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ASSESSING UNCERTAINTY IN A MULTISPECIES AGE-STRUCTURED ASSESSMENT FRAMEWORK: THE EFFECTS OF DATA LIMITATIONS AND MODEL ASSUMPTIONS

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ABSTRACT. Performance of a multispecies age-structured assessment (MSASA) model in the Gulf of Alaska (GOA) relative to changes in data and model assumptions was examined through simulation exercises. Species included arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), Pacific halibut (*Hippoglossus stenolepis*), and Steller sea lion (*Eumetopias jubatus*). Age-specific predation mortality was estimated as a flexible function of predator and prey abundances and fitted to diet data. Simulated data sets were constructed by applying random error to estimates of catch, survey, and diet data from an operating model, whose structure was identical to that of the estimating model. Simulations explored the effects of data variability, mismatched assumptions regarding model structure, and lack of diet data on model performance. Model misspecification and uninformative diet data had the greatest influence on model performance. Given the current emphasis on the development of ecosystem-based models and management, prioritizing the rigorous sampling of diet data would best facilitate the development of predation models useful to management agencies.

KEY WORDS: Multispecies, predation, Gulf of Alaska, walleye pollock, arrowtooth flounder, Pacific cod, stock assessment, Pacific halibut, Steller sea lion.

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1. Introduction.

Statistical age-structured modeling of fish populations uses information from a variety of data sources regarding mortality, growth, and other dynamics that may vary with age or size to create an assessment of the dynamics of the population of interest (Quinn and Deriso [1999]). Natural mortality, defined as all sources of mortality apart from those due to fisheries removals, is a key parameter in accurate fisheries modeling and stock assessment (NRC [1998], Clark [1999]). The majority of natural mortality for nonapex species is due to predation mortality (Andersen and Beyer [2006], Gaichas et al. [2010]), which can exceed fishing mortality (Bax [1998]) and often varies relative to prey age (Tsou and Collie [2001]). A multispecies approach to modeling may therefore be useful when setting biological reference points for harvest control rules sensitive to population variability arising from predation (Collie and Gislason [2001], Tyrell et al. [2011]). Separation of predation mortality from other sources of natural mortality has been an ongoing process in fisheries research (Jurado-Molina et al. [2005], Moustahfid et al. [2009], Garrison et al. [2010]); current models that distinguish predation from other natural mortality (e.g., Aydin et al. [2007]) are often used as adjunct sources of information about species interactions, but they are rarely directly integrated into stock assessments.

Stock assessments deal with uncertainty from a variety of sources, including sampling variability (the processes by which data are accumulated through the sampling of fisheries or surveys) and errors in model specification (where model assumptions regarding the dynamics of the modeled population are incorrect) (Quinn and Deriso [1999], Maunder and Punt [2013]). Modeling predation introduces new sources of uncertainty, depending on model structure and assumptions. Diet data may be subject to ageing error for both predator and prey, along potential misidentification of prey species due to digestion level. Assumptions regarding predator evacuation rates, feeding frequencies and selection of prey species and size may be incorrect. While modeling predation mortality increases the realism of fisheries models, it also increases the uncertainty in estimates of derived quantities necessary for fisheries management. Alternatively, it could be stated that single-species models simply produce unrealistically precise estimates of derived quantities, and that integrating predation mortality into fisheries models produces more accurate assessment of both population dynamics and uncertainty (Tyrrell et al. [2011], Deroba and Schueller [2013]).

Our objective was to examine the response of a multispecies age-structured assessment model (MSASA) that explicitly models predation mortality-at-age to changes in data and assumptions regarding model structure through a series of simulation exercises. An operating model was used to generate estimates of catch, survey, and diet information, referred to hereafter as "true value(s)". Simulated data sets were constructed by adding random errors drawn from prespecified distributions and variances to the true values. An estimating model was then run using the simulated data sets to determine whether the true values were recoverable. We focused on

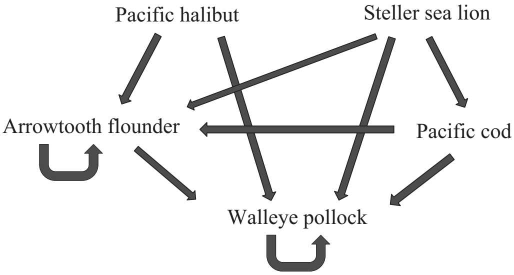

FIGURE 1. Predation linkages in the GOA MSASA model; curved arrows indicate cannibalism.

evaluating which assumptions and changes to data affected estimates of predation and abundance. If predation models are to be of use to fisheries managers, the factors that contribute the most to model variability need to be examined (Punt [2006], Curti et al. [2013]).

2. Methods.

2.1. Model structure. We previously developed a MSASA model for the Gulf of Alaska (GOA) that extended a set of single-species age-structured models by linking them via predator-prey relationships (Van Kirk et al. [2010, 2012]). Designed to integrate predation into a simplified form of an age-structured stock assessment framework, MSASA uses standard equations of single-species stock assessment models (Quinn and Deriso [1999]) to model year-class strength, fishing mortality, survey indices and commercial catch, but partitions total mortality Z into fishing mortality F, predation mortality P, and a residual natural mortality term, M_0. Age-specific predation mortality for each year is estimated from predator size- and species-preference parameters in conjunction with annual predator dietary requirements and is a dynamic function of predator and prey abundances.

Fishery, survey, and diet data were used for fitting the GOA model via maximum likelihood methods with AD Model Builder (Fournier et al. [2011]). By assuming that these data were sampled with error, MSASA departs from the methodology of multispecies virtual population analysis (MSVPA), thereby allowing the error associated with estimates of predation mortality to be quantified.

