

A Spatial Multi-species Operating model of the Antarctic Peninsula krill fishery and its impacts on land-breeding predators

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SUMMARY

1. An updated version of the Spatial Multi-species Operating Model (SMOM) of krill-predator-fishery dynamics is described. This has been developed in response to requests for scientific advice regarding the subdivision of the precautionary catch limit for krill among 15 small-scale management units (SSMUs) in the Scotia Sea, to reduce the potential impact of fishing on land-based predators.
2. The numerous uncertainties regarding the appropriate choice of parameter values in multi-species models is a major impediment. A pragmatic method proposed involves use of an operating model comprising alternative combinations that essentially try to bound the uncertainty in, for example, the choice of survival rate estimates as well as the functional relationships between predators and prey.
3. The operating model is assumed to simulate the “true” dynamics of the resource and is used to test decision rules for adjusting fishing activities (e.g. catch limits) based on field data forthcoming in the future.
4. An illustrative Management Procedure (MP) that includes a feedback structure is shown to perform better in terms of low risk to predators within each SSMU, than an approach lacking the ability to react and self-correct.
5. This modeling framework provides an example of a method for bounding some of the uncertainty associated with multi-species models used for management. Results are presented as probability envelopes rather than in point estimate form, giving a truer reflection of the uncertainty inherent in outcomes predicted on the basis of multi-species models, as well as highlighting how such probability envelopes could be narrowed given improved data on key parameters such as survival. Results are useful for evaluating the relative merits of different spatial allocations of krill catches. An example is given of

how such a framework can be used to develop a management scheme which includes feedback through management control rules.

Key words: Antarctic Peninsula, krill, Management Procedure, Multi-species model, Operating model, predator-prey, uncertainty

INTRODUCTION

This paper summarises a model framework that can be used to take into account some of the major sources of uncertainty in a multi-species model with applications to management. The framework includes a Spatial Multi-species Operating Model (SMOM) of krill-predator-fishery dynamics, and advocates using this for testing the efficacy of a Management Procedure (MP).

MP (Butterworth and Punt 1999), or analogously Management Strategy Evaluation (MSE) (Smith *et al.* 1999), frameworks are formal methods for addressing uncertainty in formulating management advice for fisheries. They focus on the identification and modelling of uncertainties as well as on balancing different resource dynamics representations (Cooke 1999, Sainsbury *et al.* 2000, Rademeyer *et al.* 2007). A key aspect of the MP approach is that the method proposed to compute quantitative management advice has been tested across a wide range of scenarios for the underlying dynamics of the resource using computer simulation.

The methods described here are based on the standard use of MPs in the Scientific Committees of the International Whaling Commission (e.g. IWC 1994), the Commission for the Conservation of Southern Bluefin Tuna (e.g. CCSBT 2005), and as implemented in the fisheries management process for the major fisheries in South Africa since the early 1990's (e.g. Butterworth *et al.* 1997, Geromont *et al.* 1999, De Oliveira and Butterworth 2004, Johnston and Butterworth 2005, Plagányi *et al.* 2006) – the one difference being that the current MP includes both spatial and (ecological) multi-species considerations. The Antarctic system is an ideal ecosystem to take the lead in the implementation of ecosystem models because krill dominates the diet of predators in the region, so that predator-prey relationships are simplified.

SMOM has been developed in response to requests for scientific advice by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Both SMOM and the Krill-Predator-Fishery-Model (KPFM) (Watters *et al.* 2005, 2006) 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. The primary aim is to assess and to ameliorate current and future potential impacts of fishing on land-based predators, given that krill catches may increase substantially in the future. SMOM is thus used to compare five options for allocating the catch limit among the SSMUs in the Scotia Sea, as presented in Hewitt *et al.* (2004): (1) historical catch within the SSMU; (2) estimated predator demand in the SSMU; (3) estimated standing stock of krill in the SSMU; (4) standing stock less predator demand in the SSMU and (5) dynamic allocation based on land-based predator monitoring conducted just prior to or early in the fishing season.

SMOM essentially builds on the modelling work of Thomson *et al.* (2000) and Mori and Butterworth (2004, 2006). The latter authors developed a model to investigate whether predator–prey interactions alone can broadly explain observed population trends since the onset of seal harvests in 1780. Their model components include krill, four baleen whale (blue *Balaenoptera musculus*, fin *B. physalus*, humpback *Megaptera novaeangliae* and Antarctic minke *B. bonaerensis*) and two seal (Antarctic fur *Arctocephalus gazella* and crabeater *Lobodon carcinophagus*) species in two large sectors of the Antarctic. However, given this model's focus on broad trends, it lacks the smaller scale spatial structure that is required to address questions concerning options for subdivision of the precautionary krill catch limit amongst SSMUs.

Based on experience with South African fisheries, Rademeyer *et al.* (2007) recommend using a Reference Set in preference to a single Reference Case when choosing core operating models for MP testing for populations for which there are a number of sources of major uncertainty about the dynamics. This approach is adopted here, and a Reference Set comprising 12 alternative versions of a basic operating model is used to bound the range of uncertainty associated with the krill-predator-fishery system. In this way, the MP approach has the potential to complement multi-species approaches through its focus on the identification and modelling of uncertainties, as well as through balancing different resource dynamics representations and associated trophic dependencies and interactions (Butterworth and Punt 1999, Sainsbury *et al.* 2000).

The simulation-testing framework used includes i) the operating model – in this case the SMOM which simulates the “true” dynamics of the resource, and ii) a separate MP module which contains the methods and rules that are used to compute krill allocations for each of the

15 SSMUs. Different MPs can then be simulation tested with the performance of alternative MPs being compared on the basis of performance statistics which in this case focus on the risks of reducing the abundance of various predator species in the SSMUs. An illustrative MP is presented that seeks to ensure reasonably robust performance in terms of anticipated krill catches and risk to the krill and predator populations in each SSMU, given prevailing uncertainties about resource status and dynamics.

METHODS

MODEL STRUCTURE

The model includes all 15 SSMUs and uses a six-month (two seasons) timestep to update the numbers of krill in each of the SSMUs, as well as the numbers of predator species in each of these areas. The model currently includes four predator groups (penguins, seals, fish and whales). The model is coded in AD Model Builder (AD Model Builder™, Otter Research, Ltd.). A description of the Operating Model is given in the Appendix and a consolidated list of symbols used in this paper, together with their definitions, is given in Table 1. Values of parameters and their sources are listed in Table 2. The details of the illustrative Management Procedure and performance statistics are as given in Plagányi and Butterworth (2006b).

There are a number of ways in which predator performance could be linked to the abundance of krill. In the interests of constructing as simple a model as possible (a minimally realistic model) here, this is not effected through a consumption term. Rather it is assumed that breeding success is likely to be the most sensitive of the various demographic parameters to changes in prey abundance. A breeding success factor $f(B_y^a)$ (see **Equation 4**) is thus formulated as a function of the available biomass of krill (i.e. krill in SSMU a in year y) and acts as a multiplier to the juvenile recruitment parameters, namely the reproductive rate P and/or the juvenile survival rate.

A single parameter value h (see Equation 11) determines the breeding success relationship for each area and predator species. It controls the “steepness” of the curve, and hence the level of krill abundance (relative to the carrying capacity) below which predator breeding success is negatively impacted. Given that this is not known or easily determined, a prudent approach adopted involved selecting two values that roughly bound the likely range in this relationship by reflecting a near-linear decrease in breeding success as krill abundance decreases compared

with a scenario in which predator breeding success is negatively impacted only at relatively low levels of krill abundance (see Fig. 1). Thus in the former case breeding success drops to half its maximum level when krill biomass is 22% of K compared with a much lower 8% of K in the latter case. The range has been narrowed to exclude hyperdepletion scenarios given that the CCAMLR WG considered that hyperstable-type relationships are more likely for penguins and seals. These values are also used to compute B_j^a in the predator consumption term in the krill dynamics equation (Equation 1), effectively representing the krill biomass when the birth rate of predator species j in SSMU a drops to half of its maximum level. Moreover, rather than assuming a deterministic relationship, variability has been added such that the extent of variability about the curve can be changed by adjusting the parameter σ_{BR} (see Equation 10).

A Reference Case to Bound Uncertainty

Given the numerous uncertainties regarding the choice of parameter values, a Reference Set is used in preference to a single Reference Case Operating Model (OM) (Rademeyer *et al.* 2007). The initial Reference Set used comprises 12 alternative combinations per predator that essentially try to bound the uncertainty in the choice of survival estimates as well as the breeding success relationship. Sensitivity analyses showed that these are the most sensitive model parameters, and they are also the least well determined parameters based on a review of the literature.

