CCAMLR Science, Vol. 13 (2006): 217–277

A FIRST STEP TOWARDS MODELLING THE KRILL–PREDATOR DYNAMICS OF THE ANTARCTIC ECOSYSTEM

M. Mori
MARAM (Marine Resource Assessment and Management Group)
Department of Mathematics and Applied Mathematics
University of Cape Town
Rondebosch 7701, South Africa
Current address: Institute of Cetacean Research
4-5 Toyomi-cho, Chuo-ku
Tokyo, 104-0055, Japan
Email – mori@cetacean.jp

D.S. Butterworth
MARAM (Marine Resource Assessment and Management Group)
Department of Mathematics and Applied Mathematics
University of Cape Town
Rondebosch 7701, South Africa

Abstract

The history of human harvests of seals, whales, fish and krill in the Antarctic is summarised briefly, and the central role played by krill emphasised. 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 Ocean sectors of the Southern Ocean in view of the much larger past harvests in the former. A reference case and six sensitivities are fitted 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, to explain observed trends – crabeater seals seemingly play an important role and constitute a particular priority for improved abundance and trend information; (iii) the Atlantic/Indian Ocean sector shows major changes in species abundances, in contrast to the Pacific Ocean sector, 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 tonnes for the krill surplus may be appreciably too high as a result of his calculations omitting consideration of density-dependent effects in feeding rates.

Résumé

Les auteurs font un bref résumé de l'histoire de l'exploitation par l'homme des phoques, des cétacés, des poissons et du krill en Antarctique et mettent l'accent sur le rôle pivot du krill. Ils décrivent le contexte de l'hypothèse d'un surplus de krill au milieu du 20e siècle et discutent des nouvelles informations sur l'effectif des populations et leurs tendances qui ont été présentées depuis les premières discussions de cette question. L'objectif de cette étude est de déterminer si, à elles seules, les interactions prédateurs–proies peuvent expliquer les tendances des populations observées sans que l'on ait besoin d'avoir recours aux hypothèses de changements environnementaux. Un modèle a été créé, portant sur les espèces de krill, de quatre baleines mysticètes (la baleine bleue, le rorqual commun, la baleine à bosse et le petit rorqual) et de deux phocidés (l'otarie et le phoque crabier). Le modèle commence en 1780 (début de la chasse au phoque) et distingue le secteur Atlantique/Indien du secteur Pacifique de l'océan Austral, pour tenir compte de l'exploitation nettement plus importante dans ce premier secteur par le passé. Un cas de référence et six sensibilités sont adaptés aux données disponibles sur l'abondance des prédateurs et ses tendances ; la plausibilité des résultats et des hypothèses sur lesquelles ils reposent font l'objet d'une discussion dans laquelle il est suggéré de poursuivre l'étude dans d'autres secteurs. Parmi les inférences clés de l'étude, on note que : i) les effets de l'interaction des espèces peuvent suffire à expliquer les tendances observées, mais cela pourrait s'avérer difficile ; ii) il est nécessaire de prendre d'autres espèces en considération, outre les baleines mysticètes et le krill, pour expliquer les tendances observées – les phoques crabiers semblent jouer un rôle important et leur étude constitue une priorité pour obtenir de meilleures informations sur l'abondance et les tendances ; iii) le secteur de l'océan Atlantique/Indien présente des variations importantes d'abondance des espèces, alors que le secteur de l'océan Pacifique est nettement plus stable ; iv) les baleines mysticètes doivent pouvoir atteindre des taux de croissance relativement élevés pour expliquer les tendances observées ; et v) l'estimation de Laws (1977) évaluant le surplus de krill à quelque 150 millions de tonnes risque d'être considérablement trop élevée du fait que ses calculs ne tenaient pas compte des effets dépendant de la densité dans les taux d'alimentation.

Резюме

Кратко излагается история ведения человеком промысла тюленей, китов, рыбы и криля в Антарктике и подчеркивается центральная роль, которую играет криль. Описываются предпосылки гипотезы об избытке криля в середине 20-го столетия и рассматривается информация об уровнях популяции и изменений, которая появилась после того, как впервые был выдвинут этот постулат. Цель исследования – определить, может ли взаимодействие хищники–криль само по себе в целом объяснить наблюдаемые тенденции изменения популяции без необходимости прибегать к гипотезам об изменении окружающей среды. Разработана модель, включающая криль, 4 вида гладких китов (синий, финвал, горбатый и малый полосатик) и 2 вида тюленей (южный морской котик и крабоед). Модель начинается в 1780 г. (возникновение промысла морских котиков) и выделяет в Южном океане сектор Атлантического/Индийского океанов и Тихого океана, учитывая, что в первом масштабы промысла в прошлом были гораздо больше. К имеющимся данным о численности и тенденциях хищников подобраны контрольный вариант и 6 функций чувствительности; рассматривается правдоподобие результатов и допущений, на которых они строятся, а также предлагаемые направления дальнейших исследований. Основными выводами данной работы является следующее: (i) результаты взаимодействия видов сами по себе могут объяснить наблюдаемые тенденции изменения численности хищников, хотя и с некоторым затруднением; (ii) для объяснения наблюдаемых тенденций необходимо рассматривать и другие виды, кроме гладких китов и криля – тюлени-крабоеды, по-видимому, играют важную роль и являются особо приоритетным видом в плане получения улучшенной информации о численности и тенденциях изменения; (iii) сектор Атлантического/Индийского океанов демонстрирует существенные изменения в численности видов в отличие от гораздо более стабильного Тихоокеанского сектора; (iv) для объяснения наблюдаемых тенденций необходимо, чтобы коэффициенты роста гладких китов достигали сравнительно высоких значений; и (v) оценка Лоуза (Laws, 1977), согласно которой избыток криля составляет около 150 млн. т, вероятно, является сильно завышенной в результате того, что в его расчетах не принимаются во внимание зависящие от плотности факторы в интенсивности питания.

Resumen

Se presenta un breve resumen de la historia de las capturas de focas, cetáceos, peces y kril por el hombre, destacándose el papel fundamental del recurso kril. Se describen los fundamentos de la hipótesis de que a mediados del siglo veinte hubo un excedente de kril, y se analiza la información obtenida acerca de las poblaciones y de las tendencias desde que se postuló esta hipótesis por primera vez. El objetivo de este estudio es determinar si las interacciones depredador-presa por sí solas son capaces de explicar en términos generales las tendencias observadas en la población, sin tener que recurrir a hipótesis relacionadas con cambios en el medio ambiente. Se desarrolló un modelo que incluye el kril, cuatro especies de ballenas de barba (la ballena azul, el rorcual común o ballena de aleta, la ballena jorobada y el rorcual aliblanco) y dos de pinnípedos (el lobo fino antártico y la foca cangrejera). El modelo comienza en 1780 (cuando empezó la caza del lobo fino) y distingue los sectores del Océano Atlántico, Océano Índico y Océano Pacífico del Océano Austral, en vista de la explotación mucho más intensa del primer sector en el pasado. Se ajustó un caso de referencia y seis sensibilidades a los datos disponibles sobre la abundancia y las tendencias de los depredadores, y se discute la verosimilitud de los resultados y las suposiciones sobre las cuales se basaron, y a la vez se proponen otros campos que podrían investigarse. Las conclusiones más importantes del estudio son: (i) que los efectos de la interacción entre especies por sí solos pueden explicar las tendencias observadas de la abundancia de los depredadores, pero no con facilidad; (ii) que se deben considerar otras especies, además de las ballenas de barba y el kril, para poder explicar las tendencias observadas – la foca cangrejera aparentemente juega un papel importante, y su estudio es prioritario para poder mejorar la información sobre la abundancia y tendencias; (iii) los sectores de los Océanos Atlántico e Índico del Océano Austral muestran los mayores cambios en la abundancia de las especies, en contraste con el sector del Océano Pacífico, que es mucho más estable; (iv) las ballenas de barba deben poder alcanzar tasas de crecimiento relativamente altas para dar cuenta de las tendencias observadas; y (v) es posible que la estimación de Laws (1977), que calcula el excedente de kril en unos 150 millones de toneladas, sea perceptiblemente demasiado alta, ya que sus cálculos no consideraron los efectos dependientes de la densidad en las tasas de alimentación.

Keywords: Antarctic, ecosystem modelling, predator–prey, competitive release, krill surplus, krill, baleen whale, seal, CCAMLR

Introduction

This paper extends the Antarctic blue whale–minke whale–krill interaction model introduced in Mori and Butterworth (2004) in various ways, as detailed in the 'Data and methods' section. First, however, the background motivating this study is summarised.

Brief history of human harvesting in the Antarctic

The Antarctic is a region where the largest human-induced perturbation of a marine ecosystem anywhere in the world has taken place (Mori and Butterworth, 2004). 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 century. More recently finfish exploitation commenced in the 1960s, and that of Antarctic krill (*Euphausia superba*) (hereafter called 'krill') in the 1970s.

Seals (including Antarctic fur seals (*Arctocephalus gazella*), sub-Antarctic fur seals (*A. tropicalis*) and southern elephant seals (*Mirounga leonina*)) were taken around South Georgia from the 1790s. Weddell (1825) calculated that 1.2 million fur seals had been harvested at South Georgia by 1822[1] (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, 1987). 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 1). Antarctic blue whales (*Balaenoptera musculus*) were harvested legally from 1904 for almost 60 years, fin whales (*B. 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 microcephalus*) were taken in substantial numbers from the 1950s, and after the depletion of the other major baleen species, the sei whales (*B. borealis*) distributed further to the north were heavily impacted in the 1960s and 1970s. 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 at 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 (2005a, 2005b) have demonstrated that the humpback whale populations were reduced by harvesting to about 1–5% of their estimated pre-exploitation abundance, depending on the breeding stock considered. 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. In 1969 and 1970, the bottom-dwelling marbled Antarctic rockcod (*Notothenia rossii*) almost vanished from the vicinity of South Georgia after 514 000 tonnes were taken

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[1] Much of the harvesting in the Antarctic takes place during an austral summer season. The notation adopted in this paper is to refer, for example, to the 1986/87 season as 1986.

(Constable et al., 2000). Following this depletion, mackerel icefish (*Champsocephalus gunnari*) became a target of the former Soviet Union fleets in the mid-1970s, and the mean annual catch of this species declined substantially over the first 20 years of the fishery, from 1970 to 1990 (Kock, 1992). Fishing for 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 longline fishery in 1987. Substantial levels of IUU fishing[2] developed around South Georgia, and from 1996 there was a rapid rise in such activities in the Indian Ocean, leading to a catch substantially above the aggregate global limit recommended by CCAMLR for its Convention Area. The rapid declines of the stocks around Crozet Island and the Prince Edward Islands Exclusive Economic Zones (EEZs) have been of great concern (Constable et al., 2000; Brandão et al., 2002).

The first large-scale krill harvests began in the late 1960s, with catches peaking at over half a million tonnes 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 tonnes of krill was taken between 1973 and 2001 (Miller, 2002). The fishery has been stable for the past nine years with the catch in 2002 being 98 414 tonnes (SC-CAMLR, 2001). This level is not considered excessive, being much less than the precautionary catch limit of 4 million tonnes 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 tonnes. 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 Antarctic Peninsula and the South Shetland Islands (SC-CAMLR, 2001).

Antarctic food web and the central role of krill as prey

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 the 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[3]. 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 fulfil 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 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), Kerguelen Islands (Cherel et al., 1997), Marion Island (Klages and Bester, 1998) and Bouvet Island (Kirkman et al., 2000). Most studies are based on analysis of scat samples, and

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[2] IUU fishing means fishing that is either illegal (when taken without permission in the EEZ of a sovereign State), unregulated (when taken by non-members of the pertinent Regional Fisheries Management Organisation (RFMO), here CCAMLR), or unreported (when taken but not reported by members of the RFMO).

[3] Some other food organisms may also be found in small quantities in the diet of these species depending on the extent of the southern migration of the species, where those that migrate further to the south around the ice-edge probably overlap more with the distribution of krill. Baleen whales may also feed on *Euphausia crystallorophias*, which is generally found further south than *E. superba*. Tamura and Konishi (2005) report that in the deep parts of the Ross Sea and Prydz Bay, minke whales feed on *E. crystallorophias*, but that the overall consumption is far less than of *E. superba*. While there has not been any assessment of the abundance of *E. crystallorophias*, suspicions are that this is far less than that of *E. superba* (D. Miller, S. Nicol, pers. comm.).

krill seems to constitute the major dietary item for Antarctic fur seals around South Georgia, the South Shetland Islands, the South Orkney Islands and Bouvet Island. Around Kerguelen, Heard Island, and Marion Island, fish seem to be the major prey (Cherel et al., 1997; Green et al., 1989, 1991; Klages and Bester, 1998). These studies show that Antarctic fur seals feed not only on krill but also fish, and the amount of krill and fish consumption 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 as a whole is considered.

Some supporting evidence for the 'surplus' krill hypothesis – competitive release?

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 (1962, 1977) suggested that following this exploitation, some 150 million tonnes 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 tonnes was based on the coarse estimates available at that time of the population sizes of baleen whales, estimates of mean body weight, and the assumption that krill consumption by baleen whales was between 3 and 4% of their body mass per day (see further details 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, 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). Analyses of catch-at-age data using the ADAPT-VPA method (Butterworth et al., 1999, 2002; Mori and Butterworth, 2005) also suggest a statistically significant increase (about 5% per year) in minke whale recruitment during the period from about 1940 to 1965. Two sets of research cruise observations support this low minke whale abundance in the 1950s. Zenkovich (1962) reports that during a cruise in the Indian Ocean sector of the Southern Ocean in 1957 over the December–February period, 266 blue, 1 429 fin, 527 humpback but only 81 minke whales were seen. In coverage of the Pacific Ocean sector of the Southern Ocean in April, similar numbers of blue, fin and humpback whales were sighted; no figures are reported for minke whales in this region, but comments in the paper suggest these to be very low. Similar results had been reported in Clarke and Ruud (1954). They recount the voyage of the *Enern* to the Atlantic Ocean sector in November–December 1953, when 35 blue and 228–237 fin, but only 22 minke whales were sighted[4] during an expedition focused on marking. 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, which could have arisen for the same reason of increased availability of food in the form of krill that is postulated for minke whales. 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% per year. Observations at other breeding sites such as the South Shetland, Bouvet, Marion, Possession and Heard Islands also show that Antarctic fur seals increased from 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 large baleen whales. Since there is no

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[4] Some care must, however, be exercised in interpreting this result, as Clarke and Ruud (1954) also suggest that the lookout may not always have reported sightings of the smaller whales (minke and southern bottlenose), presumably because of their lesser financial importance at that time.

obvious evidence of any other appreciable environmental or human-induced changes that could have led to increases in these populations commencing 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 certainly 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 in the International Whaling Commission (IWC) Management Areas (see Figure 2) using various statistical and population-modelling approaches. Their GLM analysis took different management areas into account and indicated 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 among areas, with the population levels 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 off west Australia (termed 'breeding stock D' by the IWC (Annex H of IWC, 2004)) 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 Japanese Whale Research Programme under Special Permit in the Antarctic (JARPA) 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 an indication of the recovery of breeding stock C – east Africa. For breeding stock A (Brazil), Zerbini (2004) used a Bayesian 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 abundance in Areas IIIE (35°–70°E) and IV using JARPA sighting data from 1989 to 2003; however, there are large yearly fluctuations in the abundance estimates for the area south of 60°S in Areas IV and V, which may arise because the distribution area for fin whales lies mainly 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. Analyses of catch-at-age data using the ADAPT-VPA method (Butterworth et al., 1999, 2002; Mori and Butterworth, 2005) suggest an increase in minke whale recruitment in IWC Management Areas IV and V until a peak in the late 1960s, followed by a drop and then stabilisation over more recent years. Mori and Butterworth (2005) suggested a reduction in the total (1+) minke whale population in these areas from 1970 to 2000 at a rate of 2.4% per year. The relatively low levels of minke whale catches over this period are much too small to account fully for these trends. Analysis of the age-at-sexual-maturity of minke whales by Zenitani and Kato (2005) indicated 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 program commenced (Tamura and Konishi, 2005).

An increase in the age-at-sexual-maturity of crabeater seals has also been postulated. Bengtson and Laws (1985) suggested a steady increase through the 1960s and 1970s. A more recent study by Hårding and Härkönen (1995) also reached this conclusion, suggesting strong evidence for a true increase in age-at-sexual-maturity of crabeater seals from 1964 to 1989 based on calculations of the mean age-at-first-ovulation. Erickson and Hanson (1990) suggested 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 suggested a reduction in crabeater seal density of 30–60%. They attributed 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 proportion of the seal population observable on the ice during moults. No firm conclusion on this matter has been reached, but the trends in the age-at-sexual-maturity of crabeater seals, at least, suggest that any earlier increase rate in their abundance has slowed (and could perhaps even have reversed).

Reid and Croxall (2001) examined the relationship between the trends in krill biomass and those of its predators (Antarctic fur seals, Adélie (*Pygoscelis adelia*) and macaroni (*Eudyptes chrysolophus*) penguins) around South Georgia, and found that the numbers of all these predators have been declining since 1990, and that the length of krill in their diets has become smaller, which indicates a lesser abundance of adult krill. These authors suggest 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 to be crucial for understanding and predicting trends in abundance for these populations.

