Estimating recruitment variability and productivity in Antarctic krill

Douglas Kinzey*, George M. Watters, Christian S. Reiss

Antarctic Ecosystem Research Division, NOAA Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA, 92037, USA

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ABSTRACT

Three alternative forms of the spawner-recruit relationship – the Beverton-Holt and two expressions of the Ricker function - and a fourth form representing annual recruitment deviations without an explicit relationship to spawning biomass, were applied in an integrated assessment model for Antarctic krill. Model data were from the international krill fishery and U.S. AMLR surveys in the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Subarea 48.1, the area around the Antarctic peninsula where the majority of recent fishing for krill has taken place. Sensitivity tests using pre-specified values for the standard deviation of the logarithm of annual recruitment residuals (σ_R) and productivity (steepness, h) for the relationship between spawning biomass and subsequent recruitment indicated that neither the Beverton-Holt nor Ricker functions were superior to configurations of the model that did not assume a spawner-recruit relationship. As the predictive power of the spawner-recruit functions was reduced by increasing the value of σ_R the fit to the data improved. All the functions fitted the data best when σ_R was large enough so that random recruitment with respect to spawning biomass was produced. The alternative functions produced the same time series of recruitment and spawning biomass estimates when they were determined by the data rather than forced towards an assumed relationship. Although the Beverton-Holt and Ricker models were poor predictors of the data, cross-correlations of the recruitment predictions with the spawning biomass predictions from the best models indicated that recruitment was statistically correlated with spawning biomasses in the previous two to four years. The highest correlation (0.58) was with spawning biomass three years previously. Correlations in the reverse direction, with spawning biomass following recruitment were insignificant. These results suggest that recruitment variability does not influence subsequent spawning biomass in krill. They leave open the possibility that krill spawning biomass could influence subsequent recruitment, but not as modeled in the Beverton-Holt or Ricker functions with a one-year lag and the pre-specified von Bertalanffy growth.

1. Introduction

The strength of the relationship between the spawning population in one year and recruitment in subsequent years is uncertain. The role of the spawner-recruit relationship vs. other potential factors controlling recruitment such as environmental, ecosystem, or similar external drivers, particularly for forage species, is also uncertain and under debate (e.g., Vert-pre et al., 2013; Essington et al., 2015; Hilborn et al., 2017; Pikitch et al., 2012, 2018). Myers and Barrowman (1996) used 364 time series of vertebrate spawner abundance and recruitment from the database they assembled from stock assessments and similar sources to evaluate this relationship. They calculated the relative rank of spawner abundance associated with the highest recruitment, the lowest recruitment, and whether the mean recruitment was the same when spawner abundance was below or above its median value. They found a generally positive relationship between spawner and recruit abundance, although it varied by taxonomic order. Gilbert (1997) used a version of the Myers database to suggest recruitment varies around a mean value that shifts with environmental conditions rather than following spawning biomass and that spawning biomass may be caused by variable recruitment rather than the reverse. Szuwalski et al. (2014) did not find a positive relationship between spawners and recruitment in 61% of 224 worldwide marine stocks they examined from an updated version of the Myers database after they eliminated stocks in which recruitment estimates were derived directly from an assumed stock-recruitment relationship. They suggested environmental effects are a stronger influence on recruitment than spawning biomass for many stocks. Other previous studies (e.g., Conn et al., 2010; Dickey-Collas et al., 2015) have found little difference in estimates of spawners and recruits between models with loosely constrained stock-recruitment functions and models with no assumed relationship.

The size of the annual spawning population relative to its unfished

size is a proxy for "reproductive potential", the capacity of the stock to increase after depletion. Spawning biomass is one metric, but alternative metrics of reproductive potential, such as total lifetime egg production, or the slope of the spawner-recruit curve at its origin, possibly normalized by the spawning potential per recruit, have also been proposed (Myers et al., 1999; Morgan et al., 2009, 2011; Mehault et al., 2010; Hillary et al., 2012; Kell et al., 2016).

An integrated assessment model for Antarctic krill (*Euphausia superba*, hereafter krill) around the Antarctic peninsula (Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Subarea 48.1) estimates 96 parameters by fitting to data from research surveys and the fishery. Twenty-two quantities are pre-specified as model inputs instead of estimated. Earlier attempts to estimate these pre-specified values within the model did not converge or did not pass diagnostics for stationarity (Kinzey et al., 2015, 2018).

Harvests of krill by the fishery in CCAMLR Subarea 48.1 (annual catch limit of 155,000 tonnes) appear to be a small proportion of the total biomass, annually removing about one percent of the total krill biomass established for this Subarea by a multinational survey in 2000 (Hewitt et al., 2004). Although the fishery impact on the population is expected to be small, krill annual biomass varies by one to two orders of magnitude. Most of this annual variation is thus expected to be due to causes other than the fishery.

If the spawner-recruit relationship is a biological attribute of a population and there is enough variability in spawning biomass to allow its compensatory potential to be realized, the compensation strength should be measurable whether or not population changes are driven by a fishery. Over an order of magnitude of annual variability in krill biomass is measured using both hydroacoustics and trawls. A question evaluated in this study is, how much of the apparent variability in krill recruitment appears to be driven by variability in spawning biomass? This is an important initial issue to be considered before devising management policies that are based on an assumed relationship between spawning biomass and recruitment that may not exist.

Some of the pre-specified values used in the model are based on previous studies of krill and derive from measured quantities. Examples include the weight-at-length relationship and maturity-at-age. The former has been periodically rechecked against field measurements of length and weight (unpublished) and has remained stable since an earlier study by Hewitt et al. (2004). Mean values of maturity-at-age are calculated from measurements of maturity-at-length in the trawl samples, in combination with pre-specified von Bertalanffy growth parameters.

Other pre-specified values must be assigned not because they are well known but because they are not able to be estimated simultaneously with other parameters. Examples of these in the krill model are the von Bertalanffy growth parameters mentioned above, variability in log-recruitment (σ_R) and steepness (h). These quantities are important in establishing the productivity of the stock and the relationship between spawning biomass and subsequent recruitment. σ_R scales the random effects portion of recruitment. The dependence of recruitment numbers on spawning biomass in models with an assumed spawner-recruit function decreases as σ_R increases. It is not uncommon in fisheries assessment models to fix σ_R at 0.6 when it cannot be estimated (Maunder and Deriso, 2003). Steepness (h) represents the proportion of unfished recruitment that would be obtainable from 20% of the unfished spawning biomass. This quantity is also commonly fixed in fisheries assessment models when it cannot be estimated. Simulation studies have indicated estimates of steepness often have low precision and high bias, although it may be estimable in specific cases (Lee et al., 2012).

