Incorporating predation interactions in a statistical catch-at-age model for a predator–prey system in the eastern Bering Sea

Jesús Jurado-Molina, Patricia A. Livingston, and James N. Ianelli

Abstract: Virtual population analysis and the statistical catch-at-age methods are common stock assessment models used for management advice. The difference between them is the statistical assumptions allowing the fitting of parameters by considering how errors enter into the models and the data sources for the estimation. Fishery managers are being asked to consider multispecies interactions in their decisions. One option to achieve this goal is the multispecies virtual population analysis (MSVPA); however, its lack of statistical assumptions does not allow the use of tools used in single-species stock assessment. We chose to use a two-species system, walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*), to incorporate the predation equations from MSVPA into an age-structured multispecies statistical model (MSM). Results suggest that both models produced similar estimates of suitability coefficients and predation mortalities. The adult population estimates from the single-species stock assessment and MSM were also comparable. MSM provides a measure of parameter uncertainty, which is not available with the MSVPA technologies. MSM is an important advancement in providing advice to fisheries managers because it incorporates the standard tools such as Bayesian methods and decision analysis into a multispecies context, helping to establish useful scenarios for management in the Bering Sea.

Résumé : L'analyse des populations virtuelles et les méthodes statistiques reliées aux captures en fonction de l'âge sont des modèles courants d'évaluation des stocks utilisés pour générer des avis sur l'aménagement. La différence entre ces deux approches réside dans les présuppositions statistiques qui permettent l'ajustement des paramètres en considérant comment les erreurs entrent dans les modèles et les sources de données utilisés pour les estimations. Les gestionnaires de la pêche doivent considérer les interactions plurispécifiques dans leurs décisions. Une façon d'atteindre cet objectif est d'utiliser l'analyse des populations virtuelles plurispécifiques (MSVPA); cependant, l'absence de présuppositions statistiques ne permet pas l'emploi des outils qui servent dans l'évaluation des stocks monospécifiques. Nous avons choisi un système comprenant deux espèces, la goberge de l'Alaska (*Theragra chalcogramma*) et la morue du Pacifique (*Gadus macrocephalus*), afin d'incorporer les équations de prédation de MSVPA dans un modèle statistique plurispécifique (MSM) structuré en fonction de l'âge. Les résultats montrent que les deux modèles produisent des estimations semblables des coefficients d'adéquation et des mortalités dues à la prédation. Les estimations des populations adultes réalisées à partir des évaluations de stocks monospécifiques et de MSM sont aussi comparables. MSM fournit une mesure de l'incertitude des paramètres, ce qui n'est pas disponible dans les méthodologies MSVPA. MSM représente un progrès important dans la production d'avis pour les gestionnaires, parce qu'il incorpore les outils habituels, tels que les méthodes bayésiennes et l'analyse décisionnelle, dans un contexte plurispécifique, aidant ainsi à établir des scénarios utiles pour l'aménagement dans la mer de Béring.

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Introduction

Single-species catch-at-age models are some of the more common methods currently used in data-rich fisheries stock assessments. These models permit the historical reconstruction of the numbers-at-age of exploited fish stocks and provide estimates of vital mortality rates. These estimates serve as the primary basis for providing management advice in many world fisheries (Megrey 1989). Two main types of catch-at-age methods are recognized (Hilborn and Walters 1992). The first method, virtual population analysis (VPA) or cohort analysis, is a recursive algorithm that calculates stock size based on catches with no underlying statistical assumptions. The second class of catch-at-age-methods relies on the statistical fitting of parameters by explicitly considering how errors enter into these models. They are called sta-

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tistical catch-at-age methods. Instead of relying only on catch estimates, as VPA does, statistical catch-at-age models use a variety of data sources to estimate population parameters. A more detailed review of these models can be found in Hilborn and Walters (1992) and Megrey (1989).

Single-species models play an important role in fisheries management because they allow the establishment of target reference points and setting of allowable harvest limits. Scientists involved in stock assessment have acknowledged the possibility that predator–prey interactions can influence population dynamics estimation and reference points, but the general belief is that the effects of predation and competition are subordinate to the direct effect of fishing (Sissenwine and Daan 1991). Fishery managers are increasingly asked to consider multispecies interactions in their harvesting decisions because there is an increasing tendency to recognize that fish populations are not isolated entities. Scientists acknowledge the fact that harvest limits of some prey species may depend on harvest limits of predators (Collie and Gislason 2001); thus, there is a real need to link assessment models. Therefore, several attempts have been made to include different kinds of interactions (biological or technological) in models. Among the biological interaction models, the multispecies VPA (MSVPA) and the multispecies forecasting (MSFOR) model, developed by a working group of the International Council for the Exploration of the Sea, have the potential to provide additional information to fisheries managers to improve management policies. These models have been used in the North Sea (Anonymous 1989; Sparre 1991), the Baltic Sea (Sparholt 1991), Georges Bank (Tsou and Collie 2001), and recently in the eastern Bering Sea (Livingston and Jurado-Molina 2000; Jurado-Molina and Livingston 2002*a*, 2002*b*).