Objective of this study

A decrease in sea-ice cover until the mid-21st century as a consequence of global warming has 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 also likely to be 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 IWC in collating 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 for the whale species heavily depleted last century 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, the hypothesis in this paper is that the effects of human-induced harvesting of the species in the Antarctic has indeed played a major role in, and continues to impact on, 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 both 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, it is hoped 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 and methods

Species considered in the model

Baleen whales, some squid, fish, seabirds and some seals all prey directly on krill. The amount of krill consumed by each species group 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 predator groups on krill biomass, approximate estimates of krill consumption by each predator group in the Antarctic are summarised 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 on krill of consumption by baleen whales and seals in the Antarctic is relatively large, and therefore baleen whales (specifically blue, minke, humpback and fin whales) and seals (Antarctic fur 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 estimate 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 such values for these species (particularly for squid and fish) is still very limited, and any estimates remain heavily dependent on what are often rather sweeping assumptions. Similar comments could be made for other cetacean species such as killer and beaked whales. Due to this lack of data, the effect of consumption by these further species on krill and on the predator–prey dynamics in the Antarctic is not considered directly in the model developed. 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 2), as their distribution is essentially restricted to the Atlantic Ocean sector.

Incorporating regional effects

The model developed divides the Antarctic into two regions: one is the Atlantic and Indian Ocean sectors, which corresponds essentially to the IWC Management Areas II, III and IV, and the other the Pacific Ocean sector, which corresponds to the Areas V, VI and I. The two regions, together with the IWC management areas, are shown in Figure 2. For convenience, the former region is termed Region A, and the latter 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 in Region A (Figure 3), bringing most of the large baleen whale populations and the Antarctic fur seals to the verge of extinction. The whales on the Pacific side of the continent were harvested in much lesser numbers (Figure 3). This suggests an uneven pre-exploitation distribution of large baleen whales: abundant in Region A, but relatively scarce in Region P. Thus, the impact of whaling and sealing may have different effects in these two regions, which is the reason for this division.

Historical catch

Baleen whales

Annual catches by region for the baleen whales species considered in the model are listed in Table 2(a). These include all catches taken in the southern hemisphere. Catches for blue whales have been taken from Rademeyer et al. (2003), except that some minor errors found there have been corrected. The pygmy blue whales (*B. m. brevicauda*) identified in Branch et al. (2004) are excluded from these data, as are the whales for which the species name is indicated only as 'probably blue whales' (this occurs over 1905–1913, involving a total of 1 063 whales).

Catches for fin whales have been provided by C. Allison of the IWC Secretariat. For some of the early catches, species were not recorded. In these cases, the total catch by the vessels concerned have been allocated to species in the same proportions as for the same vessels in the same region for the nearest year for which species information is given. A similar basis was used to allocate catches to Regions A and P when no information on catch position was given, except that all South Shetland catches were allocated to Region A. When compared to the cumulative catch of fin whales over time, the contributions from allocations from catches for which the species were not specified total only about 2%.

The catch series for minke whales have been provided by C. Allison. For humpback whales, the series developed by C. Allison and K. Findlay during the 2005 meeting of the IWC Scientific Committee were used, with catches for breeding stocks A, B, C and D allocated to Region A, and for E, F and G to Region P (see IWC, 2004 for the geographical locations of these breeding stocks).

It should be noted that aspects of the early catch histories and more recent Soviet misreporting for these species remain under investigation, but any consequent future changes to the values in Table 2(a) are likely to be minor.

Seals

Since no details on yearly catches of Antarctic fur seals exist, a plausible catch history for this species based on the available knowledge of these catches was developed. Details of how this was accomplished are given in the appendix. 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 (Boyd, pers. comm.). The consequent historical catches of Antarctic fur and crabeater seals assumed for the model are shown in Table 2(b).

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. Note that the estimates of abundance for blue, humpback and minke whales in Table 3 refer to the region south of 60°S, which probably includes most of the blue and minke whales. For the fin whales, the estimates obtained for south of 60°S by Branch and Butterworth (2001) are extrapolated by a factor of 7, based on the results of Butterworth and Geromont (1995), who used Japanese scouting vessels (JSVs) sighting rate data, for which the surveys extended as far north as 30°S, as an index of relative density to extrapolate abundance estimates obtained from the IWC/IDCR-SOWER surveys to the region north of 60°S.

Since the abundance trends for fin whales and crabeater seals are not well known, they are not included in Table 4, so that no related information is used in fitting the population model developed below.

Population dynamics of the species

Functional response

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 (SC-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) are likely to follow Type III curves. In the analyses following, 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 intraspecific density-dependent parameter (η) for each predator in order to admit a non-trivial coexistence equilibrium of the species considered.

Dynamics of krill –

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

Dynamics of the predators –

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

where

B_y^a	is the biomass of krill in region *a* in year *y*;
r^a	is the intrinsic growth rate of krill in region *a*;
K_a	is the carrying capacity of krill (in the absence of predators) in region *a*;
λ^j	is the maximum per capita annual consumption rate of krill (in tonnes) by predator species *j* (*j* could be either *b* (blue whale), *m* (minke whale), *h* (humpback whale), *f* (fin whale), *s* (Antarctic fur seal) or *c* (crabeater seal));
$N_y^{j,a}$	is the number of predator species *j* in region *a* in year *y*;
$B^{j,a}$	is the krill biomass when the consumption, and hence also the birth rate, of species *j* in region *a* drops to half its maximum level;

μ^j is the maximum annual birth rate of predator species *j* (which can be considered to include calf-survival rate, as usually only the net effect of these two processes in combination is measurable);

M^j is the natural annual mortality rate 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);

$C_y^{j,a}$ 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 (typically by some two or more orders of magnitude) (SC-CAMLR, 2001). Terms involving the parameter $\eta^{j,a}$ can apply to either or both 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 the 'Discussion' section).

Note also that the krill production function in equation (1) is changed from the Pella-Tomlinson form of the earlier model of Mori and Butterworth (2004) to a Schaefer form. This was done to facilitate computations: the problem is that otherwise the computation of K_a from equation (3) (see next subsection) can lead to discontinuous derivatives, which is not permissible for the minimisation process of the ADMB package used for these computations. The effect of this change is not large: the MSY level (MSYL) for krill increases from 40 to 50% of K_a.

Model fitting procedure and parameter estimation

In order to estimate the yearly abundances of krill and its predators using equations (1) and (2), the initial abundance for each species in the year 1780, before any exploitation began (taken to correspond to a co-existence equilibrium level for the species considered), needs to be estimated. The condition that all the species considered in the model were in equilibrium (balance) in the year 1780 provides relationships between the parameter values. Thus, by setting $B_{y+1}^a = B_y^a$ in equation (1), it follows that if a Type III functional response form is assumed:

$$r^a\left(1-\left(\frac{B_{1780}^a}{K_a}\right)\right)=\sum_j \frac{\lambda^j\left(B_{1780}^a\right)^2 N_{1780}^{j,a}}{\left(B^{j,a}\right)^2+\left(B_{1780}^a\right)^2} \qquad (3)$$

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

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

for each predator species *j*.

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

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

Given values of $B^{b,a}$ and $\eta^{b,a}$ as inputs (see Table 6), and choices from their plausible ranges for the other blue whale parameters ($M^b, N_{1780}^{b,a}$ and μ^b) (see Table 5), the initial biomass of krill in region *a* in year 1780 (B_{1780}^a) is specified. Similarly, by solving equation (4) for $B^{j,a}$, this functional response parameter is specified for each 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 minimised to estimate parameters $M^j, N_{1780}^{j,a}, \lambda^j, \mu^j$ for all the predator species *j*, and r^a for krill, is:

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

where this function (–ln*L*) comprises the contributions of LL_{abun}^j and sometimes LL_{tren}^j from each predator species *j*. LL_{abun}^j is the component that compares the model-estimated abundance of predator species *j* to the observed abundance (estimated directly from surveys) and assumes distribution lognormality, and LL_{tren}^j is a similar component pertinent to the abundance trend which assumes distribution normality.

Blue whale component

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

$$LL^{b}_{tren} = \sum_{y=1}^{n}\left[\ln\sigma_y + \frac{1}{2\sigma_y^2}\left(\ln N_y^{b,obs} - \ln q - \ln \hat{N}_y^{b}\right)^2\right], \tag{8}$$

where $\ln q = \dfrac{\sum_{y=1}^{n}\frac{1}{\sigma_y^2}\left(\ln N_y^{b,obs} - \ln \hat{N}_y^{b}\right)}{\sum_{y=1}^{n}\frac{1}{\sigma_y^2}}$,

with q reflecting a possible multiplicative bias in the abundance estimates utilised, and the summation being over years for which circumpolar estimates of abundance (i.e. for regions A and P combined) are available.

Minke whale component

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

$$LL^{m}_{tren} = \left(R^{m,A}_{1970-2000} - \hat{R}^{m,A}_{1970-2000}\right)^2 / 2\left(\sigma^{m,A}_{1970-2000}\right)^2 + \left(R^{m,P}_{1970-2000} - \hat{R}^{m,P}_{1970-2000}\right)^2 / 2\left(\sigma^{m,P}_{1970-2000}\right)^2 \tag{10}$$

Humpback whale component

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

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

Fin whale component

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

Antarctic fur seal component

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

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

Crabeater seal component

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

where $\sigma_y^{j,a}$ is the CV of the observed abundance (or abundance trend) of species j in region a in year(s) y; and $R^{j,a}_{y_1-y_2}$ is the rate of increase of species j in region a from year y_1 to year y_2 which is calculated from the equation:

$$R^{j,a}_{y_1-y_2} = \left(\frac{N^{j,a}_{y_2}}{N^{j,a}_{y_1}}\right)^{\frac{1}{y_2-y_1}} - 1\,.$$

Biological parameters

Details of the plausible bounds imposed on the parameters to be estimated are provided in Table 5[5]. Computations were conducted using the ADMB package, which treats this information as providing boundaries for uniform priors for each of these parameters, so that the estimates ultimately provided can be considered either as maximum likelihood estimates or as the modes of Bayesian posteriors. The range for r^a was selected on the same basis as in Mori and Butterworth (2004), and ranges for the other parameters were chosen based on various sources of information available to date.

Values for the input parameters $B^{b,a}$ and $\eta^{j,a}$ (see Table 6) were chosen so that the resultant populations' trajectories are able to reflect the patterns evident from available data. Note in particular that the apparent greater suitability of the Atlantic for

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[5] Given that the model developed here is age-aggregated rather than age-structured, biases can arise between values of parameters and variables in such models and the observed/actual values of these quantities (that likely better correspond to age-structured model constructs) (see, for example, Punt, 1989, Figure 2 of which provides an example of such a bias for biomass estimates). Thus the ranges considered in Table 5 for consumption rates (for example) may not be the most appropriate for the aggregated model developed here, but it was nevertheless considered desirable to impose such bounds so as not to stray too far from biological realism.

blue, fin and humpback whales and of the Pacific for minke whales is reflected by choosing comparatively smaller values for the η parameter for these respective regions.

Results

Figure 4 shows the 'reference-case' model 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 six 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[6]. Once the fit had converged, a check was made that the associated initial coexistence equilibrium was stable. Figure 5 shows the projected trajectories (up to the year 2500) for this 'reference-case' model under zero future catches for all the species. Figure 6(a) shows the annual consumption of krill by each predator in Regions A and P; note that the relatively greater increase in consumption by minke whales in the latter region arises from their greater abundance there compared to the other predator species. Figure 7(a) shows the annual production of krill itself for each region; the greater changes in Region A reflect the higher initial abundances and subsequent much greater harvests there, particularly of blue and fin whales (see Figure 3).

Six other scenarios to investigate the sensitivity of these results were considered. These are as follows:

(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 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. de la Mare, 1997; Gille, 2002; Atkinson et al., 2004), what if carrying capacity K_A of krill was linearly reduced to half of its original value between the mid-1950s and early 1970s (specific computations assumed the decrease to commence in 1951 and end in 1970)?

(iii) What if only whales were considered in the model (i.e. no Antarctic fur 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 a higher density-dependent mortality rate ($\eta^{c,A}$) than is assumed for that scenario?

(vi) What if the lower limits of the bounds for the initial (1780) abundances of crabeater seals were set higher?

Table 6 shows the values of the input and estimated parameters for these six scenarios. The trajectories of krill and their main predators in the Antarctic for each of the above sensitivity scenarios respectively are shown in Mori (2005).

The main feature of the 'reference-case' results of a sharp increase from about 1930, followed by a decrease in krill biomass in Region A starting at about 1950 (as shown in Figure 4), does not change for scenarios (i), (ii) and (vi) detailed above. 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. For the model to reflect minke whales starting to decrease from about 1970, a fairly large drop in krill biomass from about the 1950s to the 1990s, together with a relatively high density dependent η parameter for this species, is required.

When minke whale abundance is doubled (scenario (i)), the consumption of krill by this species increases compared to the 'reference case' (compare Figures 6a and 6b) 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 the 'reference case' and scenario (ii)). This is mainly due to an 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. When the lower limits for the bounds of the initial abundances of crabeater seals are set higher, the results do not change qualitatively compared to the 'reference case'; however, more recent absolute abundances of crabeater seals are increased in response to these increases in initial abundance.

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

Note that for all these scenarios the substantial changes, particularly in krill abundance, take place in Region A, with Region P much more stable.

Table 7 lists 95% confidence intervals for the parameter values estimated, based on the likelihood profile method. These profiles are compared to the input ranges for each parameter in Figures 8(a) and 8(b). To aid the reader in determining the extent to which the data used to fit the model are informative for estimating these parameter values, the comparisons are presented as if they reflected prior and posterior distributions in a Bayesian context. The priors are exact representations across the ranges specified (throughout which values are assumed to be equally likely); however, the 'posteriors' are not exact representations, as they make the assumption that likelihood profiles provide close approximations to the corresponding posteriors (numerical convergence difficulties were encountered in attempting a Markov Chain Monte Carlo (MCMC) approach to obtain Bayesian posteriors directly).

For the estimates of the numbers of animals for the initial year considered in this model (i.e. 1780), these 'posterior' distributions are somewhat narrower than the prior distributions for all the species considered, although the differences are rather small for minke whales (Figure 8a). For humpback whales and Antarctic fur seals in Region A, the confidence intervals for the estimated initial numbers of these animals are very narrow (Figure 8a, Table 7). For humpback whales, this could be due to the low observed abundance estimate for 1997, despite the high growth rate observed for this species since 1977, which necessitates a high density-dependent mortality rate parameter η and also allows little scope for estimates of the initial number for this species. The low abundance estimate for Antarctic fur seals in 1930 means that the species must have been virtually extinct when exploitation ceased in the 19th century; this, together with the relatively short period of the harvest, indicates that the cumulative historic catch alone dominates any estimate of numbers in 1780. The narrow confidence interval for the initial abundance estimate for Antarctic fur seals probably results from the steep increase rate in the middle decades of the 20th century that is indicated by the survey estimates of abundance (see Table 4).

For the estimates of maximum birth rates, again the 'posterior' distributions are somewhat narrower than the prior distributions for all species considered in the model; in all cases, fairly high maximum birth rates are preferred. For the estimates of natural morality rates, there is not much improvement in the 'posterior' distributions compared to the priors, except for blue and minke whales and both seal species (Figure 8b).

For maximum consumption rates (the λ parameters), higher values are preferred in all cases. For the intrinsic growth rate of krill, the model prefers a low estimate for Region A, but for Region P the data contain insufficient information to meaningfully update the prior (see Figures 13.13(c) and 13.13(d) of Mori (2005)).

Discussion

The underlying assumptions of the model are:

(1) before the exploitation of seals and whales in the Antarctic (i.e. in 1780), the species considered were coexisting in a stable equilibrium;

(2) there is competition both between and within the species.

This study shows that:

(i) under assumptions (1) and (2) above;

(ii) under scenarios in which the consumption and birth rates of the predators considered in the model show a Holling Type III functional response to krill biomass;

(iii) provided 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 sequence of primary factors indicated to be 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 the expanding minke whale and seal populations, it started to drop again.

4. Finally, following this decline in krill biomass and because of high density-dependent mortality effects, predators such as minke whales and crabeater seals (which originally benefited from the earlier krill increase) started to decrease from around 1970, while the larger baleen whale species (by that time fully protected) commenced recovery.

The important key features required of the model to enable minke whales to decrease from around 1970 are first the drop in krill biomass from around the 1950s to the 1990s, and secondly a relatively high density-dependent mortality rate (η parameter) for this species. When only baleen whales and krill are included in the model (scenario (iii)), no success has been achieved in attempting to find a combination of parameters for which krill abundance starts to decrease from around the 1950s to the extent that then causes minke whales to start to decrease from around 1970. 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 6, which shows that it is the increases in other krill predators, such as crabeater seals, that are essential to give rise to the appreciable reduction in minke whales since about 1970 that is indicated by VPA assessments (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 for minke whales to start to decrease from around 1970.

The following sub-sections 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 validated 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 for the estimable parameters.

(2) Existence of competition between and within species

Most ecologists recognise 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, in contrast, is 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., 1999).