In this study, we perform a sensitivity analysis by pre-specifying different values of σ_R and h to identify the values for these quantities that provide the best fit to the krill data for Beverton-Holt and Ricker stock-recruitment relationships, and for random recruitment. We choose the best fits of these models to the data and evaluate cross-

Table 1

Eleven corresponding values of Beverton-Holt steepness (h_{BH}), their reproductive potential (λ), and Ricker values of steepness (h_{Ricker_A}) for the same λ. The Beverton-Holt and Ricker$_B$ were undefined for $h > 1$.

h_{BH}	λ	h_{Ricker_A}
0.2	1.00	0.28
0.22	1.13	0.30
0.3	1.71	0.42
0.445	3.21	0.70
0.5	4.00	0.84
0.545	4.79	0.97
0.555	4.99	1.00
0.7	9.33	1.65
0.85	22.67	3.35
0.97	129.33	13.50
0.99	396.00	33.04

correlations between the lagged estimates of spawning biomass and recruitment to see if either estimate leads or follows the other in their annual fluctuations.

2. Methods

The krill model is age-structured and assumes that krill begin recruiting to the spawning population after one year. Individual krill have been kept alive more than 9 years in laboratory conditions (Ikeda and Dixon, 1987 cited in Nicol, 2006). Fishery and survey selectivities for one- and two-year old krill are estimated to be low (Kinzey et al., 2015, 2018). Siegel (1987) used a distribution mixture analysis of krill lengths to suggest that krill are born in December and after a year as larvae/ juveniles reach an age 1+ length of approximately 30 mm in March to April, varying by location and year (Siegel, 1987 Table 1). Ikeda (1985) estimated krill would reach 30 mm length, half of their maximum size, in less than 1.5 years, and a potential spawning size of 40 mm in less than 2 years, if they grew for 6 months during the year (Ikeda Fig. 3).

The krill data on compositions and proportion mature are measured in lengths. The transition from ages in the model to lengths in the data is through a pre-specified von Bertalanffy relationship. The model has 6 ages, with the last one being a plus-group. Aging techniques for krill have not been available historically, although some recent progress has been made (Kilada et al., 2017). Attempts to use the integrated model to estimate the parameters of the von Bertalanffy growth function for krill in Subarea 48.1 were made in the past (Kinzey et al., 2015), but subsequent work with Markov chain Monte Carlo (MCMC) diagnostics indicated these estimates were not reaching stationary distributions (Kinzey et al., 2018). The values for von Bertalanffy parameters in the current models were prespecified to those used by CCAMLR in the Generalised Yield Model for krill (values obtained from the CCAMLR Secretariat, Kinzey et al., 2018). The CCAMLR values were derived from the distribution mixture analysis work of Siegel (1987). Krill begin maturing in the model, based on proportion mature at length and the von Bertalanffy growth function, at age 1+, with 48% of age 1+ krill mature. By age 4+, over 99% are mature.

The krill model supports four alternatives for modeling recruitment: the Beverton-Holt relationship, two forms of the Ricker function, or a simple annual deviation around a mean without a deterministic spawner-recruit relationship. Each of these alternatives uses a different function for the deterministic portion of recruitment ($\hat{R}_y$) in year y. $\hat{R}_y$ is the "fixed effect" for recruitment that is constant over all years, before the random component ($e^{\varepsilon_y^R}$) is estimated for each year y.

The deterministic part of recruitment in the krill models calculated using one of four options:

$$\hat{R}_y = B_{y-1}/(\alpha + \beta * B_{y-1}) \text{ (Beverton-Holt)} \tag{1}$$

$$\hat{R}_y = B_{y-1} e^{\alpha - B_{y-1} * \beta} (\text{Ricker}_A) \tag{2}$$

$$\hat{R}_y = \frac{B_{y-1}}{B_0/R_0} e^{\alpha*(1-B_{y-1}/B_0)} \, (\text{Ricker}_B) \tag{3}$$

from Eq. (3) in Kimura (1988).

$\hat{R}_y$

$\quad = e^R$ (no assumed relationship between recruits and spawning biomass) (4)

In Eqs. (1)–(3), B_{y-1} is the spawning biomass the previous year. R_0 is the unfished recruitment and B_0 is unfished spawning biomass. In the Beverton-Holt configuration α and β are determined from h as $\alpha = B_0(1-(h-0.2)/(0.8h))/R_0$ and $\beta = (0.5h-1)/(4hR_0)$ (Appendix 1 of Francis, 1992). In the Ricker functions the α and β parameters are calculated from h as $\alpha = ln(R_0/B_0) + \beta B_0$ and $\beta = ln(5h)/(0.8B_0)$ in Eq. (2), and $\alpha = ln(-4h/(h-1))$ in Eq. (3).

In all configurations model recruitment in year y was initially estimated as $e^{R+\varepsilon_y^R}$ where the logarithm of mean recruitment, $\bar{R}$, and the logarithm of annual recruitment deviations, ε_y^R, were estimated parameters. The range of annual deviations from the deterministic value of $\hat{R}_y$ by the ε_y^R parameters is constrained by σ_R. The effect of σ_R is applied to the estimates of ε_y^R in the penalty functions described below.

Recruitment variability in the model is constrained by $\hat{R}_y$ and by σ_R in the likelihood (using negative log-likelihood as the loss function) by four penalties Λ_{1-4}:

$$\Lambda_1 = 0.5(ln(R_0)-\bar{R})^2 \tag{5}$$

$$\Lambda_2 = Yln(\sigma_R) + \sum_y \left(ln\left(\frac{N_{1,y}}{\hat{R}_y}\right) + 0.5(\sigma_R)^2 \right)^2 / 2(\sigma_R)^2 \tag{6}$$

where y = 1982 to 2016 (the years with length-composition data), Y = 35 (the number of model years y), and $N_{1,y}$ is the model estimate of recruitment ($N_{1,y} = e^{\bar{R}+\varepsilon_y^R}$);

$$\Lambda_3 = \sum_y (e^{\varepsilon_y^R})^2 \tag{7}$$

where y = 1971–2016 (from 6 years before the fishery started in 1976 to the final year modeled);

$$\Lambda_4 = 0.5 \sum_y (e^{\varepsilon_y^R})^2 / (\sigma_R)^2 + Y\sigma_R \tag{8}$$

where y = 1971–1981 (model years before composition data were available), Y = 10.

Parameters were estimated in 9 phases and the Λ_4 penalty was only applied during the final phase.

Λ_1 penalizes large deviations of $\bar{R}$ from R_0, particularly in the case of Eq. (4) where no relationship between recruitment and spawning biomass is assumed to constrain annual recruitment deviations. The Λ_2 penalty constrains the estimates of the model-estimated recruitment in each year, $N_{1,y}$, to match the predicted recruitment for that year $\hat{R}_y$, with the weight of the penalty determined by σ_R. The Λ_3 penalty increases as recruitment variability σ_R increases. The Λ_4 penalty smooths deviations of the recruitment variability in individual years towards the overall variability σ_R.

