to reduce the inherent variability in the data set as well as the amount of missing data (Van Kirk et al. 2010), while still capturing the temporal trends.

## Model description

Equations for the progression of year class abundance, commercial catch-at-age, and fishing mortality-at-age (assuming separable fishing mortality) follow those equations traditionally used in age-structured, single-species stock assessments (Quinn and Deriso

mortality was set to 0.2 for cod and 0.1 for silver hake and herring. A sensitivity analysis was conducted to examine the impacts of the assumed residual natural mortality values in the multispecies model. This analysis indicated that the assumptions regarding $M1$ impacted the scale of predicted indices such as total annual abundance and biomass, but exhibited only minimal impacts on estimated rates of predation and total mortality. Furthermore, in all sensitivity runs, the temporal trends in predicted indices remained the same. Therefore, the multispecies model was robust to assumptions of residual natural mortality.

Calculation of predation mortality follows that of MSVPA and is calculated from suitability coefficients, incorporating the preference for a particular prey species by a predator (Sparre 1991). Predator $j$, age $b$ size preference for prey $i$, age $a$ is modeled as a lognormal function of the ratio of predator-to-prey weight (Andersen and Ursin 1977; Helgason and Gislason 1979):

$$(4) \qquad g_{i,a,j,b,t} = \exp\left[\frac{-1}{2\sigma_{i,j}^2}\left(\ln\frac{W_{j,b,t}}{W_{i,a,t}} - \eta_{i,j}\right)^2\right]$$

where $\eta_{i,j}$ represents the preferred lognormal predator-to-prey weight ratio, and $\sigma_{i,j}^2$ reflects the variance in this ratio (i.e., how selective the predator species is with regards to the size of its prey). A distinct set of size-preference coefficients is estimated for each species interaction. Preliminary analyses with simulated data indicated that predator size-preference coefficients were not estimable within the model framework because the full data set was not structured by prey length. Consequently, the subset of data for which both predator and prey lengths were available was used to empirically calculate observed predator size-preference coefficients.

The calculated average predator-to-prey weight ratio was used to approximate the preferred ratio, $\eta$, and the observed variance in that ratio was assumed to be equivalent to $\sigma$. To calculate these coefficients, season-specific length–weight relationships (Wigley et al. 2003) were used to convert observed predator and prey lengths to weights. These empirical size-preference parameters were then inputted into the model framework as known constants. In preliminary runs with the Georges Bank data, we also explored whether these size-preference parameters could be estimated using priors. However, this analysis again indicated a high sensitivity to parameter confounding and only minimal movement from starting parameter estimates when confounding was not apparent; therefore, the base run with empirical size-preference parameters treated as known constants was used.

From age-specific, size-preference coefficients, the suitability of each prey $i,a$ to predator $j,b$ is calculated as

$$(5) \qquad v_{i,a,j,b,t} = \rho_{i,j} \cdot g_{i,a,j,b,t}$$

where $\rho_{i,j}$ represents the general vulnerability of prey species $i$ to predation by predator species $j$ (i.e., the species preference of a predator). Vulnerability incorporates all differences in food selection, for example, behavioral and vertical distribution differences, that are not attributable to size differences (Gislason and Helgason 1985). Species preference is relative to a reference prey species, in this case "other food", whose $\rho_{\text{other}}$ is set to one. The suitability of "other food" is also equal to one because it is assumed to be of the preferred size.

Suitability and underlying size-preference coefficients are permitted to vary annually as a function of annual variation in the input time series of individual weight-at-age. Suitability coefficients are scaled across all prey species and ages to facilitate comparisons between estimated available (suitable) prey biomass and food-habits data such that the suitabilities for a predator age class sum to one (Sparre 1980):

$$(6) \qquad \tilde{v}_{i,a,j,b,t} = \frac{v_{i,a,j,b,t}}{\Sigma_i\Sigma_a\, v_{i,a,j,b,t} + v_{\text{other}}}$$

These scaled suitability coefficients are then used to calculate the biomass of prey $i,a$ available to each predator $j,b$:

$$(7) \qquad \phi_{i,a,j,b,t} = \tilde{v}_{i,a,j,b,t} \cdot B_{i,a,t}$$

and the available biomass of other food:

$$(8) \qquad \phi_{\text{other}} = \tilde{v}_{\text{other}} \cdot B_{\text{other},t}$$

where $B_{\text{other},t}$ represents the total biomass of other food in the system. Following Sparre (1980), the total biomass of other food is calculated as

$$(9) \qquad B_{\text{other},t} = \text{EB} - \sum_i \sum_a B_{i,a,t}$$

where EB represents the total biomass of the ecosystem (15 million metric tons; Tsou and Collie 2001a), and $\Sigma_i\Sigma_a B_{i,a,t}$ is the total biomass of those species included in the model, permitting the biomass of other food to vary annually. The total available prey biomass then represents the sum of the available biomass of the modeled species and the available other-food biomass:

$$(10) \qquad \phi_{j,b,t} = \phi_{\text{other}} + \sum_i \sum_a \phi_{i,a,j,b,t}$$

The ratio of the available biomass of prey $i,a$ to the total available prey biomass is equivalent to the proportion, by weight, of prey $i,a$ in the stomach of the predator, or

$$(11) \qquad \frac{S_{i,a,j,b,t}}{S_{j,b,t}} = \frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}$$

where $S_{i,a,j,b,t}$ is the weight of prey species $i,a$ in the stomach of predator $j,b$, and $S_{j,b,t}$ is the total stomach content weight of predator $j,b$. The scaling of the suitability coefficients creates a one-to-one direct correspondence between the stomach contents of the predator and the relative suitable prey biomass. Diet proportions were predicted for each year and then averaged over 5-year intervals.

Finally, following Lewy and Vinther (2004), the mortality due to predation is approximated as

$$(12) \qquad M2_{i,a,t} \approx \frac{1}{N_{i,a,t}W_{i,a,t}} \sum_j \sum_b \text{CB}_{j,b}B_{j,b,t}\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}$$

where $\text{CB}_{j,b}$ represents the age-specific consumption-to-biomass ratio for each predator species. Owing to the time invariance of these consumption estimates, it is assumed that predators are not food-limited (Magnússon 1995). These definitions of predation mortality and predator stomach contents correspond to a Type II functional response (Sparre 1980). To obtain an instantaneous rate of predation mortality, estimates of average annual predator biomass and prey abundance should ideally be used instead of beginning year abundance, making the equation for predation mortality recursive (Lewy and Vinther 2004). As in Van Kirk et al. (2010), an approximation of predation mortality was used to avoid the extensive iterations that would be required for parameter estimation.

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## Parameter estimation

The set of estimated model parameters includes age-specific abundances in the first year ($N_{i,a,1}$), annual recruitment ($N_{i,1,t}$; years 2 through the end of the time series), annual fully recruited fishing mortality rates ($F_{i,t}$), age-specific fishery ($s_{i,a}$) and survey ($r_{i,a}$) selectivity coefficients, and vulnerability parameters ($\rho_{i,j}$). Annual recruitment and fishing mortality parameters are each estimated as a mean parameter plus a vector of annual deviation parameters that are constrained to sum to zero. Model parameters were estimated using AD Model Builder (Fournier et al. 2012). The statistical estimation of model parameters allows the assumption that commercial catch, survey index, and food-habits data are subject to observation error, with some prior distributions assumed to constrain the model and improve parameter estimability.

The objective function contained five likelihood components (Table 3). Total commercial catch and aggregate survey indices were assumed to be lognormally distributed. Commercial catch age proportions, survey age proportions, and predator food habits (average proportions by weight) were assumed to follow multinomial distributions.