For ‘exploitation competition’ to exist, the resources in question must be in limited supply. The observations/inferences of increases 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, indirectly support this assumption of a limited supply of krill to krill predators, as they link plausibly to the postulate of competitive release following the overharvesting of the larger baleen whales. Indeed results in Table 6 and Figure 4 suggest that these whales were ‘overexploiting’ krill by ‘harvesting’ it at below its MSYL.

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 a resource limitation applies. They argue first that 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 and sperm whales in thieving Patagonian toothfish from longlines in fisheries off both Marion Island and South Georgia (Kock et al., 2006; C. Heinecken, Capricorn Fisheries Monitoring, pers. comm.) provide a counter-example to these arguments, though admittedly such competition is between, rather than within, species.

The model developed here 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 coexistence equilibria, and are relatively easy to motivate for seals on the grounds of breeding site limitations. 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 the arguments of Clapham and Brownell (1996). 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 modelled here may be a surrogate for inter-species interference, of which recent observations of increased humpback: minke whale abundance ratios in Area IV concurrent with a drop in stomach fullness and blubber thickness for minke whales (Konishi and Tamura, 2005; Tamura and Konishi, 2005) may constitute indirect evidence;

(iii) the effect is principally operative at a calf survival level, i.e. there are limitations on preferred calving/weaning locations for these animals, as suggested by observed increases in the spatial extent of the distribution of calving whales as the South African right whale population has recovered (Best, 1981).

As mentioned earlier, the density-dependent term involving the η parameter, introduced into the predator dynamics equation (2), can be considered as a modifier of some combination of overall natural death rate and birth-plus-calf-survival rate. Figure 9 plots time trajectories for predator natural mortality rates for the 'reference case' under the assumption that this term contributes in its entirety to a time-variable natural mortality rate ($\tilde{M}_y^{j,a}$) where:

$$\tilde{M}_y^{j,a} = M^j + \eta^{j,a} N_y^{j,a} \,. \tag{17}$$

Figure 9 indicates that the annual $\tilde{M}_y^{j,a}$ are initially in the range of 0.04–0.10 per year for all species considered except for humpback whales. For these whales, this rate is much higher (≈0.16 per year), and (to the extent that this value is realistic) would probably be more reflective of lower calf survival or pregnancy rates than of a high overall natural mortality rate. A major feature of these plots is the large drop in $\tilde{M}$ for humpback whales once their numbers were reduced by harvesting, thus allowing for a potentially rapid recovery rate. The increases in $\tilde{M}$ for minke whales and crabeater seals over the middle decades of the 20th century in both regions lead to an arrest of the increases in abundance in these populations in response to the krill surplus before there has been any appreciable recovery of the larger baleen whales.

Plausibility of the estimates for factors suggested to be driving the dynamics of the species in the Antarctic

Plausibility of the estimated magnitude of krill biomass

The long-term trend in krill biomass estimated by the reference-case model suggests that the initial krill biomass under unexploited coexistence was around 150 million tonnes, which then gradually increased to about 700 million tonnes during the first half of the 20th century (with virtually all this increase occurring in Region A), after which it declined again to around 200 to 300 million tonnes in recent years.

Estimating the abundance 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 in these regions is covered with pack-ice. Furthermore, the uneven distribution of krill and its occurrence in patches of various sizes, ranging from hundreds of metres in diameter and several metres thick, to 12 km in diameter and 230 m 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 700 million tonnes (Miller and Hampton, 1989). A recent study by Voronina (1998) estimated the total krill biomass to be 272 million tonnes based on published data and using a map of quantitative krill distribution compiled from commercial trawling made by Soviet fishing and research vessels. Nicol et al. (2000) calculated circumpolar abundance estimates for krill using: (i) historical information on the overall range of krill; and (ii) recent measurements of krill density from various acoustic surveys. They suggest circumpolar krill abundance to be in the range of 60 to 155 million tonnes. There are various uncertainties associated with acoustic survey methods, however, as are well summarised 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), it seems reasonable to the authors to argue that this abundance estimate of krill could cover a range of several hundred million tonnes.

More recently, Hewitt et al. (2002) estimated the total abundance of krill in the Scotia Sea to be 44.3 million tonnes 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 characterisation of krill target strength, suggested that these improvements will lead to a krill biomass estimate that is nearly 2.5 times greater. Such an adjustment would raise the estimate by Nicol et al. (2000) to about 150 to 400 million tonnes. This is quite compatible with estimates from the reference-case population model in the 200–300 million tonnes range, and would also seem to exclude sensitivity scenarios (iii) and (iv) considered earlier where respectively ignoring seal predators or assuming Type II functional responses suggest recent krill biomass to be in the 700–800 million tonnes range. Unfortunately, there are no direct observations that allow the plausibility of the estimate of 700 million tonnes of krill biomass in the mid-20th century that is suggested by the reference-case model to be assessed. However, consideration of information on relative trends in krill biomass could potentially provide some insight into the possible magnitude of krill biomass in those previous years, and is addressed below.

Plausibility of the predicted biomass trend estimate of krill

Despite the broad distribution and several areas of high concentration 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 commencing about 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) show these for South Georgia over the period from 1981 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 (sampling was less frequent 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 1926–1939 and 1976–2003 in order to examine spatial and temporal changes in krill distribution. They found that the productive southwest Atlantic Ocean 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 to 1970, where the reference-case model predicts an initial increase in krill biomass, followed by a drop since the 1950s. According to Atkinson (pers. comm.), comparison of krill abundance between the period 1926–1939 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. its 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 the reference-case 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.

The reference-case model, and also scenarios (i), (ii) and (vi), do indicate substantial increases in krill production (as well as abundance) in Region A, starting from about 1920 (Figure 7). These models indicate that in the absence of human exploitation, natural predators 'harvest' krill sufficiently heavily in this region that its biomass drops well below the overall (predator consumption included) MSY level. Krill productivity thus increases when human harvests of predators lead to a reduction in predator-induced mortality of krill. This does, of course, imply that in the pre-exploitation situation, krill is 'cropped down' by predators to the extent that it cannot make full use of all the available primary productivity, which presumably therefore feeds back more directly to detritus (e.g. via salps perhaps).

This implication that krill fails to make full use of the available primary productivity is supported by the results of Holm-Hansen and Huntley (1984), who assessed the food requirements of krill in the Scotia Sea. The mean krill biomass in the upper 200 m of the water column was estimated at 10.6 mg dry wt m^{-3} and this was calculated to require a food ration of 0.105–0.211 mg C m^{-3} day^{-1}. The corresponding value for krill in a super-swarm off Elephant Island was 2.4–5.4 mg C m^{-3} day^{-1}. On the other hand the phytoplankton (which is the primary prey of krill) productivity for the upper 200 m in the Scotia Sea and the super-swarm area was estimated to be 4.8 and 4.2 mg C m^{-3} day^{-1} respectively. On this basis it would appear that there was ample phytoplankton to provide for the food requirements of krill. Holm-Hansen and Huntley (1984) estimated that krill in the super-swarm were consuming between 58 and 81% of the daily production, and that the krill population in the Scotia Sea as a whole on average consumed only between 2.5 and 3.5% of the daily primary production. Miller et al. (1985) came to a similar conclusion for the Indian Ocean sector.

Difference between Laws' (1977) estimate of 150 million tonnes of 'surplus' krill and this analysis

Laws (1977) suggested that following the exploitation of large baleen whales in the Antarctic, some 150 million tonnes 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 tonnes was based on coarse estimates of the population sizes of baleen whales which 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 8). However, the reference-case estimate of consumption of krill by large baleen whales in the Antarctic shown in Figure 6 suggests much less consumption of krill by the large baleen whales prior to their harvesting: approximately 50 million tonnes per year.

Table 8 provides a detailed comparison of the consumption of krill as estimated by Laws (1977) and in this study. The main reason for the difference in the estimated consumption by baleen whales from these two studies is their different assumptions for predator consumption rates in relation to the biomasses of their prey. In Laws (1977) it is assumed that the amounts of krill consumed per capita by whales are independent of the biomass of krill. In other words, predators each consume a certain amount of krill regardless of the amount of prey available. 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, for example) compared to a situation where a large amount of krill is available. The model developed in this study includes Holling Type III functional response forms, which incorporate the effect of the dependence of consumption on prey biomass, and suggest 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 the model developed here estimates a lower pre-exploitation abundance of fin whales (see further remarks below) than that assumed by Laws (1977), 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 the modelling framework in this study takes account of the fact that krill productivity changes with krill abundance, as discussed above.

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 between the abundance estimates for krill obtained by these two methods (those obtained from acoustic surveys are much smaller than the ones calculated from predator consumption), and suggested that this discrepancy may be caused by: (i) bias in acoustic studies, (ii) the possibility of large krill population components that are either too deep, too shallow or too dispersed to be detected, and/or (iii) an overestimation of the demand for krill by predators. The results from the reference-case model lend support to 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 rates in the abundance of minke whales and crabeater seals from 1940 to 1970 in Region A for the reference-case model are 4% and 9% respectively. Mori and Butterworth (2005) infer the increase rate in minke whale recruitment to be 5% per year for the period between 1945 and 1970, based on the data available for this species in Areas IV and V (indeed, this can be considered as an independent verification of a prediction of the reference-case model, as this increase rate was not amongst the trend information included when fitting the model – see Table 4). This suggests that the 4% per year increase for minke whales 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 that this species increased at a rate of 9% 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 9% 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 6 is substantial (exceeding, for example, the 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 large increase in consumption of krill by crabeater seals is lowered by about 65% as also shown in Figure 6. 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.

Plausibility of the estimated fur seal population trend

The model suggests (Figure 4) that fur seals were virtually extirpated by 1830, persisted for the next century in very low numbers, and have been in meaningful recovery only since about 1960. This result is driven primarily by the very low 1930 population estimate for this species (see Table 3). The functional response forms and density-dependent mortality terms of the model act in such a way that fur seals can commence recovery only once the depletion of the large baleen whale species by harvesting has enabled krill abundance to increase considerably.

Effect of other krill predators 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 (*P. 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 stabilised 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) estimated total consumption of crustaceans by penguins in the Antarctic to be about 14 million tonnes per year.

For squid, Everson (1977) noted 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 tonnes. As squid tend to be relatively short-lived and have fast growth rates (Nesis, 1983), Everson (1984) suggested 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 in the order of 34–56 million tonnes. As far as fish are concerned, myctophid biomass in the Antarctic has been estimated to be 70–200 million tonnes (Lubimova et al., 1987), although this estimate may include all myctophids as far north as 40°S. From these data, Kock (1992) estimated that if a substantial proportion of this biomass is present south of the South Polar Frontal Zone, then even under the 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 tonnes 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 tonnes (Hureau, 1994). Interestingly, Agnew (pers. comm.) remarks that the rockcod and icefish populations that appear to have been present around South Georgia in the 1970s and early 1980s in high abundance (given the large catches at that time) have not recovered despite 2–3 decades of little or no exploitation, which suggests that those high levels might be a further indication of a transient response to a temporary period of krill surplus.

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 whales and seals considered in the model developed here. In the context of this model, then, results for crabeater seals should perhaps be considered as reflecting a conglomerate of these seals together with some other seals, birds, squid and fish, thereby rendering the large krill consumption increase for crabeater seals in the 1950s and 1960s under the reference case (Figure 6a) somewhat more plausible (see also discussion in the section following).

In summary, it seems that the results for the reference-case model do pass the various plausibility tests, though admittedly by something of a stretch as regards crabeater seals. Certainly an assumption of a deterioration in the environment (modelled as a lessening of the food production available for krill) assists in improving the plausibility of some model outputs (Table 6), 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 with the current model. First, although information on recent abundances and trend 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 the trend estimate from VPA for Areas IV and V was used in this model, and it was assumed that the trend for these areas is representative of the trends in the appreciably larger 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, render the model's predictions the less reliable.

It has been found to be very difficult to find sets of parameter values that will result in a stable coexistence equilibrium at the time of the first year considered in the model (i.e. 1780) and also give a reasonable fit to the data. This becomes understandable when one considers the relatively large number of species considered and their complex non-linear interactions.

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 the fact of the cumulative fin whale catch having been about twice as large (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 whale catches than previously assumed reflects enhanced productivity rather than a fishing down of pristine abundance. This is reflected in Figure 10, 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, increased values of these per-capita growth rates first occur over a period when blue whales were already substantially depleted, so could not take full 'advantage', unlike the situation for fin whales. Thus, essentially, fin whales were the first beneficiaries of the krill 'surplus', even before minke whales and crabeater seals.

Although the baleen whale abundance estimates of Table 3 that have been used for the analyses presented here apply to the area south of 60°S (except in the case of fin whales), the model in principle applies to the region over which the krill distribution extends. While, for the most part, this might be taken to be south of 60°S, there are areas, particularly in the Indian Ocean sector, where this distribution can extend as far north as 50°S (Miller, pers. comm.). Interestingly, this corresponds to a vicinity (the north of Areas III and IVW) where JSV and IWC/IDCR-SOWER transit data indicate a relatively high abundance of fin whales (Miyashita et al., 1995; Best, 2005; Branch, pers. comm.).

Finally, the need to introduce density-dependent mortality has its less-than-satisfactory aspects, as the associated η parameters play an 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 to go from here

A decline in the area covered by sea-ice, linked to warming of the Southern Ocean, 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 to 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 these species in a quantitative way. This is probably due to the lack of data and difficulties associated with the modelling as discussed above. However, in order to understand more fully the possible mechanisms that might be controlling the dynamics of the species in the Antarctic, it would seem that these effects should be accorded at least as much attention as environmental studies, and that the two should be modelled jointly (i.e. that both top-down and bottom-up control mechanisms should be considered together). The results presented in this paper do not, of course, exclude the possibility that the observed/inferred trends in predator abundances could be dominated by bottom-up effects, with predator–prey interactions having little real impact. However, this raises the question of whether such bottom-up approaches can account for these trends in a more plausible and parsimonious manner without recourse to ad hoc assumptions to account for the times of the changes in these trends (which do correspond suggestively to the period of harvesting of the large baleen whale species).

Due to the difficulties already mentioned, this study is not regarded 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. Continued monitoring of the abundance and various biological parameters of the prey and predator species in the Antarctic, as well as of environmental change and its effect on the dynamics of these species, will be essential to improve such models and to be able to incorporate environmental effects explicitly. In due course, a move from an age-aggregated to an age-structured model for the various species might be justified, and this would allow 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 the quantification of uncertainties is desirable. In principle, this is achievable through a Bayesian estimation approach, but the associated computations would prove decidedly non-trivial given the high level of non-linearity in the model and the fact that the maximum likelihood estimates of a number of the biological parameters lie at the boundaries of their specified ranges[7]. Furthermore, it would seem advisable to wait for the availability of the SCAR Antarctic Pack-Ice Seals Program results for crabeater seal abundance and culmination of the IWC Scientific Committee's plan to provide consolidated advice on southern hemisphere minke whale abundance estimates and trends at its 2006 meeting. Finally, and importantly, consideration needs to be given to including further predator species that are not included in the current model, even if only as a lumped

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[7] The fact (see Table 6 and Figure 8b) that many birth (μ) and natural mortality (M) rate estimates tend towards their respective maximum and minimum bounds suggests that population trend data 'seek' higher natural growth rates than demographically likely. The reason for preference for higher consumption rate (λ) estimates may be related to the partial confounding of λ and krill biomass (B) values in the model. If all feeding rates had saturated at their maxima when krill biomass is relatively large, then model fits could not distinguish between higher absolute values of krill abundance and lower λ values, and vice versa, as there are no data on krill abundance available for use when fitting the model. Thus it is only the non-linearities introduced by the Holling Type II or III functional relationships in equations (1) and (2) that inform (weakly) on the estimates of λ, so that it is not altogether surprising that all of these tend towards their maximum or minimum bounds.

variable explicitly representing all such species[8]. Prior to doing so, however, a careful evaluation of the likely biomass of, and krill consumption by, these other species in comparison to those already included in the model would assist in focusing further modelling refinements.

In recent years, the importance of ecosystem-based management of fisheries and wildlife resources has been recognised worldwide. Both 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 modelling 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, 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 modelling 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 an appropriate next step.

Some concluding summary comments

There are many inferences to be drawn from this work thus far. The following are likely to be amongst the more interesting and important.

- 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 that consequently need to be better understood and taken into account in management decisions. Fin whales, for example, need to be considered in the context that they may effectively have been the first beneficiaries of the krill surplus, brought about by early heavy harvesting of blue whales.

- It is not sufficient to consider the interactions between the Antarctic baleen whales and krill alone. The major seal species, at least, need also to be taken into account explicitly, and probably some other predator species in addition.

- There are major differences in the historic dynamics of Region A and P, 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 showing maxima mainly closer to 10% than 1%) (see Figure 10).

- Nevertheless, in the absence of future harvesting, blue whales in Region A are predicted to need some three to four centuries to recover to their pre-exploitation level (see Figure 5), essentially because they also need to out-compete 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 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 fairly high 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

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[8] It may, however, prove problematic to include squid in such a grouping, as it could result in faster dynamics because of its higher maximum growth rate.

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. A review of the likely biomass of, and consumption of krill by, predators not as yet included in the model, compared to the six species which are, would be a desirable precursor to further modelling which takes more explicit account of these other species.