Each model configuration in this study used one of Eqs. (1)–(4) as the basis for estimating recruitment. Configurations using smaller pre-specified values of σ_R forced the model to fit the fixed effect, $\hat{R}_y$, of the recruitment function more closely. Larger σ_R allowed the recruitment estimates in the model to deviate more from these expectations. Recruitment variability around $\hat{R}_y$ was penalized by Eqs. (5)–(8) so that values above those that improved the fit to the data had higher negative log-likelihood (-LL) values than the recruitment variability that best matched the data.

2.1. Steepness and λ in the Beverton-Holt and Ricker models

Steepness, in combination with growth and mortality, specifies the resilience of the stock. Steepness is bounded between 0.2 and 1.0 in the Beverton-Holt function (Eq. 1). In the standard Ricker function (Ricker$_A$, Eq. 2) steepness can vary from 0.2 to infinity because the Ricker$_A$ equation predicts declining recruitment as spawning biomass increases above the biomass that produces maximum recruitment (Hillary et al., 2012). The Ricker$_B$ function (Eq. 3), like the Beverton-Holt, is undefined for $h > 1$. Hillary et al. (2012) suggest comparison of Beverton-Holt and Ricker models using a nonlinear generalized equation with a derived parameter (λ) calculated as the product of the slope of the stock-recruit function at its origin (the maximum recruitment potential) and the reproductive potential-per-recruit (Table 1). Lambda allows the meaning of steepness in terms of potential stock productivity in the Ricker model to correspond to a given steepness in the Beverton-Holt model. For Beverton-Holt, $\lambda = 4h/(1-h)$ and for Ricker$_A$, $\lambda = 5h^{5/4}$ (Hillary et al., 2012). For a given Beverton-Holt steepness the Ricker$_A$ steepness with a corresponding normalized spawning potential per recruit is $\lambda_{BH}/5^{4/5}$. Thus, values of steepness for the Ricker$_A$ model in the range 0.23 to 33.0 correspond in terms of normalized spawning potential per recruit to Beverton-Holt values ranging from 0.2 to 0.99 (Table 1).

Despite potential differences in the range of steepness among different spawner-recruit functions, its meaning is the same in all three functions. It is the proportional reduction in equilibrium recruitment expected at a spawning potential of 20% of maximum spawning potential (Hillary et al., 2012). The proportional reduction produced by selected steepness values for the Ricker$_A$ is reported in Table 1 for the corresponding Beverton-Holt value with the same λ.

For each of the four configurations of the krill model using one of the recruitment Eqs. (1)–(4), we specified 80 combinations of steepness and σ_R. These pre-specified quantities were 10 values of σ_R (0.01, 0.05, 0.1, 0.2, 0.5, 0.7, 0.9, 1.2, 2.0, and 3.0) and 8 values of steepness (0.2, 0.22, 0.3, 0.5, 0.7, 0.85, 0.97 and 0.99). The Ricker$_A$ configurations were assigned 6 additional values of steepness (0.28, 0.42, 1.65, 3.35, 13.05 and 33.04) with λ values corresponding to some of the Beverton-Holt values (Table 1).

At least ten replicates for each of the 80 configurations were estimated in different randomized sequential phase orders of the 96 estimated parameters to identify sequences representing local minima (Kinzey et al., 2018). Typically this produced multiple replicates with the best (lowest) observed -LL for that combination of σ_R and steepness. In some of the forced fits ($\sigma_R < 0.2$) only one of the replicates had the lowest -LL. In these cases the differences between the best replicates were less than one unit of -LL, far less than the differences of hundreds of -LL units between configurations with different values of σ_R and steepness. The best replicate from the configurations using different values of σ_R and steepness with the lowest-LL was selected for each of Eqs. (1)–(4). These best replicates from the four recruitment functions were compared among one another, and to the best replicates of the configurations that were forced to fit each of the recruitment functions using σ_R = 0.01.

3. Results

The model configurations that best fitted the data produced essentially identical estimates of spawning biomass and recruitment using each of Eqs. (1)–(4) (Fig. 1). The best-fitting values of σ_R and steepness (Table 2) included σ_R values that were sufficiently large to remove the differences due to the individual fixed effect functions $\hat{R}_y$ on spawning biomass and recruitment. Small differences in the estimates were probably due to the discrete values of σ_R and steepness that were assigned.

The potential differences among the recruitment functions constrained using σ_R = 0.01 so that the models were forced to fit one of the
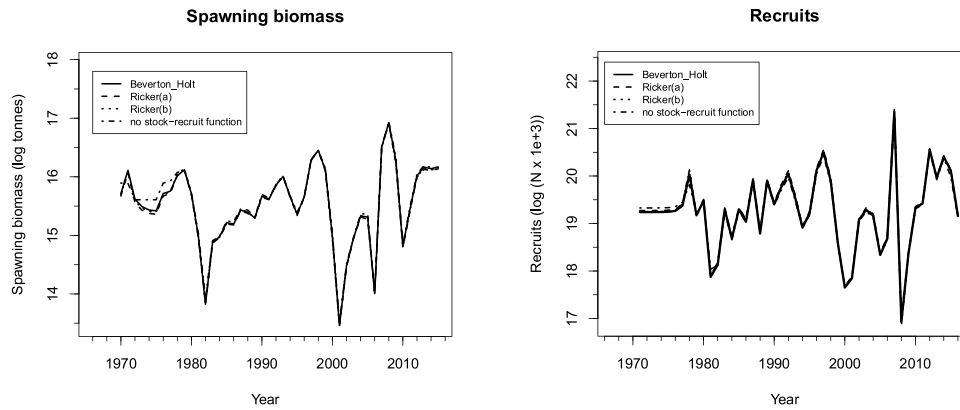
Spawning biomass

Recruits

Fig. 1. Estimated spawners and recruits from 1970 to 2016 from the best-fitting models with h and σ_R values from Table 2 for the models using Beverton-Holt, Ricker$_A$, Ricker$_B$, and the model with no assumed relationship between spawning biomass and recruitment.

Table 2

Values of steepness and σ_R in the best-fitting model configurations that produced the lowest negative log-likelihoods for each of the recruitment models represented by Eqs. (1)–(4).

