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Title **CONDITIONING SMOM USING THE AGREED CALENDAR OF OBSERVED CHANGES IN PREDATOR AND KRILL ABUNDANCE: A FURTHER STEP IN THE DEVELOPMENT OF A MANAGEMENT PROCEDURE FOR KRILL FISHERIES IN AREA 48**

ABSTRACT

The updated version of the Spatial Multi-species Operating Model (SMOM) of krill-predatorfishery dynamics described in an accompanying paper is conditioned using the WG-SAM set of reference observations for Area 48 (the SAM calendar). Results are presented for two implementations of SMOM, one with the time series of krill abundance fixed on input, and the other incorporating an explicit model of krill dynamics. Additional versions of SMOM that may need to be conditioned are discussed. In general the two SMOM implementations are broadly successful in reproducing the direction and timing of observed changes in predator abundance. The main method of conditioning involved estimating a shape parameter (the "steepness") of the predator-prey interaction formulation. The steepness values estimated suggest that penguins respond sooner than other predators to decreasing levels of krill abundance. Given data on fish catches, the model estimates the starting (1970) fish abundance level, with results suggesting that fish populations in several of the SSMUs are much reduced compared to their 1970 levels. The conditioned operating models presented here constitute a further step towards the development of a spatially-structured Management Procedure (MP) for the krill fishery by contributing to the set of such operating models to be used to simulation test candidate MPs for robust performance. The next step involves agreeing the relative plausibilities (weights) for the different operating models. An outline of suggested future steps in the MP development process is discussed.

SUMMARY OF FINDINGS AS RELATED TO NOMINATED AGENDA ITEMS

EMM2.2; SAM 5.2, 6.3 Description of conditioning of SMOM (Spatial Multi-species Operating Model), for use in a Management Procedure Framework for assisting in developing approaches to subdivide the precautionary catch limit for krill in Area 48. Discussion provided of suggested future steps in the MP development process.

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Conditioning SMOM using the agreed calendar of observed changes in predator and krill abundance: a further step in the development of a Management Procedure for krill fisheries in Area 48

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ABSTRACT

The updated version of the Spatial Multi-species Operating Model (SMOM) of krillpredator-fishery dynamics described in an accompanying paper is conditioned using the WG-SAM set of reference observations for Area 48 (the SAM calendar). Results are presented for two implementations of SMOM, one with the time series of krill abundance fixed on input, and the other incorporating an explicit model of krill dynamics. Additional versions of SMOM that may need to be conditioned are discussed. In general the two SMOM implementations are broadly successful in reproducing the direction and timing of observed changes in predator abundance. The main method of conditioning involved estimating a shape parameter (the "steepness") of the predator-prey interaction formulation. The steepness values estimated suggest that penguins respond sooner than other predators to decreasing levels of krill abundance. Given data on fish catches, the model estimates the starting (1970) fish abundance level, with results suggesting that fish populations in several of the SSMUs are much reduced compared to their 1970 levels. The conditioned operating models presented here constitute a further step towards the development of a spatiallystructured Management Procedure (MP) for the krill fishery by contributing to the set of such operating models to be used to simulation test candidate MPs for robust performance. The next step involves agreeing the relative plausibilities (weights) for the different operating models. An outline of suggested future steps in the MP development process is discussed.

INTRODUCTION

The Spatial Multi-species Operating Model (SMOM) (Plagányi and Butterworth 2007, 2006a,b) and the FOOSA model (Watters *et al*. 2005, 2006) of krill-predator-fishery dynamics have been used to preliminarily explore alternative scenarios involving subdivision of the precautionary catch limit for krill (*Euphausia superba*) among 15 small-scale management units (SSMUs) in the Scotia Sea. An accompanying paper provides an updated description of SMOM while this paper focuses on presenting the results of conditioning SMOM using the SAM calendar. The calendar comprises a set of reference observations for validating and tuning proposed models to evaluate krill catch allocation options for Area 48. These observations in the form endorsed by WG-EMM were largely qualitative and relative, and have recently been translated into numerical terms (the numerical calendar) (Hill *et al*. 2008).

WG-EMM (CCAMLR 2006) has supported the development of Management Procedures (MPs; Butterworth and Punt 1999; or similarly Management Strategy Evaluation MSE, Smith *et al.* 1999) because they provide formalisations of long-term, robust strategies that are designed to satisfy multiple conflicting objectives. Conventionally there is an ordered set of tasks that need to be achieved in the adoption of a MP, and these are listed below and discussed further at the end of the document to provide an overall context to the work presented here.

