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# Including predation mortality in stock assessments: a case study for Gulf of Alaska walleye pollock

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A separable catch-age stock assessment model that accommodates predation mortality is applied to the Gulf of Alaska walleye pollock (*Theragra chalcogramma*) assessment. Three predators are incorporated in the model: arrowtooth flounder (*Atheresthes stomias*), Pacific halibut (*Hippoglossus stenolepis*), and Steller sea lion (*Eumetopias jubatus*). The effect of these predators is examined by defining the predation mortality as a type of fishery. The model is used to quantify changes in the relative fit to the survey, fishery, and predator data when the assumption of constant natural mortality is relaxed. Specifically, we examine the effect of assumptions regarding the functional feeding response, residual naturaly mortality, and uncertainty in predator biomass on stock assessment. Total natural mortality rates (including predation) tended to be higher than estimated from life history characteristics of the stock. Models that did not account for uncertainty in natural mortality underestimated uncertainty in current stock biomass by as much as 20%. Our results indicate that independent estimates of survey selectivity, additional food habits data, and estimates of the feeding responses of predators to different prey densities are all needed to improve our ability to develop stock assessment models that address ecosystem concerns.

Key words: predation, stock assessment, uncertainty, walleye pollock.

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## Introduction

A long-term goal of fisheries management is to employ harvest practices that sustain the diversity and productivity of fish stocks. To provide appropriate advice, stock assessment scientists must account for changes in the physical and biological factors that influence production (Botsford *et al.*, 1997). Shifts in predation mortality are one biological factor that can impact stock assessments. Recent developments in catch-age assessment models provide an analytical framework for incorporating predator–prey interactions to account for age-specific variability in natural mortality (Larkin, 1996). In this paper, we present a catch-age modelling framework that incorporates predator–prey interactions and employ this model for the assessment of the walleye pollock (*Theragra chalcogramma*) stock in the Gulf of Alaska.

Although numerous studies have identified the potential for biased stock projections caused by erroneous assignment of a constant natural mortality rate (e.g., Sims, 1984; Lapointe *et al.*, 1989; Mertz and Myers, 1997), predation mortality is still commonly assumed to be constant. The assumption of constant natural mortality has been relaxed by modelling age-specific predation mortality in stock assessments (e.g. Macer and Shepherd, 1987; Gislason, 1991; Sparholt, 1991; Sparre, 1991; Magnússon, 1995; Mohn and Bowen, 1996; Livingston and Jurado-Molina, 1999; and Livingston and Methot, in press), and by developing stochastic simulation models that account for errors in estimation of natural mortality (e.g. Schnute and Richards, 1995). Simulation approaches are often favoured in producing harvest recommendations because of the uncertainty surrounding the interaction parameters, such as consumption rates, diet preference, and daily ration. When reasonable estimates of interaction parameters exist, information regarding trends in predator abundance should be used to account for interannual variability in age-specific natural mortality rates.

In the Gulf of Alaska, walleye pollock is an important component of the diet of several marine fish, birds,

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Table 1. Summary list of data sets and time frames used (BTS: bottom trawl survey; EIT: echo integration trawl survey; SS: Shelikof Strait; p.p.u.e.: predation per unit of predator effort).

| Dataset | Years |
|---|---|
| Catch | 1964–1997 |
| BTS biomass | 1975, 1984, 1987, 1990, 1993, 1996 |
| EIT biomass for SS | 1981, 1983–1986, 1988–1997 |
| Egg production spawning biomass for SS | 1981, 1985–1992 |
| Fishery catch at age | 1964–1997 |
| BTS numbers at age | 1984, 1987, 1990, 1993 |
| EIT numbers at age | 1973, 1981, 1983–1991 |
| EIT size frequency by length bin | 1981, 1983–1986, 1988–1997 |
| Fishery length frequency by length bin | 1964–1975 |
| Arrowtooth flounder abundance | 1964–1997 |
| Pacific halibut abundance | 1964–1997 |
| Sea lion abundance | 1964–1997 |
| Arrowtooth flounder p.p.u.e. | 1990, 1993, 1996 |
| Pacific halibut p.p.u.e. | 1990, 1993, 1996 |
| Sea lion p.p.u.e. | 1977, 1985 |
| Arrowtooth flounder catch-at-age | 1990, 1993, 1996 |
| Pacific halibut catch-at-age | 1990, 1993, 1996 |
| Sea lion catch-at-age | 1985 |

and some mammals (Pitcher, 1981; Hatch and Sanger, 1992; Merrick and Calkins, 1996). The three primary predators of pollock in the Gulf of Alaska are Pacific halibut (*Hippoglossus stenolepis*), arrowtooth flounder (*Atheresthes stomias*), and Steller sea lions (*Eumetopias jubatus*). Unlike the Bering Sea, cannibalism is not a major source of predation mortality in the Gulf of Alaska. Dramatic shifts in predator abundance in recent years prompted us to investigate the functional relationship between walleye pollock and its predators. The abundance of adult arrowtooth flounder has doubled over the last decade (Turnock *et al.*, 1996), while the decline in populations of Steller sea lions during the same period (Fritz *et al.*, 1995) led to its listing as an endangered species in June 1997 (Anon., 1997). Quantifying selectivity and catchability of pollock by Steller sea lions by incorporating predation mortality in stock assessments is expected to improve our understanding of the potential role of pollock in impacting predator populations. These parameters can be used in simulation models that evaluate natural and anthropogenic factors influencing the dynamics of predator populations (Butterworth *et al.*, 1995; Shima, 1996).

We developed a statistical catch-at-age model for the Gulf of Alaska walleye pollock that relaxes the assumption of constant natural mortality for a single species by accounting for predation mortality from the three predators identified above. The model was made possible by NOAA's commitment to the collection and analysis of food habits data in Alaska waters that was driven by the need to improve single-species, multispecies, and ecosystem models which include trophic interactions (Livingston, 1985, 1986). Predation mortality is modelled through a retrospective analysis of existing data on predator abundance and predation rates.

## Methods

### Data

Commercial fishery and survey data used (Table 1) consist of estimates of total catch, bottom trawl biomass estimates (Hughes and Hirshhorn, 1979; Stark and Clausen, 1995; Martin and Clausen, 1995; Hollowed *et al.*, 1996), echo integration trawl (EIT) survey estimates of the spawning biomass in Shelikof Strait (Traynor and Nelson, 1985; Guttormsen and Wilson, 1997), egg production estimates of spawning biomass in Shelikof Strait (Picquelle and Megrey, 1993), fisheries catch-at-age, and survey size and age compositions (cf., Hollowed *et al.*, 1997).

Walleye pollock is a semi-demersal schooling fish that is widely distributed throughout the North Pacific in temperate and sub-arctic waters. In the Gulf of Alaska (GOA), major exploitable concentrations are found primarily in the central and western regulatory areas (147–170°W, Fig. 1). Pollock from this region are managed as a single stock that is separate from the Bering Sea and Aleutian Islands pollock stocks. Major spawning concentrations of pollock have been observed in Shelikof Strait and near the Shumagin Islands.

