CCAMLR Science, Vol. 20 (2013): 81–96

EFFECTS OF RECRUITMENT VARIABILITY AND NATURAL MORTALITY ON GENERALISED YIELD MODEL PROJECTIONS AND THE CCAMLR DECISION RULES FOR ANTARCTIC KRILL

D. Kinzey⊠, G. Watters and C.S. Reiss
Antarctic Ecosystem Research Division
Southwest Fisheries Science Center
NOAA National Marine Fisheries Service
8901 La Jolla Shores Drive
La Jolla, CA 92037, USA
Email – doug.kinzey@noaa.gov

Abstract

The generalised yield model (GYM) was used by CCAMLR to establish the precautionary catch limit for the Antarctic krill (*Euphausia superba*) fishery. The current precautionary catch limit was based on supplying the GYM with a natural mortality rate of 0.8 and recruitment variability generated using a Beta distribution for proportional recruitment of krill. In this study, krill sampling data for empirical size frequencies were supplied to the GYM as the 'vector of recruitments' input option to simulate the population dynamics of krill around the Antarctic Peninsula (Subarea 48.1) along with increasing rates of natural mortality. The annual proportions of krill less than 36 mm in length to the total captured in net samples in four sampling areas of the Peninsula were used as proxies for recruitment variability. The variability of proportional recruitment in the CCAMLR study areas was similar to the variability in other krill studies and in the annual size distributions of krill in penguin diets. Simulations with either no fishing, or with fishing at the trigger level (lowest catches), at approximately half the precautionary catch limit (intermediate), or at the precautionary catch limit (highest) were conducted. As the values for natural mortality, recruitment variability and catch were increased, fewer of the scenarios were able to meet the CCAMLR decision rules. The higher precautionary level of catch was not obtainable while meeting CCAMLR decision criteria for at least two of the four recruitment vectors based on net sampling, regardless of how the specified parameters for recruitment and mortality were combined. Any substantial future increases in krill harvests in Area 48 beyond the trigger level require verification that the krill recruitment variability, natural mortality, and other parameters specified in the scenarios used to test management criteria, adequately represent the range of plausible values encompassing krill population biology.

Introduction

The annual catch of Antarctic krill (*Euphausia superba*) in the Scotia Sea (FAO Statistical Subareas 48.1, 48.2, 48.3 and 48.4) is limited by a trigger level of 620 000 tonnes until a procedure for division of the precautionary catch limit of 5.61 million tonnes into smaller management units has been established (CCAMLR, 2012: CM 51-01). This precautionary catch limit was calculated using the generalised yield model (GYM) (Constable and de la Mare, 1996; Constable et al., 2003). The GYM is a simulation approach that can be used to compare population responses to proposed levels of harvest against decision criteria.

From the early 1990s until 2009 the catch by the Antarctic krill fishery remained around 120 000 tonnes per year. Since then, annual catches have increased to over 200 000 tonnes and there is potential for additional increases in catch. The total precautionary catch limit of 8.6 million tonnes for all areas regulated by CCAMLR is over 40 times the current catch (Nicol et al., 2012).

Recent fishing has occurred mainly in Area 48, where about 28% of the Antarctic krill stock is estimated to occur (Atkinson et al., 2009; Nicol et al., 2012). Krill from the region around the Antarctic Peninsula and northern Weddell Sea are believed to be the source of production for a larger area to the north and east, including supplying the sometimes dense aggregations observed around South Georgia (Hofmann et al., 1998; Murphy et al., 1998; Murphy and Reid, 2001; Siegel et al., 2003; Tarling et al., 2007; Reid et al., 2010).

The objective of this study is to examine the effects of different assumptions regarding recruitment and natural mortality on the outputs of the GYM in general and, in particular, on the precautionary catch limit and whether the precautionary catch limit of 5.61 million tonnes for Area 48 meets the CCAMLR decision rules for plausible scenarios developed using available data on recruitment variability and natural mortality. A data series for recruitment based on the observed size frequencies in net samples from the US Antarctic Marine Living Resources (AMLR) Program research surveys (e.g. Van Cise, 2011) during 1992 to 2010 is supplied as a recruitment vector input to the GYM. The effect of different natural mortality rates is also explored. Published estimates of natural mortality for *E. superba* range from 0.45 to 2.92 (Siegel, 2000, Table 4). Siegel (2000) considered realistic values of natural mortality for postlarval *E. superba* to be between 0.66 and 1.35 based on maximum age. Murphy and Reid (2001) suggested that a value of 1.25 produced the best match for size frequencies in the South Georgia area. In this study, natural mortality rates supplied to the GYM are sequentially increased from the 'base-case' value of 0.8 (the value used to calculate the precautionary catch limit), to a uniform distribution between 0.8 and 2 (annual survivals of 14 to 45%) and finally to 3 (5% annual survival). The scenarios with a variable range of annual natural mortalities represented a situation with annual rates of mortality that can vary widely. Scenarios with point values were intended to explore the effects of higher and lower values for mortality on meeting the decision criteria.

The GYM can estimate the distribution of annual spawning biomasses for a modelled population resulting when a constant fraction (gamma) of the pre-exploitation biomass is removed each year by the fishery (gamma = catch/pre-exploitation biomass). A proposed value of gamma is determined outside the GYM and supplied as an input to it. Population parameters associated with that level of harvest are then calculated and compared to decision criteria to determine whether or not the population effects associated with the proposed catch are acceptable. For krill in Area 48, a total biomass estimate of 60.3 million tonnes was established based on CCAMLR surveys conducted in 2000 (Hewitt et al., 2004; Fielding et al., 2011). The trigger level of 620 000 tonnes has been fixed at its present level since 1991. With the current estimate of pre-exploitation biomass of 60.3 million tonnes the trigger level is equivalent to a gamma of 0.0103. The precautionary catch limit is based on a gamma of approximately 0.093 (CCAMLR, 2012: CM 51-01). In practice, the trigger level of catch is apportioned among subareas, with 25% (155 000 tonnes) currently allocated to Subarea 48.1 (CCAMLR, 2012: CM 51-07).

The precautionary catch limit for krill was obtained based on the application of two CCAMLR decision rules to the distributions of spawning biomasses resulting from GYM trials with different gammas (Constable et al., 2000; Constable et al., 2003). The rules are:

(i) achieve a median spawning biomass of at least 0.75 of the unfished median spawning biomass over a twenty-year period, a rule variously called the 'target status', 'escapement', or 'predator' criterion

(ii) achieve a less than 10% chance that the spawning biomass falls below 20% of its pre-fishing median level over a twenty-year period, called the 'threshold', 'depletion', or 'recruitment' criterion.

Each of these criteria is used to evaluate different levels of gamma based on the output of GYM models supplied with pre-specified input parameters (see below). The highest value of gamma at which both criteria are met is then used to calculate the precautionary catch used as an upper limit for the fishery.

The approach that underlies the GYM has been developed over several decades. The krill yield model (KYM) (Butterworth et al., 1994) used a simulation procedure that combined decision rules with a model for population dynamics that extended an earlier dynamic model for fisheries management (Beddington and Cooke, 1983). The framework underlying the KYM was generalised by Constable and de la Mare (1994, 1998).

