

THE SENSITIVITY OF MULTIPLE OUTPUT STATISTICS TO INPUT PARAMETERS IN A KRILL–PREDATOR–FISHERY ECOSYSTEM DYNAMICS MODEL

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Abstract

There is a global need to develop strategic frameworks for assessing uncertainty in ecosystem dynamics models. Such models have been used within CCAMLR to evaluate options for managing the Antarctic krill fishery in the Scotia Sea and southern Drake Passage. The model analysed here required 2 311 input values for each of four scenarios and produced 68 output statistics. Small perturbations to input values affected output statistics indicating the status of predator groups more than they affected statistics indicating the status of the target stock or the fishery. Output statistics were most sensitive to a parameter controlling predator recruitment through pre-recruit mortality. A parameter mediating the effect of a forcing function on krill recruitment, which was used to condition the model on past dynamics, was also important, and some of the parameter estimates resulting from conditioning were unstable. This highlights the tension between the parameter stability benefits of well-constrained models and the use of model conditioning to identify plausible alternative hypotheses in data-poor situations. Apparent sensitivity is a function of both input values and output statistics. Clearer specification of ecosystem-based management objectives would help to identify the important statistics for consideration when assessing uncertainty in ecosystem dynamics models.

Introduction

Watters et al. (2013) describe a spatially resolved stochastic simulation model representing one prey and target species, its natural predators and a fishing fleet. Its authors developed this model to provide advice to CCAMLR on the spatial allocation of the Antarctic krill catch limit for the Scotia Sea and southern Drake Passage (Statistical Subareas 48.1 to 48.3). As such, they configured the model to represent the krill stock, its predators and fishery within the small-scale management units (SSMUs) proposed by Hewitt et al. (2004) (Figure 1). During its development, this model was variously referred to as KPFM, KPFM2 and Foosa in Watters et al. (2005; 2006; 2008a), Hill et al. (2007a, 2007b) and Plagányi (2007). This paper follows Watters et al. (2013) and Hill (2013) and refers to it simply as ‘the model’.

The model incorporates only ecosystem components and interactions considered directly important to the focal species and therefore

resembles a minimum realistic model (Plagányi, 2007). Nonetheless, in its simplest form it requires 50 distinct inputs (18 point values, 29 vectors and 3 matrices). In the 15 SSMU–four predator configuration developed by Watters et al. (2013), it required 2 311 separate inputs for each of four alternative scenarios (Table 1). The word scenario here means a mathematical representation of a hypothesis about ecosystem dynamics consisting of a model and its inputs (*sensu* Rademeyer et al., 2007). This reference set of alternative scenarios brackets key uncertainties about ecosystem operation that were identified by CCAMLR scientific working groups (SC-CAMLR, 2005, 2006, 2007a). These uncertainties concern the movement of krill between areas and the sensitivity of predator reproduction to variations in krill abundance. The alternative scenarios were an essential part of the evaluation of competing methods for spatially allocating the catch, known as catch allocation options (Hewitt et al., 2004; Hill et al., 2007a; Plagányi and Butterworth, 2012).

Table 1: Summary of the types of model input specified by Watters et al. (2013) to generate each of their four reference models. The components column specifies the number of separate model components (prey, fishery and four predator taxa) that the input is specified for.

Category	Type	Parameters	Length ¹	Components	Seasons	Total
Arguments ²	Point values	11				11
General	Point values	7				7
SSMU	Vectors	2	18			36
Predators – general	Vectors	4	15	4		240
Predators – seasonal	Vectors	10	15	4	2	1200
Krill – general	Vectors	2	18	1		36
Krill – seasonal	Vectors	4	18	1	2	144
Catch	Vectors	1	15	1	2	30
Threshold density	Vector	1	15	1		15
Available fraction	Vector	1	18	1		18
Time series ¹	Vectors	4	38	1	2	304
Foraging	Matrices	1	18	4	2	144
Movement	Matrices	1	18	1	2	36
Competition	Matrix	1	18	5		90

¹ Vector or matrix length is the number of relevant modelled areas, except for time series where it is the number of relevant modelled years (although the model can also resolve seasons shorter than a year)

² There are, in fact, 29 arguments for the main function. Eleven of these are numerical arguments that affect model structure and parameterisation. The remaining arguments identify input objects and control outputs, and the number of Monte Carlo trials.

Watters et al. (2008a; 2009; 2013) considered four types of output statistic which correspond to the goals of ecosystem-based management as defined by McLeod and Leslie (2009): ecosystem productivity, health, resilience and services. These objectives are also consistent with CCAMLR's conservation principles and commitment to rational use (Table 2) (Grant et al., 2013). The output statistics were illustrative as there was no information available to the modellers about appropriate reference points or levels of aggregation (i.e. the combination of the modelled area- and taxon-specific abundance trajectories that the reference points apply to). In total, Watters et al. (2013) generated 68 statistics, including one each for krill (productivity) and fishery performance (services) and two (health and resilience) for each of 33 SSMU- and taxon-specific predator groups.

Plagányi (2007) commented that accounting for key uncertainties, within a strategic and practical framework, has lagged unsatisfactorily behind other aspects of ecosystem model development for marine living resource management. Link et al. (2012) noted that this lack of attention to uncertainty means that ecosystem dynamics models lack the credibility of single species models, but identified CCAMLR's use of ecosystem dynamics

models, as described in Hill et al. (2007a, 2007b), as an example of good practice for addressing several types of uncertainty. The effort of CCAMLR's scientific working groups to evaluate alternative model structures (SC-CAMLR, 2005, 2006, 2007a, 2007b, 2008) was an important part of this good practice. However, conventional model evaluation also includes analysis of the model's sensitivity to uncertainties in inputs. Such analysis identifies the relative contribution of uncertainty in each input to variability in model outputs, and provides an objective basis for targeting data collection and modelling effort to reduce uncertainty.

The current contribution describes a local sensitivity analysis to assess the effect of changes to model inputs on the output statistics used by Watters et al. (2008a; 2009; 2013). A local sensitivity analysis varies one input at a time, maintaining all others at their representative values, and is distinct from a global analysis which varies all inputs simultaneously but independently (Cariboni et al., 2007). The contribution also assesses the output response to values across the feasible ranges of selected inputs, including the key uncertainties represented in the four alternative scenarios. It assesses these responses across the rather complex analysis process that includes initialisation, conditioning,

Table 2: Model output statistics, with the relevant text and article numbers from the Convention on the Conservation of Antarctic Marine Living Resources in brackets. Each statistic indicates the probability of a specific undesirable outcome. The predators group comprises four component taxa: fish, penguins, seals and whales.

Statistic	Definition	Components	Spatial resolution
Productivity (II.3(a) prevention of decrease in the size of any harvested population to levels below those which ensure its stable recruitment)	Probability that krill abundance falls below 20% of median abundance at beginning of fishing period.	Krill	Whole model
Health (II.3(b) maintenance of the ecological relationships between harvested, dependent and related populations)	Probability that the abundance of the relevant component is <75% of the abundance in equivalent no-fishing trials at the end of the fishing period.	Predators	SSMU
Resilience (II.3(c) prevention of changes or minimisation of the risk of changes in the marine ecosystem which are not potentially reversible over two or three decades)	Probability that the abundance of the relevant component is <75% of the abundance in equivalent no-fishing trials at the end of the recovery period.	Predators	SSMU
Services (II.2 the term ‘conservation’ includes rational use)	Average proportion of allowable catch that is not caught.	Fishery	Whole model

multiple simulations and data processing. As it was necessary to repeat the initialisation stage many times, this contribution includes a revised initialisation that allows automation. The objectives are: (i) to inform users of the model and the advice that it provides about the sensitivity of this advice to input parameters and the stages of the analysis process, including the choice of output statistics; (ii) to objectively evaluate the key uncertainties identified in SC-CAMLR (2006, 2007a) and; (iii) to help identify the requirements of a strategic framework for assessing uncertainty in ecosystem dynamics models.

Methods

Previous use of the model to provide management advice

The appendices that accompany Watters et al. (2013) describe the model in detail (see also Watters et al., 2005; 2006; 2008a). The model is available for download as an [R] package with accompanying documentation from <http://swfsc.noaa.gov/aerd-kpfm>. The current analysis also made extensive use of [R] (R Development Core Team, 2012).

Figure 1 summarises the spatial, temporal and trophic structure, and data inputs and outputs in the current implementation of the model, which largely reproduces that of Watters et al. (2013).