Originally, walleye pollock was a by-catch in the Japanese Pacific ocean perch (POP) fishery in the Gulf of Alaska (Hollowed *et al.*, 1991). The commercial fishery started as a foreign fishery in the early 1970s (Megrey, 1988). Catches increased rapidly during the

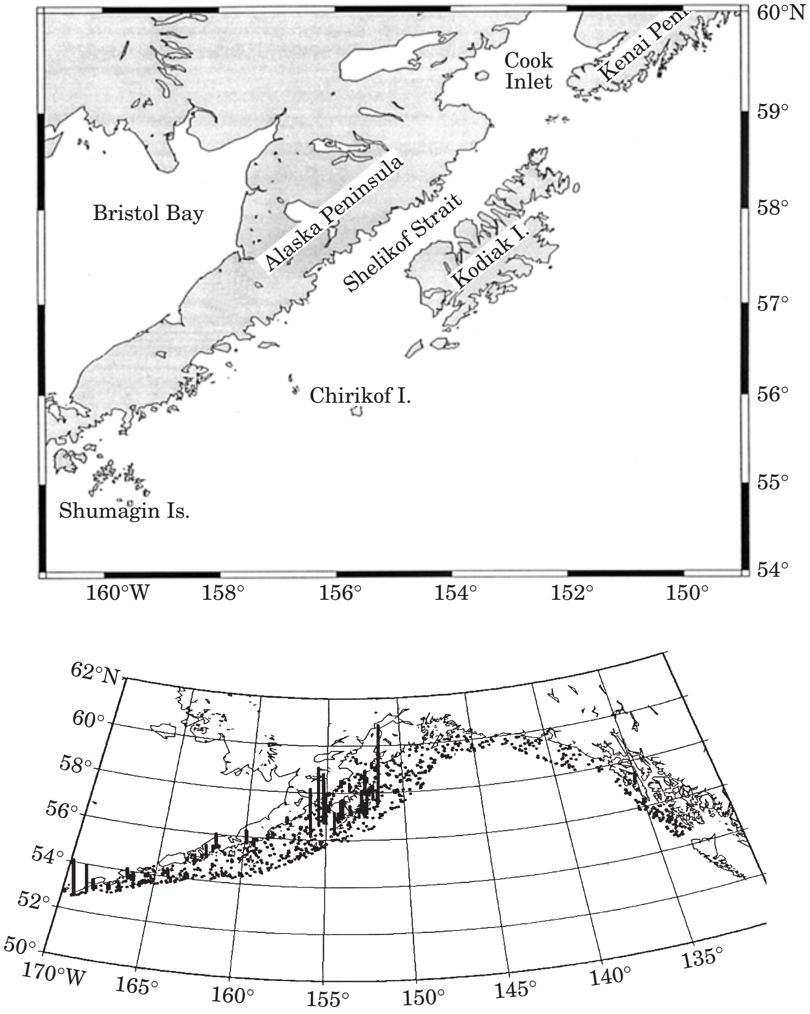

Figure 1. Map showing the area of the Alaska Peninsula with geographical names referred to (top panel) and the main areas of abundance in the entire Gulf of Alaska (lower panel: bars represent c.p.u.e. values from the 1996 bottom-trawl survey).

late 1970s and early 1980s (Table 2). Major spawning concentrations of pollock were discovered in Shelikof Strait in 1981 and roe fisheries quickly developed. After a short period of joint venture operations in the mid-1980s, the fishery was fully domesticated by 1988.

Survey abundance was assumed to be proportional to total abundance as modified by the estimated survey selectivity pattern. The mid-date of the survey period was specified in the model to account for differences in abundance between surveys due to growth or mortality during the year. Egg production estimates of spawning stock biomass were included in the model by setting the age-specific selectivity pattern equal to the estimated percent mature at age (Hollowed *et al.*, 1991). The catchability coefficient (q) for the egg production estimates was assumed to equal that estimated for the EIT survey of Shelikof Strait.

Incorporation of predation mortality in the pollock assessment utilized four sources of information: (a) a time series of predator abundance (analogous to fishing effort) over the entire period (1964–1997); (b) annual pollock consumption rates per unit of predator for years where food habits data were available; (c) age composition of pollock consumed by predators during years for which data on size composition in the diet were available, and (d) mean weights at age of pollock consumed, averaged over all years.

Arrowtooth flounder, Pacific halibut, and Steller sea lions have relatively large populations in the Gulf of Alaska (Fig. 2). Estimates of arrowtooth flounder mid-year biomass were obtained from Turnock *et al.* (1996) for two age groups: age 3–6 (approx. 20–39 cm) and age 6+ (approx. ≥40 cm). Because pollock consumption rates vary by age, a standardized total biomass of these

Table 2. Catches (landings+discards; '000 t) of walleye pollock in the western and central region of the Gulf of Alaska, 1977–1997 (sources: foreign and joint venture catches, 1997–1984; Berger *et al.*, 1986; 1985–1988: Pacific Fishery Information Network – PacFIN, Pacific Marine Fisheries Commission; domestic catches 1978–1980; Rigby, 1984; 1981–1990; PacFIN, 1991–1997: NMFS Alaska Regional Office) and biomass estimates ('000 t from echo integration trawl surveys of Shelikof Strait (EIT), Gulf-wide bottom trawl surveys (BTS), estimates of spawner stock biomass from egg production surveys of Shelikof Strait (EPS), and biomass estimates from ADF&G trawl surveys (TS).

| | | Biomass | | | |
|---|---|---|---|---|---|
| Year | Catch | EIT | BTS | EPS | TS |
| 1975 | NA | — | 825* | — | — |
| 1976 | NA | — | — | — | — |
| 1977 | 112.3 | — | — | — | — |
| 1978 | 95.8 | — | — | — | — |
| 1979 | 99.8 | — | — | — | — |
| 1980 | 120.4 | — | — | — | — |
| 1981 | 139.2 | 2786 | — | 1789 | — |
| 1982 | 165.1 | — | — | — | — |
| 1983 | 215.5 | 2278 | — | — | — |
| 1984 | 306.7 | 1757 | 730 | — | — |
| 1985 | 284.8 | 1176 | — | 768 | — |
| 1986 | 93.6 | 586 | — | 376 | — |
| 1987 | 69.5 | — | 847 | 484 | 92 |
| 1988 | 65.6 | 302 | — | 504 | 186 |
| 1989 | 78.2 | 290 | — | 434 | 128 |
| 1990 | 90.5 | 375 | 799 | 381 | 70 |
| 1991 | 107.5 | 380 | — | 370 | 80 |
| 1992 | 93.9 | 580 | — | 616 | 70 |
| 1993 | 107.4 | 296 | 761 | — | 46 |
| 1994 | 104.0 | 367 | — | — | 40 |
| 1995 | 69.9 | 573 | — | — | 58 |
| 1996 | 49.8 | 589 | 654 | — | 101 |
| 1997 | 84.0 | 450 | — | — | 63 |
| 1998 | NA | 387 | | | 46 |

*Estimate expanded from BTS estimate of the Chirikof area using 400 mesh eastern trawl.

two age groups was obtained using the methods described in Hilborn and Walters (1992) for standardizing the effort of classes of fishing vessels. Total biomass was defined as the sum of the standardized age 3–6 biomass and the age 6+ biomass.

