

Stock Reduction Analysis using catch at length data: Length-SRA

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Abstract

Many modern stock assessments convert length frequency data from catches to age compositions to then conduct age-structured assessment. These assessments must estimate age- or length-based vulnerability to fishing, often using simple parametric functions describing asymptotic or dome-shaped vulnerability. We present a length-based stock reduction analysis (Length-SRA), which bypasses the requirement of estimating a vulnerability by estimating exploitation rate at length directly from observed catch at length data. We test the performance of Length-SRA with a simulation-evaluation framework under three exploitation rate trajectories and under fixed and time-varying vulnerability scenarios. The model yields relatively low bias in parameter estimates and conservative management benchmarks. Length-SRA is relatively accurate when tracking changes in selectivity through time. We further use Length-SRA to assess two species, Pacific hake and Peruvian jack mackerel, to show that vulnerability is quite variable in both species over time, leading to time-varying management reference points. Length-SRA provides assessment results with accuracy comparable to other methods, such as Virtual Population Analysis and Statistical Catch at Age. However, Length-SRA has the additional advantage of providing accurate estimates of vulnerability over time.

1 Introduction

Modern stock assessments typically attempt to fit population dynamics models to catch at age and catch at length data, in hopes of extracting information from these data about age/size vulnerability, cohort strength and fishing mortality patterns (Methot and Wetzel, 2013; Hilborn and Walters, 1992). Some assessment methods attempt to put aside the length frequency data, by converting these data to age compositions using age-from-length tables, perhaps using iterative methods to estimate proportions of fish at age for each length interval

25 (Kimura and Chikuni, 1987). In cases where age data are lacking, models like MULTIFAN-CL attempt to
26 obtain estimates of vulnerability, fishing mortality and population dynamics parameters only from size distri-
27 bution data (Fournier et al., 1998). Combined with a few assumptions regarding the structure and variability in
28 length at age, this procedure can even be used to attempt to recover information about changes in body growth
29 patterns if there is a strong age-class signal in the length frequency data (Fournier et al., 1998). It is typical for
30 assessment results from length-based assessment models to show substantial deviations between predicted and
31 observed length distributions of catches, reflecting both sampling variation in the length composition data and
32 incorrect assumptions about stability of growth and vulnerability patterns (Hilborn and Walters, 1992).

33 Vulnerability to fishing is the combination of two processes: selectivity of the fishing gear and availability
34 of the fished population in the area being fished (Beverton and Holt, 1957). Both processes can vary over
35 time and therefore modify the resulting selectivity. Although selectivity process can often be directly measured
36 through gear experiments, availability is generally harder to measure as it depends on the size-based distribution
37 of the exploited population and the spatial distribution of the fishing fleet. Fish movement, size-structured
38 changes in fish distribution, and changes in fleet distribution, can all affect availability and consequently lead to
39 vulnerability changes. Changes in vulnerability are not uncommon (Sampson and Scott, 2012) but are usually
40 difficult to track over time. This difficulty is associated with an inability to distinguish between changes in
41 fishing mortality and changes in vulnerability in most age- and length-based stock assessment methods. For
42 this reason, many assessment methods rely on ad hoc parametric vulnerability models that may or may not
43 include changes over time (Maunder et al., 2014). If misspecified, such models might lead to severe bias in
44 fishing mortality estimates and other model parameters, which could result in misleading management advice
45 (Martell and Stewart, 2014).

46 Here we suggest an alternative approach to assessment modeling that begins by assuming that the as-
47 sessment model should exactly reproduce the observed catch at length composition. This approach follows
48 the dynamics of an age structured stock reduction analysis (SRA) (Walters et al., 2006; Kimura et al., 1984;
49 Kimura and Tagart, 1982) which follows a “conditioned on catch” format, subtracting observed catches at age
50 from modeled numbers at age in estimation of numbers at age over time. This assumption is analogous to
51 the classical assumption in virtual population analysis that reconstructed numbers at age should exactly match
52 observed catch at age data (Hilborn and Walters, 1992). The suggested approach may have two key advantages
53 over statistical catch at age and/or catch at length models: (1) it does not require estimation of age or size
54 vulnerability schedules, and (2) catch at length data are commonly available for every year, even when age
55 composition sampling has not been conducted.

We named this approach a Length-SRA assessment model. Here we present the model formulation, the demonstrate its performance with a simulation-evaluation analysis and apply it to real fisheries data from the Peruvian jack mackerel (*Trachurus murphyi*) and Pacific hake (*Merluccius productus*) fisheries.

2 Methods

2.1 Stock reduction analysis with catch at length data - length-SRA

The stock reduction analysis (SRA) described here proceeds through the following steps: (1) compute numbers at age (based on recruitment estimates and mortality in the previous year); (2) convert numbers at age into numbers at length using the proportions of individuals at length given each age class; (3) calculate the exploitation rate at length using numbers at length and observed catch at length; (3) convert the exploitation rate at length to exploitation rate at age; (4) compute numbers in the following year using the exploitation rate at age, natural mortality, and recruitment estimates.

A crucial component of the length-SRA is the calculation of proportions of individual at length given each age class ($P_{l|a}$ - eqs. T3.1-T3.5). The calculation of such proportions (eq. T3.1) relies on four main assumptions regarding the distribution of length at age: (1) The mean length at age follows a von Bertalanffy growth curve (eq.T3.4), (2) The length at age is normally distributed (eqs. T3.1 -T3.3), (3) The standard deviation of the length at age is defined (e.g. eq.T3.5), and (4) $P_{l|a}$ is constant for all lengths equal or greater than a maximum length L (eq.T3.3).

