

## POSSIBLE EFFECTS OF DIFFERENT LEVELS OF KRILL FISHING ON PREDATORS - SOME INITIAL MODELLING ATTEMPTS

D. S. Butterworth

Department of Applied Mathematics, University of Cape Town  
Rondebosch 7700, South Africa

R.B. Thomson

Department of Zoology, University of Cape Town  
Rondebosch 7700, South Africa

### Abstract

An initial attempt is made to develop the modelling framework suggested by the Joint Meeting of CCAMLR's Working Group on Krill (WG-Krill) and Working Group for the CCAMLR Ecosystem Monitoring Program (WG-CEMP) in 1992, in order to investigate the possible effects of krill fishing on krill predators. First, estimates are made of the parameters of predator survival rates as functions of krill abundance, by considering a krill dynamics model incorporating recruitment fluctuations together with preliminary information on adult survival and breeding success patterns for certain krill predator species. A 'one-way' interaction model is developed, in which krill abundance fluctuations impact on the predator population, but not *vice versa*. Computations based on this model indicate that variability in the annual recruitment of krill results in predator populations being less resilient to krill harvesting than deterministic evaluations would suggest. The analyses have also facilitated discussion on the interpretation of the preliminary estimates of adult survival rate provided for some krill predator populations, and on the possibility of biases in their estimation. These matters will need to be taken into account in future developments of this approach, before the latter can claim sufficient realism to provide a possible basis for management recommendations. A mathematical framework for a 'two-way' interaction model (including also the effect of differing predator consumption levels on krill) is developed, but computations based on this approach are deferred pending further development of the 'one-way' analyses.

### Résumé

Afin d'examiner les effets possibles de la pêche de krill sur les prédateurs, les auteurs tentent d'établir une première structure de base de la modélisation, comme cela avait été suggéré pendant la réunion conjointe du Groupe de travail sur le krill (WG-Krill) de la CCAMLR et du Groupe de travail chargé du Programme de contrôle de l'écosystème de la CCAMLR (WG-CEMP) en 1992. Tout d'abord, les auteurs procèdent à des estimations des paramètres des taux de survie des prédateurs en fonction de l'abondance de krill, en considérant un modèle de la dynamique de krill incorporant les fluctuations du recrutement dans les informations préliminaires sur la survie des adultes et les tendances de la réussite de la reproduction pour certaines espèces prédatrices de krill. Ils créent un modèle d'interaction 'à sens unique' dans lequel les fluctuations de l'abondance du krill ont un effet sur la population prédatrice mais pas *vice versa*. Selon les calculs fondés sur ce modèle, la variabilité du recrutement annuel de krill rend les populations prédatrices plus sensibles à l'exploitation du krill que ne le laissent entendre les évaluations déterministes. Les analyses ont également facilité la discussion des estimations préliminaires du taux de survie des adultes de certaines populations prédatrices de krill et la possibilité qu'elles soient biaisées. A l'avenir, il conviendra de tenir compte de ces facteurs dans les décisions concernant cette approche afin que celle-ci soit suffisamment réaliste pour pouvoir servir de base à des avis de gestion. Une structure mathématique de modèle d'interaction 'à double sens' (couvrant également l'effet de divers niveaux de consommation des prédateurs sur le krill) est mise au point, mais les calculs reposant sur cette approche sont reportés, en attendant l'avancement des analyses 'à sens unique'.

### Резюме

В целях изучения возможных последствий промысла криля для питающихся крилем хищников в настоящей работе делается первая попытка разработать параметры модели, предложенной на совместном совещании Рабочей группы по

крилю (WG-Krill) и Рабочей группы по Программе АНТКОМа по мониторингу экосистемы (WG-CEMP), проходившем в 1992 г. Во-первых, были получены оценки уровней выживания хищников как функции численности криля путем рассмотрения модели динамики криля, в которой учтены величины колебания пополнения совместно с предварительной информацией о выживаемости взрослых особей и эффективности воспроизводства у ряда питающихся крилем хищников. Разработана 'однонаправленная' модель взаимодействия, в которой колебания в численности криля влияют на популяции хищников, а обратные взаимодействия отсутствуют. Результаты основанных на этой модели расчетов указывают на то, что изменчивость в ежегодном пополнении криля обозначает, что популяции хищников являются менее устойчивыми по отношению к промыслу криля, чем предполагают детерминистические оценки. Кроме этого, результаты анализов способствовали рассмотрению вопроса об интерпретации предварительных оценок уровня выживания взрослых особей в ряде популяций питающихся крилем хищников, а также вопроса о возможности возникновения смещений в этих оценках. Эти вопросы должны быть приняты во внимание при дальнейшей работе над данным подходом до того, как он будет считаться достаточно реалистичным для принятия его за основу при разработке рекомендаций по управлению промыслом. Разработана математическая структура 'двусторонней' модели взаимодействия (включая также воздействие на криль различных уровней потребления криля хищниками), однако проведение основанных на этом подходе расчетов было отложено до дальнейшей разработки 'однонаправленных' анализов.

#### Resumen

Se intenta crear la estructura preliminar del modelado propuesta por la reunión conjunta de los Grupos de Trabajo de la CCRVMA relacionados con el Kril (WG-Krill) y con el Programa de Seguimiento del Ecosistema (WG-CEMP) en 1992, para investigar los posibles efectos de la pesca de kril en los depredadores de este recurso. Para empezar, se estiman los parámetros de los índices de supervivencia de los depredadores en función de la abundancia de kril, tomando en cuenta un modelo de la dinámica de poblaciones de kril que incluye fluctuaciones del reclutamiento junto con información preliminar sobre la supervivencia adulta y las características del éxito de la reproducción de ciertas especies depredadoras de kril. Se crea un modelo de interacción 'unidireccional', en el cual las fluctuaciones de la abundancia de kril tienen efecto en la población depredadora, pero no *vice versa*. Los cálculos basados en este modelo indican que la variabilidad del reclutamiento anual de kril tiene como resultado el que las poblaciones de depredadores son más vulnerables a la explotación de kril que lo sugerido por evaluaciones determinísticas. Los análisis han facilitado también la discusión sobre la interpretación de los cálculos preliminares de los índices de supervivencia adulta proporcionados para algunas poblaciones de depredadores de kril, y sobre la posibilidad de desviaciones en los cálculos. Estos asuntos deberán ser tomados en cuenta en el futuro desarrollo de este enfoque, a fin de que éste sea suficientemente realista como para servir de posible base a recomendaciones de ordenación. Se crea la estructura matemática para un modelo de interacción 'bi-direccional' (que incluye también el efecto que diferentes niveles de consumo de kril por el depredador tienen sobre el kril), pero los cálculos basados en este enfoque se han postergado hasta el futuro desarrollo de los análisis 'uni-direccionales'.

Keywords: predator, krill, fishing, modelling, CCAMLR

#### INTRODUCTION

This paper constitutes an initial attempt to take forward the suggestions made by the Joint Meeting of CCAMLR's Working Group on Krill (WG-Krill) and Working Group for the CCAMLR Ecosystem Monitoring Program (WG-CEMP) in 1992 (SC-CAMLR, 1992) with regard to evaluation of the extent to which different levels of krill fishing may affect krill predators.

The underlying concepts may be explained by reference to Figure 1, which shows the distribution of krill biomass under various levels of fishing intensity as indicated by the value of the parameter  $\gamma$ . The biomass follows a distribution, rather than remaining fixed at a single value as in deterministic models, because of the variability in the annual recruitment to the krill population. The solid curve depicts the situation in the absence of krill fishing. Once

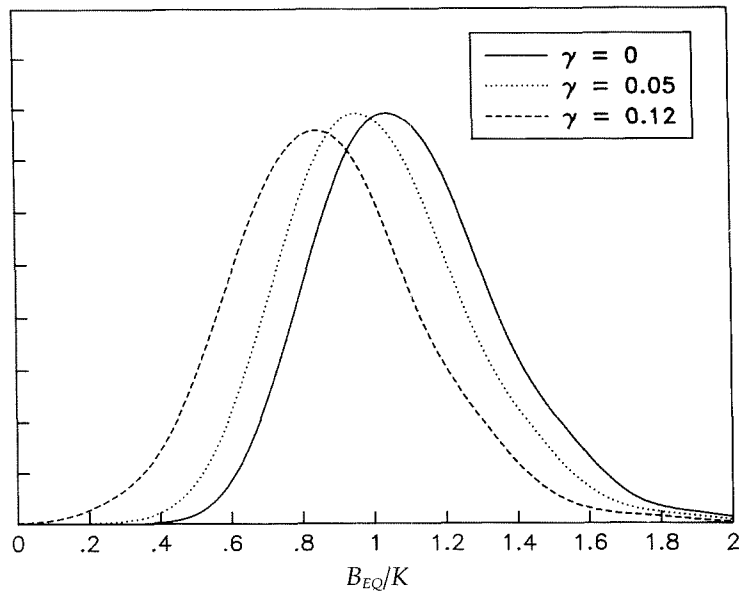


Figure 1: The distribution of krill biomass under various levels of krill harvesting intensity, as indicated by the value of the parameter  $\gamma$  (see sub-section 'Deterministic Evaluations of the Effect of Fishing' for a definition of  $\gamma$ ). The solid curve ( $\gamma = 0$ ) reflects an absence of any krill fishing, and  $K$  is the median 1+ krill biomass in those circumstances.  $B_{EQ}$  indicates an 'equilibrium' 1+ biomass value, i.e. one realised after any transient effects from the commencement of fishing at an intensity  $\gamma$  have disappeared. The results shown were calculated using the summer (December to February) fishing season variant of Model 2 of Butterworth *et al.* (1994).

fishing for krill occurs, this distribution shifts to the left and broadens. The heavier the level of fishing, the greater are both the shift and the widening.

The survival rates and breeding success of krill predators must depend, to some extent at least, on the level of krill biomass. Both will tend to be good at high biomass levels, and poor at low levels, as indicated by appropriate functional relationships. Thus, as krill fishing levels increase and the (average) krill biomass level drops, the ratio of good to poor years for krill predators will decrease. The aim of subsequent modelling is to attempt to link the estimated size of this decrease to the size of the resultant drop in predator numbers.

