



Hiding or dead? A computationally efficient model of selective fisheries mortality

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ARTICLE INFO

Article history:

Received 6 July 2012

Received in revised form 28 August 2012

Accepted 29 August 2012

Keywords:

Stock Synthesis

Rosa Lee's Phenomenon

Selective mortality

Dome-shaped selectivity

ABSTRACT

100 years after Rosa Lee (1912) showed that higher mortality on faster growing fish can alter length-at-age distributions in fish populations, we present a computationally-efficient and parsimonious method for modeling size-selective mortality within a commonly-used assessment model, Stock Synthesis. Stock Synthesis allows the normal distribution of length-at-age to be partitioned into three or five overlapping platoons with slow, medium, or fast growth trajectories. The platoons are tracked separately in the model, and experience different degrees of size-selective fishing pressure and mortality, but are assumed to be unobservable except through changes in the length distribution. Simulations are used to explore this phenomenon in conjunction with dome-shaped selectivity, an alternative explanation for observing fewer than expected large fish in sampled data, but with very different implications for population productivity. For data simulated both with and without platoons, misspecification of the assumptions about growth are found to bias model results, with selectivity often incorrectly identified as the cause of fewer observations of larger fish. Trends in dome-shaped selectivity were explored as a potential diagnostic of model misspecification.

Published by Elsevier B.V.

1. Introduction

Lee (1912), examining back-calculated growth rates for herring, haddock, and trout, noted that fish caught at young ages grew faster at any given age than fish caught at older ages. Ricker (1969) identified two potential causes of this pattern, which has been referred to as “Rosa Lee's Phenomenon” (Walker et al., 1998): biased sampling and selective mortality. Estimating growth within integrated stock assessment models such as Stock Synthesis (SS) is a way to correct for biased sampling of length-at-age (Methot, 2009), and internally estimated growth is now common practice in stock assessments that use integrated models. However, the effect of selective mortality (fishing pressure removing faster-growing fish from the population, such that fish captured at older ages are drawn from a slower-growing subset of the population), although subject of many valuable analyses (Kristensen et al., 2006; Parma and Deriso, 1990; Walker et al., 1998), has not been commonly included in stock assessment models used for management. Two factors that hinder the exploration of selective mortality in stock assessment models are the additional computational complexity required and the potential difficulty in distinguishing this phenomenon from other potential causes of the observed patterns. In this paper, we describe a relatively simple and parsimonious way of

exploring changes in length-at-age due to fishing pressure that has been implemented in SS. We then explore confounding of this phenomenon with dome-shaped selectivity, and consider a potential diagnostic of the presence of selective mortality in the dynamics of a population.

The approach taken by many modern age-structured stock assessment models, including SS, is to track numbers-at-age, often within some potential set of divisions such as gender or spatial area. The length distributions of individuals at each age are typically assumed to be normally distributed around a growth curve representing the mean population length-at-age. In SS, selectivity can be age- or length-based, but in both cases, the impact of the fishery has typically been converted into a mortality rate applied equally to the numbers at each age (within a given gender, area, etc.). The calculation of selected biomass-at-age includes the product of selectivity and the normally-distributed length-at-age when selectivity is length-based. However, the remainder of each cohort surviving the fishery is assumed in the following year to once again have a normal length distribution around the same growth curve. This common assumption is reasonable if inter-year variability in growth of individual fish is high. However, the assumption of repeatedly regenerated normal distributions could lead to biased assessment results if inter-year variability in growth is low and Rosa Lee's Phenomenon is occurring in a population.

Dome-shaped selectivity is a common explanation for length distributions that contain fewer large fish than expected. Many possible causes of such patterns exist, including fisheries targeting

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areas with high catch rates which may not include the largest fish. Sampson et al. (2011) showed that the combined effect of multiple fishing fleets each with different asymptotic selectivity patterns could lead to a dome-shaped pattern in aggregate. Dome-shaped selectivity and size-dependent mortality could both lead to similar patterns in distributions of length-at-age, but they have very different implications for management. In the one case, the oldest (and perhaps most fecund) fish are alive and contributing to future recruitment, but unavailable to the fishing gear. In the other case, these fish are absent from the population because they have been removed by size-selective fishing pressure at an earlier age.

Consideration of length-dependent mortality in SS is made possible by dividing the population into overlapping growth “platoons”, each with their own growth curve, distributions of length-at-age, and independently changing numbers. This is very similar to the treatment of each gender as having potentially different growth trajectories, but it is assumed that no data could distinguish between faster and slower growing subsets of a population, so expected values are aggregated across platoons in the observation sub-model of SS (whereas data from males and females may be either aggregated or left separate to match the format of the observed data). SS also allows consideration of separate growth “morphs” within each gender to account for phenomenon such as spatial differences in growth rates. Growth morphs each have a separate set of growth parameters. Unlike platoons, growth morphs are assumed to be identifiable (via spatial location, stable isotopes, or some other data). Growth morphs are not considered in this paper.

Evolutionary change in growth rates (Conover and Munch, 2002) is not modeled in SS, so the distribution of recruits among platoons is independent of the distribution of spawners among platoons. For longer-lived fish, such as the simulated population in this analysis, the mean generation time and the duration of strong fishing pressure are on the same order of magnitude, so the potential for evolutionary change is likely small compared to the effects of selective mortality regardless of the degree of heritability in growth rates.

Inclusion of selective mortality in simulation models (e.g. Goodyear, 2004; Kristensen et al., 2006) is more common than in estimation models, and in that context, the computational demands of additional complexity may not be a factor. Indeed, in a simulation context, an individual-based model can be used to capture the full spectrum of options for modeling selective mortality and variability in growth. However, it is necessary to have a computationally efficient way to model selective mortality if it is to be considered in an applied stock assessment model.

The “growth groups” approach of Punt et al. (2001, 2002) divides the population into a set of growth trajectories in a similar way to the approach presented here. However, Punt et al. (2001, 2002) did not include variability within growth groups, only between them, thus requiring a large number of groups to obtain a smooth distribution of lengths. This approach also does not allow for the possibility of annual variability in growth within a group. Another parsimonious method for modeling length-based mortality in an age-structured model is the “slicing” method of McGarvey et al. (2007). This approach is an efficient way to model the effect of a legal minimum length within an age-structured model, but the benefits of this approach may be reduced for stocks without such a limit.

2. Methods

The impact of including platoons to model selective mortality was quantified by simulating populations with and without platoons using SS as both simulation and estimation model. An initial set of deterministic simulations was conducted to examine changes

in measures of population productivity, including mean weight and mean length, resulting from including platoons in SS. The sensitivity of these changes to the selectivity of the fishery was also examined. A second set of simulations involved generating bootstrap data sets to be used as input in a collection of estimation models. All combinations of simulation and estimation models with either one or five platoons each were considered to quantify the accuracy of estimated parameters and derived quantities under matching or mismatching assumptions about how growth occurs.