The proportions of length at age are used to convert the length-based quantities into age-based quantities which are used to propagate the age structured population dynamics forward (Table 3). We assume that recruitment follows a Beverton-Holt type recruitment curve (eq. T3.6), that harvesting occurs over a short, discrete season in each time step (year or shorter time period), and that natural survival rate is known and stable over time (eqs. T3.6-T3.10). The computation of numbers at age in the initial year (i.e., first year in which data is reported - t_{init}) is different from that in the remaining years (eq. T3.12). Recruitment in the initial year is given by the parameter R_{init} , which allows the model to reflect that the population has been fished prior to the beginning of the time series. If the population is initially unfished, this parameter can be set to equal to R_0 . We used equilibrium yield per recruit quantities to calculate MSY and U_{MSY} (Table 4 - eqs.T4.6 to T4.12). As in all yield per recruit calculations, our MSY and U_{MSY} estimates depend on the vulnerability curves calculated for each year (eq. T4.8).

In order to assess how well the model tracked changes in selectivity over time, we produced summary plots of of exploitation rate at length ($U_{l,t}$).

The Length-SRA model estimates three main parameters: average unexploited recruitment R_0 , recruitment compensation ratio κ , and recruitment in the initial year R_{init} . In addition, the annual recruitment deviations w_t are estimated for all cohorts observed in the model. That is, the number of recruitment deviations is equal to the number of years in the time series plus the number of age classes greater than recruitment age.

The objective function (eq. T5.13) is composed of a negative log-likelihood component, three penalties, and a prior component for the recruitment compensation ratio κ . The negative log-likelihood component minimizes the differences between the predicted and observed index of abundance (eq. T5.1). We assume that such differences are lognormally distributed (eqs. T5.3-T5.4) and use the conditional maximum likelihood estimator described by Walters and Ludwig (1994) to estimate the survey catchability coefficient q (eq. T5.2). A lognormal penalty is added to the negative log-likelihood function to constrain annual recruitment residuals so that the estimates have mean of zero and fixed standard deviation σ_R (Maunder and Deriso, 2003) (eq. T5.5). A second penalty, $P_{U_{max}}$ was implemented in order to prevent estimated values of exploitation rate at length greater than one ($U_{l,t} > 1$) (eq. T5.9) and a third penalty P_U was added to limit variability in vulnerability at length across years, and therefore limit the influence of observation error on vulnerability estimates. Lastly, an informative normal prior for $\log(\kappa)$ was included in the objective function (eq. T5.12).

2.2 Simulation-evaluation

Model performance was evaluated using a simulation-evaluation populated with the biological parameters of an hypothetical fish species. We used the same model structure described in Table 3 for both the simulation and estimation models. However, the operating model was modified to control annual exploitation rate (eq. T4.2), time varying selectivity (eq. T4.4), and observation and process errors.

The simulation model was initialized at unfished conditions (eq. T4.1) but only started reporting data for the simulation-evaluation procedure after the t_{init} year. The period between the first time step and t_{init} is used as a burn-in period. Selectivity in the operating model was computed with the three parameter selectivity function described by Thompson (1994) (eq. T4.4). We chose to use this three parameter selectivity curve because of its flexibility, which allowed us to switch between logistic and dome-shaped selectivity curves in the scenarios in which time varying selectivity was considered. The observation error in the operating model included lognormal error in the index of abundance and logistic multivariate error (Schnute and Richards, 1995)

113 in the catch numbers at length (Table 2). Recruitment deviations were assumed to be lognormally distributed
114 with constant σ_R (Table 1).

115 We considered a total of six different scenarios in simulation-evaluation trials, including three historical
116 exploitation rate trajectories (contrast, one-way trip and U -ramp) and two selectivity patterns (constant and
117 time-varying). In the contrast scenario the exploitation rate (U_t) starts low and increases beyond U_{MSY} and then
118 decreases until $U_t = U_{MSY}$. In the one-way trip scenario U increased through time until $U = 2 \cdot U_{MSY}$. In the U -
119 ramp scenario, U_t increases steadily until $U_t = U_{MSY}$ and remains constant thereafter. In the constant selectivity
120 scenario, selectivity was assumed to follow a sigmoid shape. In the time varying selectivity scenario, the
121 selectivity curve was assumed to vary every year, progressively changing from a dome shaped curve to sigmoid
122 and back to dome shaped. The complete list of scenarios and the acronym used for them is presented in Table
123 6.

124 All simulations had 30 years of data and 200 simulation trials were performed for each scenario. We
125 evaluated the distribution of the relative proportional error ($\frac{estimated-simulated}{simulated}$) for the main parameter estimates
126 (R_0 , R_{init} , and κ) and for four derived quantities (Depletion: $\frac{SB_t}{SB_0}$, MSY , U_{MSY} , and q).

127 2.3 Real data examples

128 Two case studies were chosen to illustrate the application of the Length-SRA to real datasets: Pacific hake
129 and Peruvian jack mackerel. Both species are believed to be subject to time varying selectivity.

130 The Pacific hake fishery is believed to exhibit time varying selectivity due to cohort targeting and annual
131 changes fleet spatial distribution (Ruttan, 2003). The population is known to have spasmodic recruitment, with
132 high recruitment events occurring once or twice every decade (Ressler et al., 2007). Pacific hake tends to
133 segregate by size during their annual migration (Ressler et al., 2007), allowing the fishing fleet to target strong
134 cohorts by changing the spatial distribution of fishing effort as the cohort ages. Hake catch at length data was
135 available for the period between 1975 and 2013. The survey index of abundance was available intermittently
136 from 1995 to 2013.

137 The movement pattern of jack mackerel is not as well known, although fish appear to move between spawn-
138 ing and feeding areas (Gerlotto et al., 2012). Variability in selectivity patterns for the jack mackerel fishery are
139 believed to be associated both with evolution of fleet capacity and gear utilization and with compression and
140 expansion of the species range associated with abundance changes (Gerlotto et al., 2012). Jack mackerel catch
141 at length data was available from 1980 to 2013 and the survey index was available for the years between 1986
142 and 2013, with the exception of the year of 2010.