One weakness of the MSVPA is its lack of statistical assumptions that impede the inclusion of uncertainty into multispecies model parameter estimation. Explicit estimates of uncertainty in model estimates provide useful advice to decision-makers. Thus, it is important to include assumptions on process and (or) observation errors in multispecies models. This task requires a change in the approach used to assess the dynamics of populations in a multispecies framework. Currently, MSVPA is based on Gulland's (1965) method, which is a deterministic backward nonlinear sequential method. A new approach requires the inclusion of the separable fishing mortality assumption (Doubleday 1976; Pope 1977), which allows for common statistical estimation procedures in a multispecies context. These include estimation of the likelihood profile and the posterior distribution of parameters and also indicators of performance used in the analysis of decision or risk analysis. This could provide new insights for fisheries management in a multispecies context, a task that is not possible with the current available MSVPA–MSFOR technology. We will show how the predation equations from MSVPA can be introduced into a statistical catch-at-age model and we will also discuss some advantages of this approach.

Materials and methods

To facilitate model development and verification, we reduced the number of species in the system used for the eastern Bering Sea in previous studies (Livingston and Jurado-Molina 2000; Jurado-Molina and Livingston 2002*a*, 2002*b*) to include only walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*). These species were chosen based on the important role they played in the eastern Bering Sea. Walleye pollock is the dominant species in the Bering Sea and comprises over half the total biomass and catch of groundfish in the eastern Bering Sea (Bakkala 1993). Walleye pollock is important not just in terms of biomass but also in its role in the food web as predator and prey. Many species prey on walleye pollock and Pacific cod is one of its main predators but is also a prey for walleye pollock (Livingston and Jurado-Molina 2000). In addition, cannibalism is also observed in Pacific cod. Thus, these two species comprise a majority of the species interactions in the eastern Bering Sea.

To assess the dynamics of these two species, we applied the MSVPA model and the multispecies statistical catch-at-age model (MSM). We compared the results from the two models with the single-species statistical stock assessments carried out by scientists from the Alaska Fisheries Science Center (AFSC) as well as the results from the MSVPA base run that includes all predator species and complete predator stomach content data. A brief description of the models used is presented below.

Models

MSVPA is a retrospective analysis that is an extension of the VPA model (Gulland 1965). It uses catch-at-age data, predator ration, and predator diet information to estimate fishing mortality, recruitment, stock size, suitability coefficients, and predation mortality. Some of the model's principles with regard to predation are based on the work of Anderson and Ursin (1977) on predator–prey preferences and estimates of suitability coefficients. In addition to the standard equations from VPA (Gulland 1965), MSVPA uses three additional equations related to predation. The first equation represents the assumption of the separation of natural mortality M into two components:

$$(1) \qquad M = M1 + M2$$

where $M1$ is the residual mortality and $M2$ is the predation mortality. The second equation estimates the predation mortality:

$$(2) \qquad M2_{p,a} = \sum_i \sum_j \frac{\bar{N}_{i,j} R_{i,j} S_{p,a,i,j}}{\sum_{p,a} \bar{N}_{p,a} W_{p,a} S_{p,a,i,j}}$$

where $\bar{N}_{i,j}$ represents the average stock size of the predator i of age j, $R_{i,j}$ is the annual ration of the predator, and $S_{p,a,i,j}$ is the suitability coefficient for each combination of predator–prey–age. This parameter reflects the diet composition of the predator relative to the available food (Sparre 1991). The denominator of eq. 2 represents the total suitable biomass available to the predator. In the denominator, $\bar{N}_{p,a}$ represents the average stock size of prey p of age a and $W_{p,a}$ represents the weight-at-age of the prey in the stomach of the predator. The third equation estimates the suitability coefficients:

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$$S_{p,a,i,j} = \frac{U_{p,a,i,j}/(\bar{N}_{p,a} W_{p,a})}{\sum_p \sum_a U_{p,a,i,j}/(\bar{N}_{p,a} W_{p,a})} \tag{3}$$

where $U_{p,a,i,j}$ represents the fraction of prey p of age a found in the stomach of predator i of age j. These equations (1–3) are set up in a quarterly form and are solved iteratively within the MSVPA (Gislason 1991). More details of the MSVPA model can be found in Sparre (1991), Magnusson (1995), and Gislason (1991).

In addition to the predation equations (1–3), in the multispecies statistical model MSM, we use the following equations from single-species statistical catch-at-age models:

$$N_{a+1,t+1,q+1} = N_{a,t,q}\, e^{-(F_{a,t}+M_a)} \tag{4}$$

$$N_{a+1,t+1,1} = N_{a,t,4}\, e^{-(F_{a,t}+M_a)}$$

$$C_{a,t} = \frac{F_{a,t} N_{a,t} [1 - e^{-(F_{a,t}+M_a)}]}{F_{a,t} + M_a} \tag{5}$$

$$F_{a,t} = s_a F_t \tag{6}$$

$$s_a = \frac{1}{1 + e^{u-va}} \tag{7}$$

where $N_{a,t,q}$ represents the number of individuals of age a in year t in quarter q, $F_{a,t}$ is the fishing mortality at age, M_a is the natural mortality at age, $C_{a,t}$ is the catch-at-age, s_a is the age-dependent gear selectivity (u and v are its parameters), F_t is the full fishing mortality.