- 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.

Acknowledgements

Support from the Nakajima Foundation, Japan, to one of the authors (M. Mori) is gratefully acknowledged. The authors also thank many colleagues, too numerous to list individually, for discussions and input during the process of developing this work. This document has been revised in response to helpful comments received during discussions of an earlier version (IWC document SC/57/O21) during the June 2005 meeting of the Scientific Committee of the International Whaling Commission, and has also benefited from feedback from subsequent meetings of the CCAMLR Working Group on Ecosystem Monitoring and Management and reviewers David Agnew and Beth Fulton.

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Table 1: Estimates of annual consumption of krill by its predators in the Antarctic. - no estimate is provided; * – this estimate also includes other euphausiids; ? – the estimate is coarse, being based on sweeping assumptions. (Note that the analyses of this paper (see Table 8) suggest that the estimates of Laws (1977) are too high.)

Species	Krill consumption (million tonnes)			References
	Pre-exploitation (Laws, 1977)	1985–1990	1991–1997	
Baleen whales (blue, fin, humpback, minke)	190	6–120	3–53	Chapter 3, Table 3.6 of Mori (2005)
Seals (Antarctic fur, crabeater)	64	24–73		Chapter 3, Table 3.6 of Mori (2005)
Birds (dominated by penguins)	-	Min. 14*		Woehler (1995)
Cephalopods	-	Min. 34–56 (?)		Everson (1984)
Fish	-	40–50 (?)		Hureau (1994)

Table 2a: Historical catches in the southern hemisphere of the baleen whale species considered in this study (see text for details on sources).

Year	Blue whale		Fin whale		Minke whale		Humpback whale	
	Region A	Region P	Region A	Region P	Region A	Region P	Region A	Region P
1900	0	0	0	0	0	0	0	0
1901	0	0	0	0	0	0	0	0
1902	0	0	0	0	0	0	0	0
1903	0	0	0	0	0	0	0	0
1904	11	0	4	0	0	0	180	0
1905	51	0	104	4	0	0	288	23
1906	68	0	133	0	0	0	240	229
1907	106	0	163	0	0	0	1 261	130
1908	237	0	295	0	0	0	2 170	1 248
1909	176	32	433	4	0	0	3 936	1 575
1910	359	28	825	7	0	0	6 578	2 246
1911	1 235	0	2 322	11	0	0	8 566	1 689
1912	2 319	186	5 118	13	0	0	8 818	1 320
1913	2 772	2	5 594	7	0	0	9 856	1 446
1914	5 031	96	4 818	47	0	0	6 256	651
1915	5 536	100	5 967	137	0	0	3 254	177
1916	4 323	64	2 881	35	0	0	915	36
1917	3 097	76	1 676	579	0	5	73	84
1918	1 978	68	2 016	909	0	0	95	104
1919	1 994	15	3 160	528	0	0	211	181
1920	2 948	54	3 673	2 251	0	0	283	157
1921	4 443	78	1 732	1 044	1	0	229	21
1922	6 689	85	3 036	1 265	0	0	1 503	135
1923	4 657	261	2 509	1 405	0	0	1 386	107
1924	6 510	456	3 579	1 785	0	0	1 000	126
1925	5 787	635	7 833	2 337	0	0	1 957	387
1926	6 976	1 689	4 426	2 593	0	0	1 345	407
1927	7 827	2 281	3 867	2 220	0	0	1 128	41
1928	8 954	4 831	5 915	1 841	0	0	1 198	63
1929	18 267	459	10 781	2 112	0	0	227	805
1930	26 637	3 820	9 745	1 425	0	0	1 159	287
1931	6 613	46	3 330	6	0	0	255	163
1932	18 308	148	5 513	4	0	0	464	39
1933	17 307	56	7 781	43	0	0	1 030	59
1934	16 569	28	13 110	123	0	0	3 219	65
1935	17 672	198	10 210	84	0	0	5 874	315
1936	14 420	174	15 533	235	0	0	12 562	91
1937	15 022	97	29 195	170	0	0	13 637	125
1938	13 092	1 035	19 282	2 096	0	0	4 596	129
1939	11 010	508	18 520	1 063	0	0	2 447	87
1940	3 245	1 723	4 398	3 711	0	0	455	2 508
1941	51	0	1 226	0	0	0	92	86
1942	127	0	980	0	0	0	0	71
1943	349	0	1 459	0	0	0	84	90
1944	1 048	2	1 892	61	0	0	175	88
1945	3 604	42	9 350	80	0	0	284	107
1946	8 533	704	14 264	706	0	0	123	126
1947	5 470	1 498	20 083	1 696	0	0	134	122
1948	6 565	1 166	17 105	2 861	0	0	289	173
1949	3 517	2 723	17 738	2 898	1	0	5 693	1 508
1950	4 004	3 031	15 899	4 264	0	0	4 858	1 478
1951	3 422	1 725	18 643	5 277	4	0	3 299	1 164
1952	2 954	1 048	19 893	4 052	6	0	2 039	1 487
1953	2 483	405	24 879	3 689	12	0	1 794	1 156

(continued)

Table 2a (continued)

Year	Blue whale		Fin whale		Minke whale		Humpback whale	
	Region A	Region P	Region A	Region P	Region A	Region P	Region A	Region P
1954	1 484	1 060	24 578	4 269	0	0	1 540	2 527
1955	1 018	731	20 266	7 468	36	0	2 401	3 767
1956	677	1 038	17 420	10 953	45	0	1 270	1 879
1957	996	773	20 405	7 416	10	1	1 946	2 814
1958	726	524	22 720	4 757	9	1	3 700	4 354
1959	514	112	23 023	2 561	3	1	4 279	11 564
1960	425	191	23 456	3 840	2	1	3 250	11 698
1961	523	231	23 085	4 000	2	1	1 069	6 105
1962	300	57	15 789	2 121	8	11	1 826	1 932
1963	178	37	13 055	1 163	114	6	515	306
1964	191	47	6 979	978	58	5	91	162
1965	356	255	2 654	1 277	74	7	1 150	1 048
1966	216	178	2 418	1 480	381	8	427	1 240
1967	89	34	2 015	864	1 113	5	580	859
1968	79	16	2 385	1 375	606	21	0	2
1969	37	7	2 729	402	752	15	0	0
1970	20	4	3 237	185	914	0	0	0
1971	15	4	2 149	185	4 157	4	0	3
1972	2	1	1 344	478	6 583	0	3	0
1973	1	0	750	591	7 271	1 270	1	0
1974	0	0	503	523	5 280	2 757	0	0
1975	0	0	22	211	5 350	1 835	0	0
1976	0	0	0	8	6 117	2 559	0	0
1977	0	0	0	2	4 126	1 874	0	0
1978	0	0	0	0	4 954	1 202	0	0
1979	0	0	0	0	5 609	2 288	0	0
1980	0	0	0	0	4 697	2 445	0	0
1981	0	0	0	0	4 845	3 058	0	0
1982	0	0	0	0	3 935	3 366	0	0
1983	0	0	0	1	4 136	2 544	0	0
1984	0	0	0	0	3 504	2 064	0	0
1985	0	0	0	0	3 470	2 097	0	0
1986	0	0	0	0	2 935	2 034	0	0
1987	0	0	0	0	273	0	0	0
1988	0	0	0	0	0	236	0	0
1989	0	0	0	0	327	0	0	0
1990	0	0	0	0	0	323	0	0
1991	0	0	0	0	288	0	0	0
1992	0	0	0	0	0	327	0	0
1993	0	0	0	0	330	0	0	0
1994	0	0	0	0	0	330	0	0
1995	0	0	0	0	439	1	0	0
1996	0	0	0	0	0	440	0	0
1997	0	0	0	0	438	0	0	0
1998	0	0	0	0	0	389	0	0
1999	0	0	0	0	439	0	0	0
2000	0	0	0	0	0	440	0	0
Total	312 221	36 971	613 870	112 786	83 654	33 971	151 563	75 172
Grand total	349 192		726 656		117 625		226 734	

Table 2b: Assumed historical catches of Antarctic fur seals (see Appendix 1); all were taken in the south Atlantic (i.e. from Region A, the Atlantic/Indian Ocean sector). 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	11 000
1792	22 000
1793	33 000
1794	44 000
1795	55 000
1796	66 000
1797	77 000
1798	88 000
1799	99 000
1800	110 000
1801	104 500
1802	99 000
1803	93 500
1804	88 000
1805	82 500
1806	77 000
1807	71 500
1808	66 000
1809	60 500
1810	55 000
1811	49 500
1812	44 000
1813	38 500
1814	33 000
1815	27 500
1816	22 000
1817	16 500
1818	11 000
1819	5 500
1820	0
1821	320 000
1822	284 444
1823	248 888
1824	213 332
1825	177 776
1826	142 220
1827	106 664
1828	71 108
1829	35 552
1830	0
Total	3 249 984

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

Species		Abundance estimate	CV	Sources
Blue whale	$N^{b,A}_{2000}$	1 104	0.4	Rademeyer et al. (2003)
	$N^{b,P}_{2000}$	762	0.4	
Fin whale	$N^{f,A}_{1997}$	10 591	0.5	Branch and Butterworth (2001); Butterworth and Geromont (1995)
	$N^{f,P}_{1997}$	27 594	0.5	
Humpback whale	$N^{h,A}_{1997}$	5 044	0.2	Branch and Butterworth (2001)
	$N^{h,P}_{1997}$	4 868	0.2	
Minke whale	$N^{m,A}_{1985}$	327 369	0.1	IWC (1991)
	$N^{m,P}_{1985}$	420 572	0.1	
Antarctic fur seals	$N^{s,A}_{1930}$	100	0.5	Payne (1977, 1979)
	$N^{s,A}_{1975}$	369 000	0.5	Payne (1977, 1979); MacCann and Doidge (1987)
	$N^{s,A}_{1990}$	1 550 000	0.5	Boyd (1993)
Crabeater seals	$N^{c,A}_{2000}$	4 000 000	0.5	J. Laake (pers. commn)*; see Section 6.3 of Mori (2005)
	$N^{c,P}_{2000}$	4 000 000	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 Seals (APIS) Program (Ackley et al., 2003). This sector corresponds to only part of Region P. The estimates from surveys of the Australian sector which covered from 60°E to 150°E are not yet available and information for the remainder of the Region A is scarce. 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 fairly large numbers of crabeater seals are also found in the vicinity of sub-Antarctic islands. Thus abundances of 4 million crabeater seals for each region are assumed in this analysis. The CVs associated with the estimates are not available so that a tentative CV of 0.5 is assumed.

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 to provide a basis to infer an estimate in the process of fitting the population model (see text).

Species		Fitted trend	CV	Sources
Blue whale	N^{b}_{1981}	546	0.41	Branch and Rademeyer (2003)
	N^{b}_{1988}	680	0.52	
	N^{b}_{1996}	1891	0.42	
Humpback whale	$R^{h,A}_{1977-1991}$	0.11	0.14	Bannister (1994)[1]
	$R^{h,P}_{1981-1996}$	0.12	0.07	Brown et al. (1997)[2]
Minke whale	$R^{m,A}_{1970-2000}$	–0.024	0.31	Mori and Butterworth (2005)[3], Chapter 8 of Mori (2005)
	$R^{m,P}_{1970-2000}$	–0.024	0.31	
Antarctic fur seals	$R^{s,A}_{1957-1972}$	0.17	0.5	Payne (1977), Boyd et al. (1995)
	$R^{s,A}_{1976-1990}$	0.10	0.5	Boyd (1993), SCAR (2000)
	$R^{s,A}_{1990-1999}$	0.10	0.5	

[1] For west Australia (Area IV) only

[2] For east Australia (Area V) only

[3] For Areas IV and V only

Table 5: Plausible bounds for the parameters to be estimated.

Parameters to be estimated		References/Notes
	Bounds	
$N_{1780}^{b,A}$	100 000–300 000	See footnote (1)
$N_{1780}^{b,P}$	10 000–100 000	
$N_{1780}^{m,A}$	10 000–200 000	
$N_{1780}^{m,P}$	10 000–300 000	
$N_{1780}^{h,A}$	10 000–250 000	
$N_{1780}^{h,P}$	10 000–100 000	
$N_{1780}^{f,A}$	10 000–400 000	
$N_{1780}^{f,P}$	10 000–200 000	
$N_{1780}^{s,A}$	500 000–5 000 000	
$N_{1780}^{c,A}$	100 000–10 000 000	
$N_{1780}^{c,P}$	100 000–10 000 000	
μ_b	0.05–0.16	See footnote (2)
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 footnote (2)
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 footnote (3)
λ_m	3.8–32.1	
λ_h	37.8–108	
λ_f	27.6–110.4	
λ_s	0.68–2.71	
λ_c	3.31–5.51	
r^A	0.4–0.6	Mori and Butterworth (2004)
r^P	0.4–0.6	

(continued)

Table 5 (continued)

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(1) These bounds are included primarily to assist computations. They were guided in many cases by cumulative catch information. Figure 8a shows that the data available to fit the population model proves informative from most of these parameters so that the exact choices for these ranges are not of very great concern.

(2) 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. These constraints are considered reasonable given observed increase rates for some baleen whale and seal species in the Antarctic as reported in Chapters 5 and 6 of Mori (2005).

(3) 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 8. 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 than that for blue, humpback and minke whales. Though euphausiids are still thought to be the primary source of food in that area (Ohsumi, Tamura pers. comm.), these may well be from a different stock to the 'krill' (*Euphausia superba*) on 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 tonnes in mass, compared with the normal adult cow weight of less than 0.05 tonnes (Payne, 1977), in order to give a range for the consumption of krill by the seals, ranges for the weights of 0.05–0.2 tonnes for Antarctic fur seals and 0.15–0.25 tonnes for crabeater seals have been used. 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 to be 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’ population model and six sensitivity scenarios (i) to (vi). See text for details of the sensitivity scenarios. Parameters under the estimated parameter heading which are shown in square parenthesis were fixed rather than estimated. The contributions (*LL*) from various species to –ln*L* are also shown. For sensitivity (vi), the lower 1780 abundance bounds for crabeater seals (*) were set to 300 000.

	Input parameters						
	Reference	(i)	(ii)	(iii)	(iv)	(v)	(vi)
$B^{b,A}$	1.70E+08	1.70E+08	1.70E+08	2.30E+08	5.00E+08	1.70E+08	1.70E+08
$B^{b,P}$	7.00E+07	7.00E+07	7.00E+07	5.00E+07	2.00E+08	7.00E+07	7.00E+07
$\eta^{b,A}$	4.00E-08	4.00E-08	4.00E-08	2.00E-07	3.00E-08	4.00E-08	4.00E-08
$\eta^{m,A}$	3.00E-07	2.50E-07	3.00E-07	2.00E-07	1.35E-08	3.00E-07	3.00E-07
$\eta^{h,A}$	1.25E-06	1.25E-06	1.25E-06	8.00E-07	5.25E-07	1.25E-06	1.25E-06
$\eta^{f,A}$	4.00E-08	4.00E-08	4.00E-08	5.00E-08	4.00E-08	4.00E-08	4.00E-08
$\eta^{s,A}$	3.50E-09	3.50E-09	3.50E-09	-	1.50E-08	3.50E-09	3.50E-09
$\eta^{c,A}$	7.00E-09	7.00E-09	7.00E-09	-	5.00E-10	2.00E-09	4.00E-09
$\eta^{b,P}$	1.00E-06	1.00E-06	1.00E-06	6.00E-07	1.00E-06	1.00E-06	1.00E-06
$\eta^{m,P}$	2.00E-07	1.70E-07	2.00E-07	1.70E-07	2.00E-07	2.00E-07	2.00E-07
$\eta^{h,P}$	1.50E-06	1.50E-06	1.50E-06	1.00E-06	1.50E-06	1.50E-06	1.50E-06
$\eta^{f,P}$	7.00E-08	7.00E-08	7.00E-08	9.00E-07	7.00E-08	7.00E-08	7.00E-08
$\eta^{c,P}$	6.00E-09	6.00E-09	6.00E-09	-	1.00E-09	6.00E-09	5.00E-09

(continued)

Table 6 (continued)

	Estimated parameters and ln*L*							
	Bounds	Estimates						
		Reference	(i)	(ii)	(iii)	(iv)	(v)	(vi)
$N_{1780}^{b,A}$	100 000–300 000	162 332	161 308	164 299	219 188	231 293	224 771	151 407
$N_{1780}^{b,P}$	10 000–100 000	26 861	24 656	27 019	28 475	28 816	29 839	25 872
$N_{1780}^{m,A}$	10 000–200 000	47 155	200 000	56 551	200 000	29 997	75 149	200 000
$N_{1780}^{m,P}$	100 000–300 000	271 720	300 000	270 128	300 000	300 000	300 000	267 517
$N_{1780}^{h,A}$	10 000–250 000	71 589	71 547	71 670	68 630	82 733	73 100	71 372
$N_{1780}^{h,P}$	10 000–100 000	47 095	44 189	47 475	45 685	49 703	48 193	45 919
$N_{1780}^{f,A}$	10 000–400 000	151 505	149 883	155 177	182 749	2 85 203	126 350	140 028
$N_{1780}^{f,P}$	10 000–200 000	87 187	70 937	88 586	52 077	105 171	95 580	79 459
$N_{1780}^{s,A}$	500 000–5 000 000	2898 590	2938 280	2904 180	-	2 569 970	2 905 380	2 876 600
$N_{1780}^{c,A}$	100 000*–10 000 000	241 045	100 000	602 942	-	100 000	1 537 310	300 000
$N_{1780}^{c,P}$	100 000*–10 000 000	733 511	100 000	1585 280	-	1 491 330	1 604 670	300 000
λ^{b}	115.875–450.625	450.62	450.63	412.20	450.63	450.63	450.63	398.10
λ^{m}	3.78–32.13	32.13	32.13	32.13	32.13	32.13	32.13	32.13
λ^{h}	37.8–108	108.00	108.00	108.00	108.00	108.00	108.00	108.00
λ^{f}	27.6–110.4	[110.40]	[110.40]	[110.40]	110.36	110.40	[110.40]	[110.40]
λ^{s}	0.678–2.713	2.71	1.42	2.71	-	0.68	2.71	2.63
λ^{c}	3.306–5.511	5.51	5.51	5.51	-	5.51	5.51	5.51

