MULTISPECIES AND SINGLE-SPECIES MODELS OF FISH POPULATION DYNAMICS: COMPARING PARAMETER ESTIMATES

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ABSTRACT. Population features inferred from single-species, age-structured models are compared to those inferred from a multispecies, age-structured model that includes predator-prey interactions among three commercially harvested fish species—walleye pollock, Atka mackerel, and Pacific cod—on the Aleutian Shelf, Alaska. The multispecies framework treats the single-species models and data as a special case of the multispecies model and data. The same data from fisheries and surveys are used to estimate model parameters for both single-species and multispecies configurations of the model. Additionally, data from stomach samples and predator rations are used to estimate the parameters of the multispecies model. One form of the feeding functional response, predator pre-emption, was selected using AIC from seven alternative models for how the predation rate changes with the densities of prey and possibly other predators. Differences in estimated population dynamics and productivity between the multispecies and single-species models were observed. The multispecies model estimated lower mackerel population sizes from 1964–2003 than the single-species model, while the spawning biomass of pollock was estimated to have declined more than three times faster since 1964 by the multispecies model. The variances around the estimates of spawning biomass were smaller for mackerel and larger for pollock in the multispecies model compared to the single-species model.

KEY WORDS: Multispecies stock assessment, predator-prey modeling, fisheries, integrated analysis, statistical catch-at-age analysis, predator functional response.

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1. Introduction. Interactions among species affect the population dynamics of every species in an ecological system. Although fisheries are embedded in such a system of interacting predators and preys, traditional methods of fisheries stock assessment are typically based on single-species models (Quinn [2003], Quinn and Collie [2005], Marasco et al. [2007]). The dynamics and productivity of harvested fish stocks are consequently modeled for management purposes using an approach that assumes that natural mortality is constant over time.

An alternative approach is to combine time-series information on diets from stomach samples from various species that interact as predator and prey, with the more traditional data sources used for stock assessment modeling and hence to treat the single-species modeling framework as a special case of a multispecies modeling framework. Predators can be considered as another sampling device, analogous to a fishery or a survey, providing information about the population dynamics of the species preyed upon. Similar to a fishery, a predator will exhibit a "selectivity" for a given age or size of a prey species. This selectivity, combined with a measure of predator effort (its feeding rate or *functional response*), will impose a rate of mortality due to that predator on the prey. The interaction of predator selectivity and abundance of prey is reflected in the predator's diet, observations of which can then be used to estimate the parameters of, and perhaps the functional form for, the predator functional response. Estimating the parameters of the predator functional response within a conventional stock assessment model extends the strengths of single-species methods of stock assessment into the realm of ecosystem modeling and management (Link [2002], Pikitch et al. [2004], Marasco et al. [2007]), using additional information on ecological interactions when estimating variables of interest.

Many previous multispecies fisheries assessments have been based on multispecies virtual population analysis (MSVPA) and its variants (see Magnússon [1995] for a summary and critique of MSVPA models). MSVPA is an extension to single-species virtual population analysis (VPA) that estimates current and historical biomass while explicitly accounting for predation among modeled species. A core component of MSVPA is the notion of the "suitability" of each type of prey to each predator. Suitability and the age structure of fishery catches are assumed to be known without error in MSVPA, which is problematic

for regions for which catch-at-age data are not available for all years for many species.

An alternative to the MSVPA is Ecopath-with-Ecosim (EwE; Christensen and Walters [2004]). This method was originally developed to represent each trophic compartment of an ecosystem as a single dynamic pool without age structure, although subsequent additions incorporated "stanzas" to represent ordinal stages of life history. It is a simulation approach rather than a statistical estimation method, which limits its use for tactical purposes of fisheries management such as setting annual catch limits.

This paper develops a statistical framework for simultaneously modeling multiple interacting species to assess their status and productivity, using data from stomach samples to estimate predator–prey relationships among the species included in the model. The framework differs from MSVPA by allowing for uncertainty regarding the predator functional response to prey densities and in not requiring an assumed value for fishing mortality in the terminal year. The framework is similar to Gadget (Begley [2003], Stefansson [2003]), a likelihood-based approach that allows for multiple stocks, fisheries, and surveys for each species, and for several spatial areas, with migration among them. Gadget has been used to model multispecies/fishery dynamics in boreal systems such as the interactions among cod, capelin, and shrimp in Icelandic waters. Unlike Gadget, the approach outlined here can make explicit use of both length and weight compositions of prey in predator diets when estimating the parameters of predation functions and allows a wider range of predator functional responses to be considered.

The model is applied for illustrative purposes to three commercial fish species on the Aleutian shelf, Alaska: walleye pollock (*Theragra chalcogramma*), Atka mackeral (*Pleurogrammus monopterygius*), and Pacific cod (*Gadus macrocephalus*). Diet data indicate that cod is an important predator of pollock and of mackerel in this region, although large individuals of all three species consume at least some small individuals of one another, and there is also cannibalism. These species provide the basis for the main fisheries in the region as well as are important food items for apex predators such as Steller sea lions (*Eumetopias jubatus*), which have exhibited recent local declines in abundance and for which food web effects of fishing have been posited as

a contributory cause (National Research Council [2003]). Other important predators of these fish in the Aleutians include Pacific halibut (*Hippoglossus stenolepis*), arrowtooth flounder (*Atheresthes stomias*), and Northern fur seals (*Callorhinus ursinus*). Model outputs are compared between the multispecies and single-species approaches with the ultimate goal of identifying better potential trade-offs among fisheries for different species, and between fisheries and the trophic roles of the harvested populations, than is achievable by considering each species in isolation.

Past assessment studies of North Pacific fish populations that incorporate predation aspects of multispecies interactions include MSVPA-based models (Livingston and Jurado-Molina [2000], Jurado-Molina and Livingston [2002], Jurado-Molina et al. [2005a, b]); EwE based-models (Trites et al. [1999], Aydin et al. [2002], Ciannelli et al. [2004], Guénette et al. [2006]); statistical catch-at-age assessments with predation applied as an external "forcing function" (Livingston and Methot [1998]); models that combine MSVPA and statistical catch-at-age approaches (Jurado-Molina et al. (2005a)); and surplus-production models for multispecies, composite stocks without age structure (Mueter and Megrey [2006]). However, none of these studies fully integrated predation and the diet data when estimating model parameters.

1.1 Alternative structural models: predator functional response. There is a large body of work developing models on the rate at which an individual predator is able to obtain its prey in given prey and predator densities. This rate may be affected by factors such as predator searching time, time to handle each captured prey, digestive processing (satiation), and competition with other predators. Alternative models emphasize different aspects of these processes.

The simplest model for how an individual predator's feeding rate responds to changes in the density of prey or other predators is that there is no response, that is, a constant proportion of the available prey is consumed regardless of the prey (or predator) density. This is the classical Lotka–Volterra model for predation. Jeschke et al. [2002] summarize studies subsequent to the Lotka–Volterra model using a "family tree" and organizing 38 types of functional response that have been described in the literature. This range of functional responses can be condensed into seven general types (Koen-Alonso and Yodzis [2005], Skalski and Gilliam [2001]): *linear* (Lotka–Volterra),

asymptotic (Holling Type II), *sigmoid* (Holling type III), *predator interference*, *predator pre-emption*, *Hassell–Varley*, and *Ecosim*. A predator's rate of feeding depends only on the density of prey in the first three of these seven types, but it may also depend on the densities of other predators in the last four types.

The most commonly used model of the predator response is the Holling Type II, in which the rate of predation increases with prey density up to an asymptote. The Holling Type III, in which the rate of feeding decreases at low prey densities as well as at high densities, is also widely applied. The predator interference model represents a case in which the densities of other predators affect a predator's feeding rate at all prey densities. The interference due to other predators decreases asymptotically with the prey density in the predator pre-emption model, so that at high enough densities of prey, predators no longer interfere with one another. The Hassell–Varley model has been proposed as a generalized form that reduces to Type II with appropriate parameter values (Skalski and Gilliam [2001]). Essington and Hansson [2004] modified the Hassell–Varley model to represent a range of possible responses, including satiation, and applied the modified form to cod predation on herring and sprat in the Baltic Sea. The Ecosim form of predator response incorporates the concept of prey refuges or proportions of prey that are invulnerable to predation at times (Christensen and Walters [2004]).

Field studies using fisheries data to select among alternative forms of the predator functional response are rare. Alternative parameterizations of the Ecosim model have been constructed as one means of representing a range of alternative predator functional responses (i.e., Mackinson et al. [2003]). Koen-Alonso and Yodzis [2005] selected among alternative forms of predator functional response using fisheries data for a marine community off Patagonia.

