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Title **A SPATIAL MULTI-SPECIES OPERATING MODEL (SMOM) OF KRILL-PREDATOR INTERACTIONS IN SMALL-SCALE MANAGEMENT UNITS IN THE SCOTIA SEA**

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ABSTRACT

A Spatial Multi-species Operating Model (SMOM) of the underlying krill-predator-fishery dynamics is 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. The model is intended to complement the outputs from the KPFM. The model includes all 15 SSMUs and uses an annual 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 only two predator groups (penguins and seals) but is configured so that there is essentially no upper limit on the number of predator species which can be included. Given the numerous uncertainties regarding the choice of parameter values, a Reference Set is used in preference to a single Reference Case operating model. The initial Reference Set used comprises 12 alternative combinations that essentially try to bound the uncertainty in the choice of survival estimates as well as the breeding success relationship. The model is coded in AD Model Builder and quickly generates large numbers of stochastic replicates to explore different hypotheses such as that related to the transport of krill. The SMOM developed here is intended for use as an operating model in a formal MP framework described in an accompanying paper. Different MPs are simulation tested with their performances being compared on the basis of an agreed set of performance statistics which essentially compare the risks of reducing the abundance of predators below certain levels, as well as comparing the variability in future average krill catches per SSMU associated with each MP.

SUMMARY OF FINDINGS AS RELATED TO NOMINATED AGENDA ITEMS

Agenda Item	*Findings*
2 (ii)-(iii), 5.3, 6.2	A Spatial Multi-species Operating Model (SMOM) is developed for use as an operating model in a formal MP framework to explore alternative management rules regarding the subdivision of the precautionary catch limit for krill among 15 SSMUs. Preliminary illustrative results are presented comparing different static krill allocation options.

A Spatial Multi-species Operating Model (SMOM) of Krill-Predator Interactions in Small-Scale Management Units in the Scotia Sea

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ABSTRACT

A Spatial Multi-species Operating Model (SMOM) of the underlying krill-predator-fishery dynamics is 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. The model is intended to complement the outputs from the KPFM. The model includes all 15 SSMUs and uses an annual 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 only two predator groups (penguins and seals) but is configured so that there is essentially no upper limit on the number of predator species which can be included. Given the numerous uncertainties regarding the choice of parameter values, a Reference Set is used in preference to a single Reference Case operating model. The initial Reference Set used comprises 12 alternative combinations that essentially try to bound the uncertainty in the choice of survival estimates as well as the breeding success relationship. The model is coded in AD Model Builder and quickly generates large numbers of stochastic replicates to explore different hypotheses such as that related to the transport of krill. The SMOM developed here is intended for use as an operating model in a formal MP framework described in an accompanying paper. Different MPs are simulation tested with their performances being compared on the basis of an agreed set of performance statistics which essentially compare the risks of reducing the abundance of predators below certain levels, as well as comparing the variability in future average krill catches per SSMU associated with each MP.

INTRODUCTION

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has requested scientific advice regarding the subdivision of the precautionary catch limit for krill among 15 small-scale management units (SSMUs) in the Scotia Sea (Fig. 1) in such a way as to reduce the potential impact of fishing on land-based predators. Hewitt *et al.* (2004) presented five options for allocating the catch limit among the SSMUs in the Scotia Sea: (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 (Table 1). Clearly if krill catches increase there is a need to assess these various options within a dynamic framework.

Watters *et al.* (2005) developed a Krill-Predator-Fishery-Model (KPFM) for evaluating candidate management procedures. They stress the considerable uncertainties in the krill-predator-fishery system and use Monte Carlo simulations to capture some of this uncertainty. Given the level of uncertainty, it is preferable to have more than one model of the system. This paper thus presents an alternative (and arguably simpler) Operating Model of the underlying dynamics that is intended to complement the outputs from the KPFM. Ecosystem/multi-species models are difficult to validate and hence if different models give qualitatively similar results, this can increase one's confidence in the models. To facilitate model comparisons, wherever possible the same model inputs have been used as used in Watters *et al.* (2005).

The Spatial Multi-species Operating Model (SMOM) developed here essentially builds on the modelling work of Thomson *et al.* (2000) and Mori and Butterworth (2004, 2006). Mori and Butterworth (2004, 2006) 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, fin, humpback and minke) and two seal (Antarctic fur and crabeater) 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.

Operational Management Procedure (OMP) (Butterworth and Punt 1999), or analogously Management Strategy Evaluation (MSE) (Smith *et al.* 1999) frameworks, or simply Management Procedures (MPs) 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, Plaganyi *et al*. 2006). 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. In this case, it is necessary to ensure that the likely performance of the OMP in terms of low risk to predators within each SSMU is reasonably robust to the primary uncertainties about such dynamics. The SMOM developed here is intended for use as an operating model which simulates the "true" dynamics of the resource. A separate MP module contains the methods and rules that are used to subdivide the krill catch between SSMUs (see accompanying paper Plaganyi and Butterworth 2006). Different MPs are then simulation tested with their performances being compared on the basis of an agreed set of performance statistics which essentially compare the risks of reducing the abundance of predators below certain levels, as well as comparing the variability in future average krillcatches per SSMU associated with each MP.

Management Procedures (MPs) have been implemented for the major fisheries in South Africa since the early 1990's (e.g. Butterworth *et al.* 1997, Cochrane *et al.* 1998, Geromont *et al.* 1999, Punt 1993, Rademeyer 2003, DeOliveira and Butterworth 2004). Based on experience with these fisheries, Rademeyer *et al.* (2006) 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 combinations of a basic operating model is used to bound the range of uncertainty associated with the krill-predator-fishery system. Moreover, a range of robustness tests, reflecting other likely less important uncertainties/less plausible hypotheses, needs to be considered (see e.g. Rademeyer *et al.* 2006).

MODEL DIMENSIONING

The model includes all 15 SSMUs and uses an annual 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 only two predator groups (penguins and seals) but is configured so that there is essentially no upper limit on the number of predator species which can be included.

Given adequate data, it is thus possible to include individual species rather than generic predator groups.
The model is coded in AD Model Builder (AD Model Builder™, Otter Research, Ltd.), which permits fast, reliable and powerful (in terms of the number of parameters readily estimable) minimisation when fitting nonlinear models to data and addressing questions of uncertainty. Users are able to alter inputs and settings stored in text files before running the executable file. The current version of the model is illustrative only, as further work is needed to refine model parameter estimates. A description of the model is provided below and a list of parameter definitions given in Table 2.

KRILL DYNAMICS EQUATION

The krill population is modelled following Mori and Butterworth (2004), 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 (γ^a) which accounts for total consumption by predators not explicitly included in the model.

$$B_{y+1}^a = B_y^a + r^a B_y^a \left(1 - \left(\frac{B_y^a}{K_a}\right)\right) - \gamma^a \Big/ q^j \sum_j \frac{\lambda^j \left(B_y^a\right)^n N_y^{j,a}}{\left(B_j^{\ a}\right)^n + \left(B_y^a\right)^n} - F_y^a B_y^a + D_y^a \qquad (1)$$

where:

B_y^a is the biomass of krill in SSMU *a* in year *y*,
r^a is the intrinsic growth rate of krill in SSMU *a*,
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*,
$N_y^{j,a}$ is the number of mature females of predator species *j* in SSMU *a* 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),
q^j is the proportion of the mature population for predator species *j* comprised of mature females;
γ^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_y^a is the fishing proportion (catch=$F_y^a B_y^a$) on krill in SSMU *a* in year *y*, and
D_y^a is the net movement of krill (immigration-emigration) into SSMU *a* in year *y* (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. As a first step, 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 user thus inputs a single parameter *Em* which represents the average proportion of krill that move between areas each year. By varying *Em*, a range of movement hypotheses can thus 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:

$$D_y^a = Em * B_y^a + I_y^a \tag{2}$$

where I_y^a is the randomly-determined number of immigrants into SSMU *a* in year *y*, scaled such that (on average) in each year:

$$\sum_a I_y^a \approx Em \sum_a B_y^a \tag{3}$$

PREDATOR DYNAMICS EQUATION

The same delay difference equation is used for all predators, with the number of mature females (i.e. adult females past the age-at-first-parturition) given by:

$$N_{y+1}^{j,a} = N_y^{j,a} S^j + \left(N_{y-T+1}^{j,a}\right) \cdot q^j \cdot f(B_y^a) \cdot P^j \cdot S_{juv}^{*,j} \left(1 - N_y^{j,a} \big/ K^{*,j,a}\right) \left(S^j\right)^{T-1} \tag{4}$$

where:

$N_y^{j,a}$	is the number of predator species *j* in SSMU *a* in year *y*,
S^j	is the post-first-year annual survival rate of predator species *j* (assumed to be independent of area),
T	is the average age at first breeding (taken here to be 3),
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;
$f\left(B_y^a\right)$	is a breeding success factor (multiplier for *P*) 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*.