The objective function weights for each data set were determined with an iterative approach. In particular, weightings for the lognormal components were chosen to achieve approximately a 10% coefficient of variation (CV) for total commercial catch and a 30%–40% CV for aggregate survey indices. A higher CV was assumed for the trawl-survey component because of the large interannual variability apparent in the observed time series. It is presumed that this interannual variability results from variation in availability to survey gear and spatial heterogeneity in abundance (Overholtz et al. 1999). Weightings for the multinomial components were chosen to best approximate the average effective sample size. Following McAllister and Ianelli (1997), the effective sample size for species $i$ in year $t$ was calculated as

$$(13) \quad \text{EfN}_{i,t} = \frac{\Sigma_a \widehat{P}_{i,a,t}(1 - \widehat{P}_{i,a,t})}{\Sigma_a(P_{i,a,t} - \widehat{P}_{i,a,t})^2}$$

where $P_{i,a,t}$ is the observed proportion-at-age for species $i$ in year $t$, and $\widehat{P}_{i,a,t}$ is the predicted proportion-at-age. Annual effective sample sizes were then averaged over time. Sensitivity runs were conducted to determine the influence of the food-habits weighting on resulting predation rates.

Penalty functions were imposed on initial abundances, annual recruitment, and age-specific biomasses (Table 3). The penalty imposed on initial abundances (Yp) prevents age-specific abundances from deviating substantially from those predicted by exponential decay (Yr1), assuming a total mortality equal to the age-specific average. The penalty imposed on annual recruitment (Rp) prevents the coefficient of variation for the log recruitment of any species from becoming greater than a predefined threshold value. The threshold values for cod, silver hake, and herring were set at 1, 0.7, and 0.4, respectively. The penalty imposed on age-specific biomasses (Bp) prevents any age-specific biomass from falling below a predefined threshold of 10 kg. The weights for each of these penalties, $\text{Pwt}_Y$, $\text{Pwt}_R$, and $\text{Pwt}_B$, and their corresponding threshold values were selected iteratively.

## Monte Carlo simulations

Parameter estimates from the best fit three-species model were used to create a known simulated data set without error. Measurement errors of varying magnitudes were then added sequentially to each of the three data sets (commercial catches, survey indices and predator diet) to evaluate the sensitivity of predicted indices, including recruitment, predation mortality, and fishing mortal-

**Table 3.** Components of the likelihood function.

| Equation | Description |
|---|---|
| $\text{LL}_{\text{Total}} = \text{LL}_{\text{TC}} + \text{LL}_{\text{TS}} + \text{LL}_{\text{CP}} + \text{LL}_{\text{SP}} + \text{LL}_{\text{FH}} + \Sigma_i\text{Pen}_i$ | Total log likelihood |
| $\text{LL}_I = D_I \cdot \Sigma_{t,i} [\ln(I + 10^{-3}) - \ln(\hat{I} + 10^{-3})]^2$ | Lognormal distribution |
| $\text{LL}_I = D_I \cdot \Sigma_{t,i,a} [(I + 10^{-30}) \cdot \ln(\hat{I} + 10^{-30})]$ | Multinomial distribution |
| $\text{Pen}_i = \text{Pwt}_{Y_i} \cdot \text{Yp}_i + \text{Pwt}_{R_i} \cdot \text{Rp}_i + \text{Pwt}_{B_i} \cdot \text{Bp}_i$ | Total penalty |
| $\text{Yp}_i = \Sigma_a(N_{i,a,1} - \text{Yr1}_{i,a,1})^2$ | Initial abundance penalty |
| $\text{Rp}_i = 0.01 \cdot [\text{CV}(N_{i,1,t}) - \text{Rth}_i]^2 \quad \text{for} \quad \text{CV}(N_{i,1,t}) > \text{Rth}_i$ | Recruitment penalty |
| $\text{Bp}_i = \Sigma_{a,t} 0.01 \cdot (B_{i,t,a} - \text{Bth}_i)^2 \quad \text{for} \quad B_{i,t,a} < \text{Bth}_i$ | Biomass penalty |

**Note:** $I$ represents a data set index, $D_I$ is the corresponding objective function weighting, $\text{LL}_I$ is the log likelihood for data set $I$, $\text{Pen}_i$ is the total likelihood penalty for each species, and $\text{Pwt}_p$ is the objective function weighting for penalty $p$. All additional symbols are defined in Table 1.

ity. In all simulations, initial parameter values were set to the final parameter estimates from the single-species runs.

Lognormal errors were applied to both total annual survey indices and commercial catches, with standard deviations of 0.2, 0.4, 0.6, and 0.8. Multinomial errors were added to age proportions and predator food habits assuming known effective sample sizes. When measurement error was added to either commercial catch or survey index data sets, errors were added simultaneously to both annual total catches and age proportions. The standard deviations for lognormal multiplicative errors and sample sizes for the random multinomial draws were chosen to achieve approximately the same percent difference between observed and true catches. Accordingly, effective sample sizes of 500, 75, 40, and 20 were chosen for commercial catch age proportions; 1000, 200, 100, and 60 for survey age proportions; and 2500, 500, 100, 50, and 10 for predator food habits. As the multinomial effective sample size decreases, the magnitude of measurement error incorporated into the proportions increases.

Initial simulations tested the stability of parameter estimates and their variances in relation to the number of replicates. Analysis of trends in 95th percentiles and scaled root mean squared error over time indicated that both measures generally achieved stable values at approximately 200–300 simulations (Supplemental Fig. S1[1]). Based on these initial results, 400 randomizations were completed for each error level.

In an effort to portray the magnitude of error present in the input data, measurement error was simultaneously incorporated into all three data sets in levels comparable to the standard deviations of the residuals of the best model fit. Total commercial catch and survey index standard deviations for lognormal errors were set to 0.1 and 0.4, respectively. Multinomial effective sample sizes for commercial catch age proportions, survey index age proportions, and predator diet were set to 1000, 200, and 10, respectively. For this simulation, 500 randomizations were conducted. Scaled mean error and coefficient of variation were used to quantify resulting parameter bias and precision, respectively (Walther and Moore 2005).
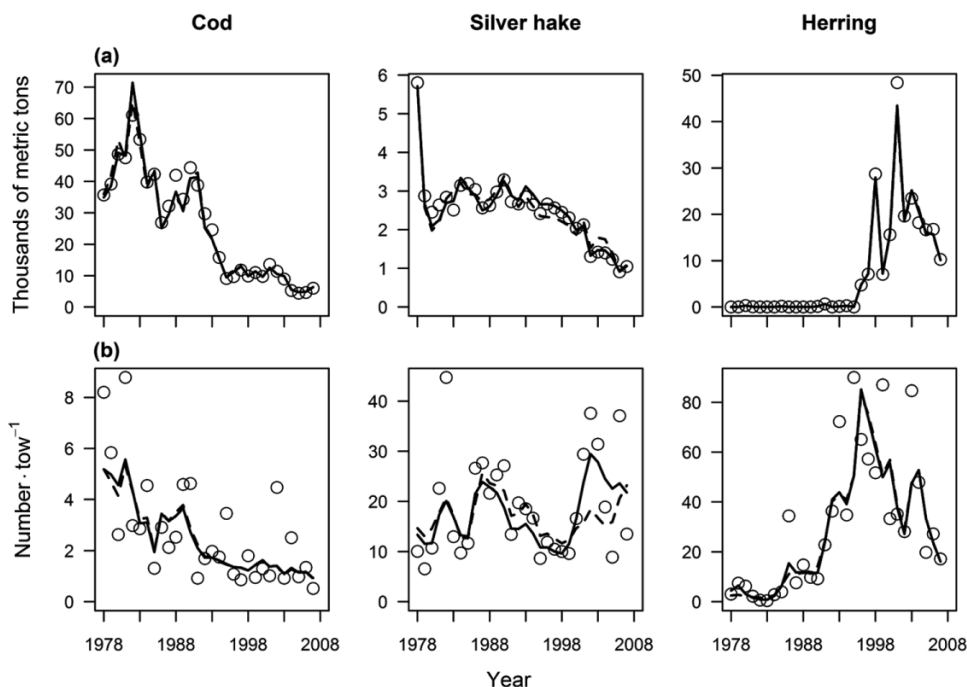
## Results

### Model fitting

We compare single-species and multispecies fits to examine both the consistencies and points of deviations between the two approaches. These model fits are compared with the observed

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[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2012-0229.