2. Materials and methods

2.1 The data.   A variety of data sources are used for parameter estimation. Some of these are assumed to be subject to measurement error but others are considered to be known exactly. The former are included in the likelihood function whereas the latter are used to directly

specify some of the parameters of the model. The traditional sources of data from fisheries and surveys that are included in the likelihood function are: (i) total biomass of the catches by fishery and year, (ii) the age- or length-composition of the catches by fishery and year, and (iii) survey biomass indices and the associated survey age- or length-compositions for each year for which survey data are available. When the predation data are used for parameter estimation, the following additional data sources are included in the likelihood function: (iv) stomach samples (length-frequencies of prey for each predator length over the entire period modeled, biomass-frequencies of prey species by predator length each year) and (v) data on predator rations (calculated from weight-at-age using the approach of Essington et al. [2001]). Maturity-at-age, weight-at-length, and the probability of being a given length at each age (the age–length transition matrix) are prespecified based on data collected from surveys.

The application to walleye pollock, Atka mackerel, and Pacific cod considers the years 1960–2003. Fishery catches start in 1978 for all three species in the model, although a small catch of Atka mackerel was recorded in 1977. The ages included in the application to pollock, mackerel, and cod were 0–15, 0–15, and 0–12 years, respectively, with the last age being a plus-group, while the length-structure of diets and the fishery and survey catches were modeled using 5-cm length classes (1–80 cm for walleye pollock, 1–65 cm for Atka mackerel, and 1–120 cm for Pacific cod). The composition data from the fisheries and surveys for pollock and mackerel were in ages, but the cod compositions were by length. A single fishery was modeled for each of mackerel and pollock, while three fisheries (trawls, pots, and longlines), each of which was allowed to have a different age-specific selectivity pattern, were considered for cod.

The effective sample sizes for the fishery and survey age-compositions for pollock and mackerel were set to the values used in Anon [2003]. These ranged between 10 and 50 for the 8 years of pollock fishery samples, 100 for each of three pollock surveys, between 25 and 100 for the 20 years of mackerel fishery samples, and 50 for each of five mackerel surveys. Effective sample sizes for the cod fisheries for each of 14, 10, and 14 sample years for trawls, pots, and longlines, respectively, were assigned to a value of 10, and each of 5 years of cod surveys were assigned a value of 40.

Data on prey weights and lengths in stomach samples from the Aleutian shelf for each of the three species as predators in 5-cm length classes were obtained during the 25-year period, 1978 to 2003. During this period, 1,987 pollock stomachs (in 17 individual years), 1,033 mackerel stomachs (11 years), and 3,278 cod stomachs (20 years) contained at least one of the other three species as prey. Number of predator stomachs recorded for a given combination of predator-length class and year for prey weights, which contained at least one of the modeled prey species, ranged from 0 to 706 for pollock, 0 to 701 for mackerel, and 0 to 480 for cod. The number of stomachs examined for prey lengths was smaller. Maximum sample size of 20 was assigned to each length class of predator per year to reduce the influence of years in which many stomachs were examined, but the assumption of independence of each stomach is not likely to be satisfied.

Data on consumption rates (kg/kg/day) of total prey mass required by a unit of predator mass by predator species and age calculated from weight-at-age (Essington et al. [2001]) are shown in Figure 1.

2.2 The model. The model of the population dynamics is age-structured, allows for multiple fishing fleets for each species, assumes that recruitment is distributed about an underlying Beverton–Holt stock–recruitment relationship, and accounts for mortality due to fishery catches and other sources. The nonfishing mortality can be separated into (i) mortality due to predation by the species in the model,
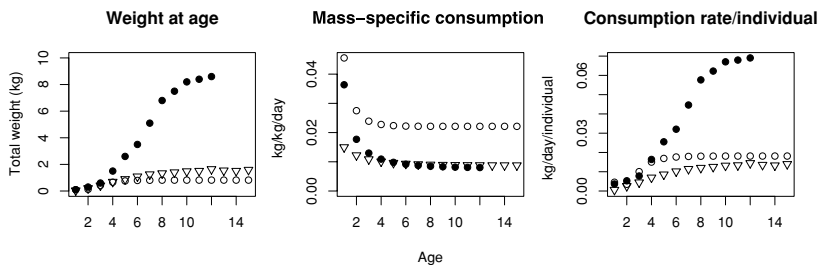

FIGURE 1. Weights-at-age (left), mass-specific consumption rates (center), and mass consumed by an individual of a given age in a day (right) for Pacific cod (closed circles), Atka mackerel (open circles), and walleye pollock (triangles).

and (ii) residual mortality due to species outside the model and other factors. The model can be run in two modes: (i) "predation on," when the model incorporates predator–prey interactions and uses diet data to estimate the model parameters; or (ii) "predation off," when inter-specific predation is assumed to be included as part of the residual mortality and only conventional data sources from fisheries and surveys are used for parameter estimation. The values for the parameters of the model are estimated by fitting it to data on total catches, survey indices of abundance, age- and length-compositions from catches and surveys, and diet data (for the "predation on" variant). A schematic of the overall framework is provided in Figure 2.

2.2.1 *Basic dynamics.* The numbers-at-age for the years $y_\mathrm{P} + 1$, $y_\mathrm{P} + 2, \ldots, y_\mathrm{L}$, where y_P and y_L are, respectively, the first and last year considered in the model, are given by

(1)
$$N_{k,a,y} = \begin{cases} R_{k,0} e^{\varepsilon^{\mathrm{R}}_{k,y}} & \text{if } a = 0 \\ N_{k,a-1,y-1} L_{k,a-1,y-1} & \text{if } 1 \le a < A_{k,\mathrm{L}} \\ N_{k,A_{k,\mathrm{L}}-1,y-1} L_{k,A_{k,\mathrm{L}}-1,y-1} + N_{k,A_{k,\mathrm{L}},y-1} L_{k,A_{k,\mathrm{L}},y-1} & \text{if } a = A_{k,\mathrm{L}} \end{cases}$$

where

$N_{k,a,y}$ is the number of animals of age a and species k at the start of year y,

$R_{k,0}$ is the mean unfished recruitment for species k,

$L_{k,a,y}$ is the survival rate for animals of species k and age a during year y:

(2)
$$L_{k,a,y} = e^{-Z_{k,a,y}}$$

$Z_{k,a,y}$ is the total mortality rate for animals of species k and age a during year y,

$\varepsilon^{\mathrm{R}}_{k,y}$ is the logarithm of the deviation from the mean recruitment for species k in year y, and

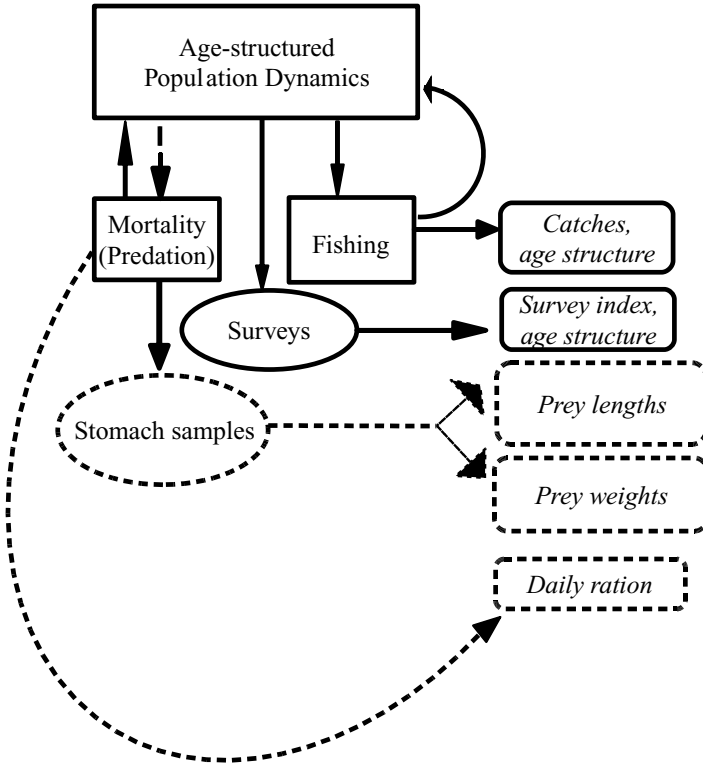$A_{k,\mathrm{L}}$ is the oldest age considered for species k.

FIGURE 2. Schematic of the multispecies model. Model predictions for which data are available are italicized. Solid lines indicate the "predation off" configuration.

2.2.2 *Total mortality.*   The total mortality on animals of age a and species k during year y is due to (i) fishing, (ii) predation by predators included in the model (used for the "predation on" configurations only), and (iii) residual natural mortality due to factors not included in the model (for "predation off" configurations this includes all the predation mortality), that is:

$$(3) \qquad Z_{k,a,y} = \sum_{f} F_{k,a,y}^{f} + P_{k,a,y} + M_k$$

where

$F^f_{k,a,y}$ is the fishing mortality rate by fleet f on animals of species k and age a during year y, that is:

(4)
$$F^f_{k,a,y} = \begin{cases} S^f_{k,a,y}\, e^{\mu^f_k + \varepsilon^f_{k,y}} & \text{if } C^f_{k,y} > 0 \\ 0 & \text{otherwise} \end{cases}$$

$C^f_{k,y}$ is the observed catch (in weight) of species k by fleet f during year y,

μ^f_k is the logarithm of the mean fishing mortality rate by fleet f on animals of species k over all years,

$\varepsilon^f_{k,y}$ is the logarithm of the deviation from the mean fishing mortality for species k and fleet f during year y,

$S^f_{k,a,y}$ is the selectivity of fleet f on animals of species k and age a during year y,

$P_{k,a,y}$ is the mortality rate for prey of species k and age a during year y due to the modeled predators, and

M_k is the mortality rate for prey species k due to causes not included in the model.