Pacific halibut biomass estimates were obtained from Sullivan and Parma (1995) and transformed from pounds net weight to metric tonnes (t) whole weight. Because the International Pacific Halibut Commission stock assessment covers the period 1974–1996, biomass estimates prior to 1974 were input at the 1974 level. Halibut biomass was not standardized because pollock consumption rates for age 7+ halibut are similar.

Steller sea lion biomass estimates were derived from the sea lion count database of the National Marine Mammal Laboratory (Richard Merrick, pers. comm., Alaska Fisheries Science Center, Seattle, WA). Counts of juveniles and adults were taken from the Western and Central GOA, part of the Eastern GOA, and part of the eastern Aleutian Islands. Counts from areas east of Cape St Elias, inside Prince William Sound, and eastern Aleutian sites west and north of the Shumagin International North Pacific Fisheries Commission statistical area boundaries were excluded, as described in Hollowed *et al.* (1997). A correction factor of 1.33 (estimated by Loughlin *et al.*, 1992) was used to correct for animals at sea. Because counts were not available for years before 1976, abundance during this period was assumed equal to the 1976 value. Numbers were transformed into biomass assuming an average sea lion weight of 212 kg (Perez, 1990).

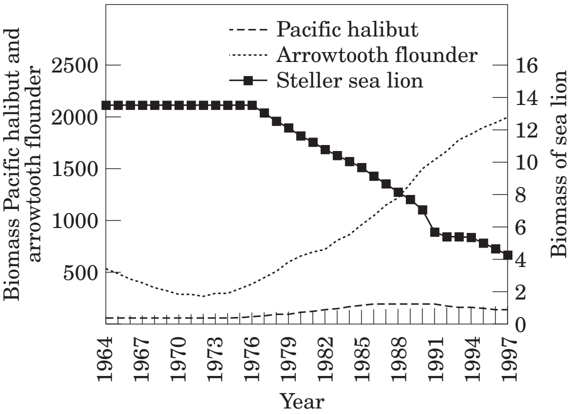

Figure 2. Trends in predator biomass ('000 t) in the Gulf of Alaska, 1964–1997: Pacific halibut, arrowtooth flounder, and Steller sea lion.

Consumption rates of pollock by arrowtooth flounder and Pacific halibut were estimated from stomach samples (3020 and 604, respectively) taken during the 1990, 1993, and 1996 bottom-trawl surveys of the Gulf of Alaska. A detailed description of the methods for field collection and laboratory analysis of stomach samples can be found in Yang (1993) and a description of the methods for calculating consumption rates is found in Livingston and Methot (in press). Age 0 fish (<14 cm standard length) were excluded to correspond to the pollock assessment model, which considers only age 1 and older fish.

Sea lion consumption rates were estimated from published estimates of sea lion diet composition in 1976–1978 and 1985 (with respective sample sizes of 153 and 74), assuming a daily ration of 20 668 kcal $d^{-1}$ per individual, energy content of the diet at 1.3 kcal $g^{-1}$ (Perez, 1990; Perez *et al.*, 1990), and an annual feeding period of 365 days. The proportions by weight of pollock in the diet were taken directly from Pitcher (1981) and Merrick and Calkins (1996), and were assumed to be representative of the region. Because sample sizes and amounts of pollock in the diet indicated that the 1976–1978 diet data of sea lions largely reflected

Table 3. Model equations describing population dynamics.

| Equations | Description |
|---|---|
| $N_{t,1}=R_t=R_0e^{\tau_t}, \quad \tau_t \sim N(0,\sigma_R^2)$ | Recruitment |
| $C_{t,a}=\frac{F_{t,a}}{Z_{t,a}}(1-e^{-Z_{t,a}})N_{t,a} \quad 1 \le t \le T \quad 1 \le a \le A$ | Catch |
| $N_{t+1,a+1}=N_{t,a}e^{-Z_{t,a}} \quad 1<t \le T \quad 1 \le a<A$ | Numbers |
| $S_t=\sum_{a=0}^{20+} w_{t,a}\phi_a N_{t,a}$ | Spawners |
| $N_{t+1,A}=N_{t,A-1}e^{-Z_{t,A-1}}+N_{t,A}e^{-Z_{t,A}} \quad 1 \le t \le T$ | Numbers in "plus" group |
| $Z_{t,a}=F_{t,a}+M_{t,a}$ | Total mortality |
| $M_{t,a}=M_a^{\text{residual}}+\sum_{j \text{ predators}} q_j E_{j,t} e^{-\alpha\left(\frac{U_{j,t}}{U_j^{\max}}\right)-1+\varepsilon_t}$ | Components of natural mortality |
| $C_t=\sum_{a=1}^{A} C_{t,a}$ | Total catch |
| $p_{t,a}=C_{t,a}/C_{t.}$ | Proportion at age in catch |
| $Y_t=\sum_{a=1}^{A} w_{t,a}C_{t,a}$ | Yield |
| $F_{t,a}=\mu_F e^{\varepsilon_{f,t}} s_{f,a} \quad \varepsilon_{f,t} \sim N(0,\sigma_F^2)$ | Fishing mortality |
| $s_{f,a}=\exp(\eta_{f,a}) \quad \eta_{f,a} \sim N(0,\sigma^2_{s_{f,a}}$ | Age effect of fishing |

1977, we used this year to represent pollock consumption per unit of sea lion biomass.

## The model

We used an explicit age-structured model (Tables 3, 4) with the Baranov catch equation (Ricker, 1975) as the underlying population model (e.g., Fournier and Archibald, 1982; Deriso *et al.*, 1985; Hilborn and Walters, 1992). Fishing mortality in each year was scaled so that total catch biomass was fitted with a CV of 3%. The model was tuned with time series of catch, survey and fishery age composition, survey biomass estimates, and predation-per-unit-predator-effort (p.p.u.e.).

A single selectivity pattern was assumed for the three commercial fishery periods (POP fishery 1964–1971; foreign fishery 1972–1984; domestic fishery 1984–1997). Since natural mortality and fishery or survey selectivity estimates can be confounded, selectivity for the EIT and bottom-trawl surveys and the POP fishery were all fixed to be asymptotic when natural mortality was estimated.

The population model begins in 1964, in conjunction with total catch data and length data from the early Pacific ocean perch fishery. The model tracks numbers and catches of pollock in the age groups 1–15 (for a more complete description see Hollowed *et al.*, 1997). We assumed that the initial age distribution of the stock was at equilibrium with an exponential decay rate, that is, a function of natural mortality. Recruitment is estimated for each year from 1964 to 1996. For later years until 2002, recruitment is set equal to the median of the annual estimates, assuming no stock–recruitment

Table 4. List of variables and definitions used (a: age, t: year).

