A COMPILATION OF PARAMETERS FOR ECOSYSTEM DYNAMICS MODELS OF THE SCOTIA SEA – ANTARCTIC PENINSULA REGION

S.L. Hill✉, K. Reid and S.E. Thorpe
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET
United Kingdom
Email – sih@bas.ac.uk

J. Hinke
Southwest Fisheries Science Center
NOAA Fisheries
Antarctic Ecosystem Research Division
8604 La Jolla Shores Drive
La Jolla, CA 92037, USA

G.M. Watters
Southwest Fisheries Science Center
NOAA Fisheries
Protected Resources Division
1352 Lighthouse Avenue
Pacific Grove, CA 93950, USA

Abstract

Expansion of the krill fishery in the Scotia Sea–Antarctic Peninsula region beyond the current operational catch limit requires the development and assessment of methods for subdividing the precautionary catch limit amongst smaller spatial units. This paper compiles parameters for use in the ecosystem dynamic models that are needed to assess these methods. These parameters include life history and krill consumption parameters for the fish, whale, penguin and seal species that feed on krill in this region. Maximum krill transport rates are also derived from the OCCAM global ocean circulation model. This parameter set, like most others, is associated with considerable uncertainty, which must be taken into account when it is used. The sources, assumptions and calculations at every stage of the compilation process are therefore detailed, and plausible limits for parameter values are provided where possible. The results suggest that fish are the major krill consumers in all SSMUs, with perciform fish taking as much krill as whales, penguins and fur seals combined and myctophid fish taking double that amount. However, estimates of krill consumption per unit predator biomass suggest that this is an order of magnitude higher in penguins and seals than in whales and fish.

Résumé

L'expansion de la pêcherie de krill de la région de la mer du Scotia–péninsule antarctique, au-delà de la limite de capture actuellement en vigueur, nécessite la mise au point et l'évaluation de méthodes de subdivision de la limite de précaution des captures en unités spatiales plus petites. Le présent document dresse la liste des paramètres à utiliser dans les modèles de la dynamique de l'écosystème, qui sont nécessaires pour évaluer ces méthodes. Ces paramètres comprennent, entre autres, les paramètres du cycle biologique et de la consommation de krill des espèces de poissons, de cétacés, de manchots et d'otaries qui se nourrissent de krill dans la région. Les flux maximum de krill proviennent du modèle OCCAM de circulation océanique globale. Cet ensemble de paramètres, comme bien d'autres, est entouré d'une incertitude considérable, dont il faut tenir compte lors de son utilisation. Les sources, les hypothèses et les calculs, à chaque étape du processus de compilation, sont donc détaillés et des limites plausibles sont fournies lorsque cela est possible pour les valeurs paramétriques. Les résultats laissent penser que les poissons sont les principaux consommateurs de krill dans toutes les SSMU, les poissons perciformes en ingurgitant autant que les cétacés, les manchots et les otaries réunis et les poissons myctophidés, le double de cette quantité. Les estimations de la consommation de krill par unité de biomasse de prédateurs semblent néanmoins indiquer que celle des manchots et des otaries est supérieure à celle des cétacés et des poissons, la différence étant de l'ordre d'un facteur 10.

Резюме

Превышение крилевым промыслом в районе моря Скотия – Антарктического п-ова рамок существующего рабочего ограничения на вылов требует разработки и оценки методов подразделения предохранительного ограничения на вылов между более мелкими пространственными единицами. В данной статье собраны необходимые для оценки этих методов параметры, применяемые в динамических моделях экосистемы. Эти параметры включают данные о жизненном цикле и потреблении криля для видов рыб, китов, пингвинов и тюленей, которые питаются крилем в этом регионе. Максимальная скорость переноса криля также приводится по модели глобальной циркуляции океана OCCAM. Для этого набора параметров, как и для большинства других, характерна значительная неопределенность, которую следует учитывать при его использовании. В связи с этим, на каждом этапе компиляционного процесса источники, допущения и расчеты детализируются и, по возможности, приводятся вероятные пределы значений параметров. Согласно результатам, основным потребителем криля во всех SSMU является рыба, причем рыбы отряда окунеобразных съедают столько же криля, сколько киты, пингвины и тюлени вместе взятые, а миктофиды – вдвое больше. Однако оценки потребления криля на единицу биомассы хищников говорят о том, что у пингвинов и тюленей этот показатель на порядок выше, чем у китов и рыбы.

Resumen

La expansión de la pesquería de kril en la región del Mar de Escocia–Península Antártica más allá del límite operacional de captura actualmente vigente, requiere de la formulación y evaluación de métodos para subdividir el límite de captura precautorio en áreas más pequeñas. Este trabajo compila parámetros para las simulaciones de la dinámica del ecosistema requeridas en la evaluación de estos métodos. Los parámetros incluyen el ciclo de vida y el consumo de kril de las especies de peces, cetáceos, pingüinos y pinnípedos que se alimentan del recurso en esta región. Las tasas máximas de transporte de kril también se derivan del modelo OCCAM de circulación oceánica global. La magnitud de la incertidumbre inherente a este conjunto de parámetros, al igual que la de muchos otros, es considerable y debe ser tomada en cuenta al utilizarlo. Por lo tanto, se han detallado las fuentes, suposiciones y cálculos efectuados en todas las etapas de la compilación, y en la medida de lo posible, se proporcionaron los márgenes verosímiles de los valores de los parámetros. Los resultados indican que los peces son los mayores consumidores de kril en todas las UOPE, y de éstos, los peces perciformes consumen tanto kril como el consumido colectivamente por ballenas, pingüinos y lobos finos, y los peces mictófidos consumen el doble de esta cantidad. No obstante, las estimaciones del consumo de kril por unidad de biomasa de los depredadores indican que en el caso de los pingüinos y pinnípedos, dicho consumo es un orden de magnitud mayor que el de las ballenas y los peces.

Introduction

Expansion of the krill fishery in the Scotia Sea–Antarctic Peninsula region (FAO Statistical Area 48) beyond the current operational catch limit requires the development and assessment of methods for subdividing the precautionary catch limit among smaller spatial units. CCAMLR's Working Group on Ecosystem Monitoring and Management (WG-EMM) has defined such small-scale management units (SSMUs) and proposed a set of candidate options for subdivision of the catch limit (Hewitt et al., 2004a). The evaluation of these options will involve simulating their effects on krill and its predators using ecosystem dynamics models.

Such models must be spatially resolved at least to the scale of SSMUs and must represent krill and predator populations within these areas. WG-EMM has also recognised that the temporal resolution of such models must distinguish at least two seasons (summer and winter) to represent differences between SSMUs in the temporal overlap of fishing and predator breeding (SC-CAMLR, 2005). In order to represent the population dynamics of the focal species (krill and its dependent predators), such models will need information on key life history and population parameters. The functions representing the interactions between species must also be parameterised. The models must also account for uncertainties associated with the structure and

functioning of the ecosystem. One of the key uncertainties concerns the influence of advection on the local dynamics of krill (Hill et al., 2006).

This paper compiles and derives key parameters for the fish, whale, penguin and seal predators of krill. It is intended for general use in modelling studies of krill and its dependent predators in the Scotia Sea–Antarctic Peninsula region. However, it is particularly relevant to the ecosystem dynamics models presented at two WG-EMM workshops on Management Procedures (SC-CAMLR, 2005, 2006). These models represent the dynamics of predator populations with delay-difference equations in which individuals recruit to the adult population at the age of first breeding. The models are similar in their treatment of krill dynamics: the krill–predator–fishery model (KPFM), developed by Dr G. Watters (NOAA Fisheries, USA) and colleagues (at BAS, UK and NOAA Fisheries, USA), models krill numbers but assumes a constant mean mass, whereas the spatial multi-species operating model (SMOM) developed by Dr É. Plagányi and Prof. D. Butterworth (University of Cape Town, South Africa) directly models krill biomass. Although the population demographic structure and individual growth of krill are potentially important characteristics, they are not discussed in more detail because they are not explicitly considered in these models. As these models consider a limited number of predator taxa, a way of combining parameters for different species to represent 'generic' predators is suggested. The predator parameters derived here, their symbols, and their relevance in the KPFM are listed in Table 1.

