Data conflicts in fishery models: incorporating hydroacoustic data into the Prince William Sound Pacific herring assessment model

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Data conflicts present difficulties in running integrated assessment models as shown by the age-structured assessment (ASA) model for the Pacific herring population in Prince William Sound (PWS), Alaska. After the 1989 "Exxon Valdez" oil spill in PWS, the Pacific herring (*Clupea pallasi*) ASA model indicated a significant decline in the population, starting in winter 1992. Back-calculated estimates from hydroacoustic abundance surveys that started in 1993 suggested that the ASA model overestimated herring biomass from 1990 to 1992 and that the population decline actually began in 1989. To expose data conflicts, we incorporated the hydroacoustic survey information with all available spawning population indices directly into the age-structured model. In this way, the substantial uncertainty about population parameters from 1989 to 1992 attributable to data conflicts was quantified. Consequently, the magnitude of declines for that period estimated from both linear and ASA models depend on the type of integrated datasets and weighting, particularly with indices of male spawners. Our view is that a major decline started in 1992 when disease affected a large population that was in weakened condition. Other views are consistent with the existing data too.

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Introduction

Arguably the most crucial scientific activity in fisheries management is stock assessment: determining the status of a commercially or recreationally important fish population and what levels of harvest are sustainable. Fisheries management is in crisis around the world owing to spectacular fisheries collapses and public perception that sufficient attention is not being paid to the ecological effects of fisheries. Without good information and analysis in a stock assessment, there can be major errors in management which may not be observed until it is too late to take action. Although the stock assessment process has evolved to develop models with increasingly complex biological processes (Quinn and Deriso, 1999), there is still a need to improve assessment models (NRC, 1998; Quinn and Collie, 2005).

Fishery age-structured assessment (ASA) models that integrate multiple data sources are ubiquitous (Quinn and Deriso, 1999), but data conflicts often arise through associated measurement and process errors. A common conflict is between fishery catch per unit effort (cpue) and a survey index of abundance (NRC, 1998; Booth and Quinn, 2006). As stock assessments evolve to incorporate a wider variety of data (reproduction, size-structure, spatial strata), conflicts become more prominent.

With multiple datasets in an ASA model, an analyst must choose how much weight to give to each dataset's component in the objective function for parameter estimation. Controversy frequently arises when different weightings produce more optimistic harvest recommendations and when hypotheses are tested on the basis of model output (Deriso et al., 2007). Theoretically, weighting should be based on the ratio of variances, but in almost all cases, such variances are unknown. The Prince William Sound (PWS), Alaska, population of Pacific herring (*Clupea pallasi*) provides a good example of data conflicts and the effects of dataset weighting.

Pacific herring that spawn in PWS are an important forage species for marine fish and wildlife, and a valuable commercial resource (Thomas and Thorne, 2003). In 1992, >130 000 t were predicted to be available in 1993 by an ASA model, but only some 30 000 t actually returned to spawn (Meyers et al., 1994; Quinn et al., 2001). Because of the population decline over the winter of 1992/1993, the Alaska Department of Fish and Game (ADF&G) closed the 1993 fishery, and it has remained closed except for relatively small openings in 1997 and 1998.

It has been hypothesized that a disease was responsible for this unexpected natural mortality (Meyers et al., 1994); in 1993, the

North American strain of viral haemorrhagic septicemia virus (VHSV) was isolated from Pacific herring sampled from PWS. There was some microscopic evidence of lesions consistent with VHSV in 1989, but not between 1990 and 1992 (Kocan *et al.*, 1996; Marty *et al.*, 1999). In 1994, a systematic and unique time-series of disease prevalence commenced. That time-series documented the significance of three major diseases or pathogens in PWS Pacific herring: ulcers related to filamentous bacteria, VHSV, and the mesomycetozoan *Ichthyophonus hoferi* (Quinn *et al.*, 2001; Marty *et al.*, 2003).

An alternative hypothesis indicated that the significant decline in the PWS herring population started in 1989 (Thomas and Thorne, 2003). Hydroacoustic surveys were initiated in autumn 1993 to determine the condition of the herring stock as a consequence of the unexpected biomass decline, and these surveys generated more than a decade's worth of data. From a back-calculation of a regression relationship between hydroacoustic survey biomass estimates and a measure of male spawning activity (mile-days of milt production), herring biomass was extrapolated back to the early 1970s. Smaller values than those from the ASA model were obtained for the years 1990–1992, suggesting that the ASA model had overestimated biomass in those years by including other data sources, including egg deposition survey estimates and age-structured catch and survey data. Consequently, harvest rates calculated from the hindcast estimates are larger than those from the ASA model. In 1991 and 1992, the estimated exploitation rates of the fishery approached nearly 40% (35% and 39%, respectively; Thomas and Thorne, 2003). These high harvest rates, because of inaccuracies in the ASA methodology, were concluded to have contributed to the decline in the population.

The goal of this study is to evaluate explicitly the conflicts present in the data sources for PWS Pacific herring and to revisit the hypotheses pertaining to mortality after 1989 with an alternative analytical approach. Rather than relying on a simple linear regression, we estimate mortality using the ASA model by integrating the hydroacoustic survey dataset with all available index and age-structured data. Therefore, the data conflicts are evaluated through determination of uncertainty and model comparison over a variety of weighting scenarios and natural mortality parameterizations. We evaluate the estimation behaviour of the hydroacoustic hindcast procedure with available indices of male spawners, compare estimates of exploitation rates from 1989 to 1992 between the linear regression and ASA models, and assess the value of the new acoustic dataset as an index in the PWS Pacific herring ASA model.

Methods
Data
The ASA model integrates various data sources relevant to Pacific herring in PWS from 1980 to 2004. Herring datasets include the age distribution of catch for the purse-seine fishery ($n = 88$; 500–7000 fish sampled annually), spawning age composition ($n = 158$; 600–8000 fish sampled annually), estimates of total egg deposition from diver surveys ($n = 10$), and measures of male spawning from annual aerial surveys ($n = 25$).

Egg deposition was estimated from a two-stage sampling design (Blankenbeckler and Larson, 1982, 1987; Schweigert *et al.*, 1985) with random sampling at the primary stage (transects) and systematic sampling in the second stage (Willette *et al.*, 1999). There are two related indices for male spawner abundance. The first is

miles of milt, the total linear distance of beaches receiving spawn, and the second is mile-days of milt, which includes both the linear distance and the duration of spawn. Both date back to the early 1970s, and the ASA model in PWS has historically used the index mile-days of milt. For illustrative purposes, the mile-days of milt and egg deposition datasets are shown in Figure 1, with ellipses encircling the period of conflict between the two indices.

Disease indices for ulcers, VHSV, and *I. hoferi* are available for the years 1994–2004. The indices are stratified by age (3–4, 5–9) and originate from disease-prevalence values adjusted to reflect the significance of each component (Marty *et al.*, 2003). Other data sources include weight- and fecundity-at-age, total seine catch, and catch-at-age in other fisheries.

We obtained two sets of hydroacoustic biomass estimates. The first, from 1995 to 2004 (Table 1), is a recompilation of data collected by PWSSC (Thomas and Thorne, 2003) and ADF&G. In 1995 and 1996, the estimates were taken directly from PWSSC through unpublished contract reports to ADF&G. The first year that ADF&G had acoustic gear and conducted its own survey was 1997 (Biosonics 70 kHz, single beam). From 1997 to 2004, the estimates were taken from a combination of PWSSC and ADF&G surveys except 2000, in which year ADF&G did not conduct a survey so only PWSSC data were used. The second hydroacoustic dataset is from 1993 to 2004 (Thorne and Thomas, 2008; Table 1). This dataset includes two additional years of data (1993, 1994) collected during autumn, requiring the assumption that spring and autumn surveys measure population biomass consistently. In this study, we notate the integrated PWSSC and ADF&G acoustic dataset as A, and the acoustic dataset from Thorne and Thomas (2008) as B. In previous assessment analyses, the hydroacoustic dataset was used as a constraint on the minimum value of spawning biomass rather than as an index.

ASA model
To investigate the ASA model thoroughly, it is necessary to present its full structure as implemented in PWS. The ASA model is a standard implementation of an ASA model (Quinn and Deriso, 1999, chapter 8), modified to include the impact of disease on mortality and abundance (Quinn *et al.*, 2001; Marty *et al.*, 2003). The observations are compared with model estimates in a least-squares setting to obtain parameter estimates of recruitment, initial abundance in the first year, maturity, gear selectivity, a milt calibration coefficient, a hydroacoustic calibration coefficient, and disease coefficients. Notation is given in Table 2.

The recruitment, initial abundance, natural mortality, and gear selectivity parameters are utilized to obtain a population matrix of pre-fishery total abundances for ages 3 to 9+ and the years 1980–2004. Pre-fishery total abundance $N_{a,t}$ starts with recruitment and initial abundance parameters: abundances (in millions of fish) for age 3 from 1980 to 2004, and ages ≥ 4 in 1980. It is given by:

$$N_{a+1,t+1} = [((N_{a,t} - (C_t^s \Theta_{a,t}^s + C_{a,t}^g + P_k C_{a,t}^p)) S_{a,t}^{1/2}) - C_{a,t}^{f/b}] S_{a,t+1}^{1/2}, \tag{1}$$

in which a cohort at age a and year t becomes 1 year older the next year. The pre-fishery population decreases as a consequence of four commercial fishery catches (s, seine; g, gillnet; p, pound utilization; f/b, food and bait), and natural mortality (expressed in terms of natural survival S). S is written as a function of age and year to accommodate disease prevalence. A half-year convention
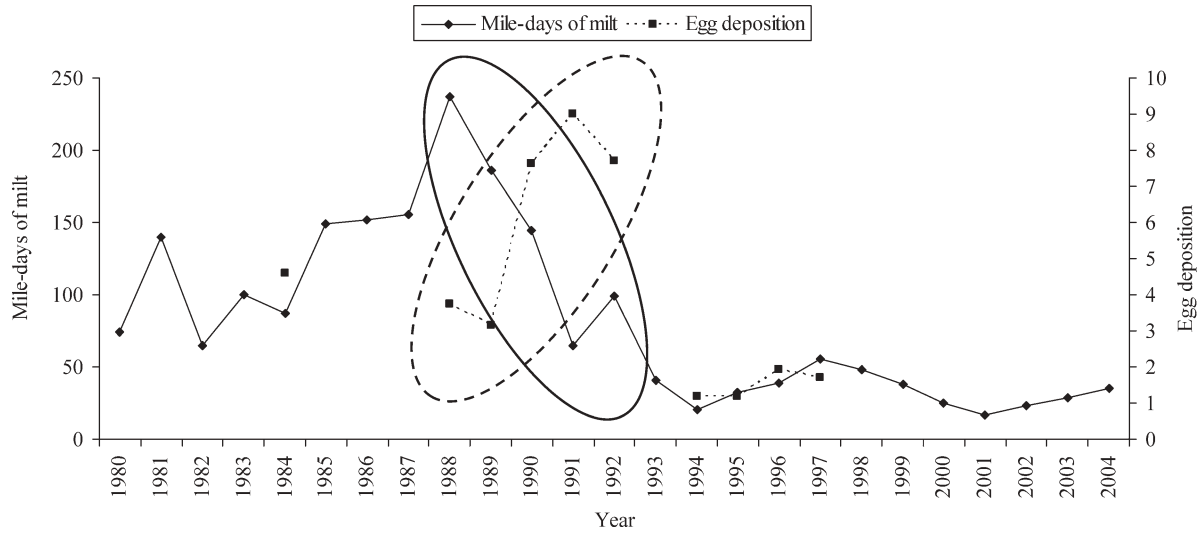
Figure 1. Observed mile-days of milt and egg deposition survey datasets. The ellipses encircle the trends in each dataset from 1988 to 1992 following the same line format as in the observed value plots.

to survival is applied, because the seine, gillnet, and pound utilization fisheries are in spring and the food and bait fishery in autumn. Mortality in the pound fishery is the number of fish impounded $C_{a,t}^{p}$ times the proportion P_k of impounded herring killed. ADF&G sets P_k to 0.75, based on previous studies.

The seine catch-at-age is expressed as total catch C_t^s multiplied by age composition $\Theta_{a,t}^s$, corresponding to data sources. The seine age composition is assumed to be measured with error attributable to sampling variability and age-determination error. Gear selectivity parameters are used to estimate the proportion of fish in the pre-fishery total population matrix that are vulnerable to fishing gear with respect to age. Gear selectivity is assumed to be a logistic function:

$$V_a = \frac{1}{1 + e^{-\omega(a-\xi)}}, \qquad (2)$$

in which ω and ξ are estimated parameters.

