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Progress on Multi-species Modeling in the Antarctic

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Abstract

This paper introduces a multi-species predator-prey model of whales, seals and krill in the Antarctic that is currently in development, and illustrates some example results that are obtained from the model. Due to limited time, sensitivities of the output of the model to various input parameter values and functional response forms have not yet been investigated, and are planned for future work. Preliminary results show the possible role of predator-prey interactions in influencing the dynamics of the Antarctic species considered in the model.

Introduction and aim of this work

This paper is an expansion of the work of Mori and Butterworth (2004) which considered blue and minke whales and krill. There are three major new aspects that are introduced in this paper:

1. The Southern Ocean is divided into two regions as detailed in the “Incorporating Regional Effect” section.
2. Other baleen whales and seals that mainly feed on krill, specifically humpback whales, fin whales, Antarctic fur seals and crabeater seals, are also included in the model.
3. An intra-specific density dependent term is incorporated in the population dynamics of the predators.

The framework for introducing these aspects will be detailed later.

The main objective of this paper is to investigate the following question:

> Simply by considering the krill-centric major predator-prey interactions and the available knowledge concerning these species (including their historical catches), to what extent can these interactions alone reproduce the abundances and their trends as observed in recent surveys of these species? In other words, is it possible to qualitatively and quantitatively evaluate to what extent predator-prey interactions may be controlling the population abundances and trends of krill and its major predators?

By answering this question, we hope to provide further insight on the extent to which predator-prey interactions may have influenced krill and their predators in the Antarctic, and improve understanding of the functioning and hence predictability of the Antarctic marine ecosystem.

Species considered in the model

Figure 1 provides a schematic diagram of the krill-centric major trophic interactions in the Antarctic. Unlike other marine ecosystems in lower latitudes where many species interact with each other in a complex manner, the trophic interactions in the Antarctic are fairly simple. Baleen whales, some squid, fish, seabirds and some seals prey directly on krill. The amount of krill consumed by each group of species differs depending on their abundances, diet compositions, daily intake of food and the period over which they feed in the Antarctic.

In order to evaluate the magnitude of impact of consumption by the predator groups shown in Figure 1 on krill abundance, we summarize approximate estimates of krill consumption by each predator group in the Antarctic in Table 1. The derivations of the consumption estimates for baleen whales since the 1980s, and also for those for seals, are detailed in Mori (in preparation).

It can be seen from Table 1 that, before their exploitation began, baleen whales were probably the major predators of krill, followed by seals. This indicates that the impact of consumption by whales and seals in the Antarctic on krill is large, and thus baleen whales (specifically, blue, minke, humpback and fin whales[1]) and seals (Antarctic fur seals and crabeater seals[2]) are considered in the model developed. A particular difficulty, as is evident from Table 1, is that no detailed information exists on the consumption of krill by cephalopods, fish and birds for the period prior to the exploitation of the baleen whales. Even for recent years, knowledge of abundances of and consumption by these species (particularly for squid and fish) is still very limited, and the estimates are heavily dependent upon various assumptions. Due to this lack of data, we do not in this paper directly consider the effect of consumption by these species on krill and on the predator-prey dynamics in the Antarctic. Instead, the potential impacts of these species on predator-prey dynamics will be considered at a later stage of this study. Thus, in summary, blue, minke, humpback and fin whales, and Antarctic fur and crabeater seals are considered as the major krill predators in the model developed. Antarctic fur seals are considered only in Region A (defined below) since their distribution is essentially restricted to the Atlantic side of the Antarctic.

Incorporating regional effects

The model to be developed divides the Antarctic into two regions: the one is the Atlantic and Indian Oceans region, which corresponds essentially to the IWC Management Areas II, III and IV, and the other is the Pacific Ocean region, which corresponds to the IWC Management Areas V, VI and I. The two regions together with the IWC Management Areas are shown in Figure 2. For convenience, we refer to the former region as Region A, and the latter as Region P. The reason for dividing the Antarctic in this way is that the majority of the commercial harvesting of baleen whales and Antarctic fur seals took place on the Atlantic side of the Antarctic (Figure 3), bringing most of the large baleen whale populations and the Antarctic fur seals to the verge of extinction. The whales on the Pacific side of the Ocean were harvested in much lesser numbers (Figure 3). This suggests an uneven pre-exploitation distribution of large baleen whales: abundant on the Atlantic side of Antarctica, but relatively scarce in the Pacific. This uneven distribution may in turn mean that large baleen whales may have different vital rates (i.e. consumption rates, birth rates, etc.) for the two Regions because the Atlantic side apparently provides more favourable habitat. The model is developed so as to be able to reflect these possible regional differences in vital rates of the predators.

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[1] Other large whale species are not considered in the model developed, since their major prey is not krill.

[2] Other seal species are not considered in the model developed, since their major prey is not krill.

Data and Methods

Data

Historic catch

Baleen whales

Annual catches by Area of the baleen whales considered in the model were provided by C. Allison of the IWC Secretariat for minke and fin whales. For humpback whales, data were taken from Johnston and Butterworth (2001), and for blue whales from Rademeyer *et al*. (2003) (Table 2a). Blue whales were harvested legally from 1904 for almost 60 years, fin whales from 1913 to 1976, and humpback whales until 1967 (though there were some illegal takes after these dates, Yablokov *et al*. 1998). Laws (1977) suggests that the stocks of baleen whales overall were reduced by whaling to about a third of their former numbers, and that blue, fin, sei and humpback whales combined declined to about 18% of their pre-exploitation level. This was based on the then current knowledge of the population sizes of the baleen whales and represented the (qualitative) consensus of whale biologists at that time. He also suggests that blue whale and humpback whale were the two species that were most heavily harvested and were respectively reduced to about 3 and 5% of their estimated initial abundances. The commercial harvest of minke whales began in the 1970s and ended in 1986[3] (when a moratorium on commercial whaling came into force), though this species was not nearly as heavily exploited as the other baleen whales. In 1987, following the moratorium on commercial whaling by the International Whaling Commission (IWC), Japan proposed a feasibility study (see IWC 1989) for what came to be called the ‘Japanese Whale Research Programme under Special Permit in the Antarctic’ or JARPA. JARPA currently catches about 400 minke whales primarily from IWC management Areas IV and V (see Figure 2 for the location of these Areas) alternately each austral summer season in the Antarctic (RIWC 1998, p378).

Seals

Before any commercial whaling commenced in the region, Antarctic and sub-Antarctic fur seals were exploited virtually to extinction in the 18th and 19th Centuries (Croxall 1992). Antarctic fur seals were harvested at South Georgia and the South Shetland, South Orkney and Marion Islands, but hardly any accurate records of the numbers harvested exist. The first known sealing trip to South Georgia for this species took place between 1790 and 1792. Weddell (1825) calculated that 1.2 million fur seals had been harvested at South Georgia by 1822, peaking at about 1800 when 112,000 skins were collected (McCann and Doidge 1984). This extensive harvesting of the Antarctic fur seals almost rendered the population extinct (McCann and Doidge 1984). As the numbers at South Georgia declined rapidly, the South Shetland Islands became the next location for the sealers in 1819. Some 320,000 skins were collected over 1821-22, and by 1830 the fur seal population there had almost been exterminated. Very few visits to the South Shetland Islands occurred again until 1871 when United States sealers began supplying furs to the London market. This continued until 1892, but the number of fur seals harvested during that period was only a small fraction of previous levels (Palmer, ref to be confirmed).

Harvesting of Southern elephant seals occurred over the same general period as for Antarctic fur seals and this species was also substantially reduced in numbers, mainly during the 19th Century (Palmer, ref to be confirmed).

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[3] For convenience in this paper, the convention is adopted of referring to the austral summer (whaling) season as the later of the two years concerned, e.g. the 1986/87 season is referenced as 1987.

Other seal species (crabeater seals, leopard seals, Ross seals and Weddell seals) were either not exploited, or not taken in appreciable numbers (Croxall 1992). For crabeater seals, 750 animals were taken per year over some 10 years (Boyd, pers. commn) and here it is assumed that this occurred at the same time that Antarctic fur seals were harvested.

Since no details on yearly catches of Antarctic fur seals exist, we developed a plausible catch history of this species based on the knowledge summarized above. The consequent historical catches of Antarctic fur seals and crabeater seals assumed for the model are shown in Table 2b. Details of how this series of catches for the fur seals was developed are detailed in Mori (in preparation).

