Modelling the predator-prey interactions of krill, baleen whales and seals in the Antarctic

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ABSTRACT

The history of human harvests of seals, whales, fish and krill in the Antarctic is summarized briefly, and the central role played by krill emphasized. The background to the hypothesis of a krill surplus in the mid 20th Century is described, and the information on population and trend levels that has become available since the postulate was first advanced is discussed. The objective of the study is to determine whether predator-prey interactions alone can broadly explain observed population trends without the need for recourse to environmental change hypotheses. A model is developed including krill, four baleen whale (blue, fin, humpback and minke) and two seal (Antarctic fur and crabeater) species. The model commences in 1780 (the onset of fur seal harvests) and distinguishes the Atlantic/Indian and Pacific sectors in view of the much larger past harvests in former. A reference case and five sensitivities are fit to available data on predator abundances and trends, and the plausibility of the results and the assumptions on which they are based is discussed, together with suggested further areas for investigation. Amongst the key inferences of the study are that: i) species interaction effects alone can explain observed predator abundance trends, though not without some difficulty; ii) it is necessary to consider other species in addition to baleen whales and krill only to explain observed trends, with crabeater seals seemingly playing an important role and constituting a particular priority for improved abundance and trend information; iii) the Atlantic/Indian region shows major changes in species abundances, in contrast to the Pacific which is much more stable; iv) baleen whales have to be able to achieve relatively high growth rates to explain observed trends; and v) Laws' (1977) estimate of some 150 million tons for the krill surplus may be appreciably too high as a result of his calculations omitting consideration of density dependent effects in feeding rates.

INTRODUCTION

Brief history of human harvesting in the Antarctic

The Antarctic is a region where the largest human-induced perturbation of the marine ecosystem anywhere in the world has taken place. Species were harvested sequentially, with many heavily depleted as a consequence. Initially seals were taken from the end of the 18th century, followed by whales at the start of the 20th. More recently fin fish exploitation commenced in the 1960s, and that of *Euphausia superba* (hereafter called "krill") in the 1970s.

Seals (including Antarctic fur seals *Arctocephalus gazella*, sub-Antarctic fur seals *Arctocephalus tropicalis*, and Southern elephant seals *Mirounga leonina*) were taken around South Georgia from the 1790s (Figure 1). Weddell (1825) calculated that 1.2 million fur seals had been harvested at South Georgia by 1822 (peaking in about 1800 when 112 000 skins were collected) and this extensive harvesting almost rendered the population extinct in this region (McCann and Doidge 1984). As the numbers in South Georgia declined rapidly, the South Shetland Islands became the next location for the sealers, and by 1830 the fur seal population there had also almost been exterminated.

After this exploitation of the Antarctic fur seals, and commencing at the beginning of the 20th century, large baleen whale species were depleted sequentially, some almost to extinction (Figure 2). Antarctic blue whales *Balaenoptera musculus* were harvested legally from 1904 for almost 60 years, fin whales *Balaenoptera physalus* from 1913 to 1976, and humpback whales *Megaptera novaeangliae* until 1962 (though there were some illegal takes after these dates, Yablokov *et al*. 1998). Sperm whales *Physeter macrocephalus* were taken in substantial numbers from the 1950s, and after the depletion of the other major baleen species, sei whales *Balaenoptera*

borealis were heavily impacted in the 1960s and 70s. Based on historical catch information for blue whales and the fit of a logistic model to several sighting survey series, Branch *et al*. (2004) estimated that by the start of World War II, the Antarctic blue whale population was already about only a quarter of its pristine level, and by 1963 had been reduced to about 0.5% of this pre-exploitation abundance. Similar studies by Johnston and Butterworth (2002) have demonstrated that the humpback whale populations were reduced by harvesting to about 1 to 5% of their estimated pre-exploitation abundance depending on the breeding stock. The commercial harvest of minke whales began in the 1970s and ended in 1986 (when a moratorium on commercial whaling came into force), though this species was not nearly as heavily exploited as the other baleen whales.

More recently, some finfish species have been appreciably overharvested. Over 1969 and 1970, the bottom-dwelling marbled Antarctic rockcod *Notothenia rossii* almost vanished from the vicinity of South Georgia after 514000 tons were taken (Constable *et al*. 2000). Following this depletion, mackerel icefish *Champsocephalus gunnari* became a target of the Soviet fleets in the mid-1970s, and the mean annual catch of this species declined over the first 20 years of the fishery, from 1970 to 1990 (Kock 1992). Fishing for the Patagonian toothfish *Dissostichus eleginoides* began in the 1970s as part of the mixed bottom-trawl fishery around South Georgia, followed by the introduction of a long-line fishery in 1987. Substantial levels of IUU fishing[1] developed around South Georgia, and then from 1996 there was a rapid rise in such activities in the Indian Ocean, leading to a catch substantially above the recommended aggregate global limit set by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) for its Convention area. The rapid declines of the stocks around Crozet Island and the Prince Edward Islands Exclusive Economic Zone (EEZ) have been of great concern (Constable *et al*. 2000, Brandão *et al*. 2002).

The first full-scale krill harvesting experiments began in the late 1960s, with catches peaking at over half a million tons in the 1981 season, and then declining sharply until 1984 as a result of marketing and processing problems brought about by the discovery of high levels of fluoride in the exoskeleton of krill (Nicol and de la Mare 1993, Nicol and Endo 1999). These problems were overcome and catch increased again until the break-up of the Soviet Union in 1991 caused another sharp decline in catches as former member states of the USSR reassessed the economic viability of their krill fisheries. A total of 6.1 million tons of krill was taken between 1973 and 2001 (Miller 2002). The fishery has been stable for the past 9 years with the catch in 2002 being 98 414 tons (CCAMLR 2001). This level is not considered excessive, being much less than the precautionary catch limit of 4 million tons set by CCAMLR for the Scotia Sea sector (Area 48). The latter limit is based on an acoustic survey estimate of krill abundance of 44.3 million tons. The fishery currently operates in the South Atlantic with a winter fishery around South Georgia, moving south in spring and summer to the waters of the Antarctic Peninsula and the South Orkney Islands (Nicol and Foster 2003). Lately, because of reduced winter sea ice, the winter fishery has remained in the waters around the Peninsula and the South Shetlands (CCAMLR 2001).

Antarctic food web and the centric role of krill as prey

Figure 3 shows the major trophic interactions in the Antarctic (Miller 2002). Unlike most other marine ecosystems in lower latitudes, where many species interact in a complex manner with each other, trophic interactions in the Antarctic may be fairly simple. Baleen whales, some squid, fish, seabirds and some seals all feed predominantly on krill. Various qualitative and quantitative analyses of diet composition of baleen whales in the Antarctic (Mackintosh and Wheeler 1929, Mackintosh 1942, Nemoto 1959, Kawamura 1994, Ohsumi 1979, Bushuev 1986, Nemoto 1970, Ichii and Kato 1991, Tamura and Konishi 2005) confirm this for blue, fin, humpback and minke whales[2]. Kawamura (1994) reviewed the feeding of baleen whales in the Antarctic and concluded that although there are some local and seasonal variations, all southern baleen whale species (apart from the Bryde's whale *Balaenoptera edeni* which does not enter Antarctic waters and the sei whale which shows a strong preference for copepods and amphipods) largely fulfill their nutritional requirements by feeding on krill, a key species within the Southern Ocean ecosystem.

Among the seals in the Antarctic, crabeater seals *Lobodon carcinophagus* and Antarctic fur seals feed mainly on krill. Øritsland (1977) estimated the diet composition of crabeater seals to be 94% krill, 3% fish and 2% squid, based on samples taken from surveys in the Scotia Sea and Weddell Sea pack ice. The diet of the Antarctic fur

[1] IUU fishing means fishing that is either illegal (when taken in the Exclusive Economic Zone of a sovereign state), unregulated (when taken by non-members of the permanent Regional Fisheries Management Organisations (RFMO) here CCAMLR), or unreported (when taken by members of the RFMO).

[2] Some other food organisms may also be found in small quantities depending on the extent of the southern migration of the species, where those that migrate further to the south around the ice-edge probably have more overlap with the distribution of krill.

seals has been studied at numerous sites throughout their range, namely at South Georgia (Bonner 1968, Croxall and Pilcher 1984, Costa *et al.* 1989, Reid and Arnould 1996), the South Orkney Islands (Daneri and Coria, 1992), the South Shetland Islands (Daneri 1996, Casaux *et al*., 1998, Daneri *et al*., 1999), Heard Island (Green *et al*., 1989, 1991), Iles Kerguelen (Cherel *et al*., 1997), Marion Island (Klages and Bester, 1998) and Bouvetøya (Kirkman *et al*., 2000). Most studies are based on analysis of scat samples, and krill seems to constitute the major dietary item for Antarctic fur seals around South Georgia, the South Shetland Islands, the South Orkney Islands and Bouvetøya. In Kerguelen, Heard Island, and Marion Island, fish seem to be the major prey (Cherel *et al*. 1997, Green *et al*., 1989, Green *et al*., 1991, Klages and Bester, 1998). These studies show that Antarctic fur seals are feeding not only on kill but also fish, and the amount of krill and fish eaten differs greatly between regions. However, as more than 95% of the breeding population of Antarctic fur seals is located at South Georgia (Reid 1995), it is evident that krill is the main source of food when the population is considered as a whole.

Some supporting evidence of the "Surplus" krill hypothesis – competitive release?

Figure 4 shows consumption of krill by baleen whales in the Antarctic before and after the major exploitation of the baleen whales, as estimated by Laws (1977). Considering the extensive exploitation of Antarctic baleen whales in the early 20th century and the fact that krill is virtually the only prey item for those species, Laws (1977) suggested that following this exploitation, some 150 million tons of "surplus" annual production of krill became available for other krill-feeding predators, such as minke whales, crabeater seals, fur seals, penguins and some albatrosses. This suggestion of 150 million tons was based on coarse estimates available at that time of the population sizes of the baleen whales, estimates of mean body weight, and the assumption that krill consumption by baleen whales was between 3-4% of their body mass/day (details discussed below in the Discussion section).

Although no direct inferences can be made, there are several studies and observations that support this "surplus" krill hypothesis. The estimated trend in age at maturity of minke whales, as indicated by transition phase observations from earplugs, was downwards from the 1950s to the 1980s during the period of commercial whaling, indicating a likely increased abundance of minke whales in the mid 20th century, plausibly in response to increased krill abundance following the depletion of the large baleen whales (Kato 1983, Thomson *et al*. 1999, Zenitani and Kato 2005). Analysis of catch-at-age data using the ADAPT-VPA method (Butterworth *et al*. 1999, 2002, Mori and Butterworth 2005) also suggests a statistically significant increase (about 5%/year) in minke whale recruitment during the period 1940 to 1965. Furthermore there is anecdotal evidence of increased abundance of minke whales from observations on whaling vessels over the same period (Ash 1962). Bengtson and Laws (1985) suggest a similar trend in the age at sexual maturity for crabeater seals. They examined this trend both by back-calculation from the transition layers observed in teeth and by examining the ovaries of the female crabeater seals, and showed a drop in the age at sexual maturity from the 1959 to the 1963 cohort. They also showed that after 1963 there was a steady increase in female age at maturity through to the 1976 cohort Further evidence is provided by the once extensively harvested Antarctic fur seals. By counting the pups as well as using mark recapture methods, Payne (1977) estimated the approximate number of Antarctic fur seals in South Georgia, and suggested an annual rate of population increase of 16.8% between 1957 and 1972. Following this study, Boyd (1993) calculated the total population of Antarctic fur seals in South Georgia based on counting female fur seals ashore, and suggested the population increase from 1977 to 1991 to be 9.8%. Observations at other breeding sites such as the South Shetland Islands, Bouvetøya Island, Marion Island, Possession Island and Heard Island also show that Antarctic fur seals increased during the 1980s to the 1990s (Hucke-Gaete *et al*. 2004, Hofmeyr *et al*. 1997, Guinet *et al*. 1994, Shaughnessy and Goldsworthy 1990).

The timing of all these changes in biological parameters and population trends of minke whales, crabeater seals and Antarctic fur seals (which all feed mainly on krill), corresponds well with the period of extensive commercial harvesting of the krill-feeding baleen whales. Since there is no obvious evidence of any other appreciable environmental or human induced changes that could have led to increases in these populations beginning in the middle decades of the 20th Century, the hypothesis that some large quantity of "surplus" annual production of krill became available for other krill-feeding predators (competitive release), following the depletion of the large baleen whales, seems particularly plausible.

More recent trends in whales and seals in the Antarctic

More than 30 years have now passed since the reduction and subsequent protection of the populations of large baleen whales in the Antarctic, and there are several indications of recovery of these previously heavily exploited species. A recent analysis by Branch *et al*. (2004) of blue whale abundance estimates using Bayesian approaches yields an annual 7.3% (95%CI: 1.4-11.5%) increase for this species since its protection in 1964. A similar analysis by Rademeyer *et al*. (2003) investigated whether there has been a significant increase in abundance for

this species by IWC-Management Area using various statistical and population modelling approaches. Their GLM analysis took different Management Areas into account and indicates an annual 11% (S.E. 5%) increase in the density of blue whales over the period 1978-2000, though the extent of recovery of the species compared to its pre-exploitation abundance differed between Areas with the depletion in Areas II and IV still being particularly low.

Recoveries of humpback whales have also been confirmed by several studies. Bannister (1994) estimated the increase rate of humpback whales (breeding stock D - west Australia) by fitting an exponential increase model to the number of whales seen per flying day, and suggested an annual 10.9% (95%CI: 6.9-13.9%) increase over the period 1963 to 1991. For the same breeding stock, a recent study by Matsuoka *et al*. (2004) using sighting-based estimates of abundance from the JARPA program estimated the annual rates of increase for humpback whales to be even higher. A similar recovery rate has been indicated for breeding stock E – east Australia (Brown *et al*. 1997, Matsuoka *et al*. 2004). Findlay *et al*. (2004) recently reported indication of recovery of breeding stock C – East Africa. For breeding stock A (Brazil), Zerbini (2004) used a Bayesian statistical method to estimate a maximum net recruitment rate of 8.5%, though he concluded nevertheless that this population is still low relative to its pre-exploitation size and requires continued conservation efforts. Information on breeding stock B (west Africa) is still lacking, but at least for other Areas (the Indian Ocean and Australian east coast), it is likely that humpback whales have been recovering at about 10% per year since there has been effective protection of this species. For fin whales, Matsuoka *et al*. (2005) reported some increase in fin whale abundance in Areas IIIE and IV using JARPA sighting data from 1989 to 2003; however, there are large yearly fluctuations in the area south of 60°S in Areas IV and V, which may be because most of the distribution area for fin whales lies to the north of 60°S.

In contrast to the recent recovery of large baleen whales in the Antarctic, there are some indications of recent reductions in increase rates and perhaps even declines in other predators of krill, especially those that once seemed to have benefited from the "surplus" krill, such as minke whales and crabeater seals. Analysis of catch-at-age data using the ADAPT-VPA method (Butterworth *et al*. 1999, 2002, Mori and Butterworth 2005) suggests an increase in minke whale recruitment in IWC Management Areas IV and V until a peak in the late 1960's followed by a drop and then stabilisation over more recent years. Mori and Butterworth (2005) suggest a reduction in the total (1+) minke whale population in these Areas from 1970 to 2000 at a decrease rate of 2.3%/year. Analysis of the age at sexual maturity of minke whales by Zenitani and Kato (2005) indicates that the declining tendency of age at sexual maturity gradually slowed down around the 1960s, and almost stopped from about 1965 to 1980;. For females, a slight increasing trend is evident for the year classes from 1990. Direct observations of the age at physical maturity provide stronger evidence for a recent increase (Bando *et al*. 2005). Supportive indications for recent declines in food availability for minke whales are provided by analyses indicating a decrease in blubber thickness since the 1980s (Ohsumi *et al*. 1997, Konishi and Tamura 2005), and also by a steady pattern of decreasing weights of stomach contents of mature minke whales since 1987 when the JARPA programme commenced (Tamura and Konishi 2005).

An increase in the age at sexual maturity of crabeater seals has also been postulated. Bengtson and Laws (1985) suggest a steady increase through the 1960s and 1970s. A more recent study by Hårding and Kärkönen (1995) also reached this conclusion, suggesting strong evidence for a true increase in age at sexual maturity of crabeater seals through 1964 to 1989 based on calculations of the mean age at first ovulation. Erikson and Hanson (1990) suggest that there has been a decline in the population of crabeater seals in the Western Weddell Sea south of 70°S and to a lesser extent in the Pacific Ocean sector. Their critical comparison of shipboard and aerial census data from 1968 and 1969 with those from 1984 suggests a reduction in crabeater seal density of 30-60%. They attribute this decline to increased foraging competition between the large baleen whales that are showing signs of recovery after protection from commercial whaling. However, Green *et al*. (1995) argue that this apparent decline is an artefact of the censusing protocol, which did not take into account the possibility of a change in the composition and numbers of the seal population observable on the ice during moults. No firm conclusion on this matter has been reached, but at least trends in the age at sexual maturity of crabeater seals suggest that any earlier increase rate in their abundance has slowed (and hence could perhaps have reversed).

Reid and Croxall (2001) examined the relationship between the trends in krill biomass and those of its predators (Antarctic fur seals, Adélie penguin *Pygoscelis adeliae* and macaroni penguin *Eudyptes chrysolophus*) around South Georgia, and found that the numbers of all these predators have been declining since 1990, and the length of krill in their diets has become smaller, suggesting that an increase in the adult mortality rate of krill has occurred. These authors suggest further that the biomass of krill was sufficient to support predator demands at South Georgia in the 1980s but not in the 1990s, so that the period of the "krill surplus" might now be at an end. Thus

multi-species studies of these predator-prey interactions are likely crucial for understanding and predicting trends in abundance for these populations.