The models all had a fishing fleet and a survey. The fishery and survey had asymptotic selectivity in the simulation models. In the estimation models, the fishery was assumed (correctly) to have asymptotic selectivity, but survey selectivity was allowed to be dome-shaped. This choice was made to focus the exploration of dome-shaped selectivity on the survey for which age samples were assumed to be available for assessment purposes while avoiding the additional complexity of interacting dome-shaped patterns for both the survey and the fishery. The number of fleets is likely to be larger and the complexity of selectivity patterns much greater in most actual applications of SS, than the approach chosen here for illustration purposes.

2.1. Growth platoons

Growth was assumed to follow the von Bertalanffy growth curve, with males and females having identical growth rates. Length-at-age was assumed to be either normally distributed or the sum of multiple normal distributions (Fig. 1). The distribution of length at each age within each platoon was assumed fixed across all years, but the relative distribution of numbers across each platoon (starting with a specified allocation at recruitment) changes over time in a given cohort as a result of length-based selectivity leading to different rates of removals from each platoon.

SS allows variability in length-at-age to be a 2-parameter function of age or length. The partitioning of variability in growth within and between platoons is inspired by a pattern that would be true with infinite number of platoons. The total variance in length-at-age in the case of one platoon is assumed to be the sum of the variances within and between multiple platoons:

$$\sigma_{\text{total},a}^2 = \sigma_{\text{within},a}^2 + \sigma_{\text{between},a}^2 \quad (1)$$

where $\sigma_{\text{total},a}$ is the standard deviation of length at age a for when there is one platoon, $\sigma_{\text{within},a}$ is the standard deviation of length at age a for each of the five platoons, and $\sigma_{\text{between},a}$ is the parameter used to calculate the variability in mean length between platoons at age a . $\sigma_{\text{between},a}$ is treated as the difference in mean lengths between platoons, rather than a standard deviation of the mean values (which would also depend on the numbers-at-age within each platoon) in the simple approximation of three or five platoons.

The ratio $\rho = \sigma_{\text{within},a} / \sigma_{\text{between},a}$ allows the individual components to be calculated as:

$$\sigma_{\text{between},a} = (\rho^2 + 1)^{-1/2} \sigma_{\text{total},a} \quad (2)$$

and

$$\sigma_{\text{within},a} = \rho(\rho^2 + 1)^{-1/2} \sigma_{\text{total},a} \quad (3)$$

The difference in mean length-at-age between platoons at each age a is $\sigma_{\text{between},a}$. Thus, for example, if an age-class is assumed to have a mean length of 100 cm with a CV of 0.2, then $\sigma_{\text{total},a} = 20$. $\sigma_{\text{between},a} \approx 8.9$ and $\sigma_{\text{within},a} \approx 17.9$ if there are five platoons and ρ is assumed to be 2. The mean lengths at this age for the five platoons would be 82.1 cm, 91.1 cm, 100.0 cm, 108.9 cm, and 117.9 cm (each ~ 8.9 cm apart).

The distribution of recruits assigned to each platoon can be chosen by the user in SS. The default proportions of 3.1% for the 1st

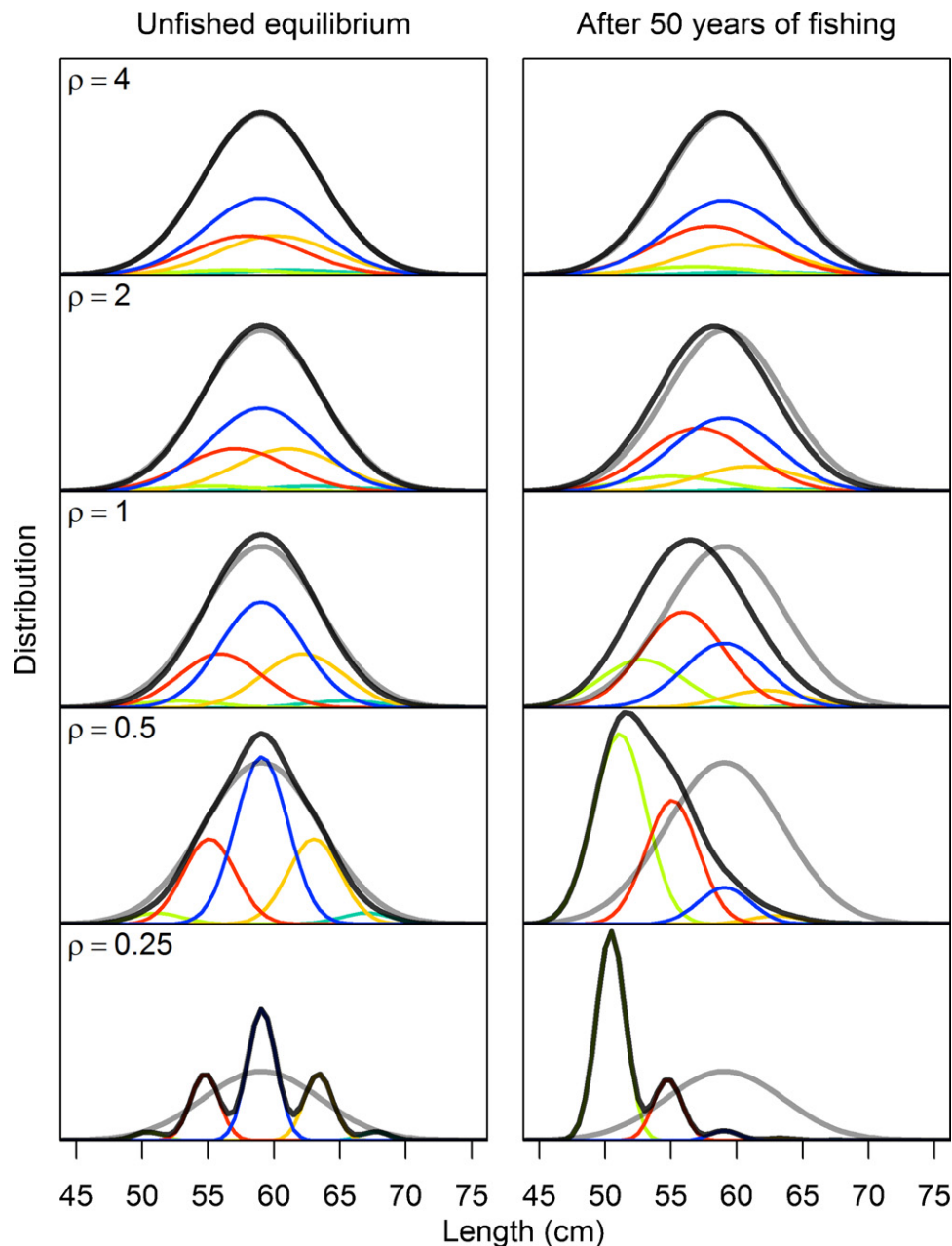


Fig. 1. Distribution of length at age 50 for the one platoon (thick gray line) and the five platoon (thick black line indicating sum of thin colored lines) cases. The left column shows unfished equilibrium distributions and the right column the effect of 50 years of fishing. Rows differ in ρ , the ratio of standard deviation within each platoon to standard deviation across platoon means. To facilitate comparisons, distributions are rescaled so that total under each case is equal. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and 5th platoons, 23.7% for the 2nd and 4th platoons, and 46.4% for the 3rd (central) platoon were assumed here. These proportions were chosen to make the distribution of length-at-age, aggregated across five platoons, reasonably approximate a normal distribution. SS also allows there to be three platoons, although that case is not considered in this paper.