Following guidance from CCAMLR’s scientific working groups (SC-CAMLR, 2005, 2006, 2007a, 2007b, 2008), Watters et al. (2008a, 2008b, 2009, 2013) applied the following risk assessment approach to advise on krill catch allocation options:

- (a) Define plausible values for the model inputs based on a review of the literature and expert knowledge (Hill et al., 2007b).
- (b) Identify a small number of key uncertainties and define plausible extreme values for the relevant inputs (SC-CAMLR, 2006, 2007a).
- (c) Develop a set of alternative parameterisations, each containing all of the inputs required to implement a scenario. There were four parameterisations, combining two sets of alternative values for movement parameters (significant krill movement between SSMUs versus no krill movement) and two sets of alternative value for predator resilience parameters

(reproductive success is proportional to foraging success versus reproductive success is relatively insensitive to foraging success) (SC-CAMLR, 2007a; Hill et al., 2007a, 2007b; Watters et al., 2008b).

- (d) Identify plausible dynamics for the modelled taxa (except fish, for which there was insufficient information) for the period 1970 to 2006 based on data and expert opinion (SC-CAMLR, 2007a, 2008; Hill et al., 2008).
- (e) Initialise the models for 1970 by setting organism abundances consistent with the plausible dynamics and adjusting krill recruitment parameters and boundary area krill abundance so that, in each SSMU, krill gains through recruitment and import balance losses through predation and export over a year (Watters et al., 2008b). Krill dynamics are not explicitly represented in the boundary areas which notionally exist outside the SSMUs. Nonetheless boundary area krill abundance can be specified to serve as a source of krill imported into SSMUs.
- (f) Adjust the values of selected taxon-specific parameters defining predator recruitment dynamics (S_p for seals, J for penguins and R_p for all species except fish: Table 3) to optimise the fit to past ecosystem dynamics, and produce a reference set of alternative scenarios. This process is known as conditioning (Rademeyer et al., 2007). The four input parameterisations led to four alternative scenarios (Watters et al., 2008b).
- (g) Perform multiple stochastic simulations of 40 years nominally beginning in 2007 and partitioned into 20 years of fishing, using a candidate catch allocation option and a specified allowable catch, followed by 20 years without fishing (SC-CAMLR, 2007a; Watters et al., 2008a).
- (h) Extract output statistics to compare the candidate catch allocation options (SC-CAMLR, 2008; Watters et al., 2008a).

Modifications to the initialisation process and input data

The current analysis used largely the same inputs as Watters et al. (2013) (steps (c) and (d) of the risk assessment approach) and replicated steps (e) to (h)

to generate output statistics, but there were two key differences. Firstly, the analysis used a single basic parameterisation, with representative average values, which required some adjustments to the input data in step (c). Secondly, an algorithmic approach replaced the ad-hoc balancing of initial krill losses and gains in step (e).

The ‘movement linear’ scenario, one of the four reference scenarios produced by Watters et al. (2013), was the basis for the step (a) input values in the current analysis. This analysis introduced a new scalar, μ : a multiplier with range (0,1) of the ‘movement linear’ movement matrices (Tables 3 and 4 in Hill et al., 2007b), which describes the maximum plausible movement of krill between model areas. The representative average value for μ was 0.5. ϕ is a shape parameter determining the proportion of adults that breed for a given level of prey consumption. The representative average value of ϕ was 0.685, midway between the values 0.37 and 1 explored by Watters et al. (2013).

The algorithmic approach to balancing krill losses and gains allows automation of risk assessment steps (e) to (h) but requires additional constraints. It also allows the introduction of another new scalar, d : a multiplier of the year-specific krill abundances in the boundary areas chosen by Watters et al. (2013: their Table B15) which was assigned a representative average value of 1 and used to explore the sensitivity of output statistics to the assumptions about krill abundance. The parameter symbols in the description of the approach are the same as those used in Watters et al. (2013). Subscript i refers to the spatial units of the model, SSMUs ($i = 1$ to 15) and boundary areas ($i = 16$ to 18). Subscript t applies to state variables and refers to time-steps. In Watters et al. (2013), time-steps were implemented as seasons within years. The current description uses the notation 1970(1) refers to the combination of year (1970) and season (1 = summer), and the notation 1970 indicates the sum of values across the two seasons in a year. Subscript s denotes season (1 = summer, 2 = winter) and applies to parameters, some of which had different values in each of the two seasons (Table 1).

The following assumptions apply:

- (i) For each SSMU, the adult abundance that produces half of maximum recruitment, $\beta_{i,s}$, had an arbitrarily low value of 1 000. This produces a relatively flat stock-recruit relationship with

Table 3: Parameters included in the sensitivity analysis. The table gives the notation used for these parameters in the current study, and the more complex corresponding notation used in the appendices of Watters et al. (2013). The predators group comprises four component taxa: fish, penguins, seals and whales.

Notation here	Notation in Watters et al. (2013)	Description	Component	Range ¹
ϕ	$\Phi_{k,i,s}$	Shape parameter determining the proportion of adults that breed for a given level of prey consumption. ²	Predators ³	0.37 to 2.7
R_p S_p	$Rpeak_{k,i,s}$ $Speak_{k,i,s}$	Maximum recruitment when all adults breed. Adult abundance that produces maximum recruitment.	Predators ^{3,4} Predators ^{3,4}	
J	$Jphi$	Shape parameter determining the relationship between pre-recruit foraging success and pre-recruit mortality.	Predators ^{3,4}	0 to 1.07
M	$\bar{M}_{k,i,s}$	Instantaneous rate of natural mortality	Predators ³	
θ	$\Phi_{i,s}$	Scalar that mediates environmental effects on krill recruitment.	Krill	
β	$\beta_{i,s}$	Adult abundance that produces half of maximum recruitment.	Krill	
α	$\alpha_{i,s}$	Maximum recruitment.	Krill	
w	\bar{w}_i	Average mass of an individual krill.	Krill	
d		Multiplier of the krill abundances in the three boundary areas chosen by Watters et al. (2013).	Krill	
μ		Multiplier with range (0,1) of the movement array. Changes to this parameter allow exploration of degrees of movement between the two extremes of no-movement and maximum movement examined by Watters et al. (2013). ²	Krill (via environment)	0 to 1
κ	$\kappa_{k,i,s}$	Krill density at which predators achieve half of maximum potential per-capita consumption.	Predators	
\hat{Q}	$Q_{k,i,s}^*$	Maximum per-capita potential consumption.	Predators	

¹ Range is specified only for the parameters analysed in Figures 6 to 8.

² The parameter specifies one of the key uncertainties identified by WG-EMM.

³ The parameter was also perturbed at the taxon scale.

⁴ The parameter was adjusted (for selected taxa) during conditioning.

recruitment, $R_{i,t}$, approximately equal to the user-defined maximum, $\alpha_{i,s}$, when stock abundance $K_{i,t} \gg \beta_{i,s}$.

(ii) The seasonally resolved parameter $\alpha_{i,s}$ was 0 for season 2. Consequently, all modelled recruitment directly depends on its value in season 1, $\alpha_{i,l}$.

(iii) The krill stock in each SSMU was in steady state in 1970:

$$K_{i,1971(1)} = K_{i,1970(1)} \quad (1)$$

(iv) Initial krill abundances in the boundary areas ($K_{16,1970(1)}$ to $K_{18,1970(1)}$) were the values used by Watters et al. (2013).

(v) Krill recruitment in SSMUs 13–15 was 0.

(vi) Krill density in each SSMU in 1970 was twice that in 2000:

$$K_{i,1970(1)} = 2K_{i,2000(1)} = \frac{2B_{i,2000(1)}}{w} \quad (2)$$

where $B_{i,2000(1)}$ is an empirically derived estimate of krill biomass in SSMU i in summer 2000 and w is the mean mass of an individual krill.

Watters et al. (2013) also made assumptions (i) to (v). Assumption (vi) is consistent with, but more specific than, that of Watters et al. (2013), who assumed that overall krill density in 1970 was double that in 2000. Assumption (iii) allows analytical estimation of $\alpha_{i,l}$ as follows:

The delay difference equation describing krill dynamics in the model can be written as

$$K_{i,t+1} = K_{i,t}S_{i,t} + R_{i,t+1} + \sum_{j \neq i} K_{j,t}T_{ji,t} \quad (3)$$

where $R_{i,t+1}$ is the recruitment of krill;

$$S_{i,t} = \exp\left(-Z_{i,t} - \sum_{j \neq i} v_{i \rightarrow j,s}\right) \quad (4)$$

is the proportion of the krill stock in SSMU i at the beginning of time-step t that remains in i at the end of the time-step; and

$$T_{ji,t} = \frac{v_{j \rightarrow i,s}}{Z_{j,t} + \sum_h v_{j \rightarrow h,s}} \left(1 - \exp\left(-Z_{j,t} - \sum_h v_{j \rightarrow h,s}\right)\right) \quad (5)$$

is the number of krill that arrive in i from area $j \neq i$ during time-step t . $v_{j \rightarrow i,s}$ is the instantaneous rate of movement from area i to area j and $h \neq j$ is the set of all areas except j .

$$Z_{i,t} = M0_{i,t} + M2_{i,t} + F_{i,t} \quad (6)$$

is the total instantaneous mortality rate consisting of predation mortality, $M2_{i,t}$, fishing mortality $F_{i,t}$ and natural non-predation mortality, $M0_{i,t}$.