Objective of this study

Global warming and a consequent decrease in sea ice cover until the mid 21st century have been suggested by several studies (Levitus *et al.*, 2000, de la Mare 1997). Warming of the Southern Ocean seems to be the fastest worldwide (Gille 2002). This has generated concern about the consequential changes affecting the dynamics of the species within the Antarctic ecosystem.

In addition to understanding the relationship between environmental change and its influence on the dynamics of the species in the Antarctic, an evaluation of the possible consequences of the past extensive human-induced harvesting of whales and seals on the Antarctic food-web via predator-prey interactions is likely also crucial for understanding the dynamics of this ecosystem. For example, by correlating changes in Antarctic seabird populations with regional climate change, Croxall *et al*. (2002) concluded that in addition to the effect of such climate change on species in the Antarctic, harvest driven changes (of whales and seals in the Antarctic) may also play a role and the combination of the two may induce rapid shifts between alternative trophic pathways. As a result of a substantial effort by the International Whaling Commission (IWC) in collecting past historical catches of whales, and by both the IWC and the Japanese Government in conducting continuing whale sighting surveys in the Antarctic for almost three decades, population abundance and trend estimates of the formerly depleted whale species have recently become available. These facilitate important improvements in understanding the effects of past human-induced harvesting of these species in the Antarctic and in the prediction of future trends.

Considering likely increases in minke whales, crabeater seals and Antarctic fur seals in response to extensive harvesting of large baleen whale species, and the more recent observations suggesting that these increases have reduced or even reversed for some of these species concomitant with the recovery of the larger baleen whale species, we hypothesize that the effects of human-induced harvesting of the species in the Antarctic has indeed played a major role in, and continues to impact upon, the dynamics of krill and its major predators in the Antarctic. The objective of this paper is thus to investigate the following question:

> By considering the krill-centric major predator-prey interactions and the available knowledge concerning these species (including harvesting thereof by humans), 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 addressing this question, we hope to provide further insight on the extent to which predator-prey interactions (compared also to the argued impact of changing environmental factors) may have influenced krill and their predators in the Antarctic, and thereby improve understanding of the functioning and hence predictability of the Antarctic marine ecosystem.

DATA & METHODS

Species considered in the model

Baleen whales, some squid, fish, seabirds and some seals all prey directly on krill (Figure 3). 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 the impact of consumption by the predator groups shown in Figure 3 on krill biomass, we summarize approximate estimates of krill consumption by each predator group in the Antarctic in Table 1. Before human exploitation began, baleen whales were probably the major predators of krill, followed by seals (Table 1). This indicates that the impact of consumption by baleen whales and seals in the Antarctic on krill is relatively large, and thus baleen whales (specifically, blue, minke, humpback and fin whales) and seals (Antarctic fur seals and crabeater seals) are considered in the model developed. A particular difficulty, as is evident from Table 1, is that no detailed information exists to relate the abundances and hence 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 the abundances of, and consumption by, these species (particularly for squid and fish) is still very limited, and any estimates remain heavily dependent upon various assumptions. Due to this lack of data, we do not directly consider the effect of consumption by these further species of krill and on the predator-prey

dynamics in the Antarctic. Instead, their potential impacts on these dynamics will be addressed further in the Discussion section. Thus, in summary, only 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 included only in Region A (see Figure 5) as 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 the Pacific Ocean region, which corresponds to the Areas V, VI and I. The two regions together with the IWC Management Areas are shown in Figure 5. 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 6), 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 6). This suggests an uneven pre-exploitation distribution of large baleen whales: abundant on the Atlantic side of Antarctica, but relatively scarce in the Pacific. Thus, the impact of whaling and sealing may have different effects in these two regions, which is the reason for this division.

Historic catch -Data

Baleen whales

Annual catches by Area of the baleen whales considered in the model are listed in Table 2a. These were provided by C. Allison of the IWC Secretariat for minke and fin whales. For humpback whales, data were taken from Johnston and Butterworth (2002) and for blue whales from Rademeyer *et al*. (2003).

Seals

Since no details on yearly catches of Antarctic fur seals exist, we developed a plausible catch history for this species based on the available knowledge of these catches. Details of how this historical series of catches for the Antarctic fur seals was developed are given in Appendix 1. Crabeater seals have hardly been harvested, but 750 animals were taken per year in Region A for 11 years during the period from 1967 to 1977 (I. Boyd, pers. commn). The consequent historical catches of Antarctic fur seals and crabeater seals assumed for the model are shown in Table 2b.

Absolute abundance estimates and their 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. 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. Similarly, it has been suggested by a CCAMLR Working Group (CAMLR 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. baleen whales that forage on krill) likely manifest Type III curves. In this analysis both Type II and Type III functional response forms are explored.

The model

The model presented here is similar to that of Mori and Butterworth (2004), but has 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

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

-Dynamics of the predators

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

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 of krill in region *a*,

λ^{j} is the maximum per capita consumption rate of krill by predator species *j*,

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

Bj^{a} is the krill biomass when the consumption and hence also 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*,

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

$\eta^{j,a}$ is a parameter governing the density dependence of natural mortality and/or birth (and calf survival) rate for predator species *j* in region *a*,

n is a parameter that controls whether a Type II or a Type III functional response is assumed (n=1 for Type II and n=2 for Type III), 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 as (to date) this has been small compared to krill abundance (CCAMLR 2001). Terms involving parameter $\eta^{j,a}$ can apply to either or both of birth (together with calf survival) and death rates; biologically these terms could reflect the impact of limitations on the numbers and sizes of breeding sites for seals, and correspond to intra-species competition for food for whales (see also further comments in Discussion section).

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 year 1780, before any exploitation began, which we consider to correspond to a co-existence equilibrium level for the species considered, needs to be estimated. The condition that all the species considered in this model were in equilibrium (balance) in year 1780 provides relationships between the parameter values. Thus, by setting $B_{y+1}^{a} = B_{y}^{a}$ in equation (1), it follows if a Type III functional response form is assumed that:

$$r^{a}\left(1-\left(\frac{B_{1780}^{a}}{K_{a}}\right)\right) = \sum_{j}\frac{\lambda^{j} B_{1780}^{a} N_{1780}^{j,a}}{\left(Bj^{a}\right)^{2}+\left(B_{1780}^{a}\right)^{2}} \quad (3)$$

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

$$\frac{\mu^{j}\left(B_{1780}^{a}\right)^{2}}{\left(Bj^{a}\right)^{2}+\left(B_{1780}^{a}\right)^{2}} = M^{j} + \eta^{j,a} N_{1780}^{j,a} \quad (4)$$

for each predator species *j*.

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

$$B_{1780}^{a} = \frac{Bb^{a}\sqrt{\left(M^{b} + \eta^{b,a} N_{1780}^{b,a}\right)}}{\sqrt{\mu^{b} - M^{b} - \eta^{b,a} N_{1780}^{b,a}}} \quad (5).$$

Given values of Bb^{a} and $\eta^{b,a}$ as inputs, and choices from their plausible ranges for the other blue whale parameters (M^{b}, $N_{1780}^{b,a}$ and μ^{b}), the initial biomass of krill in region *a* in year 1780 (B_{1780}^{a}) becomes specified. Similarly, by solving equation (4) for Bj^{a}, this functional response parameter becomes specified for the other predator species. Once all these parameters are specified, K_a can be calculated from equation (3). Similar equations apply when a Type II functional response form is assumed.

The Likelihood function

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

$$-\ln L = LL_{abun}^{b} + LL_{tren}^{b} + LL_{abun}^{m} + LL_{tren}^{m} + LL_{abun}^{h} + LL_{tren}^{h} + LL_{abun}^{f} + LL_{abun}^{s} + LL_{tren}^{s} + LL_{abun}^{c} \quad (6)$$

where this function ($-\ln L$) is comprised of the contributions of LL_{abun}^{j} and sometimes LL_{tren}^{j} from each predator species *j*. LL_{abun}^{j} is the component that relates the model estimated abundance of predator species *j* to the observed abundance, and LL_{tren}^{j} is a similar component pertinent to the abundance trend.

Blue whale component

$$LL_{abun}^{b} = \left(\ln N_{2000}^{b,A} - \ln \hat{N}_{2000}^{b,A}\right)^{2} \Big/ 2\left(\sigma_{2000}^{b,A}\right)^{2} + \left(\ln N_{2000}^{b,P} - \ln \hat{N}_{2000}^{b,P}\right)^{2} \Big/ 2\left(\sigma_{2000}^{b,P}\right)^{2} \quad (7)$$

$$LL_{tren}^{b} = \sum_{y=1}^{n}\left[\ln \sigma_{y} + \frac{1}{2\sigma_{y}^{2}}\left(\ln N_{y}^{b,obs} - \ln q - \ln \hat{N}_{y}^{b}\right)^{2}\right], \text{ where } \ln q = \frac{\sum_{y=1}^{n}\frac{1}{\sigma_{y}^{2}}\left(\ln N_{y}^{b,obs} - \ln \hat{N}_{y}^{b}\right)}{\sum_{y=1}^{n}\frac{1}{\sigma_{y}^{2}}} \quad (8)$$

Minke whale component

$$LL_{abun}^{m} = \left(\ln N_{1985}^{m,A} - \ln \hat{N}_{1985}^{m,A}\right)^{2} \Big/ 2\left(\sigma_{1985}^{m,A}\right)^{2} + \left(\ln N_{1985}^{m,P} - \ln \hat{N}_{1985}^{m,P}\right)^{2} \Big/ 2\left(\sigma_{1985}^{m,P}\right)^{2} \quad (9)$$

$$LL_{tren}^{m} = \left(R_{1970-2000}^{m,A} - \hat{R}_{1970-2000}^{m,A}\right)^{2} \Big/ 2\left(\sigma_{1970-2000}^{m,A}\right)^{2} + \left(R_{1970-2000}^{m,P} - \hat{R}_{1970-2000}^{m,P}\right)^{2} \Big/ 2\left(\sigma_{1970-2000}^{m,P}\right)^{2} \quad (10)$$

Humpback whale component

$$LL_{abun}^{h} = \left(\ln N_{1997}^{h,A} - \ln \hat{N}_{1997}^{h,A}\right)^{2} \Big/ 2\left(\sigma_{1997}^{h,A}\right)^{2} + \left(\ln N_{1997}^{h,P} - \ln \hat{N}_{1997}^{h,P}\right)^{2} \Big/ 2\left(\sigma_{1997}^{h,P}\right)^{2} \quad (11)$$

$$LL_{tren}^{h} = \left(R_{1977-1991}^{h,A} - \hat{R}_{1977-1991}^{h,A}\right)^{2} \Big/ 2\left(\sigma_{1977-1991}^{h,A}\right)^{2} + \left(R_{1981-1996}^{h,P} - \hat{R}_{1981-1996}^{h,P}\right)^{2} \Big/ 2\left(\sigma_{1981-1996}^{h,P}\right)^{2} \quad (12)$$

Fin whale component

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

Antarctic fur seal component

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

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

Crabeater seal component

$$LL^{c}_{abun} = \left(\ln N^{c,A}_{2000} - \ln \hat{N}^{c,A}_{2000}\right)^2 \Big/ 2\left(\sigma^{c,A}_{2000}\right)^2 + \left(\ln N^{c,P}_{2000} - \ln \hat{N}^{c,P}_{2000}\right)^2 \Big/ 2\left(\sigma^{c,P}_{2000}\right)^2 \quad (16)$$

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 *y*1 to year *y*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 plausible bounds imposed on the parameters to be estimated are provided in Table 5. The range for r^a was selected on the same basis as in Mori and Butterworth (2004), and ranges for the other parameters were selected based on various sources of information available to date. Values for the input parameters Bb^a and $\eta^{j,a}$ are chosen so that the resultant populations' trajectories are able to reflect the patterns evident from available data. Note in particular that the apparent greater suitabilities of the Atlantic for blue, fin, humpback whales and of the Pacific for minke whales is reflected by choosing comparatively lesser values for the η parameter for these respective regions.

RESULTS

Figure 7 shows the "reference case" trajectories for krill and their main predators in the Antarctic when a Type III functional response form is assumed, and Table 6 shows the values of the input and estimated parameters for this reference case and for five sensitivity scenarios detailed below. Convergence proved difficult to achieve if estimation of certain parameters was attempted when fitting the model to the data, so these were fixed on input[3]. Once the fit had converged, a check was made that the initial coexistence equilibrium was stable. Figure 8 shows the projected trajectories (up to 2500) for this "reference case" model under no future catch of all of the species, Figure 9 (a) shows the consumption of krill by each predator in Regions A and P, and Figure 10 (a) shows the production of krill itself for each Region.

Five other scenarios were considered to investigate the sensitivity of these results. These are:

(i) What if the minke whale abundance estimates from surveys ($N^{m,A}_{1985}$ and $N^{m,P}_{1985}$) were doubled (since there could be some under-counting of the animals, especially in the pack-ice and as a result of the $g(0)=1$ assumption)?

(ii) In the light of the environmental changes that have been reported recently (e.g. Gille 2002, de la Mare 1997), what if carrying capacity K_A of krill was linearly reduced to half of its original value between the mid 1950s and early 1970s?

[3] These parameters are λ^f, μ^h and μ^f.

(iii) What if only whales were considered in the model (no Antarctic fur seals and crabeater seals)?
(iv) What if a Type II functional response form was assumed instead of a Type III form?
(v) For the "reference case" scenario, what if crabeater seals in Region A had higher density dependent mortality rate ($\eta^{c,A}$) than what is assumed for the "reference case"?

Figures 11 to Figure 15 show the trajectories of krill and their main predators in the Antarctic for each of the above sensitivity scenarios respectively, and Table 6 shows the values of the input and estimated parameters for these five scenarios.

The main feature of the "reference case" results of a sharp increase from about 1930 followed by a decrease in krill biomass in the Atlantic/Indian region starting at about 1950 (as shown in Figure 7) does not change for scenarios (i) and (ii) detailed above (see Figures 11 and 12). However, for scenarios (iii), (iv) and (v), the subsequent decrease in krill biomass is not as appreciable as for the other scenarios, and consequently minke whale abundance does not show as marked a decrease since the 1970s, if indeed it decreases at all (Figures 13-15). For the model to reflect minke whales starting to decrease from about 1970, requires a largish drop in krill biomass from about the 1950s to the 1990s as well as a relatively high density dependent η parameter for this species. When minke whale abundance is doubled (scenario (i)), the consumption of krill by this species increases compared to the "reference case" (compare Figures 9 (a) and (b)) but there are no qualitative changes to results. The effect of linearly reducing K_A to half of its original level between the mid 1950s and early 1970s results in a marginally better fit than the "reference case" (compare $-\ln L$ in Table 6 for "reference" and (ii)). This is mainly due to improvement in the fit of the abundance estimate for crabeater seals in Region A. The high abundances of and consumption of krill by crabeater seals, which peak in the 1970s, are somewhat reduced for this scenario.

Note that neither ignoring non-whale predators (Figure 13) or assuming a Type II functional response (Figure 14) reflects a recent decline in minke whale abundance. Figure 15 shows that inhibiting the extent of growth in the crabeater seal abundance during the 1960s and 1970s by increasing the associated η parameters precludes as substantive a recent minke whale reduction as for the reference case.

Note that for all these scenarios the substantial changes, particularly in krill abundance, take place in the Atlantic/Indian (A) region, with the Pacific much more stable.

DISCUSSION

The underlying assumptions of the model are:

1) before the exploitation of the seals and whales in the Antarctic (i.e. in 1780), the species were co-existing in a stable equilibrium, and
2) there is competition both between and within the species.

This study thus shows that under these assumptions and that when the consumption and birth rates of the predators considered in the model show a Holling Type III functional response to krill biomass, and certain biological parameters do lie in the ranges presumed for them (i.e. within the bounds specified in Table 5), then simply by considering the krill-centric major predator-prey interactions and the available knowledge concerning the species (including their harvests by humans), it is possible to broadly reproduce the population abundances and trends of the major predators of krill considered in the model.

The suggested sequence of primary factors driving the dynamics of these major species in the Antarctic is as follows:

1. krill biomass increased over the period from about 1920 to 1950 as a result of a reduction in predators due to the extensive harvesting of the large baleen whales (note that earlier seal harvests seem to have had only a rather limited effect),
2. as a result of this increase in krill biomass, minke whales, crabeater seals and Antarctic fur seals increased: minke whales primarily during the period from 1930 to 1970, with the seals following a little later,
3. by about 1950, krill biomass had almost reached its carrying capacity, but due to the increase in consumption by minke whales and seals, it started to drop again, and
4. following this decline of krill biomass and because of high density-dependent mortality effects, predators such as minke whales and crabeater seals which originally benefitted also start to decrease again from

around 1970 while the protected larger baleen whale species commence recovery.

The important key features required of the model for minke whales to decrease from around 1970 are 1) the drop in krill biomass from around the 1950s to the 1990s and 2) a relatively high density-dependent mortality rate (η parameter) for this species. When only baleen whales and krill are considered in the model (scenario (iii)), we have not been able to find a combination of parameters where krill starts to drop from around 1950s to the extent that then causes minke whales to start to decrease from around 1970 (see Figure 13). This is because the increase in minke whale abundance and the associated greater consumption of krill by this species is not sufficient to counter the increase in krill biomass resulting from the harvesting of the larger baleen whales. This is evident from Figure 9, which shows that it is the increases in other krill predators such as crabeater seals that are essential to give rise to take appreciable reduction in minke whales since about 1970 that is indicated by VPA (Butterworth *et al*. 1999, 2002, Mori and Butterworth 2005).