The gamma parameter values and/or input data that satisfy a particular management criterion in the GYM depend on many values that are supplied to the model. These include the values explored in this paper for recruitment variability and natural mortality. Other potentially important inputs to the GYM include the CV of the unexploited biomass B_0, weight-at-length/age relationships, maturity schedules and spawning seasons. This study uses default values for the inputs other than natural mortality and recruitment from the 'base-run' values used for calculating the precautionary catch limit. The original GYM data files were obtained from the CCAMLR Secretariat.

The GYM has three options for modelling recruitment:

(i) proportional recruitment (randomly generated from a Beta distribution)

(ii) lognormal recruitment (randomly generated from a lognormal distribution)

(iii) recruitment vector (data supplied from outside the model).

Past modelling studies on the support provided by the CCAMLR decision rules for different gamma levels have been based on the Beta distribution or 'proportional' option for recruitment (de la Mare, 1994a; Constable and de la Mare, 1996; Peatman et al., 2011; SC-CAMLR, 2011 (Annex 6, paragraphs 2.72 to 2.78); SC-CAMLR, 2012 (Annex 4, paragraphs 2.28 to 2.30 and 2.62 to 2.65). In the base runs, the mean proportion of the stock as recruits was set at 0.557 with a standard deviation of 0.126. Natural mortality was set to 0.8, representing an annual survival rate (calculated as e^{-M}) of 45%. These values of recruitment variability and natural mortality (the 'base-case Beta model') were supplied to the GYM to calculate the precautionary catch limit for krill used in CCAMLR's management of the krill fishery.

Peatman et al. (2011) showed that the effect on the 'stable recruitment', or depletion, criterion of increasing the standard deviation of the base-case recruit proportions from 0.126 to 0.164 while keeping the mean at 0.557, assuming annual catches equal to the trigger level, was very small. Ratios of fished spawning biomass to unfished were above 0.2 in more than 10% of the trials. For example, the simulations with a maximum standard deviation of 0.164 produced populations with a 0.628 probability of being above 20% of unfished spawning biomass. Peatman et al. (2011) noted that when standard deviations above about 0.176 were assigned, the GYM projections started terminating prematurely, so it was not possible to consistently assess the effects of higher values of recruitment variability.

Methods

Krill data

Annual research cruises to sample krill populations in four areas of Subarea 48.1 (Elephant Island, Joinville, South and West) (Figure 1) of the Antarctic Peninsula in summer using combined acoustic and trawl net-based methods were conducted by AMLR from 1992 to 2011 (Reiss et al., 2008; Cossio et al., 2011; Van Cise, 2011). Some portion of the AMLR sampling grid was sampled annually, but not every station or area was sampled every year. For each year and area for which samples were obtained in January, the net sampling data were combined across stations and the proportion of krill of 36 mm length or less was calculated. These proportions of small krill were assumed to represent recruitment for that year and area. This produced four recruitment vectors representing variable numbers of measured years (Table 1). This method of calculating size frequencies differs somewhat from the CMIX-based method more commonly used in CCAMLR studies (de la Mare, 1994b; de la Mare et al., 2002) but produces very similar length-frequency distributions (Figure 2). As evident in Figure 2, the distributions of length frequencies in 2002 with high proportions of individuals less than 36 mm in all areas and legs that were sampled suggest it was a year with relatively high recruitment. Other years, such as 1995 or 2005 (Table 1), had much lower proportions of small krill. This annual variability in krill size proportions provided the information on recruitment variability that was supplied to the GYM.

Correlations in the annual proportions of krill <36 mm among areas were high (Table 2). Elephant Island, Joinville and the South area had Pearson correlation coefficients greater than 0.7. The West area was the least correlated with the other areas, with coefficients under 0.7 for Elephant Island and the South area. Elephant Island and the West area were the least correlated with a value of 0.61.

Table 1: Proportions of krill <36 mm of the total abundance captured annually during the January sampling leg in each area. Values shown are before standardisation to have mean 1. n/a indicates no January samples that year. EI – Elephant Island; JI – Joinville Island; SA – South area; WA – West area.

Year	EI	JI	SA	WA
1992	0.659	n/a	n/a	n/a
1993	0.165	n/a	0.369	0.075
1994	0.026	n/a	0.643	0.055
1995	0.053	n/a	0.062	0.102
1996	0.690	n/a	0.977	0.099
1997	0.264	0.790	0.610	0.268
1998	0.279	n/a	0.690	0.462
1999	0.022	n/a	0.168	0.042
2000	n/a	n/a	n/a	n/a
2001	0.106	n/a	0.641	0.002
2002	0.458	0.935	0.957	0.810
2003	0.627	0.911	0.944	0.460
2004	0.105	0.250	0.549	0.101
2005	0.061	0.235	0.038	0.008
2006	0.029	0.335	0.130	0.002
2007	0.346	0.983	0.882	0.404
2008	0.652	0.896	0.824	0.600
2009	0.024	0.125	0.690	0.046
2010	0.154	n/a	0.649	0.000

Table 2: Pearson correlation coefficients among areas in the abundance density proportions from Table 1. Refer to Table 1 for abbreviations of areas.

	EI	JI	SA	WA
EI	1	0.87	0.75	0.69
JI		1	0.73	0.87
SA			1	0.61
WA				1

GYM Scenarios

The four vectors of proportional values from Table 1 were each standardised to have a mean of 1 and then supplied to the GYM as the vector of recruitments option. Supplying the standardised recruitment proportions rather than total numbers of sampled individuals less than 36 mm equalised the recruitment CV and standard deviation, put added recruitment CVs for different years on the same scale, and helped account for differences in absolute sample sizes in different years and areas.

Using either standardised proportions or absolute numbers of recruits produced the same results for the annual status of the spawning stock compared to median unfished biomass. This is the value used in the CCAMLR decision criteria. The model values for abundances and biomass differed between simulations using standardised proportions and absolute numbers because they were scaled differently, but these values for population size were not used in generating the results reported here.

To investigate the effect of increasing uncertainty about the recruitment data on model outputs, the standardised recruitment proportions had additional associated CVs assuming lognormally distributed residuals of either 0, 0.1, 0.2 or 0.3 added to the discrete values supplied. The same added CV was used for all years of the recruitment vector in a single trial.

Four values of gamma were modelled: no catch (gamma = 0), the trigger level (gamma = 0.0103), approximately half the precautionary catch limit (gamma = 0.045) and the precautionary catch limit (gamma = 0.093). For an initial total biomass of 60.3 million tonnes, these gamma values correspond to annual catches of 0, 620 000, 2.7 million and 5.61 million tonnes respectively. GYM configurations were supplied with different combinations of these four gamma levels, four recruitment time series, three values of natural mortality and four values of additional recruitment CV. These combinations were used to illustrate the range of outcomes obtainable at different catches using the two CCAMLR decision criteria. Each trial of 10 001 simulations was run for 21 years and CCAMLR criteria calculated both for any given year in all years, and for only the final year, of the simulated period. The simulations based on the recruitment vectors were compared to the simulations based on proportional recruitment using the Beta distribution.