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:

$$S_{juv} \rightarrow S^{*}_{juv}\left(1-{N_y}\big/{K^{*}}\right) \tag{5}$$

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. 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.

The Antarctic system is an ideal ecosystem to take the lead in the implemention of ecosystem models because krill dominates the diet of predators in the region, so that predator-prey relationships are simplified. 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 most sensitive to changes in prey abundance. A breeding success factor $f(B^a_y)$ 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 reproductive rate P in Equation (4). 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^a_y:

$$f(B^a_y) = \frac{\alpha^a B^a_y}{\beta^a + B^a_y} \tag{6}$$

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 (6) becomes:

$$f(B^a_y) = \frac{\alpha^a \, {B^a_y}\big/{K_a}}{(\alpha^a - 1) + {B^a_y}\big/{K_a}} e^{(\varsigma_{ay} - \sigma^2_{BR}/2)} \tag{7}$$

where

ς_{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 $f(B^a_y)\cdot P^j$ does not exceed biologically plausible limits (e.g. the average annual seal pup production for females does not exceed 1).

By ignoring the random variation term and choosing a single parameter value α^a, the breeding success relationship can thus be set for each area and predator species. The parameter α^a may be thought of as controlling 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 may be to select two values that roughly bound the likely range in this relationship (see e.g. Fig. 2). 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}.

For the deterministic case, Equation (7) 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 (7) is thus used to solve for B_y^a / K_a when $BR = 0.5$, yielding:

$$B_j^a = \frac{0.5 \cdot K_a \cdot (\alpha - 1)}{(\alpha - 0.5)} \tag{8}$$

A consolidated list of symbols used in this paper, together with their definitions, is given in Table 1.

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 (Rademeyer *et al.* 2006). The initial Reference Set used comprises 12 alternative combinations that essentially try to bound the uncertainty in the choice of survival estimates as well as the breeding success relationship. 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 (α1,α2) for the parameter α^a that roughly bound the likely "steepness" of the breeding success relationship.

This leads to a total of 3x2x2=12 alternative operating models to represent the dynamics of each predator. The initial illustrative values chosen for penguins and seals are shown in Table 2.

DATA AND MODEL INITIALIZATION

Krill

The krill intrinsic growth rate parameter is set at 0.45, this being the average of the values estimated by Mori and Butterworth (2004). 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 current (year 2000) krill biomass and predator number estimates and catches per SSMU are taken from Hewitt *et al.* (2004) and are shown in Table 3 together with the $F_y^a = C_y^a / B_y^a$ values corresponding to Catch Options 1-4, which are used to initialise Equation (1). The λ^j parameters are similarly based on the estimates presented in Hewitt *et al.* (2004), and converting numbers to biomass assuming an average krill mass of 0.7 g (ref) (Table 4). Hewitt *et al.* (2004) give the total predator demand per SSMU. In model versions such as this initial formulation which does not include all predator groups, it is possible to estimate a scaling factor γ^a as the total predator demand in SSMU *a* divided by the total demand of all predators explicitly included in the model. As such data are available for one year only, it is necessary (initially at least) to assume that γ^a is year-independent. For this reason, model simulations were conducted for scenarios both with γ^a computed as described above and with γ^a = 1. The main difference between these two options is that it affects the calculation of the remaining unknown krill dynamics parameter, namely K_a. 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:

$$R = r^a \left(1 - \left(\frac{B_y^a}{K_a}\right)\right) - \gamma^a \Big/ q^j \sum_j \frac{\lambda^j N_y^{j,a}}{\left(Bj^a\right) + \left(B_y^a\right)} - F_y^a \tag{9}$$

and hence solving for K_a for each SSMU as follows:

$$K_a = B_y^a \Bigg/ 1 - \frac{R + F_y^a + \gamma^a \Big/ q^j \sum_j \frac{\lambda^j N_y^{j,a}}{\left(Bj^a\right) + \left(B_y^a\right)}}{r^a} \tag{10}$$

The simplest assumption possible is that the biomass of krill is currently stable (i.e. *R* = 0), but recent studies suggest long-term declines in krill abundance (Atkinson *et al.* 2004). Ideally data on trends in each SSMU should be used to provide estimates of *R*. For current purposes, an estimate of *R* for krill of *R* = -0.04 yr^{-1} was obtained by fitting to krill biomass density estimates from the South Georgia region (Hewitt *et al.* 2004) and the same value was used for all areas.

Predators

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:

$$\left(1 + R^j\right)^T = \left(1 + R^j\right)^{T-1} S^j + q^j \cdot f(B_y^a) \cdot P^j \cdot S_{juv}^{*,j} \left(1 - N_y^{j,a} \Big/ K^{*,j,a}\right) \left(S^j\right)^{T-1} \tag{11}$$

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

$$K^{*,j,a} = N_y^{j,a} \Bigg/ 1 - \frac{\left(1 + R^j\right)^T - \left(1 + R^j\right)^{T-1} S^j}{q^j \cdot f(B_y^a) \cdot P^j \cdot S_{juv}^{*,j} \left(S^j\right)^{T-1}} \tag{12}$$

Once again, data on trends in predator abundance per SSMU should be used to provide estimates of R^j. Based on estimates from the literature (summarised in Mori and Butterworth 2006), seal populations in the Antarctic are thought to be increasing by approximately 10% per year and hence $R^j = 0.1$. In the case of penguin populations, a rough initial estimate of R^j=0.04 was set by fitting to CEMP data on Macaroni penguins (Fig. 3) (Ramm and Turner 2005).

The only parameter not yet accorded a value in Equation (12) is the maximum breeding success parameter P^j. Note that the average number of offspring per 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. Initial estimates used are $P^{seals} = 0.88$ (Boyd *et al*. 1995) and $P^{peng} = 0.91$ (Crawford *et al.* 2006).

PERFORMANCE STATISTICS

The following performance statistics are used to compare the Catch Options and will be particularly useful when comparing different scenarios for the dynamics. Core outputs for presentation purposes include the median and 10%- and 90%-iles of distributions. Projections are conducted over 20 years: 2005-2024.

Resource status-related

1) $N_{2015}^{j,a} / N_{2005}^{j,a}$

1) $N_{2025}^{j,a} / N_{2005}^{j,a}$

Shown separately for each predator and for all SSMUs.

Krill catch variability

1) $AAV(per\,SSMU) = \frac{1}{19}\sum_{y=2006}^{2024} \left|C_y - C_{y-1}\right| / C_{y-1}$ (*AAV* is Annual Average Variability)

In addition, time trajectories (both worm plots and probability envelopes) are plotted for predator abundance $N^{j,a}$ and krill biomass B_y^a.

