Abstract—The natural mortality rate (M) of fish varies with size and age, although it is often assumed to be constant in stock assessments. Misspecification of M may bias important assessment quantities. We simulated fishery data, using an age-based population model, and then conducted stock assessments on the simulated data. Results were compared to known values. Misspecification of M had a negligible effect on the estimation of relative stock depletion; however, misspecification of M had a large effect on the estimation of parameters describing the stock recruitment relationship, age-specific selectivity, and catchability. If high M occurs in juvenile and old fish, but is misspecified in the assessment model, virgin biomass and catchability are often poorly estimated. In addition, stock recruitment relationships are often very difficult to estimate, and steepness values are commonly estimated at the upper bound (1.0) and overfishing limits tend to be biased low. Natural mortality can be estimated in assessment models if M is constant across ages or if selectivity is asymptotic. However if M is higher in old fish and selectivity is dome-shaped, M and the selectivity cannot both be adequately estimated because of strong interactions between M and selectivity.

Interactions of age-dependent mortality and selectivity functions in age-based stock assessment models

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Correctly specifying the instantaneous rate of natural mortality (M) in stock assessment models is important because misspecification may lead to over- or underestimates of critical assessment quantities, including stock depletion, maximum sustainable yield (MSY), virgin biomass, and density dependence (Lapointe et al., 1989; Thompson, 1994; Mertz and Myers, 1997; Punt and Walker, 1998; Clark, 1999; Wang et al., 2006). It is widely believed that natural mortality varies with age or size; young (small) fish have higher natural mortality rates due to higher predation risks, disease, or starvation (Lorenzen, 1996), whereas older (larger) fish may have increased natural mortality with senescence or because of cumulative reproductive stress (Mangel, 2003; Moustahfid et al., 2009).

In spite of the widely held perception that natural mortality varies considerably with age, most stock assessment models assume that M is constant for all ages, mainly because there are insufficient data with which to estimate natural mortality on an age-specific basis. Another reason for assuming constant M in stock assessment models is that natural mortality is typically highly correlated with other key parameters, including stock recruitment and selectivity parameters (Lapointe et al., 1992; Thompson, 1994; Schnute

and Richards, 1995; Fu and Quinn, 2000), quantities that are often quite difficult to estimate with accuracy (Maunder et al.[1]).

In previous studies a variety of approaches have been developed to estimate natural mortality, including the use of maximum observed age (Hoenig, 1983) and life-history parameters (Alverson and Carney, 1975; Gunderson, 1980; Myers and Doyle, 1983; Roff, 1992; Jensen, 1996; Gunderson, 1997). In other studies, life-history data and environmental variables have been combined to establish empirical relationships to predict natural mortality (Pauly, 1980; Gislason et al., 2010). These studies have provided estimates of natural mortality that can be useful for stock assessments but these estimates may not be sufficient for species-specific stock assessment because of bias (e.g., only a subset of possible life histories was considered). Other studies have shown that unless species-specific data were collected before exploitation of the species, estimates of

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[1] Maunder, M. N., H. H. Lee, and K. R. Piner. 2010. A review of natural mortality, its estimation, and use in fisheries stock assessment. Unpubl. manuscr, 35 p. Inter-American Tropical Tuna Commission, 8604 La Jolla Shores Drive, La Jolla, CA.

natural mortality are impractical, if not impossible, to derive from fishery or survey data, because of the interaction between fishing and natural mortality (Vetter, 1988; Quinn and Deriso, 1999). Clark (1999) examined the effects of incorrectly specifying M for a simple age-structured stock assessment and concluded that errors in M mainly affect estimates of fishing mortality and abundance, but not estimates of age-specific selectivity.

In most regions of the world, where statistical stock assessments of single species provide the basis for management advice (Worm et al., 2009), it is commonplace to assume a constant natural mortality rate for all exploitable ages or sizes (or for both). Moreover, natural mortality is also typically assumed to be constant over time and identical among regions (Punt, 2003; Yin and Sampson, 2004; PFMC, 2008). Uncertainty in the use of constant natural mortality in these assessment models is usually evaluated by an approach that is similar to likelihood profiles, where M values are changed and other parameters are fixed. However, this approach is highly dependent on the specific model structure and parameter settings being evaluated. For example, if stock recruitment relationships or selectivity functions are fixed in an assessment model, likelihood profile methods on natural mortality can provide only the validity of the model fitted to fixed values of natural mortality and not the validity of the model for its interactions with other model parameters.

In this study, we compare stock assessment results among simulated populations with different natural mortality schedules. The simulation data were generated with an age-based population model characterized by exploitation from a single fishery with a constant selectivity pattern over an extended period of time, representing somewhat ideal conditions. Simulations were crafted to reflect conditions in the U.S. west coast groundfish fishery—the source of most available fishery data for the last 40 years, a period when fishing intensity was high in the early years and has been low in recent years. In the simulation operating model, two different natural mortality patterns were used: 1) constant natural mortality for all ages; and 2) elevated values of M in both juvenile and old fish. The data, along with sampling errors, were input into the assessment models. In the assessment model, natural mortality was assumed to be known and constant for all ages, estimated to be constant for all ages, or was estimated to follow an age-specific pattern. Estimated quantities from the assessments were then compared with the simulation models that generated the data. Important assessment results, e.g., stock depletion and stock-recruit relationships, were then compared to evaluate the effect of misspecification of natural mortality and selectivity on stock assessment estimates. In addition, results from the assessment models were compared with and without an informative parameter prior for spawner-recruit steepness parameters.

Methods

Simulation model

The simulation or operating model in this study was an age-structured population model with a max age of 30 years. The last age was an age plus group. The Beverton-Holt stock-recruitment function was used to model stock recruitment. In particular, the "steepness" parameterization of Mace and Doonan[2] with $h=0.6$ was used (see also Dorn, 2002). Recruitment variability was lognormal with σ_R set equal to 0.5 and lognormal survey variability set to equal 0.25. Specifics of the simulated population dynamics are presented in the Appendix. Base values for biological, fishery, and modeling parameters are presented in Table 1. Because of variability in recruitment and catchability, the model was run for 260 years, with the first 200 years as a "burn-in" period with no fishing to minimize the effect of initial conditions in the model. Only the last 40 years of data were provided for the assessment model.

Biological parameters, including growth, fecundity, and the length-weight relationship were patterned after widow rockfish (*Sebastes entomelas*) off the U.S. west coast (He et al., 2009). Although widow rockfish shows differences between the sexes in biological parameters, the same values were used for both sexes to simplify the model.

We modeled two different functional types of age-dependent natural mortality (M) in the simulations including 1) constant natural mortality for all ages (0.15/yr); and 2) high M in both juvenile and old fish (Table 2; Fig. 1). The annual sample size for age compositions was 500 for all simulations—a size that ensured that informative age composition data were available to the assessment models.

We used only one fishery in the operating model, and catches began in the last 40 years of the simulations. Fishing mortalities (F) were modeled as proportions of F_{MSY}, which varied over time. During the first 20 years, fishing at F_{MSY} occurred, and in the last 20 years fishing mortality was 10% of F_{MSY}. Two types of fishery selectivity patterns were simulated, i.e., simple asymptotic logistic and double normal curves (Fig. 2). The later was moderately dome-shaped and is implemented in the stock synthesis model (Methot, 2009a), a widely used stock assessment model. In all simulations the ascending limbs of the two selectivity curves were constrained to be similar, i.e., 50% of individuals were selected at age 8. The above specific values and patterns in M, F, and selectivity were based on typical life history patterns of fish, and fishing patterns, off the U.S. west coast (e.g., those of widow rockfish).

[2] Mace, P. M., and I. J. Doonan. 1988. A generalized bioeconomic simulation model for fish population dynamics. New Zealand Fishery Assessment Res. Doc., 88/4, 21 p. MAF Fisheries, Greta Point, Wellington, New Zealand.

Table 1

Biological, fishery, and modeling parameters used in the simulation model to evaluate interactions between mortality and selectivity. See Appendix for equations, definitions of parameters, and symbols. Parameters are the same for both sexes. True values are the base parameter values used in the simulation models. Lower and upper bounds are boundary limits used in the stock assessment program. NA=not applicable.