| | |
|---|---|
| $R_t$ | Age 1 recruitment in t |
| $R_0$ | Geometric mean of age 1 recruitment, 1964–1997 |
| $R_0'$ | Geometric mean of age 1 recruitment prior to 1964 (establishes initial age composition) |
| $\tau_t$ | Recruitment deviation in t |
| $T$ | Number of years of fishing (i.e. for 1964 t=1; for 1997 t=T) |
| $A$ | Number of age classes (A=15; a=15 corresponds to fish age 15 and older) |
| $N_{t,a}$ | Number of fish age a in t |
| $C_{t,a}$ | Catch number of age a in t |
| $P_{t,a}$ | Proportion of the total catch in t, that is of age a |
| $C_t$ | Total catch in t |
| $W_{t,a}$ | Mean body weight (kg) of fish of age a in t |
| $\varphi_a$ | Proportion mature at age a |
| $Y_t$ | Total yield weight in t |
| $F_{t,a}$ | Instantaneous fishing mortality for age a, in t |
| $M_{t,a}$ | Instantaneous natural mortality for age a, in t |
| $M_a^{\text{residual}}$ | Unexplained natural mortality component for age a |
| $q_j$ | Catchability coefficient of predator j |
| $E_{j,t}$ | Abundance of predator j in t |
| $\varepsilon_{j,t}$ | Normally distributed random variable of predator j, distributed with a CV related to the uncertainty in the estimate of its abundance |
| $Z_{t,a}$ | Instantaneous total mortality for age a, in t |
| $S_{f,a}$ | Age-effect of fishing for age a in fishery f, normalized to average 1.0 over ages a=1 to A |
| $\mu_F$ | Median year effect of fishing mortality |
| $\varepsilon_{f,t}$ | Residual year effect of fishing mortality (note that effective effort fluctuates in fidelity to the total catch each year) |
| $U_{j,t}$ | Consumption rate of predator j in t |
| $U_j^{\max}$ | Consumption satiation point of predator j |
| $\alpha$ | Parameter governing satiation response curve (range 0–1.0) |

relationship. To reduce the freedom of the parameter estimates, the variation in the fishing mortality rates ($F_{t,a}$) was restricted by assuming that this variation is represented by the product of year and age effects, where the latter component is primarily linked to fitting the catch.

The approach used to model the effect of predation mortality begins in a form analogous to the way fishing mortality is commonly modelled and was first applied in this basic form to the Bering Sea pollock stock assessment (Livingston and Methot, in press). For a given year, the mortality due to predation, $M_{pred}$ can be written as $M_{pred}=qE$, where E is the predator *effort* (or abundance) and q is a proportionality constant. The predation rate expressed as a unit of pollock biomass consumed p.p.u.e. is assumed to be proportional to mean pollock stock size present during the time predation ("fishing") takes place (Ricker, 1975).

Here we improve upon the original formulation by allowing a threshold storage capacity for consumed prey (satiation point). In our model the per capita rate of consumption is expected to have a maximum beyond which further increases in prey abundance will result in no further increases in p.p.u.e. (Holling, 1965). The maximum p.p.u.e. ($U_{max}$) was estimated as the total amount of food that a unit predator could have consumed in a year given the rations and number of feeding days per year. The estimates of $U_{max}$ for pollock consumed per tonne of predator were: 27.37 t for sea lion, 0.4357 t for arrowtooth flounder, and 0.9792 t for Pacific halibut. As the pollock abundance increases to stock sizes beyond the satiation point, then the effective effort of the predator declines. This effect is modelled by using a multiplicative term to the above equation as:

$$M_{pred}=q\ E\ \exp[-I(U/U_{max}-1)].$$

where U is the anticipated p.p.u.e. in the current year (computed prior to adjusting the $M_{pred}$ value). The addition of uncertainty in predator abundance (E) is modelled using a stochastic term with assumed variance (see Table 3). This function is flexible and allows approximation that conform to different Holling Type of functional response curves. The parameter I sets the degree of curvature where a value of 0.0 conforms to a modified Type 1 response (i.e., proportional ration without satiation) and a value of 1.0 approximately conforms to Type 4 response. A Type 2 response was best approximated with a value of I equal to 0.7. We used values of 0.0 and 0.7 to contrast the effect of predator satiation on model results.

Predation mortality by the three selected predators does not account for all sources of natural mortality. To account for additional sources of natural mortality in pollock we estimated a residual component of natural mortality ($M_1^{residual}$) for age 1 and ages 3 years and older ($M_3^{residual}$). The residual mortality of age 2 individuals was assumed to be half way between the values estimated for ages 1 and 3.

Thompson (1994) noted that estimates of natural mortality can be confounded with selectivity assumptions. Our approach to resolving this problem was to use prior distributions about estimates of the residual mortality component. We devised a prior distribution of age-1 natural mortality based on a study by Bailey *et al.* (1996) in the Shelikof Strait, who estimated total natural mortality to be between 0.8 and 3.0. Similarly, we devised a prior distribution for pollock aged 3 years and older based on estimates of total pollock mortality including: (a) growth parameters (Alverson and Carney, 1975; Pauly, 1980), (b) the gonadosomal index (Gunderson and Dygert, 1988), and (c) cohort abundance. These methods produced estimates of natural mortality that ranged from 0.24 to 0.30. Alternative prior distributions for these mortality rates were evaluated.

The statistical aspects of this age-structured model are similar to those used in the Stock Synthesis program of Methot (1986, 1990) and are more fully described in Hollowed *et al.* (1997). The likelihood components include the combined fishery catch-at-age composition estimates (and the total annual catch estimates) and the survey indices. Multinomial likelihoods are estimated for age (and size) composition data and lognormal likelihoods for survey biomass estimates. Model parameters are estimated by maximizing the log-likelihood of the data, viewed as a function of the parameters. All series of abundance indices are treated as being lognormally distributed about their expected values (i.e., having a negative log-likelihood). Ageing error for all age composition data was incorporated by use of a transition matrix (with elements associated with the probability of an observed age being true age).

The survey catchability coefficients can be fixed or freely estimated in this model. For the results presented below, we selected a prior variance on the catchability for the triennial trawl survey to have a mean value of 1.0 and a coefficient of variation of 13%. Catchabilities for all other indices were estimated, assuming that they were constant. Standard errors in survey biomass estimates were incorporated with survey estimates. Standard errors for the EIT biomass estimates observed in 1992 were applied for all subsequent EIT surveys.

For some models presented below, over 200 parameters were estimated, most of which are associated with year-to-year and age-specific deviations in coefficients. Schnute (1994) presents a broad discussion of this type of approach to modelling errors-in-variables. To facilitate the estimation of such a large number of parameters in a non-linear model, automatic differentiation software extended from Greiwank and Corliss (1991) and developed into C++ class libraries was used.

Table 5. List of models presented according to increasing degree of complexity and/or amount of assumptions relaxed (Pred: predation; Sat: satiation; Unc: uncertainty in Pred; SS: EIT survey selectivity; $M^{residual}$: residual mortality in age groups 1 and 3).

| Model | Description | Pred | Sat | Unc | SS | $M^{residual}$ |
|---|---|---|---|---|---|---|
| A | Assessment | No | No | No | Free | $M_1=0.8$, $M_3=0.3$ |
| B | Baseline | Yes | No | No | Asymptotic | $M_1=0.5$, $M_3=0.1$ |
| C | Satiation | Yes | Yes | No | Asymptotic | $M_1=0.5$, $M_3=0.1$ |
| D | Uncertainty | Yes | Yes | Yes | Asymptotic | $M_1=0.5$, $M_3=0.1$ |
| E | Estimated M | Yes | Yes | Yes | Asymptotic | $M_1$ and $M_3$ estimated |

This software provided the derivative calculations needed for finding the likelihood mode via a quasi-Newton function minimization routine (e.g., Press *et al.*, 1992). The model implementation language (ADModel Builder, Ianelli and Fournier, 1998) gave simple and rapid access to these routines and provided the ability to estimate the variance–covariance matrix for all dependent and independent parameters of interest.