2.2.3 *Fishery and survey selectivity.* Selectivity for a sampling method is the relative proportion of the population at age that is available to that sampling method. Selectivity is allowed to vary between the surveys and the fisheries for each species and is modeled by estimating selection parameters for each age (*sensu* Maunder and Watters [2003]). The possibility of time-varying selectivity is accounted for by estimating age-specific selectivity parameters for periods of years. Selectivity for species k is assumed to be independent of age above age $A_{k,\mathrm{M}}$.

(5)
$$S^f_{k,a,y} = \begin{cases} e^{\eta^f_{y,a}} & \text{if } a \leq A_{k,\mathrm{M}} \\ e^{\eta^f_{y,A_{k,\mathrm{M}}}} & \text{otherwise.} \end{cases}$$

An analogous approach is used to model survey selectivity.

2.2.4 *Initial conditions.* Each species is assumed to be in deterministic unfished equilibrium at the start of the first year considered in the model (year y_P). Year y_P is chosen to be 4 years before the first year for which recruitment is estimated, that is, year $y_{k,R} = y_{k,C} - A_{k,L} + 1$, where $y_{k,C}$ is the earliest year for which catch data are available for any species k.

2.2.5 *Predation.* When predation is "on," the mortality rate during year y for prey of species k and age a, $P_{k,a,y}$, is:

$$(6) \qquad P_{k,a,y} = \sum_{r,u} V^{r,u}_{k,a,y},$$

where $V^{r,u}_{k,a,y}$ is the mortality rate during year y for prey of species k and age a due to predators of species r and age u:

$$(7) \qquad V^{r,u}_{k,a,y} = N_{r,u,y}\, \phi^{r,u}_{k,a,y}\, \gamma^{r,u}_{k,a}$$

$\phi^{r,u}_{k,a,y}$ is the predation rate due to an individual predator of species r and age u during year y on "fully selected" prey of species k and age a (see Section 2.2.5.2), and

$\gamma^{r,u}_{k,a}$ is the selectivity of a predator of species r and age u for prey of species k and age a.

2.2.5.1 *Numbers of prey eaten, prey mass, and daily ration.* The total number of prey of species k and age a eaten during year y by predators of species r and age u, $E^{r,u}_{k,a,y}$, is given by

$$(8) \qquad E^{r,u}_{k,a,y} = \frac{V^{r,u}_{k,a,y}}{Z_{k,a,y}} N_{k,a,y} \left(1 - e^{-Z_{k,a,y}}\right).$$

The number of prey of species k and age a eaten by predators of species r in length-class l during year y is then

$$(9) \qquad E^{r,l}_{k,a,y} = \sum_{u} \left(E^{r,u}_{k,a,y}\, \chi^{r,u,l}\right),$$

where $\chi^{r,u,l}$ is the age-to-length transition matrix for species r (the proportion of animals of species r and age u that are in length-class l).

The mass of prey species k (including "other") consumed during year y by predators of species r in length-class l, $Q_{k,y}^{r,l}$, is given by

$$(10) \qquad Q_{k,y}^{r,l} = \sum_u Q_{k,y}^{r,u} \chi^{r,u,l},$$

where $Q_{k,y}^{r,u}$ is the mass of prey species k consumed during year y by predators of species r and age u:

$$(11) \quad Q_{k,y}^{r,u} = \begin{cases} \displaystyle\sum_{a=0}^{A_{\mathrm{L},k}} \left(E_{k,a,y}^{r,u}\, w_{k,a} \right) & \text{for modeled prey species } k \\[2mm] Q_o^r \left(1 - e^{-O_y^{r,u}} \right) & \text{for other prey} \end{cases}$$

$w_{k,a}$ is the mean weight of an individual of age a and species k in the population,

$O_y^{r,u}$ is the mortality rate due to predators of species r and age u on "other" prey:

$$(12) \qquad O_y^{r,u} = \phi_o^{r,u} N_{r,u,y}$$

$\phi_o^{r,u}$ is the predation rate by predators of species r and age u on "other" prey (assumed to be linear and independent of year), and

Q_0^r is the mass of "other" prey.

The model estimate of the daily ration of a predator of species r and age u during year y is given by

$$(13) \qquad \hat{\Omega}_y^{r,u} = \frac{1}{365} \left(\sum_k Q_{k,y}^{r,u} \right) \Big/ \bar{N}_{r,u,y}$$

where $\bar{N}_{r,u,y}$ is the average number of predators of species r and age u during year y, approximated by

$$(14) \qquad \bar{N}_{r,u,y} = N_{r,u,y}\, e^{-Z_{r,u,y}/2}.$$

2.2.5.2 *Predator functional response.* Seven alternative forms ("types") of predator functional response (the predation rate by an individual predator at given densities of prey and other predators— see equation 7) are considered (Table 1). Types II, IV, V, and VI (Table 1) correspond to reparameterized versions of equations (1) to (4), respectively, from Skalski and Gilliam [2001]. Types III and VII in Table 1 correspond to reparameterized versions of equations (9) and (12), respectively, from Koen-Alonso and Yodzis [2005], expressed in numbers instead of predator and prey biomass.

The rate at which predation varies with age is taken to be

$$(15) \qquad \theta^{r,u} = 1 + \omega^r \tilde{\omega}^r / (u + \tilde{\omega}^r),$$

TABLE 1. Alternative hypotheses for the form of the predator functional response. The symbols v_k^r, $\tilde{v}_k^r$, and $\tilde{\tilde{v}}_k^r$ are used for the parameters of the functional responses, although these parameters do not have the same meaning for each form. See equations (16) and (17) for the definitions of $\Phi_y^{r,u}$ and $\Psi_y^{k,a}$, respectively.

Response name	Type	Number of estimable parameters	$\phi_{k,a,y}^{r,u}$ (from equation 7)
Linear	I	1	$\theta^{r,u} v_k^r$
Asymptotic (Holling Type II)	II	2	$\dfrac{v_k^r \theta^{r,u} [1 + \tilde{v}_k^r]}{1 + \tilde{v}_k^r \, \Phi_y^{r,u}}$
Sigmoid (Holling Type III)	III	3	$\dfrac{v_k^r \theta^{r,u} (1 + \tilde{v}_k^r) (\Phi_y^{r,u})^{\tilde{\tilde{v}}_k^r - 1}}{1 + \tilde{v}_k^r (\Phi_y^{r,u})^{\tilde{\tilde{v}}_k^r}}$
Interference	IV	3	$\dfrac{v_k^r \theta^{r,u} [1 + \tilde{v}_k^r]}{1 + \tilde{v}_k^r \Phi_y^{r,u} + \tilde{\tilde{v}}_k^r (\Psi_y^{k,a} - 1)}$
Pre-emption	V	3	$\dfrac{v_k^r \theta^{r,u} [1 + \tilde{v}_k^r]}{(1 + \tilde{v}_k^r \, \Phi_y^{r,u}) [1 + \tilde{\tilde{v}}_k^r (\Psi_y^{k,a} - 1)]}$
Hassell–Varley	VI	3	$\dfrac{v_k^r \theta^{r,u} [1 + \tilde{v}_k^r]}{\tilde{v}_k^r \Phi_y^{r,u} + (\Phi_y^{r,u})^{\tilde{\tilde{v}}_k^r}}$
Ecosim	VII	2	$\dfrac{v_k^r \theta^{r,u}}{1 + \tilde{v}_k^r (\Psi_y^{k,a} - 1)}$

where $\theta^{r,u}$ determines the extent to which predation mortality due to predator r changes with predator age u (in the absence of fluctuations in predator and prey numbers for those feeding functional relationships that depend on predator and prey numbers), ω^r is fraction by which predation mortality is higher at age 0 than at "infinite age," and $\tilde{\omega}^r$ determines the rate at which predation mortality drops with age.