RESULTS

For each of the 12 operating models (termed the 12 simulations), 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. 4-7). Results are shown for all SSMUs with penguins and/or seals present and for each of the four Hewitt *et al* (2004) Catch Options as preliminary illustrations of differences resulting from possible allocations of the krill catch limit among the SSMUs. The accompanying paper (Plagányi and Butterworth 2006) provides a comparison when these are transformed into dynamic (feedback) options. Three randomly selected individual trajectories are also superimposed on each plot (termed worm plots). Illustrative performance statistics to be used for the MP tests are shown in Fig. 8. Note that in the model the predators do not go extinct immediately the kill population crashes because the model is not designed to represent this region which management hopefully succeeds in avoiding

Consistent with the approach in Watters *et al*. (2005), and in the interests of brevity, selected results are shown only for SSMUs 3 (Drake Passage West), 10 (South Orkney East) and/or 14 (South Georgia West).

Table 5 presents a comparison of the estimated current depletion level (as a proportion of a carrying capacity-related term K^*) for krill, penguins and seals in the various SSMUs. Values highlight the sensitivity to the assumption regarding the assumed (or estimated) initial steady krill growth rate (R) used to initialise the model. This highlights the importance of trying to use available data to obtain the best possible initial estimate of R.

Figure 9 shows illustrative trajectories of krill biomass, penguin and seal abundance (i.t.o. numbers) under scenarios ranging from an assumption of zero transport of krill between SSMUs to gradually increasing levels of assumed krill transport (set by parameter *Em* in the model). This 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 met in a SSMU even when static mass balance calculations suggest otherwise.

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*., 2005). 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.

The SMOM is relatively simple and has been constructed to require as few parameters as possible – the 12 alternative Reference Case combinations are useful in bounding two key areas of uncertainty: the choice of survival estimates as well as the breeding success relationship. The SMOM developed here is intended for use as an operating model in a formal MP framework described in Plaganyi and Butterworth (2006). The latter provides examples of a feedback management rule whereas in the current paper model results are compared across the four static Catch Options presented in Hewitt *et al.* (2004).

Preliminary results are presented for illustrative purposes, but it is acknowledged that further refinement of model parameters is required. Two of the most important aspects requiring further investigation are estimates of current growth rates of krill and predators (as determined for example by fitting to abundance indices) and further discussion regarding the best way to include consumption by predators not explicitly included in the model. The model currently includes only two predator groups (penguins and seals) but it is relatively straightforward to include additional predator species in the model.

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Table 3. Data from Hewitt *et al*. (1994) showing the estimated number of krill per SSMU as well as the current krill catch (in kgs). The krill Catch Options 1-4 presented in Hewitt *et al*. (2004) propose catches per SSMU which have here been converted to fishing mortality (as a proportion of available biomass) *F* values for use in the model. The last two columns show estimates of the numbers of penguins and seals per SSMU, calculated from annual predator demand estimates. 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	Krill N	Catch (kg)	*F* : Opt 1	Op 2	Op 3	Op 4	Penguins no.	Seals no.
1	APPA	5.41E+09	2.54E+07	0.015	0.021	0.048	0.049	0	0
2	APW	1.38E+09	7.40E+06	0.017	0.061	0.048	0.038	1.353E+06	0
3	APDPW	5.96E+08	2.28E+08	1.232	0.062	0.047	0.039	5.826E+05	1.165E+04
4	APDPE	6.18E+08	1.03E+08	0.539	0.061	0.049	0.039	6.042E+05	3.529E+02
5	APBSW	8.29E+08	1.15E+07	0.045	0.060	0.048	0.039	8.107E+05	0.000E+00
6	APBSE	1.08E+09	5.95E+06	0.018	0.061	0.048	0.039	1.058E+06	0.000E+00
7	APEI	1.36E+09	9.49E+07	0.225	0.061	0.048	0.038	1.334E+06	1.059E+03
8	APE	2.32E+09	2.50E+04	0.000	0.031	0.048	0.046	0	0
9	SOPA	1.98E+10	6.25E+06	0.001	0.003	0.048	0.054	0	0
10	SOW	2.42E+09	2.17E+08	0.290	0.050	0.048	0.041	1.472E+05	0
11	SONE	1.62E+09	1.59E+07	0.031	0.052	0.048	0.041	1.967E+05	0
12	SOSE	2.33E+09	1.95E+07	0.027	0.070	0.048	0.036	1.673E+06	0
13	SGPA	2.27E+10	7.82E+06	0.001	0.003	0.048	0.053	0	0
14	SGW	1.68E+09	3.14E+07	0.060	1.125	0.048	0.000	1.724E+07	2.456E+06
15	SGE	2.17E+09	2.09E+08	0.310	0.108	0.048	0.026	7.182E+05	2.471E+04

Table 1. List of model parameters and descriptions, in the order in which they appear in the text.

Parameter	Description
B_y^a	Biomass of krill in SSMU *a* in year *y*
r^a	Intrinsic annual growth rate of krill in SSMU *a*
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)
q^j	Proportion of mature females in the mature population of predator species *j*
γ^a	Scaling factor (year-independent) computed as the ratio of the total predator demand in SSMU *a* divided by the total demand of all predators explicitly included in the model
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 move between 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 breeding
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
$f\left(B_y^a\right)$	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 post-fledging or post-weaning (juvenile) survival rate 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. Reference Set illustrative parameter values for penguin and seal predator groups.

	Penguins	Seals
$\alpha1$	1.1	1.1
$\alpha2$	1.4	1.4
S1	0.85	0.92
S2	0.82	0.85
S3	0.88	0.94
SJ1	0.5	0.6
SJ2	0.6	0.7

Table 4. Maximum consumption of krill (in numbers) per SSMU per predator as indicated (from Watters *et al.* 2005). Maximum values are converted to units of kg's by multiplying by an assumed average weight for krill (0.7g).

	QQmax	
Area	Penguins	Seals
1	4.30E+05	1.70E+06
2	4.30E+05	1.70E+06
3	4.30E+05	1.70E+06
4	4.30E+05	1.70E+06
5	4.30E+05	1.70E+06
6	4.30E+05	1.70E+06
7	4.30E+05	1.70E+06
8	4.30E+05	1.70E+06
9	4.30E+05	1.70E+06
10	4.30E+05	1.70E+06
11	4.30E+05	1.70E+06
12	4.30E+05	1.70E+06
13	4.50E+05	1.70E+06
14	4.50E+05	1.70E+06
15	4.50E+05	1.70E+06

Table 5. Comparison of the estimated current depletion level (as a proportion of a carrying capacity-related term K^*) for krill, penguins and seals in each SSMU as indicated. Values highlight the sensitivity to the assumption regarding the assumed (or estimated) initial steady krill growth rate (R) used to initialise the model.

	With *Rpeng* = -0.04			With *Rpeng* = 0		
SSMU	Krill	Penguin	Seals	Krill	Penguin	Seals
2	0.23	0.32		0.50	0.27	
3	0.02	0.01	0.01	0.47	0.25	0.29
4	0.11	0.01	0.01	0.50	0.27	0.31
5	0.22	0.31		0.50	0.27	
6	0.23	0.32		0.49	0.27	
7	0.17	0.18	0.01	0.50	0.27	0.31
10	0.21	0.28		0.96	0.43	
11	0.29	0.40		0.93	0.42	
12	0.18	0.20		0.62	0.33	
14	0.01	0.01	0.01	0.01	0.01	0.01
15	0.29	0.40	0.08	0.81	0.39	0.43