Table 1. Hydroacoustic estimates of herring biomass.

Year	Biomass estimate (t)	
	A	**B**
1993	–	18 812
1994	–	12 555
1995	13 284	12 070
1996	23 000	23 203
1997	40 002	37 400
1998	17 655	17 655
1999	20 324	17 301
2000	7 281	7 280
2001	6 384	6 330
2002	10 700	10 700
2003	27 100	23 200
2004	19 098	12 700

Dataset A denotes data obtained by integrating PWS Science Center and ADF&G acoustic surveys, and B are estimates from Thorne and Thomas (2008).

Table 2. Notation used in the formulae for the ASA model.

Notation	Description
Observed quantities	
$C_{a,t}^{i}$	Catch in the ith fishery at age a in year t
P_k	Proportion of impounded herring killed
$w_{a,t}$	Weight-at-age in year t
$\Theta_{a,t}^{i}$	Age composition in the ith dataset at age a in year t
$f_{a,t}$	Fecundity at age a in year t
$x_{i,t}$	Disease prevalence variables
H_t	Hydroacoustic survey biomass in year t
E_t	Egg deposition survey in year t (trillions of eggs)
L_t	Mile-days of milt in year t
$\%F_t$	Percentage of females present in the spawning population
Quantities derived from estimated parameters	
$N_{3,t}$	Age 3 recruits in year t
$N_{a,1980}$	Initial abundance for all ages
V_a	Gear vulnerability of age a with parameters ω and ξ
$mat_{a,t}$	Maturity at age a in year t with parameters δ and ϵ
$M_{a,t}$	Mortality with disease parameter β
$S_{a,t}$	Survival of age a in year t
$\hat{\Theta}_{a,t}$	Estimated age composition
$\hat{E}_t$	Estimated egg deposition in year t
$\hat{L}_t$	Estimated mile-days of milt in year t with parameter ψ
$\hat{H}_t$	Estimated hydroacoustic biomass in year t with parameter γ
R_t	Ricker estimates of recruits in year t with parameters α and τ
Population quantities	
$N_{a,t}$	Total abundance at age a in year t in millions of fish
$PB_{a,t}$	Pre-fishery spawning biomass at age a in year t
$SN_{a,t}$	Natural spawning population after spring fisheries at age a in year t
SB_t	Total spawning biomass in year t (after spring fisheries)
B_t	Pre-fishery biomass in year t

After 1993, natural mortality is assumed to be a linear function of disease prevalence variables $\{x_{it}\}$. In Quinn *et al.* (2001) and Marty *et al.* (2003), it was assumed that natural survival $S_{a,t}$ decreases linearly as a function of disease prevalence variables rather than natural mortality. Here, disease with respect to natural mortality is used because this convention allows more enhanced fit to the data (results not shown), and parameter estimation becomes more stable by avoiding negative survival values. Expressed mathematically,

$$M_{a,t} = M_0 + \sum_i \beta_i x_{it}, \tag{3}$$

in which M_0 is background natural mortality attributable to other natural phenomena (predation in particular), and β_i is a disease coefficient that scales the disease index to a mortality value. A separate natural mortality parameter is estimated for the last half-year in 1992 and the whole year in 1993 for age groups 3–4 and 5–8, to accommodate the population crash. Before that year, natural mortality is initially set to 0.25 (Quinn *et al.*, 2001), because it cannot be estimated accurately because of the sparseness of information (but see later for alternative scenarios). In all years, natural mortality for the plus age class (ages 9 and older) is estimated using a multiplier on natural mortality at earlier ages. The half-year survival used in Equation (1) is then

$$S_{a,t}^{1/2} = e^{-M_{a,t}/2}. \tag{4}$$

Maturity parameters are used to transform the pre-fishery total abundance matrix into both pre- and post-fishery spawning population matrices. Maturity of PWS herring is not measured through sampling, but is estimated from spawning age composition. Maturity for ages 3 and 4 is estimated directly, and analysis of residuals suggested that maturity changed before and after 1997, so different parameters were estimated for the two periods. Maturity for ages 5 and older is set to 1, which implies that all these herring are present on the spawning grounds.

For a given age class and year, pre-fishery spawning biomass is

$$PB_{a,t} = w_{a,t}\,\text{mat}_{a,t}N_{a,t}, \tag{5}$$

such that $w_{a,t}$ is the observed weight-at-age in year t and $\text{mat}_{a,t}$ is the maturity at age a in year t. The abundance of the natural spawning population after the spring fisheries is

$$SN_{a,t} = \text{mat}_{a,t}(N_{a,t} - (\Theta_{a,t}^s C_{a,t}^s + C_{a,t}^g + P_k C_{a,t}^p)). \tag{6}$$

The corresponding spawning biomass in a given year is

$$SB_t = \sum_a w_{a,t} SN_{a,t}. \tag{7}$$

Other model quantities, seine age composition ($\hat{\Theta}_{a,t}^s$), spawning age composition ($\hat{\Theta}_{a\,,t}^{SP}$), mile-days of milt ($\hat{L}_t$), egg deposition ($\hat{E}_t$), hydroacoustic biomass ($\hat{H}_t$), and the Ricker spawner–recruit relationship, are all derived from the pre-fishery total abundance ($N_{a,t}$), post-fishery spawning abundance ($SN_{a,t}$), and post-fishery spawning biomass calculations (SB_t). Seine age composition is the proportion of seine catch with respect to age, related to gear selectivity and abundance by

$$\hat{\Theta}_{a,t}^s = \frac{V_a N_{a,t}}{\sum_a V_a N_{a,t}}. \tag{8}$$

In the ASA model, spawning age composition, the proportion of the population that has reached sexual maturity and is available on the spawning grounds, is the ratio of spawning abundance-at-age to total spawning abundance after the spring fisheries from Equation (6). It is computed as

$$\hat{\Theta}_{a,t}^{SP} = \frac{SN_{a,t}}{\sum_a SN_{a,t}}. \tag{9}$$

The mile-days of milt variable is assumed to be proportional to male spawning biomass and is obtained by

$$\hat{L}_t = \frac{(1 - \%F_t)SB_t}{\psi}, \tag{10}$$

in which $1 - \%F_t$ is the percentage of male spawners and ψ the milt calibration coefficient. Egg deposition is female spawning abundance multiplied by fecundity-at-age $f_{a,t}$, or

$$\hat{E}_t = \%F_t \sum_a f_{a,t} SN_{a,t}, \tag{11}$$

for which fecundity data are available in all years in which the egg deposition survey was conducted. When modelling the hydroacoustic data, biomass from the hydroacoustic survey in the spring is assumed to be an index of the total estimated pre-fishery biomass. The estimated hydroacoustic biomass values from the model are then

$$\hat{H}_t = B_t e^\gamma, \tag{12}$$

in which γ is the estimate of the logarithm of the hydroacoustic survey calibration coefficient, and B_t is the pre-fishery estimated biomass:

$$B_t = \sum_a N_{a,t} w_{a,t}. \tag{13}$$

If the log calibration coefficient γ is equal to 0, then the hydroacoustic survey provides an absolute estimate of abundance ($e^0 = 1$). If the log calibration coefficient is <0, then the hydroacoustic survey provides a relative index of abundance (less than pre-fishery abundance). A Ricker spawner–recruit relationship is introduced into the model to stabilize recruitment parameters. This relationship models the recruitment $\{R_t = N_{3,t+3}\}$ in year $t + 3$ as a dome-shaped function of spawning biomass in year t, or

$$\hat{R}_t = \alpha e^{-\tau SB_t + \varepsilon_t}, \tag{14}$$

with lognormal process error ε allowed, and estimated parameters for productivity (α) and density-dependence (τ).

Objective function

The least squares setting of the age-structured model follows from consideration of the statistical distributions of the various datasets: seine age composition, spawning age composition, mile-days of milt, egg deposition, and hydroacoustic biomass. Each dataset is assumed to follow a normal distribution, sometimes after transformation, to satisfy the requirements of a normal likelihood function that obtains the maximum likelihood parameter estimates.

The age composition datasets (seine and spawning) are considered to follow a multinomial distribution. The residuals for these datasets are not transformed, and the residual sum of squares for seine age composition (RSS_S) and spawning age composition (RSS_{SP}) is

$$RSS_i = \sum_t \sum_a (\Theta^i_{a,t} - \hat{\Theta}^i_{a,t})^2, \qquad (15)$$

such that the subscript and superscript i represents either the seine (S) or spawning (SP) age composition and the observed proportion ($\Theta^i_{a,t}$) is compared with the estimated proportion ($\hat{\Theta}^i_{a,t}$).

The mile-days of milt (L_t), egg deposition (E_t), hydroacoustic biomass (H_t), and recruitment parameters (R_t) are modelled with a log-normal statistical distribution. Thus, the residual sum of squares compares the logarithms of the observed and estimated values. The residual sum of squares for the mile-days of milt (RSS_L), egg deposition (RSS_E), hydroacoustic biomass (RSS_H), and Ricker estimated recruits (RSS_R) is obtained from

$$RSS_i = \sum_t (\ln O_t - \ln P_t)^2, \qquad (16)$$

in which O is the observation and P the estimate in year t. Consequently, the introduction of a residual sum of squares term between the model's estimates of recruitment and the estimated Ricker curve on a log scale prevents recruitment estimates from going to zero or negative values.

The objective function to be minimized is the total weighted sum of squares, representing the negative log-likelihood of the modelled datasets. This is computed as

$$RSS_{tot} = \sum_i \lambda_i RSS_i, \qquad (17)$$

in which λ_i is a weighting term for each dataset. The weighting term influences the model's fit to the dataset, with a lower weight translating to less influence by the dataset on the parameter estimates. The initial weighting used was $\lambda_S = 1$, $\lambda_{SP} = 1$, $\lambda_L = 0.5$, $\lambda_E = 0.5$ (S, seine age composition; SP, spawning age composition; L, mile-days of milt; E, egg deposition). These weightings were chosen to prevent unwelcome patterns in residuals among the various datasets, as was done similarly by Quinn *et al.* (2001, except that $\lambda_E = 1$) and Marty *et al.* (2003, except that $\lambda_{SP} = 10$, $\lambda_E = 1$). This weighting reflects our perception that age composition data are estimated with greater precision than indices of abundance. The weighting $\lambda_S = 0.25$, $\lambda_{SP} = 1$, $\lambda_L = 2$, $\lambda_E = 0.25$ is currently employed by ADF&G in stock assessment. This weighting reflects the perception of ADF&G personnel that fishery age composition and egg deposition have not been collected in several years and may have low precision. The contribution of each dataset to the objective function increases as the number of years (and data points) increases. None of these models had a Ricker spawner–recruit relationship,

and the weight λ_R was chosen to be 0.03 so recruitment estimates did not converge to 0 and sufficient stochasticity was obtained to account for environmental anomalies.

Model scenarios

Here, a sensitivity analysis with several ASA modeling scenarios was performed to evaluate data conflicts. The purpose of the analysis in the ASA model was to examine the sensitivity of the model's parameter and uncertainty estimates, in particular estimates of natural mortality from 1988 to 1992, to datasets and weighting. ASA model estimates that were evaluated in this study include recruitment, spawning biomass, maturity-at-ages 3 and 4, disease index coefficients, fishery exploitation rates, and natural survival. To aid presentation of results, natural mortality parameters estimated from 1988 to 1992 were converted to annual natural survival [Equation (4)]. Additional linear regression model scenarios were evaluated to compare the results from linear regression and ASA model estimation. The model scenarios considered in this study are described in Table 3. The 71 parameterization and weighting scenarios investigated by the ASA model that were bootstrapped are described in detail below.

In the ASA model scenarios, we examined the influence of the hydroacoustic, mile-days of milt, and egg deposition indices on parameter estimates and uncertainty. The base model scenario, M0, started with the initial ASA dataset weighting. The hydroacoustic datasets were added to the ASA model and sensitivity analysis was performed by ranging the weights on these datasets (λ_H) from 0 to 10. Weights were selected in subsequent model scenarios M1–M4 for the hydroacoustic indices to represent both low precision, comparable with age-structured data ($\lambda_H = 0.5$), and high precision ($\lambda_H = 2$).

In model scenarios M1–M4, alternative parameterizations of natural mortality from 1988 to 1992 were investigated. Indices of male spawning (mile-days of milt and miles of milt), the hindcast estimation, and egg deposition indicate a decline in the population

Table 3. ASA model scenarios with bootstrap uncertainty.