For each predator species, the following parameter values are thus input:

- i) an average S2, low S1 and high S3 adult annual survival rate;
- ii) a low SJ1 and high SJ2 maximum juvenile annual survival rate; and
- iii) two alternative values (h_1, h_2) to roughly bound the likely “steepness” of the breeding success relationship.

This leads to a total of $3 \times 2 \times 2 = 12$ alternative OMs to represent the dynamics of each predator. This number of combinations then needs to be raised to a power equal to the number of predators included, so that the number of OMs can become extremely large. Given computational constraints in the current application, the same h_1, h_2 parameters were assumed for seals and penguins, and coupled low, medium and high survival scenarios assumed for penguins and seals, to restrict the number of operating models to 12. A total of ten replicates of each OM were run, yielding a total of 120 simulations per scenario. The initial values chosen for penguins and seals are shown in Table 3.

Accounting for seasonality

The CCAMLR WG suggested that these models include a seasonal component to temporally separate the fishery from predator demands, particularly for the South Georgia SSMU which is characterized by a fishery which operates during the winter months. The revised SMOM model has taken this into account in as simple a manner as possible, which involves splitting each year into a “summer” $s1$ season and “winter” $s2$ season. The krill population in each SSMU is thus updated each year using two time-steps, with the possibility of setting different growth rates, fishing proportions and movement rates for each of half years $s1$ and $s2$ (Equation 1). Moreover, whereas consumption estimates for $s1$ are computed based on the numbers of predators present in each SSMU (and assumed confined to that SSMU because of their breeding), during $s2$ the predators are assumed to range widely and to distribute themselves in the same proportions as the relative abundance of krill per SSMU at the end of $s1$.

Alternative representations of the breeding success relationship can be substituted in the model whereby this depends, for example, on either the krill biomass in a SSMU during the summer breeding season, or on the average krill biomass in a SSMU throughout the year.

Environmental forcing

SMOM is capable of representing environmental forcing through the following:

- a) The krill intrinsic growth rate r is modelled as a function of year, season and area (Equation 1). Spatial and seasonal changes in temperature that affect growth rate are thus modelled by appropriately changing r for different areas and for $s1$ and $s2$. In the illustrative results presented, different summer and winter r values are assumed (Table 3) and it is further assumed that r is 20% higher in the South Georgia SSMUs as a consequence of the higher temperatures in these lower latitude SSMUs. Climate change scenarios are simplistically simulated by introducing an appropriate temporal trend in r to reflect changes in this vital parameter as a result of changes in temperature and/or the extent of the sea ice.
- b) Different krill movement scenarios can be considered by amending Equation 2 to explore hypothesized changes in movement in response to environmental forcing.

- c) The predator adult survival rate is split into a “summer” and “winter” component such that, for example, decreased survival as a consequence of poorer environmental conditions during the winter months can be simulated.

MODEL PARAMETERS

To facilitate model comparisons, wherever possible SMOM and KPFM used the same model inputs in evaluations conducted as part of CCAMLR’s 2006 Workshop on Management Procedures to evaluate options for subdividing the krill catch among SSMU’s (CCAMLR 2006). Most of these inputs, including essential information on the total demand for krill from key predator species in each SSMU, are summarised in Hill *et al.* (2007). Parameters for different species were combined by Hill *et al.* (2007) to represent “generic” predators as this was considered the most pragmatic way to proceed, notwithstanding that individual species differences may be important to bear in mind.

Krill

The krill intrinsic growth rate parameter is set at 0.4 (Mori and Butterworth 2006). Ideally this parameter should be estimated by fitting to time series data on krill abundance in the SSMUs. Its importance in determining krill dynamics depends on the assumed extent of movement of krill between SSMUs, as set by the parameter *Em*.

The overall exploitation rate γ for the 15 SSMUs under consideration was set at 0.091, which is higher than the current krill exploitation rate. The krill catches per SSMU corresponding to Catch Options 1-4 were then computed by dividing γ in the same proportions as given in Hewitt *et al.* (2004). For comparison purposes with the results from the KPFM model, it was assumed that the krill fishery would not operate in a SSMU once krill density falls below a threshold value, set for illustrative purposes at 20% of the starting level. This provided a rough way of accommodating an economic concern of the fishery regarding threshold krill densities below which fishing becomes uneconomical (CCAMLR 2005). Fishing is assumed to occur for the first 20 years, with zero fishing thereafter, in order to assess resource recovery over the next 20 years.

The λ^j parameters are similarly based on the estimates presented in Hewitt *et al.* (2004), when converting numbers to biomass assuming an average krill mass of 0.46 g (Hill *et al.* 2007) (Table 4). Hewitt *et al.* (2004) give the total predator demand per SSMU.

Recent studies suggest long-term declines in krill abundance (Atkinson *et al.* 2004). However, the simplest assumption possible is that the biomass of krill is currently approximately stable over the past few years (i.e. $R = 0$), and the Working Group suggested assuming stable initial krill and predator population sizes (i.e. $R^j = 0$) in initial investigations. Ideally data on trends in each SSMU should be used to provide estimates of R and R^j .

Predators

After setting $R^j = 0$, the only parameter not yet accorded a value in Equation (15) is the maximum breeding success parameter P^j . The average number of offspring per mature female that survive the first year of life is given by the product $f(B_y^a) \cdot P^j \cdot S_{juv}^j$ which includes both intra- and inter-specific density-dependent components. In combination, these terms thus roughly capture the pregnancy rate, survival until fledging (for penguins) / until pups leave their natal colony (for seals) and survival of juveniles to the end of the first year of life. Estimates used are $P^{seals} = 0.88$ (Boyd *et al.* 1995) and $P^{peng} = 0.91$ (Crawford *et al.* 2006). Density dependence in predators such as seals and penguins is assumed to primarily affect the youngest age classes.

RESULTS

For each of the 12 operating models, 10 replicates are run, yielding a total of 120 model outcomes. Projections are conducted over 20 years: 2005-2024. For presentation purposes, trajectories of both krill and predator (by group) abundance are plotted showing the median value and 90% probability envelopes (Figs. 2-6). Three randomly selected individual trajectories are also superimposed on each plot (termed worm plots). In the interests of brevity, selected results are shown mainly for SSMUs 3 (Drake Passage West), 10 (South Orkney East) and/or 14 (South Georgia West).

Previous simulations to compare Fishing Option 1 (historical catch within the SSMU) and Option 4 (standing stock less predator demand in the SSMU) demonstrated that the former resulted in relatively higher fishery performance and the latter relatively higher ecosystem performance (Fig. 2). These results were taken to support the notion that Option 1 results in lower ecosystem performance, particularly given there was general qualitative agreement in predictions made by SMOM and KPFM2.

A comparison was provided at last year's WG_EMM meeting when these were transformed into dynamic (feedback) options. The results of an illustrative run using the feedback control rule are shown in Fig. 3. The run shown included the following features: no movement of krill between SSMUs; initially stable (i.e. $R=0$) trends in the abundance of predators; and parameter values as given in Table 3. By focusing on a comparison of the median trend under each scenario, it is clear that the introduction of a feedback mechanism is partially successful in reversing the extent of the downward trends in abundance that would otherwise have occurred. It is important to note that this is an illustrative example only, and as such the MP applied has not been finely tuned as would be done in the later stages of developing a MP.

The result above was based on the assumption that there was a moderate amount of monitoring information available. Plagányi and Butterworth (2006 a,b) illustrated the importance of having as much monitoring information available as possible to effectively monitor future changes in the abundance of predators (and krill) in the various SSMUs.

Illustrative results from the revised model including four predator groups are shown in Figs. 4-6. Fig. 4a shows results for all SSMUs with penguins and/or seals present, whereas Fig. 4b is for the other SSMUs. The example shown is when using Catch Option 4 (standing stock less predator demand in the SSMU) (Hewitt *et al.* 2004) as the starting catch allocation in the simulations and when assuming no movement of krill between SSMUs. By comparison, Fig. 5 shows results for selected SSMUs when using a model version with krill movement based on the outputs of the OCCAM model. There was almost no difference in whale trajectories with and without krill movement being assumed (Fig. 6).