**Fig. 1.** Observed (open circles) and predicted total annual (*a*) commercial catch and (*b*) survey indices from the single-species (dashed line) and multispecies (solid line) runs.



data and predicted indices from recent stock assessments. The assessment-predicted indices are not considered to be known underlying values. We do not expect the multispecies results to completely agree with the assessment-predicted indices, but instead are using these single-species estimates as a basis for comparing the catch-at-age models presented here.

In both formulations, single-species and multispecies predicted total annual commercial catch closely followed observed catches with only minor differences apparent between runs (Fig. 1*a*). Total annual survey indices also followed temporal trends in the observed time series, but greater interannual variability was apparent (Fig. 1*b*). For both commercial and survey age proportions, the predicted trends captured much of the apparent interannual variability. However, both formulations predicted an accumulation of biomass in the older age classes of cod and silver hake during the end of the time series that was inconsistent with the observed age proportions (Supplemental Figs. S2–S7[1]).

The objective-function weightings for each data set were selected iteratively to reflect prespecified coefficient of variations for lognormal variables and calculated effective sample sizes for multinomial variables (Supplemental Table S1[1]). The resulting standard deviations of total commercial catch residuals across both model formulations ranged from 0.04 to 0.11, whereas those for total survey indices ranged from 0.34 to 0.56 (Supplemental Table S2[1]). Contributions of each data set to the objective function further indicated a better fit to commercial catches than to trawl-survey indices (Table 4). Multinomial data set weightings approximated average effective sample sizes over the time series (Supplemental Figs. S8–S10[1]). Across all runs, the maximum observed correlation between parameter pairs was 0.80.

Agreement among models in predicted total annual abundance varied across species (Fig. 2*a*). For cod, both single-species and multispecies predictions closely matched the decline in total abundance estimated in the single-species stock assessment. For silver hake and herring, total abundance estimated from the multispecies model was generally greater than that estimated from the single-species run. For herring, both multispecies and single-species predictions were the same order of magnitude as that

predicted by the assessment; predicted abundance increased and peaked between 1995 and 2003. In the case of silver hake, total abundance estimated with both model formulations consistently exceeded estimates of minimum swept biomass from the trawl surveys. Silver hake abundance varied without a clear trend, with peaks in the 1980s and 2000s. For all species, trends in predicted recruitment for both model formulations generally followed the same trends as total annual abundance (Fig. 2*b*).

As expected, the single-species models generally produced higher estimates of fully recruited fishing mortality rates than the multispecies models (Fig. 2*c*). For cod, fishing mortality estimated in both the single-species and multispecies models closely followed the rates estimated in the assessment. In the beginning of the time series, both models consistently predicted higher fishing mortality rates than those of the assessment, while both models predicted consistently lower rates during the latter half of the time series. For herring, the trends in fishing mortality predicted by the assessment drastically differed from those predicted using both catch-at-age models. The VPA conducted during the herring stock assessment predicted a decline in fishing mortality over the time series, while the results of both the single-species and multispecies catch-at-age models developed here predicted a strong increase in fishing mortality.

Estimated predation mortality (*M2*) varied across species, prey age, and time (Fig. 3*a*). Predation mortality only represented a maximum of 15% of total mortality for cod (Fig. 3*b*) and declined in parallel with cod abundance (as associated with cannibalism). For silver hake and herring, however, predation accounted for as much as 91% of total mortality. As with cod, silver hake *M2* mirrored the pattern of silver hake abundance. By contrast, herring *M2* was high but declined over time as herring abundance increased. For cod and silver hake, predation mortality decreased with increasing age, whereas herring *M2* increased from age-1 to age-2, beyond which it decreased with age.

For silver hake, predation mortality constituted a substantial proportion of total mortality even for the oldest age classes. In this multispecies model, predation size selectivity is dictated by predator size-preference coefficients, which were empirically calcu-

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**Table 4.** The contributions of each objective function component in both the single-species and multispecies models.

| | Single-species | | | Multispecies | | |
|---|---|---|---|---|---|---|
| | Cod | Silver hake | Herring | Cod | Silver hake | Herring |
| Total commercial catch | 27.24 | 71.08 | 6.80 | 29.45 | 28.59 | 3.16 |
| Total survey index | 464.12 | 441.05 | 896.28 | 459.03 | 328.88 | 456.82 |
| Commercial age proportions | 96.66 | 130.49 | 2.89 | 100.88 | 150.20 | 3.46 |
| Survey age proportions | 149.13 | 292.73 | 595.15 | 156.20 | 341.63 | 718.93 |
| Food habits | NA | NA | NA | 146.22 | 66.51 | 0 |
| Abundance penalty | 0 | 0 | 0 | 0 | 0 | 0.53 |
| Recruitment penalty | 0 | 0 | 0.24 | 0 | 0 | 0 |

**Note:** The abundance penalty constrains the age distribution in the initial year; the recruitment penalty constrains the CV of estimated recruitment each year (Table 3).

**Fig. 2.** Comparison of predicted annual (a) total abundance, (b) recruitment, and (c) fishing mortality from the single-species run (dashed line), multispecies run (solid line), and the most recent stock assessments (open circles; Cod: NEFSC 2008; silver hake: Brodziak et al. 2001; herring: Overholtz et al. 2004 and Shepherd et al. 2009). For silver hake total abundance and recruitment, absolute estimates were not available; therefore, the points represent minimum swept area estimates.
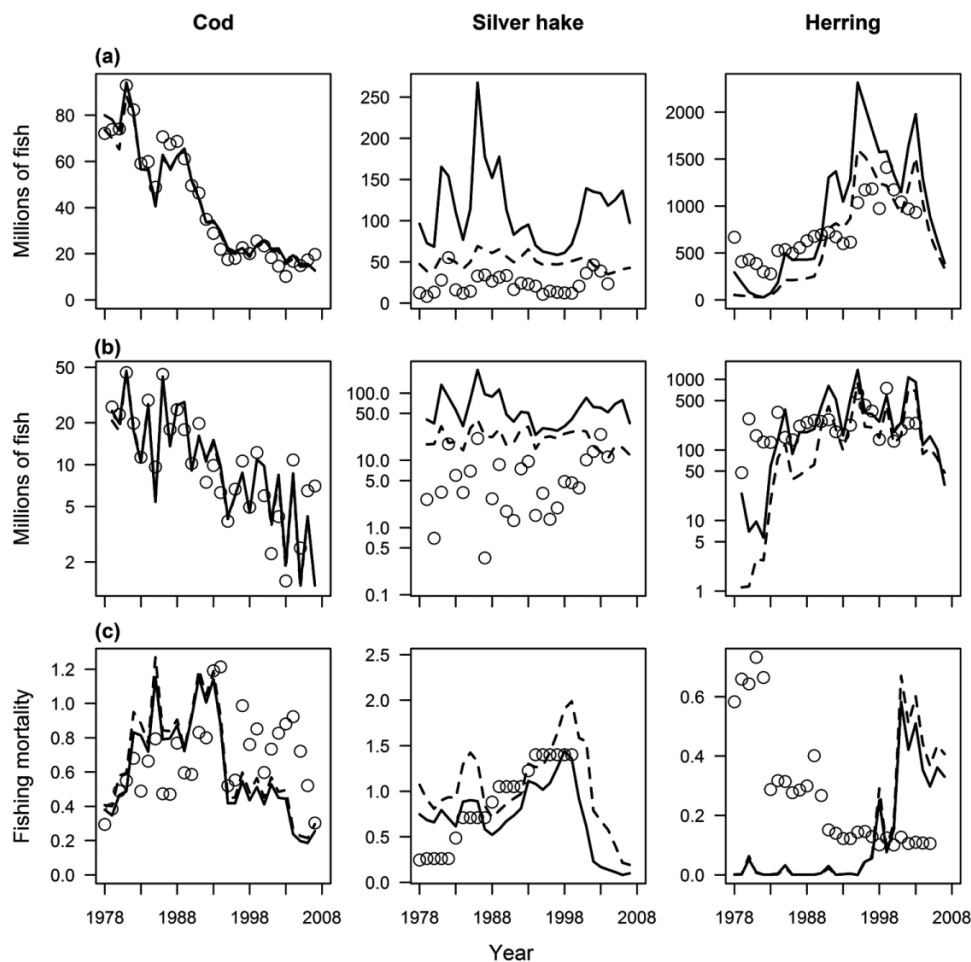


lated from observed predator and prey lengths. Across the time series, the dominant source of silver hake predation was cannibalism (Fig. 3c). Accordingly, the size-preference parameters for silver hake cannibalism can provide insight as to the source of these large predation mortality rates on older age classes. In particular, the large estimated variance in the observed predator–prey weight ratio ($\sigma$) resulted in a wide distribution of silver hake size preference (Table 5).