The first section of the paper describes how preliminary information received from members of WG-CEMP on predator dynamics has been used to fix parameters of the functional relationships assumed between juvenile and adult predator annual survival rates, and krill abundance.

Next, a 'one-way' interaction model is developed, in which the effect of fishing on krill

influences krill abundance and thereby impacts on the predator population, but the reverse effect of different levels of loss of krill to natural mortality because of changing predator numbers is ignored. The approach adopted is to consider first the predictions of this model for deterministic krill dynamics (i.e., no noise about the krill stock-recruitment relationship), and then to examine the manner in which the introduction of recruitment variability for krill modifies these results.

A basis for extending this approach simply to a 'two-way' interaction model, which takes explicit account of the effects of consumption by the predator on the krill population dynamics, is then put forward. Finally, some concluding remarks, which include suggestions for further research on this topic, are made.

#### THE RELATIONSHIPS BETWEEN PREDATOR SURVIVAL RATES AND KRILL ABUNDANCE

SC-CAMLR (1992) suggested that initial modelling attempts make use of the functional forms, illustrated in Figure 2, for the relationship

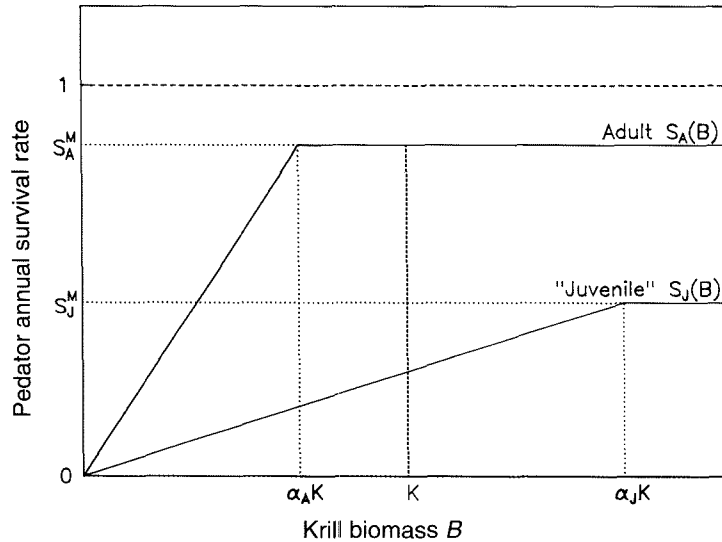


Figure 2: The relationships assumed between annual predator survival rates and krill abundance, taken here to be the krill biomass ( $B$ ). The median krill biomass in the absence of exploitation is indicated by  $K$ . The juvenile (first year) 'survival rate' incorporates the effects of (changing) pregnancy rate as well as the higher-than-average natural mortality rate early in life.

between predator survival rates and krill abundance. These relationships are:

$$S_{A/J}(B) = \begin{cases} B/[\alpha_{A/J}K] S_{A/J}^M & \text{for } B \leq \alpha_{A/J}K \\ S_{A/J}^M & \text{for } B > \alpha_{A/J}K \end{cases} \quad (1)$$

where  $S_{A/J}$  is the annual adult ( $A$ ) or 'juvenile' ( $J$ ) predator survival rate;  
 $S_{A/J}^M$  is the maximum value of this survival rate; and  
 $B$  is the krill biomass, with  $K$  its median value in the absence of exploitation.

Note that the 'juvenile survival rate' incorporates the effects of pregnancy rate (see equation (3) following).

WG-CEMP has circulated a tabulation of information on the population dynamics of a number of krill predators (CCAMLR, 1993), much of which is incorporated in Tables 1 and 2. (It must be stressed that the estimates given in CCAMLR (1993) are preliminary, and do not necessarily reflect finalised analyses of the data concerned. The intent was to make parameter values available which were thought to be typical of those for various predators of Antarctic krill, in order to allow for illustrative calculations of model behaviour.) This tabulation lists the

proportion of years which were 'good', 'poor' or 'bad' for each predator, to be interpreted respectively as follow: years in which both adult survival and breeding success are high, those where adult survival is high but breeding success poor, and those in which both adult survival and breeding success are poor.

This information has been translated into estimates of the parameters  $\alpha_j$  and  $\alpha_A$  of the relationships shown in Figure 2. In the absence of exploitation, the annual krill biomass is distributed about its median value ( $K$ ) - see the solid curve in Figure 1. If  $p$  is the proportion of years in which adult survival is poor (i.e., the 'bad' years), then  $\alpha_A$  is chosen so that the krill biomass drops below the level  $\alpha_A K$  in this same proportion  $p$  of the years when there is no krill fishing. Similarly, the krill biomass drops below the level  $\alpha_j K$  in a proportion  $q$  of the years, where  $q$  is the proportion of years in which breeding success is poor (i.e., both the 'poor' and the 'bad' years).

Krill biomass projections based upon Model 2 of Butterworth *et al.* (1994) were used to evaluate these proportions and hence estimate the parameters  $\alpha_A$  and  $\alpha_j$ . However, this model includes two components of variability: first, annual fluctuations in krill recruitment; and secondly, uncertainty about appropriate values for some of the parameters. To render the effects at work in the analysis of this paper more

Table 1: Preliminary information provided on proportions of years which are poor for adult predator survival and for predator breeding success (from CCAMLR, 1993 as modified in SC-CAMLR, 1993a for the Antarctic fur seal), with consequent estimates of the parameters  $\alpha_A$  and  $\alpha_j$  in the relationships of equation (1) between predator survival rate and krill abundance.

Predator	Poor Adult Survival		Poor Breeding Success	
	Proportion of 'Bad' Years, $p$	$\alpha_A$	Proportion of 'Bad' and 'Poor' Years, $q$	$\alpha_j$
Adélie penguin	0.38	0.936	0.69	1.157
Antarctic fur seal*	0.22	0.846	0.67	1.143
Crabeater seal	0.23	0.852	0.64	1.130
Black-browed albatross**	0.33	0.898	0.64	1.130

\* Average of three sets of proportions given in SC-CAMLR (1993a - paragraph 7.28)

\*\* Average of two sets of proportions given in CCAMLR (1993)

Table 2: Values used for age-at-first-reproduction and maximum adult annual survival rate of the various predators considered. (Developed from the preliminary estimates provided in CCAMLR (1993) as explained in the text, where explanations of the figures in parentheses are also given. An error in the original version of this paper regarding the age-at-first-reproduction for the Antarctic fur seal, as pointed out in SC-CAMLR (1993a - paragraph 7.24) has now been corrected.)

Predator	Age-at-First-Reproduction $T$ (yr)	Maximum Adult Survival Rate $S_A^M$ (yr <sup>-1</sup> )
Adélie penguin	4	0.65 (0.78)
Antarctic fur seal	4	0.79 (0.88)
Crabeater seal	5	0.93
Black-browed albatross	10	0.934

transparent, it seems preferable to restrict consideration at this early stage to the first of these components only. Hence, the parameter values for the krill dynamics were set to the mid-points of the ranges specified by the Third Meeting of the Working Group on Krill (SC-CAMLR, 1991), viz:

$$\left. \begin{aligned} M &= 0.7 \text{ yr}^{-1} && \text{(natural mortality rate)} \\ \sigma_R &= 0.5 && \text{(recruitment variability measure} \\ &&& \text{= CV, approximately)} \\ \ell_r^{50} &= 40 \text{ mm} && \text{(length at 50\% recruitment)} \\ \ell_m^{50} &= 37 \text{ mm} && \text{(length at 50\% maturity)} \end{aligned} \right\} \quad (2)$$

The krill biomass ( $B$ ) was taken to be the biomass of age classes 1 and above (i.e., the '1 + biomass') at the 'start' of the year (i.e., 1 November, see Butterworth *et al.*, 1994).

The values of the proportions given in CCAMLR (1993) for each predator, and the consequent estimates of  $\alpha_A$  and  $\alpha_j$ , are listed in Table 1. (For the Antarctic fur seal, the values originally provided (and used in an earlier

version of this paper) have now been modified as indicated in paragraph 7.28 of SC-CAMLR, 1993a.) The matter of choosing values for parameters  $S_A^M$  and  $S_j^M$  will be discussed in the following section.

#### ONE-WAY INTERACTION: PREDATORS AFFECTED BY KRILL ABUNDANCE

##### Methods

##### The Basic Model

Only the female, reproductively mature, component of the predator population is modelled. The population dynamics equation is:

$$N_{y+1} = \begin{cases} N_y S_A(B_y) + N_{y-T+1} S_j(B_{y-T+1}) \\ * \left[ \prod_{y'=y-T+2}^y S_A(B_{y'}) \right] [1 - \beta N_{y-T+1} / K_p] \\ N_y S_A(B_y) & \text{if } N_{y-T+1} / K_p > 1 / \beta \end{cases} \quad (3)$$

where  $N_y$  is the number of female predators capable of reproduction at the start of year  $y$ ;  
 $K_p$  is the number of such female predators at deterministic equilibrium in the absence of fishing on krill;  
 $\beta$  is a parameter set so that  $N = K_p$  at that equilibrium;  
 $T$  is the age at which a female predator can first reproduce; and  
 $S_{A|f}(B)$  are as defined by equation (1).

Note that  $T$  is taken to be the same for each female predator in the population. For seals,  $T$  represents the age-at-first-parturition (sexual maturity plus a gestation period of essentially one year), while for birds it is the age at first laying.

The values of  $T$  were taken from the central estimates provided by CCAMLR (1993), which were rounded to the nearest appropriate integer. These values are listed in Table 2, which also shows values for the maximum adult survival ( $S_A^M$ ). This rate is taken (in the first instance) to be equal to the estimate of mean adult survival rate provided by CCAMLR (1993) (but see further discussion at the end of this sub-section).