This paper also provides information on SSMUs and historical catch, which is necessary for modelling the catch allocation options in Hewitt et al. (2004a). Furthermore, it derives maximum krill transport rates between SSMUs to define an upper bound on this important source of uncertainty. The intention is to provide a parameter set that best reflects current knowledge of the system. However, this knowledge is far from complete. Details are therefore provided of sources, methods and assumptions, which serve as an audit trail. Plausible limits are also estimated for parameter values where possible. This is intended to provide the information required to stimulate debate and research that will challenge current assumptions and address important gaps in this knowledge.

Approach: parameters, uncertainty and model inputs

The parameter estimates are derived from four main sources: the published literature; direct calculation when data were available; model output in the case of the krill transport parameters; and, finally, assumptions based on similar species, expert opinion or unpublished studies when values were unavailable from the other sources. Assumptions based on similar species were made only when they were necessary to derive the parameters in Tables 14 and 15. The parameters $\rho_{k,j}$ and $\alpha_{k,j}$ for fish were not included in these tables as they would have been based largely on such assumptions.

Parameters were derived for two seasons, corresponding to the six months from 1 October (summer) and the six months from 1 April (winter). However, natural mortality rate estimates tend to be annual rather than seasonal. Lifetime averaged annual rates (indicated by the symbol μ) were divided by 2 to obtain estimates of $M_{k,j,s}$. The derivation of the krill transport parameters is described in a self-contained section of the main text and frequently used equations are described in the present section. However, the derivation of many predator parameters required specific calculations, which are described in accompanying notes (following 'References'), along with details of the data sources used.

Uncertainty is dealt with by reporting minimum and maximum plausible values for parameters alongside average values. These limits are either the extremes of reported values or the 95% confidence intervals of estimates. Values shown without limits indicate that there was insufficient information to assess this uncertainty.

$\alpha_{k,j}$ was calculated depending on the available information as follows:

$$\alpha_{\max} = r_{\max} + 1 - e^{-\mu_A} \tag{1a}$$

$$\alpha_{\min} = \Lambda . e^{-(\mu_J)\rho} \tag{1b}$$

where μ_A and μ_J are the adult and pre-recruit annual mortality rates, $r_{\max}$ is the maximum observed rate of population increase and Λ is the observed number of live offspring produced per breeding adult per year.

Derived krill demand estimates are for the adult portion of the relevant populations (except for whales, where separate abundance estimates were not available for adults). The demand of adults foraging to feed their offspring is included, but the demand of independently feeding juveniles is not.

In compiling KPFM parameters, four predator taxa were considered: baleen whales, seals, penguins and fish. Each of these groups is composed
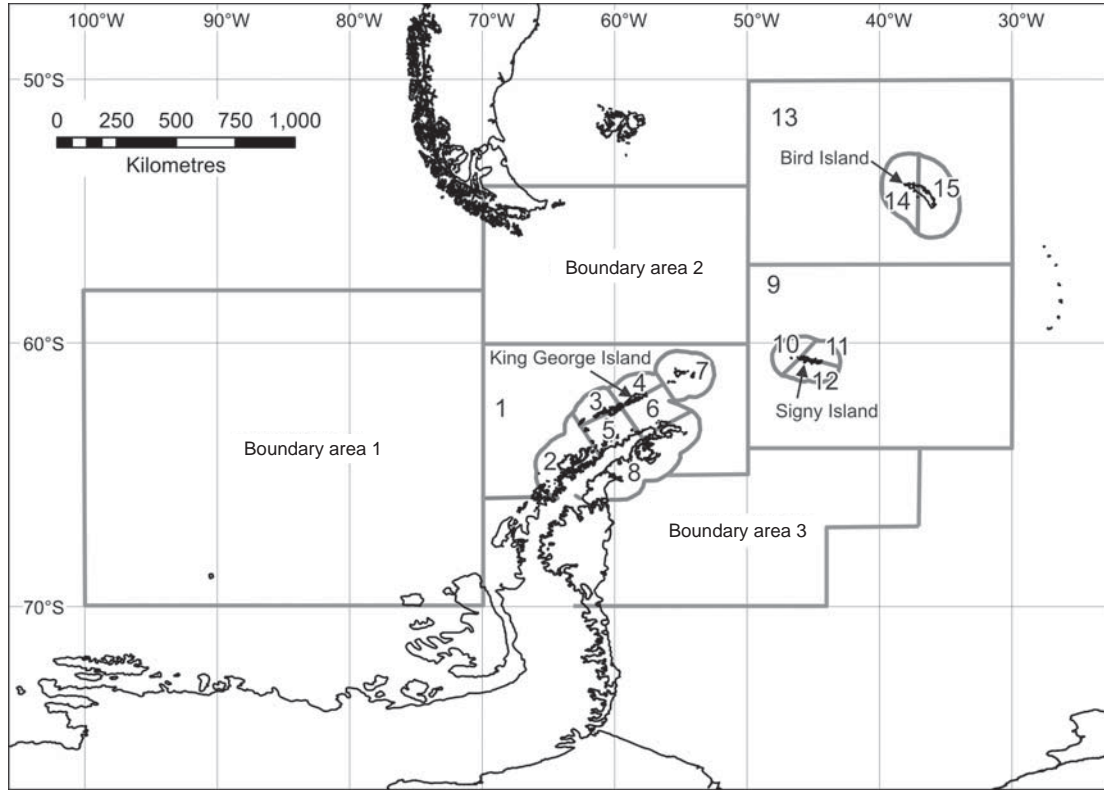
Figure 1:   The Scotia Sea–Antarctic Peninsula region, showing the SSMUs (names in Table 2), boundary areas and sites mentioned in the text.

of several species in the Scotia Sea–Antarctic Peninsula region, and the members of some groups, particularly fish, have very different characteristics. Parameters for generic members of each group were calculated as averages weighted by the krill consumption of the initial population of each species within the group. The basic calculation for a generic predator was:

$$\tilde{X}_{k,j} = \frac{\sum_{i=1}^{l} D_{i,j} X_{i,j}}{\sum_{i=1}^{l} D_{i,j}} \qquad (2)$$

where $\tilde{X}_{k,j}$ is the generic value of parameter X for taxon k, $X_{i,j}$ is its value for the i'th of l species in taxon k in SSMU j, and $D_{i,j}$ is the total annual krill consumption of species i in SSMU j.

SSMU areas

The basic spatial unit of the current parameter set is the SSMU. The KPFM includes additional spatial units, known as 'boundary areas', that border these management units and represent the spatial boundaries of the model. This parameterisation considers three boundary areas corresponding to areas in the Bellingshausen Sea, the Drake Passage and the Weddell Sea respectively (Figure 1). These boundary areas are essentially boxes fitted around the greatest distances that particles originating in the SSMUs could travel over six months, and the greatest distances from which particles could reach the SSMUs in six months. These distances were estimated by tracking particle advection in model velocity fields on a horizontal grid of resolution 0.25° latitude by 0.5° longitude (see next section).

The area within each SSMU was provided by the CCAMLR Secretariat and was calculated from the global sea-floor topography database of Smith and Sandwell (1997). Boundary areas were calculated from the GEBCO bathymetric database (IOC, IHO and BODC, 2003). For the purposes of this paper, the marine habitat in each SSMU is divided into two types: waters with depth ≤500 m are defined as 'shelf' areas and waters deeper than 500 m were defined as 'off-shelf' areas. Basic information on each SSMU, including the total krill catch from 1988 to 2002, is given in Table 2.