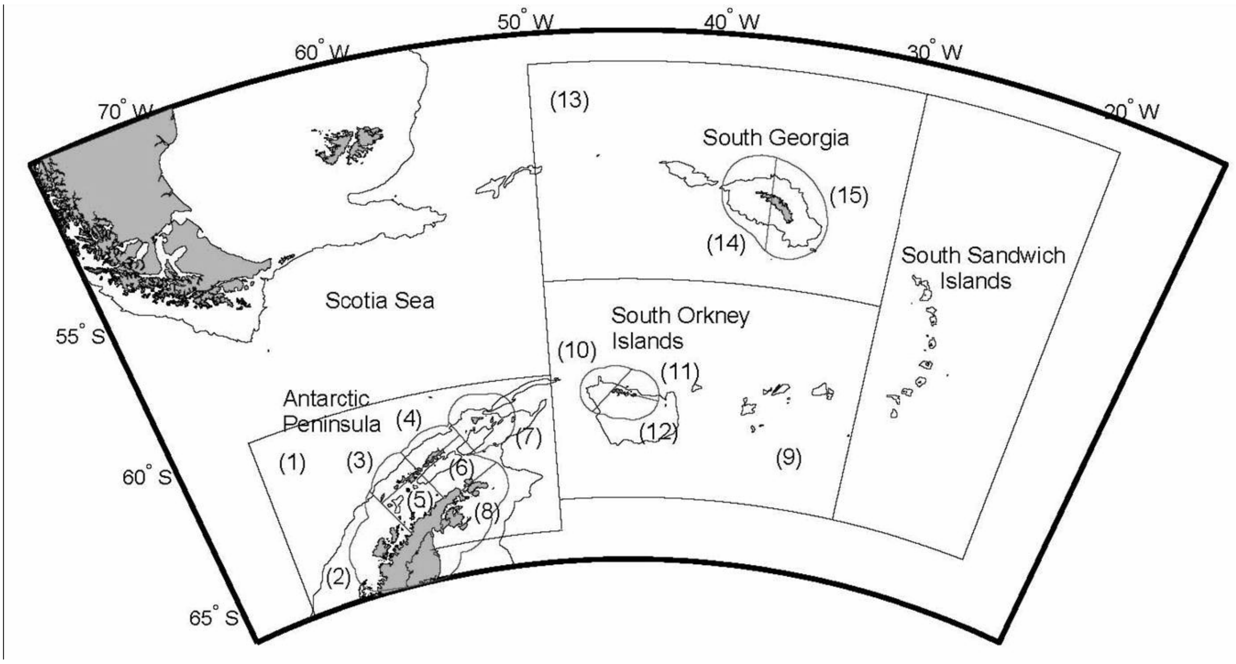

Figure 1. Small-scale management units in Subareas 48.1, 48.2 and 4.3 (from Hewitt *et al.* 2005). The 1000 m isobath is also shown to indicate the approximate edge of the continental shelf surrounding the archipelagos in the Scotia Sea. SSMUs are (1) Antarctic Peninsula Pelagic Area (APPA); (2) Antarctic Peninsula West (APW); (3) Drake Passage West (APDPW); (4) Drake Passage East (APDPE): (5) Bransfield Strait West (APBSW); (6) Bransfield Strait East (APBSE); (7) Elephant Island (APEI); (8) Antarctic Peninsula East (APE); (9) South Orkney Pelagic Area (SOPA); (10) South Orkney West SOW); (11) South Orkney North East (SONE); (12) South Orkney South East (SOSE); (13) South Georgia Pelagic Area (SGPA); (14) South Georgia West (SGW); (15) South Georgia East (SGE).

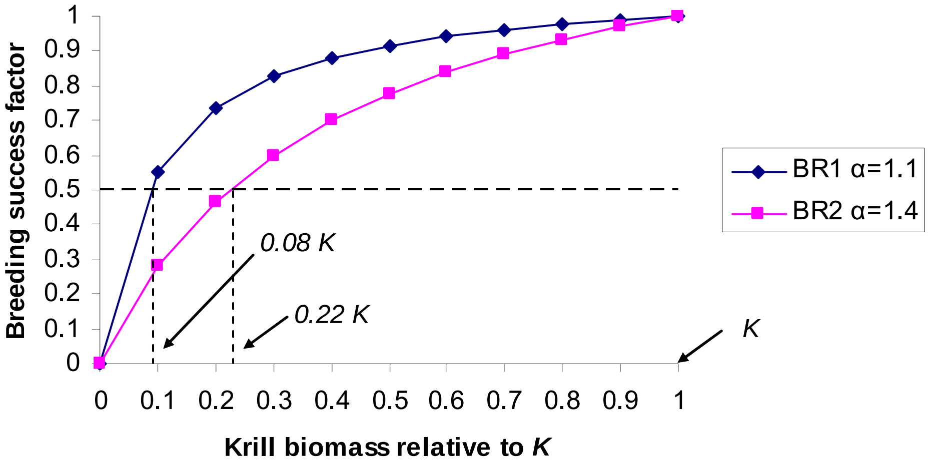

Fig. 2. Plot of the modelled relationship between predator breeding success and krill abundance relative to the krillcarrying capacity level *K* in each SSMU. The shape of the curve is determined by a single parameter α and two values of α have been chosen as examples of a near-linear decrease in breeding 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 .

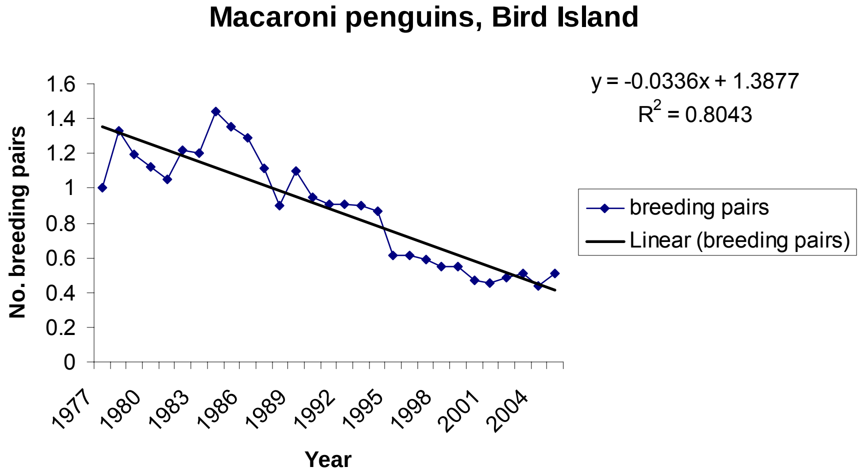

Fig. 3. CEMP data on the numbers of breeding pairs of Macaroni penguins at Bird Island, used to compute an estimate of the average annual rate of increase/decrease of penguin populations in the Scotia Sea. CEMP data (from Ramm and Turner 2005) kindly reproduced with permission from CCAMLR.