The value of ρ controls the degree to which the growth platoons overlap. This may be viewed as a measure of the variability of the growth trajectories of individual fish. Less overlap between platoons (i.e. a lower value for ρ) corresponds to the assumption that growth trajectories are more determined from an early age. More overlap between platoons approaches the assumption inherent in current common practice that annual growth of individuals is highly variable, and the distribution of length at each age is

independent of any length-based fishing pressure applied to the previous year.

2.2. Selectivity

A 5-parameter double-normal, length-based selectivity function was used in all simulation and estimation models (Table 1). The simulation models had asymptotic (monotonically increasing to 1.0) selectivity for both the fishing fleet and survey, which was implemented as a high value for the descending slope parameter in the double-normal selectivity function. In the estimation models, the fishing fleet was assumed to have asymptotic selectivity, so the parameters controlling the width of the peak selectivity (selectivity = 1) and descending slope were fixed at the values in

Table 1
Simulated and median estimated parameter values. Medians with relative error greater than 10% are bolded. Dashes indicate parameters fixed at simulation values in estimation models. Details of the growth, weight, maturity, recruitment, and selectivity functions are provided by Methot and Wetzel (this issue).

Symbol	Description	Simulated value	Median estimated value			
		Case:	A	B	C	D
		Platoons in sim., est.:	1, 1	5, 5	1, 5	5, 1
Growth and maturity parameters						
M	Natural mortality (year ^{−1})	0.050	0.051	0.050	0.081	0.045
L_1	Length at age 1 (cm)	18.0	18.0	18.0	18.0	18.1
L_2	Length at age 70 (cm)	62.0	62.0	62.0	62.0	61.7
K	Growth coefficient (year ^{−1})	0.0470	0.0470	0.0470	0.0470	0.0458
CV_1	Length CV at age 1	0.130	0.130	0.130	0.147	0.145
CV_2	Length CV at age 70 (exponential offset)	−0.600	−0.598	−0.599	−0.597	−0.549
Ω_1	Weight coefficient (kg cm ^{−3} 10 ^{−6})	9.77	–	–	–	–
Ω_2	Weight exponent	3.17	–	–	–	–
Ω_3	Length at 50% maturity (cm)	38.78	–	–	–	–
Ω_4	Maturity slope (cm ^{−1})	−0.44	–	–	–	–
Recruitment parameters						
R_0	Initial recruitment (log)	5.60	5.65	5.61	10.98	5.31
h	Stock-recruit steepness	0.440	0.416	0.430	0.466	0.445
σ_R	Recruitment variability	0.5	–	–	–	–
Selectivity parameters–fishery						
β_1	Size at which selectivity = 1 begins (cm)	55.0	54.9	55.0	53.5	53.2
β_2	Determines width of peak selectivity	−2.00	–	–	–	–
β_3	Determines slope of ascending section	5.00	4.99	4.99	4.75	4.81
β_4	Determines slope of descending section	15.0	–	–	–	–
β_5	Logit of selectivity at $L_{\min}$	−15.00	−11.3	−10.1	−8.6	−7.0
Selectivity parameters–survey						
β_1	Size at which selectivity = 1 begins (cm)	50.0	50.0	50.0	49.9	49.3
β_2	Determines width of peak selectivity	−2.00	−1.99	−2.00	−2.00	−1.52
β_3	Determines slope of ascending section	5.00	5.01	5.00	4.81	4.88
β_4	Determines slope of descending section	15.0	14.7	14.7	14.7	5.3
β_5	Logit of selectivity at $L_{\min}$	−15.0	−11.0	−8.8	−8.5	−6.7

the simulation model and only three parameters were estimated (length at peak selectivity, ascending slope, and initial selectivity). Survey selectivity was allowed to be dome-shaped in the estimation models, with five parameters estimated.

This double normal selectivity function can have 4–6 parameters in SS, depending on whether each half-normal distribution describing the ascending or descending limb of the function has a parameter controlling the initial (or final) selectivity in addition to those controlling the peak and slope (Methot and Wetzel, this issue). The choice to use the additional parameter on the ascending, but not the descending (right-hand), side was based on the belief that the ascending selectivity is generally better informed by length data than the dome-shape or lack thereof.

2.3. Parameter trends

Temporal trends in the descending slope of the selectivity function were considered in the estimation models. Such trends were not included in any of the simulations, so estimation of parameter trends may be diagnostic of model misspecification. The functional form of temporal parameter trends in SS is based on the standard cumulative normal distribution, Φ , where the parameter value in a given year is given by,

$$p(y) = p_{\text{base}} + p_{\text{offset}} \Phi \left(\frac{y - p_{\text{infl}}}{p_{\text{width}}} \right) \quad (4)$$

where y is the year in which the parameter value is being calculated, p_{base} is the base (initial year) parameter value, p_{offset} is the maximum (final year) change in parameter value, p_{infl} is the year in which half of the offset has occurred, and p_{width} is the standard deviation of the cumulative normal distribution which controls the rate at which the parameter value changes.

2.4. Simulations

Initial simulations were conducted to explore the properties of growth platoons, the implications of different choices for ρ , and the sensitivity of biological quantities (length, weight, and spawning output) to the position of the fishery selectivity curve relative to the growth platoons. These simulations involved only projecting SS with different values for ρ or peak selectivity, and involved no estimation step. Recruitment was assumed to be related deterministically to spawner biomass in these simulations.

A larger set of simulation models was then run for two cases differing in the number of growth platoons (1 or 5). For each case, 100 simulations were conducted, each with a unique time-series of randomly generated recruitment deviations. SS was the simulation model to reduce the possibility of biases in estimation model results due to structural differences, and should allow a better investigation into the effects of making matched or mismatched assumptions about growth platoons.