In the illustrative results presented, the probability envelopes from 120 model version and projection replicates for predator trajectories are very wide, primarily as a consequence of the uncertainties associated with key population parameters. Sensitivity analyses have revealed that

predator population trajectories are most sensitive to changes in the survival parameters. Figure 7 illustrates how such probability envelopes could be narrowed given improved data on key parameters such as survival. The biggest effect is seen if adult survival rates are known better - the illustrative scenario uses a single S value per predator in place of three values to bound the likely range in these parameters. Fixing both juvenile and adult survival rates at a single value dramatically narrows the probability envelopes (Fig. 7). The remaining width of the probability envelopes in Fig. 7 is primarily due to uncertainty regarding the relationship between predator breeding performance and the abundance of krill.

DISCUSSION

The Spatial Multi-species Operating Model (SMOM) described here can potentially contribute to the provision of scientific advice regarding the subdivision of the precautionary catch limit for krill among 15 small-scale management units (SSMUs). The modelling efforts described have built to some extent on those related to recent increasing pressure on the South African purse-seine fishery management system to ensure adequate escapement of anchovy and sardine above a threshold limit calculated to avoid negatively impacting the breeding success of vulnerable land breeding marine predator species such as the African penguin *Spheniscus demersus* (Crawford *et al.*, 2006). Attempts there are being made to incorporate functional relationships between predators and prey into the operating models for sardine and anchovy, with these in turn augmented by population dynamic model/s for the predator/s of concern (Plagányi and Butterworth 2007).

The SMOM is relatively simple and has been constructed to require as few parameters as possible – the 12 alternative Reference Set operating model versions are useful in bounding two key areas of uncertainty: the choice of survival rate estimates as well as the breeding success relationship. Preliminary results are presented for illustrative purposes, but it is acknowledged that further refinement of model parameters is required. One of the most important aspects requiring further investigation concerns estimates of growth rates of krill and predators, as determined for example by fitting to time-series of abundance indices. Results highlighted how probability envelopes associated with predator trajectories could be narrowed given improved data on key parameters such as survival.

Comparing results under contrasting scenarios of no movement of krill and extensive movement based on the OCCAM model, highlights the importance of checking the robustness of model conclusions to a wide range of krill transport assumptions – with increasing krill transport it is obvious that the demands of predators may be much more easily met in a SSMU. Given that whales, unlike the other predators in the model, are assumed to be much more mobile and able to integrate krill availability across all SSMUs, they do not show much difference under different krill movement scenarios.

Model Limitations

One of the main problems with the current Operating Model is that the illustrative parameter values selected are in need of revision. Further refinement of these will become possible once an agreed data set becomes available for use either in conditioning models or comparing model trends with observed trends.

The results and candidate MP presented here are still in the early stages of development. Further work would include testing the robustness of candidate MPs to a wide range of alternative hypotheses. For example, it is possible to use robustness tests (see Rademeyer *et al.* 2007) as part of the framework presented here to test the effect of future environmentally-driven changes, such as a change in the overall carrying capacity of krill.

GENERAL CONCLUSIONS

SMOM has been revised from the original version presented in Plagányi and Butterworth (2006a) in three main ways: 1) Accounting for seasonality; 2) Explicitly modeling fish and whales in addition to penguin and seal predators; and 3) Addition of an alternative movement model based on the results from the OCCAM model.

SMOM has been useful in demonstrating the usefulness of an adaptive management framework involving a move towards strategic advice based on stochastic probabilities rather than a short-term tactical approach based on deterministic outputs. One clear advantage of the approach considered here (see (Plagányi and Butterworth 2006b) for details) is thus that management

decisions are based on a trend in data - reducing the risk of responding simply to noise in monitoring data each year.

In summary, an illustrative adaptive management framework is developed that could be used to assist in providing advice regarding the allocation of krill catches between SSMUs. An example is provided of an empirical Management Procedure (MP) which reacts to CEMP monitoring data in setting krill catches per SSMU. The advantages of including a feedback mechanism are demonstrated.

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APPENDIX

KRILL DYNAMICS EQUATION

The krill population is modelled following Mori and Butterworth (2006), with the following modifications to their discrete equation:

- (1) the krill catch is subtracted;
- (2) a net movement term is added which links the various SSMUs;
- (3) the consumption term is scaled upwards to account for the fact that mature predator numbers are calculated in terms of mature females only;
- (4) the consumption term is scaled upwards by a second factor (μ^a) which accounts for total consumption by predators not explicitly included in the model.

$$B_{t+1}^a = B_t^a + r_t^a B_t^a \left(1 - \left(\frac{B_t^a}{K_a} \right) \right) - \frac{1}{\omega} \sum_j \frac{\lambda^j (B_t^a)^n N_{y,seas}^{j,a}}{(B_j^a)^n + (B_t^a)^n} - F_t^a B_t^a + D_t^a \quad (1)$$

where:

B_t^a is the biomass of krill in SSMU a at time-step t (with the base-case model using two time-steps per year y),

r_t^a is the intrinsic growth rate of krill in SSMU a during time-step t ,

K_a is the carrying capacity of krill in SSMU a ,

λ^j is the maximum per capita consumption rate of krill by predator species j ,

$N_t^{j,a}$ is the number of mature females of predator species j in SSMU a during season $seas$ ($s1=summer, s2=winter$) in year y ,

B_j^a is the krill biomass when the consumption and hence also birth rate of species j in SSMU a drops to half of its maximum level,

n is a parameter that controls whether a Type II or a Type III functional response is assumed ($n=1$ for Type II as assumed here; $n=2$ for Type III),

ω is the proportion of the mature population for predator species j comprised of mature females;

μ^a is a consumption scaling factor (year-independent) computed as the total predator demand in SSMU a divided by the total demand of all predators explicitly included in the model;

F_t^a is the fishing proportion (catch= $F_t^a B_t^a$) on krill in SSMU a at time-step t , and

D_t^a is the net movement of krill (immigration-emigration) into SSMU a at time-step t (see below).

Given that there is likely to be substantial movement of krill between areas, it is important to include a term in Equation (1) to describe this. However, there is limited information available on which to base this term. There are two alternative movement models included in SMOM. In the first, a simplistic movement term has been developed by assuming that the net annual immigration in each area is randomly determined in such a way that the total immigration between areas approximately equals the total emigration i.e. there is conservation of krill in the overall area considered. The parameter Em represents the average proportion of krill that emigrate from an area into other areas each year. By varying Em , a range of movement hypotheses can be tested, from an assumption of zero movement to extensive movement. In

initial simulations this parameter is set to zero as the addition of movement complicates interpretation of the dynamics. Mathematically:

$$D_t^a = -Em * B_t^a + I_t^a \quad (2)$$

where I_t^a is the randomly-determined number of immigrants into SSMU a at time t , scaled such that (on average) in each year:

$$\sum_a I_t^a \approx Em \sum_a B_t^a \quad (3)$$

The second option for modelling krill movement in SMOM is based on the method used by KPFM (Watters *et al.* 2006), based on outputs from the OCCAM global numerical ocean circulation model. Hill *et al.* (2006) present summer and winter matrices detailing the instantaneous transport rate between SSMUs and three adjacent “bathtub” areas. These matrices are here rescaled by a parameter ϕ such that the recalled values in matrices \underline{M}^{summer} and \underline{M}^{winter} represent the proportion of krill in each SSMU and bathtub that immigrate to or emigrate from every other SSMU and bathtub at each time-step. The proportions remain constant over time as they represent the relative amounts of krill that can be expected to move between different SSMUs, These proportions are in each case multiplied by the absolute numbers of krill in the different areas, with the numbers in the bathtub regions assumed to remain constant over time. Both the parameter ϕ and the bathtub krill abundance estimates can be adjusted to increase or decrease krill movement in the model.