Scenario	Description	Index weighting	Parameters	Weightings
M0	Hydroacoustic survey data added to model used in Quinn *et al.* (2001) and Marty *et al.* (2003), with mortality modelled as a linear function of disease prevalence	Hydroacoustic 0–10	42	7
M1	Natural mortality from 1988 to 1992 assumed constant at 0.25	Mile-days of milt, egg deposition 0.1–2	42	16
M2	Natural mortality from 1988 to 1992 estimated	Mile-days of milt, egg deposition 0.1–2	43	16
M3	Natural mortality for ages 3–4 and 5–8 from 1988 to 1992 estimated	Mile-days of milt, egg deposition 0.1–2	44	16
M4	Natural mortality estimated for each year from 1988 to 1992	Mile-days of milt, egg deposition 0.1–2	47	16

from 1988 to 1989. In 1989, the ASA model estimates abundance just before the spawning event, as does the hindcast extrapolation, because the datasets available (no seine catch data in 1989) were collected during and after spawning. The 1989 oil spill happened before Pacific herring spawned in PWS, so any immediate mortality caused directly by the oil spill while herring were schooling in the sound before spawning would be reflected in the ASA model's estimate natural mortality for 1988. For each of these scenarios, alternative objective function weights on the two spawning population indices available from 1988 to 1992 were evaluated. Weights of 0.1, 0.5, 1, and 2 on the mile-days of milt (λ_L) and on egg deposition values (λ_E) allow for adequate model evaluation, resulting in 16 weighting sub-scenarios. The parameterization of natural mortality in the model scenarios was as follows:

- M1: natural mortality from 1980 to 1992 is assumed constant and set at 0.25.

- M2: natural mortality is assumed constant from 1988 to 1992 and estimated.

- M3: natural mortality is estimated separately for age groups 3–4 and 5–8 from 1988 to 1992.

- M4: natural mortality is estimated annually from 1988 to 1992.

A bootstrap procedure (Quinn *et al.*, 2001) was used to obtain standard errors for estimated parameters in all ASA model scenarios. Bootstrap replicates for age composition data (seine, spawning) are generated from the multinomial distribution. For population indices (egg production, mile-days of milt, hydroacoustic data), residuals (on a logarithmic scale) are resampled with replacement and added to estimate values from the original model. The number of replications is 1000, the recommended level for calculating confidence intervals (CIs) (Efron and Tibshirani, 1993). All ASA model optimization was performed in AD Model Builder (ADMB; Fournier, 1996). The bootstrapping of model scenarios was conducted by customized Visual Basic code that integrated data generation in Microsoft Excel to optimization in ADMB.

The most parsimonious ASA model was chosen based on AICc (Akaike Information Criterion, corrected) comparisons outlined in Burnham and Anderson (1998). AICc values can only be compared for models with the same datasets and weighting scenario. To calculate AICc, the likelihood must be calculated first from the equation

$$\ln L = \sum_i -\frac{1}{2}\left[n_i \ln(2\pi\sigma_i^2) + \frac{\text{RSS}_i}{\sigma_i^2}\right] \quad (18)$$

[Quinn and Deriso, 1999, p. 170, Equation (4.55)], in which σ_i^2 is the unexplained variance and n_i is sample size. Each weighting term λ_i is the variance of the first dataset (seine age composition) relative to the variance of the ith dataset, or $\lambda_i = \sigma_1^2/\sigma_i^2$. The maximum log likelihood is

$$\max \ln L = \sum_i -\frac{n_i}{2}\left[\ln\left(\frac{2\pi\hat{\sigma}_1^2}{\lambda_i}\right) + 1\right], \text{ in which}$$

$$\hat{\sigma}_1^2 = \frac{\sum \lambda_i \text{RSS}_i}{\sum n_i}, \text{ and } \hat{\sigma}_i^2 = \frac{\hat{\sigma}_1^2}{\lambda_i}. \quad (19)$$

Therefore, the maximum likelihood corresponds to the minimum weighted residual sum of squares. The AIC and its

corrected version for small sample sizes (AICc) are then obtained from

$$\text{AIC} = -2\ln L + 2p$$
$$\text{AICc} = \text{AIC} + 2p(p+1)/(n-p-1), \quad (20)$$

where p is the number of estimated parameters, and n the combined sample size. When comparing between models, the most parsimonious model is the one with the lowest AICc value. Differences in AICc < 4 are considered statistically insignificant.

The linear regression model scenarios were evaluated to investigate the hindcast estimation procedure performed by Thomas and Thorne (2003, 2008). Each model is applied to the mile-days of milt index, and we first use the integrated acoustic dataset [scenario L(A)]. Then we repeat the linear regression procedure with the hydroacoustic survey dataset from Thorne and Thomas [2008, scenario L(B)]. Hindcast estimates of biomass and exploitation rates were explicitly evaluated in these scenarios.

A simulation study was performed to investigate the impact of commercial fishery openings in 1997 and 1998 on the PWS herring population. It has been argued that the opening in 1998 induced significant fishing mortality on the population inducing an exploitation rate of ~33% (Thomas and Thorne, 2003). On the other hand, high VHSV prevalence during this period could also have caused larger natural mortality (Quinn *et al.*, 2001). We examine the impact of the fishery by removing the catch data from the ASA model and projecting the population based on no fishing mortality in 1997 and 1998.

Results

In the initial ASA model scenario M0, the estimates of spawning biomass from 1980 to 2004 and the parameter estimates of recruitment, survival, and maturity-at-age were much less sensitive to small weights ($\lambda_H < 1$) than to large weights on the hydroacoustic survey indices. The pattern of age 3 recruitment appears cyclic, with a period of 4–5 years throughout the time-series, and an apparent decrease in large recruitment events after 1993 (Figure 2, series to the left). Before 1992, recruitment estimates were not sensitive to λ_H. However, after 1992, recruitment estimates increased as λ_H increased. Overall, λ_H had little effect on total spawning biomass estimates in scenario M0 (Figure 2, series to the right). Regardless of λ_H, the estimated spawning biomass stayed within the 95% CIs estimated for λ_H of 0.5 (Figure 2). The estimated survival for age group 3–4 was not very sensitive to λ_H during the period for which disease information was available (1993–2004; Figure 3a, series to the left). In contrast, estimated survival for age group 5–8 was sensitive to λ_H, and increased substantially as λ_H was increased for all years (Figure 3a, series to the right). The estimated coefficient for the VHSV index did not change much as a consequence of λ_H, and was fairly precise (Figure 3b, series to the left). However, the coefficient for the *I. hoferi* index was sensitive to λ_H with increasing values and uncertainty as λ_H was increased (Figure 3b, series to the right). Further, the hydroacoustic datasets (A or B) had little effect on the disease coefficient estimates. Maturities for ages 3 and 4 shifted in 1997 from lower to higher values at small λ_H and, as λ_H increased, the shift in maturity disappeared and the maturity values decreased (Table 4). The estimated uncertainty in the maturity estimates also increased as λ_H increased, although more appreciably for age 4 than for age 3 (Table 4). The estimated coefficient for the hydroacoustic index,
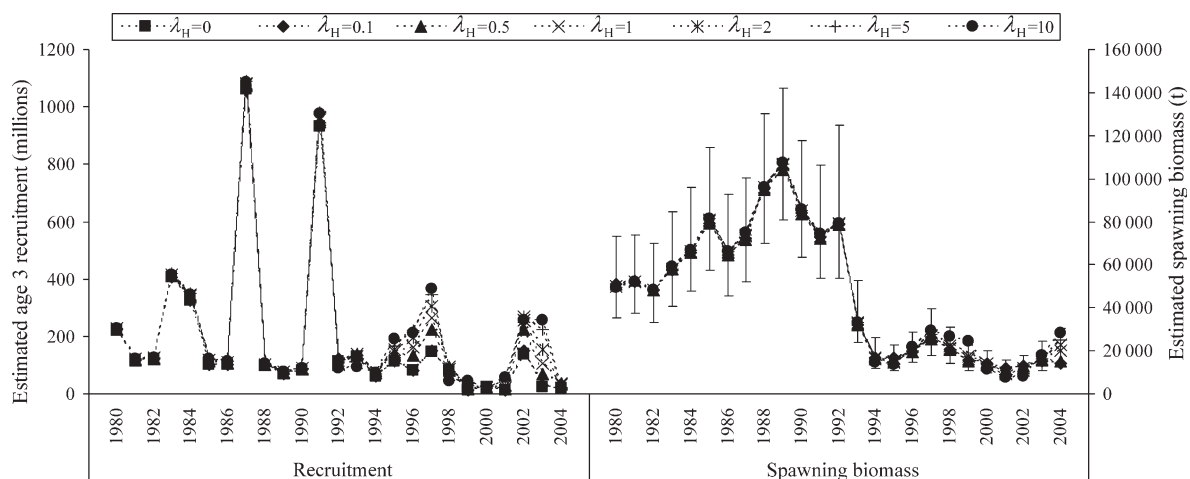
Figure 2. Age 3 recruitment (in millions of fish, plotted on the left) and spawning biomass (t, plotted on the right) estimated from model scenario M0 at hydroacoustic index weights λ_H = 0, 0.1, 0.5, 1, 2, 5, 10 (denoted λ_H = 0.1, for example). For illustration, 95% CIs from the bootstrap with a hydroacoustic weight of 0.5 are shown.
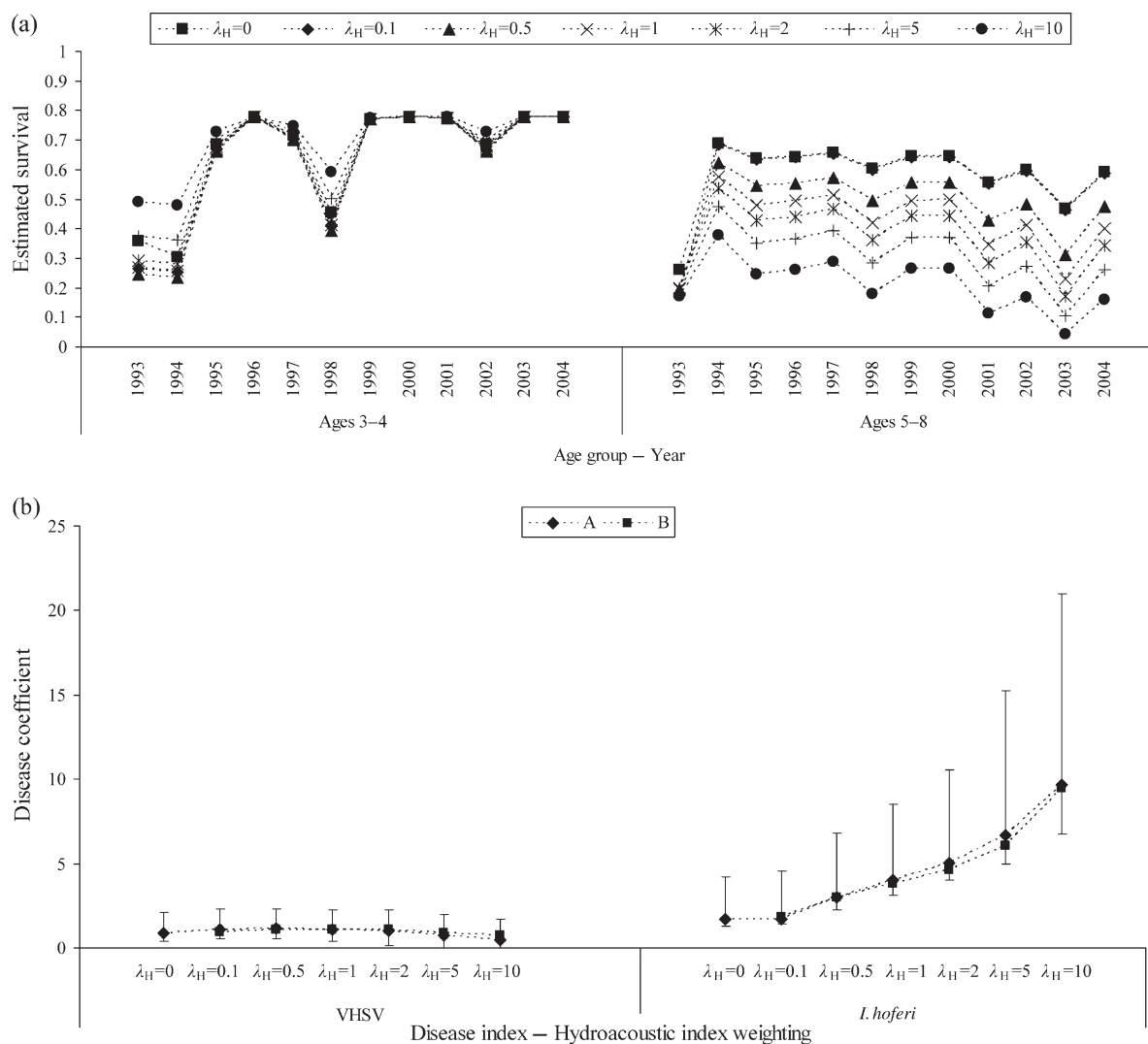
Figure 3. (a) Estimated survival for age groups 3–4 (plotted on the left) and 5–8 (plotted on the right), 1993–2004. (b) Estimated disease index coefficients with 95% CIs from the bootstrap. The VHSV index coefficient is plotted to the left and *I. hoferi* to the right with PWSSC and ADF&G integrated hydroacoustic dataset (A) and data from Thorne and Thomas (2008; B).