- 1. Agree broad objectives for the management of the populations in the region under consideration.
- 2. Agree on the data (observations) available which are pertinent to the dynamics of these populations (e.g. Hill *et al.* 2008).
- 3. Develop a wide range of operating models (in terms both of model structure and input parameter values) that span the uncertainties concerning the dynamics of the populations (e.g. FOOSA, SMOM and EPOC).
- 4. Fit (condition) each of these models to the data agreed under 2; this involves estimating values for the remaining free parameters of each model; such conditioning must, for each model in turn, be agreed to reflect a sufficiently satisfactory fit to the data to be acceptable.
- 5. Agree relative plausibilities (weights) for the different operating models based on *a priori* considerations and on how well they are able to fit to the data agreed.
- 6. Specify statistics in terms of which the performances of alternative candidate MPs are to be assessed and compared.
- 7. Agree guidelines and or thresholds that candidate MPs need to meet/achieve to be acceptable in terms of the agreed broad objectives for management.
- 8. Develop candidate MPs.
- 9. Subject those candidate MPs to a set of trials based on forward projections over a number of years of each operating model under the management actions output annually by the MP.
- 10. Consider and compare the performance statistics for each candidate MP across all the operating models, taking due account of the relative plausibility weightings agreed for each; select from amongst the candidates that MP which best achieves the broad objectives and (since there will be conflicts amongst these objectives) appropriate tradeoffs between them.

The current situation in regard to this set of tasks is that the first two have already been achieved, and tasks 3 and 4 are to be presented to and finalized (or further advanced) during this year's meeting. Step 5 will similarly be initiated at the meeting and continued to the extent appropriate given progress on 4. Initial work has been conducted with respect to steps 6 and 7, and this needs to be extended and finalized. It is suggested that steps 8 and 9, together with any aspects of 4 and 5 still outstanding, might be carried out intersessionally, rather than necessarily await the next meeting, if an appropriate process can be determined at this meeting, and finally that step 10 could then be initiated at the next meeting.

METHODS

ALTERNATIVE OPERATING MODELS

There are three different broad operating models considered here.

- Model 1: This uses a fixed input series of krill biomasses from the SAM calendar as a driving variable to generate predator trajectories for comparison with the SAM calendar.
- Model 2: A no-krill-movement scenario with krill dynamics determined by the combination of sea surface temperature (SST), historic removals by the fishery and predators, and density dependent effects.
- Model 3: Krill movement is assumed based on OCCAM, and krill dynamics determined by the factors listed under Model 2.

Note that each of the operating models above incorporates a Reference Set that comprises 12 alternative combinations of predator parameter values that essentially try to bound the uncertainty in the choice of survival rate estimates as well as in the breeding success relationship.

As described in Plagányi and Butterworth (2008), a multiplier to the krill growth rate parameter *r* is derived based on available historic SST data. The resulting temporal variability in *r* is illustrated in Fig. 1. Based on the SAM calendar, 1986 is set as an anomalous year, and in Models 2 and 3 a second scenario is explored in which there is a step-down in the average krill growth rate from 1984 to 1988, and then remains at this lower level for all following years.

METHOD FOR CONDITIONING MODELS

The methodology used is outlined in Plagányi and Butterworth (2008), with the following summarizing the two main estimation steps.

- a) For each of the three predator groups penguins, seals and whales, the shape parameter *h* for the relationship between breeding success and krill abundance is estimated by finding the best fit to the calendar numerical values for each combination of survival values. The mathematical function minimized is as described in Plagányi and Butterworth (2008).
- b) For fish, there are no calendar observations describing the change in the relative abundance over time, hence the model is used to estimate the 1970 starting abundance of fish in each SSMU that would result in the recent abundance given the historic catch record.

CONDITIONING MODEL 2

In Model 2 the krill dynamics are determined by the combination of sea surface temperature (SST), historic removals by the fishery and predators, and density dependent effects. This model assumes no movement of krill between SSMUs (although predators move during the winter period, thereby partially integrating krill availability over the whole region under consideration). This scenario is useful because the no movement assumption is an extreme that provides a bound, and essentially represents a particularly conservative approach when simulating the effects of different spatial distributions of krill catch on the various SSMUs. As a first step in the conditioning process, the estimates of *h* for each predator were fixed at the values estimated previously, but as they did not give satisfactory fits to the calendar observations, they were re-estimated in subsequent simulations. Simulations revealed that the starting krill biomass estimates were too low to maintain the dependent populations, and hence the starting krill biomass in each SSMU was re-estimated in such a way that predator trajectories roughly matched the observed calendar trends. The historic SST series and derived krill growth rate series (Fig. 1), together with simulated predation pressure by dependent populations, were insufficient to result in the calendar-specified decrease in krill biomass. An additional environmental anomaly was thus introduced with its value estimated such that it results in a decline in krill biomass of approximately 50% over the period 1984 to 1988.

CONDITIONING MODEL 3

The major change introduced by Model 3 is that it includes explicit movement of krill between SSMUs and also three bathtub regions. The direction of movement is set by the OCCAM input matrices, but the model is then conditioned by estimating the rate of movement that leads to predator trajectories that match those specified by the calendar. There was insufficient time to finalise the conditioning results for Model 3 for inclusion in the current document.

RESULTS

Model 1 is treated as the basic model here as it focuses on projecting predator abundance as a function of a given krill biomass, and hence discussion focuses on this case. The other models are more complicated in having to model the krill dynamics explicitly, and hence it is only once this step is captured adequately that the effect of predator dynamics on krill abundance can be taken into account.

Conditioning of SMOM is complicated because it involves simultaneously assessing 12 penguin, 5 seal, 1 whale and 15 fish populations in the various SSMUs, with movement of both krill and predators as specified in each model considered. Rather than attempting to simultaneously estimate all the parameters for each SSMU so as to achieve a close fit to the calendar reference observations, a structured approach was adopted. The first step involved using a Leslie matrix approach (see Plagányi and Butterworth 2008) to set basic survival estimates because the previous values (based partly on literature sources) were mostly too low to yield the observed growth rates.

As explained previously, SMOM (and indeed every multi-species / ecosystem model) is sensitive to the assumed form of interaction between predators and prey. The key parameter controlling this relationship is the "steepness" parameter *h* which may be thought of as specifying the level of prey biomass below which breeding success is negatively impacted (Plagányi and Butterworth 2008). Low values (around 0.2) of *h* reflect scenarios in which there is a near-linear decrease in predator breeding success as krill abundance decreases, whereas high values of *h* (close to 1) reflect scenarios in which predator breeding success is negatively impacted at relatively low levels of krill abundance only. Model estimates of *h* for each predator are shown in Table 1. The values reflect averages over the Reference Set for Model 1 – slightly different values of *h* are estimated for different combinations of adult and juvenile survival rate values. The model could be further refined by allowing different *h* values for different SSMUs (or groupings of SSMUs), but the approach adopted here has been to start as simple as possible so that it seemed pragmatic to assume a common *h* for each predator group.

Although fish are not included in the SAM calendar, they are major consumers in the system modeled and hence their presence impacts on the other predators. It was therefore considered important to try and represent the fish dynamics as realistically as possible in the model. This step therefore consisted of estimating the 1970 (starting) number of fish in each SSMU (Table 2) that would give the observed current number of fish when accounting for the historic catches, and with other aspects of the dynamics modeled as for the other predators, i.e. recruitment determined by krill availability etc. The corresponding current depletion estimates (here the ratio of current fish abundance to the 1970 level) for each SSMU are listed in Table 2. Table 2 also gives the average juvenile survival rate for penguins and seals in each of the SSMUs, given that these "realised" survival values are much less than the maximum possible juvenile survival parameter values which are input.

The conditioned trajectories of penguin, seal and fish abundance (expressed as numbers) for each SSMU, whale abundance for all SSMUs combined and krill biomass are shown in Figs 2a,b. The plots show comparisons with the empirical abundance estimates from Hill *et al.* (2008). For fish, the historic catches are also shown. The historic krill catches have been small compared to krill biomass, and hence these are plotted on a different scale for easier viewing. To aid comparison with FOOSA results presented in Watters *et al.* (2008), similar plots of the natural logarithm of relative abundance (i.e. abundance over time expressed as a fraction of starting abundance) are presented in Fig. 3 (which shows averages of results over the component models of the Reference Set for Model 1).

Model 2

Here the krill biomass trajectories vary across the SSMUs. In general starting krill biomass values were tuned so that on average the final krill biomass was approximately half the starting biomass. Plots of the natural logarithm of relative abundance of penguin, seal and fish for each SSMU, whale abundance for all SSMUs combined and krill biomass are shown in Fig. 4. The major difference of the results for Model 2 conditioning when compared to those for Model 1 is that a much lower estimate of steepness *h* is required for the fish-krill interaction relationship. In contrast, the average steepness *h* controlling the interaction between penguins and krill increased slightly to around 0.25 (Table 1).

DISCUSSION

The conditioning process has proved useful in reducing some of the uncertainty associated with key model parameters. For example, lower survival rate estimates can be excluded as these have been shown to be incompatible with observed rates of population increase. Moreover, the conditioning process has assisted in resolving some of the uncertainty in the response of predators to krill biomass, with penguins predicted to respond earlier to decreasing levels of krill abundance because of the low steepness value estimated for that species. In the absence of calendar reference observations for fish, one earlier suggestion was to assume that the abundance of this group remained approximately constant over time. However the analyses presented here take account of the sometimes large historical fish catches taken, and suggest that fish populations in several of the SSMUs are much reduced compared to their starting (1970) levels (Table 2, Figs 2a,b).

Overall the basic model (Model 1), as conditioned, successfully reproduces the direction and timing of changes in predator abundances as specified by Hill *et al*. (2008). However, in order to fit the recent declines in penguin abundance, an estimate of steepness *h* of about 0.2 is required for penguin breeding relationship. This is not critically problematic, as such an estimate would be for a stock-recruitment relationship where it would imply an absence of density dependence and hence no resilience to the effects of fishing; this is because there is also another density dependent term in the predator dynamics equations (see Equations A1.4 and A1.5 of Plagányi and Butterworth, 2008). Nevertheless it does raise the question of whether the model as conditioned will reflect an unrealistically high sensitivity of penguins to reduction in localized krill abundance caused by krill fishing. For Model 2 the estimate of steepness *h* of the penguin breeding success relationship is slightly higher at about 0.25.

Although there is uncertainty regarding the exact trajectories in krill biomass in the various SSMUs over the past few decades, Model 2 is broadly successful in simulating the empirical observations of changes in predator abundance in response to variability in krill abundance, coupled with a general decrease of about 50% over the period considered.

FURTHER TASKS

The discussion below is formulated in terms of the ordered set of tasks listed in the Introduction.

3. *Develop a wide range of operating models*

In developing the trials for determining the anticipated performance of an MP, once agreement has been reached on the choice of an appropriate Reference Set of operating models, a wider range of robustness-test scenarios needs to be identified (Cooke, 1999). Rademeyer *et al*. (2007) note that such scenarios typically reflect true dynamics that may vary more widely and be less plausible or have less impact than the scenarios included in the Reference Set. In the current context, such further tests could, for example, include different hypotheses about:

- 1) resource dynamics: for example, in SMOM it is possible to change the intensity of the predator-prey interaction term and/or the extent of density dependence;
- 2) the environment: for example, changes in future productivity/recruitment levels of krill in response to global warming;
- 3) dynamics of the fishery: changes in the behaviour of the fishery in terms of spatial distribution and threshold krill density below which it becomes inefficient to operate.

If the MP to be developed is to be subject to such further tests, a start (at least) on their specification needs to be made at the current meeting.

4. *Agreeing the conditioning of each operating model*

Securing formal agreement that operating models have been adequately conditioned to data is a very important step in the overall process. Otherwise, if a candidate MP fails to show satisfactory performance for the trial associated with the operating model concerned, the proponents of that candidate can reasonably argue that such a result can be discounted as the trial concerned was inconsistent with reality. It may be useful to discuss whether a process could be developed which would allow such agreement to be reached intersessionally, rather than only at meetings.

5. *Agreeing relative plausibility weights*

It is important that the relative plausibility of the scenarios reflected by the different operating models be formally agreed *before* the process of comparing the performance statistics achieved by alternative candidate MPs commences. This avoids the difficulty of debates on this topic being influenced by trial results – e.g. proponents of a particular candidate MP arguing for low weight to be accorded to scenarios for which their preferred candidate shows poor performance. Probably a qualitative categorization of *high, medium* and *low* weight for scenarios would be adequate (and likely as much as is possible to reach agreement upon). Then in considering results, perhaps scenarios accorded *low* weight can then be disregarded, with candidate MPs applied to scenarios accorded *medium* weight required to meet a lesser standard for risk-related performance statistics (see task 7 discussion below) than is the case for scenarios accorded high weight.

Plausibility weights need to be considered as a combination of two considerations: how likely *a priori* the scenario is to represent the true underlying reality, and how well the conditioning for that scenario is able to fit to the agreed data. Thus, completion of the plausibility weighting process requires first completion of task 4, the conditioning of all models.

6. *Agree performance statistics*

Ideally earlier discussions on this topic need to be finalized at this meeting so that there is general agreement on the statistics to be considered in choosing from amongst different candidate MPs put forward. For the SAM calendar, transient effects from earlier perturbations may still be present at the time future projections commence. As previously agreed, it is thus useful to report future abundance levels in terms of what they would have been in the absence of future krill fishing, which factors out the impact of the transient effects.

7. *Agree performance guidelines and/or thresholds*

This is desirable so that those developing candidate MPs have some idea of the targets at which they need to aim. Furthermore, guidelines and thresholds might need to differ depending on the plausibility of the scenario under consideration.

For the same reason as in task 5 above, this process is ideally finalized *before* results of trials are available, again to avoid possible undue influence. However, there is the danger that desired trade-offs may be specified amongst such guidelines and thresholds which are not achievable given the dynamics of the system. Hence is might be appropriate to allow limited iteration in this process, so that final thresholds and guidelines set are informed by some initial results from trials of some simple MP candidates.

8. *Develop candidate MPs*

MPs can be constructed to be model-based or 'model-free' (data-based, empirical), with the latter providing recommendations directly based on appropriate feedback in the form of recent upward or downward trends in abundance indices. Model-free approaches are typically simple to develop and easily understood by all stake-holders. Furthermore, as highlighted by Rademeyer *et al.* (2007), they require relatively little computer power for testing (because no iterative minimisation routines are required for fitting models to data) and consequently allow for many simulations to be performed quickly (McAllister *et al*. 1999). Testing with even relatively simple age-structured population models or age-aggregated production models can be lengthy and intensive, so that more complex MPs are seldom considered. A recent international review meeting of best practices in fisheries ecosystem modelling expressed the view that whereas ecosystem models have an immediate role as operating models within a MP framework, the use of tactical ecosystem models as estimators within the MPs themselves still seems some time off (FAO 2008). A further difficulty with the use of complex population models as estimators is that the non-linear minimization involved in fitting the model to data has to be completely automated in the testing process because of the many replications this requires, unlike the careful checking possible for the one-off application needed in an assessment process. Thus, for example, during testing often local rather than global minima may be found; this can raise problems of non-uniqueness of output when such an MP actually comes to be applied in practice.

Although empirical MPs have the advantage of simplicity, population model-based approaches often perform somewhat better, because they reflect the behaviour of the resource over relatively longer periods, and hence exhibit less variability in forecasts and consequently in TACs (Rademeyer *et al.* 2007). Estimators based on simple population models have often been shown to perform as well or better than those based on more complex ones (Punt 1993; Punt and Smith 1999). An example of an illustrative 'model-free' MP that uses data directly, for example in the form of recent upward or downward trends in abundance indices, to feedback appropriately through krill catch allocation changes in the same direction, is given in Plagányi and Butterworth (2008).

The question arises of whether candidates MPs need to be formulated to incorporate certain design features: for example, explicit incorporation in control rules of (some of the) thresholds specified under task 7 above. General practice seems to be that this is not seen as necessary or necessarily appropriate. Both stochastic effects and differences between the operating model and the estimation model within an MP mean that there is no guarantee that a deterministic feature of, say, a catch control rule will be reflected in performance statistics. Rather it is consideration of the performance statistics alone which should determine whether or not a candidate MP meets pre-agreed performance guidelines and thresholds, so that no restrictions need be placed on the form of the candidate MPs themselves.

9. *Subject MPs to trials*

Candidate MP developers need to be able to test their procedures against *all* operating models developed. This requires the code for these procedures to be readily available. Code should be developed on a modular basis, in particular so that candidate MPs can be set up within a separate sub-routine, to avoid the risk that operating model code is unintentionally altered. If the computer language in question allows, all code other than the subroutine containing the MP might desirably be provided in compiled form to preclude such alteration.