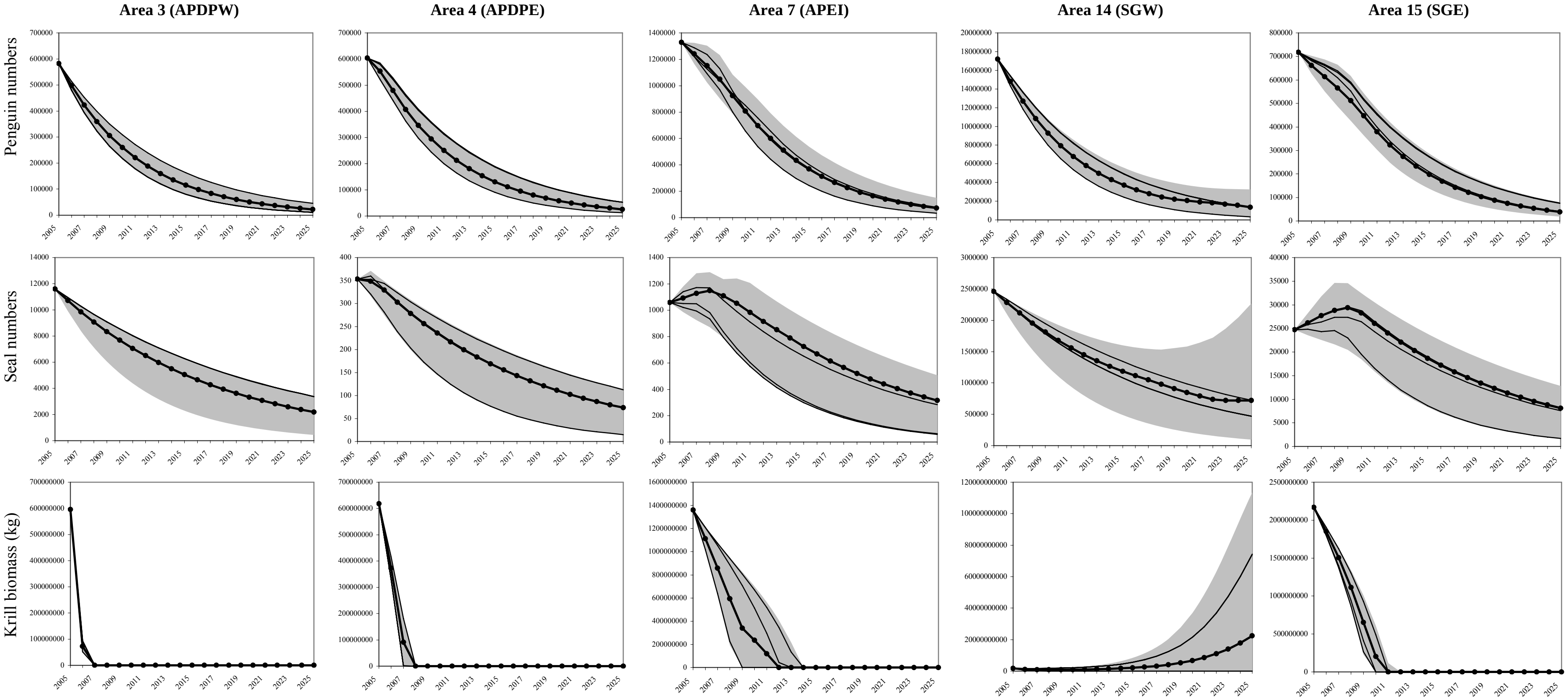

Fig. 4a. Trajectories of krill biomass under ***Catch Option 1***, penguin and seal abundance (i.t.o. numbers) in all SSMUs with both penguins and seals present, from 120 model representations and when using a model version that assumes no krill movement ($Em = 0$). Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes. Note that in the model the predators do not go extinct immediately the kill population crashes because the model is not designed to represent this region which management hopefully succeeds in avoiding.

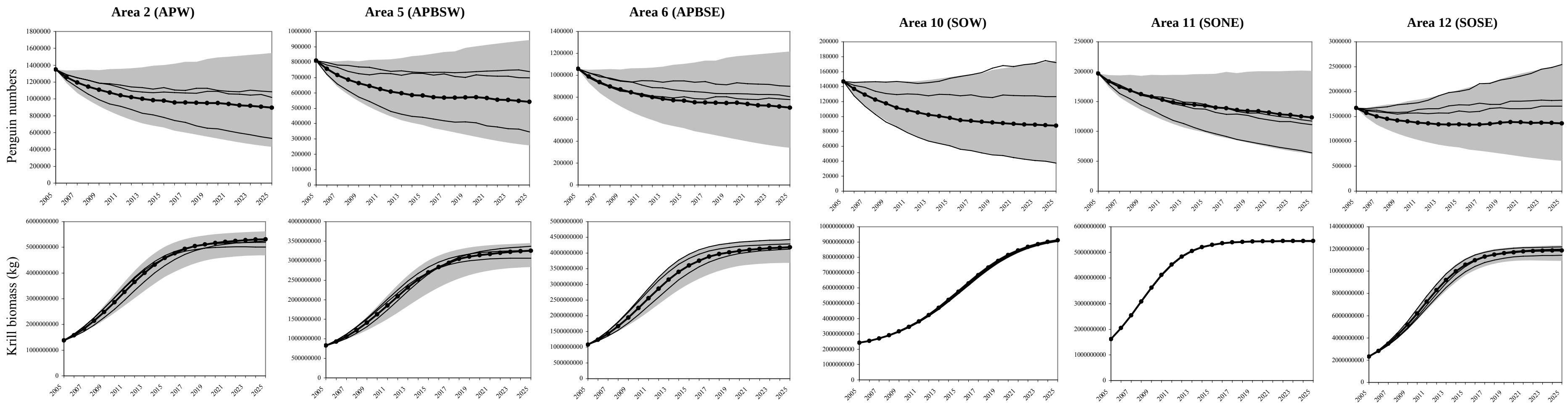

Fig. 4b. Trajectories of krill biomass under ***Catch Option 1***, penguin and seal abundance (i.t.o. numbers) in all SSMUs **without seals** present, from 120 model representations and when using a model version that assumes no krill movement (*Em* = 0). Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

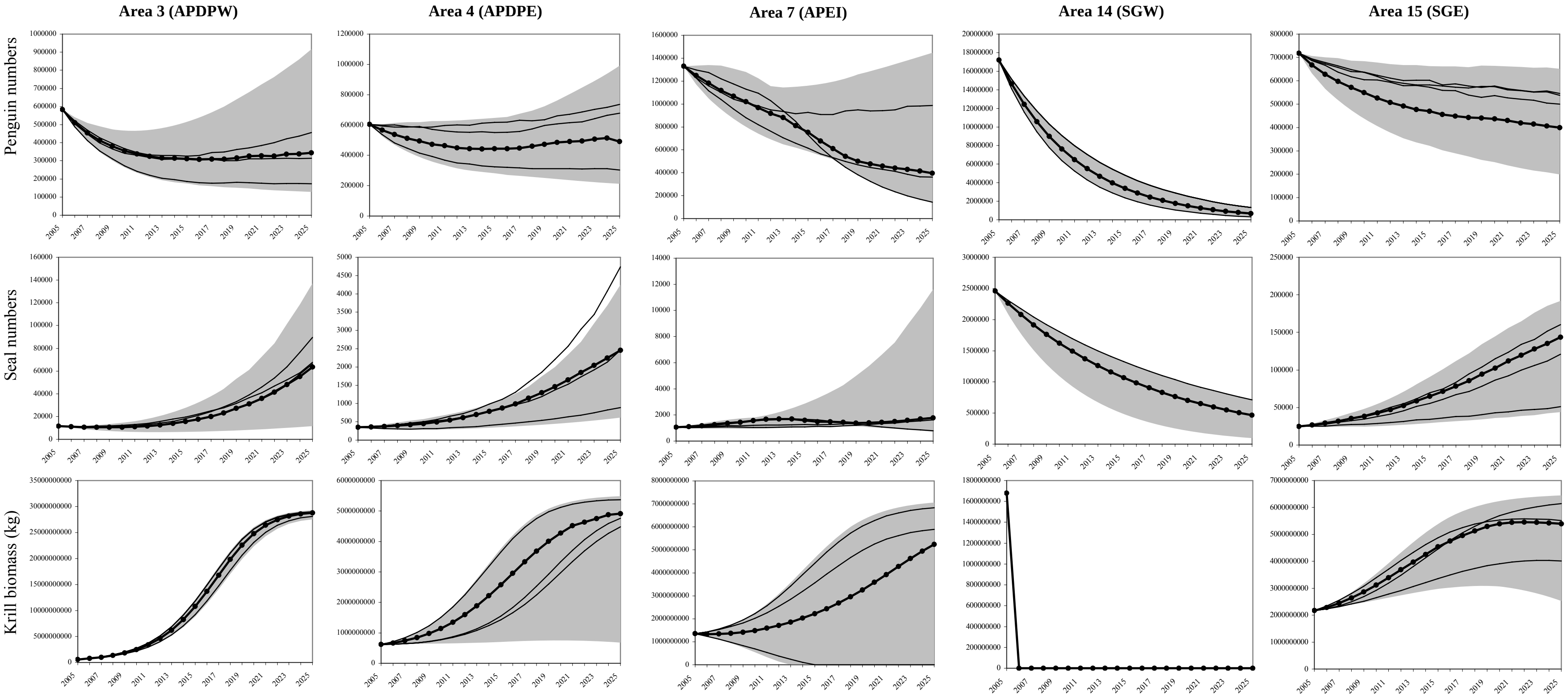

Fig. 5a. Trajectories of krill biomass under ***Catch Option 2***, penguin and seal abundance (i.t.o. numbers) in all SSMUs with both penguins and seals present, from 120 model representations and when using a model version that assumes no krill movement (*Em* = 0). Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