Table 4. Maturity estimates at ages 3 and 4, with uncertainty from M0 at different weights given to the hydroacoustic index.

| λ_H	Maturity			
	1980–1996	s.e.	1997–2004	s.e.
Age 3				
0	0.246	0.057	0.684	0.134
0.1	0.259	0.061	0.626	0.125
0.5	0.252	0.055	0.464	0.114
1	0.262	0.062	0.406	0.119
2	0.266	0.069	0.349	0.109
5	0.272	0.076	0.300	0.112
10	0.292	0.092	0.307	0.119
Age 4				
0	0.815	0.123	1.000	0.128
0.5	0.833	0.123	0.749	0.153
1	0.847	0.128	0.660	0.159
2	0.851	0.130	0.592	0.170
5	0.852	0.133	0.538	0.181
10	0.860	0.140	0.529	0.214

or the proportion of the total abundance detected by the acoustic survey, was greatest (0.85) at the smallest hydroacoustic index weight with the integrated acoustic dataset ($\lambda_H = 0.1$; Figure 4). The estimated coefficient decreased as λ_H increased, with the largest uncertainty at a weight of 10. Further, the estimated coefficient for the hydroacoustic index was smaller with dataset B (Thorne and Thomas, 2008) than with integrated dataset A (Figure 4).

Increased λ_H degraded the model fit to the age composition and egg deposition datasets in model scenario M0, whereas model fit to the miles-days of milt datasets improved. Unsurprisingly, the unweighted residual sum of squares for both hydroacoustic datasets in scenario M0 decreased as λ_H was increased (Figure 5), because the greater weight made the non-linear procedure fit the hydroacoustic data better. In contrast, there was a nearly exponential degradation in fit to spawning

age composition (increasing residual sum of squares) as λ_H increased on both acoustic datasets (Figure 5). At the same time, there was linear degradation in the fits to the seine age composition and egg survey, with the former being far more sensitive to λ_H (Figure 5). For both acoustic datasets as λ_H increased initially, the fit to mile-days of milt improved (decreasing residual sum of squares), then deteriorated as λ_H was increased to large weights (Figure 5). The initial decrease in the mile-days of milt unweighted residual sum of squares indicated a strong correlation with the hydroacoustic survey indices. Because of this correlation, the addition of the hydroacoustic data essentially doubled the contribution of the mile-days of milt, the fit to one being improved by an increase in weight on the other.

Estimated recruitment and spawning biomass among scenarios M1–M4 resulted in large ranges of possible values for some years (Figure 6a). The range between the minimum and the maximum estimated recruitment among scenarios M1–M4 was generally not large except for the years in which large abundances were estimated (1987, 1991; Figure 6a, series to the left). On the other hand, the ranges between minimum and maximum values of spawning biomass were fairly substantial from the late 1980s to the early 1990s (Figure 6a, series to the right). From 1988 to 1992, the pattern in the maximum estimated biomass was not similar to that of the minimum estimates, and from 1990 to 1991 the minimum biomass values decreased, while the maximum values increased (Figure 6a). Using model scenario M1 as an example, from 1988 to 1990 the maximum values were obtained from model scenarios that weighted the mile-days of milt higher than the egg deposition index (Figure 6b, series to the left). Conversely, from 1991 to 1993 the maximum values were obtained from models that weighted the egg deposition higher than the mile-days of milt (Figure 6b, series to the right). Moreover, the spawning biomass estimates were not sensitive to the hydroacoustic dataset (A or B) or to the weight in the objective function (Figure 6b).

There was a strong relationship in model scenarios M1–M4 between the maturity estimates for ages 3 and 4, and index weight (Table 5). From 1980 to 1997, increased weight on the mile-days of milt index decreased the estimated maturity,
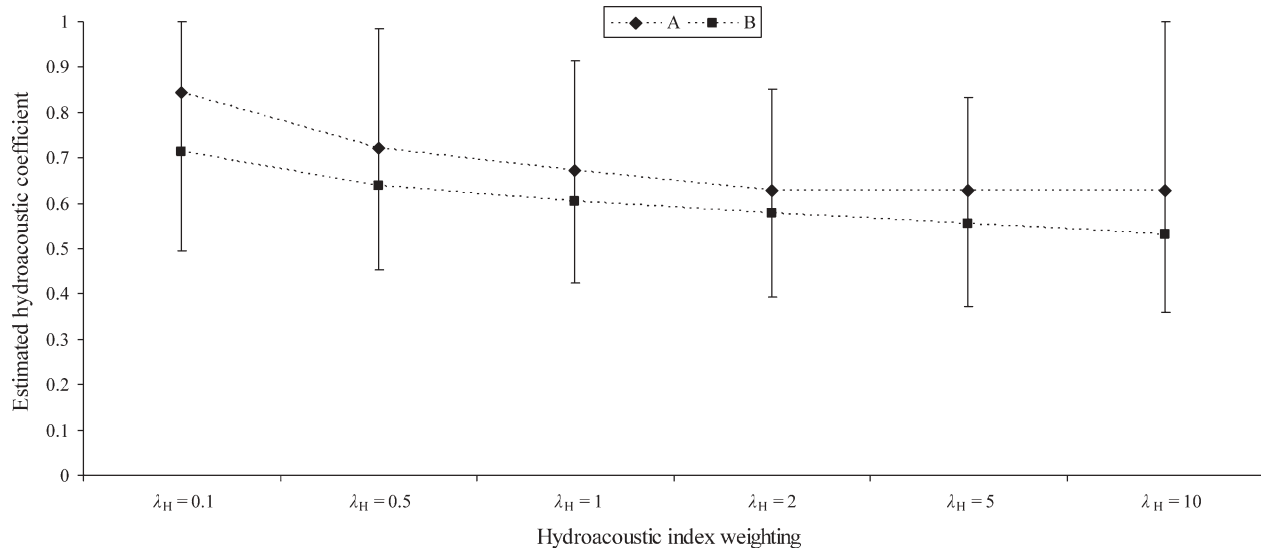
Figure 4. Estimated hydroacoustic survey coefficients from PWSSC and ADF&G integrated hydroacoustic dataset (A) and data from Thorne and Thomas (2008; B). 95% CIs from a bootstrap are shown for the ASA model with hydroacoustic dataset A.
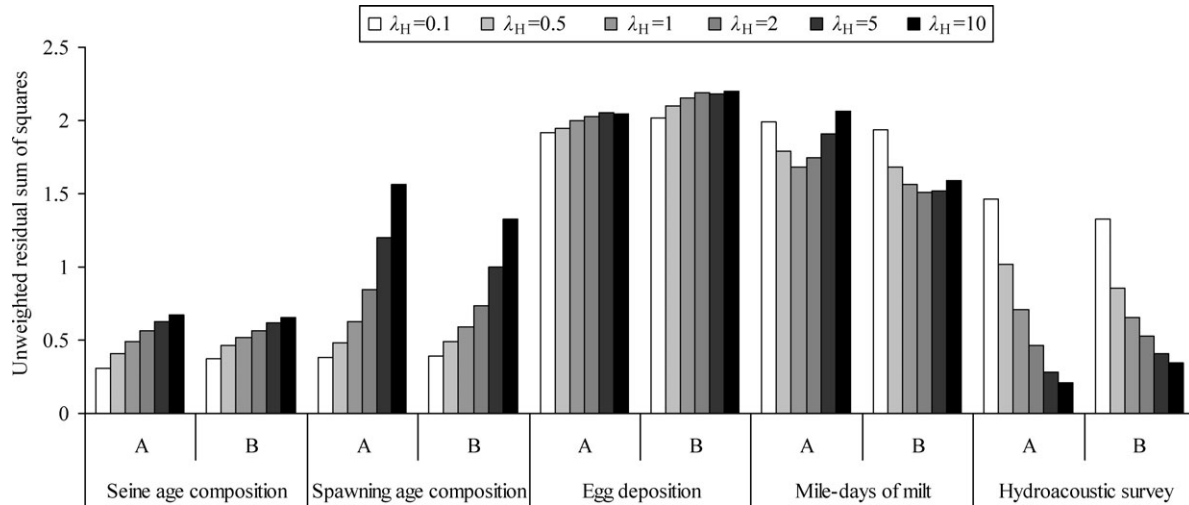
Figure 5. Unweighted residual sum of squares for the estimated datasets in the ASA model as the weights (λ_H) on the hydroacoustic indices (A, integrated PWSSC and ADF&G; B, Thorne and Thomas, 2008) are increased in scenario M0.

whereas increased weight on the egg deposition index increased the estimated maturity for both ages 3 and 4 (Table 5). In contrast, from 1998 to 2004, increased mile-days of milt weight increased maturity, and increased egg deposition weight decreased maturity

for both ages. Furthermore, uncertainty in estimated maturity also increased as a function of weight on either index (Table 5).

The estimated hydroacoustic calibration coefficient in scenarios M1−M4 was not very sensitive to the weight given to the mile-days
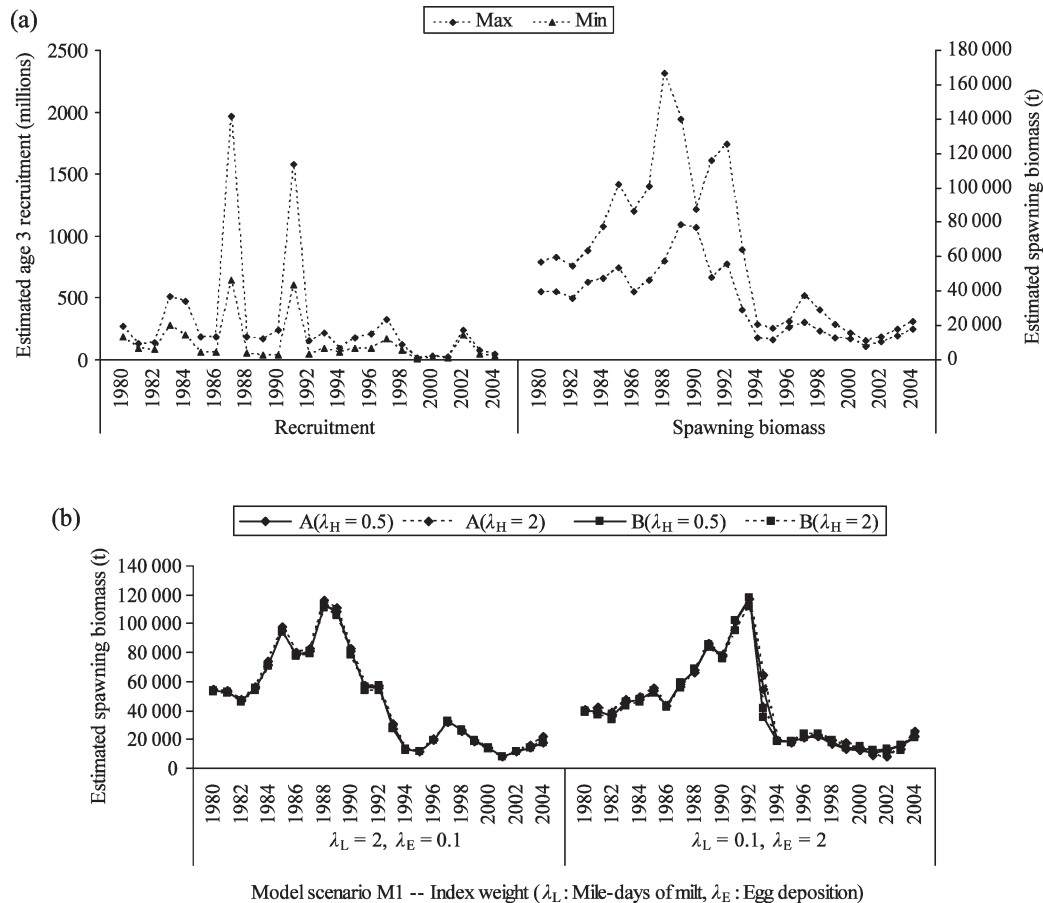
Figure 6. (a) Maximum and minimum estimated recruitment (plotted to the left) and spawning biomass (plotted to the right) from model scenarios M1−M4. (b) Estimated spawning biomass from model scenario M1 for hydroacoustic datasets (A, integrated PWSSC and ADF&G; B, Thorne and Thomas, 2008) at weight of 0.5 and 2 in the objective function.