In early trials, a fifth recruitment vector consisting of a combination of the individual area vectors in Table 1, weighted by proportion of the total area represented by each individual sampling area, was also supplied to the GYM. The results from these runs were inside the ranges of values produced using the vectors from the individual areas and so are not reported further.

Results

These results are based on the population status in the final year of simulations in each of the 10 001 trials. The CCAMLR criteria were slightly more likely to be triggered when only the final year, rather than all years, was evaluated, however, for the input values used in this study the results based on either time frame had the same effect on whether or not the CCAMLR decision rules were triggered.

As reported in Peatman et al., 2011, the results of trials based on the base-case Beta model produced population distributions with spawning biomasses well above the CCAMLR decision criteria at all four levels of gamma. The values in Table 1 of Peatman et al., 2011 were reproduced in this study, as was the premature termination of the GYM projections with proportional distribution CVs above about 0.17.

The base-case Beta model produces a smooth distribution (Figure 3) which differs in several respects from distributions for standardised recruitment calculated from the data on length frequencies (Figures 4 to 6). When the added CV was zero, the GYM randomly recycled the discrete, standardised recruitment values in the input vector for the 10 001 randomisations (Figure 4). Unlike the smooth distribution of standardised recruitments produced using the Beta distribution (Figure 3), the values of standardised recruitment or their logarithms were separated by gaps representing proportions that did not occur in the original time series (Figures 4 and 5). Supplying an additional CV greater than 0 to the vector of recruitments allowed the GYM to select from a different set of annual recruitment values for each simulation instead of resampling from only the original input vector, filling the gaps between the original proportions but also widening the distributions of annual recruitments (Figure 6). The logarithms of standardised krill recruitments from the Beta distribution fall mostly between –2 and 2 (Figure 3). The logarithms of recruitment proportions from the AMLR samples with added CVs were between –4 and 4 or wider (Figure 6).

Similar to the findings of Peatman et al. (2011), premature termination of the GYM projections was observed in a small number (about 2%) of the configurations based on AMLR sampling data applied in this study. All of these were for the Elephant Island pattern of recruitment variability. From a total of 240 configurations of natural mortality and added CV for each of four levels of catch (including zero catch) with recruitment variabilities from one of the four areas, four Elephant Island configurations at gamma = trigger level and one Elephant Island configuration at gamma = half precautionary catch limit failed to complete all 10 001 trials. In each of these cases more than 5 000 trials were successfully completed before termination, and configurations with higher gammas but otherwise identical parameter values to the configurations that terminated completed all 10 001 trials.

As expected, as gamma was increased, the distribution of spawning stock biomasses shifted towards more trials with lower final biomass. This shift in the distribution had more of an effect on triggering the depletion rule than on the escapement rule. The median values used by the escapement rule differed less than the 10% ratio of spawning biomasses that define the depletion rule. The Elephant Island recruitment proportions with no additional CV on the recruitment vector and natural mortality set to 0.8 illustrate this (Figure 7).

In each plot of Figure 7 the areas to the left of the dotted lines represent trials with the Elephant Island pattern of recruitment that failed to meet either the depletion rule (left line) or the escapement rule (right). If these lines cross the x-axis below the respective criterion level of 0.2 or 0.75, the CCAMLR decision criterion is triggered. The number of runs producing extremely low spawning biomasses increased from half the precautionary catch limit to the precautionary catch limit (Figure 7, bottom plots). Catch levels up to approximately half the precautionary catch limit did not trigger either decision rule for the Elephant Island base case, but at the precautionary catch limit both the decision rules, especially for depletion, were triggered (Figure 7).

The distributions in Figure 7 correspond to the dashed lines representing the Elephant Island base case in Figure 8 (depletion rule) and Figure 9 (escapement rule). Figure 8 shows the lower 10% quantile of the ratio of the spawning biomass in the final year to the pre-exploitation median spawning biomass (the SSB Status) for the 10 001 trials for each scenario. Scenarios with values that fall below the dashed line at 0.2 do not meet the depletion criterion. The base-case runs for the recruitment vectors from all four regions were all above the CCAMLR depletion decision rule at no catch, at the trigger level, and at approximately half the precautionary catch limit (Figure 8(a), left plot). At the highest level of catch, the precautionary catch limit (gamma ~ 0.09), two of the four recruitment vectors, those from Elephant Island and the West area, triggered the depletion rule. This indicates that populations with either of these patterns of recruitment variability and a natural mortality of 0.8 would not support catches of about 9% of unfished biomass while satisfying the depletion rule.

As natural mortality was increased above 0.8 (Figure 8a), the proportion of recruitments that supported particular gamma levels of catch while conforming to CCAMLR decision rules decreased. At natural mortality = 3, two of the four levels of recruitment variability would not support any catch under the CCAMLR depletion rule (Figure 8(a), right plot). When natural mortality was held constant at 0.8 but CVs of 10%, 20% and 30% were added to the recruitment vectors, the proportion of recruitment vectors supporting a particular gamma level of catch likewise decreased (Figure 8b).

The population based on the recruitment vectors from the Elephant Island and West areas could not support the precautionary catch limit of harvest under the depletion rule with an added CV of 10% and a natural mortality of 0.8 (Figure 8(b), left plot). With 30% added CV, neither the Elephant Island's nor the West areas' level of recruitment could support half the precautionary catch limit under the depletion rule.

The CCAMLR escapement criterion was less susceptible to being triggered at the levels of natural mortality and recruitment variability examined in this study. Only at the highest level of natural mortality considered, $M = 3$, was the escapement rule with catches at the precautionary catch limit appreciably triggered for the recruitment levels from the four areas (Figure 9(a), right). At the highest levels of recruitment variability (Figure 9b), there was a slight triggering of the escapement rule with catches at the precautionary catch limit.

An 'effective' CV (Table 3) was calculated from the recruitment time series generated as model output after running the GYM supplied with the input recruitment parameters and other data. These effective CVs calculated from the model outputs for recruitment were greater than the input CVs. The effective CVs based on the AMLR sampling proportions with natural mortality of 0.8 and no added CV ranged from 0.531 for the South area to 1.104 for the West area.

Table 3: Values of sampling CV added to the vector of recruitments and the effective CVs of the recruitments produced by the GYM for models with natural mortality = 0.8. Refer to Table 1 for abbreviations of areas.

Added CV	EI	JI	SA	WA
0	0.934	0.568	0.531	1.104
0.1	1.636	0.655	0.860	2.342
0.2	4.981	1.005	1.849	3.757
0.3	9.835	1.754	3.068	4.514

Table 4: Effective CVs from the base-case Beta model, using published data for proportional recruitment from other studies in the Scotia Arc, and from penguin diets in the AMLR sampling grid and the Palmer LTER, as inputs to the vector of recruitments option in the GYM.