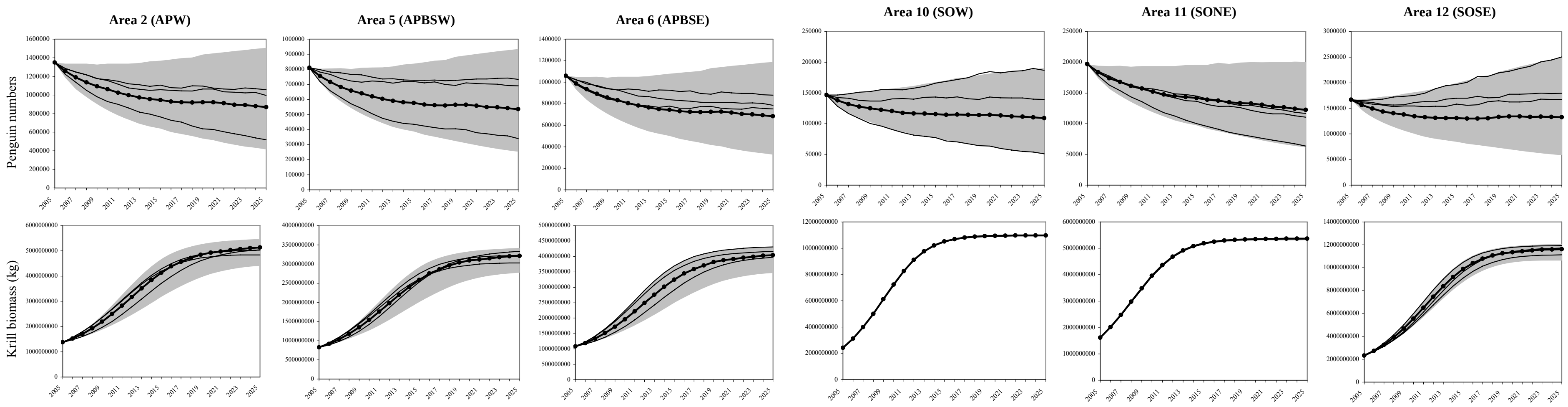

Fig. 5b. Trajectories of krill biomass under ***Catch Option 2***, penguin and seal abundance (i.t.o. numbers) in all SSMUs **without seals** present, from 120 model representations and when using a model version that assumes no krill movement (*Em* = 0). Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

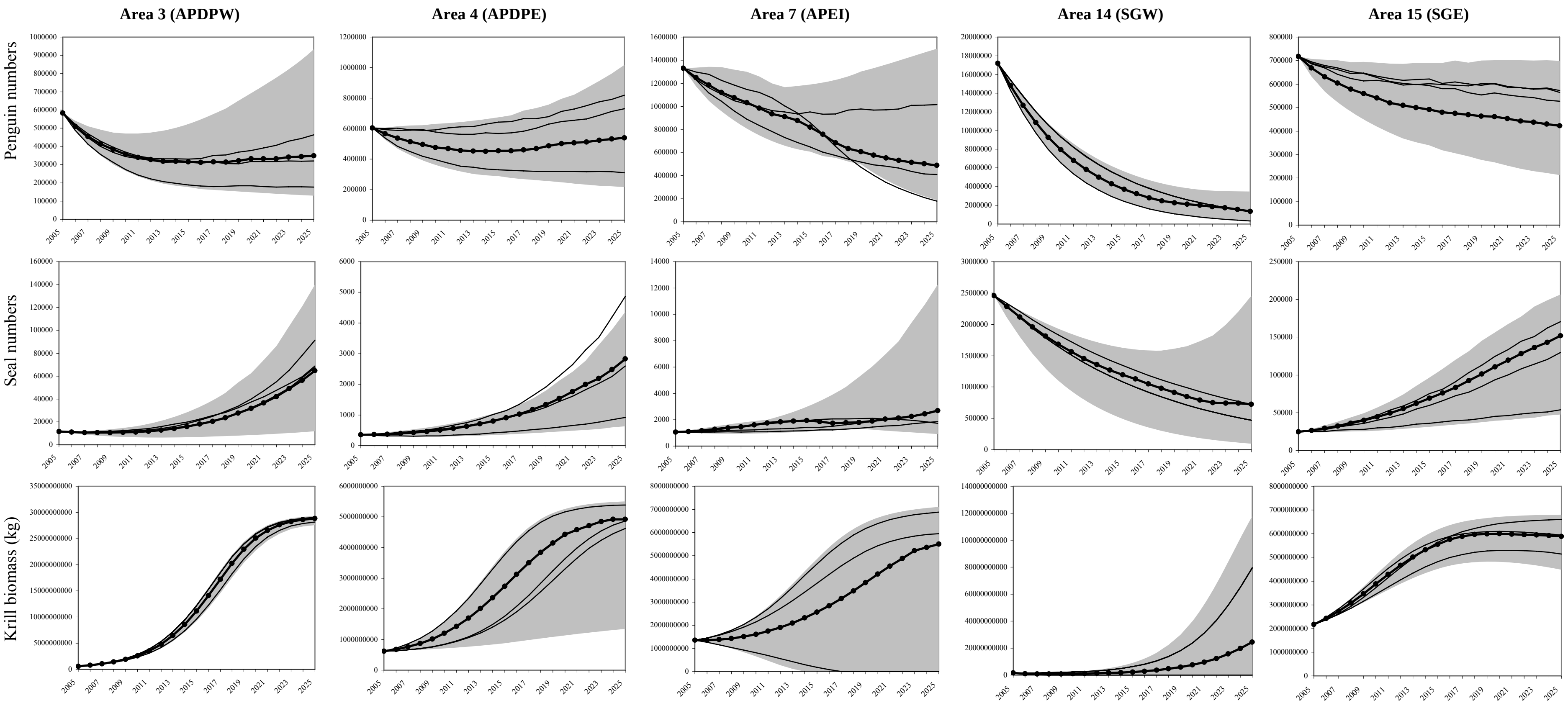

Fig. 6a. Trajectories of krill biomass under ***Catch Option 3***, penguin and seal abundance (i.t.o. numbers) in all SSMUs with both penguins and seals present, from 120 model representations and when using a model version that assumes no krill movement (*Em* = 0). Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

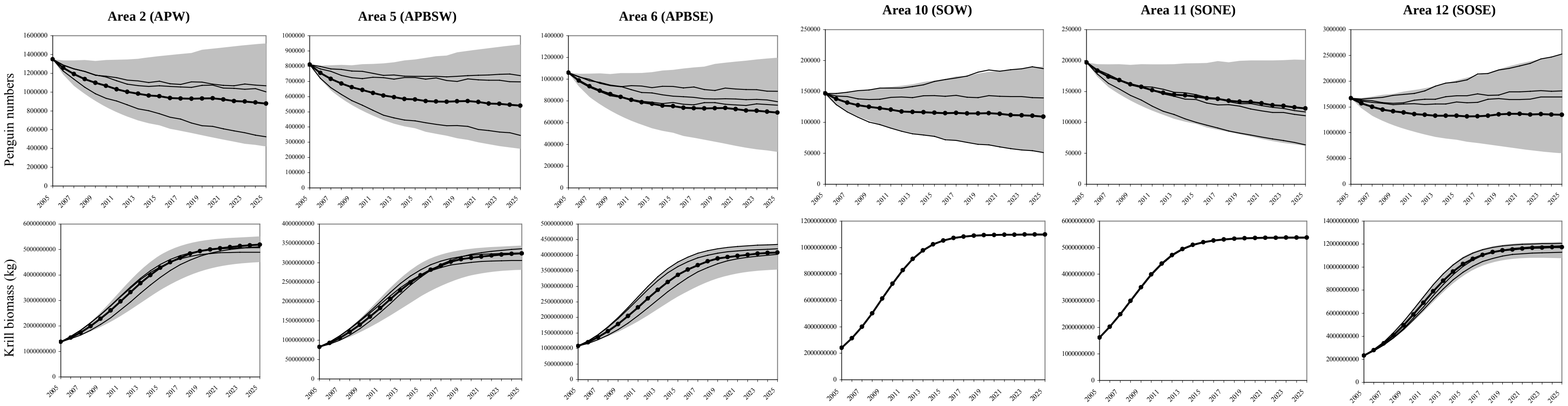

Fig. 6b. Trajectories of krill biomass under ***Catch Option 3***, penguin and seal abundance (i.t.o. numbers) in all SSMUs **without seals** present, from 120 model representations and when using a model version that assumes no krill movement (*Em* = 0). Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

