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Modelling the krill-predator dynamics of the Antarctic ecosystem

by

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August 2005

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DECLARATION

I declare that this thesis is my own unaided work, both in concept and execution, and that apart from the normal guidance from my supervisor, I have received no assistance except as stated below.

André Punt (University of Washington) kindly provided program code for earlier versions of the minke whale catch-at-age analyses. I checked the code, and adjusted it to be able to effect the further modifications introduced for the calculations carried out in Chapter 8. (All other code used I developed from scratch).

My supervisor, Doug Butterworth spent considerable time in assisting with editing the English throughout the thesis, and some other members of the MARAM research group at UCT also helped with this.

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Finally, the material reported in Chapter 12 was submitted for publication, so that I benefited from the comments made by journal reviewers. The resultant paper was:

Mori, M. and Butterworth, D. S. 2004. Consideration of multispecies interactions in the Antarctic: a preliminary model of the minke whale – blue whale – krill interaction. *Afr. J. mar. Sci.* 26: 245-259.

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ABSTRACT

The main objective of this thesis is to model the krill-predator dynamics of the Antarctic ecosystem so as to determine whether predator-prey interactions alone can broadly explain observed population trends of the species considered in the model without any appeal to systematic effects possibly caused by environmental change.

The history of human harvesting in the Antarctic is summarized briefly, and the central role played by krill is emphasized. The background to the hypothesis of a krill surplus in the mid 20th Century is described, and the information, particularly regarding population trends, that has become available since the postulate was first advanced is discussed. By reviewing the consumption and abundance estimates for various species in the Antarctic, it is evident that among the baleen whales, blue, fin, humpback and minke whales feed mainly on krill, and could collectively be consuming up to 120 million tons of krill in this region for each of the years around 1990. Of the seals, the Antarctic fur seals and crabeater seals also feed mainly on krill, and these two species could be consuming up to 70 million tons of krill each year. Consumption estimates for other krill predators (birds, fish and cephalopods) are relatively poorly determined by comparison. Of these four baleen whale species, minke whales currently make the greatest impact on krill due to their large number at present compared to the other larger whale populations which are still depleted. Trend information suggests that the large baleen whales that were heavily depleted during the commercial whaling period are now recovering at rates in the vicinity of 10% per year, but there are some indications of a recent decrease in minke whale numbers. Thus, the consumption of krill by these large baleen whales has probably been increasing over recent years, though decreasing for minke whales.

Updated and refined catch-at-age analyses of minke whales for the International Whaling Commission (IWC) Management Areas IV and V suggest an increase in abundance of this species in the middle decades of the 20th Century to peak at about 1970, followed by a decline for the next three decades. Fitting the recruitment time trend obtained from these analyses to a stock-recruitment model suggests that minke whale carrying capacity first increased from about 1940 to 1960 followed by a 60% decrease from the 1960s to the present. General trends in the biological parameters of this species are consistent with such a decline.

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A predator-prey interaction model is developed including krill, four baleen whale (blue, fin, humpback and minke) and two seal (Antarctic fur and crabeater) species. The model commences in 1780 (the onset of fur seal harvests) and distinguishes the Atlantic/Indian and Pacific sectors in view of the much larger past harvests in the former. A reference case and six sensitivities are fit to available data on predator abundances and trends, and the plausibility of the results and the assumptions on which they are based is discussed, together with suggested areas for future 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, with crabeater seals seemingly playing an important role and constituting a particular priority for improved abundance and trend information; iii) the Atlantic/Indian region shows major changes in species abundances, in contrast to the Pacific which is much more stable; iv) baleen whales have to be able to achieve relatively high growth rates to explain observed trends; v) 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 they need to be better understood and taken into account in management decisions, and vi) Laws' (1977) estimate of some 150 million tons for the krill surplus may be appreciably too high as a result of his calculations omitting consideration of density dependent effects in feeding rates.

A priority for future work is to obtain improved estimates of the amount of krill consumed by other species, such as birds, cephalopods and fish as well as to obtain consensus on current abundance estimates for crabeater seals and baleen whales (especially minke whales and also the associated abundance trend). Once such information is improved, more thorough sensitivity tests to the assumptions of the model and uncertainties in the abundance estimates of the species considered need to be explored. With such further development, it is hoped that such a model may ultimately assist in providing scientific advice for appropriate sustainable harvesting strategies for the Antarctic marine ecosystem taking species interactions into account, as this is a matter of key importance for the IWC and for the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR).

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CHAPTER 1

INTRODUCTION AND OVERVIEW OF THESIS

1.1 Introduction

There are a number of motivations to model the krill *Euphausia superba* -predator dynamics of the Antarctic ecosystem. The first is related to the abundance trend estimates for the krill-feeding predators in this region. It has now been about half a century since the protection of the large baleen whales in the Antarctic following the extensive commercial harvesting of these species during the early 20th Century. A number of recent studies report the recovery of these previously exploited large baleen whales since such protection. On the other hand, some studies suggest recent declines in other species which were not extensively harvested and share the same prey with the large baleen whales. These recent opposing trends among these species together with a number of studies consistent with Laws' (1962, 1977) hypothesis of a krill "surplus" arising from the depletion of the large baleen whales, strengthen inferences and that the main krill-feeding predators are probably competing for krill, and hence affecting each others population dynamics as well as that of krill in the Antarctic.

The second motivation is that while much has recently been published concerning the possible impact of environmental changes (e.g. global warming, decrease in sea-ice extent etc.) on Antarctic marine species, little has been attempted by way of explaining population trends on the basis of predator-prey interactions. This is despite the fact that past whale harvesting in the Antarctic provided likely the largest human-induced perturbation of any marine ecosystem[1].

A final motivation is the increasing need in fisheries management to look beyond target species only and to consider the impacts of fishing on the ecosystem, as a whole as well as the impacts of the ecosystem on fisheries. If reliable multi-species models of marine ecosystems are to be achieved anywhere, the Antarctic provides a primary candidate where success needs first to be demonstrated, since the food web is fairly simple compared to other marine ecosystems. Furthermore, the ability to reliably predict the consequences of such multi-species effects is of key

[1] Compare Laws' (1977) estimate of the annual amount of krill no longer consumed by large baleen whales of 150 million tons to the recent annual worldwide harvest of marine species of less than 100 million tons.

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importance for the International Whaling Commission (IWC) and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) to be able to determine appropriate sustainable harvesting strategies for the Antarctic marine ecosystem.

The main objective of the thesis is to model the krill-predator dynamics of the Antarctic ecosystem and to determine whether predator-prey interactions alone can broadly explain observed population trends of the species considered in the model without any appeal to other systematic effects, possibly caused by environmental change. The thesis consists of three sections. In the first, the information and data available for modelling the krill-predator dynamics in the Antarctic are reviewed. In the second, evidence for multi-species effects from the analyses of Southern Hemisphere minke whale *Balaenoptera acutorostrata* dynamics is discussed. Finally in the last section, krill-predator interaction models of the Antarctic ecosystem are developed.

This thesis intends to provide further insight on the extent to which predator-prey interactions may have influenced krill and their predators in the Antarctic, and thereby improve understanding of the functioning and hence the predictability of the Antarctic marine ecosystem.

1.2 Overview of Section 1 – Review of data for Antarctic multi-species model development

Chapter 2 describes the history of human harvesting in the Antarctic, focusing particularly on species that prey on krill.

Chapter 3 describes the Antarctic food web and reviews information on consumption of krill by its predators. Annual consumption of krill by the main krill-feeding baleen whales (blue *Balaenoptera musculus*, fin *Balaenoptera physalus*, humpback *Megaptera novaeangliae* and minke whales) and seals (Antarctic fur *Arctocephalus gazella* and crabeater seals *Lobodon carcinophagus*) in the Antarctic is estimated.

Chapter 4 describes the basic biology (e.g. stock structure, reproduction and age at sexual maturity) and ecology (migration, distribution and habitat overlap) of the main krill-feeding predators.

Chapter 5 reviews the available abundance and trend estimates for the main krill-feeding baleen whales in the Antarctic.

Chapter 6 reviews the available abundance and trend estimates for the main krill-feeding seals in the Antarctic.

Chapter 7 reviews the available abundance and trend estimates for krill.

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1.3 Overview of Section 2 – Evidence for multi-species effects from the analyses of Southern Hemisphere minke whale dynamics

Chapter 8 reports results for recruitment and population trends from catch-at-age analyses for the Southern Hemisphere minke whales.

Chapter 9 discusses the implications of the results of Chapter 8 for minke whale dynamics.

Chapter 10 provides information on very recent trends in biological parameters for the Southern Hemisphere minke whales, and relates these to the results in Chapter 8.

1.4 Overview of Section 3 – Development of an krill-centric Antarctic multi-species model

Chapter 11 summarises the broad features of observed trends in the abundance of krill and its main predators in the Antarctic, and develops and discusses hypotheses for the causes of these population changes.

Chapter 12 develops a preliminary model of the minke whale – blue whale – krill interaction in the Antarctic, and discusses the results obtained.

Chapter 13 extends the model developed in Chapter 12 to include four baleen whale (blue, minke, humpback and fin) and two seal (Antarctic fur and crabeater) species as well as krill. Results from the model are discussed, and a summary of suggested future work is presented.

Chapter 14 summarises the main conclusions from throughout the thesis and suggests priorities for future work.

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1.5 Definition of terms used in this thesis

- For convenience in this thesis, the convention is adopted of referring to the austral summer season as the former of the two years concerned, e.g. the 1986/87 season is referenced as 1986.
- Krill refers to Antarctic krill *Euphausia superba* throughout this thesis.
- Unless specified, blue whales refer to Antarctic true blue whales *Balaenoptera musculus* and minke whales refer to the common species *Balaenoptera acutorostrata* throughout this thesis.
- The region of interest in this thesis is essentially south of the Antarctic Convergence (see Figure 1.1), or more precisely, the region over which the krill distribution extends. While generally this distribution 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. Dedicated sighting surveys and hence population estimates for baleen whales generally apply to the region south of 60°S, and consequently do not exactly match the region over which krill extends. However, as most of the austral summer distributions of the main krill-feeding baleen whales (except for fin whales) are concentrated south of 60°S, this slight mismatch has been ignored for the purpose of this thesis.

- Unless otherwise indicated, "significant" means statistically significant at the 5% level.

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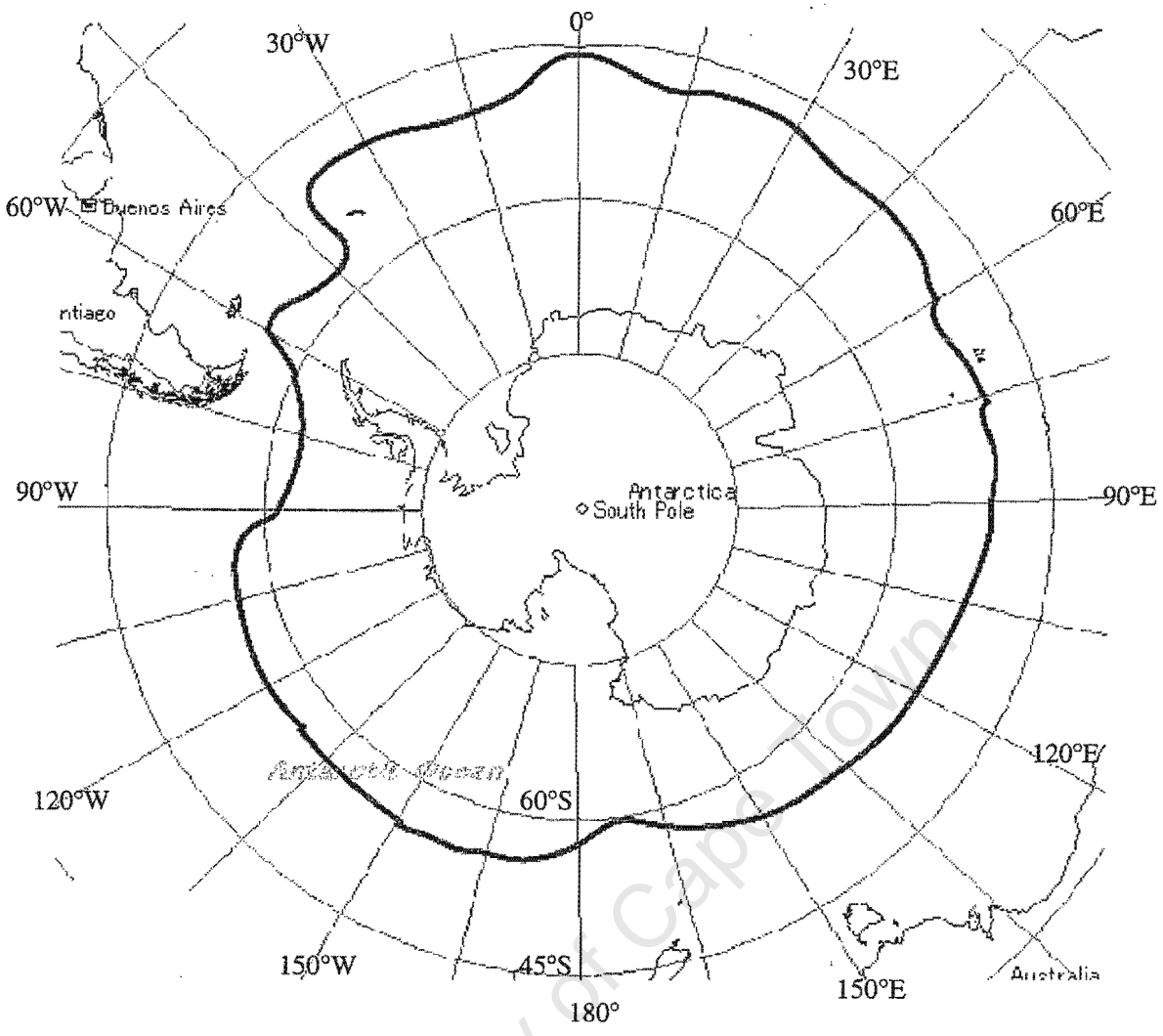


Figure 1.1 Map of the Antarctic indicating the approximate area of the Antarctic Convergence in thick lines (drawn from Kock 1992).

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SECTION 1:

REVIEW OF DATA FOR ANTARCTIC MULTI-SPECIES MODEL DEVELOPMENT

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CHAPTER 2

HISTORY OF HUMAN HARVESTING IN THE ANTARCTIC

In the Antarctic, species were depleted virtually sequentially. Once catches had reduced one species below an economically viable level, harvesting focused on the next. Figure 2.1 illustrates this sequential harvesting. This Chapter presents a brief history of human harvesting in the Antarctic. It focuses particularly on species that prey on krill.

2.1 Sealing

The main seal species that have been harvested in the Antarctic are the Antarctic fur seals, the sub Antarctic fur seals *Arctocephalus tropicalis* and the Southern elephant seals *Mirounga leonina.*

Before any commercial whaling commenced in the Antarctic, Antarctic and sub Antarctic fur seals were exploited virtually to extinction in the 18th and 19th Centuries. For Antarctic fur seals, the first known sealing trip to South Georgia was made between 1790 and 1792. Antarctic fur seals were harvested at South Georgia and the South Shetland, South Orkney and Marion Islands (see Figure 2.2), but hardly any accurate records of numbers harvested exist. The only useful information on these numbers is provided by Weddell (1825), who calculated that 1.2 million fur seals had been harvested at South Georgia by 1822, peaking at about 1800 when 112,000 skins were collected (McCann and Doidge 1987). This extensive harvesting of the Antarctic fur seals almost rendered the population extinct in South Georgia (McCann and Doidge 1987). As the numbers in South Georgia declined rapidly, the South Shetland Islands became the next location for the sealers in 1819. Some 320,000 skins were collected in 1821-22, and by 1830 the fur seal population there was again almost exterminated (Bonner 1968). Very few visits to the South Shetland Islands occurred again until 1871 when United States sealers began supplying furs to the London market. This continued until 1892, but the numbers of fur seals harvested during this period was only a small fraction of previous levels (Palmer 2004).

A similar harvesting history is reported for the sub Antarctic fur seals. Bester (1987) reports that at the Gough Island (Tristan da Cunha), American sealers commenced operations in 1790 when 5,600

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fur seal pelts were taken. Sealing gangs lived on the islands for considerable periods, and in 1811, some 1,100 fur seal skins were taken there. After about 1820 fur sealing in the islands declined due to overexploitation of the stocks. Bester (1987) notes that it is impossible to make a reasonable estimate of the total numbers of seals taken since 1790 from the island(s) during the course of sealing activities. Roux (1987) reports that between 1789 and 1832 regular and intensive harvesting of this species were commenced in Saint Paul and Amsterdam Islands, and sub Antarctic fur seals appeared to have stopped breeding on Saint Paul Island after 1835. In the Macquarie Island, Shaughnessy and Fletcher (1987) report that harvesting began when it was discovered in 1810, and by the end of 1812, over 120,000 seal skins were taken, and after 1812 catches were much smaller. Kerley (1987) reports that at the Prince Edward Islands, since its discovery in 1772, sub Antarctic fur seal were harvested, and within 30 years the population there were extensively exploited.

Sealing of the Southern elephant seals also occurred over the same general period as for Antarctic fur seals and these were also substantially reduced in numbers, mainly during the 19th Century (Palmer 2004).

Other seal species (Crabeater seals, Leopard seals *Hydrurga leptonyx*, Ross seals *Ommatophoca rossii* and Weddell seals *Leptonychotes weddellii*) were either not exploited or not taken in appreciable numbers (Croxall 1992). For crabeater seals, 918 animals were taken over 1970-1973 (Laws and Christie 1976), and 750 per year over the 11 years from 1967-1977 (I. Boyd, pers. commn).

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2.2 Whaling

After the exploitation of the Antarctic fur seals, and commencing at the beginning of the 20th Century, large baleen whale species were depleted sequentially, some almost to extinction (Figure 2.3). Blue whales were harvested legally from 1904 for almost 60 years, fin whales from 1913 to 1976, and humpback whales until 1963 (though there were some illegal takes after these dates, Yablokov *et al.* 1998). Sperm whales *Physeter macrocephalus* were taken in substantial numbers from the 1950s, and after the depletion of the other major baleen species, sei whales *Balaenoptera borealis* were heavily impacted in the 1960s and 70s. Based on historical catch information for blue whales and the fit of a logistic model to several sighting survey series, Branch *et al.* (2004) estimated that by the start of World War II, blue whale population was already about only a quarter of its pristine level, and by 1962 had been reduced to about 0.5% of this pre-exploitation abundance.

Similar studies by Johnston and Butterworth (2005a, b) have estimated that the humpback whale populations were reduced by harvesting to about 1 to 5% of their pre-exploitation abundance, depending on the breeding stock.

The commercial harvest of minke whales began in the 1970s and ended in 1986 (when a moratorium on commercial whaling came into force), though this species was not nearly as heavily exploited as the other baleen whales. In 1987, following the moratorium on commercial whaling by the IWC, Japan proposed a feasibility study (see IWC 1989a) for what came to be called the 'Japanese Whale Research Programme under Special Permit in the Antarctic' or JARPA. JARPA currently catches about 400 minke whales from IWC Management Areas IV and V (see Figure 2.2 for the location of these Areas) alternately each austral summer season in the Antarctic (e.g. IWC 1998a, p.378).

2.3 Harvesting of krill

The first full-scale krill harvesting experiments began in the late 1960s, with catches peaking at over half a million tons in the 1981 season, and then declining sharply until 1984 as a result of marketing and processing problems brought about by the discovery of high levels of fluoride in the exoskeleton of krill (Nicol and de la Mare 1993, Nicol and Endo 1999). These problems were overcome and catches increased again until the break-up of the Soviet Union in 1991 caused another sharp decline in catches as former member states of the USSR reassessed the economic viability of their krill fisheries.

A total of 6.1 million tons of krill has been taken between 1973 and 2001 (Miller 2002). The fishery has been stable for the past decade with the catch in 2001 being 98,414 tons (CCAMLR 2001). This level is not considered excessive, being much less than the precautionary catch limit of 4 million tons set by CCAMLR for the Scotia Sea sector (Area 48) from which most of the catch is taken. The latter limit is based on an acoustic survey estimate of krill abundance of 44.3 million tons, details of which are provided in Chapter 7. The fishery currently operates in the South Atlantic with a winter fishery around South Georgia, moving south in spring and summer to the waters of the Antarctic Peninsula and the South Orkney Islands (Nicol and Foster 2003). Lately, because of reduced winter sea-ice, the winter fishery has remained in the waters around the Peninsula and the South Shetlands (CCAMLR 2001). Figure 2.4 shows the historical catches of krill in the Antarctic by Management Area as defined by CCAMLR (see Figure 2.2 for a map showing these areas).

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2.4 Fishing

Together with krill harvesting, the exploitation of finfish began in the mid-1960s. Over 1969 and 1970, the bottom-dwelling marbled Antarctic rockcod *Notothenia rossii* almost vanished from the vicinity of South Georgia after 514,000 tons were taken (Constable *et al.* 2000). Following this depletion, mackerel icefish *Champsocephalus gunnari* became a target of the Soviet fleets in the mid-1970s, and the mean annual catch of this species declined over the first 20 years of the fishery, from 1970 to 1990 (Kock 1992).

Fishing for the Patagonian toothfish *Dissostichus eleginoides* began in the 1970s as part of the mixed bottom-trawl fishery around South Georgia, followed by the introduction of a long-line fishery in 1987. Substantial levels of IUU fishing[1] developed around South Georgia, and then from 1996 there was a rapid rise in such activities in the Indian Ocean, leading to a catch substantially above the recommended aggregate global limit set by CCAMLR for its Convention area. The rapid declines of the stocks in the Exclusive Economic Zones (EEZ) of Crozet Island and the Prince Edward Islands have been of great concern (Constable *et al.* 2000, Brandão *et al.* 2002).

At present CCAMLR regulates commercial fishing for krill, Patagonian/Antarctic toothfish *Dissostichus mawsoni*, icefish, lantern fish *Electrona carlsbergi*, squid *Martialia hyadesi* and crabs *Paralomis* spp..

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[1] IUU fishing means fishing that is either illegal (when taken in the Exclusive Economic Zone of a sovereign state), unregulated (when taken by non-members of the pertinent Regional Fisheries Management Organisations (RFMO) here CCAMLR), or unreported (when taken but not admitted by members of the RFMO).

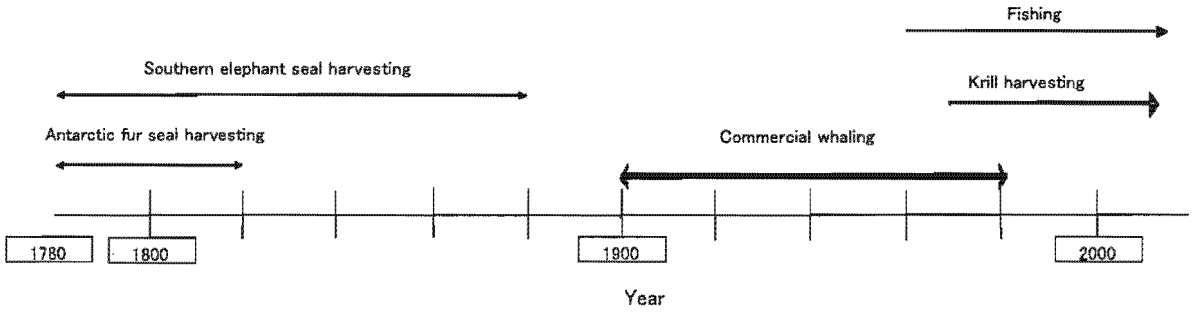


Figure 2.1 Schematic diagram that shows the historical harvesting of species in the Antarctic.

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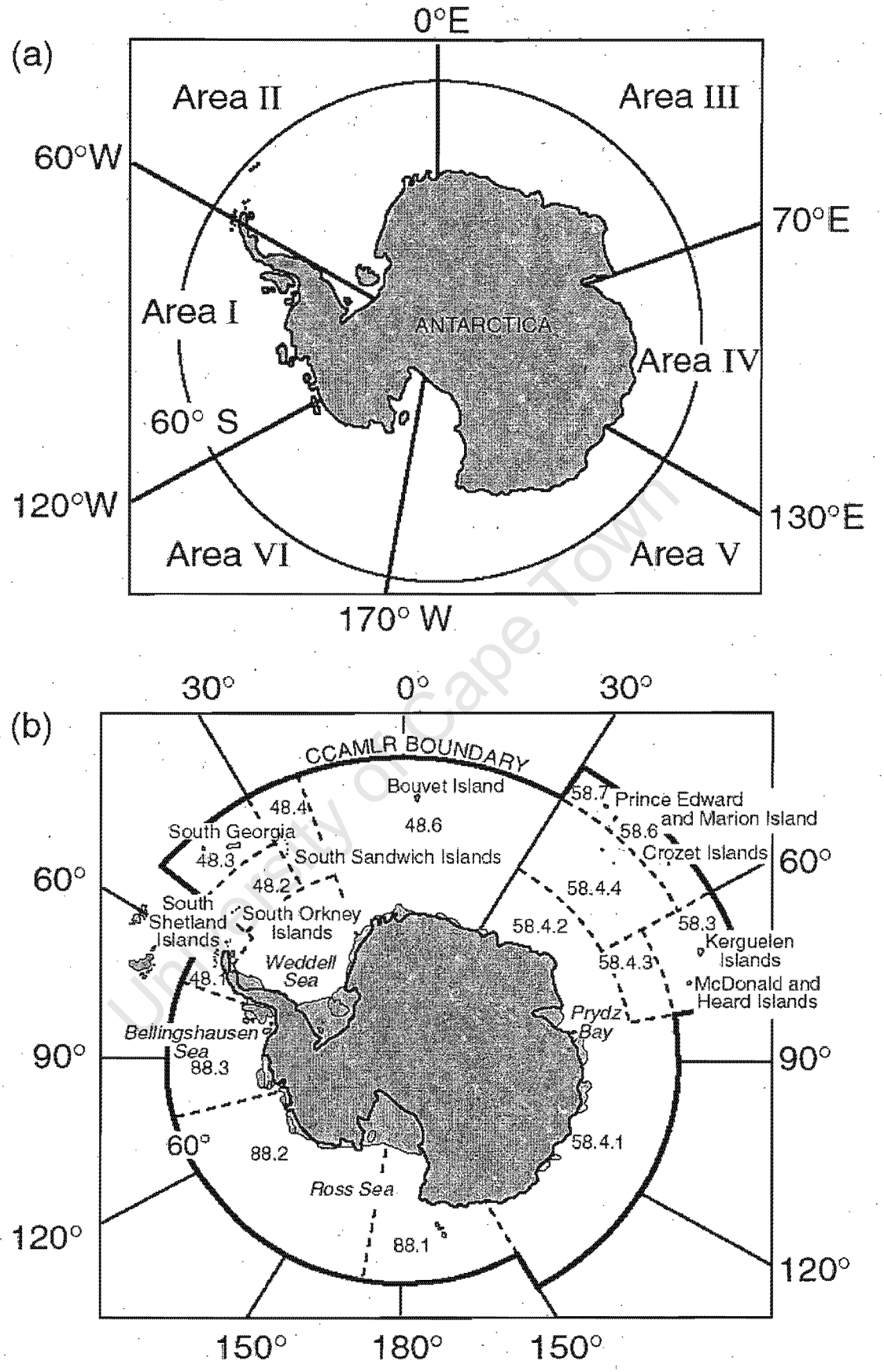
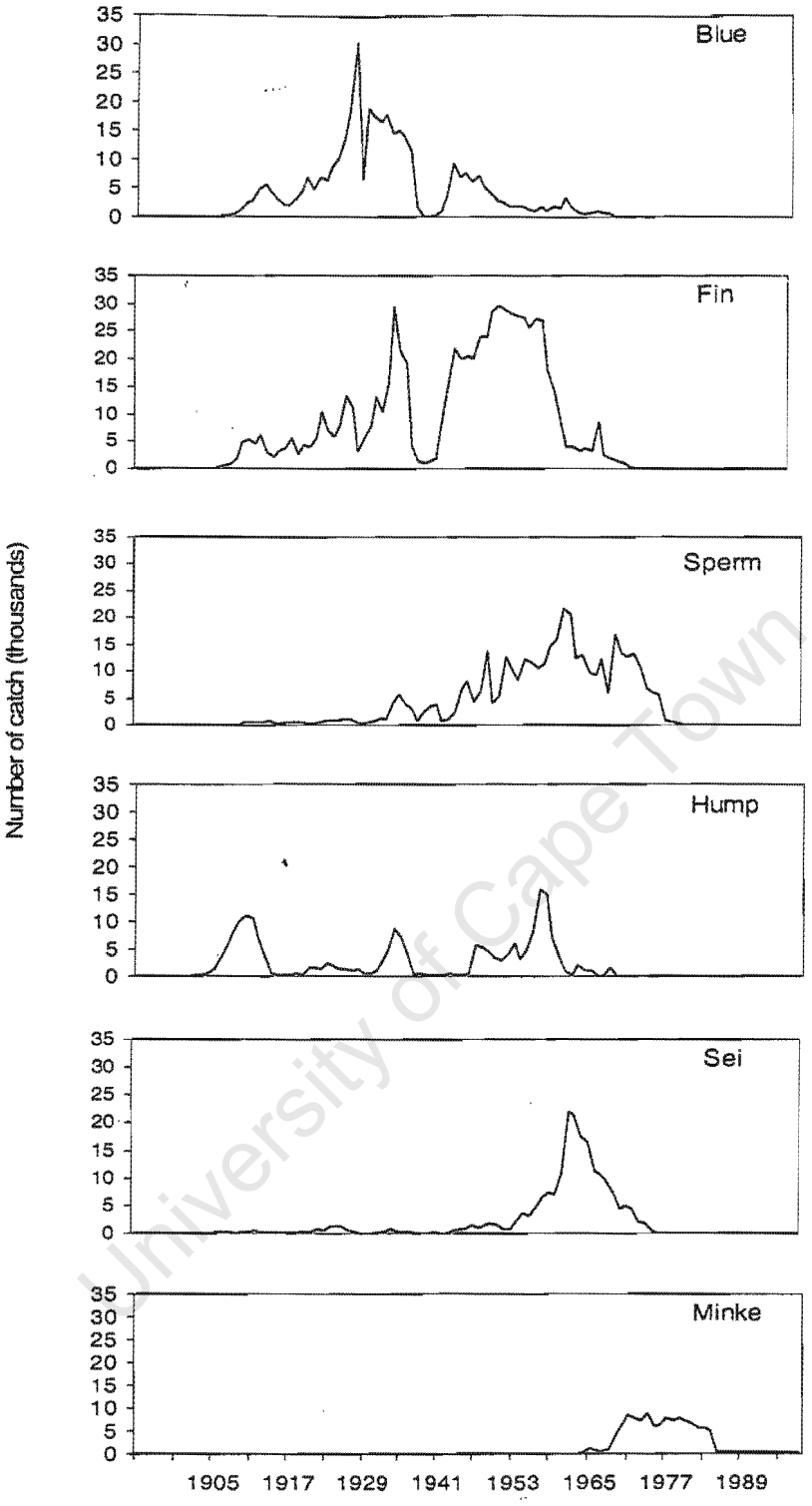


Figure 2.2 Antarctic Management Areas as defined by international organizations: (a) by the IWC, (b) by the CCAMLR.

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Figure 2.3 Annual catches (in thousands) of blue, fin, sperm, humpback, sei and minke whales caught in the Southern Hemisphere, corrected for Soviet misreporting. Source: C. Allison, International Whaling Commission, December 2002.

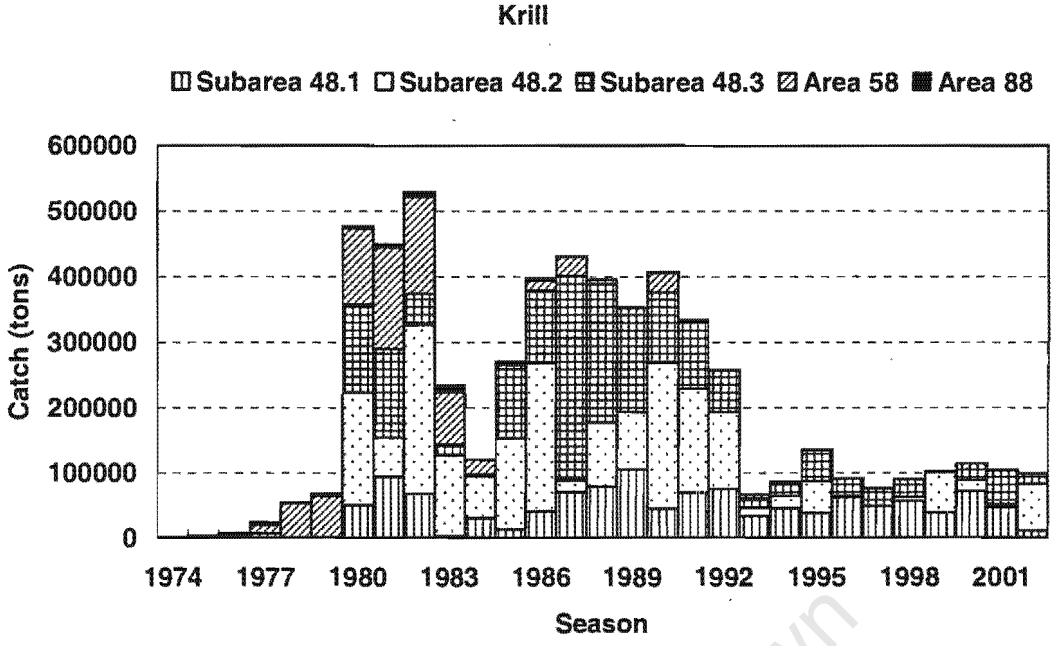


Figure 2.4 Catches of krill in the Antarctic by Management Area, as defined by the CCAMLR.

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CHAPTER 3

THE ANTARCTIC FOOD WEB AND CONSUMPTION OF KRILL BY ITS PREDATORS

3.1 Antarctic food web

Figure 3.1 shows the major trophic interactions in the Antarctic. 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.

In order to estimate annual per capita consumption of prey by krill predators in the Antarctic, information on the diet composition of the predator species, the duration of the feeding period in the Antarctic and the daily intake of prey are required. In this Chapter, information on each of these topics is summarized.

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3.2 Consumption of krill by baleen whales

3.2.1 Diet composition

Information on the diet composition of large baleen whales in the Antarctic is limited primarily because they have been protected since the end of 1960s. Thus much of the information available comes from samples taken during the commercial whaling period earlier in the 1900s, and most of this is qualitative, indicating only the names of the species that were found in the stomachs and a general impression of their amount. However, it is generally understood that although there are some local and seasonal variations, most of the southern baleen whale species (apart from the Bryde's whale, *Balaenoptera edeni*, which does not enter Antarctic waters and sei and right whales *Eubalaena australis* which mainly feed on copepods), largely fulfill their nutritional requirements by feeding on krill.

Qualitative examination of the diets of blue, fin and humpback whales

Apart from their main prey of krill, small quantities of other food organisms are also found in the stomach contents of these baleen whales. Mackintosh and Wheeler (1929) reported that the whales caught at South Georgia (i.e. humpback, fin and blue whales) feed exclusively on krill and had no other food whatsoever in their stomachs, apart from a few specimens of the amphipod *Euthemisto* which is so abundant in the plankton around South Georgia that the whales can hardly help swallowing a certain quantity. A subsequent study by Mackintosh (1942), based on the examination of whale samples collected from factory ships around South Georgia during 1936 to 1938, suggests that fish are eaten occasionally (usually the 'ice-fish' *Chionodraco hamatus*) and further that squid are sometimes present in the stomachs of blue and fin whales. Mackintosh (1942) concludes that during the Antarctic summer, blue, fin and humpback whales consume large quantities of krill; in warmer regions in winter, these whales manage to a large extent without food except for a very meager diet of certain small euphausiids, some lobster krill *Munida gregaria* and perhaps an occasional meal of fish. Nemoto (1959) found that together with krill, *Euphausia crystallorophias, Euphausia vallentini* and *Euphausia spinifera* are also consumed by humpback whales. A more recent study by Kawamura (1994) show that for fin whales, some other euphausiids such as *Euphausia lucens*, *Euphausia diomedea* and *Thysanoessa macrura* are also found in their stomachs.

Qualitative examination of the diet of minke whales

Apart from krill, some other species, such as *E. spinifera* and *Calanus tonsus*, are also found in the stomach contents of minke whales (Ohsumi *et al.* 1970). However, in a subsequent study, Ohsumi (1979) suggests that krill may for practical purposes be considered the only food source for these whales. Attention is drawn to the local importance of *E. crystallorophias* in some areas by several authors (Bushuev 1986, Tamura and Konishi 2005). 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 that of krill. While there has not been any survey or assessment of the abundance of *E. crystallorophias*, suspicions are that this is far less than that of krill (D. Miller, S. Nicol, pers. commn).

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Quantitative examination of the diets of blue, fin, humpback and minke whales

There are hardly any studies that provide quantitative diet composition information from examination of stomach contents of blue, fin and humpback whales. Nemoto (1970) analyzed the stomach contents of baleen whales in the Japanese pelagic catch in the southern hemisphere (the specific locations of the samples collected are not specified in the text) from 1961 to 1965, and shows that amongst those for which stomach contents were examined, 98% of the stomachs (excluding those that were empty) were filled with euphausiids for blue whales, 99% for fin whales and 100% for humpback whales (note however that the sample size for humpback whale was only nine). For minke whales, Ichii and Kato (1991) analyzed the stomach contents of 273 minke whales taken in the region from 55°S to the ice-edge and between 105°E and 115°E during a Japanese survey in 1987. They show that krill is the dominant food source, comprising 100% and 94% by weight of the stomach contents of these whales in the ice-edge and offshore zones of the Antarctic respectively. They also note that in the offshore zone, minke whales tend to feed on krill rather than *T. macrura*, which is found more frequently than krill in net samples. Tamura and Konishi (2005) examined the composition of the main prey found in the stomachs of minke whales sampled on JAPRA surveys from 1987 to 2003 in IWC Management Areas III-East (35°E to 70°E), IV, V and VI-West (170°W to 145°W). They found that among those stomachs that were not empty, 98-100% contained euphausiids (i.e. krill, *E. crystallorophias*, *Euphausia frigida* and *T. macrura*); in the coastal (shallow) areas of Prydz Bay and the Ross Sea, the dietary split ranges over 0-17% *E. crystallorophias* and 83-100% krill.

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Qualitative and Quantitative examination of the diets of other baleen whales (Bryde's, sei and right whales)

Bryde's whales

Bryde's whales are unique amongst the baleen whales, in that they do not undertake extensive feeding migrations into the higher latitudes of either hemisphere in summer, and thus do not cross the Antarctic Convergence (Best 2001). They are thus of limited pertinence to the analyses that follow.

Best (2001) reports the percentage frequency of occurrence of prey items in stomachs of Bryde's whales off southern Africa. There are three populations of Bryde's whales in this region: the

South African inshore stock, the southeast Atlantic stock and the southwest Indian Ocean stock. Among the Bryde's whales of the South African inshore stock that were examined between 1962 and 1965, of those that had food in their stomachs, almost 100% contained only fish (sample size n=39). For the southeast Atlantic stock, of those that had food in their stomachs, 80% contained euphausiids (50% of the euphausiids were not possible to identify, but among those that were identified 25% were *E. lucens*), 18.5% fish and 1.5% a mixture of fish and euphausiids (n=65). For the Bryde's whales taken under special permit south of Madagascar in the Indian Ocean in March 1977, all the stomachs with food contained only euphausiids (*Euphausia recurva* and *E. diomedea*) (Best 2001).

Sei whales

Nemoto (1970) analyzed the stomach contents of sei whales taken in the southern hemisphere by Japanese pelagic operators from 1961 to 1966, and reports that these whales feed on various plankton, i.e. animals such as carnivorous amphipods (*Parathemisto gaudichaudai*) and herbivorous copepods (*Drepanopus pectinatus*, etc.) which are found mostly along the Antarctic and subtropical Convergences. On their summer feeding grounds, sei whales occur mainly north of 60°S, and so are also of limited pertinence to the analyses that follow.

Right whales

Although there is relatively little direct information on the feeding habits of the southern right whale, it has been reported that this species feeds mainly on copepods (Kawamura 1978). Kawamura (1978) analyzed the relationship between the whaling grounds[1] for southern right whales where they were heavily harvested from the mid-18th to the early 20th Century, and the zoogeography of planktonic crustaceans in those areas. Based on this analysis, he suggests that the principal food sources for the southern right whale are *C. tonsus*, *Calanus simillimus*, *Drepanopsis pectinatus*, *Clausocalanus laticeps*, *Parathemisto gaudichaudii* and *E. vallentini* in the pelagic region, but that there is considerable variation between localities in the regions closer to the land. Based on some observations of southern right whales near the Antarctic Peninsula during 1983-1985, Hamner *et al.* (1988) reports some instances where this species fed on krill. No quantitative information on the diet composition of this species exists. On their summer feeding grounds, right whales occur mainly between 40°S and 50°S, and so are also of limited pertinence to

[1] The principal whaling grounds are found in the mid-latitudes between 30° and 40°S over the sectors from the Pacific towards the Atlantic through the Indian Ocean sector.

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the analyses that follow.

Do baleen whales actively select certain sizes of krill?

Whether whales actively select certain sizes of krill is not yet known. Mackintosh (1974) suggests that whales take the bulk of their food by mass from krill between 27-50 mm and impose the heaviest mortality in numbers in the 15-40 mm range. Further studies by Ichii and Kato (1991) suggest that although krill of body length 25-28 mm (1 year-old) are numerically more abundant than the 41-48 mm (3-4 year-old) krill, the latter dominate the diet by weight, and thus larger krill are the more important food for minke whales.

Summary

From the observations discussed above, it seems reasonable to conclude that krill is the main prey for blue, fin, humpback and minke whales in the Antarctic. Some other food organisms may also be found in small quantities depending on the extent of the southern migration of the species, where those that migrate further to the south around the ice-edge probably have more overlap with the distribution of krill. Bryde's whales mainly feed on fish and some euphausiids (mainly species other than krill), sei whales mainly on carnivorous amphipods and herbivorous copepods, and right whales mainly on copepods. Since Bryde's, sei and right whales are not major krill predators, and also show distributions with limited overlap of the region of interest in this thesis (essentially south of the Antarctic Convergence), these species will not be considered further in this Chapter.

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3.2.2 Prey switching

Prey-switching occurs when a predator's dietary preferences exhibit a sudden change as a function of prey abundance, such as when a predator switches to another prey species if its original preferred prey species drops below a certain level of abundance. Mechanisms responsible for switching include predators developing a search image for a certain prey type, an increase in capture success with increasing abundance and the occupation of different sub-habitats by different prey types (Murdoch *et al.* 1975).

Prey-switching behaviour in minke whales has been observed in the Barents Sea, where following a collapse in the capelin stock in 1992, minke whales foraging in the northern Barents Sea switched from a capelin-dominated diet to a diet almost completely comprised of euphausiids (Haug *et al.*

2002). No such appreciable predator-switching behaviour has been observed in the Antarctic; this is hardly surprising since there is no other substantial alternative prey species to krill in the Antarctic, especially for the ice-edge related predators.

3.2.3 Duration of the period feeding in the Antarctic

The approximate average periods that baleen whales are present (and feeding) in the Antarctic are shown in Figure 3.2 (from Figure 2-38 of Kasamatsu 2000). These inferences are based on the seasonal variation of encounter rates for these whales sighted from Japanese research vessels and the IWC/IDCR (International Decade of Cetacean Research) surveys conducted between 1976 and 1988 (see Figure 3.3). Although the specific calculations that lead to Figure 3.2 are not explained in detail in Kasamatsu (2000), it appears from Figure 3.3 that, generally, blue whales are present in the Antarctic from about December to March (approximately 125 days), whereas minke whales feed there from around December to February (approximately 90 days) and show a peak period around in late January, and fin and humpback whales are present for intermediate periods. Kasamatsu (2000) also found that these periods are closely related to body length, with a positive correlation between the two. The reason for this seems likely to be that those species that have a shorter body length also have a less efficient heat conservation budget compared to the larger species, and thus are not able to stay as long in a cold environment such as the Antarctic.

3.2.4 Daily intake

A brief summary of past studies of the daily intake of prey by whales and their resultant estimates is provided below.

Sergeant (1969) analysed the feeding rates for captive porpoises and dolphins based on the weight of daily food ingested and the animals' body weights. He found that above a body weight of 600 kg, the feeding rates remained constant at 4-6% of body weight/day up to the largest species for which these had been measured, the killer whale *Orcinus orca* (body weight of about 2 tons). He also found that the ratio of heart weight to body weight equals approximately one tenth of the daily feeding rate in large whales, and from this heart weight/body weight ratio he calculated that the daily feeding rate of adult rorquals is about 4% of the body weight. In another study, Kato and Shimadzu (1986) examined the ratios of stomach contents (krill) weight for minke whales to their body weight for those sampled in the Antarctic during 1978-1981, and obtained daily feeding rates in the range of 1.9 to 5.1% of body weights. By using a similar approach, Horwood (1990)

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suggests daily feeding rates to be in the range of 0.6 to 2.1%.

A more recent study by Tamura (2003) calculates the daily rate of prey consumption using three different methods. The first method was proposed by Innes *et al.* (1986), who estimated the daily prey consumption of a cetacean in relation to its average body weight as $I=0.42M^{0.67}$, where I is daily consumption (kg day^{-1}) and M is average body weight (kg). This formula was derived from re-analysing the values proposed by Sergeant (1969) for ingestion rates and heart masses for cetaceans of known body mass, using linear least squares regression of log-transformed data. The second method was proposed by Sigurjónsson and Víkingsson (1997) who estimated consumption by using the following formula: $D=206.25M^{0.783}$, where D is daily caloric value of prey intake (kcal day^{-1}). This method was developed by using Lockyer's (1981a) "near-basal metabolic rate" and assuming an assimilation rate of 80% and an activity coefficient of 1.5. The third method was proposed by Klumov (1963) who estimates daily consumption from the average body weight of each cetacean species as $I=0.035M$. The constant (i.e. 0.035) was derived from stomach volumes of large cetacean species (i.e. blue, fin and sei whales). The results from these three methods suggest that the daily rate of intake is estimated to be 1.4 to 4% of body weight for humpback, 1 to 4% for fin, 0.9 to 3.5% for blue and 2.4 to 4% for minke whales (Tamura 2003).

3.2.5 Consumption of krill by baleen whales

Per capita consumption of krill by baleen whales in the Antarctic is estimated by the following formula:

$$\lambda_j = \overline{w}_j \cdot c_j \cdot d_j \cdot p_j \qquad (3.1)$$

where λ_j is the per capita annual consumption of krill for baleen whale species j;

$\overline{w}_j$ is the mean weight of baleen whale species j;

c_j is the consumption of prey/day for baleen whale species j expressed as a proportion of its weight;

d_j is the number of days spent feeding in the Antarctic for baleen whale species j; and

p_j is the estimated proportion of krill in the diet of baleen whale species j.

Table 3.1 summarises the per capita annual consumption of krill by blue, fin, humpback and minke whales in the Antarctic calculated using equation (3.1). This ranges from 116-451 tons, 28-110 tons, 38-110 tons, and 4-32 tons for blue, fin, humpback and minke whales respectively. The

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proportion of krill in the diet of fin whales is assumed to be 50% for this calculation. The fin whale feeding distribution in the austral summer is located appreciably further north of that for blue, humpback and minke whales (as detailed in Chapter 4). Though euphausiids are still thought to be the primary source of food for fin whales south of the Antarctic Convergence (S. Ohsumi, T. Tamura pers. commn), these may well be from different populations to the krill upon which to predators feeding closer to the ice-edge mainly depend. The "50%" assumption is a crude approach to take account of this for the purposes of the multi-species model calculations that follow.

Table 3.2 shows the total annual consumption of krill over recent years by the major krill-feeding baleen whales in the Antarctic, estimated by multiplying the per capita consumption estimates shown in Table 3.1 by the minimum and maximum abundance estimates for these baleen whales listed in Table 5.5. Detail discussions of the abundance and trend estimates for these populations may be found in Chapter 5. This total consumption of krill over 1985-1990 is estimated to be about 6-120 million tons/year, and about 3-53 million tons/year more recently. Minke whales are the major consumers of krill among these baleen whale species; however, their impact seems to be decreasing, and that of the other species increasing over the past two decades. The latter effect arises because of the recovery over recent decades of large baleen whales in the Antarctic which is discussed further in Chapter 5.

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3.3 Consumption of krill by seals

3.3.1 Diet composition

Among the different seal species in the Antarctic, crabeater seals, Antarctic fur seals and to a lesser extent leopard seals feed mainly on krill. The number of studies that have been carried out on diet composition differs greatly between these species. A considerable number of studies have been conducted for Antarctic fur seals and leopard seals, but very few quantitative studies have been carried out for crabeater seals, probably due to their limited accessibility on the pack-ice. Available details on the diet composition of seals in the Antarctic are summarized below.

Crabeater seals

It is generally understood that crabeater seals feed almost exclusively on krill; however, quantitative studies on the diet composition of this species are very limited. Øritsland (1977) calculated the

diet composition of crabeater seals based on samples taken from a single cruise in 1964 that operated in the Scotia Sea and Weddell Sea pack-ice. The stomach contents of 65 crabeater seals were examined and indicated that this species eats krill almost exclusively. Combining these data with those from previous cruises, Øritsland (1977) estimated the diet composition of this species to be 94% krill, 3% fish and 2% squid.

Antarctic fur seals

The diet of the Antarctic fur seals has been studied at numerous sites throughout its range, namely at South Georgia (Bonner 1968, North *et al.* 1983, Croxall and Pilcher 1984, Costa *et al.* 1989, Reid 1995, 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, Osman *et al.* 2004, Casaux *et al.* 2004), Heard Island (Green *et al.* 1989, 1991, 1997), Iles Kerguelen (Cherel *et al.* 1997), Marion Island (Klages and Bester 1998) and Bouvetøya Island (Klages *et al.* 1999, Kirkman *et al.* 2000). Most studies are based on analysis of scat samples, but stomach contents have also been obtained from animals that were shot (e.g. Croxall and Pilcher 1984).

The main diet of Antarctic fur seals varies depending on their location, and probably relates to the extents of the distributions of potential prey species. Krill seems to be the major dietary item for Antarctic fur seals in South Georgia, the South Shetland Islands, the South Orkney Islands and Bouvetøya. In South Georgia, lactating females feed mainly on krill, which occurs in 88% of all scats (n=497), whereas fish occurs in 47% and squid in only 5% (Reid and Arnould 1996). Reid (1995) reports that during the austral winter, the male fur seals which are present around South Georgia at that time target their foraging on a krill and also a fish community, which is probably associated with the krill aggregations. In the South Shetland Islands, several studies suggest that during the austral summer period, krill is the main food for Antarctic fur seals, as it occurs in about 75% of all scats, whereas fish occur in about 60% (Casaux *et al.* 1998, Osman *et al.* 2004, Casaux *et al.* 2004). In the South Orkney Islands, where large numbers of sub-adult and adult males may be found during the summer/autumn and where numbers have increased dramatically in recent years (Smith 1988), krill occurs in 100% of scats, and fish in 78% (n=105) (Daneri and Coria 1992). In Bouvetøya, Antarctic fur seals feed almost exclusively on krill, which occurs in 97% of the scats sampled (n=123) (Kirkman *et al.* 2000).

Laws (1977) assumed that Antarctic fur seals consume 34% krill, 33% squid and 33% fish year-round. This is based on the qualitative information of Bonner (1968) which suggests that the

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fur seals at South Georgia feed almost exclusively on krill, but fish (commonly) and squid (rarely) are also found in the stomachs sampled there. Based on the results of more recent studies on diet composition of Antarctic fur seals in South Georgia discussed above, the assumption of 33% squid in the diet of Antarctic fur seals in South Georgia seems to be too high. Probably over recent years, 60% krill, 35% fish and 5% squid would be better estimates, though these figures will also vary somewhat by season, year, and the sex and maturity stage of the seals, and are a broad approximation.

In Kerguelen, Heard Island and Marion Island, fish seem to be the major prey for Antarctic fur seals (Cherel *et al.* 1997, Green *et al.* 1989, Green *et al.* 1991, Klages and Bester 1998). In the vicinity of the Antarctic Peninsula, either krill or fish is the dominant prey for non-breeding males, and the relative amount eaten seems to differ greatly across the survey years (Casaux *et al.* 2003).

From these studies it is evident that Antarctic fur seals are feeding not only on krill but also on fish, and that the proportions of krill and fish eaten differ greatly between regions. However, because more than 95% of the breeding population of Antarctic fur seals is at South Georgia (Reid 1995), it nevertheless remains the case that krill comprises most of the total food consumed by this population.

In terms of prey selection, Reid and Arnould (1996) suggest from their examination of the distribution of krill sizes taken by Antarctic fur seals in South Georgia that these animals are not actively selecting particular sizes of krill and, therefore, that the proportions of krill of different sizes in the diet reflect these proportions in the krill available around South Georgia. A recent study by Osman *et al.* (2004) offers a different opinion. They examined the size distribution of krill collected from faecal samples obtained from the South Shetland Islands over 1997-2001, and argue that in this vicinity there is a preference for larger krill (>34 mm) in the diet, despite the broader size range of prey items that is available in that region.

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Sub Antarctic fur seals

Sub Antarctic fur seals seem to feed predominantly on fish. Klages and Bester (1998) analysed scats collected between 1989 and 1994 from this species on Marion Island, and reported that they feed predominantly on fish of the family Myctophidae (lanternfishes). Robinson *et al.* (2002) also report that this species feeds predominantly on fish near Macquarie Island. Diet information is lacking for Amsterdam, Crozet and Kerguelen Islands, but probably fish remains the main dietary

item as is the case for the Antarctic fur seals at those locations.

Leopard seals

The diet of the leopard seals in the pack-ice is reported to consist of diverse prey items which most commonly include other seals, such as crabeater seals (Gilbert and Erickson 1977, Øritsland 1977, Siniff *et al.* 1979), fish (Green and Williams 1986), cephalopods (Siniff and Stone 1985) and krill (Lowry *et al.* 1988). A recent study by Walker *et al.* (1998), based on the analysis of scat samples (n=162) taken from Bird Island (over 1983-95), suggests that Antarctic fur seals are the main prey item (occurring in 58% of the scats collected), followed by macaroni penguins (*Eudyptes chrysolophus*) (28.0%) and that there is hardly any krill. From the samples (n=45) taken during 1994 and 1995, Walker *et al.* (1998) show that 53% was fur seal hairs, 24% fish, 20% penguin feathers and 2% krill.

Relative proportions in the diet suggested by Laws (1984) are 50% krill, 20% penguins, 14% seals, 9% fish and 6% cephalopods, based on the studies of Øritsland (1977) and Stone and Siniff (1983). Øritsland (1977) examined the stomach contents of leopard seals (n=38) based on samples taken from a single cruise in 1964 that operated in the Scotia Sea and Weddell Sea pack-ice, and concluded that the diet comprised 58% krill, 16% penguins, 12% fish, 9% cephalopods and 3% seals. Stone and Siniff (1983) examined 52 stomach and 16 faecal samples obtained during November-March (the year that the samples were taken is not made clear) along the west coast of the Antarctic Peninsula, and found that the diet comprised 54% krill, 27% penguins (mainly adélie *Pygoscelis adeliae*), 25% seals (mostly crabeater), 8% fish and 6% squid. These proportions of krill found in the diet of leopard seals differ quite markedly from the results of more the recent studies of Walker *et al.* (1998), which suggests that the amount of krill eaten by leopard seals may have decreased in recent years compared to the past, and krill been replaced by Antarctic fur seals as the primary prey species, though it seems clear that leopard seals feed on a wide range of species.

Southern elephant seals

Southern elephant seals consume mainly squid and fish, and Laws (1977) assumed that their year-round diet comprises about 75% cephalopods and 25% fish, though this was based on a very small sample (n=6). By using fatty acid analysis of blubber, Bradshaw *et al.* (2003) determined that a high proportion of the Southern elephant seals surveyed during 1999 to 2001 at Macquire Island had diets dominated by fish during the winter and when foraging around the Antarctic

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continental shelf, but that the majority had summer diets dominated by squid when they foraged pelagically.

Ross seals

Ross seals also feed mainly on cephalopods and fish. Øritsland (1977) calculated the diet composition of Ross seals based on samples taken on a single cruise in 1964 that operated in the Scotia Sea and Weddell Sea pack-ice. Stomach contents of 7 Ross seals were examined and the diet composition of this species was estimated to be 86% cephalopods and 14% fish. Combining these data with those from previous cruises, the diet composition of this species was estimated to be 64% cephalopods, 22% fish, 9% krill and 5% other invertebrates (Øritsland 1977).

Weddell seals

Weddell seals are yet another species that take mainly fish and cephalopods. Casaux *et al.* (1997) and Lake *et al.* (2003) show from analysis of faecal samples that fish are the most frequent prey, occurring in 95.7% of the faeces (n=41) and regurgitations (n=5) sampled during January and February in 1996 at the South Shetland Islands. *Euphausia* sp. occurred in 41.3% of the samples (Casaux *et al.* 1997). The diet composition estimated earlier by Øritsland (1977) was 53% fish, 11% cephalopods, 1% krill and 35% of other invertebrates.

Summary

Among the seals in the Antarctic, crabeater and Antarctic fur seals feed mainly on krill, but other seals such as southern elephant, Ross and Weddell seals feed mainly on fish and cephalopods. Leopard seals feed not only on krill, fish and cephalopods but also on other species of seals. Since sub Antarctic fur, southern elephant, Ross, Weddell and leopard seals are not major krill predators, these species will not be considered further in this Chapter. Instead the focus is on those species that feed mainly on krill (i.e. crabeater and Antarctic fur seals).

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3.3.2 Duration of the period feeding in the Antarctic

Crabeater seals

Laws (1984) suggests that observations on the behaviour of crabeater seals indicate that neither male nor female feeds during the suckling period (end of October to end of November). Øritsland (1977) reports a substantial increase in the relative frequency of empty stomachs in September and October. Among 155 crabeater seals examined from 27 August to 10 October, 65% of the stomachs were empty, whereas among the 64 examined from 11 to 31 October a larger proportion of 84% were empty. From these observations, Laws (1984) concluded that for the purpose of estimating annual food consumption, the crabeater seals should be considered to fast for an average of about 30 days annually.

Antarctic fur seals

For Antarctic fur seals, McCann (1980) reports that the territorial males (bulls) hold territories from late October to late December for an average period of 34 days (range 1-53 days) (see Figure 4.5 for a representation of colony attendance by Antarctic fur seals), during which these bulls do not feed. This result was based on data obtained from a survey at South Georgia in 1976 during the breeding season for this species. McCann (1980) notes that the period of tenure depends on the body size of the animal (which reflects its ability to sustain long fasts), the climate and the duration of the mating period. Based on these observations, Laws (1984) estimated that Antarctic fur seals feed for some 315-331 days each year.

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3.3.3 Daily intake

The average daily food intake is tentatively proposed by Øritsland (1977) and Laws (1984) to be about 7% of body weight for the pack-ice seals, with a similar rate for fur seals. This suggestion is based on information obtained from several studies (Keyes 1968, Geraci 1975, Sergeant 1973) which examined the daily intake of food by captive seals. The daily feeding rates of captive seals reported by various authors range from 4 to 10% of total body weight. Øritsland (1977) notes that even if captive seals have lower energy requirements than non-captive seals, they can nevertheless probably utilize relatively large amounts of food, and thus their feeding rates in nature may well lie within the range recorded for captive seals when periods of active feeding are considered.

3.3.4 Functional response of feeding to krill abundance

An aspect clearly of crucial importance to a consumer is the local density of its food (and hence its immediate availability) since, generally, the greater the density of food, the more the consumer eats (Begon *et al.* 1999). The relationship between an individual's consumption rate and local food density is known as the consumer's functional response (Solomon 1949). Boyd and Murray (2001) found a statistically significant non-linear functional response (similar to the Holling Type II functional response form) between the combined standardized index (CSI) (a combination of population size, breeding performance, growth rate of off-spring, foraging behaviour and diet) for the predator population and krill biomass for Antarctic fur seals, macaroni penguins and gentoo penguins *Pygoscelis papua* around South Georgia. This is the first characterization of a functional response between seals or penguins and their food supply in the Antarctic.

3.3.5 Consumption of krill by seals

Table 3.3 summarises the per capita consumption of krill by Antarctic fur seals and crabeater seals in the Antarctic. Per capita consumption of krill ranges from 0.7-2.7 tons and 3.3-5.5 tons for Antarctic fur seals and crabeater seals respectively. These ranges are based only on the ranges given for mean body weight, which differs for territorial bulls and cows, as few error estimates have been put forward for the other parameters. Since bull fur seals (at 0.2 tons) weigh some four times as much as normal adult cows (at 0.05 tons) (Payne 1977), and such bulls comprise only a smallish proportion of total population numbers, the maximum consumption rates quoted are probably too high.

Table 3.4 shows the total annual consumption of krill by the major krill-feeding seals in the Antarctic as estimated by multiplying the per capita consumption estimates shown in Table 3.3 by the minimum and maximum abundance estimates for these seals discussed in Chapter 6 which are listed in Table 6.4. This total consumption is estimated to be about 24-73 million tons around 1990. Crabeater seals seem to take the greater proportion. The consumption of krill by these two species combined is of a similar magnitude to that estimated for the baleen whales as listed in Table 3.2.

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3.4 Consumption of krill by other predators

3.4.1 Toothed whales and Beaked whales

Large male sperm whales are present as far south as the Antarctic continent, though females seldom penetrate further south than the Subtropical Convergence. Sperm whales feed primarily on squid (Clarke 1980, Kawakami 1980); however, they are also known to feed on Patagonian toothfish both north and south of the Antarctic Convergence (Korabelnikov 1959, Solyanik 1963, Yukhov 1972, 1982), though the quantities they take are unknown. Antarctic toothfish have been mentioned as also being taken by sperm whales (Abe and Iwami 1989). Furthermore squid are known to be the preferred food of many other odontocetes such as pilot whales (Sergeant 1962). Bottlenosed and beaked whales feed almost exclusively on cephalopods (Tomilin 1967).

Three different ecotypes (Types A, B and C), or possibly species, of killer whales have been identified in the Antarctic (Berzin and Vladimirov 1983, Pitman and Ensor 2003), and have different dietary preferences. Type A killer whales prey primarily on minke whales (Pitman and Ensor 2003). Type B killer whales prey primarily on seals in the Antarctic, although minke and humpback whales may also be targeted. Type C killer whales (putative *O. glacialis*, Berzin and Vladimirov 1983) prey mostly on Antarctic toothfish.

In summary, none of the toothed and beaked whales seem to be a major krill predator. However, it needs to be appreciated that these species may be impacting krill indirectly (through some of their prey, such as squid and minke whales).

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3.4.2 Sea birds

Penguins

Woehler (1995) summarizes diet composition for seven species of penguins that breed south of the Antarctic Convergence using abundance estimates available up to 1989. For emperor penguins *Aptenodytes forsteri*, crustaceans[2] comprise approximately 3-10% of the diet, for king penguins *Aptenodytes patagonicus* 0-0.1%, adélie penguins 79-99%, chinstrap penguins *Pygoscelis antarctica* 96-98%, gentoo penguins 7-84% and macaroni penguins 59 -97%. From these figures,

[2] Here, crustaceans include euphausiids, amphipods and copepods.

it is evident that crustaceans are the main contributor to the diet of adélie, chinstrap and macaroni penguins. Croxall (1984) reports that most crustaceans consumed by penguins are krill, except near the Antarctic continent where this is replaced by *E. crystallorophais*, and in the New Zealand area where other euphausiids such as *T. macrura* and *Nyctiphanes australis* may also be locally important.

From consideration of the total annual energetic demand of the species, Woehler (1995) estimated that a total of 13.9 million tons of crustaceans is consumed annually by the breeding populations of seven penguin species (emperor, king, adélie, chinstrap, gentoo, macaroni and rockhopper *Eudyptes chrysocome*), mainly in the vicinities of South Georgia and of the South Sandwich Islands. Woehler (1995) comments that this estimate of 13.9 million tons should be considered as a minimum estimate, since no corrections have been made to the abundance estimate to account for non-breeding, failed and pre-breeding birds.

Other sea birds

The majority of the Southern Ocean's flying seabirds consist of albatrosses and petrels (Procellariiformes), and skuas, gulls and terns (Charadriiformes). Very few fully quantitative diet studies of Antarctic flying seabirds are available. Based on such studies as are available, Croxall (1984) reports the principal natural dietary preferences for the Antarctic flying seabirds. Table 3.5 lists the Antarctic flying seabirds for which the primary dietary component is reported to be crustaceans. Croxall (1984) remarks that in the studies conducted to that date, most of the crustaceans consumed are krill, but with the identical exceptions near the Antarctic continent and New Zealand that are listed above for penguins. He also notes that other groups of crustacean may be important, e.g. copepods in the diet of broad-billed and dove prion, diving petrels and possibly storm petrels. Amphipods, and particularly *Parathemisto gaudichauadii*, may be important to the narrow-billed prion *Pachyptila belcheri*, and there are significant differences in the proportions taken by blue petrels and dove prions of amphipod species that are common to the diet of both (Prince 1980).

Croxall (1984) estimates that the biomass of Antarctic sea birds (other than the penguins) in the Antarctic is about 3 million tons. Although this estimate is very crude, it is much smaller (only about 2%) than that for the Antarctic penguins. Thus, the amount of krill consumed by the Antarctic flying seabirds is likely to be much smaller than that by the penguins.

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3.4.3 Cephalopods (squid)

Filippova (2002) analysed the stomach contents of 325 specimens of squid collected during Antarctic expeditions from 1967 to 1987, and suggests that there are at least two trophic groups of squid in the Antarctic. The first group includes species feeding to some extent on krill, and the second those which have no direct connection to krill. The first includes *Brachioteuthis* sp., which live in the surface region of the Antarctic pelagic zone and feed exclusively on crustaceans (euphausiids, hyperids and mysids). Crustaceans are estimated to comprise up to 98% of their diet, with squid and fish making up the remainder (up to 10%). Amongst the crustaceans, krill predominate, and very often the stomach contents consist only of euphausiids. Based on these findings, Filippova (2002) suggests that the role of Antarctic squid as consumers of krill seems to be much more important than has previously been believed. This is consistent with the results of Nemoto *et al.* (1988), who show that krill was the predominant prey item for 300 specimens of squid collected in the Antarctic from trawling operations during the summers of 1980 to 1982.

Everson (1977) notes that no direct information is available on either the standing stock or production of squid; however, indirect estimates, based on consumption by predators, suggest that the annual production of squid is in excess of 17 million tons. As squid tend to be relatively short-lived and have fast growth rates (Nesis 1983), Everson (1984) suggests that squid have a high efficiency in converting their food to body-mass of squid, perhaps of the order of 30-50%, suggesting food consumption of the order of 34-56 million tons.

3.4.4 Fish

Kock (1985, 1987) estimates that the annual krill consumption by the seven fish species which are the most abundant fish predators of krill around South Georgia was about 5 million tons prior to their exploitation (in the mid 1960s). This is based on the assumptions of a gastric evacuation time of 48 hours for krill, feeding being negligible during a two-month spawning season, and a reduction in the feeding rate on krill during winter. Because of the various assumptions that have to made, Kock (1985, 1987) notes that the 5 million tons figure is a coarse estimate and indicates only the order of magnitude.

Myctophid biomass in the Antarctic (south of 40°S) has been estimated to be 70-200 million tons based on survey data and model calculations (Lubimova *et al.* 1987). From these data, Kock (1992) estimated that if a substantial proportion of this biomass is present south of the Antarctic

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Convergence, then even conservative assumptions that krill comprises 5% of the food by mass and that annual food intake is 5-10 times body mass, would result in an estimated annual krill consumption of 20-35 million tons. This would mean that the total consumption of krill by all fish south of the Antarctic Convergence would be estimated, as a rough figure, to be about 40-50 million tons (Hureau 1994).