PREDATOR DYNAMICS EQUATION

The same delay difference equation is used for all predators (penguins, seals, icefish) except whales, with the number of mature females (i.e. adult females past the age-at-first-parturition) at the start of year y , where year y is assumed to commence on the first day of the “summer” season sI , given by:

$$N_{y+1}^{j,a} = N_y^{j,a} \sqrt{(S_{s1}^j)(S_{s2}^j)} + (N_{y-T+1}^{j,a}) \cdot q^j \cdot f(B_{y-T+1}^a) \cdot P^j \cdot S_{juv}^{*,j} \left(1 - \frac{N_y^{j,a}}{K^{*,j,a}}\right) \left((S_{s1}^j)(S_{s2}^j)\right)^{(T-1)/2} \quad (4)$$

and the number of mature females at the start of winter season $s2$ given by:

$$N_{y,s2}^{j,a} = N_y^{j,a} (S_{s1}^j) + (N_{y-T+1}^{j,a}) \cdot q^j \cdot f(B_{y-T+1}^a) \cdot P^j \cdot S_{juv}^{*,j} \left(1 - \frac{N_y^{j,a}}{K^{*,j,a}}\right) (S_{s1}^j)^{(T-1)/2} (S_{s2}^j)^{(T-2)/2} \quad (5)$$

where:

$N_y^{j,a}$ is the number of predator species j in SSMU a at the start of season $s1=summer$ in year y ,

$N_{y,s2}^{j,a}$ is the number of predator species j in SSMU a at the start of season $s2=winter$ in year y ,

S_{s1}^j is the post-first-year annual survival rate of predator species j in season $s1$ (assumed to be independent of area),

S_{s2}^j is the post-first-year annual survival rate of predator species j in season $s2$,

T is the average age at maturity, assumed here for simplicity to be one year less than the age at first reproduction (i.e. a common gestation period of 1 year is assumed, though clearly this is less for some of the predator species considered),

q^j is the fraction of chicks/pups that are female,

P^j is the maximum number of fledged chicks or pups leaving the natal colony per pair of predator species j per year;

$f(B_{y-T+1}^a)$ is a breeding success factor (multiplier for P or S_{juv}) which is a function (see below) of the biomass of krill in SSMU a in year y ,

$S_{juv}^{*,j}$ is the maximum first year post-fledging or post-weaning (juvenile) survival rate of predator species j , and

$K^{*,j,a}$ is a carrying capacity-related term for predator species j in SSMU a , used to introduce density dependence into the predator dynamics through the dependence of S_{juv} on predator abundance N .

Note from the above that it is possible to set different adult survival values S^j for each of the 6-month seasons. Births are assumed to occur at the start of the summer season. The second term on the right hand side of Equation (4) represents animals born $T+1$ years ago that are

now reproducing for the first time, and is slightly different in Equation (5) because the adult survival rate is only applied for half (i.e. the summer half) of the last pre-maturity year in order to estimate the numbers of animals present at the start of the winter (the survivors from these maturing animals will be assumed to give birth at the start of the following summer).

Note that during the “summer” months, the number of predators feeding in each SSMU is simply given by:

$$N_{y,summer}^{j,a} = N_y^{j,a} \quad (6)$$

However, predators in the Antarctic Peninsula region are not confined to their SSMUs during the winter months (CCAMLR 2006). In the model they are assumed to distribute themselves according to the relative abundance of krill in the region, and then to return again to their natal SSMUs at the start of spring/summer. To compute the impact of predators on krill in each SSMU during season $s2$, the number of predators feeding in each SSMU is thus calculated as:

$$N_{y,winter}^{j,a} = \frac{B_{s2}^a}{\sum_a B_{s2}^a} \times \sum_a N_{y,s2}^{j,a} \quad (7)$$

The “breeding success” factor in the model above is essentially a component of the first-year or juvenile survival rate S_{juv} . It is not adequate in a model of this form to assume that survival depends on prey abundance without also introducing density dependence into the predator dynamics through the dependence of S_{juv} (say) on N . If S_{juv} is a decreasing function of N , as well as an increasing function of prey abundance B , the model behaviour will yield broadly stable levels of predator abundance for a range of prey abundances. Density dependence in predators such as seals and penguins is assumed to primarily affect the youngest age classes.

The selected density-dependent formulation is based on the form suggested in Thomson *et al.* (2000) adapted as follows:

$$S_{juv} \rightarrow S_{juv}^* \left(1 - \frac{N_y}{K^*} \right) \quad (8)$$

Note that the value of the density dependent multiplier lies between zero and 1, so that, for example, when the population size is very small relative to the carrying capacity related term K^* , this term approaches 1. If at any stage $N_y > K^*$, the whole term is set to zero. Estimating or specifying the value of S_{juv}^* is not straightforward: one approach is to set this value based on the maximum realistic population growth rate. The value for K^* is computed as explained in the next section.

A breeding success factor $f(B_y^a)$ is formulated as a function of the available biomass of krill, which can be determined either as the krill in SSMU a during season sl or the average krill in SSMU a during year y . It acts as a multiplier to the reproductive rate P in Equation (4) but could also be thought of as acting as a multiplier for the juvenile survival rate S_{juv} or a multiple of the product of P and S_{juv} . To reduce the number of parameters in the model, the breeding success factor is scaled such that it is 1 when the local krill abundance is at the carrying capacity level for an area, i.e. breeding success is at a maximum in these circumstances. A useful functional form to use is that classically referred to as a Beverton-Holt stock-recruitment relationship, modified here to represent breeding success as a function of krill biomass B_y^a :

$$f(B_y^a) = \frac{\alpha^a B_y^a}{\beta^a + B_y^a} \quad (9)$$

where α^a and β^a are parameters for SSMU a , with $\beta = (\alpha - 1) \cdot K_a$.

By scaling as above, multiplying through by the krill carrying capacity K_a and adding a term to allow for fluctuations about this relationship, Equation (9) becomes:

$$f(B_y^a) = \frac{\alpha^a B_y^a / K_a}{(\alpha^a - 1) + B_y^a / K_a} e^{(\zeta_{ay} - \sigma_{BR}^2/2)} \quad (10)$$

where

ζ_{ay} reflects fluctuation about the expected curve for area a in year y , which is assumed to be normally distributed with standard deviation σ_{BR} (whose value is input in the applications considered here). Note that values of σ_{BR} are such that the product

$f(B_y^a) \cdot P^j$ does not exceed biologically plausible limits (e.g. the annual seal pup production for females does not exceed 1).

In order to work with estimable parameters that are more meaningful biologically, Equation (10) is re-parameterised in terms of the maximum krill biomass, B_{MAX}^a , and the “steepness” h of the relationship, where “steepness” is the fraction of, for example, maximum fledging success that results when B_y^a drops to 20% of its maximum level, from which it follows that:

$$h = \frac{\alpha}{5\alpha - 4} \quad (11)$$

By ignoring the random variation term and choosing a single parameter value h , the fledging success relationship can thus be specified. The parameter h may be thought of as controlling the level of prey biomass below which breeding success is negatively impacted (Fig. 3).

For the deterministic case, Equation (10) can also be used to calculate B_j^a in Equation (1) given that it represents the krill biomass when the birth rate (as a proxy for consumption) of species j in SSMU a drops to half of its maximum level. Equation (10) is thus used to solve for B_y^a / K_a when $f(B_y^a) = BR = 0.5$, yielding:

$$B_j^a = \frac{0.5 \cdot K_a \cdot (\alpha - 1)}{(\alpha - 0.5)} \quad (12)$$

Given values for all the other parameters in Equation (1) (including $n=1$), and assuming that krill have shown a steady growth rate R over the past few years, the value of K_a can be calculated by rewriting Equation (1) (and assuming zero net immigration/emigration) as:

$$R = r^a \left(1 - \left(\frac{B_y^a}{K_a} \right) \right) - \mu^a / q^j \sum_j \frac{\lambda^j N_y^{j,a}}{(B_j^a) + (B_y^a)} - F_y^a \quad (13)$$

and hence solving for K_a for each SSMU as follows:

$$K_a = B_y^a \left/ 1 - \frac{R + F_y^a + \mu^a}{q^j \sum_j \frac{\lambda^j N_y^{j,a}}{(B_j^a) + (B_y^a)}} \right/ r^a \quad (14)$$

Analogous to the method outlined above for krill, if the predators in each SSMU have shown a fixed growth rate R^j over the past few years, the values of $K^{*,j,a}$ can be calculated by rewriting Equation (4) as:

$$(1 + R^j)^T = (1 + R^j)^{T-1} \sqrt{(S_{s1}^j)(S_{s2}^j)} + q^j \cdot f(B_y^a) \cdot P^j \cdot S_{juv}^{*,j} \left(1 - \frac{N_y^{j,a}}{K^{*,j,a}} \right) \left((S_{s1}^j)(S_{s2}^j) \right)^{(T-1)/2} \quad (15)$$

and rearranging to solve for $K^{*,j,a}$ as:

$$K^{*,j,a} = N_y^{j,a} \left/ 1 - \frac{(1 + R^j)^T - (1 + R^j)^{T-1} \sqrt{(S_{s1}^j)(S_{s2}^j)}}{q^j \cdot f(B_y^a) \cdot P^j \cdot S_{juv}^{*,j} \left((S_{s1}^j)(S_{s2}^j) \right)^{(T-1)/2}} \right/ \quad (16)$$