Absolute abundance estimates and its relative trends

The absolute abundance estimates for the predator species considered are shown in Table 3, while their relative trends are listed in Table 4 together with the sources for this information. Details of the baleen whale abundance estimates and their associated uncertainties are discussed in Mori (in preparation). Mori (in preparation) also provides a similar discussion for seals; the CV's for these abundance estimates are guesses, since the original paper does not provide CVs for these estimates. Details of the estimated trends shown in Table 4 are also given in Mori (in preparation). Since the abundance trends for fin whales and crabeater seals are not well known, we do not include any information on these trends when fitting the model to data.

Population dynamics of the species

Functional response

One of the most obvious issues of crucial importance to a consumer is the local density of its food, and hence its immediate availability, since, generally, the greater the density of food, the more the consumer eats (Begon *et al*. 1999). The relationship between an individual's consumption rate and local food density is known as the consumer's functional response (Solomon 1949).

There is almost no information on the functional response of baleen whales to their prey. Turchin (2002) comments that specialist predators are thought to be typified by a hyperbolic shaped response, whereas generalists are commonly thought to exhibit sigmoidal shaped responses. On this basis, baleen whales would be assumed to have a hyperbolic shaped response (similar to the Holling Type II form) since they prey almost exclusively on krill. Similarly, it has been suggested in a CCAMLR Working Group report (2004) that for those predators whose foraging is based on interactions with individual prey organisms (e.g. killer whales that forage on seals), Type II response curves might be appropriate. On the other hand, predators whose foraging is based on interactions with prey organisms that must be aggregated to exceed some threshold density (e.g. a baleen whale that forages on krill) manifest Type III response curves.

Boyd and Murray (2001) found a significant non-linear functional response (similar to the Holling Type II form) between the combined standardized index (CSI) (a combination of population size, breeding performance, growth rate of off-spring, foraging behaviour and diet) of the predator population and krill biomass for Antarctic fur seals, macaroni penguins and gentoo penguins around South Georgia. This is the first characterization of a functional response between seals or penguins and their food supply.

Since the information on functional responses of whales and seals to their prey is still scarce, sensitivities of results to different assumptions for functional responses need to be investigated. For the Base Case here, we assume a Holling Type III functional form for the baleen whale and seal species considered in this paper.

The model

The model presented here is similar to that of Mori and Butterworth (2004), but with an added an intra-specific density-dependent parameter (η) for each predator in order to admit a non-trivial coexistence equilibrium of the species considered.

-Dynamics of krill

$$B_{y+1}^{a} = B_{y}^{a} + r^{a} B_{y}^{a}\left(1-\left(\frac{B_{y}^{a}}{K_{a}}\right)\right) - \sum_{j} \frac{\alpha_{j}^{a} \lambda^{j} \left(B_{y}^{a}\right)^{2} N_{y}^{j,a}}{\left(Bj^{a}\right)^{2} + \left(B_{y}^{a}\right)^{2}} \tag{1}$$

-Dynamics of the predators

$$N_{y+1}^{j,a} = N_{y}^{j,a} + \frac{\alpha_{j}^{a} \mu^{j} N_{y}^{j,a} \left(B_{y}^{a}\right)^{2}}{\left(Bb^{a}\right)^{2} + \left(B_{y}^{a}\right)^{2}} - M^{j} N_{y}^{j,a} - \eta^{j}\left(N_{y}^{j,a}\right)^{2} - C_{y}^{j,a} \tag{2}$$

where

B_{y}^{a} is the biomass of krill in region *a* in year *y*,

r^{a} is the intrinsic growth rate of krill in region *a*,

K_{a} is the carrying capacity for krill in region *a*,

α_{j}^{a} is a parameter that adjusts for the differences in consumption and birth rates between regions and refers to region *a* for predator species *j*,

λ^{j} is the maximum per capita consumption rate of krill by predator species *j* (for $\alpha_{j}^{a}=1$),

$N_{y}^{j,a}$ is the number of predator species *j* in region *a* in year *y*,

Bj^{a} is the krill biomass when the consumption and birth rate of species *j* in region *a* drops to half of its maximum level,

μ^{j} is the maximum birth rate of predator species *j* (for $\alpha_{j}^{a}=1$),

M^{j} is the natural mortality of predator species *j* in the limit of low population size,

η^{j} is a parameter governing the density dependence of natural mortality for predator species *j*, and

$C_{y}^{j,a}$ is the catch of predator species *j* in region *a* in year *y*.

Note that no krill catch is considered in the model as (to date) this has been small compared to krill abundance.

The new density dependent term $\eta^j (N^j)^2$ introduced in the equations for predator dynamics can be considered as either increasing the natural mortality rate or decreasing the birth rate (or some combination of the two) as the abundance of the predator increases. For the land-breeding fur seals, this could be a reflection of space-limitation effects leading to increasing frequency of disease or a drop in pregnancy rate as numbers increase. For baleen whales, such a term could reflect increased competition between the animals as their numbers grow for access to the most desirable prey aggregations.

Model fitting procedure and parameter estimation

In order to estimate the yearly abundances of krill and its predators using equations (1) and (2), the initial abundance for each species in the year 1780, before any exploitation began, which we consider to correspond to the co-existence equilibrium level for the species considered, needs to be estimated. The condition that all the species considered in the model were in equilibrium (balance) in year 1780 provides relationships between the parameter values. Thus, by setting $B^a_{y+1} = B^a_y$ in equation (1), it follows that:

$$r^a\left(1-\left(\frac{B^a_{1780}}{K_a}\right)\right) = \sum_j \frac{\alpha^a_j \lambda^j B^a_{1780} N^{j,a}_{1780}}{\left(Bj^a\right)^2 + \left(B^a_{1780}\right)^2} \tag{3}$$

Similarly, setting $N^{j,a}_{y+1} = N^{j,a}_y$ in equation (2) yields:

$$\frac{\alpha^a_j \mu^j \left(B^a_{1780}\right)^2}{\left(Bj^a\right)^2 + \left(B^a_{1780}\right)^2} = M^j + \eta^j N^{j,a}_{1780} \tag{4}$$

for each predator species *j*.

For blue whales, equation (4) can be rewritten as:

$$B^a_{1780} = \frac{Bb^a \sqrt{\left(M^b + \eta^b N^{b,a}_{1780}\right)}}{\sqrt{\alpha^a_b \mu^b - M^b - \eta^b N^{b,a}_{1780}}} \qquad (5).$$

Given values of Bb^a, η^b and α^a_b as inputs, and choices from plausible ranges for each of the other parameters ($M^b, N^{b,a}_{1780}$ and μ^b), the initial biomass of krill in region *a* in year 1780 becomes specified. Similarly, by solving equation (4) for Bj^a, this value becomes specified for other predator species. Once all these parameters have been specified in this manner, K_a can be calculated from equation (3).

The Likelihood function

The complete negative log-likelihood function minimized to estimate the remaining parameters M^j, $N^{j,a}_{1780}$, λ^j and μ^j for all the predator species *j*, and r^a, is:

$$-\ln L = LL^b_{abun} + LL^b_{tren} + LL^m_{abun} + LL^m_{tren} + LL^h_{abun} + LL^h_{tren} + LL^f_{abun} + LL^s_{abun} + LL^s_{tren} + LL^c_{abun} \tag{6}$$

where this function ($-\ln L$) is constructed from the contributions of LL^j_{abun} and LL^j_{tren} from each predator species *j*.

LL^j_{abun} is the component that relates the model estimate of the abundance of predator species *j* to the observed abundance, and LL^j_{tren} is a similar component related to the abundance trend.

Blue whale component

$$LL^b_{abun} = \left(\ln N^{b,A}_{2000} - \ln \hat{N}^{b,A}_{2000}\right)^2 \Big/ 2\left(\sigma^{b,A}_{2000}\right)^2 + \left(\ln N^{b,P}_{2000} - \ln \hat{N}^{b,P}_{2000}\right)^2 \Big/ 2\left(\sigma^{b,P}_{2000}\right)^2 \qquad (7)$$

$$LL^b_{tren} = \sum_{y=1}^{n}\left[\frac{1}{2\sigma^2_y}\left(\ln N^{b,obs}_y - \ln q - \ln \hat{N}^b_y\right)^2\right], \text{ where } \ln q = \frac{\sum_{y=1}^{n}\frac{1}{\sigma^2_y}\left(\ln N^{b,obs}_y - \ln \hat{N}^b_y\right)}{\sum_{y=1}^{n}\frac{1}{\sigma^2_y}} \qquad (8)$$

The reason the blue whale trend estimates are dealt with in this way is that the blue whale abundance estimates given in Table 3 ($N^{b,A/P}_{2000}$) and in Table 4 ($N^{b,obs}_y$) are based in part on the same data. To avoid "double counting" through having the Table 4 as well as the Table 3 estimates informing the model inferences about absolute values, a constant of proportionality *q* is estimated for the Table 4 values so that the model utilizes only the trend information that they contain.