Following Watters et al. (2013) both $M0_{i,t}$ and $F_{i,t}$ were 0 in 1970, therefore

$$Z_{i,1970} = M2_{i,1970} = -\ln\left(1 - \frac{\sum Q_{i,1970}}{K_{i,1970}}\right) \quad (7)$$

where $\sum Q_{i,1970}$ is total krill consumption by predators in SSMU i (Q is summed across multiple predator taxa).

Equation (3) can be rewritten as

$$K_{i,t+1} = K_{i,t}S_{i,t} + \alpha_{i,l} + \sum_{j \neq i} K_{j,t}T_{ji,t} \quad (8)$$

using assumptions (i) and (ii) ($R_{i,t} \approx \alpha_{i,l}$) and solved for $\alpha_{i,l}$ using assumption (iii):

$$\alpha_{i,l} = (1 - S_{i,t})K_{i,t} - \sum_{j \neq i} K_{j,t}T_{ji,t}. \quad (9)$$

Local sensitivity analysis

A local sensitivity analysis varies one input value at a time to assess its effect on model output statistics. In the model, there are many more inputs than parameters as the latter can apply to different taxa, areas and time-steps, taking a different value for each (Table 1). It was beyond the scope of the current analysis to vary every taxon- and SMMU-specific input separately, so some were varied simultaneously (see ‘Controlling complexity and inputs considered’).

The sensitivity of an output statistic, p , to a single input, a , is its rate of change, $\frac{\partial p}{\partial a}$, when other inputs are held constant. Sensitivity is usually calculated as a linear response to a small perturbation in a .

The analysis used the following numerical approximation:

$$\Delta p(a^*) = \frac{p(1.01a^*) - p(0.99a^*)}{2} \quad (10)$$

where a^* is the average value of a . Each output statistic (Table 2) is a probability and $\Delta p(a^*)$ is therefore an estimate of the linear change in the probability, p , of an undesirable outcome as a result of a 1% change in a . A positive value of $\Delta p(a^*)$ indicates that an increase in a leads to an increase in the probability of an undesirable outcome. It was necessary to use a small perturbation (as opposed to, say, 10%) as many of the perturbed inputs control strongly nonlinear functions.

Each of the values $p(1.01a^*)$ and $p(0.99a^*)$ were calculated using steps (e) to (h) of the risk assessment approach described above. Perturbations were applied to the inputs supplied in step (e). Each data point in Figures 2 to 4 summarises the results of 1 001 Monte Carlo simulations but, because of resource constraints, the further investigations summarised in Figures 4 to 7 used 101 Monte Carlo simulations per data point (see Watters et al., 2013,

Appendix C for implications). Table 3 lists the parameters considered in the sensitivity analysis, which includes the new scalars, μ and d . The representative average values for each parameter were taken from Watters et al. (2013, their Tables B4 to B18) except, as described above, for μ , ϕ and d .

Further analysis

Further analyses considered the output responses across the plausible range of input values for selected inputs. The scalar μ was given input values in the range 0 to 1 where 0 is equivalent to the no-movement parameterisations and 1 is equivalent to the maximum movement parameterisations of Watters et al. (2008a, 2008b, 2009, 2013). Input values for the shape parameter ϕ were in the range 0.37 to 2.70, which includes the linear ($\phi = 1$) and hyperstable ($\phi = 0.37$) relationships evaluated by Watters et al. (2013) as well as the hyperdepleting ($\phi = 2.70$) relationship identified in SC-CAMLR (2006) (Figure 7). The analysis used the same input value of ϕ simultaneously for all relevant SSMU and taxon combinations. Values for the shape parameter J are specified in step (c) for most taxa, but are estimated for penguins in step (d). The analysis considered the effects of J for seals in the range 0 to 1.07.

Controlling complexity and inputs considered

Watters et al. (2013) used 2 006 input values per scenario (this total does not include time series) and assessed four catch allocation options at a range of allowable catches, producing results in terms of 68 output statistics. This implies 545 632 combinations of output statistic, p , and perturbed input, a , each of which gives a vector of responses at different allowable catches. The current analysis included the following simplifications to make it tractable:

- (i) The analysis considered two allowable catch levels: 11% and 100% of the modelled precautionary catch limit. The former represents CCAMLR's operational krill catch limit, or trigger level, which is 11% of the current precautionary catch limit (Conservation Measure 51-01: CCAMLR, 2011).
- (ii) The analysis considered three of the catch allocation options, namely 'Catch', where the

allocation was proportional to the total reported catch in each SSMU between the 2002/03 and the 2006/07 fishing seasons; 'Demand', where the allocation was proportional to the consumption requirements of predators, calculated within the model; and 'Stock' where the allocation was proportional to the biomass of krill, calculated within the model.

- (iii) Each taxon-specific health or resilience output statistic is the arithmetic mean of the ≤ 15 relevant taxon-and-SSMU-specific statistics.
- (iv) All SSMU-specific values for a given parameter were perturbed simultaneously.
- (v) All taxon-specific values for a given predator parameter were initially perturbed simultaneously. Further analysis considered taxon-specific perturbation of five of the seven predator parameters, but used only the higher allowable catch and the 'Demand' catch allocation option.

Results

Comparison of initialisation methods

Table 4 compares SSMU-specific estimates of $\alpha_{i,1}$, the maximum krill recruitment, from the current study with those of Watters et al. (2013). Watters et al. (2013) estimated higher values for coastal SSMUs in Subareas 48.1 and 48.2 with the movement case than with the no-movement case, indicating that modelled movement causes a net loss of krill from these SSMUs. In oceanic SSMUs in these subareas, movement causes a net gain of krill. In the current study, values for the movement case were higher for oceanic SSMUs than were those of Watters et al. (2013), whereas the rest were lower. This more uniform set of values is due to the simultaneous balancing of krill losses and gains in all SSMUs. The differences for Subarea 48.3 are due to the contrasting assumptions of zero recruitment in the current study and finite recruitment in that of Watters et al. (2013).

In the no-movement case, krill recruitment simply balances losses due to predation mortality. The differences between values from the current study and Watters et al. (2013) were mainly smaller than for the movement case. However, the two initialisation approaches are clearly not equivalent.

Table 4: Comparison of SSMU-specific values for the krill recruitment parameter $\alpha_{i,1}$ (units: 10^{13} krill) estimated in the current study and Watters et al. (2013).

SSMU	Subarea	Movement		No-movement		Average movement
		(Watters et al., 2013)	(Current study)	(Watters et al., 2013)	(Current study)	(Current study)
		$\mu = 1$	$\mu = 1$	$\mu = 0$	$\mu = 0$	$\mu = 0.5$
1 (oceanic)	48.1	0.173	0.450	1.730	0.680	0.422
2	48.1	2.066	0.549	0.356	0.359	0.471
3	48.1	1.449	0.285	0.106	0.107	0.233
4	48.1	0.924	0.337	0.176	0.222	0.306
5	48.1	1.864	0.448	0.213	0.255	0.384
6	48.1	1.370	0.482	0.228	0.232	0.372
7	48.1	1.453	0.584	0.215	0.244	0.480
8	48.1	2.715	0.964	0.724	0.742	0.864
9 (oceanic)	48.2	0.000*	0.443	2.391	2.309	0.904
10	48.2	3.505	0.893	0.065	0.065	0.759
11	48.2	2.300	0.514	0.089	0.109	0.446
12	48.2	3.085	0.842	0.261	0.327	0.699
13 (oceanic)	48.3	0.001	0.000	3.063	0.000	0.000
14	48.3	0.006	0.000	0.600	0.000	0.000
15	48.3	0.003	0.000	0.280	0.000	0.000

* Value at higher precision: 8.967×10^8

Sensitivity analysis 1: Simultaneous perturbation

This section describes results from perturbation, simultaneously across taxa and SSMUs, of inputs for parameters with SSMU-specific values (e.g. w) or SSMU-and-taxon specific values (e.g. J). There were differences between output statistics in the magnitude and direction of the maximum response and the input parameters that were most influential. These characteristics also varied between catch allocation options and allowable catches. The productivity statistic was insensitive to all perturbations. The services statistic was the only output that was sensitive to all relevant perturbations. It was most sensitive to the parameter \hat{Q} , although the magnitude of the response was never greater than 0.0029 (meaning that a 1% perturbation to the input changed the estimated risk by 0.29%), and was not consistent across allowable catches or catch allocation options (Figure 2). The strongest responses by taxon in the health statistic ranged from 0.0005 for whales to -0.1642 for penguins, and the strongest responses in the resilience statistic ranged from 0.0041 for fish to -0.1570 for penguins (Figures 3 and 4).