Subsequent to these studies, Pakhomov *et al.* (1996) investigated the feeding ecology of myctophids using data collected during five South African scientific cruises to the Southern Ocean from 1985 to 1995. They found that krill was usually poorly represented in the stomachs of all but one myctophid species (lantern fish: *Electrona carlsbergi*), and suggested that their study does not support the hypothesis that krill plays a major role in the feeding ecology and budget of myctophids. They further reported that krill is an important food source for lantern fish only during the summer season. Copepods were the most important component in the diet of almost all myctophid species examined (Pakhomov *et al.* 1996).

3.5 Summary

Table 3.6 summarizes broad estimates of recent annual consumption of krill by its predators in the Antarctic. The baleen whales could be consuming up to 120 million tons of krill and seals up to 70 million tons each year in this region. Of the whales, minke currently make the greatest impact on krill due to their large number at present compared to the other depleted larger baleen whale populations. However, it is noteworthy that the consumption of krill by these larger baleen whales has probably been increasing in recent years, though decreasing for minke whales. Crabeater seals are the seal species with the greatest current impact on krill.

The wide ranges in the consumption estimates shown in Table 3.6 arise mainly from the wide range of uncertainties associated with the abundance estimates for these predator species. Nonetheless, the estimates for baleen whales and seals are much more accurate than those for other species. High priority therefore needs to be given to improving estimates of the amount of krill consumed by these other species (particularly birds, cephalopods and fish) because one cannot at present rule out the possibility that these species might be making comparable impacts on krill to those by baleen whales and seals.

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Table 3.1 Estimates of per capita annual consumption of krill by the major krill-feeding baleen whales in the Antarctic. See text for details.

Species	Mean body weight (t) $\overline{w}_j$	Weight/day (%) c_j	Days feeding in the Antarctic d_j	Krill in the diet (%) p_j	Per capita consumption of krill (t) λ_j
Blue whale	103	0.9 - 3.5	125	100	115.9 - 450.6
Fin whale	46	1.0 - 4.0	120	50	27.6 - 110.4
Humpback whale	27	1.4 - 4.0	100	100	37.8 - 108.0
Minke whale	7	0.6 - 5.1	90	100	3.8 - 32.1

Table 3.2 Minimum and maximum estimates of recent annual consumption of krill by the four baleen whale species considered in this thesis. See text for details.

Species	Abundance (millions) (see Table 5.5)				Consumption (million tons)			
	1985-1990		1991-1997		1985-1990		1991-1997	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Blue whale	0.001	0.001	0.002	0.003	0.1	0.5	0.3	1.4
Fin whale	0.012	0.018	0.027	0.056	0.3	2.0	0.7	6.2
Humpback whale	0.026	0.096	0.025	0.095	1.0	10.4	0.9	10.3
Minke whale	1.200	3.300	0.330	1.100	4.6	106.0	1.3	35.3
Total	1.239	3.415	0.384	1.254	6.0	118.8	3.2	53.2

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Table 3.3 Estimates of per capita annual consumption of krill by the major krill-feeding seals in the Antarctic. See text for details.

Species	Mean body weight (t) $\overline{w}_j$	Weight/day (%) c_j	Days feeding in the Antarctic d_j	Krill in the diet (%) p_j	Per capita consumption of krill (t) λ_j
Antarctic fur seals	0.05 - 0.2	7	323	60	0.68 - 2.71
Crabeater seals	0.15 - 0.25	7	335	94	3.31 - 5.51

Table 3.4 Minimum and maximum estimates of abundances and annual consumption of krill by Antarctic fur and crabeater seals around 1990. See text for details.

Species	Abundance around 1990		Consumption around 1990	
	Min. (millions)	Max. (millions)	Min. (million tons)	Max. (million tons)
Antarctic fur seals	1.0	2.5	0.7	6.8
Crabeater seals	7.0	12.0	23.2	66.1
Total	8.0	14.5	23.9	72.9

Table 3.5 Common and scientific names of the Antarctic flying sea birds for which the major natural dietary item is crustaceans (modified from Croxall 1984).

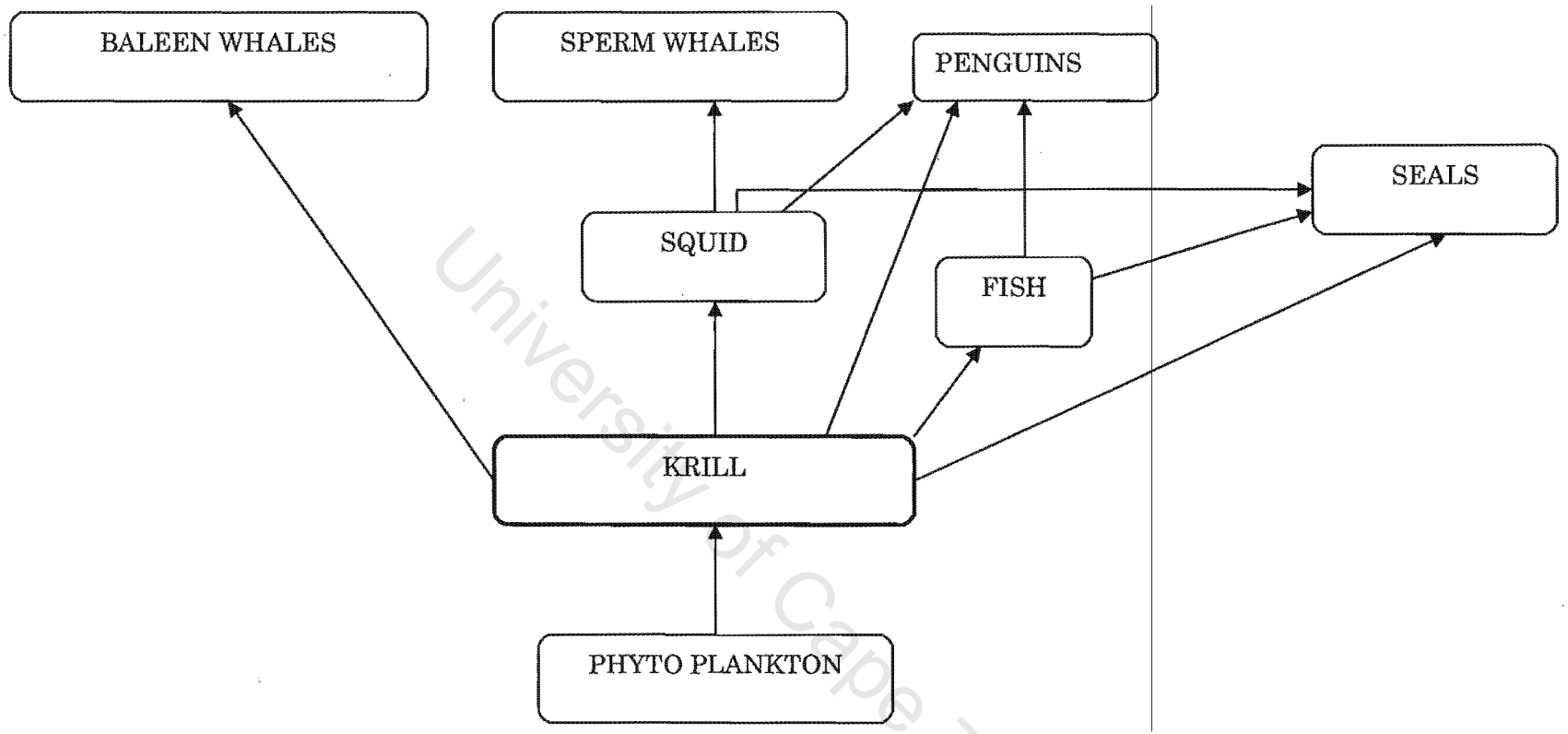
Common name	Scientific name
Sooty albatross	*Phoebetria fusca*
Light-mantled sooty albatross	*Phoebetria palpebrata*
Black-browed albatross	*Diomedea melanophris*
Cape petrel	*Daption capense*
Snow petrel	*Pagodroma nivea*
Antarctic petrel	*Thalassoica antarctica*
Southern Fulmar	*Fulmarus glacialoides*
Blue petrel	*Halobaena caerulea*
Prion	*Pachyptila spp.*
Georgian diving petrel	*Pelecanoides Georgicus*
Common diving petrel	*Pelecanoides urinatrix*
Storm petrel	*Hydrobates pelagicus*

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Table 3.6 Estimates of annual consumption of krill by its predators in the Antarctic. * denotes that this estimate also includes other euphausiids; ? indicates that the estimates is coarse, being based on sweeping assumptions.

Species	Krill consumption (million tons)		References
	1985-1990	1991-1997	
Baleen whales (blue, fin, humpback, minke)	6-120	3-53	This thesis
Seals (Antarctic fur, crabeaater)	24-73		This thesis
Birds (dominated by penguins)	min 14*		Woehler (1995)
Cephalopods	min 34-56 (?)		Everson (1984)
Fish	40-50 (?)		Hureau (1994)

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Figure 3.1 A simplified representation of the Antarctic marine food chain indicating krill's central position (after Miller 2002).

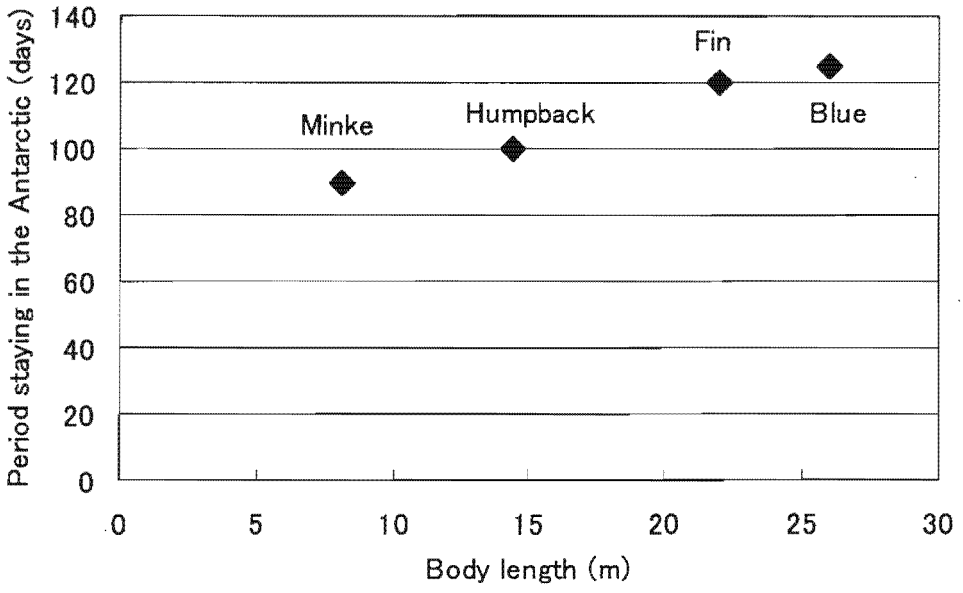


Figure 3.2 The approximate annual periods spent feeding in the Antarctic by the Southern Hemisphere baleen whales considered in this thesis (after Figure 2-38 of Kasamatsu 2000).

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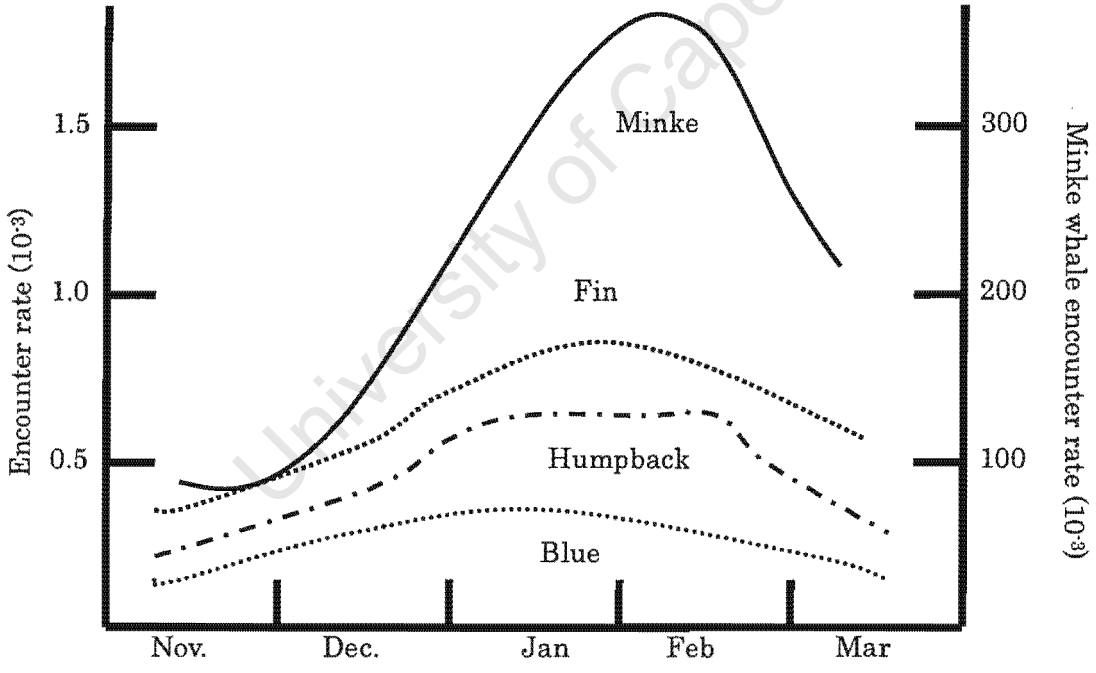


Figure 3.3 Seasonal occurrences of Southern Hemisphere baleen whales in the Antarctic (after Figure 2-37 of Kasamatsu 2000).

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CHAPTER 4

BASIC BIOLOGY AND ECOLOGY OF THE MAIN KRILL-FEEDING PREDATORS

4.1 Baleen whales

4.1.1 Migration

Humpback whales

Humpback whales are (in the main) found in Antarctic waters in summer and in tropical regions in winter. Movements up and down the African and Australian coasts have been followed by direct observation (e.g. Matthews 1937) and thus the migration of this species along these coasts is fairly well understood compared to the migratory behaviour of other baleen whale species, such as blue or fin whales. Occasional sightings and strandings have been reported for the Brazilian coast; however, distribution and density are poorly known for a great portion of the humpback whales around this coast (Zerbini *et al.* 2004). Based on the statistics of catches at different times and places during the early 20th Century, Mackintosh (1942) concluded that there is no doubt that the humpback whales undertake regular migrations to the Antarctic in summer where they find plenty of food, and to the coastal waters of the southern continents in winter where breeding takes place but where food seems relatively scarce. He also commented that probably the vast majority of the humpback whales take part in this migration; however, evidently some remain in high latitudes over the winter, because humpbacks have been taken at South Georgia, where limited winter whaling took place up to 1917-18. Furthermore, it is possible that some, especially the immature whales, remain in the warmer latitudes over the summer.

There is a very clear temporal segregation between different classes or categories of humpback whales throughout the seasonal cycle. The southward spring migration is led by recently pregnant females and immature males, followed by resting females and mature males, and finally females in early lactation. On the Antarctic feeding grounds the different groups apparently become fully mixed, but on the northward migration they again segregate. Females at the end of lactation

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accompanied by weaning yearling calves depart northward first, followed in succession by immature animals, mature males with resting females, and finally females in late pregnancy. Pregnant females therefore spend the greatest amount of time on the feeding grounds south of 60°S (about 6.5 months, late November-May), and lactating females accompanied by their calves the least (about 4.5 months, late December-April) (Brown and Lockyer 1984).

Blue whales and fin whales

The migrations and distributions of blue and fin whales are less clearly understood than those of humpback whales. Mackintosh (1942) notes that only one instance of migration between the Antarctic and warmer waters had been demonstrated by whale marking for blue whales, but that there is abundant circumstantial evidence that such migrations take place. Southward migration by fin whales from subtropical South American waters to the Antarctic feeding grounds, and northward migration from these grounds to South African waters, has been demonstrated by whale marking (Brown 1962).

Little is known of the destination of these whales when they move northwards in winter, but it is supposed that most of them become dispersed in temperate waters. In the Antarctic, blue and fin whales are more evenly distributed than humpbacks, but the positions of capture and marking show that they have at least a same tendency (more definite in blue than fin whales) to concentrate in the same areas as humpbacks. Whale marking has shown, furthermore, that they generally return to the same part of the Antarctic after their northward migration, but unlike the humpbacks these species sometimes move from one area to another (Mackintosh 1942). Brown (1962) reports that one blue whale marked after World War II moved through at least 170° of longitude from Area III into Area VI in a little over two years, and this information suggests that there is no limit to the range of dispersal in this species. However, Brown (1962) also reports that most of the mark returns fall within the 90° range, so that it may be that very few animals disperse over these extreme distances. Harmer (1931) analyzed the catches around South Georgia during June-August 1914-1919 and found that some blue and fin whales are present in the Antarctic even during the winter.

Some recent studies on Southern Ocean blue whale songs by McDonald *et al.* (2005) suggest a circumpolar distribution around the Antarctic continent. They also report that blue whale songs have also been recorded in tropical latitudes, off the coast of Peru during July and off the southwest coast of Australia in June, suggesting some movement to lower latitudes during the southern winter

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(McDonald *et al.* 2005). Galletti *et al.* (2005) report similarly that during marine, aerial and land-based platform surveys conducted over 31 January to 15 March 2005, blue whales were sighted as far north as 41° 45'S. These studies suggest the movement of blue whales to lower latitudes.

A year-round blue whale presence is documented from fixed hydrophones deployed near the western part of the Antarctic Peninsula (Širović *et al.* 2004). Mckay *et al.* (2005) detail similar features for the eastern Antarctic. Based on blue whale calls detected from data recorded on an Acoustic Recording Package (ARP) deployed offshore of Mawson Station in this region during February 2003 to January 2004, Mckay *et al.* (2005) report that peak calling was detected in autumn (April to June), with a secondary peak in November. The lowest calling rates occurred in summer (December to March) and winter (July to September).

As part of the IWC's SOWER (Southern Ocean Whale and Ecosystem Research) blue whale research programme, two sighting vessels surveyed the Madagascar Plateau between 25° and 35°S, 40°and 45°E, in December 1996. The two vessels combined made a total of 95 sightings of 110 animals assigned in the field to pygmy blue whales, 14 sightings of 21 'unidentified' blue whales and 12 sightings of 13 'like' blue whales (Best *et al.* 2003). There were no sightings classified as true blue whales. These results suggest the dominance of pygmy blue whales in this region compared to the true blue whales.

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Minke whales

As for the larger baleen whales, seasonal migrations take minke whales from tropical latitudes in winter to the high latitudes of the Antarctic in summer. Kasamatsu *et al.* (1995) investigated the southbound migration of minke whales based on sighting data (encounter rates) derived from the Japanese sighting surveys in waters from 0° to 30°S during October to December from 1976 to 1987. By analyzing the encounter rate by latitude and by month, they found that minke whales move southward from the breeding areas in October-November, and most of them have migrated into Antarctic waters by January.

Based on the catch of minke whales from the whaling station at Durban (29°53'S 31°03'E) on South Africa's east coast and from the aircraft sightings around the area from 1968 to 1975, Best (1982) showed that in general, minke whales were rarely seen off Durban in February and March but increased in abundance in April and May, and that their abundance then remained at about the

same level until the last month of the local whaling season (September), when it increased further to a maximum value for the eight months of operation. Holt *et al.* (1982), from consideration of the catch and sightings of minke whales in Brazilian waters (around 7°S) from 1979 to 1980, found increasing abundance from June to October and a rapid decline thereafter, with a sharp peak in the abundance of minke whales off Brazil in the months September and October.

In the light of these studies, Kasamatsu *et al.* (1995) concluded that minke whales undertake regular annual migrations between tropical and polar regions, and suggested that younger whales leave the breeding areas earlier than mature ones and begin returning to the breeding grounds after February. Most other whales leave the feeding grounds by March, and the northbound migration continues into the early austral summer. It appears that breeding populations of minke whales are relatively dispersed in open waters, and tend to move almost directly south from these breeding areas to feeding areas, subsequently dispersing after arriving at those areas.

4.1.2 Stock structure

Humpback whales

Based on the positions of previous Soviet Antarctic catches, mark-recovery information from the International Marking Scheme, and the distribution of sightings on IWC/IDCR-SOWER cruises, seven concentration areas (reflecting feeding grounds) are recognized in the Antarctic, with seven closely corresponding breeding grounds (A-G) in lower latitudes (IWC 1998b).

Further studies on the stock structure of this species have suggested a possible substructure in breeding stocks in grounds C, E and F (IWC 2004a) (see Figure 4.1). Best *et al.* (1998) investigated the distribution and seasonality of humpback whales in the southwest Indian Ocean using a number of data sources. These included sighting and acoustic data collected on shore and ship-based surveys, together with aerial sighting data, historical catch data, and incidental sightings data from a research ship and transiting merchant vessels in the southwest Indian Ocean. Based on these data, the possibility of further division within breeding grounds C was suggested as C1: coastal Mozambique; C2: coastal central Mozambique Channel Islands; and C3: coastal Madagascar (Best *et al.* 1998, IWC 2004a). In breeding ground E there is the possibility of a further division based on comparison of photographic catalogues: E1 for animals breeding close to the east Australian coast, E2 for animals breeding close to New Caledonia, and E3 for animals breeding close to Tonga (Garrigue *et al.* 2002, IWC 2004a). Based on a similar study, there is the

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possibility that there are two breeding stocks within F centered on French Polynesia and the Cook Islands (Garrigue *et al.* 2002, IWC 2004a) (Figure 4.1).

Blue whales and Fin whales

The stock structure of blue whales and fin whales is not as well known as for humpback whales. Based mainly on evidence from the concentrations of whales reflected in commercial catches and sightings in the Antarctic, Mackintosh (1942) reports that in the Antarctic summer, blue whales and possibly also fin whales tend to segregate in the same regions as the humpbacks. However, while for humpbacks the segregation by area is almost complete, for blue whales this tendency is apparent only insofar as rather larger numbers are to be found in these areas of concentration than elsewhere. Mackintosh (1942) concluded that blue and fin whales are less clearly segregated in different feeding areas than humpbacks, and that they move more readily from one area to another. He proposed that the distribution of blue whales could be divided into six areas each extending through some 60-70 degrees of longitude (Figure 2.2). These feeding concentrations were initially considered as stocks, at least for management purposes, and were believed to correspond to biological stocks.

Fin whales are considered to have similar stock divisions to those of blue whales, with the addition of a subdivision of the fin whales in the Atlantic (Area II) and western Indian Ocean sectors (Area III) into eastern and western groupings, to give a total of eight stocks (Gambell 1985).

Minke whales

Based on sighting data (encounter rates) derived from the Japanese sighting surveys in waters from 0° to 30°S in the Indian and Pacific Oceans during October to December of 1976 to 1987, Kasamatsu *et al.* (1995) suggest that there are at least four separate breeding areas, one in the eastern South Pacific, one in the western South Pacific (main area 150°-170°W) with a possible boundary at about 120°-130°W, and the other two in the eastern Indian Ocean (main area 100°-110°E) and the western Indian Ocean with a possible boundary at about 60°-70°E.

More recent studies by Pastene *et al.* (2005) have investigated the stock identity of minke whales by means of different analytical approaches using samples obtained during the JARPA surveys from 1987 to 2003 in Areas IIIE, IV, V and VIW. The analytical approaches used were genetics (mtDNA RFLP and microsatellite) and non-genetic (mean body length of physically matured

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whales, morphometrics and distribution of the parasite *Anisakis simplex*). The results of the different approaches were consistent and showed substantial longitudinal heterogeneity. The general pattern of differentiation was well correlated with geography, with the most distant strata being differentiated from each other, e.g. IIIE + IVW was different from VIW+VE, and this pattern was evident from the results of all approaches used. Based on this analysis, Pastene *et al.* (2005) propose a stock boundary at about longitude 165°E. This result clearly suggests that there is more than one stock in the region of the Antarctic investigated by JARPA; however, whether there are more than two stocks is questionable.

4.1.3 Distribution and habitat overlap between the krill-feeding whales in the Antarctic

Kasamatsu *et al.* (1996) remark that possible latitudinal habitat segregation (or separation) in the Antarctic feeding grounds between whale species is suggested by their different peaks of occurrence. Figure 4.2 shows the latitudinal occurrence of the most abundant Antarctic baleen whale species, and Figure 3.3 shows the seasonal occurrences of these whales deduced by these authors on the basis of analyses of the encounter rate patterns evident from the sightings on Japanese scouting vessels (JSV)[1] and IWC/IDCR surveys from 1976 to 1988. Based on the encounter rates, Kasamatsu *et al.* (1996) suggest that blue whales and minke whales occur in the southernmost waters (south of 66°S), humpback whales over a wide range of latitudes (peaking in 62°S-66°S) and fin whales in the northern part of the Antarctic waters (peaking in 54°S-58°S).

In a further study, Kasamatsu *et al.* (2000a) examined the interspecific relationships among whale communities, together with the effects of environmental variables (sea surface temperature, distance from the ice-edge, and sea floor-slope type) in the Antarctic using data derived from the IWC/IDCR-SOWER surveys conducted over 1978-1996. They found a significant negative correlation between minke whale density and the distance from the ice-edge. Blue whales also tend to concentrate in waters close to the ice-edge, whereas fin whales tend to be abundant in waters much further to the north. Furthermore the encounter rate for minke whale shows density gradients, with more frequent sightings over the continental shelf than other areas (continental shelf > shelf break > shelf slope > plane). The humpback whale distribution does not show any gradient,

[1] There were two different systems for the Japanese whale sighting operations: (1) scouting vessels attached to the whaling fleets, (2) research vessels chartered by the Fisheries Agency surveying according to pre-specified designs independent of the whaling fleets. The former system began in 1965 and the latter in 1976. Abundance indices calculated from JSV data are considered less reliable because of their pattern of search effort was linked to whaling operations. These research vessels both extended as far north as 30°S.

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and fin whales tend to distribute in the deep-sea area. Kasamatsu *et al.* (2000a) found a substantial overlap in the distribution of blue and minke whales, and no apparent habitat segregation between the two species. In contrast, the humpback whales distribution peaks to the north of the ice-edge, and fin whales still further north, so that these two species do not overlap to nearly the same extent as blue and minke whales. Murase *et al.* (2002) found that the distributions of humpback whales are correlated with high euphausiid density zones, irrespective of the bottom topographic features.

The minke whale distribution around the ice-edge shows an interesting segregation between the sexes. Kasamatsu and Ohsumi (1981) demonstrated that there is a considerable temporal and spatial segregation of the sexes for these high latitude feeding grounds from an analysis of Japanese whaling data from IWC Management Area IV from 1971-1979. Females predominate nearest to the ice-edge, while males are more abundant away from the edge of the pack-ice even though they arrive earlier and stay longer on the feeding grounds than the females. Furthermore, Fujise and Kishino (1997) examined the segregation pattern of minke whales in Antarctic Areas IV and V based on data collected during the JARPA surveys from 1987 to 1995 using a logistic regression model. They found that the proportion of males increases away from the ice-edge in both Areas, especially in Area V, that mature females dominate in Area V, and that the proportion of females that are mature decreases away from the ice-edge. However, the point to make clear here is that this sexual segregation applies only close to the ice-edge within the overall distribution which was examined as for north as 60°S.

Kasamatsu *et al.* (2000b) investigated the relationship between the distribution of minke whales in the Bellingshausen and Amundsen Seas (longitude between 60°W and 120°W), and environmental and physiographic variables (sea-surface temperature, sea-ice extension, and sea-floor-type), to determine whether these factors affect the distribution and density of minke whales, by using sightings data obtained from the 1982 and 1989 IWC/IDCR surveys. They found that the distribution of minke whales differed substantially between the two surveys, with the density and abundance being greater and closer to the ice-edge in 1982 than in 1989. They concluded that the warmer sea-surface temperatures, fewer cold-water intrusions, and the smaller extent of sea-ice in 1989 may explain the difference in distribution from that in 1982, possibly owing to a shift in available prey. This study is based on only two cruises, and does not give information about other large baleen whale species; further understanding of baleen whale distributions and their relation to various environmental factors will become possible as more data become available.

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4.1.4 Brief initial discussion on spatial overlap and the potential for species competition in the Antarctic

Due to small sample sizes, the studies by Kasamatsu *et al.* (1996, 2000a) pooled the sighting data for the 1978 to 1996 surveys and drew conclusions based on the general trend for these years combined. Even after pooling over years, the encounter rates for blue whales and to a lesser extent fin whales are very small and are associated with large standard errors (especially for Kasamatsu *et al.* 1996). More precise temporal and spatial distributions for these two species will be obtainable only once the population abundances increase further so that the number of sightings increases. Moreover, the general trend suggested by Kasamatsu *et al.* (1996, 2000a) may differ appreciably for some years due to differences in distribution of the prey species (mainly krill) as a result of variable environmental factors.

Nevertheless, although the sample size for the blue whale encounter rate is small for these studies, it seems likely that the blue and minke whales share the same feeding grounds in the Antarctic near the ice-edge, so that some competition for prey (krill) between these species might be occurring. Furthermore, humpback whales and, to a lesser extent, fin whales prey on krill so that some competition for prey among these species might be occurring as well.

Most ecologists recognize this form of competition as *exploitative* competition (Keddy 1989). Exploitative competition involves reduction (by consumption or utilization) of a limited resource, but with no direct interactions between the competing species (Clapham and Brownell 1996). Confirming this type of competition directly from observations of whales in the Antarctic is almost impossible due to their wide circumpolar distribution, and because it is often difficult to link the causes of species declines or increases to this effect. Nevertheless, the possibility of exploitative competition among the baleen whale species in the Antarctic cannot be ignored, and there are a number of indirect observations that suggest such competition is playing a role in the Antarctic.

Interference competition is another form of competition well recognized in ecology. Interference competition occurs when one species somehow disrupts the activities of another (e.g. by aggressively defending access to food) (Clapham and Brownell 1996). Clapham and Brownell (1996) argue that there is no direct observation of this kind of competition between the baleen whales in the Antarctic, and comment that it is generally understood that baleen whales are not territorial animals. However, Kawamura's (1994) suggestion that minke whales break up the larger euphausiid patches required by blue whales merits further consideration as a possible

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manifestation of interference competition (Clapham and Brownell 1996).

The potential for exploitative and interference competition in the Antarctic is discussed further in the discussion section of Chapter 13.

4.1.5 Reproductive biology

Breeding seasons

Lockyer (1984) points out that the reproductive cycle has a minimum duration governed by gestation time, which in all baleen whales is about one year. Brown and Lockyer (1984) report that the usual two-year reproductive cycle of the baleen whales is closely tied to the annual migratory and feeding cycle. Births, which occur in warm waters within a year of conception, are not normally followed immediately by another pregnancy, even if there has been a post-partum ovulation. With the exception of the minke whale, one ovulation occurs approximately every 1.5 years. Few females become pregnant during the southern summer, a condition which would result from a post-lactation ovulation and put the reproductive cycle out of phase.

Normally one calf is produced (Brown and Lockyer 1984). Lockyer (1984) notes that the timing of the migratory and feeding cycle means that optimally the cow can bear one calf annually, whilst simultaneously lactating and pregnant. This is usual in minke whales and has been observed occasionally in humpback whales (Glockner-Ferrari and Ferrari 1984), but normally a calf is produced only every two or three years for blue, fin and humpback whales.

The ovulation rate has been determined first by histological examination of the seasonal activity in the ovaries, considered together with the relative sizes and numbers of Graafian follicles and corpora albicantia and lutea. Secondly, direct determination has been achieved through the correlation of numbers of corpora with the actual age of the whale as determined from ear plugs (Laws 1961, Gambell 1968). Table 4.1 summarizes the peak breeding seasons of southern hemisphere baleen whales.

Age at sexual maturity and its trend for baleen whales

It is widely accepted that the position where growth layer spacing changes (the transition phase) in the earplugs of whales corresponds to the age at physical and sexual maturity of the animal

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(Lockyer 1972, Masaki 1979, Kato 1983). Lockyer (1972) explains that the ear plug layer formation during the juvenile growth phase is very irregular and the layers are unevenly spaced; however, after maturity, the new layers become more compact and evenly spaced. A summary of information on the age at sexual maturity and its trend for the various baleen whales considered in this thesis is provided below.

Fin whales

Lockyer (1972) analysed the age at sexual maturity for fin whales taken within the 0°W-60°W longitudinal sector (IWC Management Area II) between 1960 and 1965 using various methods. From counts of the age at transition for ear plugs of 175 males and 232 females, she suggests a decline in mean age at maturity from 10 years for the 1910 year class to 6 years for the 1958 year class for both sexes, where the first hint of a decline occurred during the 1930s.

Sexual maturity in females is determined from the first ovulation and immediately prior to this when ripening follicles are present, and in males from when the individual testis weight is at least 2.5 kg (Ohsumi 1964, Ichihara 1964). By plotting the proportion of sexually mature whales by age, Lockyer (1972) suggests that 50% of the whales[2] are mature between 6 and 7 years. Furthermore, by regressing the mean age (as estimated by ear plug layer counts) to the ovarian corpora number for mature female fin whales, she estimates that the mean ovulation rate for all age groups of mature females approximates to one corpus luteum per 1.4 years; from this an estimate of the age at sexual maturity of approximately 7 years follows.

Lockyer (1972) notes that the mechanisms leading to the decline in mean age at maturity are likely to be complex, but the simplest possible explanation is that the lower population size has diminished competition for space and food, resulting in a greater availability of food for the remaining fin whales.

Blue whales

Lockyer (1981b) analysed the age at sexual maturity of 36 blue whales (20 females and 16 males, the years and locations of these samples are not clearly specified) by counting the layers of their ear plugs and suggests sexual maturity occur at about 5 years. Since blue whales and fin whales have

[2] The corresponding year classes are not specified in Lockyer (1972); however, speculating from the results that they obtained, probably these are those from around the 1940-1950 year classes.

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similar body-length and breeding characteristics, speculation has arisen that the age at maturity of this species may also have declined in the mid-20th Century, as suggested above for fin whales.

Humpback whales

Chittleborough (1959, 1965) has examined the age at sexual maturity of humpback whales. His 1959 study was based on 391 females and 238 males, but the subsequent 1965 publication reflected a much larger sample size. This latter study reports that based on 1603 females whose ovaries and ear plugs (in place of the baleen plates used for ageing in the earlier study) were examined at Australian stations, the ages at sexual maturity range from 2 years to an extreme of 12 years, and the majority of individuals (70%) attain sexual maturity at 4 or 5 years of age. For 1967 samples for males, he found on the basis of testes weights that sexual maturity can be said to be reached at 3-6 years of age, 11.8% being mature at 3 years, 33.0% at 4 years, 85.4 % at 5 years, and 95.0% at 6 years.

Minke whales

Kato (1983) examined the age at sexual maturity of minke whales using three approaches: the transition phase in ear plugs, the relationship between age and percentage of animals that are sexually mature, and the relationship between age and the number of ovulations based on samples collected between 1976 and 1980 from Japanese whaling expeditions in Area IV. Data from 793 males and 936 females were used. The examination of the transition phase in the ear plugs (taking into account the bias due to truncation problems[3]) showed a decline in the age at sexual maturity for this species from 14-15 years (1945 year class) to 7 years (1965 year class) for both sexes, and thereafter a constant trend at around 6 years for the 1965 to 1972 year classes. Furthermore, Kato (1983) reports that the examination of the age at first ovulation also suggests a decline in the age at sexual maturity for this species from the 1952-1954 to the 1967-1969 year classes.

Taking account of two effects that potentially introduce bias (truncation error and fringe effect[4]) in the estimation of the age at sexual maturity of this species, and also the possibility that readers with more experience in reading the transition phase may recognize this phase in a greater proportion of

[3] Truncation error occurs from the under-representation of older animals in the most recent cohorts sampled.

[4] Fringe effect relates to the low proportion of animals recorded as having ages only slightly greater than the age corresponding to their transition phase (Cooke and de la Mare 1984). A likely reason for this is that detection of the transition phase requires contrast – a number of narrowly spaced rings after the transition phase, as well as the broadly spaced rings for the early years of life. Thus, unless a few years have elapsed between transition and capture, the presence of the transition phase is unlikely to be recognized.

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the earplugs, Thomson *et al.* (1999) estimated that the average age at transition declined from roughly 11 for the cohorts of the 1950s to roughly 7 for those of the 1970s. They suggest that minke whale transition-phase readings are related to a real signal in the data and are not simply an artifact (as had been argued by Cooke and de la Mare 1984), and further that there has been a real decline in the age to which this signal corresponds (Thomson *et al.* 1999).

Recently, Zenitani and Kato (2005) examined longer term changes in the age at sexual maturity of minke whales by identifying the transition phase layer in earplugs collected both during 1971 to 1986 (the commercial whaling period) and 1987 to 2003 (the JARPA period) in Area IV. Their results indicate that the tendency of the age at sexual maturity to decline gradually slowed around the 1960s, and almost stopped from about 1965 to 1980.

Possible causes of this decline followed by its termination are discussed in Chapter 11.

4.2 Seals

4.2.1 Distribution and migration

Although seals feed exclusively at sea, their pups are born on land, or on ice, and remain at their birth site until weaned. In most parts of the world, seals must return to land, at least during the breeding season, so that their distribution is discontinuous and limited to areas where suitable islands or reefs occur. In polar regions, however, some species breed on the drifting pack-ice and this has allowed them to colonize a much larger geographic area and enabled their breeding system to closely match the spatio-temporal distribution of their prey (Knox 1994). Chapter 3 identified that among the Antarctic seals, Antarctic fur seals and crabeater seals feed mainly on krill, so that the focus here will be on these two species.

Antarctic fur seals

The distribution of breeding sites of Antarctic fur seals is shown in Figure 4.3. With the exception of small colonies on Marion, Crozet, Kerguelen, McDonald, Heard and Macquarie Island, the breeding range of the Antarctic fur seal is limited to islands south of the Antarctic Convergence and north of about 65°S (Bonner 1981). The main breeding populations are on Bird Island, Willis Islands, and the neighbouring coast of South Georgia. Individuals tagged on Bird Island have later been observed breeding on South Georgia and as summer visitors to the South Orkney Islands and

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Elephant Island (Hunt 1973, Payne 1979).

The distribution of non-breeders is less well-known. Almost nothing is known about the pelagic distribution of the fur seal, with the adults absent from the breeding islands between May and October. It is not known whether there is a directional migration or a widespread dispersal from South Georgia (Laws 1984)[5].

Crabeater seals

Crabeater seals seem to have a circumpolar breeding distribution in the pack-ice (inferred from distributions in the summer, non-breeding season) (Laws 1984). The six residual pack-ice regions presumed to constitute population centers for pelagic Antarctic seals in the austral summer are shown in Figure 4.4 (from Figure 7 of Gilbert and Erickson 1977). They reproduce in spring on the pack-ice wherever there is access for hauling out, which in practice restricts breeding to a zone near the periphery of the pack-ice. For logistical reasons, direct observations in the pack-ice at the time of the breeding season are difficult to make, so that these are very few and confined to the Antarctic Peninsula (Siniff *et al.* 1979, Bengtson and Siniff 1981) and to the vicinity of the South Orkney Islands (Øritsland 1970). Studies of protein and enzyme polymorphisms have given no indication of genetically separate sub-populations, so that homogeneity has been inferred (Seal *et al.* 1971a, b). Siniff *et al.* (1980) report that two adult male crabeater seals were recovered two years later in the same area where they were tagged, suggesting some site-fidelity for these animals.

4.2.2 Reproductive biology

Breeding behaviour

Payne (1978) reports that pupping of Antarctic fur seals occurs about two days after haul out when harems form averaging ten cows in size. Pupping is very synchronized, with 50% of the pups being born by 4 December and 80% within a 17 day period. Mating occur about eight days post-partum, and at the peak period the male territories average about $22m^2$ in area. Territories are held from late October to late December for an average period of 34 days (range 1- 53 days), during which the bulls do not feed (McCann 1980). Figure 4.5 shows a schematic representation of colony attendance by Antarctic fur seals during the year.

[5] Afternote: Boyd (pers. commn) advises that recent observations of fur seal movements suggest that they spend important amounts of time outside the area considered in this study.

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Owing to their inaccessibility in the pack-ice during the breeding season, not much is known about the breeding behaviour of crabeater seals. The pupping season for these seals is from late September until early November, with a peak in early to mid-October (Siniff *et al.* 1979). Table 4.2 summarizes the approximate duration of stages in the annual cycle of the female seals.

Age at sexual maturity and its trend for seals

The age at sexual maturity is defined here as the age of first ovulation in the female and production of sperm by the male (Laws 1956). For the female fur seals, Payne (1977) reports that from examination of 54 uteri, mean sexual maturity is attained by about three years. The percentages of pregnant females in each age class increases from zero at two years, to 55% at three, to 75% at four, 85% at five and 90% by six years. The age at maturity for males has not been established, but males are not socially mature and able to participate fully in mating activity until about eight years of age (Laws 1984).

For crabeater seals, Laws (1977) used tooth back-calculation (back-calculating age at maturity evidenced by the transition phase in rates of cementum deposition in teeth) from crabeater seals in the Marguerite Bay area to demonstrate a decrease in age at maturity from approximately 4.5 years in 1945 to 2.5 years in the late 1960s. In a subsequent study, Bengtson and Laws (1985) examined the trend in the age at sexual maturity by tooth back-calculation and by examining the ovaries of female crabeater seals collected between 1964 and 1984. They suggested that an apparent decrease in maturity as evident from the transition zone of tooth cementum was unrelated to population trends, but rather to a differential mortality within cohorts (those individuals maturing earlier apparently dieing sooner). Thus they suggested that tooth back-calculation is an unsuitable method to assess past trends in sexual maturity. Nevertheless, the estimates of mean age at maturity for each year as calculated from ovarian material showed a drop in the age of maturity from the 1959 to the 1963 cohort, followed by a steady increase through the 1960s and 1970s. A more recent study by Hårding and Härkönen (1995) also reached this conclusion, agreeing that there was strong evidence for a true increase in the age at maturity of crabeater seals over 1964 to 1989. They used two different methods. The first took account of the proportion of mature females in each age-class to calculate mean age at first ovulation and corresponding 95% confidence intervals. The second method was based on the following assumptions: female crabeater seal ovulate once each year in alternating ovaries; the erupted follicle forms a corpus lutetium (CL) that is converted into a corpora albicantia (CA) after gestation; the CA persists, and can be distinguished from other structures at least five years after formation. Thus, to obtain the

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age at first ovulation of a female seal, the total number of ovarian corpora is subtracted from her age. The mean age at first ovulation was calculated as the arithmetic mean of these back-calculated ages (Hårding and Härkönen 1995).

4.3 Summary

- The southern baleen whale species considered in this thesis tend to migrate from tropical latitudes in winter where breeding takes place to the higher latitudes of the Antarctic in summer where they feed mainly on krill. However not all migrate every year, and some seem to remain at both high and lower latitudes.
- The stock structure for humpback whales is well studied and seven concentration areas in the Antarctic are indicated. The stock structure of blue, fin and minke whales are not as well known, but recent study by Pastene *et al.* (2005) suggests a boundary between minke whale stocks at about longitude 165°E.
- Analysis of the encounter rate patterns evident from the whale sighting surveys in the Antarctic suggests that blue whales and minke whales occur in the southernmost waters close the ice-edge (south of 66°S), humpback whales over a wide range of latitudes (peaking in 62°S-66°S) and fin whales in the northern part of the Antarctic waters (peaking in 54°S-58°S) (Kasamatsu *et al.* 1996, 2000a).
- Blue, fin and humpback whales normally reproduce every two to three years. Minke whales reproduce more frequently, usually producing one calf every year (Brown and Lockyer 1984).
- Lockyer (1972) suggests a decline in mean age at maturity of fin whales from 10 years for the 1910 year class to 6 years for the 1958 year class for both sexes. Lockyer (1981b) reports mean age at sexual maturity for blue whales to be 5 years. Chittleborough (1965) suggests this age for female humpback whales to be 4-5 years, and for males to be about 5 years. For minke whales, Kato (1983) and Thomson *et al.* (1999) suggest that the average age at transition declined from roughly 11 for the cohorts of the 1950s to roughly 7 for those of the 1970s. A more recent study by Zenitani and Kato (2005) indicates that the tendency of the age at sexual maturity of minke whales to decline slowed gradually around the 1960s and almost stopped from about 1965 to 1980.
- The main breeding population of Antarctic fur seals occurs in the vicinity of South Georgia. Crabeater seals appear to have a circumpolar breeding distribution in the pack-ice.
- Female Antarctic fur seals attain sexual maturity at about 3 years; males participate in reproduction through holding territories from about 8 years of age, though they may mature

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earlier. The age at sexual maturity of crabeater seals declined from the 1959 to the 1963 cohorts, but subsequently there has been a steady increase in this age through the 1960s and 1970s (Bengtson and Laws 1985, Hårding and Härkönen 1995).

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Table 4.1 Peak breeding seasons of Southern Hemisphere baleen whales (source: Kasamatsu 2000).

	Month of conception	**Month of birth**
Blue whale	June	May
Fin whale	June - July	May
Humpback whale	July - August	July - August
Minke whale	August - September	May - June

Table 4.2 Approximate durations (in days) of the reproductive stages in the annual cycle of female seals (source: Laws 1984).

Species	**Lactation period**	**Parturition to conception**	**Conception to implantation**	**Parturition to implantation**	**Implantation to parturition**
Antarctic fur seal	110	8	125	133	232
Crabeater seal	28	30	80	110	255

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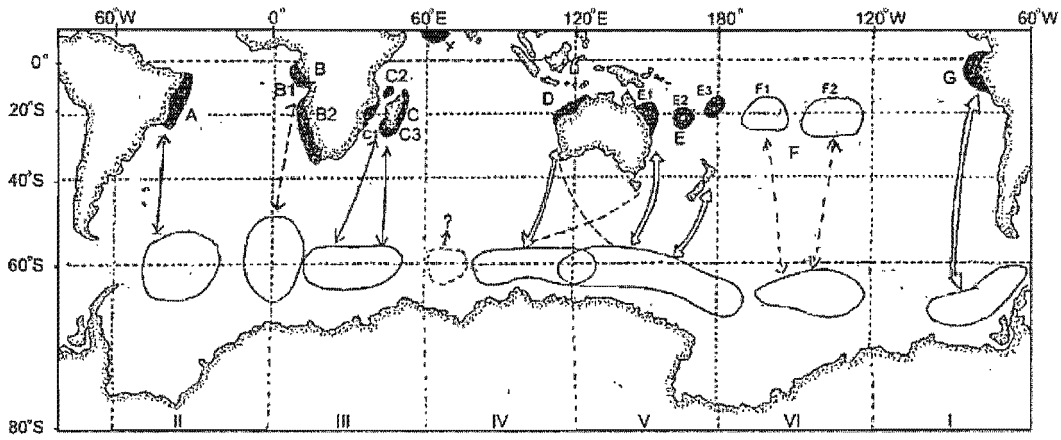


Figure 4.1 Current hypothesized stock structure for Southern Hemisphere humpback whales. The areas and sub areas identified reflect approximate, rather than necessarily exact boundaries. A dotted line represents a hypothesised connection, thin lines represent a small number of documented connections between areas from Discovery tags, photo-identification or genetics, or satellite tracked whales, and thick lines represent a large number of documented connections between areas from such linkages (source: Annex H of IWC 2004).

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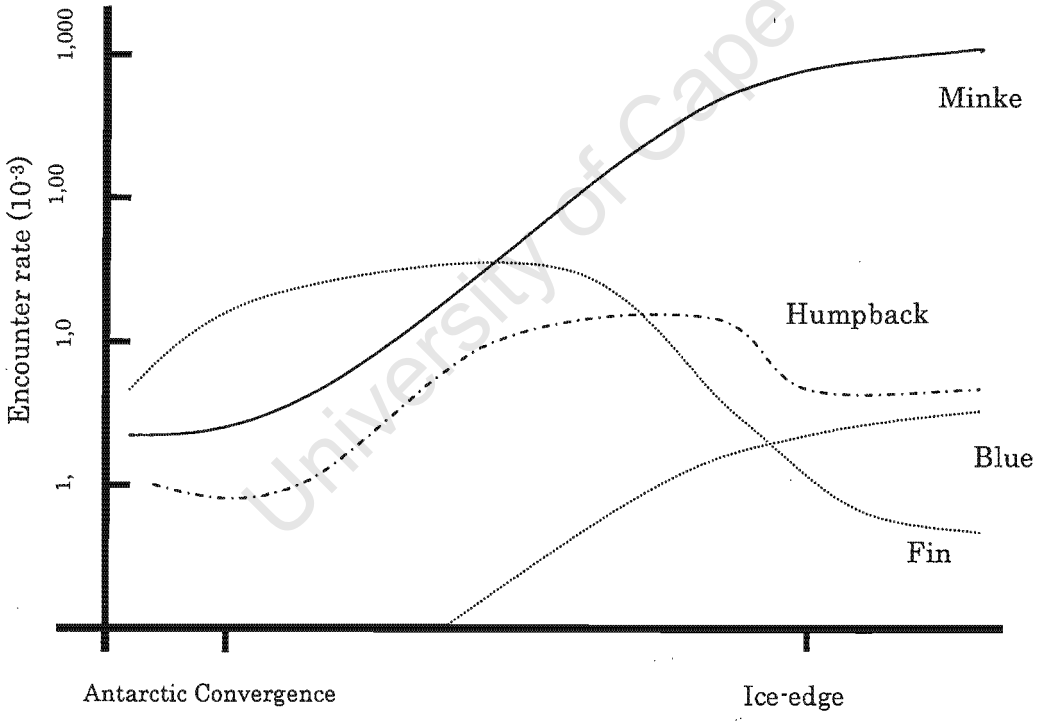


Figure 4.2 Latitudinal occurrences of baleen whales in the Antarctic (source: Kasamatsu *et al.* 1996).

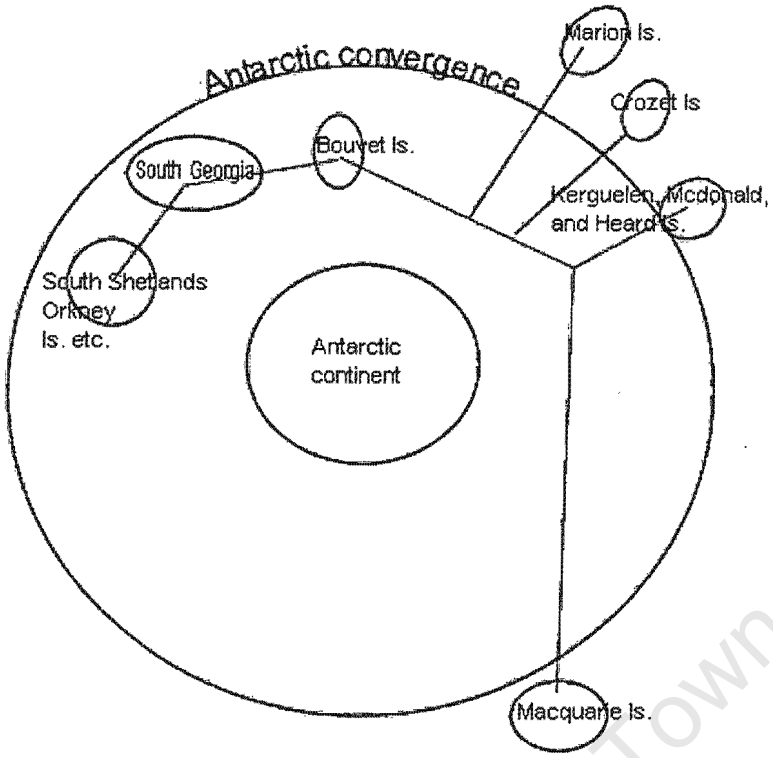


Figure 4.3 Distribution of breeding sites of Antarctic fur seals. The lines are drawn to join breeding localities (modified from Fig. 1b of Laws 1984).

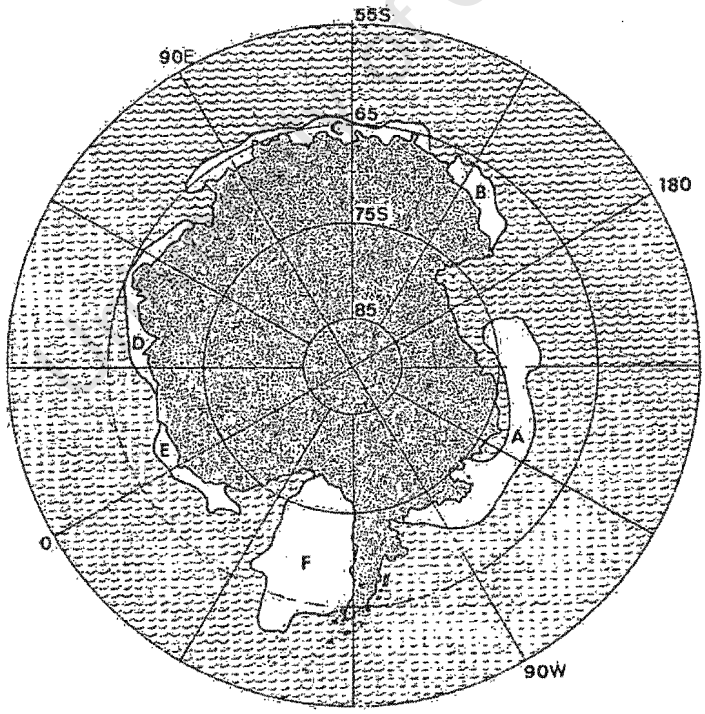


Figure 4.4 Six residual pack ice regions presumed to constitute population centers for pelagic Antarctic seals in the austral summer. These regions are as follows: A, Amundsen and Bellingshausen seas; B, Oates Coast; C, Wilkes Land; D, Queen Maud Land; E, Halley Bay; and F, Weddell Sea (reproduced from Fig. 7 of Gilbert and Erickson 1977).

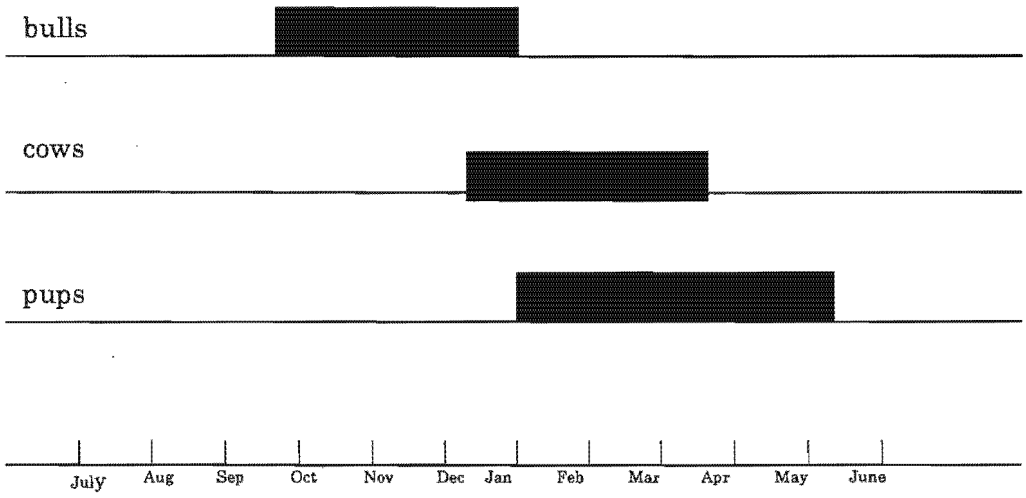


Figure 4.5 Schematic representation of colony attendance by Antarctic fur seals during the year (reproduced from Payne 1977).

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CHAPTER 5

ABUNDANCE AND TREND ESTIMATION FOR THE MAIN KRILL-FEEDING BALEEN WHALES

The most recent published circumpolar abundance estimates for the baleen whale species are presented in Branch and Butterworth (2001a, 2001b). Due to the wide circumpolar distribution of the baleen whales in a severe environment, where in winter the area is covered with pack-ice, surveys of these species are particularly difficult. Furthermore, the migratory nature of the baleen whales together with their diving and surfacing behavior adds to the difficulties of abundance estimation. Nonetheless, extensive efforts, in terms both of surveys and analyses, have been made to estimate the abundances and trends of the baleen whales in the Antarctic. In this Chapter, abundance and population trend estimates of minke, blue, humpback and fin whales are reviewed.

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5.1 Review of the abundance estimates derived using the "standard methodology" for the IWC/IDCR-SOWER cruises

Table 5.1 shows recent reported absolute abundance estimates for these four baleen whale species. These estimates are as calculated by Branch and Butterworth (2001a, 2001b), Branch (2003) and Rademeyer *et al.* (2003a), and are based on the cetacean sightings data collected during first the IDCR and then the SOWER circumpolar survey programs coordinated by the IWC since 1978. These surveys have been conducted every austral summer predominantly south of 60°S and (usually) in one of the IWC Management Areas (Figure 2.2) in turn. At the time when Branch and Butterworth (2001a, 2001b) calculated their abundance estimates, a total of 23 shipborne surveys had been completed, falling into three circumpolar sets: 1978-1983, 1985-1990 and 1991-2000 (still incomplete). The areas surveyed during each of the three circumpolar sets are shown in Figures 5.1.1 to 5.1.3, and the survey periods in Figure 5.2. The primary aim of the surveys has been to estimate minke whale abundance; however, all cetacean sightings are recorded, which makes it possible to estimate abundance for species other than minke whales.

The abundance estimates calculated by Branch and Butterworth (2001a) and shown in Table 5.1 reflect a decrease of about 50% in minke whale abundance from the second circumpolar set of surveys (1985-1990) to the third (1991-2000). This estimate of a substantial decrease in minke whale abundance has led to an in-depth assessment of these estimates by the IWC Scientific Committee, and there has been considerable debate as to whether the decline is real or is an artifact of changes in various aspects of the survey procedures. Extensive reviews of this topic by the Scientific Committee of the IWC are reported in IWC (2002), IWC (2003), IWC (2004b) and IWC (2005). In this section, first the basic equation used by Branch and Butterworth (2001a) for estimating the abundance of whales (in terms of the so called "standard methodology") is introduced; this is followed by consideration of the potential biases associated with these estimates together with an evaluation of their likely magnitudes. The biases are considered not only in absolute terms, but also in relative terms (particularly in comparing abundance estimates for the second and third circumpolar sets of surveys), as this has important implications for estimates of trends in abundance.

5.1.1 Basic equation

The basic equation applied in Branch and Butterworth (2001a, 2001b) to estimate the abundances of whales is:

$$P = \frac{A \cdot \bar{s} \cdot n}{2 \cdot w_s \cdot L} \tag{5.1}$$

where:

P = uncorrected abundance (assumes all schools on the trackline are sighted and makes no correction for random school movement);

A = open ocean area of stratum;

$\bar{s}$ = mean school size;

n = number of schools sighted during primary search mode;

w_s = effective search half-width for schools, equal to the inverse of the detection function intercept $f(0)$; and

L = search effort (distance steamed in primary search mode).

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Effective search half-width (w_s) is estimated from the following equation:

$$f(y) = \frac{g(y)}{w_s} \tag{5.2}$$

where:

$f(y)$ = the probability density function for the sighting distribution in relation to perpendicular distance from the trackline (y); and

$g(y)$ = the probability that a school at a perpendicular distance y from the trackline will be sighted.

In the analyses of Branch and Butterworth (2001a, 2001b) it is assumed that $g(0) = 1$, which means that all schools on the trackline are seen so that $w_s = \frac{1}{f(0)}$. The function $f(y)$, and hence its intercept $f(0)$, is estimated by fitting a hazard rate form: $f(y) = f(0)\left[1 - \exp\left\{-\left(\frac{y}{a}\right)^{1-b}\right\}\right]$ to the observed distribution of sightings within a truncation distance W. W is chosen to include about 95% of the sightings, and for minke whales is accordingly set at 1.5 n. miles.

Survey effort is divided into closing and IO (independent observer) mode. In closing mode, when a school is sighted, the vessel suspends primary searching effort, turns off the trackline and closes in with the sighting (Branch and Butterworth 2001a). In IO mode, the vessel continues steaming along the trackline after a sighting, with observers in the barrel and the IO platform (both located on the main mast) maintaining full search effort while those on the upper bridge concentrate on tracking and identifying the sighting (Branch and Butterworth 2001a). IO mode is considered less biased because of the absence of "end effects" when the vessel goes off primary searching effort when closing and disregard of "secondary" sightings seen during that period; however, it does not allow for accurate school size estimation, which is based on closing mode (Branch and Butterworth 2001a). Since the start of the second circumpolar set of surveys, transects have alternated between closing and IO mode.

Mean school size ($\bar{s}$) is estimated by comparing the results obtained from two different methods. One method is to take the actual mean of the schools sighted within the truncation distance W, whereas the other takes the estimate of $y = 0$ of a regression of $\ln s$ *vs.* $g(y)$. The latter method is used if the regression is significant at the 15% level and has a slope in the downward direction

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expected as proportionally more smaller schools are likely to be missed at larger perpendicular distances (Branch and Butterworth 2001a).

5.1.2 Potential biases associated with the estimate

Various biases are associated with abundance estimation of whales in the Antarctic. The reasons for these arise partly from the widespread circumpolar distribution of these whales and the difficulties in finding and identifying species which are not always above the surface but instead are repeatedly surfacing and diving. The major difficulties in estimating the abundance of the baleen whale species considered in this thesis are listed in Table 5.2, together with a qualitative assessment of their potential impacts on abundance estimates (evaluated as H=High, M=Medium and L=Low) for each. Work that has been carried out to address these biases and to estimate the potential magnitude of their effects on abundance estimates is summarized below.

Plausibility of the assumption of all whales on the trackline is detected (i.e. $g(0)=1$)

The assumption that $g(0)=1$ was used in the analyses of Branch and Butterworth (2001a, 2001b) because of many difficulties associated in estimating how much less than 1 this value might be. Historically, over the period 1981 to 1983, the Scientific Committee of the IWC used results of analyses of variable speed and parallel ship experiments to select $g(0)$ values that were less than 1 in computing minke whale abundance estimates (see, for example, Butterworth *et al.* 1982, 1984 for more details of these experiments and their analyses). However, at the 1984 Scientific Committee meeting, methodological questions about these approaches were raised, and in the absence then of their resolution, the Committee effectively decided to set $g(0)=1$. Despite considerable efforts to obtain a satisfactory estimate of $g(0)$ from these experiments and from IO mode duplicate sightings data over the next six years, problems in interpreting the data continued (see, e.g., IWC 1988, p.78, IWC 1989b, p.72-73). In the absence of any agreed estimate of $g(0)$, use of the value $g(0)=1$ was continued for abundance estimation purposes. Finally, during the 1990 Comprehensive Assessment of Southern Hemisphere minke whales, the results of a review (Butterworth 1991) of estimates of $g(0)$ for the barrel from IO survey[1] data were noted, together with the fact that applying these to sightings from the barrel alone yielded density estimates not

[1] In passing (or IO) mode in these surveys (no closure on whales sighted), observations are made independently from these two separate platforms (the barrel and the IOP) on the main mast and reported to the bridge, where an assessment is made of whether or not a particular whale school has been sighted by only one or by both platforms (if the latter it is termed a duplicate). The two platforms are kept unaware of each others sightings.

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much different from those based on sightings from all platforms linked to the assumption $g(0)=1$ (IWC 1991, p.116). This was followed by agreement to continue the use of the value $g(0)=1$, a decision reconfirmed two years later (IWC 1993, p.106) (Branch and Butterworth 2001a).

Several more recent studies (Mori *et al.* 2002, 2003) suggest that for minke whales, $g(0)$ may depend on the size of the school, the experience of the observer and on some environmental factors. Mori *et al.* (2002) analysed the duplicate sighting data (here considered as a surrogate for $g(0)$ as a lesser proportion of duplicate sightings suggests lower $g(0)$) between the topmen in the barrel and the IOP (independent observer platform) for IO mode during the IWC/IDCR-SOWER surveys. Using Generalized Linear Models (GLMs) which assumed a binomial error distribution, the effect of school size on the probability of duplicate sightings was statistically significant at the 5% level for minke and humpback whales. Duplicate sightings of blue whales showed no significant dependence on school size, which is not surprising as for this species the body and the blow size are large enough for easy detection even of a solitary animal. For minke whales, the probability of a duplicate sighting for schools of size 2 was 1.56 times larger (95% CI: 1.21; 1.78) than for a solitary animal, and for school sizes exceeding 2 was 1.84 times larger (95% CI: 1.68; 1.93). They concluded that this provides strong evidence that $g(0)$ depends on school size, and in particular that $g(0)$ for solitary whales is smaller than for schools of larger size.

If some of the whales on the trackline are missed (i.e. $g(0)<1$), then the abundance estimates shown in Table 5.1 will be negatively biased. Several authors (Mori *et al.* 2003, Murase *et al.* 2004) have hypothesized that the suggested 50% decline in minke whale abundance calculated by Branch and Butterworth (2001a) may partly be an artifact of a decrease in $g(0)$ in the third circumpolar set of surveys compared to the second set due to changes in observer experience and in school size. Mori *et al.* (2003) examined the effect of observer experience on minke whale sighting rates using the sighting data obtained during the third circumpolar set of IWC/IDCR-SOWER surveys, and found that sighting rates decreased about 20% for observers with experience of only four or fewer past surveys. They concluded that $g(0)$ could well be less than one, especially for the third circumpolar set of surveys when less experienced observers were introduced. In addition, Murase *et al.* (2004) found that the mean school size $\bar{s}$ in closing mode dropped from 2.5 in the second circumpolar set of surveys to 1.5 in the third circumpolar set of surveys, suggesting a possible decrease in $g(0)$ (i.e. the average value over the distribution of school sizes encountered) from the former to the latter.

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Overall, these studies suggest that $g(0)$ may depend on school size, observer experience, and it may be notably less than one especially for minke whales which have smaller body-length and less visible sighting cues than the other larger baleen whales.

Butterworth *et al.* (2003) examined the magnitude of the effect of $g(0)<1$ (but increasing with school size) on the minke whale abundance estimates shown in Table 5.1, using a simple Kelker strip approach. This approach calculates the abundance estimates by considering only sightings made within a small perpendicular distance (≈0.1-0.2) of the trackline over which $g(y)$ is assumed constant, and their calculations assumed different values for $g(0)$ depending on the school size (here classified as 1, 2 or >2). Values of 0.3-0.5 for $g^1(0)$ (being $g(0)$ for schools of size 1) were investigated, based on estimates for this quantity from a hazard-rate model analysis of duplicate sighting data by Okamura *et al.* (2003) and applying a simple model for the dependence of $g(0)$ on school size developed by Cooke (1985). The effects of this adjustment on the absolute abundance estimates were increases of 20-70% and 30-100% for closing mode during the second and third circumpolar set of surveys respectively, and correspondingly 50-140% and 60-150% for IO mode, depending on the value assumed for $g^1(0)$ and whether or not to include sightings for which school size was unconfirmed in the calculation. The effect of this adjustment on the abundance estimate ratio for the third circumpolar set of surveys compared to the second was an increase of 8-15% for closing mode, and 5-7% for IO mode depending on these same two factors.

In summary, the impact of the assumption that $g(0)=1$ on minke whale abundance estimate is evaluated as "H" in Table 5.2 based on the various studies summarised above, and the fact that minke whales have shorter body-length (7-11m) compared to other larger whales which makes it relatively more difficult for observers to sight them.