Parametric bootstrap data sets were generated by sampling from the appropriate distributions for each data type. This is done automatically within SS, although some additional variability was added to the bootstraps for the conditional age-at-length data. Indices of abundance were created by generating lognormal random variables from a distribution with mean determined by the simulated biomass selected in each sampling year under the assumed selectivity function, and standard deviation fixed at the assumed value for each survey point. Length and conditional age-at-length compositions were generated using the following multi-step process:

1. Observed length compositions were generated within SS from a multinomial distribution with chosen sample size and

proportions equal to the expected numbers of selected fish in each length bin in each sampling year

2. The length compositions of fish to be aged were generated by sampling outside SS from a multinomial distribution with the chosen age sample size and proportions equal to the length compositions chosen in step 1.
3. For each length bin with non-zero numbers of fish to be aged chosen in step 2, the conditional age-at-length composition was generated by sampling outside SS from a multinomial distribution with sample size equal to the value from step 2 and proportions equal to the expected distribution of observed ages conditioned on the given length bin.

The expected conditional age-at-length distributions used in step 3 include ageing error. Sampling from this distribution simulates the process of producing a set of age readings that reflects observation uncertainty as well as the sampling error. The use of additional sampling steps outside SS allows the age compositions to be associated with a different set of lengths for each bootstrap sample, unlike conditional age-at-length samples that are produced by SS automatically. The impact of this additional variability was not examined in this analysis.

The simulated populations were projected for 60 years (labeled 1951–2010), with random normal recruitment deviations from 1921 to create a non-equilibrium initial age structure. A simulation was conducted for both the 1 and 5 platoon cases for each of the 100 recruitment deviation vectors, to isolate differences in model specification from those due to simulated recruitment.

Many parameter values for the simulation model were based on a recent stock assessment for yelloweye rockfish, *Sebastes ruberrimus* (Taylor and Wetzel, 2011) to gain some biological realism. This includes growth rates, maturity and fecundity relationships, and the ageing error matrix. Likewise, the catch time-series matched that used for yelloweye for the period 1951–2010. Yelloweye rockfish are a long-lived, slow-growing species that are estimated to have become overfished during the 1990s after a rapid decline in abundance and are now in a protracted rebuilding plan. This analysis is in no way intended as a reflection of the true dynamics of yelloweye rockfish. The use of a single fishery and survey and their respective selectivities are very different from the much more complex spatial and fishery structure in the actual yelloweye stock assessment. The simulation models accounted for males and females separately, but for simplicity, the two genders were assumed to have identical growth patterns, which is not the case for the actual yelloweye stock assessment.

The method of modeling growth according to platoons explored here is no more or no less likely to be appropriate for yelloweye rockfish than any other species. However, a few qualities of the biology of yelloweye would make them more susceptible to the presence of length-based fishing mortality. First, the relatively slow growth rate means that a fast growing fish may be susceptible to a fishery with length-based selectivity for many years before a slow-growing fish from the same cohort (Fig. 2a). Second, spawning output of yelloweye is not proportional to weight, with the largest individuals producing a disproportionate fraction of the spawning output (Dick, 2009). This means that removal of even a small fraction of the fastest growing fish may have a noteworthy impact on the fecundity of the population (Fig. 2d).

SS allows the bin structure used for the population dynamics to differ from that used for the data. The initial simulation to illustrate the effect of ρ used 0.5 cm length bins to better illustrate the distribution of length-at-age across platoons. The population dynamics in both the simulation and estimation models used 2 cm length bins from 10–90 cm, but the length data were binned over a narrower range from 20 to 80 cm for all other cases. Likewise, the population dynamics had an accumulator age at 80 years (starting at age 0),

but the bins for age compositions spanned a narrower range (ages 1–70). The use of a broader range for the population dynamics than the data for these data types is intended to ensure that the underlying processes and associated calculations such as spawning output and depletion are not too influenced by the binning. However, the observed range of sampled fish with the chosen sample sizes may not warrant a similarly broad range for the data bins.

The simulated data included the following:

1. *Catch*. 60 years of catch rising from 50 mt in 1951 to a peak of 462 mt in 1982, and falling below 25 mt from 2002.
2. *Index of abundance*. A survey conducted every 3rd year from 1980 to 2010, with each of the 11 observations having a standard error on a log scale of 0.25.
3. *Length compositions*.
 - a. Fishery lengths with sample size 100 for the 30 years 1981–2010, and
 - b. Survey lengths with sample size 400 for each of the 11 survey years.
4. *Conditional age-at-length compositions*.
 - a. Survey ages with sample size 100 for each of the 11 survey years conditioned on length bin (no fishery age data were simulated).

2.5. Estimation

For each of the 100 bootstrap data sets generated with 1 or 5 platoons, estimation models were applied with 1 or 5 platoons resulting in a total of 400 estimation models falling into four groups labeled as:

- *Case A*. 1 platoon in simulation, 1 platoon in estimation (match),
- *Case B*. 5 platoons in simulation, 5 platoons in estimation (match),
- *Case C*. 1 platoon in simulation, 5 platoons in estimation (mismatch),
- *Case D*. 5 platoons in simulation, 1 platoon in estimation (mismatch).

106 parameters were estimated in each estimation model (see Table 1). The quantity ρ is not estimable in SS. The estimation models with five platoons (B and C) had ρ set to the same value as the simulation models with five platoons (B and D). The effects of misspecifying ρ in a model with multiple platoons and the ability to estimate ρ through iterative methods are topics left to future research. The estimations were repeated with three additional parameters included to allow a trend in the degree of dome-shape for survey selectivity. Of particular interest in these additional estimations is Case D in which the five platoons in the simulation model allow a reduction over time in the proportion of larger fish at each age while the estimation model with one platoon and a trend in selectivity may misinterpret the reduction in larger fish as an increase over time in the degree of dome-shape of the survey selectivity pattern.

The remaining parameters in the estimation model were fixed at the true values used in the simulation stage, including those controlling weight-at-length, fecundity-at-length and maturity-at-length, to focus the investigation on the impact of incorrect assumptions about growth platoons. In stock assessments, these quantities are often estimated externally. Two parameters that are notoriously difficult to estimate, natural mortality and steepness were estimated, but given informative priors. The prior for natural mortality was $N(0.05 \text{ yr}^{-1}; 0.0226 \text{ yr}^{-2})$. This variance was equal to that used in the actual yelloweye stock assessment (Taylor and Wetzel, 2011), but the mean was chosen to match the value used in the simulations. The prior on steepness was a beta distribution with standard deviation of 0.1 around a mean value of 0.44, which again