(continued)

Table 6 (continued)

	Estimated parameters and ln$L$							
	Bounds	Estimates						
		Reference	(i)	(ii)	(iii)	(iv)	(v)	(vi)
μ^b	0.05–0.16	0.16	0.16	0.16	0.14	0.16	0.10	0.16
μ^m	0.07–0.2	0.20	0.20	0.20	0.20	0.20	0.20	0.20
μ^h	0.06–0.18	[0.18]	[0.18]	[0.18]	0.18	[0.18]	[0.18]	[0.18]
μ^f	0.05–0.16	[0.16]	[0.16]	[0.16]	[0.16]	[0.16]	[0.16]	[0.16]
μ^s	0.18–0.28	0.28	0.28	0.28	-	0.28	0.28	0.28
μ^c	0.11–0.28	0.24	0.27	0.15	-	[0.25]	0.18	0.25
M^b	0.03–0.06	0.03	0.03	0.03	0.03	0.03	0.06	0.03
M^m	0.04–0.1	0.04	0.04	0.04	0.04	0.04	0.04	0.08
M^h	0.03–0.08	0.08	0.08	0.08	0.06	0.08	0.08	0.08
M^f	0.03–0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
M^s	0.07–0.3	0.07	0.09	0.07	-	0.07	0.07	0.07
M^c	0.07–0.3	0.07	0.07	0.07	-	0.07	0.07	0.07
r^A	0.4–0.6	0.40	0.41	0.40	0.40	0.40	0.41	0.40
r^P	0.4–0.6	0.58	0.40	0.60	0.50	[0.40]	0.40	0.51
LL^b_{abun}		0.000	0.000	0.001	0.000	0.000	0.000	0.000
LL^b_{tren}		–1.806	–1.860	–1.926	0.009	–1.739	–1.281	–1.818
LL^m_{abun}		0.001	11.952	0.003	0.000	1.077	0.117	0.014
LL^m_{tren}		0.002	0.001	0.002	–2.226	0.018	0.002	0.003

(continued)

Table 6 (continued)

	Estimated parameters and ln$L$							
	Bounds	Estimates						
		Reference	(i)	(ii)	(iii)	(iv)	(v)	(vi)
LL^{h}_{tabun}		0.000	0.000	0.000	0.000	0.000	0.000	0.000
LL^{h}_{tren}		0.186	0.164	0.187	0.005	0.211	0.184	0.170
LL^{f}_{abun}		0.000	0.014	0.000	0.000	0.000	0.000	0.001
LL^{s}_{abun}		0.959	0.970	1.504	-	14.332	0.455	0.751
LL^{s}_{tren}		0.692	1.824	0.703	-	3.170	0.755	0.738
LL^{c}_{abun}		2.347	2.531	0.693	-	1.768	8.098	2.426
$-\ln L$		2.381	15.597	1.166	–2.212	18.839	8.330	2.284

Table 6 (continued)

	Derived parameters and other quantities							
	Model							Observed
	Reference	(i)	(ii)	(iii)	(iv)	(v)	(vi)	
K_A	8.22.E+08	1.08.E+09	8.04.E+08	6.82.E+08	5.38.E+08	1.71.E+09	9.70E+08	-
K_P	1.25.E+08	2.10.E+08	1.49.E+08	1.63.E+08	2.11.E+08	3.06.E+08	1.48E+08	-
$B^{m,A}$	1.45.E+08	9.24.E+07	1.51.E+08	2.15.E+08	5.35.E+08	3.64.E+08	6.00E+07	-
$B^{m,P}$	5.29.E+07	5.04.E+07	5.68.E+07	3.08.E+07	1.09.E+08	1.92.E+08	3.61E+07	-
$B^{h,A}$	2.33.E+07	2.31.E+07	2.44.E+07	3.08.E+08	6.89.E+07	5.57.E+07	2.37E+07	-
$B^{h,P}$	2.31.E+07	2.42.E+07	2.39.E+07	5.10.E+07	1.92.E+07	8.23.E+07	2.39E+07	-
$B^{f,A}$	1.28.E+08	1.26.E+08	1.36.E+08	4.34.E+08	2.41.E+08	3.46.E+08	1.29E+08	-

(continued)

Table 6 (continued)

	Derived parameters and other quantities							
	Model							Observed
	Reference	(i)	(ii)	(iii)	(iv)	(v)	(vi)	
$B^{f,P}$	7.19.E+07	6.98.E+07	7.64.E+07	3.38.E+07	2.08.E+08	2.64.E+08	7.20E+07	-
$B^{s,A}$	1.46.E+08	1.27.E+08	1.54.E+08	-	2.37.E+08	3.89.E+08	1.45E+08	-
$B^{c,A}$	1.34.E+08	1.54.E+08	9.71.E+07	-	3.86.E+08	3.01.E+08	1.45E+08	-
$B^{c,P}$	7.34.E+07	8.41.E+07	5.06.E+07	-	2.90.E+08	2.19.E+08	8.13E+07	-
B^{A}_{1780}	9.26.E+07	9.24.E+07	9.76.E+07	3.27.E+08	1.50.E+08	2.47.E+08	9.35E+07	-
B^{P}_{1780}	5.21.E+07	5.04.E+07	5.46.E+07	4.08.E+07	1.16.E+08	1.93.E+08	5.21E+07	-
$N^{b,P}_{2000}$	1 109	1 100	1 118	1 104	1 112	1 094	1 100	1 104
$N^{b,A}_{2000}$	758	760	752	762	755	766	764	762
$N^{m,A}_{1985}$	325 963	457 592	324 999	326 783	327 664	325 621	322 023	327 369
$N^{m,P}_{1985}$	420 598	603 088	420 416	421 160	363 157	400 815	421 972	420 572
$N^{h,A}_{1997}$	5 046	5 041	5 044	5 044	5 045	5 041	5 044	5 044
$N^{h,P}_{1997}$	4 859	4 856	4 859	4 867	4 861	4 861	4 858	4 868
$N^{f,A}_{1997}$	10 649	10 595	10 625	10 591	10 624	10 551	10 597	10 591
$N^{f,P}_{1997}$	27 361	25 358	27 359	27 561	27 668	27 453	27 106	27 594
$N^{s,A}_{1930}$	175	166	200	-	875	142	162	100
$N^{s,A}_{1976}$	262 422	231 244	229 260	-	110 195	296 599	274 382	369 000
$N^{s,A}_{1991}$	1 234 240	1 414 310	1 251 060	-	569 684	1 220 680	1 232 610	1 550 000
$N^{c,A}_{2000}$	11 794 500	12 269 700	7 184 970	-	10 241 300	29 908 300	11 936 700	4 000 000

(continued)

Table 6 (continued)

	Derived parameters and other quantities							
	Model							Observed
	Reference	(i)	(ii)	(iii)	(iv)	(v)	(vi)	
$N_{2000}^{c,P}$	3 753 920	3 638 290	3 777 040	-	3 947 840	3 856 120	3 505 290	4 000 000
$R_{1970-2000}^{m,A}$	–0.017	–0.010	–0.014	0.001	0.036	–0.017	–0.006	–0.024
$R_{1970-2000}^{m,P}$	–0.003	–0.007	–0.003	0.008	0.001	0.000	–0.002	–0.024
$R_{1977-1991}^{h,A}$	0.09	0.10	0.10	0.11	0.08	0.10	0.09	0.11
$R_{1981-1996}^{h,A}$	0.08	0.08	0.08	0.11	0.08	0.08	0.08	0.12
$R_{1958-1971}^{s,A}$	0.19	0.19	0.18	-	0.12	0.18	0.19	0.17
$R_{1977-1991}^{s,A}$	0.17	0.18	0.14	-	0.12	0.15	0.17	0.10
$R_{1991-2000}^{s,A}$	0.10	0.12	0.12	-	0.11	0.10	0.10	0.10

Table 7: 95% confidence intervals for the estimated parameters for the 'reference-case' population model based on likelihood profiles. All values have been rounded to three significant figures.

	Lower 95% CI	Estimate	Higher 95% CI
$N_{1780}^{b,A}$	143 000	162 000	226 000
$N_{1780}^{b,P}$	21 200	26 900	29 800
$N_{1780}^{m,A}$	16 600	47 200	198 000
$N_{1780}^{m,P}$	114 000	272 000	296 000
$N_{1780}^{h,A}$	59 900	71 600	72 800
$N_{1780}^{h,P}$	34 200	47 100	50 400
$N_{1780}^{f,A}$	134 000	152 000	169 000
$N_{1780}^{f,P}$	46 700	87 000	122 000
$N_{1780}^{s,A}$	2 880 000	2 900 000	3 010 000
$N_{1780}^{c,A}$	120 000	241 000	1 480 000
$N_{1780}^{c,P}$	191 000	734 000	5 540 000
λ^b	449	451	451
λ^m	31.6	32.1	32.1
λ^h	107	108	108
λ^s	1.46	2.71	2.71
λ^c	5.25	5.51	5.51
μ^b	0.143	0.160	0.160
μ^m	0.112	0.200	0.200
μ^s	0.259	0.280	0.280
μ^c	0.158	0.236	0.280
M^b	0.030	0.030	0.038
M^m	0.041	0.044	0.092
M^h	0.044	0.080	0.080
M^f	0.031	0.049	0.050
M^s	0.070	0.070	0.113
M^c	0.071	0.074	0.123
r^A	0.400	0.400	0.524
r^P	0.401	0.576	0.597

Table 8: Comparison of pre-exploitation consumption of krill suggested by Laws (1977) and the estimates provided by the 'reference-case' model of this paper. 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				
	Numbers (thousands)	Mean weight (tonnes)	Days feeding in the Antarctic	Weight/day (%)	Consumption of krill/year (10^3 tonnes)
Blue whale	200	88	120	3.4	71 702
Fin whale	400	50	120	3.4	81 480
Humpback whale	100	27	120	3.4	11 000
Minke whale	200	7	365	3.9	19 827
Crabeater seals	-	-	-	-	-
Antarctic fur seals	-	-	-	-	-
Total (whales)					184 009
Total (whales + seals)					-

	This study (for 1920)							
	Numbers (thousands)	Mean weight (tonnes)	Days feeding in the Antarctic	Weight/day (%)			Consumption of krill/year (10^3 tonnes)	
				Maximum	For 1920 krill abundance		Maximum	For 1920 krill abundance
					Region A	Region P		
Blue whale	187	103	125	3.5	1.30	2.72	84 220	31 388
Fin whale	235	46	120	4	1.47	2.60	51 802	11 821
Humpback whale	75	27	100	4	3.77	3.94	8 098	7 313
Minke whale	335	6	90	5.1	2.26	4.05	9 218	5 403
Crabeater seals	1 097	0.2	335	7	3.43	5.28	5 145	2 392
Antarctic fur seals	0.09	0.2	323	7	3.04	-	0.41	0.11
Total (whales)							153 339	55 925
Total (whales + seals)							158 485	58 317

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 the annotations to Table 5.

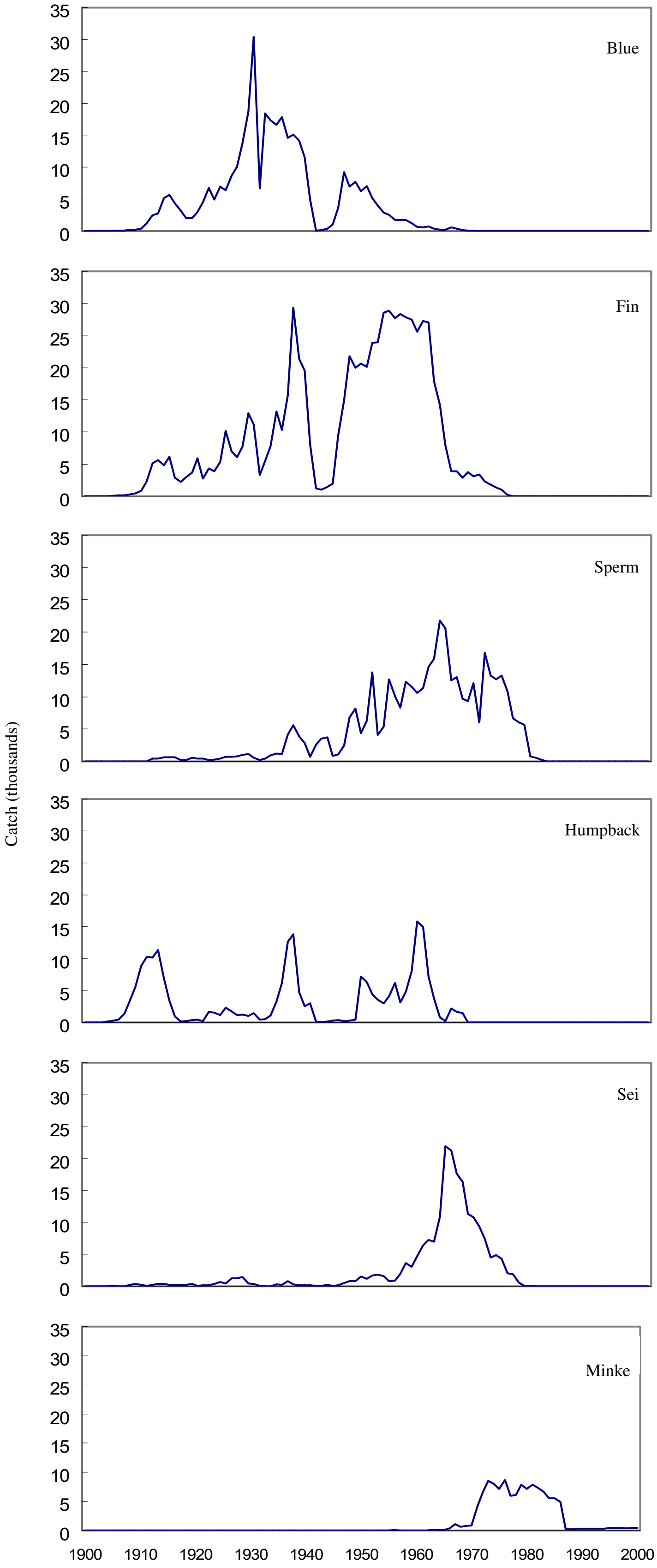


Figure 1: Annual catches of blue, fin, sperm, humpback, sei and minke whales caught in the southern hemisphere, corrected for former Soviet Union misreporting (see text for details on sources).