Krill transport

The exact role of advective transport on local krill dynamics is uncertain. The plausible limits on this uncertainty identified by WG-EMM (SC-CAMLR, 2006) were no krill transport between SSMUs versus the transport of krill as passive drifters. A more extreme scenario, which cannot be discounted but was not considered, would involve krill swimming with the currents. Parameters for the passive-drifter hypothesis were derived by tracking particle movements in velocity fields output from the ocean circulation model of the Ocean Circulation Climate Advanced Modelling Project (OCCAM). This model has 66 vertical levels, with a horizontal resolution of 0.25° by 0.25° (Coward and de Cuevas, 2005). A subset of output was used. This covered the model domain 45°–75°S 100°–20°W and the upper 100 m of the water column (upper 14 model levels). For each calendar month, a depth-weighted mean velocity field was calculated over a 19-year run of this model (1985 to 2003). Prior to use in the advection scheme, the monthly mean velocity fields were modified according to Killworth (1996) to avoid errors associated with linear interpolation between mean fields.

The particles were advected using a second-order Runge-Kutta advection scheme, following Murphy et al. (2004). The advection scheme used a timestep of 0.1 day and did not explicitly include diffusion. The scheme applies a no-slip boundary condition at coasts and, once particles leave the model domain, they take no further part in the simulations. Particles were released on a regular grid within predefined areas of SSMUs and boundary areas, with a resolution of 0.25° latitude by 0.5° longitude. The particles were advected through the velocity fields for 183 days (~6 months) beginning on either 1 October or 1 April to derive the summer and winter transport rates respectively.

The instantaneous transport rate between model spatial units (SSMUs and boundary areas) was calculated as follows:

$$v_{m,n \neq m} = -\ln\left(1 - \frac{\theta_{m,n}}{\tilde{\theta}_m}\right) \tag{3a}$$

$$v_{m,n=m} = 0 \tag{3b}$$

where $\tilde{\theta}_m$ is the number of particles released in area m at the beginning of the advection period and $\theta_{m,n}$ is the number of these particles that were found in area n at the end of the period. The resulting summer and winter matrices are given in Tables 3 and 4.

Krill mean mass

The mean body mass of individual krill caught in nets during the CCAMLR 2000 Krill Synoptic Survey of Area 48 was calculated from data supplied by Dr V. Siegel (Sea Fisheries Institute, Hamburg, Germany). The overall mean mass was 0.46 g, but there was considerable between-haul variability in mean mass (range: 0.11 to 1.27 g, SD: 0.31 g, $n = 93$).

Fish

The krill-eating fish fauna are composed largely of demersal members of the order Perciformes (mainly families Nototheniidae and Channichthyidae, the icefish) and pelagic members of the family Myctophidae. The assumption was made that off-shelf areas are populated by a generic myctophid and that shelf areas are populated by a generic perciform. Generic parameters were estimated separately for these two taxa, and then combined according to estimated krill demand within SSMUs to estimate parameters for generic fish (equation 2). The body mass and mortality rates of these two taxa are very different, so the characteristics of generic fish varied with the relative area of the two habitats in each SSMU.

Although Kock (1992) reported the results of virtual population analyses (VPAs) for some Scotia Sea fish species, no stock-recruit information is available for relevant myctophid species. Also, life history information is scarce for many of the important krill-consuming fish. Therefore, the two parameters relating to recruitment ($\rho_{k,j}$ and $\alpha_{k,j}$) were not estimated for fish. Uncertainty was not evaluated for many of the derived parameters as it is unlikely that the limited available data fully reflect the spatial and temporal variability in fish population sizes.

Myctophid fish

Pusch et al. (2004) provided biomass density and krill consumption estimates for myctophids based on a limited study on the shelf slope near King George Island, suggesting that *Gymnoscopelus nicholsi* and *Electrona antarctica* are responsible for the majority of krill consumption by myctophids. $Q^*_{k,j,s}$ and $P_{k,j}$ estimates were based on data from Pusch et al. (2004) for these species (Notes F1 to F6; Tables 5 and 7). μ values for similar species were obtained from Kock (1992).

Perciform fish

$Q_{k,j,s}^*$ and $P_{k,j}$ estimates for perciform fish were based on estimates of abundance and krill consumption from extensive trawl surveys in three areas of the Scotia Sea, reported in Kock (1985) (Note F7; Table 6). Life history parameters for perciforms were based on *Champsocephalus gunnari*, which was the main krill consumer identified by Kock (1985). The μ for perciforms in Table 7 is the average of the range of values quoted for *C. gunnari* at South Georgia in Kock (1992). Growth parameters for *C. gunnari* from Agnew et al. (1998) were used to estimate mean mass, which, in turn, was used to estimate $P_{k,j}$ from biomass density data (Note F8).

Seals

Only one seal species was considered: the Antarctic fur seal (*Arctocephalus gazella*). There are considerable differences between the sexes of this species, in characteristics including age-at-first-reproduction, body size and mortality rate (Table 9). In addition, a substantial proportion of adult females do not breed each year, and these non-breeders are likely to have lower food requirements than those nursing pups. Average characteristics were therefore calculated across these three different groups of adult fur seals. This required the construction of a simple demographic projection to calculate sex ratios (Note S2; Table 8).

The life history parameters used in this demographic projection and to calculate $M_{k,j,s}$ and $\rho_{k,j}$ were obtained from McCann and Doidge 1987; Boyd et al. (1995); Wickens and York (1997); Boyd (2002b) and Goebel et al. (2006). The population growth rate reported by Payne (1977) was used to calculate α_{max}.

$P_{k,j}$ estimates were obtained from SC-CAMLR (2002). This lists the position of fur seal breeding colonies and the estimated number of breeding females in each colony. These colonies were assigned to the SSMUs they were located in and the abundance estimates were scaled up to include males and non-breeding females.

Estimates of annual krill requirements were taken from Boyd (2002a) (see Note S3). These were converted to $Q_{k,j,s}^*$ estimates using the arbitrary ratios in Table 9. The first-season requirement of pups was added to that of breeding females.

Penguins

Generic penguin parameters were calculated using specific parameters for Adélie (*Pygoscelis adeliae*), chinstrap (*P. antarctica*), gentoo (*P. papua*) and macaroni (*Eudyptes chrysolophus*) penguins. Abundance data from SC-CAMLR (2002) (derived largely from Woehler, 1993), were supplemented with data for four additional Adélie penguin colonies, provided by the CCAMLR Secretariat (Table 10), and $P_{k,j}$ was calculated using these data.

$M_{k,j,s}$, $\rho_{k,j}$ and $\alpha_{k,j}$ were calculated from basic life-history parameters in Williams (1995) and from the monitoring programs of BAS at Bird Island and Signy Island and the US Antarctic Marine Living Resources Program at Copacabana Beach, Admiralty Bay, King George Island. However, arbitrary values were used for juvenile μ and the proportion of non-breeding adults for all species (Notes P1 to P3). An arbitrary value was also used for the adult μ of chinstrap penguins.

$Q_{k,j,s}^*$ for Adélie, chinstrap and gentoo penguins were calculated from the krill consumption estimates and population structures in Croll and Tershy (1998) (Note P4). An arbitrary 1:1 sex ratio was assumed for the adult population and the individual krill requirements of adults were arbitrarily assumed to be constant throughout the year. Chick requirements during the breeding season were added to those of adults (Notes P5 and P6). The annual krill demand estimates for macaroni penguins in Boyd (2002a) were used to obtain $Q_{k,j,s}^*$ for this species (Note P6; Table 12).

Whales

Reilly et al. (2004) estimated the abundance and krill requirements of fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), minke (*B. bonaerensis*) and southern right whales (*Eubalaena australis*) as well as the overall abundance of 'large baleen' whales including humpback, fin, southern right, blue (*B. musculus*) and sei (*B. borealis*) whales in strata corresponding to the Scotia Sea and Antarctic Peninsula regions. Branch and Butterworth (2001) reported the number of pods, by species, sighted on surveys of larger strata that also overlap these areas. These two data sources were used to calculate $P_{k,j}$ limits for the species listed by Reilly et al. (2004) (Note W1). There was very good correspondence between these two data sources, with the Reilly et al. (2004) data estimating total whale abundance as (mean and 95% confidence intervals) 36 069 (9 831–42 274) and the Branch and Butterworth (2001) data estimating 34 145 (13 163–52 380).

These data, together with life history parameters from Laws (1977), Boness et al. (2002) and unpublished studies (Notes W4 and W5) were used to estimate separate generic parameters for the Scotia Sea and Antarctic Peninsula regions on the arbitrary assumption that whale fauna was comparable between the individual SSMUs in each region (Notes W1 to W8; Table 13).