Source	Approximate scale*	Effective CV
base-case Beta (SD = 0.126)	Scotia Arc (1 000 000s km^2)	0.547
EI+LTER+South Georgia[1]	Scotia Arc (1 000 000s km^2)	0.689
EI+LTER[1]	100 000s km^2	0.769
AMLR combined	100 000 km^2	0.768
South Georgia[2]	10 000s km^2	1.328
LTER[1]	10 000s km^2	1.153
Elephant Island[1]	10 000s km^2	0.689
Cape Shirreff chinstrap	100s km^2	0.764
Copacabana Adélie	100s km^2	0.725
Copacabana chinstrap	100s km^2	0.975
LTER Adélie[3]	100s km^2	0.768

1 Siegel et al., 2003
2 Watkins, 1999
3 Fraser, 2013
* see text for details

Discussion

The actual values of natural mortality and annual recruitment variability for Antarctic krill are not known. The question remains as to what the best values for such parameters are to use in GYM simulations of the krill population, and more generally, any stock assessment for Antarctic krill. Simulations using recruitment variability based solely on ideal distributions such as the Beta distribution are insufficient if they are unable to represent the range of values observable in the data. Conversely, simulations based on a particular data series may be susceptible to vagaries associated with that specific series of values. Careful consideration should also be given to what a plausible range of natural mortality might be for an important prey species such as krill.

The size distributions from the AMLR study area might suggest a tendency towards individual years having gaps in the mid-range proportions (Figures 4 and 5), rather than the continuous decline from lower to higher proportional recruitment produced using the standardised Beta distribution (Figure 3). Assuming the AMLR data accurately represent the overall pattern of recruitment variability in Area 48 would indicate that most years have either a high proportion or a low proportion of recruits, with fewer years having intermediate proportions of recruits. Of course it is always possible that more data would eventually validate the base-case parameter values used in the Beta distribution or some other continuous pattern for recruitment variability, but the possibility that the natural distribution of recruitment events is uneven with intermediate recruitments less common than one extreme or the other cannot be ruled out based on current data.

For comparison with the effective CVs produced using the AMLR data, several other data sources were supplied to the GYM using the vector of recruitments option (Table 4). These were previously published proportional recruitment vectors (Watkins, 1999; Siegel et al., 2003), annual proportions of krill of less than 36 mm in the diets of chinstrap and Adélie penguins at two AMLR field stations inside the sampling grid (unpublished AMLR data) and at the Palmer long-term ecological research (LTER) (Fraser, 2013). The 'approximate scale' column (Table 4) indicates the order of spatial magnitude that the recruitment variabilities from the various samples were intended to represent.

The 'EI' data in Table 4 were from the R_1 column in Siegel et al. (2003, Table 2). This database shares some samples with the AMLR EI data series (Table 3, this paper) but also includes samples that differ spatially and temporally from the AMLR data. The 'LTER' data in Table 4 were from Siegel et al. (2003, Table 1) and represent a portion of the Bellingshausen Sea in the West Antarctic Peninsula south to the eastern Subareas 48.1 and 88.3. The South Georgia series were R_1 data from Watkins (1999, Table 5). The 'AMLR combined' series uses the aggregated length frequencies from all four AMLR sampling areas instead of calculating the proportions separately for each area. Combinations of the recruitment series from GYM models based on individual datasets represent the variability at larger scales (i.e. 'EI+LTER+South Georgia' combines recruitment variability from Elephant Island, the Bellingshausen Sea and South Georgia).

The effective CV of 0.547 produced using the base-case Beta model was amongst the smallest of the effective CVs obtained in the GYM models based on AMLR and other proportional recruitment vectors (Tables 3 and 4). The effective CVs produced using the vector data and combinations of these data (Table 4) suggest general agreement across a range of scales with the amount of variability obtained using the AMLR proportional recruitments (Table 3). The highest recruitment variabilities (CVs > 1) were obtained for South Georgia, the Bellingshausen Sea (LTER) and the West area of the AMLR grid.

There are two general issues to consider concerning the approach taken in this paper. Firstly, the use of proportional recruitment, based here on observable size ratios and in GYM simulations based on the Beta distribution, depend on these relative proportions being independent of absolute population size in order to be interpreted as annual recruitment success. In actuality, if total abundance varies widely among years, high proportions of recruits in years with low total abundance would have less effect on future population sizes than smaller proportions in high-abundance years. The overall population dynamics would depend largely on the recruitment in the high-abundance years even when it might appear small in terms of proportion of all individuals in those years.

The second point to consider is that the method for representing recruitment used in this paper, or in such methods as CMIX, is based on the size distribution in each year being independent of the size distributions in other years. Yet krill recruitment success is thought to be episodic on an approximately five- to six-year cycle (Siegel et al., 2003; Ducklow et al., 2007). In absolute terms, the number of two-year olds in one year must be fewer than the number of one-year olds the previous year. Such dynamics should produce correlations in the time-series of krill recruitment. An alternative way to estimate recruitment is to use some form of cohort modelling that uses multiple measurements of the size of a cohort as it is observed through the years. The integrated model under development for krill in the Antarctic Peninsula (Kinzey et al., 2011) is an example of this kind of model.

In relation to proportional recruitment, krill biomass measured acoustically in the AMLR sampling area varied over about an order of magnitude from 1992 to 2010 (Kinzey et al., 2011), so a high-abundance year with 20% recruitment would produce twice the recruits as a low-abundance year with 90% recruitment during this period if mortalities, etc. were similar. Regarding time-series relationships, there is some indication from the integrated model that krill recruitment in the Antarctic Peninsula might be serially correlated over time, with good recruitment periods of a year or two occurring on approximately a five-year cycle. However, time-series correlation in recruitment patterns was not modelled in the GYM trials reported here.

Conclusions

This study developed from the perspective that it is useful to evaluate the results of decision rules with models based on empirical data as well as theoretical data. The precautionary catch limit is based on the application of CCAMLR decision rules to a GYM model that uses: (i) a single value for natural mortality, and (ii) a theoretical distribution of recruitment variability that is more narrow than the observed variability in krill size distributions in the AMLR sampling data. The proportional recruitment option in the GYM does not appear to be able to consistently model recruitment that is as variable as can be modelled using the vector of recruitments option or with the same kind of variability as displayed by krill size-proportions in the AMLR dataset. Using the vector of recruitments option in the GYM to supply recruitment vectors with the observed levels of variability, together with higher values for natural mortality than 0.8, suggests that the precautionary catch limit established using the base-case Beta model may not meet the CCAMLR decision rules for some plausible models of krill.

The trigger level of catch meets the CCAMLR decision rules in GYM models based either on the base-case Beta model or the models using AMLR size data at all but the very highest levels of natural mortality. If natural mortality is about 0.8 and recruitment variability is no more than the observed variability in the size data, then higher catches of approximately half the precautionary catch limit meet the decision rules. If natural mortality varies annually between 0.8 and 2, the scenario based on size data from the West area does not meet the decision criteria at half the precautionary catch limit (Figure 8(a), middle). This study illustrates that better information is required about krill recruitment variability and natural mortality before using the GYM to potentially show that increasing catches in Area 48 much beyond the trigger level will meet the CCAMLR decision rules.

Acknowledgements

We thank David Ramm of the CCAMLR Secretariat for providing the GYM data files used at WG-EMM-11, Tom Peatman of MRAG, UK, for discussion of recruitment modelling in the GYM and providing the data files used in Peatman et al., 2011, and an anonymous reviewer. Data on penguin diets from the Palmer LTER data archive were supported by Office of Polar Programs, NSF Grants OPP-9011927, OPP-9632763 and OPP-0217282.