The numbers of prey and of predators are both expressed relative to their equilibrium values in Table 1. The number of prey available to predators of species r and age u during year y relative to the number in equilibrium (i.e., in year y_P), $\Phi_y^{r,u}$ is:

$$(16) \qquad \Phi_y^{r,u} = \frac{\sum_{k,a} \left(N_{k,a,y} \gamma_{k,a}^{r,u} \right)}{\sum_{k,a} \left(N_{k,a,y_p} \gamma_{k,a}^{r,u} \right)}$$

and the number of predators who would consume prey of species k and age a during year y relative to the number in equilibrium, $\Psi_y^{k,a}$ is:

$$(17) \qquad \Psi_y^{k,a} = \frac{\sum_{r,u} \left(N_{r,u,y} \gamma_{k,a}^{r,u} \right)}{\sum_{r,u} \left(N_{r,u,y_p} \gamma_{k,a}^{r,u} \right)}.$$

2.2.5.3 *Predator–prey age selectivity.* The selectivity by predators of species r and age u for prey of species k and age a is modeled using a gamma function:

$$(18) \qquad \gamma_{k,a}^{r,u} = \left(G_{k,a}^{r,u} / \tilde{G}^r \right)^{\alpha^r - 1} \exp\left[- \left(G_{k,a}^{r,u} - \tilde{G}^r \right) / \beta^r \right],$$

where

$G_{k,a}^{r,u}$ is the logarithm of the ratio of the expected length of an animal of species r and age u to that of an animal of species k and age a,

$\tilde{G}^r = (\alpha^r - 1)\beta^r$, is the value of $G_{k,a}^{r,u}$ at which predator selectivity is 1, and

α^r, β^r are the parameters of the predation selectivity function for predator species r.

2.2.6 *The objective function and implementation details.*   Table 2 summarizes the (potentially) estimable parameters of the model. Recruitment was estimated from 1964 for pollock and Atka mackerel and from 1967 for Pacific cod (the number of modeled years with variable recruitment before fishing equals the number of modeled age classes). The objective function (Tables 3 and 4) consists of contributions from the data (the likelihood) and from penalties (essentially priors on the parameters). The observed catches are assumed to be lognormally distributed about the model-predicted catches, whereas the survey indices of biomass are assumed to be lognormally distributed indices of absolute abundance. The catch and survey age- and size-compositions are assumed to be multinomially distributed about the model-predicted values. The way these data are treated in the likelihood function is identical to how they have been incorporated into recent assessments for Atka mackerel and pollock (Anon [2003]). The data on daily ration (by age-class and species) is assumed to be lognormally distributed about the model estimate of average daily ration by age from 1960–2003. The data on the breakdown of the diet in mass of each predator length-class by prey species (including "other") and the data on the size-composition of each prey species in the stomachs of each predator length-class are also assumed to be multinomially distributed. The variances for all of the likelihood components are prespecified rather than being treated as estimated parameters of the model.

The model is always fitted to fishery catches, age- and size-compositions from fisheries, survey indices, and age- and size-compositions from surveys. When predation is "on," diet data from stomach samples are also used for parameter estimation. Prespecified model parameters (Table 5), such as penalty weights, number of age classes, and start-ending dates, were chosen to match those used in Anon [2003] where feasible (i.e., the single-species parameters for pollock and Atka mackerel) and from outside sources or the results of initial model runs where assessment values were not available (i.e., predation). The Pacific cod assessment reported in Anon [2003] was based largely on data from the Bering Sea and on a different, length-based modeling framework so some prespecified values for the Aleutian-specific cod inputs in Table 5 were chosen to be consistent with the values used for pollock and Atka mackerel in Anon [2003]. Sensitivity tests can be used to explore the impact of different values for such parameters.

TABLE 2. (Potentially) estimable parameters for the Aleutian Island stocks of pollock, mackerel, and cod. The actual number of predation parameters depends on the choice of the predator functional relationship.

Parameter symbol	Description	Number of parameters		
		Pollock	Mackerel	Cod
M_k	residual mortality rate for prey species k due to causes not included in the model.	1	1	Prespecified (0.37 per year)
$\hat{\alpha}^r$	prey size selectivity for predator r	1	1	1
$\hat{\beta}^r$	prey size selectivity for predator r	1	1	1
v_k^r	functional response (all Types)	4	4	4
$\tilde{v}_k^r$	functional response (Types II, III, IV, V, VI, VII)	3*	3*	3*
$\tilde{\tilde{v}}_k^r$	functional response (Types III, IV, V, VI)	3*	3*	3*
ω^r	predator age effect on mortality (fraction)	3*	3*	3*
$\tilde{\omega}^r$	predator age effect on mortality (rate of decline)	3*	3*	3*
$R_{k,0}$	mean unfished recruitment	1	1	1
$\varepsilon_{k,y}^R$	log of year-specific deviation in recruitment	41	42	34
$\eta_{k,a,y}^f$	log of fishery selectivities from age 0 to age A_M	12	270	10
$\eta_{k,a}^s$	log of survey selectivites from age 1 to age 10	10	10	10
$\varepsilon_{k,y}^f$	log of year-specific deviation in fishing mortality	24	25	63
μ_k^f	log of average fishing mortality over all years	1	1	3

*If estimated.

TABLE 3. The objective function. L_1 to L_7 are likelihood components, and Λ_1 to Λ_7 are penalty terms.

Component	Equation
Catches	$L_1 = \displaystyle\sum_k \left(\frac{1}{(2\sigma_{k,\mathrm{C}})^2} \sum_f \sum_y \ln\left(C_{k,y}^f / \hat{C}_{k,y}^f \right)^2 \right)$
	where $\hat{C}_{k,y}^f = \displaystyle\sum_a \left(W_{k,a,y}^f N_{k,a,y} \frac{F_{k,a,y}^f}{Z_{k,a,y}} \left(1 - e^{-Z_{k,a,y}} \right) \right)$
Compositions from fisheries	$L_2 = \displaystyle\sum_k \sum_f \sum_y \left(n_{k,y}^f \sum_a \left(\left(A_{k,a,y}^f + 0.001 \right) \right.\right.$
	$\left.\left. \ln\left(\hat{A}_{k,a,y}^f + 0.001 \right) \right) \right)$
	where $\hat{A}_{k,a,y}^f = \dfrac{N_{k,a,y}\, S_{k,a,y}^f}{\displaystyle\sum_{h=0}^{A_{k,\mathrm{L}}} \left(N_{k,h,y}\, S_{k,h,y}^f \right)}$
	and the index a can represent either ages or lengths
Survey biomass	$L_3 = \displaystyle\sum_k \sum_s \sum_y \left(\frac{1}{2(\sigma_{k,y}^s)^2} \left(I_{k,y}^s - \hat{I}_{k,y}^s \right)^2 \right)$
	where $\hat{I}_{k,y}^s = \displaystyle\sum_a \left(S_{k,a,y}^s\, W_{k,a,y}^s\, N_{k,a,y} \right)$
Compositions from surveys	$L_4 = \displaystyle\sum_k \sum_s \sum_y \left(n_{k,y}^s \sum_a \left(\left(A_{k,a,y}^s + 0.001 \right) \right.\right.$
	$\left.\left. \ln\left(\hat{A}_{k,a,y}^s + 0.001 \right) \right) \right)$
	with variables defined analogously to fishery compositions.
Ration	$L_5 = \dfrac{(\Omega^{r,u} - \bar{\hat{\Omega}}^{r,u})^2}{2\sigma_d^2}$
	where $\Omega^{r,u} = \dfrac{1}{365} \dfrac{K^r}{A^r} (w^{r,u})^{d^r} (w^{r,\infty})^{d^r-1}$ (Essington et al. [2001])
Diet length compositions	$L_6 = \displaystyle\sum_r \sum_l \sum_k \left(H_k^{r,l} \sum_m \left(\tau_{k,m}^{r,l} \ln \tilde{T}_{k,m}^{r,l} \right) \right)$

TABLE 3. (Continued)

Component	Equation

$$\text{where } \tilde{T}_{k,m}^{r,l} = \frac{\sum_y n_y^{r,l} \sum_a \left(\chi^{k,a,m} E_{k,a,y}^{r,l} \right)}{\sum_y n_y^{r,l} \sum_{a'} E_{k,a',y}^{r,l}}$$

Diet weight proportions

$$L_7 = \sum_r \sum_l \sum_y G_y^{r,l} \sum_k \left(\varpi_{k,y}^{r,l} \ln \tilde{Q}_{k,y}^{r,l} \right)$$

$$\text{where } \tilde{Q}_{k,y}^{r,l} = Q_{k,y}^{r,l} \bigg/ \sum_{k'} Q_{k',y}^{r,l}$$

Selectivity of fisheries

$$\Lambda_1 = \sum_k \sum_f \sum_a \lambda_k \left(\eta_{k,a+2}^f + \eta_{k,a}^f - 2\eta_{k,a+1}^f \right)$$

$$\Lambda_2 = \sum_k 20 \sum_f \left(\bar{\eta}_k^f \right)^2$$

Selectivity of surveys

$$\Lambda_3 = \sum_k 20 \sum_s \left(\bar{\eta}_k^s \right)^2$$

Prior on recruitment

$$\Lambda_4 = \sum_k \left(\frac{1}{2(\sigma_{k,\mathrm{R}})^2} \sum_{y < y_{k,\mathrm{E}}} \left(\varepsilon_{k,y}^{\mathrm{R}} \right)^2 + (y_{k,\mathrm{E}} - y_{\mathrm{p}}) \ln(\sigma_{k,\mathrm{R}}) \right)$$

$$\Lambda_5 =$$

$$\sum_k \left(\frac{1}{2(\sigma_{k,\mathrm{R}})^2} \sum_{y \geq y_{k,\mathrm{E}}} (\ln N_{k,0,y} - \ln \hat{R}_{k,y} + (\sigma_{k,\mathrm{R}})^2/2)^2 \right.$$

$$\left. + (y_{\mathrm{L}} - y_{k,\mathrm{E}}) \ln (\sigma_{k,\mathrm{R}}) \right)$$

Fishing mortality

$$\Lambda_6 = \sum_k 20 \sum_f \left(\bar{\varepsilon}_k^f \right)^2$$

Prior on natural mortality

$$\Lambda_7 = \sum_k \frac{(M_k - \tilde{M}_k)^2}{2(\sigma_{k,\tilde{M}})^2}$$

2.2.7 *Penalty terms.* In addition to the contributions to the objective function based on data, the values for the parameters of the model are constrained based on penalty functions. The recruitment deviations $\varepsilon_{k,y}^{\mathrm{R}}$ (equation 1) are constrained to be normally distributed

TABLE 4. The additional quantities on which the objective function is based.