Different indices of relative abundance and the catch-at-age data were used to fit the model. In the case of walleye pollock, we used data collected during the AFSC's bottom trawl survey (BTS) and echo-integration trawl (EIT) survey were used. For Pacific cod, we used the biomass estimate from the AFSC's EBS bottom trawl survey. In this model, we assumed observation error in the catch-at-age and the relative indices of abundance. The log-likelihood function for each index was defined as

$$\ln L = \frac{\sum (\ln I_t - \ln \hat{I}_t)^2}{2\mathrm{CV}^2} \tag{8}$$

where CV is the coefficient of variation and I_t is the observed relative index of abundance. The predicted relative index of abundance $\hat{I}_t$ was estimated as

$$\hat{I}_t = \hat{q}\hat{B}_t \tag{9}$$

where $\hat{B}_t$ represents the estimated biomass.

The catchability coefficient was estimated using the following equation:

$$\hat{q} = \exp\left[\frac{1}{n} \sum \ln\left(\frac{I_t}{\hat{B}_t}\right)\right] \tag{10}$$

Similarly, the log-likelihood for the catch-at-age was assumed to be log-normal distributed:

$$\ln L \frac{\sum (\ln C_t - \ln \hat{C}_t)^2}{2\mathrm{CV}^2} \tag{11}$$

The sum of the log-likelihood components associated with each species was used as the objective function. In the estimation process for both species, a CV of 0.2 was used. Although the log-likelihood was used in the estimation process, the likelihood can be easily estimated applying the exponential function to eq. 11. In the estimation process, the Solver subroutine from Microsoft Excel® and the sample–importance–resample (SIR) algorithm (Mcallister and Ianelli 1997) implemented in Visual Basic were used. In particular, in the SIR algorithm, we used uniform priors for all parameters except the recruitment (walleye pollock and Pacific cod) whose priors were assumed lognormal with the mean and standard deviation calculated from recruitment estimates from MSVPA. In general, the results from Bayesian methods were used to estimate the posterior distribution to assess the uncertainty of the suitability coefficients.

In this first version of the model, the stomach contents were assumed to be measured without error. As in MSVPA, the multispecies statistical model was set up in a quarterly fashion and we assumed that the "other food" parameter remains constant. We assumed that recruitment of age-0 fish takes place in the third quarter of the year after fish complete the larval phase.

The MSM is a complex model that estimates population numbers and predation mortality based on catch-at-age data, relative indexes of abundance, predator annual ration, and predator stomach contents using estimation procedures for the statistical part and the predation mortality. The MSM statistically estimates parameters ($N_{a,0}$, R_t, F_t, and selectivity coefficients) using either an optimization algorithm (e.g., Newton–Raphson) or Bayesian methods. In both cases, for a given set of parameter values, MSM projects population trajectories (for each species) over the specified time frame (e.g., 1979–2002). These trajectories are computed based on catch-at-age (assumed known) and on predation mortality. The predation mortality, a component of the natural mortality, requires an iterative solution, since its value in each year is confounded with the abundance of other species in that year. This iterative process is referred to as the "predation algorithm" (Sparre 1991). Given fixed values for the parameters ($N_{a,0}$, R_t, F_t, and selectivity coefficients) and an initial guess for $M2$, the population trajectories are computed. These population estimates together with given values of the suitability coefficients allow the estimation of the predation mortality. The predation algorithm then adjusts the $M2$ values and updates population estimates until two consecutive iterations converge to marginally different $M2$ and suitability coefficients values according to established criteria (Sparre 1991). Once the criteria are reached and the estimates of predation mortality, suitability coefficients, and population have converged, the likelihood (eqs. 9 and 10) is used in the criteria of the main data-fitting routine. This procedure (the main part and the internal estimation for $M2$) is repeated until the negative log-likelihood is minimized (by adjusting main parameters) or in the Bayesian methods until the posterior distribution is adequately represented.

The parameters we estimated with MSM included the initial age structure in 1979 (12 parameters), age-0 recruitment from 1979 to 2002 (24 parameters), yearly full fishing mortality from 1979 to 2002 (24 parameters), and two parame-

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Fig. 1. Multispecies statistical model (MSM) fit to the abundance indices. (*a*) Walleye pollock (*Theragra chalcogramma*) 2002 echo-integration trawl (EIT) survey in the eastern Bering Sea: observed values of the EIT survey (circles); predicted EIT values (maximum likelihood estimate) with solver (line). (*b*) Walleye pollock 2002 bottom trawl survey (BTS) in the eastern Bering Sea: observed values of the BTS (circles); predicted BTS values (maximum likelihood estimate) with solver (line).