The number of parameters estimated varied considerably between models. Parameters estimated were: (1) q values for each abundance index; (2) average recruitment for the entire time frame ($R_0$) and for initial conditions ($R_0'$); (3) recruitment in each year since 1964 ($\tau_t$); (4) fisheries and surveys age-effects coefficients $\eta_{fa}$ (if any); and (5) annual (residual) effect of fishing mortality in each year $\varepsilon_{f,t}$ and the median effect of fishing ($\mu_F$).

The complete objective function upon which our estimation is based had the following component (negative logarithm) likelihood parts:

$$L_1=\sum_C\sum_t \log(I_t^c/\hat{I}_t^c)^2/2(s^c)^2,$$

where c represents the hydro-acoustic survey, bottom-trawl survey, egg-production survey, arrowtooth flounder p.p.u.e., Pacific halibut p.p.u.e., and sea lion p.p.u.e., consecutively:

$$L_2=\sum_c n^d\sum_{t,a} p_{t,a}\ln(\hat{p}_{t,a}),$$

where d represents fishery catch-at-age data, fishery size composition data, survey catch-at-age data, survey size composition data and predator catch-at-age data, consecutively:

$$L_3=\lambda_{\varepsilon_j}\sum_t \varepsilon_{j,t}^2+\lambda_{\varepsilon f}\sum_t \varepsilon_{f,t}^2+\lambda_{\eta f}\sum_t \mu_{f,a}^2,$$

$$L_{tot}=\sum_i^3 L_i.$$

## Runs

Five model configurations were evaluated (Table 5). Model A approximates a typical stock assessment where natural mortality is fixed and survey selectivities and catchabilities are estimated within the model. Model B represents the predation model where survey selectivities are fixed to be asymptotic, predation mortality is estimated but residual natural mortalities, $M_1^{residual}$ and $M_3^{residual}$, are fixed. Predator biomass was assumed to be known with certainty in Model B. Model C is identical to B except that the satiation threshold is imposed on sea lions. Errors in predator biomass are incorporated into Model D based on variance estimates surrounding stock assessments for arrowtooth flounder, Pacific halibut, and sea lion counts. Model E is similar to Model D with the exception that residual mortalities are estimated parameters (with priors).

Variance estimates on arrowtooth flounder biomass were provided by Turnock *et al.* (1996) from bootstrap methods. Variance estimates on Pacific halibut biomass were based on Sullivan and Parma (1995). York *et al.* (1996) estimated a CV of 0.04 around estimates of breeding female sea lions. This value should be considered a minimum estimate, because breeding females are the easiest animals to monitor. Juvenile and adult male abundance estimates are less certain. In each case, confidence bounds were estimated for recruitment estimates, biomass estimates, and ages 1, 2, 3, and 4+ natural mortality. Variances estimates of such derived parameters were computed using the Delta method (Seber, 1982).

We encountered estimation problems during initial runs of Model E resulting from the lack of constraints on the initial age composition, the survey selectivities and catchability coefficients, and the residual mortality parameters. These problems were resolved by adding selectivity constraints for the bottom-trawl survey (to avoid confounding with very high residual mortality rates and a shift in selectivity to older pollock) and reducing the influence of the initial age composition. Also, we evaluated use of a prior distribution on the residual mortality parameters.

The estimate of age 1 natural mortality for Model A was based on exploratory runs of the model when predation mortality was incorporated. Estimates of age 1 natural mortality ranged from 0.81 to 0.86, when predation mortality was incorporated into the

Table 6. Summary results of different models. The effective N values were computed as outlined in McAllister and Ianelli (1997), where a higher value represents a better fit, whereas lower values of root-mean squared errors (RMSE) represent better fits to those types of data.

| Model | A | B | C | D | E |
|---|---|---|---|---|---|
| Fits: Effective N | | | | | |
| EIT age | 21 | 22 | 24 | 25 | 26 |
| EIT size | 18 | 19 | 18 | 17 | 17 |
| Domestic fishery | 30 | 48 | 48 | 47 | 48 |
| Foreign fishery | 43 | 39 | 40 | 40 | 40 |
| Fishery size comps | 8 | 19 | 21 | 21 | 22 |
| Bottom trawl age | 64 | 56 | 56 | 55 | 54 |
| Fits: RMSE $(\sqrt{\ln(\text{obs/pred})^2/n})$ | | | | | |
| EIT | 0.260 | 0.238 | 0.280 | 0.272 | 0.272 |
| Egg production | 0.257 | 0.179 | 0.227 | 0.205 | 0.222 |
| Bottom trawl | 0.142 | 0.117 | 0.134 | 0.141 | 0.145 |
| AFT p.p.u.e. | NA | 0.096 | 0.122 | 0.074 | 0.073 |
| Halibut p.p.u.e. | NA | 0.025 | 0.020 | 0.020 | 0.016 |
| Sea lion p.p.u.e. | NA | 0.470 | 0.181 | 0.127 | 0.147 |
| Pollock stock condition | | | | | |
| Current stock size ('000 t) | 1347 | 2196 | 2024 | 1824 | 1560 |
| CV current stock size | 12% | 14% | 12% | 16% | 15% |
| Avg recruitment (1972–1997) | 1958 | 5160 | 4174 | 4492 | 3951 |
| Avg CV of recruitment | 13% | 16% | 12% | 15% | 19% |
| Avg F 1988–1997 | 0.17 | 0.13 | 0.14 | 0.14 | 0.15 |
| CV avg F 1988–1997 | 12% | 12% | 12% | 12% | 12% |
| 1997 spawners/avg since 72 | 76% | 60% | 60% | 57% | 57% |
| CV 1997 spawners/avg since 72 | 9% | 9% | 9% | 11% | 11% |
| Predation | | | | | |
| Total M age 1, 1997 | 0.80 | 0.84 | 0.85 | 0.90 | 0.93 |
| CV total M age 1, 1997 | 0% | 5% | 5% | 13% | 16% |
| Total M age 4+, 1997 | 0.30 | 0.38 | 0.36 | 0.38 | 0.34 |
| CV total M age 4+, 1997 | 0% | 5% | 5% | 9% | 11% |
| 1988–1997 avg M Age 1 | 0.80 | 0.80 | 0.82 | 0.84 | 0.86 |
| 1988–1997 avg M Age 2 | 0.55 | 0.72 | 0.71 | 0.75 | 0.76 |
| 1988–1997 avg M Age 3 | 0.30 | 0.55 | 0.53 | 0.59 | 0.58 |
| 1988–1997 avg M Age 4+ | 0.30 | 0.42 | 0.42 | 0.43 | 0.39 |
| Arrowtooth flounder | | | | | |
| Consumption 1997 ('000 t) | NA | 344 | 314 | 340 | 321 |
| CV estimated consumption 1997 | NA | 18% | 16% | 31% | 30% |
| Avg consumption 1988–1997/1978–1987 | NA | 118% | 138% | 112% | 111% |
| CV avg consumption 1988–1997/1978–1987 | NA | 6% | 6% | 16% | 16% |
| Pacific halibut | | | | | |
| Consumption 1997 ('000 t) | NA | 55 | 54 | 50 | 50 |
| CV estimated consumption 1997 | NA | 13% | 13% | 18% | 18% |
| Avg consumption 1988–1997/1978–1987 | NA | 82% | 88% | 78% | 79% |
| CV avg consumption 1988–1997/1978–1987 | NA | 5% | 5% | 8% | 8% |
| Steller sea lions | | | | | |
| Consumption 1997 ('000 t) | NA | 150 | 113 | 105 | 103 |
| CV estimated consumption 1997 | NA | 20% | 7% | 11% | 11% |
| Avg consumption 1988–1997/1978–1987 | NA | 30% | 45% | 43% | 42% |
| CV Avg consumption 1988–1997/1978–1987 | NA | 5% | 2% | 4% | 4% |

model (Table 6). Based on these estimates, the age 1 natural mortality rate for Model A was set at 0.8.