References

Atkinson, A., V. Siegel, E.A. Pakhomov, M.J. Jessop and V. Loeb. 2009. A reappraisal of the total biomass and annual production of Antarctic krill . *Deep-Sea Res. I*, 56: 727–740.

Beddington, J.R. and J.G. Cooke. 1983. The potential yield of fish stocks. *FAO Fish. Techn. Pap.*, 242: 47 pp.

Butterworth, D.S., G.R. Gluckman, R.B. Thomson, S. Chalis, K. Hiramatsu and D.J. Agnew. 1994. Further computations of the consequences of setting the annual krill catch limit to a fixed fraction of the estimate of krill biomass from a survey. *CCAMLR Science*, 1: 81–106.

CCAMLR. 2012. *Schedule of Conservation Measures in Force, 2011/12*. CCAMLR, Hobart, Australia: 226 pp.

Cossio, A., C. Reiss and R. Driscoll. 2011. A re-analysis and update of the Antarctic krill biomass in the South Shetland Islands, through 2011. Document *WG-EMM-11/26*. CCAMLR, Hobart, Australia: 16 pp.

Constable, A.J. and W.K. de la Mare. 1996. A generalised model for evaluating yield and the long-term status of fish stocks under conditions of uncertainty. *CCAMLR Science*, 3: 31–54.

Constable, A.J. and W.K. de la Mare. 1998. Bias in the estimation of krill yield from using a deterministic formulation of the median unexploited spawning biomass. *CCAMLR Science*, 5: 1–8.

Constable, A.J., W.K. de la Mare, D.J. Agnew, I. Everson and D. Miller. 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES J. Mar. Sci.*, 57 (3): 778–791.

Constable, A.J., A.T. Williamson and W.K. de la Mare. 2003. *Generalised Yield Model: User's*

Manual and Specifications. Version 5.01b. Australian Antarctic Division, Kingston, Australia: 165 pp.

de la Mare, W.K. 1994a. Modelling krill recruitment. *CCAMLR Science*, 1: 49–54.

de la Mare, W.K. 1994b. Estimating krill recruitment and its variability. *CCAMLR Science*, 1: 55–69.

de la Mare, W.K., A. Constable, E. van Wijk, T. Lamb, D. Hayes and B. Ronai. 2002. *CMIX: User's Manual and Specifications*. Australian Antarctic Division, Kingston, Australia: 50 pp.

Ducklow, H.W., K. Baker, D.G. Martinson, L.B. Quetin, R.M. Ross, R.C. Smith, S.E. Stammerjohn, M. Vernet and W. Fraser. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Phil. Trans. R. Soc. Lond. B*, 362: 67–94.

Fielding, S. and J. Watkins and ASAM participants: A. Cossio, C. Reiss and G. Watters, L. Calise and G. Skaret, Y. Takao, X. Zhao, D. Agnew and D. Ramm and K. Reid. 2011. The ASAM 2010 assessment of krill biomass for Area 48 from the Scotia Sea CCAMLR 2000 Synoptic Survey. Document *WG-EMM-11/20*. CCAMLR, Hobart, Australia: 10 pp.

Fraser, W.R. 2013. LTER Dataset Catalog. Available at: http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets?action=summary&id=96.

Hewitt, R.P., J. Watkins, M. Naganobu, V. Sushin, A.S. Brierley, D. Demer, S. Kasatkina, Y. Takao, C. Goss, A. Malyshko, M. Brandon, S. Kawaguchi, V. Siegel, P. Trathan, J. Emery, I. Everson and D. Miller. 2004. Biomass of Antarctic krill in the Scotia Sea in January/February 2000 and its use in revising an estimate of precautionary yield. *Deep-Sea Res. II*, 51: 1215–1236.

Hofmann E.E., J.M. Klinck, R.A. Locarnini, B. Fach and E.J. Murphy. 1998. Krill transport in the Scotia Sea and environs. *Ant. Sci.*, 10 (4): 406–415.

Kinzey, D., G. Watters and C. Reiss. 2011. Modelling Antarctic krill: scale, movement, and age-structure. Document *WG-EMM-11/43 Rev. 1*. CCAMLR, Hobart, Australia: 37 pp.

Murphy, E.J. and K. Reid. 2001. Modelling Southern Ocean krill population dynamics: biological processes generating fluctuations in the South Georgia ecosystem. *Mar. Ecol. Prog. Ser.*, 217: 175–189.

Murphy, E.J., J.L. Watkins, K. Reid, P.N. Trathan, I. Everson, J.P. Croxall, J. Priddle, M.A. Brandon, A.S. Brierley and E. Hofmann. 1998. Interannual variability of the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. *Fish. Oceanogr.*, 7 (3/4): 381–390.

Nicol, S., J. Foster and S. Kawaguchi. 2012. The fishery for Antarctic krill – recent developments. *Fish Fish.*, 13 (1): 30–40.

Peatman, T., J. Moir Clark and D.J. Agnew. 2011. Estimation of management reference points consistent with the catch trigger level for the Antarctic krill fishery in Area 48. Document *WG-EMM-11/17*. CCAMLR, Hobart, Australia: 6 pp.

Reid, K., J.L. Watkins, E.J. Murphy, P.N. Trathan, S. Fielding and P. Enderlein. 2009. Krill population dynamics at South Georgia: implications for ecosystem-based fisheries management. *Mar. Ecol. Prog. Ser.*, 399: 243–252.

Reiss, C.S., A.M. Cossio, V. Loeb and D. Demer. 2008. Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996–2006. *ICES J. Mar. Sci.*, 65 (4): 497–508, doi: 10.1093/icesjms/fsn033.

SC-CAMLR. 2011. *Report of the Twenty-ninth Meeting of the Scientific Committee (SC-CAMLR-XXIX)*. CCAMLR, Hobart, Australia: 420 pp.

SC-CAMLR. 2012. *Report of the Thirtieth Meeting of the Scientific Committee (SC-CAMLR-XXX)*. CCAMLR, Hobart, Australia: 454 pp.

Siegel, V. 2000. Krill (Euphausiacea) life history and aspects of population dynamics. *Can. J. Fish. Aquat. Sci.*, 57 (S3): 130–150.

Siegel, V., R.M. Ross and L.B. Quetin. 2003. Krill (*Euphausia superba*) recruitment indices from the western Antarctic Peninsula: are they representative of larger regions? *Polar Biol.*, 26 (10): 672–679.

Tarling, G.A., J. Cuzin-Roudy, S.E. Thorpe, R.S. Shreeve, P. Ward and E.J. Murphy. 2007. Recruitment of Antarctic krill *Euphausia superba* in the South Georgia region: adult fecundity and the fate of larvae. *Mar. Ecol. Prog. Ser.*, 331: 161–179.

Van Cise, A.M. (Ed.). 2011. *AMLR 2009/2010 Field Season Report: Objectives, Accomplishments, and Tentative Conclusions*. US Department of Commerce, NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFSC-470: 52 pp.