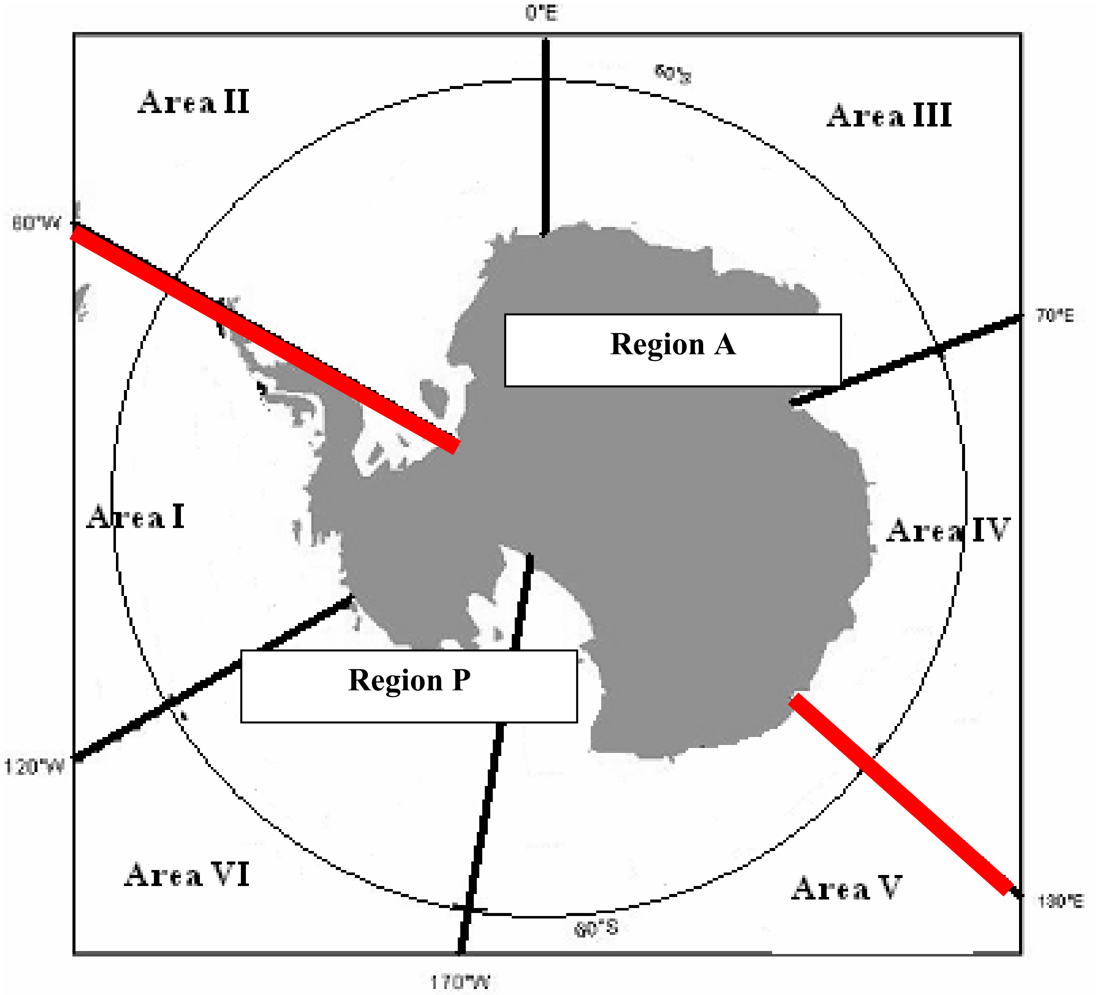


Figure 2: Map of the IWC Management Areas (I to VI), and the two regions (Region A and Region P) considered in the population model developed.

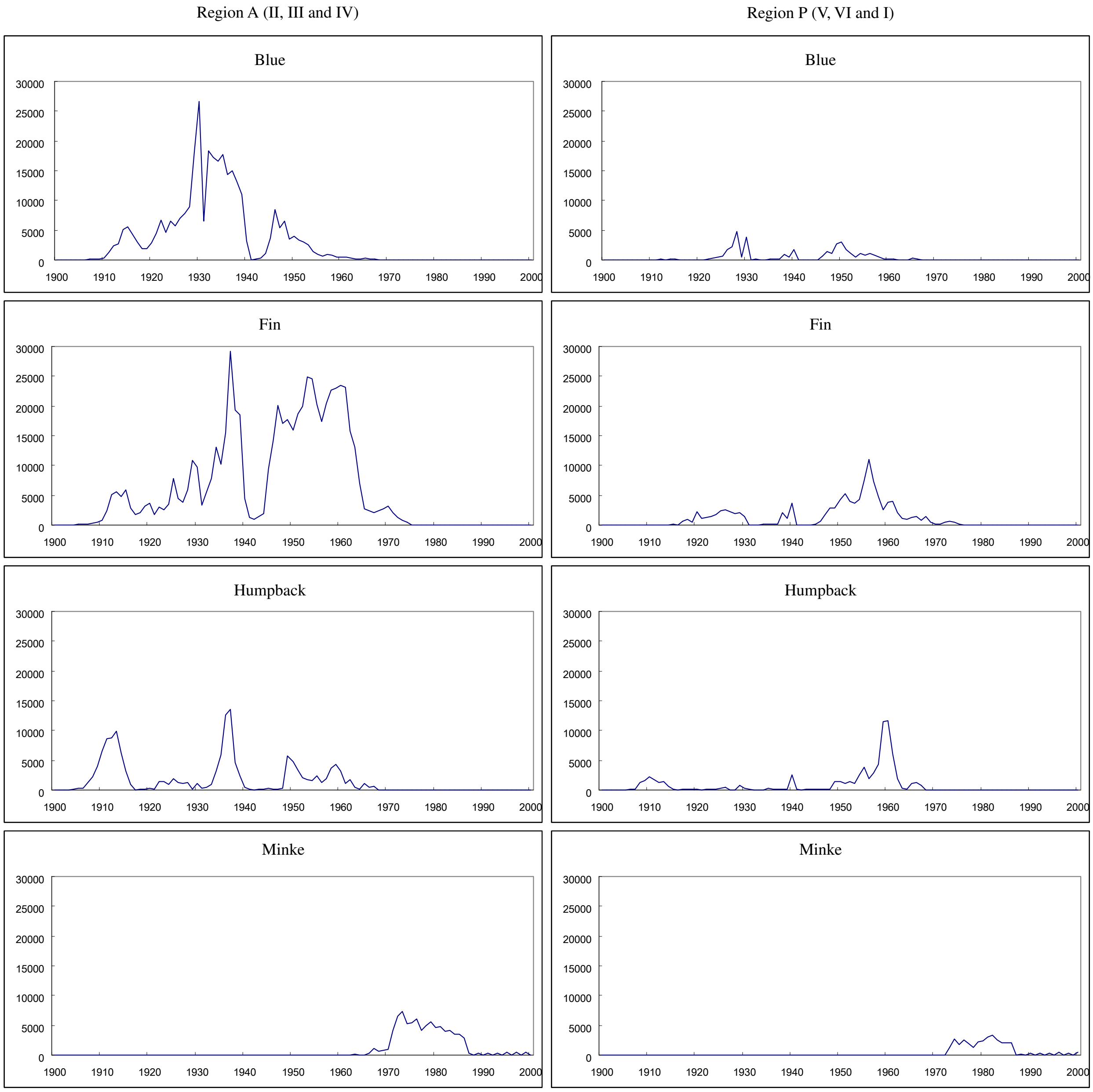


Figure 3: Historical catches of blue, minke, humpback and fin whales for Region A (IWC Management Areas II, III and IV) and Region P (IWC Management Areas V, VI and I).

Figure 4: ‘Reference-case’ population model trajectories for krill and its main predators in the Antarctic. A black dot/cross shows a survey-based abundance estimate for the Pacific and Atlantic Ocean sectors respectively, to which the model was fitted. 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 fitted to reflect the abundance trend indicated by these estimates. Whale and seal number estimates are as indicated, and krill in millions of tonnes.

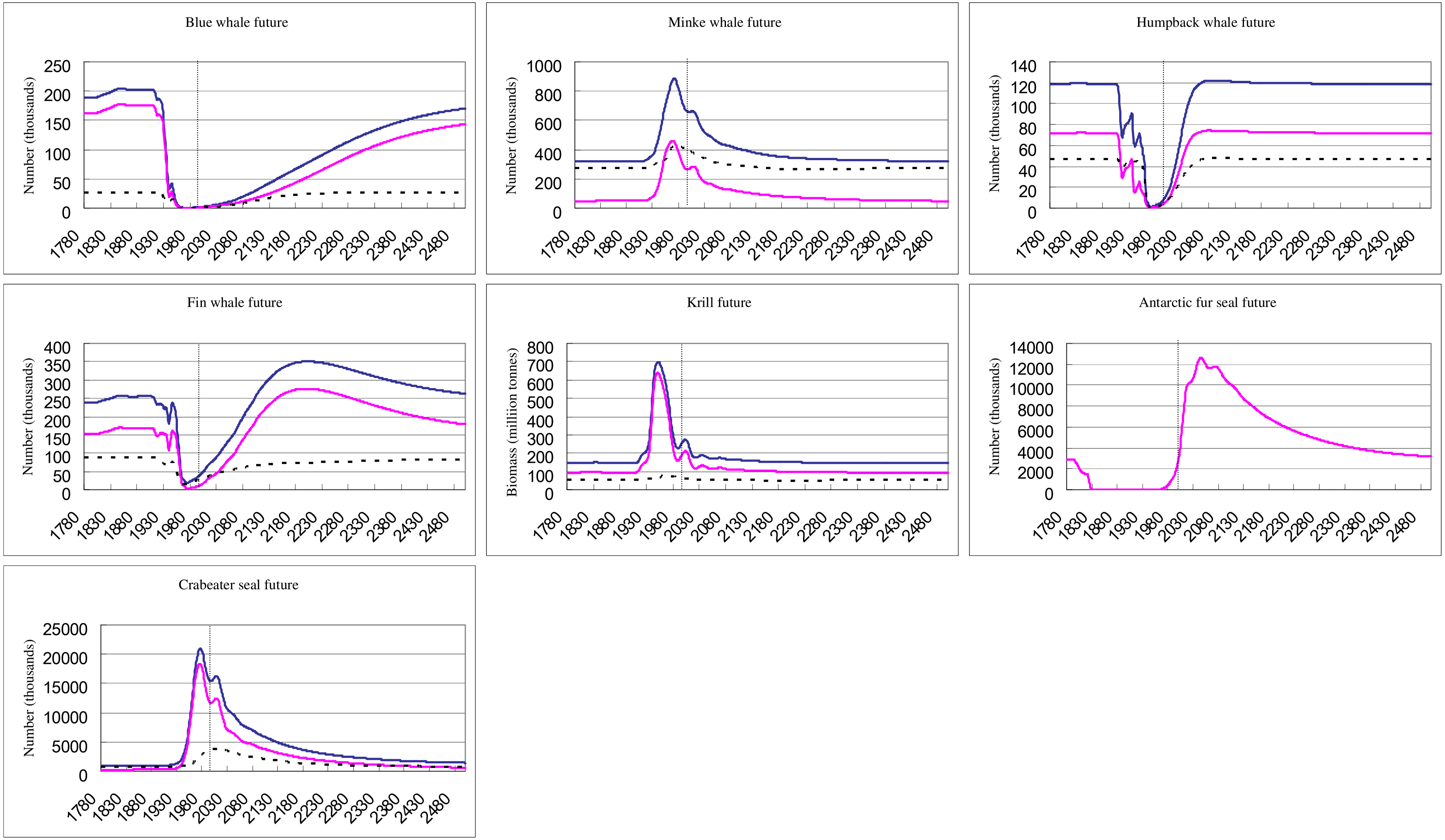


Figure 5: ‘Reference-case’ population model projections for future trajectories (up to the year 2500) for krill and its main predators in the Antarctic under the assumption of zero catches for all species after 2000.

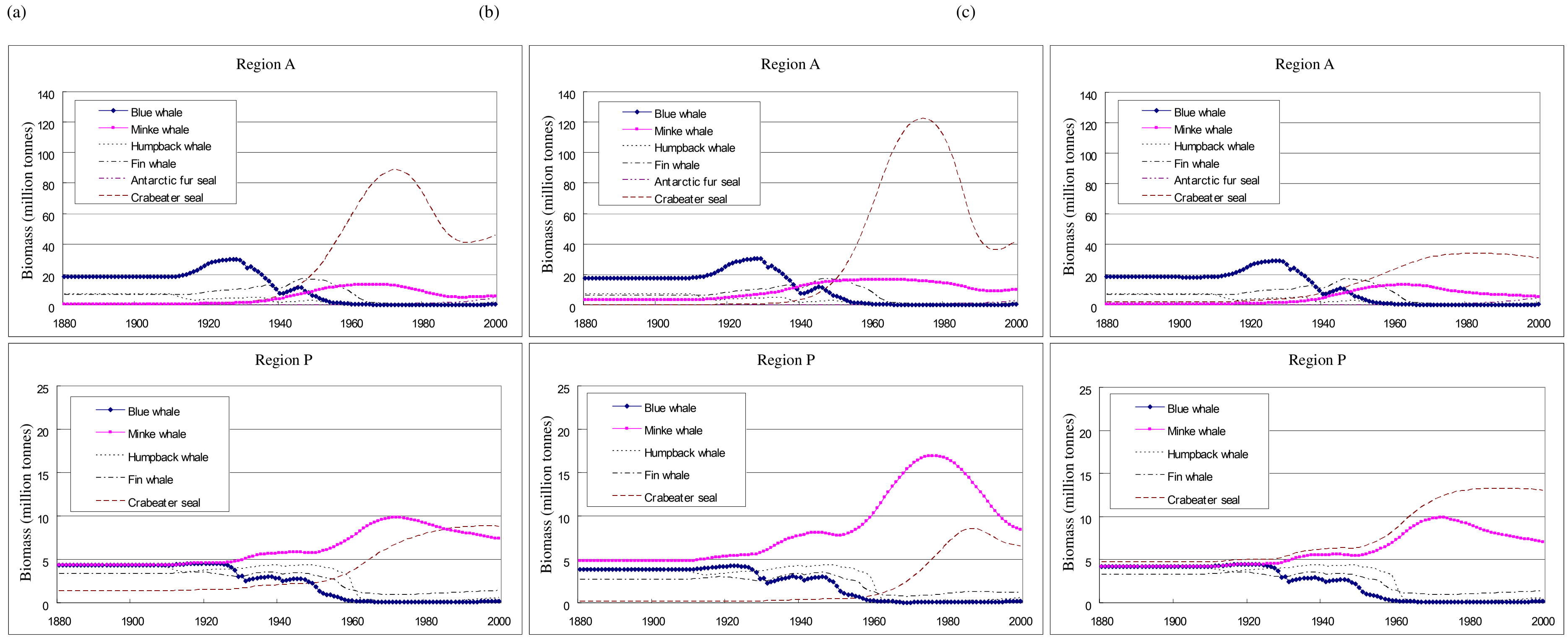


Figure 6: Annual consumption of krill biomass (millions of tonnes) by predators considered in the model for Region A and Region P for (a) 'reference case', (b) scenario (i) for which available minke whale abundance estimates are doubled, and (c) scenario (ii) where krill carrying capacity for Region A drops by 50% over 1951–1970.

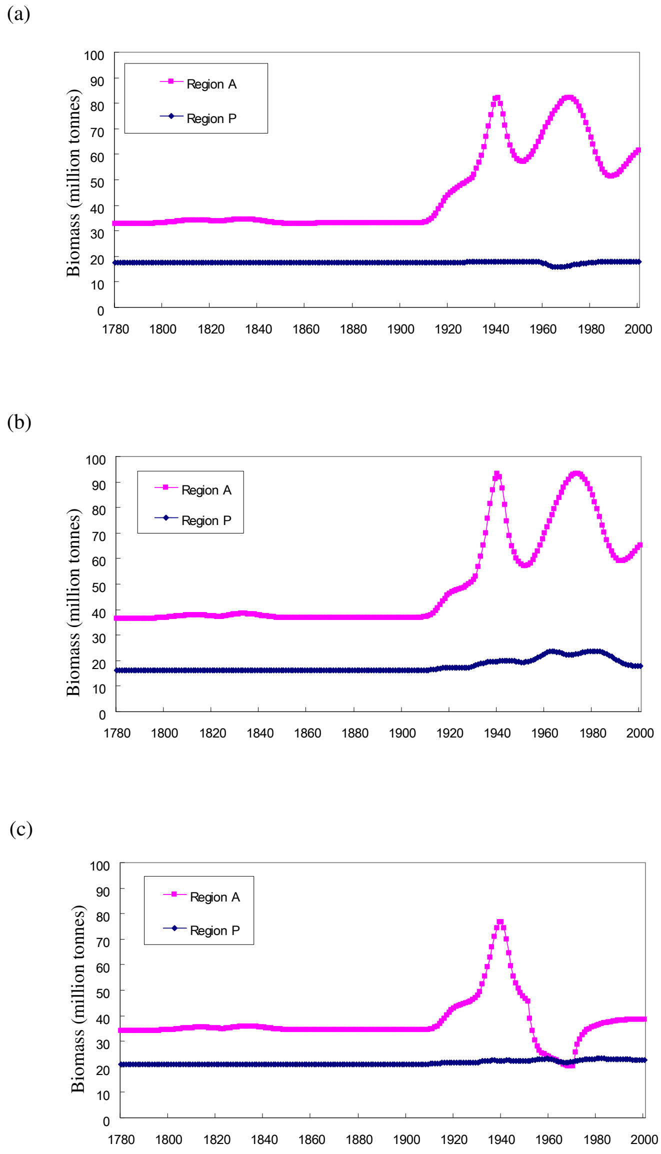


Figure 7: Estimated annual production of krill (millions of tonnes) for Region A and Region P for (a) the 'reference case', (b) scenario (i) and (c) scenario (ii).