Previous experience suggests that the random numbers used to generate stochastic components of recruitment and measurement errors should be pre-specified in data files or data statements in the program. This avoids the problems which frequently arise from the non-transferability of random number generators across different computer platforms, and also reduces Monte Carlo error when comparing results for different candidate MPs.

10*. Selection amongst candidate MPs*

If all other tasks above have been completed in time, and results of tests are available, the next meeting could proceed with selection amongst the candidate MPs put forward. Some discussion of how best to structure that discussion process would seem desirable at this meeting.

Before an MP might be formally adopted by the Commission, it is preferable that the trial results upon which its selection was based are independently checked, and that the coding of the MP is made available to the CCAMLR Secretariat first for validation, and then for use for implementation when associated management advice is needed. Discussion is needed as to who would undertake such checks.

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Table 1. Summary of the averages of the estimates of the biological interaction steepness parameter *h* for each of the predator groups across the Reference Sets for the first two of the broad operating models considered.

Table 2. Summary of the basic model (Model 1) estimates and outcomes, averaged over its associated Reference Set. The first column shows the current fish depletion per SSMU relative to the 1970 abundance as estimated during the conditioning process. The next column shows the model estimated 1970 fish biomass (after converting units from numbers to tons for easier comprehension and comparison with fish catch statistics). In SMOM the realised juvenile survival rate is reduced compared to the maximum value that is input, and the Table shows the average juvenile survival rate for penguins and seals in each SSMU in which they are present. The final column shows the starting krill depletion per SSMU after conditioning.

Fig. 1. Temporal variability in the krill growth rate parameter *r*, which depends on sea surface temperature (CARTON-GIESE SODA Version 2.0.2-3), over the period 1967 to 2006. The same relationship is assumed to apply to a southern box (57°S-64°S; 30°W-70°W) spanning SSMUs 1-12 (Antarctic Peninsula to South Orkney Islands), and a northern box (50°S-57°S; 30°W-50°W) spanning SSMUs 13-15 (South Georgia).

Fig. 2a. Conditioned trajectories of penguin, seal and fish abundance (expressed as numbers) in SSMUs 1-8 from 12 model versions which constitute the Reference Set for the basic model (Model 1), and when using the calendar krill biomass as an input. The crosses (X) represent the empirical abundance estimates from Hill *et al.* (2008). For krill and fish, the historic catches are shown as the shaded regions in the plot. As the krill catches were very small compared to krill biomass, these are plotted on a different scale which is shown on the right side vertical axis for easier viewing.

Fig. 2b.Conditioned trajectories of penguin, seal and fish abundance (expressed as numbers) in SSMUs 9-15 from 12 model versions which constitute the Reference Set for the basic model (Model 1), and when using the calendar krill biomass as an input. The crosses (X) represent the empirical abundance estimates from Hill *et al.* (2008). For krill and fish, the historic catches are shown as the shaded regions in the plot. As the krill catches were very small compared to krill biomass, these are plotted on a different scale which is shown on the right side vertical axis for easier viewing. The bottom right figure shows whale abundance summed over all SSMUs.

Fig. 3. Trajectories of ln(relative abundance) averaged over the Reference Set for the basic model (Model 1). Trajectories are shown relative to initial abundance for each of penguins (blue), seals (red), whales (green hash) and krill (black dash). The whale trajectory represents whales summed across the entire region, but is plotted in SSMU 1 for ease of viewing. The empirical abundance estimates from Hill *et al.* (2008) are shown for penguins (crosses), seals (diamonds) and whales (squares).

Fig. 4. Trajectories of ln(relative abundance) averaged over the Reference Set for Model 2 which explicitly models krill. Trajectories are shown relative to initial abundance for each of penguins (blue), seals (red), whales (green hash) and krill (black dash). The whale trajectory represents whales summed across the entire region, but is plotted in SSMU 1 for ease of viewing. The empirical abundance estimates from Hill *et al.* (2008) are shown for penguins (crosses), seals (diamonds) and whales (squares). Note that the graphs are all plotted on the same scale for purposes of comparison, and that negative values don't reflect populations going extinct but rather a decrease in the population relative to the starting value.