The final component of the rightmost term of equation (3) requires explanation. This is most easily effected by considering the deterministic situation of a value for the krill biomass ( $B$ ) which is fixed in time (this is allowed in the context of this simple model, as the assumption is being made that consumption of krill by the predator has a negligible effect on the krill population, so that krill abundance can remain unchanged as predator numbers increase or decline). In these circumstances, were this final component of the equations to be omitted, predator equilibrium would be possible for a single value of  $B$  only. Higher or lower values of  $B$  would lead respectively (ignoring initial transients) to unlimited geometric growth or decline. The final component is an *ad hoc* fix, to allow for equilibrium across a continuum of values of  $B$ , as is necessary to allow the effect of krill fishing on the predator to be examined. This component can be thought of as a combination of a number of effects which would contribute to limiting the size of the predator population: high predator abundances would impact on the krill population to lessen growth rates, and other density-dependent mechanisms such as space-limitation would also play some role.

As is evident from the form of equation (3),  $S_f$  incorporates pregnancy rate, and the final component of the equation is taken to pertain to the first year of the predator's life, because space-limitation at breeding colonies (for example) would most likely lead to impacts at that life-stage.

Two parameters of equations (1) and (3) remain to be specified:  $\beta$  and  $S_f^M$ . Given  $S_f^M$ ,  $\beta$  is readily deduced from the condition that  $N = K_p$  at (deterministic) unexploited equilibrium, which yields:

$$\beta = 1 - [1 - S_A(K)] / [S_f(K) S_A(K)^{T-1}] \quad (4)$$

Now, given the values of  $p$  and  $q$  in Table 1, for the cases considered here:

$$\left. \begin{aligned} S_A(K) &= S_A^M && \text{(because all } p < 0.5) \\ S_f(K) &= S_f^M / \alpha_f && \text{(because all } q > 0.5) \end{aligned} \right\} \quad (5)$$

Since sensibly (given the form of equation (3))  $\beta > 0$ , a lower bound for  $S_f^M$  follows:

$$S_f^M > \alpha_f (1 - S_A^M) / (S_A^M)^{T-1} \quad (6)$$

This reflects the requirement that additions to the adult female population must, under optimal conditions, be capable of more than balancing the losses to natural mortality.

In setting an upper bound for  $S_f^M$ , account must be taken of the fact that this incorporates the effects of annual pregnancy rate ( $\rho$ ) (laying rate in the case of birds), and that only the female component of the population is modelled. Assuming a 50:50 sex ratio at birth, and making the further plausible assumption that the true first-year survival rate is less than the maximum annual adult rate  $S_A^M$ , leads to the bound:

$$S_f^M < 0.5 \rho^M S_A^M \quad (7)$$

where  $\rho^M$  is the maximum possible annual 'pregnancy' rate.

(The fact that true survival rates cannot exceed 1 leads to the weaker bound:  $S_f^M < 0.5 \rho^M$ .)

Table 3 lists values assumed for  $\rho^M$  for the predators considered, and the lower and upper

Table 3: The maximum pregnancy rates assumed for each of the predators considered, together with the bounds for the maximum 'juvenile survival rate' ( $S_j^M$ ) provided by inequalities (6) and (7). The values used for  $S_j^M$  in this paper are chosen to be roughly midway between these two bounds, where this is possible. For the first two species listed, the choice is instead midway between the figures in parenthesis, for reasons detailed in the text.

Predator	Maximum 'Pregnancy' Rate $\rho^M$ ( $\text{yr}^{-1}$ )	$S_j^M$ ( $\text{yr}^{-1}$ )		
		Lower Bound:	Upper Bound:	Value Used
Adélie penguin	2	1.47 (0.54)	0.65 (0.78)	0.65
Antarctic fur seal	1	0.67 (0.23)	0.40 (0.44)	0.35
Crabeater seal	1	0.11	0.47	0.3
Black-browed albatross	1	0.14	0.47	0.3

bounds for  $S_j^M$  provided by inequalities (6) and (7). It was originally planned that, in the interests of brevity, this paper consider only a single value for  $S_j^M$  for each predator, which was to be the value midway between these two bounds. However, this procedure leads to an immediate problem for the Adélie penguin and the Antarctic fur seal: no  $S_j^M$  choice is possible, because the lower bound exceeds the upper bound in both these cases! Such a situation is not feasible: reproduction would be unable to offset losses to natural mortality, and the population would not persist. One reason for this apparent inconsistency is that the mean adult survival rate estimates provided by CCAMLR (1993) do not pertain to conditions optimal for adult survival, but rather to an average over a number of years of varying conditions (see SC-CAMLR, 1993a - paragraphs 7.17 to 7.20). Another is that the estimate for the Adélie penguin is known to be negatively biased due to band loss and is possibly further influenced by band-induced mortality (Trivelpiece, pers. comm.). In the interests of taking the illustrative calculations of this paper further for these two species, the associated values for  $S_A^M$  have been increased somewhat arbitrarily, as indicated by the figures in parenthesis in Table 2. The corresponding entries in parentheses in Table 3 then admit a choice for  $S_j^M$  at a level intermediate between the associated revised bounds.

#### Deterministic Evaluations of the Effect of Fishing

The calculations carried out here assume a summer fishing season (December to February),

together with Model 2 of Butterworth *et al.* (1994) and the parameter values of equation (2). Those authors use a parameter  $\gamma$  to reflect the intensity of krill fishing, where  $\gamma$  is the multiple of a single pre-exploitation biomass survey estimate of krill which fixes the constant annual catch to be taken in subsequent years. As  $\gamma$  is increased, the median value of the (1+) krill biomass drops. This median value is taken to be representative of  $B$  for the purpose of the deterministic evaluations. The extent to which the predator population declines under various levels of krill fishing ( $\gamma$ ) can then be calculated by considering the equilibrium solution of equation (3) for the corresponding values of  $B$ :

$$N / K_p = (1 / \beta) \left[ 1 - \{1 - S_A(B)\} / \{S_j(B) S_A(B)^{T-1}\} \right] \quad (8)$$

Transient dynamics, which reflect how quickly the predators respond to changed levels of krill harvesting, are readily calculated by direct application of equation (3).

#### Incorporating Krill Recruitment Variability

When krill recruitment varies from year to year, krill biomass ( $B_y$ ) is no longer steady (even for fixed  $\gamma$ ), but fluctuates over time. This means that  $S_A$  and  $S_j$  also fluctuate over time, as determined by equation (1).

To investigate the consequences of different fixed-catch harvesting strategies for krill (i.e., fixed values of  $\gamma$ ) on predators, 100 time series of  $B_y$  values were generated for each  $\gamma$  considered, using the krill dynamics model specified in the preceding sub-section. Each series was 200 years

in length. These series were used to provide the  $B_y$  values for 100 projections of the predator population, each of 200 years duration, using equation (3). The distribution of  $N/K_p$  in year 200 then provides the stochastic analog of equation (8) for the effect of krill fishing on the predator population. The reason for the long projection period is to attempt to eliminate transient effects, as these can die out rather slowly for species such as albatross which have high adult survival rates and long times to first reproduction. Thus, the assumption being made is that the distribution of  $N/K_p$  will have stabilised after 200 years.

To examine transient effects, the predator population was set at its median level in the absence of krill fishing, in the first (and all preceding) years. This initial state was then repeatedly projected forward in time to allow comparison of the distribution of biomass over time with its deterministic analog, for a number of different values of  $\gamma$ .

## Results

Figure 3(i) compares plots of predator abundance (expressed as  $N/K_p$ ) against krill harvesting intensity (reflected by  $\gamma$ ) for each of the four predator species considered for the deterministic model, as evaluated by means of equation (8). The initial derivative discontinuity in each plot corresponds to the krill biomass dropping below the level at which the predator adult survival rate begins to fall. Comparative results when krill recruitment variability is taken into account (the 'stochastic' model) are shown in Figure 3(ii) for the medians of the distributions of  $N$  after 200 years of a constant annual catch of krill (this catch is reduced in a particular year if an upper bound of  $1.5 \text{ yr}^{-1}$  on the effective annual fishing mortality for fully selected age-classes would be exceeded - see Butterworth *et al.* (1994)). Note that the stochastic results are normalised to their median value after 200 years in the absence of krill harvesting ( $\gamma = 0$ ), which is a level less than  $K_p$ . (In the interests of reducing the effects of Monte Carlo variability, the figure actually used was the average of the medians over the last 50 years of the 200-year projection period.) Figure 4 compares deterministic and stochastic results for each predator species separately, and includes 10 and 90 percentiles as well as medians for the stochastic model distributions.

Two points are readily apparent from these plots of model results:

- (i) the crabeater seal, by virtue of the preliminary estimates of parameter values which indicate the combination of a low age-at-first-parturition, high adult survival rate, and lesser frequency of poor breeding success (Tables 1 and 2), is suggested to be the best able of the four predator species considered to cope with the impact of fishing on krill; by contrast, Adélie penguins would be the least well equipped for this, in terms of these preliminary values; and
- (ii) the predicted decline in predator numbers resulting from krill fishing in circumstances of krill recruitment variability, is considerably greater than deterministic evaluations would suggest.

Presumably, the underlying reason for (ii) is the Type II nature of the survival rate functions of Figure 2. In consequence, when krill biomass fluctuates, the net losses to the predators when the krill biomass is low are not entirely compensated by gains when this biomass is high.

Figure 5 shows plots of predator numbers ( $N$ ) against time for three different values of  $\gamma$  (including  $\gamma = 0$ ) for each predator species considered. To illustrate transient effects, the starting condition sets  $N$  equal to its 'equilibrium level' in the absence of harvesting ( $\gamma = 0$ ) for the first and all preceding years. For the stochastic model, this 'equilibrium level' is taken to be the median of the distribution of  $N$  following a 200-year projection under varying krill recruitment. (For the same reason as explained above, the average of the medians over the last 50 years of this period is the figure actually used.)