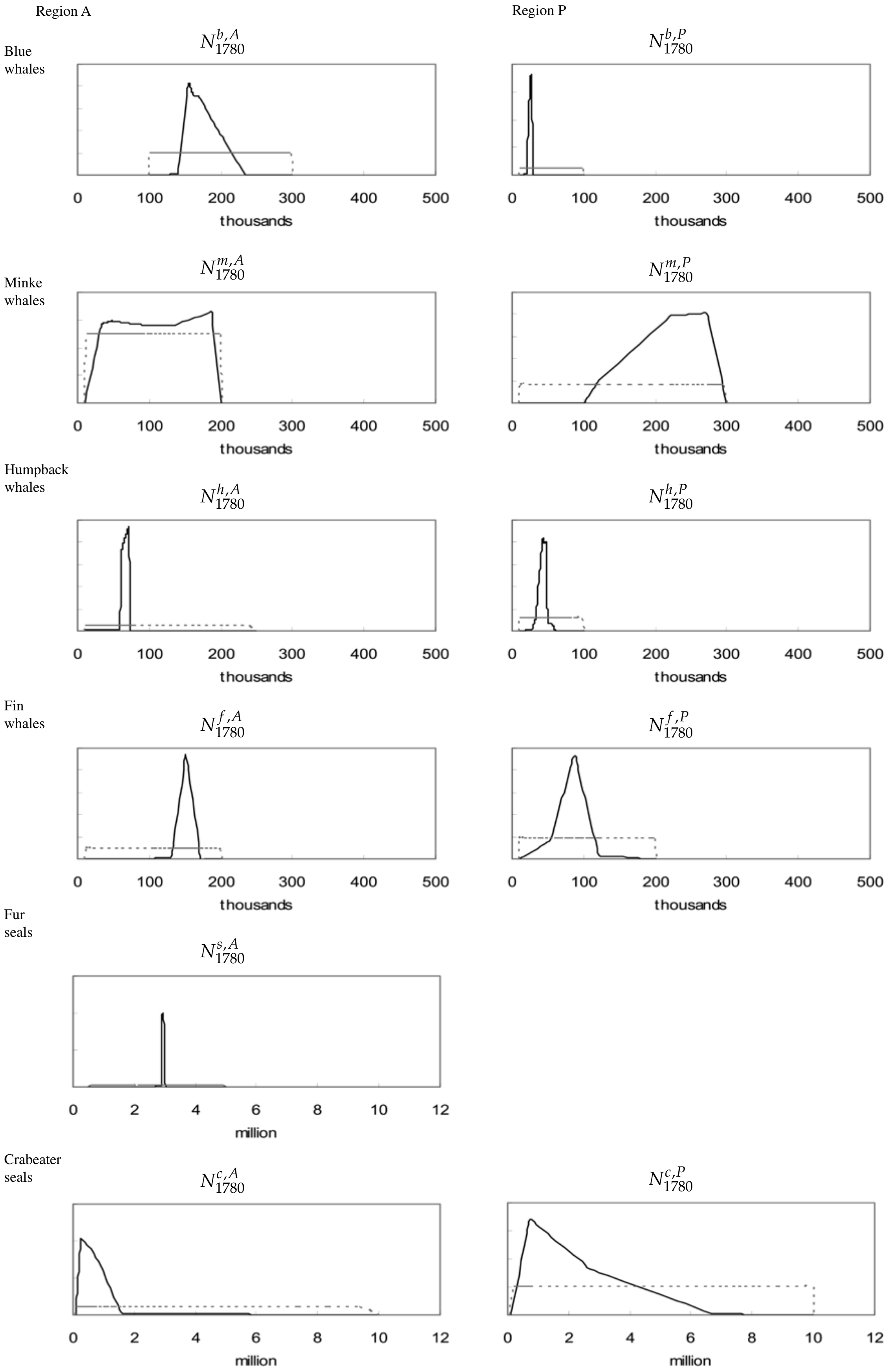


Figure 8(a): Probability density distributions for the initial number of animals in the year 1780. The solid lines are the model estimates (likelihood profiles used to approximate posteriors) and the dotted lines represent the effective priors.

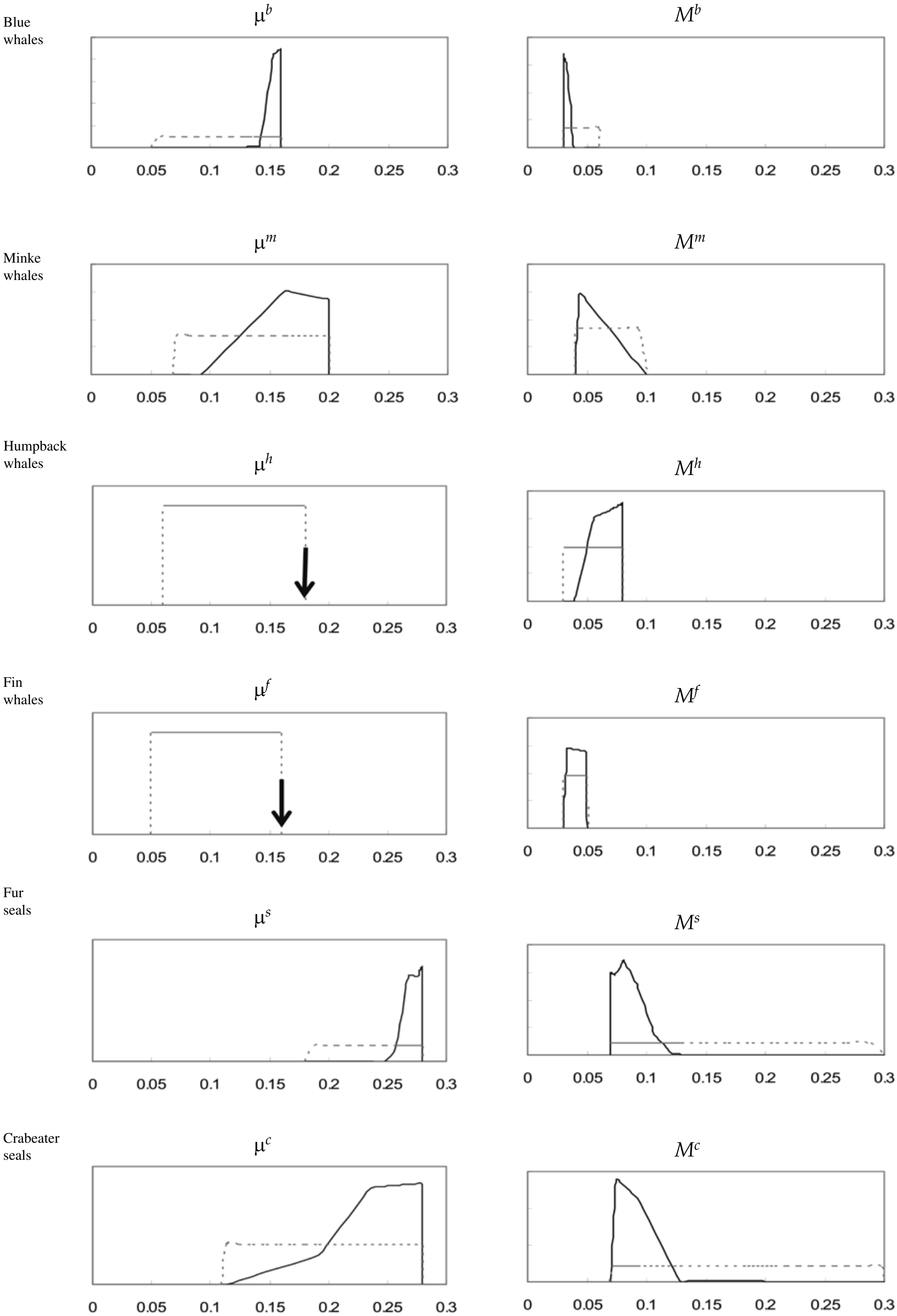
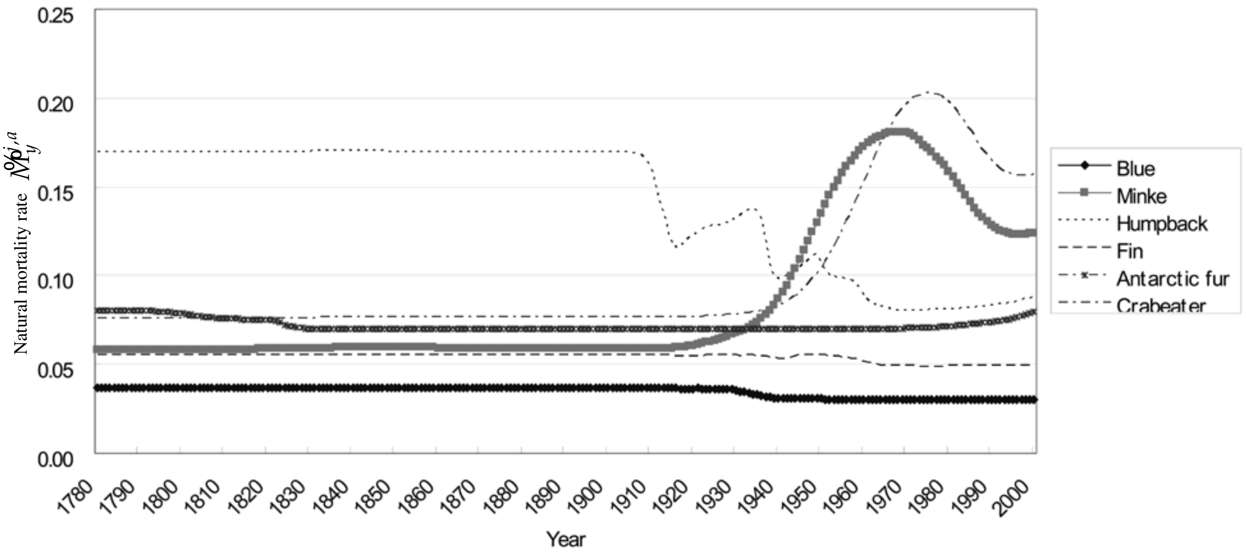


Figure 8(b): Probability density distributions for annual birth and natural mortality rates. The solid lines are the model estimates (likelihood profiles used to approximate posteriors) and the dotted lines represent the effective priors. The μ^h and μ^f parameters were fixed at the maximum of their ranges (see arrows), rather than estimated.

Region A



Region P

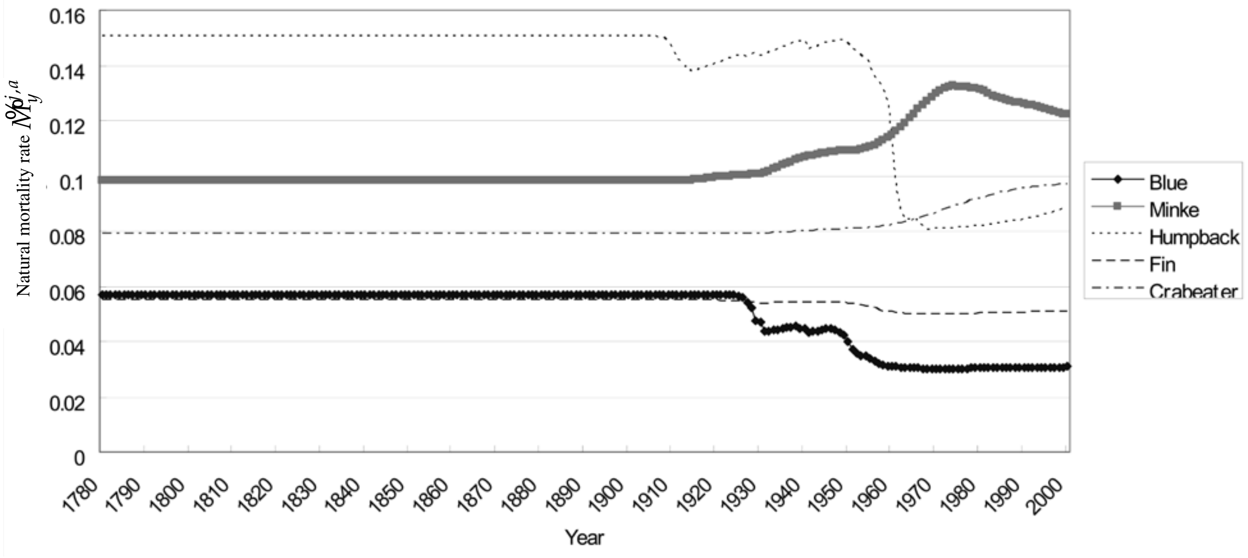


Figure 9: Annual per-capita natural mortality rate ($\tilde{M}_y^{j,a} = M^j + \eta^{j,a} N_y^{j,a}$) changes over time for the predator species considered in this study for the 'reference-case' model under the assumption that the density-dependent (η) factors operate entirely on natural mortality rates for all ages, without causing any change to pregnancy and/or calf survival rates.

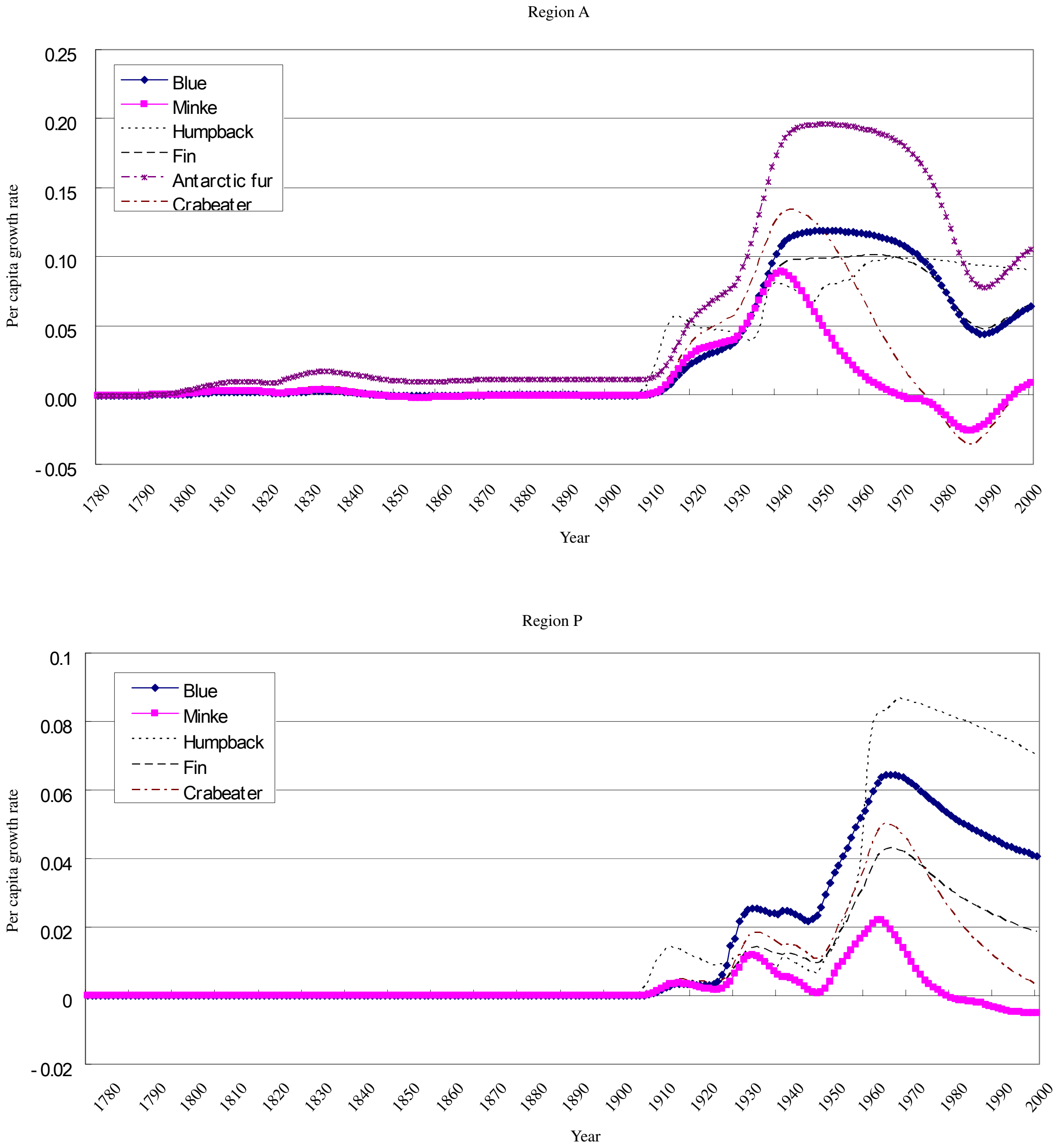


Figure 10: Annual per capita growth rate $[\frac{\mu^j \left(B_y^a\right)^n}{\left(Bb^a\right)^n + \left(B_y^a\right)^n} - M^j - \eta^{j,a} N_y^{j,a}]$ changes over time for the predator species considered in this study, as estimated for the 'reference-case' model (for which n = 2).

Liste des tableaux

Tableau 1: Estimations de la consommation annuelle de krill par ses prédateurs en Antarctique. – Aucune estimation n'est fournie ; * cette estimation compte également d'autres euphausiidés ; ? – l'estimation est approximative, elle ne repose que sur des suppositions péremptoires. (Noter que les analyses du présent document (voir tableau 8) laissent penser que les estimations de Laws (1977) sont trop élevées.)

Tableau 2a: Captures anciennes dans l'hémisphère sud des espèces de baleines mysticètes faisant l'objet de cette étude (voir le texte pour obtenir des précisions sur la source des informations).

Tableau 2b: Captures anciennes présumées des otaries de Kerguelen (voir appendice 1) ; toutes provenaient du sud de l'Atlantique (à savoir de la région A, celle du secteur Atlantique/Indien de l'océan Austral). A l'égard des phoques crabiers, il est présumé que sur les 11 années de 1967 à 1977, 750 individus ont été capturés par année dans la région A.

Tableau 3: Estimations de l'abondance observée/inférée des prédateurs de krill examinés dans le modèle.