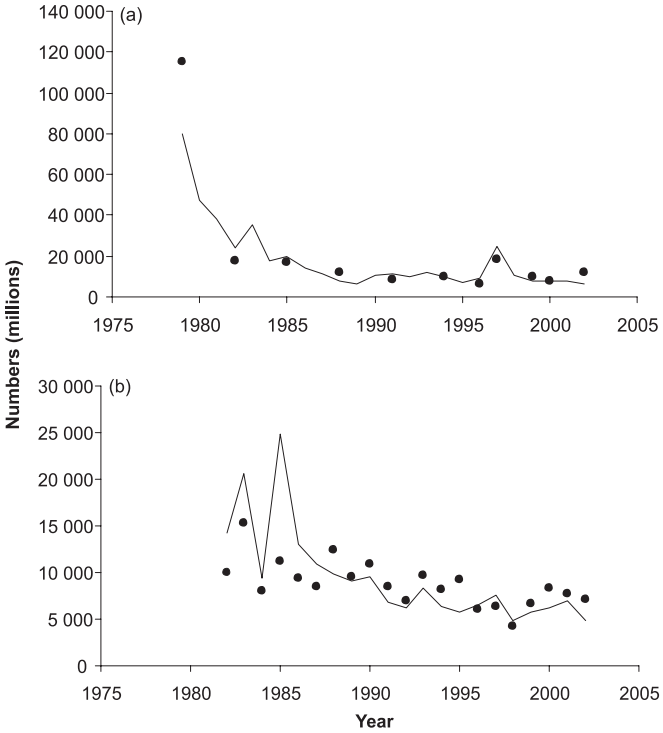
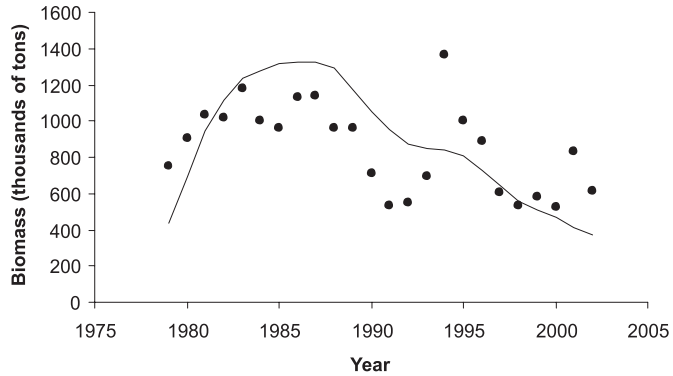


Fig. 2. Multispecies statistical model (MSM) fit to the Pacific cod (*Gadus macrocephalus*) 2002 biomass index in the eastern Bering Sea: observed values of the biomass index (cirlcles); predicted biomass index (maximum likelihood estimate) (line).



ters for selectivity (eq. 7) for each species, giving a total of 124 parameters.

We compare results from the MSVPA, MSM, and single-species statistical age-structured stock assessments from the AFSC. Details about the models used in the single-species stock assessment of walleye pollock and Pacific cod can be found in the 2002 North Pacific Fishery Management Council's groundfish stock assessment and fishery evaluation reports (Ianelli et al. 2002; Thompson and Dorn 2002).

Data

Common input data for all models included catch-at-age data (landings and discards), maturity-at-age, and weight-at-age. The common input data of the MSVPA and MSM included stomach content data, prey weight-at-age in the predator stomach contents, predator annual ration, and residual natural mortality. The AFSC fish food habits database contains stomach content information of several groundfish predators collected annually since 1985. However, stomach content data and estimates of weight-at-age in the stomach contents of predators from 1985 and 1987 were used because those years had complete quarterly information for the two species. We used the annual ration that was previously described in Livingston and Jurado-Molina (2000). The estimation of the residual natural mortality $M1$ involved an iterative process that starts with an initial run of the MSVPA for the two-species system assuming $M1 = M$ (natural mortality from the single species model). This iterative procedure was needed to incorporate the predation mortality of walleye pollock and Pacific cod by groundfish predators not included in the two-species model. An initial set of values of $M2$ was obtained in this step. These values were subtracted from the estimates of natural mortality from the base run of MSVPA that included all of the species (Livingston and Jurado-Molina 2000) to obtain new estimates of $M1$. A second run of the MSVPA for the two-species system was made with these new values of $M1$. This procedure was repeated until the following criterion of convergence was reached:

$$|M1_{\text{previous}} - M1_{\text{current}}| \leq 0.0001 \quad (12)$$

A particular input for MSVPA is the terminal fishing mortalities that were tuned to minimize the differences between single-species cohort analysis estimates and the estimates from stock assessment models used by National Marine Fisheries Service (NMFS) scientists (Livingston and Jurado-Molina 2000). Finally, relative indices of abundance (BTS and EIT) also used in the 2002 single-species stock assessment carried out by the NMFS (Ianelli et al. 2002; Thompson and Dorn 2000) were incorporated into the MSM.

For comparative purposes, we also did a MSVPA base run including all predators and all predator stomach content information (Livingston and Jurado-Molina 2000).

Results

The fit of the MSM model to the walleye pollock and Pacific cod abundance indices is illustrated in Figs. 1 and 2, respectively. The correlation matrix for the estimated parameters did not show significant correlations; therefore, no potential confounding among parameters can be observed. The estimates of the suitability coefficients from both models (MSVPA and MSM) for both species were similar (Fig. 3). A regression to test the similarity between both types of estimates carried out taking the suitability coefficients from MSVPA as the independent variable was significant ($p \sim 0$) with a slope of 0.99 ± 0.01 and explained 99% of the variability observed. Percent deviations of suitability coefficients

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Fig. 3. Comparison of estimates of average suitability coefficients for walleye pollock (*Theragra chalcogramma*) as predator from the multispecies virtual population analysis (MSVPA) and multispecies statistical model (MSM).