The MSASA model developed for the GOA included walleye pollock (*Theragra chalcogramma*), arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), and Steller sea lion (*Eumetopias jubatus*) (Figure 1). Annual abundance-at-age, fishing mortality, fishery and survey selectivity, predation mortality, and a residual mortality M_0 term were estimated for pollock, cod, and flounder for 1981 through 2010. Fishery selectivity, survey selectivity, and residual mortality were assumed constant over time.

Steller sea lions and Pacific halibut functioned as predators only; their abundances were estimated externally and input for each year. Length/weight-at-age and annual predator ingestion rate were input and assumed constant over time. The exception was Pacific halibut, for which the annual weights-at-age, and therefore annual rations, changed each year.

Catch and survey data were taken from the North Pacific Fishery Management Council (NPFMC) Stock Assessment and Fishery Evaluation (SAFE) reports, and diet data for fish species were supplied by the Resource Ecology and Ecosystem Modeling (REEM) database of the Alaska Fisheries Science Center (AFSC). Pacific halibut weights-at-age were supplied by the International Pacific Halibut Commission. A complete description of model structure and analyses of results is given in Van Kirk et al. ([2010, 2012]); model equations are presented in Tables A1 – A3.

Age-structured diet data for Steller sea lions are rare, and none exist with detail equivalent to other diet data used in the GOA MSASA model. We drew on Aydin et al. [2007] and Trites and Calkin [2008] to define general proportions by weight of each prey species contained in sea lion stomachs, independent of explicit prey age-structure. A penalty was implemented in the objective function should the model-estimated prey proportions deviate from those suggested by the literature (pollock = 0.4; cod = 0.15; flounder = 0.1). The age-structured maximum/minimum bounds used for sea lion diet in earlier model configurations (Van Kirk et al. [2012]) were discarded due to concerns over potential disproportionate influence on simulation results.

2.2. Simulation structure. Five scenarios were constructed. For each configuration, 1000 simulated data sets each 30 years long were generated in the statistical programming language R, version 3.1.2 (R Development Core Team [2014]) by the application of random error to the true values of catch, survey, and diet data estimated by the operating model; these errors were drawn from the assumed distributions of the AFSC catch and survey data and the best model fits from Van Kirk et al. ([2012]) to diet data (Table 1). Measurement errors for total annual catch and total annual survey abundance were drawn from lognormal distributions; proportions-at-age in both the surveys and commercial fisheries were generated from multinomial distributions with assumed sample size $n = 100$. Diet data were assumed root-normally distributed (Table A3, equation 5), for which the square root was normally distributed, with probability density function

$$\frac{1}{2\sigma\sqrt{x}\sqrt{2\pi}}\exp\left(-\frac{\left(\sqrt{x}-\mu\right)^2}{2\sigma^2}\right) \tag{1}$$

for which x is an observed diet data point, μ was set to 0, and the variance σ was set to 0.05 (reflecting an assumed sample size of 400) for all diet data points over all fish species and ages (Table 1). Using equation (1) resolved issues with poor

TABLE 1. Operating model objective function weights and the associated variances used for random draws to construct simulated data sets.

Component	Distribution	Weight	Variance for random draws
Total annual catch	Lognormal	$1/\sigma^2$	Flounder: 0.02; Cod: 0.02; Pollock: 0.05
Total survey biomass	Lognormal	$1/\sigma^2$	Flounder: 0.014; Cod: 0.053; Pollock: 0.08
Commercial catch proportions-at-age	Multinomial	100	Effective sample size = 100
Survey proportions-at-age	Multinomial	100	Effective sample size = 100
Diet data	Root normal	$1/\sigma^2$	0.05 for all fish species

performance of random samples drawn from lognormal, multinomial, or normal distributions when generating simulated data sets for which many of the values were close to zero, and departs from the methodology in Van Kirk et al. [2010, 2012] for diet data.

The five simulations differed from the assumptions of the operating model regarding data availability, data variability, and model structure; except where explicitly defined, all aspects of the simulations remained as in SIM 1, and the structures of the operating model and estimating models were identical.

SIM 1: Random draws were used to generate simulated data sets for all key derived quantities from the operating model: commercial catch proportions-at-age, total annual commercial catch, survey proportions-at-age, total survey biomass, and diet data for all ages of all predators except sea lions. In contrast to the relatively uninformative diet data available to the operating model, SIM 1 contained simulated diet data for every potential combination of predator and prey species and age. The simulated diet data had therefore a greater influence on parameter estimates than data available to the GOA MSASA operating model due to a larger number of data points.

SIM 2: Random error was applied solely to the diet data to examine model sensitivity to predation mortality apart from errors in other data sets; values for catch and survey indices were assumed known without error and set to the true values (the operating model output).

SIM 3: Diet data were thinned to reflect the diet data available to the operating model. As discussed above, the operating model output a diet coefficient for each combination of predator-prey species and age, indicating the proportion of prey species i age a in the stomach of predator species j age b. The data available to the operating model, however, were not as complete, especially in early model years.

If the operating model contained no data indicating the presence of prey species i age a in the stomach of predator species j age b after accounting for size limitations (a fish was assumed unable to feed on prey equal to or exceeding its own weight—the size-preference function presented in Table A2), this data point was removed from the simulated diet data available to the estimating model in SIM 3. In some instances, this reduced the diet data available to SIM 3 by up to 95% from that available to the other simulations. Priors for relative proportions of sea lion diet did not change.

SIM 4: The variances used to generate the simulated data sets were doubled from their original values; objective function weights remained unchanged. By doubling the variance and keeping the objective weights unchanged, the estimating model effectively underestimated the uncertainty in all data sets, assessing model sensitivity to the mismatch between the magnitude of variance used to generate the simulated data set and the level of possible precision assumed by the model.