Table 5. Maturity estimates at ages 3 and 4, with standard errors from scenarios M1–M4 at different weights given to the mile-days of milt index (λ_L) and egg deposition index (λ_E).

Scenario	λ_L	λ_E	Maturity at age 3				Maturity at age 4			
			1980–1997	s.e.	1998–2004	s.e.	1980–1997	s.e.	1998–2004	s.e.
M1	0.1	0.1	0.246	0.034	0.452	0.090	0.866	0.086	0.790	0.128
		0.5	0.259	0.056	0.397	0.088	0.773	0.123	0.722	0.132
		1	0.301	0.087	0.355	0.095	0.736	0.152	0.672	0.133
		2	0.377	0.132	0.305	0.100	0.735	0.177	0.605	0.149
	0.5	0.1	0.226	0.042	0.524	0.120	0.866	0.104	0.783	0.148
		0.5	0.252	0.055	0.464	0.114	0.833	0.123	0.749	0.153
		1	0.286	0.083	0.411	0.131	0.805	0.145	0.717	0.167
		2	0.353	0.139	0.343	0.126	0.784	0.181	0.658	0.179
	1	0.1	0.214	0.050	0.576	0.128	0.914	0.096	0.759	0.158
		0.5	0.243	0.060	0.520	0.138	0.891	0.110	0.734	0.166
		1	0.271	0.085	0.464	0.143	0.862	0.135	0.709	0.179
		2	0.324	0.136	0.383	0.156	0.830	0.168	0.672	0.199
	2	0.1	0.193	0.055	0.644	0.136	0.984	0.074	0.747	0.148
		0.5	0.220	0.064	0.608	0.141	0.975	0.083	0.729	0.157
		1	0.248	0.079	0.567	0.153	0.953	0.098	0.710	0.166
		2	0.291	0.117	0.497	0.167	0.914	0.133	0.686	0.196
M2	0.1	0.1	0.238	0.039	0.446	0.088	0.853	0.093	0.784	0.126
		0.5	0.328	0.058	0.453	0.089	0.898	0.101	0.768	0.140
		1	0.365	0.076	0.427	0.096	0.872	0.122	0.735	0.140
		2	0.434	0.116	0.389	0.097	0.859	0.148	0.686	0.141
	0.5	0.1	0.183	0.034	0.496	0.107	0.795	0.099	0.766	0.143
		0.5	0.260	0.062	0.471	0.123	0.846	0.124	0.752	0.159
		1	0.331	0.093	0.460	0.131	0.890	0.136	0.744	0.176
		2	0.422	0.125	0.442	0.142	0.925	0.145	0.727	0.184
	1	0.1	0.168	0.036	0.528	0.110	0.822	0.100	0.735	0.138
		0.5	0.225	0.057	0.501	0.133	0.858	0.119	0.725	0.160
		1	0.288	0.090	0.485	0.148	0.895	0.132	0.718	0.181
		2	0.386	0.139	0.479	0.160	0.952	0.146	0.714	0.208
	2	0.1	0.148	0.035	0.581	0.114	0.853	0.095	0.711	0.133
		0.5	0.191	0.050	0.563	0.124	0.888	0.106	0.706	0.141
		1	0.236	0.078	0.550	0.152	0.922	0.115	0.704	0.166
		2	0.321	0.132	0.548	0.182	0.987	0.130	0.701	0.197
M3	0.1	0.1	0.260	0.044	0.448	0.088	0.874	0.094	0.786	0.123
		0.5	0.328	0.057	0.453	0.093	0.896	0.102	0.768	0.136
		1	0.365	0.076	0.427	0.094	0.872	0.119	0.735	0.140
		2	0.434	0.114	0.389	0.100	0.859	0.147	0.686	0.144
	0.5	0.1	0.189	0.038	0.496	0.111	0.804	0.103	0.770	0.136
		0.5	0.258	0.063	0.471	0.117	0.844	0.123	0.751	0.154
		1	0.322	0.088	0.459	0.142	0.874	0.129	0.740	0.174
		2	0.418	0.124	0.439	0.141	0.915	0.152	0.724	0.189
	1	0.1	0.170	0.040	0.528	0.115	0.826	0.098	0.735	0.138
		0.5	0.220	0.060	0.501	0.127	0.849	0.118	0.723	0.152
		1	0.274	0.086	0.487	0.147	0.871	0.137	0.714	0.176
		2	0.357	0.132	0.478	0.168	0.897	0.161	0.701	0.202
	2	0.1	0.153	0.037	0.582	0.117	0.863	0.096	0.713	0.128
		0.5	0.184	0.051	0.563	0.126	0.875	0.107	0.704	0.147
		1	0.222	0.079	0.552	0.140	0.894	0.120	0.697	0.165
		2	0.287	0.119	0.548	0.177	0.918	0.146	0.687	0.195

Continued

Table 5. *Continued*

Scenario	λ_L	λ_E	Maturity at age 3				Maturity at age 4			
			1980–1997	s.e.	1998–2004	s.e.	1980–1997	s.e.	1998–2004	s.e.
M4	0.1	0.1	0.218	0.037	0.385	0.077	0.823	0.094	0.715	0.117
		0.5	0.272	0.051	0.375	0.084	0.889	0.099	0.694	0.122
		1	0.305	0.066	0.363	0.085	0.920	0.112	0.675	0.124
		2	0.336	0.087	0.338	0.088	0.943	0.118	0.638	0.136
	0.5	0.1	0.158	0.035	0.450	0.101	0.758	0.100	0.743	0.135
		0.5	0.200	0.049	0.425	0.110	0.779	0.124	0.709	0.145
		1	0.233	0.062	0.406	0.121	0.806	0.133	0.684	0.158
		2	0.287	0.087	0.360	0.120	0.875	0.136	0.638	0.175
	1	0.1	0.183	0.037	0.515	0.102	0.786	0.100	0.725	0.134
		0.5	0.166	0.044	0.479	0.122	0.751	0.124	0.717	0.151
		1	0.192	0.061	0.451	0.144	0.773	0.139	0.692	0.174
		2	0.236	0.085	0.399	0.152	0.822	0.155	0.652	0.196
	2	0.1	0.176	0.040	0.568	0.108	0.814	0.099	0.704	0.120
		0.5	0.192	0.048	0.549	0.120	0.815	0.111	0.694	0.138
		1	0.155	0.053	0.518	0.153	0.765	0.131	0.692	0.169
		2	0.174	0.073	0.480	0.169	0.803	0.158	0.669	0.198

of milt or to the egg deposition survey (Figure 7). In scenario M1, the most robust results were obtained for the coefficient. The largest change in the coefficient was at large weights (1, 2) on the mile-days of milt, for which increased egg deposition weight decreased the coefficient (Figure 7). For scenarios M2–M4, increased weight on the mile-days of milt slightly decreased the proportion of the population detected by the acoustic survey, whereas increased weight on the egg deposition slightly increased the hydroacoustic coefficient value (Figure 7). Moreover, the uncertainty in the estimated coefficients in scenarios M1–M4 remained somewhat stable and did not indicate a relationship with index weight (Figure 7). The estimated hydroacoustic coefficient was larger with acoustic dataset A than with dataset B. Further, with a larger weight on the hydroacoustic index, or treating this index as more precise than the age-structured data, indicated that the

proportion of the population detected by the acoustic survey was less for both types of acoustic dataset (Figure 7).

The estimated coefficients for the disease indices describing VHSV and *I. hoferi* prevalence from 1993 to 2004 in model scenarios M1–M4 were sensitive to the index weight (Figure 8a and b). In model scenario M1, the estimated VHSV coefficient decreased as the weight on the mile-days of milt index was increased, but it increased with increased weight on the egg deposition index (Figure 8a). On the other hand, in scenarios M2–M4, as the weight on either index increased, the estimated coefficient decreased. For the most part, the uncertainty in the estimated VHSV coefficient increased as the index weights increased (Figure 8a). The estimated coefficient for *I. hoferi* increased as the weight on the mile-days of milt index increased in model scenarios M1–M4 (Figure 8b). At a weighting of 0.1 on the mile-days
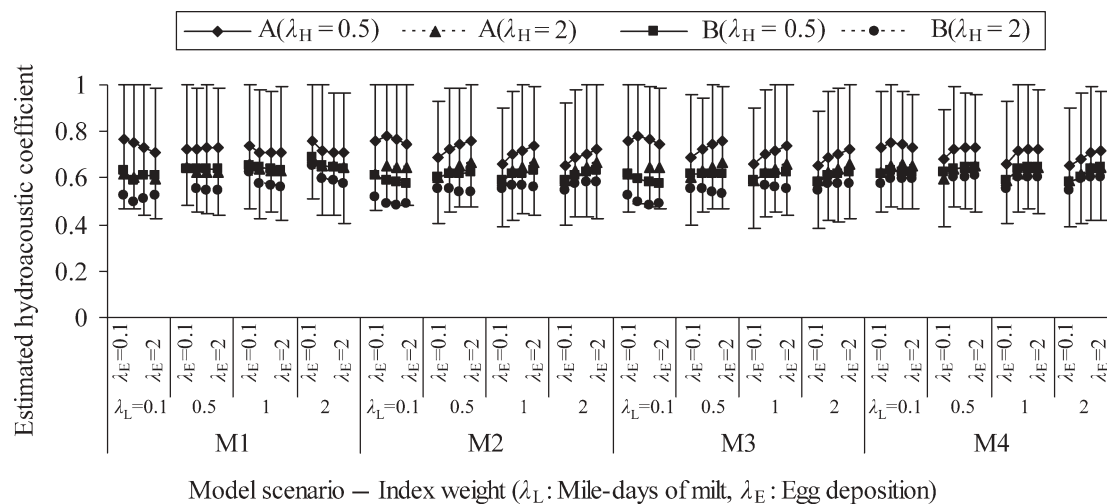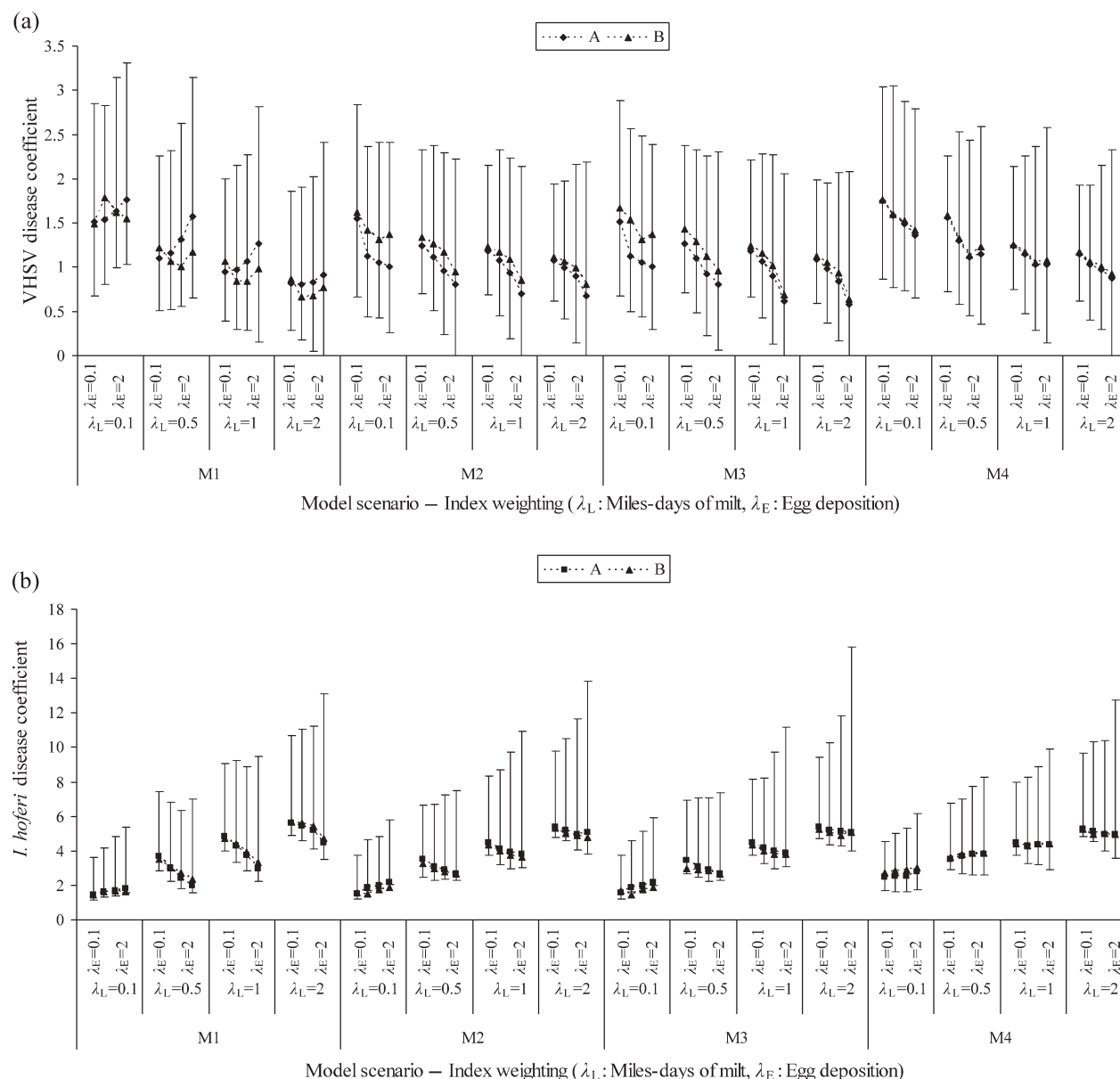

Figure 7. Estimated hydroacoustic survey coefficient for the hydroacoustic datasets (A, integrated PWSSC and ADF&G; B, Thorne and Thomas, 2008) at weights of 0.5 and 2 in the objective function from scenarios M1–M4 with 95% CIs from the bootstrap.