Quantity	Definition
Data	
$A^f_{k,a,y}$	observed proportion that animals of age a constitute of the catch of species k by fleet f during year y
$A^s_{k,l,y}$	observed proportion that animals in length-class l constitute of the catch of species k by survey s during year y
$C^f_{k,y}$	observed catch of fish of species k by fleet f during year y
$I^s_{k,y}$	observed survey index of abundance for survey s, species k, and year y
$W^f_{k,a,y}$	mean weight in fishery f of an animal of age a and species k during year y
$W^s_{k,a,y}$	mean weight in survey s of an animal of age a and species k during year y
$n^{r,l}_y$	number of stomachs from predators of species r in length-class l that were sampled during year y
$w^{r,u}$	observed mean weight (kilograms) at age u for a predator of species r
$w^{r,\infty}$	maximum weight approached asymptotically with age for a predator of species r
$\Omega^{r,u}$	observed average predator ration for animals of species k and age u (based on the method of Essington et al. [2001])
$\varpi^{r,l}_{k,y}$	observed proportion that prey species k constitutes of the diet during year y of predators of species r in length-class l
$\tau^{r,l}_{k,m}$	observed fraction that animals in length-class m make up of the component of the diet of predators of species r in length-class l that is made up prey of species k
Model predictions	
$\hat{A}^f_{k,a,y}$	model-estimate of the proportion that animals of age a constitute of the catch of species k by fleet f during year y
$\hat{A}^s_{k,l,y}$	model-estimates of the proportion that animals in length-class l constitute of the catch of species k by survey s during year y, that is: $\hat{A}^s_{k,l,y} = \sum\limits_a \hat{A}^s_{k,a,y} \chi^{k,a,l}$

TABLE 4. (Continued)

Quantity	Definition
$B_{k,y}$	spawning biomass of species k during year y:

$$B_{k,y} = \left(\sum_{a=1}^{A_{k,L}} \omega_{k,a} m_{k,a} N_{k,a,y} \right) e^{(-M_k)^{\rho_k}}$$

Quantity	Definition
$B_{k,0}$	spawning biomass of species k in an unfished state
$\hat{C}_{k,y}^f$	model-estimate of the catch of fish of species k by fleet f during year y
$\hat{I}_{k,y}^s$	model-estimate of the survey index of abundance for survey s, species k, and year y
$\tilde{Q}_{k,y}^{r,l}$	model-estimate of fraction of the diet (in mass) during year y of a predator of species r in length-class l that consists of prey species k
$\hat{R}_{k,y}$	model-estimate of the number of age 0 animals of species k at the start of year y, that is:

$$\hat{R}_{k,y} = \frac{4 h_k R_{k,0} B_{k,y}}{(1 - h_k) B_{k,0} + (5 h_k - 1) B_{k,y}}$$

Quantity	Definition
$\tilde{T}_{k,m}^{r,l}$	model-estimate of the fraction that animals in length-class m make up of the component of the diet of predators of species r in length-class l that is made up prey of species k
$\bar{\hat{\Omega}}^{r,u}$	average estimated daily ration over the years included in the model
$\bar{\eta}_k^f$	mean selectivity deviation for fleet f and species k over all years and ages
$\bar{\eta}_k^s$	mean selectivity deviation over all years for survey s and species k

for the years before the fishery started while for the years thereafter, a penalty is placed on the number of recruits $\hat{R}_{k,y}$ for each species and year based on the assumption that recruitment is lognormally distributed about a Beverton–Holt stock–recruitment relationship. The

TABLE 5. Quantities that define the dimension of the model, the weights used in the objective function, and the prespecified values of model parameters.

Index	Description	Pollock	Mackerel	Cod
Model dimensions				
$A_{k,\text{L}}$	last age class (a plus group) for stock k	15^*	15^*	12^*
$A_{k,\text{M}}$	age after which fishery selectivity is uniform for stock k	12^*	10^*	10^*
				(3 fleets)
k^f	number of fisheries for stock k	1^*	1^*	3
k^s	number of surveys for stock k	1^*	1^*	1
$y_{k,\text{C}}$	first year with catch data for stock k	1978^*	1978	1978^*
$y_{k,\text{E}}$	first year for which recruitment is constrained by a Beverton–Holt stock-recruitment function for stock k	1983^*	1977^*	1983
y_L	last year modeled	2003^*	2003^*	2003^*
y_p	first year modeled	1960	1960	1960
Weights in the likelihood components and the penalties terms				
$G_y^{r,l}$	effective sample size for the diet data on prey mass for predator species r and length-class l during year y		See text	
$H_k^{r,l}$	effective sample size for diet data on prey lengths for predator species r and length-class l		See text	
$\tilde{M}_k$	prior mean for M for species k	0.3^*	0.3^*	0.37^*
$n_{k,y}^\text{f}$, $n_{k,y}^\text{s}$	Effective sample sizes for the composition data		See text	

TABLE 5. (Continued)

Index	Description	Pollock	Mackerel	Cod
λ_k	weight assigned to the selectivity penalty for species k	12.5[*]	3[*]	12.5 (3 fleets)
σ_d	standard deviation of the logarithm of the daily ration	0.05	0.05	0.05
$\sigma_{k,\mathrm{C}}$	coefficient of variation of the catch data for species k	0.05[*]	0.05[*]	0.05
$\sigma_{k,\mathrm{R}}$	extent of recruitment variability	0.5[*]	0.6[*]	0.5
$\sigma_{k,y}^s$	survey standard deviations	Taken from Anon [2003]		
$\sigma_{k,\mathrm{M}}$	standard deviation for the prior on M for species k	0.1[*]	0.05[*]	0.1
Prespecified parameters				
A^r	assimilation efficiency for a predator of species r	0.6[**]	0.6[**]	0.6[**]
K^r	mass-specific rate of energy loss with age for a predator of species r	1.9[**]	4.8[**]	1.7[**]
$\ln(Q_0^r)$	mass (g/g/year) of "other" prey	9.2	9.2	9.2
d^r	allometric scaling constant for consumption by predators of species r	0.8[**]	0.8[**]	0.8[**]
h_k	stock productivity at 20% of unfished biomass (steepness)	0.6[*]	0.8[*]	0.6
$m_{k,a}$	proportion of fish of species k and age a that are mature	Taken from Anon [2003]		
ρ_k	adjustment for mortality before spawning for species k	0.17[*]	0.58[*]	0.08
$\omega_{k,a}$	weight at the time of spawning of a fish of age a and species k	Taken from Anon [2003]		

[*]Values from Anon [2003].
[**]See Essington et al. [2001].

parameter that determines the shape of the stock–recruitment relationship (steepness, h) was prespecified (0.6 for pollock and Atka mackerel and 0.8 for cod). The stock–recruitment relationship imposes a weak penalty on recruitment and was included in the analyses for consistency with the analyses in Anon [2003]. There is a slight inconsistency in this model and the stock assessments in Anon [2003] in how recruitment is treated, viz. Equation (1) implies that recruitment is lognormally distributed about a mean value whereas penalty term 5 in Table 3 implies that recruitment after year $y_{k,\mathrm{E}}$ is lognormally distributed about the Beverton–Holt stock–recruitment relationship.

Consistent with Anon [2003], fishery selectivities for Atka mackerel were allowed to vary annually but those for pollock were time-invariant. Cod fishery selectivities were also assumed to be time-invariant. A penalty was placed on the second differences of the deviations in selectivity from one age to the next each year to prevent abrupt changes in selectivity for mackerel; this approach is common when separate parameters are estimated for each age (e.g., Maunder and Watters [2003]). A penalty was also placed on the average deviation in selectivity over all years and ages for each combination of fleet (or survey) and species to force selectivity to tend to be flat (penalties 2 and 3 in Table 3). The age from which selectivity was assumed to be flat ($A_{\mathrm{M},k}$) was set to 10 for Atka mackerel and pollock and 12 for cod as these choices led to adequate fits to the age- and length-composition data.