The effect of the assumption that $g(0)=1$ on humpback whale abundance estimate is evaluated as "M" in Table 5.2, based on the analysis of Mori *et al.* (2002) which showed that duplicate sighting probability for this species sighted in the Antarctic also differs significantly between school sizes of 1, 2 and >2. As the school size increases, the duplicate sighting probability increases by about 30%. This suggests that $g(0)$ for humpback whales depends on school size and could be less than one, especially for solitary animals. The reason that the impact has not been evaluated as "H" is that humpback whales typically have larger body-lengths (11-15m) compared to minke whales,

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and hence are probably easier to detect, and that the duplicate sighting probability does not increase as much for greater school sizes as is the case of minke whales. Calambokidis and Barlow (2004) estimated $g(0)$ for humpback and blue whales to be 0.9 in the eastern North Pacific (west coast of the U.S. and Mexico) based on independent observer data collected during line-transect surveys conducted in 1991, 1993 and 1996. Due to the low number of sightings detected only by the independent observers (n=13), this estimate was not stratified by group size (Calambokidis and Barlow 2004). Whether this high estimate of $g(0)$ applies to the humpback whales in the Antarctic (where the sighting conditions are probably more severe than that of the west coast of the U.S) regardless of the school size is questionable. No quantitative study of the effect of $g(0)<1$ on the humpback whale abundance estimates shown in Table 5.1 has been carried out; however, it seems reasonable to assume that this would not be as large as that for minke whales.

The impacts of the assumption that $g(0)=1$ on fin whale and blue whale abundance estimates are evaluated as "L" in Table 5.2. Again this is based on the analyses of Mori *et al.* (2002) which was unable to detect a significant difference in the duplicate sighting probability of blue whales for different school sizes. This could be a result of lower power given the small sample size of the sightings (n=13); however, it seems more likely to be due to the large body-length of this species which is typically 24-28m, which makes it rather easy for observers to detect. Furthermore, Best *et al.* (2003) suggests that based on dive times and surfacing behaviour of blue whales recorded in just over 21 hours of monitoring around the Madagascar Plateau between 25° and 35°S, 40° and 45°E in December 1996, the assumption that $g(0)=1$ is reasonable for this species.

As the typical body length of fin whales (18-25m) is similar to that of blue whales, it seems safe to conclude that the impact of assuming $g(0)=1$ for fin whale abundance estimates is also low.

Abundance of whales in the unsurveyed area south of 60°S

As shown in Figures 5.1.1 to 5.1.3, there are some areas that were not surveyed within the region south of 60°S during the IWC/IDCR-SOWER cruises. For the third circumpolar set of cruises (Figure 5.1.3), nearly all of the area south of 60°S was surveyed (by design), so that no major extrapolations are needed to estimate abundances of whales within this area. However, cruises during the second circumpolar set of surveys reflect a fair amount of unsurveyed area within this region (Figure 5.1.2).

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This inconsistency in the area surveyed precludes direct comparison of abundance estimates from the two set of circumpolar cruises, necessitating in some kind of extrapolation of density estimates to the unsurveyed areas to be able to make such a comparison. Branch and Butterworth (2001a, b) estimated the abundances of the whales in the unsurveyed area by assuming that the unsurveyed northern areas have the same density of whales as the northern strata surveyed in each survey, to scale estimates to the whole region south of 60°S. The results of this extrapolation on abundance estimates are also shown in Table 5.1, in combination with longitudinal extrapolations needed for the third circumpolar set to allow for its incomplete nature. For minke whales, the net effect is to increase the abundance estimate by about 15% for the second set of circumpolar surveys and about 29% for the third. For blue, humpback and fin whales, the effects are to increase abundance estimates for the second set of circumpolar cruises by 24%, 30% and 5% respectively, and by 11%, 16% and 12% respectively for the third.

As is noted in Branch and Butterworth (2001a), this assumption probably introduces some positive bias into the resultant abundance estimates of minke whales, as minke whale density tends to decrease with movement north away from the ice-edge. Rademeyer *et al.* (2003b) use the IWC/IDCR-SOWER survey data to show that the sighting rate for minke whales increases with latitude. The sighting rates in the 60°-62°S latitudinal band are about half or less of those in 63°-64°S, so that they scaled down the extrapolated abundance estimates for unsurveyed northern areas in Branch (2003) by a factor of 0.5 as a sensitivity test. This decreased the minke whale abundance estimates for the second circumpolar by about 10% on average compared to the original extrapolations of Branch and Butterworth (2001a) shown in Table 5.1.

The opposite effect occurs for fin whales. The sighting rate for these whales tends to be higher in latitudes immediately north of 60°S (Kasamatsu *et al.* 1996). In the 60°-62°S latitudinal band this rate is almost three times larger than that south of 62°S, suggesting that the extrapolation of the fin whale abundance estimates in Table 5.1 may be negatively biased.

Moreover, the region surveyed in the third circumpolar set of surveys for Area IV in 1994 was a very small fraction (70°-80°E) of this Area (70°-130°E), thus the abundance estimates for humpback and fin whales in the third set of circumpolar surveys could be affected largely by this unsurveyed latitudinal area.

This effect thus seems to affect the abundance estimate of all the species considered in this thesis by about 10-30%, depending on the species. Thus the impact of this effect in Table 5.2 is considered

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to be "M" for all the species.

Abundance of whales in the unsurveyed area within the pack-ice

Some studies reveal that minke whales are present within the pack-ice (Naito 1982, Ensor 1989, Thiele and Gill 1999), which the standard cetacean sighting survey vessels cannot enter. Shimada *et al.* (2001) coarsely estimated the number of minke whales within the pack-ice region during the second circumpolar set of surveys by assuming various densities of minke whales in relation to the ice concentration observed in the previous studies by Naito (1982) and by Ainley (1985). Shimada *et al.* (2001) provides estimates ranging from about 100,000 to 700,000 depending on the underlying assumption made for minke whale density, and suggests that some hundreds of thousands of whales within the pack-ice region should be added to the abundance estimates of Branch and Butterworth (2001a) for the second circumpolar set of surveys. This calculation is very crude since the density estimate of Naito (1982) is based on that of either from one or two years of surveys by an ice-breaker in the pack-ice region (Naito 1982); however, it nevertheless raises the possibility that the number of minke whales within the pack-ice region is quite substantial, and research to address this issue further in the future is needed.

For this reason the effect on minke whale abundance is assigned as "H". Minke whales and killer whales were the only species that were sighted within the pack-ice region (Thiele and Gill 1999). "M" is assigned for blue whales; since their distribution is close to the ice-edge as for minke whales, and the reason for not being able to detect blue whales within the pack-ice during the ice-breaker surveys could be because of the current small size of this population. "L" is assigned for humpback whales, since they are sufficiently numerous that they would likely have been seen if they were there. "L" is also assigned for fin whales since their main distribution is far from the ice-edge.

Abundance of whales in the unsurveyed area north of 60°S

As described in Chapter 4, Section 4.1.3, Kasamatsu *et al.* (1996) analysed the relationship between encounter rate and latitudinal occurrences of Antarctic baleen whales during mid-December to mid-February using IWC/IDCR-SOWER and JSV data in Antarctic waters (here defined as those south of the Antarctic Convergence, considered to be at 50°S between 60°W-160°E in the South Atlantic-Indian Ocean Sector and at 58°S between 160°E-60°W in South Pacific Sector) from 1976 to 1988. They found that the main concentrations of blue and minke whales occur in the

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southernmost latitudes (66°S-70°S for blue whales and south of 66°S for minke whales), of humpback whales over 62°S-66°S, and of fin whales in the northern part of the region (54°S-58°S). This suggests that the estimated abundances of minke and blue whales, and to a lesser extent that of humpback whales, south of 60°S as calculated by Branch and Butterworth (2001a, 2001b) may be reasonably representative of the abundance of these species in the Southern Hemisphere (if corrected for various other biases discussed here). However, this is likely not to be the case for fin whales, since their main summer distribution is north of the area where the IWC/IDCR-SOWER surveys have been conducted and hence the abundance estimates for this species from these surveys are almost certainly appreciably negatively biased.

Butterworth and Geromont (1995) used JSV sighting rate data from 1965 to 1987 as an index of relative density to extrapolate abundance estimates obtained in the IWC/IDCR-SOWER surveys to the region north of 60°S. They estimated the multiplicative extrapolation factor for fin whales to be in the range of about 5.5 to 7, which is much larger than estimates of 1.1 to 1.5 for blue whales and 2.3 to 3.4 for humpback whales. A similarly based extrapolation factor for minke whales was estimated to be 1.18 (Borchers 1991). This information can be used to provide a rough total abundance estimate for the whales in the unsurveyed areas north of 60°S.

For this reason, the impact of this effect on fin whale abundance estimate is classified as "H" in Table 5.2. The impact of this effect is classified as "L" for both blue and minke whales since the main austral summer distributional range for these species lies south of 60°S. For humpback whales the impact is classified as "M".

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Dealing with the sightings that were classified as "like-species"

Not all the schools sighted on the surveys can be classified to species with certainty, so that some are classified instead as "like-species". The general guideline for the identification of a "like-minke whale" is as follows (from Matsuoka *et al.* 2003):

> "The cue observed is usually the whale blow. In most cases there is no observation of the body or the view obtained is poor and insufficient to observe the diagnostic features of the species. Characteristics of the blow indicate it is probably a minke whale."

Because it is unclear what proportion of such "like-species" sightings are actually of the species in question, it seems sensible to bound abundance estimates for the species by conducting computations both including and excluding those that were classified as "like-species".

Abundance estimates including the "like-species" together with the extrapolation of the abundance estimate to full region south of 60°S are also shown in Table 5.1. In the analyses of Branch and Butterworth (2001a), inclusion of "like-minke whale" sightings increased the total abundance estimate by 11% for the second circumpolar set of surveys and by 18% for the third. For blue whales and humpback whales, this effect is negligible; however, for fin whales, the inclusion of the like-fin whale sightings increased the abundance estimate for the third circumpolar set of surveys by almost 70% compared to a mere 10% for the second (Branch and Butterworth 2001b). From these figures it is obvious that this factor has an appreciable impact for fin whales and to a lesser extent for minke whales (thus "M" is assigned for both species).

Estimation of mean school size ($\bar{s}$)

Brandão *et al.* (2001) note that a method that takes the average of observed school sizes as an estimate of the underlying mean school size for minke whales would be positively biased, since larger schools are less likely to be missed than smaller schools as one moves away from the trackline. They applied three different mean school size estimation methods ("average", "regression" and "kernel") to the IWC/IDCR-SOWER surveys' closing mode sighting data from 1978 to 1997, and compared estimation on performances amongst these three approaches. The average CVs for the method that takes the average of the sighted schools were some 20-40% higher than for the other methods, and they concluded that the ln(s) *vs.* g(y) regression method should be used irrespective of the statistical significance of the regression, unless the regression shows a positive correlation or provides an estimate less than 1 (the IWC Scientific Committee consequently agreed to amend its "standard methodology" to incorporate this adjustment (IWC 2002, p.196-7). When this approach is used instead of the one used in Branch and Butterworth (2001a), minke whale abundance estimates are reduced by 7% and 1% for the second and third sets of circumpolar surveys respectively (Butterworth *et al.* 2001).

Based on the study of Brandão *et al.* (2001), "L" is assigned for this effect on minke whale abundance estimates. Given that body-lengths for blue and fin whales, and to a lesser extent humpback whales, are larger than those of minke whales, estimation of individual and hence also mean school size is probably better for these species than for minke whales, and hence "L" is also assigned for these other species.

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Survey timing and the migration peak of the whales

As detailed in Matsuoka *et al.* (2003), and shown in Figure 5.2, from 1994 the survey period for the IWC/IDCR-SOWER surveys was typically two to three weeks later compared to earlier surveys. Before 1994, the surveys started mainly around mid-December and ended around mid-February; however, since 1994 the surveys have generally started near the beginning of January and ended about the end of February or early in March. The aim of this delay in the survey period was to facilitate cruise track construction by increasing the likelihood of the ice-edge having receded prior to the survey to form a compact edge at a position consequently more readily determined (Matsuoka *et al.* 2003).

This delay for the later surveys subsequently raised concerns that perhaps many of the third circumpolar set of surveys did not match the migration peak of minke whales to the Antarctic very well (Branch and Butterworth 2001a). Kasamatsu *et al.* (1996) reported a decrease in minke whale sighting rates of about 50% from late January to late February, using the data from surveys (IDCR and other) south of 50°S from 1976 to 1987. Analysis by Free (1983) similarly show a decrease of about the same size in commercial minke whale catch rates from their peak in January to February. Butterworth *et al.* (2003) attempted to correct for the migration peak of minke whales that was suggested by Kasamatsu *et al.* (1996) by using a simple GLM approach to allow for the fact that the time of the apparent peak may be confounded by other factors such as different latitudes and areas surveyed; however, they found that because of the high variability in the data, they were unable to detect a statistically significant decrease in minke whale density from January to February.

Thus "L" is assigned for the likely impact of survey timing on minke whale abundance estimates. "L" is similarly assigned for blue and fin whales since Kasamatsu *et al.* (1996) in their analysis of sighting rate *vs.* seasonal occurrence using the IWC/IDCR-SOWER survey data between 1976 to 1988 found that the peak occurrences of these species were in late January, followed by a drop in February, which seems to fall within the survey period for all three sets of circumpolar surveys. "L" is also assigned for humpback whales since the highest densities were found throughout January though this is followed by a drop in mid to late February.

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5.1.3 Net effect of various biases on abundance estimates of the species

Various biases associated with the abundance estimates of four important baleen whale species in the Antarctic have been discussed above, and the potential impact of each of these biases on abundance estimates has been evaluated qualitatively but only sometimes quantitatively. Below, an attempt is made to quantify the net effect of these various biases in combination on abundance estimates provided by Branch and Butterworth (2001a, 2001b) for each species.

Minke whales

As can be seen from Table 5.2, the effects of at least the following four factors on abundance estimates of minke whales need to be considered:

1) the assumption that $g(0)=1$;
2) unsurveyed areas south of 60°S;
3) unsurveyed areas in the pack-ice; and
4) sightings that were classified as "like-minke whales".

Butterworth *et al.* (2001) roughly quantified the net effect of five factors on the abundance estimation of minke whales. Those were:

1) the proportion of like-minke sightings and their increase over time;
2) comparable latitudinal (all to 60°S) and longitudinal coverage;
3) the effect of using the ln(s) *vs.* g(y) regression method proposed by Brandão *et al.* (2001) to estimate mean school size;
4) the increase in less experienced observers over time (with implications for $g(0)$)[2]; and
5) the change in survey timing over time.

Since Butterworth *et al.* (2001) did not account completely for the effect of $g(0)<1$, Table 5.3 shows a similar but an updated version of the corrected abundance estimates of Butterworth *et al.* (2001), which now takes into account the subsequent result of Butterworth *et al.* (2003) which examined the magnitude of the effect of $g(0)<1$ (but increasing with school size) on minke whale abundance estimates for comparable areas for the second and third sets of circumpolar surveys for three values of $g^1(0)$. Further, the proportion of animals north of 60°S is taken into account by

[2] This difference is not accounting completely for $g(0)<1$, as is attempted e.g. in Butterworth *et al.* (2003) on page 68 of this thesis.

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using the extrapolation factor of 1.18 for minke whales estimated by Borchers (1991). These corrections results in a 40-100% and a 60-150% increase in closing mode absolute abundance estimates of minke whales for the second and third circumpolar sets of cruises respectively, depending on whether like-minke whales are included or not and on the value assumed for $g^1(0)$. For IO mode the corresponding increases are 70-190% and 90-260% respectively.

Table 5.3 adjusts the minke whale abundance estimates for most of the factors listed in Table 5.2, except for the number of minke whales in the unsurveyed area in the pack-ice. Shimada *et al.* (2002) preliminarily estimated the abundance of minke whales within the pack-ice area for the second and third IWC/IDCR-SOWER circumpolar surveys using sea-ice concentration data, and assuming three different scenarios for the relationship between the encounter rate of minke whales and ice conditions based on the studies of Naito (1982) and Ainley (1985). Table 5.4 shows the estimated abundance estimate of minke whales within the pack-ice area calculated by Shimada *et al.* (2002) as well as the combined abundance estimate for these whales when those in the pack-ice are added to the adjusted abundance estimates shown in Table 5.3. Scenario 1 in Table 5.4 uses the 1979 sighting rate data from Naito (1982), which surveyed the animals in the pack-ice in IWC Management Area III using an icebreaker. Scenario 2 uses the same data but also adds the survey data obtained in 1981 (Naito 1982). Scenario 3 uses the survey data from 1976-1980 in the Ross Sea Area (IWC Management Area V) of Ainley (1985). The relationships between the encounter rate and ice conditions used in these three scenarios are shown in Figure 5.3.

The abundances of minke whales in the pack-ice calculated by Shimada *et al.* (2002) should be considered as approximate numbers with probably very large associated uncertainties because there have been rather few surveys in the pack-ice. Nevertheless these calculations are utilizing the information available to date, which do suggest that there could be some several hundred thousand minke whales in the pack-ice region where the IWC/IDCR-SOWER vessels could not survey, thus underestimating the abundances of minke whales in the Antarctic.

In conclusion, consideration of the biases listed in Table 5.2 indicates that all increase the "base" abundance estimates of Branch and Butterworth (2001a). The corrected estimates would lie in the approximate ranges of 1.2 to 3.3 million minke whales for the period 1985 -1990 and 0.33 to 1.1 million minke whales for the periods 1991-1997[3] (Table 5.4). The largest contributions to these uncertainties are estimates of the number of whales in the pack-ice and the extent to which $g(0)$ is

[3] Note that these results relate to data available at a time before the third circumpolar set of surveys had been completed.

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less than 1.

Blue whales

Table 5.2 indicates that there is less likelihood of substantial bias in the abundance estimate for blue whales shown in Table 5.1 then for other species; however, consideration should also be given to the possible biases which could arise from: (1) unsurveyed area in the pack-ice and (2) unsurveyed area north of 60°S. The effect of the unsurveyed area in the pack-ice on blue whale abundance estimates could be large; however, since there have been no observation of these animals in this region during the ice-breaker surveys, it is not possible to estimate the magnitude of this impact. To assess the contribution of the unsurveyed area north of 60°S on blue whale abundance estimates, the multiplicative extrapolation factor of 1.1 to 1.5 estimated by Butterworth and Geromont (1995) may be applied to the estimates shown in Table 5.1. A difficulty with this extrapolation is the possible confusion of species identification between the pygmy blue whales. In the analysis of Butterworth and Geromont (1995), animals sighted further north than 50°S were considered to be pygmy blue whales, so that this extrapolation factor is calculated based on blue whales sighted south of 50°S only[4]. Given that the analysis by Kasamatsu *et al.* (1996) which reports that concentrations of blue whales occur in the southernmost latitudes (66°S-70°S), the extrapolation factor estimated by Butterworth and Geromont (1995) does not seem unreasonable.

To summarise, the minimum abundance estimates for blue whales considered here are 750 and 2,300 for the periods 1985 -1990 and 1991-1997 respectively (the "Extrapolate" estimates in Table 5.1 multiplied by a 1.1 factor to allow for animals north of 60°S), and the maximum estimates are 1,000 and 3,100 for these same periods (calculated by multiplying the estimates shown under "Extrapolate + like-blue" in Table 5.1 by a factor of 1.5). The possible effect of $g(0)<1$ is not considered here, since blue whales are probably large enough to be detected on the trackline with near certainty (furthermore, there is in any case no quantitative evaluations of $g(0)$ for this species in the Antarctic).

Humpback whales

For humpback whales, the abundance estimates shown in Table 5.1 should be regarded as negatively biased even after taking into account the extrapolation to 60°S and the inclusion of

[4] See section 5.3 for a discussion of whether these estimates may be biased by inclusion of some pygmy blue whales.

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sightings that were identified as like-humpbacks. This is primarily because adjustments for the following two factors have not yet been incorporated: (1) the assumption that $g(0)=1$ and (2) unsurveyed areas north of 60°S. Attempts to correct the abundance estimate of humpback whales for $g(0)=1$ have not yet been made, but the maximum possible impact of this factor on humpback whale abundance estimates may be inferred from information obtained for other baleen whale species in the Antarctic. For example, it seems reasonable to assume that this effect should not be as large as that for minke whales which are more difficult to detect due to their smaller body length. For minke whales, as discussed previously, Butterworth *et al.* (2003) examined the magnitude of the effect of $g(0)<1$ (but increasing with school size) on minke whale abundance estimates for comparable areas for the second and third sets of circumpolar surveys. Depending on survey mode and whether to include unconfirmed as well as confirmed school size sightings or not, this adjustment increased the minke whale abundance estimates by multiplicative factors of about 1.2 to 2.4 and about 1.3 to 2.5 compared to the case when $g(0)=1$ was assumed for the second and the third set of circumpolar surveys respectively. Thus, in broad terms, when the effect of the possibility of $g(0)<1$ is taken into account for humpback whales, the numbers shown in Table 5.1c could be about 20-150% larger, resulting in estimates in the range about 14 to 30 thousand humpback whales. This maximum estimate could be an over-estimate if the $g(0)$ estimate of 0.9 (regardless of the school size) estimated by Calambokidis and Barlow (2004) for the humpback whales sighted in the eastern North Pacific also applies to those in the Antarctic.

The bias that could be caused by failure to take account of the unsurveyed area north of 60°S can be very broadly estimated by using information from Butterworth and Geromont (1995), in which JSV sighting rate data were used as an index of relative density to extrapolate abundance estimates obtained in the IWC/IDCR-SOWER surveys to the region north of 60°S. They estimated the multiplicative factor for humpback whales to be in the range of about 2.3 to 3.4.

To summarise then, the minimum abundance estimates for humpback whales considered here are 26,000 and 25,000 for the periods 1985-1990 and 1991-1997 respectively (the "Extrapolate" estimate in Table 5.1 multiplied by a northward extrapolation factor of 2.3 but making no adjustment for $g(0)<1$), and the maximum estimates are 96,000 and 95,000 for these same periods (which is 8.5 times[5] the estimate shown in "Extrapolate to 60°S + like- blue whales" in Table 5.1).

[5] This number of 8.5 comes from multiplying the maximum value of the two factors (2.5×3.4), one inferred from the effect of $g(0)<1$ (for minke whales), and the other from animals in the unsurveyed area north of 60°S.

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Fin whales

For fin whales, most of the factors considered as "M" or "H" in Table 5.2 are considered in the abundance estimate shown in Table 5.1 except for that related to unsurveyed areas north of 60°S. As a broad approximation, the extrapolation factor suggested by Butterworth and Geromont (1995) of about 5.5 to 7 might be applied to the estimate shown in Table 5.1. This would result in an estimate of abundance of 12,000 to 18,000 for the second circumpolar set of surveys, and 27,000 to 56,000 for the third. Thus, the minimum abundance estimates for fin whales considered here are 12,000 and 27,000 for the periods 1985-1990 and 1991-1997 respectively, and the maximum estimates of 18,000 and 56,000 for the same periods. The possible impact of $g(0)<1$ is not considered here for the same reason as for blue whales, since both these species are probably large enough to be detected on the trackline with near certainty.

Summary

Table 5.5 summarises the possible minimum and maximum abundance estimates of the four baleen whales considered in this thesis when the effects of the possible bias factors shown in Table 5.2 are taken into account for the IWC/IDCR-SOWER second and third sets of circumpolar surveys. Note that the third set of circumpolar surveys are still incomplete. Except for the minke whales, the abundance estimates appear stable or increasing in recent years, which will be discussed later in this Chapter.

5.2 Comparison with abundance estimates derived from other sources

Minke whales

Tables 5.6 and 5.7 show abundance estimates of minke whales in IWC Management Areas IV and V respectively calculated by Hakamada *et al.* (2005) from data obtained from JARPA surveys (which cover all the area south of 60°S) using a similar abundance estimation method to that applied by Branch and Butterworth (2001a, 2001b). The first JARPA surveys provided sightings data only from vessels involved also in taking whales, and furthermore used a survey design involving "skipping" to a planned waypoint if the full transect length planned for the day was not covered, which gave rise to concerns about negative bias arising from undersampling of higher density areas because of the resultant tendency to "skip" these because of the extra time required for additional catches on such days. However, since 1997, an extra vessel devoted to sightings alone has also

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participated in these surveys, and acts in exactly the same way as vessels surveying in passing mode on the IWC/IDCR-SOWER surveys. The JARPA estimates of abundance incorporate data from both types of operation, with the density estimates from the catching vessel calibrated to that from the sighting vessel used as the standard by the same approach used to combine results from closing and IO mode for the IWC/IDCR-SOWER surveys (Haw 1991). Figure 5.4 plots these estimates as well as those obtained from the IWC/IDCR-SOWER surveys for comparison purposes. These IWC/IDCR-SOWER estimates are extrapolated to 60°S (see "Extrapolate" column in Table 5.1), but also involve a combination of different surveys from the third circumpolar set as detailed in Chapter 8, page 151.

Comparison is not straightforward for two reasons. The first is the small number of surveys in Area IV and V under the IWC/IDCR-SOWER surveys compared to the JARPA surveys. Secondly the abundance estimates from JARPA surveys are available only from 1987. It should also be noted that the JARPA surveys extend over a larger period of the year than the IWC/IDCR-SOWER surveys (see Tables 5.6 and 5.7), and so might be negatively biased because some of this period might correspond to lower proportions of minke whales migrated to the area surveyed. Thus, direct comparison of the two surveys is hardly possible. Nonetheless, the abundance estimates calculated from these two surveys seem fairly compatible, and suggest an abundance of about 60 thousand minke whales in Area IV over the 1990s. The abundance of minke whales in Area V is much larger, about 200 thousand animals over this period.

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Blue whales

Tables 5.8 and 5.9 show abundance estimates of blue whales in IWC Management Areas IV and V respectively calculated from data obtained from the JARPA surveys[6], again using a similar abundance estimation method used by Branch and Butterworth (2001a, 2001b). Figure 5.5 plots these estimates as well as those obtained for comparable areas south of 60°S (using extrapolation where necessary) from the IWC/IDCR-SOWER surveys for comparison purposes. Again, although comparison is not straightforward for reasons given in the previous section, the abundance estimates calculated from these two surveys seem fairly compatible, suggesting an abundance of blue whales of about 300 animals in Area V over the 1990s and also in Area IV over the latter part of this period. However, the confidence intervals of the abundance estimates are very large as a

[6] While the "skipping" survey design for JARPA catcher vessel may cause non-random sampling of minke whales and hence some bias in resultant estimates of abundance, this does not necessary apply to other species (not caught by these vessels) as their distributions do not seem to be highly correlated with those of minke whales.

result of the small numbers of animals sighted. Thus, these abundance estimates should be regarded as very approximate figures only.

Humpback whales

Tables 5.10 to 5.15 show various abundance estimates available for humpback whales for breeding stocks A to G[7] (see Figure 4.1 for the map of the location of these stocks) obtained from various surveys ranging from winter sighting surveys on migration corridors to sighting surveys in the Antarctic in summer. Abundance estimates for breeding stock A (corresponding roughly to whales feeding in Area II), B (corresponding roughly to whales feeding in Area II and III) and C (corresponding roughly to whales feeding in Area III) are about 3,000, 1,000 and 12,000 respectively in the early 2000s (Tables 5.10 to 5.12). The estimate for breeding stock C involves adding an estimate for C3 for 1994, extrapolated to allow for the population increase rate for C1, to the later estimate for C1 (Johnston and Butterworth 2005b).

For breeding stock D (corresponding roughly to whales feeding in Area IV), abundance estimates calculated based on sighting data obtained during JARPA surveys in Area IV in the summer season seem to be large compared to those calculated from sighting data obtained from aerial surveys around the western Australian coast during the winter season (Table 5.13). This may partly be due to some animals from breeding stock E also feeding in Area IV and thus being sighted here. Also there could be some possibility that not all the animals found in the Antarctic migrate to lower latitudes in winter. Because of these complications, it is difficult to draw conclusions about the probable abundance of this stock; nonetheless, it seems likely that there were more than 10 thousand animals by the year 2000. For breeding stocks E (corresponding roughly to whales feeding in Area V) and G (corresponding roughly to whales feeding in Area I), abundances may be about 7,000 and 2,000 animals respectively in recent years (Tables 5.14 and 5.15).

Thus, sighting data obtained from various surveys other than from the IWC/IDCR-SOWER surveys suggest that, combining areas, there seems to be at least some 35 thousand humpback whales in the Southern Hemisphere over recent years. This number is within the range of adjusted abundance estimates calculated from data obtained from the IWC/IDCR-SOWER surveys as shown in Table 5.5.

[7] No population abundance estimate is available for stock F.

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Fin whales

Tables 5.16 and 5.17 show abundance estimates for fin whales in IWC Management Areas IV and V respectively, calculated from data obtained from JARPA surveys using a similar abundance estimation method to that applied by Branch and Butterworth (2001a, 2001b). There were no sightings of fin whales in Area IV[8] during the third circumpolar set of surveys for the IWC/IDCR-SOWER surveys; however, data obtained from JARPA surveys suggest that recently there have been at least 1,000 of these whales in this Area (Table 5.16). This difference between the two surveys could be partly caused by the small longitudinal area surveyed during the 1994 IWC/IDCR-SOWER surveys.

The abundance estimates shown in Table 5.16 fluctuate considerably, and this could be due to the fact that the main concentrations of these animals are north of 60°S and the extent of the southern migration to higher latitudes varies between years.

For the abundance estimates in Area V, although again the comparison between the IWC/IDCR-SOWER surveys and the JARPA surveys are not straightforward with only a single survey (1991) in Area V for the third set of circumpolar surveys for which the estimate was 540 (CV 0.76), this seems reasonably compatible with the abundance estimate of 726 (CV 0.31) obtained from the JARPA survey in 1990.

5.3 Abundance trend estimation for baleen whales

More than 30 years have now passed since the reduction and subsequent protection of the populations of large baleen whales in the Antarctic, and it is of great interest to determine whether the populations that once were exploited extensively have been recovering in recent years. Various surveys have been carried out to monitor the abundance trends of the baleen whale species in the Antarctic, and there are some indications of recovery for humpback whales, blue whales and to a lesser extent fin whales. However, these indications are often restricted to certain stocks or certain areas in the Antarctic. The evidence on trends for each of the four species considered here is reviewed below.

[8] Note that only 10 degrees of longitude was covered in this Area in 1994 which the analysis is based on.

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Minke whales

As detailed in section 5.1 above, Branch and Butterworth (2001a) suggest that minke whale population estimates declined by about 50% from the second set of IWC/IDCR-SOWER circumpolar surveys (1985-1990) to the third (1991-1997), although their calculations required some extrapolations as at the time they were carried out the third circumpolar set of surveys had not yet been completed. There have been in-depth discussions in the IWC Scientific Committee on the plausibility of this as a real decline, since there are various biases associated with the estimates as have been detailed earlier in this Chapter. However, even after quantifying most of the biases associated with the minke whale abundance estimates that are listed in Table 5.2, the adjusted abundances shown in Table 5.5 still show a major decline.

As reported in Table 5.6 and Table 5.7, calculations of minke whale abundance trends in IWC Management Areas IV and V based on JARPA sightings over the period for 1989–2003 give small positive point estimates of rates of increase in minke whale abundances in Areas IV and V, but these estimates do not differ significantly from zero (see 95% CIs on estimated rates of increase shown in these Tables).

Butterworth *et al.* (1999, 2002) in an analysis of minke whale catch-at-age data for Areas IV and V, together with JARPA and IWC/IDCR-SOWER estimates of abundance, suggest a statistically significant increase in minke whale recruitment and abundance until a peak in the late 1960's, followed by a drop and then stabilization for more recent years. An updated and also extended version of these studies have been conducted by Mori and Butterworth (2005), the details of which are provided in Section 2 of this thesis. Those computations suggest a statistically significant reduction in the total (1+) minke whale population in the IWC Management Areas IV and V combined from 1970 to 2000 at a rate of 2.4% per year, a result discussed further in Section 2.

Whether the decrease in minke whale abundance suggested by Branch and Butterworth (2001a), Butterworth *et al.* (1999, 2002), and in Section 2 of this thesis (arising from Mori and Butterworth 2005) is real or an artifact (and if it is real, what the magnitude of the decline might be) is still in the process of discussion in the IWC Scientific Committee. Final conclusions should be drawn only once the analysis of the third set of circumpolar surveys has been completed. However, information from IWC/IDCR-SOWER surveys, catch-at-age analyses of minke whales and some analyses of time-trends in biological parameters for this species which will be discussed in Chapter 10, all suggest some decline in the abundance of this species from about 1970-1980, perhaps

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stabilizing in more recent years[9].

Blue whales

A recent analysis of blue whale abundance estimates from surveys by Branch *et al.* (2004) yields an estimated 7.3% per year (95% CI: 1.4;11.6%) increase. This approach uses Bayesian models to fit information from three long-term series of sighting surveys: IWC/IDCR-SOWER, JSV and JARPA, which cover the period from the late 1960s to the present. Information used to develop the prior distributions for the maximum possible population growth rate used for the Bayesian analysis included blue whale biology, meta-analyses of other populations of blue whales, and meta-analyses of formerly depleted populations of other large baleen whales. The results were not too dependent on the priors, being driven mainly by the increasing trends in the abundance estimates, particularly those from the IWC/IDCR-SOWER surveys.

The Branch *et al.* (2004) analyses assume that the abundances in Areas IV and V (obtained from JARPA surveys) are representative of changes in the entire circumpolar abundance of blue whales. However, some concern arises whether this assumption is appropriate, since most of the commercial catch of blue whales came from IWC Management Area II and eventually brought that population to near extinction. Mackintosh (1942) concluded that blue whales are less clearly segregated into different areas than humpback whales. Nevertheless, based mainly on evidence from the concentrations of blue whales reflected in commercial catches and sightings in the Antarctic, he proposed that the distribution of these whales could be divided into six areas extending through some 60-70 degrees of latitude; these he considered could be treated as stocks for management purpose, and believed that they corresponded to biological stocks. Thus, if there is more than one stock of blue whales in the Antarctic, the trend in blue whale abundance could be different depending on which stock (area) of the Antarctic is considered, and the suggested increase rate of 7.3% per year may be different on the Atlantic side of the Antarctic (from which most of the historic catches were taken), and the Pacific side where historic catches were much less (see Figure 13.2). Another point to note here is the wideness of the confidence interval (95% CI: 1.4; 11.6%) associated with the estimate of 7.3% per year.

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[9] Nevertheless some caution should accompany this conclusion as other than for the abundance estimates derived from the IWC/IDCR-SOWER surveys, these results all pertain to Areas IV and V, and it is unclear whether trend for other Areas would be the same.

Rademeyer *et al.* (2003a) considered density estimates for blue whales from IWC/IDCR-SOWER surveys by IWC Management Area, and investigated whether there is a statistically significant increase in abundance for this species by using various statistical approaches as well as a population modeling approach. GLM analyses taking different Management Areas into account as factors indicated an 11% per year (95% CI: 2.0; 20.0%) increase in the density of blue whales. Fitting an age-aggregated production model to the abundance estimates obtained from IWC/IDCR-SOWER surveys and JARPA surveys indicated the abundances in Areas II and IV to be particularly low relative to their estimated pre-exploitation levels. This point is important if blue whales indeed consist of more than one stock.

There is also a concern that the IWC/IDCR-SOWER surveys extended further north to 60°S in the third circumpolar set of surveys, possibly into waters containing a higher proportion of pygmy blue whales. Alternatively, the migration patterns of pygmy blue whales may have shifted further south over time, increasing their numbers south of 60°S. Either factor may have inflated the number of blue whale sightings over time. However, Branch *et al.* (2004) note that the proportion of pygmy blue whales south of 60°S is thought to be small, no more than 7% (IWC 2003), which is hardly enough to explain the observed increase in blue whale sightings. Furthermore, they note that recent analyses based on genetics (LeDuc *et al.* 2003), morphology and behaviour (Kato *et al.* 2002), and song type (McDonald *et al.* 2005) provide little evidence for a southward shift in the pygmy blue whale populations. Thus, any such effect can probably be disregarded.

In summary, the two studies discussed above indicate an average increase rate in blue whale abundance of about 7 to 11% per year, and the rate may depend on whether one considers blue whales in the Southern Hemisphere to be one or more than one stock, and the CVs associated with these estimates are high. At present, there is not enough information to determine this, but caution should be exercised as the recovery of these whales in regions where historic whaling was more intensive than in others (i.e. Areas II, III and IV) might be slower than the other regions where there was comparatively less harvesting during the commercial whaling period. Continuation of sighting surveys such as IWC/IDCR-SOWER and JARPA will be very valuable to improve the precision of the estimated rate of recovery of this species.

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Humpback whales

Abundance estimates for humpback whales estimated from different series of surveys are shown in Tables 5.10 to 5.15 for the various breeding stocks. Only for breeding stocks C, D and E are replicate surveys available to allow the direct estimation of increase rates.

- Breeding stock C (corresponding roughly to whales feeding in Area III) -

Recent studies by Findlay *et al.* (2004) calculated the increase rate of this stock to be 8% per year (95% CI: -1; 17), based on comparison of the results of surveys in 1991 and in 2003. However, given only two surveys, the confidence interval is wide, and the authors note that this estimate must be regarded with caution as analyses of the surveys for both years assume $g(0)$ to be 1 (that all groups were sighted on the trackline) in circumstances where sighting probabilities may have been higher on the more recent survey due to both platform design and observer team size.

- Breeding stock D (corresponding roughly to whales feeding in Area IV) -

By fitting an exponential increase model to the number of whales seen per day of flying, Bannister (1994) calculated the increase rate of this stock to be 10.9% per year (95%CI: 6.9; 13.9) over the period 1963 to 1991. Recent analyses by Matsuoka *et al.* (2005) estimated the annual rates of increase for this species for the corresponding Area IV feeding ground to be 16.2% (95%CI: 9.7; 22.7). This calculation was based on the abundance estimates obtained from the sighting survey data from JARPA (1989 to 2003). The confidence interval for the estimate by Matsuoka *et al.* (2005) is quite large; however, JARPA surveys have been conducted in an almost identical manner for more than 10 years, so that the data should give a fairly good indication of the trend in the abundance of this stock. However, as is suggested by mark recapture analysis and mtDNA analysis (Pastene *et al.* 2000), it is evident that humpback whales move between areas, so that there is a possibility that animals from breeding stock E are also being sighted, resulting in a positively biased estimate of the rate of increase of this stock. Thus, the impact of migration to different areas needs to be considered more closely in future analysis. Based primarily on the coastal survey information, it seems appropriate to infer that this stock has been recovering at an increase rate of about 11% per year.

- Breeding stock E (corresponding roughly to whales feeding in Areas V) -

Brown *et al.* (1997) estimated the increase rate of this stock to be 12.1% per year (95% CI: 8.4; 15.8) based on results obtained from analyses of shore based sightings of humpback whales from 1986 to 1996. This followed from fitting a GLM with an assumed over-dispersed Poisson error

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distribution to a sequence of relative population estimates. More recent surveys of a similar kind suggest an increase rate of 10.6% per year (95% CI: 10.1; 11.1) (Noad *et al.* 2005). Analyses by Matsuoka *et al.* (2005) estimated the annual rate of increase to be 6.4% (95% CI: -2.7; 15.5%) based on data obtained from JARPA surveys in the feeding ground of Area V from 1990 to 2002. Again, the confidence interval for the estimate by Matsuoka *et al.* (2005) is quite large, and this may be due to different patterns of movements across Areas for humpback whales in different years.

In summary, humpback whale breeding stocks D and E seem to be recovering at slightly more than 10% per year. Breeding stock C shows a similar increasing trend in abundance, though further surveys are necessary to confirm this result. There is no information on increase rates for stocks migrating to the IWC Management Areas I, II and VI. Abundance estimates obtained from the IWC/IDCR-SOWER surveys shown in Table 5.1 suggest that there are reasonable numbers of humpbacks sighted in these areas, but in the absence of adequate time series of direct observations, any conclusions about the recovery of these stocks has to rest on analogies with the behaviour of breeding stocks C, D and E.

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Fin whales

Recent analyses by Matsuoka *et al.* (2005) using the JARPA sighting data suggest that the fin whales in Area IV and V are increasing at relatively high rates. The annual increase rate of this species is estimated to be 22.9% (95% CI: 8; 38) and 12.9% (95% CI: 6; 19) for Areas IV and V respectively. Abundances estimated by Branch and Butterworth (2001b) also show an increasing trend between the second and third circumpolar set of surveys (see Table 5.1d). However, fin whales are most common in the 50-60°S latitude band, and thus the areas surveyed by the JARPA cruises do not cover the complete summer distributional range for these whales. Accordingly these abundance estimates represent an unknown fraction of total abundance, and Branch and Butterworth (2001b) note further that it is probable that the greater latitudinal range covered in the later years of the IWC/IDCR-SOWER surveys is a contributing factor to the increase in their point estimates of abundance over time. More survey information, particularly for the 50-60°S region, is necessary before firmer conclusions on increase rates can be drawn.

Summary

Table 5.18 summarizes the approximate average annual increase rates for the four major krill-feeding baleen whales considered in this thesis. The general trend of these increase rates

suggests that the large baleen whales that were heavily depleted during the commercial whaling period are now recovering at about 10%/year, whereas there are some indications of a decrease in minke whales which is estimated to be about 2%/year over recent decades[10]. Discussions on possible causes of these trends may be found in Section 3 of this thesis.

5.4 Addendum

At the time this thesis was under final editing, abundance estimates for minke whales based on the full set of cruises constituting the third set of circumpolar surveys became available (Branch 2005). Table 5.A1 compares these estimates with the earlier extrapolated values reported in Table 5.1a. The differences are not large.

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[10] Here the estimate from the catch-at-age analyses has been used since the abundance estimate for the third circumpolar set of surveys for the IWC/IDCR-SOWER surveys had not yet been completed at the time this thesis was written, and because these analyses incorporate results from both the JARPA and the IWC/IDCR-SOWER surveys.

Table 5.1 Absolute abundance estimates for the baleen whale species in the Southern Hemisphere which are considered in this thesis from circumpolar (CP) sighting surveys (note: the CPIII survey had not yet been completed at the time results quoted were evaluated). "Extrapolate" refers to extending the strata from the region surveyed to the full area south of 60°S. For CPII this involves extrapolation northwards, but not longitudinally. For CPIII there is little northward extrapolation as nearly all surveys extended to 60°S, but there is substantial longitudinal extrapolation given the incomplete nature of CPIII. The 1999 estimate for minke whales was not estimated in Branch (2003) because the survey area covered was a subset of the area covered by the 1993 survey.

a) Minke whales (source: Branch and Butterworth 2001a and Branch 2003).

	Survey Year	Region surveyed		Extrapolate		Extrapolate + like-minke		IWC Management Area
		Abundance	CV	Abundance	CV	Abundance	CV	
CPII	1985	299793	0.14	290724	0.14	323474	0.13	V
	1986	131177	0.18	166000	0.20	172888	0.20	II
	1987	138022	0.27	230761	0.32	261037	0.32	III
	1988	58170	0.23	60180	0.18	64192	0.19	IV
	1989	63972	0.17	104076	0.19	110664	0.19	I
	1990	56807	0.28	60462	0.27	80900	0.27	VI
CPIII	1991	98682	0.18	190081	0.18	217623	0.18	V
	1992	25363	0.22	25363	0.22	29912	0.22	III (0-40°E)
	1993	37479	0.21	37479	0.21	44307	0.21	I (110-60°W)
	1994	31620	0.20	31620	0.20	32296	0.21	III (40-80°E)
	1995	37839	0.21	37839	0.21	45312	0.21	VI (170-140°W)
	1996	28158	0.24	21828	0.26	29820	0.26	II (0-30°W)
	1997	15428	0.28	15506	0.26	16863	0.25	II (25-60°W)
	1998	6586	0.34	6586	0.34	9125	0.33	IV (80-130°E)
	2000	35691	0.31	35691	0.31	39443	0.31	I & VI (140-110°W)
	SUM CPII	747941	0.09	931477	0.11	1031229	0.11	
	SUM CPIII	312167	0.09	402474	0.10	473092	0.10	

b) Blue whales (source: Rademeyer *et al.* 2003a).

	Survey Year	Region surveyed		Extrapolate		Extrapolate + like-blue		IWC Management Area
		Abundance	CV	Abundance	CV	Abundance	CV	
CPII	1985	196	0.70	196	0.70	194	0.70	V
	1986	130	0.62	164	0.68	163	0.69	II
	1987	115	0.76	115	0.76	114	0.76	III
	1988	0	-	0	-	0	-	IV
	1989	87	0.88	184	0.99	183	0.99	I
	1990	22	0.84	22	0.84	22	0.84	VI
CPIII	1991	226	0.55	462	0.59	469	0.60	V
	1992+1994	214	0.64	214	0.64	214	0.64	III
	1993+2000	80	0.55	80	0.55	80	0.56	I
	1995+2000	456	0.65	456	0.65	454	0.65	VI
	1996+1997	260	0.41	232	0.42	235	0.42	II
	1998	630	0.65	630	0.65	632	0.65	IV (80-130°E)
	SUM CPII	549	0.48	680	0.40	675	0.40	
	SUM CPIII	1865	0.41	2074	0.29	2085	0.29	

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c) Humpback whales (source: Branch and Butterworth 2001b)

	Survey Year	Region surveyed		Extrapolate		Extrapolate + like minke		IWC Management Area
		Abundance	CV	Abundance	CV	Abundance	CV	
CPII	1985	528	0.51	568	0.47	566	0.47	V
	1986	467	0.42	424	0.38	423	0.39	II
	1987	756	0.48	1104	0.54	1100	0.55	III
	1988	3138	0.54	3701	0.50	3786	0.49	IV
	1989	1320	0.39	2777	0.37	2768	0.37	I
	1990	2378	0.55	2717	0.49	2708	0.49	VI
CPIII	1993	1033	0.33	1033	0.33	955	0.31	I (110-60°W)
	1996+1997	1405	0.70	1256	0.29	1224	0.80	II
	1992+1994	2900	0.28	2900	0.28	2764	0.28	III
	1994	117	0.37	117	0.47	67	0.47	IV (70-80°E)
	1991	2066	0.47	3734	0.35	4308	0.34	V
	1995	1769	0.41	1769	0.57	1861	0.39	VI (170-140°W)
	SUM CPII	8587	0.17	11292	0.16	11349	0.16	
	SUM CPIII	9289	0.19	10808	0.18	11179	0.19	

d) Fin whales (source: Branch and Butterworth 2001b)

	Survey Year	Base case		Extrapolate		Extrapolate + like fin		IWC Management Area
		Abundance	CV	Abundance	CV	Abundance	CV	
CPII	1985	291	0.72	211	0.72	202	0.74	V
	1986	479	0.57	520	0.57	499	0.59	II
	1987	324	0.75	338	0.73	324	0.75	III
	1988	0	-	0	-	0	-	IV
	1989	70	0.81	70	0.81	67	0.83	I
	1990	980	0.56	1125	0.57	1468	0.61	VI
CPIII	1993	411	1.74	411	1.74	518	1.74	I (110-60°W)
	1996+1997	1513	0.67	637	0.64	803	0.64	II
	1992+1994	0	-	0	-	0	-	III
	1994	0	-	0	-	0	-	IV (70-80°E)
	1991	269	0.82	540	0.76	681	0.76	V
	1995	3263	0.62	3263	0.62	6034	0.66	VI (170-140°W)
	SUM CPII	2144	0.32	2264	0.34	2561	0.38	
	SUM CPIII	5455	0.43	4850	0.46	8036	0.51	

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Table 5.2 Factors that may affect the abundance estimates of minke, humpback, fin and blue whales in the Antarctic and their potential impact (evaluated as H=High, M=Medium and L=Low) on these estimates. In virtually all instances, ignoring the factor leads to "underestimation" (negatively biased estimation) of abundance.

Factors that may affect the abundance estimates	**Potential impact by species**			
	Minke	**Humpback**	**Fin**	**Blue**
Assumption of $g(0)=1$	H	M	L	L
Unsurveyed area within 60°S	M	M	M	M
Unsurveyed area in the pack ice	H	L	L	M
Unsurveyed area north of 60°S	L	M	H	L
Sightings that were classified as "like-species"	M	L	M	L
Estimation of mean school size	L	L	L	L
Survey timing and the migration peak	L	L	L	L

Table 5.3 Minke whale abundance estimates which adjust the estimates of Branch and Butterworth (2001a) for various potential bias factors. The comparable abundance estimates are taken from Branch (2003), the multiplier for the timing of the survey and the minimum and maximum possible effect of $g(0)<1$ are taken from Table 8 of Butterworth *et al.* (2003), those for the alternative school size estimation method and for including the like-minke whales are taken from Butterworth *et al.* (2001), and the extrapolation factor for animals north of 60°S is taken from Borchers (1991). Since Butterworth *et al.* (2003) did not extend their estimates of the effect of $g(0)<1$ to the first circumpolar set of surveys, the adjustments used below for this factor for these surveys is assumed to be the same as for the second circumpolar set of surveys. The * used to denote that the CPIII has not yet been completed.

a) Closing mode

Survey	Comparable abun. est.	Timing of the survey	Alt. school size mean	Min effect of $g(0)<1$	Max effect of $g(0)<1$	Extrapolation to north of 60°S	Include like-minke	Min. Bias corrected abun. est.	Max. Bias corrected abun. est.	Min. Bias corrected abun. est. + like	Max. Bias corrected abun. est. + like
1978	110938	1.00	1.00	1.24	1.71	1.18	1.00	161932	223851	161932	223851
1979	145967	1.02	0.97	1.24	1.71	1.18	1.00	210768	291361	210768	291361
1980	212916	1.00	0.91	1.24	1.71	1.18	1.00	282814	390956	282814	390956
1981	55778	1.00	0.97	1.24	1.71	1.18	1.00	78974	109172	78974	109172
1982	92999	1.00	0.98	1.24	1.71	1.18	1.00	133032	183900	133032	183900
1983	84956	1.04	0.92	1.24	1.71	1.18	1.00	118608	163961	118608	163961
1985	225102	1.03	0.90	1.24	1.71	1.18	1.08	304568	421028	329169	455035
1986	142837	1.00	1.00	1.24	1.71	1.18	1.01	208493	288216	209730	289926
1987	157285	1.00	0.80	1.24	1.71	1.18	1.00	183666	253896	183125	253148
1988	81223	1.00	0.97	1.24	1.71	1.18	1.04	115001	158975	119310	164931
1989	128279	1.00	0.99	1.24	1.71	1.18	1.08	185371	256253	200565	277256
1990	57572	1.00	0.96	1.24	1.71	1.18	1.16	80674	111522	93532	129297
1991	210202	1.00	1.00	1.33	1.97	1.18	1.07	329891	488636	354021	524376
1992	23322	1.00	1.00	1.33	1.97	1.18	0.98	36602	54214	35823	53061
1993	30993	1.01	1.00	1.33	1.97	1.18	1.13	48903	72435	55479	82176
1994	24234	1.12	0.94	1.33	1.97	1.18	0.73	40115	59418	29216	43275
1995	31950	1.09	0.97	1.33	1.97	1.18	1.15	52943	78420	60826	90095
1996	25616	1.01	1.01	1.33	1.97	1.18	1.17	41022	60762	47815	70824
1997	20798	1.08	0.99	1.33	1.97	1.18	0.79	34825	51583	27481	40705
CPI	703554							986128	1363201	986128	1363201
CPII	792298							1077774	1489890	1135431	1569593
CPIII*	367115							584300	865467	610661	904513

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b) IO mode

Survey	Comparable abun. est.	Timing of the survey	Alt. school size mean	Min effect of $g(0)<1$	Max effect of $g(0)<1$	Extrapolation to north of 60°S	Include like-minke	Min. Bias corrected abun. est.	Max. Bias corrected abun. est.	Min. Bias corrected abun. est. + Like	Max. Bias corrected abun. est. + Like
1985	307451	1.03	0.92	1.52	2.40	1.18	1.06	522052	820758	553375	870004
1986	159596	1.00	1.00	1.52	2.40	1.18	1.00	287005	451223	287005	451223
1987	244408	1.00	0.80	1.52	2.40	1.18	1.15	351619	552808	404362	635729
1988	55549	1.00	0.98	1.52	2.40	1.18	1.06	97897	153912	103771	163146
1989	97823	1.00	0.99	1.52	2.40	1.18	1.06	174158	273807	184607	290236
1990	57134	1.00	0.97	1.52	2.40	1.18	1.36	99663	156688	135541	213095
1991	174496	1.00	1.00	1.61	2.54	1.18	1.14	331302	522176	377684	595280
1992	24970	1.00	1.00	1.61	2.54	1.18	1.20	47409	74722	56890	89667
1993	37459	1.01	1.00	1.61	2.54	1.18	1.16	71730	113056	83207	131145
1994	32761	1.11	0.94	1.61	2.54	1.18	1.45	64731	102025	93860	147936
1995	36988	1.08	0.95	1.61	2.54	1.18	1.15	72234	113851	83069	130928
1996	20457	1.02	1.01	1.61	2.54	1.18	1.41	40111	63220	56556	89140
1997	11802	1.04	1.00	1.61	2.54	1.18	1.15	23342	36790	26843	42308
CPII	921961							1532393	2409195	1668661	2623433
CPIII*	338933							650858	1025839	778109	1226404

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Table 5.4 Estimated minke whale abundances considering also animals in the pack-ice region (for details, see text). The * is used to denote that the CPIII has not yet been completed.

a) Closing mode

	Year	Animals in the pack ice (Shimada *et al*. (2002))			Combination abundance (Table 5.3)+pack ice						Combination abundance (Table 5.3) +like-minke+pack ice					
					Scenario 1		Scenario 2		Scenario 3		Scenario 1		Scenario 2		Scenario 3	
		Scenario 1	Scenario 2	Scenario 3	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
CPII	1985	14025	79891	41868	318593	435053	384459	500919	346436	462896	343194	469060	409060	534926	371037	496903
	1986	33923	194747	95522	242416	322139	403240	482963	304015	383738	243653	323849	404477	484673	305252	385448
	1987	18604	106579	53258	202270	272500	290245	360475	236924	307154	201729	271752	289704	359727	236383	306406
	1988	21018	119951	61902	136019	179993	234952	278926	176903	220877	140328	185949	239261	284882	181212	226833
	1989	10282	57632	34216	195653	266535	243003	313885	219587	290469	210847	287538	258197	334888	234781	311472
	1990	28781	165983	78184	109455	140303	246657	277505	158858	189706	122313	158078	259515	295280	171716	207481
CPIII	1991	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	1992	12978	75146	34168	49580	67192	111748	129360	70770	88382	48801	66039	110969	128207	69991	87229
	1993	6015	33767	19821	54918	78450	82670	106202	68724	92256	61494	88191	89246	115943	75300	101997
	1994	4963	28633	13465	45078	64381	68748	88051	53580	72883	34179	48238	57849	71908	42681	56740
	1995	23757	138333	59515	76700	102177	191276	216753	112458	137935	84583	113852	199159	228428	120341	149610
	1996	3584	20533	10246	44606	64346	61555	81295	51268	71008	51399	74408	68348	91357	58061	81070
	1997	22671	131937	57084	57496	74254	166762	183520	91909	108667	50152	63376	159418	172642	84565	97789
	CP II	126633	724783	364950	1204407	1616523	1802557	2214673	1442724	1854840	1262064	1696226	1860214	2294376	1500381	1934543
	CP III*	73968	428349	194299	328377	450799	682758	805180	448708	571130	330608	454104	684989	808485	450939	574435

b) IO mode

	Year	Animals in the pack ice (Shimada *et al*. (2002))			Combination abundance (Table 5.3)+pack ice						Combination abundance (Table 5.3) +like-minke+pack ice					
					Scenario 1		Scenario 2		Scenario 3		Scenario 1		Scenario 2		Scenario 3	
		Scenario 1	Scenario 2	Scenario 3	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
CPII	1985	14025	79891	41868	536077	834783	601943	900649	563920	862626	567400	884029	633266	949895	595243	911872
	1986	33923	194747	95522	320928	485146	481752	645970	382527	546745	320928	485146	481752	645970	382527	546745
	1987	18604	106579	53258	370223	571412	458198	659387	404877	606066	422966	654333	510941	742308	457620	688987
	1988	21018	119951	61902	118915	174930	217848	273863	159799	215814	124789	184164	223722	283097	165673	225048
	1989	10282	57632	34216	184440	284089	231790	331439	208374	308023	194889	300518	242239	347868	218823	324452
	1990	28781	165983	78184	128444	185469	265646	322671	177847	234872	164322	241876	301524	379078	213725	291279
CPIII	1991	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	1992	12978	75146	34168	60387	87700	122555	149868	81577	108890	69868	102645	132036	164813	91058	123835
	1993	6015	33767	19821	77745	119071	105497	146823	91551	132877	89222	137160	116974	164912	103028	150966
	1994	4963	28633	13465	69694	106988	93364	130658	78196	115490	98823	152899	122493	176569	107325	161401
	1995	23757	138333	59515	95991	137608	210567	252184	131749	173366	106826	154685	221402	269261	142584	190443
	1996	3584	20533	10246	43695	66804	60644	83753	50357	73466	60140	92724	77089	109673	66802	99386
	1997	22671	131937	57084	46013	59461	155279	168727	80426	93874	49514	64979	158780	174245	83927	99392
	CP II	126633	724783	364950	1659026	2535828	2257176	3133978	1897343	2774145	1795294	2750066	2393444	3348216	2033611	2988383
	CP III*	73968	428349	194299	393524	577631	747905	932012	513855	697962	474393	705092	828774	1059473	594724	825423

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Table 5.5 Possible minimum and maximum corrected abundance estimates of the four baleen whales considered in this thesis when the effects of the possible bias factors shown in Table 5.2 are taken into account for the IWC/IDCR-SOWER second and third set of circumpolar surveys (CPII and CPIII). The * is used to denote that the CPIII has not yet been completed. Note that the values shown for the ratio CPIII/CPII constitute only the ratios of the minimum and maximum estimates, and thus do not reflect the full range of uncertainty for these ratios.

Species	CP II (1985-1990)		CP III* (1991-1997)		CPIII/CPII	
	Min. abundance estimate	Max. abundance estimate	Min. abundance estimate	Max. abundance estimate	Min.	Max.
Minke whales	1200000	3300000	330000	1100000	0.28	0.33
Blue whales	750	1000	2300	3100	3.07	3.10
Humpback whales	26000	96000	25000	95000	0.96	0.99
Fin whales	12000	18000	27000	56000	2.25	3.11

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Table 5.6 Abundance estimates for minke whales in IWC Management Area IV (south of 60 °S) obtained from the JARPA surveys.

Location	Year	month	Survey	Abundance estimate (CV)	ROI p.a. (%) (95% CI)	Abundance estimation methods	Reference
IWC Management Area IV	1989	Jan - mid Feb	Vessel	54539 (0.22)	0.27 (-4.57;3.91)	Line transect survey	Hakamada *et al.* (2005)
	1991	Jan - end Feb		54959 (0.24)			
	1993	End Dec - early Mar		41943 (0.22)			
	1995	End Dec - end Feb		42134 (0.22)			
	1997	Ear Jan - end Feb		32656 (0.25)			
	1999	End Dec - early Mar		49867 (0.17)			
	2001	End Dec - end Feb		68503 (0.17)			
	2003	End Dec - end Feb		47858 (0.36)			

Table 5.7 Abundance estimates for minke whales in IWC Management Area V (south of 60 °S) obtained from JARPA surveys.

Location	Year	month	Survey	Abundance estimate (CV)	ROI p.a. (%) (95% CI)	Abundance estimation methods	Reference
IWC Management Area V	1990	Mid Jan - end Feb	Vessel	195743 (0.21)	2.50 (-1.36;6.17)	Line transect survey	Hakamada *et al.* (2005)
	1992	Jan - early Mar		122048 (0.23)			
	1994	End Dec - early Mar		168566 (0.27)			
	1996	Jan - mid Mar		171332 (0.26)			
	1998	Jan - mid Mar		198423 (0.23)			
	2000	Jan - mid Mar		179796 (0.21)			
	2002	Jan - early Mar		226884 (0.16)			

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Table 5.8 Abundance estimates for blue whales in IWC Management Area IV (south of 60 °S) obtained from the JARPA surveys.

Location	Year	month	Survey	Abundance estimate (CV)	ROI p.a. (%) (95% CI)	Abundance estimation methods	Reference
IWC Management Area IV	1989	Jan - mid Feb	Vessel	65 (0.48)	14 (-9; 37)	Line transect survey	Matsuoka *et al.* (2005)
	1991	Jan - end Feb		17 (1.08)			
	1993	End Dec - early Mar		64 (0.62)			
	1995	End Dec - end Feb		6 (0.94)			
	1997	Ear Jan - end Feb		153 (0.61)			
	1999	End Dec - early Mar		218 (0.40)			
	2001	End Dec - end Feb		295 (0.44)			
	2003	End Dec - end Feb		92 (0.72)			

Table 5.9 Abundance estimates for blue whales in IWC Management Area V (south of 60 °S) obtained from JARPA surveys.

Location	Year	month	Survey	Abundance estimate (CV)	ROI p.a. (%) (95% CI)	Abundance estimation methods	Reference
IWC Management Area V	1990	Mid Jan - end Feb	Vessel	205 (1.01)	-1 (-37; 34)	Line transect survey	Matsuoka *et al.* (2005)
	1992	Jan - early Mar		231 (0.67)			
	1994	End Dec - early Mar		275 (0.64)			
	1996	Jan - mid Mar		7 (0.75)			
	1998	Jan - mid Mar		221 (2.07)			
	2000	Jan - mid Mar		294 (0.49)			
	2002	Jan - early Mar		142 (0.53)			

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Table 5.10 Various abundance estimates for humpback whales (other than from IWC/IDCR-SOWER surveys): **breeding stock A**.

Location	Year	month	Survey	Abundance estimate (CV)	ROI p.a. (%) 95% CI	Abundance estimation methods	References
Abrolhos, Brazil	1995	July - Nov	Vessel	1634 (0.09)	-	Empirical Bayesian method based on photo identification	Kinas and Bethlem (1998)
Abrolhos, Brazil (16°40'S, 19°30'S; 37°25'W, 39°45'W)	1996-2000	July - Nov	Vessel	1389-3977 (0.27)	-	Chapman-corrected Petersen estimates based on photo identification	Freitas *et al.* (2002)
Northeastern Brazil	1999-2000	Aug - Sept	Vessel	628 (0.34)	-	Line transect survey	Zerbini *et al.* (2004)
North limit of Bahia state (12°10'S) till the south limit of Espírito Santo State (20°42'S), Brazil	2001	Aug - Sept	Aerial	2291 (0.45)	-	Parallel transect survey	Andriolo *et al.* (2002)
	2002	Aug - Sept	Aerial	2663 (0.13)	-	Parallel transect survey	Andriolo *et al.* (2003)

Table 5.11 Abundance estimate for humpback whales (other than from IWC/IDCR-SOWER surveys): **breeding stock B**.

Location	Year	month	Survey	Abundance estimate (CV)	ROI p.a. (%) 95% CI	Abundance estimation methods	References
Coastal waters of Gabon	2002	August	Aerial	1259 (0.29)	-	Line transect survey	Rosenbaum *et al.* (2004)

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Table 5.12 Various abundance estimates for humpback whales (other than from IWC/IDCR-SOWER surveys): **breeding stock C**.

Sub-stock	Location	Year	Month	Survey	Abundance estimate (CV)	ROI p.a. (%) (95% CI)	Abundance estimation methods	References
C1	Cape Vidal (28°07'S, 32°33'E)	1990	June - Oct	Shore-based	1777 (≈0.12)	-	Shore-based sighting survey	Findlay and Best (1996)
	Coastal waters of southern and central Mozambique	1991	Aug - Sep	Vessel	1954 (0.38)	-	Line transect survey	Findlay *et al.* (1994)
	Between Cabo Inhaca (26° 00' S; 33° 05' E) and just north of Mozambique Island (14° 26' S; 40° 53' E)	2003	Aug - Sep	Vessel	5729 (0.12) [5039 for the same area as surveyed in Findlay *et al.* (1994)]	7.89 (-1;17)	Line transect survey	Findlay *et al.* (2004)
C3	Southern Madagascar	1994	Aug - Sep	Vessel	2532 (0.27)	-	Line transect survey	Best *et al.* (1996)

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Table 5.13 Various abundance estimates for humpback whales (other than from IWC/IDCR-SOWER surveys): **breeding stock D**.

Location	Year	Month	Survey	Abundance estimate (CV)	ROI p.a. (%) (95% CI)	Abundance/trend estimation methods	References
Off western Australian coast (Shark Bay)	1991	Mid July	Aerial	3302	10.9 (6.9;13.9)	Comparison of the 1991 aerial survey sighting rate with those from a 1963 commercial spotter	Bannister (1994)
Off northwestern Australia	1991-1992	June and July	Vessel	3878 (0.43)	-	Mark re-capture method based on photo-identification	Jenner and Jenner (1994)
Off western Australian coast (Shark Bay)	1999	June - August	Aerial	8207-13460	-	Combining standard aerial line transect methodology with a migration count approach	Bannister and Hedley (2001)
IWC Management Area IV	1989	Early Dec - mid Mar	Vessel	5230 (0.30)	16.2 (9.7;22.7)	Line transect survey	Matsuoka *et al.* (2005)
	1991	Early Dec - end Mar		5350 (0.19)			
	1993	Early Dec - mid Mar		2740 (0.15)			
	1995	End Dec - mid Mar		8850 (0.14)			
	1997	Early Dec - mid Mar		10874 (0.17)			
	1999	Early Dec - mid Mar		16211 (0.15)			
	2001	End Nov - early Mar		33010 (0.11)			
	2003	End Dec - end Feb		31750 (0.11)			

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Table 5.14 Various abundance estimates for humpback whales (other than from IWC/IDCR-SOWER surveys): **breeding stock E.**

Sub-stock	Location	Year	Month	Survey	Abundance estimate (CV)	ROI p.a. (%) (95% CI)	Abundance estimation methods	References
E1	East Australian Coast (North Stradbroke Island on the Queensland coast)	1996	End May - end Aug	Land -based	3185 (0.07)	12.1 (8.4;15.8) for the period of 1981-1996	Number of pods counted × mean pod size × correction factor for pods missed during unmonitored periods	Brown *et al.* (1997)
		2004			6555 (0.03)	10.6 (10.1; 11.1)	Stratified random sampling theory	Noad *et al.* (2005)
	IWC Management Area V	1990	Mid Dec - mid Mar	Vessel	1354 (0.20)	6.4 (-2.7;15.5)	Line transect survey	Matsuoka *et al.* (2005)
		1992	Early Dec - end Mar		3837 (0.63)			
		1994	Early Dec - mid Mar		3565 (0.31)			
		1996	End Nov - mid Mar		1543 (0.28)			
		1998	Early Jan - end Mar		8301 (0.31)			
		2000	Early Dec - mid Mar		4720 (0.22)			
		2002	Early Dec - ear Mar		2735 (0.16)			
E2	Around New Caledonia	1995-2001	July - September	Vessel	327 (0.11)	-	Petersen capture-recapture model based on photo-identification	Garrigue *et al.* (2004)
					533 (0.15)	-	Petersen capture-recapture model based on genotyping	

Table 5.15 Abundance estimate for humpback whales (other than from IWC/IDCR-SOWER surveys): **breeding stock G.**

Location	Year	Month	Survey	Abundance estimate (CV)	ROI p.a. (%) 95% CI	Abundance estimation methods	Reference
Central coast of Ecuador (1°26'S, 80°50'W), South America	1996-1997	Jun - Sep	Vessel	1992 (0.50)	-	Mark re-capture method based on photo-identification	Félix and Haase (2001)

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Table 5.16 Abundance estimates for fin whales in IWC Management Area IV (south of 60 °S) obtained from JARPA surveys.

Location	Year	month	Survey	Abundance estimate (CV)	ROI p.a. (%) (95% CI)	Abundance estimation methods	Reference
IWC Management Area IV	1989	Early Dec – mid Mar	Vessel	102 (0.84)	22.9 (8; 38)	Line transect survey	Matsuoka *et al.* (2005)
	1991	Early Dec – end Mar	Vessel	338 (0.50)			
	1993	Early Dec – mid Mar	Vessel	189 (0.45)			
	1995	End Dec – mid Mar	Vessel	1191 (0.32)			
	1997	Early Dec – mid Mar	Vessel	637 (0.34)			
	1999	Early Dec – mid Mar	Vessel	1162 (0.32)			
	2001	End Nov – early Mar	Vessel	7285 (0.28)			
	2003	End Dec - end Feb	Vessel	1388 (0.28)			

Table 5.17 Abundance estimates for fin whales in IWC Management Area V (south of 60 °S) obtained from JARPA surveys.