Sensitivity runs were conducted to investigate the influence of this variance term on silver hake size preference. Reducing this variance by either one-half or by an order of magnitude caused a substantial decline in the width of the silver hake size-preference

curve and an increase in the silver hake – silver hake species-preference coefficient ($\rho$). However, it also caused an unrealistically large increase in both silver hake recruitment and age-1 predation mortality near the end of the time series.

The principle predator varied among prey species (Fig. 3c). While the dominant sources of both silver hake and Atlantic cod predation were cannibalism (cod is only prey to itself in this submodel), the dominant predator of herring was cod even though cod abundance exhibited a precipitous decline. For both silver hake and herring, the proportion consumed by cod declined in the last decade, as expected from cod's estimated abundance. Estimated species-preference coefficients indicated that relative to

**Fig. 3.** For each prey species, the (*a*) age-specific predation mortality (M2), (*b*) proportion of total mortality (Z) due to predation, and (*c*) the predator species responsible for the observed predation.
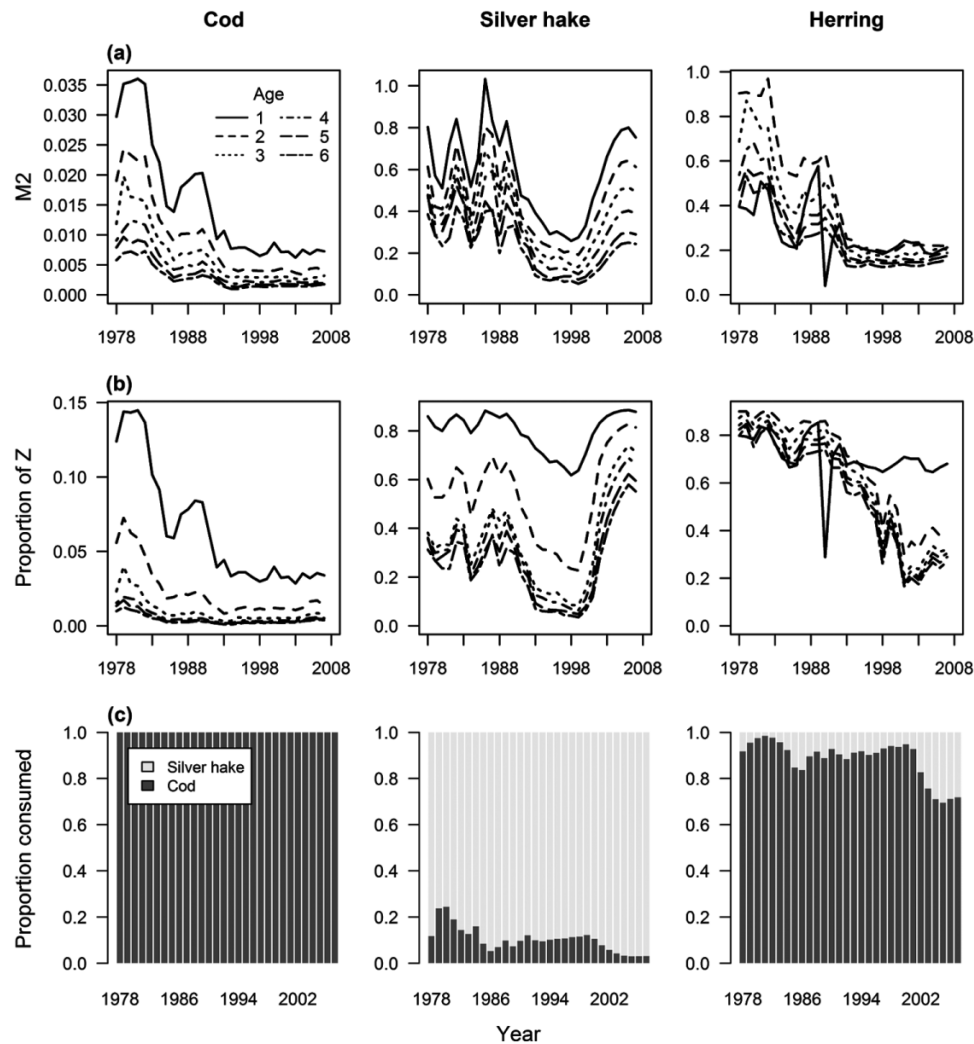


**Table 5.** Average predator–prey weight ratios ($\eta$), the variance in each ratio ($\sigma$), estimated species-preference coefficients ($\ln(\rho)$), and their associated standard deviations (in parentheses) for each species interaction.

| | | Prey species | | |
|---|---|---|---|---|
| | Predator species | Cod | Silver hake | Herring |
| $\eta$ | Cod | 4.159 | 4.833 | 3.996 |
| | Silver hake | NA | 3.946 | 2.261 |
| $\sigma$ | Cod | 2.259 | 1.875 | 1.433 |
| | Silver hake | NA | 2.979 | 1.093 |
| $\ln(\rho)$ | Cod | 0.618 (0.889) | 1.549 (0.171) | 3.255 (0.048) |
| | Silver hake | NA | 5.396 (0.029) | 3.223 (0.155) |

**Note:** Parameters $\eta$ and $\sigma$ were calculated from observed predator and prey lengths. Parameter $\rho$ was estimated as a model parameter in log space.

other food, cod had a high preference for herring, a moderate preference for silver hake, and a low preference for cannibalism (Table 5). Furthermore, the coefficient for cod cannibalism was highly uncertain, as indicated by the large corresponding standard deviation. By contrast, silver hake had a higher preference for cannibalism than for herring. Predicted diets indicated an underestimation in the proportion of modeled fish species in predator diets. In the case of cod, the model overestimated cod

consumption of herring relative to silver hake (Supplemental Figs. S11–S14[1]).

Increasing the food-habits objective-function weighting moderately impacted trends in the dominant predator for each prey species but minimally impacted other predictions including recruitment, fishing mortality, and predator diet. An increase in this objective-function weighting minimally influenced rates of predation, resulting in a 5.7% increase in the maximum observed M2 for silver hake and a 3.9% increase in that for herring. While predation mortality rates were robust to the food-habits data set weighting, the weighting influenced estimated species-preference coefficients. As the weighting increased, cod's preference for cannibalism decreased, its preference for silver hake increased, and its preference for herring slightly decreased. Likewise, the increased weighting resulted in a decreased preference for silver hake cannibalism and an increased silver hake preference for herring. These changes in species-preference coefficients resulted in enhanced roles of both cod as a predator to silver hake and silver hake as a predator to herring. However, increasing the food-habits objective-function weighting also resulted in convergence errors and an overestimation of effective sample size; therefore, the original objective-function weighting was selected for the final run.