SIM 5: Survey selectivity-at-age curves were misspecified relative to those used in the operating model. Such misspecification can alter estimates of cohort structure and residual natural mortality, skew fits to other age-structured data sets, and affect the estimates of total annual abundances used to establish catch levels (NRC [1998], Francis [2011], Crone et al. [2013]). This simulation replaced the operating model's double-logistic survey selectivity curves with nonparametric curves that were used in earlier stages of MSASA model development. The approximation estimated selectivities for younger ages (for cod and pollock, ages 1–4; for flounder, ages 1–5), set selectivities to 1 for middle ages (flounder: ages 6–12; cod: ages 5–9; pollock: ages 5–8), and estimated selectivity for older ages with a single coefficient for each species (flounder: ages 13–15; cod: ages 10–12; pollock: ages 9–10).

All weightings in the objective function of each simulation were kept at the same values as the operating model for consistency. Starting values were selected to be sufficiently informative so that model estimates of derived quantities and parameters were considered both biologically and statistically reasonable, but sufficiently uninformative to allow simulations to explore the parameter space without excessive constraint.

2.3. Nonrandomized self-test. Age-structured models are complex, and the question of whether such complex models have unique solutions sets to parameter values was a central topic at the International Council for the Exploration of the Seas (ICES) 2013 World Congress on Stock Assessment Methods (Cadrin and Dickey-Collas [2015]). If operating model parameter estimates are confounded and not unique to the data (i.e., the same model outputs of derived quantities can be replicated by more than one set of parameter estimates), this uncertainty will be incorporated into simulation efforts independently of the specific configuration of a given simulation. A nonrandomized self-test was implemented in which the estimating model was run using a simulated data set composed of catch, survey, and diet quantities directly from the operating model output without randomization. The results were used to determine whether the operating model derived quantities were recoverable using simulated data.

2.4. Evaluating simulation performance. The primary statistic to evaluate simulation performance with regard to bias was the distribution of relative errors, summarized by the median relative error (MRE)

$$\text{MRE}(\hat{\theta}) = median\left(\frac{\hat{\theta} - \theta}{\theta}\right) \tag{2}$$

for which $\hat{\theta}$ is the parameter value estimated by a given simulation replicate and θ is the true value estimated by the operating model. MRE is a measure of relative bias (the tendency of a simulation configuration to over- or underestimate parameter values).

The primary statistic to evaluate simulation performance with regard to precision was the coefficient of variation (CV), calculated for each parameter of interest within a given scenario

$$\text{CV}_{\hat{\theta}} = \frac{\sigma_{\hat{\theta}}}{|\mu_{\hat{\theta}}|} \tag{3}$$

for which $\mu_{\hat{\theta}}$ is the mean estimate of parameter $\hat{\theta}$ over the 1000 replicates of a given simulation configuration, and $\sigma_{\hat{\theta}}$ is the standard deviation of those estimates.

AD Model Builder (ADMB version 10.1) calculates the covariance matrix by inverting the Hessian matrix at the minimum log-likelihood. Where an element of the Hessian matrix is not positive, a local minimum has not been obtained, the model has not converged to set of statistically quantifiable parameters, and ADMB returns an error. Replicates returning this error were discarded and not included in the 1000 analyzed simulation runs.

Overall model performance was assessed by examining changes in model estimates of residual mortality M_0, mean age-1 abundance (recruitment), abundance-at-age, predation mortality-at-age, survey selectivity, and total annual biomass. Mean recruitment and residual mortality M_0 serve as general indicators of changes between simulations because they define the major factors influencing population dynamics: birth and death. Changes in recruitment and/or M_0 suggest that implementation of age-specific mortality by means of predation or fishery removals was insufficient to produce the derived quantities of the objective function, and that large-scale changes to M_0 (assumed constant over all years and ages) or recruitment were required to allow model convergence.

TABLE 2. Primary assessment parameter estimates from the operating model (OM), the nonrandomized self-test, and SIM 1.

Parameter	OM	Self-test	SIM 1	Self-test bias	SIM 1 bias
Age 1 Flounder	3,358,483	3,194,688	3,502,544	−0.049	0.043
Age 1 Cod	278,173	247,459	256,017	−0.110	−0.080
Age 1 Pollock	28,120,236	27,952,019	28,947,662	−0.006	0.029
Flounder M_0	0.178	0.193	0.191	0.083	0.075
Cod M_0	0.422	0.404	0.407	−0.043	−0.035
Pollock M_0	0.161	0.152	0.152	−0.056	−0.056

3. Results.

3.1. General population structures.

3.1.1. *Self-Test and SIM 1.* Estimates of the primary assessment parameters (mean recruitment and residual mortality M_0) from the nonrandomized self-test deviated from operating model values by -0.11 to -0.006 for mean age 1 abundance and -0.056 to 0.083 for M_0 (Table 2). These estimates were similar to median parameter estimates from SIM 1, but not identical (Table 2, Figure 2). Estimates of total annual biomass and predation mortality-at-age were also similar between all three model configurations (operating mode1, self-test, and SIM 1) (Figure 2), with biomass and predation mortality from the nonrandomized self-test falling within one standard deviation of operating model values. Estimates of cod and pollock biomass showed the poorest fits to true values at the end of the modeled time period. Although slight, the largest deviations in predation in the self-test outputs were predation by flounder on pollock (overestimated), and flounder cannibalism (underestimated) (Figure 2).