3 Results

3.1 Simulation-evaluation

Simulation-evaluation of the Length-SRA model demonstrated that bias for the three leading parameters was relatively consistent across scenarios (Figure 1). Higher biases were generally associated with the U -ramp scenarios (CR and VR). The contrast and one-way trip scenarios yielded the best performance for both constant and time-varying selectivity scenarios (Figure 1).

Median depletion (SB_t/SB_o) was underestimated in most scenarios with median proportional errors ranging between -0.170 and -0.013 (Figure 2). MSY was also underestimated for all scenarios, with median proportional errors ranging between -0.158 and -0.046 (Figure 2). The estimates for U_{MSY} showed very low (<0.03) median proportional errors for all scenarios (Figure 2), and were underestimated for the time varying selectivity scenarios and overestimated for the constant selectivity scenarios. The estimates of q were positively biased, particularly for the U -ramp scenarios (CR and VR); this is likely to be associated with the underestimations of both R_0 and R_{init} for those scenarios.

The simulation-evaluation exercise showed that the Length-SRA model is able to track selectivity changes over time (Figure 3). However, the estimates of selectivity are less accurate in the initial year of data (year 21) for all scenarios and particularly inaccurate for the U -ramp scenarios. Precision and accuracy of selectivity estimates were better for the contrast and one-way trip scenarios for both the constant and time-varying selectivity.

3.2 Real data examples

The model fit the Pacific hake and jack mackerel indexes of abundance relatively well (Figure 4), despite some limitation in the available data. The Pacific hake index of abundance time-series is quite short and intermittent (survey happens every three or two years). The index of abundance time series for jack mackerel was longer but it indicates a downward trend in abundance with low contrast in the last ten years of data.

The model fit for both species resulted in time varying selectivities that lead to variation in MSY and consequent changes in U_{MSY} . This is because changes in selectivity result in changes to the vulnerable biomass even if total biomass is constant. The time-varying selectivity calculated for each species (Figure 5) results in up to two-fold change in MSY throughout the time series for both species (Figure 4).

4 Discussion

We present a length-based stock reduction analysis (Length-SRA) that allows monitoring of time varying vulnerability. In the Length-SRA model, catch at length is assumed to be known without error and exploitation rate at length is calculated directly from estimates of numbers at length. In turn, numbers at length are produced based on numbers at age and on probabilities derived from growth curve parameters and coefficient of variation. This fact is important because it allows the model to bypass the requirement for the estimation of a vulnerability ogive, as is required in more traditional age- and length-based models (Sullivan et al., 1990; Mesnil and Shepherd, 1990, e.g.) and in more recent length based state-space modelling approaches White et al. (2016). Estimation of vulnerability ogives can be very difficult, especially if vulnerability is believed to vary over time unpredictably (Martell and Stewart, 2014; Linton and Bence, 2011).

Parameter and management quantities estimates from Length-SRA seem to be robust to strong changes in vulnerability, i.e. from asymptotic to dome shaped. The accuracy in the estimates of vulnerability obtained with the Length-SRA are comparable with those presented by Nielsen and Berg (2014), especially for the contrast and one-way trip scenarios. Nielsen and Berg (2014) account for time varying selectivity by treating fishing mortality at age as stochastic processes that are correlated over age and time. Their model seems to perform extremely well, however they only considered one exploitation rate trajectory, with significant contrast in the data and the changes in vulnerability considered in their study are more subtle than the ones considered in this study.

Another attractive approach to model catch at length data is the one described by White et al. (2016). Their state space model estimates annual recruitment, harvest rate, and error terms from catch at length data and seem to obtain good precision and accuracy in their estimates. However, it is important to note that their model relies on two assumptions that are likely violated in real data examples. First, they assume that vulnerability is constant over time and follows a cumulative normal distribution parametric form. Second, they assume that the growth component of the transition matrix $P(y,x)$ to be constant and given by the growth curve. This is incorrect because fishing causes changes in the age composition of fish of size x , i.e. under fishing, proportion of younger fish (with higher $y|x$) is expected to increase.

The most important advancement of Length-SRA over conventional stock-assessment models is a calculation of time-varying vulnerability. This information alone will go a long way in helping to characterize the complexity of the fishery system. Length-SRA on its own is reasonably accurate in deriving important management-oriented parameters (depletion and U_{MSY}), however another option may be to combine findings

200 from this model with another assessment model, such as a statistical catch at age (SCA) model. In this frame-
201 work, Length-SRA can be used to calculate annual vulnerability, which then becomes an input into SCA to
202 then calculate other important variables and produce management advice. This combination of models has
203 been used in the past (Walters and Punt, 1994); we suggest Length-SRA may be an extremely useful tool in
204 this context.

205 Accurate estimates of vulnerability are particularly important if the fishery management is based on yield
206 per recruit reference points. The yield per recruit of a fishery depends on the vulnerability curve (Beverton
207 and Holt, 1957) and for this reason, changes in vulnerability over time will directly affect reference points
208 (Beverton and Holt, 1957; Hilborn and Walters, 1992). We observed vulnerability changes for both Pacific
209 hake and jack mackerel and show how this variability can lead to a two-fold difference between the maximum
210 and minimum estimates of *MSY* calculated along the time series. We believe that tracking these changes is
211 important not only to ensure appropriate management recommendations, but also to illustrate the relationship
212 between vulnerability patterns and *MSY* (Vasilakopoulos et al., 2016).

213 The approach used in the Length-SRA is analogous to that used in virtual population analysis in that the
214 length composition data is assumed to be known without error. For this reason, the vulnerability estimates
215 include extra variability due to observation and sampling error. We attempted to minimize this effect by adding
216 a the time varying vulnerability penalty to the model's objective function, however this penalty is not capable of
217 completely removing the observation error effect from the vulnerability estimates. Because of the assumption
218 of known catch at length, it is important that the catch sampling is representative of the total removals from
219 the population (Pope, 1972). As in any other fisheries model, biased sampling and/or low sampling effort will
220 result in bias in parameter and fishery reference point estimates (Coggins and Quinn, 1998; Bunch et al., 2013).
221 Another important point to consider is that the Length-SRA assumes that the biological parameters used in
222 the growth curve and catch at age relationship are know without error and constant over time. Minte-Vera
223 et al. (2017) showed that misspecification in biological parameters, especially in asymptotic length, can have a
224 significant impact in assessment results.