Minke whale component

$$LL^m_{abun} = \left(\ln N^{m,A}_{1985} - \ln \hat{N}^{m,A}_{1985}\right)^2 \Big/ 2\left(\sigma^{m,A}_{1985}\right)^2 + \left(\ln N^{m,P}_{1985} - \ln \hat{N}^{m,P}_{1985}\right)^2 \Big/ 2\left(\sigma^{m,P}_{1985}\right)^2 \qquad (9)$$

$$LL^m_{tren} = \left(R^m_{1970-2000} - \hat{R}^m_{1970-2000}\right)^2 \Big/ 2\left(\sigma^m_{1970-2000}\right)^2 \qquad (10)$$

Humpback whale component

$$LL^h_{abun} = \left(\ln N^{h,A}_{1997} - \ln \hat{N}^{h,A}_{1997}\right)^2 \Big/ 2\left(\sigma^{h,A}_{1997}\right)^2 + \left(\ln N^{h,P}_{1997} - \ln \hat{N}^{h,P}_{1997}\right)^2 \Big/ 2\left(\sigma^{h,P}_{1997}\right)^2 \qquad (11)$$

$$LL^h_{tren} = \left(R^{h,A}_{1977-1991} - \hat{R}^{h,A}_{1977-1991}\right)^2 \Big/ 2\left(\sigma^{h,A}_{1977-1991}\right)^2 + \left(R^{h,P}_{1981-1996} - \hat{R}^{h,P}_{1981-1996}\right)^2 \Big/ 2\left(\sigma^{h,P}_{1981-1996}\right)^2 \qquad (12)$$

Fin whale component

$$LL^f_{abun} = \left(\ln N^{f,A}_{1997} - \ln \hat{N}^{f,A}_{1997}\right)^2 \Big/ 2\left(\sigma^{f,A}_{1997}\right)^2 + \left(\ln N^{f,P}_{1997} - \ln \hat{N}^{f,P}_{1997}\right)^2 \Big/ 2\left(\sigma^{f,P}_{1997}\right)^2 \qquad (13)$$

Antarctic fur seal component

$$LL^{s}_{abun}=\left(\ln N^{s,A}_{1930}-\ln \hat{N}^{s,A}_{1930}\right)^2\Big/2\left(\sigma^{s,A}_{1930}\right)^2+\left(\ln N^{s,A}_{1976}-\ln \hat{N}^{s,A}_{1976}\right)^2\Big/2\left(\sigma^{s,A}_{1976}\right)^2+\left(\ln N^{s,A}_{1991}-\ln \hat{N}^{s,A}_{1991}\right)^2\Big/2\left(\sigma^{s,A}_{1991}\right)^2 \qquad (14)$$

$$LL^{s}_{tren}=\left(R^{s,A}_{1958-1971}-\hat{R}^{s,A}_{1958-1971}\right)^2\Big/2\left(\sigma^{s,A}_{1958-1971}\right)^2+\left(R^{s,A}_{1977-1991}-\hat{R}^{s,A}_{1977-1991}\right)^2\Big/2\left(\sigma^{s,A}_{1977-1991}\right)^2+\left(R^{s,A}_{1991-2000}-\hat{R}^{s,A}_{1991-2000}\right)^2\Big/2\left(\sigma^{s,A}_{1991-2000}\right)^2 \qquad (15)$$

Crabeater seal component

$$LL^{c}_{abun}=\left(\ln N^{c,A}_{1968}-\ln \hat{N}^{c,A}_{1968}\right)^2\Big/2\left(\sigma^{c,A}_{1968}\right)^2+\left(\ln N^{c,A}_{1983}-\ln \hat{N}^{c,A}_{1983}\right)^2\Big/2\left(\sigma^{c,A}_{1983}\right)^2+\left(\ln N^{c,P}_{1972}-\ln \hat{N}^{c,P}_{1972}\right)^2\Big/2\left(\sigma^{c,P}_{1972}\right)^2 \qquad (16)$$

where $\sigma^{j,a}_{y}$ is the CV of the observed abundance (or abundance trend) of species *j* in region *a* in year(s) *y*, and

$R^{j,a}_{y1-y2}$ is the rate of increase of species *j* in region *a* between year 1 to year 2 which is calculated from the equation $R^{j,a}_{y1-y2}=\left(\frac{N^{j,a}_{y2}}{N^{j,a}_{y1}}\right)^{\frac{1}{y2-y1}}-1$.

Biological parameters

Details of the values input for some parameters, and the plausible bounds imposed on other parameters to be estimated, are provided in Table 5. Values for the former set of parameters have been chosen by trial and error so that the resultant trajectories can reasonably match the abundances and trends indicated by observation. Sensitivity tests on these input parameters will be conducted at a later stage of the analysis. The range for r^a was selected as the same basis as in Mori and Butterworth (2004), and ranges for the λ^j s were chosen based on information discussed in Mori (in preparation). Plausible ranges for the other parameters were selected somewhat arbitrarily.

RESULTS

What do Figure 4 and Figure 5 tell us?

Figure 4 shows "Base Case" estimated trajectories for krill and their main predators in the Antarctic from 1780 to 2000. Figure 5 shows the same trajectories, but also adds forward projection to 2500 assuming zero catches for all species after 2000. Table 6 lists values for the parameters that are fixed on input, and estimated values for the remaining parameters and other quantities for the "Base Case" analysis. Figure 6 shows the time trends of the model estimates of consumption of krill by whales and seals, together with the estimated krill biomass.

Figure 4 and Figure 5 illustrate the possible sequence of events that could have happened in the past, and might happen in the future, for krill and their main predators in the Antarctic.

(1) Before the harvesting of seals and whales in the Antarctic, all the species were in equilibrium, with a krill biomass of about 200 million tons.

(2) In the early 1800s, Antarctic fur seal harvesting began and greatly reduced the abundance of Antarctic fur seals; whales increased slightly in consequence, while krill biomass was hardly affected.

(3) In the early 1900s commercial whaling of large baleen whales began and this reduced the blue, humpback and fin whales excessively. The large reduction in consumption of krill sees krill biomass increase from about 200 to 400 million tons (roughly double) by the middle of 20th Century. (Interestingly, however, this reduced consumption is only about 30 million tons, rather than the 150 million tons estimated by Laws (1977) – the reasons for this difference merit examination.)

(4) Due to this increase in krill biomass, the abundance of other predators such as minke whales, Antarctic fur seals and crabeater seals increased rapidly. (The fur seal increase is not readily evident from the plot in Fig. 4, as the population had been reduced so low.)

(5) Due to this increase of other predators, the increase in the krill biomass was arrested.

(6) Since about the 1970s, the large baleen whales were all protected, and these species showed fairly rapid recovery.

(7) Due to the initiation of the recovery of these large baleen whales and the increase in minke whales and seals, krill abundance started to drop again from about 1970. This in turn caused the numbers of minke whales, and subsequently will cause those of the crabeater seals and Antarctic fur seals to fall. In the absence of future catches, all the species are predicted to return steadily (i.e. with hardly any oscillations) to their original equilibrium levels.

How well does the model fit the available information on abundances and trends?

The model provides reasonable fit to the observed abundances and trends of all the baleen whale species considered. It slightly over-estimates the recent increase rate of Antarctic fur seals, and substantially overestimates the most recent abundance estimate for the crabeater seals in the Atlantic. However, more realistic abundance estimates for crabeater seals probably lie in the range of 7 to 11 million, because Erikson and Hanson (1990) acknowledge substantial areas not covered by their surveys, as is discussed further in Mori (in preparation), so that this over-estimation may not be as great a problem as it seems.

Discussion and Further work

The results presented here should be considered “preliminary”, and be regarded as an example illustration of the output of the model since various aspects of the model need further investigation.