KPFM input parameters and demand estimates

The parameters compiled here were used to derive KPFM input parameters for four generic predators representing fish, whales, penguins and seals (Tables 14 and 15). Except where the notes indicate otherwise, these values are based on average component parameters. The maximum annual krill demand, by predator type, per SSMU implied by the KPFM parameters was also estimated (Table 16). This suggests that fish are the major krill consumers in all SSMUs, with perciform fish taking as much krill as whales, penguins and fur seals combined and myctophid fish taking double that amount. Of the air-breathing predators, penguins have the highest demand. Krill consumption per unit predator biomass was also calculated for each of the generic predator taxa. These estimates are not strictly comparable between taxa (see caveats in the legend to Table 16). However, they suggest an enormous range in consumption to biomass ratios from 2 year^{-1} in whales to 103 year^{-1} in penguins.

Discussion

This paper compiles information about a number of species, taken from studies at a range of spatial and temporal scales, into a coherent and spatially resolved view of the regional krill-based food web. This can be used to parameterise population dynamic models for krill-dependent predators based on delay-difference equations, and it should be a useful reference for other analyses of the system at the regional and SSMU scales. This paper also illustrates a practical method for linking output from the OCCAM ocean circulation model to ecosystem dynamics models in the form of transport rates between SSMUs.

Tables 14 and 15 provide many of the input parameters required for KPFM.

Sets of plausible limit values are also available on request from the authors. However, there are a number of KPFM input parameters that have not been derived here.

These parameters concern the distribution of predator foraging effort amongst SSMUs other than the one in which the predators breed, and the form of functional relationships (describing the functional and numerical response of predators and the stock-recruit relationship for krill). It will be necessary to make assumptions about these parameter values and their associated uncertainty, and the onus is on the analyst to justify and test these assumptions.

The complexity and scale of the system and its dynamics ensure that it will be impossible to ever describe it fully. Therefore, while the parameters used here summarise the best available information about selected krill predators, they should not be considered definitive. This paper provides a clear audit-trail of its sources, methods and assumptions to facilitate the necessary scrutiny. It also represents uncertainty, where possible, by reporting plausible limits for parameter values. It is important to remember that, where such limits are not shown, it does not imply certainty in the parameter estimate, but rather a lack of information with which to quantify uncertainty. As an understanding of uncertainty is particularly important in evaluating management options, the remainder of this discussion highlights some additional uncertainties associated with the current parameter set.

While the published literature provides a repository of knowledge, it is not always current. This is particularly true for populations whose size changes rapidly or where new information has not yet been included in published population size estimates. The values used here for Antarctic fur seals at South Georgia are considered to be unreliable (J. Forcada, BAS, pers. comm.) and those for humpback whales in the Scotia Sea are considered to be underestimates (A. Martin, BAS, pers. comm.), although no revised estimates have been published.

Empirical values have been compiled from a variety of studies focusing on different, but limited, temporal and spatial scales. These studies inevitably represent a 'snapshot' of conditions that might not apply to other scales. In particular, the abundance estimates for the various predators may represent different states in the system's dynamics. Also, myctophid fish diets and densities from the shelf slope near King George Island have been extrapolated to all waters deeper than 500 m. Since this study identifies myctophids as the taxon that consumes most krill, there is a particular need to examine the uncertainty associated with this extrapolation. Furthermore, the field studies on which demand estimates are based usually consider time

periods of less than one year, which are usually in the summer months. Extrapolating from these to other parts of the year also introduces uncertainty. In particular, there is a risk of bias in the penguin demand estimates presented here. The extrapolations and assumptions of contemporaneousness made in this study do not imply that the system is homogenous and stable at the relevant scales. They merely highlight a lack of suitable information on its heterogeneity and dynamics.

The parameters presented here concern the 'krill-dependent' penguins and seals that are an important focus of the CCAMLR Ecosystem Monitoring Program, the baleen whales and fish. This combination is intended to represent current interest in the conservation of endothermic predators and the maintenance of viable fish stocks, and to capture important sources of krill consumption. However, this is not a comprehensive survey and other potentially important species, such as crabeater seals and squid, have not been included as there are few data to assess their abundance and krill requirements. Also, this compilation does not include demand estimates for independent juveniles of the species considered, which are likely to be substantial.

There are a number of other issues: (i) different whale species may have very different patterns of habitat use and baleen whale distribution might therefore differ from the assumptions presented here; (ii) breeding and non-breeding members of the same species also have different spatial distributions, so the total adult size may not always scale linearly with the breeding population size; (iii) model estimates of krill demand are sensitive to their assumptions; and (iv) the spatial and temporal resolution of these parameters will result in some loss of information compared to finer scales. For example, the transport matrices imply transport between non-adjacent SSMUs with no information on the intermediate SSMUs that particles passed through.

The estimates of krill demand must be interpreted in the light of the above caveats, but they suggest that krill demand outstrips estimated biomass, highlighting the uncertainty associated with many of these estimates.

Conclusion

This compilation of parameter values is intended for use in ecosystem dynamic models to support the management of the krill fishery in Area 48. These parameter values are based on a combination of empirical data, published models, informed estimates and some arbitrary, but clearly stated, assumptions. Consequently, there are many uncertainties associated with these parameters, which must be taken into account when they are used. The KPFM is designed to investigate the implications of differing assumptions and parameter values and it is therefore recommend that full use be made of this facility.

Myctophid fish appear to be the main krill consumers of the taxa considered, but the myctophid abundance estimates are particularly uncertain. This suggests that priority should be given to reducing this uncertainty and investigating its implications for krill management.

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Notes

Myctophid fish

F1. The biomass density is 0.6 times biomass per $1\,000\ \text{m}^3$ (Pusch et al., 2004) on the assumption that myctophids occupy a depth range of 600 m. This value was adjusted to account for waters between 500 and 600 m deep in later SSMU-specific calculations (see Note F11).

F2. Daily krill intake was multiplied by 365 to obtain annual consumption per unit biomass, and further multiplied by biomass density to obtain annual consumption per unit area.

F3. The lower mean mass is the mean value for *E. antarctica* (calculated as biomass over individuals) and the upper value is that for *G. nicholsi*. The average is the mean of these two values weighted by krill consumption per unit area.

F4. μ is the average of values for *G. nicholsi* (1.14) and *E. carlsbergi*, a congener of *E. antarctica* (0.86), obtained from Kock (1992, original source: Konstantinova, 1987).

F5. Biomass density is the sum of values for *E. antarctica* and *G. nicholsi*.

F6. It was assumed that myctophids consume two-thirds of their annual krill requirement in summer and the remaining third in winter. Krill demand per fish per season was calculated as the biomass-weighted sum of the lower estimates (10 hours feeding) of species-specific annual consumption per unit biomass (Table 5) divided by mean mass multiplied by proportion of annual demand consumed in the relevant season.

Perciform fish

F7. Kock (1985) included data from a third survey at South Georgia in the 1980/81 season, which is omitted here to allow comparability between areas when calculating averages. Kock's (1985) krill consumption estimates for *P. georgianus* at South Georgia in 1977/78, *C. gunnari* at the South Orkneys in 1975/76 and *C. rastrospinosus* at the South Orkneys in 1977/78 were modified so that the ratio of krill consumption to trawlable biomass was constant for each species–area combination.

F8. The mean mass of perciforms is based on *C. gunnari* in age classes 3+ to 7+ using the von Bertalanffy growth parameters of North (2005), the length–weight relationship of Agnew et al. (1998), μ of 0.46 (Kock, 1992; Note F9), and a constant recruitment which replaces losses due to mortality.

F9. μ for perciforms is the average of estimates for *C. gunnari* at South Georgia listed in Kock (1992).

F10. Perciform biomass density is the sum of biomass values divided by twice the sum of areas in Table 6.