225 Some management parameters are underestimated (namely depletion and *MSY*), which may be cause for
226 concern. However, it is important to note that both parameters are underestimated for all scenarios, which leads
227 to conservative management recommendations. Although this may lead to losses in catch in the short-term,
228 it will result in healthier stocks and higher catches over the longer-term (once the stock is recovered). The
229 magnitude of bias is also dependent on the trajectory of the data: time-series with more contrast will lead
230 to more accurate estimates. The magnitude and direction of the bias in the estimates of *MSY* and depletion

231 observed in this study are comparable to the results obtained by Martell and Stewart (2014) in a simulation
232 study on the impacts of time varying vulnerability on the estimates generated by a statistical catch at age
233 model. Other studies show even higher biases in face of time-varying vulnerabilities (e.g. Linton and Bence,
234 2011; Henriquez et al., 2016). Overall, estimates derived parameters are generally within the range of many
235 other stock assessment models and the conservative bias will lead to better management overall.

236 The simple nature of the Length-SRA model makes it a good candidate model for inclusion on closed-loop
237 simulation studies. Further testing of this model in a closed-loop simulation set up would provide more insight
238 on the model performance on achieving management outcomes (Punt et al., 2014). As mentioned before, we
239 expect that the length-SRA, when used as an assessment tool, will yield slightly conservative management
240 benchmarks which might lead to higher average catch in the long term if the stock is currently overfished.
241 However, it is also possible that these conservative benchmarks result in forgone yield in the medium and long
242 term. We recommend, therefore that this approach be tested in a simulation set up before it is considered as
243 part of a management strategy.

244 In conclusion, we believe that the Length-SRA approach presented in this study is a useful approach to
245 fisheries stock assessment. We believe that this is particularly true when time varying vulnerability is believed
246 to occur, especially if the variability is not easily predictable from historical changes in gear use/fleet com-
247 position. We foresee the application of this model as an investigative tool to evaluate potential time-varying
248 vulnerability patterns, as a stock assessment tool and as part of closed loop simulation studies.

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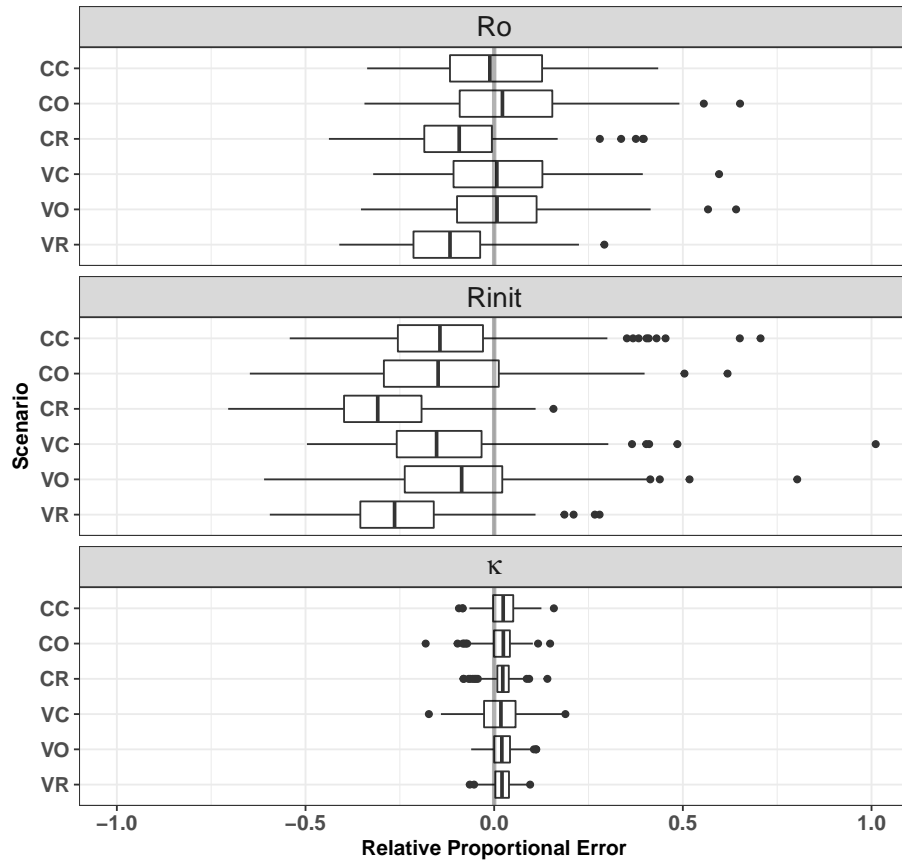


Figure 1: Relative proportional error for main parameters for all scenarios considered in the simulation-evaluation.