Parameter	Symbol	True value	Estimated in assessment model	Lower and upper bounds	Unit and note
Minimum age	a_{min}	0	No	NA	Year
Maximum age	a_{max}	30	No	NA	Age plus group
Virgin recruitment	R_0	10	Yes	0.1, 30	Log scale
Recruitment steepness	h	0.6	Yes	0.2, 1.0	
Annual recruit deviation	R_y^δ	0	Yes	−5, 5	Log scale, 76 years
Growth	K	0.14	No	NA	Per year
Growth	L_∞	50.54	No	NA	cm
Growth	t_0	−2.68	No	NA	Year
Length–weight	τ_1	5.45e-6	No	NA	
Length–weight	τ_2	3.2878	No	NA	Kg/cm
Natural mortality	M	0.15	Yes or no	0.01, 1	Per year, varied, see text
Logistic selectivity	η_1	8	Yes	0, 50	50% selectivity at age 8
Logistic selectivity	η_2	5	Yes	0, 50	Width for 95% selection
Double normal selectivity	η_1	13	Yes	−507, 533	See Appendix
Double normal selectivity	η_2	−2	Yes	−82, 80	See Appendix
Double normal selectivity	η_3	3.5	Yes	−136, 143	See Appendix
Double normal selectivity	η_4	2.6	Yes	−101, 106	See Appendix
Double normal selectivity	η_5	−5	Yes	−205, 195	See Appendix
Double normal selectivity	η_6	0.65	Yes	−25, 26	See Appendix
Catchability—survey of juveniles	q_1	0	Yes	−5, 5	Log scale
Catchability—survey of adults	q_2	0	Yes	−5, 5	Log scale
Recruitment variability	σ_R	0.6	No	NA	
Catch variability	σ_ψ	0.05	No	NA	
Variability—survey of adults	$\sigma_{i,1}$	0.25	No	NA	
Variability—survey of adults	$\sigma_{i,2}$	0.25	No	NA	
Annual age sample size	n	500	No	NA	

Stock assessment model

The simulation data were fitted to the stock assessment model by using stock synthesis (SS3, vers. 3.04b) software (Methot, 2009a, 2009b). Other than patterns in natural mortality and selectivity, a correct population structure was assumed in the assessment model, and likewise for the growth, fecundity, and the length-weight relationship. There were three ways in which natural mortality (M) was treated in the assessment models. First, M was assumed to be constant and was fixed at the same value of M=0.15/yr as in the simulation model (Fig. 1; Table 2, runs 1–12). Second, a single M was estimated (runs 13 and 15). Third, four values of M were estimated (runs 14 and 16). In the third case, we used the breakpoint method in the SS3 program, and the four breakpoints (M_1, M_2, M_3, and M_4) were defined for ages 2, 3, 24, and 25. In this case, M_1 was used for ages 0 to 2, M_2 was used for age 3, M_3 was used for age 24, M_4 for ages 25 to 30, and M values

for ages between 4 and 23 were linearly interpolated between M_3 and M_4.

Fishery data from the simulation model consisted of annual catches, annual age composition data, and survey indices. Fishing mortality was estimated by using the hybrid method in the SS3 program. The hybrid method in the SS3 program is a simplified parameterization method (see Methot, 2009a). Because of relatively small variations of catch data generated in the simulation models (coefficient of variation [CV]=0.05), this method produces nearly identical fishing mortality estimates as in fully parameterized fishing mortality (see Methot, 2009a). Other estimated parameters in the assessment model included the stock-recruit relationship, selectivity, catchability coefficients, and annual recruitment deviations from the stock-recruit curve (Table 1). Initial values for all estimated parameters were set to be the same as those in the simulation models. Noninformative priors were used in parameter

Table 2

Model and parameter specifications in simulation and assessment models used to evaluate interactions between mortality and selectivity. Constant natural mortality ($M=0.15$) is used in all runs except runs 14 and 16. A normal prior is used as h prior.

Run no.	No. of simulations	True selectivity	Selectivity function used in assessment	h prior in assessment	True M in simulation	M estimated in assessment model
1	3000	Logistic	Logistic	Yes	Constant	No
2	500	Logistic	Logistic	Yes	High M in juvenile and old fish	No
3	500	Double normal	Double normal	Yes	Constant	No
4	500	Double normal	Double normal	Yes	High M in juvenile and old fish	No
5	500	Logistic	Double normal	Yes	Constant	No
6	500	Logistic	Double normal	Yes	High M in juvenile and old fish	No
7	500	Double normal	Logistic	Yes	Constant	No
8	500	Double normal	Logistic	Yes	High M in juvenile and old fish	No
9	500	Logistic	Logistic	No	Constant	No
10	500	Logistic	Logistic	No	High M in juvenile and old fish	No
11	500	Double normal	Double normal	No	Constant	No
12	500	Double normal	Double normal	No	High M in juvenile and old fish	No
13	500	Logistic	Logistic	No	Constant	Yes (1 parameter)
14	500	Logistic	Logistic	No	High M in juvenile and old fish	Yes (4 parameters)
15	500	Double normal	Double normal	No	Constant	Yes (1 parameter)
16	500	Double normal	Double normal	No	High M in juvenile and old fish	Yes (4 parameters)

estimation except for spawner-recruit steepness (h), in which case $h=0.6$ and a normal prior with standard deviation (SD)=0.1 was either used (runs 1–8), or not used (runs 9–16) in the assessment models.

Comparisons of simulation and assessment results

For evaluating each simulation scenario (Table 2), the simulation was repeated 500 times and the simulated data from each run were inputted into the SS3 model. A successful assessment model run was then achieved if the value of the maximum gradient component was less than 0.05. If an assessment model run did not converge, that realization was flagged as a failed run and a new set of data was generated from the operating model.

Assessment model outputs were compared with known quantities from the simulation model for a subset of key assessment results. These included 1) a time series of spawning output; 2) estimated stock-recruitment parameters; 3) terminal stock depletion; 4) the overfishing limit (OFL); and 5) catchability coefficients. The OFL is a recently developed reference point used in the United States and is defined as the catch available from the estimated terminal biomass if fished at F_{MSY}. For each comparison between the simulation and assessment models, a discrepancy statistic was computed. For four
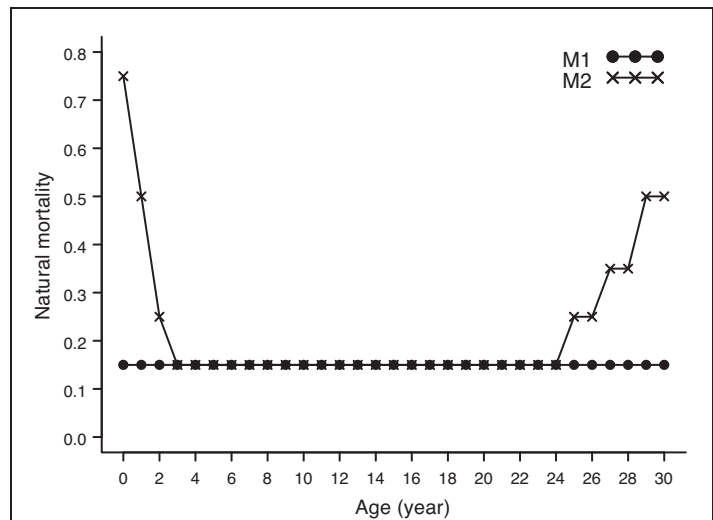

Figure 1

Patterns of natural mortality by age used in simulation models to evaluate interactions between mortality and selectivity. M1 has constant M by age, and M2 has higher M values in juvenile and old fish.

quantities, i.e., virgin spawning output (B_0), virgin recruitment (R_0), stock depletion, and OFL, the relative discrepancy ($S_\%$) was computed as a percent deviation from the simulation model:

$$S_\% = 100 \; \frac{X_a - X_s}{X_s}, \qquad (1)$$

where X_a and X_S are quantities from the assessment and simulation, respectively.

In contrast, for steepness (h) and catchability (q_i) the absolute discrepancy (S_{abs}) between the assessment and

Figure 2

Two selectivity functions (logistic and double normal) used in simulation models to evaluate interactions between mortality and selectivity.

Figure 3

Time series of spawning outputs from simulation (Sim) and stock synthesis (SS3) assessment models from run 1. Closed circles are median simulation outputs and open circles are median assessment outputs. Assessment outputs are barely visible because most of them overlap simulation outputs. Lines are 2.5% and 97.5% of quantiles from simulation (dashed lines) and assessment (solid lines) model outputs.

simulation models was computed by using absolute differences according to the following equation:

$$S_{abs} = X_a - X_s. \qquad (2)$$

To test the congruence of the simulation and assessment models, 3000 runs were conducted by using the default setup between the simulation and assessment models (Table 2). Note that in the default setup (run 1), simple logistic selectivity was used in both the simulation and assessment models. Likewise, M was constant and correctly specified in both models. Thus, no model specification errors existed in fits of the default model. For all other simulation scenarios, 500 simulations were conducted. Early testing runs indicated that 500 simulations were sufficient to capture the range of outputs. Median values from the simulation-assessment runs were then computed along with 2.5% and 97.5% of percentiles.

Performance of the assessment models was also measured by using two performance statistics. The first statistic measured the percentage of SS3 runs that were completed (% run completed). Runs were considered completed whenever the program finished estimation, regardless of how or if the assessment model produced sensible results. Incomplete runs were those when the program stopped in the middle of the procedure without producing any SS3 outputs. The second performance statistics (% maximum gradient component [MGC] satisfied) measured the percentage of runs that not only were completed, but also satisfied the convergence criteria with MGC less than 0.05 and a positive-definite Hessian matrix. It should be noted that even when MGC was <0.05 there was no assurance that the model had reached a global optimum. The threshold value for the MGC was set to be 0.05. The choice of this value was based on earlier testing runs, in which the default setup (run 1) was used and the result with the MGC of 0.05 was the same as that from other testing runs with smaller MGC values (e.g., 0.001).
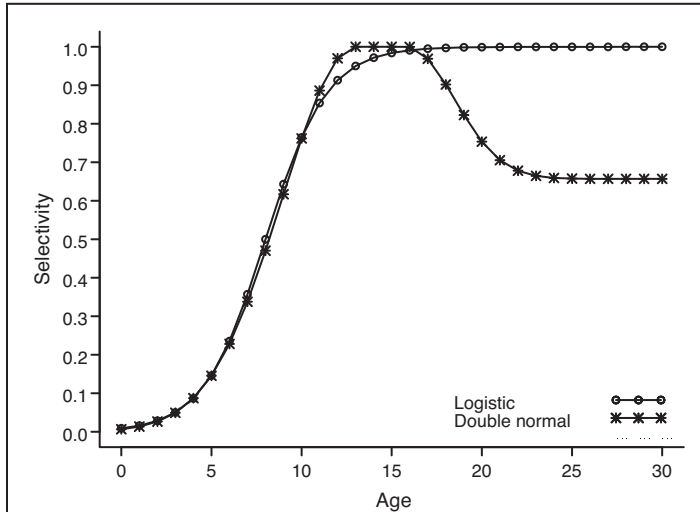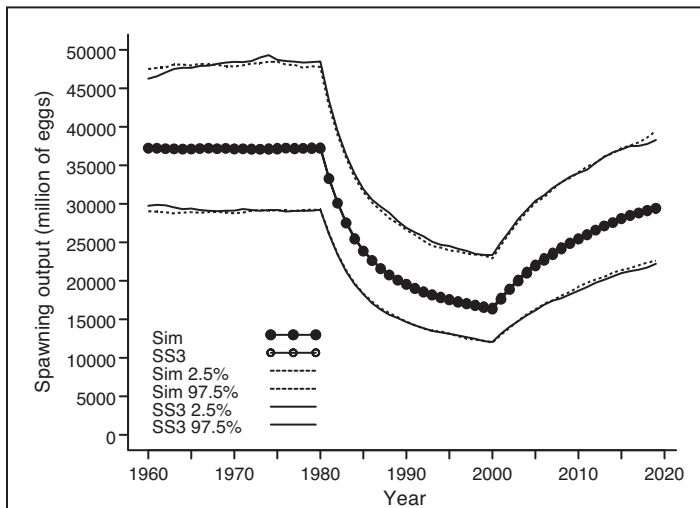
Results