Furthermore, the assumption of a Holling Type III functional response form also seems to be critical to obtain such a trajectory for minke whales. This is because when a Holling Type II form is assumed, crabeater seals do not increase as rapidly as for a Type III form, so that krill biomass does not drop sufficiently from the 1950s to the 1990s that minke whales will start to decrease from around 1970 (Figure 14). As far as the species parameters are concerned, having the model fit the data requires highish maximum consumption and maximum birth rates for all the species considered in the model, and a low intrinsic growth rate parameter (r) for krill in region A.

The following parts of the discussion address the plausibility of the underlying assumptions of the model and the suggested factors listed above as driving the dynamics of the species in the Antarctic.

Plausibility of the underlying assumptions of the model

1. Before the exploitation of the seals and whales in the Antarctic, the species were in stable equilibrium.
Naturally there are no independent observations available from this period which would allow this assumption to be checked directly. However, in circumstances where estimable parameters are numerous but data limited, there would seem to be justification in imposing this simple and plausible constraint which limits the feasible space of the estimable parameters.

2. Existence of competition between and within the species
Most ecologists recognize two forms of competition. One is called “exploitation competition” and the other “interference competition”. Exploitation competition is defined as: competition in which any adverse effects on an organism are brought about by reductions in resource levels caused by other competing organisms. Interference competition is defined as: competition between two organisms in which one physically excludes the other from a portion of habitat and hence from the resources that could be exploited there (Begon *et al*. 1996).

For “exploitation competition” to exist, the resource in question must be in limited supply. The observations of an increase in minke whales, crabeater seals and some seabirds (none of which had been subject to earlier human harvest) over about the 1940s to the 1970s likely in response to overharvesting of the krill-consuming larger baleen whales, as is detailed in the Introduction section, indirectly supports this assumption of limited supply in krill biomass to krill predators. There is some other indirect supporting evidence for this, as already discussed in detail in the sections on the “Surplus” krill hypothesis and on more recent trends of whales and seals in the Antarctic.

In regard to the possibility of “interference competition” between the baleen whales, Clapham and Brownell (1996) suggest that there are several reasons to believe that at least interference competition between baleen whales may in most cases be minimal even if resource limitation applies. They suggest that first this is because a principal mechanism for this type of competition among other taxa is establishment and defense of territories, yet it appears that most mysticetes are not territorial animals. They also suggest that there are hardly any observations of such competition in the field for baleen whales. Recent observations of direct competition (fighting) between killer *Orcinus orca* and sperm whales in thieving Patagonian toothfish from longlines in fisheries off both Marion Island and South Georgia (C. Heinecken, Capricorn Fisheries Monitoring, pers. commn) provide a counter-example to these arguments, though admittedly such competition is between rather than within species.

The model developed includes both exploitation competition (through the functional response postulated for krill consumption) and interference competition in the form of the density dependent mortality terms (with their

associated η parameters). The latter are a mathematical necessity to admit non-trivial co-existence equilibria, and are relatively easy to motivate on the grounds of breeding site limitations for seals. For baleen whales, however, though clearly the η parameters play an important role in having the model fit the data, the biological justification is more difficult given Clapham and Brownell (1996)'s arguments. Some possible explanations are that:

i) the intra-species effect is subtle and occurs only at high levels of abundance not recently evident in the Antarctic,
ii) what has been modeled here may be a surrogate for intra-species interference, of which recent observations of increased humpback:minke whale abundance rates in Area IV concurrent with a drop in stomach fullness for minke whales (Tamura and Konishi 2005) may constitute indirect evidence; and
iii) the effect is principally operative at a calf survival level, i.e. there are limitations to preferred calving/weaning locations for these animals, as suggested by observed increases in the spatial extent of distribution of calving right whales (Best 1981).

Plausibility of the suggested factors driving the dynamics of the species in the Antarctic

Plausibility of the magnitude estimated for krill biomass

The long term trend in krill biomass estimated by the reference case model suggests that the initial krill biomass under unexploited co-existence was around 150 million tons, which then gradually increased to about 800 million tons during the first half of the 20th century (with virtually all this increase occurring in the Atlantic/Indian region), after which it declined again to around 200 to 300 million tons in recent years. Estimating the abundances of krill has been a very difficult task because of its wide distribution in an environment in which surveys are expensive and difficult, particularly as during winter most of the ocean is covered with pack-ice. Furthermore, the uneven distribution of krill and its occurrence in various sizes of patches ranging from hundreds of meters in diameter and several meters thick to 12km in diameter and 230m thick makes such abundance estimation even more difficult.

Nonetheless, various attempts have been made to estimate the abundance of krill using different techniques, and these estimates vary between 14 and 7000 million tons (Miller and Hampton 1989). A recent study by Voronina (1998) estimated the total krill biomass to be 272 million tons based on published data and using a map of krill's quantitative distribution compiled from commercial trawling made by Soviet fishing and research vessels. Nicol *et al*. (2000) calculated the circumpolar abundance estimates for krill using: 1) historical information on the overall range of krill; and 2) recent measurements of krill density from various acoustic surveys. They suggest circumpolar krill abundance to be in the range of 60 to 155 million tons. There are various uncertainties associated with acoustic survey methods, however, as are well summarized in Hewitt and Demer (2000). The calculation by Nicol *et al*. (2000) required some extrapolation of density estimates to unsurveyed areas (which correspond to 67% of the whole distributional range of krill as they define this). Moreover, taking account of the large inter- and intra-annual variability of krill abundance shown around Elephant Island (Hewitt and Demer, 1994) and South Georgia (Brierley *et al*., 1999, 2002), we consider that it is reasonable to argue that this abundance estimate of krill could cover in a range of several hundred million tons.

More recently, Hewitt *et al*. (2002) estimated the total abundance of krill in the Scotia Sea to be 44.3 million tons based on data from an international echosounder and net survey; however, a reanalysis of these data by Demer and Conti (2005) which incorporated recent improvements in the characterization of krill target strength, suggests that these improvements will lead to a krill biomass estimate that is nearly 2.5 fold greater than the previous one. Such an adjustment would raise the estimate by Nicol *et al*. (2000) to about 150 to 400 million tons. This is quite compatible with our reference case model estimates in the 200-300 million ton range, and would also seem to exclude sensitivity scenarios iii) and iv) considered earlier where respectively ignoring seal predators or assuming Type II functional response suggest recent krill biomass in the 600-700 million ton range. Unfortunately, there are no direct observations that allow the plausibility of the estimate of 800 million tons of krill biomass in the mid 20th century that is suggested by our model to be assessed. However consideration of information on relative trends in krill biomass could potentially provide some insight in to the possible magnitude of krill biomass in those previous years.

Plausibility of the predicted biomass trend estimate of krill

Despite the broad distribution and several high concentration areas of krill in the Antarctic, long-term sequences of surveys of krill abundance have been conducted only in the vicinities of Elephant Island and South Georgia. In these areas, acoustic survey information as well as net sampling data have been collected and there are long term density estimates of krill in these regions since *circa* 1980. Hewitt and Demer (1994) show trends in

density estimates of krill over the period from 1981 to 1993 obtained from acoustic surveys around Elephant Island, and Brierely *et al*. (1999) shows these for South Georgia over the period from1981 to 1998. In both areas, no persistent trend in krill abundance is evident over these periods. In the Elephant Island region, net sampling of krill has also been conducted for more than 20 years, commencing in 1977. Methods for calculating the density estimates of krill from net sampling have changed from year to year, and Siegel *et al*. (1998) point out that estimates obtained in this way are probably biased by net avoidance behaviour by krill and are thus too low. The frequency of sampling as well as the spatial extent of survey areas have not been consistent over the survey period (there was less frequent sampling in the early years), and it is accordingly difficult to conclude from these data whether there was any appreciable trend in krill density between 1977 and 2000 in the Elephant Island region. Moreover, these areas where consecutive surveys have taken place correspond to only a tiny fraction of the total distribution area for krill, so that estimating any trends in circumpolar krill abundance remains problematic.

A recent study by Atkinson *et al*. (2004) combined all available scientific net sampling data from 1926-39 and 1976-2003 in order to examine spatial and temporal changes in krill distribution. They found that the productive southwest Atlantic sector contains >50% of the Southern Ocean krill abundance, but that here the density has declined since the 1970s. By regressing winter sea ice duration against krill density, they postulate that there is a positive relationship between the two. However the primary question here involves the long-term trend in krill biomass over the period from 1930-1970, where our model predicts an initial increase in krill biomass, followed by a drop since the 1950s. According to Atkinson (pers. commn), comparison of krill abundance between the 1926-39 period and the post 1976 era is not possible for three reasons: first there are statistical problems in comparing two data series of different lengths with a long gap between them; secondly there are comparatively few hauls in the modern era with nets of similar type to the past; and finally, there is possible evidence that the behaviour of krill (i.e. their vertical distribution) has changed since the earlier period, which renders it difficult to make a valid comparison of abundances, particularly as a result of possible consequential changes in net avoidance.

Thus, from the information available, there is some confirmation of a decline in krill biomass in more recent years as is indicated by our model, but whether this is part of some monotonic decline over the whole 20th Century, or a decline which occurred only after an increase in krill biomass earlier in the century as the model indicates, cannot be directly resolved.

Difference between Laws (1977) estimate of 150 million tons of "surplus" krill and this analysis

Laws (1977) suggested that following the exploitation of large baleen whales in the Antarctic, some 150 million tons of "surplus" annual production of krill became available for other krill-feeding predators, such as minke whales, crabeater seals, fur seals, penguins and some albatrosses. This estimate of 150 million tons was based on estimates of the population sizes of the baleen whales represented the consensus of whale biologists at that time, estimates of mean body weight, and the assumption that baleen whales feed on krill at 3-4% of their body mass per day (Table 7). However, our reference case estimate of consumption of krill by large baleen whales in the Antarctic shown in Figure 9 suggests much less consumption of krill by the large baleen whales prior to their harvesting: approximately about 50 million tons per year.

Table 7 provides detailed comparison of consumption of krill as estimated by Laws (1977) and in this study. The main reason for the difference in estimated consumption by baleen whales from these two studies is their different assumptions for predator consumption rates in relation to their prey biomasses. In Laws (1977) it is assumed that the amounts of krill consumed per capita by the whales are independent to the biomass of krill. In other words, predators consume a certain amount of krill regardless of the amount of available prey. This assumption seems extreme, since it is likely to be more difficult for the predators to find krill when the krill biomass is low (perhaps due to smaller patch sizes or fewer patches etc.) compared to a situation where a large amount of krill is available. Our model includes Holling-Type III functional response form which incorporates the effect of the dependence of consumption on prey biomass, and suggests that immediately before the onset of large scale commercial whale harvesting, the predators were competing for krill at a relatively low level of krill biomass so that their per capita consumption rates were reduced. Further reasons for the differences are that our model estimates a lower pre-exploitation abundance of fin whales (see further remarks below) than assumed by Laws, and that though minke whales are now estimated to be larger in number, they are no longer thought to feed throughout the year on krill as Laws (1977) assumed. It should also be noted that our modeling framework takes account of the fact that krill productivity changes with krill abundance.

Interesting inferences can also be drawn about the discrepancies in abundance estimates of krill obtained from acoustic methods and from estimates of predator consumption linked to assumed productivity/biomass ratios for

krill. Miller and Hampton (1989) and Nicol *et al*. (2000) both found a major discrepancy in abundance estimates for krill obtained by these two methods (those obtained from acoustic surveys are much smaller than ones calculated from predator consumption) and suggested that this discrepancy may be caused by: 1) bias in acoustics studies, 2) the possibility of large krill population components that are either too deep, too shallow or too dispersed to be detected, and 3) an overestimation of the demand for krill by predators. Our results give support the last of these suggestions: overestimation of the demand for krill by predators, calculations of which often ignore the likely dependence of predator consumption rates on krill abundance.

Plausibility of the predicted increase rates of and consumption of krill by minke whales and crabeater seals

The annual increase rate in the abundance of minke whales and crabeater seals from 1940 to 1970 for the reference case is 4% in Region A. Mori and Butterworth (2005) infer the increase rate of minke whale recruitment to be 5% per year for the period between 1945 to 1970 based on catch at age analysis for this species in Area IV and Area V. This suggests that the 4% per year increase indicated by the reference case is quite plausible. Although there are no comparable consecutive abundance estimates for crabeater seals, it does not seem unrealistic to suggest this species increased at a rate of 4% per year given that other seal populations have shown increase rates of this magnitude or higher. Analysis of data for the age at sexual maturity of minke whales and crabeater seals discussed in the Introduction section indicates a decrease in age at sexual maturity within this period which is an expected response to greater food availability and would contribute to an increase in population growth rate.

Although an annual increase rate of 4% for crabeater seals may not seem unrealistic, the increase in the amount of consumption of krill by this species in Region A as shown in Figure 9 is substantial (exceeding, for example estimated pre-exploitation consumption by blue whales), and raises plausibility concerns. When the possible effect of environmental change (K_A for krill linearly reduced to half of its original value between the mid 1950s and early 1970s – sensitivity scenario ii)), this enormous increase in consumption of krill by crabeater seals is lowered by about as 40% shown in Figure 9. Thus whether or not a poorer environment needs to be postulated in addition to species interaction effects to explain predator population trends in the Antarctic rests primarily on the extent of an increase in crabeater seal abundance that is considered to be realistic.

Effect of other krill predators that is not included in the model

It is important to bear in mind that although not included in this model, some other krill predators such as Adélie penguins, chinstrap penguins *Pygoscelis antarctica* and macaroni penguins also increased during the period from 1950 to the 1970s (Croxall 1992, Croxall *et al*. 2002). Adélie penguins on the western side of Antarctica, and on the Antarctic Peninsula and its associated island groups, increased substantially over this period, and then stabilized or decreased in the 1980s and, at some sites, in the 1990s (Croxall *et al*. 2002). During the late 1970s macaroni penguins at South Georgia decreased by almost 50% over five years but have remained stable subsequently (Croxall 1992). Woehler (1995) estimates total consumption of crustaceans by penguins in the Antarctic to be about 14 million tons per year.

For squid, Everson (1977) notes that no direct information is available on either the standing stock or production of squid, but indirect estimates, based on consumption by predators, suggest that the annual production of squid is in excess of 17 million tons. As squid tend to be relatively short-lived and have fast growth rates (Nesis 1983), Everson (1984) suggests that squid will have a high efficiency of conversion for the food they consume, perhaps even of the order of 30-50%, suggesting annual food consumption of the order of 34-56 million tons. As far as fish are concerned, myctophid biomass in the Antarctic has been estimated to be 70-200 million tons (Lubimova *et al*. 1987), although this estimate may includes all myctophids south of 40°S. From these data, Kock (1992) estimated that if a substantial proportion of this biomass is present south of the South Polar Front zone, then even under conservative assumptions that krill makes up 5% of the food by mass and annual food intake is 5-10 times body mass, an annual krill consumption of 20-35 million tons would result, which means that the total impact of all fish on krill in the Southern Ocean could be estimated, as a rough minimum figure, to be about 40-50 million tons (Hureau 1994).

These estimates for birds, squid and fish are somewhat coarser than those for baleen whales, but nevertheless suggest that some of these predators, at least, did respond to a krill surplus in the mid-20th Century, and furthermore that their present levels of krill consumption are not insubstantial compared to those of the whales and seals considered in the model. In the context of the model then, results for crabeater seals should perhaps be considered as reflecting a conglomerate of these seals together with some birds, squid and fish, thereby rendering

the large krill consumption increase for crabeater seals in the 1950s and 1960s under the reference case (Figure 9a) somewhat more plausible.

In summary, it seems that the results for our reference case model do pass the various plausibility tests, though admittedly by something of a stretch in regard to crabeater seals. Certainly an assumption of a deterioration in the environment (modeled as a lessening of the food production available for krill) assists in improving the plausibility of some model outputs (see Figure 12 for sensitivity scenario (ii)), but the results of the analyses of this paper suggest that predator population trends can still be explained without invoking this assumption.

Difficulties with the current model

There are several difficulties in the current model. First, although information on recent abundances and trends estimates for baleen whales has become available from sighting surveys, this is still relatively limited. In particular for minke whales, there are no agreed estimates of trends in abundance from sighting surveys (IWC 2003), so that we have used trend estimates from VPA for Areas IV and V, and assumed that the trends for these Areas are representative of the trends in Regions A and P. However, this may not be the case: for example in Areas II and III where the harvesting of blue whales was more excessive than in Areas IV and V, minke whales may have responded differently than in Areas IV and V. Furthermore little is known about the circumpolar abundance and trends for crabeater seals, which the model suggests to be playing a key role in the dynamics of the system. The few data available to fit compared to the number of estimable parameters in the model, renders the model predictions less reliable.

Secondly, we have found that it is very difficult to find sets of parameter values that will result in a stable co-existence equilibrium at the time of the first year considered in the model (i.e. 1780) and also gives reasonable fit to the data. This becomes understandable when one considers the relatively large number of species considered and their complex non-linear interactions.