(a)

(b)

Figure 8. (a) Estimated VHSV index coefficient with 95% CIs from the bootstrap for mile-days of milt and egg deposition weights. (b) Estimated *I. hoferi* index coefficient with 95% CIs from bootstrap for mile-days of milt and egg deposition weights investigated for the two hydroacoustic indices. Both (a) and (b) apply to scenarios M1–M4 using the two hydroacoustic indices (A, integrated PWSSC and ADF&G; B, Thorne and Thomas, 2008).

of milt index, the *I. hoferi* coefficient increased with larger egg deposition index weights. However, at all other weights investigated on the mile-days of milt index, an increasing egg deposition index weight resulted in smaller *I. hoferi* coefficients in model scenarios M1–M4 (Figure 8b). Furthermore, estimates for both disease coefficients were not sensitive to hydroacoustic datasets A or B.

Estimated natural survival from 1988 to 1992 in model scenarios M2 and M3 displayed a functional relationship with index weight (Figure 9a and b). In scenarios M2 and M3, estimated survival decreased as a function of increased mile-days of milt weight, but it increased with larger egg deposition index weight (Figure 9a). At a small weight on the mile-days of milt (0.1), estimated survival was virtually 100% for egg deposition weights >0.5.

Parameter estimates in scenario M2 and age group 5–8 in scenario M3 produced fairly precise values for natural survival, but there was great uncertainty for age group 3–4 in scenario M3 (Figure 9a). Further, the hydroacoustic dataset employed (A or B) and the weight on the index had little effect on the estimated natural survival from 1988 to 1992 in scenarios M2 and M3.

In scenario M4, annual parameters from 1988 to 1992 for natural survival were highly uncertain (Figure 9b). Overall, estimated survival was inversely related to the mile-days of milt weight, and proportional to the egg deposition weight (Figure 9b). Survival in 1988 was highly sensitive to index weight and very imprecise. Survival of 100% resulted in 1989 regardless of index weighting, although the lower 95% confidence limit reached 30% for some weights. The same was true in 1991 for
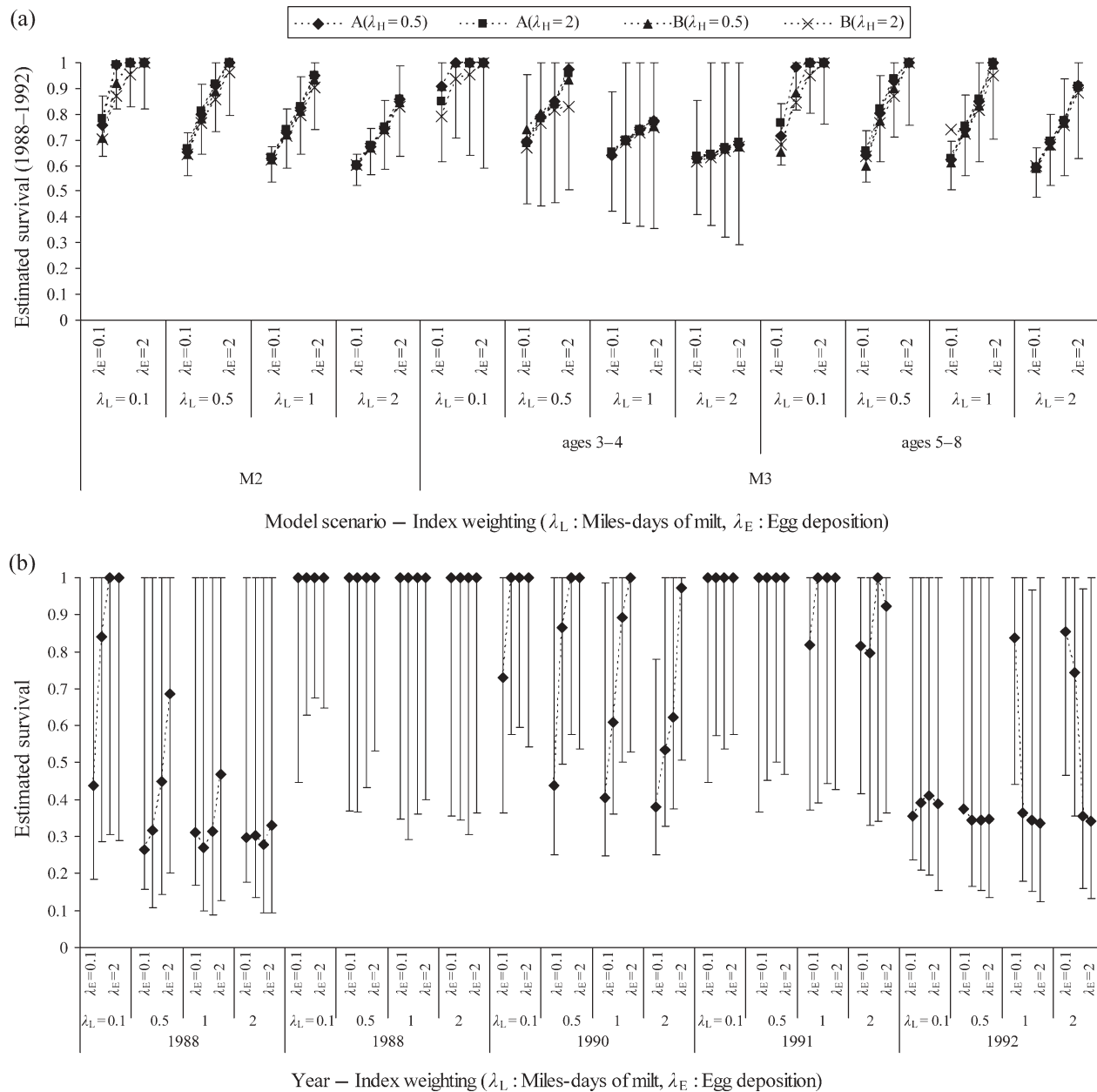
Figure 9. (a) Estimated survival from 1988 to 1992 in model scenarios M2 and M3 with 95% CIs from bootstrap. Results are shown for both hydroacoustic indices (A, integrated PWSSC and ADF&G; B, Thorne and Thomas, 2008) at weights of 0.5 and 2 in the objective function. (b) Estimated annual survival from 1988 to 1992 in model scenario M4, with 95% CIs from the bootstrap.

weights ≤ 0.5 on the mile-days of milt index. Survival decreased slightly in 1991 at larger mile-days of milt weights, but uncertainty was great. On the whole, survival estimates in 1992 were the lowest, and in that year, unlike previous years, increased weight on the egg deposition decreased survival. However, in 1992, the 95% CIs from the bootstrap ranged from 10% to 100% for some weights (Figure 9b). Estimation of natural survival in model scenario M4 allows insight into the possible results, without need for direct estimation of parameters and uncertainty, obtained if natural survival was estimated and set constant from 1989 to 1992, rather than for 1988–1992 in scenarios M2 and M3. Estimated natural survival in 1988 was less than all the annual estimates in scenario M4, except 1992 (Figure 9b). Therefore, constant natural survival estimated in

scenarios M2 and M3 from 1988 to 1992 would increase when estimated from 1989 to 1992 because the maximum likelihood estimate depicts the average natural survival over the time period evaluated. Results were only presented for the hydroacoustic dataset A at a weight of 0.5, because there was no sensitivity to the hydroacoustic dataset type or weight (results not shown).

For the 16 weighting combinations on the mile-days of milt and egg deposition indices, the AICc comparison selected scenario M1 three times, M2 three times, and M4 ten times as the most parsimonious and best fit model (Table 6). For egg deposition weights >0.1 and equal to or greater than mile-days of milt weights, model scenario M4 had the lowest AICc value. The second most parsimonious model for these weightings was M2 when the egg deposition

Table 6. AICc model comparison among scenarios M1–M4 with respect to the mile-days of milt and egg deposition index weights.

	$\lambda_L = 0.1$															
	$\lambda_E = 0.1$				$\lambda_E = 0.5$				$\lambda_E = 1$				$\lambda_E = 2$			
Scenario	M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4
Total SSQ	2.32	2.31	2.31	2.25	2.99	2.80	2.80	2.68	3.62	3.17	3.17	3.03	4.56	3.78	3.78	3.58
n	313	313	313	313	313	313	313	313	313	313	313	313	313	313	313	313
p	42	43	44	47	42	43	44	47	42	43	44	47	42	43	44	47
AICc	−385.352	−382.862	−381.368	−380.648	−321.056	−339.171	−336.527	−342.33	−268.471	−307.874	−305.165	−310.919	−203.426	−259.088	−256.379	−265.247
ΔAICc	*0.00*	**2.49**	3.98	4.70	21.27	**3.16**	5.80	*0.00*	42.45	**3.04**	5.75	*0.00*	61.82	**6.16**	8.87	*0.00*

	$\lambda_L = 0.5$															
	$\lambda_E = 0.1$				$\lambda_E = 0.5$				$\lambda_E = 1$				$\lambda_E = 2$			
Scenario	M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4
Total SSQ	3.04	2.93	2.93	2.85	4.04	4.04	4.04	3.86	4.98	4.84	4.84	4.54	6.33	5.80	5.80	5.44
n	313	313	313	313	313	313	313	313	313	313	313	313	313	313	313	313
p	42	43	44	47	42	43	44	47	42	43	44	47	42	43	44	47
AICc	−340.01	−348.863	−346.266	−346.838	−267.623	−265.205	−262.499	−268.119	−209.287	-215.354	−212.808	−224.61	−140.829	−165.588	−162.906	−174.425
ΔAICc	8.85	*0.00*	2.60	**2.02**	**0.50**	2.91	5.62	*0.00*	15.32	**9.26**	11.80	*0.00*	33.60	**8.84**	11.52	*0.00*

	$\lambda_L = 1$															
	$\lambda_E = 0.1$				$\lambda_E = 0.5$				$\lambda_E = 1$				$\lambda_E = 2$			
Scenario	M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4
Total SSQ	3.54	3.30	3.30	3.20	4.74	4.72	4.72	4.58	5.95	5.93	5.92	5.65	7.77	7.47	7.44	6.99
n	313	313	313	313	313	313	313	313	313	313	313	313	313	313	313	313
p	42	43	44	47	42	43	44	47	42	43	44	47	42	43	44	47
AICc	−309.818	−329.05	−326.361	−328.482	−234.605	−233.491	−230.852	−232.182	−170.702	−169.125	−166.773	−173.389	−94.1429	−103.687	−102.214	−113.537
ΔAICc	19.23	*0.00*	2.69	**0.57**	*0.00*	1.11	3.75	**2.42**	**2.69**	4.26	6.62	*0.00*	19.39	**9.85**	11.32	*0.00*

|	$\lambda_L = 2$															
	$\lambda_E = 0.1$				$\lambda_E = 0.5$				$\lambda_E = 1$				$\lambda_E = 2$			
Scenario	M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4
Total SSQ	4.24	3.77	3.76	3.58	5.62	5.46	5.46	5.32	7.12	7.11	7.10	6.89	9.56	9.47	9.43	9.03
n	313	313	313	313	313	313	313	313	313	313	313	313	313	313	313	313
p	42	43	44	47	42	43	44	47	42	43	44	47	42	43	44	47
AICc	−271.088	−305.501	−302.878	−310.742	−199.138	−205.189	−202.587	−202.653	−131.747	−129.708	−127.405	−128.314	−46.6314	−46.6314	−45.2513	−50.5987
ΔAICc	39.65	**5.24**	7.86	*0.00*	6.05	*0.00*	2.60	**2.54**	*0.00*	**2.04**	4.34	3.43	**3.97**	3.97	5.35	*0.00*

For each weight comparison, the model with the lowest AICc value (ΔAICc = 0) is italicized and the model with the next lowest AICc value is emboldened.