The extensions to this model compared to the earlier blue-minke-krill model of Mori and Butterworth (2004) were motivated to improve a number of possibly unsatisfactory aspects of this previous exercise:

1) Other major krill predators were being ignored, so that estimated levels of and trends in krill abundance could be appreciably biased.
2) It was difficult to get the earlier model to reflect the observed situation of both a recent increase in blue whales but a decrease in minke whales.
3) Part of the reason for 2) was the indication from that model that a large minke whale increase had led to krill abundance dropping very low over recent decades, and only starting to increase again in the 1990s.

4) Projections into the future showed initially large amplitude oscillations for all populations, continuing the pattern of 3).
5) Marked differences in historic whale catches and hence likely pre-exploitation population sizes in the Atlantic and Pacific regions.

A number of the new features were introduced to attempt to correct/take account of these aspects:

a) The density dependent $\eta^j (N^j)^2$ terms in the predator dynamics, which *inter alia* tend to damp oscillatory bahaviour.
b) The $\alpha_j^{A/P}$ factors to reflect different habitat suitabilities for each species between the Atlantic and Pacific regions.
c) Changing from a Type II to Type III form of interaction to better reflect the observed recent minke and blue whale trends.

However, this process has led to a proliferation in the number of model parameters. A first priority for future work will be to check whether all of a), b) and c) are in fact necessary – for example, could judicious region- and species-specific choices for the η parameters remove the need for the α parameters, and perhaps also for changing from a Holling Type II to Type III form?

Recent crabeater seal abundance and trend information clearly can have a major impact on the model, and this is an area where data are weak. There is a need to determine whether variants can be found of the model/parameter value choices considered here which are consistent with lower recent abundances and projected rates of increase for this species.

Finally, having hopefully developed a more parsimonious version of the model of this paper without sacrificing the ability to fit to observations of abundance and trends, sensitivity to alternative choices of input parameter values and functional responses will need to be examined to assess the robustness of model predictions.

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Table 1 Estimates of annual consumption of krill by its predators in the Antarctic (a dash indicates that no estimates are available). [Note that the analyses of this paper (see Figure 6) suggest that the estimates of Laws (1977) are too high.]

Species	Krill consumption (million tons)				Reference
	Year				
	Pre Exploitation (Laws 1977)	1970-1980	1980-1990	1990-2000	
Baleen whales	190	-	4 - 53	4 - 46	Mori (in preparation)
Seals	64	52	53	-	Mori (in preparation)
Birds	min 14				Woehler (1995)
Cephalopods	min 34-56				Everson (1984)
Fish	min 40-50				Hureau (1994)

Table 2a Historical catches in the Southern Hemisphere of the baleen whale species considered in this paper.

	blue whales		minke whales		humpback whales		fin whales	
Year/	Region A	Region P	Region A	Region P	Region A	Region P	Region A	Region P
1900	0	0	0	0	0	0	0	0
1901	0	0	0	0	0	0	0	0
1902	0	0	0	0	0	0	0	0
1903	0	0	0	0	0	0	0	0
1904	11	0	0	0	180	0	0	0
1905	51	0	0	0	311	0	0	0
1906	68	0	0	0	732	0	0	0
1907	106	0	0	0	1597	0	0	0
1908	245	0	0	0	3419	0	0	0
1909	180	32	0	0	5511	0	0	0
1910	359	28	0	0	10252	0	0	0
1911	1235	0	0	0	12004	0	0	0
1912	2319	185	0	0	10321	382	0	0
1913	2772	0	0	0	10783	671	569	0
1914	5031	94	0	0	6879	23	1026	0
1915	5536	100	0	0	3354	10	1850	0
1916	4323	64	0	0	485	15	755	0
1917	3097	76	0	0	135	15	530	500
1918	1978	68	0	0	177	23	1113	824
1919	1994	15	0	0	366	24	2508	454
1920	2948	54	0	0	428	21	3072	2227
1921	4443	78	0	0	229	21	1243	1025
1922	6689	85	1	0	1583	19	2342	1244
1923	4657	261	0	0	1481	16	2124	1325
1924	6510	456	0	0	1183	34	3393	1650
1925	5787	635	0	0	2043	248	6881	2096
1926	12148	1512	0	0	1408	261	3747	1848
1927	7822	2281	0	0	1134	22	3356	1703
1928	9067	4831	0	0	1205	36	5484	1656
1929	18267	459	0	0	229	26	8053	2422
1930	51916	3820	0	0	1158	111	1179	0
1931	6613	46	0	0	253	163	3765	0
1932	18835	148	0	0	469	39	5621	1
1933	17376	56	0	0	1024	55	7530	18
1934	16584	28	0	0	3214	65	13125	29
1935	17670	198	0	0	6051	134	10233	105
1936	14424	174	0	0	9486	91	14901	105
1937	12442	97	0	0	7338	124	29115	129
1938	13092	1035	0	0	3679	129	19922	2079
1939	10983	5752	0	0	1168	87	13940	0
1940	1514	0	0	0	455	107	4063	6
1941	51	0	0	0	95	86	717	0
1942	127	0	0	0	0	71	776	0
1943	349	0	0	0	84	90	1158	0
1944	1048	2	0	0	175	88	1665	0
1945	3604	42	0	0	284	107	9188	0
1946	8533	704	0	0	124	125	14119	478
1947	5470	1498	0	0	134	122	19700	1607
1948	6562	1167	0	0	305	156	16382	2655
1949	3516	2722	1	0	5767	1433	16708	2968
1950	4004	3028	0	0	5265	1040	15272	4103
1951	2984	2108	9	0	3387	1077	16065	5375
1952	2946	1048	0	0	2083	1442	17867	3894
1953	2483	405	12	0	1831	1119	12496	3385
1954	1483	1059	0	0	1593	2474	12078	4540
1955	1018	731	45	0	2483	3685	18075	8654
1956	676	1062	46	0	1315	1834	15321	11094
1957	995	648	12	481	2251	2502	18429	7279
1958	726	524	103	0	4284	3761	21330	4574
1959	824	112	63	143	4904	10854	22968	2070
1960	1552	191	66	96	3610	11278	12951	2453
1961	911	232	0	2	1734	5430	11927	1379
1962	1584	164	9	12	2093	1651	15035	279
1963	1244	258	98	6	493	377	12142	179
1964	2688	654	47	4	146	123	6327	77
1965	861	538	72	7	1161	1046	1864	108
1966	362	300	369	5	598	601	1568	309
1967	336	126	1096	3	788	140	1167	119
1968	561	113	607	11	1	0	1750	230
1969	760	156	746	18	0	0	1887	0
1970	681	141	917	0	0	0	1757	0
1971	449	101	4152	3	0	3	1300	1
1972	514	105	6583	0	5	4	1353	472
1973	1	0	7271	1270	1	0	763	576
1974	0	0	5280	2604	0	0	511	510
1975	0	0	5350	1835	0	0	23	206
1976	0	0	6117	2559	0	0	22	0
1977	0	0	4126	1874	0	0	0	0
1978	0	0	4954	1202	0	0	0	0
1979	0	0	5609	2288	0	0	0	0
1980	0	0	4697	2445	0	0	0	0
1981	0	0	4845	3058	0	0	0	0
1982	0	0	3935	3366	0	0	0	0
1983	0	0	4136	2544	0	0	0	0
1984	0	0	3504	2064	0	0	0	0
1985	0	0	3470	2097	0	0	0	0
1986	0	0	2935	2034	0	0	0	0
1987	0	0	273	0	0	0	0	0
1988	0	0	0	241	0	0	0	0
1989	0	0	330	0	0	0	0	0
1990	0	0	0	327	0	0	0	0
1991	0	0	288	0	0	0	0	0
1992	0	0	0	330	0	0	0	0
1993	0	0	330	0	0	0	0	0
1994	0	0	0	330	0	0	0	0
1995	0	0	439	1	0	0	0	0
1996	0	0	0	440	0	0	0	0
1997	0	0	438	0	0	0	0	0
1998	0	0	0	389	0	0	0	0
1999	0	0	439	0	0	0	0	0
2000	0	0	0	440	0	0	0	0
SUM	348998	42604	83820	34529	158717	55688	494101	91020
TOTAL	391602		118349		214405		585121	

Table 2b Assumed historical catches of Antarctic fur seals and crabeater seals in Region A as defend in this paper.