The  $\gamma = 0$  plots in Figure 5 indicate that some problems remain with the stochastic model implementations considered thus far. There appears for some species to be a continuous (albeit sometimes slow) declining trend with time in the median of the predator population size, even after considerable time has elapsed. Thus the assumption made above that the  $N/K_p$  distribution will have stabilised after 200 years, is not always valid. In other words, some populations seem not to be self-sustaining for the stochastic model (given the preliminary parameter estimates of Tables 1 and 2), even in the absence of fishing on krill. This is obviously the case for the two bird species, but it is not clear from the plots whether or not crabeater seals also fall into this category.



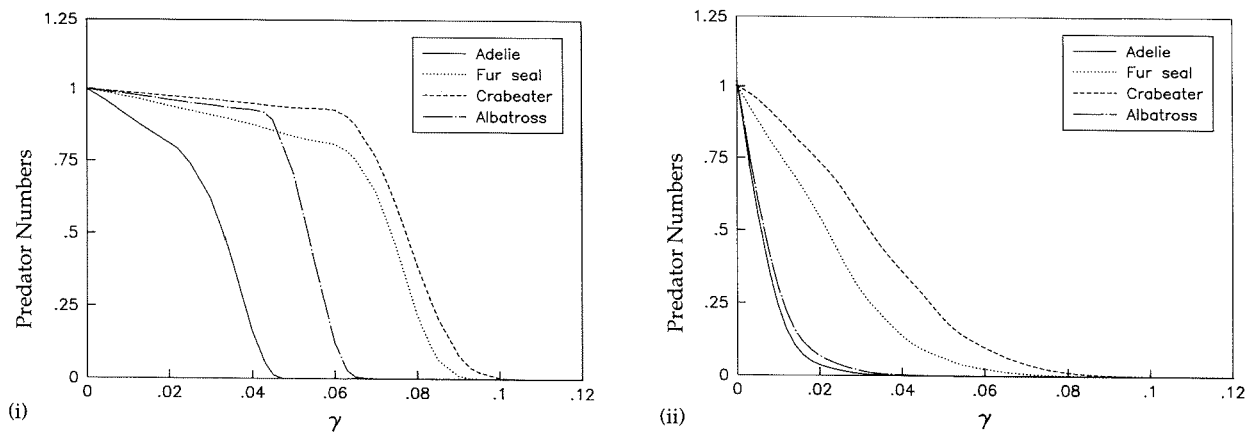


Figure 3: Plots of predator numbers ( $N$ ) (normalised to their level when  $\gamma = 0$ ) as a function of krill fishing intensity (measured by  $\gamma$ ) are compared for the four species of predator considered. Deterministic results are shown in (i), and the medians of the results incorporating krill recruitment variability in (ii).

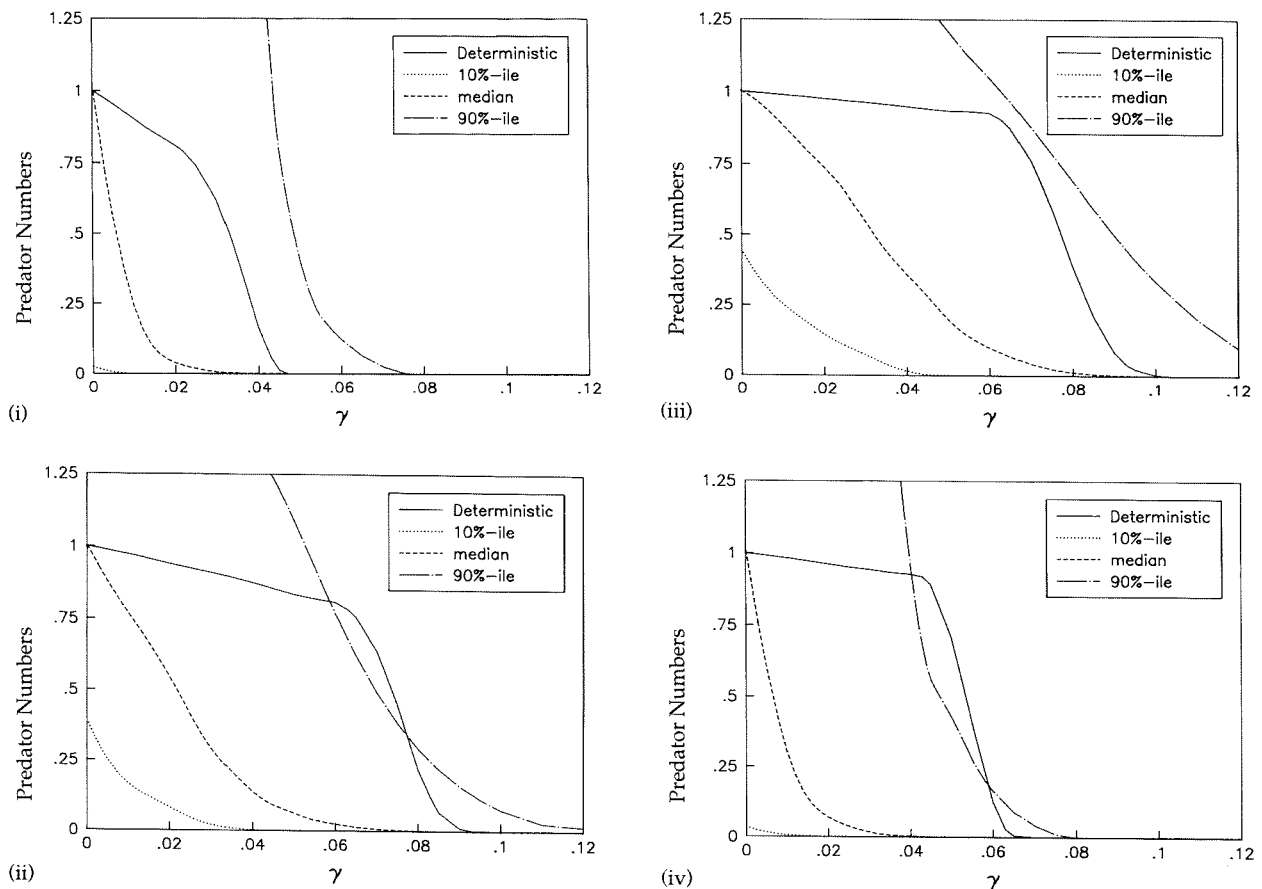
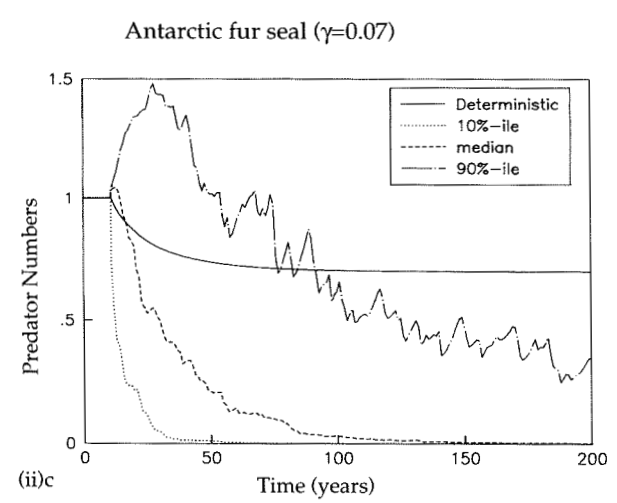
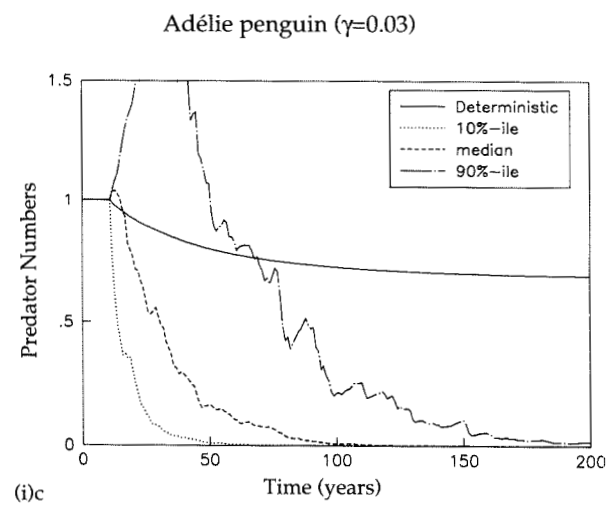
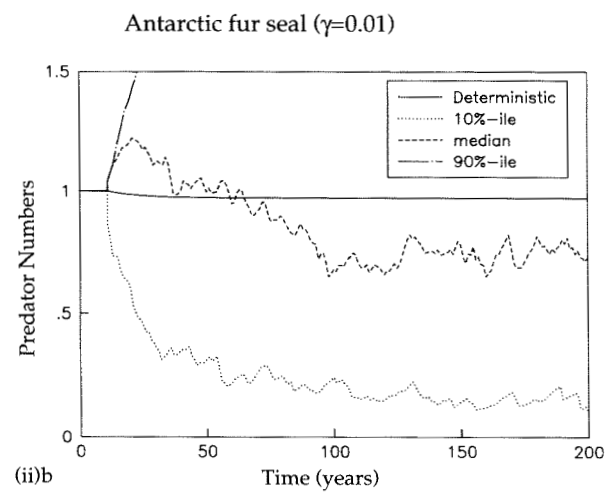
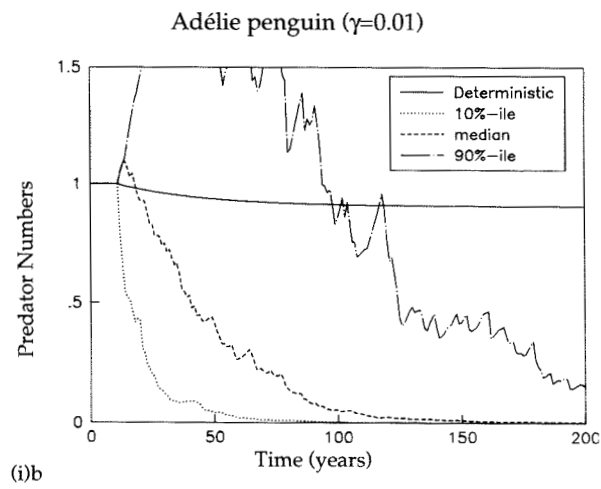
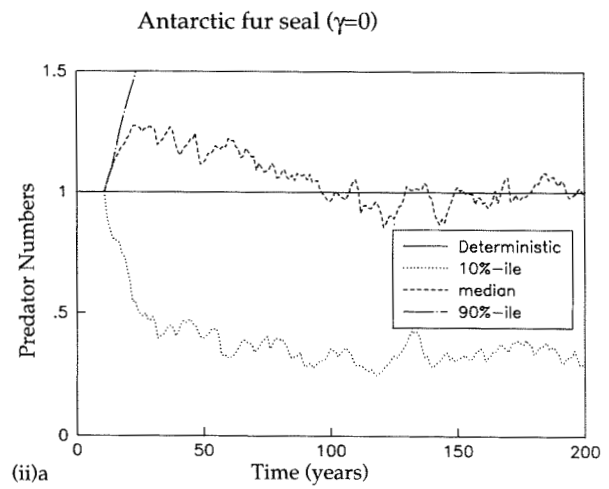
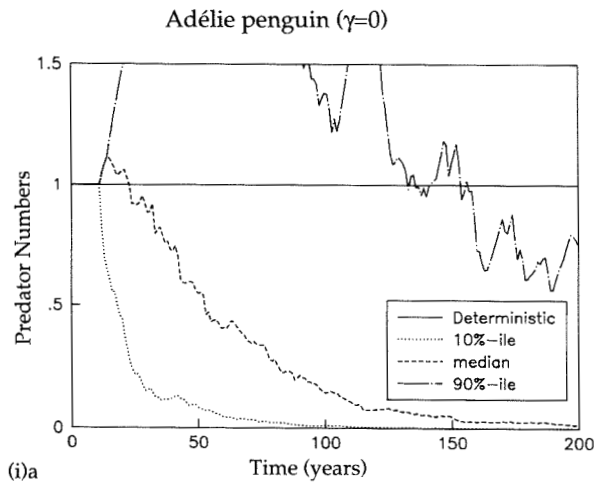