Exploratory runs of Model B revealed that the selectivity patterns of Steller sea lions and Pacific halibut were asymptotic. Therefore, subsequent runs of Model B–E were all run assuming that the selectivity pattern of Steller sea lions and Pacific halibut were asymptotic.

## Results

Summary results between all of the models are presented in Table 6. Here we emphasize the information about

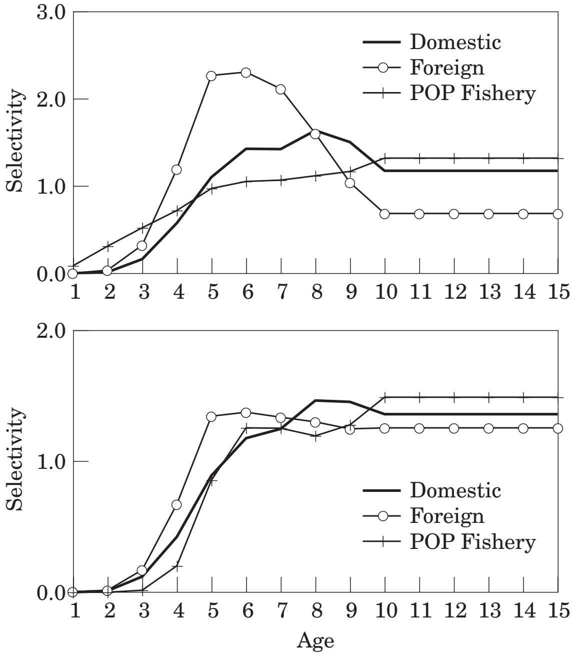

Figure 3. Estimates of fishery selectivity by Models A (upper panel) and B (lower panel).

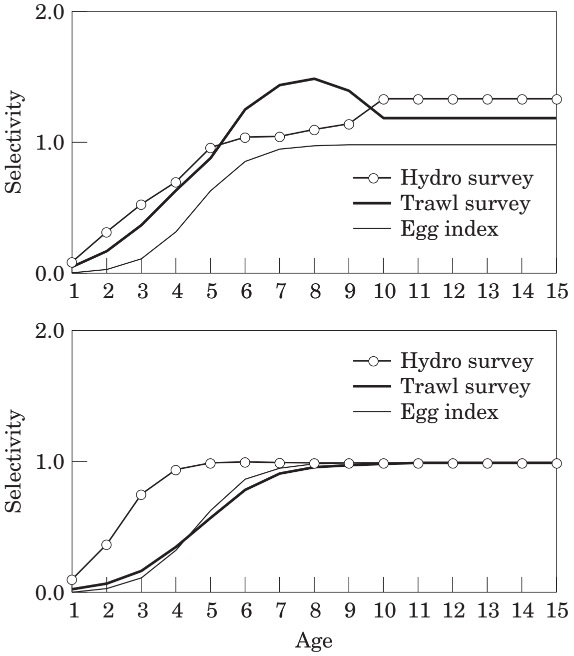

Figure 4. Estimates of survey selectivity by Models A (upper panel) and B (lower panel).

the condition of the pollock stock and fishery, and the information involving predation.

Fishery and survey selectivities were estimated in both Models A and B (Figs 3, 4). In Model A, fisheries and trawl selectivities were freely estimated and the best fit resulted in dome-shaped selectivity patterns, with the exception of the POP fishery period. In Model B, fishery and trawl survey selectivities were fixed as asymptotic with increasing age.

Selectivity by predator type shows the expected response that arrowtooth flounder has a preference for younger pollock, while Steller sea lions and Pacific halibut tend to prefer somewhat older pollock (Fig. 5).

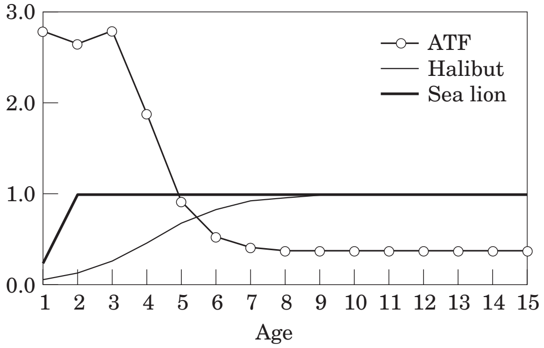

Figure 5. Estimates of predator selectivity by Model E.

Relative to Model A, average abundance at age 1 was higher for Models B–E that incorporated predation, but they were mutually strongly correlated (Table 6; Fig. 6). The recruitment of age-1 pollock shows a variable pattern of year-class strength characteristic of gadoid species (Fig. 7). Uncertainty is higher for incoming year classes, where less information is available. The uncertainty related to the recruitment of the strong 1994 year class appears in the stock in 1995, which resulted in broad 95% confidence limits, is also projected into recent abundance estimates relative to the historical biomass trajectory (Fig. 8a). This trajectory suggests that the peak abundance of pollock in the Gulf occurred in the early 1980s and the total biomass was between 2.5 and 3.5 million tonnes. Relative to Model E, the baseline model underestimated the CV of current stock size by 20% and average recruitment by 32% (Table 6). The current estimate of total biomass is between abundance 1.3 and 2.2 million tonnes, with a recent average fishing mortality rate of about 0.14 (Fig. 8c).

Average spawner biomass over the last decade has been lower than the long-term average (Table 6). Relative to the historical average, recent spawner biomass was roughly 20% lower in models that incorporated predation pressure than Model A. Spawner biomass estimates from Model A were consistently lower than Model E (Fig. 8b) because the average total natural mortality for adult fish (age 4+) was higher in Model E. Model E also exhibited larger variations in spawning stock biomass than Model A because of

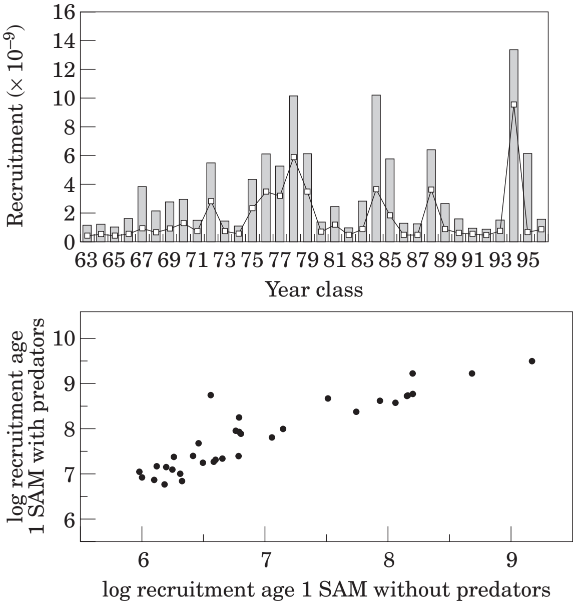

Figure 6. Time series of pollock recruitment estimates at age 1 (top panel) by Models A (lines) and E (bars). Lower panel shows the strong correlation between the log-transformed estimates from the two models.