	Antarctic fur seals	Crabeater seals
1790	0	0
1791	11000	750
1792	22000	750
1793	33000	750
1794	44000	750
1795	55000	750
1796	66000	750
1797	77000	750
1798	88000	750
1799	99000	750
1800	110000	750
1801	104500	0
1802	99000	0
1803	93500	0
1804	88000	0
1805	82500	0
1806	77000	0
1807	71500	0
1808	66000	0
1809	60500	0
1810	55000	0
1811	49500	0
1812	44000	0
1813	38500	0
1814	33000	0
1815	27500	0
1816	22000	0
1817	16500	0
1818	11000	0
1819	5500	0
1820	0	0
1821	320000	0
1822	284444	0
1823	248888	0
1824	213332	0
1825	177776	0
1826	142220	0
1827	106664	0
1828	71108	0
1829	35552	0
1830	0	0
TOTAL	3249984	7500

Table 3 Observed abundance estimates for the krill-feeding predators considered in the model.

Species		Year	Abundance estimate	CV	Sources
Blue whale	$N^{b,A}_{2000}$	2000	1104	0.4	Rademeyer *et al.* (2003)
	$N^{b,P}_{2000}$	2000	762	0.4	
Minke whale	$N^{m,A}_{1985}$	1985	327369	0.1	Rep. Int. Whal. Commn 41 (1991)
	$N^{m,P}_{1985}$	1985	420572	0.1	
Humpback whale	$N^{h,A}_{1997}$	1997	5044	0.2	Branch and Butterworth (2001)
	$N^{h,P}_{1997}$	1997	4868	0.2	
Fin whale	$N^{f,A}_{1997}$	1997	10591	0.5	Branch and Butterworth (2001)
	$N^{f,P}_{1997}$	1997	27594	0.5	Butterworth and Geromont (1995)
Antarctic fur seals	$N^{s,A}_{1930}$	1930	100	0.5	Payne (1977,1979)
	$N^{s,A}_{1976}$	1976	369000	0.5	Payne (1977,1979), MacCann & Doidge (1984)
	$N^{s,A}_{1991}$	1991	1550000	0.5	Boyd (1993)
Crabeater seals	$N^{c,A}_{1968}$	1968	2241324	0.5	Erickson and Hanson (1990)
	$N^{c,P}_{1972}$	1972	1292962	0.5	
	$N^{c,A}_{1983}$	1983	564970	0.5	

Table 4 Observed abundance trend estimates for the krill feeding predators considered in the model. The trends are shown as a proportional change per annum, except in the case of blue whales where successive abundance estimates are listed (see text).

Species		Year	Fitted trend	CV	Sources
Blue whale	N^{b}_{1981}	1981	546	0.41	Branch and Rademeyer (2003)
	N^{b}_{1988}	1988	680	0.52	
	N^{b}_{1996}	1996	1891	0.42	
Minke whale	$R^{m}_{1970-2000}$	1970-2000	-0.01	0.01	Butterworth *et al.* (1999, 2002)
Humpback whale	$R^{h,A}_{1977-1991}$	1977-1991	0.11	0.02	Bannister (1994)
	$R^{h,P}_{1981-1996}$	1981-1996	0.12	0.07	Brown *et al.* (1997)
Antarctic fur seals	$R^{f,A}_{1958-1971}$	1958-1971	0.17	0.5	Payne (1977), Boyd *et al.* (1990,1995)
	$R^{f,A}_{1977-1991}$	1977-1991	0.10	0.5	Boyd (1993)
	$R^{f,A}_{1991-2000}$	1991-2000	0.10	0.5	

Table 5 Details of the input parameter values assumed and plausible bounds for the parameters to be estimated.

Input parameters		Parameters to be estimated		
			Bounds	Reference
Bb^A	300000000	$N_{1780}^{b,A}$	100000-300000	
Bb^P	80000000	$N_{1780}^{b,P}$	10000-100000	
		$N_{1780}^{m,A}$	10000-300000	
α_b^A	1.2	$N_{1780}^{m,P}$	10000-400000	
α_b^P	1	$N_{1780}^{h,A}$	10000-200000	
α_m^A	1.2	$N_{1780}^{h,P}$	10000-100000	
α_m^P	1.3	$N_{1780}^{f,A}$	10000-400000	
α_h^A	1.4	$N_{1780}^{f,P}$	10000-200000	
α_h^P	1.4	$N_{1780}^{s,A}$	500000-5000000	
α_f^A	1.2	$N_{1780}^{c,A}$	100000-10000000	
α_f^P	1	$N_{1780}^{c,P}$	100000-10000000	
α_s^A	1.4	μ_b	0.05-0.16	
α_c^A	1.4	μ_m	0.07-0.2	
α_c^P	1	μ_h	0.06-0.18	
		μ_f	0.05-0.16	
η_b^A	**5.00E-08**	μ_s	0.18-0.28	Laws (1984), Boyd *et al*. (1995)
η_b^P	**4.00E-07**	μ_c	0.11-0.28	
η_m^A	**3.00E-07**	M_b	0.03-0.06	
η_m^P	**2.00E-07**	M_m	0.04-0.1	
η_h^A	**8.00E-07**	M_h	0.03-0.08	
η_h^P	**2.00E-06**	M_f	0.03-0.05	
η_f^A	**1.00E-07**	M_s	0.07-0.3	Laws (1984), Boyd *et al*. (1995), Payne (1977)
η_f^P	**1.00E-07**	M_c	0.07-0.3	Laws (1984)
η_s^A	**3.00E-09**	λ_b	115.9-450.6	See Appendix 1 of Mori (in preparation)
η_c^A	**1.50E-08**	λ_m	3.78-32.13	
η_c^P	**3.00E-09**	λ_h	37.8-108	
		λ_f	55.4-220.8	
		λ_s	0.969-1.292	See Appendix 2 of Mori (in preparation)
		λ_c	0.388-5.172	
		r^A	0.4-0.6	Mori and Butterworth (2004)
		r^P	0.4-0.6	

* The following constraints are imposed: $\mu^b - M^b \geq 0.02$, $\mu^m - M^m \geq 0.03$, $\mu^h - M^h \geq 0.02$ and $\mu^f - M^f \geq 0.02$. $\mu^s - M^s \geq 0.03$ $\mu^c - M^c \geq 0.03$.

Table 6 Values of the input and estimated parameters and other quantities for the "Base Case" model.