WHALE DYNAMICS EQUATION

A similar delay difference equation to Equation (4) is used to represent whales, with two main differences. Given the large movements undertaken by whales, the dynamics of whales are not determined at the individual SSMU scale but rather based on the total prey abundance across all the SSMUs. Hence the number of mature female whales at the start of year y is given by:

$$N_{y+1}^w = N_y^w \sqrt{(S_{s1}^w)(S_{s2}^w)} + (N_{y-T+1}^w) \cdot q^w \cdot f(B_{y-T+1}^w) \cdot P^w \cdot S_{juv}^{*,w} \left(1 - \frac{N_y^w}{K^{*,w}} \right) \left((S_{s1}^w)(S_{s2}^w) \right)^{(T-1)/2} \quad (17)$$

To incorporate the effect of whales on krill abundance in each SSMU during the summer months, it is assumed that whales distribute themselves according to the relative abundance of krill in the region, such that:

$$N_{y,summer}^{w,a} = \frac{B_{s1}^a}{\sum_a B_{s1}^a} \times N_y^w \quad (18)$$

As for simplicity, all whales are assumed to migrate north during winter, it follows that:

$$N_{y,summer}^{w,a} = 0 \quad (19)$$

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Table 1. List of model parameters and descriptions.

Parameter / Variable	Description
B_y^a	Biomass of krill in SSMU a in year y
r_t^a	Intrinsic annual growth rate of krill in SSMU a at time t
K_a	Carrying capacity of krill in SSMU a
λ^j	Maximum per capita annual consumption rate of krill by predator species j
$N_y^{j,a}$	Number of predator species j in SSMU a in year y
B_j^a	Krill biomass when the consumption and hence also birth rate of species j in SSMU a drops to half of its maximum level
n	Parameter that controls whether a Type II or a Type III functional response is assumed ($n=1$ for Type II assumed here)
ω	Proportion of mature females in the mature population of predator species j
F_y^a	Fishing proportion (catch = $F_y^a B_y^a$) on krill in SSMU a in year y
D_y^a	Net movement of krill (immigration-emigration) into SSMU a in year y
Em	The average proportion of krill that emigrate from an area to other areas each year
$N_y^{j,a}$	Number of predator species j in SSMU a in year y
S^j	Post-first-year annual survival rate of predator species j
T	Average age at first maturity, taken for simplicity to be one less than the age at first reproduction (i.e. assuming a one year gestation period)
q^j	Fraction of chicks/pups that are female
P^j	Maximum number of fledged chicks or pups leaving the natal colony per pair of predator j per year
$f(B_y^a)$	Breeding success factor (multiplier for P) which is a function of the biomass of krill in SSMU a in year y
$S_{juv}^{*,j}$	Maximum first year (juvenile) survival rate (post-fledging or post-weaning) of predator species j
$K^{*,j,a}$	Carrying capacity-related term for predator species j in SSMU a
α^a, β^a	Parameters for breeding success function for SSMU a , with $\beta = (\alpha - 1) \cdot K_a$
R	Krill steady annual growth rate
R^j	Steady annual growth rate of predator j

Table 2. Parameter values and their sources as used in the basic model.

Parameter	Value	Source
r_t^a	r_t^a (summer) = 0.4; r_t^a (winter) = 0.3	Mori and Butterworth (2006)
K_a	Computed; Whales initial $N/K = 0.2$	
λ^j	See Table 3	Hill <i>et al.</i> (2007)
n	1	-
ω	0.5 (penguins); 0.67 (seals); 0.5 (fish); 0.5 (whales)	Hill <i>et al.</i> (2007)
Em	0.0 – 0.3	See text
$S^{penguins}, S^{seals}, S^{fish}, S^{whales}$	0.82 – 0.88; 0.83 – 0.93; 0.6 – 0.72; 0.9 – 0.96	See Table 3
T	3 (penguins); 4 (seals); 3(fish); 5(whales)	Hill <i>et al.</i> (2007)
q^j	0.5	-
P^j	0.91 (penguins); 0.88 (seals); 3.0 (fish); 1.0 (whales)	Crawford <i>et al.</i> (2006); Boyd <i>et al.</i> (1995)
$S_{juv}^{*,penguins}, S_{juv}^{*,seals}, S_{juv}^{*,fish}, S_{juv}^{*,whales}$	0.82 – 0.89; 0.5-0.7; 0.6-0.67; 0.83-0.93	See Table 3
R, R^j	0.0	Working Group

Table 3. Reference Set illustrative parameter values for penguin, seal, fish and whale predator groups.

Parameter	Penguins	Seals	Fish	Whales
$h1$	0.5	0.5	0.5	0.5
$h2$	0.7	0.7	0.7	0.7
$S^j 1$	0.82	0.83	0.6	0.9
$S^j 2$	0.85	0.88	0.67	0.93
$S^j 3$	0.88	0.93	0.72	0.96
$S_{juv}^{*,j} 1$	0.82	0.5	0.6	0.83
$S_{juv}^{*,j} 2$	0.89	0.7	0.67	0.93

Table 4. Data from Hewitt *et al.* (1994), Hill *et al.* (2007) and S. Hill and G. Watters (pers. commn) showing the estimated number of krill per SSMU as well as the current krill catch (in kgs). The middle columns show estimates of the numbers of penguins, seals, fish and whales per SSMU, calculated from annual predator demand estimates from data provided in Hewitt *et al.* 2004. The final columns show annual predator demand in terms of numbers of krill, with these being converted to biomass of krill within the model. The penguin and seal predator demand estimates in Hewitt *et al.* (2004) considered only Adélie, chinstrap, gentoo and macaroni penguins, as well as lactating female Antarctic fur seals.

Area	SSMU	Area.(m2)	Catch (kg)	Penguins (no.)	Seals (no.)	Fish (no.)	Whales (no.)	Qmax(penguins)	Qmax(seals)	Qmax (fish)	Qmax(whales)
1	APPA	4.22E+11	2.54E+07	0	0	1.46E+10	1.12E+04	0	0	1.05E+03	1.31E+08
2	APW	3.51E+10	7.40E+06	2.37E+05	0	7.90E+08	9.30E+02	6.70E+05	0	2.53E+03	1.31E+08
3	APDPW	1.51E+10	2.28E+08	7.57E+04	1.36E+04	3.66E+08	4.00E+02	5.54E+05	3.50E+06	1.88E+03	1.31E+08
4	APDPE	1.56E+10	1.03E+08	1.11E+06	2.35E+02	3.67E+08	4.13E+02	5.47E+05	3.50E+06	2.03E+03	1.31E+08
5	APBSW	2.10E+10	1.15E+07	1.19E+06	0	4.91E+08	5.57E+02	5.48E+05	0	2.08E+03	1.31E+08
6	APBSE	2.74E+10	5.95E+06	2.79E+05	0	6.41E+08	7.28E+02	6.77E+05	0	2.09E+03	1.31E+08
7	APEI	3.53E+10	9.49E+07	1.45E+06	1.12E+03	1.11E+09	9.37E+02	5.46E+05	3.50E+06	1.20E+03	1.31E+08
8	APE	5.87E+10	2.50E+04	7.25E+05	0	1.33E+09	1.56E+03	7.97E+05	0	2.79E+03	1.31E+08
9	SOPA	8.09E+11	6.25E+06	0	0	1.26E+11	7.54E+03	0	0	1.93E+02	1.50E+08
10	SOW	1.56E+10	2.17E+08	2.35E+03	0	5.84E+08	1.45E+02	5.46E+05	0	9.47E+02	1.50E+08
11	SONE	1.03E+10	1.59E+07	5.17E+05	0	3.09E+08	9.50E+01	7.91E+05	0	1.28E+03	1.50E+08
12	SOSE	1.50E+10	1.95E+07	2.00E+06	0	3.38E+08	1.39E+02	5.89E+05	0	2.75E+03	1.50E+08
13	SGPA	9.20E+11	7.82E+06	0	0	2.37E+11	8.56E+03	0	0	1.15E+02	1.50E+08
14	SGW	4.21E+10	3.14E+07	7.58E+06	6.80E+05	1.61E+09	3.92E+02	4.94E+05	3.50E+06	8.84E+02	1.50E+08
15	SGE	5.37E+10	2.09E+08	5.97E+05	6.78E+03	2.17E+09	5.00E+02	5.29E+05	3.50E+06	8.32E+02	1.50E+08