A sensitivity run was also conducted to examine the impact of a reduction in assumed total ecosystem biomass on estimated pre-

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**Fig. 4.** 95th percentiles for estimated annual fishing mortality rate when low measurement error levels were introduced into (*a*) commercial catches, (*b*) survey indices, and (*c*) predator diets. For commercial and survey catches, error levels represent the standard deviations of the multiplicative errors incorporated into total annual catches. For food-habits data, error levels represent the number of draws from a multinomial distribution where measurement error increases as effective sample size decreases. In all plots, the solid line represents the true parameter values.
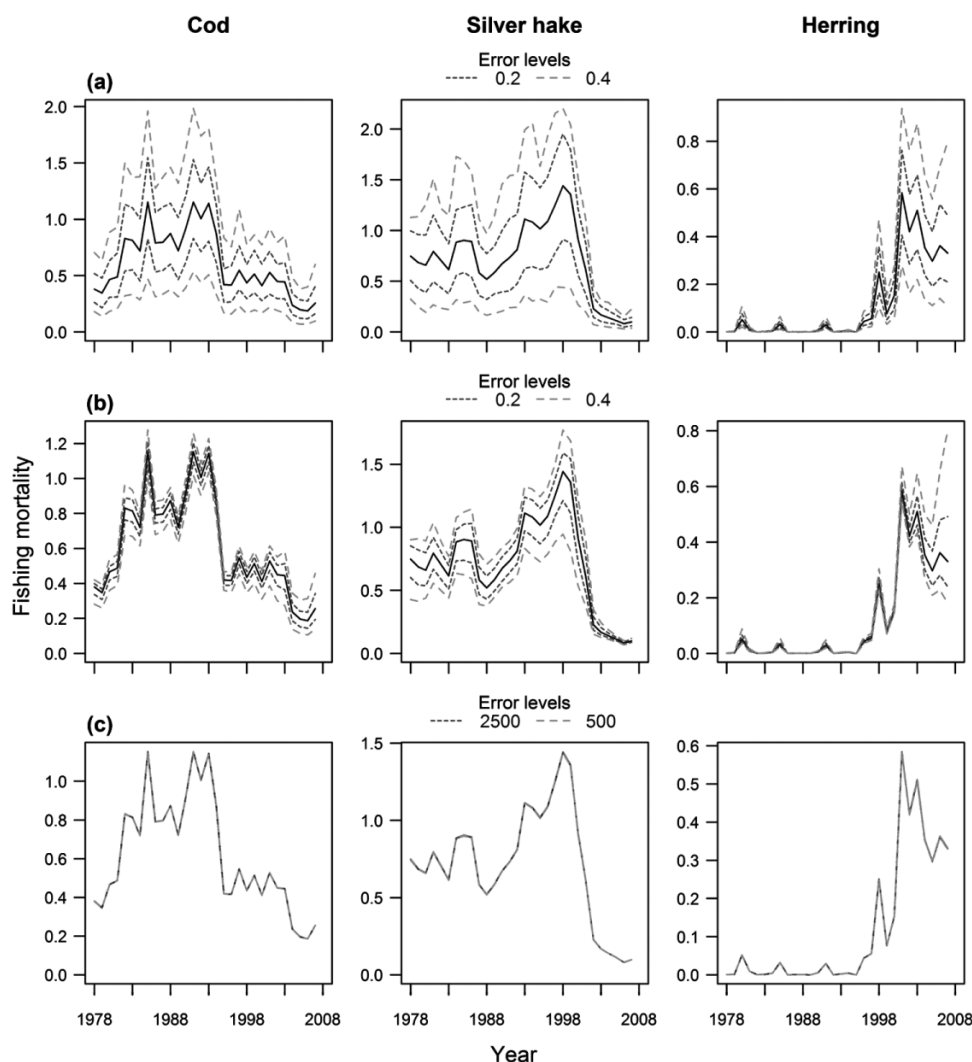


dation mortality rates and species-preference coefficients. Reducing ecosystem biomass to approximately one-half its original estimate had a negligible impact on estimated recruitment, total annual abundance, predicted predator diets, and rates of predation. For any species or age class, the maximum percent difference in predicted recruitment, total abundance, and $M2$ between runs was 0.53%, 0.59%, and 3.49%, respectively. In contrast, estimated species-preference coefficients decreased by 51%–53% owing to the definition of these coefficients as predator preferences relative to other food.

### Monte Carlo simulations

In general, the parameters of the multispecies model could be estimated, even with substantial levels of simulated error. As expected, the uncertainty in predicted indices such as recruitment and fishing mortality increased with increased measurement error in commercial catches, survey indices, and food-habits data.

At low measurement error levels ($\sigma \leq 0.4$), errors introduced into commercial catches resulted in greater uncertainty in predicted fishing mortality rates than corresponding levels of error in survey indices (Figs. 4*a*, 4*b*). However, at higher error levels ($\sigma = 0.6$ to 0.8), the model could not fully resolve fishing mortality

rates of the prey species when error was introduced into the survey data set (Supplemental Fig. S15[1]).

Across all levels of measurement error, errors in commercial catches resulted in less uncertainty in predicted recruitment than errors in survey indices (Figs. 5*a*, 5*b*). For survey index errors, recruitment estimation, particularly at the end of the time series, began to break down at an error level of 0.4. With error in the commercial catch, all error levels produced reasonable yet increasingly uncertain recruitment estimates for cod and herring (Fig. 5*a*; Supplemental Fig. S16[1]). However for silver hake, recruitment estimation broke down at an intermediate error level of 0.6.

Similar to recruitment, estimated predation mortalities were more sensitive to measurement error in survey indices than in the commercial catch (Figs. 6*a*, 6*b*). For both data sources, parameter uncertainty increased substantially at a measurement error level of 0.6. For the trawl-survey data set, an error level of 0.8 resulted in age-1 predation mortalities greater than 3.0 for both silver hake and herring. Across all estimated parameters and levels of measurement error, error in predator diets had the least effect on parameter estimates (Figs. 4–6). Species-preference coefficients were quite sensitive to measurement errors in both survey indices

**Fig. 5.** 95th percentiles for estimated annual recruitment when low measurement error levels were introduced into (*a*) commercial catches, (*b*) survey indices, and (*c*) predator diets. For commercial and survey catches, error levels represent the standard deviations of the multiplicative errors incorporated into total annual catches. For food-habits data, error levels represent the number of draws from a multinomial distribution where measurement error increases as effective sample size decreases. In all plots, the solid line represents the true parameter values.
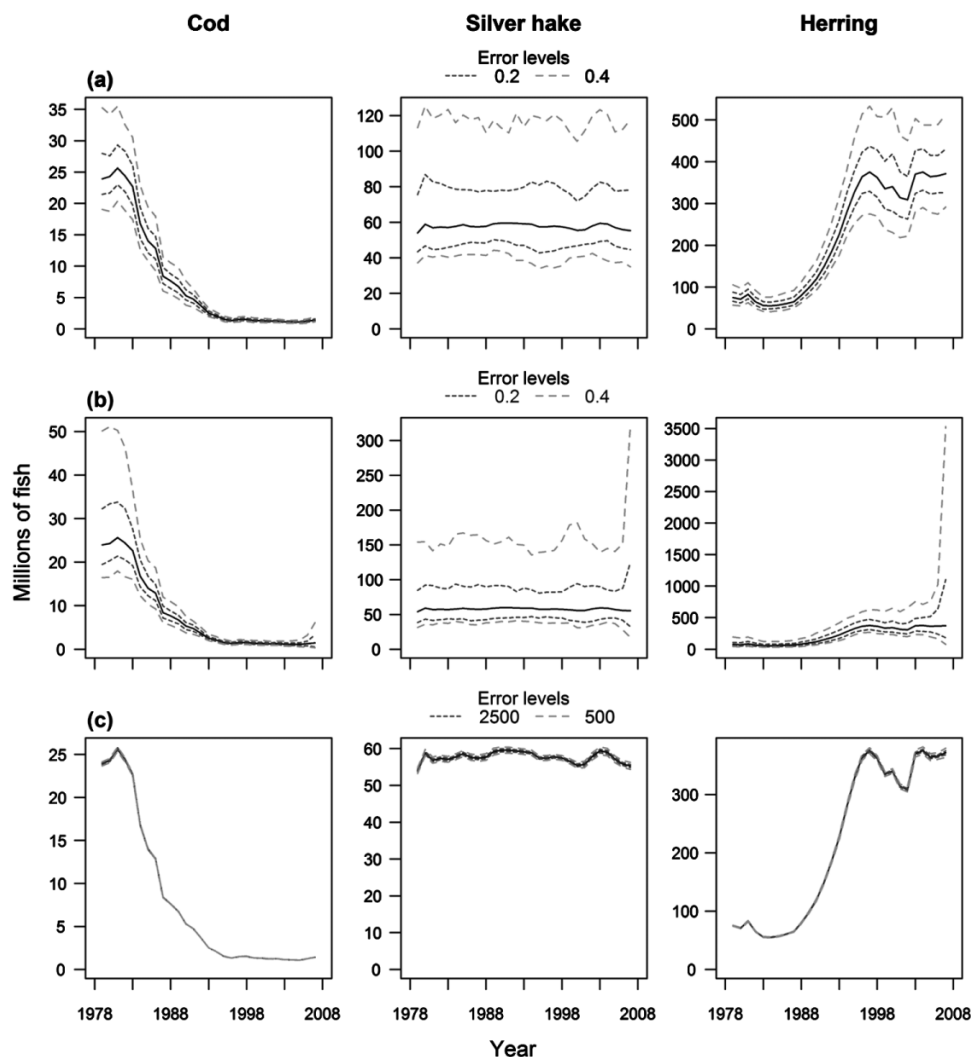