3. Results

3.1 Predation "off." The model was run in single-species mode (predation components "off"). As expected, the abundance of each cohort decreased with age with the stronger cohorts traceable through time as diagonal ridges of increased abundance (Figure 3). The associated fishing mortalities by age were very low before about ages 3 or 4 and then increased with age for all three species. Natural mortality was estimated by a single, year- and age-invariant value for pollock (estimated $M = 0.09$ per year) and mackerel (estimated $M = 0.55$ per year). It was not possible to estimate natural mortality for cod because the composition data for cod were in lengths not ages, so the value for
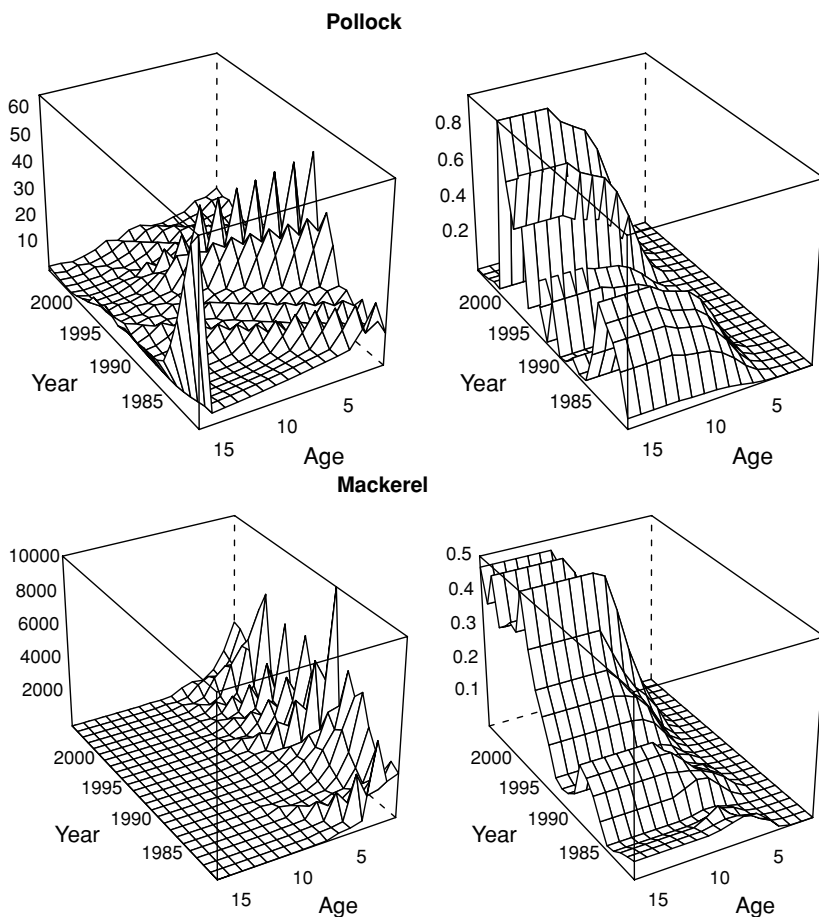
Pollock

FIGURE 3. Point estimates of numbers by age and year (in millions, left) and the associated fishing mortalities (in rates per year, right) for each species, estimated using the predation "off" variant of the model.

cod M assumed for the 2003 assessment (0.37 per year; Anon [2003]) was also assumed here.

3.2 Predation "on." The model was run with predation "on" for each of the seven feeding functional responses in Table 1. Each species was modeled as potentially both prey and predator of one
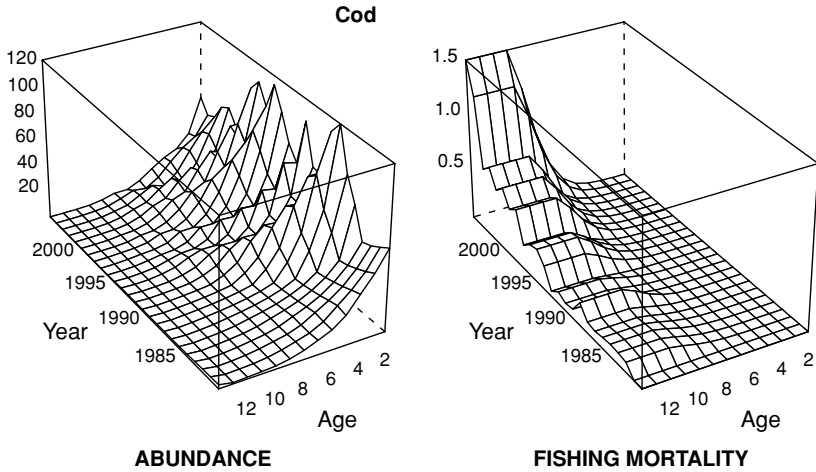
FIGURE 3. (Continued)

another at different ages, as informed by the diet data. All of the
models for the predator functional response fit the ration data well
(Figure 4).

All alternative model configurations for the feeding functional re-
sponse were able to fit the survey indices (Figure 5) and the other
data sources in a manner that was qualitatively similar to the single-
species analysis, although the fits by the latter were better (Table 6).
Differences among the alternative model configurations were greatest
for model outputs for nonobserved quantities, such as total spawning
biomass in prefishing years (Figure 6) and recruitment (Figure 7a).
The smallest value of the objective function (i.e., the best fit) for the
seven multispecies configurations was for predator pre-emption, which
was also selected as the best of the seven multispecies configurations
using AIC (Burnham and Anderson [2000]; Table 6).

The largest difference among models was for estimated recruitment,
which varied among the alternative model configurations by up to
several orders of magnitude (Figure 7a). The multispecies configu-
rations generally estimated more pollock, fewer mackerel, and about
the same numbers for cod at early ages as the single-species model
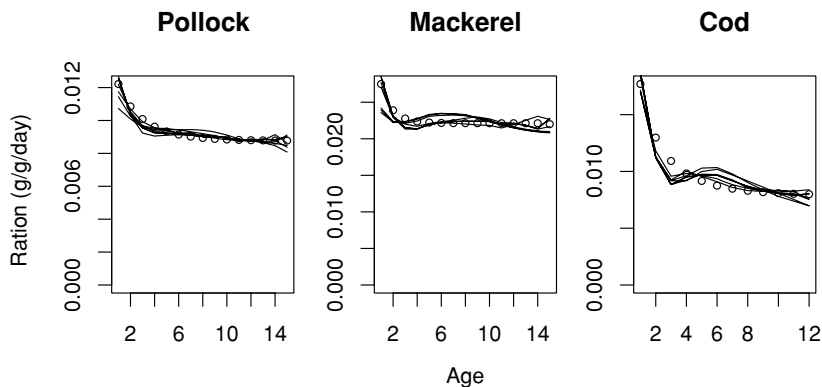
FIGURE 4. Fits to mass-specific consumption rates calculated from weight at age following Essington et al. [2001] (circles) by the models based on alternative functional responses (lines).
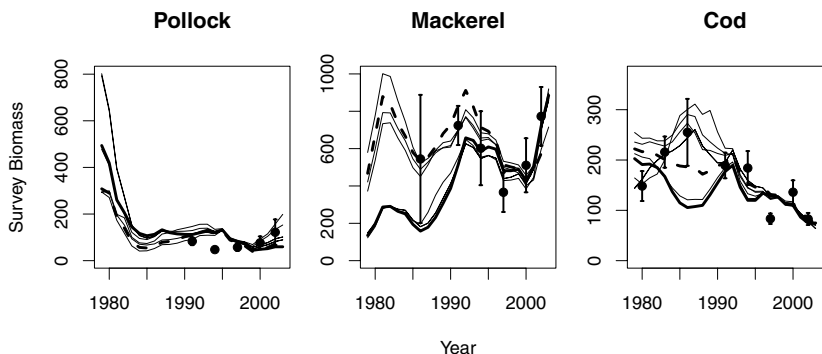

FIGURE 5. Model fits to survey biomass indices (metric tons × 1000) based on the "with predation off" (dashed lines) and on seven multispecies models (solid lines, with wider line indicating the best-fitting, pre-emption type of response).

(Figure 7b). These differences among configurations for estimated abundance at age decreased with age (Figures 7c, d).

The estimated numbers-at-age and fishing mortalities from the "best" multispecies model, predator pre-emption (Figure 8), may be compared to the numbers-at-age and fishing mortalities estimated from the

TABLE 6. AIC, objective function, and individual contributions to the objective function for the different model configurations (see Table 1 for the definitions of the alternative predator functional relationships).