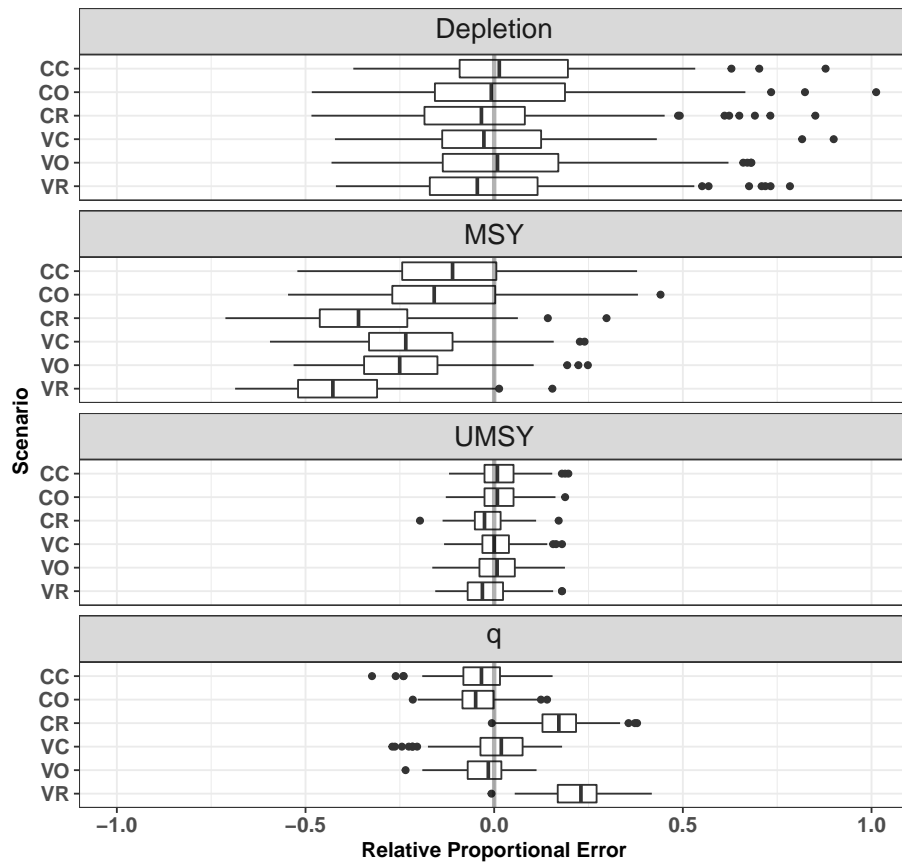


Figure 2: Relative proportional error for main parameters for all scenarios considered in the simulation-evaluation.

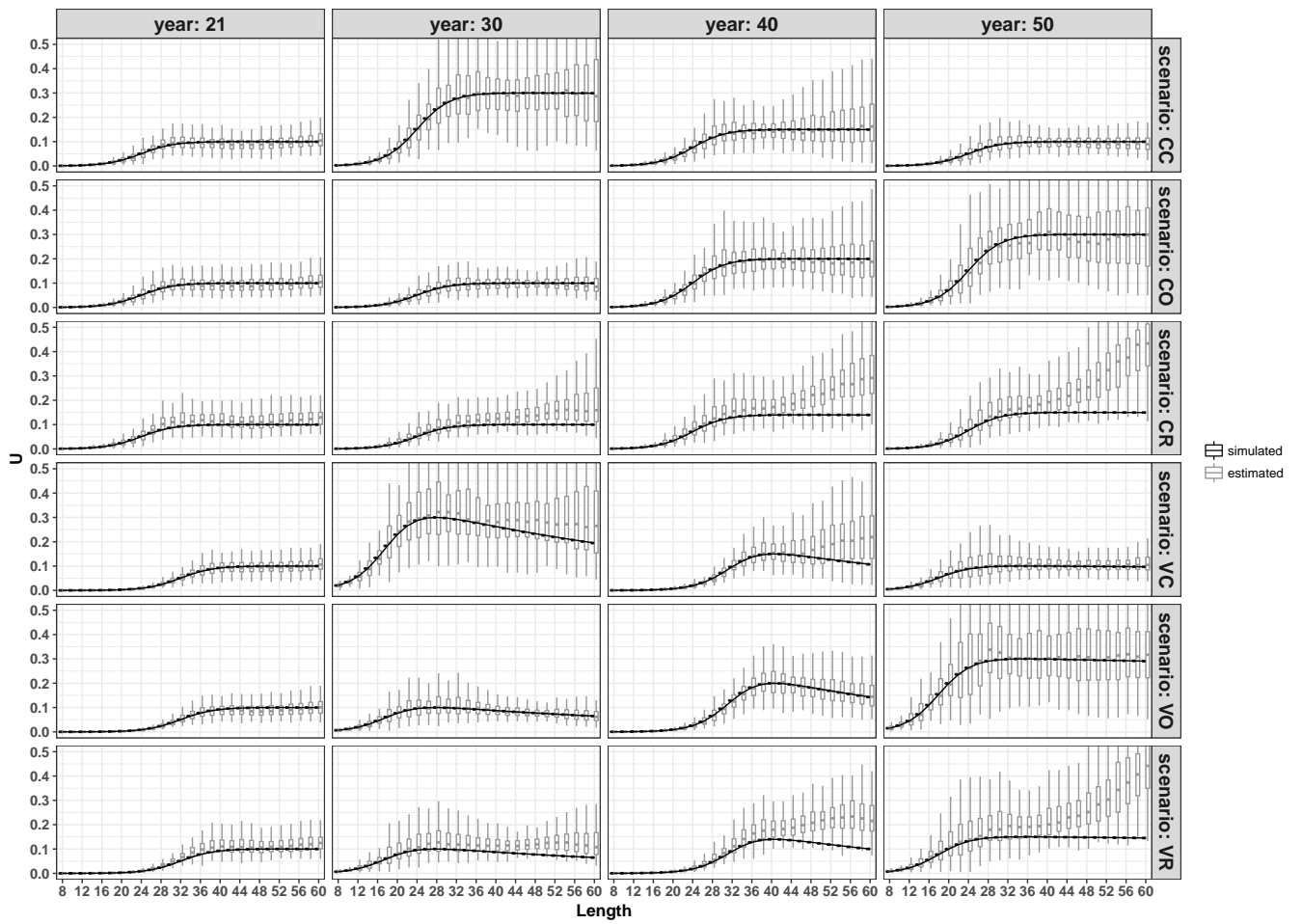


Figure 3: Simulated and realized selectivity estimates for a set of years within simulation-evaluation time series.