Recruitment	h	σ_R	-LL
Beverton-Holt	0.97, 0.99	0.9	11398.8
Ricker$_A$	0.97	0.9	11399.1
Ricker$_B$	0.7	0.9	11399.6
Eq. 4	NA	0.7	11400.6

fixed effect functions $\hat{R}_y$ were evident (Fig. 2). These forced models had -LLs that were hundreds of units worse than the best models (Figs. 3, 4; Tables 2–4). Fig. 4 shows comparable results to Fig. 3 about how negative log-likelihoods changed with σ_R for the recruitment function without a spawner-recruit relationship (Eq. 4). Fig. 4 lacks the axis for steepness that is present for Eqs. (1)–(3) in Fig. 3 because steepness has no effect in the average recruitment models without a spawner-recruit relationship. Models with σ_R values less than about 0.6 had -LLs more than 10 units away from the best-fitting configurations, increasing steeply with smaller values of σ_R. This indicates a lack of support for the forced models compared to models using the same data but with different pre-specified values for σ_R and steepness. These forced configurations are discussed here as examples of the results produced by forcing the spawner-recruit functions but are not intended as plausible alternatives to the best-fitting configurations. The best-fitting and forced recruitment functions did have very different implications for estimating the potential productivity of krill in this region, however.

The models using the Beverton-Holt and Ricker$_A$ spawner-recruit functions with different combinations of σ_R and steepness values up to

0.99 showed similar patterns in the -LL values (Figs. 3a, b). For the Beverton-Holt form, five configurations produced -LLs less than 11,400. The best fit (-LL = 11,398.8) for the Beverton-Holt model used 0.9 for σ_R and either 0.97 or 0.99 (both produced the same -LL) for steepness. The best-fitting Ricker$_A$ model also had σ_R of 0.9 and steepness of 0.97 (-LL = 11,399.1). Steepness values greater than 1 for the Ricker$_A$ model fit the data less well (Fig. 3d) than when steepness was 0.97 (Table 2).

The Ricker$_B$ form displayed a different pattern in the negative log likelihood values than the Beverton-Holt or Ricker$_A$ forms (Fig. 3c). Unlike those forms, that best fitted the data with high steepness values at 0.97 or 0.99, the best Ricker$_B$ fit had steepness of 0.7. Similar to the Beverton-Holt form, values of steepness greater than 1 were undefined in the Ricker$_B$ form. This was inconsistent with the generalized non-linear transformation of the stock-recruit relationship using λ from Hillary et al. (2012) and did not match the Ricker$_A$, which was able to produce numerical values when steepness was greater than 1.

The best-fitting models estimated maximum spawning biomass of about 15 million tonnes and a maximum recruitment of about 2e+12 individuals in one year, and fewer than 1e+12 individuals for most years (Figs. 5a, 6a, 7a).The best models using a spawner-recruit function (Eqs. (1)–(3)) had pre-specified σ_R values of 0.9. The best model with deviations around an average recruitment value instead of a spawner-recruit relationship (Eq. 4) had $\sigma_R = 0.7$ (Table 2, Fig. 3). The configurations using Eq. 4 did not include steepness as a parameter.

The best-fitting configurations for all four recruitment functions produced -LLs of approximately 11,399 (Table 2).More finely delineated assignments of these pre-specified values should produce -LLs with arbitrarily small differences among configurations using Eqs. (1)–(4).

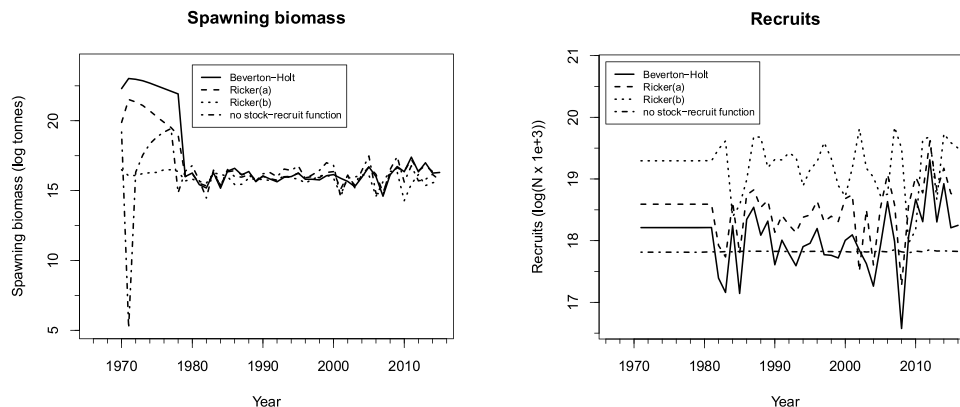The forced Beverton-Holt curve produced increasing numbers of

Spawning biomass

Recruits

Fig. 2. Estimated spawners and recruits from 1970 to 2016 from the three forced models with $\sigma_R = 0.01$ and h from Table 3 for the Beverton-Holt, Ricker$_A$, Ricker$_B$, and for the model assuming no relationship.
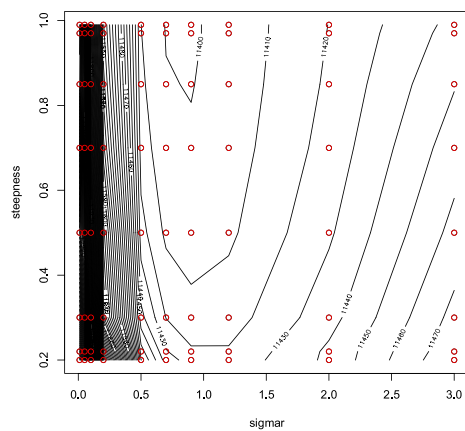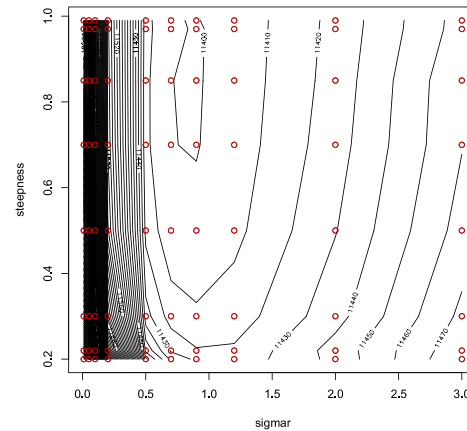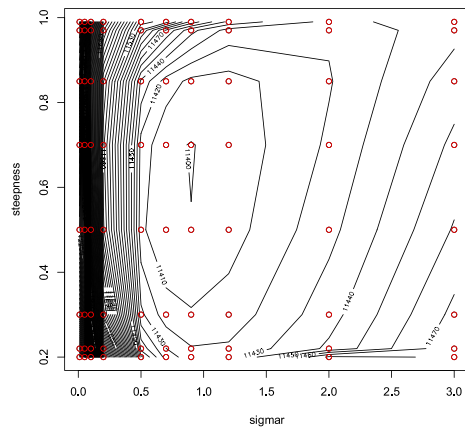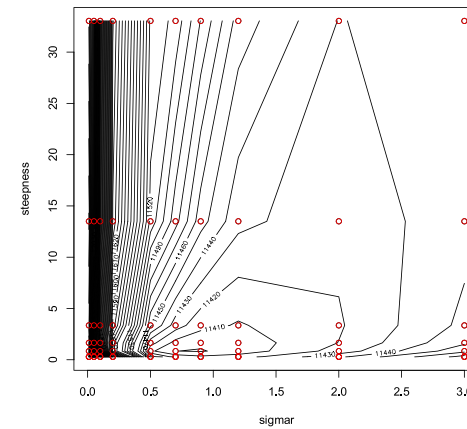
a) Beverton-Holt (*h* = 0.2 to 0.99)   b) Ricker$_A$ (*h* = 0.2 to 0.99)

c) Ricker$_B$ (*h* = 0.2 to 0.99)   d) Ricker$_A$ (*h* = 0.23 to 30.03)