Figure 4: Plots of predator numbers ( $N$ ) (normalised as in Figure 3) versus  $\gamma$ , separately for each species of predator considered: (i) Adélie penguin; (ii) Antarctic fur seal; (iii) crabeater seal; and (iv) black-browed albatross. Each plot shows the deterministic results, together with the median and 10 and 90 percentile of the distributions incorporating krill recruitment variability.



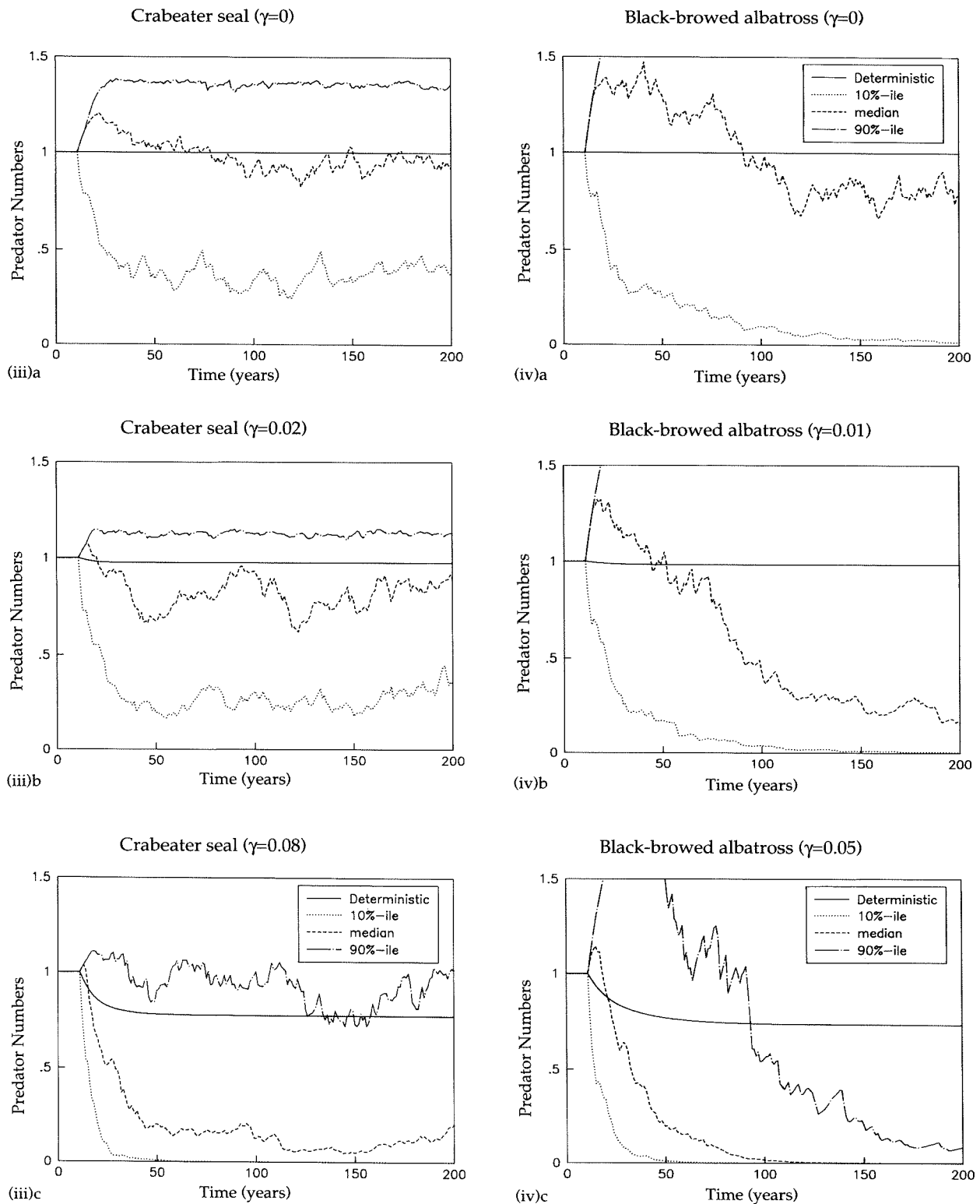


Figure 5: Plots of predator numbers ( $N$ ) versus time for deterministic projections, and for stochastic projections which take account of krill recruitment variability. Distribution medians together with 10 and 90 percentile are shown for the stochastic results.  $N$  is normalised to its starting level, which corresponds to a  $\gamma = 0$  (no krill fishing) situation; this is taken to be  $K_p$  for the deterministic projections, and the median  $N$  after 200 years for the stochastic case. Plots (i) to (iv) show results for each predator separately, as in Figure 4. Results are shown for three different  $\gamma$  values in each case:  $\gamma = 0$  and two other values, one of which corresponds roughly to depletion of predator numbers by 50% in terms of the stochastic median, and the other to depletion by 50% according to the deterministic calculation (see Figures 3(ii) and 3(i) respectively).

Two alternative approaches have been considered in an attempt to provide the necessary self-sustainability in the population dynamics of these predators in the presence of krill recruitment variability (and given the parameter estimates of Table 2). First, a crude representation of the availability of other food sources is considered. While the various predator species in the Antarctic may have differing abilities to utilise food sources other than krill, none of those species considered here are wholly dependent on krill alone, so that having both  $S_A$  and  $S_I$  tend to zero when the krill biomass itself approaches zero (as in Figure 2) seems extreme. To examine the consequences of availability of other food sources, Figure 6 shows results for the crabeater seal and

the black-browed albatross for a situation where both  $S_A$  and  $S_I$  approach one third of their maximum values, rather than zero, as krill abundance drops to very low values. The second approach is to set  $S_I^M$  values much closer to their upper bounds than was the case for the calculations considered thus far. Accordingly, Figure 7 shows results for these same two species, with the earlier choice of  $S_I^M = 0.3$  (see Table 3) replaced by  $S_I^M = 0.45$  (close to the upper bound of 0.47) in both cases.

The plots of median predator numbers against time in Figures 6 and 7 for the stochastic implementations of these approaches suggest that, in terms of these illustrative computations,