and commercial catches (Supplemental Fig. S17[1]). Across all sources of measurement error, the species-preference coefficient for cod cannibalism was the most sensitive to errors in the input data.

With measurement error added to all three data sources in levels comparable to the standard deviations of the residuals of the best model fit (Supplemental Table S2[1]), the model produced reasonable estimates for most parameters (Fig. 7). Notable exceptions included the annual recruitment of both silver hake and herring near the end of the time series (Fig. 7*a*), where some runs predicted a large increase in recruitment that was not apparent in the observed time series. Across all years, silver hake recruitment estimates were quite uncertain, where the width of the 95th percentiles was approximately twice as large as the magnitude of the true recruitment level, and the annual CV ranged from 33.6% to 156.6% (Table 6). However, the medians were within approximately 20% of the true recruitment values. For herring, predicted recruitment exhibited an average CV of 34.3% until the final year of the time series where it jumped to 196% (Table 6; Fig. 7*a*). Similarly, uncertainty in predicted fishing mortality increased substantially in the last 3 years (Fig. 7*b*), further indicating that the

model was unable to fully resolve herring dynamics at the end of the time series.

For all three species, this model overestimated age-1 predation mortality (Fig. 7*c*). This overestimation was most severe for cod $M2$, which exhibited a scaled mean error ranging from 1.47 to 1.87 and an average annual CV exceeding 120% (Table 6). Taken together with the large standard deviation of the cod cannibalism species-preference coefficient and the high sensitivity of this coefficient to measurement error in the input data sets, this overestimation in cod $M2$ further demonstrates the uncertainty in the extent of cod cannibalism. For the other two species, the model produced slightly biased but reasonable predation mortality estimates, with average annual CVs less than 35%.

## Discussion

The multispecies model fit the observed data as well as the individual single-species age-structured models, but differed in the estimated levels of abundance, fishing mortality, and natural mortality. The differences among the multispecies, single-species, and stock-assessment model results can be interpreted with respect to the trophic role of the species. Like previous modeling

**Fig. 6.** 95th percentiles for estimated age-1 predation mortality when all measurement error levels were introduced into (*a*) commercial catches, (*b*) survey indices, and (*c*) predator diets. For commercial and survey catches, error levels represent the standard deviations of the multiplicative errors incorporated into total annual catches. For food-habits data, error levels represent the number of draws from a multinomial distribution where measurement error increases as effective sample size decreases. In all plots, the solid line represents the true parameter values.
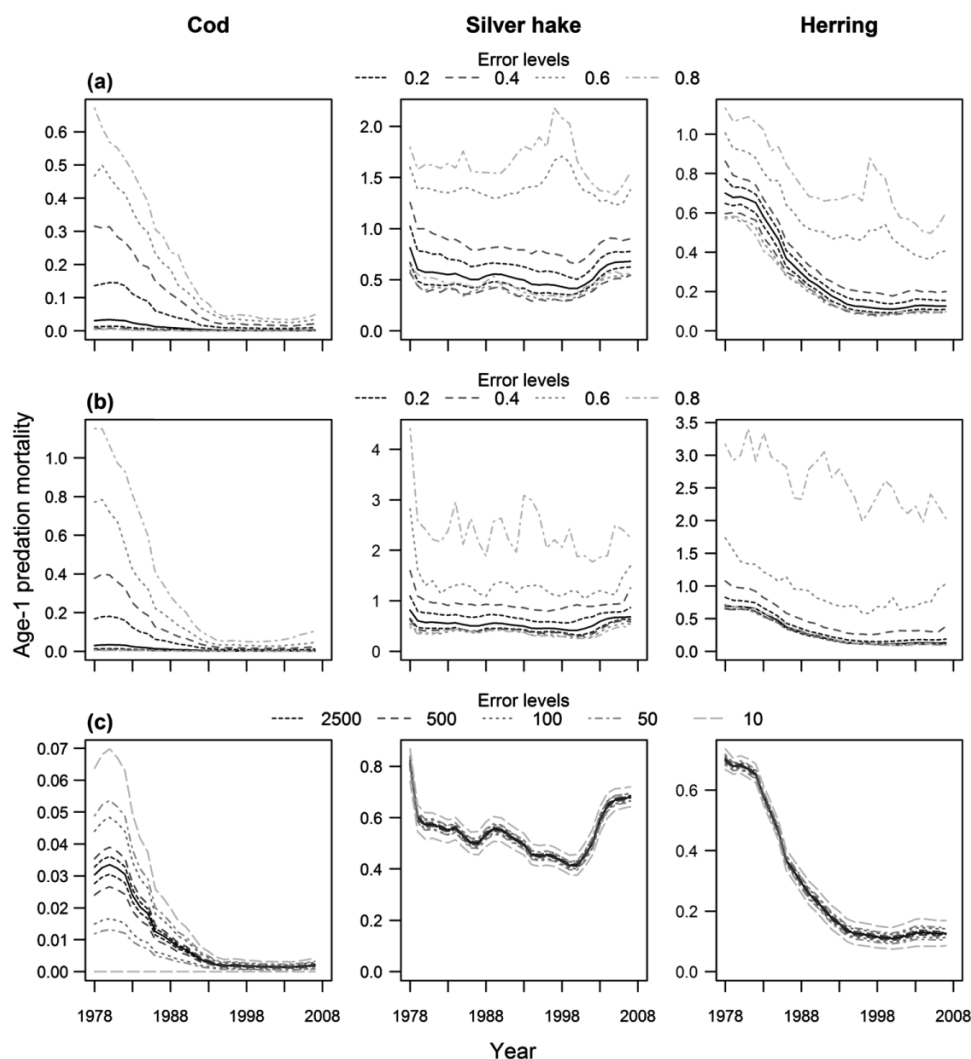


efforts (Tsou and Collie 2001*a*; Overholtz et al. 2008; Tyrrell et al. 2008), our results demonstrate temporal and ontogenetic variation in total natural mortality and the strong influence of predation on community dynamics. Abundance patterns predicted in the multispecies formulation result from the interplay between fishing and predation mortality.

In the case of Atlantic cod, the close consistency in abundance predictions across the three outputs is due to cod's primary role as a predator species in the model; the effect of predation is minimal. In this submodel, cod is only a prey species to itself through cannibalism, and the estimated species-preference coefficient indicates a low preference towards cannibalism. Furthermore, with predicted age-specific predation mortality rates less than 0.04 and constituting a maximum of 15% of total mortality, cod's total natural mortality rate was effectively constant between model formulations. Therefore, the decline in cod abundance was driven by fishing mortality.