Testing simulation models

Simulation models were tested by using the default setup in the operating model and the assessment model (run 1). As expected, the time series of median spawning output, as well as their 2.5% and 97.5% percentiles, between the simulation and assessment models matched very well (Table 3; Fig. 3). Frequency plots of the estimated differences in virgin spawning output (B_0), depletion, and OFL between simulation and assessment models showed that the differences were very

Table 3

Key assessment model estimates on biological, fishery, and management parameters and their comparisons with their correct values. For virgin spawning output, depletion, and overfishing limit (OFL, in metric tons [t]), the statistics are expressed as the percent difference of medians between simulations and assessments with 2.5% and 95% percentiles seen in parentheses. Values equal to zero indicate no difference between the simulation and assessment models. For steepness and catchability, the estimated values and their ranges are used. The true value of steepness (h) is 0.6 and the true values of two survey catchabilities (q_2 and q_2) are 1.0. Selectivity fits are indicated by three categories: good, fair, or bad.

Run no.	Virgin spawning output (B_0)	Steepness (h)	Adult survey catchability (q_1)	Juvenile survey catchability (q_2)	Selectivity fit	Depletion	OFL (t)
1	0.5 (−19.9, 26.8)	0.59 (0.35, 0.75)	0.98 (0.84, 1.14)	0.99 (0.84, 1.19)	Good	−2.0 (−27.0, 31.1)	−2.2 (−22.3, 18.2)
2	−21.3 (−41.9, 2.5)	0.76 (0.61, 0.87)	1.35 (1.16, 1.56)	3.62 (3.03, 4.28)	Fair	−6.3 (−32.9, 37.0)	−32.4 (−48.3, 11.7)
3	1.0 (−20.3, 32.3)	0.59 (0.35, 0.74)	0.97 (0.82, 1.17)	0.99 (0.83, 1.18)	Good	−2.1 (−27.7, 27.2)	−1.7 (−21.4, 19.5)
4	7.5 (−21.1, 42.0)	0.60 (0.36, 0.74)	0.95 (0.81, 1.21)	2.80 (2.36, 3.39)	Bad	−4.3 (−30.7, 31.8)	−9.7 (−26.2, 9.4)
5	5.3 (−17.7, 32.6)	0.59 (0.36, 0.73)	0.88 (0.77, 1.04)	0.96 (0.81, 1.14)	Fair	−2.7 (−28.3, 29.6)	−0.1 (−20.9, 20.6)
6	9.2 (−20.9, 47.4)	0.61 (0.35, 0.73)	0.87 (0.73, 1.02)	2.72 (2.32, 3.16)	Bad	−3.9 (−30.6, 31.7)	−10.1 (−24.9, 9.3)
7	−11.6 (−30.0, 13.2)	0.63 (0.40, 0.78)	1.13 (1.00, 1.32)	1.11 (0.95, 1.32)	Bad	0.8 (−25.8, 31.3)	−6.6 (−27.9, 11.6)
8	−29.6 (−47.4, −6.4)	0.78 (0.64, 0.90)	1.55 (1.36, 1.78)	3.96 (3.36, 4.76)	Bad	−5.1 (−32.9, 33.0)	−35.8 (−51.6, −19.1)
9	1.6 (−18.7, 25.0)	0.57 (0.31, 1.00)	0.99 (0.84, 1.13)	1.00 (0.84, 1.17)	Good	−2.0 (−26.1, 30.4)	−3.4 (−20.5, 15.9)
10	−24.1 (−43.2, −0.5)	1.00 (0.63, 1.00)	1.33 (1.13, 1.52)	3.50 (2.93, 4.22)	Fair	2.1 (−29.8, 46.6)	−29.6 (−46.5, −9.7)
11	1.8 (−19.8, 33.0)	0.58 (0.32, 1.00)	0.97 (0.83, 1.14)	0.99 (0.84, 1.17)	Good	−1.8 (−27.5, 31.8)	−2.3 (−20.5, 16.6)
12	9.5 (−18.9, 45.8)	0.60 (0.34, 1.00)	0.95 (0.81, 1.17)	2.80 (2.37, 3.32)	Fair	−6.9 (−31.1, 24.2)	−10.1 (−25.8, 6.1)
13	0.3 (−26.1, 37.8)	0.62 (0.32, 1.00)	0.98 (0.82, 1.15)	1.00 (0.77, 1.30)	Good	−1.5 (−29.0, 33.8)	−2.4 (−21.4, 22.7)
14	−0.4 (−24.1, −32.6)	0.58 (0.33, 1.00)	0.98 (0.82, 1.16)	1.19 (0.79, 1.79)	Good	−0.9 (−27.5, 36.9)	−3.7 (−24.0, 21.0)
15	−1.1 (−24.4, 35.6)	0.61 (0.33, 1.00)	0.98 (0.83, 1.16)	1.03 (0.78, 1.29)	Good	0.0 (−28.0, 31.7)	−4.1 (−22.31, 21.1)
16	22.9 (−1.9, 110.4)	0.55 (0.21, 1.00)	0.96 (0.80, 1.13)	1.67 (0.68, 4.33)	Fair	−6.0 (−33.2, 34.0)	−19.7 (−52.2, 20.3)

small (Tables 3 and 4), and their distributions were centered near zero and symmetrical (Fig. 4). Other key assessment outputs, such as steepness (h) and the two catchability coefficients (q_1 and q_2), in comparisons between the simulation and assessment models also matched very well (Table 3). Selectivity was also estimated well in the stock assessment models (Fig. 5). In this setting, with no model specification error, the estimation model performed very well; 100% of runs finished and 100% MGC values were smaller than specified critical values (Table 5).

Effects of misspecified *M* on assessment results

If selectivity functions were asymptotic and correctly specified in the assessment models (runs 1 and 2), population depletion was generally well estimated, even when natural mortality was misspecified in assessment models (Table 3). However, the OFL estimates were lower by more than 32% than the true values if young and old fish were characterized by increasing natural mortality, but *M* was assumed to be constant in the assessment (Table 3, run 2). The estimated

Table 4

Performance and convergences of assessment models. Percentages of runs finished indicate that the assessment models finished stock synthesis (SS3) runs but maximum gradient component (MGC) statistics did not satisfy convergence criteria. Percentages of MGC satisfied indicate that the assessment models finished SS3 runs and MGC statistics satisfied convergence criteria (MGC<0.05).

Run no.	No. of simulations	% of runs finished	% MGC satisfied	No. of parameters
1	3000	100.0	100.0	82
2	500	100.0	100.0	82
3	500	86.2	81.3	86
4	500	78.6	48.2	86
5	500	83.3	81.0	86
6	500	70.2	53.0	86
7	500	100.0	100.0	82
8	500	100.0	100.0	82
9	500	100.0	100.0	82
10	500	100.0	100.0	82
11	500	84.5	80.1	86
12	500	77.4	45.7	86
13	500	100.0	100.0	83
14	500	100.0	100.0	86
15	500	83.8	79.5	87
16	500	75.1	48.4	90
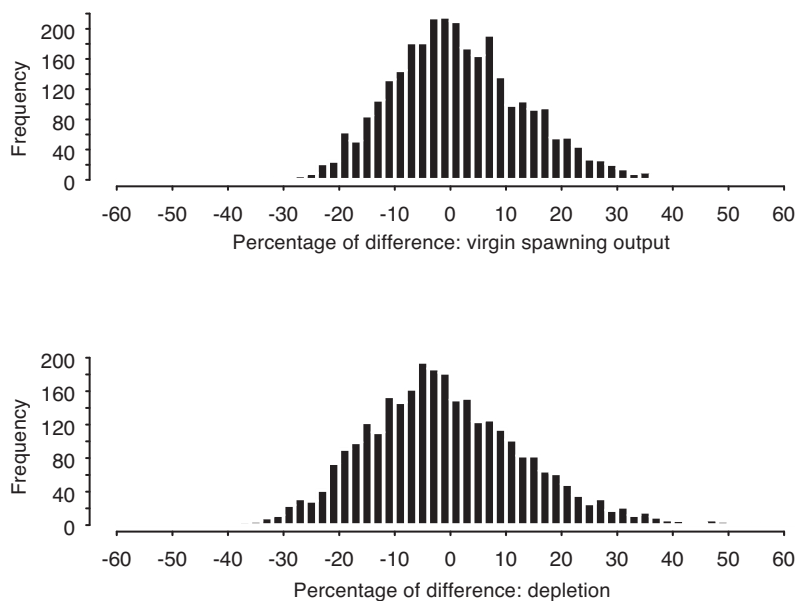
Figure 4

Frequency plots of estimated differences of virgin spawning outputs (B_0) and depletions between simulation and stock synthesis (SS3) assessment models from run 1. The differences are percentages of differences between simulation and assessment divided by true simulation values. Values equaled to zero indicate no differences between simulation and assessment models.

population trajectories were very different between the simulation and assessment models for run 2 (top right panel, Fig. 6), and stock recruitment parameters (B_0, h) were poorly estimated, with B_0 being lower and h being higher in the assessment models than those in the simulation models. The estimated catchability coefficients in the assessment models were higher than those in the simulation models. Estimated catchability coefficients for juvenile fish (q_2) were especially high (>3.6 versus the correct value of 1.0) for run 2. This result occurred also for all other scenarios in which juvenile natural mortalities were misspecified in assessment models (Table 3). However, estimated selectivity functions matched fairly well between the simulation and estimation models (top row, Fig. 7). Performance of the stock assessment models in this setting was very good; 100% of the runs finished successfully and MGC values were satisfied (Table 4).

Similar results were obtained if selectivity functions were double normal and were correctly specified in the
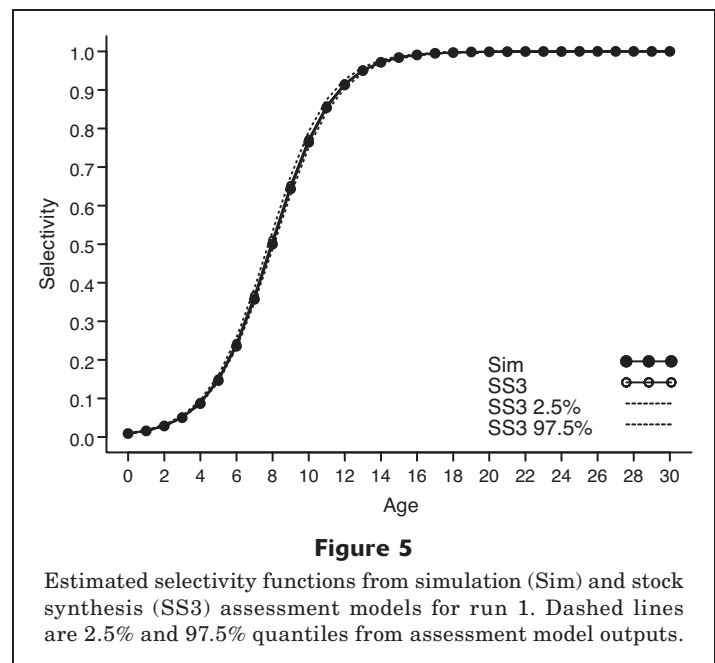
Table 5

Estimated natural mortalities (M) with 2.5% and 97.5% quantiles in parentheses for runs 13 to 16. A single M for all ages is estimated in runs 13 and 15, and four M values (break points) are estimated in runs 14 and 16. See the *Methods* section for how these four M values were assigned to each age group.

Run no.	M_1	M_2	M_3	M_4
13	0.150 (0.139, 0.161)			
14	0.448 (0.377, 0.513)	0.148 (0.108, 0.193)	0.147 (0.119, 0.169)	0.359 (0.321, 0.404)
15	0.148 (0.138, 0.163)			
16	0.285 (0.131, 0.450)	0.169 (0.068, 0.258)	0.139 (0.080, 0.225)	0.074 (0.010, 0.389)

assessment models (runs 3 and 4). Population depletion, as well as other stock assessment parameters, was well estimated if M was constant in both simulation and assessment models (run 3, second row in Fig. 6 and Table 3). The estimated double normal selectivity functions in the assessment model also matched well with that in the simulation model (run 3 in Fig. 7). Estimated population depletions were also matched reasonably well, even with misspecified natural mortalities, but the estimated OFL statistics were about 10% negatively biased (run 4, Table 3). However, if natural mortality was higher for younger and older age classes in the simulation models but was constant in the assessment models, the estimated population trajectories were different, with the estimated B_0 biased high (run 4 in Fig. 6; Table 3). Selectivity functions matched fairly well in the ascending limb between the simulation and assessment models but failed to match the descending limb of the selectivity curve (run 4, Fig. 7). Convergence of the estimation model was poor in this setting. In runs 3 and 4, 86.2% and 78.6% of 500 SS3 runs finished successfully, respectively, whereas only 81.3% and 48.2% of 500 SS3 runs produced satisfactory MGC values (Table 4).

If selectivity functions were logistic in the simulation models but were double normal in the assessment models and M was correctly specified (runs 5 and 6, Table 2), most of the estimated parameters from the stock assessment models were close to those in the simulation models, generally less than 10% of differences (Table 3). However, when natural mortality in the simulation model varied, but was assumed constant in the assessment model, the estimated catchability coefficient for the juvenile survey (q_2) was positively biased (run 6, Table 3). Time series of estimated spawning output matched reasonably well (runs 5 and 6, Fig. 6), and the estimated selectivity function showed a negative bias for old fish (runs 5 and 6, Fig. 7). Convergence performance was poor (Table 4); less than 83.3% of runs finished and only 53.0% of runs satisfied the MGC criterion (Table 5).

If selectivity functions were double normal in the simulation model but were misspecified as logistic functions

Figure 5

Estimated selectivity functions from simulation (Sim) and stock synthesis (SS3) assessment models for run 1. Dashed lines are 2.5% and 97.5% quantiles from assessment model outputs.

in the estimation model (runs 7 and 8, Table 2), the curves fits were very poor, as expected (last row in Fig. 7 and Table 3). Spawning output was poorly estimated; all estimated spawning outputs were lower than those in the simulation models in the early years (last row in Fig. 6). If natural mortality was incorrectly specified in the assessment models (run 8), estimated parameters from the stock assessment models were strongly biased (Table 3). This bias included high correlations between the two stock recruitment parameters (B_0 and h), and positive biases in both catchability coefficients (q_1 and q_2) (Table 3). Convergence of the assessment models, however, was very good. The percentages of runs finishing successfully and satisfying the MGC criterion were 100% (Table 4).

If no prior for h was used in the assessment models and natural mortality was assumed to be constant (runs 9 to12), the results in general were very similar to those from runs 1 to 4, where a prior on h was used (Figs. 8 and 9; Table 3). However, an important ex-
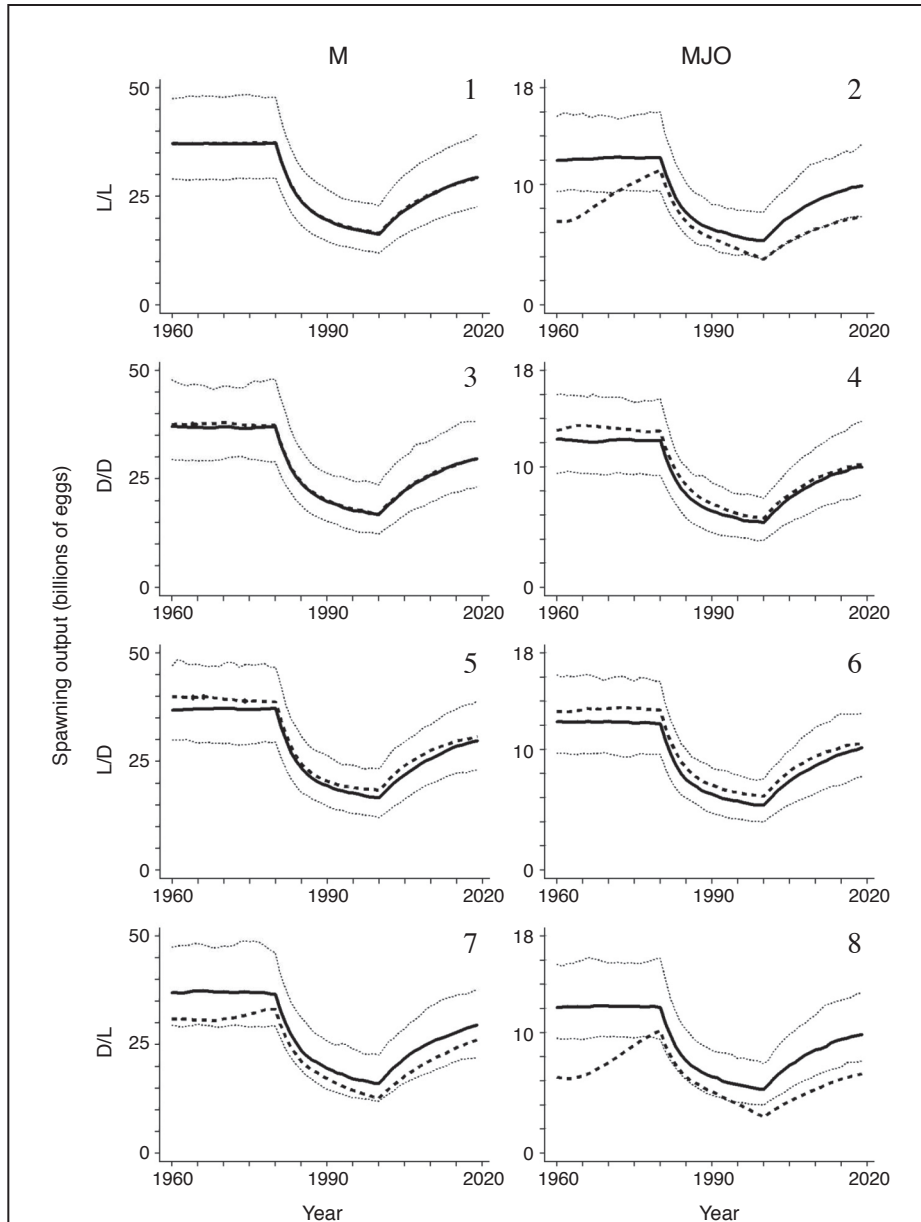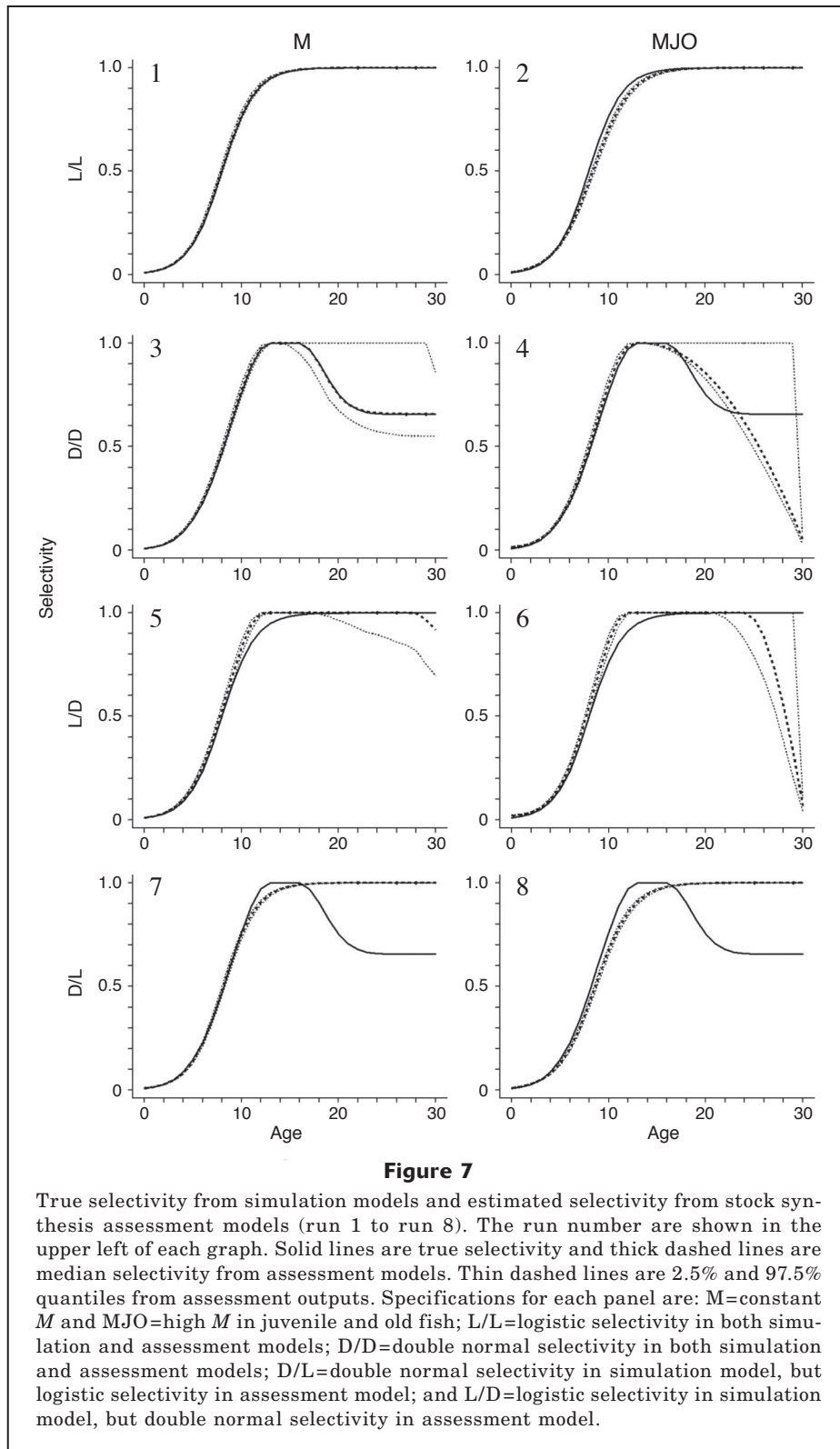
Figure 6

Time series of spawning outputs from simulation and stock synthesis assessment models (runs 1 to 8). The run number is shown in the upper right of each graph. See Table 2 for model and parameter setup for all runs. Solid lines are median simulation outputs and thick dashed lines are median assessment outputs. Thin dashed lines are 2.5% and 97.5% of quantiles from simulation outputs. Specifications for each panel are: M=constant M and MJO=high M in juvenile and old fish; L/L=logistic selectivity in both simulation and assessment models; D/D=double normal selectivity in both simulation and assessment models; D/L=double normal selectivity in simulation model, but logistic selectivity in assessment model; and L/D=logistic selectivity in simulation model, but double normal selectivity in assessment model.

ception was that a high percentage of runs estimated steepness at the upper bound of (h=1.0). If logistic selectivity functions were used and natural mortalities were correctly specified in both simulation and assessment models (run 9), there were still 16% of runs with h at the upper bound (Fig. 10). If logistic selectivity functions were used but natural mortality was incorrectly specified assessment models (run 10),

Figure 7

True selectivity from simulation models and estimated selectivity from stock synthesis assessment models (run 1 to run 8). The run number are shown in the upper left of each graph. Solid lines are true selectivity and thick dashed lines are median selectivity from assessment models. Thin dashed lines are 2.5% and 97.5% quantiles from assessment outputs. Specifications for each panel are: M=constant M and MJO=high M in juvenile and old fish; L/L=logistic selectivity in both simulation and assessment models; D/D=double normal selectivity in both simulation and assessment models; D/L=double normal selectivity in simulation model, but logistic selectivity in assessment model; and L/D=logistic selectivity in simulation model, but double normal selectivity in assessment model.

there were close to 90% of runs with h=1.0 (Fig. 10). If double normal selectivity functions were used and natural mortality was constant in both simulation and assessment models (run 11), 17% of runs settled

on the upper bound (h=1.0) (Fig. 10). Results were similar even when natural mortality was high for both juvenile and old fish in the simulation model but was assumed to be constant in the assessment model
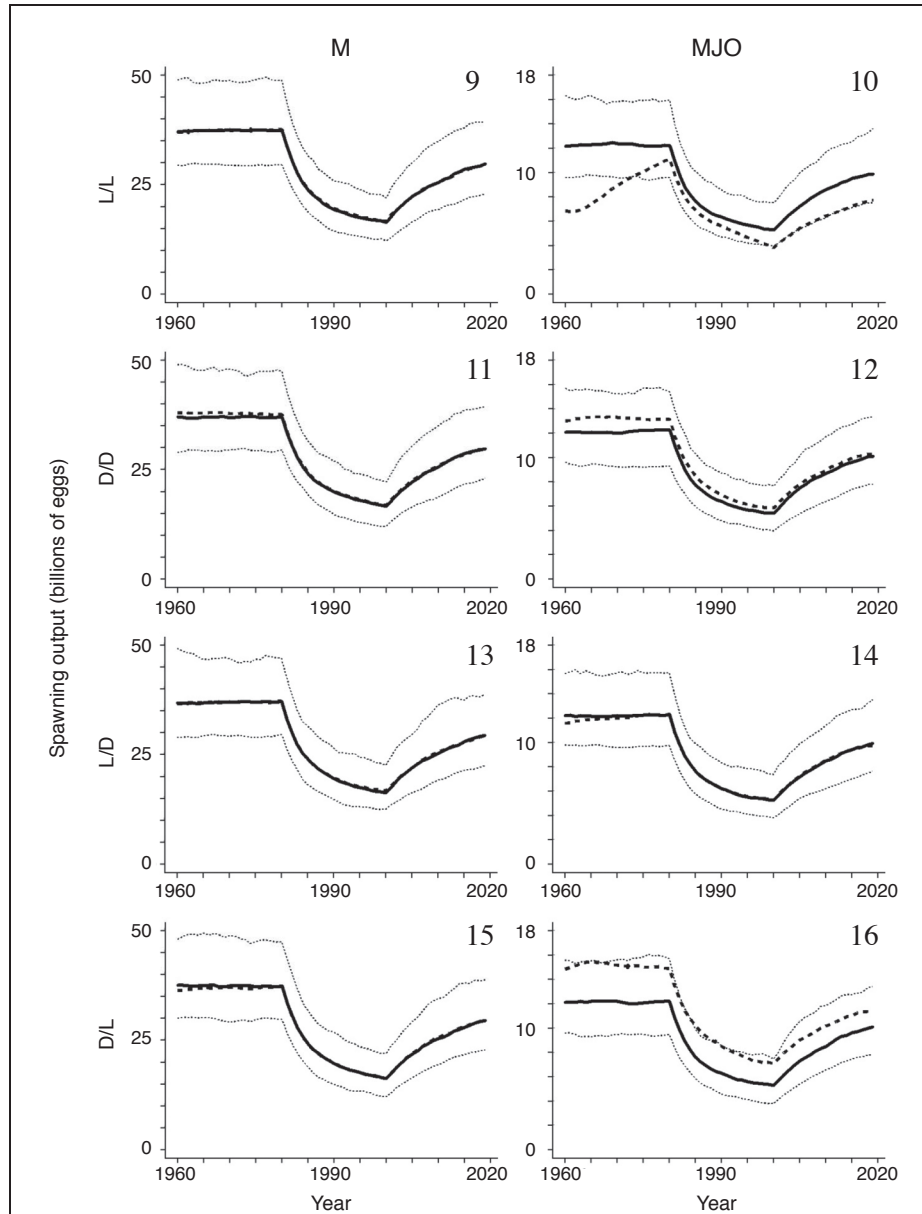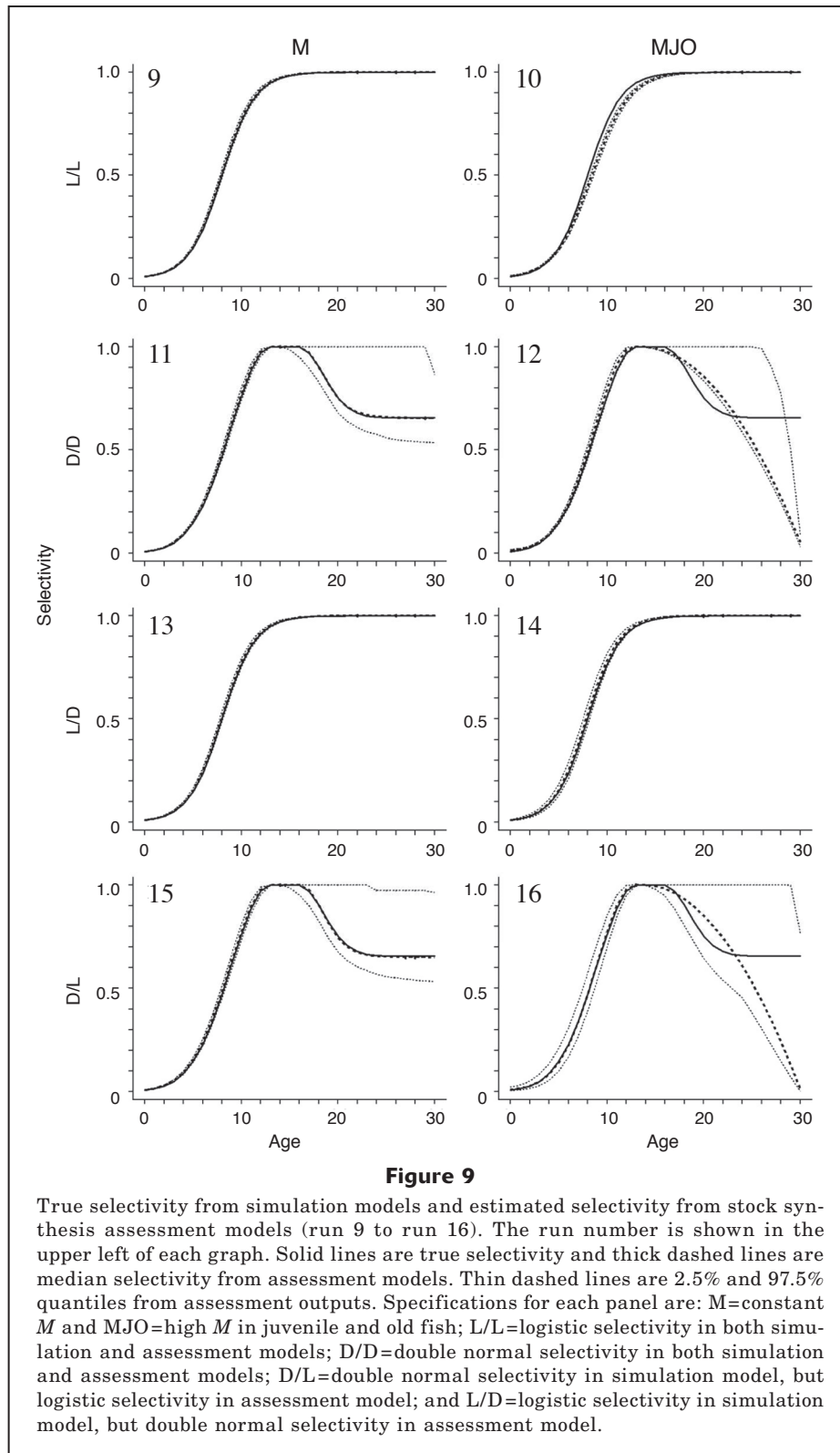
Figure 8

Time series of spawning outputs from simulation and stock synthesis assessment models (runs 9 to 16). The run number is shown in the upper right of each graph. See Table 2 for model and parameter setup for all runs Solid lines are median simulation outputs and thick dashed lines are median assessment outputs. Thin dashed lines are 2.5% and 97.5% of quantiles from simulation outputs. Specifications for each panel are: M=constant M and MJO=high M in juvenile and old fish; L/L=logistic selectivity in both simulation and assessment models; D/D=double normal selectivity in both simulation and assessment models; D/L=double normal selectivity in simulation model, but logistic selectivity in assessment model; and L/D=logistic selectivity in simulation model, but double normal selectivity in assessment model.

(Fig. 10). However, selectivity was poorly fitted for old fish (panel 12, Fig. 9). Percentages of runs that finished and that had satisfactory MGC rates were similar to those runs (runs 1 to 4) with the same

selectivity and M specifications but with h priors included (Table 4).

If no priors for h were used and natural mortality was estimated in the assessment models (runs 13 to

Figure 9

True selectivity from simulation models and estimated selectivity from stock synthesis assessment models (run 9 to run 16). The run number is shown in the upper left of each graph. Solid lines are true selectivity and thick dashed lines are median selectivity from assessment models. Thin dashed lines are 2.5% and 97.5% quantiles from assessment outputs. Specifications for each panel are: M=constant M and MJO=high M in juvenile and old fish; L/L=logistic selectivity in both simulation and assessment models; D/D=double normal selectivity in both simulation and assessment models; D/L=double normal selectivity in simulation model, but logistic selectivity in assessment model; and L/D=logistic selectivity in simulation model, but double normal selectivity in assessment model.

16), the results varied. For runs 13 and 15, in which a single natural mortality was used for all ages and was estimated in the assessment models, key assessment outputs, including spawning outputs, selectivity, and distributions of estimated h values, were very similar to runs 9 and 11 (Tables 3 and 4; Figs. 8–10). Estimated values of natural mortality (M) were also very close to the true underlying M values (Table 5).
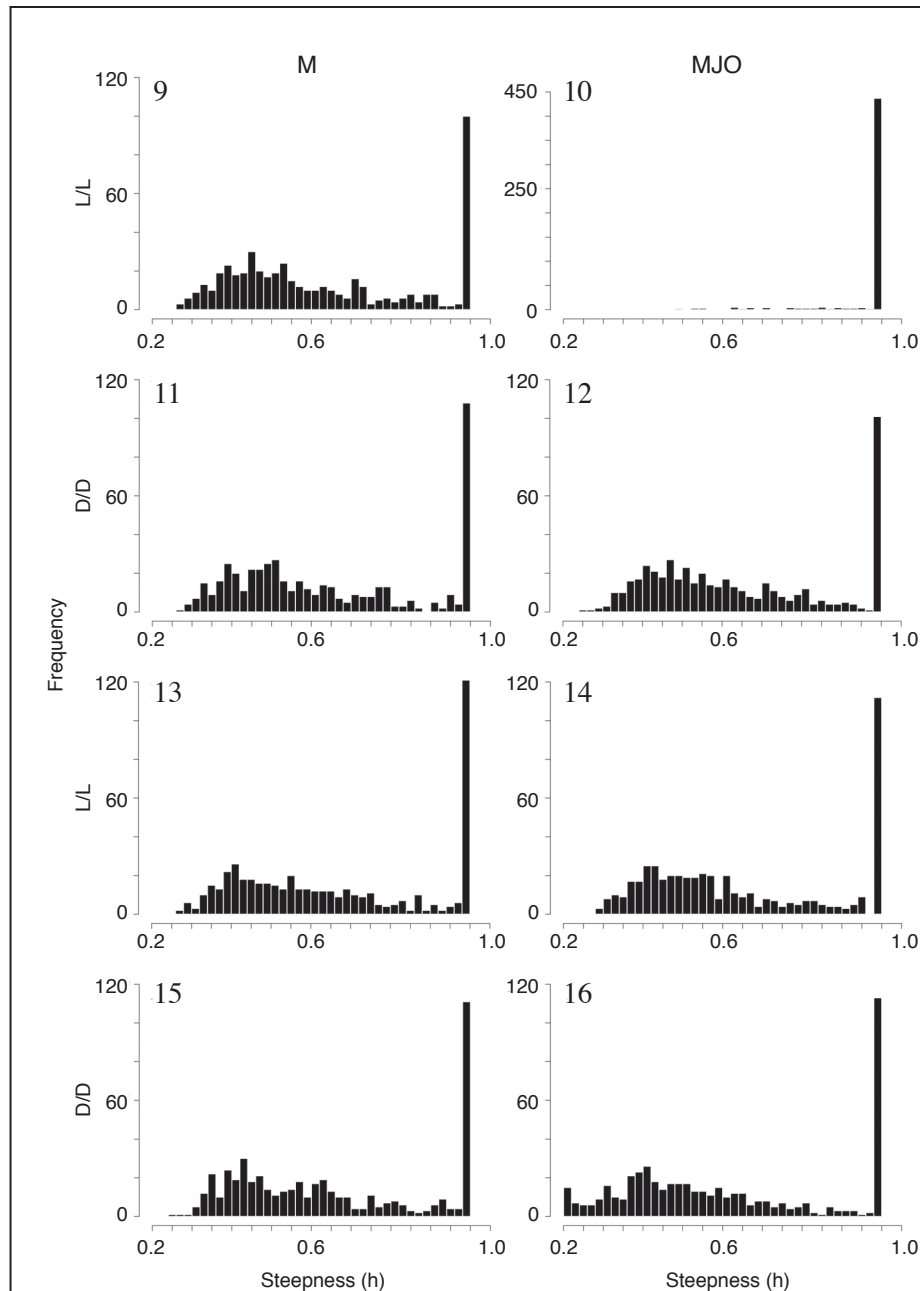
Figure 10

Frequency plots of estimated steepness (*h*) in stock synthesis assessment model for runs 9 to 16. The run number is shown in the upper left of each graph. True steepness value is 0.6. No prior for *h* was used in the assessment models. Specifications for each panel are: M=constant *M* and MJO=high *M* in juvenile and old fish; L/L=logistic selectivity in both simulation and assessment models; D/D=double normal selectivity in both simulation and assessment models; D/L=double normal selectivity in simulation model but logistic selectivity in assessment model; and L/D=logistic selectivity in simulation model, but double normal selectivity in assessment model.

For run 14, which had the same model configuration as run 10, except that four natural mortality values were used in both the simulation and estimation models, the assessment outputs matched well with those in the simulation model (Table 3; Figs. 8 and 9). Estimated natural mortalities also matched reasonably well with

the true values (Table 5). For run 16, which had the same model configuration as run 12 except that four natural mortalities were used in both models, the assessment outputs matched very poorly with those in the simulation model (Table 3; Figs. 8 and 9). Spawning outputs of all years, including B_0, estimated by the assessment model were much higher than those in the simulation model (Table 3; panel 16 in Fig. 8), and selectivity was poorly fitted for old fish (panel 16, Fig. 9). Estimated natural mortalities for old fish (M_4) showed a bi-modal distribution (Fig. 11), and there were strong interactions between estimated M_4 and selectivity for old fish (e.g., fish at age 30) (Fig. 12). There was a high proportion of cases (394 out of 500, Fig. 12) where M was estimated to be very small (mean=0.03).

Patterns of convergence performance, between runs 9 to 12 and between runs 13 to 16, were very similar to those runs between runs 1 to 4 because these runs had the same setup for selectivities (Table 4).

Discussion

Our research has shown that the assumption of a constant natural mortality for all ages when natural mortality is actually elevated in young and old fish can lead to inaccurate estimates of many important population and management quantities. The manner in which selectivity is modeled is also very important in determining which assessment parameters are poorly estimated and how these interact with one another in the model.

In general, population depletion was well estimated, even when mortality and selectivity were incorrectly specified in assessment models because population depletion is a robust indicator of population status. This is mainly because depletion is estimated as the ratio of two quantities (terminal spawning output divided by virgin spawning output), both of which exhibit similar relative biases. Estimates of another management variable, i.e., the OFL, were consistently biased, although 95% quantile intervals overlapped zero for some runs. These results indicate that OFL may be a more precautionary management indicator than population depletion. However, more research is needed to compare these two indicators because OFL depends on F_{MSY} and biomass in the terminal year and estimates of these two quantities were strongly influenced by how natural mortality, selectivity and other population parameters were modeled in the assessment.

Our results show that catchability coefficients for juvenile and adult surveys can be strongly positively biased if natural mortalities are higher in young and old fish but are misspecified in the estimation model, even when selectivity is correctly specified. If juvenile
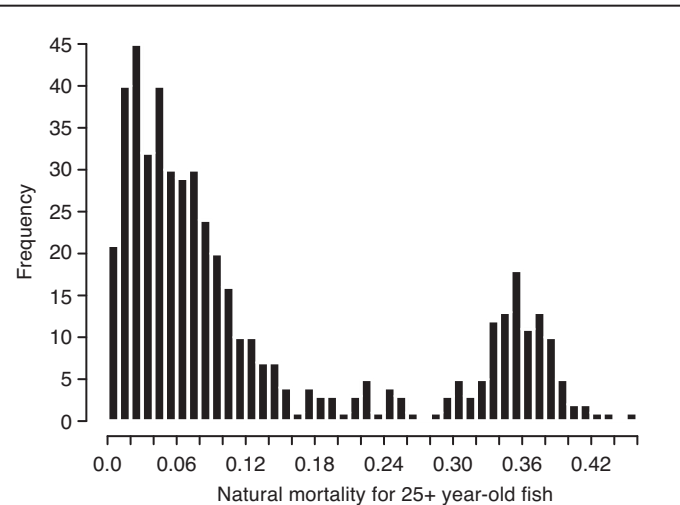

Figure 11

Frequency plots of estimated natural mortality for 25+ year-old fish (M_4) from run 16. True M_4 values ranged from 0.25 to 0.5, and no prior for steepness (h) was used in the assessment models.
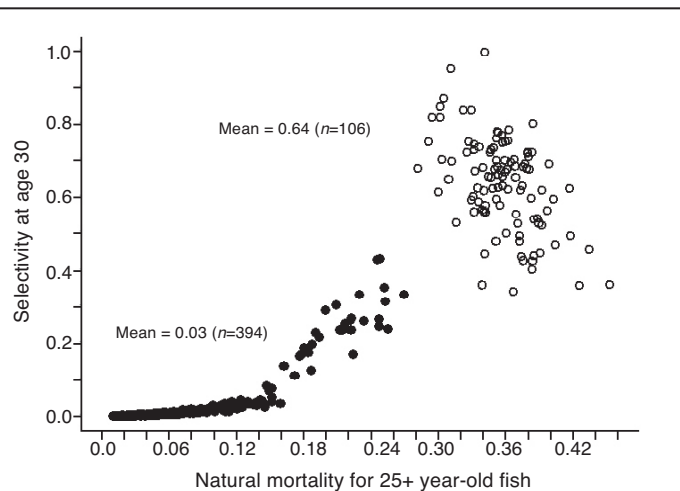

Figure 12

Estimated selectivity at age 30 versus natural mortality for 25+ year-old fish (M_4) from run 16. True M_4 values ranged from 0.25 to 0.5 and no prior for steepness (h) was used in the assessment models. Outputs were plotted in two separated groups based on the estimated M_4 values. The first group had estimated M_4 values ≤0.28 (solid dots) and the second had estimated M_4 values >0.28. Means on the graph are mean selectivities for age-30 fish.

natural mortality is higher than that for adult fish, but is assumed to be the same as that for adult fish, catchability coefficients for juveniles from surveys of precruits are poorly estimated. In many stock assessments, these coefficients are unknown and are often very small numbers because relative abundance is measured in

surveys. In this case there is no logical way within the estimation model to identify these poorly estimated parameters. In cases where survey indices are derived to measure absolute population abundances, catchability coefficients for these survey indices could be estimated to be greater than unity because of misspecified natural mortality.

The best to model selectivity in stock assessment models poses great challenges. This is especially true in modeling the selectivity of old fish. That is, one must decide if asymptotic (i.e., logistic) or dome-shaped (i.e., double normal) selectivity should be used. In most cases, no field or experimental data exist to support the choice of which form of selectivity is appropriate. As shown in this study, decreased selectivity in old fish can erroneously be attributed to increased natural mortality in old fish, and stock assessment models cannot resolve this error. In addition, the available sampling data for old fish in either age or length compositions are typically rare and render the estimation of the descending portions of selectivity curves imprecise and uncertain. Moreover, misspecifications of selectivity for old fish can still lead to moderately incorrect estimates of population status and management parameters (runs 7, 8, 11, and 12). Such incorrect estimates can have a greater effect on population status if old fish have higher weight-specific fecundity than young spawners, as is the case in many rockfish species along the U.S. west coast (Dick, 2009).

Double normal selectivity has been widely used in recent stock assessments where the SS3 program was used. It has six parameters and is a very flexible selectivity function that can model a wide range of shapes for fishery selectivity (Methot, 2009a). Our study shows that double normal selectivity can sometimes lead to "unstable" estimations in stock assessment models. That is, the model may fail to converge properly, even in the absence of model specification error (runs 3 to 6, and runs 11 and 12). In the case of run 3, in which double normal selectivity is used in both the simulation and the assessment model, and natural mortality is also correctly specified, model runs succeeded only 86% of the time and the MGC criterion was satisfied only 81% of the time. This finding further highlights the difficulty in estimating the descending portion of a dome-shaped selectivity curve and the uncertainty in estimating selectivity parameters. Unstable descending curves have also been observed in some recent west coast groundfish assessments, where selectivities for the last age (length) group drops to a very small value (He et al., 2009). Further study on the stability of double normal selectivity may be needed to address this issue.

We also conducted additional runs, in which high natural mortalities were simulated only for juvenile fish, and only for old fish, but were assumed to be constant in assessment models. The results showed that if high natural mortalities in juvenile fish existed but were misspecified in the assessment model, catchability coefficients for surveys of juveniles would be estimated to be much higher in assessment models (from 2.5 to 3.6

as compared to the true value of 1.0). Other assessment results for runs with high natural mortalities in juvenile fish, however, were very similar to runs presented in this paper. If only high natural mortalities for old fish existed but were misspecified in the assessment model, assessment results would also be very similar to those of runs presented in this study with no biases in estimates for catchability coefficients for surveys of juveniles. This conclusion would indicate that effects of misspecifications of natural mortalities for juvenile and old fish on assessment results are mostly independent of each other.