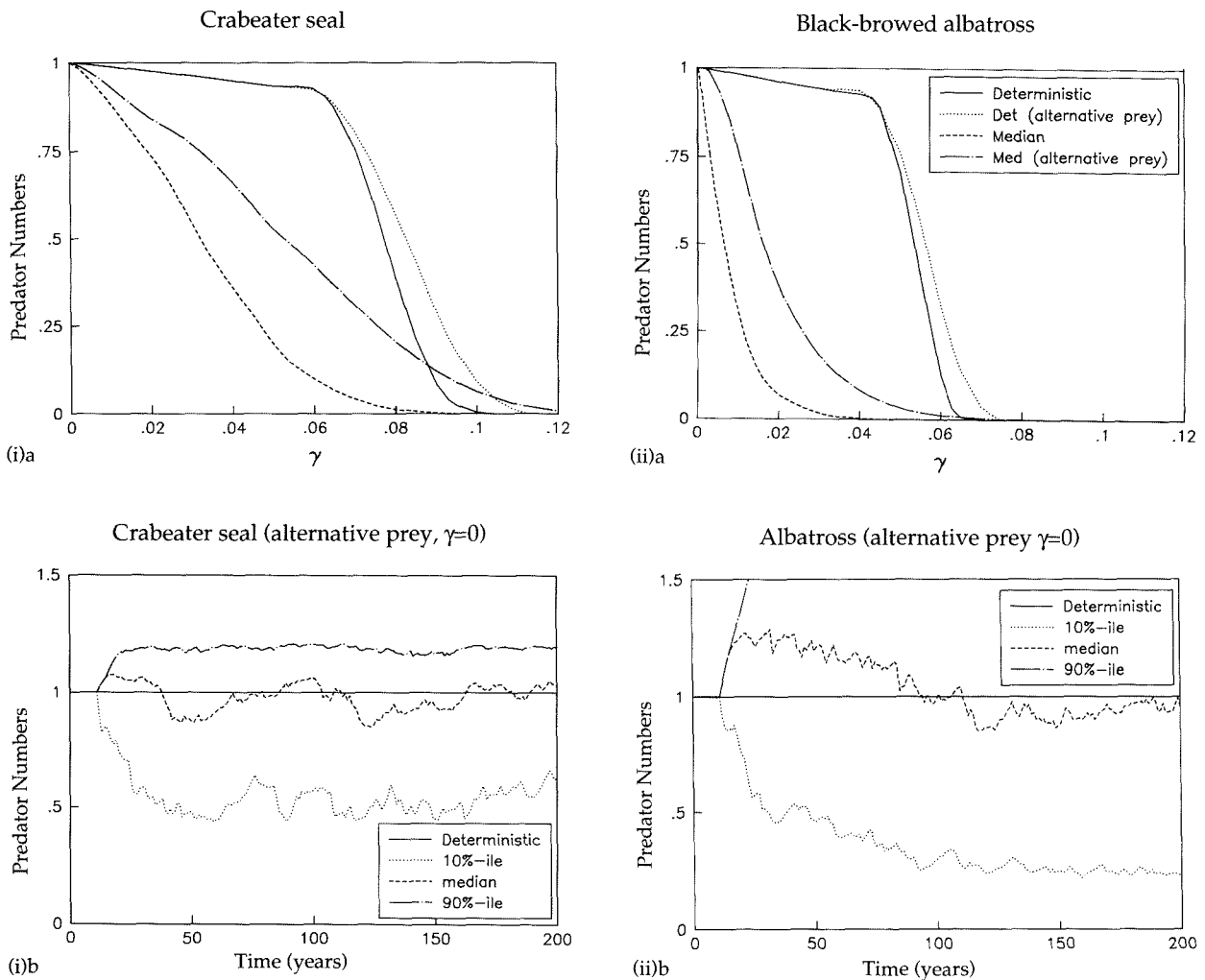


Figure 6: Results for (i) the crabeater seal, and (ii) the black-browed albatross under a scenario in which the predator is able to use other sources of prey in addition to krill, and in which the predator's survival rates tend to non-zero limits as krill abundance approaches zero. Plots of  $N$  versus  $\gamma$  are contrasted with those for the standard scenarios of Figures 4(iii) and (iv) respectively in the upper plots, which show both deterministic and stochastic median results. The lower plots show  $N$  versus time for the stochastic case with  $\gamma = 0$  in a similar manner to Figure 4.

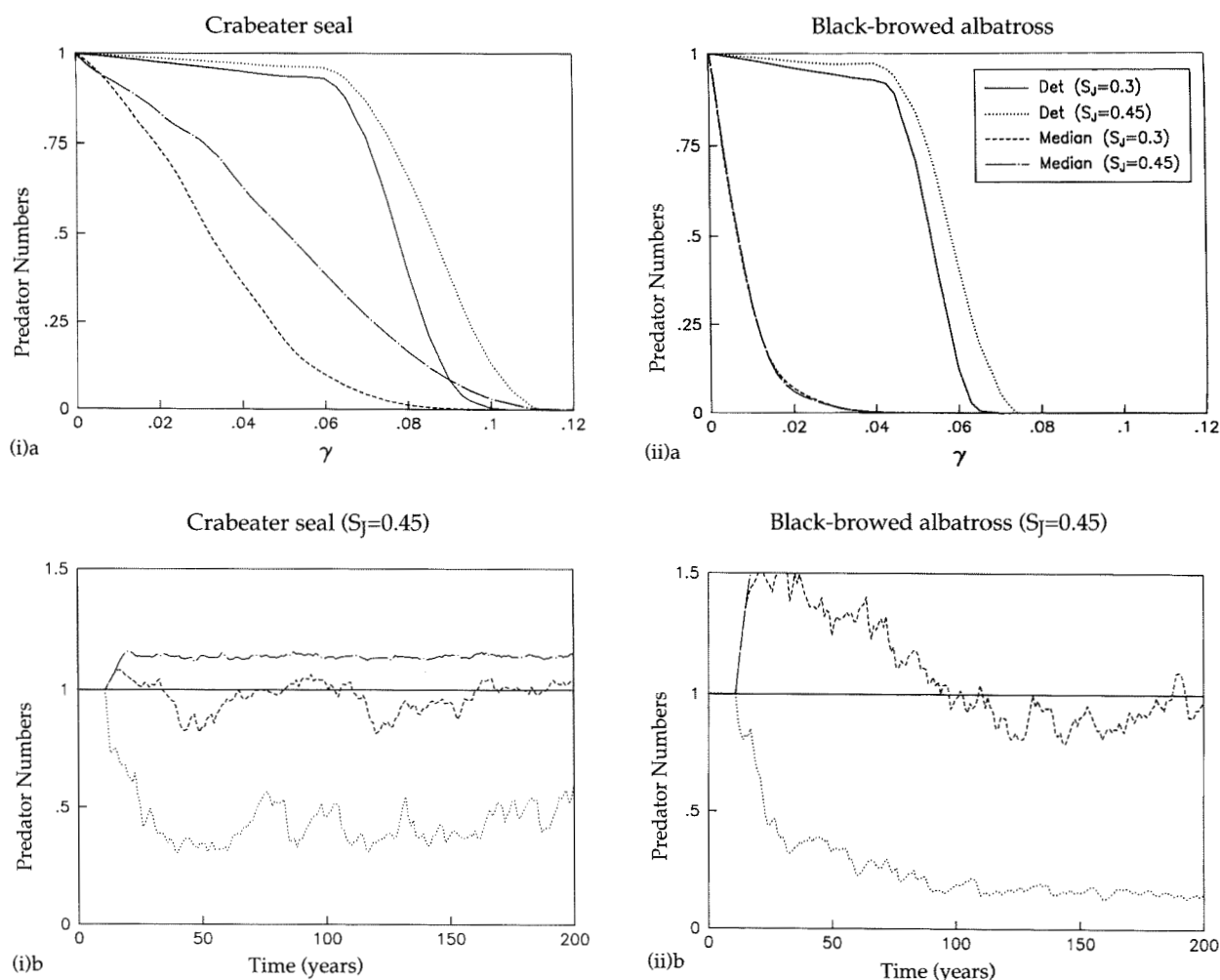


Figure 7: Results for (i) the crabeater seal, and (ii) the black-browed albatross, both with  $S_j^M$  increased to 0.45, are contrasted with the standard scenarios in Figures 4 and 5, in the same fashion as in Figure 6.

definite self-sustainability can be achieved by either of these approaches. They also show greater resilience of these predator populations to krill fishing, which indicates that both these aspects will need further consideration if subsequent developments of this approach are to be put forward as a basis for management recommendations.

#### TWO-WAY INTERACTION: KRILL ABUNDANCE EXPLICITLY AFFECTED BY CONSUMPTION BY PREDATORS

##### Methods

##### The Basic Models

Rather than work with a fully age-structured model of the krill population dynamics, a slightly simpler approach is suggested here to ease computations. The krill dynamics are governed

by the following aggregate equation for krill biomass:

$$B_{y+1} = B_y e^{-M} + r_y B_{y-2} \left[ 1 - \omega B_{y-2} / K \right] - F B_y - \lambda S_A(B_y) \tilde{N}_y \quad (9)$$

where  $F$  is the fishing mortality on krill;  
 $\lambda$  is related to the daily krill requirements for the species of predators being modelled;  
 $M$  is natural mortality of krill (taken here to be  $0.7 \text{ yr}^{-1}$ ), which includes mortality caused by species of krill predators other than the one under specific consideration here;  
 $\omega$  is a parameter introduced to allow  $K$  to retain its previous meaning; and  
 $\tilde{N}_y$  is the biomass of the species of predator under consideration at the start of year  $y$ .

Note that this approach assumes (for simplicity) that one species of predator dominates the krill-predator interaction, and that the effects caused by other species are sufficiently small that they can be adequately approximated by subsuming them into the natural mortality of krill (which is taken to be constant).

In an approximate sense, the first two terms on the right hand side of the equation correspond to the fraction of krill surviving natural mortality over the year, and to the incoming recruitment (from both individual growth and births, with a three-year time lag corresponding roughly to the delay associated with reaching maturity). To allow for recruitment variability:

$$r_y = r_{med} \exp(\varepsilon_y) \quad \varepsilon_y \text{ from } N(0; \sigma^2) \quad (10)$$

where  $N(0; \sigma^2)$  is a normal distribution with zero mean and variance  $\sigma^2$ . Values of the parameters  $r_{med}$  and  $\sigma$  are chosen so that the distribution of the 1+ biomass ( $B_y$ ) in the absence of exploitation ( $F = 0; \lambda = 0$ ) reasonably approximates the corresponding distribution for this biomass component for the fully age-structured krill model of Butterworth *et al.* (1994). This is well achieved by the choice  $r_{med} = 0.85$  and  $\sigma = 0.35$ .

The parameter  $K$  retains its interpretation of the previous section, if it is set to the deterministic value of  $B$  when  $F = 0$  and  $\lambda = 0$  (the latter because the earlier one-way interaction model corresponds to setting  $\lambda = 0$ ). Hence:

$$\omega = 1 - (1 - e^{-M}) / r_{med} \quad (11)$$

Deterministically,  $F$  of equation (9) corresponds closely to the parameter  $\gamma$  used above to measure the level of fishing intensity on krill. The final term in equation (9) reflects the annual consumption of krill by the predator species considered. The per-capita consumption of krill by this species is plausibly assumed to have the same functional form as that for adult survival rate in Figure 2 - hence the explicit inclusion of a Type II-like variation with  $B$ , in the form of the  $S_A(B)$  function. Given that  $S_A$  is typically close to 1 for higher values of  $B$ ,  $\lambda$  measures the annual krill biomass requirement for a krill predator. Taking both  $B$  and  $\tilde{N}_y$  to be measured in tonnes then, and a predator's food requirements to be some 5 to 15% of body mass per day, typical

values for  $\lambda$  would be:

$$\lambda \sim 20 - 60 \quad (12)$$

For the predator dynamics, equation (3) is used again with  $N_y$  replaced by  $\tilde{N}_y$ , i.e. the biomass of predators is assumed for simplicity to remain proportional to the number of reproducing females.