	Predation off	Response type						
		I	II	III	IV	V	VI	VII
# Parameters	568	586	595	604	604	604	604	595
AIC	2308	7411	7080	7306	7098	6696	7169	7046
ΔAIC	*	716	384	611	403	0	473	351
Objective function	586.1	3119.6	2944.9	3049.2	2945.1	2743.8	2980.3	2928.1
Traditional data sources								
Catch biomass	4.7	6.8	2.8	3.7	2.8	2.8	3.5	3.6
Fishery age composition	245.8	305.5	268.2	311.6	268.2	300.3	280.0	312.8
Fishery length composition	107.8	123.7	115.5	128.0	115.5	115.1	120.8	121.2
Survey index	46.4	63.5	42.0	36.4	42.0	53.6	49.7	53.2
Survey age composition	114.1	172.5	129.2	143.5	129.0	152.7	136.3	140.6
Survey length composition	20.9	36.4	42.7	32.7	42.6	46.1	43.7	36.5
Total	539.7	708.4	600.4	656.0	600.0	670.6	634.0	668.0
Diet data								
Daily ration	N/A	40.2	22.5	45.8	22.3	14.7	26.0	18.9
Diet (weights)	N/A	1358.3	1320.6	1259.2	1320.5	1121.2	1310.0	1226.3
Diet (lengths)	N/A	945.6	928.0	917.4	928.2	865.5	941.5	918.7
Total	N/A	2344.1	2271.0	2222.5	2271.0	2001.4	2277.4	2163.9
Penalties	46.4	67.1	73.5	170.7	74.0	71.7	68.9	96.2

*The results for predation off are not comparable to those for Types I–VII because the single-species model does not use the diet data.
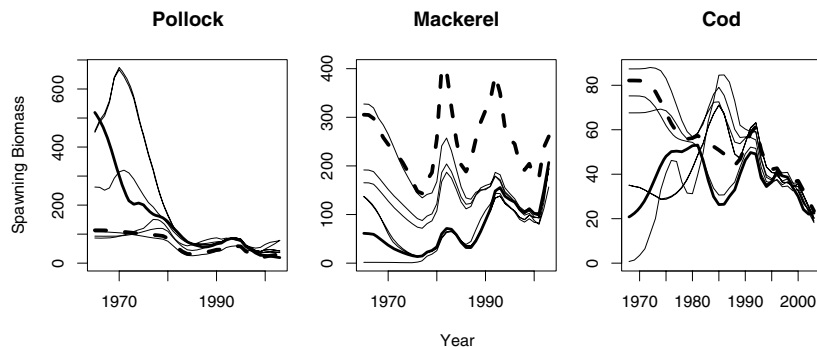
FIGURE 6. Model estimates of total spawning biomass (metric tons $\times$ 1000). The dashed line indicates a model "with predation off" while the remaining lines correspond to the seven multispecies models (the wider line indicates the best-fitting multispecies model).

single-species model (Figure 3). The predation mortality in the multispecies framework displayed strong patterns with age, in contrast to the single-species premise of age-invariant natural mortality. The residual natural mortalities for pollock and mackerel were 0.24 per year and 0.2 per year, respectively. The rate of natural mortality for age zero pollock was about 5.2 per year (P of about 5 and M of 0.24), implying that only approximately 5 individuals out of 1,000 were estimated to survive (equation 2) from age zero to 1. The portion of total natural mortality varying by age and year that was due to the other modeled species was greatest for the youngest ages in all cases, falling to nearly zero by age 5 for all species. This was about the age that fishing mortality began increasing to values over 0.1 per year (Figure 8).

3.3 Standard error estimates. Figure 9 shows asymptotic 95% confidence intervals for the time trajectories of spawning biomass by species for the single-species and the AIC-selected multispecies model. For pollock and mackerel, there was little overlap in the envelopes between these models, especially in the earlier years; the 95% confidence intervals for cod spawning biomasses generally overlap, although not for the mid-1980s. The estimates of spawning biomass were least precise for the earliest years of the modeled period, which are the years with the fewest data.

(a) Age 0
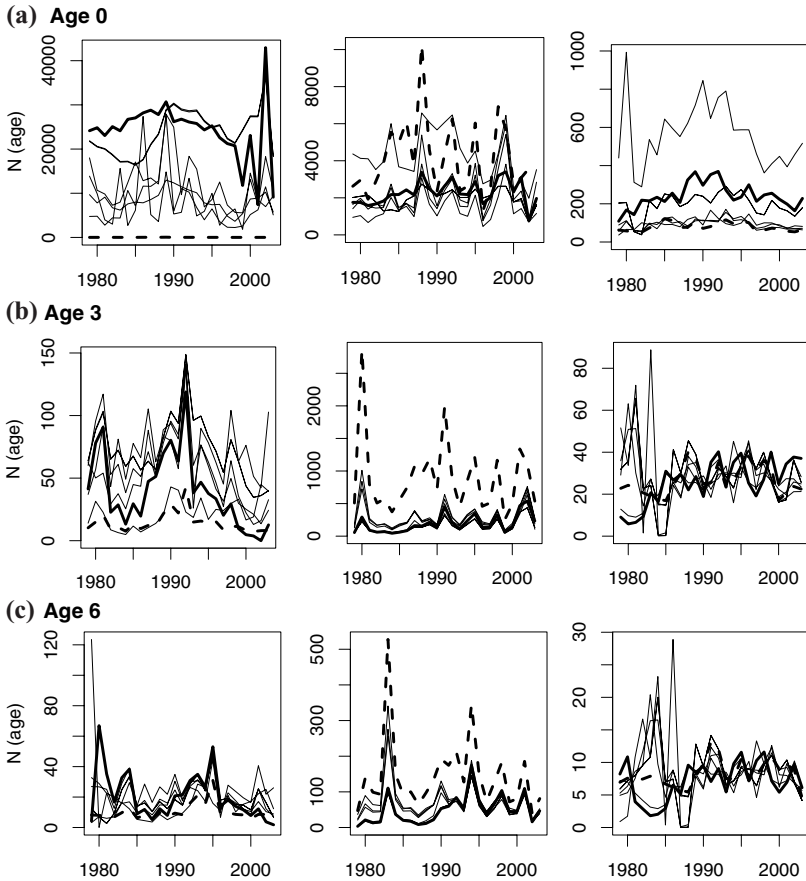
(b) Age 3

(c) Age 6

FIGURE 7. Numbers in millions per year estimated for each of four ages by the single-species and seven multispecies models with line types as for Figures 5 and 6.

4. Discussion. Catch-at-age modeling in fisheries is used to make inferences about harvested fish populations from data on catches and auxiliary information. One step in this process is parameter estimation conditional on the model and data. A separate step is measuring the associated uncertainty around the variables of interest. Although the statistical foundations and interpretation of the results of parameter

(d) Age 10
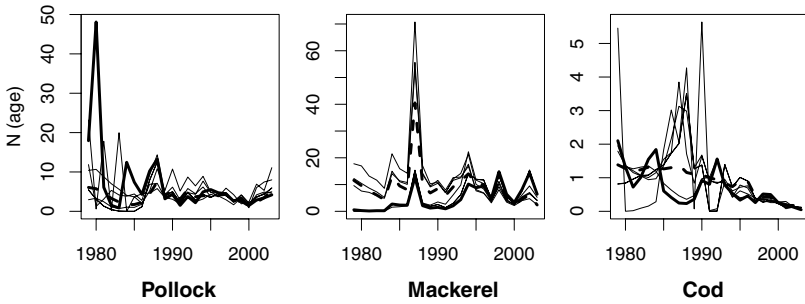
FIGURE 7. (Continued).

estimation are well established, the meaning of the calculations of uncertainty is more controversial (Pawitan [2001], Chapter 7). In particular, inferences based on the likelihood function for a statistical model do not convey uncertainty about the correctness of the model itself but only about the parameter estimates from the data given that the model is true. Decisions about the adequacy of the model depend on the modeling objectives as well as on ecological and biological knowledge of the system.

This study has demonstrated that decisions about whether or not to explicitly model multispecies interactions and include data from predator diets can affect the estimates of population features of interest and the associated uncertainty in an age-structured stock assessment and that the confidence intervals from a single-species model may not capture the full range of uncertainty (Figure 9). Choosing between the multispecies and single-species approaches depends in part on how effective the predators are as sampling devices relative to fisheries and to surveys and on how well the modeling framework is able to estimate the age selectivity patterns for each predator. However, the choice between the multispecies and single-species modeling frameworks also depends on whether the estimates from the single-species approach are likely to be markedly biased. In the context of this study, estimates of mortality for young animals (and hence the amount of food potentially available for predator species) were very sensitive to the choice of modeling framework.