Input parameters		Estimated parameters and -lnL			Derived parameters		
			Bounds	Estimates		Model	**Observed**
Bb^A	300000000	$N^{b,A}_{1780}$	100000-300000	**229124**	K_A	428799000	**-**
Bb^P	80000000	$N^{b,P}_{1780}$	10000-100000	**32820**	K_P	169311000	**-**
		$N^{m,A}_{1780}$	10000-300000	**54971**			
α_b^A	1.2	$N^{m,P}_{1780}$	10000-400000	**133882**	Bm^A	**2.21E+08**	**-**
α_b^P	1	$N^{h,A}_{1780}$	10000-200000	**77169**	Bm^P	**6.63E+07**	**-**
α_m^A	1.2	$N^{h,P}_{1780}$	10000-100000	**36548**	Bh^A	**1.12E+08**	**-**
α_m^P	1.3	$N^{f,A}_{1780}$	10000-400000	**178299**	Bh^P	**3.04E+07**	**-**
α_h^A	1.4	$N^{f,P}_{1780}$	10000-200000	**71073**	Bf^A	**2.71E+08**	**-**
α_h^P	1.4	$N^{s,A}_{1780}$	500000-5000000	**3003420**	Bf^P	**8.74E+07**	**-**
α_f^A	1.2	$N^{c,A}_{1780}$	10000-10000000	**100246**	Bs^A	**2.42E+08**	**-**
α_f^P	1	$N^{c,P}_{1780}$	10000-10000000	**792643**	Bc^A	**1.35E+08**	**-**
α_s^A	1.4	μ_b	0.05-0.16	**0.160**	Bc^P	**2.38E+07**	**-**
α_c^A	1.4	μ_m	0.07-0.2	**0.200**			
α_c^P	1	μ_h	0.06-0.18	**0.150**	B^A_{1780}	**1.58E+08**	**-**
		μ_f	0.05-0.16	**0.160**	B^P_{1780}	**4.87E+07**	**-**
η_b^A	**5.00E-08**	μ_s	0.18-0.28	**0.280**			
η_b^P	**4.00E-07**	μ_c	0.11-0.28	**0.155**	$N^{b,A}_{2000}$	**1138**	**1104**
η_m^A	**3.00E-07**	M_b	0.03-0.06	**0.030**	$N^{b,P}_{2000}$	**742**	**762**
η_m^P	**2.00E-07**	M_m	0.04-0.1	**0.064**	$N^{m,A}_{1985}$	**324402**	**327369**
η_h^A	**8.00E-07**	M_h	0.03-0.08	**0.078**	$N^{m,P}_{1985}$	**422568**	**420572**
η_h^P	**2.00E-06**	M_f	0.03-0.05	**0.031**	$N^{h,A}_{1997}$	**5054**	**5044**
η_f^A	**1.00E-07**	M_s	0.07-0.3	**0.108**	$N^{h,P}_{1997}$	**4865**	**4868**
η_f^P	**1.00E-07**	M_c	0.07-0.3	**0.125**	$N^{f,A}_{1997}$	**10691**	**10591**
η_s^A	**3.00E-09**	λ_b	115.875-450.625	**450.623**	$N^{f,P}_{1997}$	**27664**	**27594**
η_c^A	**1.00E-10**	λ_m	3.78-32.13	**32.130**	$N^{s,A}_{1930}$	**289**	**100**
η_c^P	**1.00E-10**	λ_h	37.8-108	**102.236**	$N^{s,A}_{1976}$	**162607**	**369000**
		λ_f	55.4-220.8	**55.200**	$N^{s,A}_{1991}$	**1.38E+06**	**1.55.E+06**
		λ_s	0.969-1.292	**1.290**	$N^{c,A}_{1968}$	**1.21E+06**	**2.24.E+06**
		λ_c	0.388-5.172	**5.172**	$N^{c,A}_{1983}$	**3.16E+06**	**5.65.E+05**
		r^A	0.4-0.6	**0.400**	$N^{c,P}_{1972}$	**1.33E+06**	**1.29.E+06**
		r^P	0.4-0.6	**0.402**			
					$R^{m}_{1970-2000}$	**-0.0045**	**-0.01**
		LL^{b}_{abun}		**0.00**	$R^{h,A}_{1977-1991}$	**0.11**	**0.11**
		LL^{b}_{tren}		**0.50**	$R^{h,P}_{1981-1996}$	**0.09**	**0.12**
		LL^{m}_{abun}		**0.01**	$R^{f,A}_{1958-1971}$	**0.17**	**0.17**
		LL^{m}_{tren}		**0.15**	$R^{f,A}_{1977-1991}$	**0.16**	**0.10**
		LL^{h}_{abun}		**0.00**	$R^{f,A}_{1991-2000}$	**0.15**	**0.10**
		LL^{h}_{tren}		**0.08**			
		LL^{f}_{abun}		**0.00**			
		LL^{s}_{abun}		**3.62**			
		LL^{s}_{tren}		**3.66**			
		LL^{c}_{abun}		**6.68**			
		$-\ln L$		**14.70**			

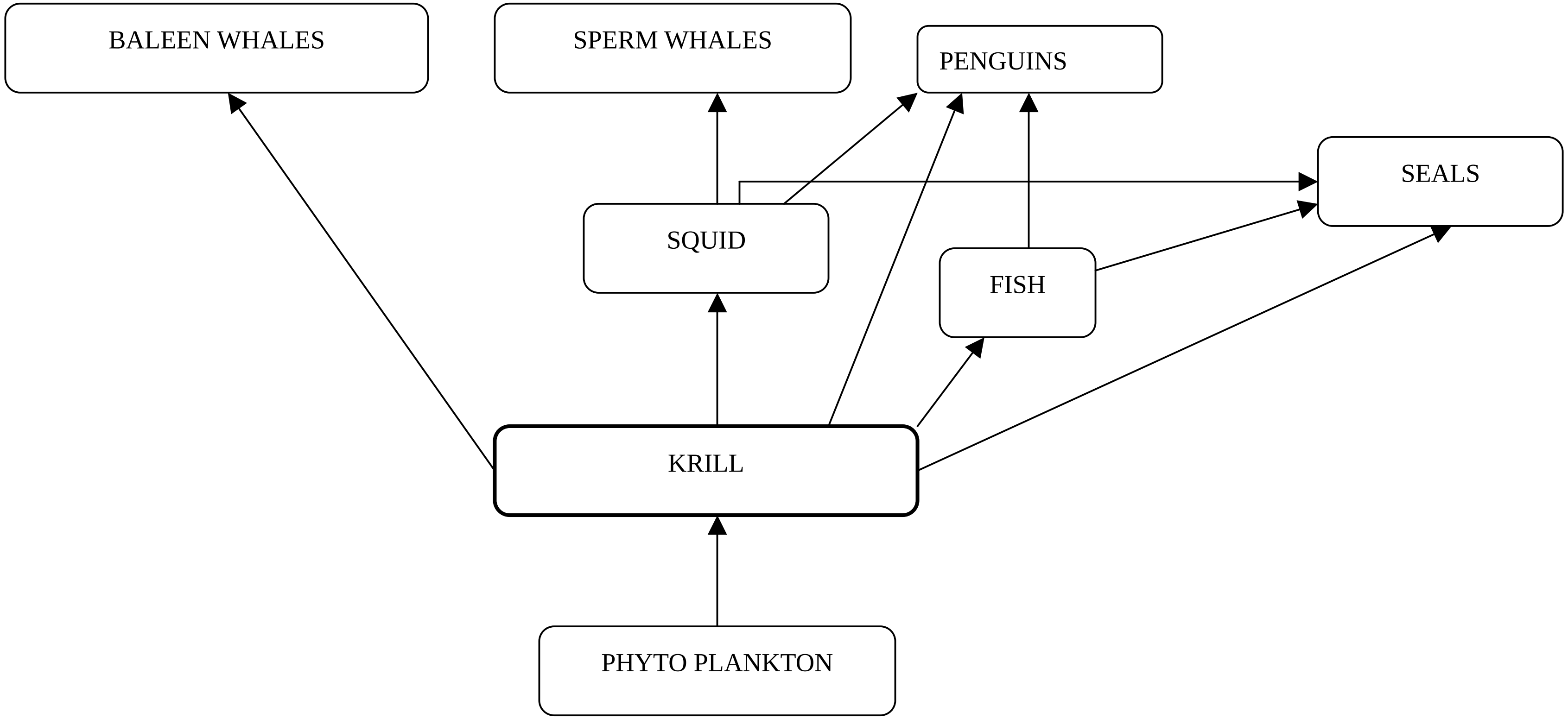

Figure 1. A simplified representation of the Antarctic marine food chain indicating krill's central position (after Miller 2002).