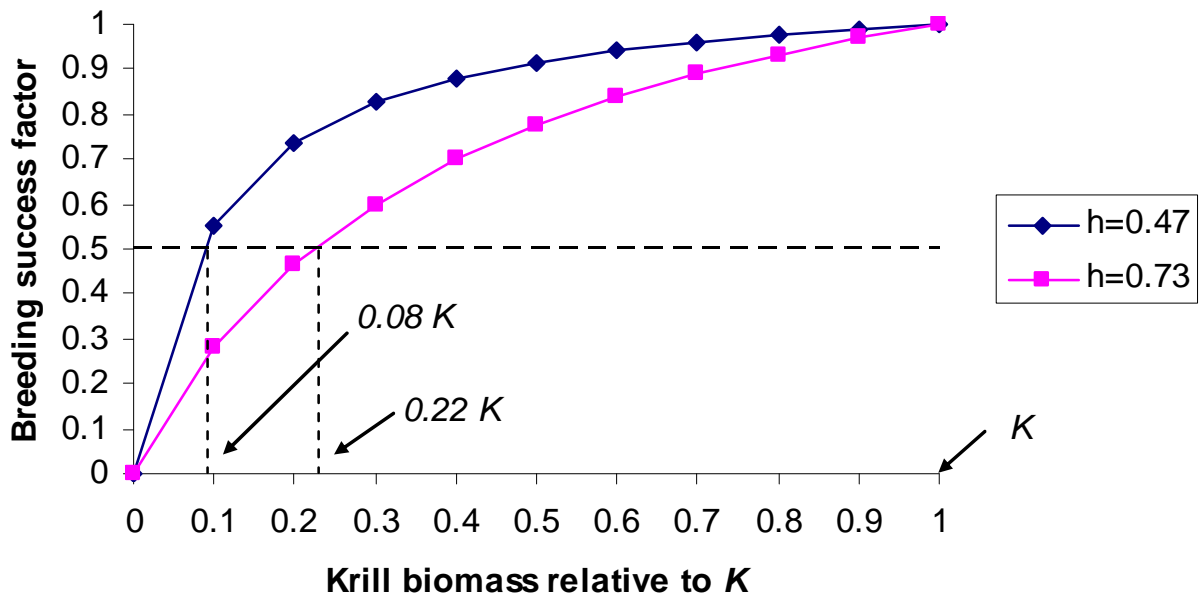


Fig. 1. Plot of the modelled relationship between predator breeding success and krill abundance relative to the krill carrying capacity level K in each SSMU. The shape of the curve is determined by a single parameter α and two values of α (and hence h – see Equation 11) have been chosen as examples of a near-linear decrease in breeding success as krill abundance decreases (square symbol) and a scenario in which predator breeding success is negatively impacted only at relatively low levels of krill abundance (diamond symbol). Thus in the former case breeding success drops to half its maximum level when krill biomass is 22% of K compared with a much lower 8% of K in the latter case. These values are also used to compute B_j^a in the predator consumption term in the krill equation, effectively representing the krill biomass when the birth rate of predator species j in SSMU a drops to half of its maximum level.

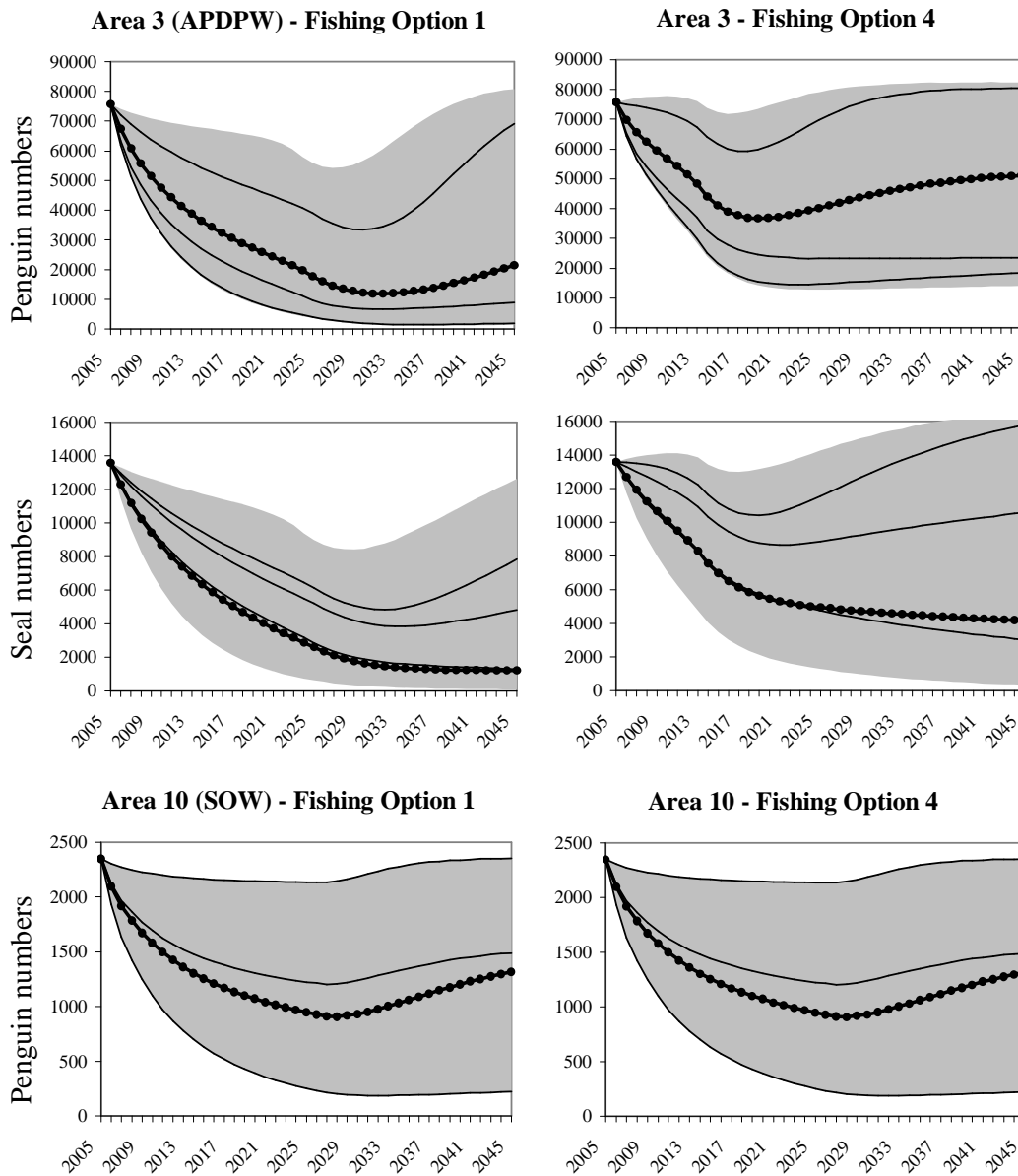


Fig. 2. Trajectories generated by SMOM of penguin and seal abundance (i.t.o. numbers) in SSMUs 3 and 10 compared under Fishing Options 1 (historical catch within the SSMU) and 4 (standing stock less predator demand in the SSMU), from 120 model version and projection replicates and when using a model version that assumes no krill movement between SSMUs. Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes. Note that trajectories assume fishing occurs for the first 20 years, but is set to zero thereafter to assess resource recovery.