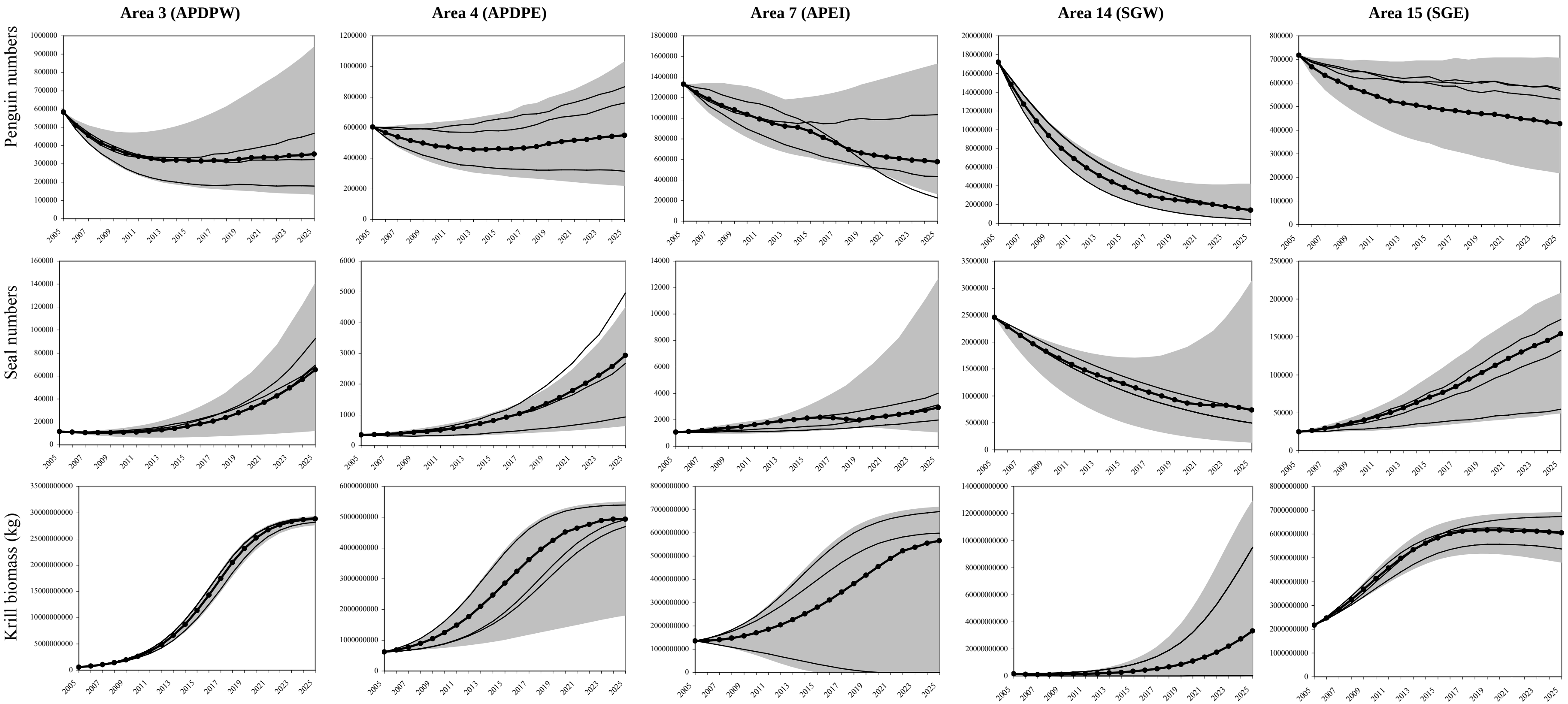

Fig. 7a. Trajectories of krill biomass under ***Catch Option 4***, penguin and seal abundance (i.t.o. numbers) in all SSMUs with both penguins and seals present, from 120 model representations and when using a model version that assumes no krill movement (*Em* = 0). Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

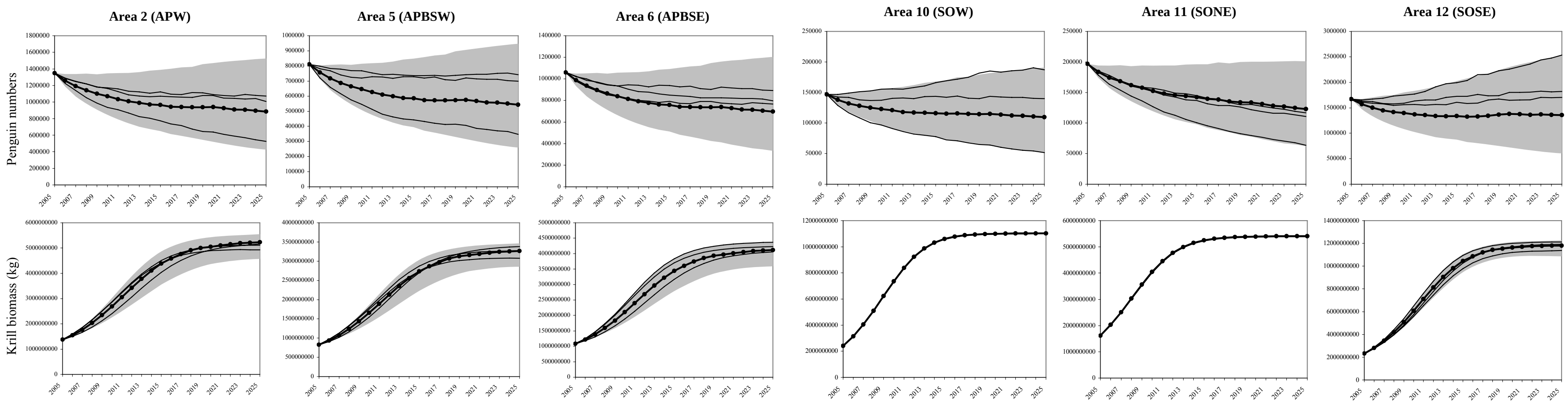

Fig. 7b. Trajectories of krill biomass under ***Catch Option 4***, penguin and seal abundance (i.t.o. numbers) in all SSMUs **without seals** present, from 120 model representations and when using a model version that assumes no krill movement (*Em* = 0). Three individual trajectories are shown, with the median a dark dotted line and the shaded areas showing 90% probability envelopes.