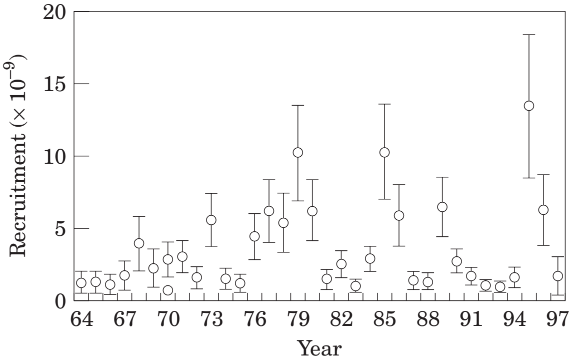

Figure 7. Time series of pollock recruitment at age 1 as estimated by Model E (bars represent 95% confidence limits).

trends in predation mortality. Comparison of spawner–recruitment plots suggests that Model E showed less compensation at high stock sizes than Model A (Fig. 9).

The overall trend in mortality due to predation has substantially increased in recent years for age 1 pollock, while older-aged pollock appear to have declined moderately in Model E (Fig. 10). Presumably this is due to the increased abundance of arrowtooth flounder and the relatively low levels of Steller sea lion abundance. The average total natural mortality over the most recent decade for adult fish was about 25% higher than assumed in the baseline (Table 6).

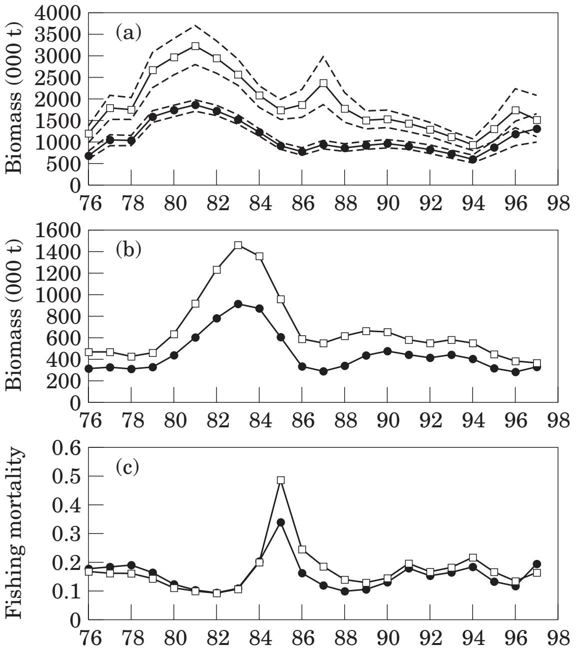

Figure 8. Time series of pollock population parameters estimated by Models A (closed circles) and E (open squares). a. Total stock biomass with associated 95% confidence limits. b. Spawning stock biomass. c. Fishing mortality.

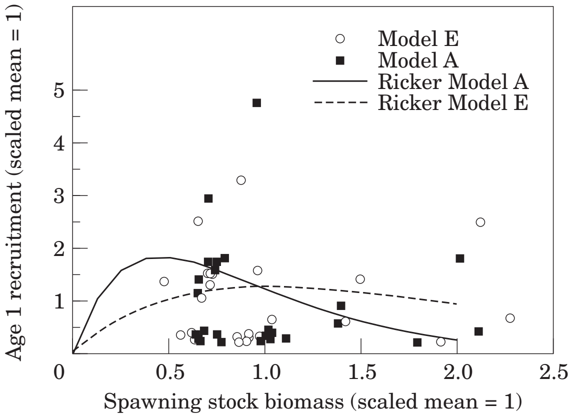

Figure 9. Pollock stock recruitment plot with estimated Ricker curves for Models A (constant natural mortality) and E (with predation).

## Discussion

This analysis represents a step toward expanded studies of the interactions between fisheries and predator populations, including marine mammals. A major difference between this model and deterministic multispecies VPA (MSVPA) models is the ability to evaluate statistically the relative fit of the model to the data. Variance estimates are readily available for any

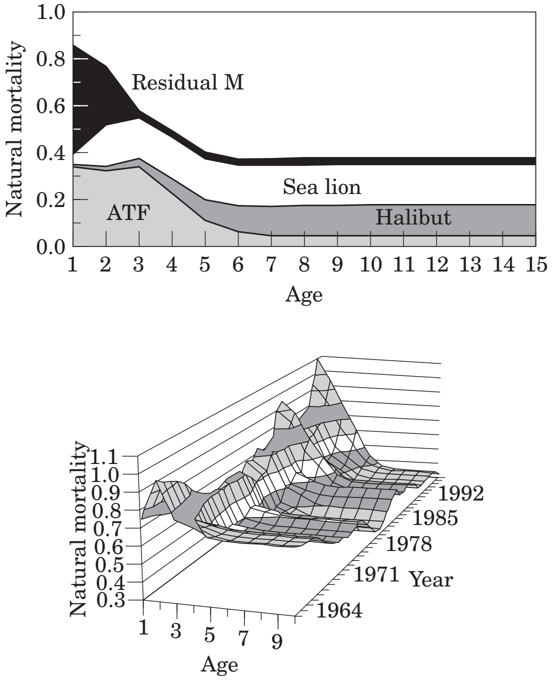

Figure 10. Trend in pollock natural mortality rate over time and age (lower panel) and the average natural mortality rate by age group over the last decade split into the components (top panel).

parameter of interest and can easily be extended to include time-series effects for processes such as selectivity.

The non-parametric smoothing treatment of selectivity allowed greater flexibility in the way the predator selectivity patterns could be modelled, yet gave results similar to the parametric form for the different fishery patterns under stock synthesis. The advantage of a non-parametric smoothing function is primarily that the parameters involved are directly interpretable and there are fewer problems with parameters becoming confounded or irrelevant (as may happen in certain parameter combinations of parametric forms).

Catchability for all surveys was estimated in this model. The prior distribution assigned to the triennial trawl survey had a mean value of 1.0 with relatively low variability (but infinitely larger than assuming a fixed value of 1.0), while for models A–D, no prior distribution was assumed for the hydro-acoustic catchability coefficient (Fig. 4). This differs from previous analyses using the stock-synthesis programme, where the triennial trawl survey was given a fixed value of 1.0. Clearly, acknowledging these sources of uncertainty allows us to express a more realistic range of model uncertainty. Without using Bayesian methods, expressing this uncertainty in a coherent fashion becomes difficult.