Thirdly, fin whales are problematic in two respects. There is the difficulty of how best to account for the fact that much of their feeding takes place north of 60°S and well away from the ice-edge zone preferred by most of the other species considered. Also there is the surprising result that the reference case model estimates initial fin whale numbers to have been about the same as blue whales despite of the fact that fin whale catch having been some 25% larger (see Table 2a). The explanation for this (according to the model) is that since peak fin whale harvests occurred a little later than for blue whales, the fin whales were able to take advantage of the krill "released" by earlier blue whale catches, so that a greater part of the fin catches reflect enhanced productivity compared to fishing down pristine abundance. This is reflected in Figure 16, which shows the per capita growth rate (sustainable yield rate) of each predator species over time in the absence of harvesting – note that while the trends shown for blue and fin whales are similar, larger values first occur over a period when blue whales are already substantially depleted, so cannot take full "advantage", unlike the situation for fin whales.

Finally the need to introduce density dependent mortality has its less then satisfactory aspects, as the associated η parameters play a very important role in the dynamics of the system, but there is no current basis to independently inform on their likely magnitudes.

Use of the model and where we go from here

Warming of the Southern Ocean and a decline in the area covered by sea ice has been postulated recently (Gille 2002, de la Mare 1997), and the possible impact of these environmental factors on the dynamics of the species in the Antarctic has become a concern. However, in contrast the increasing literature on that topic, there have been hardly any studies that have evaluated the possible influence of the past extensive harvesting of the large baleen whales and seals in the Antarctic on predator-prey dynamics of the species in the Antarctic in a quantitative way. This is probably due to the lack of data and difficulties associated with the modeling as discussed above. However, in order to more fully understand the possible mechanisms that might be controlling the dynamics of the species in the Antarctic, we consider that these effects should be accorded at least as much attention as environmental studies and the two modeled jointly.

Due to the difficulties already mentioned, we do not regard this study as definitive, but rather as a first step towards a more realistic and reliable model of the krill-centric predator-prey interactions in the Antarctic which focuses especially on the interactions between baleen whales, seals and krill. Continuing monitoring of the abundance and various biological parameters of the prey and predators in the Antarctic, as well as of environmental change and its effect on the dynamics of these species will be essential to improve the model and incorporate environmental effects explicitly. In due course, a move from an age-aggregated to an age-structured model for the various species might become justified, and this would allows for the explicit incorporation of

effects such as observed changes in age at maturity. Clearly also a more systematic exploration of sensitivity to alternative parameter choices and quantification of uncertainties is desirable. In principle this is achievable through a Bayesian estimation approach, but the associated computations will prove decidedly non-trivial given the high level of non-linearity in the model. Finally consideration needs to be given to including further predator species that were not considered for the current model.

In recent years, the importance of ecosystem based management of fisheries and wild-life resources has been recognized worldwide. The 2001 Reykjavík Declaration on Responsible Fisheries in the Marine Ecosystem and the Plan of Implementation of the 2002 World Summit on Sustainable Development highlighted the need in fisheries to look beyond target species only, and for management to consider the impacts of fishing on the ecosystem as a whole as well as the impacts of the ecosystem on fisheries. The model developed here may contribute to this as a first step in modeling the major Antarctic predator-prey interactions, which centre on krill and its major predator species, and clearly it could readily be used (in principle) to contrast the effects of alternative harvesting strategies for both krill and its predators. At this stage, however, our knowledge of the various biological parameters as well as the functional response forms for whales and seals is limited, and this restricts the potential use of such a model in a practical management context for the time being. Nevertheless, applying this modeling approach to IWC Management Areas IV and V, where extensive data have been collected over the past 20 years during the JARPA surveys, may be the most appropriate next step.

Some concluding summary comments

There are many inferences to be drawn from this work thus far. Likely amongst the more interesting and important are:

- Species interaction effects alone can account for likely trends in the abundances of major Antarctic predator species over the past 50 or so years, though not without some difficulty. Accordingly one cannot as yet conclude that the effects of environmental change in addition are essential to explain these trends.
- Species interaction effects impact the dynamics of these predators in ways that differ from what might be anticipated in a conventional single-species harvesting context, and so that they need to be better understood and taken into account in management decisions.
- It is not sufficient to consider the interactions between the Antarctic baleen whales and krill alone. The major seal species, at least, needalso to be taken into account explicitly, and possibly in addition some other predator species.
- There are major differences in the historic dynamics of the Atlantic/Indian and Pacific regions, with appreciable changes in abundance in the former while the latter has been relatively stable by comparison.
- The severe depletion of fur seals by harvesting over the turn of the 18th Century had quantitatively much less impact than that of the larger baleen whale species during the middle decades of the 20th Century.
- Accounting for likely population trends through species interaction effects suggests that baleen whale species can manifest relatively fast dynamics (sustainable yield rates typically showing maxima closer to 10% than 1%) (see Figure 16).
- Nevertheless in the absence of future harvesting, blue whales in the Atlantic/Indian region are predicted to need some three to four centuries to recover to their pre-exploitation level (see Figure 8), essentially because they also need to outcompete other predators which initially recover faster.
- Density dependent mortality is a necessary feature of the model, but problematic given the absence of independent bases to inform on likely values for the associated (η) parameters.
- The VPA-based indication of 1970 or thereabout as the time of a maximum minke whale numbers is difficult to explain within the model, as the larger baleen whale species have hardly commenced recovery at that stage, so that highish values of density dependent mortality have to be postulated for minke whales which consequently are out-competed by seals as krill abundance starts to decline.
- Crabeater seals appear to play a key role in the dynamics of the system (though this may in part reflect the model “using” them also as a surrogate for other bird, squid and fish species not explicitly included). More reliable information on abundance and its trend for this species is a particular priority.
- Laws' (1977) estimate of the krill "surplus" seems to have been too high, primarily as a result of his failing to allow for likely decreased feeding rates given a lower krill abundance prior to the onset of large scale commercial whaling in the Antarctic.

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Table 1 Estimates of annual consumption of krill by its predators in the Antarctic (a dash indicates that no estimate is available). [Note that the analyses of this paper (see Table 7) 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 whale		Minke whale		Humpback whale		Fin whale	
Year	Area A	Area P	Area A	Area P	Area A	Area P	Area A	AreaP
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	228	23	0	0
1906	68	0	0	0	240	492	0	0
1907	106	0	0	0	1281	336	0	0
1908	245	0	0	0	2171	1240	0	0
1909	180	32	0	0	4030	1481	0	0
1910	359	28	0	0	7952	2027	0	0
1911	1235	0	0	0	8558	1381	0	0
1912	2319	185	0	0	8882	1654	0	0
1913	2772	0	0	0	9562	2379	569	0
1914	5031	94	0	0	6223	679	1026	0
1915	5536	100	0	0	3135	229	1850	0
1916	4323	64	0	0	464	36	755	0
1917	3097	76	0	0	74	86	530	500
1918	1978	68	0	0	96	104	1113	824
1919	1994	15	0	0	184	206	2508	454
1920	2948	54	0	0	271	178	3072	2227
1921	4443	78	0	0	229	21	1243	1025
1922	6689	85	1	0	1395	207	2342	1244
1923	4657	261	0	0	1381	116	2124	1325
1924	6510	456	0	0	986	131	3393	1650
1925	5787	635	0	0	1919	358	6881	2096
1926	12148	1512	0	0	1305	355	3747	1848
1927	7822	2281	0	0	1128	22	3356	1703
1928	9067	4831	0	0	1189	36	5484	1656
1929	18267	459	0	0	195	26	8053	2422
1930	51916	3820	0	0	819	189	1179	0
1931	6613	46	0	0	253	273	3765	0
1932	18835	148	0	0	469	57	5621	1
1933	17376	56	0	0	1024	99	7530	18
1934	16584	28	0	0	3214	117	13125	29
1935	17670	198	0	0	6051	191	10233	105
1936	14424	174	0	0	9486	160	14901	105
1937	12442	97	0	0	7338	147	29115	129
1938	13092	1035	0	0	3679	180	19922	2079
1939	10983	5752	0	0	1168	167	13940	0
1940	1514	0	0	0	455	214	4063	6
1941	51	0	0	0	79	172	717	0
1942	127	0	0	0	0	142	776	0
1943	349	0	0	0	84	180	1158	0
1944	1048	2	0	0	175	176	1665	0
1945	3604	42	0	0	284	214	9188	0
1946	8533	704	0	0	122	235	14119	478
1947	5470	1498	0	0	134	223	19700	1607
1948	6562	1167	0	0	274	279	16382	2655
1949	3516	2722	1	0	5627	1957	16708	2968
1950	4004	3028	0	0	4734	1567	15272	4103
1951	2984	2108	9	0	3306	853	16065	5375
1952	2946	1048	0	0	1913	2249	17867	3894
1953	2483	405	12	0	1787	3099	12496	3385
1954	1483	1059	0	0	1819	4745	12078	4540
1955	1018	731	45	0	2065	2209	18075	8654
1956	676	1062	46	0	1234	2928	15321	11094
1957	995	648	12	481	2312	3471	18429	7279
1958	726	524	103	0	3172	5792	21330	4574
1959	824	112	63	143	1178	15900	22968	2070
1960	1552	191	66	96	1684	14577	12951	2453
1961	911	232	0	2	1200	6971	11927	1379
1962	1584	164	9	12	3064	901	15035	279
1963	1244	258	98	6	505	323	12142	179
1964	2688	654	47	4	173	106	6327	77
1965	861	538	72	7	1265	948	1864	108
1966	362	300	369	5	790	337	1568	309
1967	336	126	1096	3	1059	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	2	0	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	137258	86293	494101	91020

Table 2b. Assumed historical catches of Antarctic fur seals. For crabeater seals, 750 animals are assumed to be taken per year in Region A for 11 years from 1967 to 1977.

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

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

Species		Abundance estimate	CV	Sources
Blue whale	$N_{2000}^{b,A}$	1104	0.4	Rademeyer *et al*. (2003)
	$N_{2000}^{b,P}$	762	0.4	
Fin whale	$N_{1997}^{f,A}$	10591	0.5	Branch and Butterworth (2001)
	$N_{1997}^{f,P}$	27594	0.5	Butterworth and Geromont (1995)
Humpback whale	$N_{1997}^{h,A}$	5044	0.2	Branch and Butterworth (2001)
	$N_{1997}^{h,P}$	4868	0.2	
Minke whale	$N_{1985}^{m,A}$	327369	0.1	Rep. int. Whal. Commn 41 (1991)
	$N_{1985}^{m,P}$	420572	0.1	
Antarctic fur seals	$N_{1930}^{s,A}$	100	0.5	Payne (1977,1979)
	$N_{1976}^{s,A}$	369000	0.5	Payne (1977,1979), MacCann & Doidge (1987)
	$N_{1991}^{s,A}$	1550000	0.5	Boyd (1993)
Crabeater seals	$N_{2000}^{c,A}$	4000000	0.5	J. Laake (pers. commn)*
	$N_{2000}^{c,P}$	4000000	0.5	

***** Laake's coarse initial circumpolar abundance estimate of 6-8 million is based only on the segment from 170°W to 125°W which was covered by US surveys in 1999/2000 austral summer as part of the Antarctic Pack Ice Seal (APIS) program (Ackley *et al.* 2003). This sector corresponds to only part of Region P. The estimates from surveys of Australian sector which covered from 60°E to 150°E is not yet available and information for the remainder of the Atlantic/Indian region is sparse. According to Erickson and Hanson (1990), circumstantial evidence indicates that appreciable numbers of crabeater seals occur seaward from the ice edge in ice-free waters adjacent to the continent, and largish numbers of crabeater seals are also found in the vicinity of sub-Antarctic islands. Thus here we assume 4 million crabeater seals for each Region. The CV's associated with the estimates are not available so that we accord a tentative CV of 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 the successive circumpolar abundance estimates listed are used towards this end (see text).

Species		Fitted trend	CV	Sources
Blue whale	N_{1981}^{b}	546	0.41	Branch and Rademeyer (2003)
	N_{1988}^{b}	680	0.52	
	N_{1996}^{b}	1891	0.42	
Humpback whale	$R_{1977-1991}^{h,A}$	0.11	0.14	Bannister (1994)[1]
	$R_{1981-1996}^{h,P}$	0.12	0.07	Brown *et al*. (1997)[2]
Minke whale	$R_{1970-2000}^{m,A}$	−0.024	0.31	Mori and Butterworth (2005)[3]
	$R_{1970-2000}^{m,P}$	−0.024	0.31	
Antarctic fur seals	$R_{1958-1971}^{f,A}$	0.17	0.5	Payne (1977), Boyd *et al*. (1990,1995)
	$R_{1977-1991}^{f,A}$	0.10	0.5	Boyd (1993)
	$R_{1991-2000}^{f,A}$	0.10	0.5	

[1] For west Australian (Area IV) only.
[2] For east Australian (Area V) only.
[3] For Areas IV and V only.

Table 5 Plausible bounds for the parameters to be estimated.

Parameters to be estimated		
	Bounds	Reference
$N_{1780}^{b,A}$	100000-300000	
$N_{1780}^{b,P}$	10000-100000	
$N_{1780}^{m,A}$	10000-300000	
$N_{1780}^{m,P}$	10000-400000	
$N_{1780}^{h,A}$	10000-200000	
$N_{1780}^{h,P}$	10000-100000	
$N_{1780}^{f,A}$	10000-400000	
$N_{1780}^{f,P}$	10000-200000	
$N_{1780}^{s,A}$	500000-5000000	
$N_{1780}^{c,A}$	100000-10000000	
$N_{1780}^{c,P}$	100000-10000000	
μ_b	0.05-0.16	See below (1)
μ_m	0.07-0.2	
μ_h	0.06-0.18	
μ_f	0.05-0.16	
μ_s	0.18-0.28	Laws (1984), Boyd *et al*. (1995)
μ_c	0.11-0.28	
M_b	0.03-0.06	See below (1)
M_m	0.04-0.1	
M_h	0.03-0.08	
M_f	0.03-0.05	
M_s	0.07-0.3	Laws (1984), Boyd *et al*. (1995), Payne (1977)
M_c	0.07-0.3	Laws (1984)
λ_b	115.9-450.6	See below (2)
λ_m	3.78-32.13	
λ_h	37.8-108	
λ_f	55.4-220.8	
λ_s	0.678-2.713	
λ_c	3.306-5.511	
r^A	0.4-0.6	Mori and Butterworth (2004)
r^P	0.4-0.6	

(1) Parameters selected from these ranges were also required to satisfy the conditions: $\mu_b - M_b \geq 0.02$, $\mu_f - M_f \geq 0.02$, $\mu_h - M_h \geq 0.02$, $\mu_m - M_m \geq 0.03$, $\mu_s - M_s \geq 0.03$ and $\mu_c - M_c \geq 0.03$, i.e. that blue, fin and humpback whales can attain per capita growth rates of at least 2%, and minke whales, crabeater seals and Antarctic fur seals can attain per capita growth rates of at least 3% under optimal feeding conditions.

(2) λ_j is calculated as (mean weight) × (%weight consumption/day) × (days feeding in the Antarctic)× (estimated proportion of krill in diet). The mean weight and days feeding in the Antarctic (Kasamatsu 2000) assumed for the whales are shown in Table 7. The range of %weight consumption/day assumed here is 0.9-3.5% for blue whales, 1.0-4.0% for fin whales and humpback whales, and 1.9-5.1% for minke whales (Kato and Shimadzu 1986, Tamura 2003). The proportion of the diet consisting of krill is assumed to be 100% for all the whales considered here except for fin whales. For fin whales a 50% krill diet composition is assumed. The fin whale feeding distribution in the austral summer is located appreciably further north of that for blue, humpback and minke whales. Though euphausids are still thought to be the primary source of food in that area (Ohsumi, Tamura pers. commn), these may well be from a different stock to the "krill" (*Euphausia superba*) upon which the predators feeding closer to the ice-edge mainly depend. The "50%" assumption is a crude approach to take account of this.

Because there is only a single estimate for % weight consumption/day for seals, which is 7% (Laws 1984), and because bull Antarctic fur seals reach over 0.2 tons in mass, compared with the normal adult cow weight of less than 0.05 tons (Payne 1977), in order to give a range for the consumption of krill by the seals, we used the ranges for the weights of 0.05-0.2 tons for Antarctic fur seals and 0.15-0.25 tons for crabeater seals. Days feeding in the Antarctic are 323 and 353 days for Antarctic fur seals and crabeater seals respectively (Laws 1984). The proportion of the diet consisting of

krill is assumed 60% and 94% for Antarctic fur seals and crabeater seals respectively (Øritsland 1977).

Table 6. Values of the input and estimated parameters and other quantities for the "reference case" and five sensitivity scenarios (i) to (v). See text for details of the sensitivity scenarios. Parameters under the estimated parameter heading which are shown in parenthesis were in fact fixed rather than estimated.