There was no change in the output statistic in 41% (297) of 720 perturbation-response combinations (Table 5). The perturbation produced a

negative response (i.e. reduced the probability of an undesirable outcome) in 235 of the sensitive combinations and a positive response (increased the probability) in 288. The response was greater than the perturbation in 14% (103) of the combinations.

The health and resilience responses for whales were insensitive to most (66 and 50 of 72 respectively) perturbations while the responses for fish, penguins and seals were sensitive to over half of the perturbations (Figures 3 and 4). The health response for penguins and seals and the resilience response for penguins and whales included changes >0.01 in the estimated probability of an undesirable outcome. The health and resilience responses for penguins included changes >0.1 .

Penguin responses were frequently sensitive to the parameter θ . The relationship was complex with both positive and negative responses depending on the combination of allowable catch, catch allocation option and response statistic. The full set of parameters that produced a response >0.05 in penguins (in descending order of response) were: J , θ , M , κ , φ , R_p , μ and S_p . The set of parameters that produced a response >0.05 in seals (in descending order of response) were: μ , κ , w , φ , R_p , J , M and S_p . There were no responses >0.05 for other taxa.

Table 5: Responses to a 1% perturbation in each of the listed parameters. Each cell indicates the number of responses in the stated range. The 60 responses for each parameter include all combinations of the 10 output statistics, three catch allocation options and two allowable catch levels.

Response min.	Response max.	d	μ	θ	β	w	κ	\hat{Q}	M	J	ϕ	R_p	S_p
-0.18	-0.1	0	0	4	0	0	1	0	5	6	2	0	0
-0.1	-0.01	0	7	4	0	7	10	8	6	2	6	6	1
-0.01	-0.001	5	7	5	0	6	2	11	7	3	1	8	7
-0.001	0	17	10	13	2	9	9	8	5	8	6	5	6
0	0	29	22	21	54	23	22	21	19	24	19	22	21
0	0.001	6	4	8	4	7	7	7	9	12	11	4	8
0.001	0.01	3	9	2	0	7	8	5	7	2	12	10	8
0.01	0.1	0	1	3	0	1	1	0	2	3	3	5	9

Table 6 illustrates how perturbation of the parameter J for penguins affected the post-conditioning estimate of that parameter. A 2% difference in initial values produced up to 182% difference in the final estimates (in SSMU 15).

Taxon-specific perturbation

This section describes results from individual perturbation, by parameter and taxon, of input values for parameters with SSMU- and taxon-specific values (e.g. J). These results are specifically for the ‘Demand’ catch allocation option and allowable catch at the precautionary catch limit.

Responses >0.1 occurred in penguin health and resilience responses. Changes >0.05 occurred in the seal health response, and changes >0.01 also occurred in the whale resilience responses (Figure 5). The main changes in penguin resilience and health were negative responses to perturbations in J and M for penguins and a positive response to perturbations in ϕ for penguins. Penguins also responded (change >0.01) to perturbations in fish parameters (R_p , ϕ and M). Seals and whales only responded (change >0.01) to perturbations to their own parameters (R_p and ϕ respectively).

Further analysis

The results showing the responses to a wider range of values for the parameters μ , ϕ and J (the latter specifically for seals) are specifically for the ‘Demand’ catch allocation option and allowable catch at the precautionary catch limit. Figures 6 to 8 show the responses relative to the maximum response for that taxon-specific response statistic,

so the absence of a relationship with the perturbed variable does not necessarily mean that the statistic is insensitive, just that sensitivity does not change with the level of perturbation.

The constraints on krill recruitment in SSMUs 13 to 15 in the revised initialisation have implications for the case $\mu = 0$ where it is impossible to maintain krill populations in these SSMUs without an influx of krill from other areas. Figure 6 includes results for $\mu = 0$, but this is not a plausible representation of the current ecosystem. The productivity statistic was insensitive to changes in μ . The remaining statistics generally suggest a transition from high risk with low movement to low risk with high movement, as the model increasingly replaces explicit losses with imports from boundary areas. However, the pattern for penguins is noisy but implies increasing risk with increasing movement.

The risks to whales, seals and fish increased with increasing values of ϕ while the risk to the fishery (services) declined slightly (Figure 7). Watters et al. (2008a, 2009, 2013) explored values ≤ 1 , whereas the greater risks were for values > 1 . The services statistic was relatively insensitive to ϕ and the response in penguins was apparently unstructured. The health and productivity statistics for other predators had monotonic responses to ϕ with a variety of forms from quasi-linear to asymptotic.

Increasing J for seals increased the risk to seals, but all of the other statistics were insensitive to variations in the values of this taxon-specific parameter.

Table 6: Example of the interactions between perturbation and conditioning. J_a , $J_{a-1\%}$ and $J_{a+1\%}$ are the re-estimated (post-conditioning) values of J (controlling the effect of prey availability on pre-recruit mortality) for penguins based on average, average – 1%, and average + 1% input values for the same parameter.

SSMU	$J_{a+1\%}$	$J_{a+1\%}/J_a$	J_a	$J_{a-1\%}/J_a$	$J_{a-1\%}$
1					
2	3.68	68%	5.43	106%	5.74
3	19.14	71%	26.82	56%	14.94
4	11.43	121%	9.46	58%	5.46
5	4.87	49%	9.90	39%	3.83
6	2.84	85%	3.33	86%	2.88
7	5.62	132%	4.25	137%	5.83
8	3.16	81%	3.92	84%	3.28
9					
10	6.18	128%	4.83	107%	5.16
11	2.86	111%	2.58	105%	2.72
12	2.32	98%	2.37	145%	3.44
13					
14	20.79	153%	13.59	109%	14.81
15	7.42	218%	3.40	77%	2.63

Discussion

The response to perturbations in inputs varied with output statistic, catch allocation option and allowable catch. The most influential inputs affected parameters involved in the conditioning process and the most sensitive output statistics were those measuring the health and resilience of penguin and seal populations. The analysis highlights the need to explore uncertainties when the available data do not provide strong constraints.

Modification of Watters et al.'s (2013) initialisation processes was necessary to facilitate this analysis and should be useful in future applications of the model. The input parameterisation in the current analysis was a single set of representative average values and the outputs were aggregated by taxa, whereas Watters et al. (2008a, 2008b, 2009, 2013) and Hill (2013) used four parameterisations including extreme values for some parameters, and presented their results by taxa and SSMU. Consequently, the current results are a general sensitivity analysis for the model, based on the structure and parameterisation of Watters et al. (2013), but not a specific sensitivity analysis of that study.

The algorithmic approach to balancing krill losses and gains required the introduction of additional constraints to ensure that there were more

specified data than unknown parameters and thereby reduce the risk that the variability in the data would cause unstable or unreasonable estimates (Williams et al., 2002). The chosen constraints on recruitment in SSMUs 13 to 15 (South Georgia and the north Scotia Sea) are consistent with the well supported hypothesis that the krill population in this area is not self-sustaining (e.g. Tarling et al., 2007).

The model was designed to explore a range of hypotheses about ecosystem operation. In the catch allocation option evaluation process, the alternative scenarios were developed by conditioning the model on sparse and uncertain data on past ecosystem dynamics that provided limited evidence for estimating the free parameters (Watters et al., 2008b; Plagányi and Butterworth, 2012). The current study demonstrates the relative instability in some of the resulting estimates (Table 6), with the consequence that the penguin response to variability in some other parameters was apparently unstructured (Figures 6 and 7). Watters et al. (2008b) noted that the reference set of scenarios encapsulates a diverse and detailed range of hypotheses about ecosystem processes, and these scenarios were accepted as plausible by SC-CAMLR (2008). There is tension between the ideal of a well constrained model which produces stable parameter estimates, and the need to explore plausible alternative hypotheses in data-poor situations. However, there is an obvious

strategy for resolving this tension, which is to evaluate the hypotheses that the model has generated.