3.1.2. *All simulations.* Among the five simulation configurations, the number of model runs required to obtain 1000 replicates for which ADMB was able to estimate parameter variances were similar, with a maximum of 1211 runs (SIM 1), and a minimum of 1030 (SIM 5). The primary reason for rejection appeared to be the inability of ADMB to estimate the uncertainty of the Steller sea lion size-preference parameter, due to lack of age-structured diet data for sea lions.

SIM 3 and SIM 5 produced the largest median deviations in the six primary assessment parameters from true values (Figure 3), with the exception of flounder M_0 in SIM 3, which fit true values better than the other simulation configurations. MREs for cod were the least sensitive among the three species to changes in the simulation configurations.

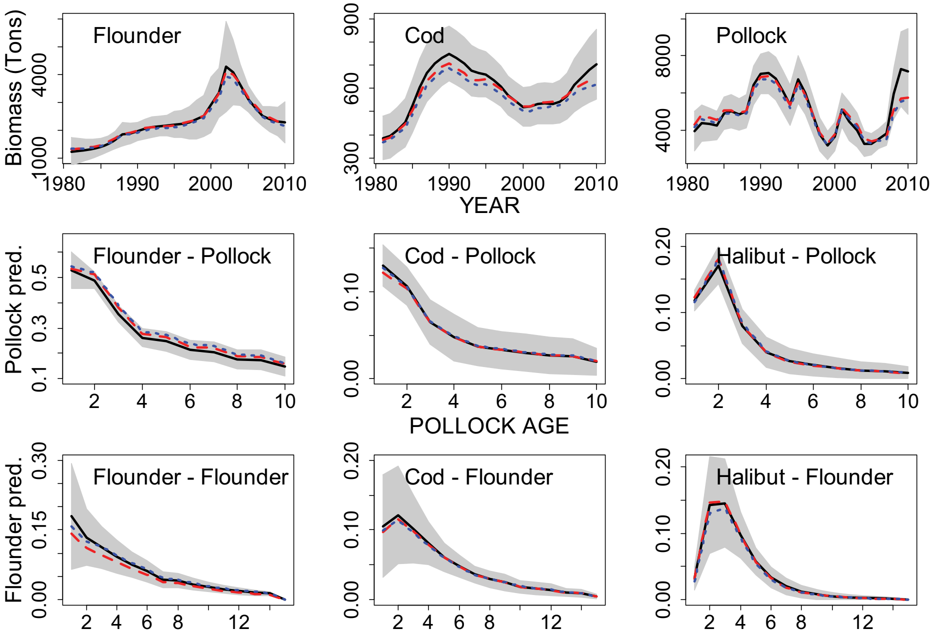

FIGURE 2. Total annual biomass (top row), predation mortality on pollock from flounder, cod, and halibut (middle row), and predation mortality on flounder from flounder, cod, and halibut (bottom row) from the operating model (black line), the nonrandomized self-test (blue line) and SIM 1 (red line).

Empirically derived coefficients of variation for the primary assessment parameters showed expected results, with SIM 2 displaying the least variability and SIM 4 the highest (Figure 4). CVs for mean recruitment were larger than those for residual mortality.

As with the primary assessment parameters, MRE for abundance-at-age trends deviated from operating model values for SIM 3 and SIM 5 more than the other simulations, and SIM 2 results had the smallest variability (Figure 5). MRE for cod showed the least variability among all three species across simulations. Pollock and flounder abundances were consistently underestimated in all simulations with the exception of SIM 3, in which flounder abundances were overestimated for ages 10 and greater and markedly underestimated for younger ages in SIM 3.

Median survey selectivity values for the SIM 1, SIM 2, SIM 3, and SIM 4 were virtually identical for cod and matched operating model values closely (Figure 6). Median survey selectivity values for flounder in SIM 3 diverged from the true values and from other simulations, with increased selectivity for younger ages and reduced selectivity for ages greater than 8. Selectivities that were set to 1.0 in SIM 5

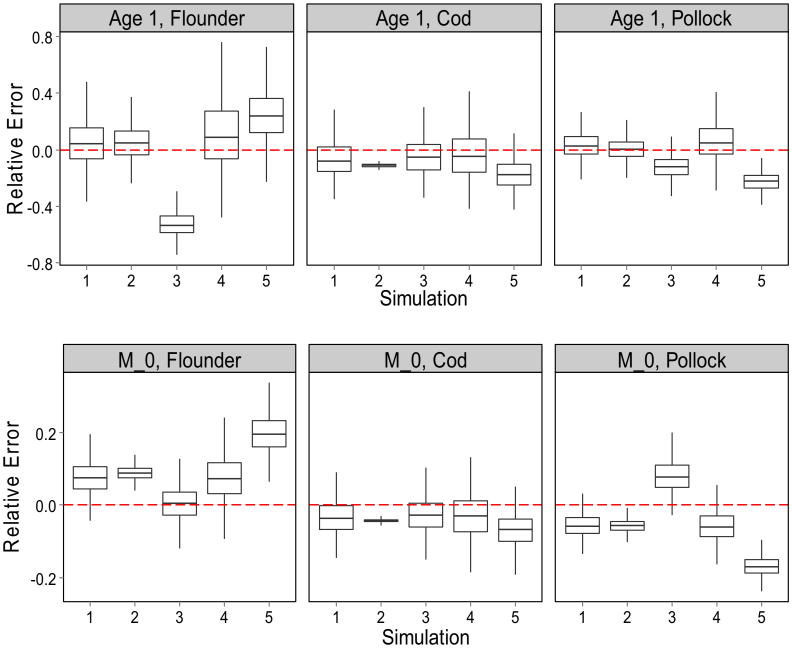

FIGURE 3. Distributions of parameter relative errors for median age-1 abundance (recruitment) and residual mortality relative to operating model values for SIM 1 (full model), SIM 2 (diet data only), SIM 3 (reduced diet data), SIM 4 (variance doubled), and SIM 5 (model misspecification). Boxes describe the interquartile range; vertical lines at ends of whiskers bounded by 1.5 times the interquartile range.

differed from operating model values more for flounder and pollock than cod. Median estimates of fishery selectivity differed little between simulations (not shown).