Input parameters							Estimated parameters and *lnL*								Derived parameters							
								Bounds	Estimates								Model						Observed
	Reference	(i)	(ii)	(iii)	(iv)	(v)			Reference	(i)	(ii)	(iii)	(iv)	(v)		Reference	(i)	(ii)	(iii)	(iv)	(v)	
Bb^A	1.70E+08	1.70E+08	1.70E+08	2.30E+08	5.00E+08	1.70E+08	$N_{1780}^{b,A}$	100000–300000	193093	194930	195115	226271	260995	208156	K_A	8.09E+08	8.58E+08	7.50E+08	7.61E+08	5.40E+08	4.30E+08	–
Bb^P	7.00E+07	7.00E+07	7.00E+07	5.00E+07	2.00E+08	7.00E+07	$N_{1780}^{b,P}$	10000–100000	27463	26511	29600	26371	32212	30563	K_P	1.56E+08	2.37E+08	1.55E+08	1.90E+08	2.27E+08	1.30E+08	–
							$N_{1780}^{m,A}$	10000–200000	52915	200000	61348	200000	33615	27709								
$\eta^{b,A}$	4.00E−08	4.00E−08	4.00E−08	2.00E−07	3.00E−08	4.00E−08	$N_{1780}^{m,P}$	100000–300000	169429	300000	248718	207706	300000	300000	Bm^A	1.47E+08	1.05E+08	1.41E+08	1.81E+08	5.75E+08	1.54E+08	–
$\eta^{m,A}$	3.00E−07	2.50E−07	3.00E−07	2.00E−07	1.35E−08	3.00E−07	$N_{1780}^{h,A}$	10000–250000	65438	65581	65430	68311	77651	63790	Bm^P	6.65E+07	5.66E+07	5.78E+07	2.77E+07	1.22E+08	5.08E+07	–
$\eta^{h,A}$	1.25E−06	1.25E−06	1.25E−06	8.00E−07	5.25E−07	1.25E−06	$N_{1780}^{h,P}$	10000–100000	56412	56057	58131	35922	59702	56826	Bh^A	3.21E+07	3.16E+07	3.28E+07	2.63E+08	7.61E+07	4.41E+07	–
$\eta^{f,A}$	4.00E−08	4.00E−08	4.00E−08	5.00E−08	4.00E−08	4.00E−08	$N_{1780}^{f,A}$	10000–400000	125736	123261	129972	197299	235957	153628	Bh^P	1.63E+07	1.61E+07	1.55E+07	4.63E+07	7.89E+06	2.25E+07	–
$\eta^{s,A}$	3.50E−09	3.50E−09	3.50E−09	–	1.50E−08	3.50E−09	$N_{1780}^{f,P}$	10000–200000	64461	55707	76138	43418	89092	82228	Bf^A	1.72E+08	1.31E+08	1.77E+08	4.23E+08	2.62E+08	1.75E+08	–
$\eta^{c,A}$	7.00E−09	7.00E−09	7.00E−09	–	5.00E−10	2.00E−08	$N_{1780}^{s,A}$	500000–5000000	2915890	2914040	2917080	–	2571660	2924650	Bf^P	9.61E+07	7.28E+07	1.00E+08	–	2.35E+08	1.01E+08	–
$\eta^{b,P}$	1.00E−06	1.00E−06	1.00E−06	6.00E−07	1.00E−06	1.00E−06	$N_{1780}^{c,A}$	100000–10000000	277991	192755	673947	–	100000	100000	Bs^A	1.49E+08	1.43E+08	1.51E+08	–	2.44E+08	1.51E+08	–
$\eta^{m,P}$	2.00E−07	1.70E−07	2.00E−07	1.70E−07	2.00E−07	2.00E−07	$N_{1780}^{c,P}$	100000–10000000	188741	100000	1520910	–	1476380	710125	Bc^A	1.34E+08	1.45E+08	8.49E+07	–	3.98E+08	1.18E+08	–
$\eta^{h,P}$	1.50E−06	1.50E−06	1.50E−06	1.00E−06	1.50E−06	1.50E−06									Bc^P	7.47E+07	8.01E+07	4.55E+07	–	3.18E+08	6.66E+07	–
$\eta^{f,P}$	7.00E−08	7.00E−08	7.00E−08	9.00E−07	7.00E−08	7.00E−08	λ^b	115.875–450.625	450.63	432.802	450.625	450.577	450.625	348.999								
$\eta^{c,P}$	6.00E−09	6.00E−09	6.00E−09	–	1.00E−09	6.00E−09	λ^m	3.78–32.13	32.13	32.1299	32.13	32.11	32.13	32.13	B_{1780}^A	9.46E+07	9.46E+07	9.56E+07	2.85E+08	1.55E+08	9.55E+07	–
							λ^h	37.8–108	108.00	108	108.00	108	108.00	108.00	B_{1780}^P	5.25E+07	5.17E+07	5.44E+07	4.05E+07	1.27E+08	5.47E+07	–
							λ^f	27.6–110.4	[110.4]	[110.4]	[110.4]	110.4	110.40	[110.4]								
							λ^s	0.678–2.713	2.71	2.71	2.71	–	0.68	2.71	$N_{2000}^{b,A}$	1102	1106	1115	1104	1108	1132	1104
							λ^c	3.306–5.511	5.51	5.51	5.51	–	5.51	5.51	$N_{2000}^{b,P}$	763	758	754	762	758	746	762
							μ^b	0.05–0.16	0.16	0.16	0.16	0.14	0.16	0.16	$N_{1985}^{m,A}$	326849	526145	325853	327244	327612	321737	327369
							μ^m	0.07–0.2	0.20	0.20	0.20	0.16	0.20	0.20	$N_{1985}^{m,P}$	420493	700703	420428	420730	365288	418978	420572
							μ^h	0.06–0.18	[0.18]	[0.18]	[0.18]	0.18	[0.18]	[0.18]	$N_{1997}^{h,A}$	5046	5045	5045	5044	5044	5057	5044
							μ^f	0.05–0.16	[0.16]	[0.16]	[0.16]	[0.16]	[0.16]	[0.16]	$N_{1997}^{h,P}$	4861	4861	4862	4868	4863	4861	4868
							μ^s	0.18–0.28	0.28	0.28	0.28	–	0.28	0.28	$N_{1997}^{f,A}$	10642	10663	10627	10591	10621	10889	10591
							μ^c	0.11–0.28	0.24	0.24	0.15	–	[0.25]	0.28	$N_{1997}^{f,P}$	27281	26020	27455	27586	27692	27451	27594
							M^b	0.03–0.06	0.03	0.03	0.03	0.04	0.03	0.03	$N_{1930}^{s,A}$	178	170	207	–	906	348	100
							M^m	0.04–0.1	0.04	0.04	0.04	0.07	0.04	0.05	$N_{1976}^{s,A}$	3.E+05	2.E+05	2.E+05	–	1.E+05	2.E+05	4.E+05
							M^h	0.03–0.08	0.08	0.08	0.08	0.04	0.08	0.07	$N_{1991}^{s,A}$	1.E+06	1.E+06	1.E+06	–	6.E+05	1.E+06	2.E+06
							M^f	0.03–0.05	0.03	0.05	0.03	0.04	0.05	0.03	$N_{2000}^{c,A}$	1.E+07	1.E+07	7.E+06	–	9.E+06	6.E+06	4.E+06
							M^s	0.07–0.3	0.07	0.07	0.07	–	0.07	0.07	$N_{2000}^{c,P}$	4.E+06	4.E+06	4.E+06	–	4.E+06	4.E+06	4.E+06
							M^c	0.07–0.3	0.08	0.07	0.08	–	0.07	0.11								
							r^A	0.4–0.6	0.40	0.43	0.41	0.43	0.40	0.40	$R_{1970-2000}^{m,A}$	−0.016	−0.010	−0.013	0.000	0.034	0.000	−0.024
							r^P	0.4–0.6	0.40	0.40	0.60	0.42	[0.40]	0.57	$R_{1970-2000}^{m,P}$	−0.004	−0.008	−0.004	0.005	0.001	−0.004	−0.024
															$R_{1977-1991}^{h,A}$	0.093	0.094	0.094	0.114	0.075	0.105	0.11
							LL_{abun}^b		0.000	0.000	0.001	0.000	0.000	0.001	$R_{1981-1996}^{h,P}$	0.090	0.090	0.090	0.118	0.089	0.093	0.12
							LL_{tren}^b		−1.917	−1.957	−1.992	−2.229	−1.787	−2.099	$R_{1958-1971}^{f,A}$	0.188	0.188	0.178	–	0.119	0.160	0.17
							LL_{abun}^m		0.000	4.059	0.001	0.000	0.993	0.016	$R_{1977-1991}^{f,A}$	0.164	0.173	0.140	–	0.119	0.154	0.10
							LL_{tren}^m		0.001	0.001	0.002	0.008	0.018	0.001	$R_{1991-2000}^{f,A}$	0.104	0.125	0.119	–	0.113	0.146	0.10
							LL_{tabun}^h		0.000	0.000	0.000	0.000	0.000	0.000								
							LL_{tren}^h		0.101	0.100	0.101	0.001	0.127	0.095								
							LL_{abun}^f		0.000	0.007	0.000	0.000	0.000	0.002								
							LL_{abun}^s		1.028	0.993	1.644	–	14.818	4.290								
							LL_{tren}^s		0.610	1.631	0.664	–	3.318	4.272								
							LL_{abun}^c		2.381	2.475	0.499	–	1.379	0.415								
							$-\ln L$		2.205	7.310	0.920	−2.221	18.866	6.997								

Table 7. Comparison of pre-exploitation consumption of krill suggested by Laws (1977) and the estimates provided by the "reference case" model. Note that for the latter calculations are shown both for feeding rates corresponding to the krill biomass as estimated for 1920 in the model, and for maximal feeding rates (corresponding to Laws' assumptions).

	Laws (1977) estimate					This study (for 1920)							
	Numbers (thousands)	Mean weight (t)	Days feeding in the Antarctic	%weight/day	Consumption of krill/year (10^3t)	Numbers (thousands)	Mean weight (t)	Days feeding in the Antarctic	%weight/day			Consumption of krill /year (10^3t)	
									Maximum	For 1920 krill abundance		Maximum	For 1920 krill abundance
										Region A	Region P		
Blue whale	200	88	120	3.4	71702	221	103	125	3.5	1.23	2.66	99791	35435
Fin whale	400	50	120	3.4	81480	203	46	120	4	1.38	2.51	46589	7146
Humpback whale	100	27	120	3.4	11000	75	27	100	4	3.75	3.93	8316	7548
Minke whale	200	7	365	3.9	19827	238	6	90	5.1	2.14	3.97	10080	3225
Crabeater seals	–	–	–	–	–	584	0.2	335	7	3.26	5.15	12757	1391
Antarctic fur seals	–	–	–	–	–	0.11	0.2	323	7	2.88	–	0.45	0
TOTAL (whales)					184009							164775	53353

- For the reference case, the krill component of the diet is assumed to be 50% for fin whales, 60% for Antarctic fur seals and 94% for crabeater seals. For other species, it is assumed to be 100%. The reason for the 50% assumption for fin whales is given in annotation to Table 5.

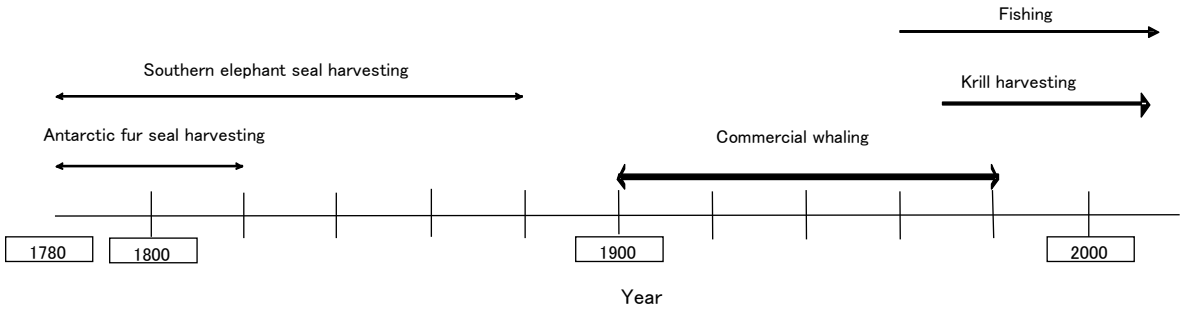


Figure 1. Schematic diagram that shows the historical harvesting of species in the Antarctic.

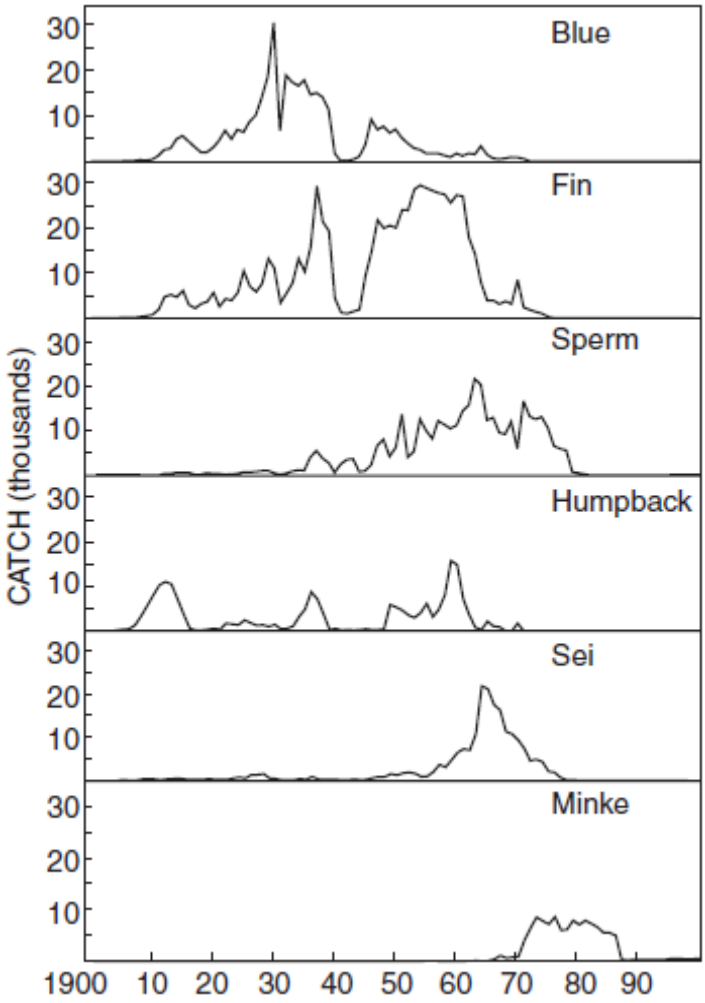


Figure 2. Annual catches of blue, fin, sperm, humpback, sei and minke whales caught in the southern hemisphere, corrected for Soviet misreporting (source: C. Allison, International Whaling Commission, December 2002).

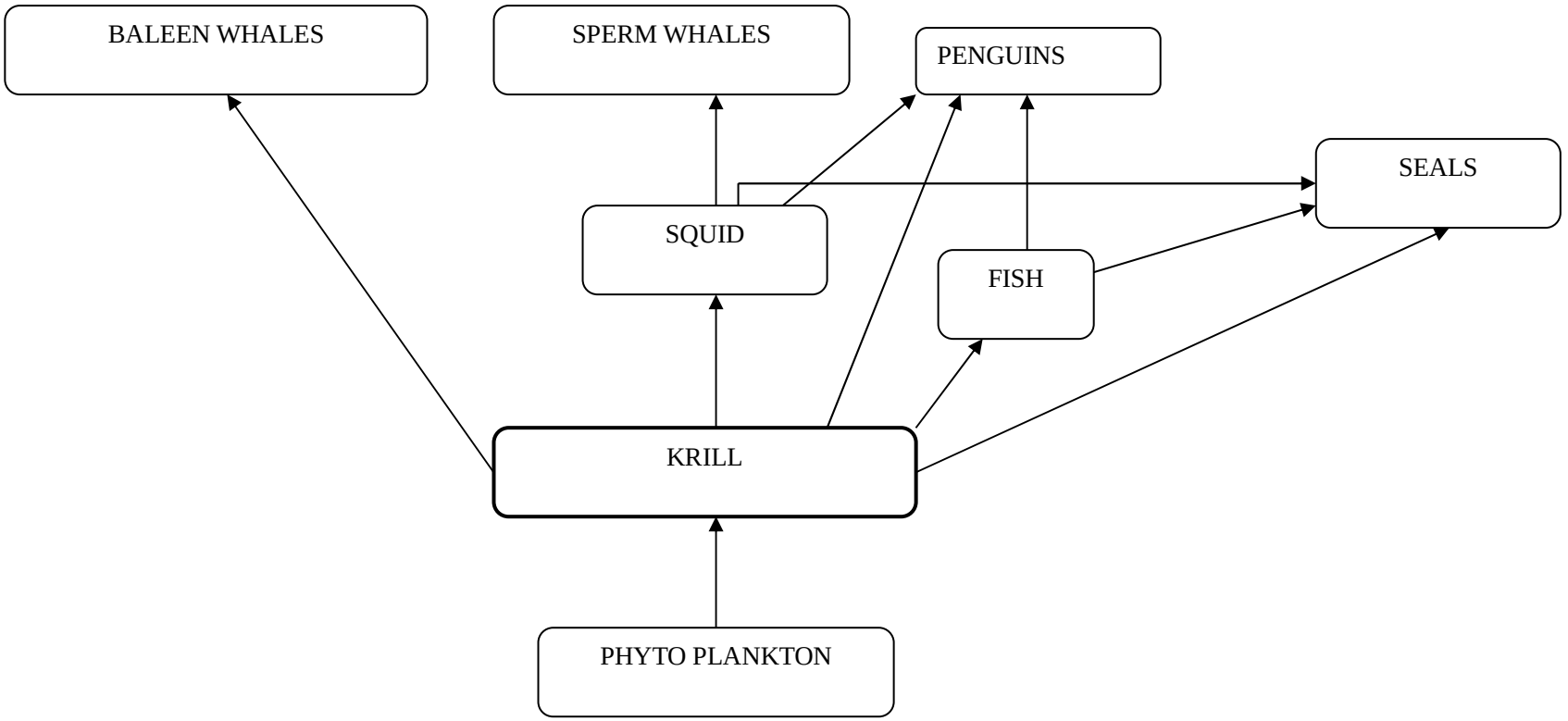


Figure 3. A simplified representation of the Antarctic marine food chain indicating krill's central position (after Miller 2002).