Location	Year	month	Survey	Abundance estimate (CV)	ROI p.a. (%) (95% CI)	Abundance estimation methods	Reference
IWC Management Area V	1990	Mid Dec – mid Mar	Vessel	726 (0.31)	12.9 (6;19)	Line transect survey	Matsuoka *et al.* (2005)
	1992	Early Dec – end Mar	Vessel	1397 (0.38)			
	1994	Early Dec – mid Mar	Vessel	6334 (0.37)			
	1996	End Nov – mid Mar	Vessel	1294 (0.32)			
	1998	Early Jan – end Mar	Vessel	4655 (0.37)			
	2000	Early Dec – mid Mar	Vessel	4802 (0.25)			
	2002	Early Dec – early Mar	Vessel	3031 (0.33)			

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Table 5.18 Approximate annual rate of increases over the last 2-3 decades for the four baleen whale species considered in this thesis. See text for detailed discussions of the plausibility of the annual rate of increase estimated for each species. Note that demographic analyses (Brandão *et al.* 2000, Clapham *et al.* 2001) indicate that closed humpback whale populations; which seemingly can at best reproduce every second year, cannot attain an increase rate higher than about 13%/year; similar constraints would apply to blue and fin whales.

Species	Approximate average annual rate of increase	References
Minke whales	-2.4%	Mori and Butterworth (2005)
Blue whales	7-11%	Branch *et al.* (2004), Rademeyer *et al.* (2003a)
Humpback whales	>10%	Bannister (1994), Brown *et al.* (1997), Matsuoka *et al.* (2005)
Fin whales	>10%	Matsuoka *et al.* (2005)

Table 5.A1 Comparison of the abundance estimates of minke whales shown in Table 5.1a for the regions surveyed with those of Branch (2005) which reports estimates for the complete third set of IWC/IDCR-SOWER circumpolar surveys.

	Survey Year	Table 5.1 a)		Branch (2005)		Ratio to Table 5.1 a)
		Abundance	CV	Abundance	CV	
CPII	1985	299793	0.14	274190	0.13	0.9
	1986	131177	0.18	140737	0.21	1.1
	1987	138022	0.27	128547	0.31	0.9
	1988	58170	0.23	79362	0.31	1.4
	1989	63972	0.17	63995	0.17	1.0
	1990	56807	0.28	43119	0.26	0.8
CPIII	1991	98682	0.18	110549	0.18	1.1
	1992	25363	0.22	24386	0.20	1.0
	1993	37479	0.21	37859	0.20	1.0
	1994	31620	0.20	29536	0.22	0.9
	1995	37839	0.21	41907	0.27	1.1
	1996	28158	0.24	36798	0.39	1.3
	1997	15428	0.28	17900	0.27	1.2
	1998	6586	0.34	6563	0.34	1.0
	1999	-	-	5999	0.34	-
	2000	35691	0.31	28946	0.20	0.8
	2001			6115	0.33	-
	2002			62020	0.20	-
	2003			120617	0.19	-

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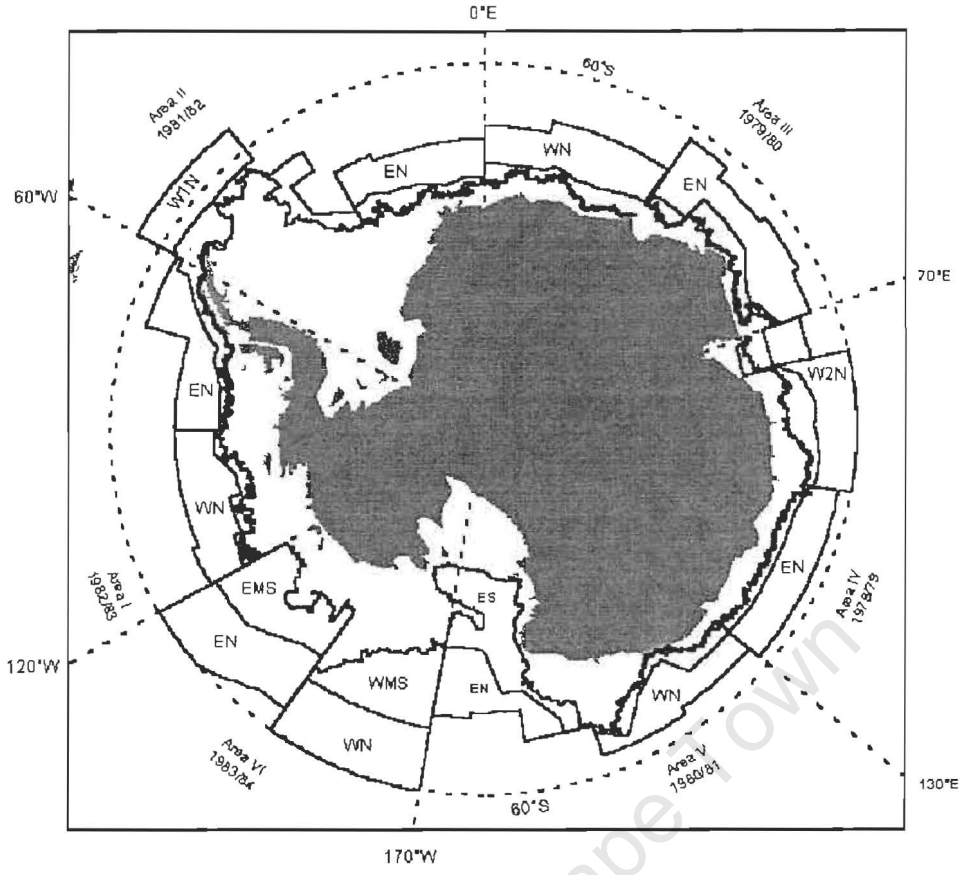


Figure 5.1.1 Areas surveyed during the first circumpolar set of cruises (1978 to 1983) (reproduced with permission from Branch and Butterworth 2001a). The inner line around the continent (shaded) reflects the packice edge found during the surveys.

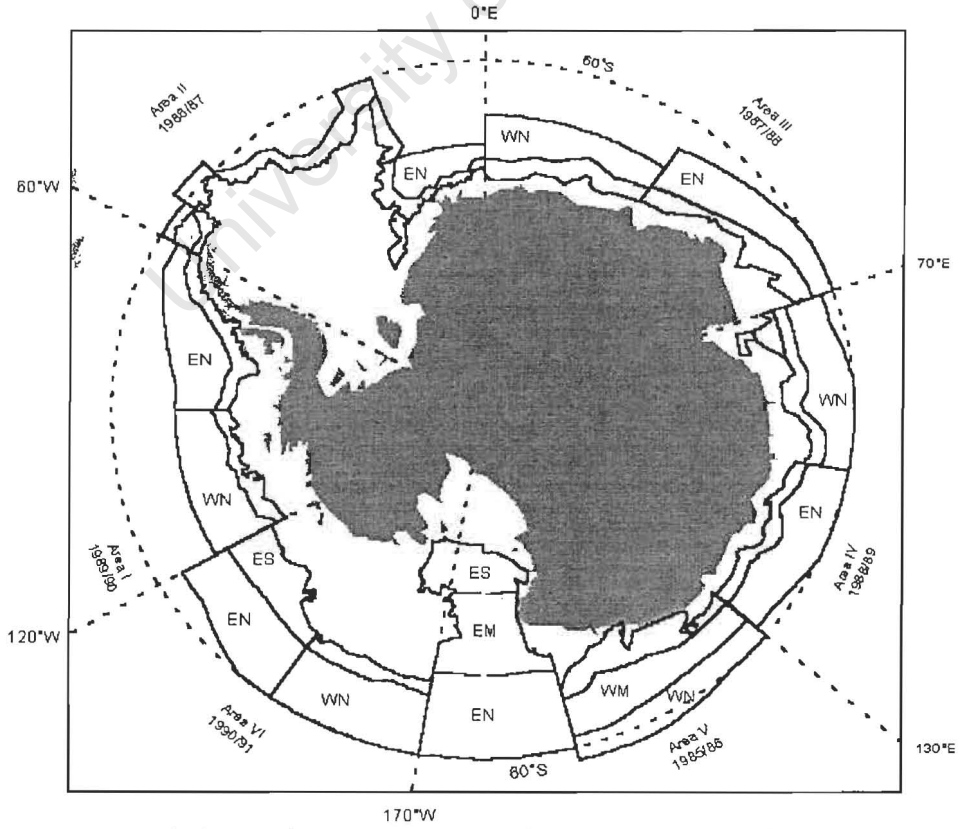


Figure 5.1.2 Areas surveyed during the second circumpolar set of cruises (1985 to 1990) (reproduced with permission from Branch and Butterworth 2001a).

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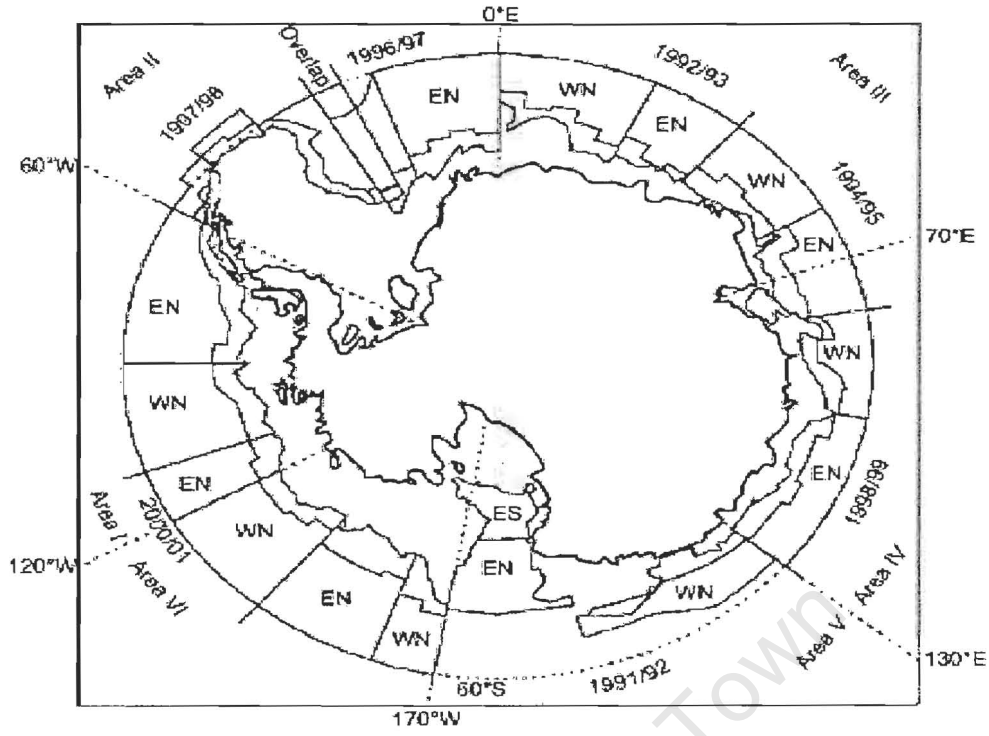


Figure 5.1.3 Areas surveyed during the third circumpolar set of cruises (1991 to 2000) (reproduced with permission from Branch 2003).

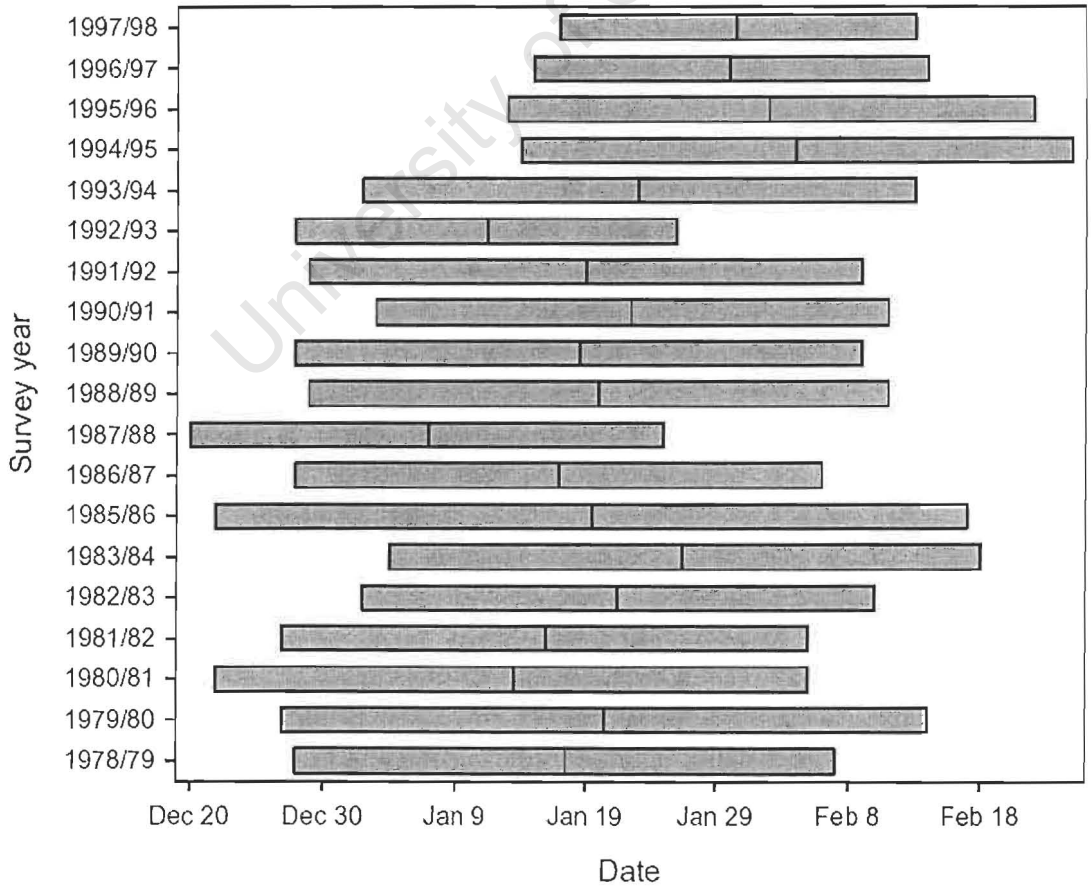


Figure 5.2 Start and end dates of IDCR/SOWER surveys (reproduced with permission from Branch and Butterworth 2001a).

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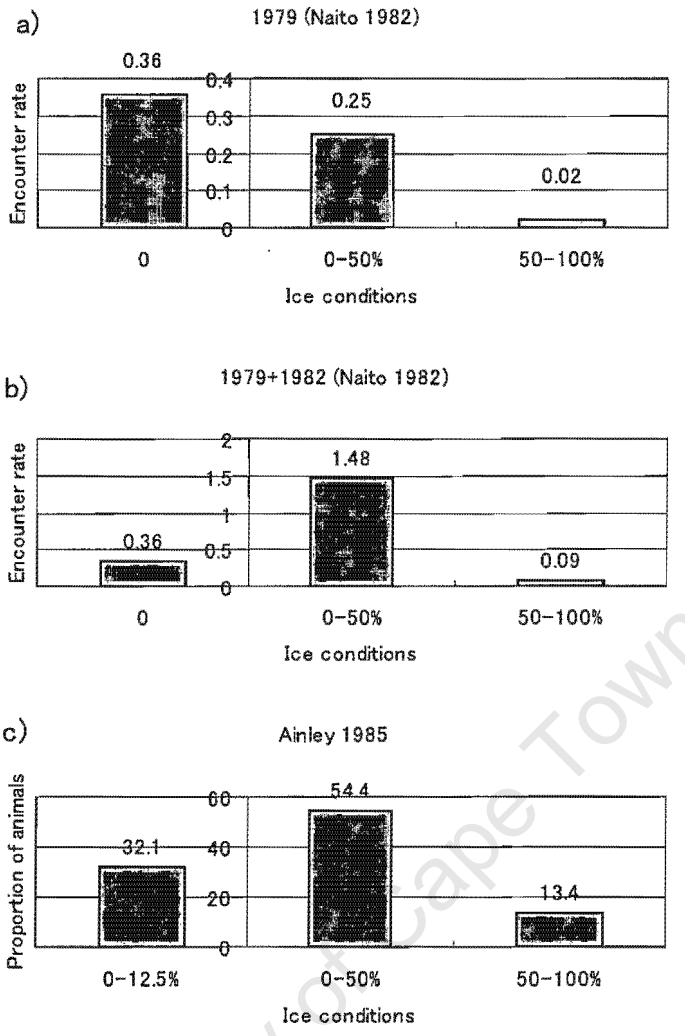
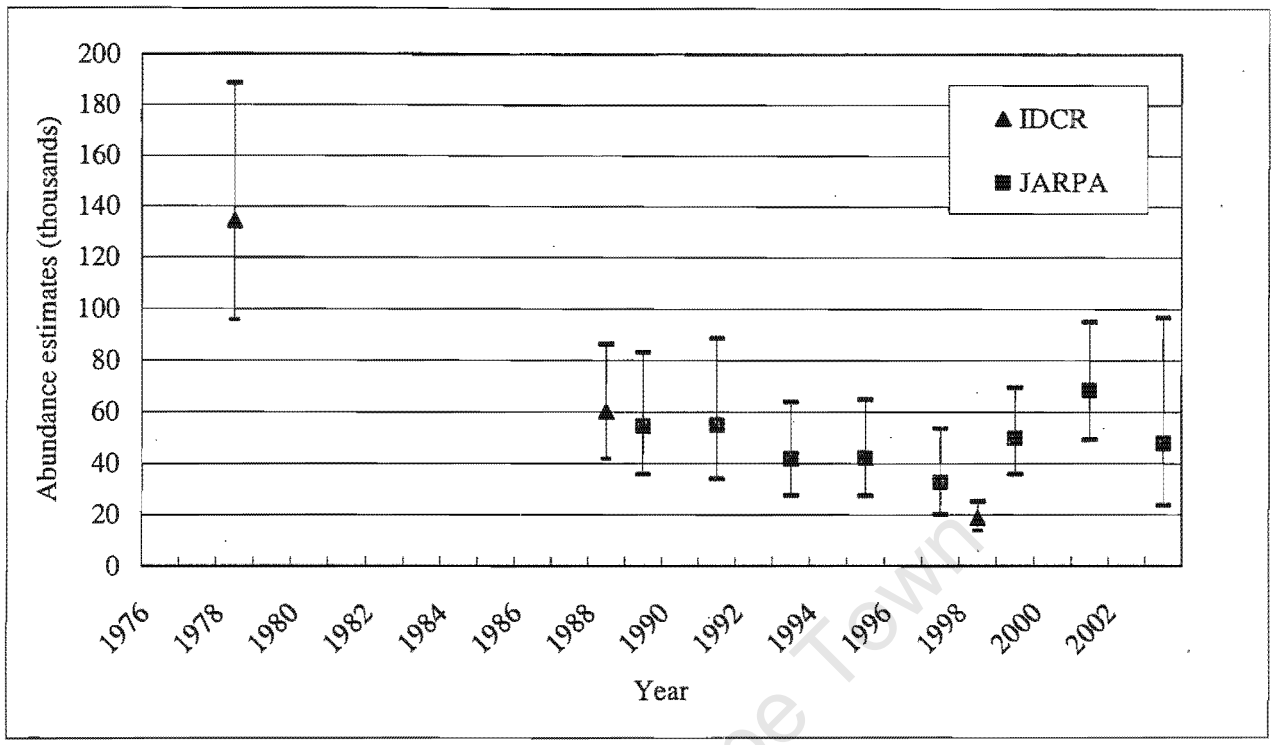


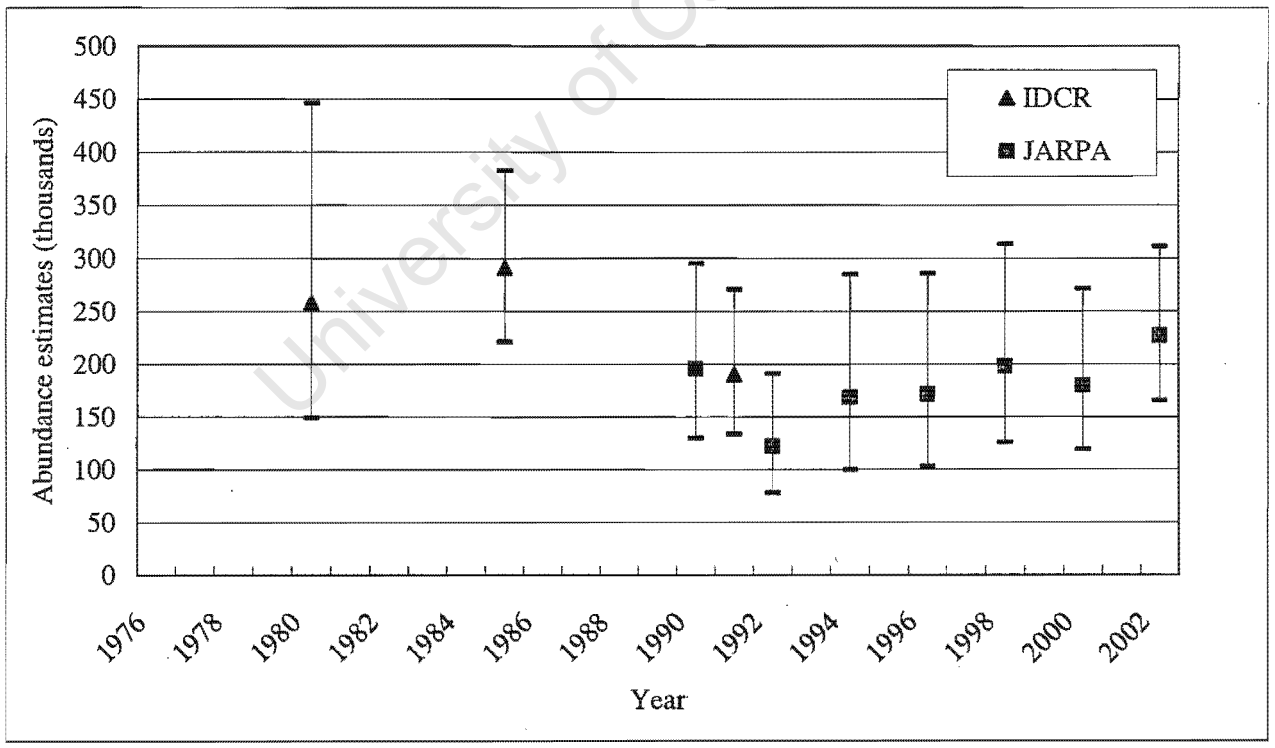
Figure 5.3 The relationship between the encounter rate of minke whales and ice conditions based on various data sources: a) 1979 survey from Naito (1982); b) 1979 and 1982 surveys from Naito (1982); and c) Ross Sea surveys from Ainley (1985) (source: Figures 2 to 4 of Shimada *et al.* 2002). The 0% ice conditions refer to an area just outside the pack ice edge, so corresponding to the southernmost strata on the IDCR-SOWER cruises.

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a) Area IV



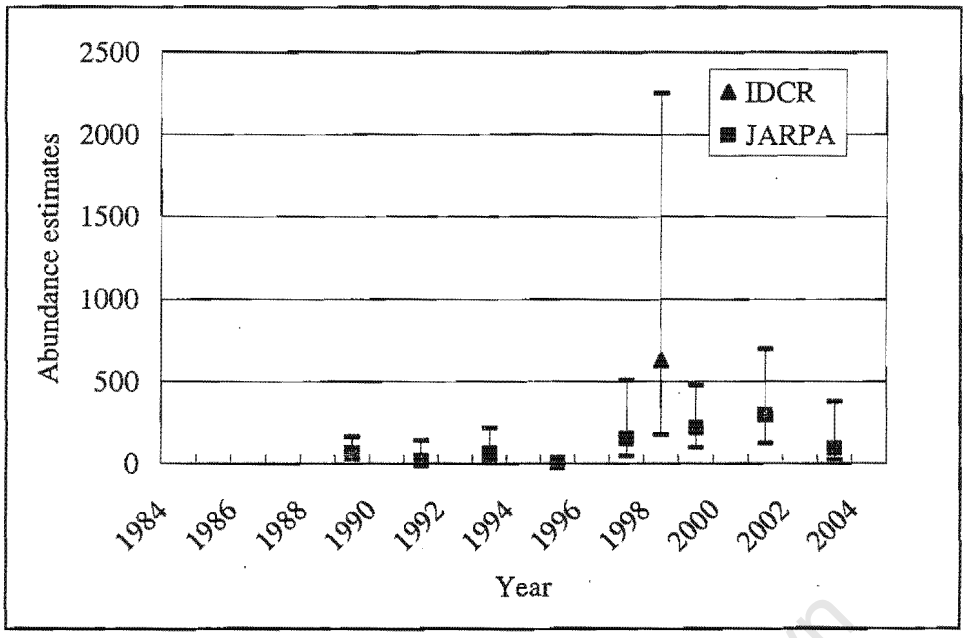
b) Area V



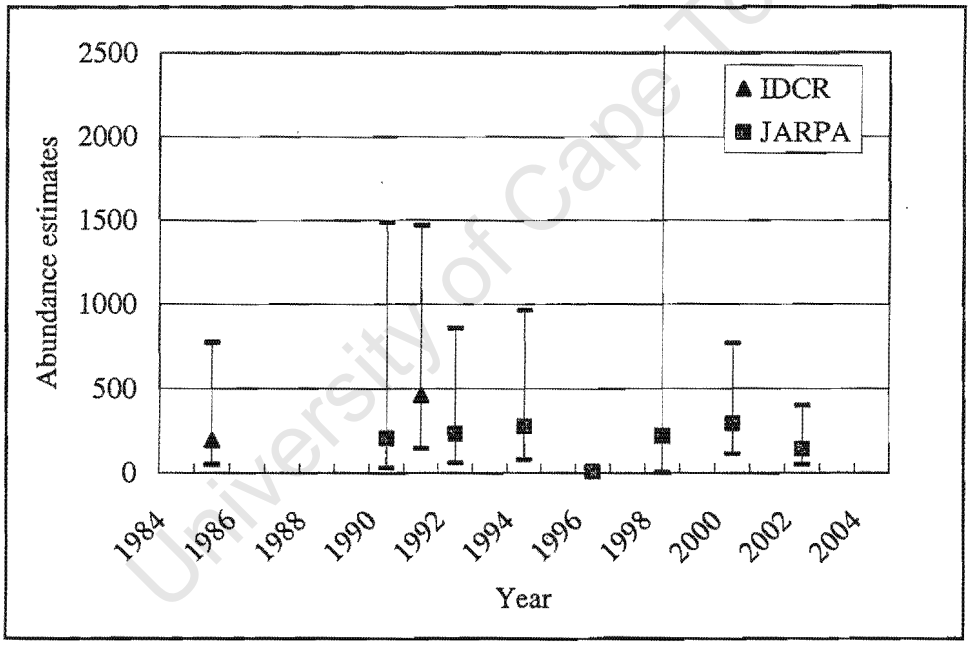
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Figure 5.4 Comparison of minke whale abundance estimates and their 95% CIs for a) Area IV and b) Area V estimated from the IWC/IDCR-SOWER and JARPA surveys. The abundance estimates for the IWC/IDCR-SOWER surveys are provided by Branch (pers. commn), with the details of how these estimates were obtained in Chapter 8, page 151. The abundance estimates for the JARPA surveys are from Hakamada *et al.* (2005) and are listed in Tables 5.6 and 5.7. Both sets of estimates referred to pertain to the whole Area south of 60°S, having been extrapolated where necessary for this purpose.

a) Area IV



b) Area V



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Figure 5.5 Comparison of blue whale abundance estimates and their 95% CIs for a) Area IV and b) Area V estimated from the IWC/IDCR-SOWER and JARPA surveys. The abundance estimates for the IWC/IDCR-SOWER surveys are taken from Table 5.1, whereas those for the JARPA surveys are from Matsuoka *et al.* (2005) and are listed in Tables 5.8 and 5.9.

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CHAPTER 6

ABUNDANCE AND TREND ESTIMATION FOR THE MAIN KRILL-FEEDING SEALS

6.1 Absolute abundance estimates for Antarctic fur seals

Table 6.1 summarizes the available absolute abundance estimates for Antarctic fur seals from various sources of information. Data and methods used to calculate these abundance estimates are described and the difficulties associated with making these estimates are discussed below.

6.1.1 Data/Methods used to calculate the abundance of Antarctic fur seals

Most abundance estimates for Antarctic fur seals are based on raw counts of animals (pups or adult females) from land or ship during the breeding season of mid November to the beginning of April. This method of counting the animals is used for colonies that contain much smaller populations compared to South Georgia, such as the South Shetland Islands, South Orkney Islands, South Sandwich Islands, Kerguelen, McDonald Island, Heard Island, Bouvetøya Island and Marion Island (see Figure 2.2 for a map). Likely errors in the counts are seldom provided for the estimates shown in Table 6.1 (except for the estimate in South Georgia in 1990). Wilkinson and Bester (1990) note that at least for Marion Island, this is due to the large area covered by the count, which prevents repeated counting of beaches within a year to obtain error estimates.

In South Georgia, where the population grew rapidly from the 1950s to the 1990s (as detailed later in this Chapter), data and methods used to calculate the abundances of Antarctic fur seals changed as the size of the population increased (Bonner 1968, Payne 1977, Boyd 1993). A brief history of abundance estimation for Antarctic fur seals in South Georgia is summarized below.

History of abundance estimation of Antarctic fur seals in South Georgia

The abundance estimate of Antarctic fur seals in the 1930s is obtained from the observations of the *Discovery* investigation team which found a total of 38 fur seals in February 1933 after thoroughly

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searching the shores of South Georgia to the north and east from a ship (Bonner 1968). In December 1936, researchers on *Discovery II* found 59 fur seals on Bird Island, of which 12 were probably pups (Bonner 1968). Based on these observations, Bonner (1968) reports that there were probably less than 100 Antarctic fur seals around South Georgia in the 1930s. No further detailed observations are available over the period from 1937 to 1955, but in December 1956, Bonner (1958) found thriving colonies on both Bird Island and on South Georgia itself. A detailed search was made for fur seal rookeries on the islands and on the coast of the mainland adjacent to Bird Sound. In each of the following seasons until 1962, visits were made to Bird Island and the pups were counted by observers from a vantage point on the beach where they checked the seals one by one on a mechanical hand tally counter (Bonner 1968). Bonner (1968) reports that the number of pups counted doubled during the period from 1957 to 1962.

Again from 1964 to 1970 no further systematic observations were made. In 1971, the survey resumed at Bird Island, and extended to mainland South Georgia in 1972, finding that almost all suitable areas on Bird Island had been colonized, as had such large stretches of the mainland coast that pup production there already exceeded that on Bird Island (Payne 1977). Pups were counted from 1971 to 1975 from ship and helicopters. Payne (1977) reports that pups are born within a short period around the same time every year, so that a high proportion of all pups born are available at the time of a count made at the end of December. Payne (1977) reports that as the density of the seals increased, some undercounting of the pups occurred, so that pup counts were calibrated by marking a known number of pups on selected beaches and then conducting mark-recapture studies.

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Pups counted on Bird Island and South Georgia in 1975 totaled 61,234, and Payne (1977) estimated that this would increase to approximately 90,000 pups if many mainland beaches (which had not been surveyed) were also taken into account. A total population estimate of 369,000 was derived by Payne (1979) by multiplying the number of pups estimated by a factor of 4.1. This factor of 4.1 is derived as follows. Information is available giving the number of pups and the numbers of breeding females by age. The latter information is adjusted to provide the total number of adult (≥3 years of age) females by dividing by estimates available for pregnancy rate-at-age. Assuming a 50:50 sex ratios for the pups, this means that only the numbers of 1 and 2 year old females are not available. These are computed from the current number of female births by adjusting for the annual rate of increase of the population (16.8%) and survival rate information for the first two years (76.1% and 95.4% respectively). Male numbers are then derived by assuming a 50:50 sex ratios to age 6, after which values are assumed subject to an additional natural mortality rate. By

using these mortality and increase rates and sex ratios, Payne (1979) estimated the total size of the population to be 4.1 multiplied by the number of pups born. The assumption that sex ratio at birth does not differ appreciably from unity was based on the work of Bonner (1968), who recorded the sex of the pups tagged (877 males and 832 female pups).

Boyd (1993) calculated the total population of Antarctic fur seals at South Georgia in 1990 to be approximately 1,550,000 (95%CI: 1,529,300; 1,980,300). This estimate was based on counting adult female fur seals ashore from land overlooking pupping sites or from a ship following the shoreline. Counts from these two sources were compared, and it was found that in most of the cases counts made from the ship were less than the numbers counted ashore, and that the shore counts were much closer to the absolute number of seals present. Together with corrections for the likelihood of a female being ashore at the time of a survey, and using an estimated pregnancy rate of 71% (obtained from the percentage of tagged females that gave birth at South Georgia in 1990), pup production was estimated from the estimated number of adult females present on the coast of South Georgia during the 1990 pupping season. The factor of 4.1 (Payne 1979) was again used to estimate the total population by multiplying the estimated number of pups born. The confidence interval shown in Table 6.1 reflects only the error associated with estimate of pregnancy rate.

In summary, the abundance estimation method at South Georgia changed from first counting the number of pups, then adding mark recapture approaches, and finally counting the number of adult females ashore.

6.1.2 Difficulties associated with estimating the abundance of Antarctic fur seals

Certain factors that may lead to bias in the abundance estimates of Antarctic fur seals are listed below, together with some discussion on their possible magnitude.

Observer counting bias

Most of the counting of the Antarctic fur seals is carried out by a single observer, so that there has been speculation that there may be some bias in the counts, which vary in size between observers. Boyd (1993) quantified the magnitude of these differences by analyzing the repeated counts of three study beaches by different observers. The differences in numbers counted by the observers were less than 3% for female fur seals, so that Boyd (1993) concluded that this effect is negligible. When territorial male fur seals were counted, the difference between the observers became 10% due

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to the differences in judgement of whether or not the animal was a territorial male. Boyd (1993) appears to be the only study which has attempted to quantify such biases, and this result does indicate that it is reasonable to assume that counts of female fur seals are not a major source of concern for possible bias in abundance estimation. This effect should also be negligible for the number of pups counted, since the judgement of whether or not an animal is a pup is straightforward.

Survey time

As shown in Figure 4.5, the pupping season is from mid November to the end of December and the breeding season is from mid November to early April (Payne 1977, Boyd 1993). Payne (1978) suggests that pups are born within a short period at the same time every year, with 50% born by 4 December (± one day) with about 80% occurring in the space of 17 days. Thus the most suitable time for counting the pups is around mid to end December, when nearly all of the pups have been born. When female fur seals are counted (as in recent surveys in South Georgia), probably the breeding season is the best time for counting; if male fur seals are also counted, the best time is probably in December - January (Figure 4.5). All the abundance estimates shown in Table 6.1 were obtained from surveys that took place during December to February, so that bias arising from the timing of the surveys does not seem likely to be a major problem.

Area searched by the survey

Most of the counts are made by walking around the island, or counting the seals from a certain viewing point on land or from a ship which is steaming along the coastline.

During the early surveys in the 1930s when about 30 animals were found around Bird Island, Bonner (1968) notes that the shores were searched thoroughly by ship except for parts of the south and west shore of mainland South Georgia. Thus, there is the possibility that some animals might have been present in the unsurveyed areas of this part of South Georgia but not counted. However, even should this be the case, the numbers missed should be rather small, since Bonner (1968) indicates that the main aggregation of fur seals occurs at the north-western tip of South Georgia.

Regarding the surveys in 1971 to 1975, Payne (1977) notes that these were conducted both by helicopters and by ships steaming around the South Georgia coastline, where most parts have been repeatedly visited since 1970. Similarly Boyd (1993) reports that for the survey in 1990, the

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whole breeding range for fur seals at South Georgia was surveyed. Thus some of the abundance estimates shown in Table 6.1 may be negatively biased because of some unsurveyed areas, but most are likely to be reasonably accurate since most of the breeding areas were covered. Similar comments apply to breeding colonies at locations other than South Georgia.

Species identification

Again this does not seem likely to be a major problem. In the main breeding islands such as South Georgia, no other similar seals are present. Even on the islands where Antarctic fur seals and Sub Antarctic fur seals co-exist (i.e. Macquarie Island, Possession Island and Marion Island), species identification does not seem a problem (Shaughnessy *et al.* 1988). Further, Condy (1978) notes that the vocalization of Antarctic and Sub Antarctic fur seal bulls are readily differentiated.

Undercounting of the animals

In South Georgia, it seems likely that undercounting of the animals tends to occur as the number of the animals increases. Payne (1977) reports that as a consequence, pup counts were calibrated by marking a known number of pups on selected beaches and applying mark-recapture approaches.

Boyd (1993) relates that after a reconnaissance exercise in 1987, it was judged that counting the increasingly larger number of pups was no longer practical. As trial censuses showed that counting females ashore gave repeatable results, this method was used to census the population in subsequent years. A problem that may be associated with counting female seals on the breeding grounds is that some of the seals may not be ashore when the counting is carried out because of being at sea searching for food, thus resulting in an undercount. In the analyses by Boyd (1993), this bias is taken into account by estimating the probability of a female being ashore at the time of the census. This was estimated by a detailed analysis of the pattern of presence of females in different habitats used during the pupping season, and an iterative procedure was used to fit a model of the presence of females ashore to the observed data (Boyd 1993).

There has been no similar attempt to correct the bias that may arise in counting the animals for areas other than South Georgia. However, since the number of fur seals inhabiting other areas seems rather small compared to that at South Georgia, undercounting is likely not a major problem for those areas that were surveyed, though these estimates should nevertheless be regarded as minimum numbers.

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Variability in pregnancy and survival rates

Counting the whole population is possible only when the number of seals inhabiting the area is small. As the size of the population increases, it becomes almost impossible to count every single individual ashore. Thus, some kind of calibration is necessary in order to estimate the total abundance of the population.

Payne (1979) estimated the total number of population by multiplying the number of pups that were counted by 4.1. Payne (1979) derived this factor of 4.1 as is detailed in the preceding section, but due to insufficient data, did not consider the implications of inter-annual variation in survival and pregnancy rates. However, from the work of Boyd *et al.* (1995), which estimated the annual survival, pregnancy and pup mortality rates for the Antarctic fur seals at Bird Island, South Georgia, it is clear that these rates differ from year to year, and it is important to consider this when estimating the precision of the estimate of total abundance. Boyd *et al.* (1995) report a mean annual survival rate of 0.83 (SD=0.10), ranging from 0.65 to 0.93, and a mean pregnancy rate of 0.70 (SD=0.11) with a range from 0.59 to 0.88. The pup mortality rate ranged from 0.07 to 0.47; the latter value occurred in a year when the mortality rate was extremely high compared to other years, probably caused by reduced food supply (Boyd *et al.* 1995).

6.1.3 Overall discussion and quantifying the magnitude of the biases

As discussed above, there are various potential sources of uncertainty in the abundance estimates. However, the consequences of most of these uncertainties for the bias and precision of abundance estimates seems likely to be negligible, except for the variations in pregnancy rate and pup survival rate and precision of the estimated rate of increases which impact the factor of 4.1 calculated by Payne (1979) for extrapolating to total abundance from the number pups counted. To assess the impact of these uncertainties on the value of the 4.1 extrapolation factor, this factor was recalculated for values at the extremes of the ranges observed to give maximum and minimum results. For the population rate of increase, a value higher than 16.8%/year seems unlikely because of demographic limitations; however, Boyd (1993) reports that by the 1970s this growth rate may have slowed to about 10%/year, so this is used as an alternative. In this way a minimum value of 3.2 (corresponding to pregnancy rate = 0.88, survival rate = 0.53 and a rate of increase = 0.168) and a maximum value of 5.3 (for corresponding rates of 0.59, 0.93, and 0.10) follow. Boyd's (1993) estimate for South Georgia considered only the confidence interval for pregnancy rate in correcting

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the number of females counted to number of pups; in Table 6.1, as a rough indication of the additional consequences of uncertainty about the 4.1 extrapolation factor, the estimated relative errors have been multiplied together to give a combined range of uncertainty in abundance.

In summary, more than 90% of the circumpolar abundance of Antarctic fur seals is estimated to be associated with South Georgia. The most recent abundance estimates for the 1990s indicate that the total population is in the range of approximately 1 million to 2.5 million individuals.

6.2 Abundance trend estimate for Antarctic fur seals

Table 6.2 shows the population growth rates of Antarctic fur seals at different breeding locations. Of all seal species in the Antarctic, the Antarctic fur seals have undergone the most rapid population increase (Payne 1977). In South Georgia, Payne (1977) calculated the annual rate of population increase to be 16.8% between 1957 and 1972 based on counts of pups, as detailed in section 6.1.1 above. He commented that this increase rate is a high figure for a population of large wild mammals to sustain, and it seemed unlikely that it would continue for more than about another 10 years. Following this study, Boyd (1993) calculated the annual population increase from 1976 to 1990 to be 9.8%. These figures suggest that the rate of increase of this species at South Georgia has slowed. Boyd (1993) suggests that the possible reason for the decline is overcrowding of the traditional breeding beaches.

Other breeding sites such as the South Shetland Islands, Bouvetøya, Marion, Possession and Heard Islands also show increases in Antarctic fur seals at various times during the 1960-2000 period as shown in Table 6.2. As discussed in sections 6.1.2 and 6.1.3, although there are some potential uncertainties in abundance estimates, the magnitudes of these uncertainties are unlikely to be substantial, so that clearly there has been a substantial real increase in abundance. Possible reasons for the increase in Antarctic fur seals since the 1930s will be discussed in Chapter 11.

6.3 Absolute abundance estimates for crabeater seals

The abundance and distribution of crabeater seals within the Antarctic pack-ice is known only in broad terms because of the remoteness of this area from human habitation and its relative inaccessibility (Gilbert and Erickson 1977). Although this species seems to have a circumpolar distribution as shown in Figure 4.4, the number of surveys that have been conducted is very limited, making precise abundance estimation very difficult. Table 6.3 summarizes the available absolute

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abundance estimates for crabeater seals (extracted from Table 4 of Erickson and Hanson 1990). The population estimates in Table 6.3 marked with an asterisk denote those surveys which Erickson and Hanson (1990) considered to be the most representative and reliable estimates. Criteria for these judgements are not clearly stated in their paper, but in general they seem to consider estimates derived from helicopter surveys to be more reliable than those obtained from ship-based observations. They note that the major difference in the abundances estimates of crabeater seals in the West Weddell Sea from the aerial and shipboard surveys in 1983 north of 70°S is due to an artifact associated with the latter, for which the contribution from the small ice area at the tip of the Antarctic Peninsula completely distorted the population estimates. Assuming a steady population over the period of the surveys (1968-1983), and hence combining the abundance estimates with an asterisk shown in Table 6.3, results in a total population estimate of approximately 7 million crabeater seals.

Based on recent survey data, J. Laake (pers. commn) coarsely estimates circumpolar abundance estimate of crabeater seals to be 6-8 million animals. This is based only on the segment from 170°W to 125°W which was covered by US surveys in the 1999 austral summer as part of the Antarctic Pack Ice Seal (APIS) program (Ackley *et al.* 2003a). 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 Atlantic/Indian region is sparse.

Data used to obtain the estimates listed in Erickson and Hanson (1990) and the potential uncertainties associated with these estimates are summarized below.

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6.3.1 Data/Methods used to calculate the abundance of crabeater seals

As indicated in Table 6.3, surveys of the crabeater seal population have been conducted by either aerial counting from helicopters, or from ships, or by both methods depending on the year of the survey. All surveys were conducted in the austral summer, sometime between January 16 and March 24. An example of the transects for the survey in the Amundsen and Bellingshausen Seas in 1972 is shown in Figure 6.1 (from Figure 1 of Gilbert and Erikson 1977), and for the survey in West Pacific Ocean in 1973 in Figure 6.2 (from Figure 2 of the same paper). Because the sample counts obtained from helicopters were not representative of the entire pack-ice region, each part of this region was divided into an inner area and an outer area as shown in Figures 6.1 and 6.2. Gilbert and Erikson (1977) explain that the outer area was defined as that extending from the outer edge of the pack-ice to a line connecting the most southerly points of the helicopter flight lines.

The inner area was the remainder of the area of pack-ice extending from this line to the edge of the Antarctic Continent. Separate estimates of seal density were made for the outer and inner segments of each part of the pack-ice region. Estimates for the outer areas were made directly from the surveys and were obtained by multiplying the mean density estimate of crabeater seals from each survey by the area of unconsolidated pack-ice in the range covered by the survey. Seal density estimates for the inner region were based on examination of fixed-wing aerial photographs (if available) and observations from helicopters of seals in pack-ice of approximately the same character as the pack-ice of the inner area (Gilbert and Erikson 1977).

Crabeater seals have been observed to display a diurnal cycle in their propensity to haul out on pack-ice where they are visible for counting (Erickson *et al.* 1989). The fact that they are not visible for much of the 24 hour period means that density estimates made over broad geographic areas at various times of the day are confounded by this daily cycle (Erickson *et al.* 1989). Thus, prior to density calculations, all counts were time-corrected to the peak haul-out period using a method described in Erickson *et al.* (1989). This method uses the data from a series of stationary counts at fixed locations on the Antarctic continental ice pack collected over several days, and fits a model to describe the haul-out pattern which is then used to adjust survey counts for the time of day.

6.3.2 Difficulties associated with estimating the abundance of crabeater seals

There are two major difficulties in assessing the abundance of crabeater seals.

Density estimate for the inner pack-ice area

In Erickson and Hanson (1990), populations in the unsurveyed inner pack-ice area were estimated by multiplying the area of the unconsolidated pack-ice in this region by the mean density of crabeater seals observed in the inner surveyed portion of the outer pack-ice. This was based on the assertion of Gilbert and Erickson (1977) that as a rule, denser and more uniform ice types were characteristic of the surveys of the deeper pack-ice and crabeater densities tended to stabilize at low levels in this area. The presumption was that these conditions persisted throughout the deeper inner unconsolidated pack-ice area. There is not enough information to confirm this assertion, and this thus serves to emphasize that these abundance estimates must be regarded as approximate.

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Correction for the peak-haul out period

Though the counts were time-corrected to correspond to peak haul-out periods, Erickson and Hanson (1990) suggest that the estimates shown in Table 6.3 should be considered minimal values since they do not include estimates for an unknown fraction of seals that did not haul out on the ice during this peak period, and thus were not included in the counts and in the subsequent abundance estimates. They suggest that population estimates for crabeater seals in pelagic pack-ice should be expanded by at least 17% to account for this fraction which would not have been counted in the surveys. The value of 17% is obtained from an observation in Weddell Sea in March 1986 where during a total of 24 activity days (an activity day = 1 seal monitored for 1 day), six of the seals observed failed to haul out during 4 (17%) of the days.

6.3.3 Overall discussion and quantifying the magnitude of the biases

Erickson and Hanson (1990) conclude that their minimal population estimate of 7 million crabeater seals in the pelagic pack-ice is very conservative for the reasons discussed above, and that it would be reasonable to assume that the population size of this species during the period of the surveys analyzed is more on the order of 11-12 million animals.

6.4 Abundance trend estimate for crabeater seals

Erikson and Hanson (1990) suggest that there has been a decline in the population of crabeater seals in the Western Weddell Sea south of 70°S and to a lesser extent in the Pacific Ocean sector. A critical comparison of shipboard and aerial survey data from 1968 and 1969 with those from 1983 suggests a reduction in crabeater seal density of 30-60%. They attribute this decline to increased foraging competition between the large baleen whales that had by the 1980s probably started to recover after their protection following substantial commercial whaling in the early 1900s. This suggested decline in the Western Weddell Sea population is particularly interesting since this area is close to that where extensive commercial whaling and (fur) sealing occurred in the past. Studies of the age at maturity of crabeater seals provide supporting evidence for a decline in food availability for these animals, given that this age increased from 1964 to 1989 following an earlier decline (Bengtson and Laws 1985, Hårding and Härkönen 1995). Trends in the age at sexual maturity of the crabeater seals are discussed in Chapter 4 of this thesis.

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A counter-argument to this suggested 30-60% decline of crabeater seals between the late 1960s to mid-1980s is put forward by Green *et al.* (1995). They suggest that it is an artifact of the counting protocol, which did not take into account the possibility of a change in composition and numbers of the seal population during the moult. Their conclusion is based on stratifying the population density estimates of crabeater seals by survey time. Dividing the 1968-1969 survey results into three periods; 30 January – 14 February, 17 February – 3 March, and 4 March – 14 March, the estimated density of the seals changes from 23.72 to 6.87 and to 10.9 seals per square nautical mile respectively. The survey in 1983 was conducted within the second period from 17 February to 3 March, thus the suggested decline may be due to the choice of this particular period for this later survey.

6.5 Summary

Table 6.4 shows the possible minimum and maximum abundance estimates of Antarctic fur seals and crabeater seals around 1990.

More than 90% of the circumpolar abundance of Antarctic fur seals is estimated to be associated with South Georgia; the most recent abundance estimates for the 1990s suggest that the population is in the range of approximately 1 million to 2.5 million individuals. Although there are some uncertainties in these abundance estimates, their magnitudes are unlikely to be substantial, so that clearly there has been a substantial real increase in the abundance of Antarctic fur seals since the 1930s.

Erickson and Hanson (1990) estimate that the abundance of crabeater seals could be in the range of 7 to 12 million, although there are substantial associated uncertainties. This estimate assumes a steady population over the period of the surveys (1968-1983). A recent coarse estimate by J. Laake (pers. commn) based on preliminary analysis of the more recent APIS surveys suggests crabeater seal abundance to be around 6-8 million animals. Erickson and Hanson (1990) suggests 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 from the end of the 1960s to the early 1980s. Studies of the age at maturity of crabeater seals provide supporting evidence for this decline, given that this age increased from 1964 to 1989 following an earlier decline.

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6.6 Addendum

At the time this thesis was under final editing, recent abundance estimates for crabeater seals off east Antarctica between longitudes 60-150°E based on the APIS program line transect survey from an icebreaker and two helicopters became available (Southwell *et al.* 2005). They estimate abundance estimate of crabeatear seals in this region to be 914,200 (95%CI: 706,900; 1,319,200) animals, and comment that this estimate is not significantly different from that of Laws (1984) of 772,000 in the early 1970s in this region. They intend shortly to determine how their estimate corresponds to those of Erickson and Hanson (1990) listed in Table 6.3 above (C. Southwell pers. commn).

J. Laake (pers. commn) notified that he will be presenting his crabeater seal abundance estimates for the segment from 170°W to 125°W of the APIS program to the Scientific Committee on Antarctic Research (SCAR) meeting to be held at the end of July 2005, and thereafter will be preparing a paper reporting these results.

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Table 6.1 Summary of the available absolute abundance estimates for Antarctic fur seals in various years and locations.

Year	Estimate of pup production	Approximate abundance	Estimated range in abundance for uncertainty in 4.1 extrapolate factor from number of pups to total population size (see section 6. 1. 3)	Location	References
1930	?	< 100		Bird Island, South Georgia	Bonner (1968)
1975	90,000	369,000	288,000 – 477,000	〃	Payne (1979)
1990	378,000	1,550,000	1,529,300 – 1,980,300* ; 1,193,600 – 2,559,900**	South Georgia	Boyd (1993)
1987	3,977	16,000	12,726 – 21,078	South Shetland Islands	Bengtson *et al.* (1990), Boyd (1993)
2002		> 21,190		〃	Hucke-Gaete *et al.* (2004)
1971	< 1,000	< 4,000		South Orkney Islands	Laws (1973), Boyd (1993)
1962	< 500	< 2,000		South Sandwich Islands	Boyd (1993)
1989	< 91	< 335		Marion Island	Boyd (1993)
1995		1,205		〃	Hofmeyr *et al.* (1997)
1981	< 100	< 400		Iles Crozet	Boyd (1993)
1984	1,693	> 5,000	5,418 – 8,973	Iles Kerguelen	Jouventin and Stonehouse (1985)
1988	248	1,000	794 – 1,314	Heard Island	Goldsworthy and Shaughnessy (1989), Boyd (1993)
1987	37	150	118 – 196	Macquarie Island	Shaughnessy *et al.* (1988), Boyd (1993)
1980	100	400	320 - 530	McDonald Island	Johnstone (1982), Boyd (1993)

* 95% CI from Boyd (1993), which takes only the uncertainty in pregnancy rate into account in calculating the number of pups.
** Adds uncertainty in the 4.1 factor to extrapolate from number of pups to total population size.

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Table 6.2 Antarctic fur seal population growth rates estimated at different breeding locations.

Year	Estimated trend (%/year)	Location	Reference
1957-1972	16.8	South Georgia	Payne (1977)
1976-1990	9.8	South Georgia	Boyd (1993)
1990-1999	6-14	South Georgia	SSG (2000)
1965-2001	18.3	South Shetlands (Livinston Island)	Hucke-Gaete *et al.* (2004)
1978-1998	14	Bouvetøya Island	Hucke-Gaete *et al.* (2004)
1988-1994	17	Marion Island	Hofmeyr *et al.* (1997)
1982-1991	17.4	Posession Island	Guinet *et al.* (1994)
1962-1987	23	Heard Island	Shaughnessy and Goldsworthy (1990)

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Table 6.3 Regional population estimates of crabeater seals in the pelagic pack ice of the Southern Ocean (source: Erickson and Hanson 1990). The population estimates marked with an asterisk denotes those surveys which Erickson and Hanson (1990) chose as the most representative reliable estimates.

Region	Census				Total pack ice area (nm^2)	Total area censused (nm^2)	Ice pack surveyed (%)	Mean seal density(nm^{-2})		Estimated populations		
	Method	Year	date					Outer pack	Inner pack	Outer pack	Inner pack	Total estimate
Amundsen-Bellingshausen Seas	Air	1972	1/23-2/15		219323	1077	46	5.99	0.24	604323*	28424	632747*
	Shipboard	1972	1/23-2/15		219323	184	20	16.12	8.35	707097	1465078	2072178
West Ross Sea	Air	1972	2/6-2/14		290720	164	33	4.69	2.9	449947*	564869	1014816
East Ross Sea	Air	1973	1/16-1/26		72680	164	90	4.09	1.46	267535*	10611	278146
	TOTAL	1972-73			363400	328				717482*	575480	1292962*
West Pacific Ocean	Air	1973	1/16-1/26		67155	452	47	3.33	0.61	634004*	21711	655715
East Pacific Ocean	Air	1974	1/18-1/28		136345	255	60	7.75	0.93	232468*	50720	283188
	TOTAL	1973-74			203500	707		4.93		866472*	72431	938903*
Pacific Ocean	Air	1983	1/30		203500	48	79	1.33	0.33	213817*	14102	227918*
	Shipboard	1983	1/24-2/2		203500	50	35	2.55	1.03	181624	136243	317867
Indian Ocean	Air	1983	2/3-2/9		130800	95	54	6.69	4.55	472528*	273376	745904*
	Shipboard	1983	2/3-2/11		130800	56	46	4.18	0.84	251502	59331	310833
East Weddell Sea	Air	1983	2/12-2/16		60000	91	100	13.44	-	806400*	-	806400*
	Shipboard	1983	2/12-2/16		60000	31	70	11.64	3.04	488880	54720	543600
West Weddell Sea	Shipboard	1968	1/30-3/13	N. of 70°S	153000	63	72	6.86	5.08	755698	217627	973325
				S. of 70°S	128340	47	48	15.08	5.08	928976	339023	1267999
	TOTAL	1968			281340	110		10.38		1684674*	556650	2241324*
	Shipboard	1969	2/18-3/24	N. of 70°S	170100	30	18	0.85	5.86	26010	816884	842894
				S. of 70°S	220500	103	29	15.96	5.86	1020562	917412	1939994
	TOTAL	1969			390600	133		12.22		1046572*	1734296	2780868*
	Shipboard	1983	2/17-3/3	N. of 70°S	155700	85	31	18.25	52.89	880873	5682213	6563086
				S. of 70°S	200700	100	20	1.89	4.21	75865*	675958	751823*
	TOTAL	1983			356400	185		9.41		956738	6358171	7314909
	Air	1983	2/17-3/3	N. of 70°S	155700	0	0	-		-	-	-
				S. of 70°S	200700	332	25	1.42	-	71248*	493722	564970*
	TOTAL				356400	332		1.42	3.28			

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Table 6.4 Possible minimum and maximum abundance estimates for Antarctic fur seals and crabeater seals around 1990.

Species	Abundance around 1990	
	Min. (million)	Max. (million)
Antarctic fur seals	1	2.5
Crabeater seals	7	12
Total	8	14.5

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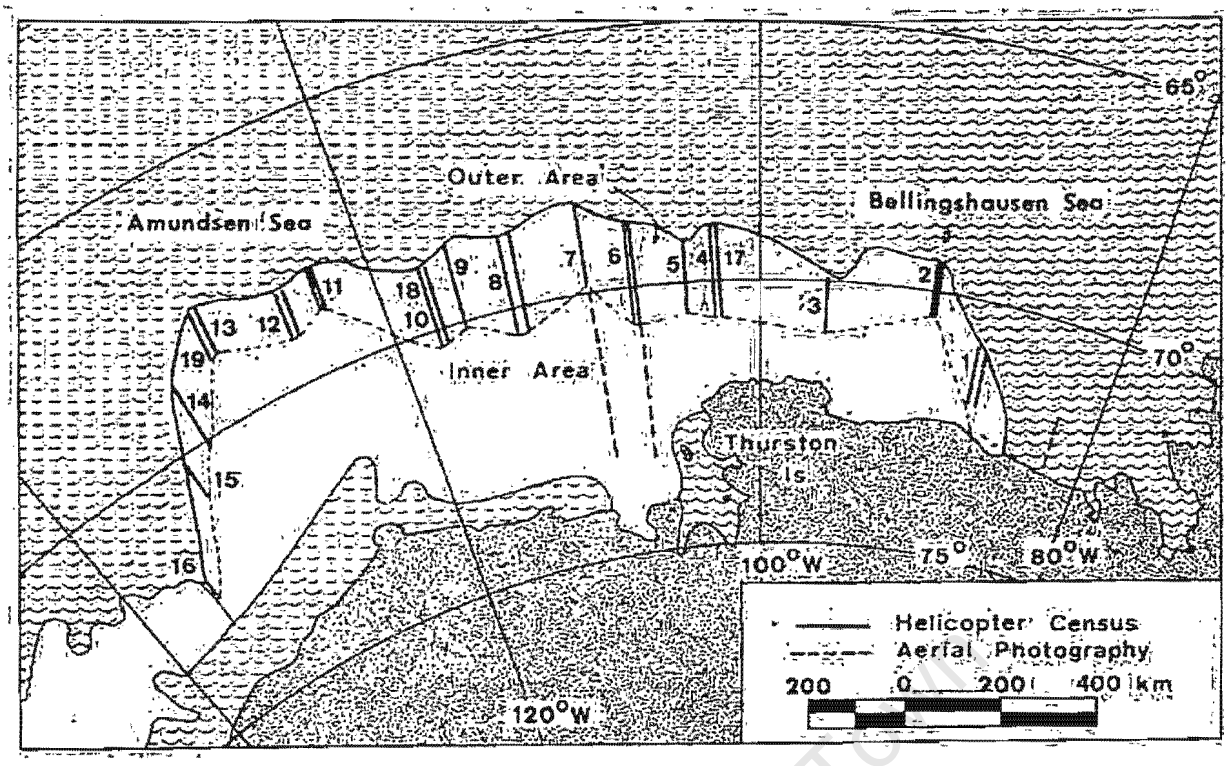


Figure 6.1 The extent of the pack ice, the location of samples obtained by helicopters and aerial photography, and the division of the total area into inner and outer pack ice areas during on-site investigations from 18 January to 15 February 1972 in the Amundsen and Bellingshausen seas (from Fig. 1 of Gilbert and Erickson 1977).

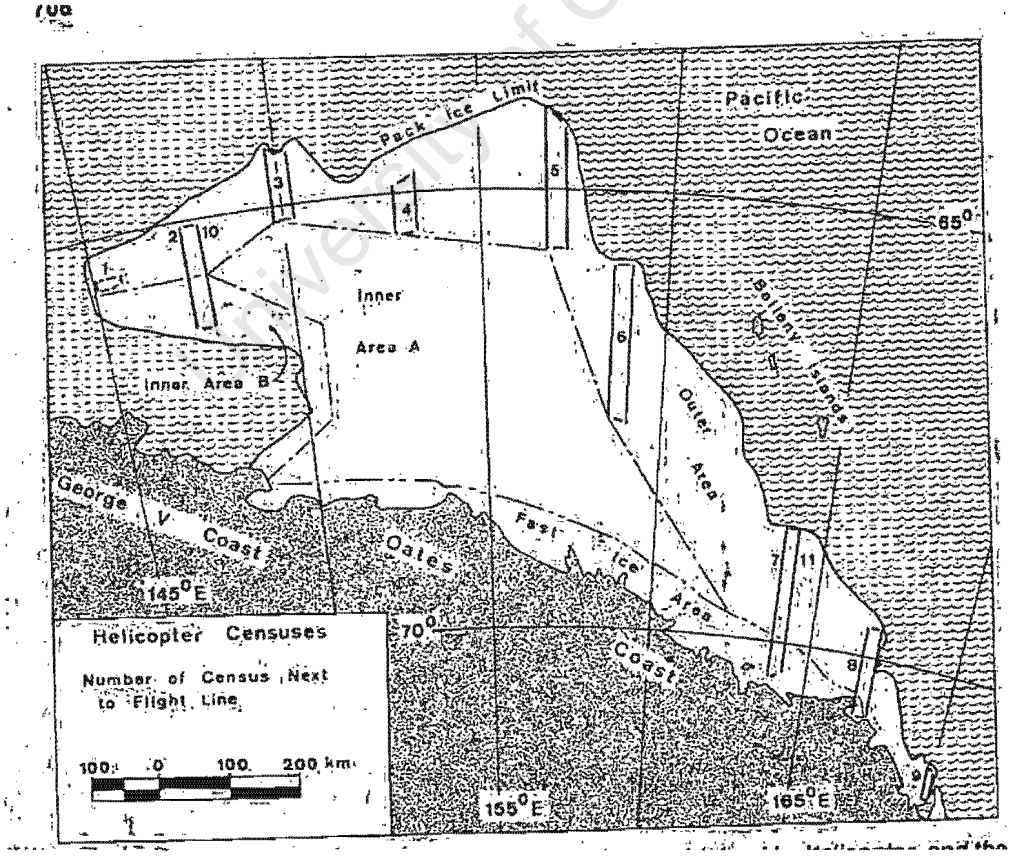


Figure 6.2 The extent of the pack ice, the location of samples obtained by helicopter, and the division of the total area into inner and outer pack ice areas during on-site investigations from 16 to 26 January 1973 off the Oates and George V coasts (from Fig. 2 of Gilbert and Erickson 1977).

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CHAPTER 7

ABUNDANCE AND TREND ESTIMATION FOR KRILL

Estimating krill abundance has proved difficult largely due to the species' wide geographical distribution south of the Antarctic Convergence and the fact that the habitat it shares with many whale species is harsh, remote and covered by ice for a good part of the year. Furthermore, the krill's contiguous distribution and its tendency to aggregate into "patches" ranging from hundreds of meters in diameter and several meters thick to 12 km in diameter and 230 m thick complicates abundance estimation even further.

Despite such difficulties, various estimates of krill's circumpolar abundance and the methods used are presented in Table 7.1. Such estimates range from 14 million tons to 300 million tons – a variation of 20 times. Each of the methods listed in Table 7.1 is discussed in section 7.2. However, initial focus is directed at reviewing circumpolar abundance estimates obtained from acoustic survey data (Nicol *et al.* 2000a) as these are considered to be the most reliable estimates for recent years.

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7.1 Reviewing the abundance estimates from acoustic surveys

Since the 1960s, the practical value of echosounders as a quantitative tool for marine stock assessment has increased dramatically with the availability of digital electronics, cheap computing power and the Global Positioning System (GPS) (Hewitt *et al.* 2002). Acoustic surveys allow detailed sampling over large areas in relatively short periods of time (Brierley *et al.* 1999). The data obtained using standardized acoustic technology (e.g. Hewitt and Demer 1994) now provide representative estimates of krill density for a variety of locations (Nicol *et al.* 2000a). The basic principles of acoustic surveys of krill are well summarized in Miller and Hampton (p. 29, 1989), and so are not repeated here. Hewitt and Demer (2000) also provide a thorough summary of the various uncertainties associated with acoustic survey methods with the more important ones being listed below.

- The largest potential bias in using acoustic techniques to estimate krill density is associated with the factor converting integrated echo energy to the absolute mass of krill reflecting sound called the target strength (TS) (Miller and Hampton 1989). Any estimate of abundance is very sensitive to the TS value used.

- Hewitt and Demer (2000) note that TS may vary with krill body shape, physical condition and orientation, and current estimates of krill target strength (Trathan *et al.* 1992) do not explicitly account for these factors.

- The accuracy of TS measurements is sensitive to system calibration factors (Foote 1983).

- There is no way to be certain that recorded echoes emanate solely from the target species of interest (Nicol and de la Mare 1993). Therefore, directed net sampling is often used for target identification and to help interpret the acoustic contributions from krill as opposed to other scatterers (Hewitt and Demer 2000). The latter difficulty has been overcome to some extent by the use of multi-frequency acoustic systems (Hewitt *et al.* 2002).

- Because acoustic techniques are dependent on reflected sound, echo-sounders work poorly in noisy environments – for instance, in rough weather or in the pack-ice, where the sound of ice against the hull of the ship at the surface may swamp echo returns from krill at depth (Nicol and de la Mare 1993).

- A substantial portion of the krill population may be located above the level of the transducer being used so leading to non-detection of krill close to the sea surface (Nicol and de la Mare 1993). Demer and Hewitt (1995) have estimated that in the Elephant Island area about 30% of the krill in the survey area are shallower than the transducer and therefore undetectable.

- Since krill have a circumpolar distribution, it is assumed that regional surveys, conducted by a limited number of vessels are not potentially substantially affected by krill moving in and out of the area being surveyed (Hewitt and Demer 2000).

- Survey results may be biased if krill react to the survey vessel's approach by adjusting their position and/or orientation (Hewitt and Demer 2000).

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Overall then, even though acoustic technology has advanced rapidly and has helped to improve abundance estimates of krill, it is important to note that there are still these various uncertainties associated with acoustic sampling methods. A number of improvements in these areas have been suggested by various authors, such as by Miller and Hampton (1989) and Hewitt and Demer (2000).

7.1.1 Review of estimate derived by Nicol et al. (2000a) – 60 to 150 million tons of krill

Nicol *et al.* (2000a) calculated circumpolar abundance estimates for krill using historical information on the overall distribution of krill and recent measurements of krill density from various acoustic surveys. Information on the distribution was extracted from the work of Marr (1962), which in turn used the information taken from townet samples taken by the Discovery Committee's vessel between 1935 and 1939 to produce a map. This map by Marr (1962 – Figure 135, p.394) is shown as Figure 7.1. For comparison, krill distribution maps produced by others are also shown as Figures 7.2 and 7.3. Figure 7.2 (from Mackintosh 1973, Figure 14, p.137) shows the general distribution of post-larval krill from January to March in the Antarctic. This distribution plot is based on information from whaling records, sightings of whales and of krill surface swarms between 1929 and 1963 (most of the data are from the late 1920s and 1930s) and the townet sample data used by Marr (1962). The use of the distribution of the whaling fleet relies on the assumption that this reflects the distribution of the whales and hence krill, given that records of the stomach contents of the whales usually reflect large amounts of krill (Mackintosh 1973). Figure 7.3 (from Miller and Hampton 1989, Figure 8, p.11) shows the distribution of major concentrations of krill obtained from Soviet trawler surveys undertaken between 1964 and 1978.