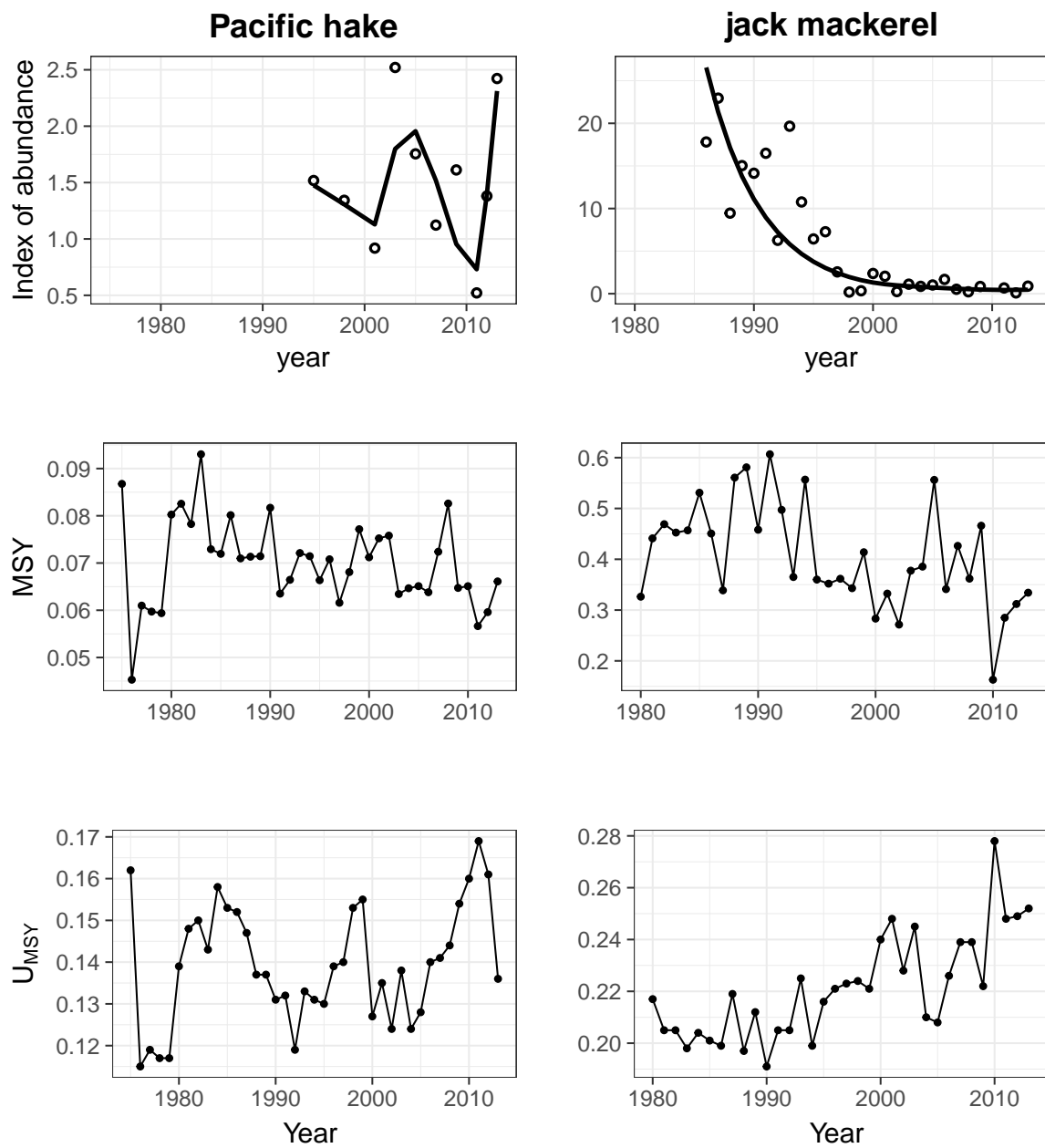


Figure 4: Fit to index of abundance for Pacific hake and jack mackerel.