Watkins, J.L. 1999. A composite recruitment index to describe interannual changes in the population structure of Antarctic krill at South Georgia. *CCAMLR Science*, 6: 71–84.

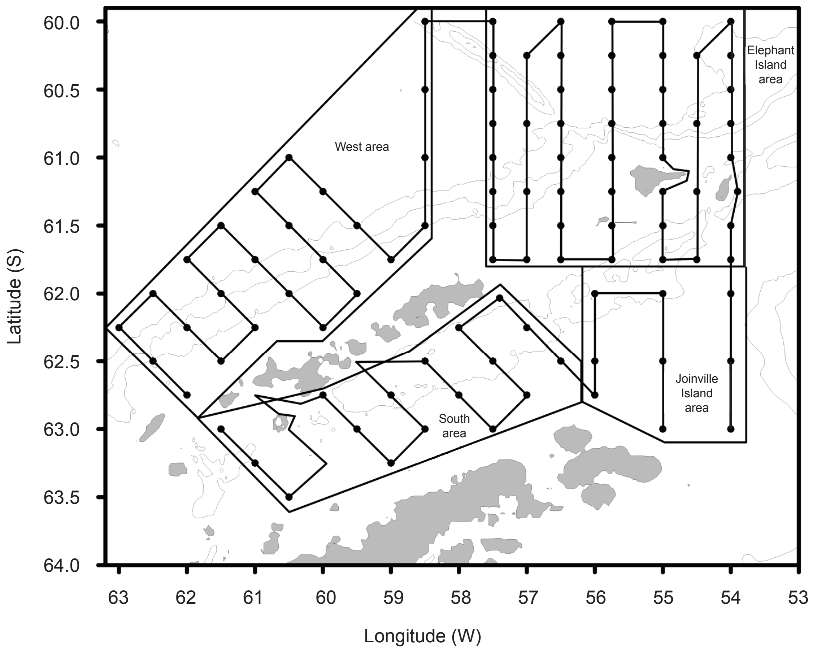


Figure 1: AMLR sampling grid for 2008 showing the survey region and the Elephant Island (43 865 km^2), Joinville Island (18 151 km^2), South (24 479 km^2) and West (38 524 km^2) krill sampling areas.

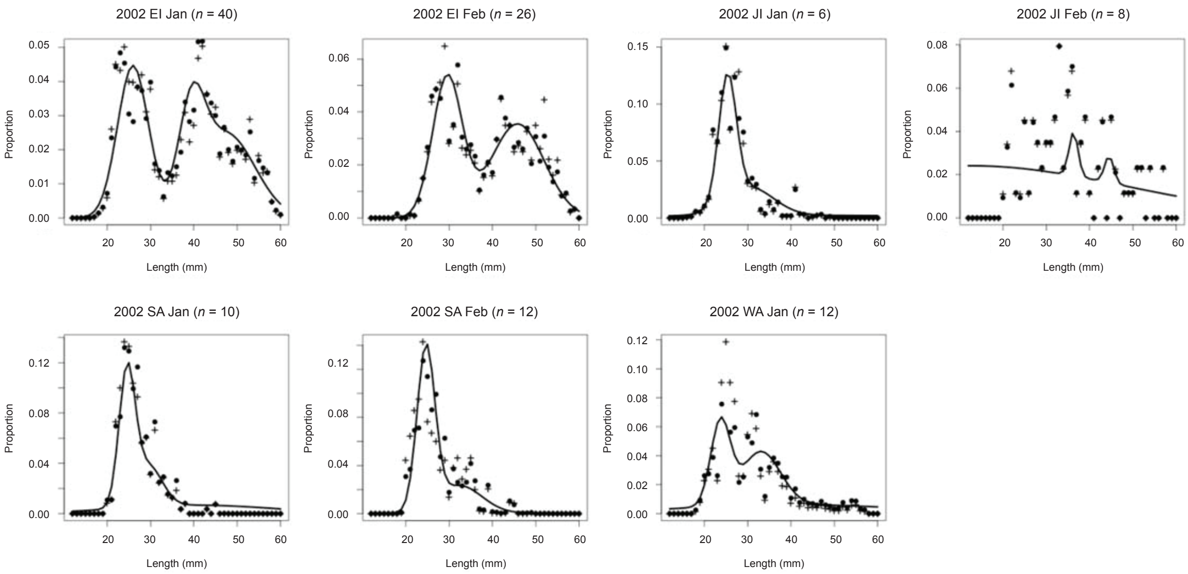


Figure 2: Example comparison between the CMIX method of fitting size frequencies for AMLR data in 2002 (solid circles and fitted lines) and the method used in this study (crosses). EI – Elephant Island; JI – Joinville Island; SA – South area; WA – West area; n – number of net trawls combined in the sampling leg to produce the distribution. Values based on CMIX and the February samples are shown for comparison only and were not used further in this study.

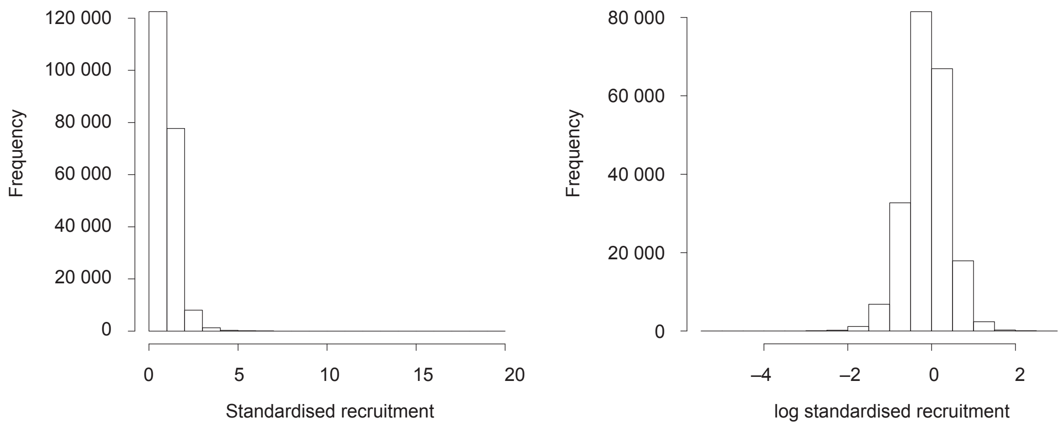


Figure 3: Histograms of standardised annual recruitments (left plot) and the logarithm of standardised recruitments (right plot) in 10 001 samples of 21 years each generated by the GYM based on the Beta distribution with a recruitment mean of 0.557 and a standard deviation of 0.126.