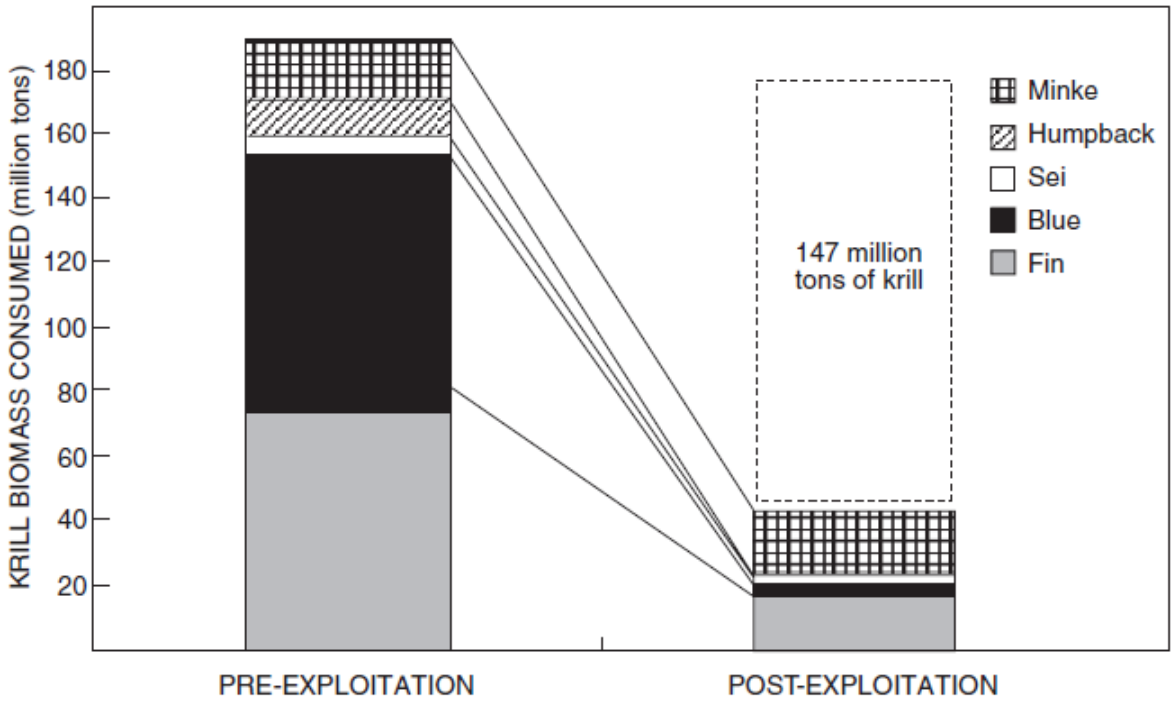


Figure 4. Estimated consumption of krill by baleen whales in the Antarctic (after Laws 1977). The plot shows the situation “pre-exploitation” and “post-exploitation” of whales.

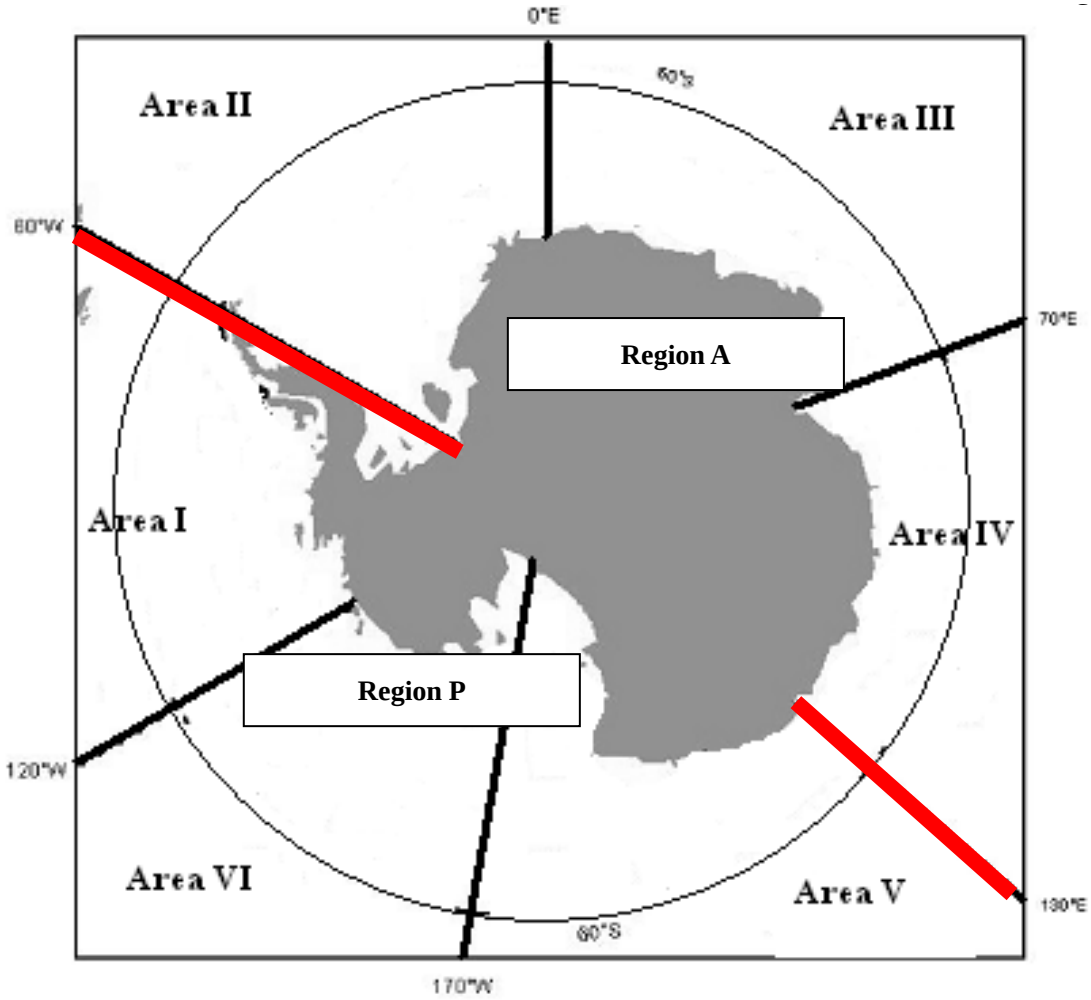


Figure 5. Map of IWC Management Areas (I to VI), and the two regions (Region A and Region P) considered in this paper.

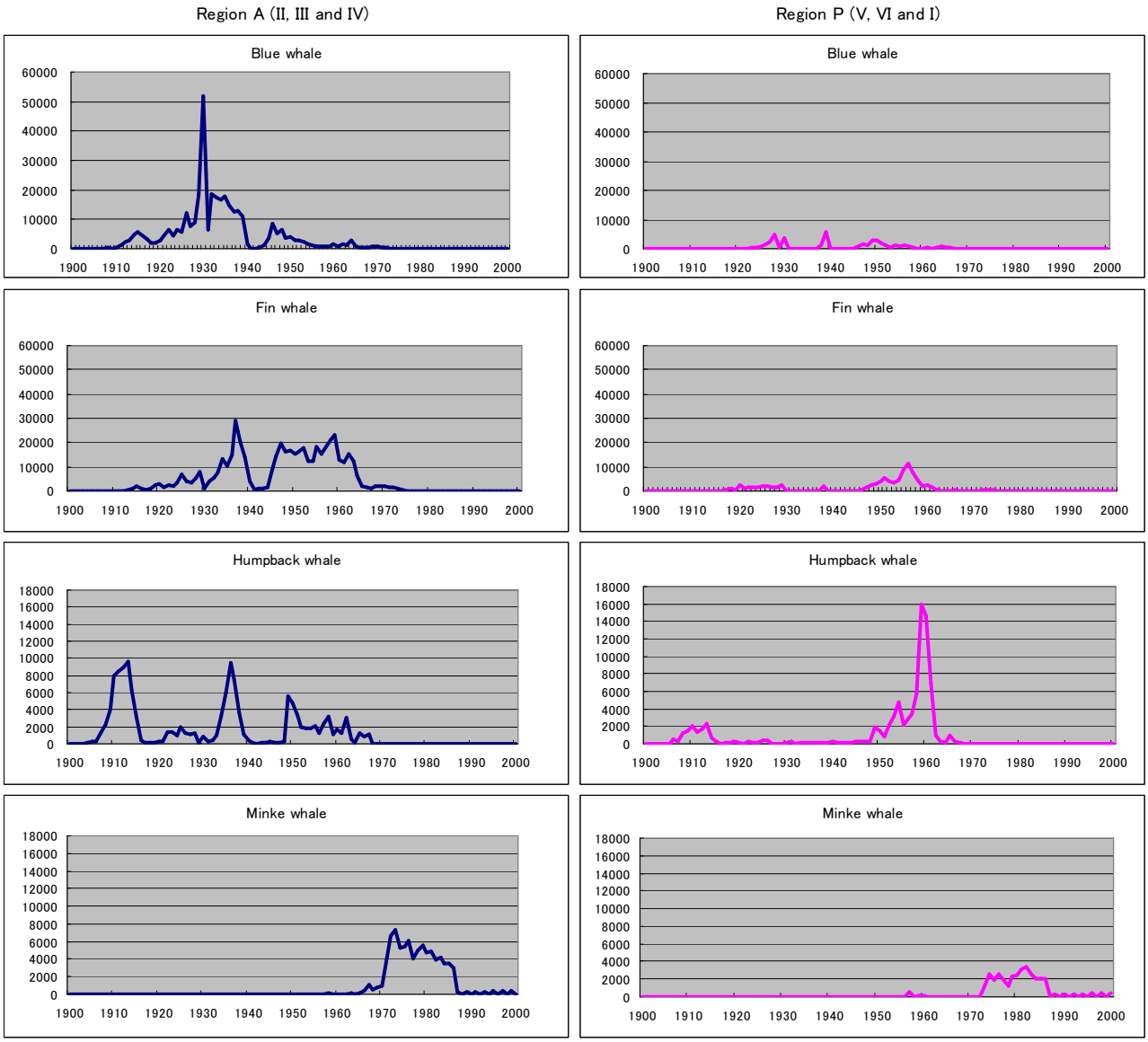


Figure 6. Historical catches of blue, minke, humpback and fin whales for Region A (IWC Management Areas II, III and IV) and Region P (IWC Management Areas V, VI and I). Note that the vertical scales differ between blue and fin whales on the one hand, and humpback and minke whales on the other.

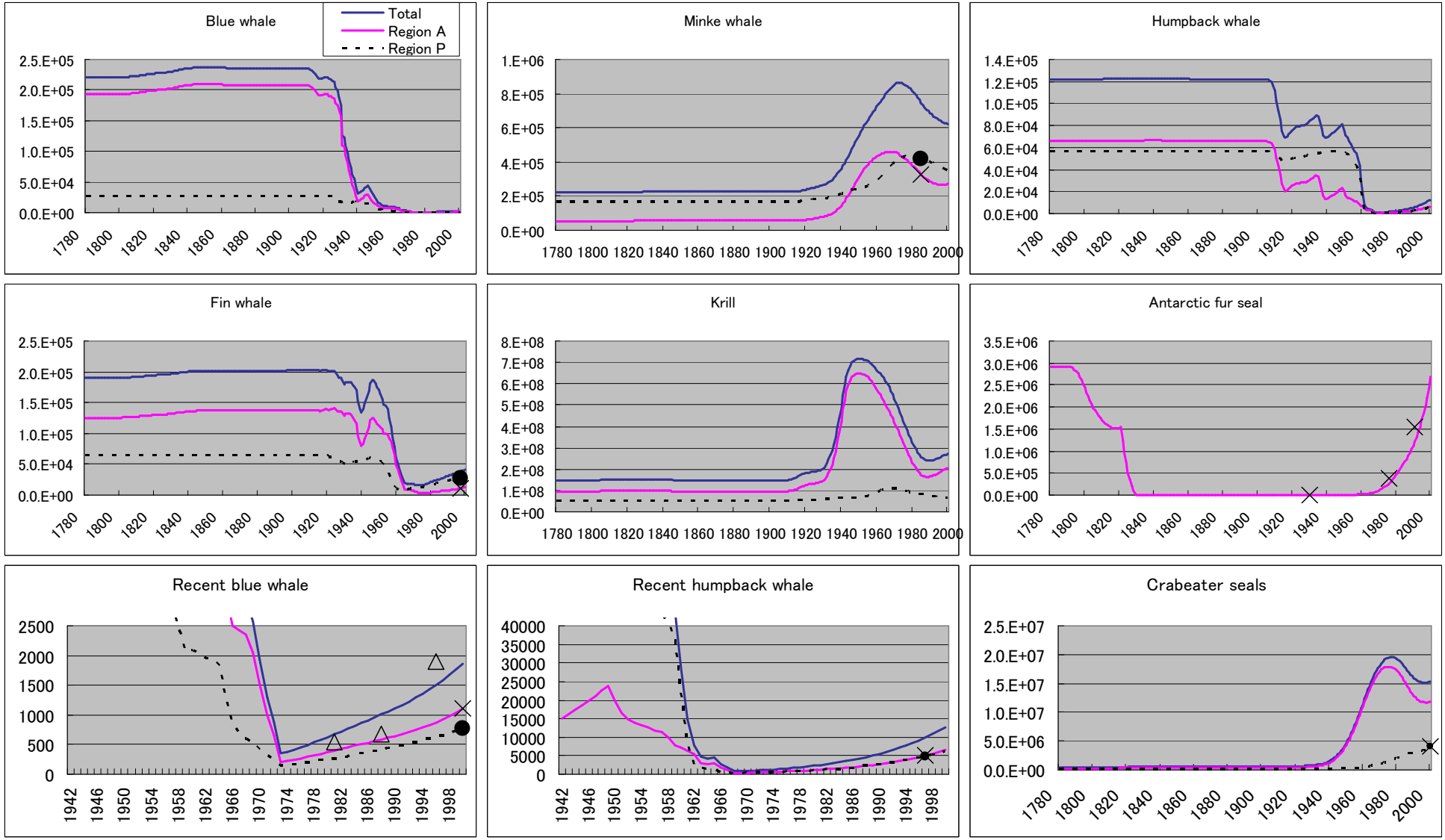


Figure 7. "Reference case" trajectories of krill and their main predators in the Antarctic. A black dot/cross shows a survey-based abundance estimate for the Pacific/Atlantic to which the model was fit. The open triangles shown in the recent blue whale trajectory plot are the blue whale abundance estimates from surveys for Regions A and P combined, to which the model was fit to reflect the trend indicated by these estimates.

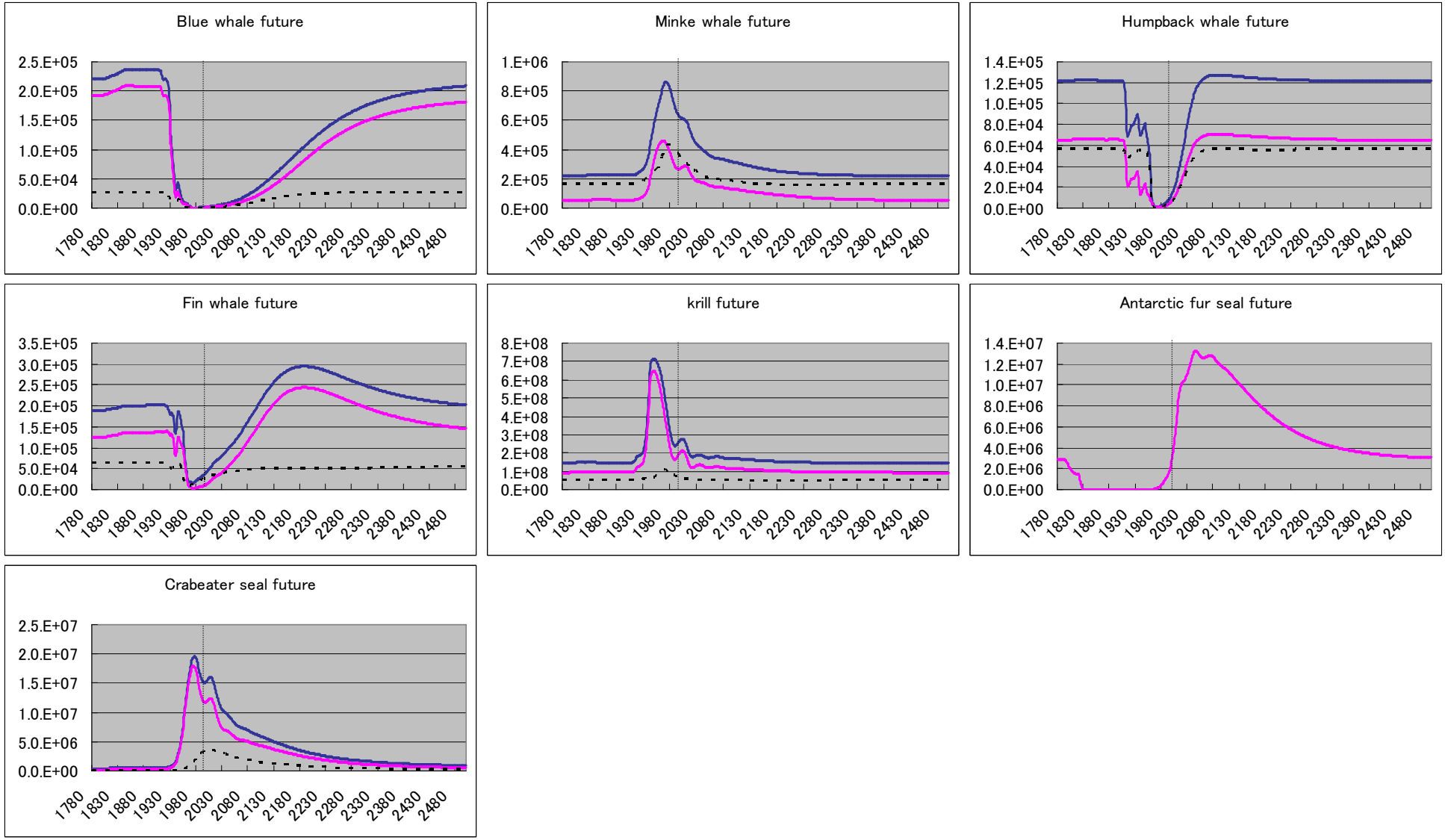


Figure 8. "Reference case" projections for future trajectories (up to 2500) for krill and their main predators in the Antarctic under the assumption of zero catches for all species after 2000.