Estimates of total annual pollock biomass from SIM 5 showed the poorest fit to true values (Figure 7), followed by estimates from SIM 3. For all simulations, fits to true values were poorest at the end of the model years, with terminal biomass in SIM 5 underestimating the true values by 49% and SIM 3 by 32%.

3.2. Predation components. Predation mortality-at-age for pollock deviated from operating model values more in SIM 3 and SIM 5 than other configurations (Figure 8). Predation in SIM 3 was generally overestimated for younger pollock and underestimated for older cohorts, while SIM 5 had increased predation on younger cohorts. Sea lion predation overestimated predation for all pollock ages in both SIM 3 and SIM 5, and displayed little variation across pollock ages (i.e., was the same for all ages), although the magnitude of that mortality was very small (0.01–0.0125, not shown).

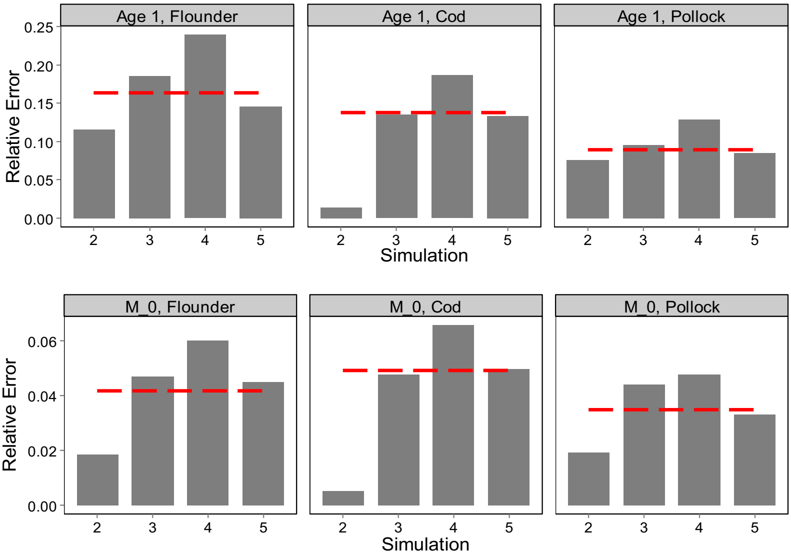

FIGURE 4. Empirically derived coefficients of variation for median age-1 abundance and residual mortality relative to SIM 1 (full model) values (red line) for SIM 2 (diet data only), SIM 3 (reduced diet data), SIM 4 (variance doubled), and SIM 5 (model misspecification). Note differences in the scales of the y-axes.

Predation mortality-at-age for flounder was similar in all simulations (Figure 9), with the exception of SIM 3, in which predation from cod and halibut was markedly reduced, and SIM 5, in which flounder cannibalism on ages 1–4 was increased. Predation from sea lions in SIM 5 was overestimated for all ages and did not vary across age, but was very minor (0.0057, not shown).

4. Discussion.

The inability of the nonrandomized self-test to perfectly match operating model parameter values and outputs suggests that the current model structure has reached the limits of estimability. While biomass and predation outputs from the self-test still fit operating model values closely, it appears that a variety of parameter values can produce those estimates, and that the parameters themselves are confounded, without a unique solution set to the data. Poorer fit between simulation estimates and true values in the end years of model runs has been observed in similar simulation self-test work (Deroba et al. [2015]), which is especially problematic, as it is the estimates from the most recent years that are relevant to managers. Whether this inherent variability has practical consequences for management purposes, given the small deviation between operating model values and the self-test outputs, has yet to be evaluated.

It is also relevant that the operating model had relatively uninformative diet data for early model years, whereas the simulated diet data for the nonrandomized

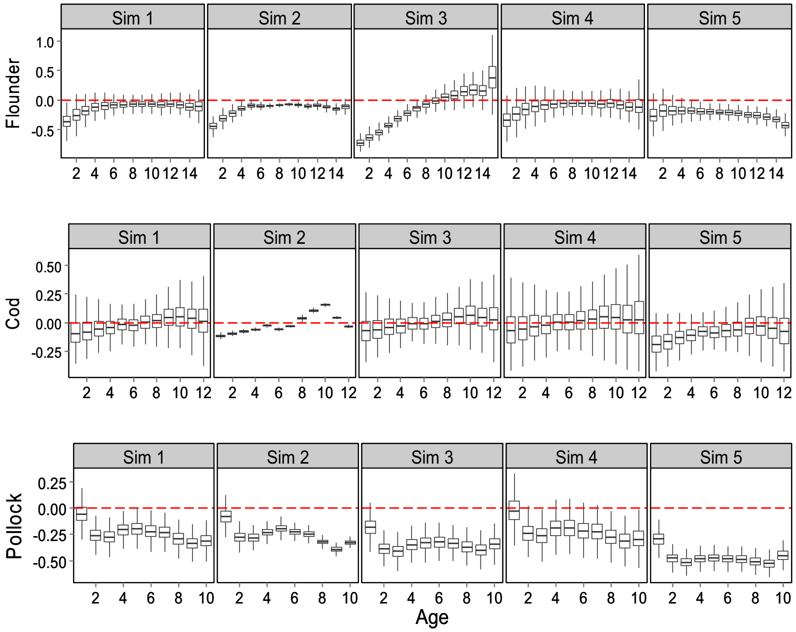

FIGURE 5. Distributions of relative error for flounder, cod, and pollock abundance-at-age for SIM 1 (full), SIM 2 (diet data only), SIM 3 (reduced diet data), SIM 4 (doubled variance), and SIM 5 (model misspecification) relative to the operating model estimates. Boxes describe the interquartile range; vertical lines at ends of whiskers bounded by 1.5 times the interquartile range. Note differences in the scales of the y-axes.

self-test and simulations were more informative, having a diet coefficient for every combination of predator-prey species and age. This discrepancy, combined with the limits of estimability inherent in models this complex, resulted in the lack of perfect fit between the operating model values, the non-randomized self-test, and the median of SIM 1 outputs.