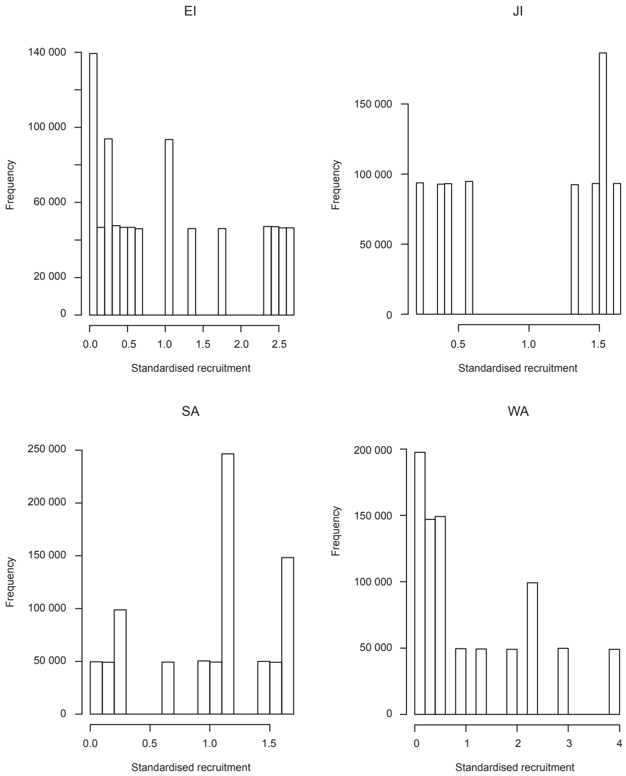


Figure 4: Histograms of the standardised annual recruitments generated by the GYM based on proportions of krill <36 mm from the four AMLR sampling areas, when added CVs were 0. Refer to Figure 2 for abbreviations of areas.

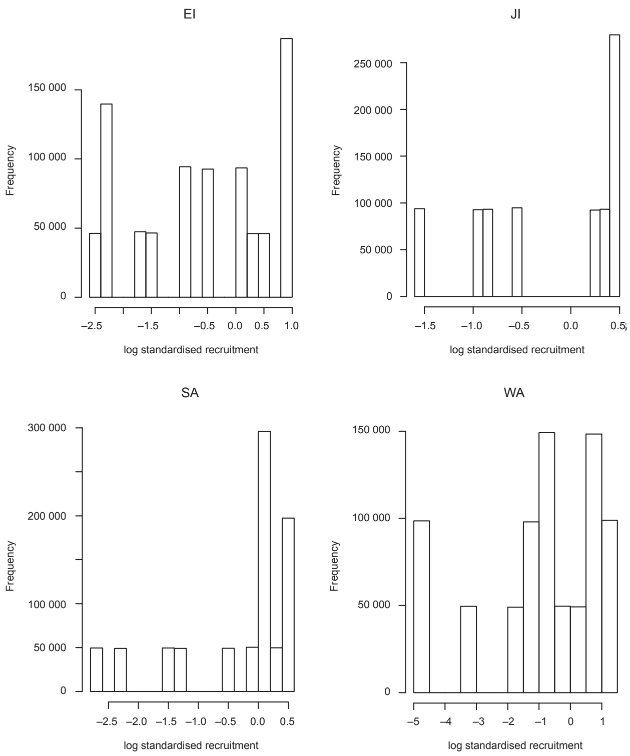


Figure 5: Histograms of the logarithms of the distributions from Figure 4. Refer to Figure 2 for abbreviations of areas.

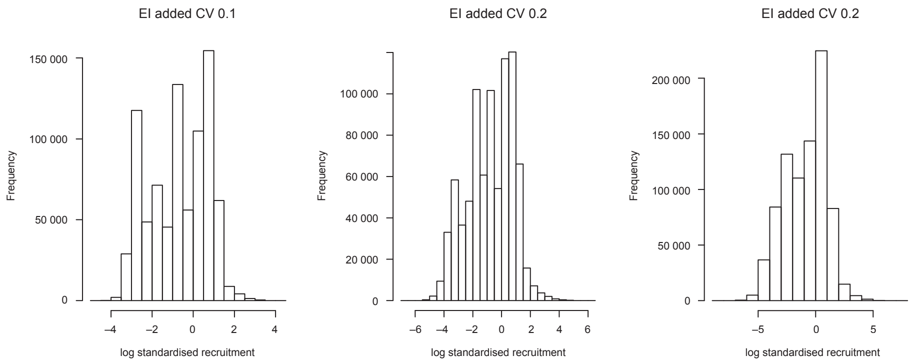


Figure 6: Histograms of logarithms of Elephant Island recruitment vectors with added CVs of 0.1, 0.2 and 0.3. Refer to Figure 2 for abbreviations of areas.

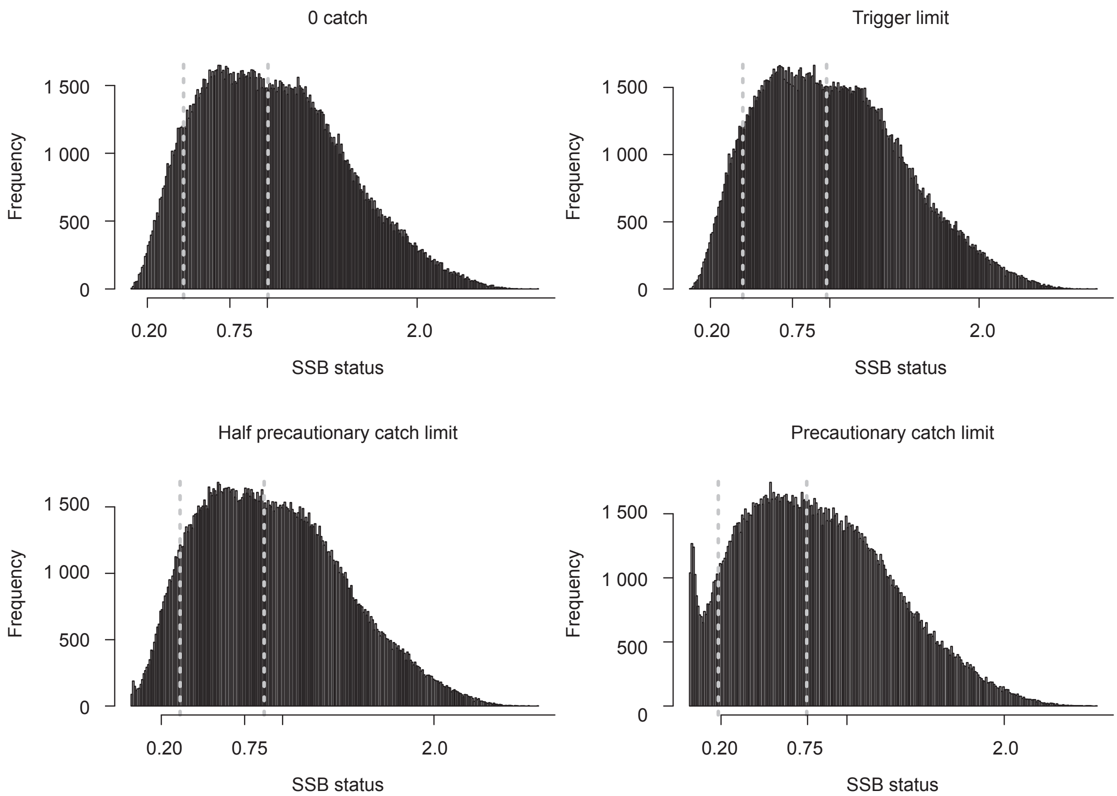
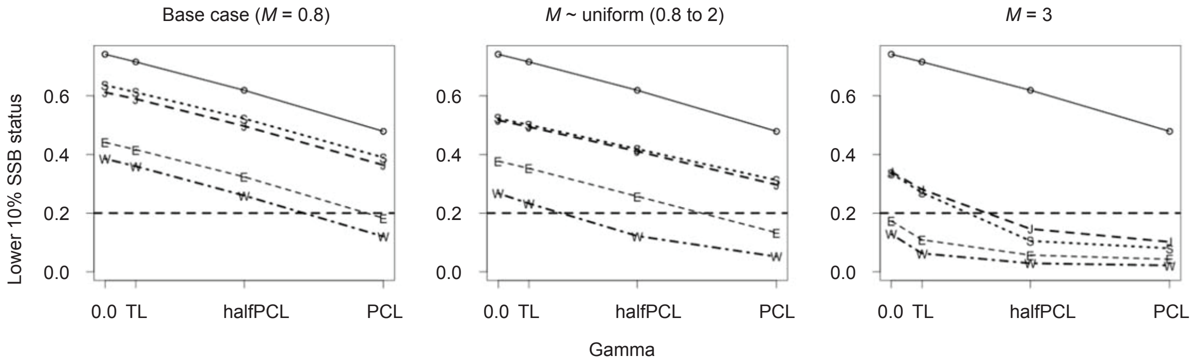