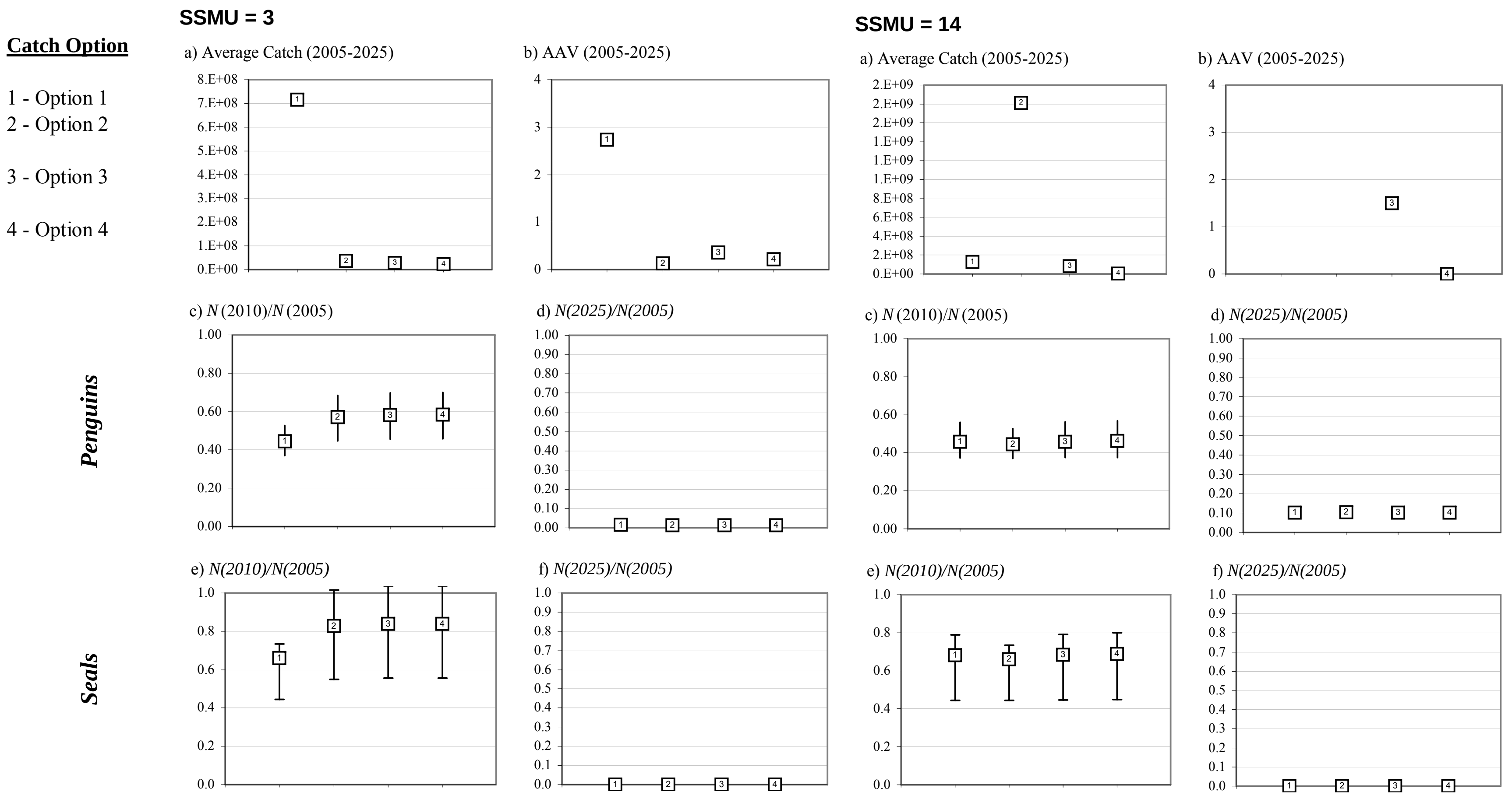

Fig. 8. Illustrative graphical summary of performance statistics for SSMUs 3 and 14, under the four constant Catch Options of Hewitt *et al.* (2004). Illustrative performance statistics include the average krill catch and catch variability associated with each option (note the latter does not vary under a constant catch), as well as the numbers of each predator species after 10 and 20 years relative to the current abundance level. Each panel shows medians together with 90%-iles.

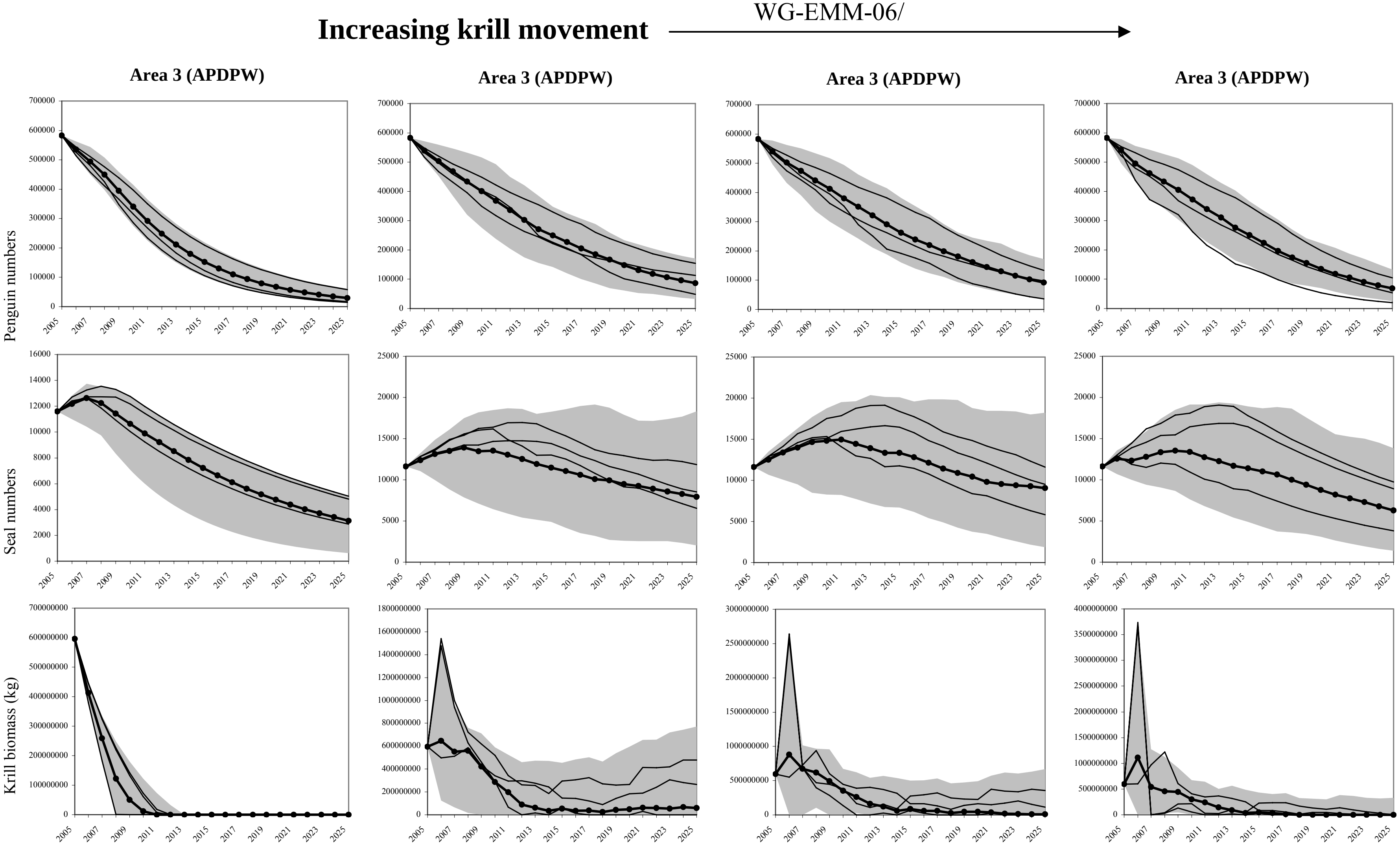

Fig. 9. Illustrative trajectories of krill biomass, penguin and seal abundance (i.t.o. numbers) under scenarios ranging from an assumption of zero transport of krill between SSMUs to gradually increasining levels of assumed krill transport (set by parameter *Em* in the model). Results are from 120 model representations with three individual trajectories shown. The median is represented using a dark dotted line and the shaded areas show 90% probability envelopes.