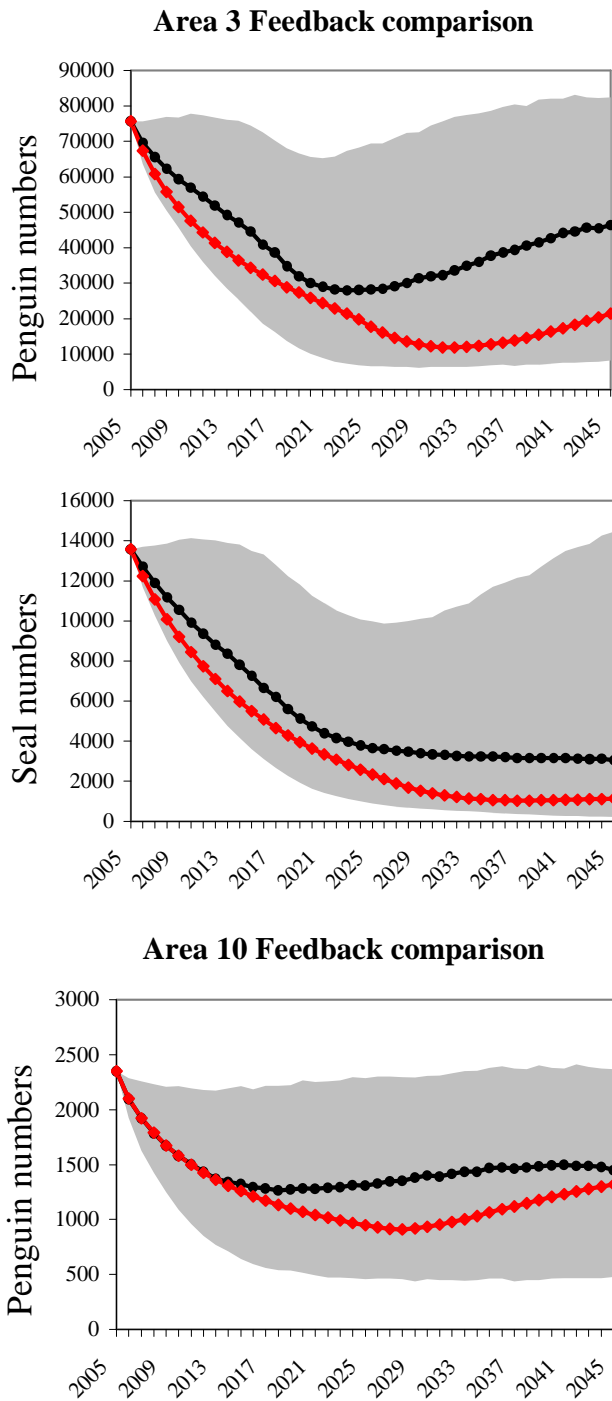


Fig. 3. Plots of the SMOM-predicted change in abundance for a) penguins and b) seals in Areas 3 and 10 (no seals) compared under two scenarios with a) no feedback in catch allocations (i.e. catches constant as per Catch Option 1) (red diamond symbols) and b) using a feedback control rule (black square symbols) based on a moderate amount monitoring information available for all SSMUs. Trajectories represent the median, and the shaded areas show the 90% probability envelopes for the feedback scenario – note that the lower 5%-ile of the corresponding probability envelope for the no feedback scenario is not shown but is lower.

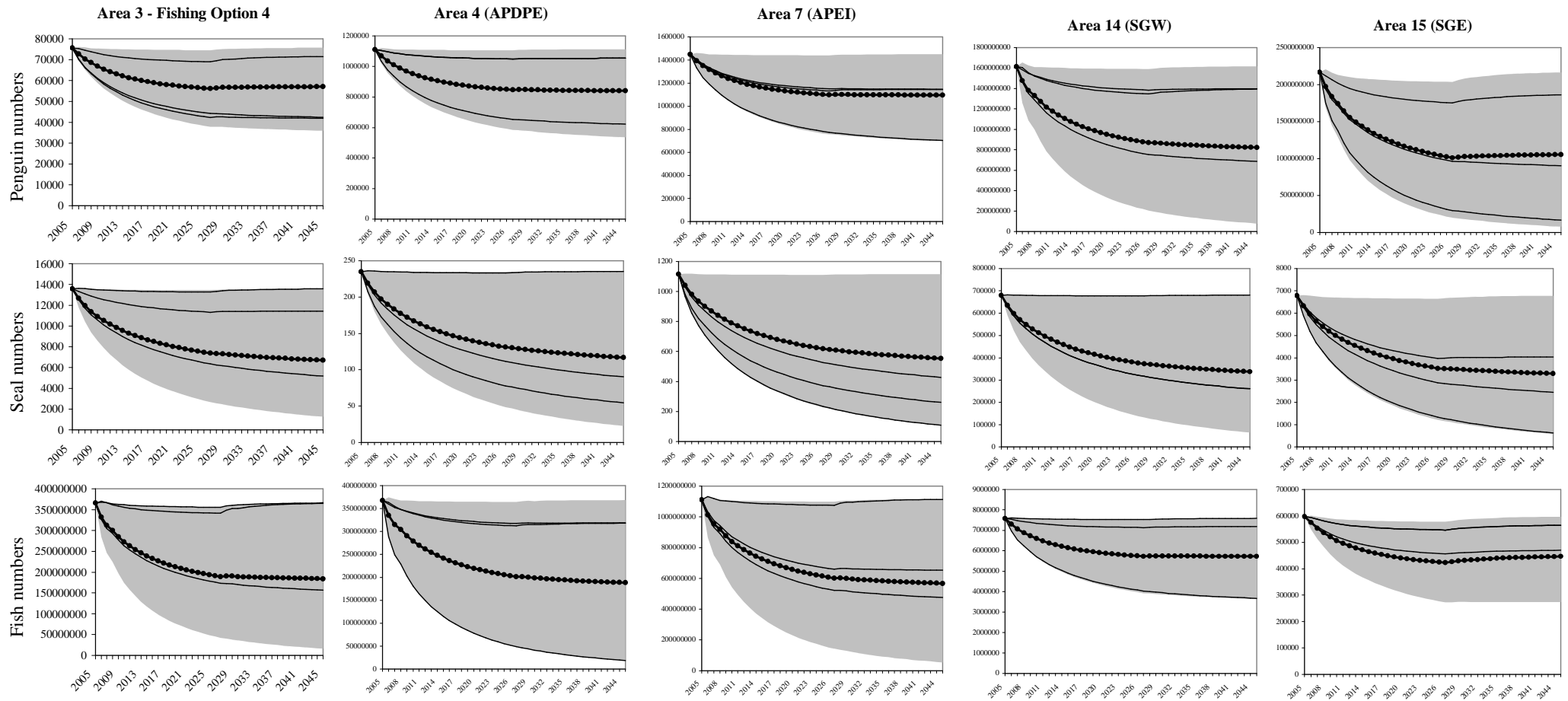


Fig. 4a. Trajectories of krill biomass under *Catch Option 4*, penguin, seal and fish abundance (expressed as numbers) in all SSMUs with all species present, from 120 model version and projection replicates, and when using a model variant that assumes no krill movement ($Em = 0$). Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