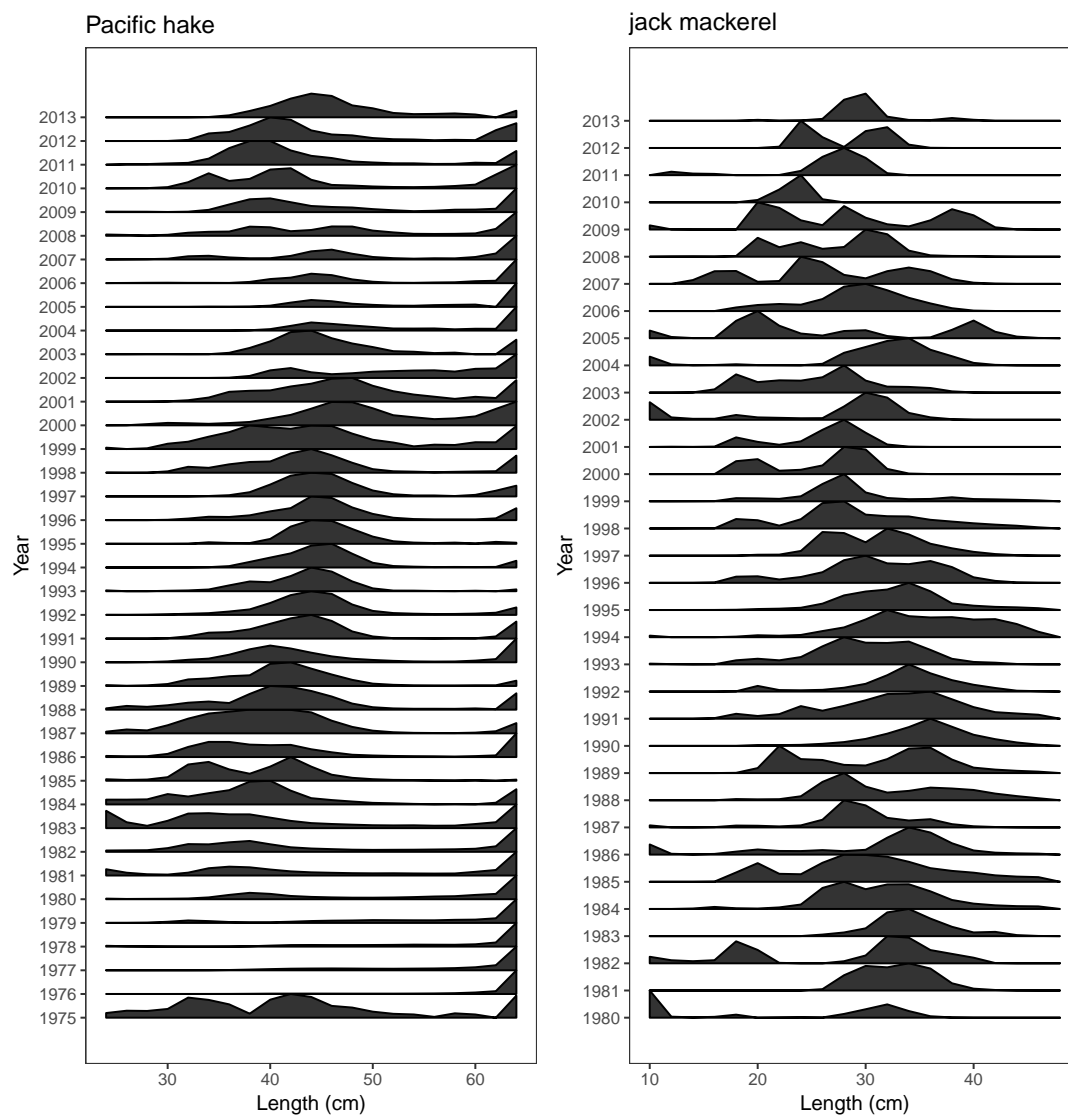


Figure 5: Realized selectivity patterns across years for Pacific hake and jack mackerel.

Table 1: Indexes, stock assessment variable definition, and values used in simulation-evaluation

Symbol	Value	Description
l	$\{l_o, \dots, L\}$	Central point of length bin, $L = 50$ cma
a	$\{a_o, \dots, A\}$	Age-class, $A = 10$ years
t	$\{1, \dots, T\}$	Annual time step, $T = 50$ years
a_o	1	First age or age of recruitment
l_{bin}	2 cm	size of length bin
l_o	8 cm	Central point of first length bin
$init$	21	Annual time step in which data starts to be reported
Distribution of length given age		
L_∞	50 cm	Maximum average length
K	0.15	Rate of approach to L_∞
t_o	-0.1	Theoretical time in which length of individuals is zero
cv_l	0.08	Coefficient of variation for length at age curve
$P_{l a}$		Matrix of proportions of length at age
Φ		Standard normal distribution
$z1_{a,l}$		Normalized z score for lower limit length bins
$z2_{a,l}$		Normalized z score for upper limit length bins
$b1_l$		Lower limit of length bins
$b2_l$		Upper limit of length bins
\bar{L}_a		Mean length at age
σ_L		Standard deviation of length at age
Population dynamics		
R_o	100	Average unfished recruitment
κ	10	Goodyear recruitment compensation ratio
S	0.7	Natural annual survival
σ_R	0.6	standard deviation for recruitment deviations
w_t	$\mathcal{N}(0, \sigma_R)$	Recruitment deviations for years $\{init-A+1, \dots, T\}$
$N_{a,t}$		Numbers of fish at age and time
SB_t		Spawning biomass at time
mat_a		Proportion of mature individuals at age
a_{rec}, b_{rec}		Beverton & Holt stock recruitment parameters
R_{init}		Recruitment in the year data starts to be reported
$U_{a,init}$		Exploitation rate at age before data starts being reported.
$U_{a,t}$		Exploitation rate at age and time
$U_{l,t}$		Exploitation rate at length and time
$C_{l,t}$		Catch at length and time
$N_{l,t}$		Numbers at length and time
lx_a		Unfished survivorship at age
Φ_e		Unfished average spawning biomass per recruit
$sel_{l,t}^{result}$		Resulting selectivity estimates at length and time

Table 2: Indexes, variable definition for operating model, MSY quantities, and values used in simulation-evaluation

Symbol	Value	Description
Operating model		
$sel_{l,t}$		Fishing selectivity at length and time
g, d, b	vary by scenario	Parameters for selectivity function
U_t	vary by scenario	Annual maximum exploitation rate
$C_{l,t}^{Sim}$		Simulated catch at length and time
$N_{l,t}^{Sim}$		Simulated numbers at length and time
I_t		Index of abundance at time
σ_{I_t}	0.1	standard deviation for index of abundance deviates
VB_t		Biomass that is vulnerable to the survey at time
q	1.0	Catchability coefficient
MSY quantities		
l_{z_a}		Fished survivorship at age
U_z	seq(0.0,1.0,by=0.001)	Hypothetical exploitation rates to calculate MSY
Φ_z		Average spawning biomass per recruit
Φ_{eq}		Average exploited biomass per recruit under U_z and sel_a
sel_a		Selectivity at age
R_{eq}		Average equilibrium recruitment under U_z
$Yield_z$		Equilibrium yield under U_z
MSY		Maximum sustainable yield based on optimum spawner per recruit
U_{MSY}		Exploitation rate that leads to maximum sustainable yield