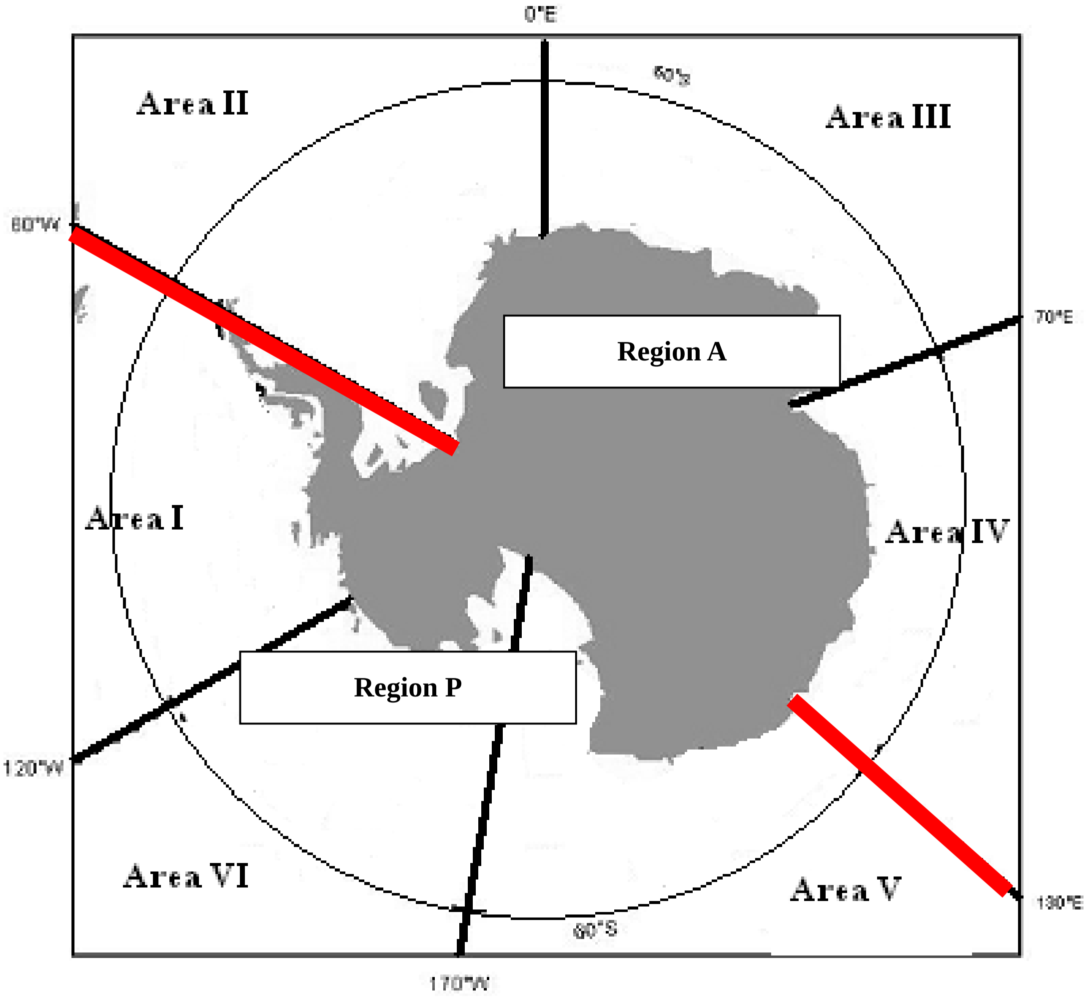

Figure 2 Map of IWC Management Areas (I to VI), and the two regions (Region A and Region P) considered in this paper.

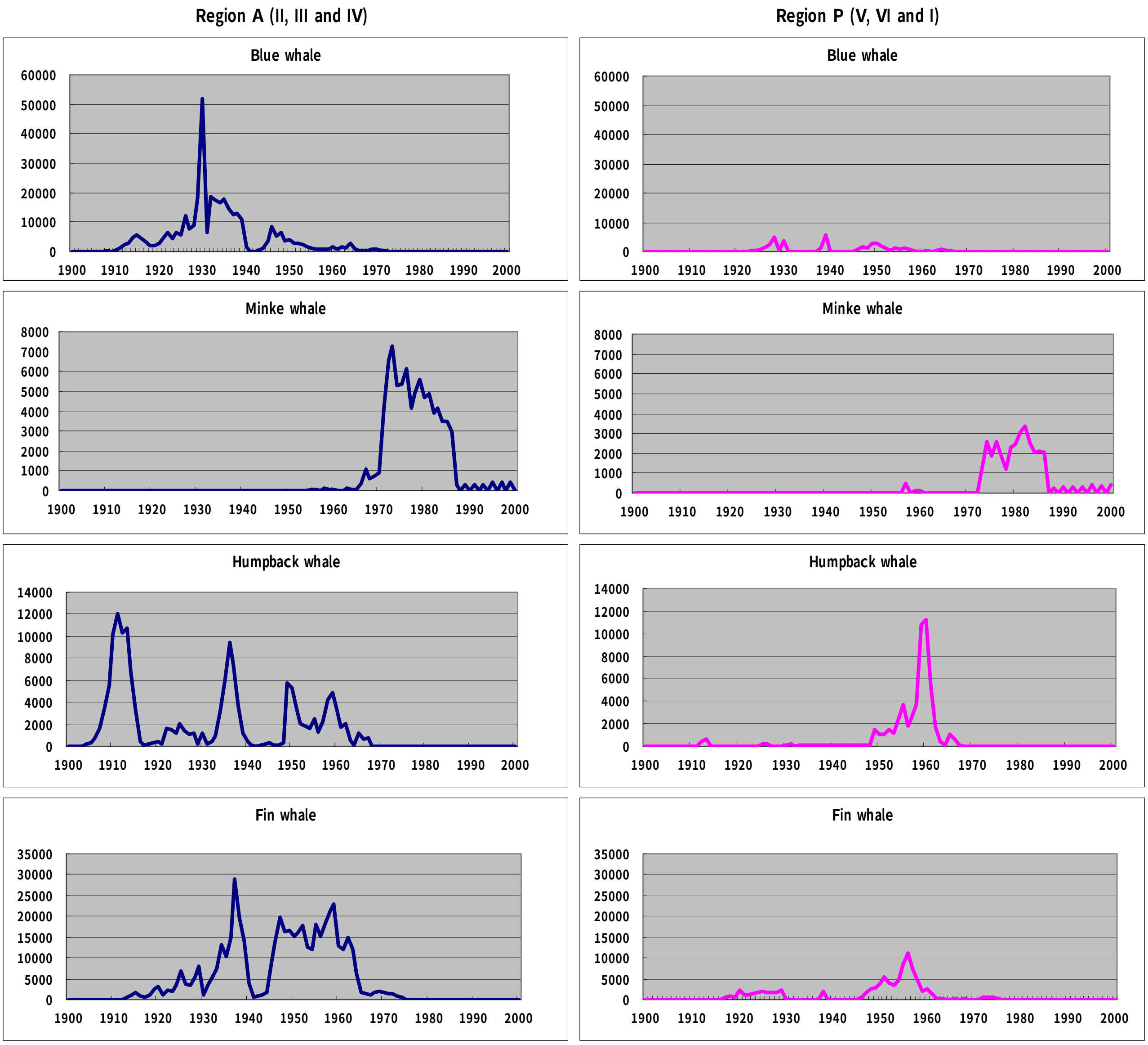

Figure 3. Historical catches of blue, minke, humpback and fin whales for Region A (IWC Management Areas II, III and IV) and Region P (IWC Management Areas V, VI and I).

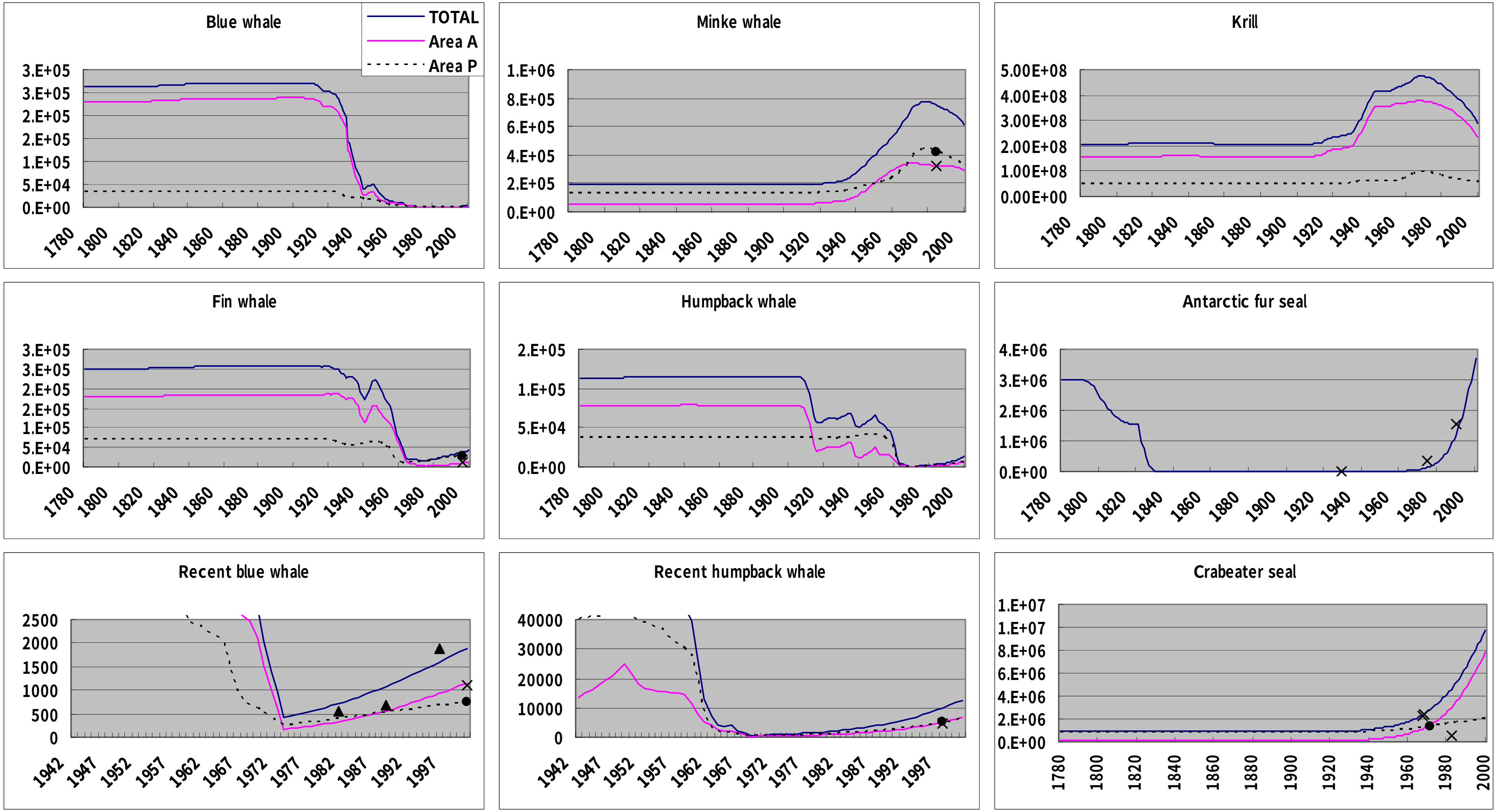

Figure 4. "**Base Case**" trajectories of krill and their main predators in the Antarctic. A black dot/cross shows an observed abundance estimate for the Pacific/Atlantic to which the model was fit. The black triangles shown in the recent blue whale trajectory plot are the observed blue whale abundance estimates for Region A and P combined, to which the model was fit to reflect trend.