Pollock

Mackerel

Cod

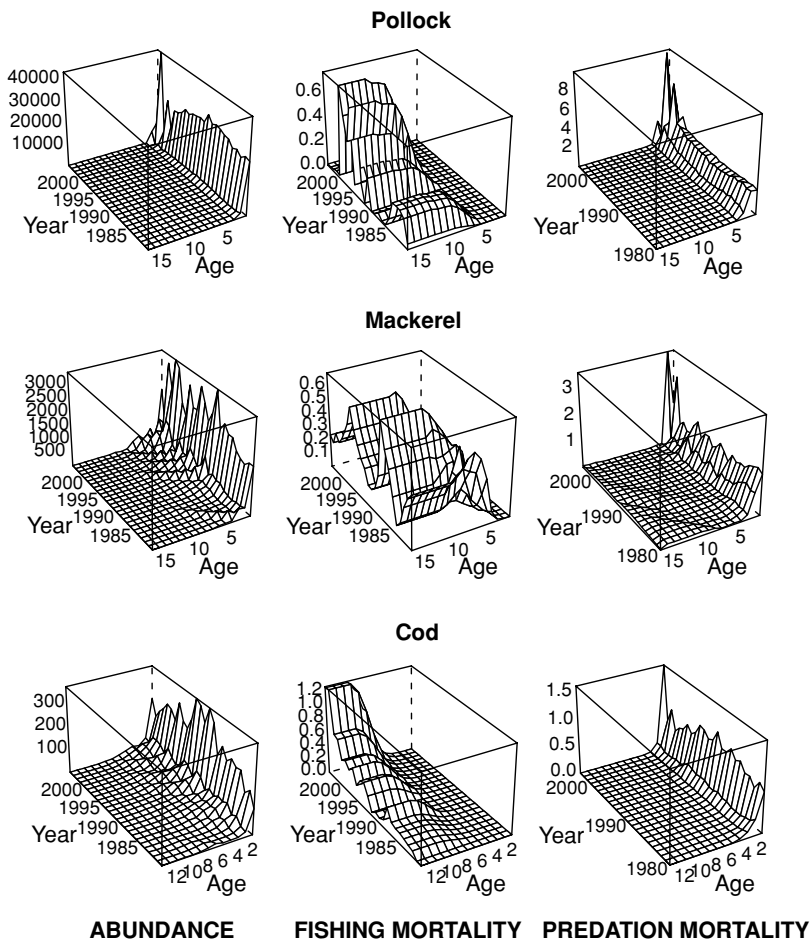**ABUNDANCE**   **FISHING MORTALITY**   **PREDATION MORTALITY**

FIGURE 8. Point estimates of numbers by age and year (in millions, left), associated fishing mortalities (per year, center) and predation mortality (per year, right) by species from the predator pre-emption multispecies model.

Decisions about which potential sources of data should be used to estimate the parameters of a model become increasingly important in models that integrate many different types of data because the effect of each data type is weighted against the others in an overall, joint

Pollock **Mackerel** **Cod**
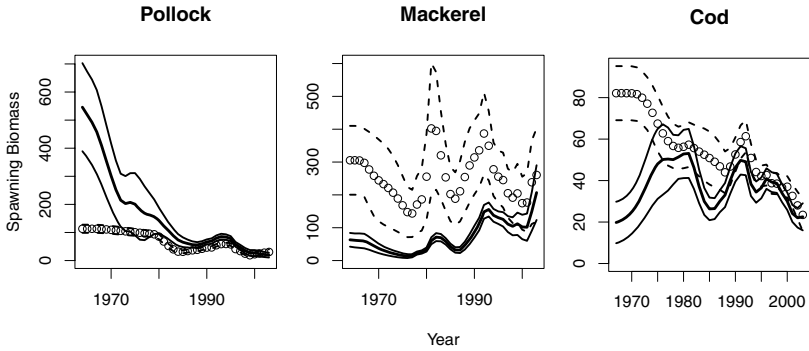
FIGURE 9. Point estimates of spawning biomass with asymptotic 95% confidence intervals from single-species (dashed circles) and multispecies (solid lines) models by three species.

likelihood. The statistical framework of "integrated analysis" (Fournier and Archibald [1982], Maunder [2003], Quinn [2003]) used in this study includes all data sources in a single objective function. Additional sources of information can be incorporated into the process of estimating the parameters by including a component in the overall objective function to represent each new source of data. Selecting the best model for a given set of data is straightforward, using a criterion such as the AIC (Burnham and Anderson [2000]). However, when the data vary among different models, as is the case in this study, these formal methods of model comparison no longer apply.

The multispecies model becomes the single-species model if the effective sample sizes for all the diet data are set to zero because the fit to the other sources of data is best when predation is ignored (Table 6). In this study, the estimates from the single-species and multispecies models diverged as effective sample sizes of the diet data were increased (results not shown). The maximum sample size of 20 used here was considered to be a conservative weighting for the diets, given that in some cases the actual numbers of stomachs examined for a given combination of predator length bin and year were in hundreds.

Issues of data weighting are generic to integrated modeling even at the single-species level (Schnute and Hilborn [1993], Maunder [2003], Cotter et al. [2004]) and can become magnified in multispecies modeling

(Stefansson [2003]). In theory, the relative weight assigned to each type of data in the model should be proportional to the inverse of the standard error of that data type, and standard errors or effective sample sizes can be calculated based on the (assumed) number of random draws from the population the sample represents. However, it is usually not straightforward to determine the "effective" sample size for data sampled from nature. This is even the case of surveys for which sampling standard errors can be computed using conventional approaches; experience in stock assessments is that sampling standard deviations can substantially underestimate the extent of difference between the estimates of abundance and true stock biomass. The problem of selecting appropriate weights becomes much more complicated when deciding the number of samples from the age classes of the prey species selected by the predators represented by the stomach data. The choice of relative weighting becomes particularly important when increasing the effective sample size for one data source can improve the fit to that data source but at the expense of the fit to some other sources and may impact the selection of the "best" model using a metric such as AIC. This is evident to some extent in this paper where, had the weight imposed on the diet data been lower, AIC might have supported one of the other functional relationships over the Type V relationship (Table 6).

An informal method of comparing models is to see how well they are able to fit each data source in terms of individual contributions to the likelihood (Table 6). The largest portion of the objective function in the multispecies models is due to the contribution of the diet data. The predation "off" configuration was able to fit the traditional data sources from fisheries and surveys more closely than any of the multispecies configurations (539.7 vs. the Type V value of 670.6, for instance) because it did not need to consider the diet data. The AIC-selected Type V multispecies model did not fit the traditional data sources as closely as, for example, the Type IV model but fit the combination of traditional and diet sources of data the best of any multispecies model. The question to ask of the closer fits of the single-species model to the fishery and survey components in Table 6 than of the fits of the multispecies model to the same components is whether the single-species model is able to spuriously overfit these data because it ignores aspects of the total system that are actually important in making realistic inferences about it.

The estimates of natural mortality in the single-species configuration (0.09 per year for pollock and 0.55 per year for mackerel) differed somewhat from the values estimated for pollock (0.14 per year) and prespecified for mackerel (0.3 per year) in Anon [2003] because the models were configured slightly differently. The framework used here was able to reproduce the Anon [2003] values almost exactly when it was configured the same as in Anon [2003]. Therefore, the low natural mortality rate for pollock for the single-species configuration is not a function of the model but rather of the nature of the data for pollock when it is interpreted in a single-species context. As a check on the robustness of the general patterns reported here, the single-species configuration was re-run prespecifying natural mortality to the values from the most recent assessment (Anon [2007]; 0.2 per year for pollock and 0.3 per year for mackerel) instead of estimating the values for these parameters. The differences between the single-species and multispecies estimates of population trends from 1964–2003 were qualitatively the same as those in Figures 3–6 (not shown), although there were of course quantitative differences between the two single-species configurations.

Although the application of this paper is primarily for illustrative purposes, the differences in estimated population trajectories for the three fish species in Figure 9 could have important implications for management. For instance, the multispecies model estimates a decline in the spawning biomass of pollock from 1964 to 2003, which is over three-fold that estimated by the single-species model for the same period. This difference could affect estimates of the degree to which declines of Steller sea lions, for which pollock is an important prey item, might have been related to prey abundance during this period (National Research Council [2003]; Trites et al. [2007]). An unexpected result of the application of the multispecies model to the data for pollock, mackerel, and cod is that the recruitment of mackerel was lower from the multispecies model (Figure 6) even through the estimates of the biomass of mackerel available to the survey were similar between the single-species and multispecies models (Figure 5). This reflects lower estimated total natural mortality, particularly for the older ages, in the multispecies model. The estimate of M of 0.55 per year from the single-species model may be valid for younger animals but seems unrealistic when applied to all ages, especially given that some fish aged over

10 years were observed in the catches. In contrast, the multispecies model estimated very high (>0.55 per year) natural mortality rates due to predation for very young mackerel (Figure 8) but much lower natural mortality rates for older fish. The high rates of predation mortality on older mackerel in the early 1980s were due to high abundances of older pollock in these early years. Fewer old pollock in recent years resulted in reduced predation mortality on older mackerel after the 1980s.

A common concern with multispecies models that include only a subset of species is whether important trophic interactions may be missing and invalid inferences drawn by ignoring species (e.g., Yodzis [1998]; Fulton et al. [2003]; Plagányi [2007]). The analyses of this model suggest that the vast bulk of the predation on young (<5 year) animals is captured by the model and the bulk of the mortality on older fish is due to fishing. However, this does not guarantee that an important link has been not omitted from the analysis. Unfortunately, adding additional species will not guarantee that more robust results will be possible because adding more species will lead to greater data demands and hence, perhaps, much poorer precision.

One way to further explore the capabilities of different modeling frameworks is through the use of simulated data sets, in which artificial data are generated with known characteristics and then supplied to the estimation framework. The estimates of the parameters and variables of interest can then be compared with the known values to evaluate estimation performance. This procedure could provide additional insight into the relative strengths and weaknesses of the multispecies and single-species approaches.

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