Nicol *et al.* (2000a) stratified the distribution of krill shown in Figure 7.1 into eight areas, based mainly on the boundaries of recent acoustic surveys, and these strata are shown in Figure 7.4. The extent of the krill distribution was estimated by joining points reflecting the northernmost positive records of krill in Figure 7.1 to indicate the northern limit, and similarly joining points for the southernmost records to form the southern limit. They then multiplied the calculated mean density of krill obtained from each of the acoustic surveys in a stratum by the corresponding ocean areas. No acoustic surveys have taken place in strata 1 and 8 of Figure 7.4, so the mean density estimate for stratum 7 was used for those regions. Nicol *et al.* (2000a) remark that this density value was chosen because it is the result of the only recent large-scale krill biomass survey in an area removed from the known high-density areas of the South Atlantic. In the strata for which sufficient density estimates exist, Nicol *et al.* (2000a) extract minimum, mean and maximum density estimates. The corresponding summations yield the range for their estimate of 60-150 million tons of krill in the

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Antarctic. Although Nicol *et al.* (2000a) note in their paper that these estimates are not intended to provide definitive figures for krill abundance, nor do they necessarily endorse any of them, a review of their analyses is carried out below in order to better understand what the plausible range of krill abundance in the Antarctic might be, given the results of various acoustic surveys. Potential uncertainties associated with their estimate are thus listed and discussed below.

Potential uncertainties associated with the estimate of krill abundance by Nicol *et al.* (2000a)

1. Strata 1 and 8 had not been surveyed in the past, so that Nicol *et al.* (2000a) used the density estimate for stratum 7 for these strata. As can be seen from Table 7.2, stratum 1 and stratum 8 have the largest ocean areas, corresponding to 67% of the whole distributional range of krill as defined by Nicol *et al.* (2000a). It is obvious that the assumption of the density for these strata must greatly affect the total abundance estimated for krill. From the maps shown in Figures 7.1 to 7.3, it would seem that the density of krill in these strata is not particularly low. Nevertheless, the density value from a single cruise in stratum 7 is enormously influential on the final abundance estimate.

2. Even among the surveyed strata, other than for strata 4 and 7, the area actually surveyed covers less than 20% of the total stratum. Applying the density estimate obtained from a small part of the stratum to the stratum as a whole may introduce substantial positive or negative bias, especially for a species like krill with its patchy distribution.

3. Except for strata 3 and 5, the density estimates are each based on the results of a single survey. It is well known that in regions such as Elephant Island and South Georgia where a long term set of consecutive surveys have been conducted, the inter-annual variability in krill abundance is large (as discussed later in this Chapter). In the Elephant Island region, comparison of the mean densities of krill obtained on surveys between 1981 to 1993 shows a 10-15 fold difference between the highest and lowest value, and indicates a CV of 20% assuming a lognormal distribution (Hewitt and Demer 1994). Still greater differences have been observed for the South Georgia region for which the CV = 34% (Brierley *et al.* 1999). These large inter-annual variabilities suggest that there could be substantial variance associated with a density estimate (intended to reflect an average over time) that is based on the results from a single survey only.

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4. The range of Nicol *et al.*'s (2000a) estimate for krill abundance takes no account of uncertainty in the estimates of density for strata 2 and 7, or of the fact that the estimate for stratum 7 is applied also to strata 1 and 8. If on the basis of the results for Elephant Island and South Georgia, one assumes that the stratum densities of 2.3 g/m^2 and 7.6 g/m^2 for strata 2 and 7 respectively are lognormally distributed with a CV of 27% (the average of the values for Elephant Island and South Georgia), then the 95% CIs for these densities are (1.4; 3.9) and (4.5; 12.9). If this is taken into account in adding minimum and maximum estimates over strata, then Nicol *et al.*'s (2000a) range of (60; 155) extends to (39; 192) million tons.

5. Not only inter-annual variability, but also intra-annual variability has been observed to be substantial in the Elephant Island (Hewitt and Demer 1994) and the South Georgia regions (Brierley *et al.* 2002). As shown in Figure 7.5, around Elephant Island, the densities of krill estimated from acoustic surveys differ within a survey season, and the trend within this season is not consistent from year to year. Mean densities vary almost 9-fold between early January to late February. Furthermore, similar variability has been observed in the South Georgia region (Brierley *et al.* 2002). Intra-annual variability thus also contributes to the imprecision of the overall abundance estimate for krill.

6. The approach assumes that krill abundance has been stable over the period for 1981 to 1996 when surveys have taken place. However, this assumption is questionable, since the recruitment index for krill obtained from net samples suggests a decline in krill abundance over the period from 1977-1983 to 1985-1994 (Siegel *et al.* 1998 and Atkinson *et al.* 2004 as discussed later in this Chapter). If this suggested decline is real and applies to the entire area of the Antarctic, it becomes difficult to specify the year to which the Nicol *et al.* (2000a) estimate should be taken to correspond.

7. In addition to the potential uncertainties discussed above, other uncertainties related to acoustic surveys as discussed earlier in this Chapter also apply to the Nicol *et al.* (2000a) abundance estimate.

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Updated information obtained from CCAMLR-2000 survey

Following the First International Biomass Experiment (FIBEX) krill survey in the southwest Atlantic in 1981, a large-scale acoustic survey was again conducted in the year 2000. This survey is called the CCAMLR-2000 Krill Synoptic Survey (CCAMLR-2000 survey) (Trathan *et al.* 2001), and it covered the southwest Atlantic as constituted by the Scotia Sea and the north of the Antarctic Peninsula (CCAMLR Statistical Subareas 48.1, 48.2, 48.3 and 48.4 – see Figure 2.2 for map). The areas surveyed are shown in Figure 7.6. The motivations for conducting this survey are detailed in Hewitt *et al.* (2002). Results for the density and biomass estimates by strata shown in Figure 7.6 are listed in Table 7.3 (from Table 1 of Hewitt *et al.* 2002). The highest densities of krill were found in the island strata, ranging from 25.8 gm^2 (CV=26.4%) near the South Sandwich Islands to 150.4 gm^2 (CV=55.5%) near the South Orkney Islands; densities in the oceanic strata ranged from 11.2 gm^2 (CV=19.3%) off the Antarctic Peninsula to 24.54 gm^2 (CV=15.3%) in the western Scotia Sea. The total krill biomass for the survey area was estimated at 44.3 million tons (CV=11.4%) (Hewitt *et al.* 2002).

The krill biomass estimate from the 1981 FIBEX survey for the Scotia Sea sector was estimated to be 32.7 million tons, but SC-CAMLR (2000) concluded that the two surveys are not directly comparable because of the different total areas covered, and different estimation techniques used in the two surveys. The areas surveyed during the FIBEX survey are shown in Figure 7.7. The density estimates obtained from the CCAMLR-2000 survey are generally much higher than those obtained from the FIBEX survey, especially in the area of South Orkney Islands, but are much lower in the Antarctic Peninsula area (see Tables 7.2 and 7.3).

A subsequent study by Demer and Conti (2005) reanalyzed the data in Hewitt *et al.* (2002), incorporating recent improvements in the estimation of krill target strength. They suggest that these improvements lead to an overall krill biomass estimate that is nearly 2.5 fold greater than the total of 44.3 million tons shown in Table 7.3.

In summary, although Nicol *et al.* (2000a) conclude that a total krill biomass of under 155 million tons may be more realistic than one as high as 500 million tons (as suggested by calculations from predator consumption of krill biomass), various uncertainties are associated with this estimate, some of which could see the upper limit of the Nicol *et al.* (2000a) estimate increased beyond even 500 million tons. Furthermore, if the adjustment of Demer and Conti (2005) alone is applied to the estimate of Nicol *et al.* (2000a), this rises to about 150 to 400 million tons. Therefore, at this stage

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it seems reasonable to conclude that the abundance estimate of krill as indicated by acoustic surveys is of the order of several hundred million tons.

7.2 Discussion of abundance estimates obtained from other methods

The abundance estimates obtained by Gulland (1970) and Everson (1977) required various assumptions for their calculations, which most of which have not been tested. Based on net surveys, Gulland (1970) estimated the standing stock of zooplankton in the Antarctic as a whole to be 150 million tons, and assumed that 50% of total herbivorous zooplankton is krill. However, as Gulland (1970) noted, that estimate of 150 million tons is subject to considerable error due, for example, to the patchiness of both the animals and survey sampling. Furthermore many of the nets used, especially in early work, were not efficient catchers of larger animals such as krill, and this would lead to negatively biased estimates.

As Ross and Quetin (1988) point out, krill abundance estimates calculated from the extent of consumption of predators are also problematic, since they require reasonably precise numbers for the krill-feeding predators (e.g. whales, seals, penguins, fish and squid). Abundances for some of these (especially for fish and squid) are very difficult to estimate, and furthermore precise estimates of predator consumption rates and the lengths of the periods for which some of the migratory predators stay in the Antarctic are required. Miller and Hampton (1989) and Nicol *et al.* (2000a) both draw attention to a major discrepancy between abundance estimates obtained from acoustic surveys and those from predator consumption rates. They suggest that this discrepancy may be caused by:

1) bias in acoustic estimates (caused for example by inaccurate estimates of target strength),
2) the possibility of a large, undetected krill population that is either too deep, too shallow or too dispersed to detect in acoustic surveys, and
3) overestimation of the quantity of krill required for predator consumption.

However, when the uncertainties associated with acoustic surveys are taken fully into account (as discussed in the previous section), no major discrepancy between the abundance estimates obtained from the two methods remains. However, it is still difficult to fix on a specific figure for an overall krill abundance estimate, and as mentioned above this seems best expressed as of the order of several hundred million tons.

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7.3 Trends in krill abundance

Despite a wide distribution with several areas of high concentration in the Antarctic, as shown in Figures 7.1 to 7.3, long-term series of consecutive surveys of krill have been conducted only in the vicinities of Elephant Island and South Georgia. As is obvious from Figure 7.6, these areas correspond to only a small fraction of the total distributional area of krill, so that a direct estimate of a circumpolar trend in krill abundance is impossible. As will be detailed below, assessing the trend in krill abundance even in the vicinity of Elephant Island has been problematic, due to small numbers of net samples taken in the earlier surveys (thus widening the confidence intervals for the associated density estimates), and also due to changes to the area surveyed over the period. Nevertheless, the results from these surveys highlight the characteristic of high inter-annual variability in krill recruitment within the region. Whether the trends in krill abundance in the vicinities of Elephant Island or South Georgia represent a circumpolar trend is accordingly questionable, but it remains worth reviewing these trends as they are the only ones available.

Two types of data for assessing trends in krill abundance are currently available. One is the abundance estimates that have been obtained from acoustic surveys, and the other is the estimates from net sampling during these cruises. In the following section inferences on trend obtained from acoustic surveys are discussed first, followed by inferences from net sampling surveys.

7.3.1 Trend in krill abundance from acoustic sampling data

Figure 7.8 shows the time series of density estimates of krill over the period of 1981 to 1993 obtained from acoustic surveys around Elephant Island (from Table 1 of Hewitt and Demer 1994). TS values used to determine these estimates have been adjusted to be consistent during this period (Hewitt and Demer 1994). The uncertainties associated with these estimates were discussed in section 7.1, and so will not be repeated here, but generally such uncertainties will apply consistently throughout the survey period, so that such biases should not constitute a major problem when assessing any trend. Nevertheless, as shown in Figure 7.5, variation in density within the same season is very large and does not show a consistent pattern from year to year, so that any trend evident in Figure 7.8 may be biased as a result of changes in the times of the surveys. From 1990 onwards, these surveys were conducted in several different months during the summer season (mainly between January to March), and the means of the densities during those months are plotted in Figure 7.8. For the years prior to 1990, only a single survey took place, so that the variances of those estimates may be large. There seems some suggestion of an increasing trend in krill

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abundance in the Elephant Island area over the period from 1981 to 1993. However, a log-linear regression indicates an annual change of 7 % (95%CI: -3; 17), which is not significantly different from zero.

Figure 7.9 shows the time series of density estimates of krill over the period from 1981 to 1998 obtained from acoustic surveys around South Georgia (from Table 1 of Brierely *et al.* 1999). The cruise tracks of some of these surveys are shown in Figure 7.10. Because the coverage of the area surveyed was not consistent over these cruises, and given the absence of surveys in a number of these years, it is difficult to conclude whether there is any consistent trend in the krill abundance in the vicinity of South Georgia. A log-linear regression suggests an annual change of 0.9% (95%CI: -11; 13) which is not significantly different from zero.

In summary, for the areas around both Elephant Island and South Georgia, acoustic surveys over the period from 1981 to the mid-1990s do not show any statistically significant trends, though there is some indication of an increase for Elephant Island.

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7.3.2 Trend in krill abundance from net sampling data

In the Elephant Island region, net sampling of krill has been conducted for more than 20 years commencing in 1977, and the information obtained has the potential to provide estimates of the trend in krill abundance and also recruitment. Methods for calculating the density estimates have changed over the period. Siegel and Loeb (1995) first calculated density estimates for krill from net sampling data using a stratified mean (Saville 1977) of standardized non-targeted net catches carried out during summer, between mid December and late February. In Siegel *et al.* (1997) the density estimates were re-calculated by using a delta distribution approach and the maximum likelihood method introduced by de la Mare (1994) (the TRAWLCI method). This method, described by de la Mare (1994), is the agreed standard method currently used by CCAMLR working groups to estimate densities from trawl surveys (Siegel *et al.* 2002).

Density estimates of krill from 1977 to 2000 based upon the TRAWLCI method are shown in Figure 7.11 (data from Table 1 of Siegel *et al.* 2002). As is noted in Siegel *et al.* (1998), data obtained by net-sampling are probably biased by avoidance behaviour, and therefore these estimates may be negatively biased in absolute terms. However, as they also note, the estimates are derived from standardized gear and methods used consistently over time, so that any estimates of trend are much less likely to be biased. The coefficients of variation of the density estimates shown in

Figure 7.11 are large, especially for the early years of the surveys as a consequence of less frequent sampling, and it is accordingly difficult to infer any systematic trend in krill density during the period from 1977 to 2000 in the Elephant Island area.

A more recent study by Atkinson *et al.* (2004) combined all the available scientific net sampling data from 1926-39 and 1976-2003 in order to examine spatial and temporal changes in krill distribution. They found that the productive southwest Atlantic sector contains >50% of the Southern Ocean krill biomass, 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. According to Atkinson (pers. commn), comparison of krill abundances between the 1926-39 period and the post-1976 era is unfortunately 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 those used in the past; and finally, there is suggestive evidence that the behaviour of krill (i.e. their vertical distribution) has changed since the earlier period, which renders it difficult to make a valid comparison of abundances, particularly as a result of possible consequential changes in the extent of net avoidance.

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Trend in krill recruitment

Recruitment indices, such as R_1 (the ratio of numbers of animals in age class one to the numbers in that age class and above) and R_2 (the ratio of numbers of animals in age class two to the numbers in that age class and above) have been produced to assess the trend in recruitment, using length density data and applying the maximum likelihood method described in detail by de la Mare (1994). These estimates are shown in Figure 7.14 (data from Table 4 of Siegel *et al.* 2002). Siegel *et al.* (2002) remark that the R_1 indices over the period from 1991 to 2000 were negatively biased due to an absence of survey in the area between 62°S to 63°S, where many juveniles were found during the survey of an extended area in 2001. Until 1990 the standard grid for the survey covered the area between 60°S and 63°S; however, since 1991 this grid was reduced so that it generally extended southward only to about 62°S. The extent of the bias which this causes is unknown (Siegel *et al.* 2002), and may be difficult to determine since it is known that the distribution of krill is highly variable within a year and also from year to year, making it difficult to assess the recruitment trend over the 1990s.

Due to this bias in estimates of R_1, Siegel *et al.* (2002) suggest rather using the recruitment index for two-year olds (R_2) in assessing recruitment trends, as this is likely less biased because of the more northerly distribution of these older krill. However, as Siegel *et al.* (1997) note, use of R_2 also presents problems, since it is often more difficult to separate the second year age group from the others, compared to separating the first year age group, because there is a greater overlap between the length distributions of two year old and older krill, resulting in a higher standard error for the R_2 estimate.

From Figure 7.12, it is obvious that krill recruitments show high inter-annual variability, and do not correspond directly to the density estimates for the following year shown in Figure 7.11. This may be because krill live to more than six years, so that the proportion of krill abundance that is comprised of recruitment is not too large (Siegel and Loeb 1995). Interestingly, however, comparison with the results obtained from the acoustic surveys shown in Figure 7.8 shows that, in six out of seven cases, the directional change in density from one year to the next matches that for recruitment strength in the previous year (Hewitt and Demer 1994).

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7.4 Summary

Abundance estimates for krill have been calculated by various authors using different methods. In recent years, acoustic techniques have become the primary approach and have made it possible to survey large areas in a short time period. However, there are still potentially large uncertainties associated with these techniques (e.g. in the target strength estimates) and further improvement of these approaches is needed. From the various studies of circumpolar abundance based on acoustic surveys of krill that have been published to date, krill abundance would seem to be of the order of several hundred million tons.

Long term series of consecutive krill surveys have taken place only in the areas around South Georgia and Elephant Island. In these areas, acoustic survey as well as net sampling data have been collected, and there are long term series of density estimates of krill in these regions available since about 1980. The variability in these density estimates is very large, within the same season as well as inter-annually. There is no statistically significant trend in krill density in either of these areas over the 1980s and 1990s. In any case, it is questionable whether any trend evident in these two very small areas could be taken to apply to the whole of Antarctic. Krill recruitment in the Elephant Island area also varies extensively from year to year.

Table 7.1 Various estimates of total (i.e. circumpolar) krill standing stock.

Estimate (million tons)	Method	Reference
75	Estimate of total secondary production: krill taken to comprise 50% of total herbivorous zooplankton	Gulland (1970)
14-277	From estimates (Gulland 1970) of total annual production (109 tons) assuming phytoplankton/euphausiid conversion ratios of between 10:1 and 40:1, and that krill comprise between 10% and 50% of total herbivorous zooplankton	Everson (1977)
±250	From estimates of predator requirements	Miller and Hampton (1989)
272	From a combination of fisheries and scientific survey data	Voronina (1998)
60-155	From acoustic surveys	Nicol *et al.* (2000a)

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Table 7.2 Areas of the strata where krill occur (Figure 7.4), and estimated krill biomass for these strata based on densities from acoustic surveys in these strata. A mean, maximum and minimum value for krill density for each stratum have been used where data are available. Where only a single density estimate is available, or where an extrapolated value is used, the same density figure is entered in the minimum, mean and maximum columns. (Table extracted from Table 1 of Nicol *et al.* 2000a.)

Stratum (Numbers in brackets refer to the stratum as shown in Fig. 7.2)	Area (million km^2)	Min. Density (tons km^{-2})	Min. Biomass (million tons)	Mean Density (tons km^{-2})	Mean Biomass (million tons)	Max. Density (tons km^{-2})	Max. Biomass (million tons)	Area Surveyed/Area (%)	Year of Survey	Number of years surveyed	Main Survey or Vessel	Reference
Southeast Atlantic (1)	3.94	7.6	29.9	7.6	29.9	7.6	29.9	0	-	0	*	-
Southwest Indian (2)	0.968	2.3	2.2	2.3	2.2	2.3	2.2	0.43	1981 (Jan - Feb)	1	FIBEX	Trathan *et al*. 1992
South Georgia (3)	0.348	1.9	0.7	49.3	17.2	151	52.5	various	1981 - 1998 (Nov - Mar)	11	Summary of 16 acoustic surveys	Brierley *et al*. 1999
South Orkneys (4)	0.111	17.1	1.9	26	2.9	64.5	7.2	59.37	1996 (Feb - Mar)	1	RV *Atlantida*	Kasatkina *et al*. 1998
Peninsula (5)	0.271	8	2.2	53	14.4	131	35.5	6.42 - 16.05	1981 - 1993 (Nov - Mar)	13	FIBEX & US AMLR Program	Trathan *et al*. 1992, Hewitt and Demer 1993,1994
Bellingshausen (6)	0.188	19.6	3.7	30	5.6	42.6	8	8.75	1992 (Nov - Dec)	1	STERNA	Murray *et al*. 1995
Southeast Indian (7)	0.904	7.6	6.9	7.6	6.9	7.6	6.9	51.02	1996 (Feb - Mar)	1	BROKE	Pauly *et al*. 1996
Pacific (8)	1.711	7.6	13	7.6	13	7.6	13	0	-	0	*	-
Total	8.441		60.5		92.1		155.2					

Table 7.3 Krill density and biomass estimates for the CCAMLR-2000 Krill Synoptic Survey for the strata shown in Figure 7.6. (Table extracted from Table 1 of Hewitt *et al.* 2002.)

Stratum	Mean krill density (t/km^2)	Area surveyed (million km^2)	Biomass (million tons)	CV (%)
1. Antarctic Peninsula	11.2	0.473	5.320	19.3
2. Scotia Sea	24.5	1.109	27.235	15.3
3. East Scotia Sea	11.3	0.321	3.642	42.5
4. South Shetland Islands	37.7	0.048	1.836	26.2
5. South Orkney Islands	150.4	0.024	3.670	55.5
6. South Georgia	39.3	0.025	0.982	30.8
7. Sandwich Islands	25.8	0.062	1.604	26.4
All Strata	21.4	2.062	44.289	11.4

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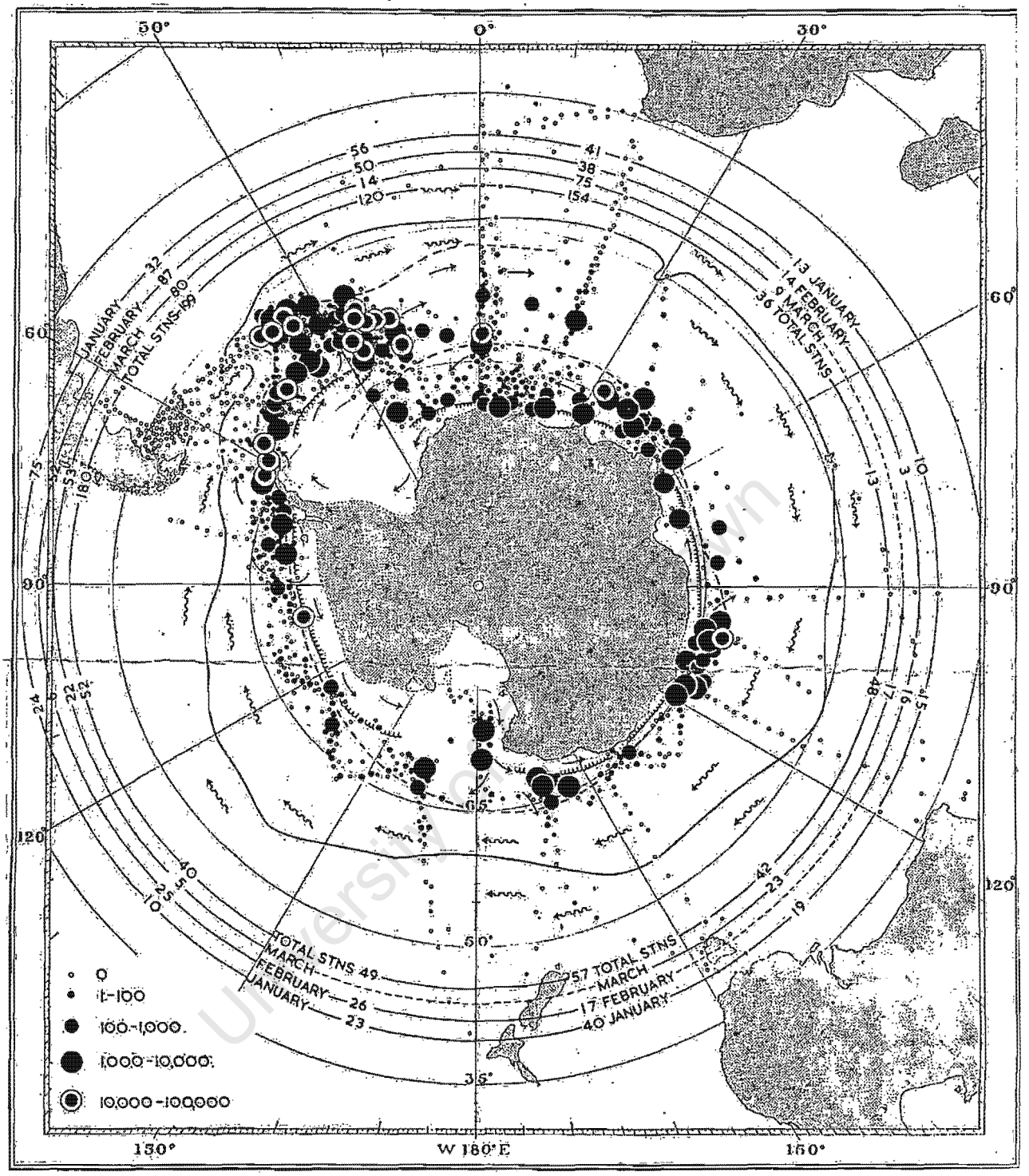


Figure 7.1 Distribution of krill obtained from net sampling data between 1935 and 1939 (reproduced from Figure 135 of Marr 1962). The circles show relative density of krill.
(~~>: Circumpolar west wind drift, ⊓⊓⊓⊓ : Ice edge – mean position in February, ---: Northern boundary of east wind drift and Weddell drift, → : Principal surface movements of the colder Antarctic water.)

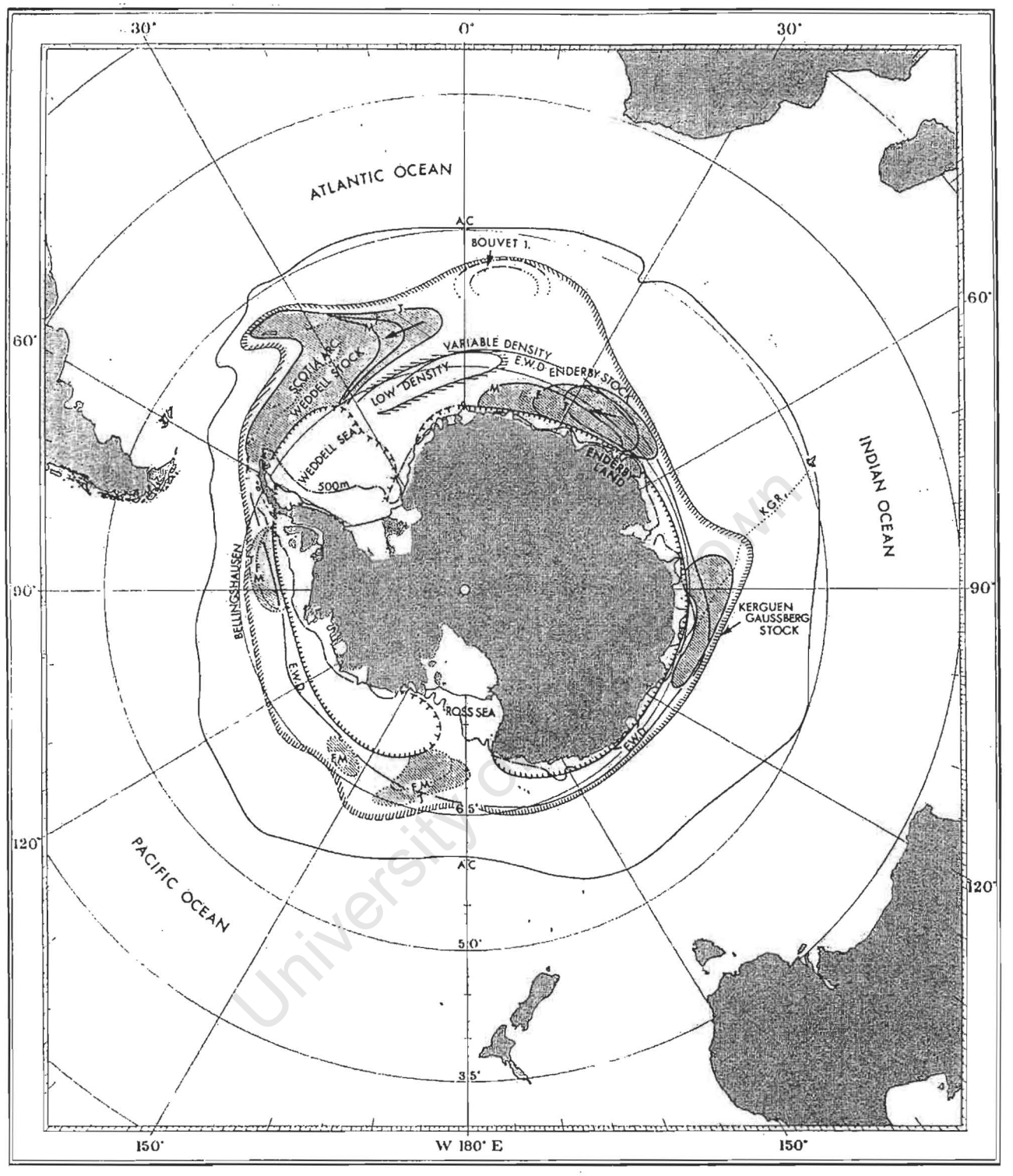


Figure 7.2 Distribution of post-larval krill during January to March based on information from whaling records, and sightings of whales and of krill surface swarms between 1929 and 1963. The outer shaded line is the limit of moderately abundant krill. The inner curved lines enclose areas of apparently higher concentrations of krill (shaded), except where marked 'low density'. J, F and M refer to January, February and March. The ice edge is shown at its lowest ebb by a combed line (reproduced from Figure 14 of Mackintosh 1973).

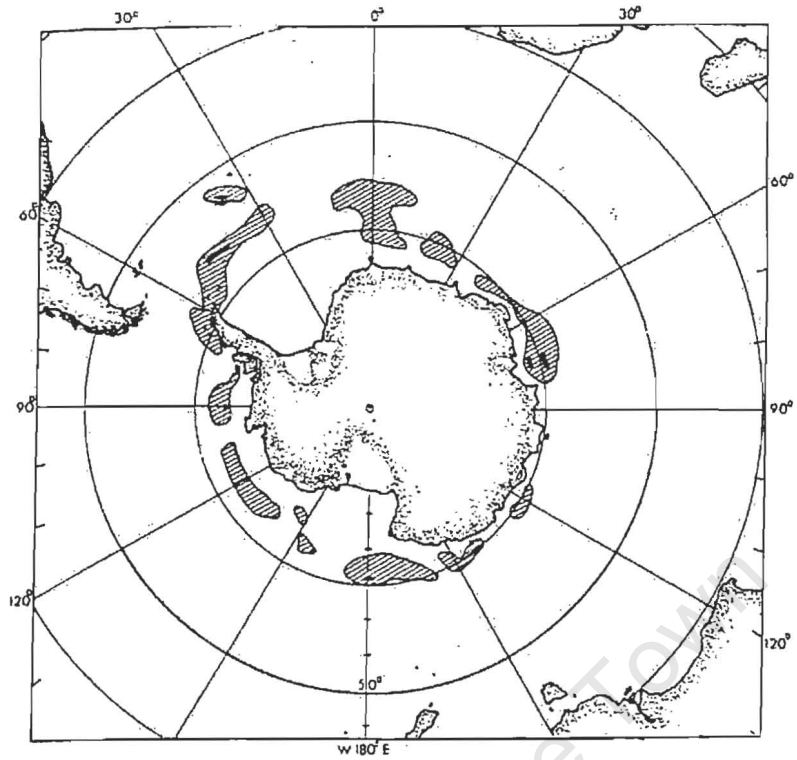


Figure 7.3 Distribution of major concentrations of krill from Soviet trawler surveys undertaken between 1964 and 1978 (reproduced with permission from Miller and Hampton 1989).

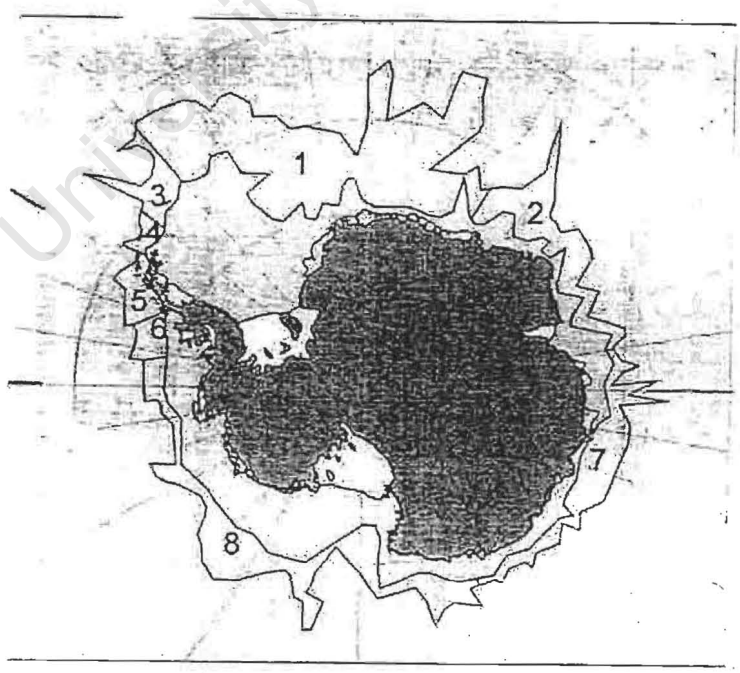


Figure 7.4 The distribution of krill and strata selected for independent density estimation by Nicol *et al.* (2000a) (reproduced with permission from Nicol *et al.* (2000a)).

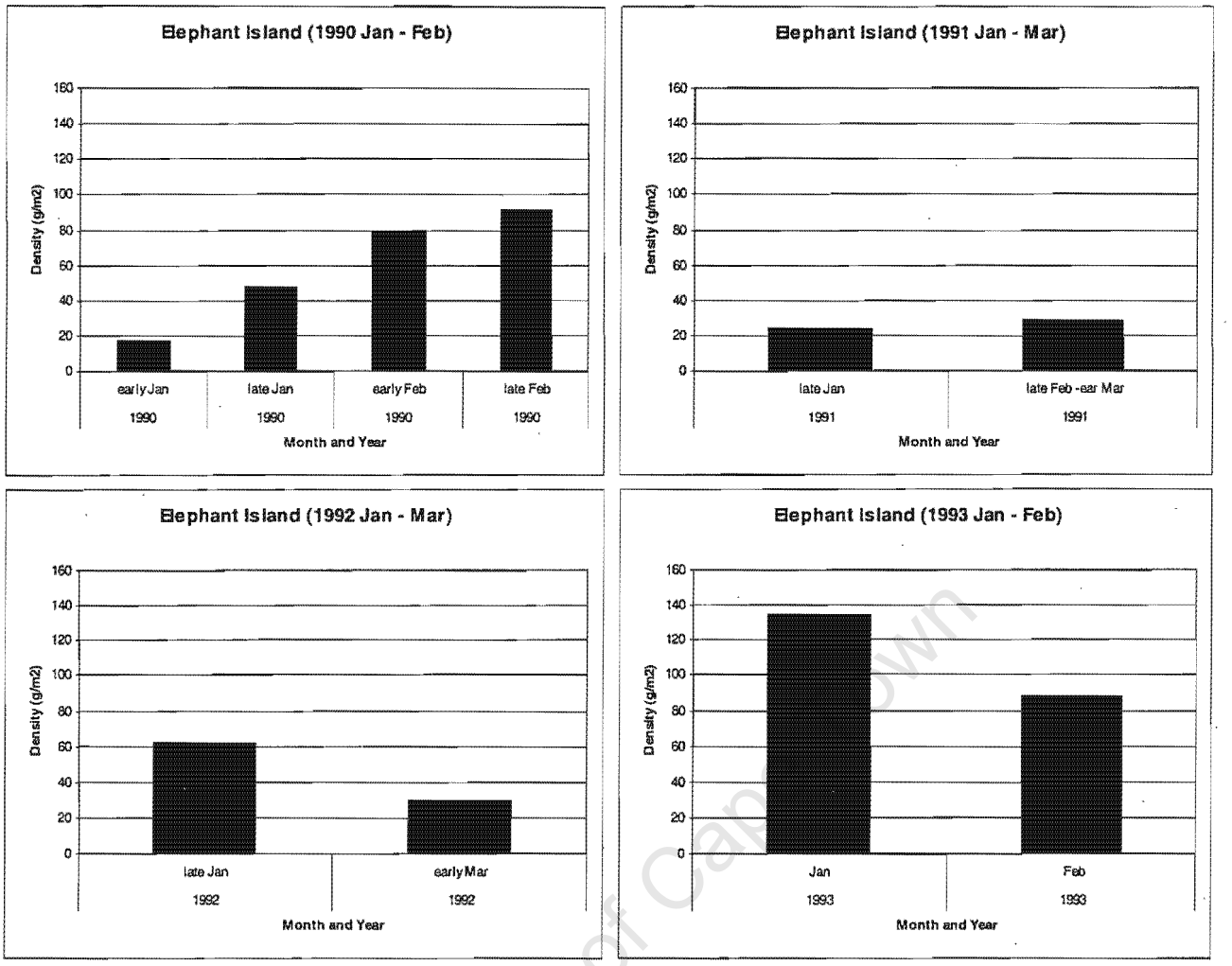
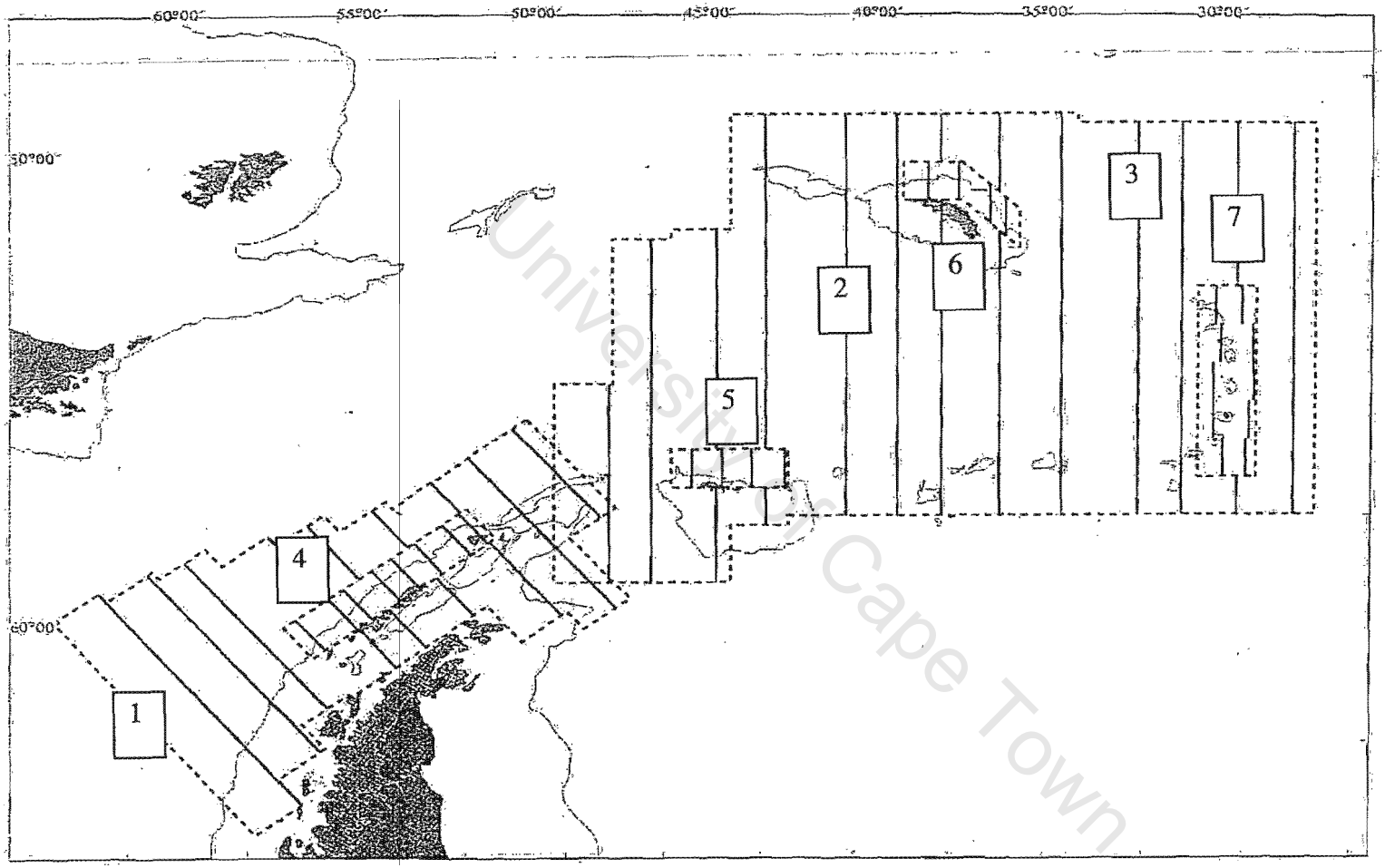


Figure 7.5 Density estimates for krill in relation to year and month, as obtained from acoustic surveys in the Elephant Island region (source: Hewitt and Demer 1994).

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Figure 7.6 The CCAMLR-2000 survey design with stratum boundaries (modified from Figure 8 of Trathan *et al.* 2001). The solid lines are the cruise track lines and the dotted lines indicate the stratum boundaries. Numbers shown are the stratum numbers given in Table 7.3: 1- Antarctic Peninsula, 2- Scotia Sea, 3- East Scotia Sea, 4- South Shetland Islands, 5- South Orkney Islands, 6- South Georgia, 7- Sandwich Islands. Elephant Island is to be found within stratum 4.

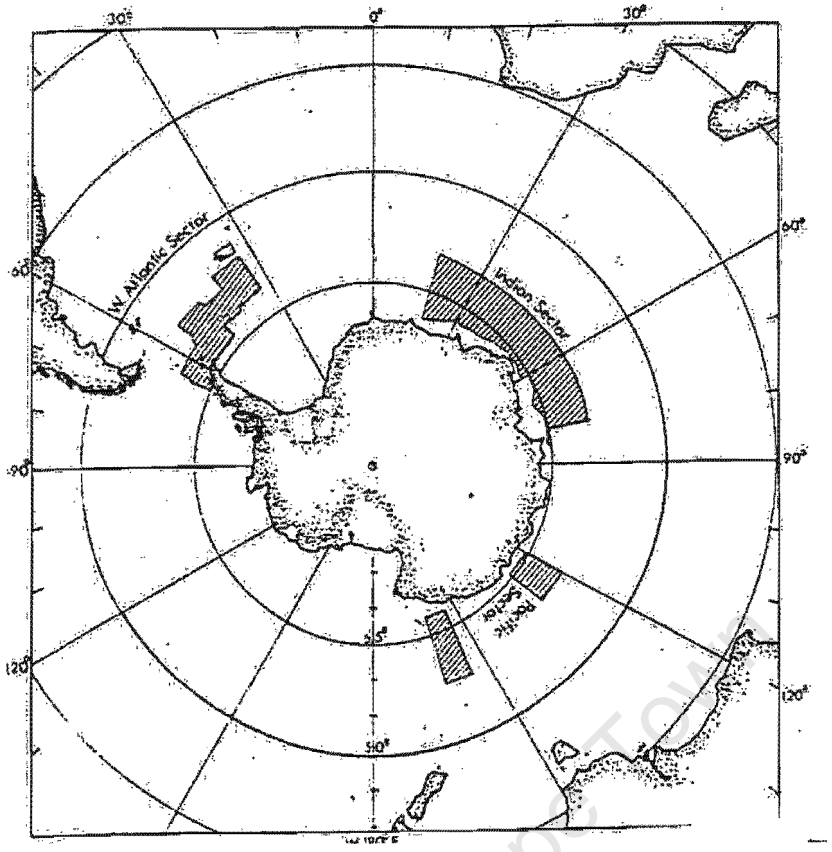


Figure 7.7 Areas covered by the 1981 FIBEX-survey (reproduced from Figure 2b of Anon 1986).

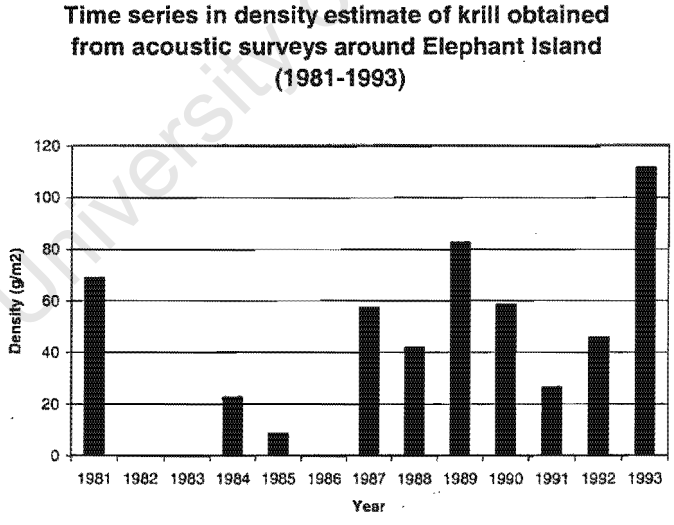


Figure 7.8 Time series of density estimates of krill obtained from acoustic surveys around Elephant Island over 1981 to 1993 (source: Table 1 of Hewitt and Demer 1994).

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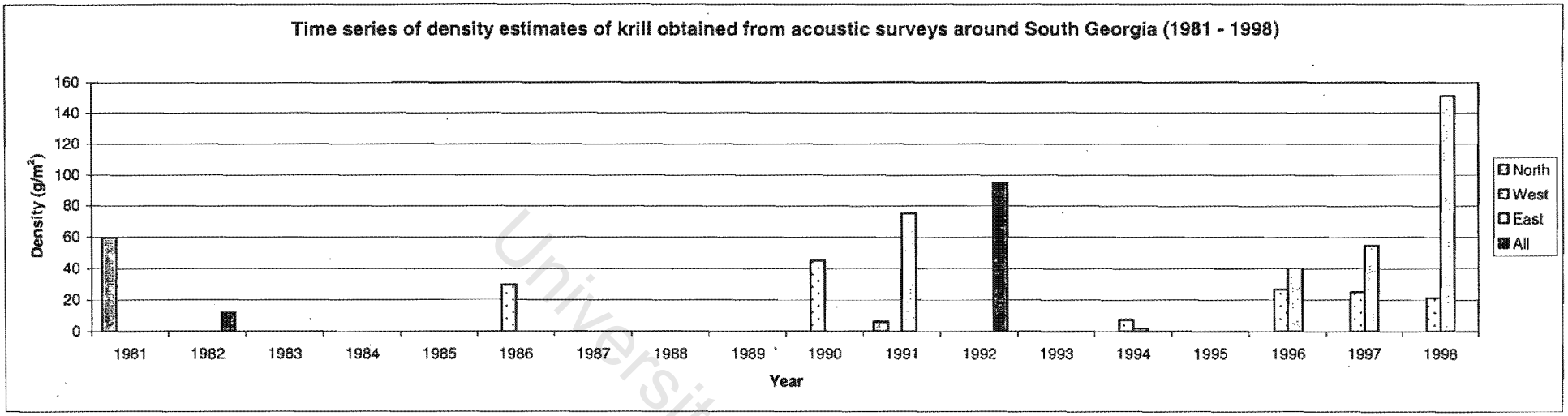
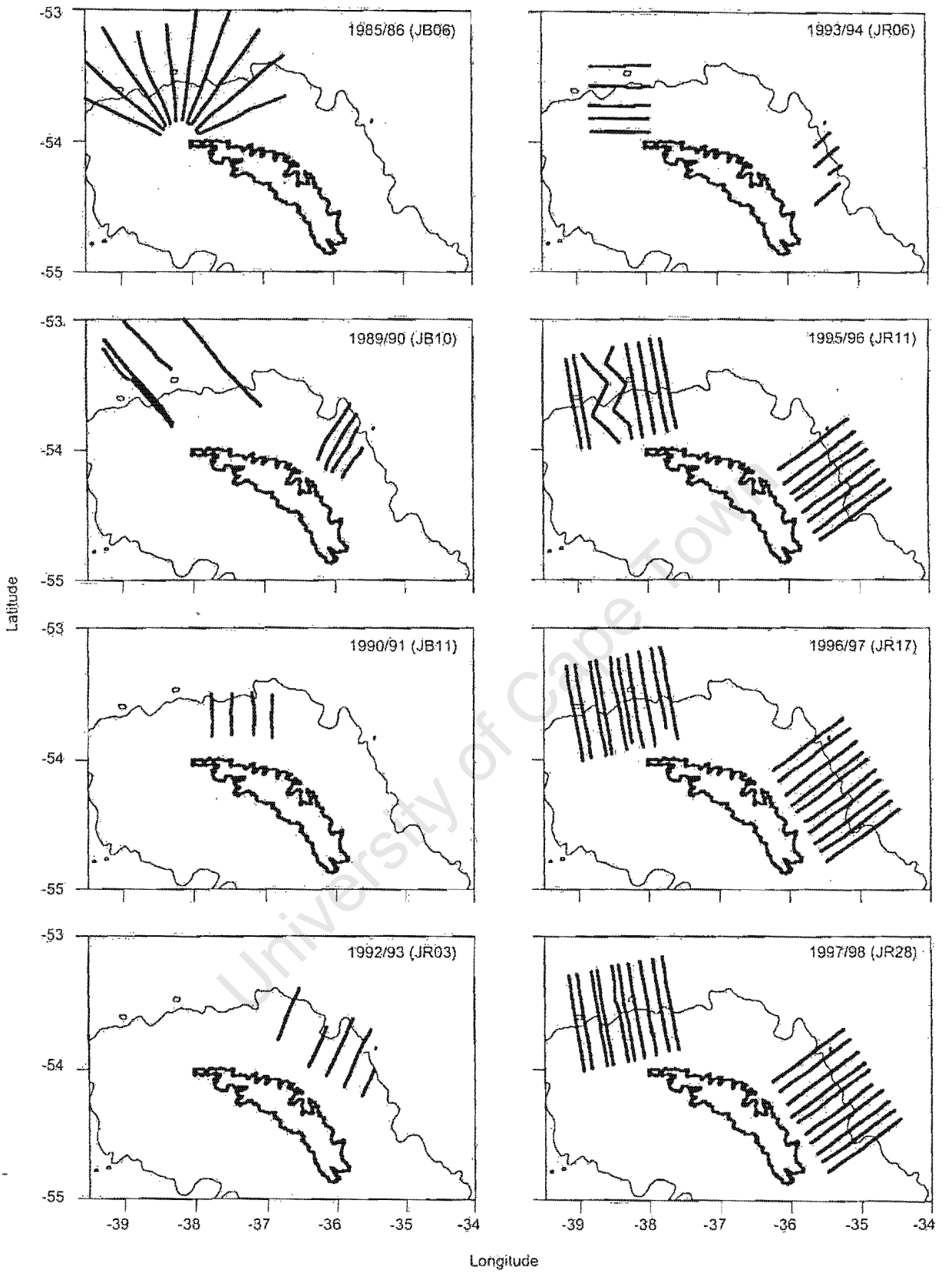


Figure 7.9 Time series of density estimates of krill obtained from acoustic surveys around South Georgia over 1981 to 1998 (source: Table 1 of Brierley *et al.* 1999).

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Figure 7.10 Maps showing South Georgia, the approximate position of the shelf-break as defined by the 1000m isobath, and sections of cruise tracks from which acoustic data for krill density estimation were taken (reproduced with permission from Figure 1 of Brierley *et al.* 1999).

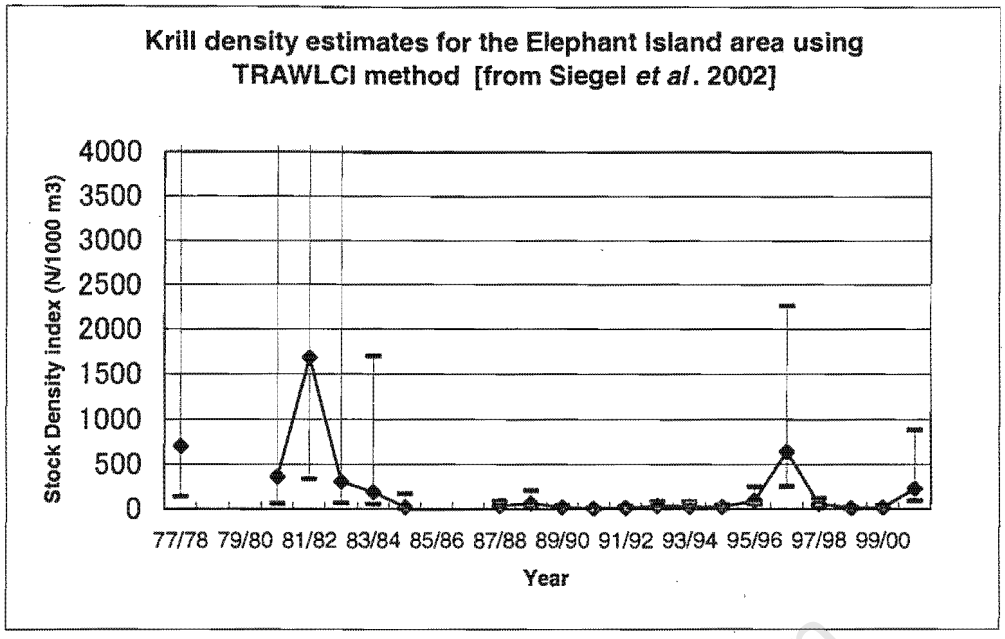


Figure 7.11 Krill density estimates for the Elephant Island area between 1978 and 2000 based upon the TRAWLCI method (source: Siegel *et al.* 2002). The confidence intervals shown are the 95% confidence intervals.

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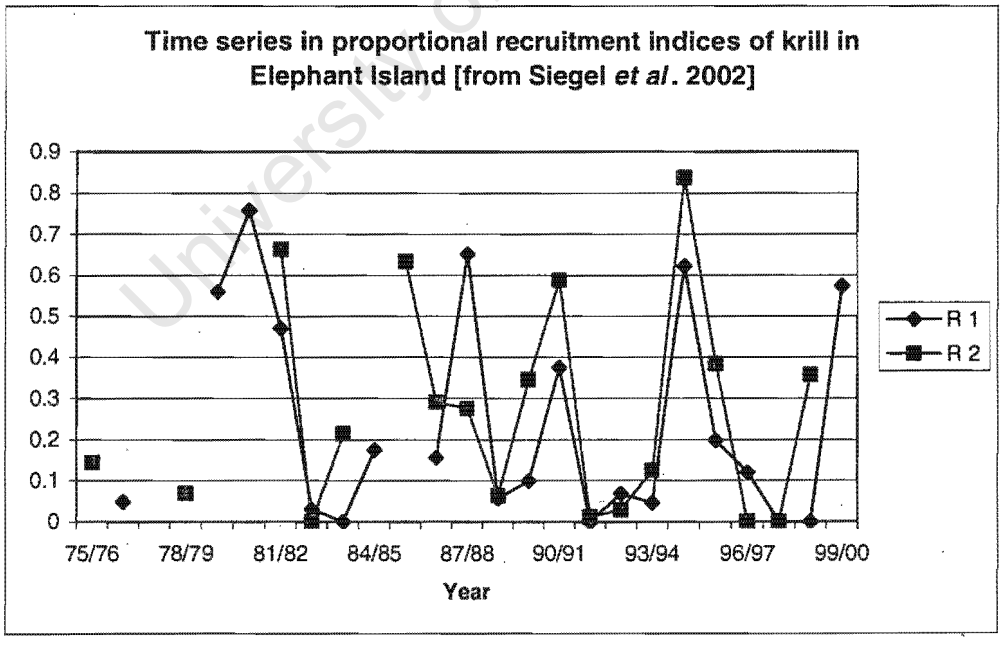


Figure 7.12 Time series of proportional recruitment indices for krill in the Elephant Island area between 1976 and 2000 (source: Siegel *et al.* 2002).

SECTION 2:

EVIDENCE FOR MULTI-SPECIES EFFECTS FROM THE ANALYSES OF SOUTHERN HEMISPHERE MINKE WHALE DYNAMICS

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CHAPTER 8

CATCH-AT-AGE ANALYSIS FOR THE SOUTHERN HEMISPHERE MINKE WHALES

8.1 Introduction

The question of whether inferences of utility for management purposes can be drawn from catch-at-age information for Southern Hemisphere minke whales has been in dispute in the Scientific Committee of the IWC for the last two decades (Butterworth *et al.* 1999). The history of the development of catch-at-age analysis approaches for these minke whales is well described in Butterworth *et al.* (1999) and thus will not be repeated here. Butterworth *et al.* (1999) applied an ADAPT-like version of Virtual Population Analysis (VPA) to commercial and research (JARPA) catches-at-age, together with estimates of abundance from IWC/IDCR-SOWER and JARPA surveys, to estimate past trends in recruitment and abundance of the minke whale populations in IWC Management Areas IV and V. The data available for those analyses extended to the 1995 season. Those analyses focused on Area IV, and used a 3-year-3-age grouping of the data to facilitate estimation. The major findings of Butterworth *et al.* (1999) were that their analyses provided an estimate of 5.5%/year (90%CI: 1.4; 9.1%) for an historic increasing trend in minke whale recruitment in Area IV over the period 1947-1968 prior to the exploitation of this resource, and that there had since been a marked drop in recruitment from 1970 to the mid-1980s. The point estimate of this increasing trend for Area V was larger, but less precisely estimated. The point estimate of age-independent natural mortality M for Area IV was 0.057/year. Butterworth *et al.* (2002) extended those analyses using data available to the 1999 season, and obtained a similar result to Butterworth *et al.* (1999): they found a statistically significant increase in minke whale recruitment (4.4%/year (90%CI: 2.2; 7.8%)) until a peak in the late 1960's followed by a drop and then stabilization for more recent years.

This Chapter extends those analyses yet further to take account of the most recent (including to the 2003 season) minke whale data and analyses now available from the JARPA surveys, specifically:

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- Updated catch-at-age data from the research samples, kindly provided by R. Zenitani (Institute of Cetacean Research, Japan).
- Updated estimates of abundance from the JARPA surveys, kindly provided by T. Hakamada (Hakamda *et al.* 2005).

Although the analysis method used in this Chapter is essentially the same as that of Butterworth *et al.* (1999), there are some important changes (primarily as regards application):

- The computations are now implemented using the ADMB package, which provides more powerful and reliable minimization capabilities when fitting the ADAPT-VPA model to the data and estimating the parameters[1].
- Given this greater power, together with the extended data set, it has become feasible to focus on a conventional 1-year-1-age analysis, instead of the previous grouping of data into 3-year-3-age blocks.
- Although analyses are conducted for Areas IV and V separately, the primary focus in this Chapter is on a joint analysis of both Areas; this treats the two as containing a single stock that distributes itself in these two feeding regions in a manner which admits some inter-Area variability from year to year.

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8.2 Data

Tables 8.1a and 8.1b list the catch-at-age matrices used for Areas IV and V respectively for these analyses, with ages grouped in 3's for economy of presentation. These reflect commercial catches from 1971 to 1986, and scientific research catches from 1987 to 2003. The commercial catch information is unchanged from that used in Butterworth *et al.* (1999) and was provided by A. Punt (pers. commn). The scientific catch information has been developed as described in Butterworth *et al.* (1999), and the specifications for the development of the catch-at-age matrices are described in Appendix 8 of this thesis. The underlying ageing information incorporates some subsequent revisions by R. Zenitani.

Tables 8.2a and 8.2b list the survey estimates of abundance for Areas IV and V respectively that are used in the analyses, together with the associated survey sampling CVs. Estimates from the IWC/IDCR-SOWER surveys were taken from Branch (2003), except for 1998 which was

[1] The basic program code in ADMB for the analyses was kindly provided by A. Punt (pers. commn), and subsequent modifications to this code were pursued.

developed by T. Branch (pers. commn) as detailed below. These estimates exclude consideration of like-minke whale sightings, and are comparable over the years, having all been extrapolated northward to 60°S as described in Branch (2003). The following process was used to obtain the abundance estimate for Area IV from the third circumpolar set of surveys that is shown in Table 8.2:

1) The 1998 estimate from Branch (2003) was used for the stratum from 80° to 130°E.
2) The 1994 estimates from Branch and Butterworth (2001a) were added to the estimate from 1) for the following strata: all of the Prydz Bay stratum, one-half of the EN stratum, and one-half of the ES stratum. The IO and closing estimates then need to be inverse-variance weighted, and the value of R=0.826 (CV=0.089) for pseudo-passing estimates, as reported in Branch and Butterworth (2001a), was used for this.

The estimates from the JARPA surveys listed in Table 8.2 were provided by Hakamada (2005). As has been described in section 5.2 of this thesis, a revised method of analysis was used to obtain these; this method incorporates estimated calibration factors to render these estimates comparable to surveying by vessels responsible for sightings only ("SV" vessels, as distinct from "SSV" vessels which also sample the whales). This in turn should render these JARPA-based abundance estimates more comparable to those from the IWC/IDCR-SOWER surveys.

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8.3 Methodology

The ADAPT estimator considered in this Chapter involves specifications for the population dynamics, the parameterization of fishing and natural mortality, and the likelihood. Each of these components is described in turn below.

Basic population dynamics

The basic population dynamics are taken to be governed by the equations:

$$N_{y+1,a+1} = \left(N_{y,a} - C_{y,a}\right) \cdot e^{-M_a} \qquad 1 \le a \le m \tag{8.1}$$

$$F_{y,a} = C_{y,a} / N_{y,a} \tag{8.2}$$

where

$N_{y,a}$ is the number of minke whales (here of both sexes combined) of age a present at the start of year y;

$C_{y,a}$ is the number of such whales taken during year y (note that the ADAPT methodology, as applied here, assumes the data provided for these catches-at-age in Table 8.1 to be known

without error);

M_a is the (possibly age-dependent) rate of natural mortality;

$F_{y,a}$ is the proportion of the animals of age a present at the start of year y that are taken (the "fishing proportion"); and

m is the oldest age considered in the model-fitting process.

Whale catches in the Antarctic are limited to a shortish period around the end of the calendar year, so that it is customary to model the population dynamics assuming a pulse fishery at the start of the year as in equation (8.1).

Consistent with Butterworth *et al.* (1999), most of the analyses in this Chapter take m=30. An argument for this approach is that sample sizes for large ages are very small, and furthermore older ages are less reliably determined because of the closer spacing of earplug rings. However, results are also shown for alternative choices for m up to 45. For analysis purposes, natural mortality M_a is presumed infinite at age 45 and above, so that animals captured above this age are ignored. For choices of $m < 45$, results are projected forward from age m to age 45 using equation (8.1) and known catches, so that all the analyses take account of minke whales up to age 45 irrespective of the choice made for m.

Model parameterization

A key aspect of the parameterization of the ADAPT-VPA model applied is the assumption that the fishing proportion F is separable (in expectation). Different selectivity patterns are assumed for the years of commercial and scientific catches:

$$F^E_{y,a} = \begin{cases} S^c_a F^E_y & y \le 1986 \\ S^s_a F^E_y & y \ge 1987 \end{cases} \qquad (8.3)$$

where

S^c_a is the selectivity-at-age for the period of commercial catches (S^c_m=1);

S^s_a is the selectivity-at-age for the period of scientific catches (S^s_m=1);

F^E_y is the fishing proportion (in expectation) for year y on age m (i.e. the fully selected fishing proportion in cases where $S^{c/s}_a \le 1$ for all a); and

$F^E_{y,a}$ is the expected fishing proportion on animals of age a for year y; this differs from the

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actual proportion $F_{y,a}$ because actual catches $C_{y,a}$ differ from their expectations ($C^E_{y,a} = F^E_{y,a} N_{y,a}$) as a result of sampling variability (at least).

The primary estimable parameters of the model are effectively:

- The natural mortality M_a (usually taken to be age-independent).
- The oldest-age numbers-at-age $N_{y,m}$.
- The most-recent-year numbers-at-age $N_{n,a}$, where n is the last year for which data are available.

Given values for these parameters, the complete numbers-at-age matrix ($N_{y,a}$) for the population can then be computed by use of equation (8.1).

The likelihood function

For single Area assessments, the likelihood function has three components related to the IWC/IDCR-SOWER estimates of abundance, the JARPA estimates of abundance and the catch-at-age data. The contribution of the first of these to the negative of the log likelihood (ignoring constants) is given by:

$$-\ln L_1 = \sum_y \frac{1}{2\sigma_y^2} \left(\ln N_y^{obs} - \ln \hat{N}_y \right)^2 \qquad (8.4)$$

where

N_y^{obs} is the IWC/IDCR-SOWER abundance estimate for year y;

σ_y is the standard error of the logarithm of N_y^{obs}, which is approximated by $\sqrt{CV_y^{\,2} + CV_{add}^{\,2}}$;

CV_y is the survey sampling CV estimated for N_y^{obs};

CV_{add} is an additional CV to reflect the fact that survey sampling error is not the only factor contributing to the difference between N_y^{obs} and $\hat{N}_y$; and

$\hat{N}_y$ is the model estimate of 1+ abundance for year y, given by:

$$\hat{N}_y = \sum_{a=1}^{45} \hat{N}_{y,a} \qquad (8.5).$$

The contribution of the JARPA estimates of abundance is similar, except that these are treated as

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indices of relative abundance:

$$-\ln L_2 = \sum_y \frac{1}{2\sigma_y^2}\left(\ln N_y^{obs} - \ln\left(q\hat{N}_y\right)\right)^2 \tag{8.6}$$

where

N_y^{obs} is the JARPA abundance estimate for year y; and

q is the multiplicative bias associated with abundance estimates from JARPA compared to those from IWC/IDCR-SOWER, and is given by its maximum likelihood estimate:

$$\ln \hat{q} = \left\{\sum_y \frac{\ln\left(N_y^{obs}/\hat{N}_y\right)}{\sigma_y^2}\right\} \Big/ \left\{\sum_y 1/\sigma_y^2\right\} \tag{8.7}.$$

Finally the contributions of the commercial and the scientific catch-at-age data are given by:[2]

$$-\ln L_3^c = -\lambda^c \sum_{y=1971}^{1986} \sum_{a=16}^{m} C_{y,a}^* \ln \hat{\rho}_{y,a} \tag{8.8}$$

$$-\ln L_3^s = -\lambda^s \sum_{y=1987}^{2003} \sum_{a=1}^{m} C_{y,a}^* \ln \hat{\rho}_{y,a} \tag{8.9}$$

where

$C_{y,a}^*$ is the effective number of animals of age a caught during year y, computed as $C_{y,a}C_y^*/C_y$;

C_y is the total catch in numbers during year y;

C_y^* is the number of animals actually aged for year y, which also are taken into account in the L_3 calculation for that year (i.e. with ages from 16 to m for the commercial, and from 1 to m for the scientific catches);

$\lambda^{c/s}$ is a factor to account for overdispersion in the commercial/scientific catch-at-age distribution (underdispersion is not admitted, so that $0 < \lambda \leq 1$); and

$\hat{\rho}_{y,a}$ is the model-estimate of the expected proportion of the catch in year y that consists of animals of age a, which from equation (8.3) is given by:

$$\hat{\rho}_{y,a} = \begin{cases} S_a^c N_{y,a} \Big/ \sum_{a'=16}^{m} S_{a'}^c N_{y,a'} & y \leq 1986 \\ S_a^s N_{y,a} \Big/ \sum_{a'=1}^{m} S_{a'}^s N_{y,a'} & y \geq 1987 \end{cases} \tag{8.10}.$$

[2] Note that this assumes a (potentially overdispersed) multinomial distribution for these data. This has, however, proved inadequate for some fish species (see Hrafnkelsson and Stefansson 2004).