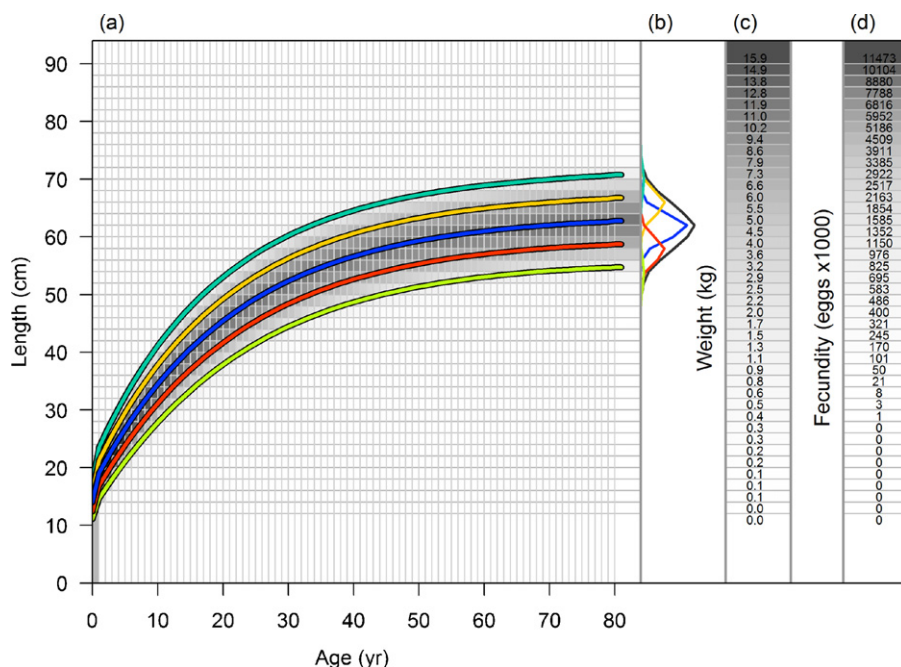


Fig. 2. (a) Mean length-at-age for each growth platoon shown on top of the grid of length $\times$ age bins used to track numbers with each growth platoon, with shading in bins indicating population proportion by length bin for each age at unfished equilibrium; (b) length distribution in the 80+ age bin at unfished equilibrium; (c) weight associated with each length bin; (d) spawning output (fecundity $\times$ maturity) associated with each length bin.

was the value used in the simulations. A sensitivity analysis was conducted in which the prior on natural mortality was made less informative with a standard deviation of 0.1 (a CV of 2.0) and the prior on steepness was widened to a diffuse beta prior with mean 0.6 and a standard deviation of 0.23, which was chosen to keep the prior likelihood associated with steepness values in the range $0.25 < h < 0.95$ above 95% of the highest prior value, to examine how the results depended on the prior distributions.

Recruitment deviations were modeled as recommended by [Methot and Taylor \(2011\)](#). This involved running each estimation model twice, where the estimated uncertainty associated with the recruitment deviates in the first run were used to adjust the lognormal recruitment distributions using a function in the R4SS software package ([Taylor et al., 2011](#)). This process is similar to that used by [Wetzel and Punt \(2011a, b\)](#) and [Garrison et al. \(2011\)](#).

3. Results

3.1. Initial simulations

The results of the initial simulations were as expected. First, less overlap between growth platoons (lower values for ρ) allows a greater impact of fishing on the distribution of length-at-age, but can also lead to cases where the length-at-age distribution is no longer normal (Fig. 1). A value of $\rho=0.5$ was chosen for the remaining simulations to illustrate an impact of fishing on length-at-age while maintaining an approximately normal distribution of length-at-age at equilibrium (Fig. 1).

Second, the initial simulations exploring the sensitivity to changes in biology-at-age to the position of the selectivity function relative to the growth platoons indicated that the greatest impact on biology occurs when selectivity strongly separates the fastest and slowest growing platoons (Fig. 3). The mean lengths in the 80+ accumulator age for each of the five growth platoons were 54.7 cm, 58.8 cm, 62.8 cm, 66.8 cm, and 70.8 cm. The greatest impact on the cohort at age 50 in the 50th year of the simulation (the first cohort to be susceptible to fishing mortality throughout

their lives) occurred when the peak selectivity of the fishery was 65 cm, right in the middle of the distribution of mean lengths for older fish. This selectivity pattern made the fastest-growing platoons more vulnerable to fishing mortality for many years while leaving the slowest-growing platoons relatively safe from fishing impacts, even at advanced ages. The impact on the biology-at-age was relatively small when either all growth platoons were fully selected at young ages (due to peak selectivity at a small size), or only the very largest fish were selected (due to peak selectivity at a large size) (Fig. 3).

The simulations with different selectivity patterns also demonstrated the extent to which impacts of changing length-at-age led to larger changes in weight and spawning output. The projection with peak selectivity at 65 cm led to a 10% reduction in the mean length of age-50 fish relative to the unfished equilibrium value. The associated reductions in weight-at-age and spawning output (Fig. 3) were about 30% and 40% respectively due to the increasing relationship between these quantities and length (Fig. 2). Spawning depletion also depended on the selectivity pattern in this simulation because the same time-series of catch was removed from different segments of the population. The greatest impact on depletion occurred when the fishery selected more small fish.

3.2. Estimation models

In common with other models written in ADMB (Fournier et al., 2011), SS provides estimates of parameter uncertainty only when it is able to successfully invert the Hessian matrix containing the variance and covariance information for the parameters and chosen derived quantities. Estimates of uncertainty in the recruitment deviations are necessary to implement the method used to determine the recruitment bias adjustment. Seven of the 400 combinations of recruitment time-series, simulation model, and operating model failed to invert the Hessian and estimate parameter uncertainty. Of these failures, none were for Cases A and B (where the number of platoons in the estimation and simulation models matched), one failure was for Case C and six were for Case

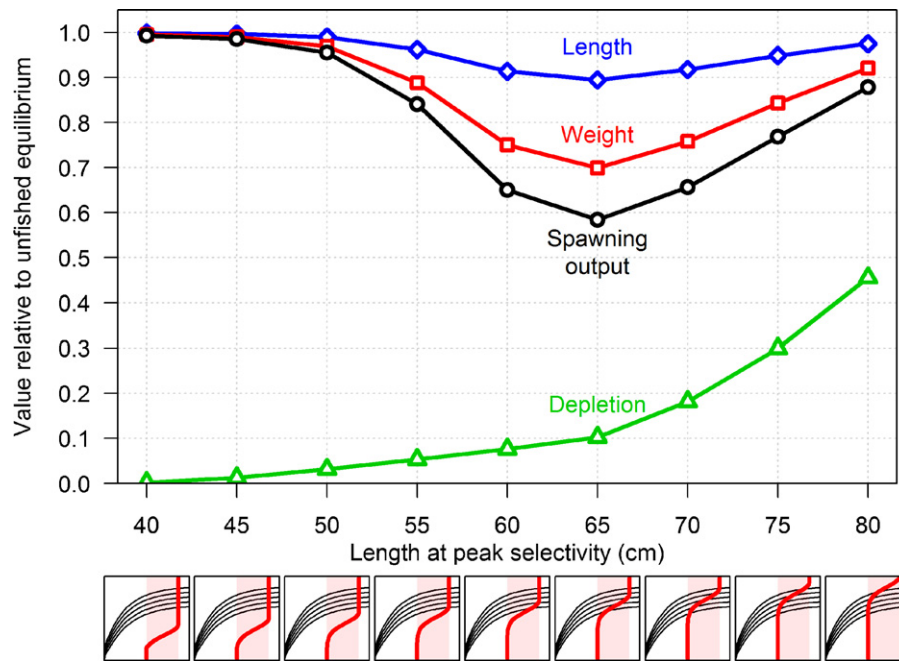


Fig. 3. Sensitivity of biology at age 50 in year 50 to changes in the position of the fishery selectivity. Curves in upper plot indicate changes relative to unfished equilibrium in mean length (blue diamonds), weight (red squares), spawning output (black circles), and spawning depletion (green triangles). The small graphics at bottom of the image show the selectivity curve (red line within the range of the pink rectangle) superimposed on the mean length-at-age for each of the five growth platoons (black lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

D (which had mismatched assumptions). This frequency of failure was seen as small enough that no accounting for their absence was made in the analysis of the median results for the remaining 393 models. The estimation model which matched the simulation model always had a higher likelihood than the model with mismatched assumptions irrespective of whether the simulation model had one or five platoons.