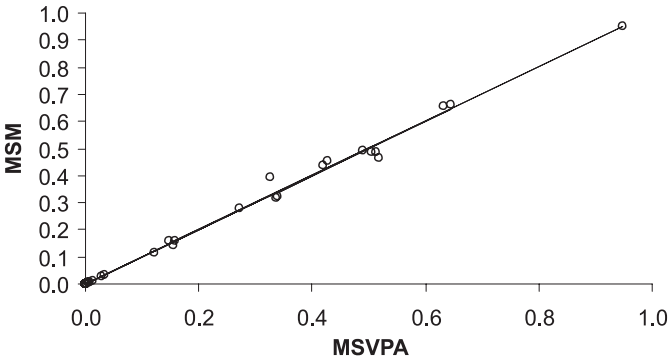
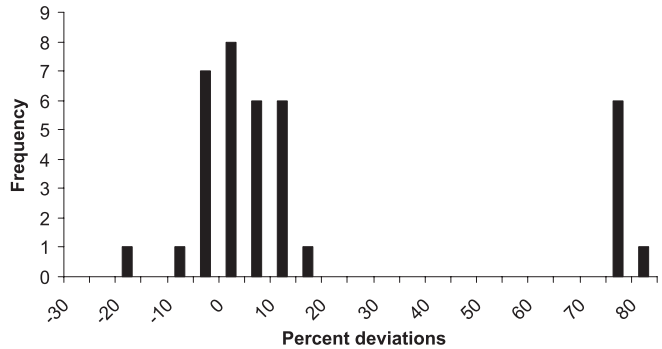


Fig. 4. Percent deviations between estimates of suitability coefficients from the multispecies virtual population analysis (MSVPA) and multispecies statistical model (MSM).



between the two models were mostly small (Fig. 4). Out of 146 average suitability estimates, only 25 had a deviation greater than 30%. Most of these (18) corresponded to Pacific cod as predator. The rest were for walleye pollock as predator, where most of the larger percent deviations were found in the first quarter. In the third and fourth quarters, no deviation was greater than 10%. The posterior distributions for the average suitability of age-0 walleye pollock as prey and walleye pollock as predator in the third quarter were estimated with MSM (as shown in Fig. 5).

The MSVPA estimates and MSM estimates (maximum likelihood estimates) of average predation mortality of walleye pollock (ages 0, 1, and 2) followed the same trend with comparable values (Figs. 6*a* and 6*b*). The highest predation mortality for age-0 walleye pollock was reached in 1983 and the lowest in 1992. The highest predation mortality for age-1 walleye pollock was reached in 1987 and the lowest in 1979. For predation mortality of age-2 walleye pollock, only the estimates from the last three years were different. For the rest of the age groups, the estimates were similar up to 1984; after that year, the estimates from MSM were larger than the estimates from MSVPA. The estimates of predation mortality for Pacific cod were not as similar as for the walleye pollock case (Figs. 6*c* and 6*d*). For age-0 Pacific cod, although both estimates followed the same trend, the estimates from MSM were larger than the estimates from MSVPA from 1979 to 1989. For ages 1, 2, and 4, these differences were much more substantial, with the estimates from MSM higher. Nonetheless, the MSM estimates always followed the same trend as the MSVPA estimates.

Comparisons of the estimates of *N*3+ walleye pollock from the MSM, the singles-species stock assessment from AFSC, the assessment from MSVPA (two species), and the MSVPA base run (all predator species) are shown in Fig. 7. In general, the majority of *N*3+ estimates produced by all of the multispecies models are larger than the single-species AFSC stock assessments. In particular, the largest deviations with respect to the AFSC stock assessment model estimates corresponded to the MSM model from 1981 to 1985, with 1981 the highest at 27%. However, in latter years of the assessment, the MSVPA (base run) and the MSM had smaller *N*3+ estimates than the ones from the AFSC assessment.

Discussion

The MSVPA model is an important tool that can provide advice to fisheries managers about potential indirect effects of fishing in a multispecies context. However, its lack of statistical assumptions does not allow the use of tools regularly used in age-structured single-species stock assessment such as Bayesian analysis, risk analysis, and decision analysis. Our intent is not to carry out a formal stock assessment but to show that it is feasible to incorporate the predation equations into a statistical catch-at-age model and to point out some of the advantages of taking this approach for providing advice to fisheries managers. It is likely that the predation equations can be incorporated into most of the statistical catch-at-age models currently used in fisheries management that have the separable fishing mortality assumption (Doubleday 1976; Pope 1977). The approach taken in this work is also being used to incorporate cannibalism in the stock assessment of hake in central Chile using a length-based model (C. Gatica and J. Jurado-Molina, Departamento de Pesquerías, Instituto de Investigación Pesquera, Casilla 350, Colón 2780, Talcahuano, Chile, personal communication).