For silver hake the difference in magnitude between model and survey-based abundance estimates occurs because the latter estimate is based on the area swept by the trawl survey and therefore represents a minimum estimate that does not take into account

species catchability. Furthermore, total abundance estimated from the multispecies run was considerably larger than that estimated from the single-species run. The dominant role of silver hake as prey of cod and silver hake resulted in the greater predicted abundance of the multispecies formulation, even though residual natural mortality was lower in the multispecies run. The decline in silver hake abundance during the late 1990s corresponded with a period of high fishing mortality. Predation mortality was higher during the abundance peaks in the 1980s and 2000s.

Predicted recruitment and total annual abundance of herring from the single-species and multispecies models roughly follow the trends of the single-species stock assessment. Total abundance estimated from the multispecies run was somewhat greater than that estimated from the single-species run, which again reflects the trophic role of herring as prey of cod and silver hake. In an application of MSVPA-X on the northeast US continental shelf evaluating the influence of predation on forage species, both age-specific and total annual predicted abundance was greater in the multispecies VPA than in the single-species formulation (Tyrrell et al. 2008). The peak in herring abundance in the late 1990s

**Fig. 7.** 95th percentiles (dashed lines), median (dotted line), and true (solid line) annual recruitment (*a*), annual fully recruited fishing mortality (*b*), and age-1 predation mortality rates (*c*) for the simulation where measurement error was incorporated into all three data sets.
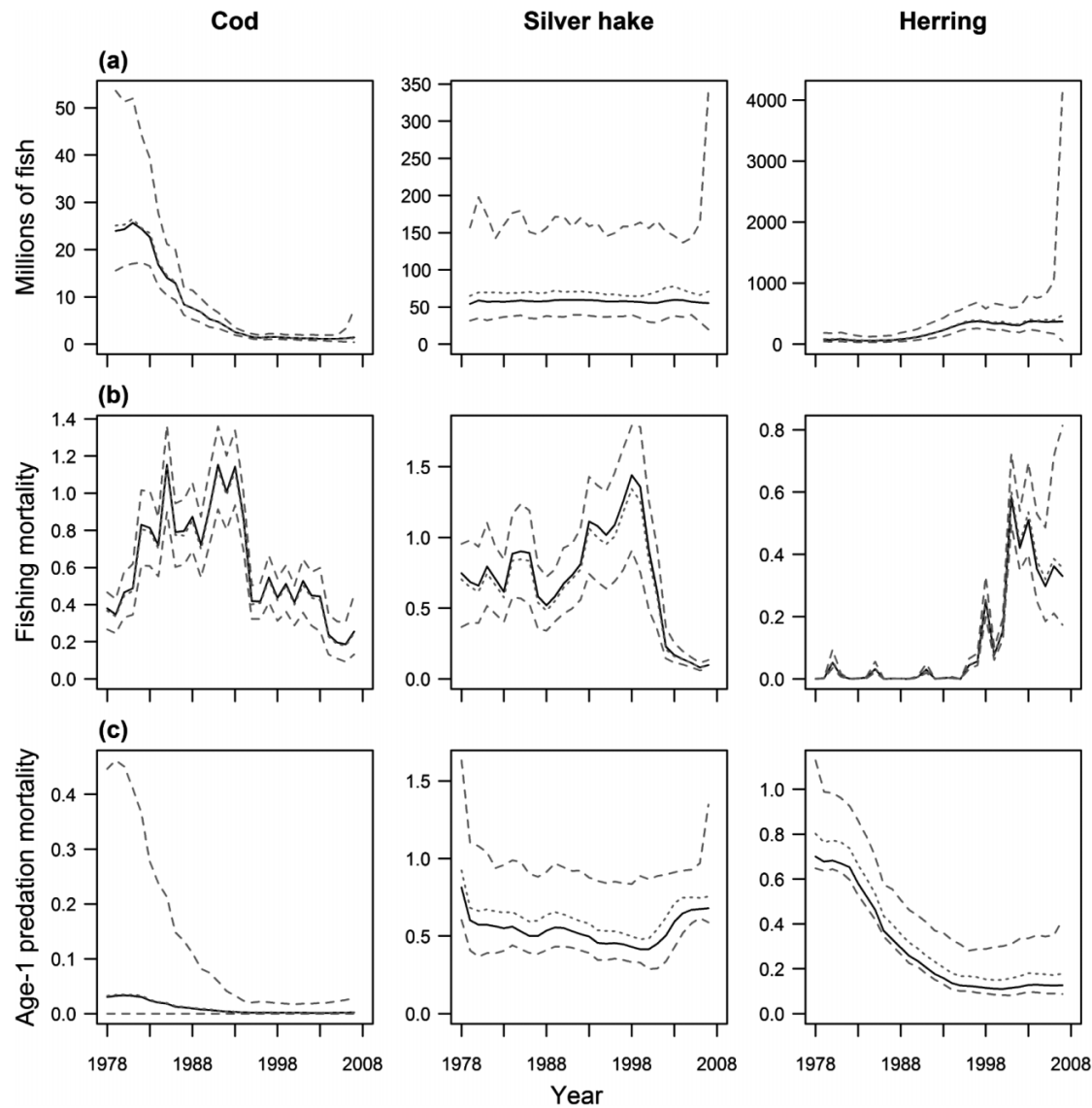


**Table 6.** The range of scaled mean error (SME) and coefficient of variation (CV) values for predicted annual fishing mortality (*F*), recruitment, and age-1 predation mortality (*M2*) for the simulation in which measurement error was incorporated into all three data sets.

| Parameter | Measure | Cod | Silver hake | Herring |
|---|---|---|---|---|
| *F* | SME | −0.04 − −0.01 | −0.07 − 0.02 | 0.03 − 0.19 |
| | CV | 9.03 − 30.62 | 15.49 − 25.58 | 9.4 − 49.07 |
| Recruitment | SME | 0.01 − 0.25 | 0.26 − 0.74 | 0.07 − 1.4 |
| | CV | 14.74 − 88.87 | 33.57 − 156.65 | 22.23 − 196.72 |
| Age-1 *M2* | SME | 1.47 − 1.87 | 0.12 − 0.25 | 0.14 − 0.56 |
| | CV | 122.39 − 136.68 | 11.75 − 33.37 | 10.84 − 43.67 |

corresponds to lower predation mortality from cod; the decline in herring abundance since 2003 can be explained by increased fishing mortality.

Similarly for fishing mortality, the consistency between cod fishing mortality rates estimated by the single-species and multi-species models is due to the low levels of predation experienced by the species. With these low predation rates and therefore similar total natural mortality rates, fishing mortality is the primary factor driving cod population dynamics in both formulations. The retrospective pattern observed between the single-species and stock assessment predictions is likely an artifact of the varying assumptions made between this statistical catch-at-age model and the VPA conducted for the single-species assessment. In the VPA, the time series was split in 1994 (NEFSC 2008); however, we assumed one continuous time series with one selectivity ogive.

For herring and silver hake, the multispecies predicted fishing mortality was consistently lower than the single-species estimate, with the substantial predation mortality rates resulting in a

smaller contribution of fishing to the total mortality experienced. For these species, both predation and fishing drive their population dynamics. The added losses experienced by prey species due to predation help to explain the differences in fishing mortality and abundance estimates between the single-species and multispecies formulations. A greater species abundance, and therefore a smaller imposed fishing mortality, was needed to account for the predation losses incurred. This result is consistent with those of other multispecies modeling efforts (Overholtz et al. 2008; Tyrrell et al. 2008; Moustahfid et al. 2009).