Fig. 3. Contour plots of the negative log-likelihoods from 80 configurations of pre-specified values of steepness (Table 1) and σ_R from 0.01 to 3.0 for four forms of spawner-recruit equations (Eqs. (1)–(3)). Points indicate the combinations of steepness and σ_R that were pre-specified for each model. The two smallest values of steepness (0.28, 0.3) specified for the Ricker$_A$ in (Fig. 3d) are indistinguishable at the scale of the plot. Contour lines represent differences of 10 negative log-likelihoods.

recruits at spawning biomass up to 1.5 billion tonnes (Fig. 5b). Although the forced Beverton-Holt estimated recruitment continuing to increase above 3.0e + 12 at a spawning biomass of 1.5 billion tonnes, the highest estimates of spawning biomass in this configuration during the model period were less than 200 million tonnes (Fig. 5b).The forced Ricker$_A$ estimated very high recruitment at much higher spawning biomass than estimated during the observation period (Fig. 6b). The forced Ricker$_B$ estimated recruitment peaked at a spawning biomass of about 5 million tonnes, with over 13 million tonnes estimated during the observed time series (Fig. 7b).

Although steepness greater than 1 was possible for the Ricker$_A$ function, the best-fitting Ricker$_A$ value of 0.97 was less than 1. This corresponded to Beverton-Holt reproductive potential values (slope at origin x spawning potential/recruit; Hillary et al., 2012; Myers, 2001) that would be produced by the Beverton-Holt function at steepness of 0.545 (Table 1).

3.1. Lagged cross-correlations between spawning biomass and recruitment

When the recruitment and spawning biomass estimates were forced using values of σ_R smaller than 0.9 towards one of the spawner-recruit relationships the models fitted the data more poorly than when the

effects of the spawner-recruit relationships were removed. However, cross-correlations from the best models between the estimates of spawning biomass and recruitment indicated significant correlation at lags of two (Spearman correlation = 0.48), three (Spearman correlation = 0.58) and four (Spearman correlation = 0.39) years (Figs. 5c, 6c, 7c). There were not significant correlations of spawning biomass lagging recruitment. Thus, the best model estimates indicated a possible effect of spawning biomass on recruitment two to four years later, and no discernable effect of recruitment on spawning biomass. This relationship was not well described by either the Beverton-Holt or Ricker functions when a one-year pre-recruit phase and the pre-specified von Bertalanffy relationship were assumed.

Cross-correlations between spawning biomass and recruitment were quite different between the models forced to be either Beverton-Holt or the two forms of Ricker. The forced Beverton-Holt and Ricker$_A$ models had a significant correlation between spawning biomass and recruitment at a one-year lag (Spearman correlation = 0.47, 0.45, respectively) but no others (Figs. 5d, 6d). The model forced to fit the Ricker$_B$ function produced negative correlations between spawning biomass and recruitment at a one-year lag, a positive effect of spawning biomass on recruitment three years later, and a positive effect of recruitment on spawning biomass one year later (Fig. 7d).
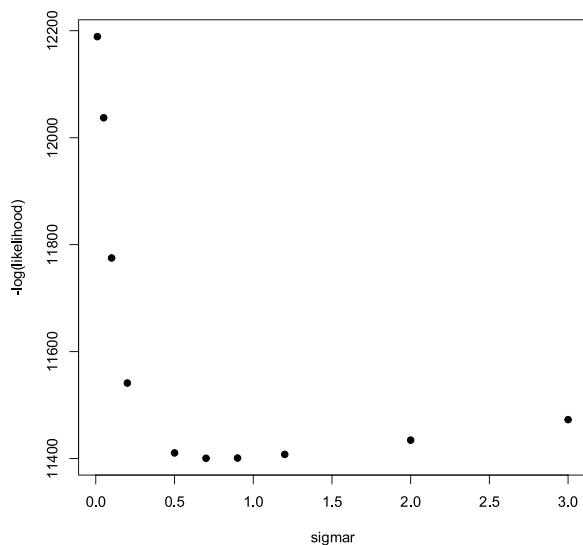
Fig. 4. Negative log-likelihoods from 30 configurations of pre-specified values of σ_R for the fourth recruitment function (Eq. 4) without a spawner-recruit relationship.

Table 3
Values of steepness and σ_R in the best-fitting model configurations with $\sigma_R = 0.01$ that produced the lowest negative log-likelihoods for each of the recruitment models represented by Eqs. (1)–(4).

Recruitment	h	σ_R	-LL
Beverton-Holt	0.85	0.01	12213.8
Ricker$_A$	33.04	0.01	12199.0
Ricker$_B$	0.85	0.01	12131.9
Eq. 4	NA	0.01	12189.0

Table 4
Differences between the best-fitting and the forced configurations using each of Eqs. (1)–(4). Negative values indicate the best-fitting configuration fit that data component worse or was penalized more than the forced model. The rows with "biomass" represent the biomass surveys and those with "comps" represent length-compositions from the surveys and from the fishery. "S" and "W" indicate summer and winter surveys, respectively. The recruitment penalties Λ_{1-4} were calculated using Eqs. (5)–(8). For the other likelihood equations and penalties see Kinzey et al. (2015, 2018).