Following the steps in the classification of multispecies models proposed by Hollowed et al. (2000*b*), the multispecies statistical model includes biological interactions with predator–prey feedback and handles age structure; however, in contrast with the traditional multispecies models (e.g., MSVPA), this new type of model uses a forward-fitting process based on likelihood fitting algorithms similar to the one used by the statistical assessment model SAM in which predators are added to a single-species stock assessment model (Livingston and Methot 1998; Hollowed et al. 2000*a*). However, the SAM does not have predator–prey feedback. Therefore, it is necessary to include a new step in the classification proposed by Hollowed et al. (2000*b*) that separates the traditional multispecies model from the multispecies statistical models.

This work presents preliminary results with an initial version of the model. Further refinements and validation of the model will be needed. However, some general conclusions can be stated from this analysis.

In general, more similarities than differences between the estimates of suitability coefficients from the MSVPA and

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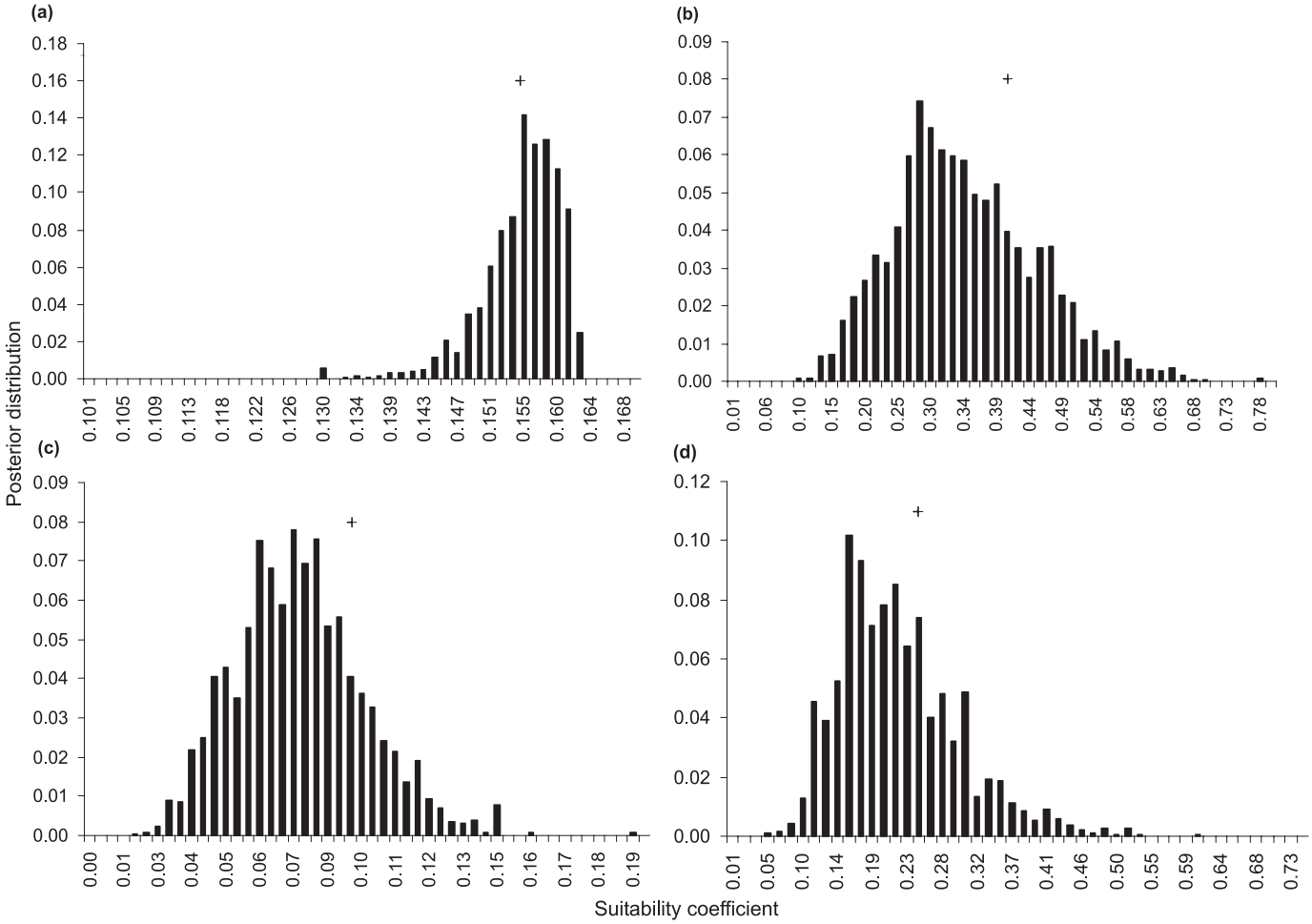
Fig. 5. Posterior distribution of the average suitability coefficients of age-0 walleye pollock (*Theragra chalcogramma*) as prey in the third quarter. (*a*) Age-1 walleye pollock as predator; (*b*) age-3 walleye pollock as predator; (*c*) age-5 walleye pollock as predator; (*d*) age-8 walleye pollock as predator. +, suitability coefficient estimate from multispecies virtual population analysis (MSVPA).