F11. Perciforms at South Georgia were assumed to consume 82% of their annual krill intake in summer, and those elsewhere were assumed to consume 80% in summer. These ratios were based on a recalculation of

Kock's (1985) consumption estimates using the summer and winter rations quoted in that paper, and the following assumptions (as specific values for some parameters were not provided in the paper):

- the proportion of krill in the diets of *N. rossii* and *C. gunnari* at Elephant Island and the South Orkneys was 0.95;

- the length of each season was 105.5 days (to account for a 64-day fast around spawning).

Similar calculations were used to estimate the limits on per capita krill demand with the following assumptions:

- the minimum and maximum proportion of krill in the diet of each species is 0.152 (based on the minimum frequency of occurrence for *N. rossii* quoted by Kock, 1985) and 1;

- the maximum daily ration (as a proportion of body mass) is 0.101 in summer and 0.013 in winter. These are the maximum values for *C. gunnari* and *N. rossii* in the appropriate seasons, quoted in Kock (1985);

- the minimum daily ration was 0.012 in both seasons. This is the minimum for *N. larseni* quoted in Kock (1985).

The annual krill requirement per fish was calculated as summed consumption over summed biomass from Table 6 multiplied by mean body mass.

Generic fish

F12. The abundance of individual fish taxa was calculated as biomass density multiplied by habitat area (shelf or adjusted off-shelf) divided by mean body mass. Myctophid habitat area was calculated as off-shelf area minus one-twelfth of the area between 500 and 600 m deep (Table 2). Abundance was multiplied by individual krill requirements to calculate total demand (Table 16). Total seasonal demand was divided by $Q_{k,j,s}^*$ for generic fish to calculate the abundance of generic fish (Table 5).

Seals

S1. μ values were calculated from survivorship estimates in Boyd (2002b) for males and Goebel et al. (2006) for females and post-weaning juveniles. ρ for each sex, the maximum breeding age of females (reproductive longevity = 23 years), and the proportion of non-breeding females (pregnancy rate = 77.4%) were taken from Wickens and York (1997).

S2. The female:male ratio (1:0.16) was calculated from the simple demographic model in Table 8, based on the μ, ρ and longevity parameters in Table 9. μ for males was assumed to be equal to the female rate until the males joined the breeding population.

S3. Annual krill demand was estimated using data from Boyd (2002a). The total annual krill demand (3.84 million tonnes) was divided amongst the different sexes and age

classes in Table 3 of Boyd (2002a) according to the sum of carbon flux and sequestration (growth) for each age class in each sex.

S4. The overall μ was calculated as the average of male and female rates, i.e. $\mu_G = \frac{o\mu_M + \mu_F}{1+o}$ where o is the number of adult males (aged ≥ 7 years) per adult female and μ_M and μ_F are the male and female mortality rates. Arbitrary values were used for the division of krill demand amongst seasons. $Q_{k,j,s}^*$ for all SSMUs was calculated as:

$$Q_{k,j,s}^* = \frac{\omega_J.P_s(\omega_J) + \omega_M.P_s(\omega_M).m + \omega_F.P_s(\omega_F).(1+n)}{1+n+m}$$

where n is non-breeding females per breeding female, m is males per breeding female, ω_J is the annual krill demand of juveniles and $P_s(\omega_J)$ is the proportion of this demand taken in season s. This calculation assigns additional demand for one juvenile to each breeding female. The scale factor was calculated as the demand-weighted average of the relative proportions of breeding and non-breeding females and males. The maximum value of α was used to calculate Tables 14 to 16.

Penguins

P1. Individual body mass for Adélie penguins was calculated as the overall mean (and range) of annual mean arrival weights at Copacabana Beach (1990 to 2005). That for macaroni penguins was the overall mean (and range) of annual mean arrival weights at Bird Island (1988 to 2005). For chinstrap penguins, the minimum is the minimum annual mean from Copacabana (1991 to 2005) and the maximum is the maximum annual average from Signy Island (1996 to 2005) while the average is the unweighted mean of the means from these two sites. Mean, minimum and maximum body mass for gentoos were calculated as the averages across sexes of the mean, minimum and maximum quoted in Williams (1995).

P2. Adult μ values for Adélie and gentoo penguins were taken from Williams (1995) with the average as the midpoint of the two extreme values although a more extreme maximum (1.81) was observed for Adélies at Copacabana Beach. Arbitrary values were used for chinstrap and macaroni penguin averages and the extreme values for macaroni penguins were based on return and non-breeding rates quoted in Williams (1995). No information on juvenile μ was available and arbitrary values were used for all species. The already high adult values were used for chinstrap and gentoo penguins.

P3. ρ values were taken from Williams (1995) for all species except chinstrap penguins, for which the gentoo penguin values were used. An arbitrary minimum was used for macaroni penguins.

P4. The average number of chicks fledged per individual were the averages (weighted by sample size) across years for Adélie (1977 to 2005) and gentoo (1991 to 2005) penguins from Copacabana Beach and chinstrap penguins (1997 to 2005) from Cape Shirreff. The minimum number

of chicks fledged per individual Adélie penguin and the maximum for gentoo penguins were also obtained from these data. The remaining values were taken from Williams (1995).

P5. The assumed proportion of non-breeding adults for all species was essentially arbitrary but based on the following figures quoted in Williams (1995): 2–14% of macaroni penguins, 4–26% of male Adélie penguins and 2–18% of female Adélie penguins join colonies but do not breed.

P6. Fledging chicks per adult was calculated as chicks per breeding adult multiplied by (1-proportion of non-breeders in the adult population). α was calculated using Equation 1b.

P7. Information on the krill demand of Adélie, chinstrap and gentoo penguins was obtained from Croll and Tershy (1998). Table 2 of Croll and Tershy (1998) contains an apparent error in the krill requirements for Adélie penguin chicks, so this value was recalculated from the energy requirements given in the same table.

P8. The number of chicks per breeding pair was calculated as 2 times chicks per breeding adult. The population structure for Adélie, chinstrap and gentoo penguins was taken from Croll and Tershy (1998).

P9. Summer Q^* for Adélie, chinstrap and gentoo penguins was calculated as

$$Q^* = 0.5\left[1.52(q_m + q_f) + \left(2 - \frac{1}{1 - U_n}\right)q_c C\right]$$

where q_m, q_f and q_c are the krill demands of males, females and chicks respectively, U_n is the proportion of non-breeders and C is the number of chicks per pair. The factor 1.52 scales the 120-day period of Croll and Tershy's (1998) estimates to half a year. Winter demand was calculated as $Q^* = 0.5\left(1.52(q_m + q_f)\right)$. This calculation assigns the requirements of unfledged chicks to their parents.

P10. $Q^*_{k,j,s}$ for macaroni penguins was derived from Boyd (2002), who estimated that 17 876 000 adults consumed 8.08 million tonnes of krill in one year. The total demand was divided equally between summer and winter.

Whales

W1. The density of whales in each stratum listed in Branch and Butterworth (2001) was calculated as the product of mean school size and number of schools sighted divided by twice the product of search distance and search half width. The density of whales in each region (the Scotia Sea and the Antarctic Peninsula) was then calculated as the stratum area weighted average of

densities in overlapping strata. Finally, the abundance by SSMU was calculated as the product of SSMU area and the relevant regional density. Upper and lower limits for these values were calculated by adjusting the regional densities by 1.96 times the CVs (to approximate 95% confidence intervals) for 'Comparable areas + like species' quoted in Branch and Butterworth (2001).

Densities estimated directly from Reilly et al. (2004) and the stratum areas in Hewitt et al. (2004b) were used to calculate another set of whale abundances, with limits based on 1.96 times CV in the SSMUs. The Branch and Butterworth (2001) data did not include southern right whales, so the abundance estimates from this dataset were supplemented by southern right whale estimates from Reilly et al. (2004). The average and minimum abundances in Table 13 are based on the Reilly et al. (2004) data while the maximum is based on the supplemented Branch and Butterworth (2001) data.

The Branch and Butterworth (2001) data suggest sei whale to blue whale ratio of 11:1, which was used to calculate parameters for the aggregated species.