Responses that were greater than the perturbation were relatively rare (14%) in the sensitivity analysis, and the distribution of negative and positive effects was near symmetrical. This suggests that despite the relative instability of parameters estimated during conditioning, the overall process used for evaluating catch allocation options was stable. Small perturbations to the following parameters were influential: the instantaneous natural mortality rate for predators (M); the krill density at which predators achieve half of maximum consumption (κ); the parameter mediating environmental effects on krill recruitment, which was used to control krill dynamics in the conditioning process (θ); the maximum recruitment when all adult predators breed (R_p); the shape parameter controlling the relationship between predator pre-recruit foraging success and pre-recruit mortality (J); and the shape parameter controlling the relationship between predator consumption and reproductive output (φ). Although the latter was one of the key uncertainties identified by CCAMLR's working groups, this analysis suggests that output statistics were less sensitive to these uncertainties than to those affecting predator mortality and feeding success and those influencing the conditioning process. However, Figures 6 and 7 suggest that greater changes in inputs representing these putative key uncertainties, on the scale of those considered by Watters et al. (2008a, 2008b, 2009, 2013), can change the probability of an undesirable outcome by over 80%.

The variability in response between output statistics is important. The model is one of a growing number of ecosystem dynamics models developed to provide advice on the management of human activities in marine ecosystems (Plagányi, 2007). Modellers need to translate complex results into a simple form that provides the appropriate information to stakeholders and decision makers. Link et al. (2012) identified unclear management objectives as one of the main uncertainties affecting this interaction. In the absence of quantitative objectives for krill predators, Watters et al. (2013) used illustrative output statistics. Hill (2013) demonstrated how the choice of such statistics can bias the evaluation of candidate management measures. More clarity about management objectives should provide better guidance about appropriate output statistics.

This, in turn, should allow objective assessment of whether sensitivity significantly influences critical outputs.

Models that incorporate inter-specific interactions typically have many more parameters than the single species models still used to evaluate management plans for many of the world's commercially harvested species. This increase in model complexity is necessary to enhance the ability of models to capture critical characteristics that are relevant to ecosystem operation and to management objectives. However, increasing complexity also leads to accumulation, and possible multiplication, of uncertainties and increased difficulty in interpreting results (e.g. Fulton et al., 2003; Raick et al., 2006; Plagányi, 2007; Hill et al., 2007a). A strategic and practical framework to account for uncertainties should therefore be developed as a matter of priority (Plagányi, 2007). The current analysis highlights some of the considerations that should inform such a process:

Firstly, model outputs result from interactions between inputs, model structure, further elements of the analysis process such as conditioning, the simulated management measure, the simulated state variables, and the statistics used to summarise them. Ideally, a strategic framework should also include global sensitivity analysis, to capture the interactions between parameters (Ginot et al., 2006; Plagányi, 2007). This suggests that there is a need to identify a limited set of model output statistics, or underlying state variables, that are useful both for assessing model sensitivity and for providing management advice. Link et al. (2012) suggested that ecosystem models should produce reference points used by management. Model outputs for the evaluation of catch allocation options for Antarctic krill have been available for several years but management reference points exist only for the target stock and not for its predators (Hill, 2013). The illustrative reference points in Table 2 provide a starting point for the dialogue between modellers, managers and other stakeholders that will be necessary to identify management reference points.

Secondly, the outcomes of formal sensitivity analysis and expert scrutiny might be different, as indicated by their different evaluations of the relative importance of the parameters describing the key uncertainties identified by SC-CAMLR (2006,

2007a). Both of these processes have a role to play in a strategic framework, but it is essential to coordinate them.

Thirdly, the use of the model to evaluate catch allocation options illustrates the tension between the ideal of well-constrained models and the reality of ecosystem-based management problems in which data are sparse, structure is complex and uncertainty is rife (Hill et al., 2007a; Plagányi, 2007; Link et al., 2012). This sort of model can help to identify plausible hypotheses that are consistent with the available data. This is important for characterising uncertainty, and it can guide data collection to reduce these uncertainties. However, the parameter estimates underlying these hypotheses may be unstable. A strategic framework must consider the implications of under-constrained models.

Finally, CCAMLR's evaluation of catch allocation options compared the results from two model structures (Plagányi and Butterworth, 2012; Watters et al., 2013) using a common suite of output statistics. This comparison was a pragmatic attempt to deal with the uncertainty that arises because different model structures can give different predictions (Hill et al., 2007a). This comparison was a form of sensitivity analysis for the effects of model structure (and any further assumptions that differ between models) on output statistics. A strategic framework should consider good practice in such multi-model comparisons (Hill et al., 2007a).

Conclusion

CCAMLR currently aims to develop feedback management for Antarctic krill, and it has an obligation to consider the effects of all fisheries on related and dependent species. This implies an increasing need to use ecosystem dynamics models to inform decision-making and therefore an expectation that its Members will continue to develop, test and evaluate such models. It is in CCAMLR's interests to build on the evaluation work of its scientific working groups and develop a strategic framework for assessing uncertainty in ecosystem dynamics models that includes sensitivity analysis. The apparent sensitivity of models varies with the chosen output statistic, and the assessment of catch allocation options for Antarctic krill illustrates that the development of models can progress faster than managers are able to identify their requirements.

There is a need for greater communication between modellers, managers and other stakeholders to identify appropriate model outputs.

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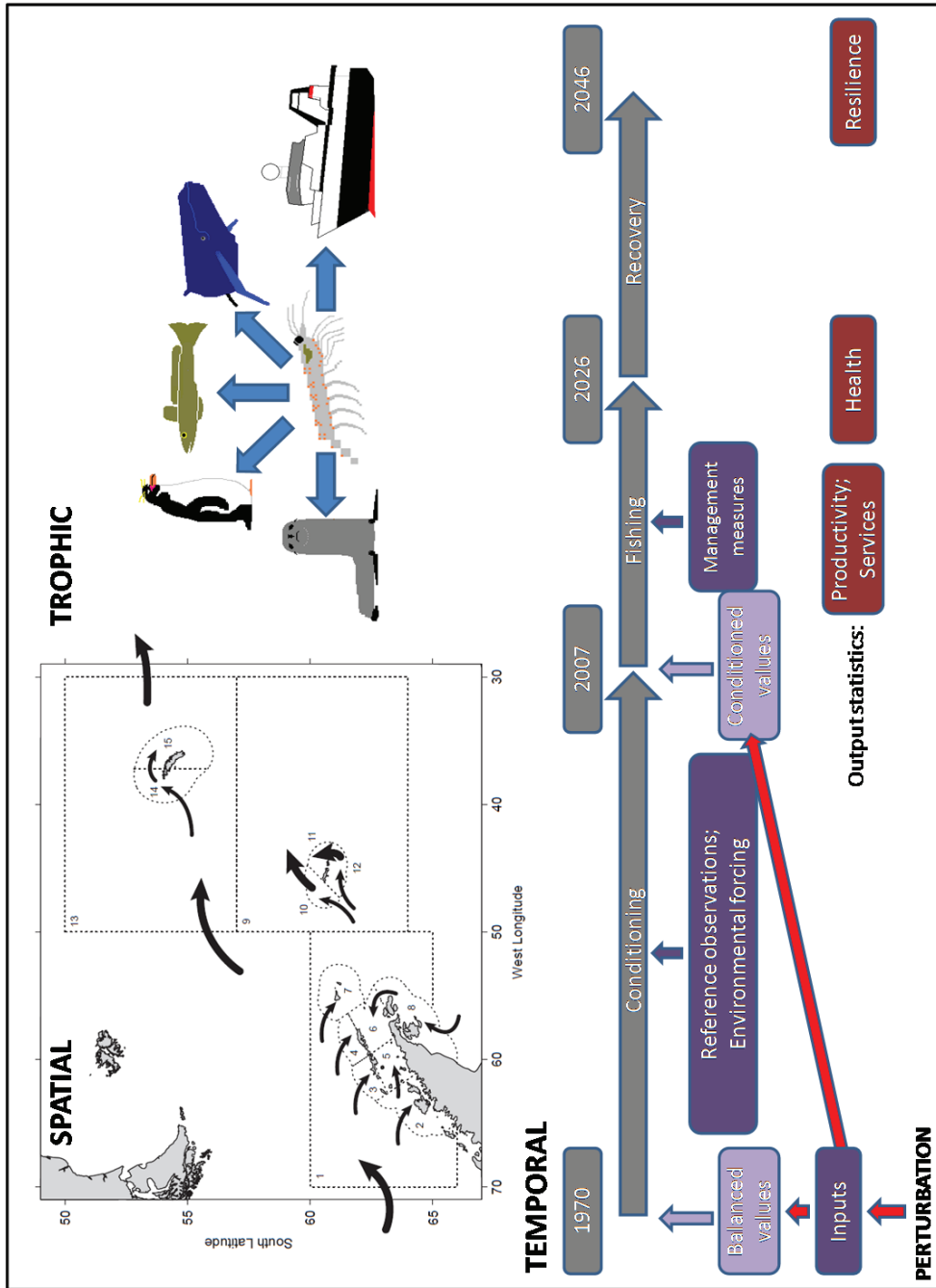


Figure 1: Structure of the ecosystem dynamics model described in Watters et al. (2013) and analysed here. The model is divided into 15 spatial units known as small-scale management units. Krill is transported between these units and the surrounding boundary areas in the movement case (black arrows). Within each unit, krill is fed upon by up to four predator groups and may be harvested by the fishery (blue arrows). Simulations were run in three phases representing the period 1970–2046 (grey arrows). Fishing occurred only during the 20-year fishing phase and was conducted according to a management measure consisting of a catch limit and a catch allocation option. In the current study, perturbations were applied to input values. Some of these values were altered during the balancing and initialisation stage. Output statistics describe conditions either during the fishing phase, at the end of the fishing phase, or at the end of the recovery phase.