The results from SIM 2 and SIM 4 were as expected. Variability was present in parameter estimates for flounder and pollock parameter in SIM 2 even with perfect catch and survey data, whereas parameter estimates for cod (subject to little predation) showed little variability, emphasizing the degree to which modeling predation can affect estimates of abundance.

The imperfect diet data in SIM 3 reflected primarily the lack of flounder as a prey item in sampled predator stomachs in early model years. As predation was heaviest on flounder aged 1–5, flounder recruitment and M_0 in SIM 3 were reduced (Figure 3), as biomass to meet the predation needs present in other simulations was not necessary. This is in contrast to pollock in SIM 3, for whom recruitment was also reduced to compensate for lower predation pressure, but for whom residual

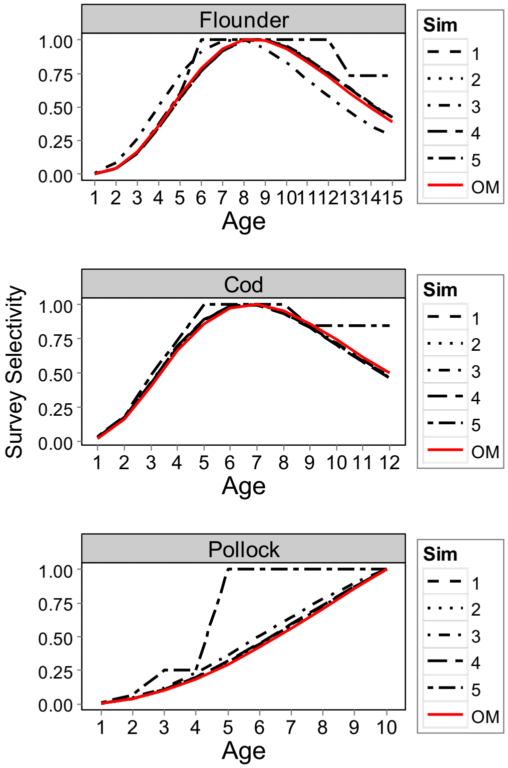

FIGURE 6. Median survey selectivity-at-age curves for the operating model (OM) and SIM 1–5.

mortality was increased. In this instance, the predation on older pollock cohorts was reduced, with the result that M_0 was increased to remove prey biomass that had been passed into older ages and was no longer subject to heavy predation. The survey selectivity curve for flounder in SIM 3 shifted to have peak selectivity for slightly younger ages and reduced selectivity for older cohorts (Figure 6) to reflect the bias in median abundance-at-age trends in that simulation (Figure 5).

By overestimating survey selectivity, SIM 5 underestimated abundance for all three species, with both recruitment and M_0 for cod and pollock being lowered. Recruitment and M_0 were overestimated, however, for flounder, even though median parameter deviations for all flounder ages were negative (Figure 5). SIM 5 overestimates selectivity for older ages, while survey selectivity for younger ages remains close to true values (Figure 6). For early ages prior to the misspecification, then, abundance should be close to SIM 1 values, and decrease only after the changes in SIM 5 survey selectivity. For cod, subject to little predation and for whom the

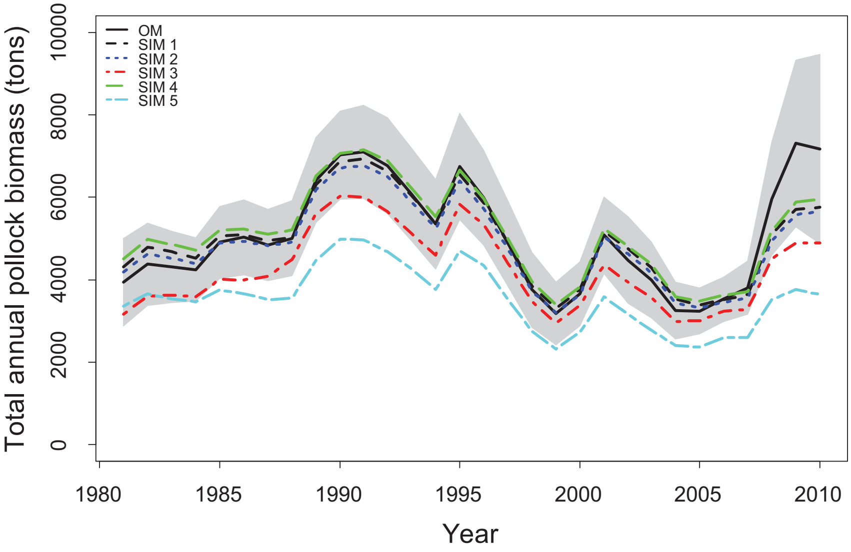

FIGURE 7. Total annual biomass for Pollock from the operating model (OM) and SIM 1–5.