MSM were found. Regression between the suitability estimates from MSVPA and MSFOR, the percent deviations between both type of estimates, and their distribution suggest their great similarity. Most of the greatest percent deviations corresponded to cases with Pacific cod as the predator. In the case of walleye pollock, some large percent deviations were found for the first quarter. However, in terms of predation mortality, the third and fourth quarters are the most important for determining the magnitude of this parameter for walleye pollock, since rations are larger in these quarters. For these quarters, none of the deviation was greater than 10%. MSVPA provides a point estimate for the suitability coefficients with no measure of the uncertainty associated with those parameters. Owing to use of Bayesian methods (SIR), MSM is capable of providing a measure of the uncertainty (posterior distribution) associated with the suitability coefficients.

In particular, the suitability coefficient for the walleye pollock combination of age 5 (predator) and age 0 (prey) is considerably smaller than the suitability coefficients corresponding to age-1, age-3, and age-8 of walleye pollock as predator. A similar result is observed in the MSVPA base run (all stomach data and predators included). This discrepancy could be associated with the available stomach data, but further confirmation will be provided when the new stomach data are added to these models.

The MSM and MSVPA produced nearly identical temporal trends for walleye pollock estimates of predation mortality. The resulting temporal trend of predation mortality of walleye pollock as prey is the result of the additive consumption of predators of different age groups preying on walleye pollock. In particular, the highest predation mortality of age-0 walleye pollock in 1983 is the result of the consumption of large adult walleye pollock population ($N3+$) and a large age-1 walleye pollock age group. For the younger age groups where predation mortality of walleye pollock is high, the estimates of MSM and MSVPA were very similar. The greater differences were observed in older ages. For Pacific cod as predator, larger differences were found for two age groups (age 1 and age 4); however, they followed the same trend. Discrepancies between estimates of suitability coefficients and predation mortality from both models might be due to the use of different estimation procedures. MSM uses a forward-fitting process based on likelihood fitting algorithms, while MSVPA uses a deterministic backward nonlinear sequential method. Therefore, it is promising that both models provide similar estimates of suitability coefficients and predation mortality.

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Fig. 6. Temporal trend of the predation mortality estimates. (*a*) Age-0 walleye pollock (*Theragra chalcogramma*); (*b*) age-1 walleye pollock; (*c*) age-0 Pacific cod (*Gadus macrocephalus*); (*d*) age-2 Pacific cod. Asterisks, maximum likelihood estimates from the multispecies statistical model (MSM); diamonds, point estimates from the multispecies virtual population analysis (MSVPA) (two species).

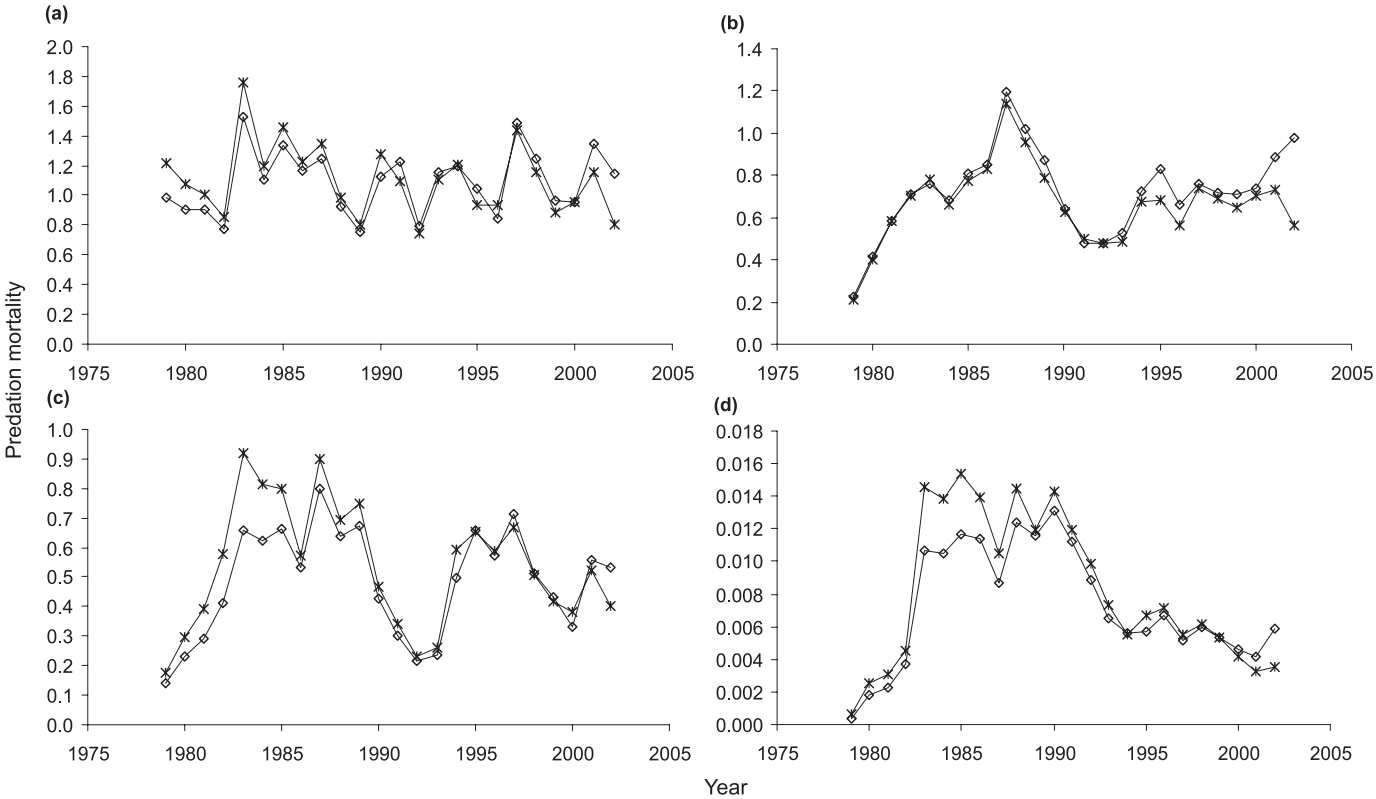
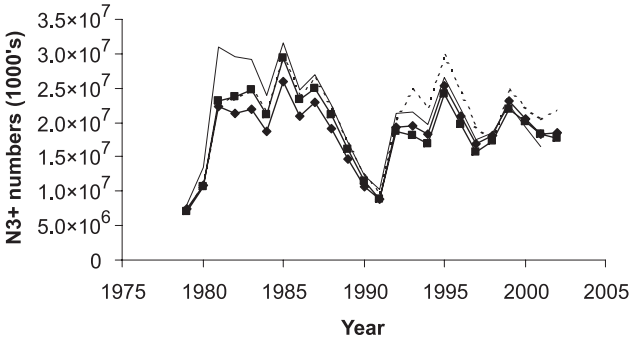