Table 3: population dynamics for Length-SRA and operating model

Distribution of length given age	
(T3.1)	$P_{l a} = \int_{z1_{a,l}}^{z2_{a,l}} \Phi(z) dz$
(T3.2)	$z1_{a,l} = \frac{b1_l - \bar{L}_a}{\sigma_{L_a}}$
(T3.3)	$z2_{a,l} = \begin{cases} \frac{b2_l - \bar{L}_a}{\sigma_{L_a}} & l < L \\ 1.0 & l = L \end{cases}$
(T3.4)	$\bar{L}_a = L_\infty \cdot (1 - e^{(-K \cdot (a - t_o))})$
(T3.5)	$\sigma_{L_a} = \bar{L}_a \cdot cv_l$
Population dynamics	
(T3.6)	$N_{a,t>init} = \begin{cases} \frac{a_{rec} \cdot SB_{t-1}}{1 + b_{rec} \cdot SB_{t-1}} \cdot e^{w_t}, & a = a_o \\ N_{a-1,t-1} \cdot S \cdot (1 - U_{a-1,t-1}), & a_o < a < A \\ \frac{N_{a-1,t-1} \cdot S \cdot (1 - U_{a-1,t-1})}{1 - S \cdot (1 - U_{a,t})}, & a = A \end{cases}$
(T3.7)	$U_{a,t} = \sum_l (P_{l a} \cdot U_{l,t})$
(T3.8)	$U_{l,t} = \frac{C_{l,t}}{N_{l,t}}$
(T3.9)	$N_{l,t} = \sum_a (P_{l a} \cdot N_{a,t})$
(T3.10)	$SB_t = \sum_a (mat_a \cdot w_a \cdot N_{a,t})$
(T3.11)	$sel_{l,t}^{result} = \frac{U_{l,t}}{\bar{U}_t}$
Initial year and incidence functions	
(T3.12)	$N_{a,init} = \begin{cases} R_{init} \cdot e^{w_{init}} & a = a_o \\ N_{a-1,init} \cdot S \cdot (1 - U_{a-1,init}) \cdot e^{w_{init}-a+1}, & a_o < a < A \\ \frac{N_{a-1,init} \cdot S \cdot (1 - U_{a-1,init})}{1 - S \cdot (1 - U_{a,init})} \cdot e^{w_{init}-a+1}, & a = A \end{cases}$
(T3.13)	$a_{rec} = \frac{\kappa}{\Phi_e}$
(T3.14)	$b_{rec} = \frac{\kappa - 1}{R_o \cdot \Phi_e}$
(T3.15)	$\Phi_e = \sum_a lx_a \cdot mat_a \cdot w_a$
(T3.16)	$lx_a = \begin{cases} 1, & a = 1 \\ lx_{a-1} \cdot S, & 1 < a < A \\ \frac{lx_{a-1} \cdot S}{1 - S}, & a = A \end{cases}$

Table 4: MSY quantities and operating model

Operating model	
(T4.1)	$N_{a,t=1}^{Sim} = l x_a \cdot R_o$
(T4.2)	$U_{l,t} = U_l \cdot sel_{l,t}$
(T4.3)	$C_{l,t}^{Sim} = N_{l,t}^{Sim} \cdot U_{l,t} \cdot P_{l a}$
(T4.4)	$sel_{l,t} = \frac{1}{1-g} \cdot \left(\frac{1-g}{g} \right)^g \cdot \frac{e^{d \cdot g \cdot (b-l)}}{1 + e^{d \cdot (b-l)}}$
(T4.5)	$I_t = q \cdot V B_t \cdot e^{(\mathcal{N}(0, \sigma_{I_t}))}$
MSY quantities	
(T4.6)	$l z_a = \begin{cases} l z_a = 1 & a = a_o \\ l z_{a-1} \cdot S \cdot (1 - U_z) & a_o < a < A \\ \frac{l z_{a-1} \cdot S \cdot (1 - U_z)}{1 - S \cdot (1 - U_z)} & a = A \end{cases}$
(T4.7)	$\Phi_z = \sum_a l z_a \cdot mat_a \cdot w_a$
(T4.8)	$\Phi_{eq} = \sum_a l z_a \cdot sel_a \cdot w_a$
(T4.9)	$R_{eq} = R_o \cdot \frac{\kappa - \Phi_e / \Phi_z}{\kappa - 1}$
(T4.10)	$Yield_z = U_z \cdot R_{eq} \cdot \Phi_{eq}$
(T4.11)	$MSY = \max(Yield_z)$
(T4.12)	$U_{MSY} = U_z \rightarrow \max(Yield_z)$

Table 5: Likelihood functions and penalties

Conditional Likelihood	
(T5.1)	$Z_t = \log(I_t) - \log(VB_t)$
(T5.2)	$q = e^{\bar{Z}}$
(T5.3)	$Zstat_t = Z_t - \bar{Z}$
(T5.4)	$LL_1 \sim \mathcal{N}(Zstat \mu = 0, \sigma = \sigma_{I_t})$
Penalties	
(T5.5)	$P_{wt} \sim \mathcal{N}(wt \mu = 0, \sigma = \sigma_R)$
(T5.6)	$\mu_{U_{t-2:t}} = \left(\sum_{t=2}^t \frac{U_{l,t}}{\bar{U}_t} \right) / 3$
(T5.7)	$U_t^{pen} = \left(\frac{U_{l,t}}{\bar{U}_t} - \mu_{U_{t-2:t}} \right)^2$
(T5.8)	$SS_{vul} = \sum_{t=3}^{t=T} U_t^{pen}$
(T5.9)	$P_U = \frac{SS_{vul}}{\sigma_{vul}}$
(T5.10)	$\sigma_{vul} = 200$
(T5.11)	$P_{U_{max}} = \sum_t^t \sum_l^l U_{t,l}^{10}$
Priors	
(T5.12)	$prior(\log(\kappa)) \sim \mathcal{N}(\log(\kappa), \sigma = 0.9)$
Objective function	
(T5.13)	$Obj = -\log(LL_1) + -\log(P_{wt}) + P_U + P_{U_{max}} + prior(\log(\kappa))$

Table 6: Simulation-estimation scenarios

Scenario Code	Selectivity	U trajectory
CC	constant	contrast
CO	constant	one-way trip
CR	constant	U -ramp
VC	time-varying	contrast
VO	time-varying	one-way trip
VR	time-varying	U -ramp