Furthermore, for Atlantic herring, the drastic difference in temporal trend between the fishing mortality predicted in the assessment and that predicted using both catch-at-age models may be a function of assumptions regarding stock dynamics. The stock assessment assumes a stock complex spanning both Georges Bank and the Gulf of Maine (Shepherd et al. 2009), while the results from the catch-at-age models are based on commercial catches from Georges Bank alone. Our assumption that a constant proportion of the stock is found on Georges Bank could have potentially biased the results. Furthermore, the large difference in predicted fishing mortality between the assessment and both catch-at-age models could be a reflection of differences in the dynamics of the Georges Bank versus Gulf of Maine populations. Previous work has indicated that the Georges Bank component of the stock complex exhibited both a more precipitous decline in abundance than that of the Gulf of Maine, as well as a more recent recovery (Overholtz and Friedland 2002).

Regardless, trends in age-specific predation mortality indicate that the losses due to predation vary substantially over both age and time. Consequently, models that assume a time- and (or) age-invariant total natural mortality do not fully capture the dynamics of the population. Increased biological realism, however, can result in increased uncertainty in parameter estimation, indicated here by the uncertainty in some of the species-preference coefficients, particularly that for cod cannibalism.

The magnitude of predation mortality experienced by the model's two primary prey species is substantial. Silver hake and herring both experience predation mortality rates exceeding 0.8, which is two and four times, respectively, the natural mortality rate assumed in the single-species stock assessments. The estimated predation rates constitute 70%–80% of the total mortality imposed on these two species, indicating the importance of predation in controlling the population dynamics of the prey species in this model. This increased total natural mortality reduces the influence of fishing on the species' population dynamics and projections for future fisheries yield.

Other multispecies models constructed for the northeast US indicate similar rates of predation. Tsou and Collie (2001a), in an MSVPA constructed for Georges Bank, estimated predation mortality rates of 0.003–0.3 for cod, 0.13–1.6 for silver hake, and 0.06–0.75 for herring. Likewise, in an MSVPA-X of the northeast US continental shelf, Tyrrell et al. (2008) estimated average age-0 and age-1 herring predation mortality between 0.94 and 3.2. Together these studies further support the importance of predation in prey population dynamics. However, age-specific rates of predation may change once the model presented here is expanded to include additional fish species on Georges Bank.

We assumed that the empirical average ($\eta$) predator–prey weight ratio and variance ($\sigma$) reflected the preferred ratio and variance because prey lengths were only available for a subset of the food-habits data. While our empirical weight ratios are similar to those estimated for cod and silver hake in the Georges Bank (Tsou and Collie 2001a) and North Sea (Gislason and Helgason 1985) MSVPA applications, some of our variance terms are greater than those either estimated or assumed in other MSVPA applications (Gislason and Helgason 1985; Van Kirk 2008). This increased variance is particularly apparent for silver hake cannibalism, resulting in a wide range of consumed prey sizes as well as a possi-

bility, albeit small, that individuals consume prey larger than themselves. This large variance estimate did not appear to be related to sample size ($n = 743$, which represented the largest sample size of any species interaction). Regardless, these high $\sigma$ estimates resulted in wide ranges of consumed prey sizes and consequently enhanced predation mortality rates of the oldest age classes. As in previous studies (Andersen and Ursin 1977; Helgason and Gislason 1979), we assumed a lognormal size selectivity function, which is symmetric on a log scale. Some authors have used asymmetric functions, which allow predators to eat prey much smaller but not larger than themselves (Tsou and Collie 2001a; Lewy and Vinther 2004). These asymmetric size-preference curves could be considered in future applications.

The majority of silver hake predation is due to cannibalism, indicating strong density dependence. This result is supported by previous modeling efforts, which indicated that cannibalism accounted for as much as 50% to 80% of silver hake predation (Tsou and Collie 2001a; Link et al. 2012). For herring, however, cod is the principle predator across the time series in this model, in contrast with previous MSVPA studies. Tyrrell et al. (2008) showed that the most important predators for herring were silver hake, white hake (*Urophycis tenuis*), summer flounder (*Paralichthys dentatus*), and goosefish (*Lophius americanus*). Likewise, while Tsou and Collie (2001a) indicated that both cod and silver hake were predators of herring, silver hake was responsible for 50% to 90% of herring consumed biomass. The dominance of cod as herring's top predator in this model is in part due to the effective sample size of the food-habits data and the resulting objective-function weighting assigned to the data set. While increasing the food-habits weighting increased silver hake consumption of herring, silver hake still exhibited a higher preference for cannibalism than herring, and cod maintained its preference for herring over silver hake. Furthermore, the emergence of convergence errors and overestimation of food-habits effective sample size ultimately prohibited its use as the final run.

The food-habits data contain important information needed to quantify predation mortality. However, as a result of the small effective sample size of the diet data, most of the statistical power for parameter estimation originates from the commercial catch and survey index data sets. Owing to the large interannual variability apparent in the trawl-survey data as a consequence of changes in availability to the survey gear (Overholtz et al. 1999), commercial catch data were assigned the greatest data set weighting and exhibited the smallest resulting CV. The use of annual food-habits data, in contrast with binning data over 5-year intervals, may have produced a greater effective sample size; yet in doing so, the model would have tried to capture the large variability inherent of food-habits data and not necessarily true changes in predation (Van Kirk et al. 2010). On the other hand, assuming time-invariant predator diets would have ignored true changes in prey availability and predation rates over the time series. Accordingly, averaging over 5-year blocks served as a compromise.

As a result of the large variability in the observed food-habits data, predicted predator diets exhibited only small changes with increases in the food-habits objective-function weighting. This result indicated that the model was unable to fully capture trends in diet even when it was given more power to fit the observed data. This pattern may change if more species, especially prey, were included in the model. While the magnitude of the species interactions was uncertain (as indicated by the underestimated proportion of modeled fish species in predator diets and the overestimated role of cod as a predator to herring), the model produced robust estimates of predation mortality rates. It is the estimation of these losses due to predation that are arguably the most critical aspect to the incorporation of ecological interactions into stock assessments.

A key benefit of the statistical multispecies model is the statistical estimation of model parameters and the recognition that

observed data sets contain measurement error. A potential draw-back of multispecies statistical models is the necessity of simultaneously estimating numerous parameters for each species as well as the predation parameters that define the interactions among species (Van Kirk et al. 2010). With Monte Carlo simulations, we evaluated robustness in parameter estimation to predetermined levels of measurement error in the three input data sets. We note that these simulations address the influence of observation error but do not consider structural uncertainty of the underlying model. The consequence of structural uncertainty, for example, through fitting single-species models to simulated multispecies data, could be examined in future simulation analyses.

As expected, uncertainty in the predicted indices increased with increasing levels of measurement error in commercial catch, survey index, and food-habits time series. Uncertainty in fishing mortality was most sensitive to increasing commercial catch measurement errors, whereas uncertainty in recruitment and predation mortality was most sensitive to increased survey index measurement error. These results demonstrate the importance of both data sets to the estimation of population parameters. Across all predicted indices, estimates were most robust to increased uncertainty in predator stomach contents. This finding was presumably due to the low effective sample size and resulting small objective-function weighting for the food-habits data.

While the model began to fail at high levels of measurement error, parameters of the multispecies model were estimable from data simulated with levels of error comparable to those in the observed data. The multispecies model was able to reconstruct the true underlying trends in predation mortality. Furthermore, while uncertainty in the resulting parameter estimates was apparent, the median estimates were not substantially biased. The small positive bias in estimated silver hake and herring predation mortality rates could arise from the approximation used to calculate $M2$. For cod, the more substantial positive bias likely results from the underlying uncertainty in the extent of cod cannibalism. The Monte Carlo simulations enhance our confidence in the performance of the statistical model, even with the increased complexity in parameter estimation inherent in the multispecies framework.

Through the development of a statistical catch-at-age model, we have expanded the multispecies modeling approaches implemented for Georges Bank and the northeast US continental shelf. Building upon previous efforts, we have demonstrated that multispecies models can be fit statistically to time series of catch, abundance, and diet data. Monte Carlo simulations indicated that parameter estimation is robust and successful when input data contain measurement errors similar to those levels found in the observed data sets. The ability to estimate the uncertainty associated with the results of multispecies statistical age-structured models should make them useful tools for furthering ecosystem-based fisheries management.

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