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A consistent commercial selectivity-at-age pattern (S_a^c) is assumed to apply only above age 15 on the basis of arguments by Sakuramoto and Tanaka (1985) that the pattern below this age varies appreciably from year to year. The overdispersion factors λ are estimated by iterative application of the formula:

$$\lambda^{c/s} = \sum_y 1 \Big/ \sum_y \left\{ \frac{C_y^* \sum_a \left(\rho_{y,a} - \hat{\rho}_{y,a}\right)^2}{\sum_a \hat{\rho}_{y,a}\left(1-\hat{\rho}_{y,a}\right)} \right\} \tag{8.11}$$

where the years and ages in the summations are as adopted above for L_3^c and L_3^s, and $\rho_{y,a}$ is the observed proportion of the catch during year y which consists of animals of age a:

$$\rho_{y,a} = \begin{cases} C_{y,a}^* \Big/ \sum_{a'=16}^{m} C_{y,a'}^* & y \le 1986 \\ C_{y,a}^* \Big/ \sum_{a'=1}^{m} C_{y,a'}^* & y \ge 1987 \end{cases} \tag{8.12}.$$

When Areas IV and V are assessed in combination, allowance needs to be made for the fact that the survey estimates now apply to only a portion of the combined IV+V minke whale abundance. If the proportion in Area IV in year y is p_y, and hence the proportion in Area V that year is $\left(1-p_y\right)$, then equation (8.4) is adjusted to read:

$$-\ln L_1 = \sum_{y(IV)} \frac{1}{2\sigma_y^2}\left[\ln N_y^{obs} - \ln\left(p_y \hat{N}_y\right)\right]^2 + \sum_{y(V)} \frac{1}{2\sigma_y^2}\left[\ln N_y^{obs} - \ln\left\{\left(1-p_y\right)\hat{N}_y\right\}\right]^2 \tag{8.13}$$

where the two summations are over years with IWC/IDCR-SOWER surveys in Area IV and in Area V respectively. Equation (8.6) for the contribution from the JARPA survey abundance estimates is adjusted similarly. The p_y s become estimable parameters of the model, though note that in years with a survey in both Areas, the same p_y is taken to apply (as any difference arising from the JARPA and IWC/IDCR-SOWER surveys taking place at slightly different times during the season seems likely to be relatively small).

Allowing the p_y s to be unconstrained (other than that $0 \le p_y \le 1$) would lead to an under-determined model, in the sense that the p_y s could then adjust for the model to match each abundance estimate exactly (except in years with surveys in both Areas). On the other hand,

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setting $p_y = p$ (constant) seems unrealistic as it does not allow for changes in the distribution of whales between the two Areas from year to year. Accordingly the p_ys have been assumed to follow a beta distribution:

$$p_y \sim \mathrm{B}(\alpha, \beta) \tag{8.14}$$

with the approximate estimation approach then used (within the MLE context applied) being the addition of the following further contribution to the negative of the log likelihood:

$$-\ln L_4 = \sum_y \left[\ln\Gamma(\alpha) + \ln\Gamma(\beta) - \ln\Gamma(\alpha+\beta) - (\alpha-1)\ln p_y - (\beta-1)\ln(1-p_y)\right] \tag{8.15}$$

where the summation extends over the years for which there is a survey in at least one of the two Areas.

In implementation, the parameter:

$$p = \frac{\alpha}{\alpha+\beta} \tag{8.16}$$

which is the average proportion of the combined abundance to be found in Area IV is treated as an estimable parameter of the model. The parameter α is fixed externally, with different values being chosen to reflect different levels of inter-annual variability (in terms of a CV) of p:

$$CV(p) = \sqrt{\frac{\beta}{[\alpha(\alpha+\beta+1)]}} \tag{8.17}.$$

8.4 Results

Base Case specification: Areas IV+V combined

The selectivity forms assumed for the Base Case assessment follow those adopted for the analyses of Butterworth *et al.* (1999):

$$S_a^c = \begin{cases} S^c & a = 16,\ldots,21 \\ 1 & a = 22,\ldots,m \end{cases} \tag{8.18}$$

$$S_a^s = \begin{cases} S^s & a = 1,\ldots,6 \\ 1 & a = 7,\ldots,m \end{cases} \tag{8.19}$$

where S^c and S^s (both constrained to be ≤ 1) are estimated in the model fitting process. For the commercial catches, a consistent selectivity-at-age pattern is assumed to apply from age a=16 and above only for reasons detailed above (see after equation 8.10). Arguments for the

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appropriateness of setting selectivity to be flat at older ages for both the commercial and the scientific catches are advanced in Butterworth *et al.* (1999), who suggest two reasons for this choice. First, although the commercial whalers would clearly have wished to select for larger (and hence older) animals, minke whale growth is (on average) very limited at older ages, with less than 0.5m growth to be expected after an animal reaches an age of 10 years. Best (1984) presents results indicating that shipboard estimates of minke whale length had a root mean square error of some 0.8m. Thus, the whalers would clearly have been unable to preferentially select older animals amongst those of age say, 20 and above on the basis of apparent size.

The second reason relates to the fact that the commercial whaling fleet did not catch at random throughout an Area (as the scientific take intends), but rather concentrated in regions of higher minke whale density near to the ice-edge. Thus non-uniform commercial selectivity-at-age could result if there is age-specific segregation of the animals. Butterworth *et al.* (1999) found by analyzing the average age of the whales sampled in JARPA between 80° and 130°E over the January-March period (covering the peak of commercial whaling operations) as a function of latitude that from 61°S southward there is a clear tendency for average age to increase, suggesting that older animals are more likely to be found closer to the ice-edge. This in turn suggests that S^c_m is not greater than 1.

Given that the scientific take intends a random sample, the scientific selectivity-at-age function (S^s_a) is taken to be flat for large ages a. The evidence for non-uniform selectivity-at-age at younger ages for both the commercial (age 16 and above) and scientific (age 1 and above) catches was examined by Butterworth *et al.* (1999) for Area IV by the use of likelihood ratio tests. Starting with a uniform function (all $S^{c/s}_a$=1), these parameters were successively freed and treated as estimable, starting with the parameter for the youngest age under consideration. This exercise suggested that the selectivities of S^c_{17} and S^c_{20}; S^s_2 and S^s_5 (note that their analyses focused on a 3-year-3-age grouping of the data, and that the age stated here is the middle of the 3-age group) were less than 1. Furthermore, however, over a wide range of age-independent values for M (0.02 to 0.14/year), no difference significant at the 5% level, between S^c_{17} and S^c_{20}, and between S^s_2 and S^s_5 was detected. Thus their base-case estimator allowed two estimable selectivity-at-age parameters: $S^c_{17} = S^c_{20} \leq S^c_{23} = 1$ and $S^s_2 = S^s_5 \leq S^s_8 = 1$ (Butterworth *et al.* 1999).

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For the Base Case assessment in this Chapter, the same assumptions are made for the selectivity-at-age parameters and sensitivities to these assumptions are examined. The remaining specifications for the Base Case assessment are:

i) $m = 30$

ii) $M_a = M$ (constant)

iii) $q = 1$

iv) $CV(p) = 0.2$ (and $CV_{add} = 0$).

The first two of these specifications maintain the approach of earlier papers (Butterworth *et al.* 1999, 2002) for consistency. The justification for the others is most easily provided by reference to the results for the IV+V combined assessments provided in Table 8.3a. This Table includes results for the case where the bias q of the JARPA surveys relative to the IWC/IDCR-SOWER surveys is estimated rather than fixed as input. The estimate is close to 1 ($\hat{q} = 1.025$) and certainly not significantly different from it, so the choice was made to treat the two sets of surveys as comparable (i.e. to fix $q = 1$) for the Base Case.

The basis for selecting CV(p)=0.2 is a little more complex. If the proportion of the population p_y in Area IV is constant over time, one finds that the differences between the observed abundances and those estimated by the ADAPT-VPA model are typically larger than the survey sampling CVs for the survey would suggest (see the case "p constant" in Table 8.3a – this difference is measured by the standard deviation of the standardized residuals - SDSR - which at 1.82 substantially exceeds 1 in this case). This discrepancy is taken into account by assuming that it is a consequence of the variation in the proportions of the population that migrate to Area IV and to Area V each year, and increase the extent of this variability (i.e. increase CV(p)) until the SDSR for abundance estimates drops to 1. This is achieved for the choice CV(p)=0.2, which also reflects consistency with the variability of the specific p_y values estimated (note SDSR(p) for the Base Case is 0.93 – very close to 1). An alternative way of accounting for the discrepancy would be to entertain a positive value of CV_{add} (see equation (8.4)). As CV_{add} and CV(p) effects are confounded, CV_{add} has been set to zero here.

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Base Case results: Areas IV+V combined

Figure 8.1 shows the estimated commercial and scientific selectivities at age, while Figure 8.2 shows the associated residuals to the fit to the catch-at-age proportions. The latter do not appear to reflect any obvious systematic patterns, except that virtually all the predicted proportions of 1-year-olds in the scientific catches are too low, indicating a need to estimate S_1^S separately to allow it to be less than, rather than force it to be equal to S_2^S. Sensitivity analyses which involved estimating scientific selectivities for ages of 6 years and less by different age-class groupings suggest that estimating S_1^S separately from $S_2^S = S_3^S = \cdots = S_6^S$ would result in a statistically better fit of the model to the data in terms of the Akaike Information Criterion (AIC)[2] as is evident from Table 8.3a (compare "Base Case" with "Est 2Sci. Sel (m=30)"). The systematic pattern of the residuals observed for the proportions of 1-year-olds no longer occur when S_1^S is estimated separately from $S_2^S = S_3^S = \cdots = S_6^S$ (Figure 8.3). However, the main features of the results for this sensitivity test hardly differ from those of the Base Case, which was consequently left unaltered. Alternative choices of age-class groupings within the first six ages of the scientific catch did not lead to improved fits in terms of the AIC.

Figure 8.4a shows the fits of the ADAPT-VPA model to the 1+ abundance estimates for Areas IV and V separately for each Area, together with the estimates for the proportions (p_y and $1-p_y$) of the total population in each Area each year. The abundance plots include the survey estimates of abundance together with their survey sampling related estimated 95% confidence intervals, nearly all of which are consistent with the overall trends estimated.

A feature of 1+ abundance plots of Figure 8.4a which needs further explanation is that both "estimated" and "adjusted" trajectories are shown. The total population estimates sum numbers-at-age ($N_{y,a}$) present each year over ages 1 to 45 (see equation (8.5)). However, limitation of the analyses to m=30 and to data from years 1971 to 2003 means that the earliest cohort for which recruitment ($N_{y,1}$) is estimable is the 1942 cohort ($N_{1942,1}$), and further that estimates of numbers at age a=45 are available only from year 1986 onwards. The "estimated" total abundance, which excludes contributions to N_y from cohorts not included in the assessment and hence effectively treated as zero, are thus negatively biased. To "adjust" them to attempt to remove this bias, a log-linear regression of recruitment *vs.* year over the period 1945 to 1968 is used

[3] AIC penalizes the goodness of fit by adding to twice the negative log-likelihood for every estimable parameter added.

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to estimate recruitment levels before 1942 back to 1930, at which time an unexploited equilibrium age-structure is assumed to apply. This then allows values to be generated for the "missing" $N_{y,a}$ s, for a better representation of the total population size in the earlier years.

Figure 8.4b shows estimated recruitment ($N_{y,1}$) and total population size trajectories for Area IV+V combined. The 95% confidence intervals (as estimated approximately from the Hessian) about these trajectories are also shown (though these do not include allowance for the "adjustment" of the total population size for earlier years). These intervals are displayed both for the case where natural mortality M is estimated, and where it is fixed at its maximum likelihood estimate. The purpose is to show that precision is fairly good for all years if M is assumed known; however, the estimation of M, though having little impact on precision for recent decades, results in increasing imprecision as one goes further back in time.

The Base Case assessment manifests values of λ^c=0.89, λ^s=0.53, i.e. slight overdispersion.

Results of Sensitivity tests for Areas IV+V combined

The sensitivity tests listed in Table 8.3a are generally self-explanatory. A number of associated Figures, which primarily compare the estimated trends in recruitment and total population size across these tests, are also shown:

- Figure 8.5 – different choices for CV(p) – variability in interannual distribution between Areas IV and V.
- Figure 8.6 – different choices for the maximum age m.
- Figure 8.7 – different choices for age-independent natural mortality M.
- Figure 8.8 – retrospective assessments for 2, 5 and 8 years earlier.
- Figure 8.9 – consequences of omitting either the JARPA or the IWC/IDCR-SOWER estimates of abundance.
- Figure 8.10 – different choices for selectivity slopes.
- Figure 8.11 – confidence intervals for M_a when various trends with age over a=1 to 30 and to 45 are admitted.

Other tests in Table 8.3a consider a different distributional form for p_y, estimating q and a 33% negative bias in abundance estimates (a consequence, perhaps, of the survey abundance estimation analysis assumption that $g(0)$=1). Some factors are tested in combination with increasing m from 30 to 45.

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The selectivity slope tests are of two types. First only commercial selectivity is assumed to have a linear trend (fixed or estimated) above age a=21 (i.e. instead of being flat with $S_a^c = 1$ as in equation (8.18)); S_{30}^c is kept fixed at 1 for these results, while S_a^s remains at 1 for $a \geq 7$. For the "Animals in the pack-ice" test, the assumption is made that selectivity changes in the same way with age for both the commercial and scientific catches because, for example, of older animals being preferentially found in that pack-ice area, and so not being available for capture (for the case $S_{26}^c > 1$). In these cases the trend in S_a^s continues down to age a=10.

Specification of Area-specific assessments

To maintain comparability with the Areas IV+V combined assessment, the Base Case specifications for each Areas treated on its own set m=30, $M_a = M$ (constant) and $q = 1$. The justification for the last choice is somewhat problematic for Area IV, as a variant of the Base Case which estimates q provides an estimate significantly larger than 1 (see Table 8.3b). However, the 1998 IWC/IDCR-SOWER abundance estimate, which is unusually low, is very influential in such an analysis. If it is omitted from consideration, the estimate of q again becomes not significantly different from 1, as is the case for Area V.

The (original) Base Cases maintain CV_{add}=0 as for the Areas IV+V combined assessment. For both Areas IV and V, this leads to the SDSR for the abundance estimates fitted exceeding 1. CV_{add} has been increased to reduce the value of SDSR to 1. Only a rather small CV_{add} is needed to achieve this for Area V, so that the associated Base Case has not been amended. However, a rather larger effect is evident for Area IV, so that the plots of results shown in Figure 8.12 are for the Revised Base Case (CV_{add}=0.2) in the case of Area IV.

Results of Base Case and Sensitivity tests for Area-Specific assessments

Figure 8.12 compares these Base Case results with those for the Areas combined Base Case assessment. For the last three decades, the Area specific assessments show a total population size which is decreasing more steeply for Area IV, but flatter for Area V. Corresponding M estimates are lower for Area V than for Area IV.

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Other sensitivity tests conducted for the Area-specific assessment include a 3-year-3-age grouping analysis for comparison with the results of Butterworth *et al.* (1999), and retrospective analyses.

8.5 Discussion

The consistent pattern shown by virtually all the assessments considered, whether for Areas IV and V in combination or separately, is of minke whale abundance that increased in the middle decades of the 20th Century to peak at about 1970, and then declined for the next three decades. Recruitment trends show a similar pattern, peaking a few years earlier than total abundance.

Of the various sensitivity tests to the Areas combined assessment, four show relatively minor effects in terms of trend estimates:

- Negative bias in estimates of abundance in absolute terms.
- A larger CV on the proportion in Area IV (p_y) distribution gives a steeper historic increase in recruitment and a flatter peak in total abundance (Figure 8.5).
- Increasing m, the largest age considered in the likelihood, leads to steeper historic increases in recruitment and abundance (Figure 8.6).
- If selectivity slopes at larger ages are treated as estimable rather than set flat, the estimates themselves are not greatly different from those when flatness is assumed (Figure 8.10).

The parameter to which trends are the most sensitive is natural mortality M. A larger M means a lesser historic increase in abundance, and a steeper current decline (Figure 8.7). Retrospective analyses indicate a decrease in the estimate of M as time has progressed (Figure 8.8 and Table 8.3a). This links to the relatively greater influences of the JARPA estimates of abundance as their number has increased with time: the IWC/IDCR-SOWER estimates tend to favour a higher M, and the JARPA a lower M, with consequential impacts on historic recruitment and population trends (Figure 8.9).

Comparing with earlier assessments using this methodology (Butterworth *et al.* 1999, 2002), CVs on estimates of M for Area-specific assessments as data have accumulated have decreased, roughly speaking, from 0.35 to 0.3 to 0.2. For the current Areas combined assessment, M is about 0.07 with a CV of about 0.12. The considerable increase in precision for these analyses compared to the earlier ones is closely linked to the revised JARPA estimates of abundance. These now seem comparable to those from the IWC/IDCR-SOWER surveys, and this assists in improving precision (the CV for M increases from 0.12 to 0.17 if q has to be estimated, see Table 8.3a).

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A number of possible forms for the dependence of natural mortality M on age a were examined. The fits showed that statistically the data could not support the estimation of more than one parameter for such dependence. Table 8.3a provides results for three alternative one-parameter formulations:

$$M_a = \begin{cases} \alpha \cdot e^{\delta \cdot a} \\ \alpha \cdot e^{\delta \cdot a^2} \\ \alpha \cdot e^{\delta \cdot \sqrt{a}} \end{cases} \tag{8.20}$$

for both the m=30 and m=45 cases. The results indicate statistically significant evidence for an increase of M with age from about 0.04 to 0.10. Although the form with a $\sqrt{a}$ dependence has a marginally greater likelihood, this suggests a downturn in M at the lowest ages which might well be an artefact of inappropriateness of the assumption that selectivity for the scientific catch-at-age 1 is the same as for ages 2-6. The form with a linear dependence on a in the exponent has therefore been preferred for the plots of M_a *vs.* a in Figure 8.11, which also show 95% Hessian-based confidence intervals.

Comparing the current Area-specific assessments with earlier analyses, the indications are of estimated historic increase rates in recruitment that have remained low for Area IV, whereas for Area V originally high values have decreased somewhat. Retrospective analyses for the current assessment reflect a trend of estimates of M that have decreased as time has progressed (as in the case of the Areas combined assessments).

8.6 Further work

Possible further work are listed in bullet point format below.

- The parameterization of selectivity factors adopted for these analyses has generally followed that of Butterworth *et al.* (1999). The data available then could justify only relatively parsimonious formulations. With more data now available, this aspect needs to be revisited and more flexible functional forms explored (e.g. logistic forms which allow also for exponential trends at higher ages).

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- The estimates of overdispersion factors for the Base Case Areas combined assessment (λ^c=0.89, λ^s=0.53) are a little surprising, particular the greater over-dispersion indicated for the scientific catch-at-age data given that they derive from an attempt at random sampling. This merits further examination, and is possibly linked to the absence of any account being taken of ageing error in this analysis.

- The estimation procedure used for the p_y parameters is somewhat *ad hoc*. However, integrating over these random effects would be computationally onerous. A more straightforward approach might be to extend the whole analysis to a fully Bayesian form, integrating over priors for all the parameters.

- As mentioned in section 4.1.2 of this thesis, Pastene *et al.* (2005) have proposed a boundary between minke whale stocks at about longitude 165°E on the basis of genetic analyses. Implications of different stock hypotheses that involve extensions of the two area/single stock models to multiple area/single stock models (i.e. to deal with the split of Area V and the inclusion of Areas IIIE and IVW) should be explored.

- Punt and Polacheck (2005) use statistical catch-at-age methodology to investigate the dynamics of minke whales in Areas IV and V. The essential difference between this approach and the ADAPT-like estimation used above is that the former does not assume catch-at-age values obtained from ageing information to be error-free. Their results are generally very similar to those obtained above. However, they do suggest that there is a notable difference in the estimated selectivity functions for the Japanese and Soviet commercial fleets when selectivity is assumed to be length-based, with that for the Japanese fleet estimated to be asymptotic and for the Soviet fleets being dome-shaped. These results suggest that further analyses based upon the ADAPT-like approach used above should explore the option of modelling the commercial catch-at-age data on a fleet-disaggregated basis.

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Table 8.1a Catch-at-age matrix for Area IV (see text for source details). For economy of space, ages have been grouped by 3, so that age 5 (for example) combines ages 4-6. Note that 1971 reflects the 1971/72 season.

Year/Age	2	5	8	11	14	17	20	23	26	29	32	35	38	41	44	47	50	54+
1971	121	256	314	310	352	319	284	235	146	95	99	45	30	25	3	7	17	4
1972	286	842	890	665	580	457	307	262	104	82	40	26	7	9	0	0	0	0
1973	495	535	620	691	529	427	398	229	213	182	93	65	62	6	12	13	0	0
1974	39	131	263	360	314	377	189	232	154	82	37	19	23	3	2	0	7	0
1975	14	110	127	176	139	140	71	33	23	23	10	6	9	0	0	0	0	0
1976	21	163	180	329	323	225	135	134	32	21	21	0	4	6	0	0	6	0
1977	46	56	131	128	156	164	77	66	69	34	17	6	11	0	0	2	0	0
1978	36	111	177	237	229	182	143	103	63	34	29	15	2	2	2	0	4	0
1979	85	174	180	222	241	268	189	139	104	79	58	39	27	19	14	15	6	0
1980	92	208	269	271	305	300	264	228	127	114	50	63	35	25	20	8	7	0
1981	65	155	195	221	211	239	171	119	106	59	41	15	17	5	4	3	1	0
1982	65	120	160	253	229	347	288	199	132	81	28	23	14	20	4	4	2	0
1983	105	225	252	334	269	300	205	188	108	76	15	9	2	7	0	0	0	0
1984	32	82	124	190	212	193	196	172	128	67	45	30	0	9	8	0	0	0
1985	14	52	97	136	192	218	211	201	107	82	33	28	31	2	0	2	0	0
1986	21	47	109	152	193	265	192	166	122	85	38	33	20	10	7	3	0	0
1987	28	44	33	24	29	25	31	14	17	13	3	6	2	1	0	0	0	0
1988	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1989	35	53	48	23	15	36	30	19	27	14	8	7	5	5	1	0	0	0
1990	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1991	39	39	39	24	20	21	18	12	16	20	15	9	7	2	2	2	1	1
1992	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993	58	47	46	42	22	25	16	11	17	12	14	7	6	1	1	2	1	1
1994	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1995	34	35	34	50	26	17	20	18	26	12	12	17	7	5	3	7	3	4
1996	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1997	87	36	36	27	20	19	14	17	10	10	15	13	10	2	5	6	0	2
1998	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1999	40	42	37	32	28	28	22	17	10	15	17	11	13	8	7	3	0	0
2000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2001	42	39	38	21	26	24	27	17	14	18	9	16	14	10	8	3	1	2
2002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2003	39	30	45	21	28	30	23	16	12	13	18	8	18	7	8	8	4	1

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Table 8.1b Catch-at-age matrix for Area V (see text for source details). For economy of space, ages have been grouped by 3, so that age 5 (for example) combines ages 4-6. Note that 1974 reflects the 1974/75 season.

Year/Age	2	5	8	11	14	17	20	23	26	29	32	35	38	41	44	47	50	54+
1974	21	62	129	133	131	89	74	48	30	3	10	4	0	0	0	0	0	0
1975	12	83	75	110	99	95	76	38	26	7	4	4	0	0	0	0	0	0
1976	10	130	150	204	286	225	145	94	76	67	27	26	7	9	9	0	0	2
1977	15	66	149	175	117	119	99	56	44	23	8	4	2	5	3	0	0	0
1978	9	19	47	72	69	72	17	43	32	19	4	9	0	4	0	0	0	0
1979	40	74	153	143	174	231	139	86	118	74	49	22	7	6	14	15	0	0
1980	10	86	123	129	152	162	108	116	109	105	32	50	30	13	13	9	0	0
1981	14	86	99	112	168	188	152	103	106	51	32	31	14	8	7	4	2	0
1982	26	113	216	258	282	295	244	175	117	72	48	16	17	12	3	1	0	1
1983	78	182	164	214	251	195	130	98	62	27	24	13	3	3	1	0	0	0
1984	24	66	88	104	112	173	128	84	56	39	13	14	5	1	1	0	0	0
1985	33	52	66	102	128	182	128	105	101	44	31	24	6	7	1	2	1	0
1986	4	32	48	102	117	141	171	125	118	80	31	25	5	6	1	2	1	3
1987	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1988	13	34	27	28	39	25	21	15	8	10	5	5	5	0	0	0	0	0
1989	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1990	4	39	30	24	35	39	42	30	23	13	12	10	9	3	4	4	0	0
1991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992	22	20	39	41	27	19	21	29	32	23	23	15	11	2	2	2	0	0
1993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1994	32	23	44	35	39	31	28	20	21	17	11	16	8	4	0	0	0	0
1995	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1996	21	24	17	40	38	21	28	21	26	18	21	13	12	15	6	2	6	0
1997	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1998	39	13	38	20	40	30	20	20	30	22	14	19	9	5	2	4	1	1
1999	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2000	16	26	29	31	33	42	9	26	28	21	18	16	15	2	6	3	4	5
2001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2002	22	33	28	37	33	37	29	22	22	16	19	8	8	3	5	2	3	1
2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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Table 8.2 Abundance estimates from sightings surveys (see text for source details).

a) Area IV

Survey	Year to which applied		Estimate (CV)
	3year–3age	1year–1age	
IDCR 1978/79	1980	1978	134308 (0.173)
IDCR 1988/89	1989	1988	60180 (0.184)
IDCR 1998/99 + part 1994/95	1998	1998	18619 (0.154)
JARPA 1989/90	1989	1989	54539 (0.215)
JARPA 1991/92	1992	1991	54959 (0.243)
JARPA 1993/94	1995	1993	41943 (0.215)
JARPA 1995/96	1995	1995	42134 (0.220)
JARPA 1997/98	1998	1997	32656 (0.252)
JARPA 1999/00	2001	1999	49867 (0.169)
JARPA 2001/02	2001	2001	68503 (0.167)
JARPA 2003/04	2004	2003	47858 (0.358)

b) Area V

Survey	Year to which applied		Estimate (CV)
	3year–3age	1year–1age	
IDCR 1980/81	1980	1980	257767 (0.280)
IDCR 1985/86	1986	1985	290724 (0.140)
IDCR 1991/92	1992	1991	190081 (0.180)
JARPA 1990/91	1992	1990	195743 (0.210)
JARPA 1992/93	1992	1992	122048 (0.229)
JARPA 1994/95	1995	1994	168566 (0.268)
JARPA 1996/97	1998	1996	171332 (0.261)
JARPA 1998/99	1998	1998	198423 (0.233)
JARPA 2000/01	2001	2000	179796 (0.210)
JARPA 2002/03	2004	2002	226884 (0.161)

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Table 8.3a Results for the Base Case and sensitivity tests for the assessment of Areas IV+V combined. $N_{y,1}$ reflects recruitment and N_y total abundance. Increase rates are given as annual proportions. The contributions to the total negative log-likelihood (-ln$L$(total)), in terms of the notation in the text, are –ln$L$(CAA)=-lnL_3, -ln$L$(indices)=-lnL_1-lnL_2, and -ln$L(p_y)$=-lnL_4. The value of $\overline{p} = \alpha/(\alpha+\beta)$is the estimated average proportion of the whales to be found in Area IV. SDSR is the standard deviation of the standardized residuals; for the abundance indices the standardization is in terms of the survey sampling CVs for each survey, whereas for the proportion p_y in Area IV it is in terms of the standard deviation assumed to apply to this distribution. Estimated CVs, where given, are based upon the Hessian approximation – this was cross-checked against likelihood profile estimation for the CV of M, and found to reflect good accuracy.

Area IV+V																	
Scenario	Ny,1 incr.rate 45-68	$N_{83,1}/N_{68,1}$	$N_{Istyr-5,1}/N_{68,1}$	M (CV)	Ny incr.rate 80-Istyr	-lnL (total)	-lnL (CAA)	-lnL (indices)	-lnL (Py)	Chi²/DF	$\overline{p}$	SDSR (abun)	SDSR (p)	Others			
"Base Case"	0.046	0.569	0.204	0.068 (0.123)	-0.027	314.156	341.423	10.590	-37.856	1.006	0.185	1.004	0.929				
Log Normal (σ=0.2)	0.046	0.561	0.197	0.069 (0.125)	-0.028	346.026	341.401	10.301	-5.676	1.009	0.201	1.075	0.883				
p constant	0.038	0.503	0.161	0.077 (0.094)	-0.035	376.405	341.690	34.715	-	0.978	0.198	1.818	-				
Beta (CV=0.1)	0.041	0.530	0.178	0.074 (0.104)	-0.032	310.662	341.560	21.542	-52.440	1.006	0.182	1.432	0.827				
Beta (CV=0.4)	0.052	0.618	0.238	0.062 (0.156)	-0.021	319.387	341.310	5.012	-26.935	1.008	0.184	0.691	0.755	q			
q estimated	0.045	0.559	0.197	0.070 (0.167)	-0.028	314.145	341.430	10.738	-38.023	1.006	0.185	1.011	0.915	1.025 (0.149)			
m=35	0.059	0.554	0.201	0.068 (0.122)	-0.026	389.808	417.072	10.497	-37.761	1.006	0.185	1.000	0.934				
m=45	0.066	0.543	0.201	0.068 (0.122)	-0.026	482.712	510.057	10.412	-37.758	0.963	0.185	0.996	0.934				
Abundance x 1.5	0.045	0.577	0.203	0.070 (0.118)	-0.028	314.524	341.572	10.786	-37.834	1.007	0.185	1.014	0.930				
Mfix=0.05	0.063	0.709	0.308	0.050	-0.011	317.100	341.512	12.017	-36.428	1.005	0.184	1.070	1.019				
Mfix=0.09	0.026	0.437	0.126	0.090	-0.045	316.591	341.812	13.203	-38.424	1.007	0.186	1.121	0.869				
M age dep (m=30)														Mmax (CV)	Mmin (CV)		
$M_a = \alpha \cdot \exp(\delta \cdot a)$	0.036	0.572	0.221	0.066	-0.027	311.801	339.377	10.426	-38.002	1.006	0.185	0.997	0.921	0.099 (0.179)	0.041 (0.310)		
$M_a = \alpha \cdot \exp(\delta \cdot a^2)$	0.037	0.578	0.222	0.067	-0.026	312.175	339.657	10.475	-37.957	1.005	0.185	0.999	0.924	0.103 (0.204)	0.052 (0.212)		
$M_a = \alpha \cdot \exp(\delta \cdot \sqrt{a})$	0.036	0.567	0.220	0.064	-0.027	311.476	339.114	10.397	-38.035	1.007	0.185	0.995	0.919	0.096 (0.167)	0.030 (0.442)		
$M_a = \alpha \cdot \exp(\delta \cdot a)$ (m=45)	0.057	0.536	0.202	0.063	-0.026	478.768	506.084	10.543	-37.859	0.965	0.185	1.002	0.929	0.107 (0.162)	0.047 (0.206)		
$M_a = \alpha \cdot \exp(\delta \cdot a^2)$ (m=45)	0.059	0.540	0.201	0.065	-0.026	479.449	506.702	10.569	-37.822	0.966	0.185	1.003	0.931	0.113 (0.190)	0.058 (0.151)		
$M_a = \alpha \cdot \exp(\delta \cdot \sqrt{a})$ (m=45)	0.056	0.533	0.202	0.062	-0.026	478.336	505.718	10.510	-37.892	0.965	0.185	1.001	0.927	0.103 (0.150)	0.036 (0.289)		
Retrospective (Istyr=2001)	0.050	0.492	0.323	0.079 (0.121)	-0.037	289.370	314.678	7.532	-32.840	1.008	0.197	0.890	0.924				
Retrospective (Istyr=1998)	0.015	0.345	0.130	0.101 (0.116)	-0.058	245.807	272.083	5.000	-31.277	1.015	0.182	0.791	0.573				
Retrospective (Istyr=1995)	0.015	0.339	0.174	0.101 (0.164)	-0.058	273.413	238.366	13.249	21.798	1.054	0.324	1.486	0.841				
Omit JARPA data	-0.070	0.258	0.038	0.124 (0.132)	-0.083	329.478	341.463	1.755	-13.741	0.988	0.182	0.765	0.417				
Omit IDCR data	0.082	0.921	0.571	0.03 (0.005)	0.010	310.605	340.904	3.431	-33.729	1.001	0.190	0.676	0.414				
Est 2Sci. Sel (m=30)	0.043	0.550	0.208	0.071 (0.119)	-0.027	298.682	326.762	9.958	-38.038	0.960	0.185	0.974	0.916				
Est3-3Sci. Sel (m=45)	0.064	0.518	0.203	0.071 (0.118)	-0.026	465.400	493.633	9.740	-37.974	0.931	0.185	0.963	0.919				
														Sc16-21	Sc22	Sc26	Sc45
Sc26=0.80 (Sc30=1)	0.084	0.561	0.202	0.068 (0.125)	-0.023	327.907	354.815	10.564	-37.472	1.021	0.186	1.003	0.946	0.532	0.600	0.800	
Est Select Slope (Sc30=1)	0.039	0.577	0.208	0.068 (0.125)	-0.027	313.687	340.995	10.577	-37.886	1.006	0.185	1.004	0.928	1.056	1.121	1.060	
Sc26=1.20 (Sc30=1)	0.024	0.597	0.221	0.066 (0.128)	-0.027	315.444	342.835	10.514	-37.904	1.010	0.185	1.001	0.926	1.355	1.400	1.200	
Sc26=1.40 (Sc30=1)	0.010	0.628	0.242	0.063 (0.135)	-0.027	321.581	349.074	10.382	-37.875	1.029	0.185	0.994	0.926	1.802	1.800	1.400	
Sc26=0.95 (m=45)	0.075	0.542	0.205	0.067 (0.125)	-0.024	488.161	515.400	10.371	-37.609	0.979	0.186	0.994	0.941	0.758	0.900	0.950	1.188
Sc26=1.05 (m=45)	0.058	0.548	0.200	0.069 (0.120)	-0.027	478.053	505.450	10.469	-37.866	0.949	0.185	0.999	0.929	0.939	1.103	1.050	0.807
Sc26=1.10 (m=45)	0.051	0.554	0.201	0.069 (0.119)	-0.027	474.806	502.219	10.514	-37.928	1.001	0.185	1.001	0.926	1.023	1.190	1.100	0.643
Est Select Slope (m=45)	0.047	0.558	0.202	0.069 (0.119)	-0.027	473.098	500.517	10.534	-37.953	0.937	0.185	1.002	0.925	1.071	1.248	1.124	0.535
Sc26=1.15 (m=45)	0.055	0.526	0.191	0.070 (0.118)	-0.027	487.262	514.731	10.488	-37.957	0.976	0.185	0.999	0.925	0.906	1.291	1.150	0.453
Sc26=0.80 (m=45, Sc30=1)	0.090	0.537	0.208	0.065 (0.128)	-0.022	500.104	527.129	10.352	-37.377	1.026	0.186	0.993	0.950	0.543	0.600	0.800	
Est Select Slope (m=45, Sc30=1)	0.065	0.544	0.201	0.068 (0.122)	-0.026	482.643	510.000	10.425	-37.782	0.962	0.185	0.996	0.933	0.873	1.036	1.018	
Sc26=1.20 (m=45, Sc30=1)	0.049	0.554	0.200	0.069 (0.118)	-0.028	487.717	515.115	10.560	-37.959	0.963	0.184	1.003	0.925	1.159	1.400	1.200	
Animals in the pack ice (Sc30=1)																	
Sc26=Ss26=0.9	0.040	0.650	0.256	0.093 (0.094)	-0.024	319.477	347.216	10.081	-37.820	1.019	0.185	0.980	0.932	0.715	0.800	0.900	
Est Select Slope	0.045	0.535	0.184	0.060 (0.176)	-0.028	313.539	340.600	10.730	-37.844	1.010	0.185	1.013	0.930	1.062	1.121	1.060	
Sc26=Ss26=1.1	0.044	0.517	0.175	0.058 (0.147)	-0.028	313.759	340.705	10.883	-37.829	1.008	0.185	1.018	0.930	1.150	1.200	1.100	

*Chi^2 is defined as $C^*_{y,a}\lambda_y \dfrac{(\rho_{y,a} - \hat{\rho}_{y,a})^2}{\hat{\rho}_{y,a}}$.

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Table 8.3b Results for the Base Case and sensitivity tests for the assessment of Area IV and of Area V each treated as closed populations. Notation is as for Table 8.3a.

Area IV											
Scenario	Ny,1 incr.rate 45-68	N83,1/N68,1	N98,1/N68,1	M (CV)	Ny incr.rate 80-lstyr	-lnL (total)	-lnL (CAA)	-lnL (indices)	Chi2/DF	SDSR (abun)	*q*
Original "Base Case"	0.020	0.422	0.129	0.090 (0.115)	-0.042	238.654	213.759	24.895	0.934	2.128	
q estimate	0.040	0.320	0.079	0.106 (0.106)	-0.059	231.392	213.748	17.644	0.934	1.791	1.740 (0.070)
omit IDCR 1998	0.033	0.510	0.201	0.076 (0.140)	-0.027	222.057	213.360	8.697	0.932	1.319	
omit IDCR 1998, *q* estimate	0.047	0.643	0.314	0.062 (0.245)	-0.012	221.024	213.213	7.811	0.932	1.250	0.716 (0.326)
m=45	0.030	0.424	0.131	0.081 (0.128)	-0.037	378.141	352.444	25.698	0.961	2.162	
3yr-3age	0.019	0.280	0.105*	0.095 (0.112)	-0.048	57.389	31.796	25.592	0.946	2.157	
Retrospective (lstyr=2001)	0.015	0.403	0.273	0.095 (0.115)	-0.044	223.863	200.287	23.576	0.937	2.172	
Retrospective (lstyr=1998)	-0.029	0.213	0.040	0.141 (0.091)	-0.085	185.987	182.205	3.782	0.969	0.972	
Retrospective (lstyr=1995)	-0.003	0.290	0.230	0.115 (0.145)	-0.062	169.052	168.776	0.276	0.974	0.303	
CVadd =0.2 (Revised Base Case)	0.029	0.468	0.161	0.080 (0.195)	-0.033	223.628	213.031	10.597	0.931	0.988	
AreaV											
Scenario	Ny,1 incr.rate 48-68	N83,1/N68,1	N98,1/N68,1	M (CV)	Ny incr.rate 80-lstyr	-lnL (total)	-lnL (CAA)	-lnL (indices)	Chi2/DF	SDSR (abun)	*q*
"Base Case"	0.067	0.628	0.267	0.051 (0.202)	-0.017	233.134	227.094	6.040	1.147	1.099	
q estimate	0.085	0.856	0.495	0.030 (0.464)	0.004	231.682	227.096	4.586	1.147	0.958	0.697 (0.255)
m=45	0.077	0.613	0.289	0.054 (0.191)	-0.015	341.545	335.865	5.680	1.135	1.066	
3yr-3age	0.060	0.604	0.330	0.050 (0.268)	-0.016	46.266	39.664	6.602	1.250	1.149	
Retrospective (lstyr=2001)	0.054	0.508	0.171	0.065 (0.196)	-0.031	213.738	209.923	3.815	1.144	0.921	
Retrospective (lstyr=1998)	0.026	0.360	0.237	0.087 (0.209)	-0.052	194.901	192.777	2.124	1.155	0.779	
Retrospective (lstyr=1995)	0.021	0.318	0.098	0.092 (0.227)	-0.060	166.291	164.624	1.667	1.200	0.770	
CVadd =0.02	0.062	0.629	0.268	0.051 (0.204)	-0.017	233.078	227.104	5.973	1.147	0.995	

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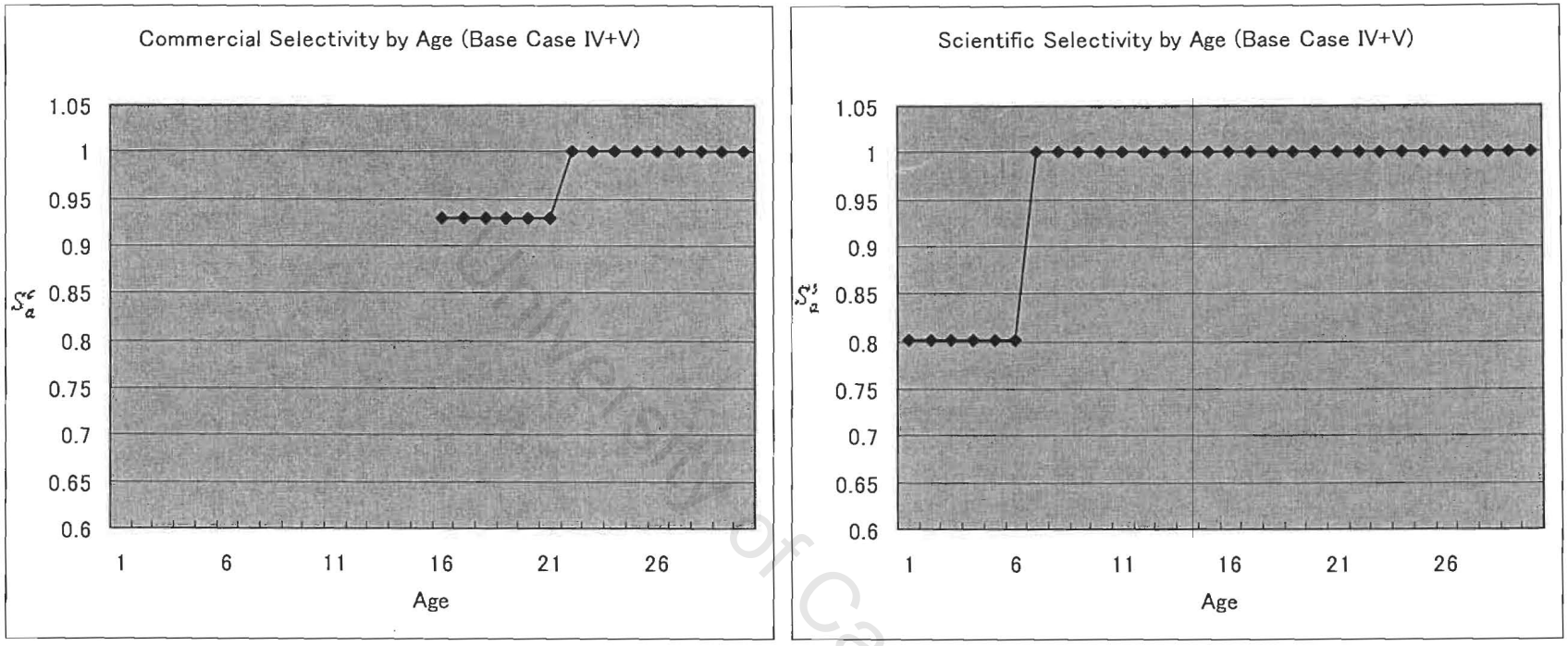
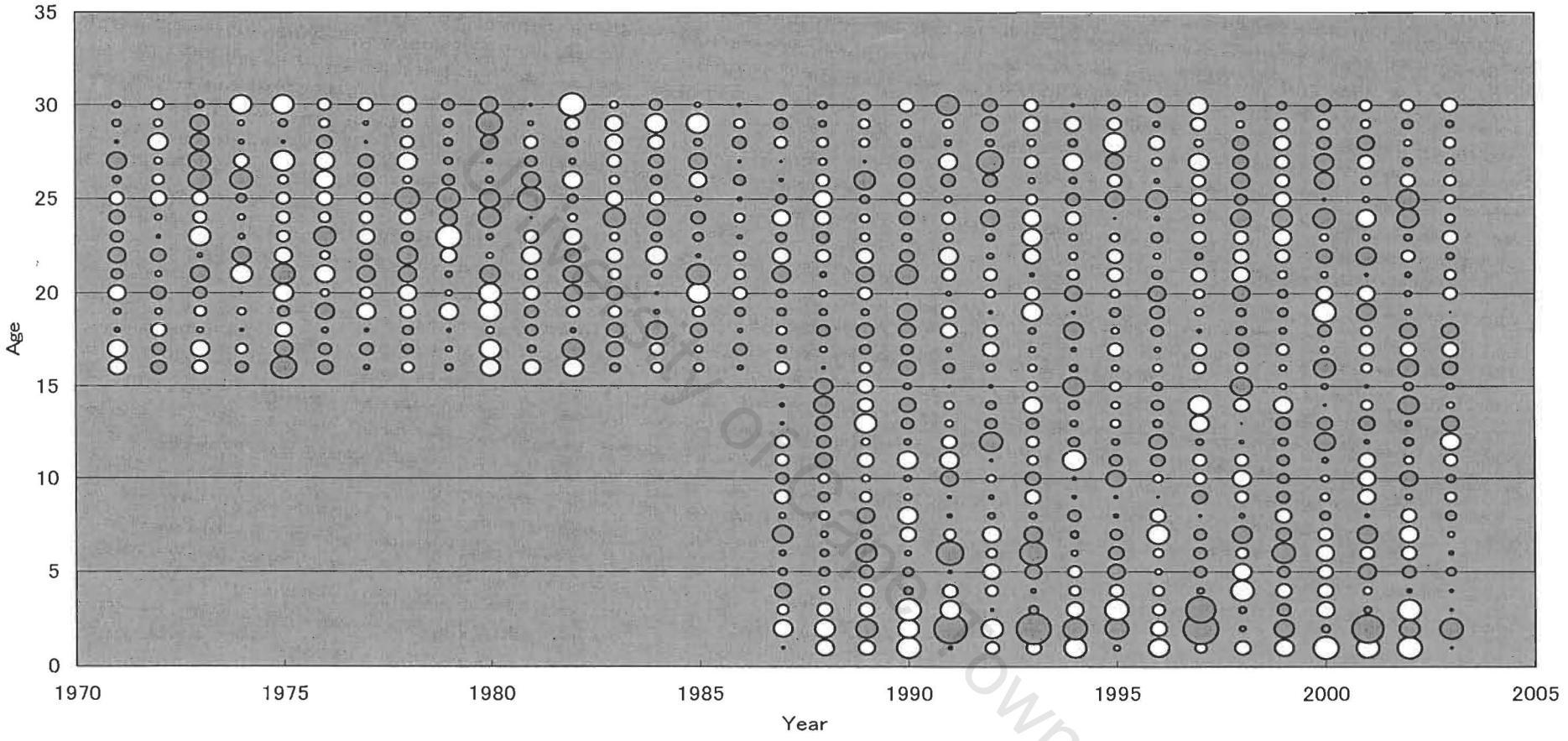


Figure 8.1 Estimated commercial and scientific selectivities by age for the "Base Case" for Areas IV+V combined.

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Figure 8.2 Standardised residuals of the model fit to the observed catch-at-age proportions for the Area IV+V combined Base Case, shown as a bubble plot. Gray bubbles are positive and white bubbles negative residuals. The size of the bubble indicates the magnitude of the residual. Standardised residuals are defined by : $\sqrt{C^*_{y,a}\lambda_y}\,\frac{\rho_{y,a}-\hat{\rho}_{y,a}}{\sqrt{\hat{\rho}_{y,a}}}$.

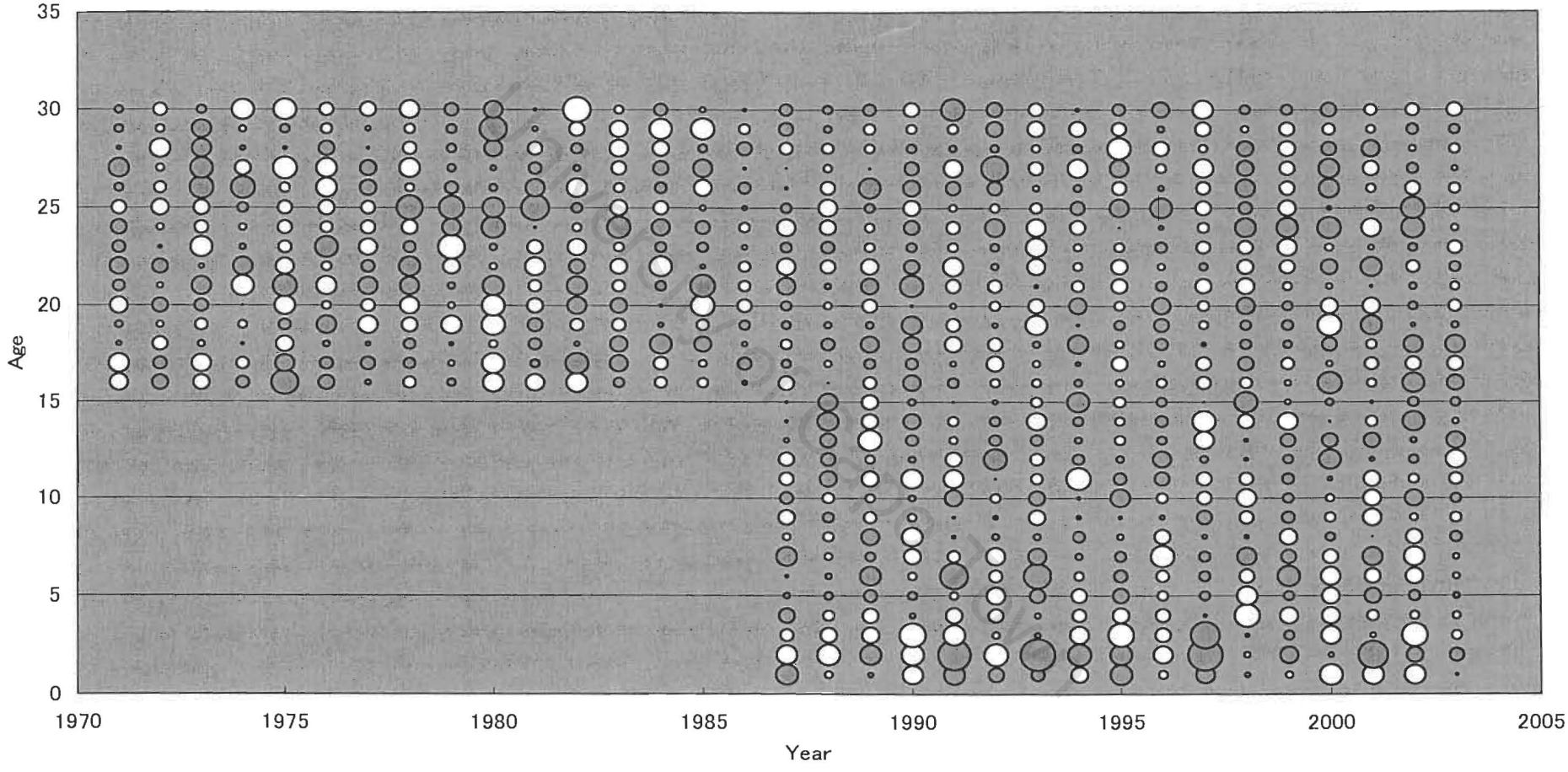
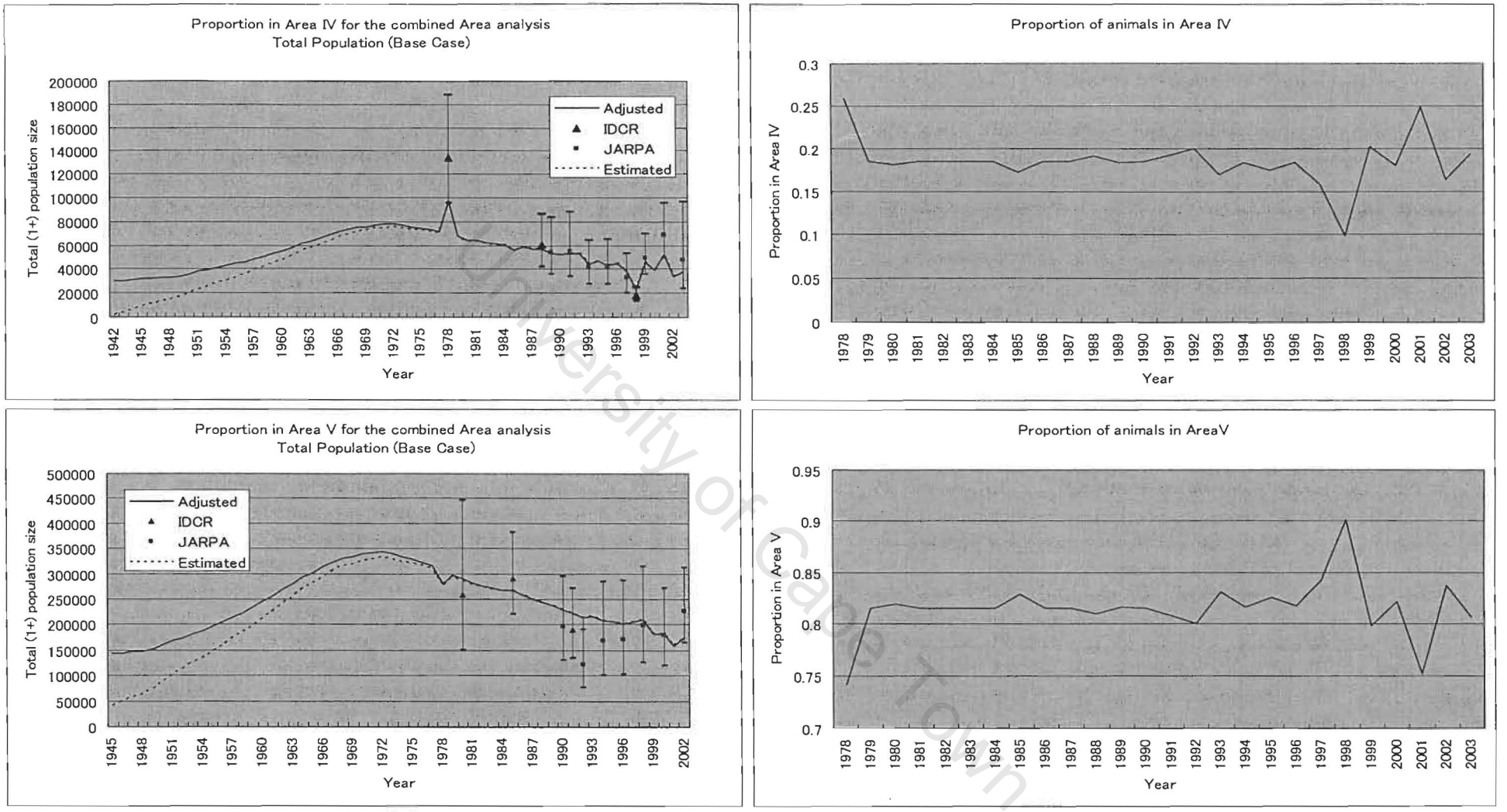


Figure 8.3 Standardised residuals of the model fit to the observed catch-at-age proportions for the Area IV+V combined Base Case adjusted so that S_1^S is estimated separately from $S_2^S = S_3^S = \cdots = S_6^S$, shown as a bubble plot (see case Est 2Sci. Sel (m=30) in Table 8.3a). The meanings of the bubbles are same as for Figure 8.2.



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Figure 8.4a Fits of the ADAPT-VPA model to the total (1+) abundance estimates for Areas IV and V separately for each Area, together with the estimates for the proportions (p_y and $1-p_y$) of the total population in each Area each year for the Area IV+V combined Base Case. The abundance plots include the survey estimates of abundance together with their survey sampling estimated 95% confidence intervals. The difference between the "estimated" and "adjusted" total population sizes is explained in the text.

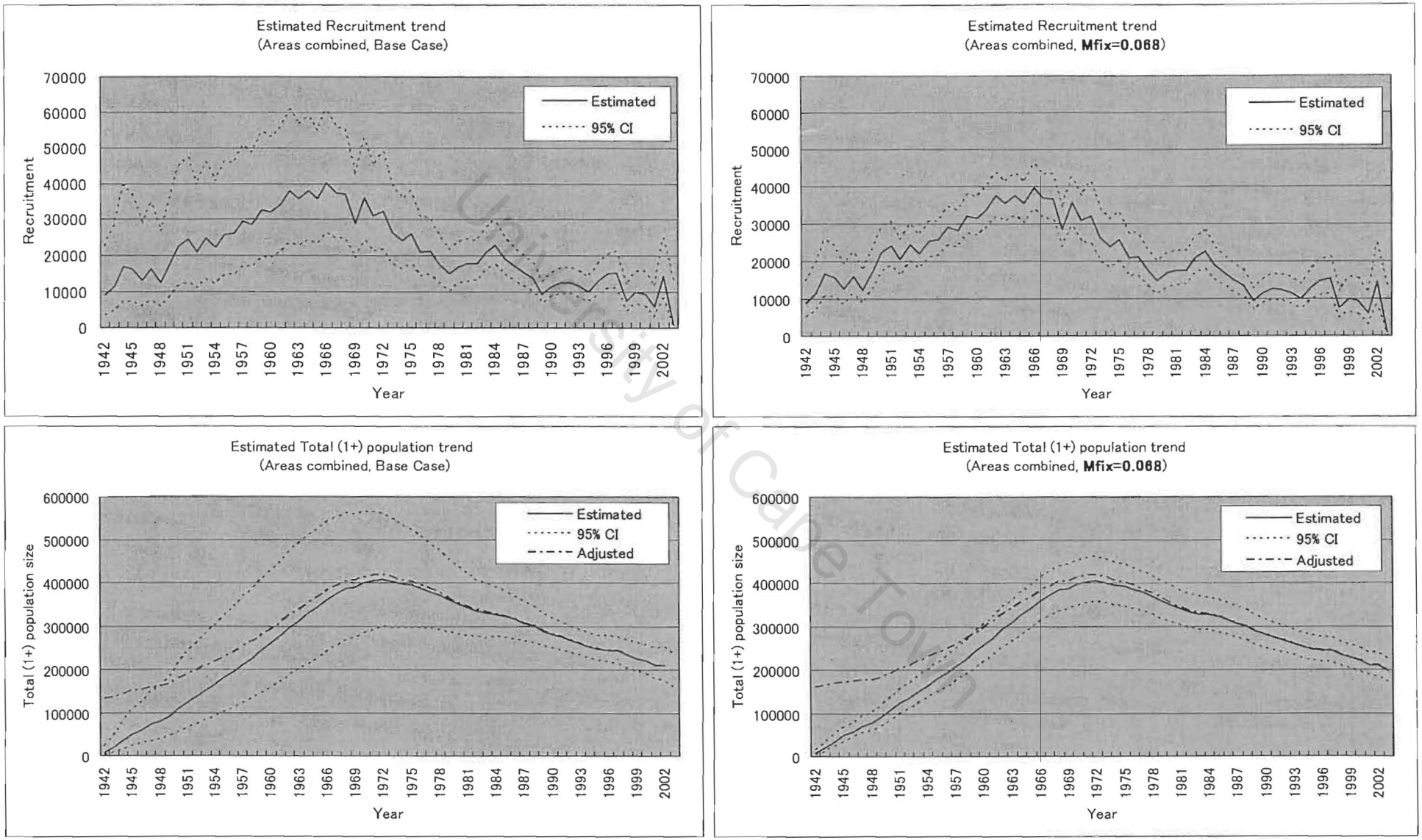
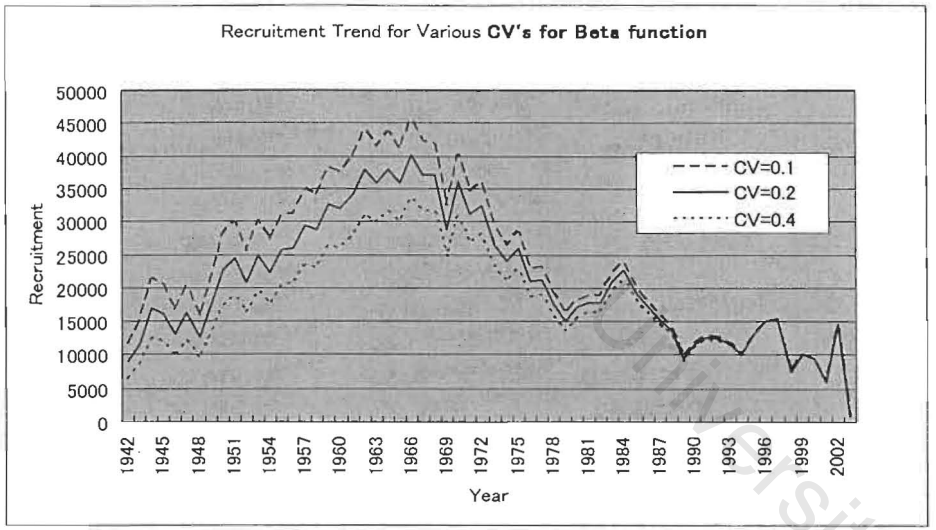


Figure 8.4b Estimated recruitment ($N_{y,1}$) and total population size trajectories for the Areas IV+V combined Base Case. In the righthand plots, natural mortality M is fixed at its maximum likelihood estimate.

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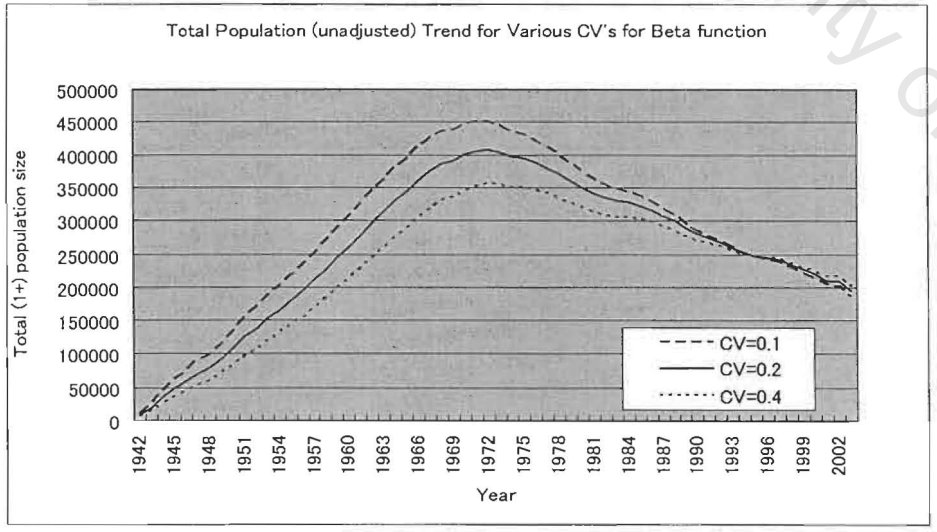
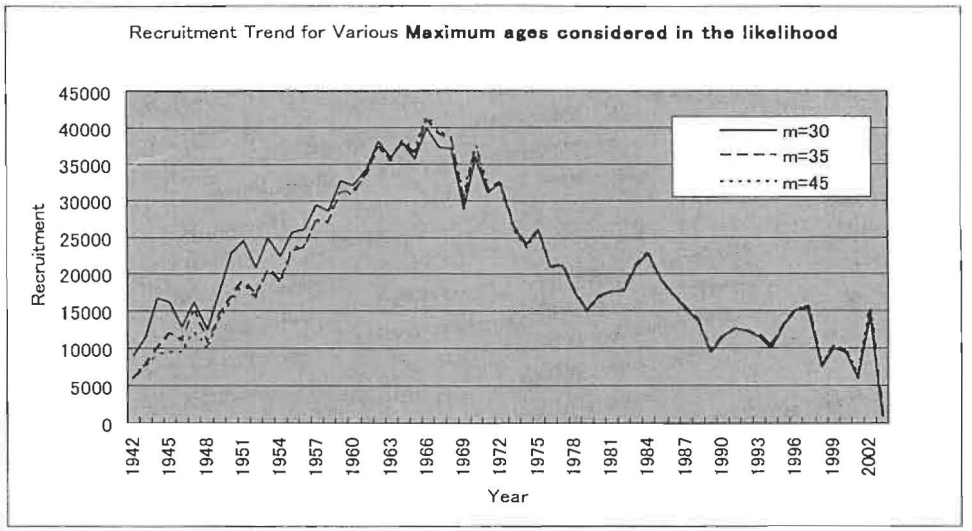


Figure 8.5 Estimated recruitment ($N_{y,1}$) and total population size trajectories for different choices of CVs for the p_y distribution for the Areas IV+V combined assessment.



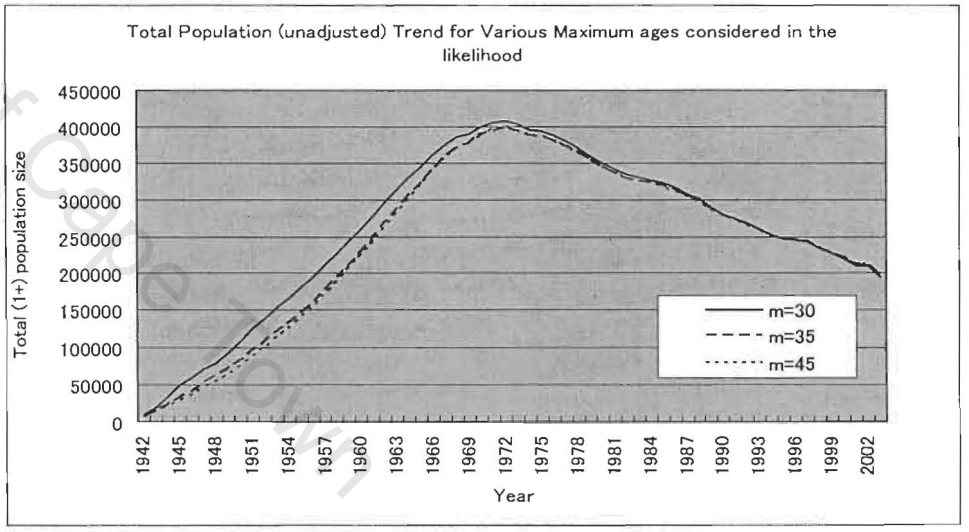


Figure 8.6 Estimated recruitment ($N_{y,1}$) and total population size trajectories for different choices of maximum age m for the Areas IV+V combined assessment.

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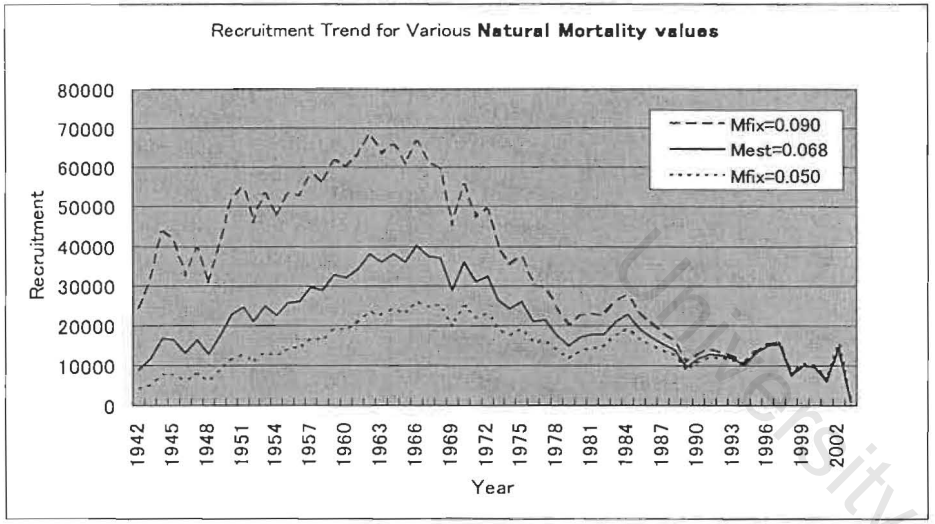


Figure 8.7 Estimated recruitment ($N_{y,1}$) and total population size trajectories for different choices of natural mortality M for the Areas IV+V combined assessment.