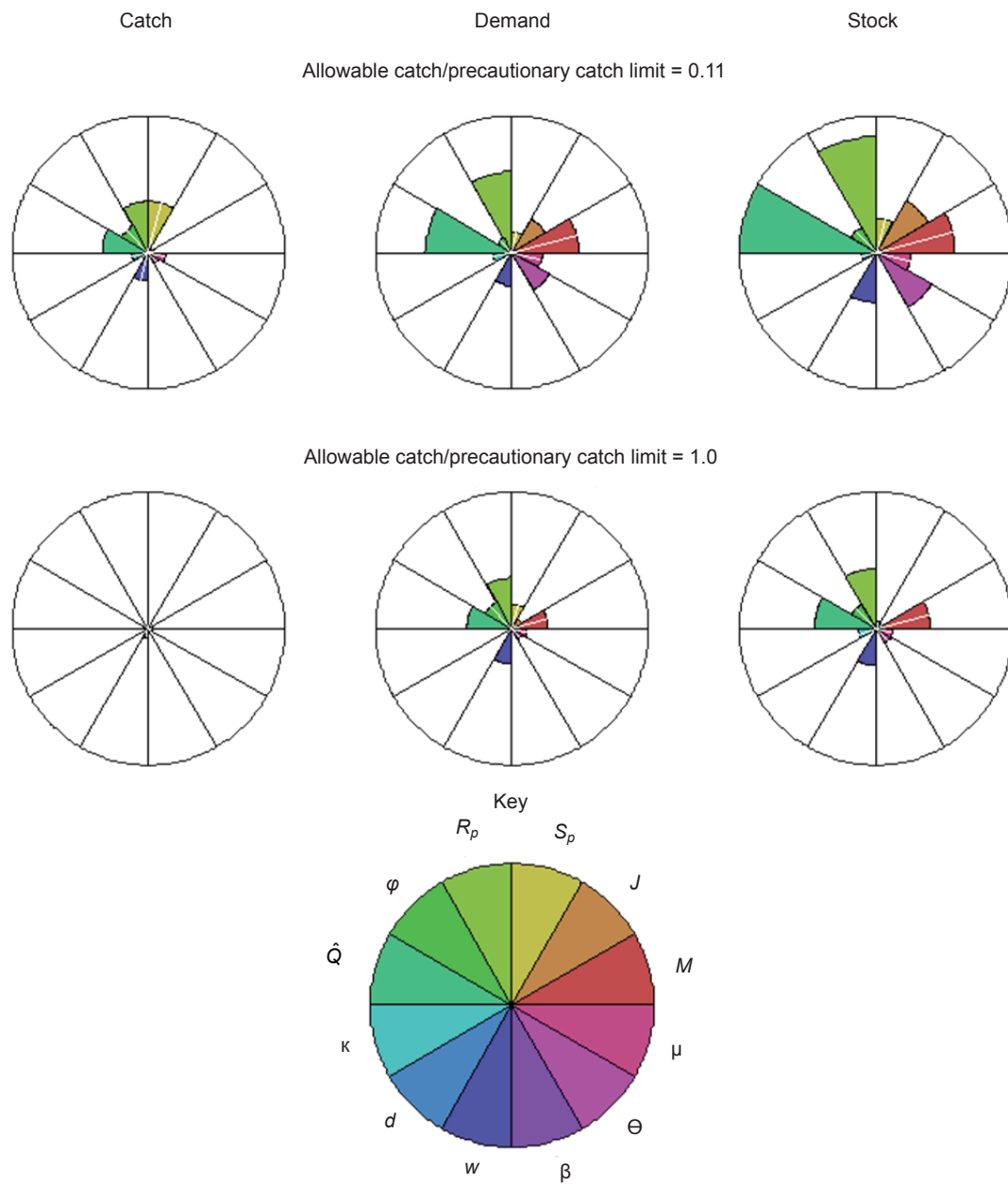


Figure 2: Wheel plots showing the response of the services output statistic to 1% perturbations to inputs. Each sector represents the response to a perturbation affecting the parameter indicated in the key. The filled fraction of the sector indicates the magnitude of the response, scaled to a maximum of 0.0029 (meaning that a 1% perturbation to the input changed the estimated risk by 0.29%) when the whole sector is coloured. A white line through a sector indicates a negative response and no line indicates a positive response. Plots are arranged in columns by catch allocation option and rows by allowable catch.

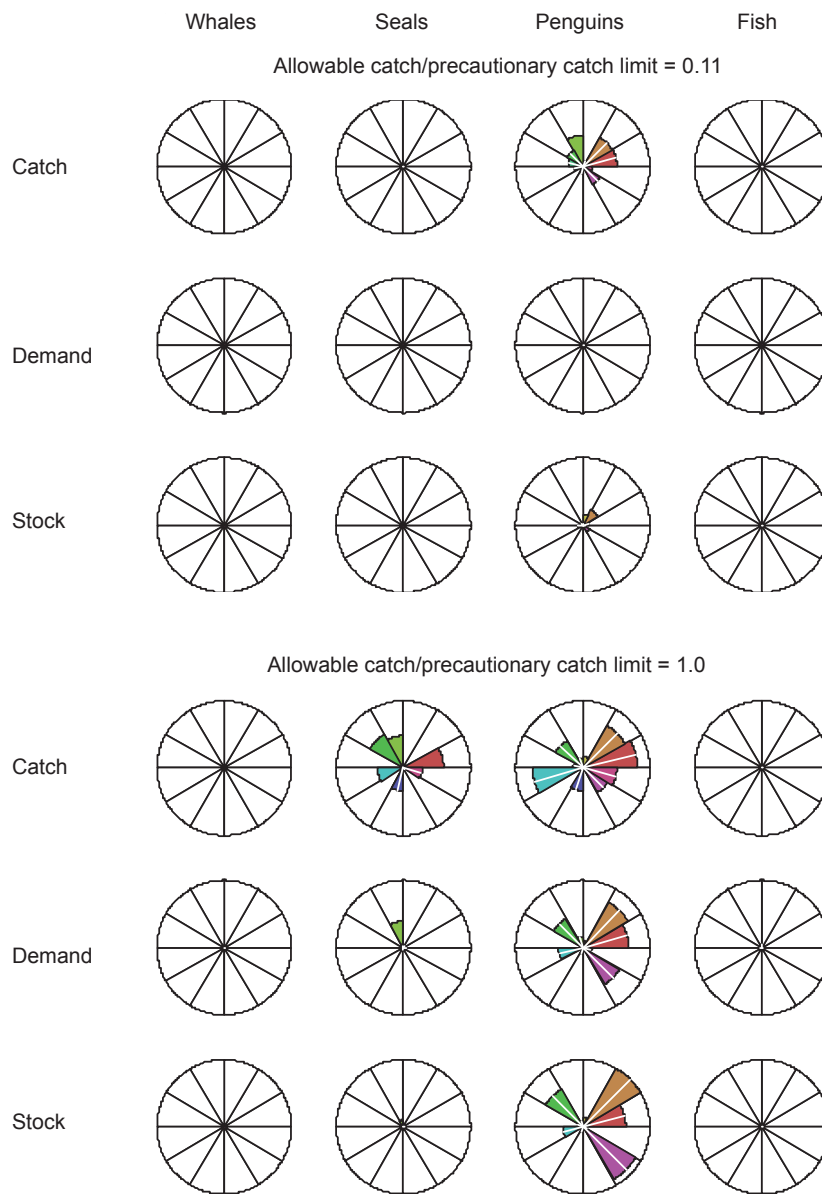


Figure 3: The response of the health output statistic to 1% perturbations to inputs (see Figure 2 for key and further explanation). Values are scaled to a maximum of 0.1642. Plots are arranged in columns by predator taxon and rows by allowable catch and catch allocation option. A white line through a sector indicates a negative response and no line indicates a positive response.