SIM 5 survey curve differed the least from true values out of all three species, lower recruitment and mortality were sufficient. For pollock, the combination of reduced recruitment (Figure 3) and the heavy predation on younger cohorts (Figure 8) was sufficient to reduce abundance to fit the overestimated survey selectivity beginning with age 5 (Figure 6). Flounder, however, experience heavy model cannibalism on ages 1–4, and it appears that reducing recruitment would have lowered abundance too far to support this predation. Model response was to increase recruitment (Figure 3) to meet predation needs, primarily cannibalism (Figure 8) and increase M_0 was well to remove remaining biomass from passing into the cohorts for which the survey selectivity was misspecified.

There appear to be two primary issues when attempting to integrate predation into contemporary age-structured stock assessments, both arising from lack of informative diet data, an issue recognized in other predation model work (Garrison et al. [2010], Tyrrell et al. [2011]). First, there is the potential for underestimating predation, as in SIM 3. Second, attempting to increase model complexity with these data may result in predation parameters being estimated in such a way as to compensate for other forms of model misspecification (Piner et al. [2011], Maunder and Punt [2013]). Lacking sufficiently informative diet data, predation models will tend toward overparameterized structures in which predation mortality functions to fit catch and survey data with poor estimates of predation. As the estimation of age-specific predation is relatively new in stock assessment methods, inaccurate predation mortality-at-age curves may be automatically assumed correct, which in

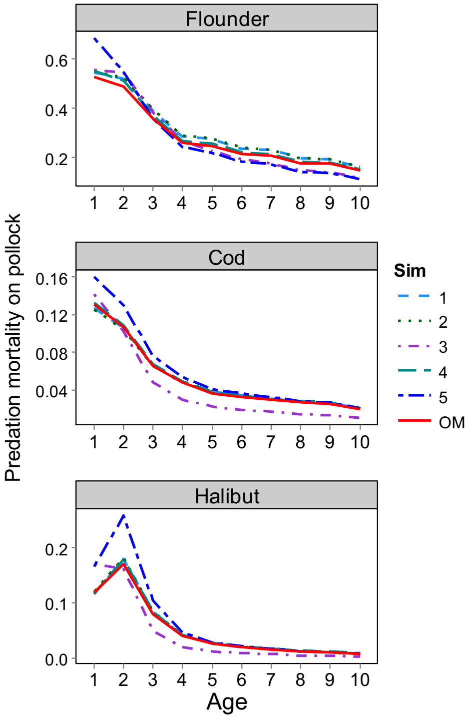

FIGURE 8. Median estimated predation-mortality-at-age for pollock from halibut, cod, flounder for the operating model (OM) and SIM 1–5.

turn can potentially affect estimates of a variety of derived quantities, including spawning biomass and the management decisions based upon it.

Temporal variability in diet data can provide information on predator and prey interactions. If changes in the time series of diet data are driven primarily by sampling efforts, however, with fewer samples and less informative data in early model years, modeling results may imply changes in abundances or predator behavior when in fact the only changes were improved data. In such a context, it may be advisable to aggregate diet data over all model years and estimate a mean predation-mortality at age. This improves model realism over the assumption of a constant natural mortality, but reduces the uncertainty associated with poor data. If other modeled species have their own indices of survey abundance, these can inform changes in survey abundance while diet data drive the interactions between predator and prey species.

Realistically, stock assessments that integrate predation are likely to incorporate one or more forms of model misspecification, Maunder and Punt, [2013] in addition to less-than-perfect diet data. In retrospect, it would have been informative to run

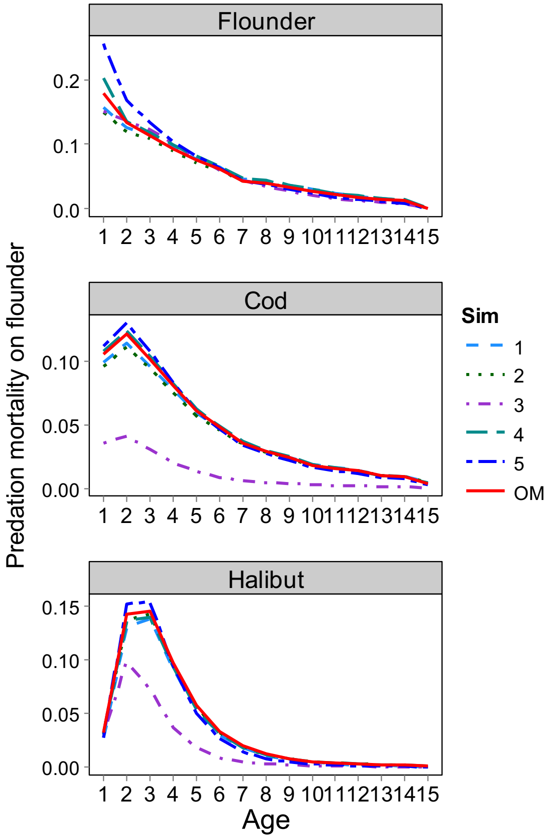

FIGURE 9. Median estimated predation-mortality-at-age for flounder from halibut, cod, flounder for the operating model (OM) and SIM 1–5.

a simulation combining survey misspecification and poor diet data, especially as these two factors are particularly confounded. In traditional single-species models, survey selectivity and natural mortality M, estimated as a free parameter, are confounded (Thompson [1994]). Andersen and Beyer [2006] and Gaichas et al. [2010] proposed that the entirety of nonfishery-related mortality is due to predation for nonapex species (i.e., $M_0 = 0$, and $Z = F + P$). As survey catchability Q is used to scale abundances, and survey selectivity curves inform model estimates of cohort structure, misspecification of survey selectivity in conjunction with poor diet data is likely to produce significantly skewed estimates of predation mortality-at-age.