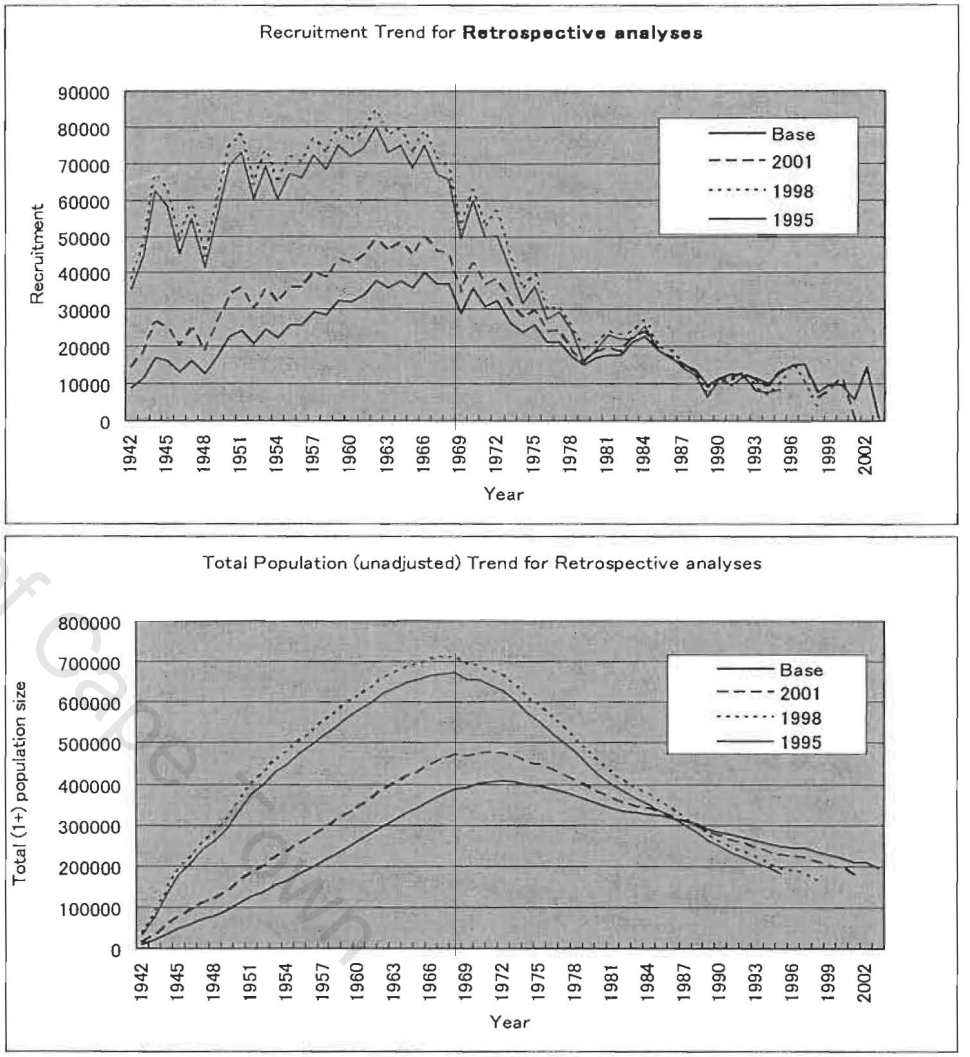


Figure 8.8 Estimated recruitment ($N_{y,1}$) and total population size trajectories for retrospective assessments for 2, 5 and 8 years earlier for the Areas IV+V combined assessment.

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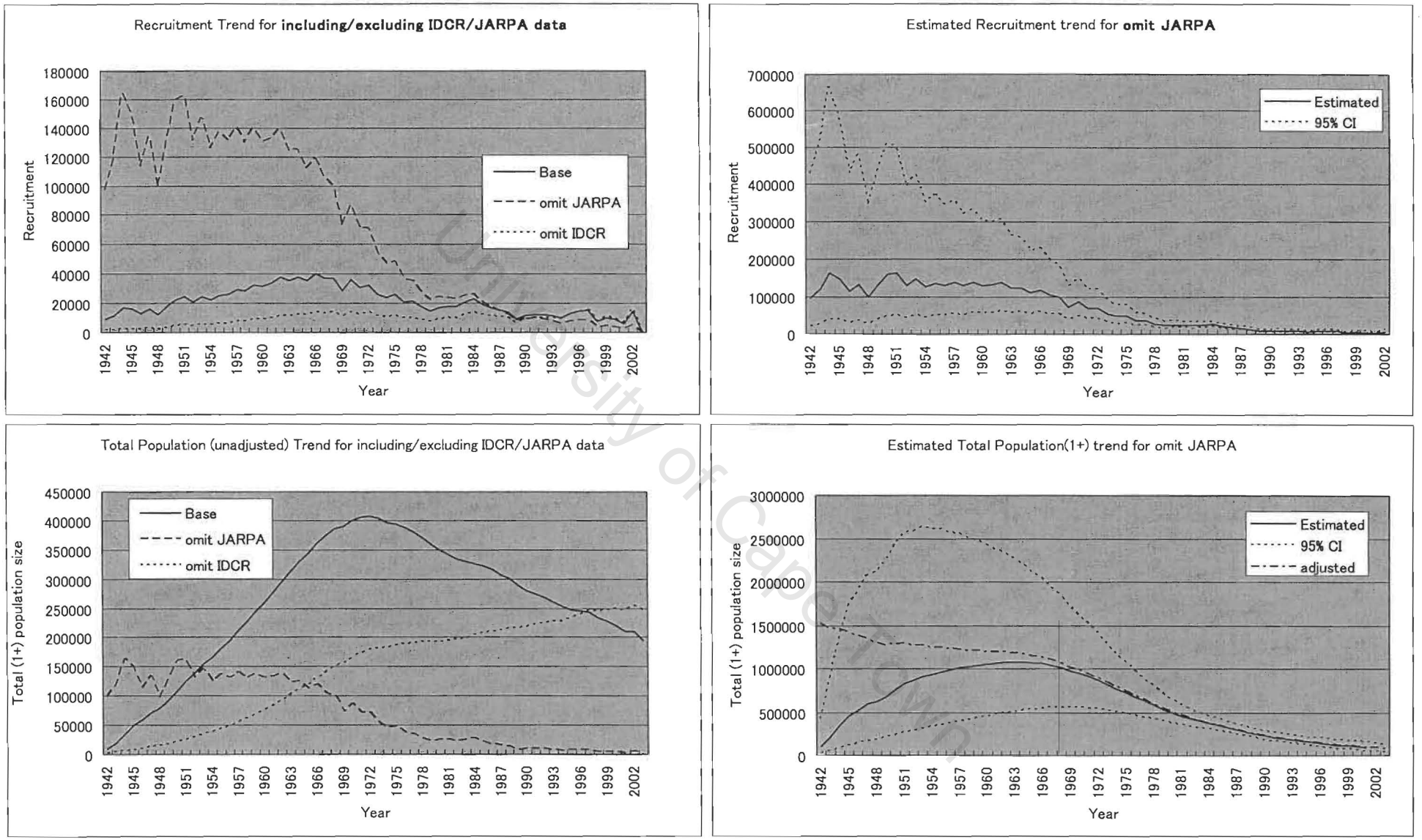


Figure 8.9 Estimated recruitment ($N_{y,1}$) and total population size trajectories for cases omitting either the JARPA or the IDCR/SOWER estimates of abundance for the Areas IV+V combined assessment. Confidence intervals for the former case are shown in the righthand plots.

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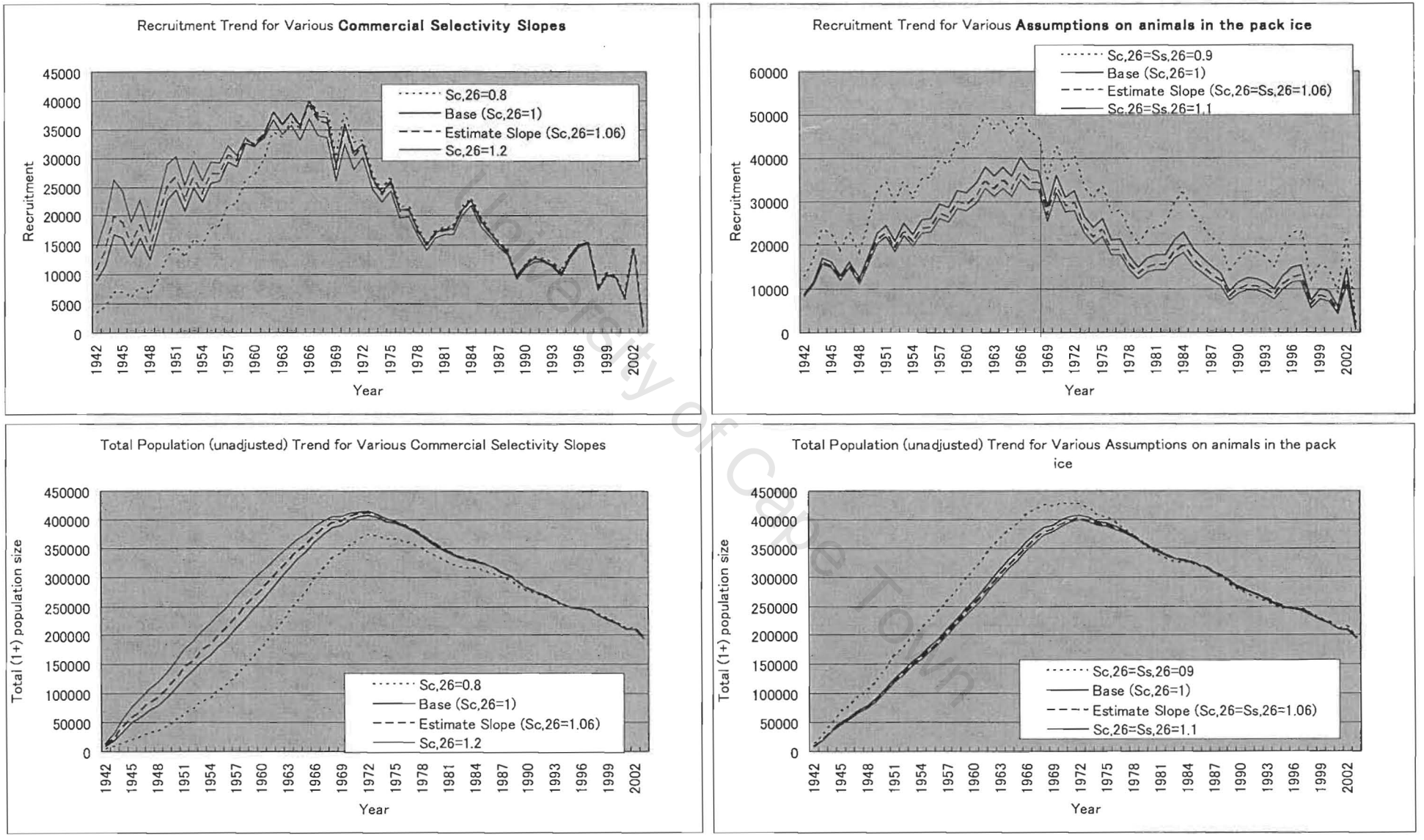
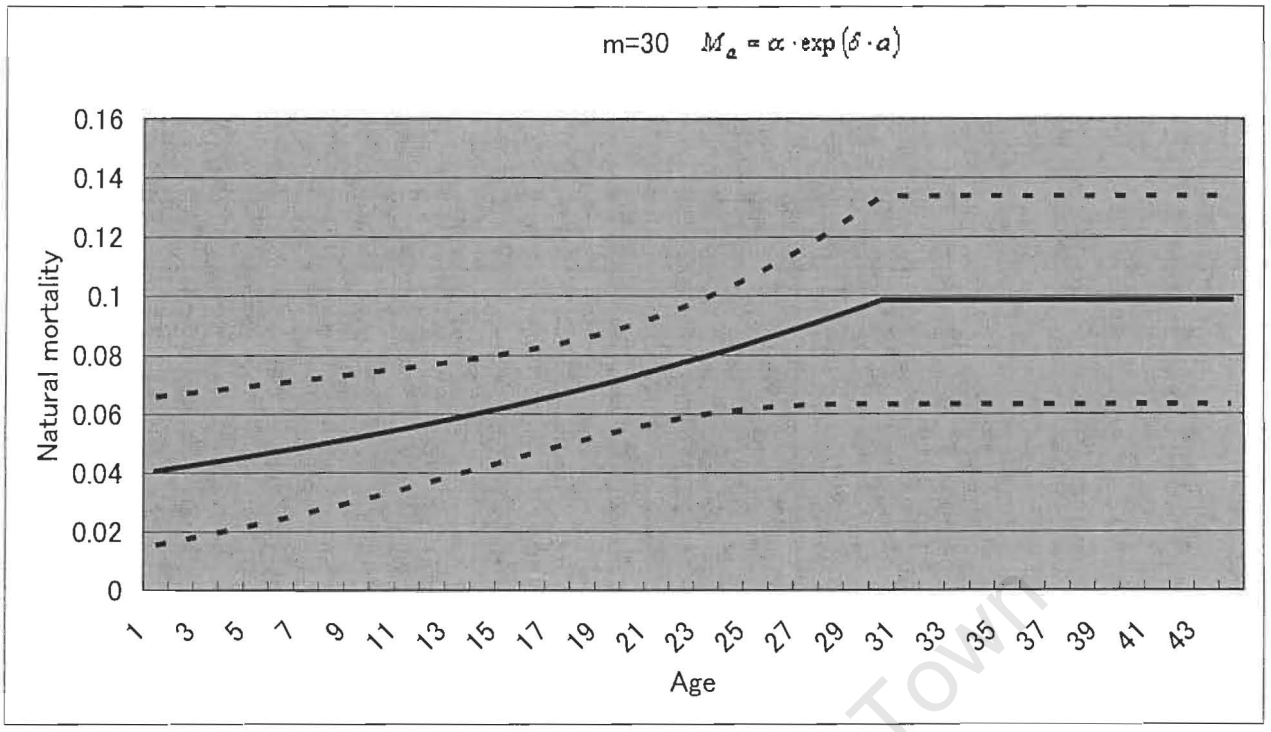


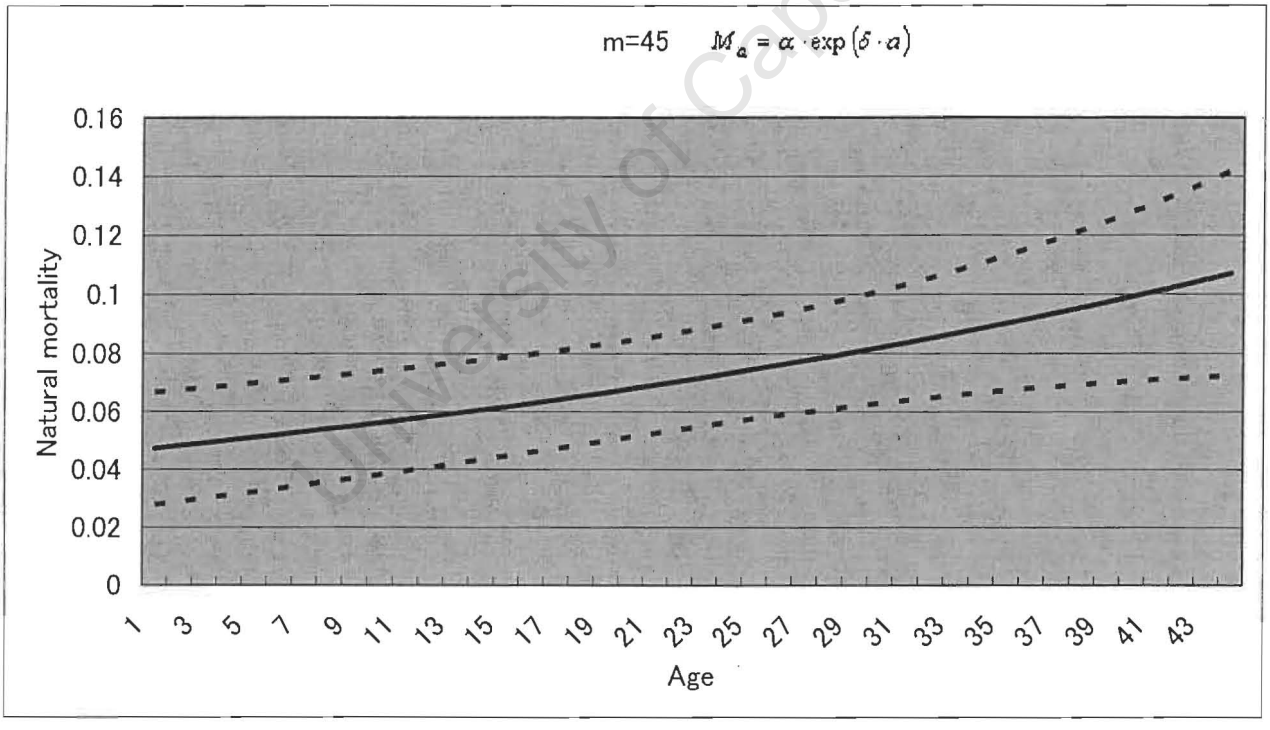
Figure 8.10 Estimated recruitment ($N_{y,1}$) and total population size trajectories for different choices for the commercial selectivity slope for the Areas IV+V combined assessments.

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a) Maximum age considered in the likelihood is 30



b) Maximum age considered in the likelihood is 45



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Figure 8.11 Confidence intervals (95% based on the Hessian) for M_a when an exponential trend ($M_a = \alpha \cdot \exp(\delta \cdot a)$) over a=1 to 30 (45 for case b)) is admitted for the Areas IV+V combined assessment.

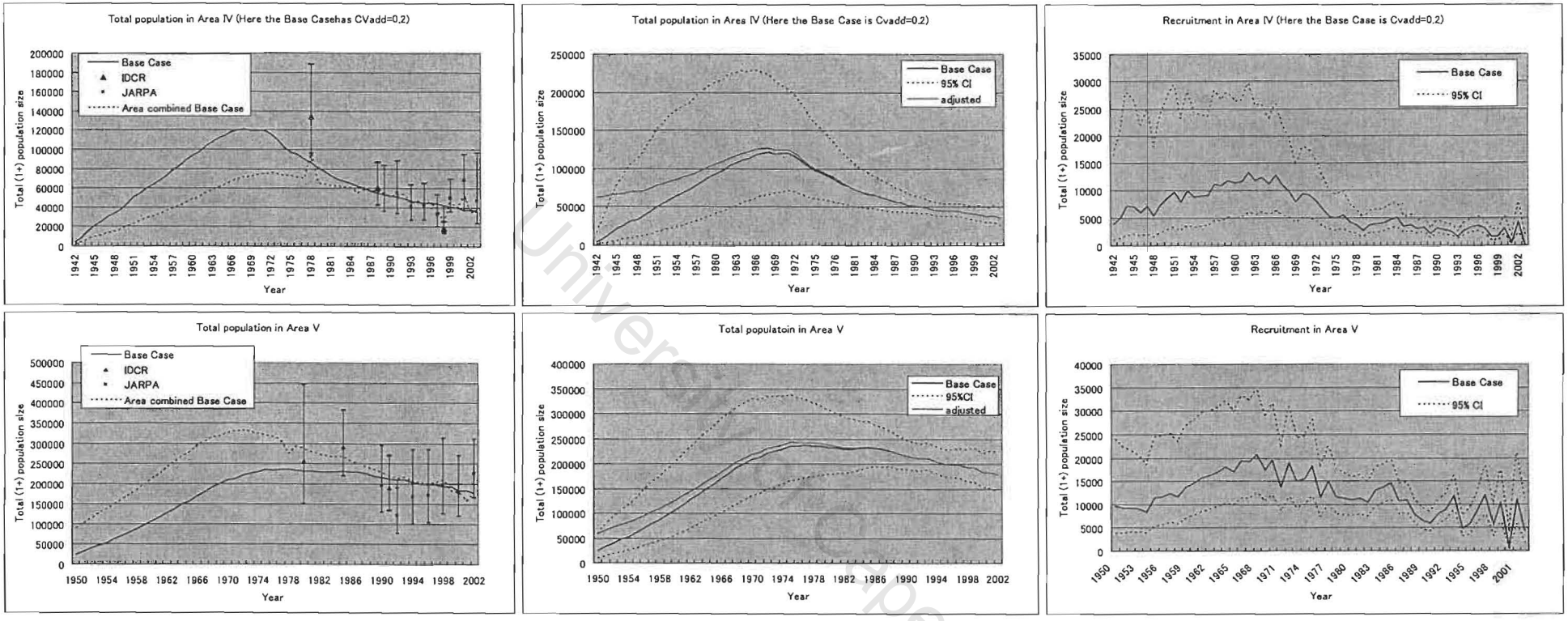


Figure 8.12 Base Case (see text) estimates of total population size and recruitment, together in Hessian-based estimates of 95% CI's, for separate Area IV and Area V assessments.

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APPENDIX 8

SPECIFICATION OF THE CATCH-AT-AGE MATRICES

The catches-at-age by sex are computed differently for the periods of commercial (1970-1986) and scientific catches (1987-present) because: (a) a much greater fraction of the scientific catch has been aged, and (b) the scientific catch is relatively small, making it difficult to develop a reliable age-length key.

App. 8.1 The scientific catch

The annual catch-at-age vector for each sex for the scientific catch is obtained by scaling the sex-specific age-frequency data obtained from aged animals upwards to the total catch, i.e.:

$$C^{m}_{y,a} = C^{m}_{y}\, C^{m*}_{y,a} \Big/ \sum_{a'} C^{m*}_{y,a'}$$
$$C^{f}_{y,a} = C^{f}_{y}\, C^{f*}_{y,a} \Big/ \sum_{a'} C^{f*}_{y,a'} \qquad \text{(App. 8.1)}$$

where $C^{m/f}_{y,a}$ is the estimated catch of males/females of age a during year y,

$C^{m/f*}_{y,a}$ is the number of males/females caught during year y assigned to be of age a, and

$C^{m/f}_{y}$ is the total catch of males/females during year y.

App. 8.2 The commercial catch

The catches-at-age by sex for the period of commercial catch are obtained by applying annual sex-specific age-length keys constructed from the subset of the catches aged by Japanese scientists to the sex-specific length-frequencies for Japan and the (former) USSR, i.e.:

$$C^{m}_{y,a} = \sum_{l} A^{m,l}_{y,a}\, C^{m,l}_{y}$$
$$C^{f}_{y,a} = \sum_{l} A^{f,l}_{y,a}\, C^{f,l}_{y} \qquad \text{(App. 8.2)}$$

where $C^{m/f,l}_{y}$ is the catch during year y of males/females in (1m) length-class l, and

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$A_{y,a}^{m/f,l}$ is the probability that a male/female in length-class l caught during year y of age a (i.e. the relative frequency of males/females of age a in the column of the age-length key for year y and length-class l), as determined by ageing by Japanese scientists.

The age-length keys do not include data for all length-classes although catches-at-length exists for some of these "missing" classes. To overcome this problem, the relative age-frequency for the 'nearest' length-class is used when applying Equation (App. 8.2). The 'nearest' length-class is selected by examining whether data are available for any of the adjacent length-classes (starting with greater length) and examining length-classes further from the length-class for which age-frequency information is needed until a length-class for which data are available is found. The small proportions of unsexed animals in the commercial catch are allocated *pro rata* between males and females.

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CHAPTER 9

IMPLICATIONS OF THE CATCH-AT-AGE ANALYSES FOR THE DYNAMICS OF SOUTHERN HEMISPHERE MINKE WHALES

9.1 Introduction

This Chapter focuses on the results of the Base Case assessment of Areas IV and V combined that is presented in the previous Chapter with a view to an improved understanding of the dynamics of the minke whales in this region.

Figure 9.1a plots the recruitment ($N_{y,1}$) time series estimated by this Base Case assessment. Figure 9.1b shows the associated stock recruitment plot: $N_{y,1}$ *vs* N^f_{y-1}, where the "adult" (reproductive) population is taken to be:

$$N^A_y = \sum_{a=7}^{45} N_{y,a} \tag{9.1}$$

and the number of adult females $N^f_y = 0.5 \cdot N^A_y$, i.e. an age at first-parturition of 7 is assumed. This plot includes a "replacement line"; this is the line where recruitment exactly balances deaths from natural mortality, i.e. for a point on this line, population size is maintained unchanged for the following year in the absence of harvesting.

For a conventional stock-recruitment relationship, recruitment levels would lie above the replacement line at low adult female population sizes; but (in the absence of harvesting) as carrying capacity K was approached, recruitments would cluster around a stable equilibrium point on the replacement line. This, however, is NOT the behaviour evident in Figure 9.1b. The recruitment series does approach the replacement line (in about 1973), but thereafter drops below this line as both recruitment and the number of reproductive animals decrease.

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Such behaviour requires not only the "conventional" assumption of an *increase* in the minke whale carrying capacity K in the mid-20th Century as the then unharvested minkes increased, presumably in response to the depletion of other krill-feeding Antarctic baleen whale species through overharvesting, but also a subsequent *decrease* in K (a result also demonstrated earlier by Butterworth and Punt 1999). Possibly this could be a response to recent recoveries of these other species and the dynamics of other Antarctic predators.

This Chapter attempts an initial model fit to the stock-recruitment information in Figure 9.1b, to assess to what quantitative extent such changes in K are required.

9.2 Methodology

The Recruitment Model

Recruitment is assumed to follow a Pella-Tomlinson form:

$$N_{y+1,1} = \lambda \cdot N_y^f \left[1 + A \left\{ 1 - \left(\frac{N_y^f}{K_y^f} \right)^z \right\} \right] \tag{9.2}$$

where

$N_{y,1}$ is the recruitment (1-year-olds) in year y;

λ is the combined pregnancy and first year survival rate when the population is at carrying capacity;

N_y^f is the number of adult (past the age of first parturition) females, taken to be given by $0.5\sum_{a=7}^{45} N_{y,a} = 0.5N_y^A$ (i.e. equal numbers of males and females are assumed);

A is the resilience parameter (related to the MSY rate *MSYR*);

K_y^f is the carrying capacity for adult females, which may change over time; and

z is the degree of compensation parameter, which is set here at 2.39, as conventional in the IWC's Scientific Committee.

When $N^f = K^f$, the recruitment must equal the number of 1+ whales dying annually as a result of natural mortality, i.e:

$$\lambda \cdot K_y^f = K^{1+}\left(1 - e^{-M}\right) \tag{9.3}$$

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(ignoring for simplicity the small correction that accounts for an assumed infinite natural morality from age 45).

Further, expressions for unexploited equilibrium numbers at age values yield:

$$\frac{K^{1+}}{K^{f}} = \frac{\sum_{a=1}^{45} e^{-M \cdot a}}{0.5 \cdot \sum_{a=7}^{45} e^{-M \cdot a}} = \mu \tag{9.4}$$

where μ can be computed given the value of M (0.068 for the assessment to be considered here).

Thus equation (9.2) can be rewritten:

$$N_{y+1,1} = \mu\left(1-e^{-M}\right)N_y^f\left[1+A\left\{1-\left(\frac{N_y^f}{K_y^f}\right)^{2.39}\right\}\right] \tag{9.5}$$

The unknown parameters of this model are A and the parameters describing K and its temporal variation. These are then estimated by minimizing:

$$SS = \sum_y \left(\ln\left(N_{y,1}^{\text{obs}}\right) - \ln\left(N_{y,1}^{\text{model}}\right)\right)^2 \tag{9.6}$$

where

$N_{y,1}^{\text{obs}}$ is the "observed" recruitment for year y from the Base Case assessment for Areas IV+V combined, as shown in Figure 9.1a; and

$N_{y,1}^{\text{model}}$ is the recruitment for year y predicted by the model of equation (9.5), which is implemented under the assumption that $N_{1930}^f = K_{1930}^f$.

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9.3 Results

Initially, the following functional form for K_y^f was considered (see Figure 9.2):

$$K_y^f = \begin{cases} K_1^f & y \le y_1 \\ K_1^f + \dfrac{\left(K_2^f - K_1^f\right)}{\left(y_2 - y_1\right)^\gamma}\left(y - y_1\right)^\gamma & y_1 + 1 \le y \le y_2 \\ K_2^f + \dfrac{\left(K_3^f - K_2^f\right)}{\left(y_3 - y_2\right)}\left(y - y_2\right) & y_2 + 1 \le y \le y_3 \\ K_3^f & y_3 + 1 \le y \end{cases} \tag{9.7}$$

with the following choices made for the "change" years: $y_1 = 1930$, $y_2 = 1955$ and $y_3 = 2000$.

Although yielding a reasonable fit to the VPA-estimated recruitment trend, this form (even when the choices for the change years y were varied somewhat) nevertheless showed same systematic deviations from the VPA results. Hence, for a more flexible form, the K_y^f of equation (9.7) was modified as follows:

$$K_y^f \to K_y^f \cdot e^{\varepsilon_y} \tag{9.8}$$

where the ε_y are estimable parameters which are constrained to change somewhat smoothly over time under the assumption:

$$\eta_y \text{ from } N\left(0, \sigma^2\right) \text{ where } \eta_y = \varepsilon_{y+1} - \varepsilon_y \tag{9.9}$$

which was implemented by adding the following term to the right hand side of equation (9.6):

$$\sum_{y=1930}^{2002} \left(\varepsilon_{y+1} - \varepsilon_y\right)^2 \Big/ 2\sigma^2 \tag{9.10}.$$

A choice of $\sigma = 0.05$ was found to yield reasonable results, with associated estimates of: A=1.67, $\gamma = 3.997$, $K_1^f = 40425$, $K_2^f = 166636$ and $K_3^f = 68689$, suggesting that carrying capacity originally increased about four-fold, but has since fallen by some 60%.

The model fit itself is shown for recruitment *vs.* year in Figure 9.3a, and for the stock recruitment plot in Figure 9.3b. The estimated trends in carrying capacity are shown in Figure 9.4.

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9.4 Discussion

The results of the analyses suggest that minke whale carrying capacity first increased from about 1940 to 1960 followed by a 60% decrease over the period from the 1960s to the present. This increase in the early 20th Century could be a result of reduced competition for prey (krill) caused by the intensive harvesting at that time of the large baleen whales which share the same prey with minke whales. The subsequent decline in the carrying capacity from the 1960s could be a result of the protection of these once harvested large baleen whales and their consequent recovery. Furthermore, as a result to the increase of minke whales and possibly also crabeater seals and other species that mainly feed on krill in the early 20th Century, the period of a surplus of krill suggested by Laws (1977), which will be detailed in Chapter 11, could have come to an end, and the predators could be competing for a smaller quantity of krill during the last decades of the 20th Century.

The estimation of the value of resilience A in turn allows an estimate of $MSYR$ ($=F_{MSY}$) to be effected. The result is:

$$MSYR_{1+}=0.050 \tag{9.11}$$

with a corresponding adult-female population size in terms of the corresponding carrying capacity:

$$MSYL_{mat} = N^f\left(F_{MSY}\right)/K^f = 0.544 \tag{9.12}.$$

The model of equation (9.5) could be used to project the abundance trajectories estimated in the previous Chapter forward in time under alternative future catch levels. Indeed, the stock-recruitment model here could be incorporated in the ADAPT-VPA assessment process itself, then also providing an improved approach to the process used in the previous Chapter to "adjust" earlier estimates of abundance for "missing" cohorts. (this approach is followed in Punt and Polacheck (2005)).

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a) b)

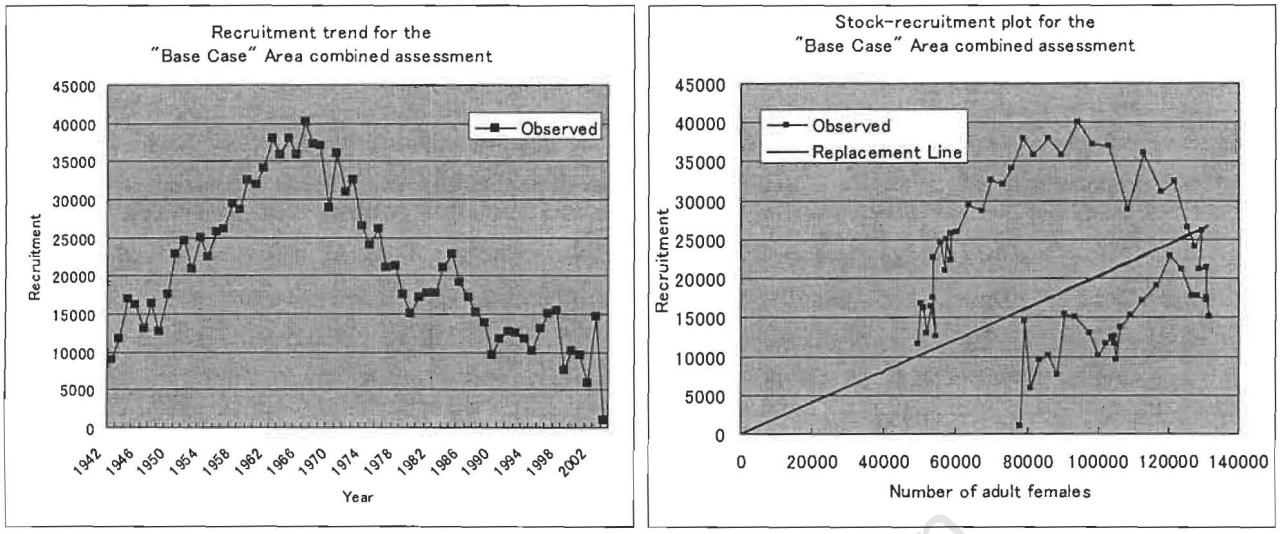


Figure 9.1 The "observed" recruitment time trend and stock-recruit plot for the Base Case Areas IV+V combined ADAPT-VPA assessment of Chapter 8.

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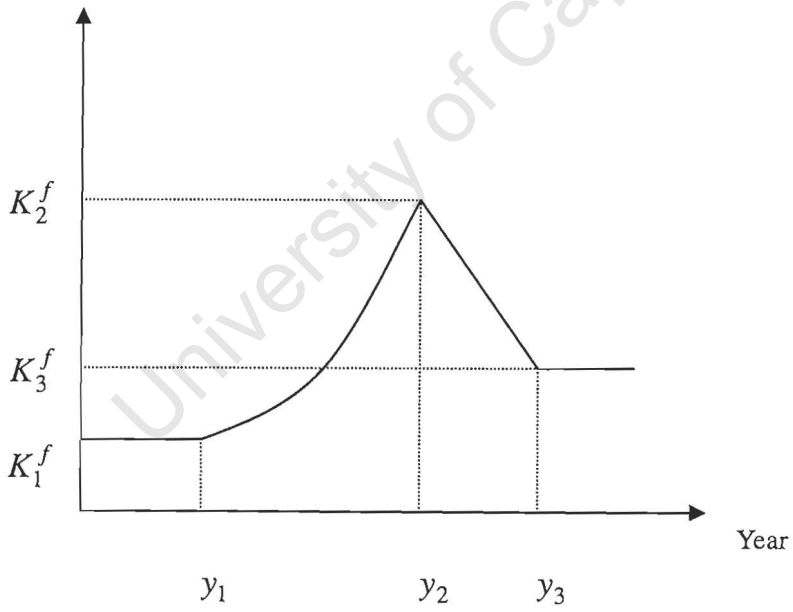


Figure 9.2 The functional form assumed for the change over time in carrying capacity of adult females.

a) b)

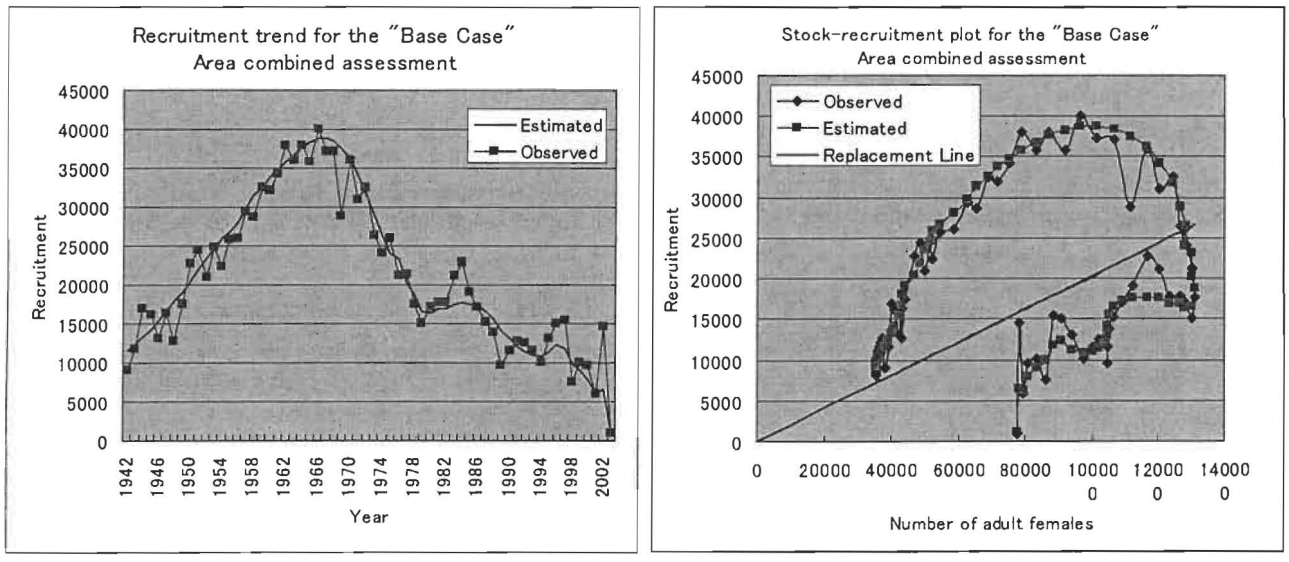


Figure 9.3 Fit of the model of equation (9.5) to the recruitment trend and stock-recruit plot for the Base Case Areas IV+V combined ADAPT-VPA assessment.

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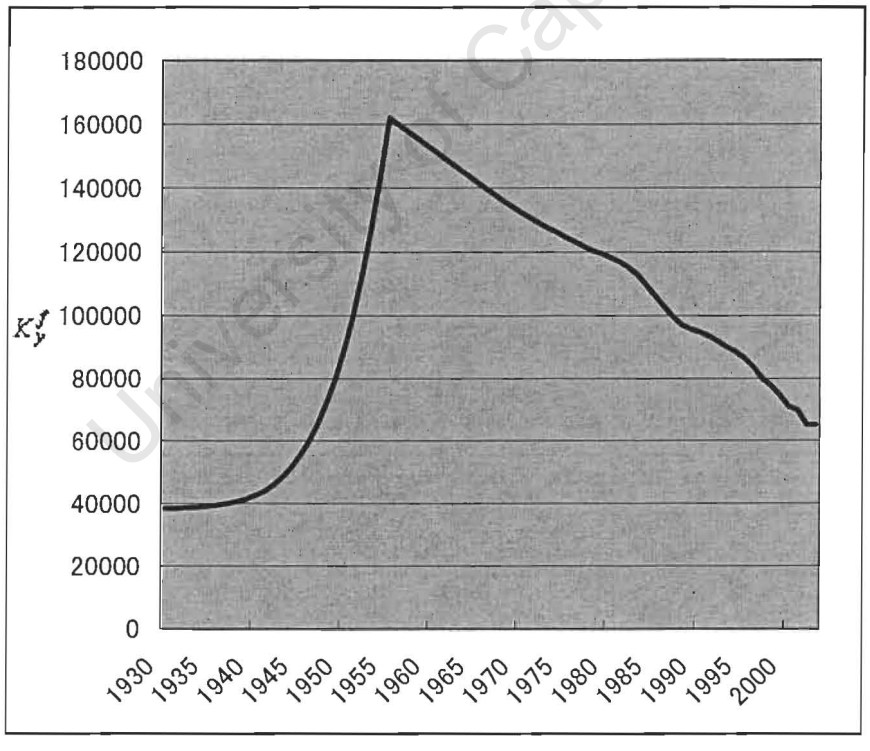


Figure 9.4 The estimated trend in carrying capacity of adult females over time.

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CHAPTER 10

RECENT TRENDS IN BIOLOGICAL PARAMETERS OF THE SOUTHERN HEMISPHERE MINKE WHALES IN RELATION TO THE RESULTS FROM THE CATCH-AT-AGE ANALYSES

10.1 Age at sexual maturity

As has been detailed in section 4.1.5 of this thesis, analyses by Kato (1983) and Thomson *et al.* (1999) indicate that the average age at transition and hence sexual maturity of Southern Hemisphere minke whales declined from roughly 11 for the cohorts of the 1950s to roughly 7 for those of the 1970s. A more recent study by Zenitani and Kato (2005) indicates that this declining trend gradually slowed during the 1960s and that the age at sexual maturity has been virtually constant from about 1965 to 1980.

10.2 Age at physical maturity

Bando *et al.* (2005) examined trends in various biological parameters obtained from samples collected by the JARPA surveys (from 1989 to 2003) and reports that the age at 50% physical maturity of minke whales has been increasing over this period, especially for females in Area IV for which the trend was significant at the 5% level ($r = 0.366$, $p<0.05$).

10.3 Blubber thickness

Ohsumi *et al.* (1997) examined blubber thickness of minke whales using data from commercial whaling which began in 1971 and the JARPA data from 1987 to 1995. They reported a reduction in blubber thickness after 1978. Konishi and Tamura (2005) analyzed blubber thickness using JARPA data from 1987 to 2003 and report that the reduction found by Ohsumi *et al.* (1997) is still evident. Blubber thickness decreased through the period of the JARPA surveys for males in both Areas, though the trend was significant only for in Area V ($r = -0.77$, $p<0.05$). There was also a decrease over this period for pregnant females in Area IV ($r = -0.78$, $p<0.05$), but no consistent trend was detected for such females in Area V ($r = 0.05$, $p=0.91$).

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10.4 Changes in stomach content weight

Tamura and Konishi (2005) also examined the stomach contents of minke whales using samples from JARPA surveys over the 1987 to 2003 seasons. They report that a decreasing trend in the mean weight of stomach contents of mature minke whales since 1987.

10.5 Discussion

Although trends in biological parameters are not completely consistent across Areas and sexes, in general they suggests that the feeding conditions for minke whales in Areas IV and V in the Antarctic have deteriorated since the 1970s which is consistent with the pattern of decreasing recruitment since that time shown by the catch-at-age analyses of Chapter 8 (see, e.g. Figure 8.4b). Possible causes of this are discussed in the next Chapter.

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SECTION 3:

DEVELOPMENT OF AN KRILL-CENTRIC ANTARCTIC MULTI-SPECIES MODEL

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CHAPTER 11

HYPOTHESISED CAUSES OF POPULATION CHANGES IN THE MAIN KRILL-FEEDING PREDATORS

Table 11 summarises broad features of trends in the abundance of krill and its main predators over the period from 1780 to 2000, as indicated by the results presented in Sections 1 and 2 of this thesis. In broad terms, at the beginning of the 19th Century, Antarctic fur seals were reduced almost to extinction by human harvests; in the early 20th Century large baleen whales including blue, fin and humpback whales were also heavily depleted, some near to extinction; and finally during the depletion of the large baleen whales, several studies indicate an increase in the abundances of minke whales, Antarctic fur seals and crabeater seals.

From the mid-1960s to mid-1970s, all the large baleen whales that had been harvested came under protection, and several recent studies indicate the subsequent recovery of a number of these populations. In contrast, recent studies also suggest that the increases in minke whales (and probably also crabeater seals) have reduced or even reversed since about 1970, concomitant with this recovery of the larger baleen whale species. Some studies also indicate a decrease in krill biomass since the 1970s (though these all refer to rather limited areas). In this Chapter, hypothesised causes of these long term population changes are put forward and discussed.

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11.1 "Surplus" krill hypothesis

Figure 11.1 shows annual consumption of krill by baleen whales in the Antarctic before and after the major exploitation of the baleen whales, as estimated by Laws (1977). Considering the extensive exploitation of large 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 tons of "surplus" annual production of krill became available for other krill-feeding predators, such as minke whales, crabeater seals, fur seals, penguins and some albatrosses. The computation of 150 million tons was based on coarse estimates available at that time of the population sizes of the baleen whales and of mean body weight, and the assumption that

krill consumption by baleen whales was between 3-4% of their body mass/day (further details are discussed in section 13.4 below).

Although no direct evidence for competitive release is available, the timing of the changes in biological parameters and population trends of minke whales, crabeater seals and Antarctic fur seals corresponds well with the period of extensive commercial harvesting of the krill-feeding large baleen whales. Some other krill predators such as Adélie, chinstrap and macaroni penguins also increased during the period from 1950 to the 1970s (Croxall 1992, Croxall *et al.* 2002). Adélie penguins on the western side of Antarctica, and on the Antarctic Peninsula and its associated island groups, increased substantially over this period, and then stabilized or decreased in the 1980s and, at some sites, also through 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).

Since there is no obvious evidence of any other appreciable environmental or human induced changes that could have led to increases in the krill-feeding predators (especially minke whales, Antarctic fur seals and crabeater seals) beginning in the early to mid-20th Century, the hypothesis that some large quantity of "surplus" annual production of krill became available for these predators (competitive release), following the depletion of the large baleen whales, is certainly plausible.

It has now been almost half a century since the protection of the large baleen whales, there are some recent studies that indicate that the time of "krill-surplus" may now be at an end. Reid and Croxall (2001) examined data on the population sizes, reproductive success and diet of krill-feeding predators (Antarctic fur seal, gentoo penguin, macaroni penguin and black-browed albatross) at South Georgia from 1980 to 2000. Indices of population size and reproductive performance showed declines in all species and an increase in the frequency of years of low reproductive output. By examining the krill length-frequency distributions based on krill consumed by Antarctic fur seals, macaroni penguins and gentoo penguins, they found appreciable differences in the population structure of krill in the diet of all these species between the periods of about 1980-1990 and 1991-2000. During the early part of the time-series the dominant modal size of krill taken by predators was 54-56 mm, whereas during the later period this mode dropped to 42-44 mm with only a small proportion of krill in the larger size class. Reid and Croxall (2001) put forward that changes in the population structure of krill and its relationship to reproductive performance suggest that the biomass of krill within the largest size class was sufficient to support predator demand in the 1980s, but not in the 1990s. They also suggest that the effects of underlying changes in the

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system on the krill population structure have been amplified by predator-induced mortality, resulting in breeding predators now regularly operating close to the limit of krill availability.

Recent observations of increased humpback:minke whale abundance ratios in Area IV concurrent with a drop in stomach fullness and blubber thickness of minke whales (Tamura and Konishi 2005, Konishi and Tamura 2005 – see previous Chapter) may constitue indirect evidence of intra-species interference/competition, and these observations also support the idea that the period of the "krill-surplus" has ended.

11.2 Effects of environmental change

Warming of the Southern Ocean seems to be the fastest worldwide (Gille 2002), and changes in sea-ice extent have been observed. By examining the correlation between regional sea-ice extent and air temperature in the Antarctic Peninsula region since the end of 1970s, Loeb *et al.* (1997) found a statistically significant correlation between these two indices (n=17, Kendall's T=-0.66, P<0.001). They report that a warming trend in mean air temperature has been documented for the Antarctic Peninsula region since the 1940s, and a decreased frequency of extensive winter sea-ice conditions has been associated with this trend. A similar suggestion was made by de la Mare (1997) who report that averaged over October to April, the Antarctic summer sea-ice edge moved southwards by 2.8° of latitude between the mid-1950s and early 1970s, suggesting a decline in the area covered by sea-ice of some 25%. de la Mare's analyses was based on a circumpolar comparison of the southern limit indicated by whaling records from 1931 to 1987 (the southern boundary for whaling was governed by the sea-ice extent) with recent satellite observations. Following this study, Ackley *et al.* (2003b) reexamined the data used by de la Mare (1997) and suggested that, while there may be a linear correlation between ice-edge position and whale catch data, the slope of the line deviates from unity and the ice-edge is also further north for the whale catch data than indicated by the satellite data for most latitudes. Ackley *et al.* (2003b) suggest that only regional perturbations took place (primarily in the Weddell Sea) from the pre-1950s to the post-1970s, without any appreciable deviations in the mean ice extents.

A recent study by Atkinson *et al.* (2004) compared annual mean density of krill across the southwest Atlantic (estimated from available scientific net sampling data over 1926-39 and 1976-2003) to indices of sea-ice (winter ice duration, winter ice latitude) and suggested that "within the southwest Atlantic, summer krill densities correlate positively with sea-ice extent the previous winter (R^2=0.21, p=0.006). Summer food and the extent of winter sea-ice are thus key factors in

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the high krill densities observed in the southwest Atlantic Ocean. Krill need the summer phytoplankton blooms of this sector, where winters of extensive sea-ice mean plentiful winter food from ice algae, promoting larval recruitment and replenishing the stock".

Nicol and Worby (2005) point out that on an ocean-wide scale there are some inconsistencies if sea-ice alone is argued to be the dominant factor in determining krill distribution and abundance. High krill densities can be found at South Georgia outside the seasonal ice zone (SIZ), whereas low densities coincides with an extensive SIZ, for example in the south west Indian Ocean sector (Atkinson *et al.* 2004).

Croxall *et al.* (2002) investigated the relationship between environmental change and changes in Antarctic seabird populations (adélie penguins, emperor penguins and snow petrels which are the most ice-dependent of all seabird species) in various localities in the Antarctic, mainly since around 1975. By correlating various population variables (e.g. adult survival rate, population size, breeding success etc.) with sea-ice extent or air temperature, they found that winter sea-ice has a profound influence on these populations; however, some effects are inconsistent between species and regions, some act in opposite directions at different stages of the breeding and life cycles, and others remain paradoxical. They report that usually the relation between population variables and sea-ice extent is a positive one – more ice means greater survival or breeding success; however, the main exceptions are hatching success in emperor penguins (probably due to increasing the time taken for adults to reach open-water feeding areas), adult survival in snow petrels (perhaps due to suppression of polynya), and the population size of adélie penguins in the Ross Sea (where too much ice may compromise juvenile survival). Croxall *et al.* (2002) suggest that the combination of historical harvest driven changes to Southern Ocean ecosystem dynamics, together with the changes engendered by global warming, may produce not just gradual changes in oceanographic and food chain dynamics, but more rapid shifts between alternative trophic pathways.

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In another study, Ainley *et al.* (2005) found that decadal-scale changes in population trajectories of adélie and emperor penguins in the western Pacific and Ross Sea sectors during the early/mid 1970s and during 1988-89 correspond to changes in weather and sea-ice patterns in those areas, which in turn are related to shifts in the semi-annual and Antarctic oscillations.

Some studies suggest that the El Niño-Southern Oscillation (ENSO) to be the cause affecting population demographics in the Antarctic. Testa *et al.* (1991) examined the fluctuations of some seal abundance indices in the Antarctic Peninsula in relation to the operational Southern Oscillation

Index (SOI), a measure of the strength of ENSO events. They found that all seal datasets showed evidence of cyclicity with an approximate five-year periodicity. Weddell seals were generally in phase with the SOI since 1970 when the Weddell series began. Leopard seals and the SOI were in phase in the 1960's, but thereafter the SOI series led the leopard seal series by about one quarter of cycle. The crabeater series was more complicated, but similarities to features of the other data sets were also apparent. In a different study, Guinet *et al.* (1994) found a significantly lower pup production (U=2, N1=4, N2=6; P<0.02) of Antarctic fur seals at Possession Island after an ENSO event, suggesting that breeding success maybe related to the ENSO events.

In summary, at least in the southwest Atlantic region of the Antarctic, there seems to be a positive correlation between krill density and the sea-ice extent for the previous winter (Atkinson *et al.* 2004). Moreover, ENSO and the semi-annual and Antarctic oscillations seem to affect the demographics of some seals and penguins in the Antarctic. Thus, it is probable that such environmental effects affect the demographics of populations in the Antarctic, especially those of the species that are ice-dependent.

Although such environmental change effects are plausible, it is not yet clear whether they are contributing to long-term population changes or only short term fluctuations. Furthermore, the studies referenced above do not rule out the possibility that other factors (i.e. predation mortality) may also be appreciably affecting the population dynamics of the species in the Antarctic. Since the objective of this thesis is to determine whether predator-prey interactions alone can broadly explain observed population trends of krill and their main predators in the Antarctic, the krill-predator dynamics model developed in the following Chapters will particularly concentrate on predator-prey interaction and the effect of human harvesting of the species.

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Table 11 Broad features in trends in the abundance of krill and its main predators during the period from 1780 to 2000. Unless indicated otherwise, there is direct observational evidence or strong indications from analyses or catch patterns of the trends indicated; (?) indicates that the evidence is relatively weaker, while (*) indicates conjecture.

	Period		
Species	**1780-1920**	**1921-1970**	**1971-2000**
Blue whale	Stable (*)	Decrease	Increase
Fin whale	Stable (*)	Decrease	Increase (?)
Humpback whale	Stable (*)	Decrease	Increase
Minke whale	Stable (*)	Increase	Decrease
Antarctic fur seal	Decrease ⟶ Stable	Increase	Increase
Crabeater seal	Stable (*)	Increase (?)	Decrease (?)
Krill	?	?	Decrease

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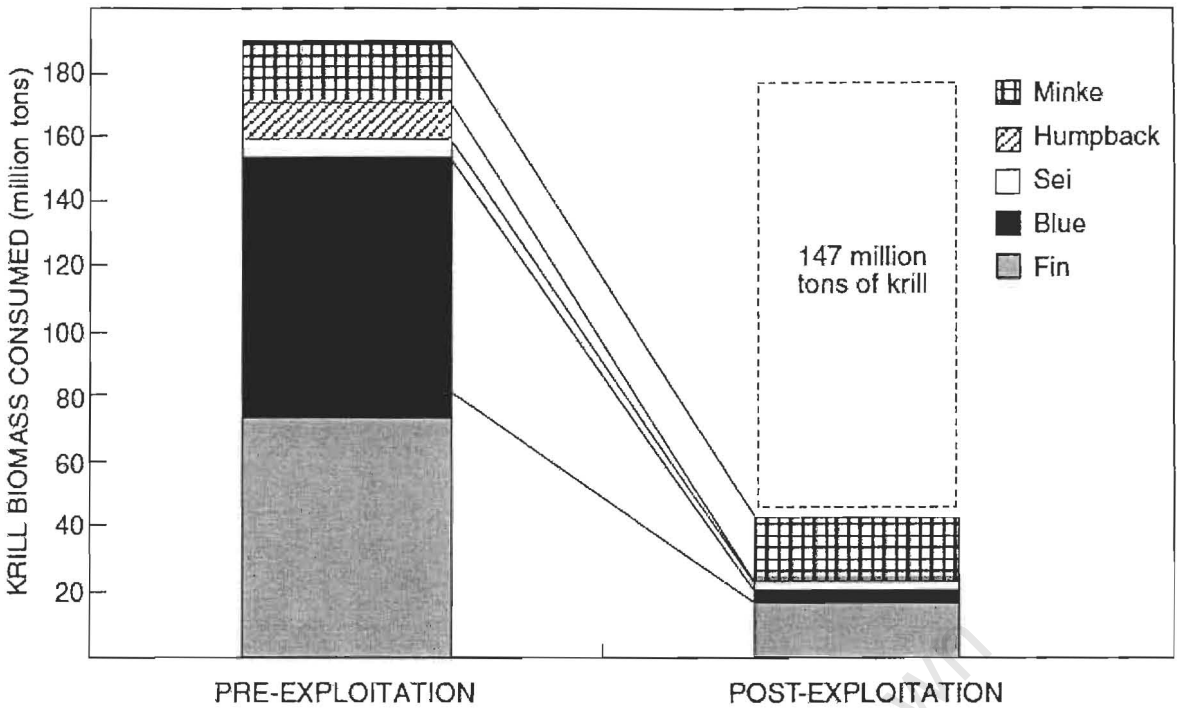


Figure 11.1 Estimated annual consumption of krill by baleen whales in the Antarctic (after Laws 1977). The plot shows the situation "pre-exploitation" and "post-exploitation" of whales.

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CHAPTER 12

A PRELIMINARY MODEL OF THE MINKE WHALE-BLUE WHALE-KRILL INTERACTION

12.1 Introduction

In this Chapter, an initial multi-species model is developed for two species in the Antarctic that feed mainly on krill, in order to gain some insight into what could have happened in the past and might occur in the future for krill and its predators. In this preliminary attempt, the interactions between blue whales, minke whales and krill are modelled. This is primarily because it is instructive to commence the development of a complex multi-species model at a simple level, and also because minke whales and blue whales share almost exactly the same feeding range (relatively close to the ice-edge) and the same prey (krill), as are detailed in Chapters 3 and 4 of this thesis. Other large baleen whales, such as humpback and fin whales, show distributions extending further to the north when in the Antarctic to feed over the summer months (as detailed in Chapter 4), and thus were not considered for this initial model.

Because of the appreciable uncertainties concerning absolute estimates of krill biomass and its trends (as detailed in Chapter 7), this model has been fit to the survey estimates of abundance for minke and blue whales only. The analysis first investigates whether a very simple predator-prey model can reproduce past population trends of these species which are discussed in Chapter 5. Then the sensitivity of the model to different parameter values is investigated, and some future projections are developed.

In earlier work of this nature, a multi-species interaction model for whales, seals and krill was investigated by May *et al.* (1979). This work used simple Lotka-Volterra-type models to analytically investigate the way multi-species food webs may respond to the harvesting of species at different trophic levels. The principal finding of May *et al.* (1979) was that simple considerations of Maximum Sustainable Yield (MSY), species by species, are insufficient for enunciating management principles in multi-species situations.

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Thomson *et al.* (2000) investigated the effect of krill harvesting on Antarctic fur seals using the "yield model" developed by CCAMLR (Butterworth *et al.* 1994) together with defining a predator survival rate function which relates to krill biomass. Application of a stochastic form of this model to an Antarctic fur seal data set from Bird Island, South Georgia indicated that the proportional annual harvest of krill that would reduce this seal population to half of its equilibrium size in the absence of such fishing lies in the range of 4 to 23%. This is to be compared with CCAMLR's present practice which is to set precautionary catch limits for krill as of 11.6% of a survey biomass estimate.

An ECOPATH-with-ECOSIM model (Christensen *et al.* 2000) focusing on the South Georgia region is also in development (A. Trites pers. commn). Murphy (1995) developed a spatial model in which the local krill abundance was regulated by a continuous, hydrodynamically mediated, supply rate and its concentration affected by abiotic-biotic interactions. He applied this model to the estimates of the annual predator demands and the krill concentration in the South Georgia area to investigate the relationship between flow rate and depletion in krill concentrations as a function of distance from a predator colony. Murphy's results suggest that concentrating factors need to be large to produce the build-up of krill densities of the order estimated to occur in the South Georgia area; however, for the estimated supply rates, the region does not need to be an area of particularly high prey concentration to support the estimated predator impact.

Other than these studies, little multi-species modeling in the Antarctic seems to have been pursued, and this study constitutes the first attempt to actually (albeit coarsely) fit such a model to estimates of abundance for some key species which have only recently become available.

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12.2 Model and data

12.2.1 An illustrative model

To illustrate how the population dynamics and interactions of the three species (minke whales, blue whales and krill) might operate, the very simple model shown in equations (12.1) to (12.3) below was developed. A Holling Type-II functional response (Holling 1965) was assumed, for which the consumption and birth rates of the predators are dependent only on the density of prey, and not on the density of predators (Figure 12.1).

Dynamics of Krill

$$B_{y+1} = B_y + rB_y\left(1-\left(\frac{B_y}{K}\right)^u\right) - \frac{\lambda^b N_y^b B_y}{B_b + B_y} - \frac{\lambda^m N_y^m B_y}{B_m + B_y} \tag{12.1}$$

where, for example, the last term on the right hand side reflects the rate at which krill is consumed by the population of minke whales.

Dynamics of Blue whales

$$N_{y+1}^b = N_y^b + \frac{\mu^b N_y^b B_y}{B_b + B_y} - M^b N_y^b - C_y^b \tag{12.2}$$

where the second term on the right hand side reflects the rate at which blue whales are born (which is assumed to depend on the rate at which the blue whale population consumes krill), and the third term the rate at which they die from natural causes.

Dynamics of Minke whales

$$N_{y+1}^m = N_y^m + \frac{\mu^m N_y^m B_y}{B_m + B_y} - M^m N_y^m - C_y^m \tag{12.3}$$

where

$N_y^{b/m}$: number of blue/minke whales at the start of year y;

B_y : biomass of krill at the start of year y;

r : intrinsic growth rate of krill;

K : carrying capacity of krill (in the absence of the blue and minke whale predators) in tons;

$\lambda^{b/m}$: maximum per capita rate of krill consumption (tons/year) by blue/minke whales;

$B_{b/m}$: level of krill biomass at which the per capita blue/minke whale consumption and hence birth rate drops by 50%;

$\mu^{b/m}$: maximum per capita birth rate for blue/minke whales;

$M^{b/m}$: blue/minke whale annual natural mortality rate; and

$C_y^{b/m}$: catch in year y of blue/minke whales from the Antarctic (and other parts of the Southern Hemisphere).

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12.2.2 Data

Historic Catch

Annual catches of blue whales (C_y^b) and minke whales (C_y^m) from 1900 onwards were provided by C. Allison of the IWC Secretariat (Table 12.1). These figures have been corrected for earlier Soviet misreporting (Yablokov *et al.* 1998).

Abundance estimates

Branch and Butterworth (2001a, b) calculate abundance estimates for minke whales and blue whales using the IWC/IDCR-SOWER survey sighting data which are detailed in Chapter 5. The abundance estimates used in this analysis and associated plausible ranges are shown in Table 12.2. For blue whales, the most recent abundance estimate of about 2000 animals is used as an central value. For minke whales, the abundance estimate of about 750 thousand animals during the survey period of 1985-1990 serves as the central value, this being the abundance estimate agreed by the IWC (IWC 1991). These estimates (and their ranges) do not exactly reflect the final conclusions in Chapter 5 (the analyses reported in this Chapter predate final information and analyses included in Chapter 5), but nevertheless remain adequate for the purposes of an initial qualitative investigation as is intended here (see also section 12.4).

Other parameters

Because of the uncertainties concerning values for the biological parameters, plausible ranges are considered and are shown in Table 12.2. The plausible ranges for the maximum per capita rate of consumption for blue and minke whales ($\lambda^{b/m}$) are taken from Table 3.1 of this thesis, with the associated details discussed in section 3.2.4. The ranges for the maximum per capita birth rate ($\mu^{b/m}$) and natural mortality ($M^{b/m}$) of blue and minke whales were chosen from discussion with whale biologists and general knowledge about the plausible ranges for these parameters. Further the constraints of $\mu^b - M^b \geq 0.02$ and $\mu^m - M^m \geq 0.03$ were added to ensure that maximum possible growth rates could be higher than 2% and 3% for blue and minke whales respectively (this seems reasonable as many recovering baleen whale populations have shown higher growth rates than this, for example as reported for humpback whales in Chapter 5). The value of u in equation (12.1) was set to 0.2 based upon the behaviour of the age-structured krill dynamics model

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developed by Butterworth *et al.* (1994), which is that used by CCAMLR to provide a basis for setting krill catch limitations (see Appendix 12 for its derivation). Each parameter is chosen randomly in the simulations by selecting from the minimum, middle or maximum value listed in Table 12.2

12.2.3 Model fitting procedure and parameter estimation

In order to estimate the yearly abundances of krill, blue whales and minke whales using equations (12.1)-(12.3), the starting value (abundance) for each species in the year 1900, before human exploitation, which corresponds to the co-existence equilibrium level for these species, needs to be estimated. The condition that all three species were in equilibrium (balance) in the year 1900 provides relationships between the parameter values. Thus, by setting $B_{y+1} = B_y$ in equation (12.1), it follows with a little algebra that:

$$r\left(1-\left(\frac{B_{1900}}{K}\right)^u\right)\left(B_b + B_{1900}\right)\left(B_m + B_{1900}\right) = \lambda^b N_{1900}^b\left(B_m + B_{1900}\right) + \lambda^m N_{1900}^m\left(B_b + B_{1900}\right). \tag{12.4}$$

Similarly, setting $N_{y+1}^b = N_y^b$ in equation (12.2), and $N_{y+1}^m = N_y^m$ in equation (12.3), yields:

$$\mu^b B_{1900} = M^b B_b + M^b B_{1900} \tag{12.5}$$

$$\mu^m B_{1900} = M^m B_m + M^m B_{1900} \tag{12.6}$$

From equations (12.5) and (12.6), it follows that:

$$B_{1900} = \frac{M^b B_b}{\mu^b - M^b} = \frac{M^m B_m}{\mu^m - M^m}. \tag{12.7}$$

Equation (12.7) indicates that given values for r, μ^b, M^b, μ^m and M^m, then once B_b is specified the value of B_m follows as does that of B_{1900}. That leaves only one quantity "free" in equation (12.4): the value of K, which follows once values for N_{1900}^b and N_{1900}^m are obtained.

N_{1900}^b and N_{1900}^m are estimated by minimizing the difference between the estimated abundances indicated by the population models of equations (12.1) to (12.3), and the survey abundance estimates shown in Table 12.2. The function minimized (*SS*) is as follows:

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$$SS = \left(N^b_{2000} - \hat{N}^b_{2000}\right)^2 + \left(N^m_{1985} - \hat{N}^m_{1985}\right)^2 \qquad (12.8)$$

where

N^b_{2000} is the survey estimate of the abundance of blue whales in the year 2000;

$\hat{N}^b_{2000}$ is the model estimate of the abundance of blue whales in the year 2000;

N^m_{1985} is the survey estimate of the abundance of minke whales in the year 1985; and

$\hat{N}^m_{1985}$ is the model estimate of the abundance of minke whales in the year 1985.

In summary, having specified one of a possible set of values for B_b, a set of values is sought for the other biological parameters that gives similar trajectories for blue whales and minke whales to those suggested by surveys and related studies. These suggested trajectories are as follows:

Blue whales: High abundance initially (1900), followed by a dramatic decrease due to exploitation. Subsequent recovery has been gradual.

Minke whales: Start low initially (1900), rise to maximum, and then start to decrease from about 1970, as suggested by the catch-at-age analyses of Butterworth *et al.* (1999, 2002) and Chapter 8 of this thesis.

In addition to these features, situations were sought where the coexistence equilibrium for the three species was stable, and where the fluctuations in krill biomass were not too large.

12.3 Results

Different sets of parameter values gave very different trajectories for the three species considered. Only some of these reflected the trends suggested by other information. Figure 12.2 shows some of the trajectories for minke whales, blue whales and krill that did reflect these trends reasonably (parameter values corresponding to these trajectories are listed in Appendix 12, Table App.12.1). Fitting to the high and low abundance estimates for minke whales and blue whales in Table 12.2 did not show trajectories that differed from those in Figure 12.2 in qualitative terms, but the absolute abundance of all three species increased when the model was fitted to higher abundance estimates (Figure 12.3).

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These trajectories suggest an interesting possible pattern of events over the last century in the Antarctic: blue whale abundance decreased dramatically after 1920 due to excessive whaling. Following this decrease, krill abundance increased because of diminished consumption by blue whales. Minke whales were not harvested until the 1970s and the population increased dramatically until that time as a result of the increase of krill biomass. However, this large increase of minke whales reduced the krill biomass to a low level. As a consequence of this reduction, minke whale abundance started to drop from the late 1970s. By the 1990s, krill biomass had increased again as a result of the minke whale decline, and this allowed for a blue whale recovery to start at a rate of about 1-2% per year.

12.3.1 Sensitivity of the model

The slopes of the population trajectories obtained are very sensitive to some of the parameter values selected, so an attempt is made below to summarize the key features that are needed to reflect the trends suggested by surveys and other information. There are essentially three of these.

The first is related to the shape of the consumption and birth rate functions for blue whales shown in Figure 12.4. None of the trajectories reflected the suggested trends when B_b was higher than 300 million tons, which suggests that the krill biomass level (B_b) at which the blue whale birth (and consumption) rate drops to half of its maximum possible value is relatively low.

The second feature concerns the relationship between the growth rates of minke whales and blue whales. The interesting point here is that the growth rate of minke whales is higher than that of blue whales only when the krill biomass is relatively high. When the krill biomass is low, the growth rate of blue whales becomes negative, but not to the same extent as that of minke whales (Figure 12.5). This may underlie the gradual recovery of blue whales in recent years, these whales being better able to cope with reductions of krill biomass to low levels than are minke whales.