Likelihood component	Beverton-Holt (Eq. 1)	Ricker$_A$ (Eq. 2)	Ricker$_B$ (Eq. 3)	no SR model (Eq. 4)
fishery catch	502.1	435.7	258.1	505.5
acoustic biomass S	9.4	9.3	4.1	10.7
acoustic biomass W	0.6	−0.1	5.5	−0.9
biomass IKMT S	−9.3	−3	−4.9	1.1
biomass IKMT W	0.9	0.6	2.5	1.6
biomass RMT8 S	3	2.9	2.7	0.6
biomass RMT8 W	10.2	8.8	3.5	5.2
comps IKMT S	144.2	169.3	4.9	0
comps IKMT W	59.5	42.9	37	0
comps RMT8 S	105	81	120.5	−37.1
comps RMT8 W	8.9	4.4	−0.3	76.6
comps fishery	213.8	272.4	529	59.3
Data component subtotals	1048.3	1024.2	962.6	1016.5
Λ_1 (Eq. 5)	6.7	5.5	0	0
Λ_2 (Eq. 6)	−171.5	−171.7	−158.6	−167.4
Λ_3 (Eq. 7)	−18.2	−21.4	−21.7	−27.7
Λ_4 (Eq. 8)	−46.6	−46.6	−46.6	−44.5
Fishing mortality penalties	−3.6	10	−3.3	11.4
Total difference	815	799.9	732.3	788.4

4. Discussion

This study identified the magnitude of recruitment variability in krill models that best fitted the fishery and survey data for CCAMLR Subarea 48.1. It attempted to separate the portion of that variability that can be attributed to recruitment "random effects" specific to each year from a deterministic expectation, $\hat{R}_y$. The integrated assessment incorporates the various data sources supplying information about interannual variability and produces a statistical model that fits the data as closely as allowed by the structural assumptions of the model equations. Recruitment variability did not follow the patterns predicted by either of the Beverton-Holt or Ricker models when data prediction (the best -LL) was used as the metric for determining the best model. All four recruitment models converged to the same estimates of recruitment numbers and spawning biomass for krill from 1982 to 2016 when the values of σ_R and steepness that provided the best fit to the data were used. The estimates of spawning biomass and recruitment from the configurations assuming a spawner-recruit relationship (Eqs. (1)–(3)) were the same as those from the configuration without an explicit relationship (Eq. 4). Small differences between the best-fitting models before 1982 (Fig. 1), before any length-composition data were available might have been due to differential effects of penalties on the models before the estimates were stabilized by matching the predictions to length-composition data available from 1982.

The values of σ_R and steepness that fit these data best produced the same estimates of substantial annual variabilities in spawning biomass and recruitment (Fig. 1). For spawning biomass the estimates of annual variability (Fig. 1 left) differed by approximately 20-fold ($e^{16.5}/e^{13.5}$). Annual recruit abundance (Fig. 1 right) was even more variable, differing by approximately 50-fold (e^{21}/e^{17}). One may ask whether these modeling results are plausible in the context of other research findings and the observed variability in the data.

High interannual variability across orders of magnitude in the recruitment and biomass density of Antarctic krill on a five to six year cycle has been noted in previous studies. Quetin and Ross (2003) described recruitment variability in krill as "episodic" and suggested that a pattern of two strong year classes followed by 3 or 4 moderate or poor year classes was commonly observed. A number of hypotheses have been developed to explain this variability, ranging from the affects of annual variations in sea-ice coverage and duration as winter habitat for juveniles, competition between adult krill and salps, competition of adult krill with juveniles for food, predation on krill eggs and larvae, and various oceanographic factors (Loeb et al., 1997; Siegel et al., 1998; Quetin and Ross, 2001, 2003; Ross et al., 2014; Ryabov et al., 2017).

High variability was observable in the survey biomass densities and length-frequencies used as data in these model configurations before any modeling occurred. Biomass densities from multi-transect hydroacoustic surveys conducted in 4 survey strata (Kinzey et al., 2013) during the summer months of January and February from 1996 to 2012 varied from 0.47 g/m^2 in January 1997 to 222.2 g/m^2 in January 2004 (unpublished data). When the survey strata were pooled the differences between the highest and lowest annual densities were still 16-fold. When differences in annual biomass densities were calculated from survey trawls the differences between the highest and lowest densities were 6-fold. Proportional differences in recruits (annual proportions of krill of lengths < 36 mm in the research trawls, a data component that along with total biomass indicates recruitment strength for the year) among survey strata ranged from low values of 0.002 in years 2001 and 2006, to a high of 0.97 in 2002 (Table 1 in Kinzey et al., 2013).

The likelihood components for the different data sources and the penalties on the parameter estimates indicate how the relative model fits improved when σ_R and steepness were specified to best fit the data (Table 4). The largest improvements were generally in fitting the catch biomass and fishery length-frequencies, with smaller improvements in the fits to the survey biomass and length-frequencies. The effects of the Λ_1 to Λ_4 penalties on increasing recruitment variability that gave small

a) BH best ($\sigma^R = 0.9$, -LL = 11,399)

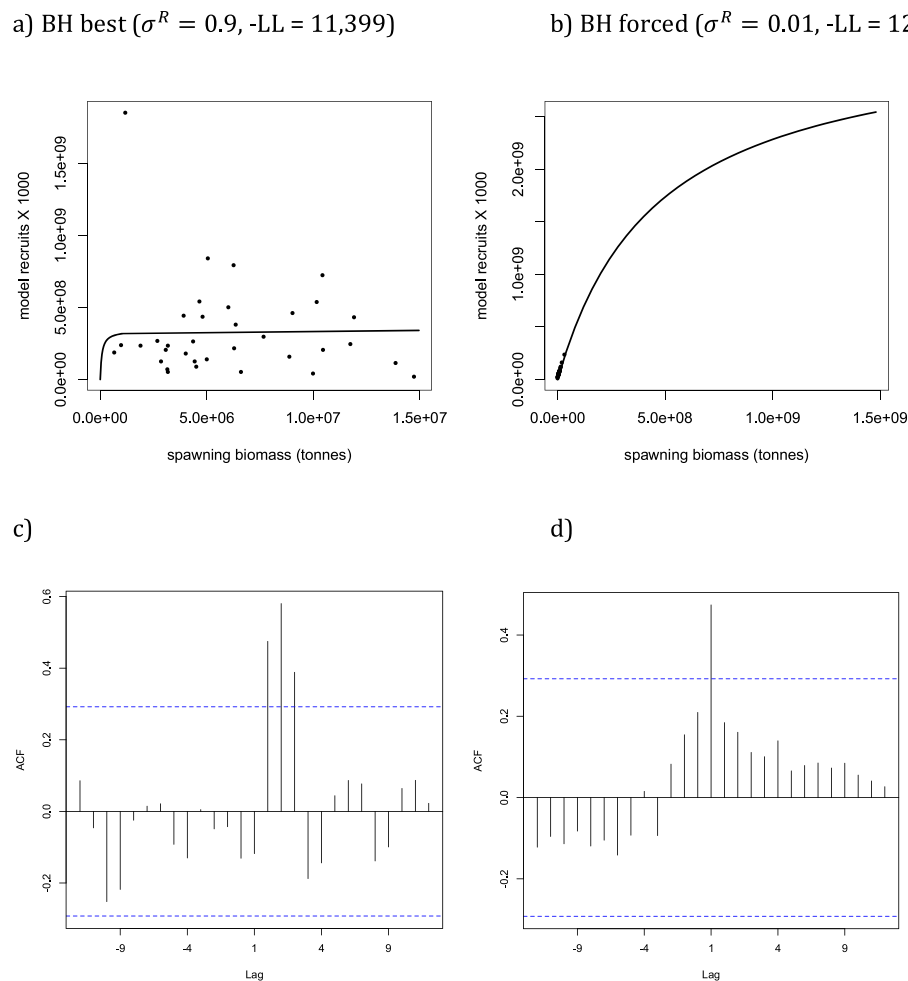## b) BH forced ($\sigma^R = 0.01$, -LL = 12,214)

c)

d)