Fig. 7. Comparison of walleye pollock (*Theragra chalcogramma*) estimates of adult population (*N*3+) in the eastern Bering Sea. Diamonds, AFSC 2002 single-species stock assessment; solid line, multispecies statistical model (MSM); broken line, multispecies virtual population analysis (MSVPA) (two species); squares, MSVPA2 base run (all predators included).



Although some differences were observed between the *N*3+ estimates from MSM and the estimates of the single-species stock assessment, the majority of estimates and the temporal trend are alike. The difference between the estimates might be due to the type of data used to fit the models. The single-species stock assessment uses age composition data from surveys and fisheries. In particular, catch-at-age data are allocated to a particular type of fishing gear. For the MSM, age composition for catch-at-age was used but was aggregated over all types of fishing gears, and survey age composition was not used. In many assessments, acknowledging time-varying selectivity has been proposed as an added source of model uncertainty. For simplicity, we have assumed constant selectivity. The assumption, if violated, may lead to underestimates of uncertainty. However, future versions of MSM will incorporate variable selectivity patterns.

In general, the MSM, MSVPA, and single-species stock assessment produced similar estimates of adult population (*N*3+), but only MSM was able to provide a measure of the uncertainty of suitability coefficients and predation mortality, a task that it is not possible with the available MSVPA–MSFOR technology.

Results from the MSM suggest that if a new estimate of the residual mortality *M*1 developed from MSVPA results (two species) is included in the model, MSM with only two species was able to reproduce fairly well the *N*3+ estimates from the MSVPA base-run model (all species included) with all predator stomach content data (Jurado-Molina and Livingston 2002*a*).

Similar to other multispecies models and aggregate models, Ecopath–Ecosim (Pauly et al. 2000), the multispecies statistical model has to be considered as a work in progress. As with any multispecies model, the MSM could play an important role in describing the indirect effects of fishing, but it may be wise to accept general rather than specific predictions (Hollowed et al. 2000*b*). Managers need to assess the potential consequences of their decisions on the ecosystem. In particular, they need to take into account the indirect ef-

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fects of fishing caused by predator–prey relationships that could cause potential changes in the structure of fish populations. Although MSVPA provides insights into the amount and direction of these indirect effects, MSM allows the incorporation of uncertainty into the estimation process. Fishery managers can then be provided with decision tables that allow the consideration of the likelihood of different states of nature that may result when changing fishing strategies on a predator or prey species.

Several improvements could be made in future versions of the model including the addition of more predator species, in particular the addition of Pacific herring (*Clupea pallasi*) and rock sole (*Pleuronectes bilineatus*) (prey), which seem to be the most sensitive species to indirect effects of fishing mortality (Jurado-Molina and Livingston 2002*a*, 2002*b*). It is also necessary to include the complete set of predator stomach content data and new data in future versions of the model. It is also important to incorporate a statistical model for the diet composition data in the future. A formal evaluation of the model through simulation of the system (adding sampling error) given a known dynamic will be necessary to see if the model is able to generate good estimates of the parameters. The final goal would be to incorporate all of the data sources used in the single-species stock assessments into the multispecies statistical model. Forward simulations to test management scenarios also need to be implemented. In those simulations, future recruitment can be lognormal distributed or modeled as either a Ricker or Beverton–Holt spawner–recruit relationship to account for compensatory effects. The validation of the model also requires a sensitivity analysis similar to the ones made for the MSVPA and MSFOR models.

The main goal in the development of this model is to incorporate the predation equations into the actual stock assessment models used to provide groundfish management advice for the Bering Sea. The development of the multispecies statistical method is an important step in its adoption in providing advice to fisheries managers because it allows consideration of uncertainty in a multispecies predator–prey modeling context and it will help to establish useful scenarios for the management of groundfish resources in the Bering Sea.

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