W2. Consumption estimates were taken from Reilly et al. (2004). Estimates for species other than minke whales are based on Reilly et al.'s (2004) revised version of the Innes et al. (1986) model (means), the unrevised Innes et al. (1986) model (minima) and a model fitted to blue whales consuming 3% of their body weight per day (maxima).

W3. Whale mean body mass estimates were taken from Reilly et al. (2004).

W4. Estimates of μ for adult baleen whales were taken from Laws (1977) except the value for southern right whales, which is based on calculations by P. Best (University of Pretoria) and co-workers (D. Butterworth, University of Cape Town, South Africa, pers. comm.) and that for minke whales for which an arbitrary value was assigned. The minimum value of 0.01 in all cases is that for southern right whales while 0.1 is an arbitrary upper limit.

W5. The ρ and inter-birth intervals are taken from Boness et al. (2002). The α values were calculated from Equation 1b with an assumed first year μ of 0.31 (value calculated for southern right whales by P. Best and co-workers).

W6. Baleen whales were assumed to feed on krill for 120 days in the summer (Reilly et al., 2004). Total summer consumption was therefore the sum of products of individual daily krill consumption and abundance of each species multiplied by 120. This was divided by the biomass of baleen whales to give krill consumption per unit baleen whale biomass for each stratum.

Table 1: Definitions of the KPFM model parameters derived in this paper.

Symbol	Description	Miscellaneous notes
$M_{k,j,s}$	Mean instantaneous natural mortality rate for predators of taxon k in SSMU j and season s.	Annual natural mortality rates are denoted μ.
$\rho_{k,j}$	Age (in years) at recruitment to the adult population for predators of taxon k in SSMU j.	The KPFM explicitly models only the adult part of predator populations.
$\alpha_{k,i}$	Maximum per capita recruitment at low adult abundance when all adults breed for taxon k in SSMU j.	This is used in the 'gamma' stock recruitment model (e.g. Quinn and Deriso, 1999) used to represent predator recruitment dynamics in the KPFM.
$P_{k,j}$	Initial abundance of predators of taxon k in SSMU j.	Used to initialise KPFM simulations.
$Q^*_{k,j,s}$	Maximum per capita potential consumption of krill for taxon k in SSMU j and season s.	A key parameter in the KPFM's predation function.

Table 2: SSMU and boundary area names, areas and total krill catch (1988 to 2002). Shelf area is the area of water with depth ≤500 m and off-shelf area is the area of water with depth >500 m. SSMU areas were calculated from the Smith and Sandwell (1997) dataset, boundary areas were calculated from the GEBCO dataset (IOC et al., 2003), krill catch data were taken from Hewitt et al. (2004a) and krill biomass is the product of density reported in Hewitt et al. (2004a) and the area reported here.

Area	Name	Shelf area (km²)	% of SSMU with depth 500–600 m	Off-shelf area (km²)	Total area (km²)	Krill catch (tonnes)	Krill biomass (tonnes)
1	Antarctic Peninsula Pelagic Area (APPA)	80 971	2.13	341 105	422 076	25 376	4 727 251
2	Antarctic Peninsula West (APW)	26 901	14.64	8 159	35 060	7 400	1 321 762
3	Drake Passage West (APDPW)	6 799	3.42	8 269	15 068	227 741	568 064
4	Drake Passage East (APDPE)	7 973	3.28	7 611	15 584	103 169	587 517
5	Bransfield Strait West (APBSW)	11 243	6.79	9 773	21 017	11 463	792 303
6	Bransfield Strait East (APBSE)	14 763	5.25	12 684	27 447	5 952	1 034 752
7	Elephant Island (APEI)	8 141	8.07	27 182	35 322	94 930	1 331 677
8	Antarctic Peninsula East (APE)	55 325	2.94	3 379	58 704	25	2 213 141
9	South Orkney Pelagic Area (SOPA)	12 303	0.67	796 861	809 163	6 248	19 824 518
10	South Orkney West (SOW)	2 591	1.89	12 978	15 569	217 374	2 341 578
11	South Orkney North East (SONE)	2 585	1.59	7 666	10 251	15 856	1 541 750
12	South Orkney South East (SOSE)	13 636	0.34	1 318	14 954	19 531	2 249 082
13	South Georgia Pelagic Area (SGPA)	5 307	0.05	914 227	919 534	7 822	22 528 583
14	South Georgia West (SGW)	16 286	1.21	25 832	42 119	31 436	1 655 237
15	South Georgia East (SGE)	19 225	1.79	34 510	53 735	208 870	2 111 786
16	Boundary area 1 (Bellingshausen Sea)				1 880 955		
17	Boundary area 2 (Drake Passage)				779 869		
18	Boundary area 3 (Weddell Sea)				523 502		

Table 3: Maximum instantaneous krill transport rates between the model areas shown in Figure 1 during summer. SSMUs and boundary areas (BAs) are numbered as in Table 2.

Name	SSMU															Boundary area		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	1	2	3
SSMU.1	0.000	0.039	0.009	0.002	0.009	0.015	0.014	0.000	0.312	0.006	0.000	0.003	0.389	0.014	0.011	0.000	0.011	0.085
SSMU.2	0.077	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.325	0.000	0.000	0.000	0.275	0.000	0.000	0.000	0.000	0.000
SSMU.3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.190	0.000	0.000	0.000	0.000	0.245
SSMU.4	0.000	0.000	0.000	0.000	0.000	0.000	0.044	0.000	0.000	0.000	0.000	0.000	0.302	0.000	0.000	0.000	0.000	1.190
SSMU.5	0.000	0.033	0.033	0.000	0.000	0.033	0.000	0.000	0.033	0.000	0.000	0.000	0.949	0.000	0.000	0.000	0.000	0.215
SSMU.6	0.024	0.000	0.000	0.000	0.024	0.000	0.000	0.000	0.024	0.000	0.000	0.000	0.150	0.000	0.000	0.000	0.000	0.765
SSMU.7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.260	0.000	0.000	0.000	0.065	0.000	0.000	0.000	0.000	0.927
SSMU.8	0.086	0.000	0.000	0.000	0.000	0.053	0.042	0.000	0.180	0.031	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.042
SSMU.9	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.011	0.006	0.002	0.000	0.000	0.000	0.000	1.011
SSMU.10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	2.996	0.000	0.000	0.000	0.051	0.000	0.000	0.000	0.000	0.000
SSMU.11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	2.773	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SSMU.12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.658	0.000	0.211	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SSMU.13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.016	0.000	0.001	1.558
SSMU.14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.047	0.000	0.229	0.000	0.000	1.299
SSMU.15	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	1.720
BA.1	0.129	0.005	0.003	0.003	0.001	0.002	0.007	0.000	0.015	0.000	0.000	0.000	0.093	0.000	0.000	0.000	0.226	0.000
BA.2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.256	0.027	0.022	0.000	0.000	0.000
BA.3	0.136	0.000	0.000	0.000	0.000	0.000	0.008	0.056	0.350	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 4: Maximum instantaneous krill transport rates between model areas during winter. SSMUs and boundary areas (BAs) are numbered as in Table 2.