Figure 7: Distributions of krill spawning stock biomass relative to unfished spawning biomass in 10 001 trials based on the recruitment vector from Elephant Island as gamma was increased from 0 to the precautionary catch limit. In each plot the left dotted line indicates the lower 10% of the distribution and the right dotted line shows the median of the distribution. The depletion and escapement criteria of 0.2 and 0.75 are labelled at the bottom of the plots.

(a) Effect of increasing *M*, no additional CV



(b) Effect of increasing CV, constant *M* = 0.8

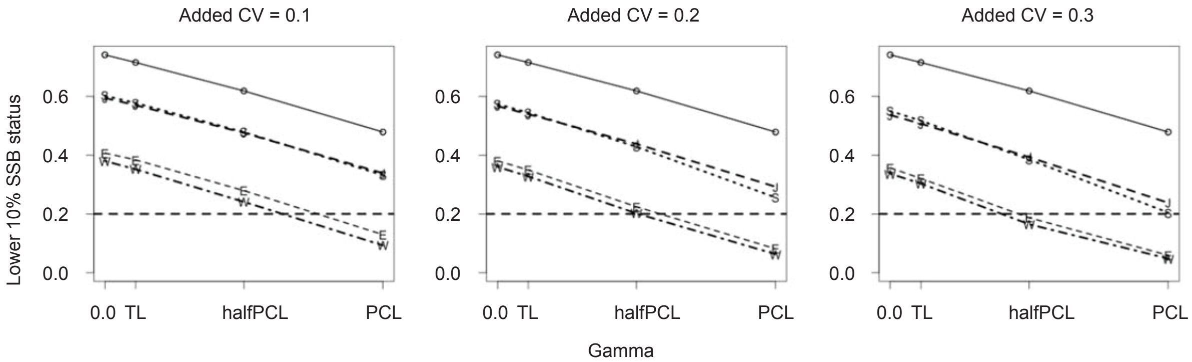
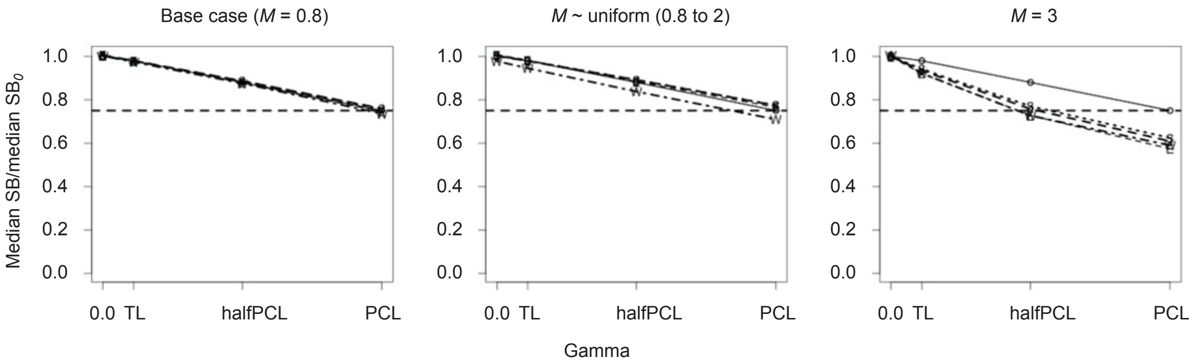


Figure 8: Scenarios meeting the depletion criterion (above the horizontal dashed line) and failing (below) based on recruitment vectors from the four sampling areas (E – Elephant Island, J – Joinville, S – South, W – West). The effects of increasing catches from no catch to the precautionary catch limit are shown (TL – trigger level, halfPCL – half precautionary catch limit, PCL – precautionary catch limit). The base-case Beta model is plotted for comparison (top line in all plots). (a) Natural mortality for recruitment vectors from the four areas increasing from 0.8 (left plot), to uniformly distributed between 0.8 and 2 (middle), to 3 (right); all added CVs 0; and (b) all trials with constant natural mortality of 0.8; added CVs to recruitment vectors of 0.1 (left plot), 0.2 (middle) and 0.3 (right).

(a) Effect of increasing *M*, no additional CV



(b) Effect of increasing CV, constant *M* = 0.8

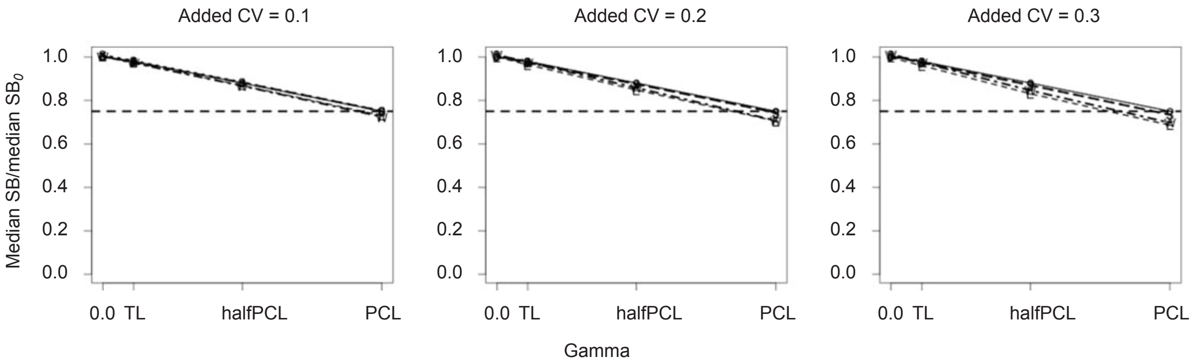


Figure 9: Escapement criterion (horizontal dashed line) and the ratios of median final spawning biomass to median unfished spawning biomass for the same trials as described for Figure 8. TL – trigger level, halfPCL – half precautionary catch limit, PCL – precautionary catch limit.