(a) Reference case (b) Scenario (i) (c) Scenario (ii)

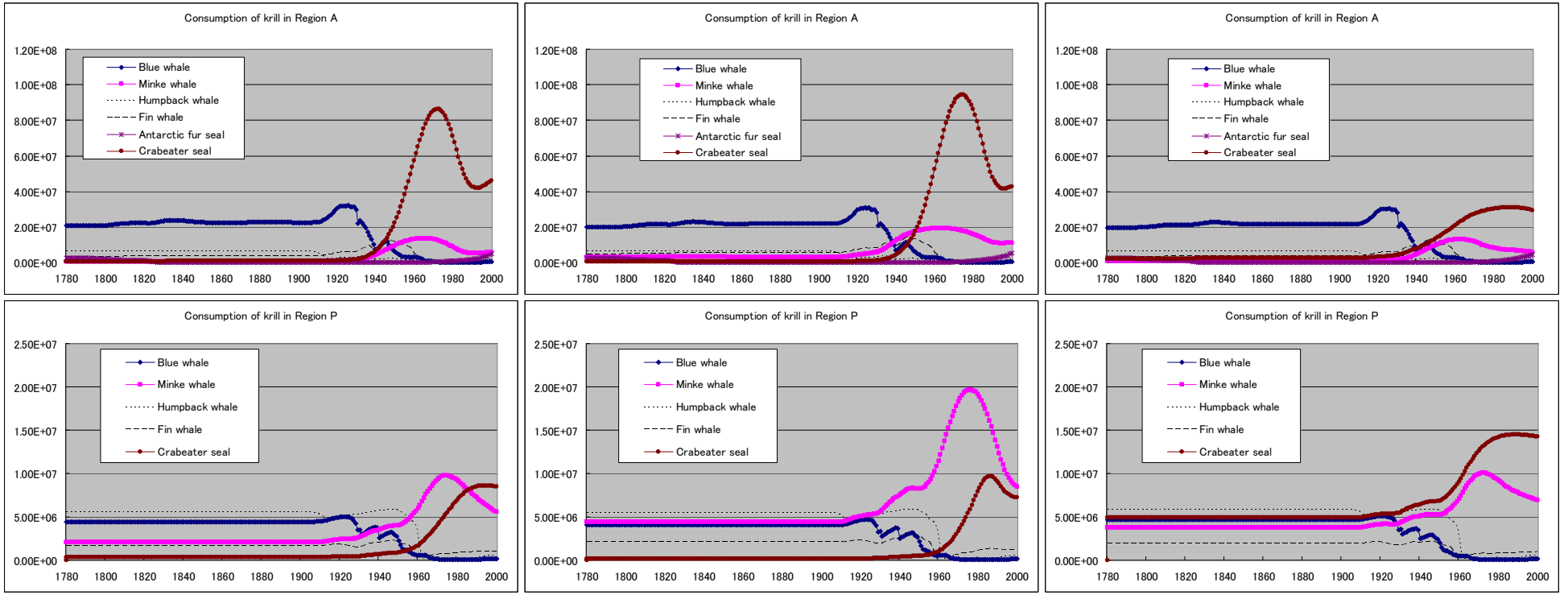
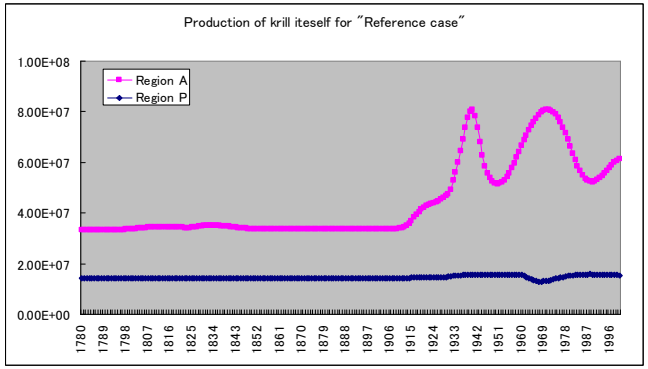
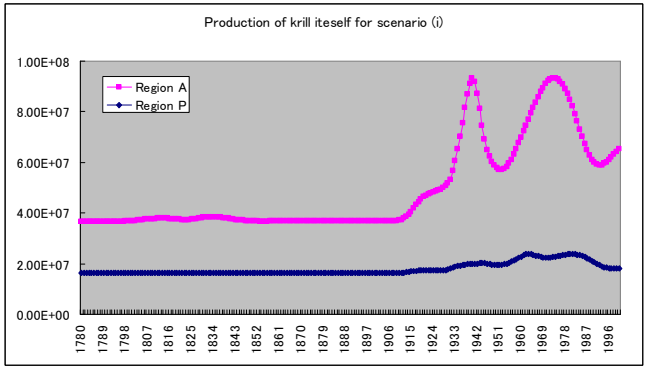


Figure 9. Consumption of krill biomass (tons) by predators considered in the model for Region A and Region P for (a) “reference case”, (b) scenario (i) and (c) scenario (ii).

(a) Reference case



(b) Scenario (i)



(c) Scenario (ii)

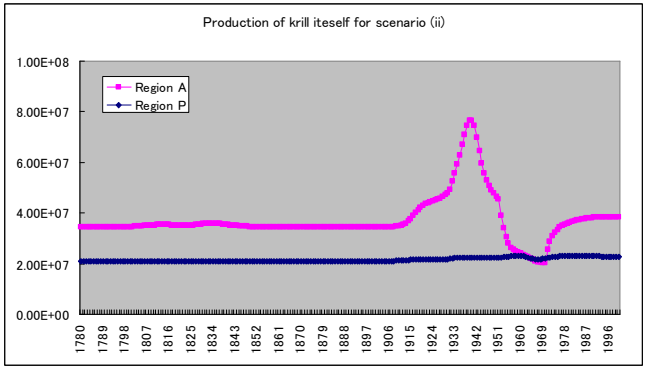


Figure 10. Estimated production of krill (tons) for Region A and Region P for (a) the “reference case”, (b) scenario (i) and (c) scenario (ii).

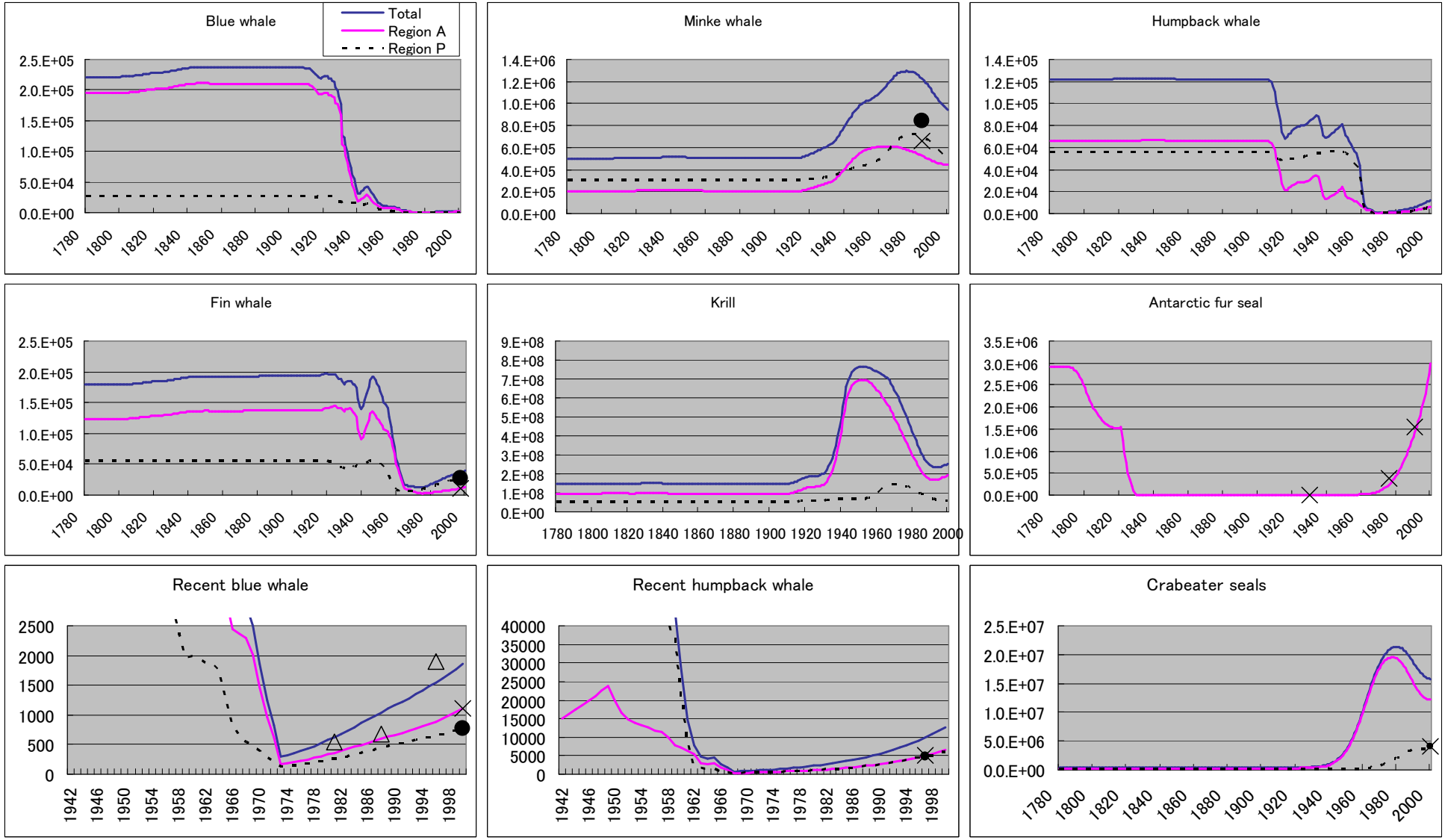


Figure 11. Trajectories of krill and their main predators in the Antarctic when **minke whale abundance as estimated from surveys is doubled**. The meanings of the symbols are same as in Figure 7.

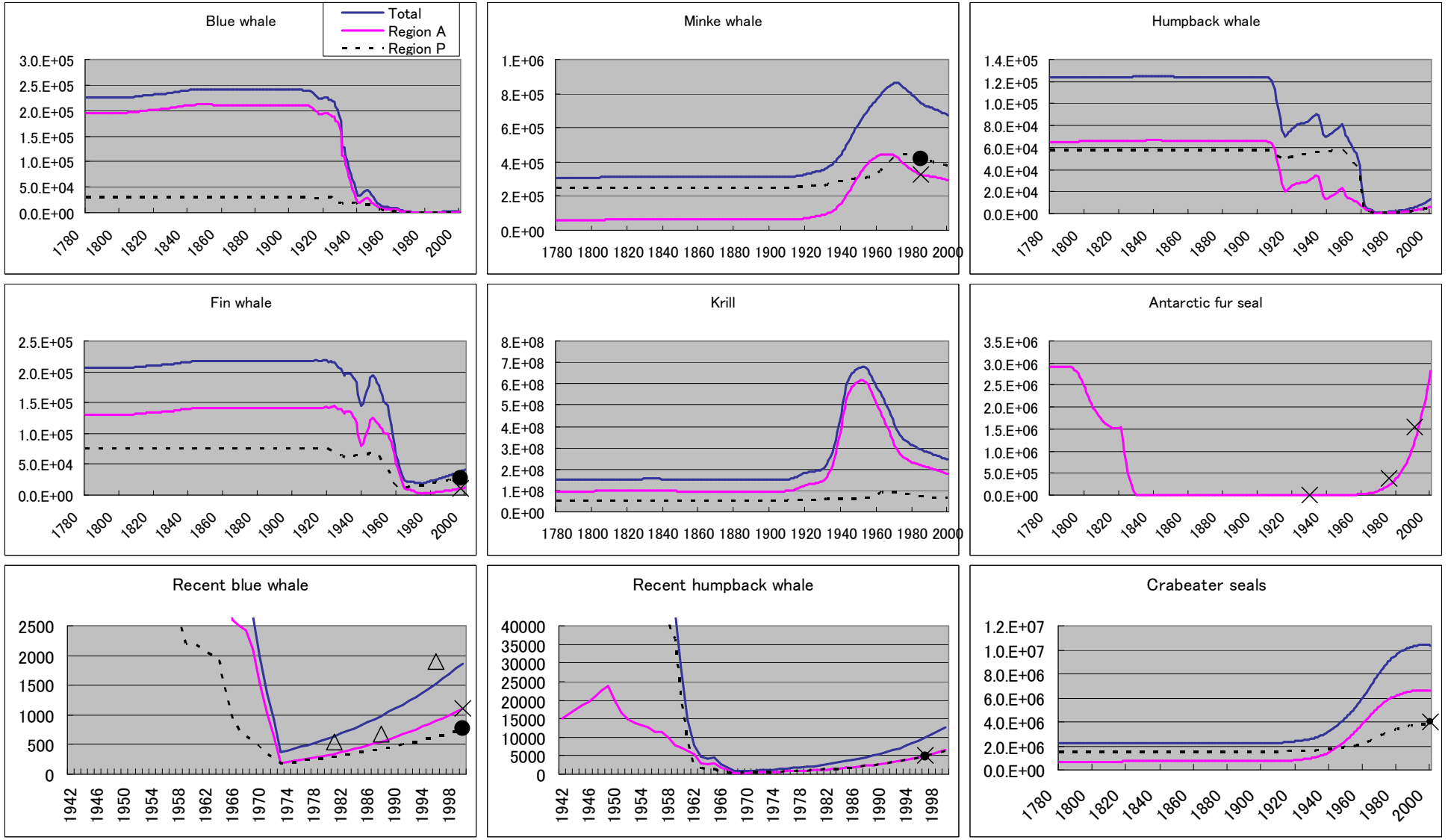


Figure 12. Trajectories of krill and their main predators in the Antarctic when observed minke whale abundance is doubled and K_A **is reduced linearly by 50% between 1950 to 1970**. The meanings of the symbols are the same as in Figure 7.

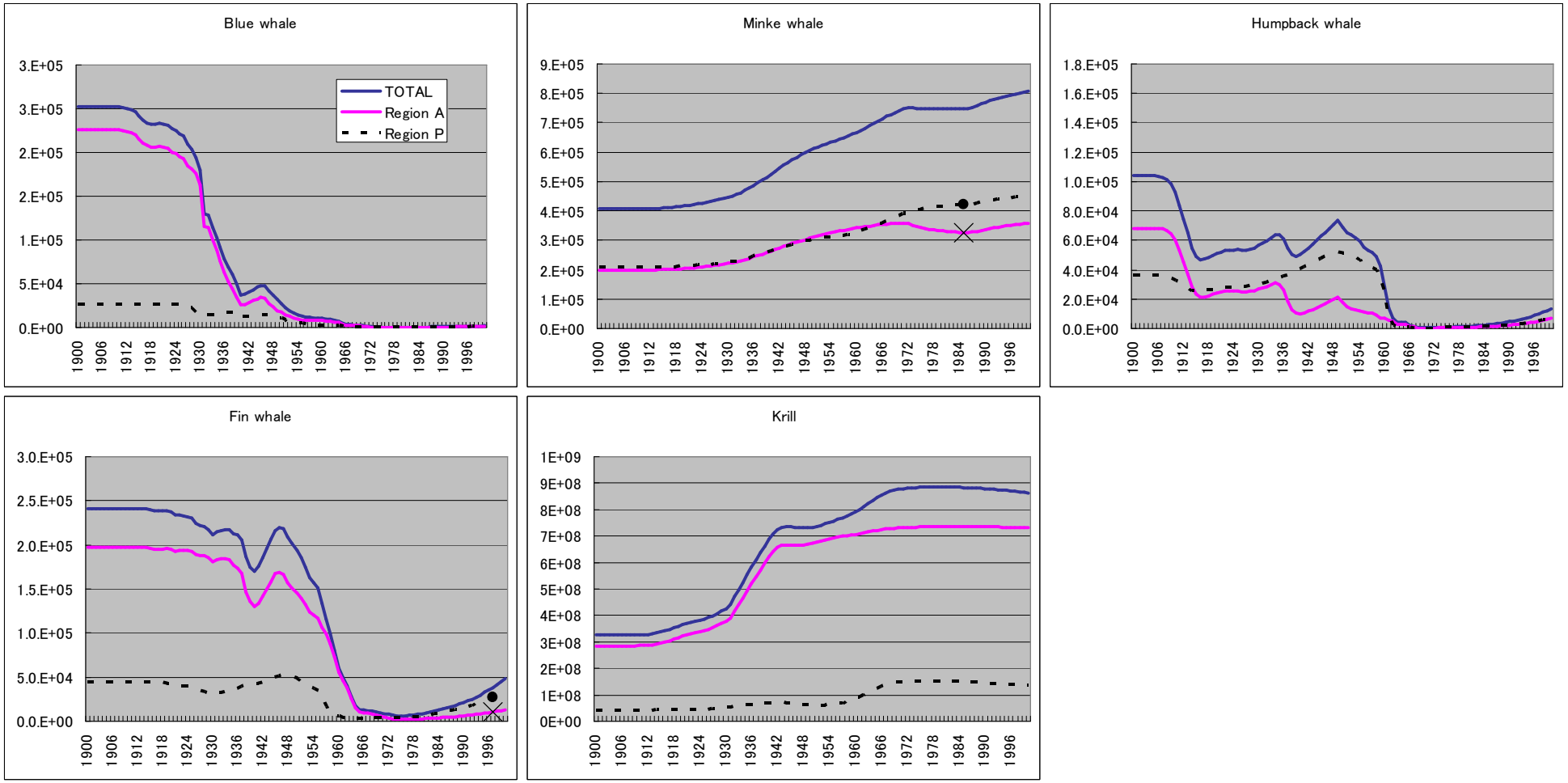


Figure 13. Trajectories of krill and their main predators in the Antarctic when **only baleen whales are considered** in the model (a Type III functional response remains assumed). The meanings of the symbols are the same as in Figure 7.