The final component of the rightmost term of equation (3) remains necessary in these circumstances, even though density dependence is introduced by growing predator populations depleting their food resource and hence becoming self-regulatory. The reason for this is clear if the deterministic equilibria are considered. In the absence of that final component, equation (3) would fix the equilibrium size of  $B$  at the same value, irrespective of the level of krill fishing. Increasing fishing would then lead, through equation (9), to exact compensation between fishery and predators: any increase in krill catch would be balanced exactly by a drop in the number of predators of such a size that the overall consumption by the predators would decrease by precisely the same amount (as long as the predators were not rendered extinct). This seems neither a realistic nor a particularly interesting scenario, so that the final component of equation (3) is retained for greater model flexibility.

#### Deterministic Analysis

In a deterministic context, at co-existence equilibrium:

$$\left. \begin{aligned} 1 &= e^{-M} + r_{med} [1 - \omega B / K] - F - \lambda S_A(B) \tilde{N} / B \\ 1 &= S_A(B) + S_J(B) S_A(B)^{T-1} [1 - \beta \tilde{N} / K_p] \end{aligned} \right\} \quad (13)$$

For a given value of  $F$ , these equations may be solved for  $B$  and  $\tilde{N}$  to indicate how both krill and predator biomasses respond to increasing krill harvest levels. Note, however, that care should be taken in contrasting results from this model with those of the one-way interaction model. This is because the value of  $M$  used in the 'one-way' model subsumes the effects of consumption by the predator species considered explicitly here, so that a lower value of  $M$  would need to be used for comparable results from the 'two-way' model.

### Incorporating Krill Recruitment Variability

Projections and biomass distributions can be generated as for the one-way interaction case, except that equation (9) is now used to calculate the krill biomass time series, instead of this being generated independently from the age-structured krill model of Butterworth *et al.* (1994).

### CONCLUDING REMARKS

It is first necessary to emphasise that it would be premature to pay undue attention to the quantitative results of these analyses. (Taken literally, Figure 3 suggests that a choice  $\gamma \geq 0.1$  for a krill harvesting strategy would render all four of the predator species considered in this paper extinct.) At this preliminary stage, cognisance should rather be taken of qualitative features of the results: for example, that krill recruitment variability indicates lesser predator resilience to krill harvesting than deterministic calculations would suggest; and that crabeater seals seem likely to be more resilient to such fishing than Adélie penguins, given the preliminary values provided in CCAMLR (1993) for their respective population dynamics parameters.

In any case, the quantitative results depend critically on these values, which are provisional and intended only to facilitate the provision of illustrations of how the models considered here behave. This paper has served to demonstrate that some of these values, as interpreted, cannot be correct. For example, were the estimates provided for adult survival rates actually unbiased values for the optimal survival level ( $S_A^M$ ) as assumed, there would seem to be little if any scope for self-sustainability of these populations, even without krill fishing. However, subsequent discussion on this point (for which the analyses of this paper served as a catalyst) has clarified both that there are likely negative biases in some of these preliminary estimates of adult survival rate, and further that they reflect averages over a variety of conditions rather than the optimum (SC-CAMLR, 1993a - paragraphs 7.17 to 7.20). Future calculations will need to attempt to take account of these aspects, before they can claim to be sufficiently realistic to provide a possible basis for management recommendations.

Other questions concern whether the manner in which survival rates have been assumed to vary with krill abundance (see Figure 2) is too 'severe', e.g. should a Beverton-Holt form be used, so that the decline is not as rapid for  $B < \alpha_{A/K}$ ; does the approach used to estimate  $\alpha_{A/K}$  lead to positive bias; and is it realistic to have these functions drop to zero at low krill abundance, given alternative food sources?

The approach of this paper assumes that predator survival rates depend on krill abundance alone in a deterministic manner. Clearly, other factors must also play a role (see comments in SC-CAMLR, 1993a - paragraph 7.35), and future calculations must attempt to make some allowance for them.

Given the fundamental nature of many of these concerns, a priority for the future should be to address these points in the context of the 'one-way' interaction model, before initiating calculations with the 'two-way' variant. This suggested priority was confirmed by WG-Krill (SC-CAMLR, 1993b - paragraph 5.16).

### ACKNOWLEDGEMENTS

This work was supported by the Foundation for Research Development, South Africa. The authors are grateful to those who provided the preliminary predator parameter estimates used in this study: Drs J.L. Bengtson and P.L. Boveng, National Marine Mammal Laboratory, who were supported by NOAA's Antarctic Marine Living Resources Program and the National Science Foundation's Division of Polar Programs (grants DPP80-20087, DPP84-20851) (crabeater seal); Drs J.P. Croxall and I.L. Boyd, British Antarctic Survey (black-browed albatross and Antarctic fur seal) who kindly provided their estimates to the authors at an early stage to facilitate initiation of this work; and Dr W.Z. Trivelpiece, Montana State University, who was supported by the National Science Foundation's Division of Polar Programs (grants DPP85-16019, DPP88-15878, DPP91-21952) (Adélie penguin). The authors are appreciative of the comments of two anonymous reviewers on an earlier version of the paper.

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#### Liste des tableaux

- Tableau 1: Informations préliminaires sur la proportion d'années considérées comme mauvaises en matière de survie des adultes et de réussite de la reproduction des prédateurs (à partir de CCAMLR, 1993 modifiées dans SC-CAMLR, 1993a pour les otaries de Kerguelen) et, de là, estimations des paramètres  $\alpha_A$  et  $\alpha_j$  dans les rapports de l'équation (1) entre le taux de survie des prédateurs et l'abondance de krill.
- Tableau 2: Valeurs utilisées pour l'âge à la première reproduction et le taux de survie maximal annuel des adultes chez les divers prédateurs étudiés. (Dérivées, comme cela est expliqué dans le texte, des premières estimations fournies dans CCAMLR (1993) dans lesquelles sont également données des explications sur les chiffres entre parenthèses. La version originale de cette communication présentait une erreur, dont fait mention SC-CAMLR (1993a - paragraphe 7.24), en ce qui concerne l'âge à la première reproduction des otaries de Kerguelen; celle-ci a maintenant été corrigée.)
- Tableau 3: Taux maximaux de gravidité présumés pour chacun des prédateurs étudiés et limites du 'taux maximal de survie des juvéniles' ( $S_j^M$ ) à partir des inégalités (6) et (7). Les valeurs retenues pour  $S_j^M$  dans cette communication se situent à peu près à mi-chemin de ces deux limites, quand cela est possible. En ce qui concerne les deux premières espèces citées, la valeur retenue se situe cette fois à mi-chemin des deux valeurs entre parenthèses et ce, pour les raisons mentionnées dans le texte.

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- Figure 2: Rapports présumés entre les taux annuels de survie des prédateurs et l'abondance de krill considérée ici comme étant la biomasse ( $B$ ) de krill. La biomasse médiane de krill en l'absence de



пêche est indiquée par  $K$ . Le 'taux de survie' des juvéniles (première année) tient compte des effets du taux de gravidité (changeant) ainsi que du taux de mortalité naturelle plus élevé que la moyenne chez les juvéniles.

- Figure 3: Courbes du nombre de prédateurs ( $N$ ) (normalisé pour  $\gamma = 0$ ) en fonction de l'intensité de la pêche de krill (mesurée par  $\gamma$ ) comparées pour les quatre espèces de prédateurs étudiées. Les résultats déterministes sont indiqués dans (i) et les médianes des résultats tenant compte de la variabilité du recrutement de krill dans (ii).
- Figure 4: Courbes du nombre de prédateurs ( $N$ ) (normalisé comme à la figure 3) par rapport à  $\gamma$  pour chacune des espèces de prédateurs étudiées: (i) manchot Adélie; (ii) otarie de Kerguelen; (iii) phoque crabier; et (iv) albatros à sourcils noirs. Chaque courbe indique les résultats déterministes ainsi que la médiane et les valeurs de 10 et 90% des distributions tenant compte de la variabilité du recrutement de krill.
- Figure 5: Courbes du nombre de prédateurs ( $N$ ) en fonction des années pour les projections déterministes et les projections stochastiques qui tiennent compte de la variabilité du recrutement de krill. Les médianes et les valeurs de 10 et 90% des distributions sont données pour les résultats stochastiques.  $N$  est normalisé à son niveau initial, et donc à une situation dans laquelle  $\gamma = 0$  (en l'absence de pêche au krill); il correspond à  $K_p$  dans les projections déterministes et à la médiane  $N$  après 200 ans, dans le cas stochastique. Les courbes (i) à (iv) donnent les résultats de chaque prédateur, séparément, comme à la figure 4. Dans chaque cas, les résultats sont donnés pour trois valeurs différentes de  $\gamma$ :  $\gamma = 0$  et deux autres valeurs dont l'une correspond en gros à l'épuisement égal à 50% du nombre des prédateurs en ce qui concerne la médiane stochastique et l'autre à l'épuisement égal à 50% selon le calcul déterministe (cf. les figures 3(ii) et 3(i), respectivement).
- Figure 6: Résultats pour (i) le phoque crabier et (ii) l'albatros à sourcils noirs dans un cas où le prédateur a accès, en plus du krill, à d'autres sources de proies, et dans lequel les taux de survie du prédateur se rapprochent de limites qui ne sont pas égales à zéro quand l'abondance de krill se rapproche de zéro. Les courbes de  $N$  par rapport à  $\gamma$  sont comparés avec celles des cas standard des figures 4(iii) et (iv) respectivement sur les courbes supérieures qui indiquent les résultats médians tant déterministes que stochastiques. Les courbes inférieures indiquent  $N$  par rapport aux années pour le cas stochastique pour  $\gamma = 0$  de la même manière qu'à la figure 4.
- Figure 7: Résultats pour (i) le phoque crabier et (ii) l'albatros à sourcils noirs, dans lesquels  $\gamma$  est accru à 0,45, comparés aux cas standard des figures 4 et 5, de la même manière qu'à la figure 6.