Curti et al. [2013] constructed a statistical age-structured multispecies model of the Georges Bank fish community. Monte Carlo simulations, which incorporated error into simulated data for catch, survey, and diet data, found results similar to this study's results, including that bias in simulation estimates of age-1 recruitment and species-preference coefficients were all highly sensitive to the inclusion of error in the simulated data. Their work also found that estimates of predation mortality-at-age and age-1 recruitment were more sensitive to uncertainty in survey data than in catch data.

Integration of predation mortality into age-structured assessments is intended to improve model realism without unacceptably high levels of uncertainty, and is currently a priority for a number of species (CIE [2012]). This is best facilitated through consistent sampling of diet data. Sufficiently robust, these data will not only increase the accuracy and precision of predation parameter estimates, but also help prevent model estimates of predation from functioning as compensatory mechanisms for model misspecification. This will result in the quantification of predator-prey relationships, permit development of multispecies fisheries management tools, and aid in the maturation of age-structured multispecies models into practical applications of ecosystem-based management.

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APPENDIX

TABLE A1. Population dynamics equations as per Van Kirk et al. [2010] and Quinn and Deriso [1999].

	Equation	Description
1	$N_{i,a+1,t+1} = N_{i,a,t} e^{-Z_{i,a,t}}$	Abundance of species i at age a in year t
2	$N_{i,a+1,t+1} = N_{i,a,t} e^{-Z_{i,a,t}} + N_{i,a+1,t} e^{-Z_{i,a+1,t}}$	Abundance of the plus group of species i year t
3	$F_{i,a,t} = s_{f\,i,a} F_{i,t}$	Fishing mortality of species i at age a in year t
4	$C_{i,a,t} = \frac{F_{i,a,t}}{Z_{i,a,t}} e^{-Z_{i,a,t}} N_{i,a,t}$	Commercial catch-at-age of species i at age a in year t
5	$S_{i,a,t} = Q_i s_{s\,i,a} N_{i,a,t}$	Survey abundance-at-age of species i at age a in year t
6	$Z_{i,a,t} = F_{i,a,t} + P_{i,a,t} + M_{0_i}$	Total mortality-at-age Z
7	Q_i	Survey catchability for species i
8	$s_{f\,i,a}$	Fishery selectivity-at-age for species i at age a
9	$s_{s_{i,a}}$	Survey selectivity-at-age for species i at age a
10	$F_{i,t}$	Full-recruitment fishing mortality for species i in year t

TABLE A2. Predation equations as per Van Kirk et al. [2010]. Subscripts *j,b* refer to a predator of species *j*, at age *b*. Subscripts *i,a* refer to a prey of species *i* at age *a*..

	Equation	Description
1	$P_{i,a,t} = \frac{1}{B_{i,a,t}} \sum_j \sum_b I_{j,b} N_{j,b,t} \frac{\varphi_{i,a,j,b,t}}{\varphi_{j,b,t}}$	Predation mortality-at-age for prey species i at age a in year t.
2	$\frac{\varphi_{i,a,j,b,t}}{\varphi_{j,b,t}}$	Proportion of prey i,a in all food available to predator species j at age b in year t.
3	$\varphi_{i,a,j,b,t} = \nu_{i,a,j,b} B_{i,a,t}$	Biomass of prey i,a in year t multiplied by a predator-prey suitability coefficient.
4	$\varphi_{j,b,t} = B_{oth} + \sum_i \sum_a \nu_{i,a,j,b,t} B_{i,a,t}$	Total food available in year t to predator j,b defined as the sum of all available modeled prey plus a constant “Other Food” term which was set to e^{15}.
5	$\nu_{i,a,j,b} = \rho_{i,j} g_{i,a,j,b}$	The product of species-preference ρ, and size-preference g. Size-preference is temporally constant; species-preference can change.
6	$g_{i,a,j,b} = \exp[-\frac{1}{2\sigma_j^2} (\ln \frac{w_{j,b}}{w_{i,a}} - \eta_j)^2]$	Size-preference function for predator j,b in which $w_{j,b}$ = weight of predator j,b, $w_{i,a}$ = weight of prey i,a, η_j = ratio of predator to prey weight preferred by all predators j (log scale), and σ_j = variance of the size-preference function for predator j. Constant over prey species; g is subscripted as prey species differ in size-at-age.

TABLE A3. Objective function components as per Van Kirk et al. [2010] with the exception of diet data, which were modified for the current work. A caret signifies model estimates.

	Equation	Description
1	$L_1 = \lambda_1 \sum_y (\ln[\frac{C_y + 0.0001}{\hat{C}_y + 0.0001}])$	Total catch (lognormal)
2	$L_2 = \lambda_2 \sum_y (\ln[\frac{S_y + 0.0001}{\hat{S}_y + 0.0001}])$	Total survey (lognormal)
3	$L_3 = \lambda_3 \sum_{styr}^{endyr} -n_y^* \sum_{a_0}^{a+} (CP_{y,a} + 0.0001) * \ln(C\hat{P}_{y,a} + 0.0001)$	Commercial catch proportions-at-age (multinomial)
4	$L_4 = \lambda_4 \sum_{styr}^{endyr} -n_y^* \sum_{a_0}^{a+} (SP_{y,a} + 0.0001) * \ln(S\hat{P}_{y,a} + 0.0001)$	Survey proportions-at-age (multinomial)
5	$L_5 = \lambda_5 \sum_j \sum_b [(\varphi_{i,a}^{1/2}) - (\hat{\varphi}_{i,a}^{1/2})]^2$	Fish diet data (root normal)

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