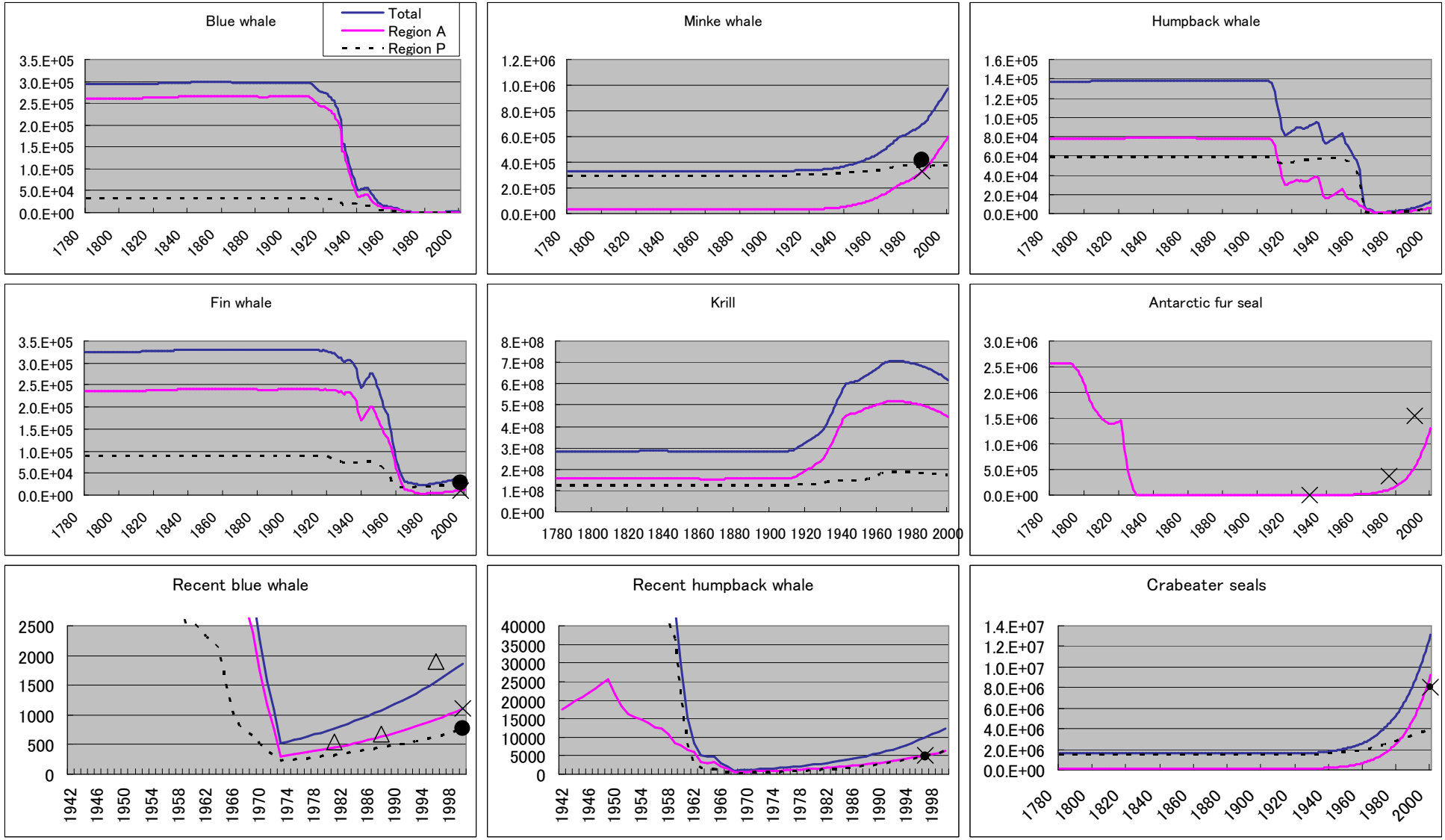


Figure 14. Trajectories of krill and their main predators in the Antarctic when a **Type II functional response form** is assumed. The meanings of the symbols are the same as in Figure 7.

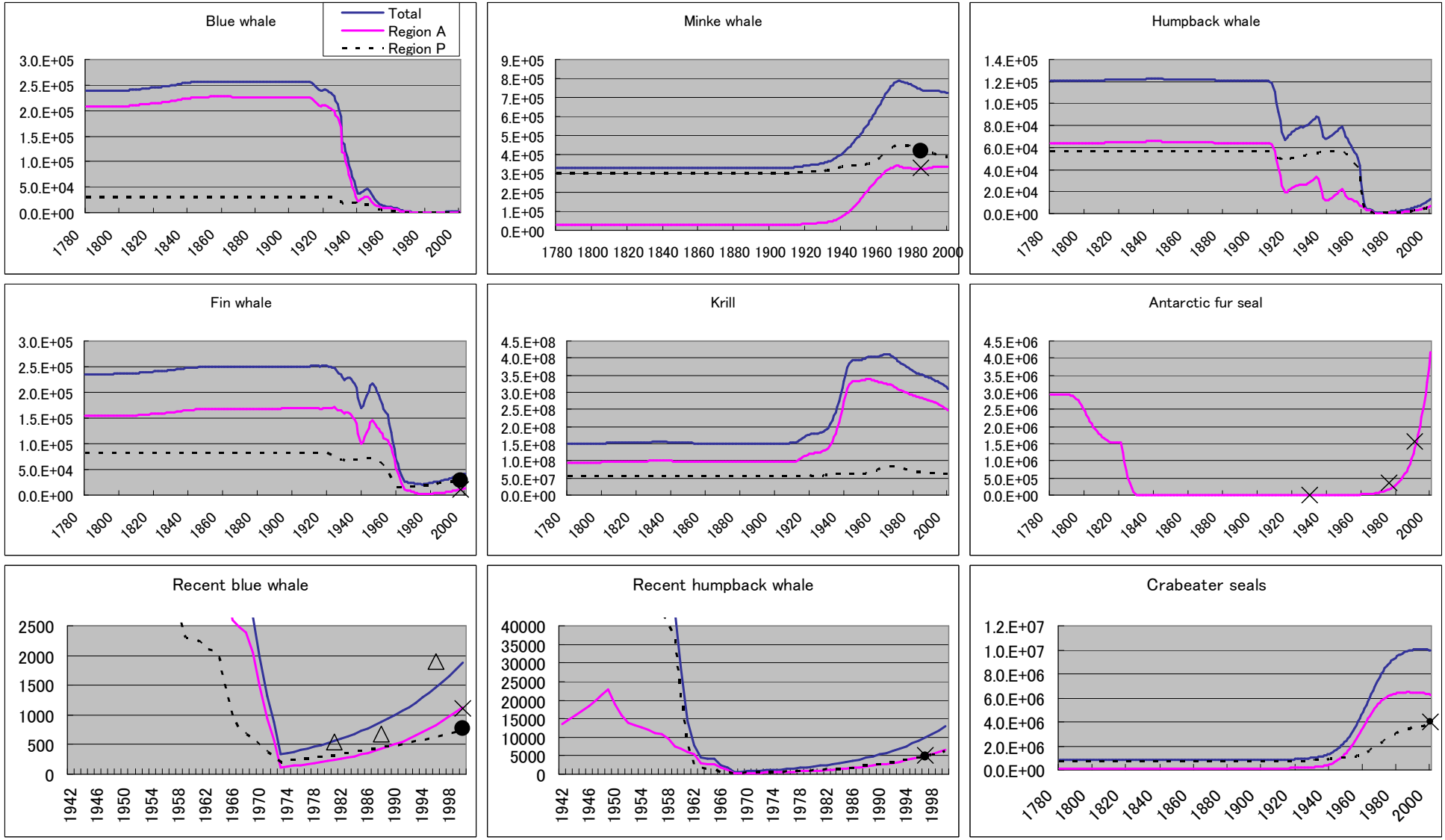


Figure 15. Trajectories of krill and their main predators in the Antarctic when **density dependent mortality of crabeater seals ($\eta^{C,A}$) is high** compared to the "reference case". The meanings of the symbols are the same as in Figure 7.

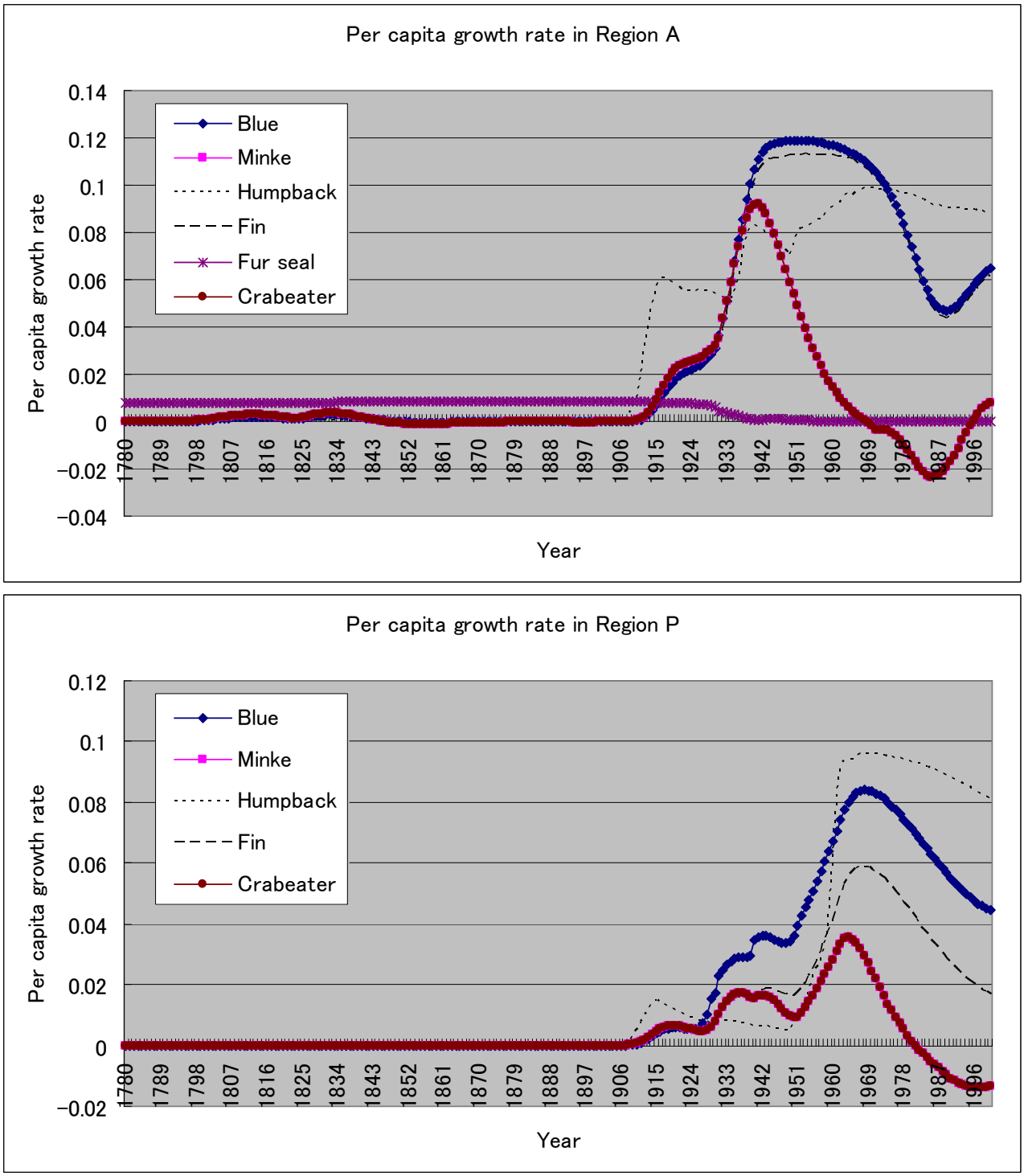


Figure 16. Per capita growth rate ($\frac{\mu^j \left(B_y^a\right)^n}{\left(Bb^a\right)^n + \left(B_y^a\right)^n} - M^j - \eta^{j,a} N_y^{j,a}$) changes over time for predator species considered in this study.

APPENDIX 1

Details for obtaining Antarctic fur seal catch by year

1. Fur seal catch trend around South Georgia

The following four pieces of information (McCann and Doidge 1984) available regarding Antarctic fur seal catch for South Georgia were used to construct a distribution of the catches by year.

(i) The first known trip to South Georgia was made between 1790 and 1792.

(ii) 1.2 million fur seals had been taken at South Georgia by 1822.

(iii) The Antarctic fur seal catch peaked in 1800 when 112000 skins were taken.

(iv) By 1820, Antarctic fur seals were almost rendered extinct at South Georgia

Assumed catch trend

The assumed catch trend for Antarctic fur seals in South Georgia is shown in Figure A3.1. For ease, we fitted two linear functions shown below:

$$C_y = 11000 \cdot (y - 1790) \qquad \text{for } 1790 \le y \le 1800 \qquad \text{(A3-1)}$$

$$C_y = 110000 - 5500 \cdot (y - 1800) \qquad \text{for } 1801 \le y \le 1820. \qquad \text{(A3-2)}$$

where C_y is the catch of Antarctic fur seals in South Georgia for year *y*.

2. Fur seal catch trend around the South Shetland Islands

Similarly, the following three pieces of information available (McCann and Doidge 1984) regarding Antarctic fur seal catch for the South Shetland Islands were used to construct a distribution of the catches by year.

(i) The first known trip to the South Shetland Islands was made in 1819.

(ii) In 1821, 320000 skins were taken.

(iii) By 1830 the stocks were almost exterminated.

Assumed catch trend

The assumed catch trend for Antarctic fur seals in the South Shetland Islands is shown in Figure A3.2. For ease, we again fit to a linear function shown below:

$$C_y = 320000 - 35556(y - 1821) \qquad \text{for } 1821 \le y \le 1829 \qquad \text{(A3-3)}$$

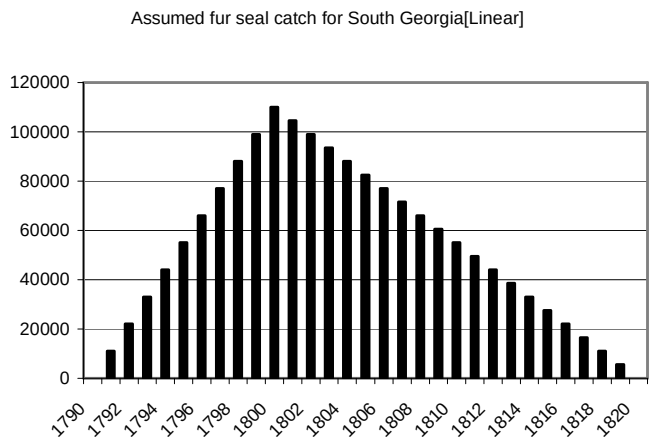


Figure A3.1 Assumed fur seal catch around South Georgia.

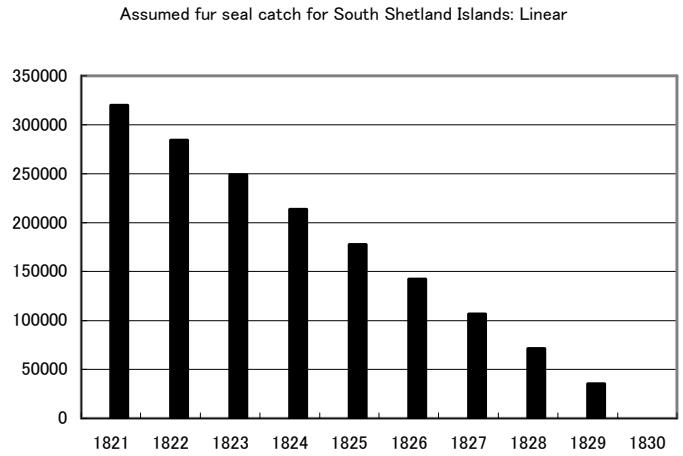


Figure A3.2 Assumed fur seal catches around the South Shetland Islands.