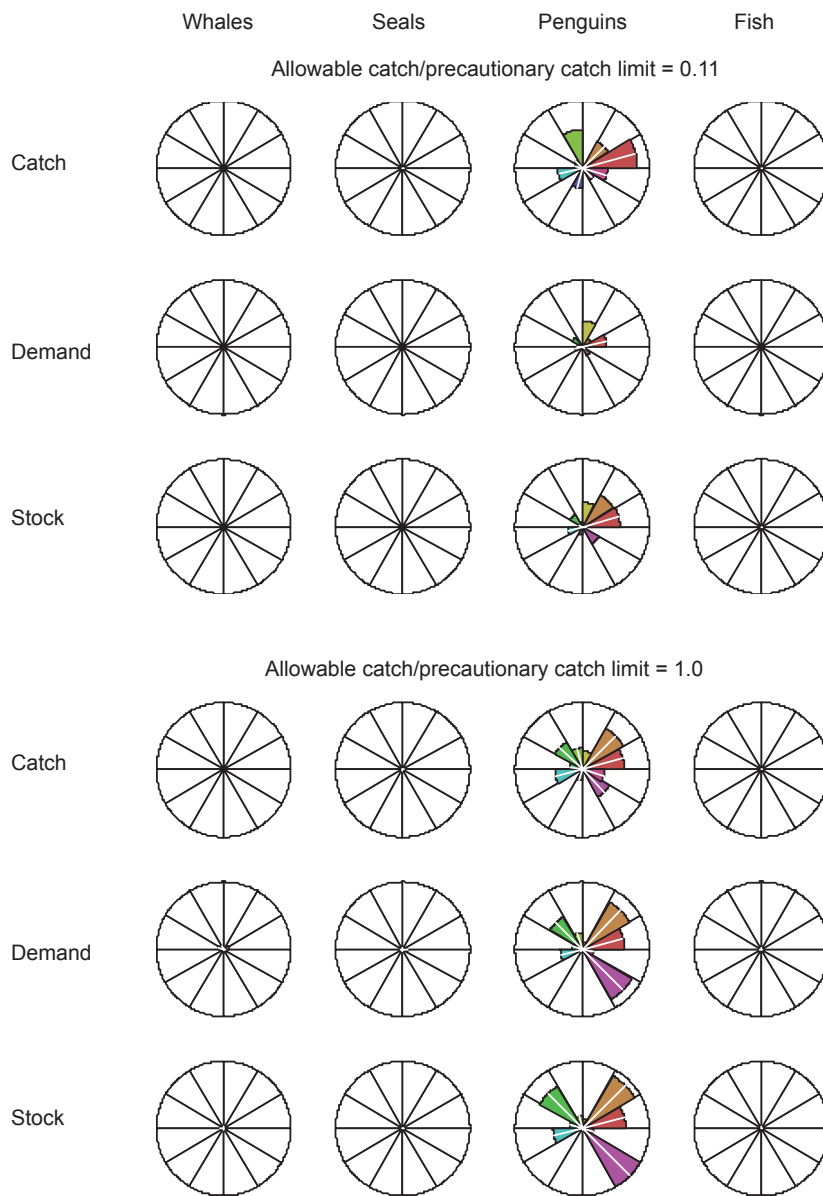


Figure 4: The response of the resilience output statistic to 1% perturbations to inputs (see Figure 2 for key). Values are scaled to a maximum of 0.1571. A white line through a sector indicates a negative response and no line indicates a positive response.

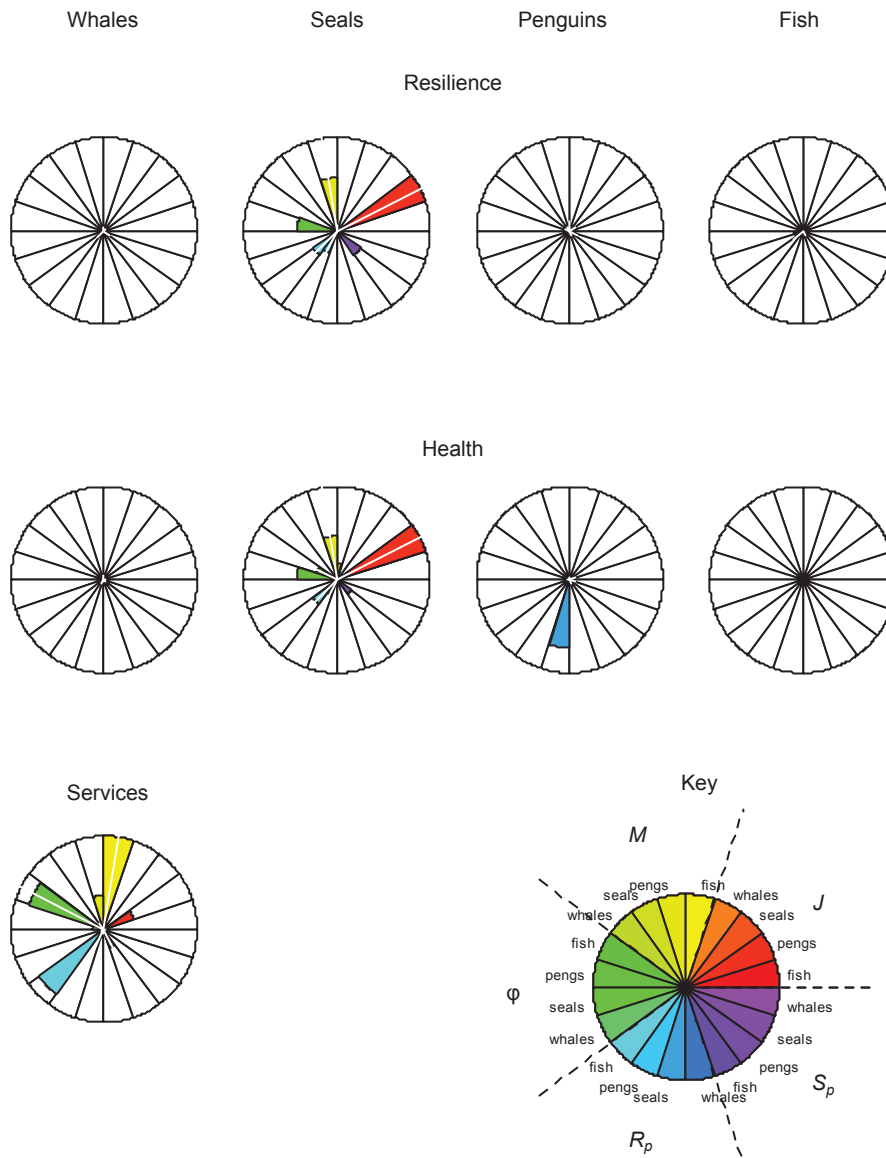


Figure 5: The response of the resilience, health and services output statistics to 1% perturbations to inputs affecting predator-specific parameters, for allocation option 2 with allowable catch = precautionary catch limit. Values are scaled within output statistics to maxima of 0.1316 (health), 0.1291 (resilience) and 0.0007 (services). A white line through a sector indicates a negative response and no line indicates a positive response.

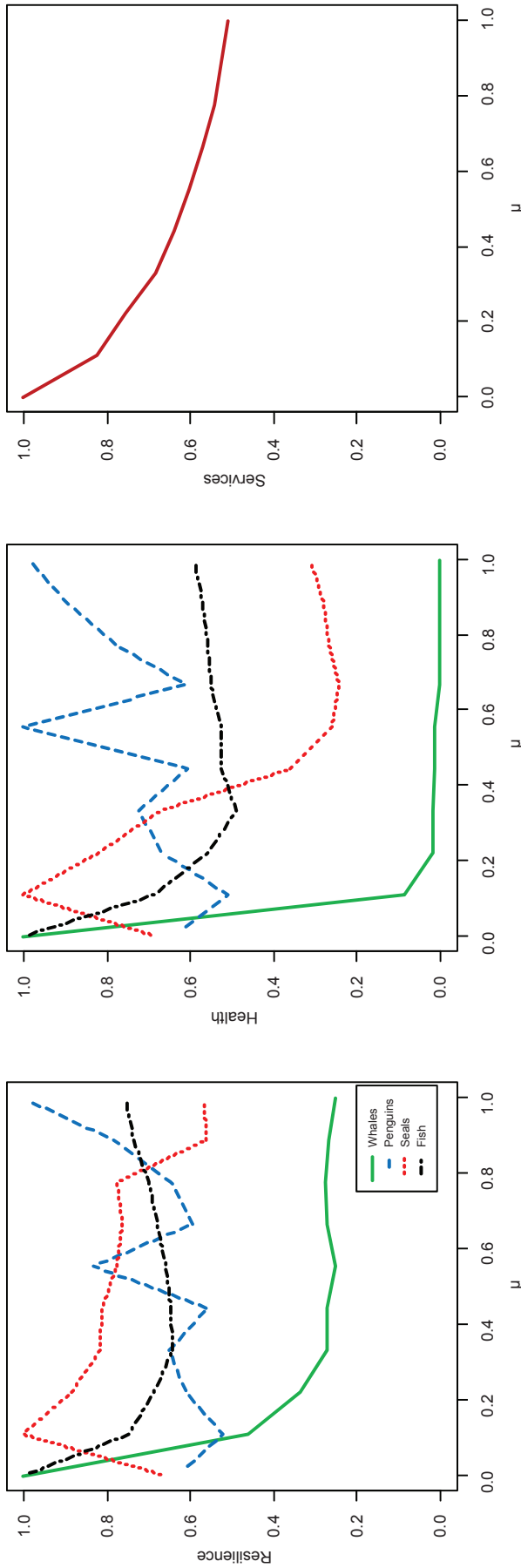


Figure 6: The response of the resilience, health and services output statistics to changes in inputs affecting the parameter μ , controlling the degree of krill movement between SSMUs. All values are risk relative to the maximum risk for that line.