Results of each estimation model were then compared to the corresponding simulation model from which the bootstrap data were generated. This was necessary because some quantities, such as spawning output and depletion, varied among simulations due to random recruitment. Cases A and B, where the growth platoon assumptions matched those in the simulation models, had generally unbiased results (Table 1). The selectivity parameters which control the selectivity for the smallest fish, β_5 were most biased. However, after the logistic transformation of these parameters, the resulting median values were all less than 0.0002, which is effectively equal to the transformed simulation parameter: $(1 + e^{-15})^{-1} < 0.000001$. Other than these selectivity parameters, the next greatest differences between estimation and simulation for Cases A and B were for steepness, where the median estimates of 0.416 and 0.430, respectively, were slightly below the simulation model's value of 0.44. Derived quantities for spawning biomass, depletion, growth, and selectivity for Cases A and B were all very similar to the corresponding simulation values (Fig. 4), generally differing by at most 1%.

Fishery selectivity, which was assumed to be asymptotic in all cases, was well estimated by the estimation models. The median survey selectivity-at-length was asymptotic, but survey selectivity was inaccurately estimated as dome-shaped in a few simulations for Cases A and B (Fig. 4e and f).

The unbiased results for Cases A and B depend on modeling recruitment using the adjustment methods of Methot and Taylor (2011). The median ratio (estimated/simulated) for unfished spawning output from the first, unadjusted, runs was 111% and 110% for Cases A and B, respectively, as compared to 100% for the

second runs after adjusting the recruitment deviations based on the standard deviations estimated in the first runs. The median standard deviation of the estimated recruitment deviations for both Cases A and B was 0.18, which is much lower than value for $\sigma_R = 0.5$ used in the simulations due to the lack of information in the data about most recruitments. The greatest variability among estimated recruitments occurs in the second half of the time-series where data were more informative (Fig. 4u and v). The median yearly recruitment deviation across estimations models for Cases A and B was close to 0, even those for 1921–1950, which are used to construct the age structure in 1951. The lower variability in estimated recruitments leads to less variability in the estimated spawning depletion in the initial year compared to the simulation models (Fig. 4m and n).

Unlike the cases with matched assumptions, Cases C and D, which have mismatched assumptions regarding the presence or absence of size-dependent mortality, performed poorly in important and opposite ways. The time-series of spawning output and depletion were dramatically different between the simulation and estimation models in Case C, where the simulation models had one growth platoon but the estimation model assumed five platoons (Fig. 4o and s). The median value of spawning depletion in the final year relative to the unfished level was 111% from the estimation model compared to a median of 27% in the simulation models. The expected length-at-age compositions would change over time for the Case C estimation model. However, this is not the case for the simulation model with one growth platoon. The estimation models for Case C have a very high equilibrium recruitment (median $\log(R_0) = 10.98$ when simulation model values were 5.6) and a strong pattern of bias in recruitments (Fig. 4w) to deal with this mismatch. The very high abundance removes the influence of the fishery on the length compositions, and the patterns in recruitment deviations lead to a better fit to the index of abundance (which varies with the fishery-induced changes in the simulation models). Case C also severely overestimated natural mortality (median of 0.081 yr^{-1} compared to 0.05 yr^{-1} in the simulations), which