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weight was greater than the mile-days of milt, and M1 when the weights were equal. Moreover, when the weights were equal, scenario M4 was not significantly better than scenario M1 (ΔAICc $<$ 4). AICc comparison between models with mile-days of milt weights greater than the egg deposition selected scenarios M1 and M2 as the best models. At a large weight on the mile-days of milt (2) and a small weight on the egg deposition (0.1), scenario M4 resulted as the best model, and with both index weights set at 0.1, scenario M1 was the best (Table 6).

The linear regression hindcast procedure extrapolated historical biomass estimates that were nearly the same regardless of the acoustic dataset utilized, and they were contained within the minimum and maximum estimates obtained from the ASA model scenarios (Figure 10a). Using the integrated hydroacoustic dataset as the dependent variable resulted in strong linear relationship with the mile-days of milt ($y = 554x$, s.e. $= 56$, $p = 0.006$). Uncertainty in biomass estimates from 1988 to 1992 was much smaller for linear regression scenario L(A) than the results of the ASA model scenarios (Figure 10b). The maximum and minimum range across ASA model scenarios M1–M4, with 95% confidence levels from the bootstrap, contained the hindcast

biomass estimates from the linear models (Figure 10b). However, the uncertainty in biomass extrapolations depicted by the linear models did not reflect the range indicated by the ASA models, and the CIs were biased towards smaller values owing to the assumption that the independent variable was measured without error (Figure 10b).

Exploitation rates in 1990–1992 and 1997–1998 estimated from both ASA and linear regression models ranged from ~10% to 30% for most years (Figure 11). The exploitation rates in 1990 were similar across all linear and ASA models, ranging from 8% to 15%. However, the range of exploitation rates in 1991 and 1992 were much larger. In 1991, both linear regression models [L(A), L(B)] estimated exploitation rates that were larger than the maximum ASA model value. However, all linear model estimates remained within the 95% CIs from the bootstrap for ASA model maximum or minimum estimates. The range of possible exploitation rates in 1992 from the ASA models was very large, from 10% to $>$50%. Linear regression exploitation estimates in 1997 and 1998 were much smaller than the maximum ASA model values, and the range in the linear estimates was narrower than the uncertainty in exploitation indicated by the ASA models (Figure 11).
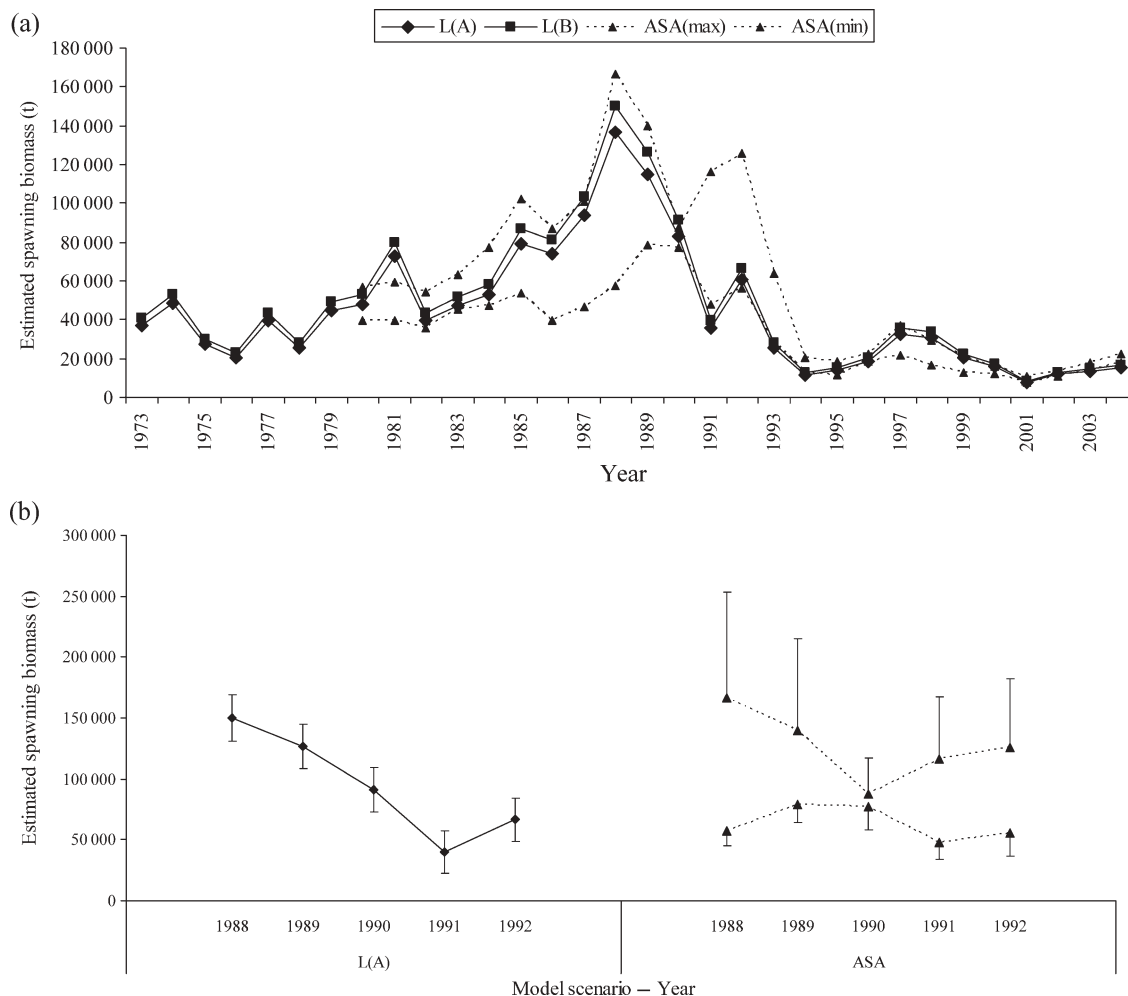
Figure 10. (a) Estimated biomass from 1973 to 2004 using the linear regression hindcast procedure for scenarios L(A) and L(B) using both hydroacoustic datasets (A, integrated PWSSC and ADF&G; B, Thorne and Thomas, 2008) with the maximum and minimum ASA model spawning biomass estimates in model scenarios M1–M4. (b) Estimated biomass with uncertainty from linear regression scenario L(A), with maximum and minimum ASA model estimates from scenarios M1–M4. For illustration, only the upper 95% confidence level from the bootstrap is shown for the maximum ASA model estimate, and the lower CI is shown for the minimum.
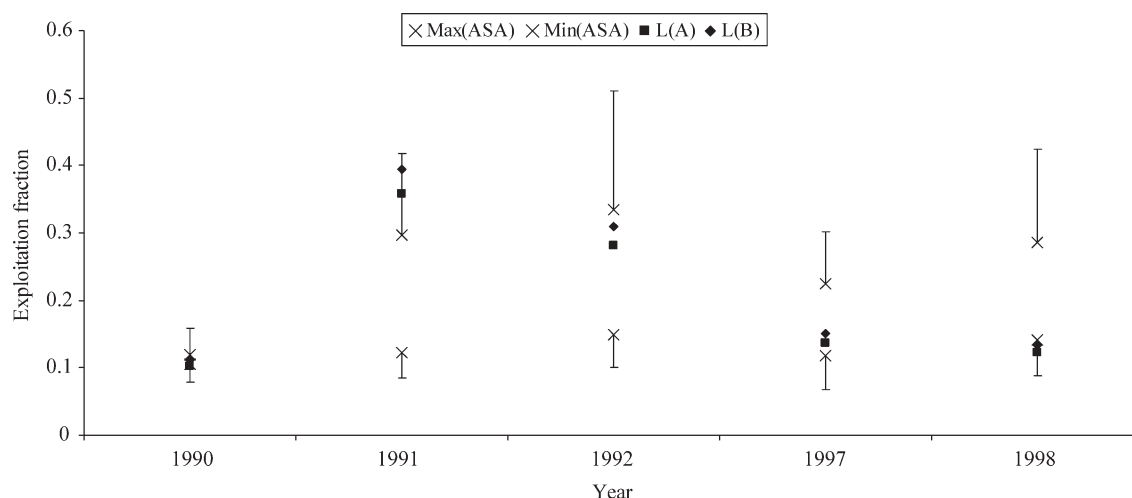
Figure 11. Estimated exploitation fractions from linear regression model scenarios L(A) and L(B), with maximum and minimum estimates from all ASA model scenarios (crosses). To illustrate the range of uncertainty in the ASA models, only the upper 95% CI from the bootstrap is shown for the maximum estimate, and the lower 95% interval is shown for the minimum.

In 1998, the ASA models indicated that uncertainty in the exploitation rate was comparable with that of 1991 and 1992 (Figure 11).

Using the ASA models with the initial weighting scheme for the datasets in model scenario M1 and the weighting scheme used by ADF&G in model scenario M2, we simulated abundances that would have occurred with no catch in 1997 and 1998. Excluding commercial catch in 1997 and 1998 from the ASA model had little consequence on the resulting biomass estimates (Figure 12). For either weighting scheme, the resulting biomass increased slightly, but by 2002 the resulting biomasses were no different from what they would have been if the catch had been taken (Figure 12).

Discussion

The biggest conflict exposed in this study is between the male and female indices of spawning abundance from 1988 to 1992. The data conflict during this period exists because the egg deposition survey indicates an increase in the population, whereas that for

mile-days of milt exhibits a decrease. It has been suggested that the egg deposition values from 1990 to 1992 were anomalous because of the lack of correlation with the mile-days of milt index in those 3 years (Thorne and Thomas, 2008). This is true when the normality of each dataset is not taken into account, but both the mile-days of milt and egg deposition indices fail the correlation coefficient test for normality. Rather, normality is obtained after logarithmic transformation, implying that those datasets follow a lognormal distribution. Upon applying appropriate normalizing transformations to these indices, there is significant correlation using all years for which data are available ($r = 0.63$, $p = 0.02$). Further, as the egg deposition dataset comes from an established statistical survey procedure (Willette *et al.*, 1999), and because there is a lack of information on the relationship between miles of spawn and egg deposition at large population sizes, we did not discount the egg deposition dataset. On including the hydroacoustic survey index into the integrated
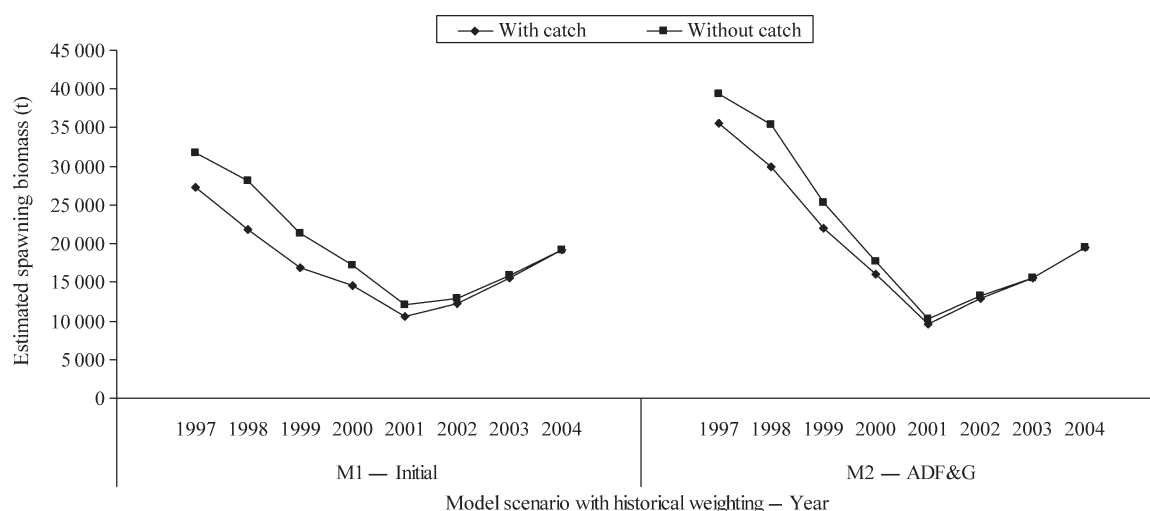
Figure 12. Estimated spawning biomass from model scenario M1, using the initial weighting ($\lambda_S = 1$, $\lambda_{SP} = 1$, $\lambda_L = 0.5$, $\lambda_E = 0.5$), and scenario M2, using the weighting employed by ADF&G ($\lambda_S = 0.25$, $\lambda_{SP} = 1$, $\lambda_L = 2$, $\lambda_E = 0.25$), allowing for catches in 1997 and 1998 to be included (squares) or excluded (diamonds).