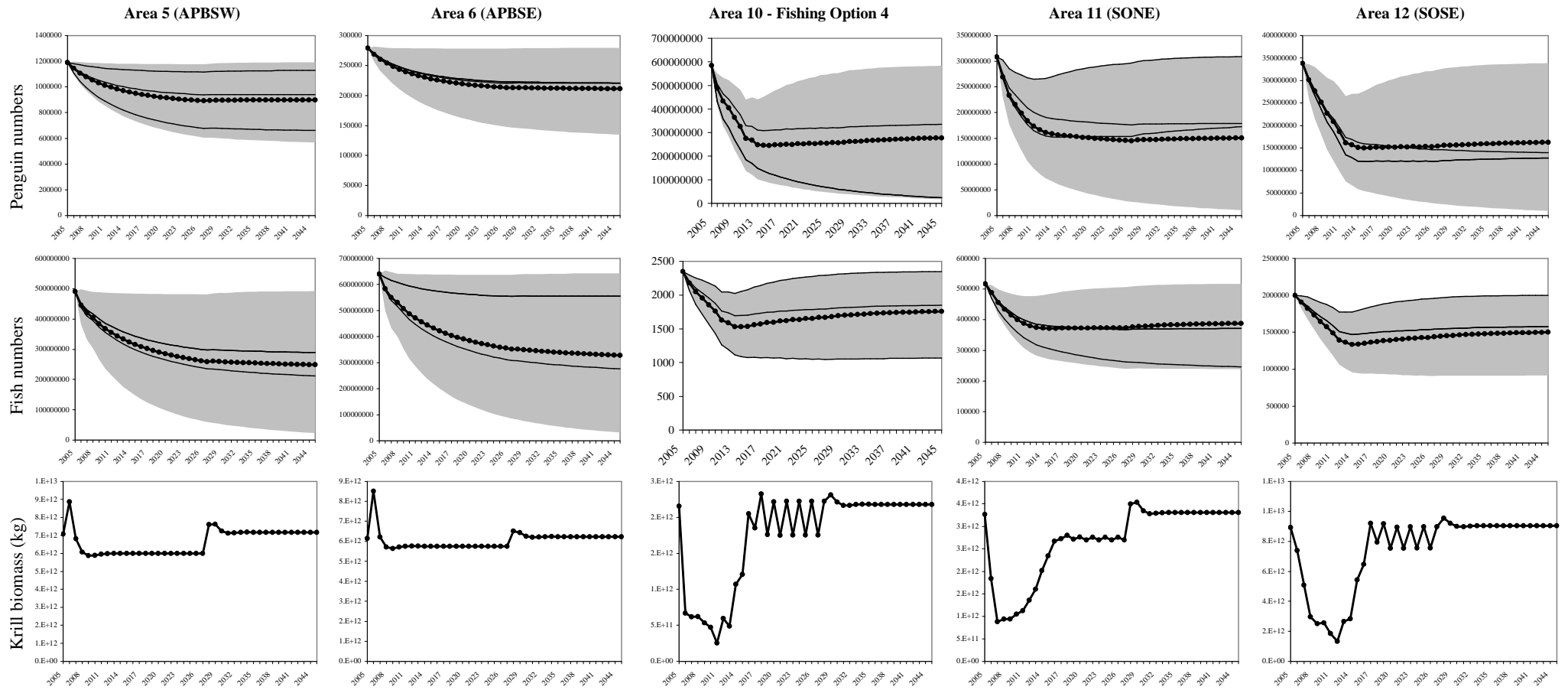


Fig. 4b. Trajectories of krill biomass under *Catch Option 4*, penguin and seal abundance (as numbers) in all SSMUs **without seals** present, from 120 model version and projection replicates and when using a model variant that assumes no krill movement ($Em = 0$). Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

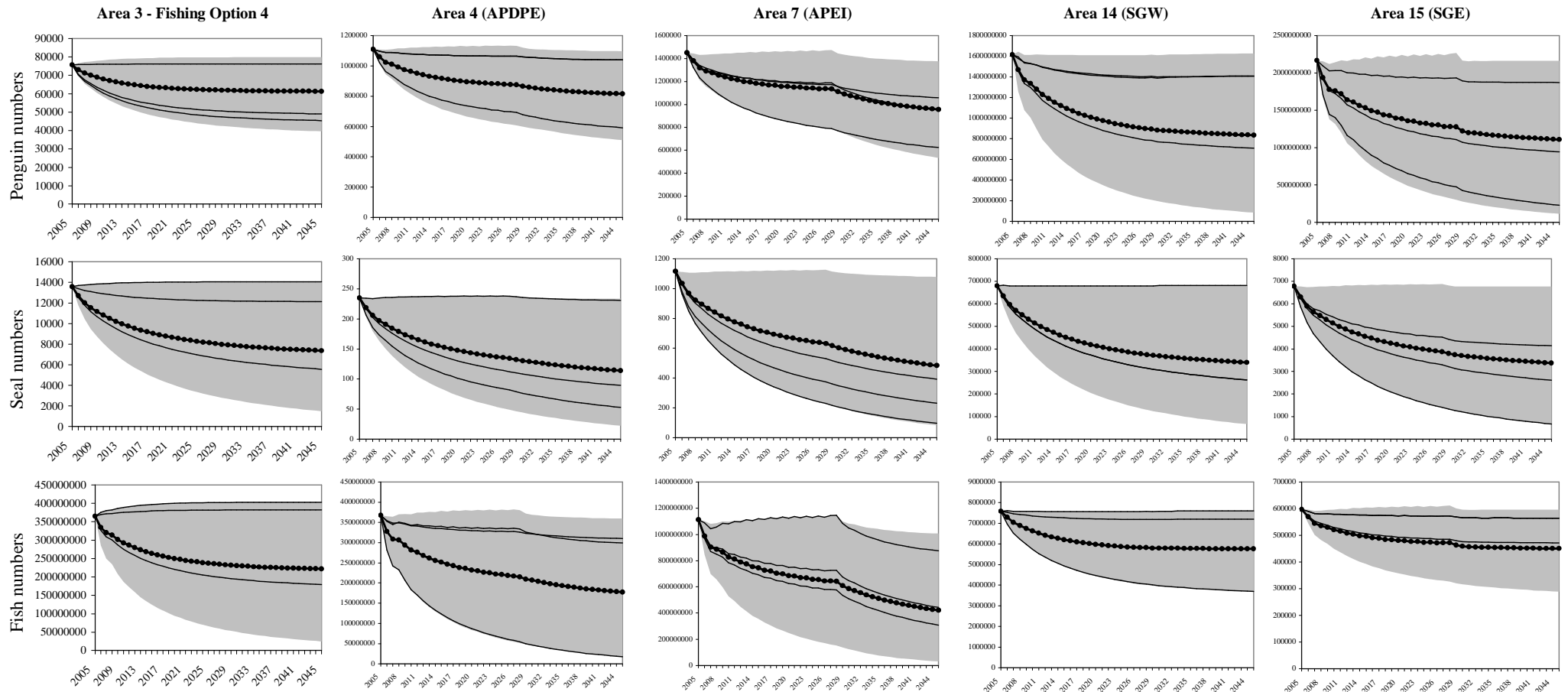


Fig. 5. Trajectories of krill biomass under *Catch Option 4*, penguin and seal abundance (expressed as numbers) in all SSMUs with both penguins and seals present, from 120 model version and projection replicates and when using a model variant that models krill movement based on the OCCAM model. Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

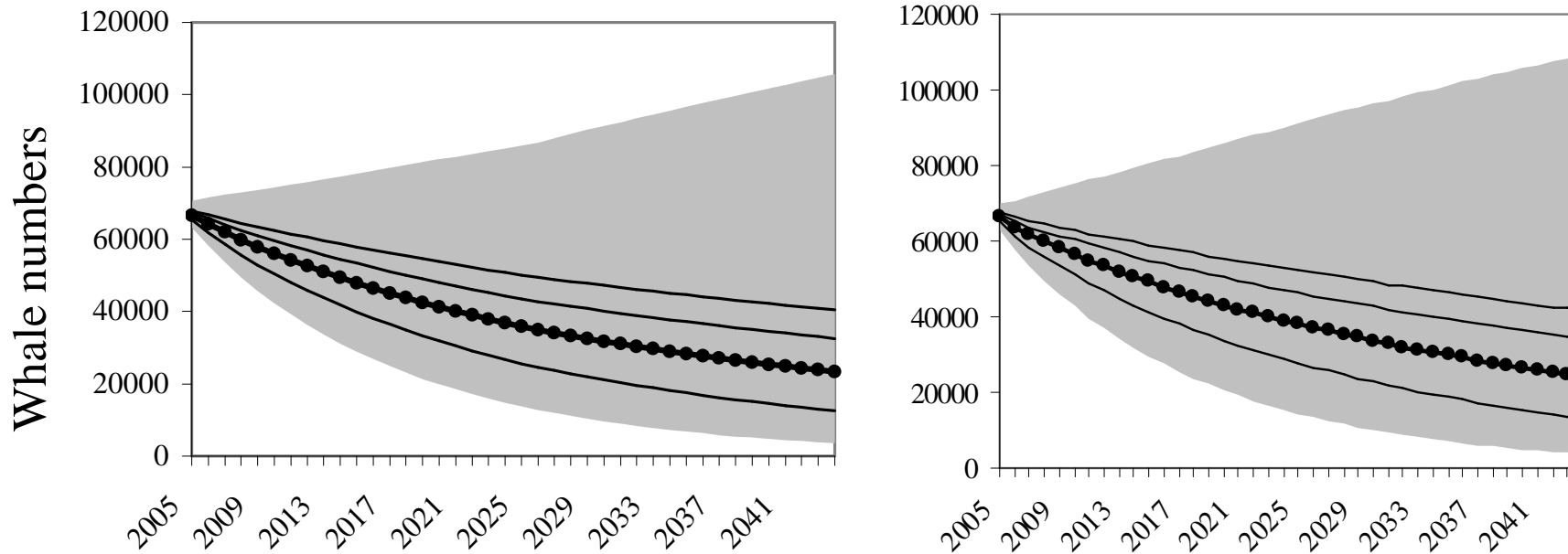


Fig. 6. Trajectories of the numbers of whales in all 15 SSMUs under *Catch Option 4* and from 120 model version and projection replicates. The LHS plot is from a scenario with no movement of krill whereas the RHS plot assumes krill movement is based on the OCCAM model. The absence of a difference between the scenarios is because whales, unlike the other predators in the model, are assumed to be able to integrate krill availability across all the SSMUs. Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

Fig. 7 (overleaf). Comparison of predator trajectories under the a) Reference Case and b-d) scenarios assuming improved information regarding parameter estimates become available. Results are shown for illustrative SSMU 3 under *Catch Option 4* and from 120 model version and projection replicates. Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes