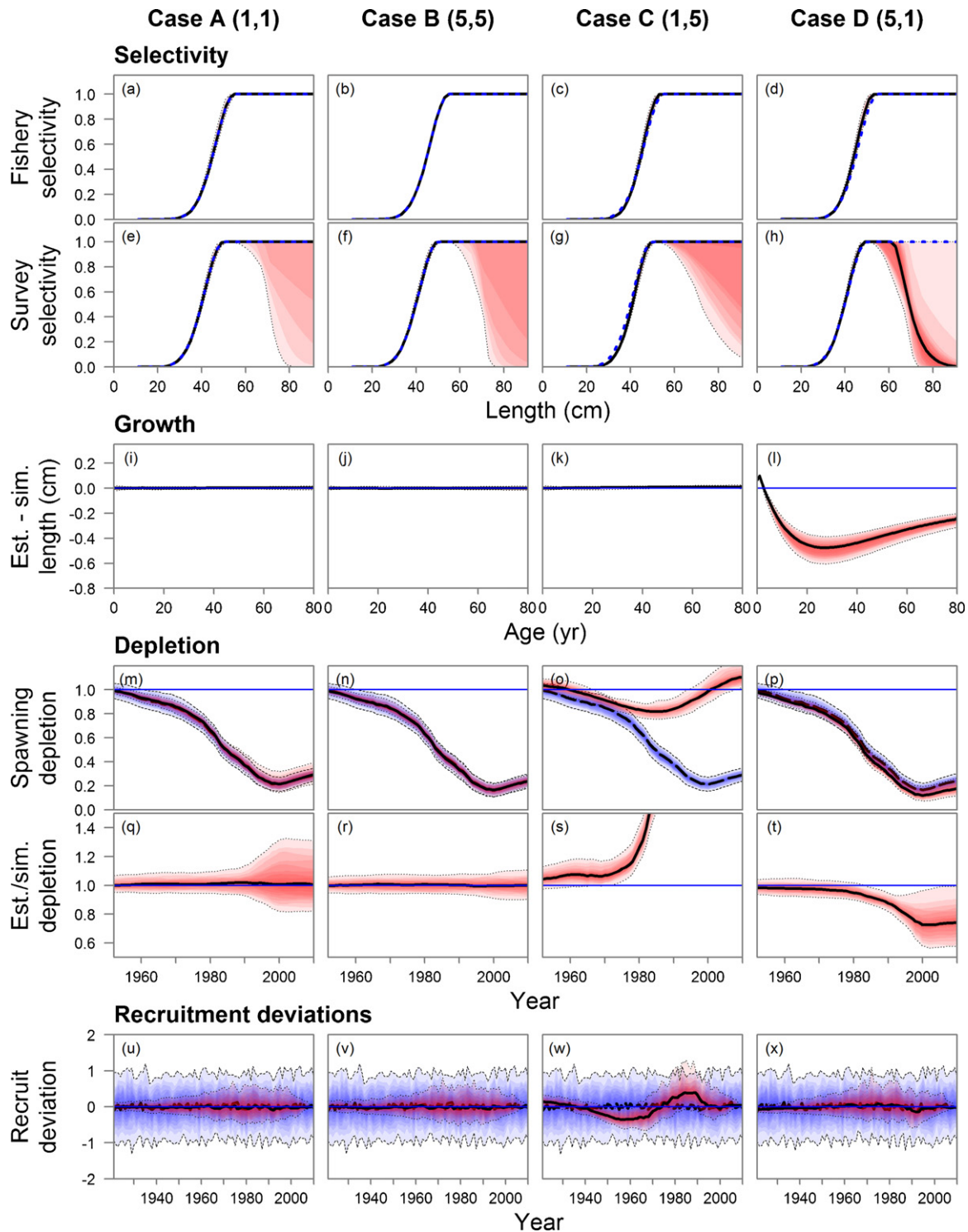


Fig. 4. Results of simulation analysis. Columns show results for each case, where the (i,j) notation at the top is respectively the number of growth platoons in the simulation and estimation models. Blue indicates simulation model output and red that from the estimation model. Each shade level represents an interval from 5 to 95% with dotted line around shading showing the 95% interval. Black lines within shaded colors show medians. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reduced the number of old fish in the expected conditional age-at-length compositions in the absence of strong fishery impacts.

The length composition data reflect differential pressure on the growth platoons in the simulation model that cannot be mimicked in the estimation models in Case D, where the simulation model had five growth platoons and the estimation model had only one. The survey selectivity was inaccurately estimated as dome-shaped

in over 90% of the models (Fig. 4h), which improved the fit to the length-composition data that were generated by simulations from which the fastest growing fish had been differentially removed. Growth was also underestimated in by about 0.3–0.6 cm for ages 10 and older (Fig. 4l). These biases in the Case D estimation models led to underestimating the spawning output and depletion in later years by about 30% (Fig. 4p and t).

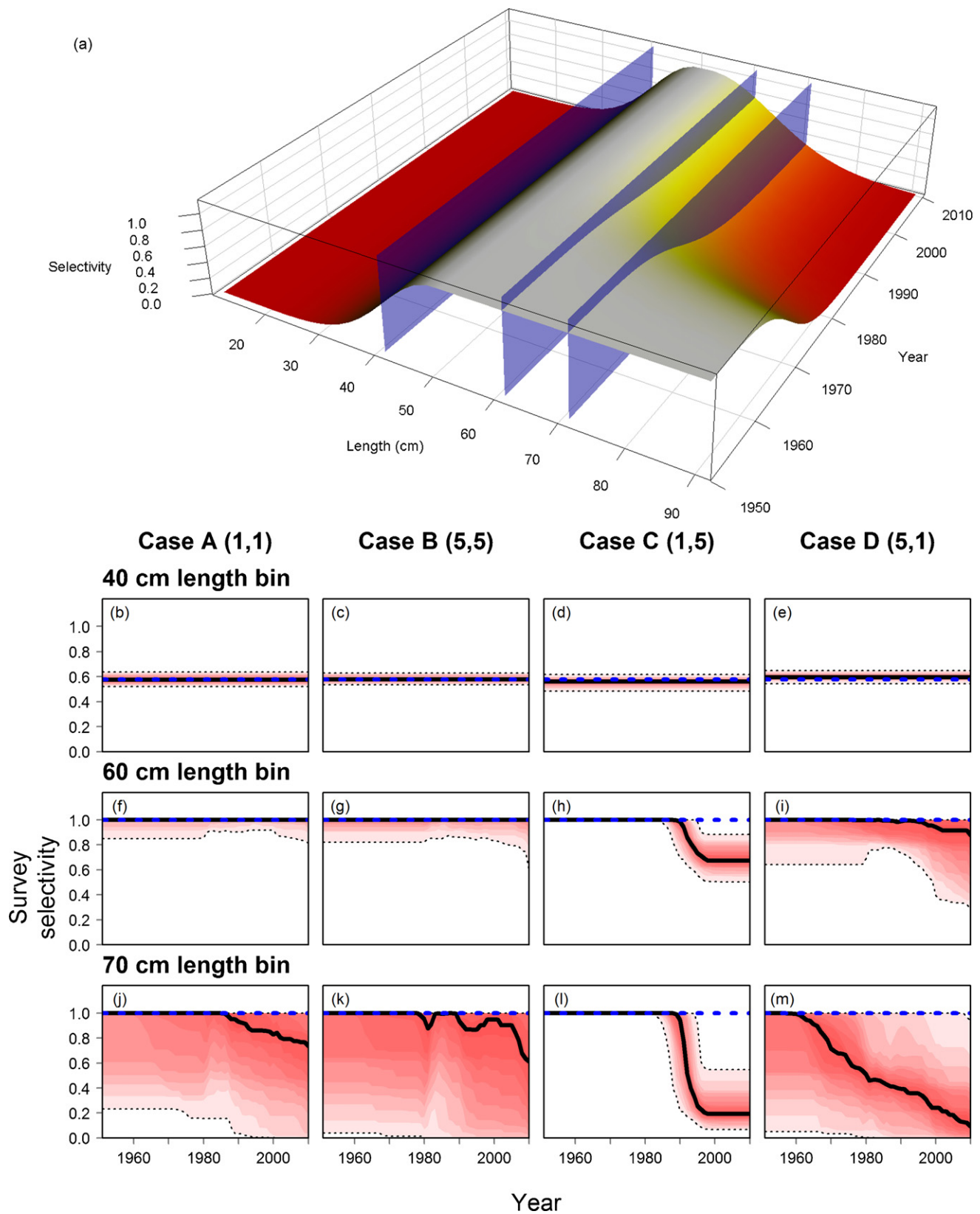


Fig. 5. Illustration of estimated trends in selectivity for each case. Upper figure (a) shows a single realization of time-varying selectivity with a trend in the degree of dome-shapeness. Lower panels show the distribution of selectivity across estimation models at the length bins indicated by the three blue planes in (a). Column labels and shading match those used in Fig. 4, with black lines within shaded colors indicating median estimates and the dashed blue line indicating the simulation value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The results were insensitive to broader priors on natural mortality and steepness. Cases A and B had estimated depletion values that were biased by 1%, rather than unbiased when more informative priors were used. The broader priors increased the variability in the estimates of natural mortality and steepness, but did not introduce large biases in Cases A and B. For instance, in Case A, the CV on estimated steepness across the 100 simulated data sets increased from 12 to 25% with the broader prior, but the median values were within 5% of the simulated value of 0.44 with both priors. However, performance was worse for Cases C and D with broader priors. For example, the median estimated steepness value increased from 0.47 with the informative prior to 0.88 with the broader prior in Case C.

3.3. Trends in selectivity

Trends in survey selectivity were often estimated when this was possible (Fig. 5). However, the pattern of trend was less consistent for Cases A and B. The median selectivity (across estimation models) for the 70 cm length bin in the first year of the model matched the simulation model at 1.0 for all cases. The median selectivity at this length for Cases A and B (Fig. 5j and k) shows a slight trend toward a dome-shape in the final 30 years of the model (including the 1980–2010 period when there are survey data). As was the case for the models without estimated trends (Fig. 4e and f), almost half of the selectivities estimated for Cases A and B showed some degree of dome-shape in all years (Fig. 5j and k) in spite of the data having come from simulation models without no dome-shaped selectivity. However, any errors in the degree of dome-shape can only be in the direction of greater dome, so variability of this type is not unexpected.

Cases C and D showed strong but different patterns of trends in selectivity. Case C showed a dramatic decrease in the selectivity of larger fish that was consistent across model runs (Fig. 5h and i). This trend was a shift from asymptotic selectivity up to the late 1980s to a strongly dome-shaped selectivity from the late 1990s. Spawning depletion was very poorly estimated for Case C (Fig. 4o) and a trend in dome-shaped selectivity is a way for the model to fit a declining index of abundance while maintaining a high biomass (the median estimate of B_0 was 60 times greater than the simulated value), which limits the impact of the fishery on the expected length compositions. A trend of declining selectivity of larger fish was also fairly consistent for Case D (Fig. 5i and m), but the estimated change over time was more gradual than for Case C. The median selectivity of the 70 cm length bin was estimated to decline steadily in this case from 1.0 in 1960 to about 0.1 in 2010.

4. Discussion

This paper describes how length-based mortality can be modeled within an age-structured model as implemented in SS. The question of the extent to which true populations exhibit such dynamics is left for future analysis. The implementation in SS is parsimonious in that it can be used without increasing the number of estimated parameters or providing additional data. Dividing the population into growth platoons has a computational cost, with the SS run times approximately proportional to the number of growth platoons, but the platoon approach is far simpler than tracking a full matrix of fish numbers by length and age.

Generalizing the results of simulation analyses to make predictions about real-world applications is always a challenge. Nevertheless, some of the results of this analysis are relatively intuitive and therefore we expect they apply in other contexts. A normal distribution of length-at-age can be reasonably approximated using a mixture of five smaller normal distributions over a

range of values for the ratio of variability within to between distributions. Less overlap between platoons leads to greater potential change in length-at-age due to fishing, but also reduces the normality of the combined distribution. Although the greatest change in biology-at-age was caused by selectivity functions in which the greatest increase in selectivity occurred near the mean asymptotic length, the fishery selectivity used in the full simulation analysis (peak selectivity at 55 cm) still interacted with the growth platoons in ways that led to bias when the estimation and simulation models were mismatched in terms of number of platoons.

Models that were misspecified by having mismatched assumptions between the simulation and estimation models regarding the presence or absence of size-dependent mortality provided very biased estimates of key model results. This suggests that inclusion of selective mortality in a stock assessment model will be necessary to reduce bias if the variability within the growth trajectories of individual fish is low for a given population compared to the variability across fish in that population. This conclusion is consistent with results of a similar analysis by Daniel Hively (UW, pers. comm.). However, the greatest bias occurred when the simulated data did not include selective mortality, but the estimation model did. This suggests that the modeling assumptions should be considered with care (and perhaps be rooted in biological studies of the growth of individuals), as no configuration can be assumed to work best in all cases. Sensitivity analyses showed that relaxing the priors that were applied to natural mortality and steepness caused models with incorrect assumptions to perform even worse, while the models with correct assumptions remained relatively unbiased.

It should be noted that Rosa Lee's Phenomenon occurs only in the presence of size-based selectivity. Stock Synthesis has options for size- and age-based selectivity or a combination of the two. Species exhibiting ontogenetic movement may be better described by age-based selectivity (Stewart et al., 2011), but any investigation into the effect of adding platoons will only be appropriate in models that include size-based selectivity.

It was possible to choose whether there should be one or five platoons based on comparing the likelihood of models with and without growth platoons using the data simulated in this analysis. This is likely due in large part to the idealized conditions of a simulation analysis, but it suggests that comparison of fits across models with and without growth platoons is useful. This analysis did not examine how to choose a value for ρ . This value cannot be estimated directly using SS, but could be chosen based on a likelihood profile. A single profile was conducted over a range of ρ values differing by 0.1 for an arbitrary example chosen from the set of simulations. A ρ of 0.4 had a slightly higher likelihood than the $\rho = 0.5$ value used when simulating the data, but values for ρ of 0.3 and below or 0.6 and above had much lower likelihoods with a change of 5 or greater units of log-likelihoods. This brief test suggests that the data can be reasonably informative about this ratio. Large values of ρ will produce results equivalent to those without growth platoons, so in those cases, the additional computation time would not be necessary.

One hypothesis considered in this paper is that if the model estimated a trend in the degree of dome-shaped selectivity (when given the flexibility to do so), it could be an indication of a misspecified model where the true process was the sequential removal of a faster growing subset of the population. Indeed, data generated with growth platoons and estimated without platoons but with flexible selectivity did lead to consistent estimates of a declining trend in the selectivity of larger fish. However, declining trends were occasionally estimated for models that were correctly specified, and they were consistently estimated for a model with the incorrect assumption of the existence of growth platoons. The trend in selectivity in this last case led to a better fit to the index of abundance, which was not well fit in the misspecified model.

Only trends in survey selectivity were considered here, but examination of fishery selectivity could be considered as well. However, fisheries may truly experience increasingly dome-shaped selectivity during periods of declining abundance if they focus on a core area of the stock. Sampson and Scott (2011) found evidence for increasingly dome-shaped selectivity of a population when modeled as age-based selectivity, which could not be the result of length-selective mortality but may be the result of changes in relative fishing effort of different gears. In summary, consideration of trends in selectivity of larger fish may provide an indication of the presence of selective mortality for models that do not have growth platoons, but is far from perfect as a predictor.

In conclusion, the implementation of growth platoons in SS allows assessment scientists to easily consider, within a commonly used assessment model, the effect of selective fishing mortality on variable length-at-age as has been well studied, but rarely applied in a management context. Only by routinely considering alternative assumptions for this process can we judge whether data provide evidence for it, and if so, how stock assessments and the management measures that they inform might differ as a result.

Acknowledgments

We are grateful to numerous members of the vibrant fisheries science community in Seattle for providing valuable feedback on this modeling approach and this manuscript describing it as both evolved over many years. We are particularly appreciative of Associate Editor André Punt for his work assembling this special issue and his valuable feedback on this manuscript. Ian Taylor was supported during some of this period through NOAA Award NA17RJ1232 to the University of Washington's Joint Institute for the Study of the Atmosphere and Ocean.

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