Natural mortality has rarely been treated as an estimable parameter and has often been set as a constant in stock assessment models. Our study shows that, given informative age composition data, natural mortality can be estimated if M is constant across ages or selectivity is asymptotic. However, if M is high in both juvenile and old fish, and selectivity is dome-shaped, estimates of M for old fish are very unreliable because that parameter strongly interacts with selectivity. Because we examined only limited scenarios of data and model configurations, further and more detailed studies are needed to fully explore the feasibility and benefits of estimating natural mortality for fishery stock assessments.

Stock assessment models in this study were fitted to data from simulation models with known model structure and error variance. In all simulation runs, the stock-recruitment function variability parameter was fixed (S_R=0.5) and is relatively small compared to that of some stock assessments of the U.S. westcoast groundfish (Field et al., 2009; He et al., 2009; Wallace and Hamel, 2009). Given that the simulation data were much "better" than those available for most stock assessments, we found that it is still difficult to estimate the stock-recruitment relationship. As shown in runs 9 to 12, in which no priors for steepness (h) were given to the model, steepness was often estimated to be near or at the upper bound of 1.0 (Fig. 10), as has been found in other studies (Magnusson and Hilborn, 2007; Haltuch et al., 2008). This finding indicates that it is very difficult, if not impossible, to accurately estimate stock productivity in practice, where other uncertainties, such as model structures or lack of recruitment surveys, may further confound this issue (Haltuch et al., 2009). Test runs on the simulation and assessment models with much longer time periods (300-year runs with 200 years of fishing down and data outputs to assessment models) show that estimates of stock recruitment relationships were reasonably close to true values. But this long period of data collection is generally not available for stock assessments. In many previous studies, the difficulty in estimating stock recruitment relationships has been emphasized, and sufficient biological information and fisheries data, which are lacking in many fisheries, are required to achieve reasonable estimation for stock recruitment relationships (Myers et al., 1995; Rose et al., 2001; Magnusson and Hilborn, 2007; Conn et al., 2010). Further studies on how or if

stock-recruitment relationships can be estimated at given levels of recruitment variability, data availability, and stock contracts are needed to provide general guidelines for estimating stock-recruitment relationship in assessment models.

We believe that even with informative data and a correctly specified estimation model, there are strong interactions between natural mortality and fishery selectivity in stock assessment models. Misspecification of both parameters can lead to poor estimates of important population and fishery parameters, which in turn can produce under- or over-estimates of important management quantities, such as stock depletion and OFL. Improvement in the assessment modeling approach itself may not resolve these problems because of the interdependence of mortality, selectivity, and stock recruitment functions within the models. Uncertainty analysis of stock assessment models on age- or length-specific mortality and selectivity is also needed and should be included for assessments of model performance and for management of assessed stocks.

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Appendix: Description of simulation model and data errors

The population is age-structured and is assumed to be subject to one fishery with constant selectivity over years. There are two survey indices. Recruits vary over years and there are sampling errors in surveys, catches, and age-composition data.

Initial condition and cohort growth

Initial conditions of the population are numbers of fish at sex x, at age a, and at the first model year ($y=0$), which is given by the equation

$$N_{x,0,a} = \begin{cases} 0.5R_0 & \text{if } a = a_{min} \\ N_{x,0,a-1}e^{-M_{x,a}} & \text{if } a_{min} < a < 3*a_{max} \end{cases}, \quad (1)$$

where R_0 = initial (virgin) recruitment;
a_{min} = age of recruitment (minimum age in model);
a_{max} = maximum age, including age-plus groups; and
$M_{x,a}$ = natural mortality for sex x, at age a, which is constant across years, and can be constant or vary by age, depending on the model setup.

Population dynamics

The numbers of fish in subsequent years are given by the equations

$$N_{x,y,a} = \begin{cases} 0.5R_y & \text{if } a = a_{min} \\ N_{x,y-1,a-1}e^{-(M_{x,a}+F_{x,y-1,a})} & \text{if } a_{min} < a < a_{max} \\ N_{x,y-1,a-1}e^{-(M_{x,a}+F_{x,y-1,a_{max}})} + N_{x,y-1,a_{max}}e^{-(M_{x,a}+F_{x,y-1,a_{max}})} & \text{if } a = a_{max} \end{cases}, \quad (2)$$

where R_y = expected recruitment at year y and is modeled by the Beverton-Holt stock recruit relationship:

$$R_y = \frac{SO_y}{\alpha + \beta SO_y},\qquad(3)$$

where R_y = recruitment at year y;
SO_y = spawning output at year y; and
α and β are recruitment parameters.

The relationship can be reparameterized by using a steepness parameter (h):

$$\alpha = \frac{\frac{B_0}{R_0}(1-h)}{4h},\qquad(4)$$

and

$$\beta = \frac{5h-1}{4hR_0},\qquad(5)$$

where B_0 is virgin spawning output ($B_0 = SO_0$), and R_0 is defined previously.

The "steepness" is the expected fraction of R_0 at 0.2 B_0 and is set to range from 0.2 to 1.0. When $h = 0.2$, recruits are a linear function of spawning output ($\beta = 0$, and $R_y = \frac{1}{\alpha}SO_y$). When $h = 1$, recruits are constant and independent of spawning output ($\alpha = 0$, and $R_y = \frac{1}{\beta}$). In the simulation, R_y is replaced by actual annual recruitment (R_y^1, see Eq. 15) which includes annual recruitment deviation (R_y^δ).

Selectivity, fishing mortality, and catch

Selectivity is same for both sexes. Logistic selectivity is given by the equation

$$S_a = \frac{1}{1+e^{-\ln(19)(a-\eta_2)/\eta_1}},\qquad(6)$$

where η_1, and η_2 are selectivity parameters.

Double normal selectivity is a special function for selectivity used by the SS3 program with two normal functions jointed by smooth functions. Details of this special function are given in Methot (2009a). There are six parameters in this selectivity function: (η_1) ascending inflection age; (η_2) width of plateau expressed as logistic between maximum selectivity and maximum age; (η_3) logarithm of ascending width; (η_4) logarithm of descending width; (η_5) selectivity at age 0 expressed as logistic between 0 and 1; and (η_6) selectivity at maximum age expressed as logistic between 0 and 1.

Fishing mortality is given by

$$F_{x,y,a} = FF_y S_a,\qquad(7)$$

where FF_y = full fishing mortality for year y; and
S_a = selectivity at age at.

Annual catch by fishery at sex x, and age a is given by

$$C_{x,y,a} = N_{x,y,a}\frac{F_{x,y,a}}{M_x + F_{x,y,a}}\left(1 - e^{-\left(M_{x,a}+F_{x,y,a}\right)}\right).\qquad(8)$$

Landing by fishery f at year y, ψ_y, is given by

$$\Psi_y = \sum_x \sum_a C_{x,y,a} W_{x,a},\qquad(9)$$

where $W_{x,a}$ = weight of fish at sex x an age a, which is assumed to be constant for all years.

Growth, weight and spawning output

Growth and length-weight relationship are given by

$$L_{x,a} = L_x^\infty\left(1 - e^{-K_x\left(a - t_x^0\right)}\right)\qquad(10)$$

$$W_{x,a} = \tau_1 L_a^{\tau_2},\qquad(11)$$

where $L_{x,a}$ = length at sex x and age a;
L_x^∞, K_x, and t_x^0 = growth parameters for sex x; and
τ_1 and τ_1 = length-weight parameters.

Annual biomass B_y is given by

$$B_y = \sum_x \sum_a N_{x,y,a} W_{x,a}.\qquad(12)$$

Annual spawning output is given by

$$SO_y = \sum_a P_a N_{1,y,a} G_a,\qquad(13)$$

where P_a = proportion of mature females at age a; and
G_a = fecundity for female at age a.

Abundance index

The abundance index (I) for year y and survey i has the following relationship:

$$I_{y,i} = q_i \sum_x \sum_a N_{y,x,a} S_{x,a},\qquad(14)$$

where q_i = catchability coefficient for survey i;
$N_{y,x,a}$ = population abundance; and
$S_{x,a}$ = selectivity for sex x and age a.

When the abundance index ($I_{y,s}$) is outputted to the assessment model, a new index ($I'_{y,s}$) is created by adding sampling error to $I_{y,s}$ (see Eq. 16).

Recruit variability and sampling errors:

Estimated annual recruitment (R'_y), annual survey indices ($I'_{y,s}$), and annual landings (ψ'_y) are all subject to log-normal errors with zero means and their respective standard deviations:

$$R'_y = R_y e^{R_y^\delta}\qquad(15)$$

$$I'_{y,i} = I_{y,i}e^{I^{\delta}_{y,i}} \qquad (16)$$

$$\Psi'_{y} = \Psi_{y}e^{\Psi^{\delta}_{y}} \qquad (17)$$

where $R^{\delta}_{y} \sim N(0,\sigma^2_R)$, $I^{\delta}_{i,y} \sim N(0,\sigma^2_i)$, and $\Psi^{\delta}_{y} \sim N(0,\sigma^2_{\Psi})$.

Age-composition data are subject to multinomial sam-

pling errors with a fixed number of aged fish (n) for all years:

$$X_{y,x,a} \in \{0,...,n\} \qquad (18)$$

$$\sum_{x}\sum_{a}X_{x,a} = n. \qquad (19)$$