Name	SSMU															Boundary area		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	1	2	3
SSMU.1	0.000	0.034	0.000	0.000	0.014	0.014	0.062	0.000	0.240	0.009	0.002	0.000	0.407	0.023	0.018	0.000	0.026	0.000
SSMU.2	0.097	0.000	0.000	0.000	0.038	0.000	0.000	0.000	0.160	0.000	0.000	0.000	0.405	0.000	0.000	0.000	0.000	0.000
SSMU.3	0.000	0.000	0.000	0.000	0.044	0.000	0.000	0.000	0.000	0.000	0.000	0.000	2.037	0.000	0.000	0.000	0.000	0.000
SSMU.4	0.000	0.000	0.000	0.000	0.000	0.000	0.044	0.000	0.000	0.000	0.000	0.000	0.302	0.000	0.000	0.000	0.000	0.000
SSMU.5	0.000	0.000	0.033	0.000	0.024	0.067	0.000	0.000	0.102	0.000	0.000	0.000	1.488	0.000	0.000	0.000	0.000	0.000
SSMU.6	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.072	0.000	0.000	0.000	0.327	0.000	0.000	0.000	0.000	0.000
SSMU.7	0.043	0.000	0.000	0.024	0.000	0.000	0.000	0.000	0.234	0.000	0.000	0.000	0.043	0.000	0.000	0.000	0.000	0.000
SSMU.8	0.031	0.000	0.000	0.000	0.000	0.053	0.075	0.000	0.086	0.000	0.000	0.000	0.086	0.000	0.000	0.000	0.000	0.010
SSMU.9	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.007	0.009	0.002	0.000	0.006	0.000	0.000	0.000
SSMU.10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.897	0.000	0.000	0.051	0.000	0.000	0.000	0.000	0.000	0.000
SSMU.11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	11.513	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SSMU.12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.946	0.000	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SSMU.13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.008	0.000	0.000	0.000
SSMU.14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.071	0.000	0.258	0.000	0.000	0.000
SSMU.15	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.062	0.000	0.000	0.000	0.000	0.000
BA.1	0.128	0.005	0.003	0.001	0.001	0.001	0.006	0.000	0.011	0.000	0.000	0.000	0.102	0.000	0.000	0.000	0.226	0.000
BA.2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.266	0.022	0.016	0.000	0.000	0.000
BA.3	0.136	0.000	0.000	0.000	0.000	0.000	0.030	0.065	0.401	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 5: Density, mean body mass and krill requirements of the two main krill-eating myctophids sampled in slope waters near King George Island in 1996. Data from Pusch et al. (2004). Consumption estimates are based on 10 (minimum) and 24 (maximum) hours' feeding per day.

	Individuals per 1 000 m^3	Biomass (g) per 1 000 m^3	Mean weight (g)	Biomass density (kg/km^2)	Daily krill intake as % fish wet weight	Annual krill consumption per unit biomass	Annual krill consumption kg/km^2
Electrona antarctica	0.595	4.080	6.86	2 448	1.06–2.54	3.87–9.27	947 085–2 269 430
Gymnoscopelus nicholsi	0.042	1.368	32.57	821	0.65–1.57	2.37–5.73	194 749–470 394
Further information				F1		F2	F2

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Table 6: Estimated biomass and annual krill requirements of seven species of perciform fish in three areas of the Scotia Sea during surveys in the mid-1970s, and the shelf area (depth ≤500 m) of non-pelagic SSMUs in these areas. Biomass and krill consumption data are adapted with permission from Kock (1985) (see Note F7). Area data are from Table 2.

Area	Shelf area (km²)	Season	Notothenia rossii	Notothenia gibberifrons	Notothenia larseni	Champsocephalus gunnari	Chaenocephalus aceratus	Pseudochaenichthys georgianus	Chionodraco rastrospinosus
Trawlable biomass (tonnes)									
South Georgia	21 593	1975/76	35 682	40 094	449	141 469	18 719	36 401	-
		1977/78	9 326	20 100	422	34 713	18 399	31 057	-
South Orkneys	18 812	1975/76	133	68 430	562	140 000	9 854	8 270	8 759
		1977/78	284	29 187	505	40 000			
Elephant Island	8 141	1975/76	9 370	16 471	100	20 000	1 249		
		1977/78	15 663	17 824	90	20 000			1 015
Sum	48 545		70 458	192 106	2 128	396 182	48 221	75 728	9 774
Krill consumption (tonnes)									
South Georgia		1975/76	160 800	18 000	1 000	630 000	33 700	131 000	-
		1977/78	42 000	9 000	900	156 200	33 100	111 800	-
South Orkneys		1975/76	1 100	30 700	1 300	1 197 000	-	-	31 500
		1977/78	2 400	13 100	1 100	342 000	17 700	29 800	-
Elephant Island		1975/76	80 100	7 400	200	171 000	-	-	-
		1977/78	133 900	8 000	200	171 000	2 200	-	3 700
Sum			420 300	86 200	4 700	2 667 200	86 700	272 600	35 200

Table 7: Further assumptions and parameters used to calculate generic fish parameters.

Taxon	Habitat	Mean mass (g)	μ	Biomass density (tonnes/km²)		Krill demand (g per fish per season)	
						South Georgia	Elsewhere
Myctophids	Offshelf waters (>500 m)	11.24 (6.86–32.6)	1.00 (0.86–1.14)	3.27	Summer		26.19
					Winter		13.09
Further information		F3	F4	F5			F6
Percriforms	Shelf waters (≤500 m)	363	0.46 (0.19–0.60)	8.18	Summer	998 (100–5 518)	1 648 (100–5 518)
					Winter	248 (100–710)	351 (100–710)
Further information		F8	F9	F10			F11

Table 8: Simple demographic projection, showing expected survivorship-at-age (from age 3) for Antarctic fur seals, and the sex ratio of adults above the age-at-first-breeding calculated from it. See Note S2 for further details.

Age	Male	Female	Age	Male	Female
3		1.000	15	0.002	0.165
4		0.861	16	0.001	0.142
5		0.741	17	0.001	0.122
6		0.638	18	0	0.105
7	0.549	0.549	19	0	0.091
8	0.274	0.472	20	0	0.078
9	0.137	0.407	21	0	0.067
10	0.069	0.350	22	0	0.058
11	0.034	0.301	23	0	0.050
12	0.017	0.259	24	0	0.043
13	0.009	0.223	25	0	0.037
14	0.004	0.192	26	0	0.032
			Totals	1.098	6.983
			Males/female	0.157	

Table 9: Basic parameters for Antarctic fur seals.

	Male	Non-breeding female	Pup	Breeding female	Generic	Source
μ	0.69	0.15	0.35	0.15	0.26	S1/S4
ρ	7			3	3.82	S1
Maximum breeding age				26		S1
Proportion of adults that do not breed					0.23	S1
Non-breeding females per breeding female					0.29	S1
Adult males per female					0.16	S2
Adult males per breeding female					0.20	S2
Maximum rate of population increase					16.8%	Payne (1977)
α					0.15–0.40	S4
Annual krill demand (kg)	3 997	1 778	1 225	2 636		S3
Proportion of annual demand in first season	0.5	0.5	0.7	0.66		S4
Proportion of annual demand in second season	0.5	0.5	0.3	0.34		S4
Summer per capita krill demand (kg)	1 998	889		1 747	1 613	S4
Winter per capita krill demand (kg)	1 998	889		889	1 040	S4
Scale factor (breeding females to whole population)					1.34	S4

Table 10: Population size data for four Adélie penguin colonies that were not included in SC-CAMLR (2002) plus species-specific totals for data included in the published version of the table.

Species	Centre no.	Longitude	Latitude	No. of pairs	Biomass (kg)
Adélie penguin	104	−45.0333	−60.7333	16 750	150 750
	105	−44.4000	−60.7167	94 462	850 158
	106	−45.9167	−60.6333	5 700	51 300
	107	−44.6833	−60.7667	24 600	221 400
Summary					
Adélie penguin				523 002	4 707 018
Chinstrap penguin				2 390 447	19 123 576
Gentoo penguin				204 563	2 454 756
Macaroni penguin				3 345 465	30 109 185

Table 11: Biomass (kg) by species of breeding penguins in each SSMU. Data from SC-CAMLR (2002) and Table 10.

SSMU	Adélie	Chinstrap	Gentoo	Macaroni
APPA				
APW	395 289	300 792	230 688	
APDPW	18	229 320	42 240	
APDPE		3 735 280	77 424	
APBSW		3 948 656	145 296	
APBSE	512 019	363 808	195 516	
APEI	18	4 922 560	31 200	
APE	2 767 041		9 432	
SOPA				
SOW		8 000		
SONE	1 921 716	40 000	12 120	
SOSE	1 284 525	5 575 160	134 640	
SGPA				
SGW			673 008	28 501 245
SGE			903 192	1 607 940

Table 12: Parameters for individual penguin species.