Fig. 5. Beverton-Holt predicted (lines) and modeled (points) spawner-recruit relationships for a) the configuration with the best negative log-likelihood, and b) forced to fit the theoretical model with $\sigma_R = 0.01$. Cross-correlations of spawning biomass during 1970–2014 with lagged recruitment during 1971–2015 for c) the best-fitting Beverton-Holt, and d) the forced Beverton-Holt.

values of σ_R an advantage over larger values were not sufficient to outweigh the improvements in fitting the data sources that were achieved by allowing more annual variability in recruitment.

Regardless of which spawner-recruit function was applied, the range of estimated recruitments for a given spawning biomass was high in the best models (Figs. 5a, 6a, 7a). High variability in recruitment around a given spawning biomass suggests stock productivity may be importantly influenced by factors other than spawning biomass (Punt et al., 2008; Morgan et al., 2009, 2011; Mangel et al., 2013; Kell et al., 2016). This highlights potential issues with using spawning biomass to represent stock productivity in calculating management reference points, particularly for species such as Antarctic krill with high natural population variability.

The positive correlation of subsequent recruitment with past spawning biomass in this study suggests that biomass might causally affect subsequent recruitment in krill, but not as modeled here using the Beverton-Holt or Ricker functions with a one-year lag time between spawners and recruits and the maturity-at-age calculated using the maturity-at-length measurements with the pre-specified von Bertalanffy relationship.

Other potential stock-recruit functions have been developed, including 11 three-parameter stock-recruitment relationships (Punt and Cope, 2017). Alternative approaches to using spawner-recruit functions as a proxy for stock reproductive potential have also been proposed. These include adding annual variation in maturation, sex ratio, and fecundity (Morgan et al., 2009, 2011), using expected total egg production instead of spawning biomass (Kell et al., 2016), using environmental forcing functions to explain recruitment variability (Loeb et al., 1997; Vert-pre et al., 2013; Szuwalski et al., 2014), and using estimates of spawning biomass relative to a reference level rather than on an absolute scale (Punt et al., 2018). These potential alternative approaches to estimating stock productivity were not applied in the model configurations evaluated in this study.

The developmental time in the wild from krill egg to spawning adult is uncertain. One potential explanation for our finding that none of the spawner-recruit functions fit the data better than random recruitment without a stock-recruitment relationship, but recruitment was still correlated with past spawning biomass, could be that the von Bertalanffy parameters used in the model are imprecise. The von Bertalanffy growth model is used in transforming the survey data on maturity-at-length to expected maturity-at-age. Any inaccuracies in the growth model could produce inaccuracy in the expected proportion mature at age so that the annual proportions mature in the model were desynchronized with the actual proportions mature.

Although this study suggests that the Beverton-Holt or Ricker functions with a one year lag to maturity may not be the best descriptor of krill recruitment dynamics, it does not resolve the issue of whether the lagged correlation observed between recruitment and previous spawning biomass in the best models was causal or only correlative. Strategies for optimal harvest management of krill will ultimately depend on the extent to which recruitment is determined by spawning biomass relative to other potential controlling factors such as

a) Ricker$_A$ best ($\sigma^R = 0.9$, -LL = 11,399)   b) Ricker$_A$ forced ($\sigma^R = 0.01$, -LL = 12,199)
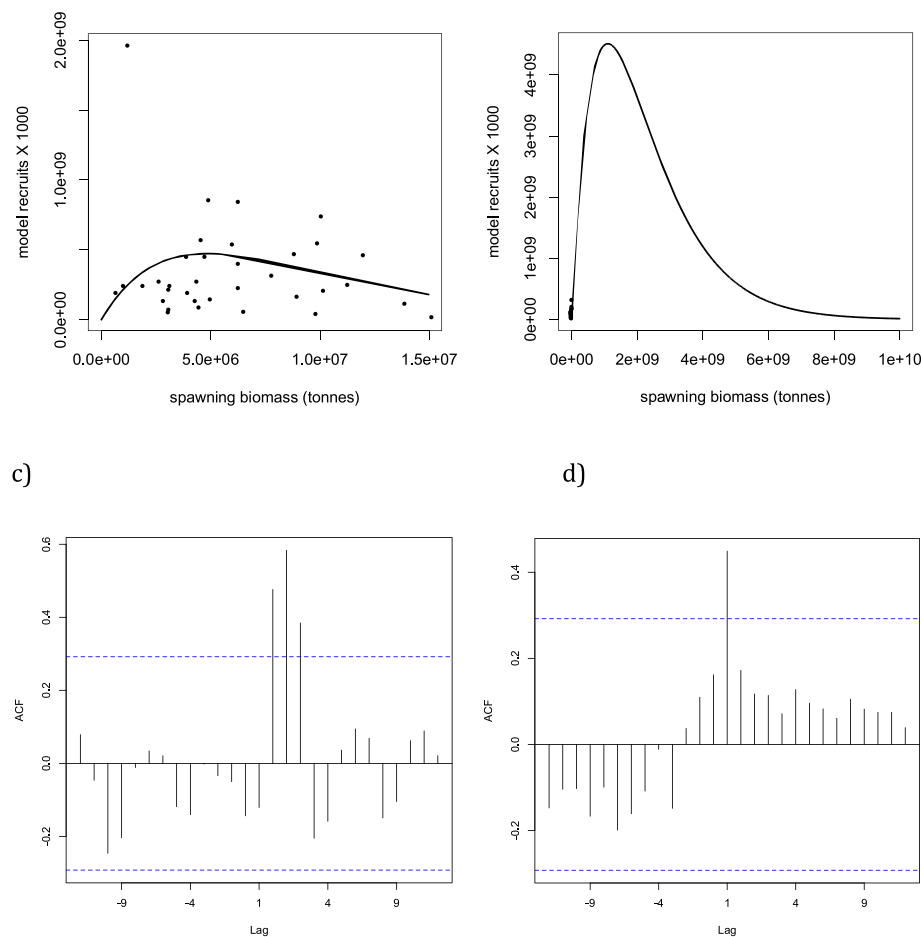

Fig. 6. Ricker$_A$ predicted (lines) and modeled (points) spawner-recruit relationships for a) the configuration with the best negative log-likelihood, and b) forced to fit the theoretical model with $\sigma_R = 0.01$. Cross-correlations of spawning biomass during 1970–2014 with lagged recruitment during 1971–2015 for c) the best-fitting Ricker$_A$, and d) the forced Ricker$_A$.

environmental conditions or endogenous population cycles.