ASA model, other conflicts were revealed; the biggest conflict was between the spawning age composition dataset and the hydroacoustic dataset.

In the ASA model for Pacific herring in PWS, parameter estimation is sensitive to the index weights used in the objective function. For the natural mortality and weighting scenarios investigated here, the trends in parameter estimates were not the same when weights on either the mile-days of milt or egg deposition were increased. Among model scenarios, it was generally the case that if the functional relationship between a parameter estimate and weight was directly proportional for one index, it would be inversely proportional to the other. This was especially true when allowing natural mortality to be estimated as a free parameter from 1988 to 1992. Estimation of a single parameter over those years, regardless of age group, showed that increasing the weight on mile-days of milt increased natural mortality, but that doing so for egg deposition decreased natural mortality. This was also true when estimating annual natural mortality in 1988, 1989, 1990, and 1991. In 1992, however, the relationship was opposite.

Most model comparisons among scenarios M1–M4 indicated that allowing natural mortality to be estimated annually from 1988 to 1992 resulted in the lowest AICc. However, determination of parameter uncertainty through the bootstrap procedure revealed great variability in the annual estimates of natural mortality. The AICc was low for scenarios M1 and M2, and in scenario M2, a constant natural mortality for 1988–1992 was estimated with good precision. Overall, taking parameter uncertainty into account, model M2 was the best model for nearly 70% of the weighting scenarios considered. However, the estimate of natural survival in scenario M2 can range from 60% to 100%, depending on which mile-days of milt or egg deposition index weight is used. With the initial weighting scheme, model M1 is the most parsimonious and best fit model when compared with the other scenarios. With the weighting scheme currently employed by ADF&G, the best fit and the most parsimonious model is scenario M2. Moreover, the estimate of natural mortality in that scenario for the weighting scenario most similar to the one used by ADF&G ($\lambda_L = 2$, $\lambda_E = 0.5$) is larger (0.39) than the currently used constant value of 0.25, and the 95% CIs from the bootstrap procedure do not include this constant value.

Inclusion of the hydroacoustic index, although strongly correlated with the mile-days of milt, does little to resolve the conflicts present in the standard datasets or aid in natural mortality estimation in the ASA model. The estimates of natural mortality were not sensitive to the hydroacoustic index, regardless of dataset (A or B) or weight in the objective function. The hydroacoustic indices have little influence on estimates of spawning biomass in the ASA model. There are modest effects, such as slight increases in the recruitment estimates $\{N_{3,t}\}$, increases in the natural mortality values for ages ≥ 5, and a convergence of pre- and post-1997 maturity values for ages 3 and 4. It appears that the hydroacoustic model produces similar spawning biomasses by introducing more age 3 recruits, while at the same time removing older age classes. The model also decreases the overall maturity of age 3 recruits and age 4 fish so that the increase in younger cohort abundance does not translate into an increase in spawning biomass. Further, estimated maturities of fish aged 3 and 4 were different for pre- and post-1997 with lower values of λ_H, but converged to a constant value at higher values of λ_H. Therefore, it remains unresolved whether there was a shift in maturity during the late 1990s.

The estimated proportion of the population detected by the hydroacoustic survey was <85% for all mile-days of milt, egg deposition, and hydroacoustic index weights in scenarios M0 and M1, and was estimated with good precision. Weighting analysis indicates that the hydroacoustic survey detects greater proportions of the total population with larger weights on the egg deposition as opposed to the mile-days of milt, when natural mortality is estimated from 1988 to 1992. Therefore, the hydroacoustic survey appears to have greater coverage of the herring population when relatively more weight is given to the egg deposition dataset than to the mile-days of milt dataset. However, coverage is reduced at large weights on the hydroacoustic index. The results of this analysis show that when treating the hydroacoustic index with more precision, the proportion of the population detected by the survey is smaller than when allowing less precision in the hydroacoustic survey.

Within the ASA model, there is virtual redundancy between the hydroacoustic and mile-days of milt indices, but the incorporation of both indices leads to quantification of the uncertainty in the population's dynamics. Therefore, future assessment of PWS herring through an ASA approach needs to include hydroacoustic data. Also, a field study of maturity conducted for PWS herring could resolve the effect of the discrepancy in maturity estimates.

From 1988 to 1992, both the mile-days of milt and the miles of milt values are upwards of ten times larger than the values from 1993 to 2004, which correspond to hydroacoustic observations. Because of the constant variance assumption in linear regressions, the uncertainty from 1988 to 1992 is determined from a highly correlated and less variable range of data (1993–2004). Therefore, the uncertainty in the extrapolated biomass is not accurately portrayed in the linear hindcast procedure. Additionally, the true relationship between the hydroacoustic measure of biomass and the milt index may not be linear. The milt index is bounded because the extent of spawning habitat for Pacific herring in PWS is finite. Therefore, we hypothesize that the true relationship may be modelled better with an asymptotic function. The constant proportionality assumption between the male spawning index and biomass is made in both the linear regression and ASA models. However, the ASA model integrates alternative datasets, and does not rely solely on the miles of spawn index to estimate abundance. Moreover, uncertainty in ASA model estimates is determined for all years of data from 1980 to 2004, and does not require that the relative variance be constant from one year to the next.

When all available data for PWS herring are integrated in an ASA model, the range of exploitation fraction estimates and uncertainty from 1990 to 1992 and 1997 to 1998 is large, and it includes estimates from the linear models. Therefore, the hypothesis that high fishing mortality accelerated the decline in the population from 1990 to 1992 (Thomas and Thorne, 2003) may be supported when using a simple linear regression model with a single dataset, but it is not supported when using all data sources in an ASA model. Simulation of spawning biomass values by excluding commercial fisheries in 1997 and 1998 indicates that the commercial fisheries did not have a substantial effect on the resulting biomass. Furthermore, uncertainty in exploitation rates from the linear regression hindcast procedure cannot be determined accurately because hydroacoustic data were first collected in 1993, after the population crashed.

A key issue in PWS herring dynamics is knowing when the decline in PWS herring actually started. With the linear hindcast

procedure, the rapid decline in herring biomass appears to start in 1989, the year of the oil spill, rather than 1993, the year that the decline was recognized by fisheries managers (Thomas and Thorne, 2003, 2008). ASA model spawning biomass estimates show some evidence of a decline in the population in 1989, but not as substantial as the decline after 1992. An alternative explanation is that natural mortality of herring increased in the late 1980s and remained elevated until the crash of 1993, when natural mortality was even greater. This hypothesis remains viable under many of the weighting schemes investigated here.

Our view is that there was a significant decline in 1992 attributable to disease affecting a large population in weakened condition. Poor body condition in spring may be the most significant risk factor for a disease epidemic (Marty *et al.*, 2003), and the greatest decline in weight-at-age in PWS herring was between autumn 1992 and spring 1993 (Pearson *et al.*, 1999). In the early 1990s, the PWS herring population biomass was high, but growth was poor and fish had inadequate energy stores entering the winter of 1992/1993 (Pearson *et al.*, 1999). This may be explained partly by a nearly non-existent zooplankton bloom in PWS during summer 1992 (Quinn *et al.*, 2001). Further, the 1989 year class of PWS herring experienced many adverse effects from EVOS (Brown *et al.*, 1996) and would have recruited to the adult stock in 1992 and 1993 (ages 3 and 4). Poor condition and limited food availability provided a mechanism for the disease epidemic in the winter of 1992. Further, poor recruitment of the 1989 year class coupled with disease could have played a role in the significant population decline from 1992 to 1993.

Some researchers believe that limitations in ASA methodology led to overestimation of Pacific herring abundance from 1989 to 1993, resulting in management actions that caused large mortality from overharvesting (Thomas and Thorne, 2003). These limitations include the ASA dependence on the egg deposition dataset and assumptions of constant mortality. We show here that the ASA model is not just dependent on egg deposition, but rather on all datasets relevant to the stock. Such synthesis of historical information lends stability to parameter estimation, proper representation of uncertainty in model estimates, and avoids problems with process errors. We have also shown that the ASA model has the flexibility to include variation in natural mortality by age group and over time. However, estimating mortality without auxiliary information usually results in highly unstable parameter estimates through data conflicts and limitations. Stable natural mortality estimation can be obtained by including disease information. Nevertheless, it is true that a change in disease or biomass condition after the previous year could lead to inaccuracy in the spawning biomass used for making management decisions.

The integration of many data sources to estimate key population parameters of the PWS herring stock is the main strength of the ASA model, because such integration leads to proper evaluation of dataset influence on modelled estimates and uncertainty. The model has been useful for understanding population dynamics in showing that multiple disease events and low recruitment may have adversely affected the population since 1993. It has been useful in fishery management, because spawning biomass is used to decide whether to open the fishery and how much fish can be caught.

A significant advantage of the hydroacoustic survey is that a large change in the population, such as from a disease outbreak, could be recognized before a fishery is opened, and this

information could be used to modify management actions. For example, all PWS fisheries were scheduled to be opened in April 1999, but they were never opened because in-season hydroacoustic estimates gave poor returns. The hydroacoustic survey can also be used to estimate fishing mortality independently, although we do not recommend this approach. Moreover, the survey cannot describe other key population parameters, such as age-specific maturity and natural mortality, or recruitment.

Integration of datasets in the ASA model connects observations with population dynamics equations to link year classes for parameter estimation. Therefore, the ASA model not only explains the observations, but it ties them together to avoid problems attributable to measurement and process error. The ASA model synthesizes datasets and exposes data conflicts in a robust manner. Further, ignoring several data sources and uncertainty in extrapolated biomass values to form hypotheses does not seem precautionary (O'Riordan, 1992; Dovers and Handmer, 1995). There is a straightforward middle ground, in which the ASA model (including hydroacoustic data) would continue to be used as a preseason tool, but in which the results from the current year's hydroacoustic survey can be scrutinized for the possibility of emergency action if there appears to be a major change in the population. This protocol has been followed by ADF&G since the late 1990s.

Each dataset used in the PWS assessment model has limitations. Egg deposition surveys have measurement errors attributable to the difficulty of detecting and locating all spawning events and ensuring diver accuracy. Further, the accuracy of the egg deposition estimate can depend on predation, dispersal, and loss to surf and wave action on the spawning beds (Rooper *et al.*, 1998; Bishop and Green, 2001). The collection of miles of milt data depends largely on weather conditions impacting the ability of aerial detection of spawning sites. It also requires that milt density be constant over years, and that milt distribution be an accurate index of spawning biomass. The hydroacoustic biomass estimate is a direct source of abundance information, but is contingent on all spawning fish being in the survey area. The accuracy of this method will be affected by the mobility of the fish schools, the temporal effects of age-dependent spawning, and the choice of target strength for herring, whose size-at-age is variable over time. The age composition datasets are dependent on the selectivity of the gear and the timing of the survey, because older fish tend to spawn earlier than younger fish (Hay, 1985).

This study has shown that data conflicts cannot always be resolved, but that they can be identified explicitly through alternative dataset weighting and parameterization, so that variability in parameter estimation and uncertainty is exposed. Assessment scientists have used several approaches for weighting data sources, with variable degrees of success. First, the magnitude of measurement errors from data sources used in integrated assessment models determined by sampling or experiments can be used (Kimura, 1989). Second, statistical theory allows estimation of the weights for multiple datasets through iterative reweighting or likelihood methods when there is no process error (Deriso *et al.*, 2007). However, we believe that substantial process error may be present in herring data sources, which means that selection of weights will continue to require the judgement of analysts. Therefore, when data conflicts arise, assessment results and hypotheses depend on the choice of weighting made by the researcher. Further, to avoid biased results when developing hypotheses during periods with conflicting data, researchers

should examine all available sources of information and how each influences key parameters and uncertainty.

Acknowledgements

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