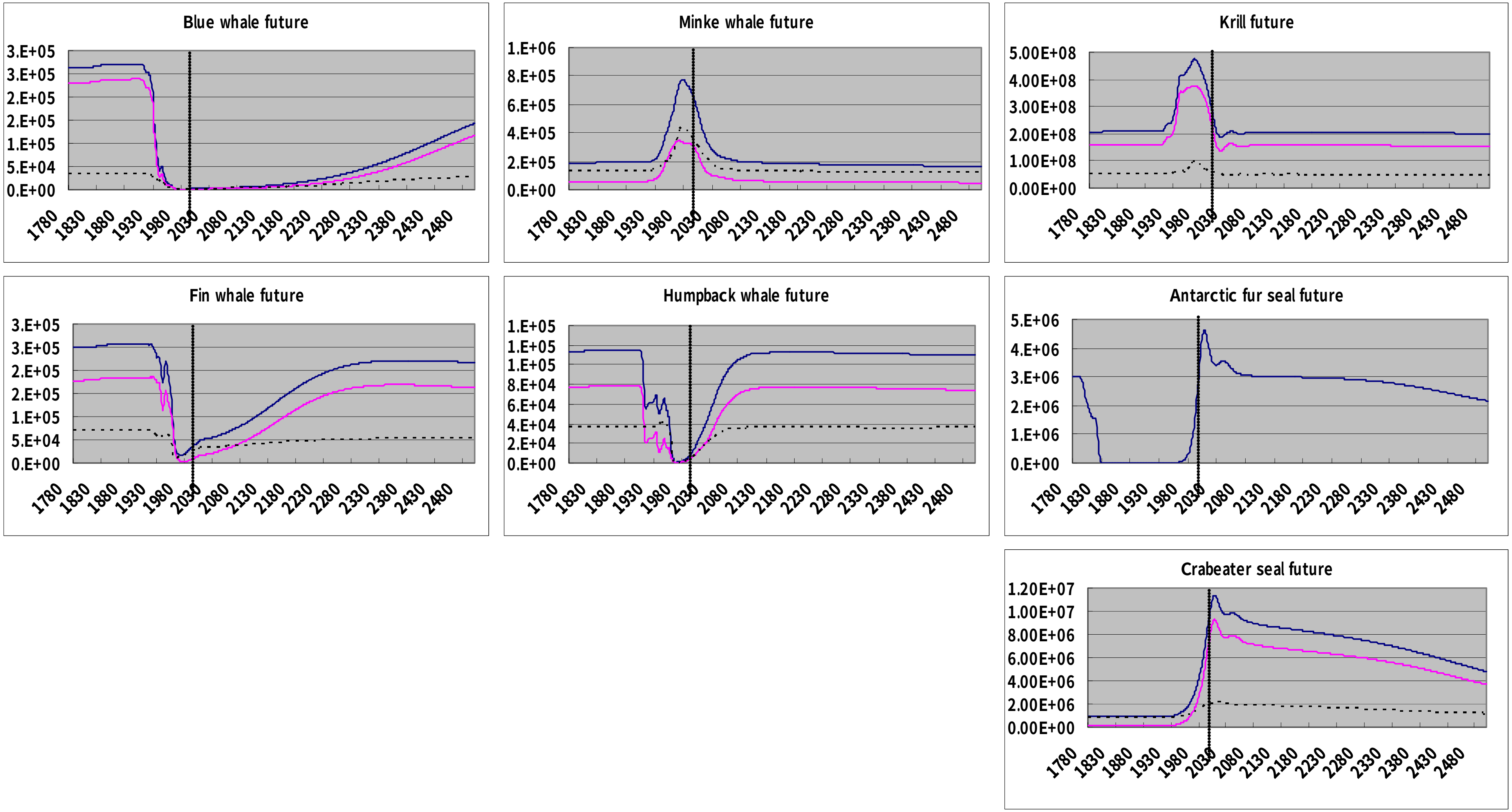

Figure 5. "**Base Case**" projected future trajectories (up to 2500) for krill and their main predators in the Antarctic under the assumption of zero catches for all species after 2000.

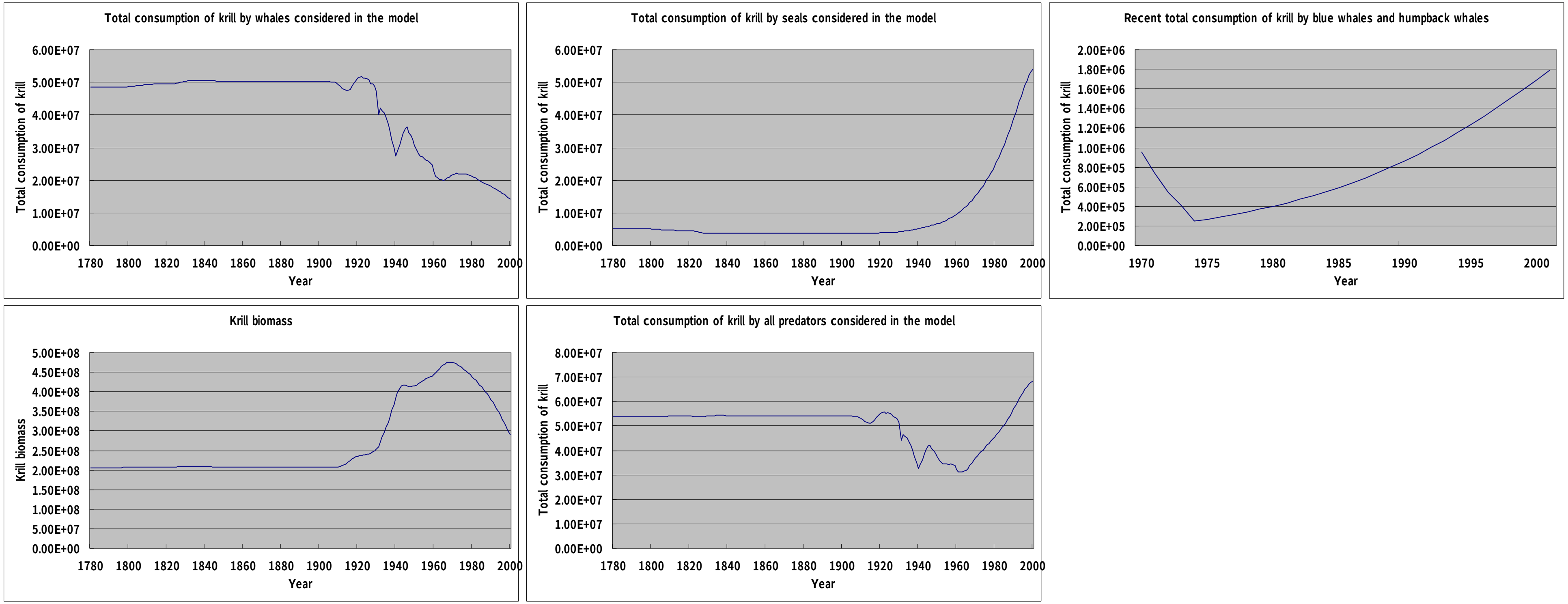

Figure 6. “Base Case” model estimates of trends in annual consumption of krill (in tons) by various species/groups of species, and of krill biomass.