Ryabov et al. (2017) used a mathematical simulation to suggest that krill juvenile abundance is controlled by competition with adults for food. In their model this competition produces population cycles with a period of five or six years due to juvenile starvation each autumn when food resources are scarce until the adult cohort reaches the end of its five to six year lifespan and the next large recruitment event is therefore made possible as competition with adults is reduced. In such a system we might expect to see a negative correlation between spawning biomass and recruitment at lags of up to five or six years. However, none of the negative correlations in the best models evaluated here were significant (Figs. 5 to 6). This result is incompatible with the hypothesis that a negative relationship between densities of older and younger krill drives patterns in recruitment.

Reference points are critical for fisheries management in order to assess whether a fishery is meeting policy objectives or if additional management actions are necessary. A final question posed by these results is, if a spawner-recruit function that fits the data has not been identified, what are the options for modeling recruitment in forward projections to predict the effects of different potential harvest levels for comparison with reference points? The values for productivity parameters such as steepness and the choice of a spawner-recruit function will strongly influence key maximum sustainable yield (MSY)-based reference points (Punt et al., 2008; Mangel et al., 2013). If the relationship between spawning biomass and recruitment is unknown or non-causal, using reference points that are based on an assumed spawner-recruit function may not be the best approach.

One of the goals of CCAMLR decision rules for krill catches is to maintain biomass sufficient for krill predators (Constable et al., 2000). An approach we have developed for the krill assessment is to project the current population into the future using the same recruitment time series as was estimated during the observed period with survey and fishery data. This decouples recruitment from spawning biomass and acknowledges the wide range of recruitments possible from a given spawning biomass as observed in the best models in this study. The CCAMLR decision rules (reference points) are defined in terms of comparing median spawning biomasses during the fished and pre-exploitation periods and so do not require an explicit spawner-recruit relationship for calculating these reference points.

Forcing the models to fit one of the spawner-recruit or average recruitment functions resulted in fishing pressure being perceived as a more important influence on krill population dynamics than in the best-fitting models. This was due to higher recruitment in the best models rather than higher annual fishing mortalities in the forced models, in which fishing mortalities were about half the values in the best models. Future 20 year projections without any catches but using the same recruitment time series as pre-specified values from each model during the observed period with fishing illustrate this. The best-fitting models estimated similar maximum spawning biomasses in the projections without catches to those from the fished period (Supplemental Fig. 1).

a) Ricker$_B$ best (σ^R = 0.9, -LL = 11,400)   b) Ricker$_B$ forced (σ^R = 0.01, -LL = 12,132)
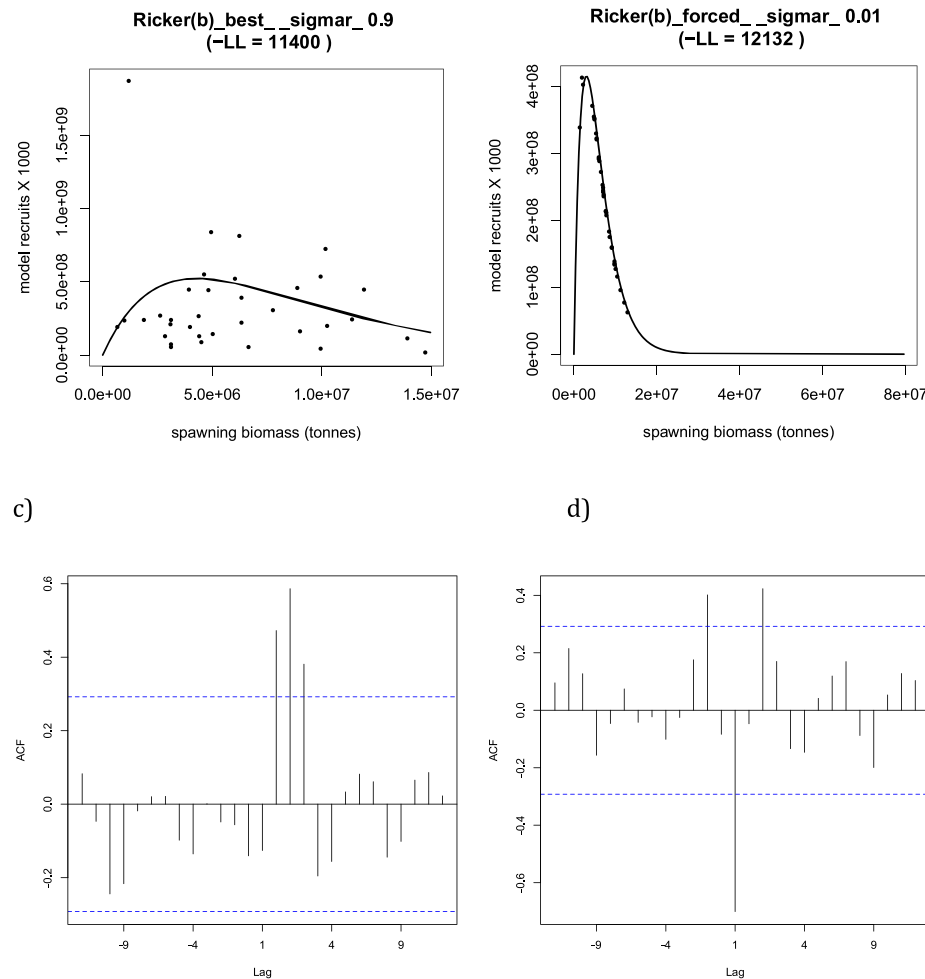

Fig. 7. Ricker$_B$ predicted (lines) and modeled (points) spawner-recruit relationships for a) the configuration with the best negative log-likelihood, and b) forced to fit the theoretical model with σ_R = 0.01. Cross-correlations of spawning biomass during 1970–2014 with lagged recruitment during 1971–2015 for c) the best-fitting Ricker$_B$, and d) the forced Ricker$_B$.

The forced models estimated increased spawning biomass after release from fishing pressure (Supplemental Fig. 2). Forcing a spawner-recruit relationship when it is not warranted by the data can have substantial impacts on model forecasts.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2018.09.027.

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