Parameter	Adélie	Chinstrap	Gentoo	Macaroni	Source
Body mass (kg)	3.96 (3.77–4.17)	4.12 (3.59–5.02)	5.37 (5.10–5.55)	5.16 (4.87–5.43)	P1
μ (adults)	0.12 (0.03–0.21)	0.22	0.22 (0.16–0.29)	0.08 (0.08–0.67)	P2
μ (juveniles)	0.20	0.22	0.22 (0.16–0.29)	0.12 (0.12–0.12)	P2
ρ	5 (4–7)	3 (2–5)	3 (2–5)	5 (5–8)	P3
Average fledging chicks/individual	0.46 (0.17–0.92)	0.47 (0.01–0.70)	0.70 (0.45–0.81)	0.22 (0.34–0.52)	P4
Proportion non-breeders	0.15 (0.15–0.15)	0.15 (0.15–0.15)	0.15 (0.15–0.15)	0.15 (0.15–0.15)	P5
Fledging chicks/adult	0.39 (0.14–0.78)	0.40 (0.01–0.59)	0.60 (0.38–0.69)	0.19 (0.29–0.44)	P6
α	0.14 (0.04–0.35)	0.21 (0.00–0.38)	0.31 (0.17–0.39)	0.10 (0.11–0.24)	P6
Individual krill requirements during breeding and rearing season (120 days in summer)					
Male (kg)	162 (113–211)	142 (99–185)	128 (90–166)		P7
Female (kg)	158 (111–205)	130 (91–169)	128 (90–166)		P7
Chick (kg)	152 (107–198)	113 (79–147)	103 (72–134)		P7
Population structure (thousands)					
Adults	131	1 620	18		P8
Chicks	129	770	19		P8
Chicks per pair	1.97 (1.97–1.97)	0.95 (0.95–0.95)	2.12 (2.12–2.12)		P8
Summer Q^* (kg)	367 (257–477)	251 (176–326)	285 (199–370)	226 (158–294)	P9/P10
Winter Q^* (kg)	243 (170–316)	207 (145–269)	195 (136–253)	226 (158–294)	P9/P10

Table 13: Parameters for individual baleen whale species.

Species	μ	ρ	Inter-birth interval	α	Body mass (kg)	Daily krill consumption	Scotia Sea abundance	Antarctic Peninsula abundance
Fin	0.04 (0.01–0.1)	5 (5–8)	2.50 (2–3)	0.12 (0.06–0.18)	48 768	693 (581–1 518)	3 180 (0–16 556)	1 492 (0–1 339)
Humpback	0.07 (0.01–0.1)	5	2.50 (2–3)	0.11 (0.08–0.18)	26 924	497 (390–874)	2 493 (0–5 050)	6 991 (2 550–679)
Minke	0.09 (0.01–0.1)	6 (6–8)	2.50 (2–3)	0.09 (0.06–0.17)	6 272	224	10 730 (4135–14 466)	7 395 (2 180–10 065)
Southern right	0.01 (0.01–0.1)	8 (7–10)	4.00 (3–5)	0.09 (0.03–0.11)	55 880	748 (637–1 723)	1 712 (0–1 712)	43 (0–43)
Blue and sei (Note W1)	0.07 (0.01–0.1)	8 (5–10)	2.50 (2–3)	0.09 (0.05–0.18)	23 326	440 (341–756)	1 772 (831–2 270)	261 (135–200)
Source	W4	W5	W5	W5	W3	W2	W1	W1

Table 14: KPFM input parameters (life history parameters) for generic predators ($M_{k,j,s}$ is assumed to be constant across seasons).

SSMU	$M_{k,j,s}$				$\rho_{k,j}$			$\alpha_{k,i}$		
	Fish	Whales	Penguins	Seals	Whales	Penguins	Seals	Whales	Penguins	Seals
APPA	0.37	0.03			5			0.11		
APW	0.25	0.03	0.08		5	4		0.11	0.20	
APDPW	0.29	0.03	0.11	0.13	5	3	4	0.11	0.23	0.40
APDPE	0.28	0.03	0.11	0.13	5	3	4	0.11	0.22	0.40
APBSW	0.28	0.03	0.11		5	3		0.11	0.22	
APBSE	0.28	0.03	0.08	0.13	5	4		0.11	0.19	
APEI	0.35	0.03	0.11		5	3	4	0.11	0.22	0.40
APE	0.23	0.03	0.06		5	5		0.11	0.14	
SOPA	0.48	0.03	0.00		6			0.10		
SOW	0.38	0.03	0.11		6	3		0.10	0.22	
SONE	0.35	0.03	0.06		6	5		0.10	0.15	
SOSE	0.24	0.03	0.10		6	3		0.10	0.20	
SGPA	0.50	0.03			6			0.10		
SGW	0.34	0.03	0.04	0.13	6	5	4	0.10	0.11	0.40
SGE	0.34	0.03	0.07	0.13	6	4	4	0.10	0.18	0.40

Table 15:   KPFM input parameters (initial abundance and seasonal per capita demand) for generic predators. Season 1 is summer and season 2 is winter.

SSMU	$P_{k,j}$				$Q^*_{k,j,1}$ (g of krill)				$Q^*_{k,j,2}$ (g of krill)			
	Fish	Whales	Penguins	Seals	Fish	Whales	Penguins	Seals	Fish	Whales	Penguins	Seals
APPA	8 402 727 132	9 233	-	-	897	54 942 525	-	-	125	-	-	-
APW	834 429 245	767	253 873	-	1 558	54 942 525	311 307	-	310	-	221 278	-
APDPW	301 932 508	330	74 798	12 204	1 325	54 942 525	255 235	1 613 386	227	-	205 329	1 039 700
APDPE	322 045 302	341	1 084 367	211	1 384	54 942 525	251 591	1 613 386	245	-	206 643	1 039 700
APBSW	438 862 551	460	1 160 224	-	1 405	54 942 525	251 988	-	252	-	206 499	-
APBSE	574 691 426	600	298 817	-	1 407	54 942 525	314 812	-	253	-	223 652	-
APEI	679 683 642	773	1 413 511	1 002	992	54 942 525	251 228	1 613 386	144	-	206 775	1 039 700
APE	1 553 175 192	1 284	823 403	-	1 628	54 942 525	366 713	-	342	-	243 211	-
SOPA	69 055 728 795	6 808	-	-	140	60 444 604	-	-	24	-	-	-
SOW	320 095 594	131	2 286	-	827	60 444 604	251 065	-	112	-	206 833	-
SONE	196 909 670	86	584 507	-	1 035	60 444 604	364 280	-	153	-	242 398	-
SOSE	389 311 850	126	2 003 958	-	1 616	60 444 604	273 603	-	336	-	213 599	-
SGPA	248 777 387 143	7 737	-	-	43	60 444 604	-	-	16	-	-	-
SGW	1 140 779 048	354	6 642 811	611 054	659	60 444 604	227 304	1 613 386	176	-	225 304	1 039 700
SGE	1 477 796 628	452	564 496	6 090	631	60 444 604	246 586	1 613 386	165	-	215 006	1 039 700

Table 16: Total krill demand (thousand tonnes), total biomass and krill consumption per unit biomass (Q/B) by taxonomic group and SSMU implied by the KPFM parameters in Table 15. Note that Q/B does not include consumption of prey other than krill and that adult consumption estimates for seals and penguins include dependent offspring. Fur seal mean body mass was assumed to be 35 kg for the purposes of estimating biomass. See also Notes F12 and S4.

SSMU	Myctophid fish	Perciform fish	Whales	Penguins	Seals
APPA	3 889	3 647	507		
APW	88	1 212	42	135	
APDPW	94	306	18	34	32
APDPE	86	359	19	497	1
APBSW	110	506	25	532	
APBSE	143	665	33	161	
APEI	308	367	42	647	3
APE	37	2 492	71	502	
SOPA	9 097	554	412		
SOW	148	117	8	1	
SONE	87	116	5	355	
SOSE	15	614	8	976	
SGPA	10 442	149	468		
SGW	295	457	21	3007	1 621
SGE	393	540	27	261	16
Subtotal	25 234	12 102	1 706	7 108	1 673
Total					47 823
Biomass (thousand tonnes)	7 224	2 324	835	69	22
Annual Q/B	3.5	5.2	2.0	103.2	76.5

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