Tableau 4: Estimations des tendances de l'abondance observée des prédateurs de krill examinés dans le modèle. Les tendances sont données en tant que variation proportionnelle par an, sauf dans le cas de la baleine bleue pour laquelle les estimations successives de l'abondance circumpolaire données sont utilisées pour servir de base à l'inférence d'une estimation dans le processus de l'ajustement du modèle de la population (voir texte).

Tableau 5: Limites plausibles des paramètres à estimer.

Tableau 6: Valeurs des paramètres d'entrée et des paramètres estimés, et autres quantités pour le modèle du "cas de référence" de la population et six scénarios de sensibilité i) à vi). Les paramètres donnés entre crochets dans la section des paramètres estimés ont été fixés et non estimés. Les contributions (*LL*) de diverses espèces à –ln*L* sont également données . Pour la sensibilité vi), les bornes inférieures de l'abondance des phoques crabiers (*) en 1780 ont été fixées à 300 000.

Tableau 7: Intervalles de confiance à 95% des paramètres estimés du modèle du "cas de référence" de la population fondé sur les profils de vraisemblance. Toutes les valeurs ont été arrondies à trois chiffres significatifs.

Tableau 8: Comparaison de la consommation pré-exploitation du krill suggérée par Laws (1977) et des estimations fournies par le modèle du cas de référence donné dans le présent document. Dans celles-ci, les calculs sont donnés tant pour les taux d'alimentation correspondant à la biomasse de krill estimée pour 1920 dans le modèle que pour les taux d'alimentation maximaux (correspondant aux suppositions de Laws).

Liste des figures

Figure 1: Capture annuelle de baleines bleues, rorquals communs, cachalots, baleines à bosse, rorquals de Rudolphi et petits rorquals dans l'hémisphère, après correction des déclarations erronées de l'ex-Union soviétique (voir le texte pour obtenir des précisions sur la source des informations).

Figure 2: Carte des zones de gestion (I à VI) de la CBI et des deux régions (A et P) examinées dans le modèle de population créé.

Figure 3: Captures anciennes de baleines bleues, petits rorquals, baleines à bosse et rorquals communs dans la région A (zones de gestion II, III et IV de la CBI) et la région P (zones de gestion V, VI et I de la CBI).

Figure 4: Trajectoires du modèle des populations du "cas de référence" pour le krill et ses principaux prédateurs en Antarctique. Un point/une croix noir(e) indique une estimation d'abondance fondée sur une campagne d'évaluation pour respectivement le secteur Pacifique et le secteur Atlantique sur lequel le modèle a été ajusté. Les triangles vides figurant dans le tracé récent de la trajectoire de la baleine bleue correspondent aux estimations d'abondance de baleines bleues dérivées des campagnes d'évaluation des régions A et P combinées, auxquelles le modèle à été ajusté pour refléter la tendance d'abondance indiquée par ces estimations.

Figure 5: Projections du modèle du "cas de référence" de la population pour les trajectoires futures (jusqu'à l'année 2500) pour le krill et ses principaux prédateurs en Antarctique, sur l'hypothèse de captures nulles de toutes les espèces après 2000.

Figure 6: Consommation annuelle de la biomasse de krill (en millions de tonnes) par les prédateurs examinés dans le modèle des régions A et P pour (a) le "cas de référence", (b) le scénario i) pour lequel les estimations d'abondance des petits rorquals ont doublé et (c) le scénario ii) pour lequel la capacité en krill de la région A baisse de 50% de 1951 à 1970.

Figure 7: Production annuelle estimée de krill (millions de tonnes) pour les régions A et P pour (a) le "cas de référence", (b) le scénario i) et (c) le scénario ii).

Figure 8a: Distributions de densité de probabilités pour le nombre initial d'individus en 1780. Les traits pleins sont les estimations du modèle (profils de vraisemblance utilisés pour se rapprocher des valeurs *a posteriori*) et les lignes pointillées représentent les valeurs réelles *a priori*.

Figure 8b: Distributions de densité de probabilités pour les taux annuels de naissance et de mortalité naturelle Les traits pleins sont les estimations du modèle (profils de vraisemblance utilisés pour se rapprocher des valeurs *a posteriori*) et les lignes pointillées représentent les valeurs réelles *a priori*. Les paramètres μ^h et μ^f ont été fixés au maximum de leur intervalle (voir les flèches) plutôt qu'estimés.

Figure 9: Changement du taux annuel de mortalité naturelle par tête ($\tilde{M}_y^{j,a} = M^j + \eta^{j,a} N_y^{j,a}$) au cours du temps pour les espèces prédatrices examinées dans cette étude pour le modèle du "cas de référence", lorsqu'il est présumé que les facteurs dépendant de la densité (η) dépendent uniquement des taux de mortalité naturelle pour tous les âges, sans causer de changement aux taux de gravidité ou de survie des baleineaux.

Figure 10: Changement du taux annuel de croissance par tête [$\frac{\mu^j \left(B_y^a\right)^n}{\left(Bb^a\right)^n + \left(B_y^a\right)^n} - M^j - \eta^{j,a} N_y^{j,a}$] au cours du temps pour les espèces prédatrices examinées dans cette étude pour le modèle du "cas de référence" (pour lequel $n = 2$).

Figure 1.1: Série chronologique présumée des captures d'otaries en Géorgie du Sud.

Figure 1.2: Série chronologique présumée des captures d'otaries aux îles Shetland du Sud.

Список таблиц

Табл. 1: Оценки ежегодного потребления криля хищниками в Антарктике. – не имеется оценки; * – в данную оценку включаются и другие эвфаузииды; ? – приблизительная оценка, основанная на широких допущениях (Заметьте, что проводимый в данном документе анализ (см. табл. 8) говорит о том, что оценки Лоуза (Laws, 1977) слишком завышены).

Табл. 2a: Ретроспективный объем добычи в южном полушарии видов гладких китов, рассматриваемых в данном исследовании (информацию об источниках см. в тексте).

Табл. 2b: Предполагаемый ретроспективный объем добычи южных морских котиков (см. Дополнение 1); весь объем получен в Южной Атлантике (т.е. в Районе A, сектор Атлантического/Индийского океанов). Что касается тюленей-крабоедов, то предполагается, что в Районе A в течение 11 лет, с 1967 по 1977 гг., ежегодно добывалось 750 особей.

Табл. 3: Оценки наблюдаемой/предполагаемой численности питающихся крилем хищников, рассматриваемых в данной модели.

Табл. 4: Оценки тенденций изменения наблюдаемой численности питающихся крилем хищников, рассматриваемых в данной модели. Эти тенденции представлены как ежегодное пропорциональное изменение, за исключением синих китов, в случае которых приведенные последовательные оценки циркумполярной численности используются в качестве основы получения оценки в процессе подбора популяционной модели (см. текст).

Табл. 5: Возможные границы подлежащих оценке параметров.

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Рис. 5: Прогнозируемые «контрольной» популяционной моделью будущие траектории (вплоть до 2500 г.) для криля и его основных хищников в Антарктике при допущении нулевого вылова всех видов после 2000 г.

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Рис. 7: Оценочная ежегодная продуктивность криля (млн. т) в Районе A и Районе P по (a) «контрольному сценарию», (b) сценарию (i) и (c) сценарию (ii).

Рис. 8(a): Распределения плотностей вероятностей для исходного количества животных в 1780 г. Сплошными линиями показаны модельные оценки (профили правдоподобия используются для аппроксимации апостериорных распределений), а пунктиром – реальные априорные распределения.

Рис. 8(b): Распределения плотностей вероятностей для годовых коэффициентов рождаемости и естественной смертности. Сплошными линиями показаны модельные оценки (профили правдоподобия используются для аппроксимации апостериорных распределений), а пунктиром – реальные априорные распределения. Параметры μ^h и μ^f зафиксированы на максимальном уровне диапазона значений (см. стрелки), а не оценены.

Рис. 9: Повременные изменения коэффициента ежегодной естественной смертности в расчете на особь ($\tilde{M}_y^{j,a} = M^j + \eta^{j,a} N_y^{j,a}$) для рассматриваемых в данном исследовании видов хищников по «контрольной» модели при допущении, что зависящие от плотности факторы (η) применяются исключительно к коэффициентам естественной смертности для всех возрастов, не вызывая изменений в коэффициентах беременности/или выживаемости детенышей.

Рис. 10: Повременные изменения коэффициента ежегодного роста в расчете на особь $[\frac{\mu^j \left(B_y^a\right)^n}{\left(Bb^a\right)^n + \left(B_y^a\right)^n} - M^j - \eta^{j,a} N_y^{j,a}]$ для рассматриваемых в данном исследовании видов хищников по оценке для «контрольной» модели (где $n = 2$).

Рис. 1.1: Предполагаемый временной ряд данных по добыче морских котиков, Южная Георгия.

Рис. 1.2: Предполагаемый временной ряд данных по добыче морских котиков, Южные Шетландские о-ва.

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Tabla 2a: Capturas históricas en el hemisferio sur de las especies de ballenas de barba consideradas en este estudio (véase el detalle de las fuentes en el texto).

Tabla 2b: Capturas históricas supuestas de lobos finos antárticos (véase el apéndice 1); todas provienen del Atlántico sur (esto es, de la región A, el sector del Océano Atlántico/Índico. Para las focas cangrejeras, se supone que 750 animales fueron cazados por año en la región A durante 11 años, desde 1967 hasta 1977.

Tabla 3: Estimaciones de la abundancia observada/inferida de los depredadores de kril considerados en el modelo.

Tabla 4: Estimaciones de las tendencias de la abundancia observada de los depredadores de kril considerados en el modelo. Las tendencias se muestran como un cambio proporcional por año, excepto en el caso de las ballenas azules, en cuyo caso las estimaciones sucesivas de la abundancia circumpolar listadas son utilizadas como base para inferir una estimación en el proceso de ajuste del modelo demográfico (véase el texto).

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Tabla 6: Valores de los parámetros de entrada y de los parámetros estimados y otras cantidades para el modelo demográfico del "caso de referencia" y seis condiciones de sensibilidad, (i) a (vi), cuyos detalles pueden verse en el texto. Los parámetros bajo el encabezamiento 'parámetro estimado', que figuran entre paréntesis cuadrado, fueron fijados en vez de estimados. También se muestran las contribuciones (*LL*) de distintas especies a $-\ln L$. Para la sensibilidad (vi), la menor abundancia de focas cangrejeras correspondiente a la del año 1780 (*) se fijó en 300 000.

Tabla 7: Intervalos de confianza del 95% de los parámetros estimados para el modelo demográfico del "caso de referencia", basados en perfiles de verosimilitud. Todos los valores han sido redondeados a tres dígitos significativos.

Tabla 8: Comparación del consumo de kril previo a su explotación propuesto por Laws (1977) y las estimaciones proporcionadas por el modelo del "caso de referencia" presentado en este trabajo. Nótese que en este último caso se muestran los cálculos tanto para las tasas de alimentación correspondientes a la biomasa de kril estimada por el modelo para 1920, como para las tasas de alimentación máximas (correspondientes a las suposiciones de Laws).

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Figura 4: Trayectorias del modelo demográfico para el "caso de referencia" del kril y sus depredadores principales en la Antártida. Un punto/cruz negros muestran estimaciones de la abundancia derivadas de prospecciones para los sectores de los Océanos Pacífico y Atlántico respectivamente, a las que fue ajustado el modelo. Los triángulos claros mostrados en el gráfico de la trayectoria reciente de la ballena azul corresponden a las estimaciones de la abundancia de esta especie de las prospecciones efectuadas en las Regiones A y P combinadas, a las cuales se ajustó el modelo para reflejar la tendencia de la abundancia indicada por estas estimaciones. Las estimaciones del número de ballenas y pinnípedos son como se indican, y las de kril en millones de toneladas.

Figura 5: Proyecciones del modelo demográfico para el "caso de referencia" para las futuras trayectorias (hasta el año 2500) del kril y sus depredadores principales en la Antártida suponiendo una captura cero para todas las especies después del año 2000.

Figura 6: Consumo anual de biomasa de kril (en millones de toneladas) por los depredadores considerados en el modelo para la Región A y la Región P para (a) el "caso de referencia", (b) sensibilidad (i) para la cual se duplican las estimaciones de la abundancia del rorcual aliblanco, y (c) sensibilidad (ii) donde la carga cinegética del kril en la Región A disminuye en un 50% de 1951 a 1970.

Figura 7: Estimación de la producción anual de kril (en millones de toneladas) para la Región A y la Región P para (a) el "caso de referencia", (b) sensibilidad (i) y (c) sensibilidad (ii).

Figura 8(a): Distribución de probabilidades de densidad para el número inicial de animales en el año 1780. Las líneas gruesas representan las estimaciones del modelo (perfiles de verosimilitud utilizados para aproximar las distribuciones posteriores) y las líneas punteadas representan los priores efectivos.

Figura 8(b): Distribución de probabilidades de densidad para las tasas anuales de nacimiento y de mortalidad natural. Las líneas gruesas representan las estimaciones del modelo (perfiles de verosimilitud utilizados para aproximar las distribuciones posteriores) y las líneas punteadas representan los priores efectivos. Los parámetros μ^h y μ^f fueron fijados en el máximo valor de su rango (ver flechas), en vez de ser estimados.

Figura 9: Cambios en la tasa de mortalidad natural anual per-capita ($\tilde{M}_y^{j,a} = M^j + \eta^{j,a} N_y^{j,a}$) en el tiempo para las especies de depredadores consideradas en este estudio para el modelo del "caso de referencia" bajo la suposición de que los factores dependientes de la densidad (η) afectan solamente las tasas de mortalidad natural de todas las clases de edad, sin producir ningún cambio en las tasas de preñez y/o de supervivencia de las crías.

Figura 10: Cambios en la tasa de crecimiento anual per-capita [$\frac{\mu^j \left(B_y^a\right)^n}{\left(Bb^a\right)^n + \left(B_y^a\right)^n} - M^j - \eta^{j,a} N_y^{j,a}$] en el tiempo para las especies de depredadores consideradas en este estudio, para el modelo del "caso de referencia" (para el cual $n = 2$).

Figura 1.1: Series cronológicas supuestas para las capturas de lobo fino antártico en las Islas Georgia del Sur.

Figura 1.2: Series cronológicas supuestas para las capturas de lobo fino antártico en las Islas Shetland del Sur.

APPENDIX 1

DETAILS OF THE APPROACH USED TO DEVELOP A PLAUSIBLE ANTARCTIC FUR SEAL CATCH HISTORY

Antarctic fur seal catch trends around South Georgia

The following four pieces of information (McCann and Doidge, 1987) available regarding the Antarctic fur seal catch for South Georgia were used to construct a sequence 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 112 000 skins were taken.
(iv) By 1820, Antarctic fur seals had been virtually rendered extinct at South Georgia.

Assumed catch trend

The assumed catch trend for Antarctic fur seals for South Georgia is shown in Figure 1.1. For simplicity, the two linear functions shown below were used:

$$C_y = 11000 \cdot (y - 1790) \qquad \text{for } 1790 \le y \le 1800 \tag{1.1}$$

$$C_y = 110000 - 5500 \cdot (y - 1800) \qquad \text{for } 1801 \le y \le 1820. \tag{1.2}$$

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

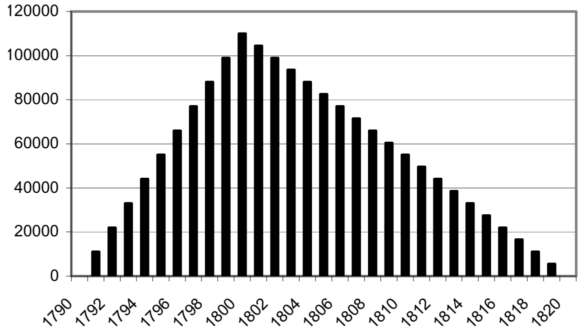

Figure 1.1: Assumed time series of fur seal catches for South Georgia.

Antarctic fur seal catch trends around the South Shetland Islands

Similarly, the following three pieces of information (McCann and Doidge, 1987) available regarding Antarctic fur seal catch for the South Shetland Islands were used to construct a sequence of the catches by year.

(i) The first known trip to the South Shetland Islands was made in 1819.
(ii) In 1821, 320 000 skins were taken.
(iii) By 1830, the population had been virtually exterminated.

Assumed catch trend

The assumed catch trend for Antarctic fur seals for the South Shetland Islands is shown in Figure 1.2. For simplicity, a linear trend was again assumed.

$$C_y = 320000 - 35556 \cdot (y - 1821) \qquad \text{for } 1821 \le y \le 1829 \tag{1.3}$$

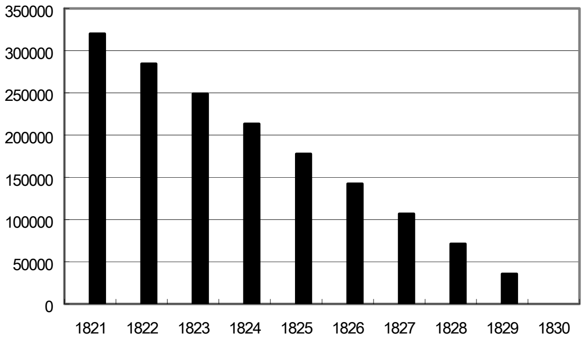

Figure 1.2: Assumed time series of fur seal catches for the South Shetland Islands.