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- Таблица 1: Предварительная информация о пропорции лет с благоприятными условиями для выживания взрослых особей хищников и для эффективного воспроизводства (из таблицы в CCAMLR, 1993, модифицированной в SC-CAMLR, 1993a для южного морского котика); также даются оценки параметров  $\alpha_A$  и  $\alpha_J$  в отношениях между уровнем выживания хищников и численностью криля в уравнении (1).
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## Список рисунков

- Рисунок 1: Распределение биомассы криля при различных уровнях интенсивности промысла криля, показанное величинами параметра  $\gamma$  (определение  $\gamma$  дается в подразделе настоящей работы - 'Детерминистические оценки воздействия промысла' ['Deterministic Evaluations of the Effect of Fishing']). Непрерывная кривая ( $\gamma = 0$ ) показывает отсутствие промысла криля;  $K$  - медианная биомасса криля 1+ в данной ситуации.  $B_{EQ}$  отражает 'равновесную' величину биомассы 1+, т.е. после исчезновения каких-либо временных эффектов начала промысла при интенсивности  $\gamma$ . Показанные результаты были рассчитаны с использованием варианта 'летний промысловый сезон' модели 2 Баттеруорта и др. (Butterworth *et al.*, 1994).
- Рисунок 2: Предполагаемые отношения между уровнями ежегодного выживания хищников и численностью криля, принятой здесь равной биомассе криля ( $B$ ).  $K$  - это медианная биомасса криля в отсутствие эксплуатации. Уровень выживания молоди в первый год жизни включает в себя воздействие (изменяющегося) коэффициента беременности и необычно высокий уровень естественной смертности на ранних стадиях жизни.
- Рисунок 3: Сравниваются кривые численности четырех видов хищников ( $N$ ) (численность нормализована на уровень  $\gamma = 0$ ) как функция интенсивности промысла криля (измеряемой с помощью  $\gamma$ ). Детерминистические результаты показаны в (i), а медианные величины результатов, включающих в себя изменчивость пополнения криля, показаны в (ii).
- Рисунок 4: Отдельные кривые численности каждого входившего в исследование вида хищника ( $N$ ) (численность нормализована как на Рисунке 3) по сравнению с  $\gamma$ : (i) пингвин Адели; (ii) южный морской котик; (iii) тюлень-крабоед; и (iv) чернобровый альбатрос. В каждом графике показаны детерминистические результаты, а также медианные, 10- и 90-перцентильные величины распределений, включающих в себя изменчивость пополнения криля.
- Рисунок 5: Кривые численности хищников ( $N$ ) в развитии со временем, отражающие результаты детерминистических прогнозов, а также стохастических прогнозов, учитывающих изменчивость пополнения криля. Показаны медианные, 10- и 90-перцентильные величины распределений по стохастическим результатам. Как в случае Рисунка 4, графики (i) - (iv) показывают результаты по каждому виду хищнику отдельно. В каждом случае даются результаты по трем величинам:  $\gamma = 0$  и еще две величины, одна приблизительно соответствует истощению численности хищников на 50% в плане стохастической медианы, а другая - истощению на 50% в соответствии с детерминистическими расчетами (см. рисунки 3(ii) и 3(i) соответственно).
- Рисунок 6: Результаты по (i) тюленю-крабоеду и (ii) чернобровому альбатросу в ситуации, согласно которой хищники могут потреблять другую пищу помимо криля и уровни выживания хищников имеют тенденцию к ненулевым пределам по мере приближения численности криля к нулю. Графики  $N$  по сравнению с  $\gamma$  сопоставлены с графиками стандартных ситуаций, изображенных на рисунках 4(iii) и (iv) и отраженных в верхних кривых, которые показывают как детерминистические, так и стохастические медианные результаты. Нижние кривые показывают  $N$  в развитии со временем в стохастическом случае при  $\gamma = 0$ , подобно Рисунку 4.
- Рисунок 7: Результаты по (i) тюленю-крабоеду и (ii) чернобровому альбатросу, при которых значение увеличено до 0,45, сравнены со стандартными ситуациями на рисунках 4 и 5, - таким же образом, что на Рисунке 6.

## Lista de las tablas

- Tabla 1: Información preliminar dada sobre la proporción de años donde la supervivencia adulta del depredador y el éxito reproductivo del depredador son bajos (de CCRVMA, 1993 y según fuera modificado en SC-CAMLR, 1993a para el lobo fino antártico), con las estimaciones consiguientes de los parámetros  $\alpha_A$  y  $\alpha_j$  en las relaciones entre el índice de supervivencia del depredador y la abundancia de kril en la ecuación (1).
- Tabla 2: Valores utilizados para la edad de primera reproducción y el índice de supervivencia adulta anual máxima de los depredadores considerados. Derivados de los cálculos preliminares dados en

CCAMLR (1993) como explica el texto, donde se dan también explicaciones de las cifras entre paréntesis. Se ha corregido ahora un error en la versión original de esta publicación con respecto a la edad de primera reproducción del lobo fino antártico, indicado en SC-CAMLR (1993a - párrafo 7.24).

Tabla 3: Las tasas de preñez máximas supuestas para cada uno de los depredadores considerados, junto con los límites para el índice máximo de supervivencia juvenil ( $S_j^M$ ) proporcionados por las desigualdades (6) y (7). Los valores usados para  $S_j^M$  en esta publicación son elegidos de manera que, en lo posible, estén situados aproximadamente en el medio de estos límites. Para las dos primeras especies citadas, la elección se hace en cambio al medio de las cifras entre paréntesis, por las razones expuestas en el texto.

#### Lista de las figuras

- Figura 1: La distribución de la biomasa de kril para diferentes niveles de intensidad de explotación de kril, como indicado por el valor del parámetro  $\gamma$  (ver sub-sección. 'Deterministic Evaluations of the Effect of Fishing' para una definición de  $\gamma$ ). La curva sólida ( $\gamma = 0$ ) refleja la ausencia de pesca de kril, y  $K$  es la mediana 1+ biomasa de kril en esas circunstancias.  $B_{EQ}$  indica un 'equilibrio' 1+ valor de la biomasa, es decir el observado después de desaparecer todos los efectos transitorios causados por el inicio de la pesca a una intensidad  $\gamma$ . Los resultados expuestos fueron calculados usando la variante del Modelo 2 de Butterworth *et al.* (1994) de la temporada veraniega de pesca (Diciembre a Febrero).
- Figura 2: Las relaciones supuestas entre los índices anuales de supervivencia de los depredadores y la abundancia de kril, interpretada aquí como la biomasa de kril ( $B$ ). La biomasa mediana de kril en ausencia de explotación está indicada por  $K$ . El 'índice de supervivencia' juvenil (primer año) incluye los efectos que tienen la tasa de preñez variable y la tasa de mortalidad natural, mayor que el promedio, que ocurre en los juveniles.
- Figura 3: Comparación de los gráficos que ilustran el número de depredadores ( $N$ ) (normalizados a su nivel cuando  $\gamma = 0$ ) en función a la intensidad de pesca de kril (medida por  $\gamma$ ) entre las cuatro especies de depredadores estudiadas. Los resultados determinísticos se presentan en (i), y las medianas de los resultados que incluyen la variabilidad en el reclutamiento del kril se presentan en (ii).
- Figura 4: Gráficos que ilustran el número de depredadores ( $N$ ) (normalizados como en la figura 3) en función de  $\gamma$ , para cada especie depredadora estudiada: (i) pingüinos adelia; (ii) lobo fino antártico; (iii) foca cangrejera; y (iv) albatros de ceja negra. Cada gráfico muestra los resultados determinísticos, junto con la mediana y 10 y 90 percentiles de las distribuciones que incluyen la variabilidad de reclutamiento de kril.
- Figura 5: Gráficos del número de depredadores ( $N$ ) en función del tiempo para las proyecciones determinísticas, y para las proyecciones estocásticas que consideran la variabilidad en el reclutamiento de kril. Se muestran las medianas de distribución junto a los percentiles 10 y 90 para los resultados estocásticos.  $N$  se normaliza a su nivel inicial, que corresponde a una situación  $\gamma = 0$  (ausencia de la pesca de kril); esto se considera como  $K_p$  para las proyecciones determinísticas, y la mediana como  $N$  después de 200 años en el caso estocástico. Los gráficos (i) a (iv) muestran los resultados para cada depredador, como en la figura 4. Se dan los resultados para tres valores diferentes de  $\gamma$  en cada caso:  $\gamma = 0$  y otros dos valores, uno de los cuales corresponde aproximadamente a una merma de 50% en el número de depredadores de acuerdo a la mediana estocástica, y el otro a una merma de 50% de acuerdo al cálculo determinístico (ver figuras 3(ii) y 3(i) respectivamente).
- Figura 6: Resultados para (i) la foca cangrejera, y (ii) el albatros de ceja negra suponiendo que el depredador pueda utilizar otras fuentes de alimento además de kril, y suponiendo que el índice de supervivencia del depredador se aproxima a límites distintos de cero a medida que la abundancia de kril se aproxima a cero. Los gráficos superiores, que muestran los resultados medianos determinísticos y estocásticos, comparan los gráficos de  $N$  en función de  $\gamma$  con los casos típicos de las figuras 4(iii) y (iv) respectivamente. Los gráficos inferiores muestran  $N$  en función del tiempo para el caso estocástico donde  $\gamma = 0$  de manera similar a la figura 4.
- Figura 7: Resultados para (i) la foca cangrejera, y (ii) el albatros de ceja negra, ambos con aumentado a 0.45, son contrastados con los casos típicos presentados en las figuras 4 y 5, tal como en figura 6.