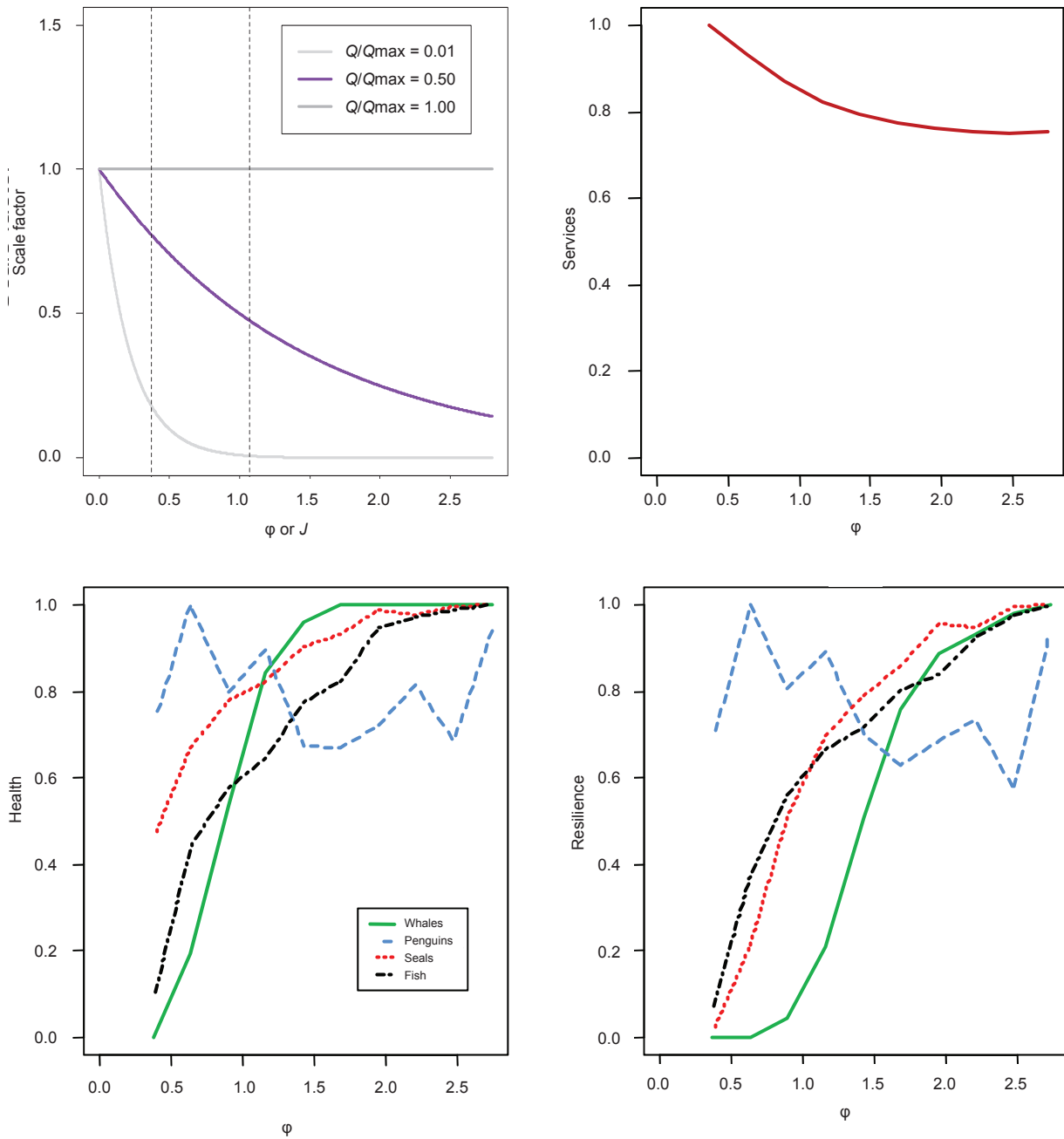


Figure 7: The response of the resilience, health and services output statistics to changes in inputs affecting the parameter ϕ , controlling the shape of the relationship between prey consumption and the proportion of adults that breed. All values are risk relative to the maximum risk for that line. The first panel shows how the parameters ϕ and J work in the model to scale predator demographic groups (the proportion of adults that breed and the proportion of potential recruits that survive) to foraging success (Q/Q_{max} , meaning realised prey consumption as a proportion of maximum potential prey consumption). The vertical reference lines show the minimum value considered in perturbations of ϕ (0.37) and the maximum value considered in perturbations of J (1.07) (Figure 8).

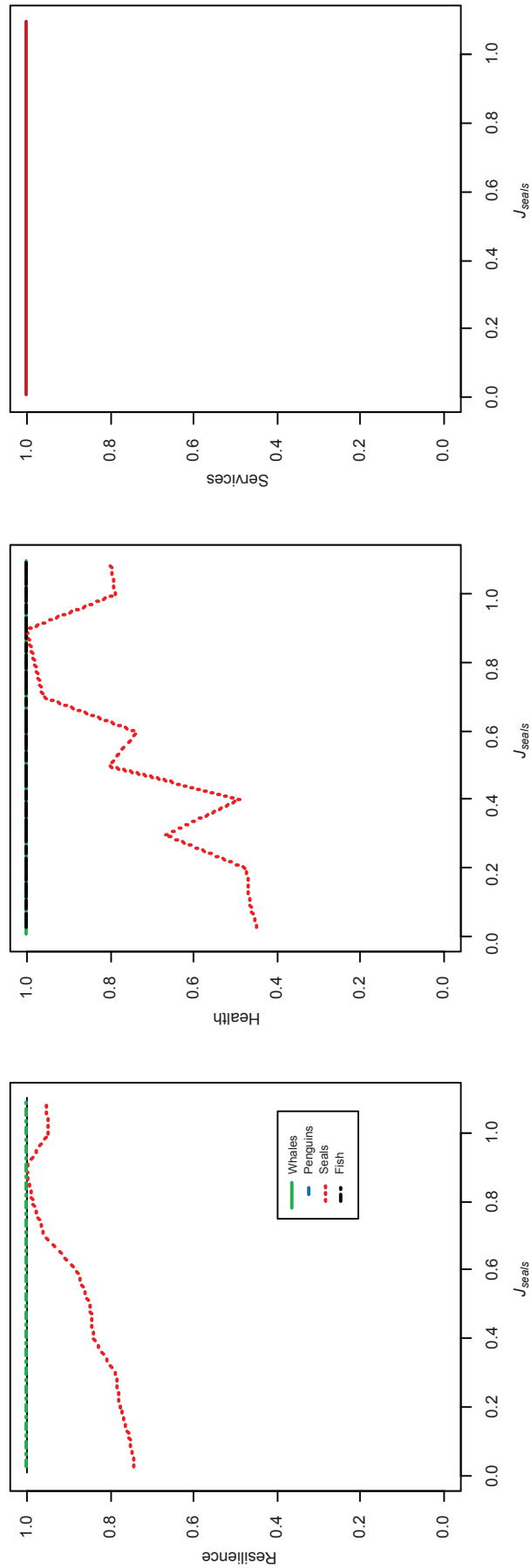


Figure 8: The response of the resilience, health and services output statistics to changes in the parameter, J_{seals} , controlling the shape of the relationship between pre-recruit foraging success and pre-recruit mortality for seals. All values are risk relative to the maximum risk for that line. The first panel in Figure 7 shows the effect of J in the model.