Using a prior distribution to model natural mortality differs from Sparholt (1990), who estimated the biomass of piscivorous fish other than those included explicitly in a multi-species virtual population analysis (MSVPA) from an estimate of the consumption (in weight) by those non-“MSVPA predators”. Estimates of the total consumption of pollock by species other than the three predators accounted for was not possible because abundance estimates were not available for many sea birds and marine mammals that are known to consume pollock. Adult pollock were not considered major pollock predators in the GOA because the incidence of cannibalism during the summer feeding period was low. This finding differs from the Bering Sea, where Dwyer *et al.* (1987) found that adult pollock were cannibalistic.

Explicitly modelling predation mortality in catch-at-age models has many advantages for addressing ecosystem concerns in stock assessments. Our results indicate that natural mortality is not constant at age and varies interannually. They also show that traditional methods for calculating natural mortality “external” to the model may underestimate mortality.

Our ability to make informed decisions regarding selectivity and natural mortality parameters will be improved through collection of additional food habits data and independent studies of selectivity. The estimated selectivity patterns were based on only 3 years of data for the fish predators and only 1 year for Steller sea lions. In addition, we assumed that the food habits information collected during the summer months was representative of predation behaviour throughout the year. We strongly recommend that a concerted effort be made to collect food habits data from commercial fisheries and surveys during different seasons of the year. Additional information on the age composition of Steller sea lion prey from seat analysis might be used to refine predator selectivity estimates.

This analysis demonstrated a high degree of uncertainty surrounding estimates of age-specific natural mortality. The best fits to the data were achieved at natural mortality rates that were higher than estimated using empirical methods. This finding is consistent with the work of the ICES Multispecies Assessment Working Group (Pope, 1991; Magnússon, 1995). The high degree of uncertainty surrounding estimates of natural mortality demonstrates that estimates based on relationships between M and parameters such as reproductive effort using the gonadosomal index (Gunderson and Dygert, 1988) and growth parameters (Alverson and Carney, 1975) should be modelled as uncertain parameters in stock assessments. Furthermore, the apparent relationships between empirical estimates of natural mortality and life history characteristics of fish are equally uncertain.

Estimates of age 1 total natural mortality (0.85–2.0) were within the range of natural mortality rates derived from other studies. Livingston and Methot (in press) estimated age 1 natural mortality rates between 0.5 and 1.8 in a stock synthesis model for Bering Sea pollock. Bailey *et al.* (1996) estimated a wide range in age 1 natural mortality (0.9 to 3.23, mean 1.87) by monitoring the decay of a cohort over time using estimates from the 1981–1991 EIT surveys. Our analysis showed that the estimate of residual natural mortality was poorly defined for age 1 pollock, which is consistent with Bailey *et al.* (1986).

Predation by arrowtooth flounder, Pacific halibut, and Steller sea lions accounted for only 40% of the age 1 natural mortality. Brodeur and Wilson (1996), in reviewing the major predators of juvenile pollock in the Gulf of Alaska, identified several potential predators that could be added to the model in future years. Of these, seabirds (murres and puffins), Pacific cod, harbor seals, and adult pollock were considered the most likely species to consume large quantities of juvenile pollock. Pollock in the Gulf of Alaska do not exhibit the high rates of cannibalism that have been estimated for pollock in the Bering Sea (Livingston and Jurado-Molina, 1999). Laboratory studies show starvation is probably not an important source of natural mortality for juvenile pollock. Sogard and Olla (in press) starved juvenile pollock for 205 days under laboratory conditions. When food was introduced, the starved juveniles were able to commence feeding and survive.

Trends in total natural mortality were observed for younger age groups (ages 1–3), while total age 4+ natural mortality was fairly constant. Total natural mortality at young ages was higher during 1988–1997 than during 1978–1987 (Table 7). This increasing trend was attributed to the growing impact of arrowtooth flounder predation Lapointe *et al.* (1989) noted that trends in natural mortality or mis-specification of natural mortality could mask trends in the magnitude of recruitment.

The larger coefficient of variation around estimates of stock biomass in models that incorporated uncertainty in sources of natural mortality illustrates that models based on assumptions of constant life history parameters may overstate the level of confidence in estimates of stock conditions. The modelling approach introduced here provides a method for statistically characterizing the accumulation of errors from various data used in the assessment.

Comparison of spawner–recruitment relationships revealed that models that assumed constant natural mortality exhibited greater compensation at high stock sizes than models that incorporated predation mortality. However, accounting for predation mortality principally scaled the age 1 recruitment time series upwards. This finding is consistent with Pope (1991), who noted that estimates of recruitment of age 1 cod from MSVPA models were larger than, but highly correlated with estimates from single-species models. Our findings are similar, but less striking, than those of Sparholt (1996) and Livingston and Methot (in press), who evaluated impacts of predators on recruitment in populations where cannibalism is an important source of mortality. In stocks where cannibalism was prevalent, accounting for temporal trends in predation mortality produced substantially different spawner–recruit patterns.

There are several areas where the model could be improved. Similar to Pope (1979), we assumed that the abundance of alternative prey is a constant proportion of the food requirements of the modelled species. However, there is some evidence that alternative prey populations may have experienced sharp declines in the last two decades. Piatt and Anderson (1996) noted that capelin populations in Pavlov Bay declined sharply after 1977, when the region experienced a major change in climatic conditions. Some improvement in estimated trends in alternative prey abundance may result from the recent passage of the forage fish amendment to the Fisheries Management Plan of the North Pacific Fishery Management Council, if this results in increased efforts to monitor forage fish populations in the Gulf of Alaska.

The assumption of constant catchability for arrowtooth flounder, Pacific halibut, and Steller sea lions implies that the spatial distributions of predator and prey are constant over time. If climatic conditions influence the distribution of pollock or its predators, the proportion consumed could be erroneous. NOAA's Fisheries Oceanography Coordinated Investigations program has conducted studies since 1984 to improve our understanding of oceanographic forcing and its impact on the distribution and abundance of marine organisms. The program has developed a primitive equation, rigid-lid, hydrostatic, eddy-resolving hydrodynamic model of the western and central regions of the Gulf of Alaska (Hermann *et al.*, 1996). Future studies may allow for comparison of fish distributions in relation to summer oceanic conditions. This type of spatial analysis may improve our understanding of the degree of overlap between predators and prey.

We considered two types of functional feeding responses: a proportional ration model (Holling Type I), with no asymptote, and a Holling Type II response. Mohn and Bowen (1996) note that there are theoretical reasons for expecting that predators could experience a Type III response, because they may switch to an alternative prey when prey density reaches a low level. The long history of research on monitoring pollock abundance with acoustic techniques provides a real opportunity to conduct studies of threshold foraging similar to those conducted by Piatt and Methven (1992). Acoustic surveys, coupled with studies of sea-lion foraging behaviour, as described by Merrick and Loughlin (1997), may provide sufficient information to introduce a Type III feeding response for this species. Identification of the threshold feeding response would be useful in establishing fisheries management decisions regarding pollock harvest that explicitly accounted for the feeding requirements of Steller sea lions.

The model presented here is an initial step towards the introduction of a formal mechanism for addressing ecosystem concerns in the process of stock assessment. The model has been presented to the Groundfish Plan Team and Scientific and Statistical Committees of the North Pacific Fishery Management Council as an alternative model structure that formally addresses ecosystem concerns with respect to management of the Gulf of Alaska walleye pollock stock (Hollowed *et al.*, 1995, 1997).

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