The last feature concerns various biological parameters for blue and minke whales as summarized in Table 12.3. These suggest that both species have a relatively high maximum birth rate: the maximum growth rate for blue whale needs to be higher than 10% per year, and for minke whales than 13% per year. These indications do not seem unrealistic when compared to the recent estimate of a 7.3% per year increase for blue whales (Branch *et al.* 2004) and of an $MSYR_{1+}$[1] of

[1] $MSYR_{1+}$ is the ratio of MSY to the population level at which it is achieved (*MSYL*), when harvesting selects uniformly from all whales aged 1 and above (1+). The maximum increase rate at low population size would

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some 5-6% for minke whales (Butterworth and Punt 1999, Chapter 9 of this thesis). Blue whales are indicated also to have a relatively low maximum consumption rate (1-2.2% of body mass/day), whereas minke whales have a relatively high maximum consumption rate (3-5% of body mass/day). This also seems plausible, since larger mammals can survive without food for longer periods than smaller ones because of their lower metabolic rate in relation to body mass (Kasamatsu 2000).

12.3.2 Projections

To get a very broad idea of future possibilities, some projections were run under a zero catch for all species. Figure 12.6 shows the trajectories for the three species for the next 500 years. Although there are some very large oscillations in population numbers, in terms of underlying trends the minke whale population decreases gradually over time, whereas the blue whale population increases gradually, both eventually returning to their original equilibrium levels.

12.4 Summary and Discussion

This model reveals some interesting possible consequences of multi-species interactions in the Antarctic:

1. There might have been an appreciable decrease in krill biomass from the 1970s to the 1990s, due to the rapid increase of minke whale abundance (and hence of their krill consumption) following the depletion of the large baleen whales.
2. The recent recovery of blue whales in spite of the decrease of minke whales can possibly be explained by the differences in growth rate of these two species in relation to krill biomass. Minke whales maintain a higher growth rate than blue whales when krill biomass is high; however, blue whales are better able to cope with periods of low krill abundance.

Trends in krill biomass

As has been detailed in Chapter 7, there are no data from which trends in krill biomass before the late 1970s can be inferred. Thus, it is not possible to confirm directly whether the suggested krill "surplus" following the reduction of the large baleen whales actually occurred. Furthermore such subsequent data as are available (e.g. Siegel *et al.* (1998, 2002) for the Elephant Island vicinity) pertain to smallish regions rather than to the Antarctic as a whole. Nonetheless, the suggested decline of krill in the southwest Atlantic sector since the 1970s (Atkinson *et al.* 2004) does

typically be some 50-100% larger than this.

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qualitatively match with the decline in krill biomass from the 1950s to the early 1990s predicted by this model, although the model also predicts an increase in krill biomass in recent years.

One should note that several studies (e.g. Loeb *et al.* 1997, Atkinson *et al.* 2004) postulate regional warming as the cause of the low level of krill biomass. Indeed as is discussed in Chapter 7 and Chapter 11, many other studies of krill abundance trends suggest environmental causes (e.g. winter sea-ice conditions) for fluctuations (e.g. Croxall *et al.* 1999, Croxall *et al.* 2002, Murphy *et al.* 1998, Nicol *et al.* 2000b, Reid and Croxall 2001, Siegel and Loeb 1995). An important insight offered by the analysis of this Chapter is that it is important to consider the impact that predator-prey dynamics may be having on longer term trends in krill abundance, as well as the impact of environmental changes. In order to test model predictions, the continuation of the surveys such as CCAMLR-2000 (SC-CAMLR 2000) is very important, and would provide useful information on krill abundance and its trend in the future. Furthermore, it might be useful to develop multi-species models for a particular region, such as the vicinity of South Georgia or Elephant Island, where relatively long time series of krill abundance in the region are already available.

Plausibility of the model and its estimated parameters

Any basis to comment upon the plausibility of the results obtained is limited because of a paucity of information. Other estimates of the pre-exploitation abundance of blue whales (e.g. as quoted by Laws 1977) rest upon similar calculations using historic catches as are conducted in this Chapter, so do not provide an independent check on the estimates of some 280,000 (Appendix 12, Table App.12.1). The recent blue whale model-predicted rates of increase listed in this Appendix (typically some 1-2% per annum) are not as high as the 8% estimated from survey results by Branch *et al.* (2004), though there is no necessary incompatibility as the latter estimate has a largish associated standard error (95% CI: 1.4; 11.6%).

Certainly the initial krill abundance estimates of about 20-40 million tons are too low, but this is a consequence of the model including only two of krill's major predators. Inclusion of other predators that mainly feed on krill would both increase krill abundance to a more realistic initial level, and also likely prevent it dropping as low over the 1970-1990 period as indicated in Figures 12.2 and 12.3. This in turn would lead to a faster predicted increase in blue whale numbers at present, more in keeping with the point estimate of Branch *et al.* (2004).

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Possible maximum abundance estimates of minke whales taking into account various bias factors listed in Chapter 5 were even higher (Table 5.5) than those that were examined in this model. However, the sensitivity analysis of this model fitting to the high (1.2 million) and low (70 thousand) abundance estimates for minke whales showed qualitatively similar results. Thus it seems reasonable to assume that the qualitative features predicted by this model will not change even if the actual 1985 abundance of minke whales was higher than considered for the results presented here.

Importance of monitoring

Given the large changes in the abundance of minke whales suggested by this model, one would expect some corresponding changes in biological parameters, such as an increase in age-at maturity or decrease in pregnancy rate or changes in blubber thickness corresponding to the suggested decline over recent decades. Studies presented in Chapter 10 of this thesis do provide evidence for some trends. It is important to monitor these biological parameters continuously in order to better understand the dynamics of the population. In addition, information on the functional response of whales to krill abundance is important. Information on the functional response of whales to krill biomass scarcely exists. The results presented here are sensitive to the shape of this functional response, and further field studies are desirable to shed light on this.

Further development of the model

The form of the model considered in this Chapter suffers from a technical problem which amounts to a lack of robustness to parameter value variation – the joint equality of equation (12.7) cannot be maintained if the value of one parameter only changes, which is unrealistic (Armstrong and McGehee 1980). This needs to be resolved by introducing terms that reflect some degree of intra- or inter-specific competition between minke whales and blue whales. This was not done in this Chapter (though it is in Chapter 13) in the interests of keeping an initial model as simple as possible, because at least one extra parameter whose value would have been difficult to specify would need to have been introduced. An advantage of such extra complexity, however, is that such terms can have the effect of damping what appear to be unrealistically large amplitude oscillations in Figures 12.2, 12.3 and 12.6.

The results of this model should therefore be interpreted qualitatively rather than quantitatively at this level of development. Further work needs to consider extensions in a number of directions for

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improved realism in respect of krill and its major predators:

i) adding further major predator species that feed on krill (particularly humpback and fin whales, and crabeater and Antarctic fur seals);

ii) incorporating age-structure and time dependence in biological parameters for some species at least; and

iii) including spatial effects, for example by distinguishing by the different IWC Antarctic Management Areas rather than pooling at a circumpolar level.

Some of these extensions are considered in the Chapter following.

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Table 12.1 Catch statistics for blue and minke whales in the Southern Hemisphere (including the Antarctic; 1900-2000). Source: C. Allison, International Whaling Commission, 2002. A moratorium on commercial whaling came into force in 1986; catches of minke whales from that time have taken place under a scientific research programme.

Year	Blue whale	Minke whale	Year	Blue whale	Minke whale
1900	0	0	1951	5 147	9
1901	0	0	1952	4 002	0
1902	0	0	1953	2 888	12
1903	0	0	1954	2 544	0
1904	11	0	1955	1 749	45
1905	51	0	1956	1 715	46
1906	68	0	1957	1 769	493
1907	106	0	1958	1 250	103
1908	245	0	1959	936	206
1909	212	0	1960	1 743	162
1910	387	0	1961	1 143	2
1911	1 235	0	1962	1 748	21
1912	2 505	0	1963	1 508	104
1913	2 774	0	1964	3 347	51
1914	4 888	0	1965	1 477	79
1915	5 636	0	1966	665	374
1916	4 387	0	1967	462	1 099
1917	3 173	0	1968	674	618
1918	2 046	0	1969	920	764
1919	2 009	0	1970	834	917
1920	3 002	0	1971	538	4 155
1921	4 521	0	1972	7	6 583
1922	6 774	1	1973	1	8 541
1923	4 918	0	1974	0	7 884
1924	6 966	0	1975	0	7 185
1925	6 422	0	1976	0	8 676
1926	8 665	0	1977	0	6 000
1927	10 108	0	1978	0	6 156
1928	13 898	0	1979	0	7 897
1929	18 726	0	1980	0	7 142
1930	30 457	0	1981	0	7 903
1931	6 659	0	1982	0	7 301
1932	18 983	0	1983	0	6 680
1933	17 432	0	1984	0	5 568
1934	16 612	0	1985	0	5 567
1935	17 870	0	1986	0	4 969
1936	14 598	0	1987	0	273
1937	15 119	0	1988	0	241
1938	14 127	0	1989	0	330
1939	11 518	0	1990	0	327
1940	1 754	0	1991	0	288
1941	51	0	1992	0	330
1942	127	0	1993	0	330
1943	349	0	1994	0	330
1944	1 050	0	1995	0	440
1945	3 646	0	1996	0	440
1946	9 237	0	1997	0	438
1947	6 968	0	1998	0	389
1948	7 731	0	1999	0	439
1949	6 240	1	2000	0	440
1950	7 035	0			

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Table 12.2 Plausible ranges assumed for the abundance estimates and biological parameter values. Parameters selected from these ranges were also required to satisfy the conditions: $\mu^b - M^b \geq 0.02$ and $\mu^m - M^m \geq 0.03$, i.e. that blue and minke whales could attain per capita growth rates of at least 2 and 3% respectively under optimal feeding conditions.

Parameter	Range	References
M^b : blue whale natural mortality rate (yr^{-1})	0.03 - 0.06	
M^m : minke whale natural mortality rate (yr^{-1})	0.04 - 0.1	
μ^b : maximum per capita birth rate for blue whales (yr^{-1})	0.05 - 0.16	
μ^m : maximum per capita birth rate for minke whales (yr^{-1})	0.07 - 0.2	
λ^b : maximum per capita rate of consumption (tons/year) by blue whales	103t × [0.9 - 3.5%] × 125days	Tamura 2003. Trites and Pauly 1998.
λ^m : maximum per capita rate of consumption (tons/year) by minke whales	7t × [0.6 or 2.85 or 5.1%] × 90days	Horwood 1990, Ichii and Kato 1991. Kasamatsu *et al.* 1996.
r : intrinsic growth rate of krill (yr^{-1})	MSYR = 0.15, 0.2, 0.25	Butterworth *et al.* 1994.
B_b: level of krill biomass (tons) at which blue whale consumption drops by 50%.	Consider different values: [100, 300, 500, 1000] × 10^6	
Abundance Estimate	**Value**	
N^b_{2000} : blue whale (year=2000)	1500, 2000, 3000	Branch and Butterworth 2001b.
N^m_{1985} : minke whale (year=1985)	700000, 750000, 1200000 (reflecting $g(0)<1$)	Branch and Butterworth 2001a.

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Table 12.3 General requirements for the biological parameters of minke whales and blue whales to reflect the population trends suggested by other information for these species.

Blue whale	**Minke whale**
High maximum birth rate (μ^b)	High maximum birth rate (μ^m)
Maximum growth rate ($\mu^b - M^b$) 10%/year	Maximum growth rate ($\mu^m - M^m$) 13%/year
Low maximum consumption rate (λ^b) (1-2.2% of body mass/day)	High maximum consumption rate (λ^m) (3-5% of body mass/day)

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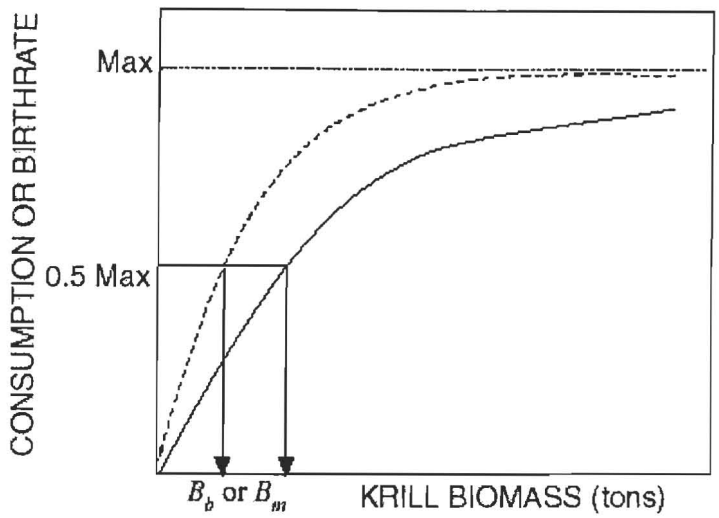


Figure 12.1. Consumption and birth rate functions for blue and minke whales in terms of krill biomass. Because of uncertainties regarding appropriate values for B_b and B_m, the model is examined for different choices for these.

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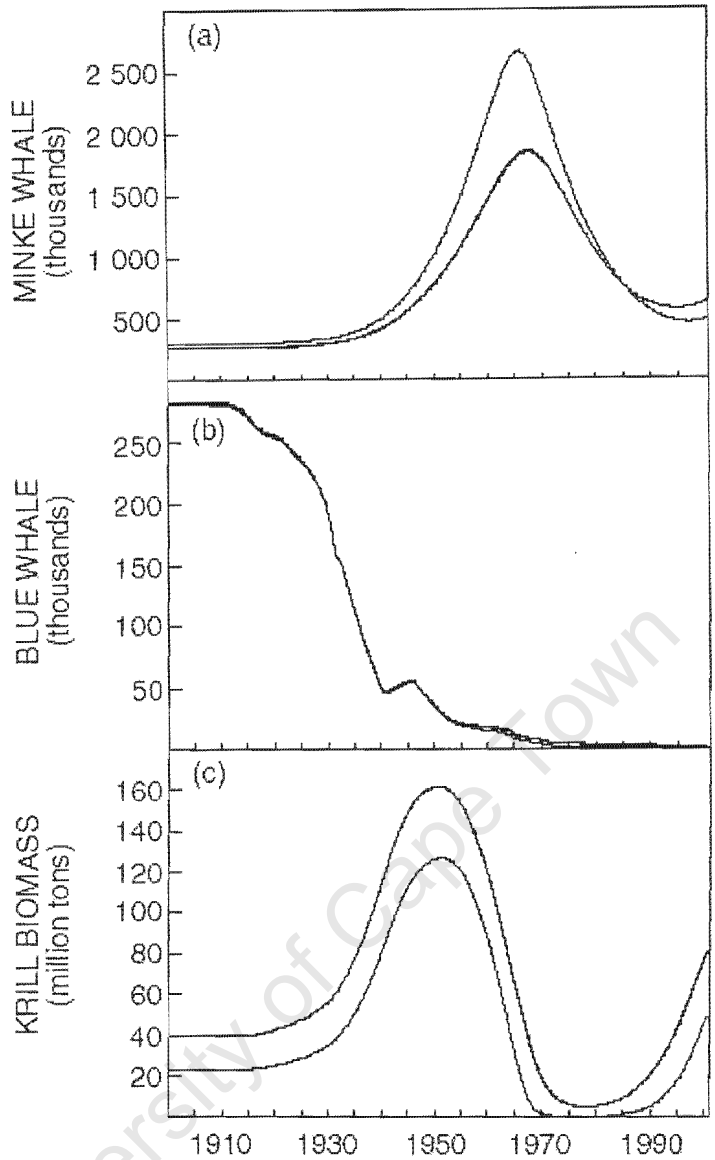


Figure 12.2 Trajectories for minke whales, blue whales and krill that reflect trends suggested by surveys and related analyses. A minke whale abundance in 1985 of 750,000 is fitted in all cases. Details of each of these scenarios are given in Table App.12.2

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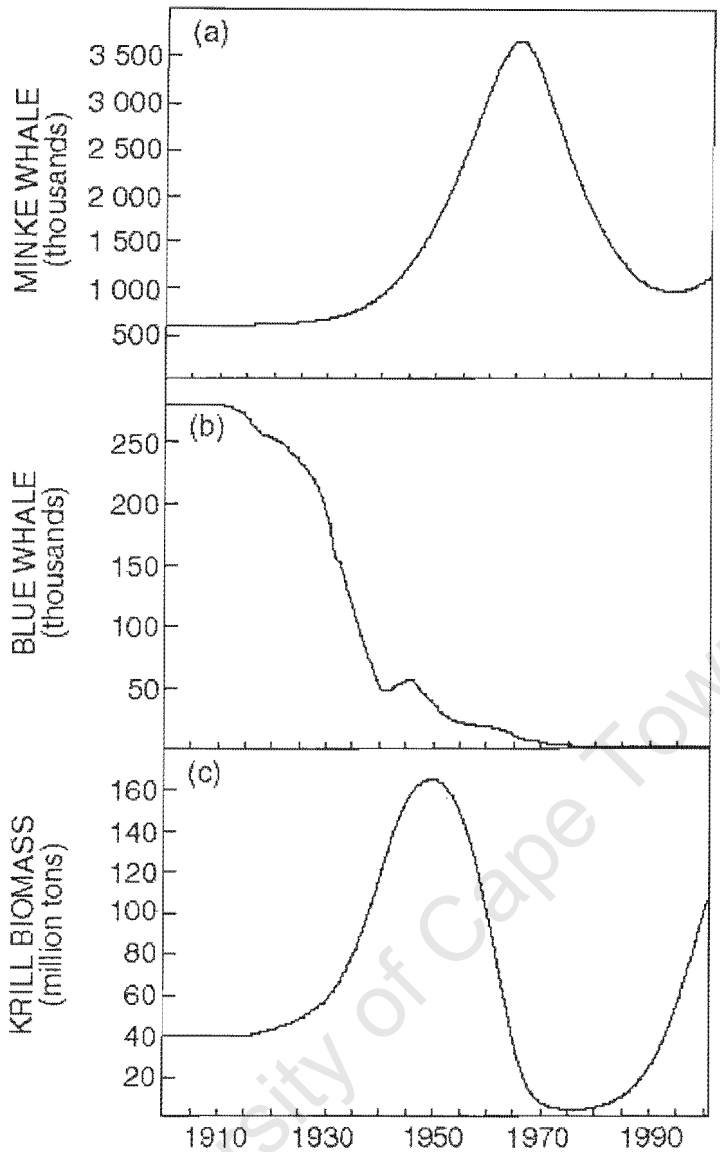


Figure 12.3 Trajectories for minke whales, blue whales and krill that reflect trends suggested by surveys and related analyses. A minke whale abundance in 1985 of 1,200,000 is fitted here.

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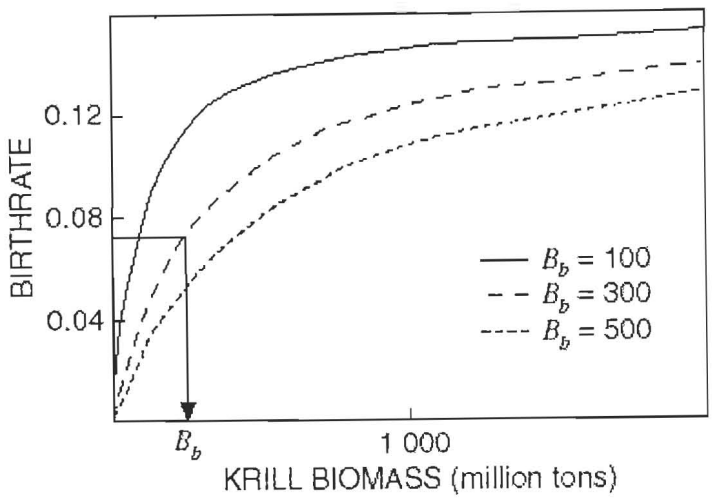


Figure 12.4 Examples of birthrate functions for blue whale in terms of krill abundance. To reflect population trends suggested by other information, the krill biomass when the blue whale birthrate and consumption rate drop to half of their maximum rate (B_b) needs to be relatively low, between 100 and 300 million tons. None of the trajectories examined reflected the trends suggested by other information when B_b was set higher than 300 million tons.

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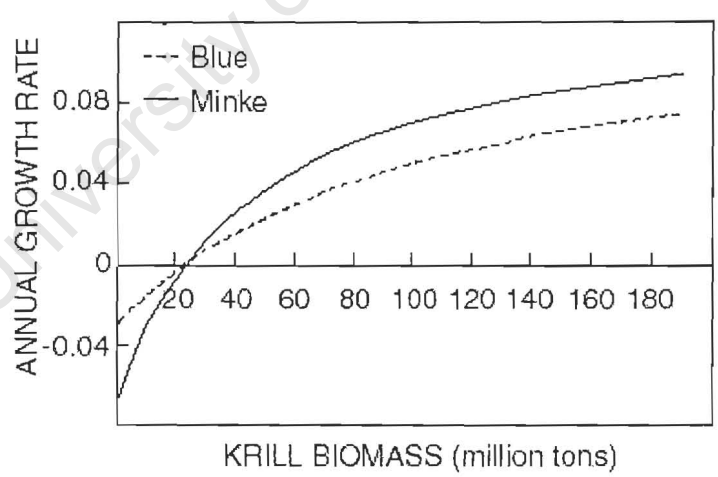


Figure 12.5 Per capita growth rates for minke and blue whales as a function of krill abundance that follow from equations (12.2) and (12.3). To reflect population trends suggested by other information, the growth rate of minke whales needs to be higher than that of blue whales when krill biomass is relatively high. However, when krill biomass is relatively low, the growth rate for blue whales does not drop below zero to as appreciable extent as does that for minke whales.

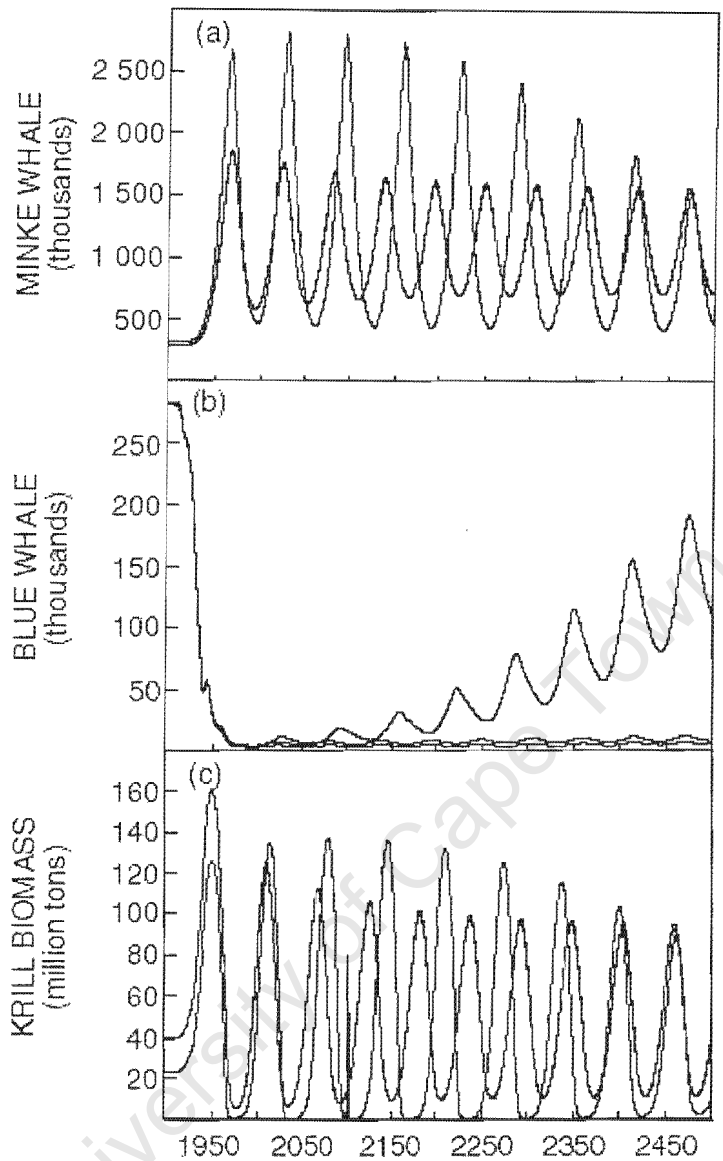


Figure 12.6 Future trajectories for minke whales, blue whales and krill for the cases shown in Figure 12.2. These simulations assume no catch of any of these species after 2000.

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APPENDIX 12

TECHNICAL DETAILS OF COMPUTATIONS FOR CHAPTER 12

App.12.1 Comparison of the krill dynamics model of Butterworth *et al.* (1994) with a Pella-Tomlinson production model form

The age-structured population model for krill developed in Butterworth *et al.* (1994) can be used to provide the curve shown in Figure App.12.1 relating annual equilibrium production (Y) to krill abundance. The Figure also shows the Pella-Tomlinson form that is used to approximate this behaviour in equation (12.1) of the main text, which models krill production:

$$Y = rB\left(1-\left(\frac{B}{K}\right)^{u}\right)$$

for which $MSYL/K = \left(\frac{1}{1+u}\right)^{1/u}$

$$MSYR = \frac{ru}{1+u}.$$

The Pella-Tomlinson curve shown in Figure App.12.1 has $MSYR$=0.2 and u=0.2 (corresponding to $MSYL/K \approx 0.4$).

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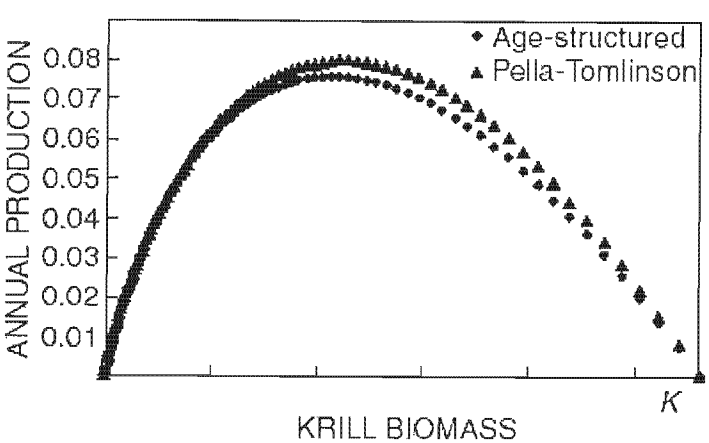


Figure App.12.1 Annual krill equilibrium production (expressed as a production of K) for the age-structured krill model of Butterworth *et al.* (1994) and for a Pella-Tomlinson approximation to this function.

App.12.2 Details of the parameter values and trends for the trajectories shown in Figures 12.2 and 12.3

The recent rates of increase (ROI) for whales over a period from y_i to y_f are computed as $\frac{1}{(y_i - y_f)} \ln\left(N_{y_i} / N_{y_f}\right)$.

Table App.12.1 Parameter values for population trajectories shown in Figures 12.2 and 12.3.

	Scenarios			
Parameters input	**Fig. 12.2-1**	**Fig. 12.2-2**	**Fig. 12.2-3**	**Fig. 12.3**
M^b (yr^{-1})	0.03	0.045	0.045	0.045
M^m (yr^{-1})	0.07	0.07	0.07	0.07
μ^b (yr^{-1})	0.16	0.16	0.16	0.16
μ^m (yr^{-1})	0.2	0.2	0.2	0.2
λ^b (tons/yr)	103x0.9%x125	103x0.9%x125	103x0.9%x125	103x0.9%x125
λ^m (tons/yr)	7x2.85%x90	7x5.1%x90	7x5.1%x90	7x2.85%x90
r (yr^{-1}) MSYR (yr^{-1})	0.9 0.15	0.9 0.15	0.9 0.15	0.9 0.15
B_0 (10^6tons)	100	100	100	100
N^b_{2000}	3000	1500	3000	2000
N^m_{1985}	750000	750000	750000	1200000
Model fit values				
B_{1900} (10^6tons)	23.1	39.1	39.1	39.1
K (10^6tons)	271.2	331.6	330.7	385.7
N^b_{1900}	283191	280451	281105	279757
N^m_{1900}	306904	276437	273456	607052
ROI $N^b_{1980-2000}$ (yr^{-1})	-0.02	-0.01	-0.01	-0.01
ROI $N^b_{1995-2000}$ (yr^{-1})	0.01	0.01	0.01	0.02
ROI $N^m_{1980-2000}$ (yr^{-1})	-0.04	-0.02	-0.02	-0.02
ROI $N^m_{1995-2000}$ (yr^{-1})	0.01	0.02	0.02	0.03

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CHAPTER 13

MODELLING THE PREDATOR-PREY INTERACTIONS OF KRILL, BALEEN WHALES AND SEALS IN THE ANTARCTIC ECOSYSTEM

13.1 Introduction

This Chapter presents work that extends the multi-species model introduced in the previous Chapter in various ways that will be detailed later in the Data and Methods section following. It is hypothesized in this Chapter that the effects of human-induced harvesting of species in the Antarctic has indeed played a major role in, and continues to impact upon, the dynamics of krill and its major predators in the Antarctic. This is based on consideration of evidence for past 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 objective of this Chapter 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, this Chapter hopes 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.

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13.2 Data and methods

13.2.1 Species considered in the model

As was discussed in Chapter 3 of this thesis, baleen whales, some squid, fish, seabirds and some seals all prey directly on krill (see Figure 3.1). The amount of krill consumed by each group of species differs depending on their abundances, diet compositions, daily intake of food and the period over which they feed in the Antarctic.

In order to evaluate the magnitude of the impact of consumption by the predator groups shown in Figure 3.1 on krill biomass, approximate estimates of krill consumption by each predator group in the Antarctic are summarized in Table 13.1. Before human exploitation began, baleen whales were probably the major predators of krill, followed by seals (Table 13.1). This indicates that the impact of consumption by baleen whales and seals in the Antarctic on krill is relatively large, and thus baleen whales (specifically, blue, minke, humpback and fin whales) and seals (Antarctic fur and crabeater seals) are considered in the model developed. A particular difficulty, as is evident from Table 13.1, 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 upon 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 of this Chapter.

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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 13.1), as their distribution is essentially restricted to the Atlantic side of the Antarctic.

13.2.2 Incorporating regional effects

The model to be developed divides the Antarctic into two regions: the one is the Atlantic and Indian Oceans region, which corresponds essentially to the IWC Management Areas II, III and IV, and the

other the Pacific Ocean region, which corresponds to the Areas V, VI and I. The two regions together with the IWC Management Areas are shown in Figure 13.1. 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 on the Atlantic side of the Antarctic (Figure 13.2), 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 13.2). This suggests an uneven pre-exploitation distribution of large baleen whales: abundant on the Atlantic side of Antarctica, but relatively scarce in the Pacific. Thus, the impact of whaling and sealing may have different effects in these two regions, which is the reason for this division.

13.2.3 Historic catch

Baleen whales

Annual catches by Region of the baleen whales considered in the model are listed in Table 13.2a. These were provided by C. Allison of the IWC Secretariat for minke and fin whales. For humpback whales, data were taken from Johnston and Butterworth (2002) and for blue whales from Rademeyer *et al.* (2003).

Seals

Since no details on yearly catches of Antarctic fur seals exist, 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 Appendix 13. Crabeater seals have hardly been harvested, but 750 animals were taken per year in Region A for 11 years during the period from 1967 to 1977 (I. Boyd, pers. commn). The consequent historical catches of Antarctic fur and crabeater seals assumed for the model are shown in Table 13.2b.

13.2.4 Absolute abundance estimates and their relative trends

The absolute abundance estimates for the predator species considered are shown in Table 13.3, while their relative trends are listed in Table 13.4 together with the sources for this information.

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Note that the estimates of abundance for blue, humpback and minke whales in Table 13.3 refer to the region south of 60°S, which likely includes most of the blue and minke whales. For the fin whales, the estimates obtained for south of 60°S by Branch and Butterworth (2001b) are extrapolated by a factor of 7, based on the results of Butterworth and Geromont (1995), who used JSV sighting rate data as an index of relative density to extrapolate abundance estimates obtained from the IWC/IDCR-SOWER surveys to the region north of 60°S.

Most of these abundance estimates do not incorporate the possible effects of bias factors discussed in Chapters 5 and 6, i.e. they are mostly the original estimates calculated by the various authors (except for fin whales as noted above). This was done so that calculations were based primarily on "firmer" estimates already reviewed by groups such as the IWC Scientific Committee. In recognition particularly of refinements of these estimates presented in those earlier Chapters, some sensitivity tests of the results to these abundance estimates are explored in the analyses, and the implications discussed in the Discussion section following.

Since the abundance trends for fin whales and crabeater seals are not well known, no information on these trends is included when fitting the model to data.

13.2.5 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 (CAMLR 2004) that for those predators whose foraging is based on interactions with individual prey organisms (e.g. killer whales that forage on seals), Type II response curves might be appropriate; on the other hand, predators whose foraging is based on interactions with prey organisms that must be aggregated to exceed some threshold density (e.g. baleen whales that forage on krill) likely manifest Type III curves. In this analysis both Type II and Type III functional response forms are explored.

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The model

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

-Dynamics of krill

$$B^a_{y+1} = B^a_y + r^a B^a_y \left(1 - \left(\frac{B^a_y}{K_a}\right)\right) - \sum_j \frac{\lambda^j \left(B^a_y\right)^n N^{j,a}_y}{\left(B^{j,a}\right)^n + \left(B^a_y\right)^n} \tag{13.1}$$

-Dynamics of the predators

$$N^{j,a}_{y+1} = N^{j,a}_y + \frac{\mu^j N^{j,a}_y \left(B^a_y\right)^n}{\left(B^{j,a}\right)^n + \left(B^a_y\right)^n} - M^j N^{j,a}_y - \eta^{j,a}\left(N^{j,a}_y\right)^2 - C^{j,a}_y \tag{13.2}$$

where

B^a_y 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 tons) by predator species j (j could be either b (blue whale), m (minke whale), h (humpback whale), f (fin whale), s (Antarctic fur seals) or c (crabeater seals));

$N^{j,a}_y$ 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 birth rate of species j in region a drops to half of its maximum level;

μ^j is the maximum annual birth rate of predator species j;

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); and

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

Note that no krill catch is considered as (to date) this has been small compared to krill abundance (CCAMLR 2001). Terms involving the parameter $\eta^{j,a}$ can apply to either or both of birth

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(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 following).

Note also that the krill production function in equation (13.1) is changed from the Pella-Tomlinson form of the earlier model (see equation (12.1)) to a Schaefer form. This was done to facilitate computations: the problem is that otherwise the computation of K_a from equation (13.3) (see next subsection) can lead to discontinuous derivatives, which is not permissible for the minimization process of the ADMB package used for these computations. The effect of this change is not large: the *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 (13.1) and (13.2), the initial abundance for each species in year 1780, before any exploitation began, (which is 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 this model were in equilibrium (balance) in year 1780 provides relationships between the parameter values. Thus, by setting $B^a_{y+1} = B^a_y$ in equation (13.1), it follows that if a Type III functional response form is assumed:

$$r^a\left(1-\left(\frac{B^a_{1780}}{K_a}\right)\right) = \sum_j \frac{\lambda^j B^a_{1780} N^{j,a}_{1780}}{\left(Bj^a\right)^2 + \left(B^a_{1780}\right)^2} \tag{13.3}$$

Similarly, setting $N^{j,a}_{y+1} = N^{j,a}_y$ in equation (13.2) yields:

$$\frac{\mu^j \left(B^a_{1780}\right)^2}{\left(Bj^a\right)^2 + \left(B^a_{1780}\right)^2} = M^j + \eta^{j,a} N^{j,a}_{1780} \tag{13.4}$$

for each predator species j.

For blue whales, equation (13.4) can also be rewritten as:

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$$B^a_{1780} = \frac{Bb^a \sqrt{\left(M^b + \eta^{b,a} N^{b,a}_{1780}\right)}}{\sqrt{\mu^b - M^b - \eta^{b,a} N^{b,a}_{1780}}} \quad . \tag{13.5}$$

Given values of Bb^a and $\eta^{b,a}$ as inputs, and choices from their plausible ranges for the other blue whale parameters (M^b, $N^{b,a}_{1780}$ and μ^b), the initial biomass of krill in region a in year 1780 (B^a_{1780}) becomes specified. Similarly, by solving equation (13.4) for Bj^a, this functional response parameter becomes specified for the other predator species. Once all these parameters are specified, K_a can be calculated from equation (13.3). Similar equations apply when a Type II functional response form is assumed.

The Likelihood function

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

$$-\ln L = LL^b_{abun} + LL^b_{tren} + LL^m_{abun} + LL^m_{tren} + LL^h_{abun} + LL^h_{tren} + LL^f_{abun} + LL^s_{abun} + LL^s_{tren} + LL^c_{abun} \tag{13.6}$$

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

Blue whale component

$$LL^b_{abun} = \left(\ln N^{b,A}_{2000} - \ln \hat{N}^{b,A}_{2000}\right)^2 \Big/ 2\left(\sigma^{b,A}_{2000}\right)^2 + \left(\ln N^{b,P}_{2000} - \ln \hat{N}^{b,P}_{2000}\right)^2 \Big/ 2\left(\sigma^{b,P}_{2000}\right)^2 \tag{13.7}$$

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

$$\text{where} \quad \ln q = \frac{\sum_{y=1}^{n} \frac{1}{\sigma^2_y} \left(\ln N^{b,obs}_y - \ln \hat{N}^b_y\right)}{\sum_{y=1}^{n} \frac{1}{\sigma^2_y}} \tag{13.8}$$

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Minke whale component

$$LL^{m}_{abun} = \left(\ln N^{m,A}_{1985} - \ln \hat{N}^{m,A}_{1985}\right)^2 \Big/ 2\left(\sigma^{m,A}_{1985}\right)^2 + \left(\ln N^{m,P}_{1985} - \ln \hat{N}^{m,P}_{1985}\right)^2 \Big/ 2\left(\sigma^{m,P}_{1985}\right)^2 \quad (13.9)$$

$$LL^{m}_{tren} = \left(R^{m,A}_{1970-2000} - \hat{R}^{m,A}_{1970-2000}\right)^2 \Big/ 2\left(\sigma^{m,A}_{1970-2000}\right)^2 + \left(R^{m,P}_{1970-2000} - \hat{R}^{m,P}_{1970-2000}\right)^2 \Big/ 2\left(\sigma^{m,P}_{1970-2000}\right)^2 \quad (13.10)$$

Humpback whale component

$$LL^{h}_{abun} = \left(\ln N^{h,A}_{1997} - \ln \hat{N}^{h,A}_{1997}\right)^2 \Big/ 2\left(\sigma^{h,A}_{1997}\right)^2 + \left(\ln N^{h,P}_{1997} - \ln \hat{N}^{h,P}_{1997}\right)^2 \Big/ 2\left(\sigma^{h,P}_{1997}\right)^2 \quad (13.11)$$

$$LL^{h}_{tren} = \left(R^{h,A}_{1977-1991} - \hat{R}^{h,A}_{1977-1991}\right)^2 \Big/ 2\left(\sigma^{h,A}_{1977-1991}\right)^2 + \left(R^{h,P}_{1981-1996} - \hat{R}^{h,P}_{1981-1996}\right)^2 \Big/ 2\left(\sigma^{h,P}_{1981-1996}\right)^2 \quad (13.12)$$

Fin whale component

$$LL^{f}_{abun} = \left(\ln N^{f,A}_{1997} - \ln \hat{N}^{f,A}_{1997}\right)^2 \Big/ 2\left(\sigma^{f,A}_{1997}\right)^2 + \left(\ln N^{f,P}_{1997} - \ln \hat{N}^{f,P}_{1997}\right)^2 \Big/ 2\left(\sigma^{f,P}_{1997}\right)^2 \quad (13.13)$$

Antarctic fur seal component

$$LL^{s}_{abun} = \left(\ln N^{s,A}_{1930} - \ln \hat{N}^{s,A}_{1930}\right)^2 \Big/ 2\left(\sigma^{s,A}_{1930}\right)^2 + \left(\ln N^{s,A}_{1976} - \ln \hat{N}^{s,A}_{1976}\right)^2 \Big/ 2\left(\sigma^{s,A}_{1976}\right)^2 + \left(\ln N^{s,A}_{1991} - \ln \hat{N}^{s,A}_{1991}\right)^2 \Big/ 2\left(\sigma^{s,A}_{1991}\right)^2 \quad (13.14)$$

$$LL^{s}_{tren} = \left(R^{s,A}_{1958\text{-}1971} - \hat{R}^{s,A}_{1958\text{-}1971}\right)^2 \Big/ 2\left(\sigma^{s,A}_{1958\text{-}1971}\right)^2 + \left(R^{s,A}_{1977\text{-}1991} - \hat{R}^{s,A}_{1977\text{-}1991}\right)^2 \Big/ 2\left(\sigma^{s,A}_{1977\text{-}1991}\right)^2 + \left(R^{s,A}_{1991\text{-}2000} - \hat{R}^{s,A}_{1991\text{-}2000}\right)^2 \Big/ 2\left(\sigma^{s,A}_{1991\text{-}2000}\right)^2 \quad (13.15)$$

Crabeater seal component

$$LL^{c}_{abun} = \left(\ln N^{c,A}_{2000} - \ln \hat{N}^{c,A}_{2000}\right)^2 \Big/ 2\left(\sigma^{c,A}_{2000}\right)^2 + \left(\ln N^{c,P}_{2000} - \ln \hat{N}^{c,P}_{2000}\right)^2 \Big/ 2\left(\sigma^{c,P}_{2000}\right)^2 \quad (13.16)$$

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

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

Biological parameters

Details of the plausible bounds imposed on the parameters to be estimated are provided in Table 13.5[1]. 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 the previous Chapter, and ranges for the other parameters were chosen based on various sources of information available to date.

Values for the input parameters Bb^a and $\eta^{j,a}$ are chosen so that the resultant populations' trajectories are able to reflect the patterns evident from available data. Note in particular that the apparent greater suitability of the Atlantic for blue, fin, humpback whales and of the Pacific for minke whales is reflected by choosing comparatively smaller values for the η parameter for these respective regions.

13.3 Results

Figure 13.3 shows the "reference case" trajectories for krill and their main predators in the Antarctic when a Type III functional response form is assumed, and Table 13.6 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[2]. Once the fit had converged, a check was made that the associated initial coexistence equilibrium was stable. Figure 13.4 shows the projected trajectories (up to 2500) for this "reference case" model under zero future catches for all the species, Figure 13.5 (a) shows the annual consumption of krill by each predator in Regions A

[1] 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 13.5 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.

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

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and P, and Figure 13.6 (a) shows the annual production of krill itself for each Region.

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

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

(ii) In the light of the environmental changes that have been reported recently (e.g. 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 what is assumed for the "reference case"?

(vi) What if the lower limits of the bounds for the initial (1780) abundances of crabeater seals were set higher (e.g. 2 million)?

Figures 13.7 to 13.12 show the trajectories of krill and their main predators in the Antarctic for each of the above sensitivity scenarios respectively, and Table 13.6 shows the values of the input and estimated parameters for these six scenarios.

The main feature of the "reference case" results of a sharp increase from about 1930, followed by a decrease in krill biomass in the Atlantic/Indian region starting at about 1950 (as shown in Figure 13.3), does not change for scenarios (i), (ii) and (vi) detailed above (see Figures 13.7, 13.8 and 13.12). However, for scenarios (iii), (iv) and (v), the subsequent decrease in krill biomass is not as appreciable as for the other scenarios, and consequently minke whale abundance does not show as marked a decrease since the 1970s, if indeed it decreases at all (Figures 13.9 to 13.11). For the model to reflect minke whales starting to decrease from about 1970, requires a largish drop in krill biomass from about the 1950s to the 1990s, as well as a relatively high density dependent η parameter for this species.

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When minke whale abundance is doubled (scenario (i)), the consumption of krill by this species increases compared to the "reference case" (compare Figures 13.5 (a) and (b)) but there are no qualitative changes to results. The effect of linearly reducing K_A to half of its original level between the mid 1950s and early 1970s results in a marginally better fit than the "reference case" (compare $-\ln L$ in Table 13.6 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 were set higher, the results do not change qualitatively compared to the "reference case"; however, the recent absolute abundances of crabeater seals are increased due to these increases in initial abundance (Figure 13.12).

Note that neither ignoring non-whale predators (Figure 13.9) or assuming a Type II functional response (Figure 13.10) leads to a recent decline in minke whale abundance. Figure 13.11 shows that inhibiting the extent of growth in the crabeater seal abundance during the 1960s and 1970s by increasing the associated η parameters precludes as substantive a recent minke whale reduction as for the reference case.

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

Table 13.7 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 13.13a to 13.13d. 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 13.13a). For

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humpback whales and Antarctic fur seals in Region A, the confidence intervals for the estimated initial numbers of these animals are very narrow (Figure 13.13a, Table 13.7). 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 the species must have been virtually extinct when exploitation stopped 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.

For the estimates of maximum birth rates, again the "posterior" distributions are somewhat narrower than the prior distributions for all the 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 whales and seals (Figure 13.13b). The narrow confidence interval for the initial abundance estimate for Antarctic fur seals likely 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 13.4).

For maximum consumption rates (the λ parameters), higher values are preferred in all cases (Figure 13.13c). As can be seen from equation (13.5), the choice of the input parameter Bb^a (which is the krill biomass when the consumption of krill by, and hence also the birth rate of blue whales in region a drops to half of its maximum level) determines the magnitude of the initial biomass of krill, which in turn affects the estimated maximum consumption rates for the species considered in the model. The narrow confidence interval for λ for blue whales is likely a consequence of the input choice for Bb^a.

Regarding 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.

13.4 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 were co-existing in a stable equilibrium, and

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

This study thus shows that under these assumptions, and 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, and certain biological parameters do lie in the ranges presumed for them (i.e. within the bounds specified in Table 13.5), 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 minke whales and seals, 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 benefitted also start to decrease again from around 1970, while the then protected larger baleen whale species commence recovery.

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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 considered 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 (see Figure 13.9). 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 13.5, 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, Chapter 8 of this thesis).

Furthermore, the assumption of a Holling Type III functional response form also seems to be critical to obtain such a trajectory for minke whales. This is because when a Holling Type II form is assumed, crabeater seals do not increase as rapidly as for a Type III form, so that krill biomass does not drop sufficiently from the 1950s to the 1990s that minke whales start to decrease from around 1970 (Figure 13.10).

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

Plausibility of the underlying assumptions of the model

1. Before the exploitation of the seals and whales in the Antarctic, the species were in stable equilibrium.

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

2. Existence of competition between and within the species

Most ecologists recognize two forms of competition. One is called "exploitation competition" and the other "interference competition". Exploitation competition is defined as: competition in which any adverse effects on an organism are brought about by reductions in resource levels caused by other competing organisms. Interference competition is defined as: competition between two organisms in which one physically excludes the other from a portion of habitat and hence from the resources that could be exploited there (Begon *et al.* 1999).

For "exploitation competition" to exist, the resource in question must be in limited supply. The observations of increases in minke whales, crabeater seals and some seabirds (none of which had

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been subject to earlier human harvest) over about the 1940s to the 1970s, likely in response to overharvesting of the krill-consuming larger baleen whales, indirectly supports this assumption of limited supply of krill to krill predators.

In regard to the possibility of "interference competition" between the baleen whales, Clapham and Brownell (1996) suggest that there are several reasons to believe that at least interference competition between baleen whales may in most cases be minimal, even if resource limitation applies. They 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.* 2005, C. Heinecken, Capricorn Fisheries Monitoring, pers. commn) provide a counter-example to these arguments, though admittedly such competition is between rather than within species.

The model developed includes both exploitation competition (through the functional response postulated for krill consumption) and interference competition in the form of the density dependent mortality terms (with their associated η parameters). The latter are a mathematical necessity to admit non-trivial co-existence equilibria, and are relatively easy to motivate 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 Clapham and Brownell (1996)'s arguments. Some possible explanations are that:

i) the intra-species effect is subtle and occurs only at high levels of abundance not recently evident in the Antarctic;
ii) what has been modelled here may be a surrogate for intra-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 (see Chapter 10 of this thesis) may constitute indirect evidence; and
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 distribution of calving whales as the South African right whale population has recovered (Best 1981).

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As mentioned earlier, the density dependent term involving the η parameter, introduced into the predator dynamics equation (13.2), can be considered as a modifier of some combination of overall natural death rate and birth-plus-calf-survival rate. Figure 13.14 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:

$$\tilde{M}_y^{j,a} = M^j + \eta^{j,a} N_y^{j,a} \qquad (13.17).$$

Figure 13.14 indicates that the annual $\tilde{M}_y^{j,a}$ are initially in the range of 0.04-0.08/year for all the species considered except for humpback whales. For these whales, this rate is much higher (≈0.16/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 over the middle decades of the 20th Century in both regions, and also for crabeater seals in the Atlantic region, lead to the increases in abundance in these populations in response to the krill surplus being arrested *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 magnitude estimated for krill biomass

The long term trend in krill biomass estimated by the reference case model suggests that the initial krill biomass under unexploited co-existence was around 150 million tons, which then gradually increased to about 800 million tons during the first half of the 20th Century (with virtually all this increase occurring in the Atlantic/Indian region), after which it declined again to around 200 to 300 million tons in recent years. As has been detailed in Chapter 7, 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 various sizes of patches ranging from hundreds of meters in diameter and several meters thick, to 12km in diameter and 230m thick, makes such abundance estimation even more difficult.

As was detailed in Chapter 7, the most recent circumpolar estimate of krill abundance are in the range of about 150 to 400 million tons. This is quite compatible with the reference case model

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estimates which are in the 200-300 million ton range; it would also seem to exclude sensitivity scenarios iii) and iv) considered earlier, in which respectively ignoring seal predators or assuming Type II functional responses suggest recent krill biomass to be in the 600-700 million ton range. Unfortunately, there are no direct observations that allow the plausibility of the estimate of 800 million tons of krill biomass in the mid 20th Century that is suggested by the model of this Chapter 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 earlier years.

Plausibility of the predicted biomass trend estimate of krill

As was detailed in Chapter 7, 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, and also scenarios (i), (ii)and (vi), do indicate substantial increases in krill production (as well as abundance) in the Atlantic/Indian region, starting from about 1920 (Figure 13.6). 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 on 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 200m 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 200m 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 the krill. Holm-Hansen and Huntley (1984) estimated that the krill in the

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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 tons of "surplus" krill and this analysis

As was discussed in Chapter 11, Laws (1977) suggested that following the exploitation of large baleen whales in the Antarctic, some 150 million tons of "surplus" annual production of krill became available for other krill-feeding predators, such as minke whales, crabeater seals, fur seals, penguins and some albatrosses. This estimate of 150 million tons was based on estimates of the population sizes of the baleen whales 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 13.8). However, the reference case estimate of consumption of krill by large baleen whales in the Antarctic shown in Figure 13.5 suggests much less consumption of krill by the large baleen whales prior to their harvesting: approximately 50 million tons per year.

Table 13.8 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 the 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 Chapter 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 in this Chapter estimates a lower pre-exploitation abundance of fin whales (see further remarks below) than that assumed by Laws, and that though minke whales are now estimated to be larger in number, they are no longer thought to feed throughout the year on krill as Laws (1977) assumed. It should also be noted that the modelling

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framework in this Chapter 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.* (2000a) 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 ones calculated from predator consumption) and suggested that this discrepancy may be caused by: 1) bias in acoustic studies, 2) the possibility of large krill population components that are either too deep, too shallow or too dispersed to be detected, and/or 3) an overestimation of the demand for krill by predators. The results of this 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 rate in the abundance of minke whales and crabeater seals from 1940 to 1970 for the reference case is 4% in Region A. The catch-at-age analysis in Chapter 8 infers the increase rate in minke whale recruitment to be 5% per year for the period between 1945 to 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 13.4). 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 this species increased at a rate of 4% per year, given that other seal populations have shown increase rates of this magnitude or higher. Analysis of data for the age at sexual maturity of minke whales and crabeater seals described in Chapter 4 indicates a decrease in age at sexual maturity within this period which is an expected response to greater food availability and would contribute to an increase in population growth rate.

Although an annual increase rate of 4% for crabeater seals may not seem unrealistic, the increase in the amount of consumption of krill by this species in Region A as shown in Figure 13.5 is substantial (exceeding, for example, the estimated pre-exploitation consumption by blue whales),

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and raises plausibility concerns. When the possible effect of environmental change (K_A for krill linearly reduced to half of its original value between the mid 1950s and early 1970s – sensitivity scenario (ii)), this enormous increase in consumption of krill by crabeater seals is lowered by about 40% as also shown in Figure 13.5. Thus whether or not a poorer environment needs to be postulated in addition to species interaction effects to explain predator population trends in the Antarctic rests primarily on the extent of an increase in crabeater seal abundance that is considered to be realistic.

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

It is important to bear in mind that although not included in this model, some other krill predators such as Adélie penguins, chinstrap penguins and macaroni penguins also increased during the period from 1950 to the 1970s as is discussed in Chapter 11 (Croxall 1992, Croxall *et al.* 2002).

As is detailed in Chapter 3, krill consumption estimates for birds, squid and fish are somewhat coarser than those for baleen whales, but nevertheless suggest that at least some of these predators did respond to a krill surplus in the mid-20th Century, and furthermore that their present levels of krill consumption are not insubstantial compared to those of the whales and seals considered in the model. In the context of the model then, results for crabeater seals should perhaps be considered as reflecting a conglomerate of these seals together with some 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 13.3) somewhat more plausible (see also discussion in the section following).

Another important point to note is that the faster dynamics of squid and fish compared to the other krill-feeding species makes it possible for them to be able to exploit "surplus" krill before, say, whales and seals, though naturally the extent to which this might have occurred depends on the sizes of the squid and fish populations which are only poorly known (see Chapter 3).

In summary, it seems that the results for the reference case model do pass the various plausibility tests, though admittedly needing 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 (see Figure 13.8 for sensitivity scenario (ii)), but the results of the analyses of this Chapter suggest that predator population trends can still be explained without invoking this assumption.

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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 (as is introduced in Chapter 5 of this thesis), 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 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, as is detailed in Chapter 6, 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 less reliable.

Secondly, it has been found that it is very difficult to find sets of parameter values that will result in a stable co-existence equilibrium at the time of the first year considered in the model (i.e. 1780) and also gives 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.

Thirdly, fin whales are problematic in two respects. There is the difficulty of how best to account for the fact that much of their feeding takes place north of 60°S and well away from the ice-edge zone preferred by most of the other species considered. Also there is the surprising result that the reference case model estimates initial fin whale numbers to have been about the same as blue whales, despite of the fact of the fin whale catch having been some 50% larger (see Table 13.1a). 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 13.15, which shows the per capita growth rate (sustainable yield rate) of each predator species over time in the absence of harvesting – note that while the trends shown for blue and fin whales are similar, larger values first occur over a period when blue whales are already substantially depleted, so cannot take full "advantage", unlike the situation for fin whales. Thus, essentially, fin whales were the first beneficiaries of the krill "surplus", even before minke whales and crabeater

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seals.

Although the baleen whale abundance estimates of Table 13.3 that have been used for the analyses presented here apply to the area south of 60°S (except in the case of fin whales), our 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 (D. Miller, pers. commn). 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, T. Branch, pers. commn). Sensitivities of the model prediction to different input values of observed abundance estimates of whales and seals taking into account various biases which were discussed in Chapters 5 and 6 of this thesis have not been fully explored in this analysis. Nevertheless such sensitivities as have been explored - to minke whale abundance estimates (scenario (i)) and to the initial number of crabeater seals in 1780 (scenario (vi)) - suggest that model results change only quantitatively but not qualitatively. Thus, the results presented here should be interpreted in qualitative rather than quantitative terms.

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

13.5 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 as is detailed in Chapter 11, 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 more fully understand 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 Chapter do not, of course, exclude the possibility that the observed/inferred trends

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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 predators in the Antarctic, as well as of environmental change and its effect on the dynamics of these species will be essential to improve the model and 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 become 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, different forms of functional response, and quantification of uncertainties is desirable. In principle this is achievable through a Bayesian estimation approach, but the associated computations will prove decidedly non-trivial given the high level of non-linearity in the model and the fact that a number of parameters are estimated to lie at the bounds of their specified ranges. Furthermore, it would seem advisable for this to wait for the availability of the APIS results for crabeater seal abundance and 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 were not considered in the current model, even if only as a lumped variable explicitly representing all such species[3]. 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 focussing further modelling refinements.

In recent years, the importance of ecosystem based management of fisheries and wild-life resources has been recognized 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

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

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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 the most appropriate next step.

13.6 Some concluding summary comments

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

- 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 they 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 the Atlantic/Indian and Pacific regions, with appreciable changes in abundance in the former while the latter has been relatively stable by comparison.
- The severe depletion of fur seals by harvesting over the turn of the 18th Century had quantitatively much less impact than that of the larger baleen whale species during the middle decades of the 20th Century.
- Accounting for likely population trends through species interaction effects suggests that baleen whale species can manifest relatively fast dynamics (sustainable yield rates typically

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showing maxima closer to 10% than 1%) (see Figure 13.15).

- Nevertheless in the absence of future harvesting, blue whales in the Atlantic/Indian region are predicted to need some three to four centuries to recover to their pre-exploitation level (see Figure 13.4), essentially because they also need to outcompete other predators which initially recover faster.
- Density dependent mortality is a necessary feature of the model, but problematic given the absence of independent bases to inform on likely values for the associated (η) parameters.
- The VPA-based indication of 1970 or thereabout as the time of 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 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.

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Table 13.1 Estimates of annual consumption of krill by its predators in the Antarctic. A dash indicates that no estimate is available; * denotes that this estimate also includes other euphausiids; ? indicates that the estimate is coarse, being based on sweeping assumptions. [Note that the analyses of this paper (see Table 13.8) suggest that the estimates of Laws (1977) are too high.]

Species	Krill consumption (million tons)			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 this thesis
Seals (Antarctic fur, crabeaater)	64	24-73		Chapter 3, Table 3.6 of this thesis
Birds (dominated by penguins)	-	min 14*		Woehler (1995)
Cephalopods	-	min 34-56 (?)		Everson (1984)
Fish	-	40-50 (?)		Hureau (1994)

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Table 13.2a Historical catches in the Southern Hemisphere of the baleen whale species considered in Chapter 13.

Year	Blue whale		Minke whale		Humpback whale		Fin 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	0	0	180	0	0	0
1905	51	0	0	0	228	23	0	0
1906	68	0	0	0	240	492	0	0
1907	106	0	0	0	1281	336	0	0
1908	245	0	0	0	2171	1240	0	0
1909	180	32	0	0	4030	1481	0	0
1910	359	28	0	0	7952	2027	0	0
1911	1235	0	0	0	8558	1381	0	0
1912	2319	185	0	0	8882	1654	0	0
1913	2772	0	0	0	9562	2379	569	0
1914	5031	94	0	0	6223	679	1026	0
1915	5536	100	0	0	3135	229	1850	0
1916	4323	64	0	0	464	36	755	0
1917	3097	76	0	0	74	86	530	500
1918	1978	68	0	0	96	104	1113	824
1919	1994	15	0	0	184	206	2508	454
1920	2948	54	0	0	271	178	3072	2227
1921	4443	78	0	0	229	21	1243	1025
1922	6689	85	1	0	1395	207	2342	1244
1923	4657	261	0	0	1381	116	2124	1325
1924	6510	456	0	0	986	131	3393	1650
1925	5787	635	0	0	1919	358	6881	2096
1926	12148	1512	0	0	1305	355	3747	1848
1927	7822	2281	0	0	1128	22	3356	1703
1928	9067	4831	0	0	1189	36	5484	1656
1929	18267	459	0	0	195	26	8053	2422
1930	51916	3820	0	0	819	189	1179	0
1931	6613	46	0	0	253	273	3765	0
1932	18835	148	0	0	469	57	5621	1
1933	17376	56	0	0	1024	99	7530	18
1934	16584	28	0	0	3214	117	13125	29
1935	17670	198	0	0	6051	191	10233	105
1936	14424	174	0	0	9486	160	14901	105
1937	12442	97	0	0	7338	147	29115	129
1938	13092	1035	0	0	3679	180	19922	2079
1939	10983	5752	0	0	1168	167	13940	0
1940	1514	0	0	0	455	214	4063	6
1941	51	0	0	0	79	172	717	0
1942	127	0	0	0	0	142	776	0
1943	349	0	0	0	84	180	1158	0
1944	1048	2	0	0	175	176	1665	0
1945	3604	42	0	0	284	214	9188	0
1946	8533	704	0	0	122	235	14119	478
1947	5470	1498	0	0	134	223	19700	1607
1948	6562	1167	0	0	274	279	16382	2655
1949	3516	2722	1	0	5627	1957	16708	2968
1950	4004	3028	0	0	4734	1567	15272	4103
1951	2984	2108	9	0	3306	853	16065	5375
1952	2946	1048	0	0	1913	2249	17867	3894
1953	2483	405	12	0	1787	3099	12496	3385
1954	1483	1059	0	0	1819	4745	12078	4540
1955	1018	731	45	0	2065	2209	18075	8654
1956	676	1062	46	0	1234	2928	15321	11094
1957	995	648	12	481	2312	3471	18429	7279
1958	726	524	103	0	3172	5792	21330	4574
1959	824	112	63	143	1178	15900	22968	2070
1960	1552	191	66	96	1684	14577	12951	2453
1961	911	232	0	2	1200	6971	11927	1379
1962	1584	164	9	12	3064	901	15035	279
1963	1244	258	98	6	505	323	12142	179
1964	2688	654	47	4	173	106	6327	77
1965	861	538	72	7	1265	948	1864	108
1966	362	300	369	5	790	337	1568	309
1967	336	126	1096	3	1059	140	1167	119
1968	561	113	607	11	1	0	1750	230
1969	760	156	746	18	0	0	1887	0
1970	681	141	917	0	0	0	1757	0
1971	449	101	4152	3	0	3	1300	1
1972	514	105	6583	0	2	0	1353	472
1973	1	0	7271	1270	1	0	763	576
1974	0	0	5280	2604	0	0	511	510
1975	0	0	5350	1835	0	0	23	206
1976	0	0	6117	2559	0	0	22	0
1977	0	0	4126	1874	0	0	0	0
1978	0	0	4954	1202	0	0	0	0
1979	0	0	5609	2288	0	0	0	0
1980	0	0	4697	2445	0	0	0	0
1981	0	0	4845	3058	0	0	0	0
1982	0	0	3935	3366	0	0	0	0
1983	0	0	4136	2544	0	0	0	0
1984	0	0	3504	2064	0	0	0	0
1985	0	0	3470	2097	0	0	0	0
1986	0	0	2935	2034	0	0	0	0
1987	0	0	273	0	0	0	0	0
1988	0	0	0	241	0	0	0	0
1989	0	0	330	0	0	0	0	0
1990	0	0	0	327	0	0	0	0
1991	0	0	288	0	0	0	0	0
1992	0	0	0	330	0	0	0	0
1993	0	0	330	0	0	0	0	0
1994	0	0	0	330	0	0	0	0
1995	0	0	439	1	0	0	0	0
1996	0	0	0	440	0	0	0	0
1997	0	0	438	0	0	0	0	0
1998	0	0	0	389	0	0	0	0
1999	0	0	439	0	0	0	0	0
2000	0	0	0	440	0	0	0	0
SUM	348998	42604	83820	34529	137258	86293	494101	91020
TOTAL	391602		118349		223551		585121	

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Addendum: After the submission of the thesis, the IWC Secretariat discovered some errors in the statistics on past whale catches that are shown in this Table. These errors will be corrected when the findings from this thesis are published in scientific journals.

Table 13.2b Assumed historical catches of Antarctic fur seals (see Appendix 13); 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.

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

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Table 13.3 Observed/inferred abundance estimates for the krill-feeding predators considered in the model.

Species		Abundance estimate	CV	Sources
Blue whale	$N^{b,A}_{2000}$	1104	0.4	Rademeyer *et al*. (2003a)
	$N^{b,P}_{2000}$	762	0.4	
Fin whale	$N^{f,A}_{1997}$	10591	0.5	Branch and Butterworth (2001b)
	$N^{f,P}_{1997}$	27594	0.5	Butterworth and Geromont (1995)
Humpback whale	$N^{h,A}_{1997}$	5044	0.2	Branch and Butterworth (2001b)
	$N^{h,P}_{1997}$	4868	0.2	
Minke whale	$N^{m,A}_{1985}$	327369	0.1	IWC (1991)
	$N^{m,P}_{1985}$	420572	0.1	
Antarctic fur seals	$N^{s,A}_{1930}$	100	0.5	Payne (1977,1979)
	$N^{s,A}_{1975}$	369000	0.5	Payne (1977,1979), MacCann and Doidge (1987)
	$N^{s,A}_{1990}$	1550000	0.5	Boyd (1993)
Crabeater seals	$N^{c,A}_{2000}$	4000000	0.5	J. Laake (pers. commn)*, see Section 6.3 of this thesis
	$N^{c,P}_{2000}$	4000000	0.5	

* Laake's coarse initial circumpolar abundance estimate of 6-8 million is based only on the segment from 170°W to 125°W which was covered by US surveys in 1999/2000 austral summer as part of the Antarctic Pack Ice Seal (APIS) program (Ackley *et al.* 2003a). 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 Atlantic/Indian region is sparse. According to Erickson and Hanson (1990), circumstantial evidence indicates that appreciable numbers of crabeater seals occur seaward from the ice edge in ice-free waters adjacent to the continent, and largish numbers of crabeater seals are also found in the vicinity of sub-Antarctic islands. Thus abundances of 4 million crabeater seals for each Region are assumed in this analysis. The CV's associated with the estimates are not available so that a tentative CV of 0.5 is assumed.

Table 13.4 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 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 this thesis
	$R^{m,P}_{1970-2000}$	-0.024	0.31	
Antarctic fur seals	$R^{s,A}_{1957-1972}$	0.17	0.5	Payne (1977), Boyd *et al*. (1990, 1995)
	$R^{s,A}_{1976-1990}$	0.10	0.5	Boyd (1993), SSG (2000)
	$R^{s,A}_{1990-1999}$	0.10	0.5	

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

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Table 13.5 Plausible bounds for the parameters to be estimated.

Parameters to be estimated		References/Notes
	Bounds	
$N_{1780}^{b,A}$	100000-300000	
$N_{1780}^{b,P}$	10000-100000	
$N_{1780}^{m,A}$	10000-200000	
$N_{1780}^{m,P}$	10000-300000	
$N_{1780}^{h,A}$	10000-250000	
$N_{1780}^{h,P}$	10000-100000	
$N_{1780}^{f,A}$	10000-400000	
$N_{1780}^{f,P}$	10000-200000	
$N_{1780}^{s,A}$	500000-5000000	
$N_{1780}^{c,A}$	100000-10000000	
$N_{1780}^{c,P}$	100000-10000000	
μ_b	0.05-0.16	See below (1)
μ_m	0.07-0.2	
μ_h	0.06-0.18	
μ_f	0.05-0.16	
μ_s	0.18-0.28	Laws (1984), Boyd *et al*. (1995)
μ_c	0.11-0.28	
M_b	0.03-0.06	See below (1)
M_m	0.04-0.1	
M_h	0.03-0.08	
M_f	0.03-0.05	
M_s	0.07-0.3	Laws (1984), Boyd *et al*. (1995), Payne (1977)
M_c	0.07-0.3	Laws (1984)
λ_b	115.9-450.6	See Chapter 3, Tables 3.1 and 3.3 of this thesis
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), Chapter 12 and Appendix 12 of this thesis
r^P	0.4-0.6	

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

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Table 13.6 Values of the input and estimated parameters and other quantities for the "reference case" 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.

Input parameters								Estimated parameters and $\ln L$								Derived parameters							
										Estimates							Model						Observed
	Reference	(i)	(ii)	(iii)	(iv)	(v)	(vi)		Bounds	Reference	(i)	(ii)	(iii)	(iv)	(v)	(vi)		Reference	(i)	(ii)	(iii)	(iv)	(v)	(vi)	
Bb^A	1.70E+08	1.70E+08	1.70E+08	2.30E+08	5.00E+08	1.70E+08	1.70E+08	$N^{b,A}_{1760}$	100000–300000	193093	194930	195115	226271	260995	208156	227958	K_A	8.09E+08	8.58E+08	7.50E+08	7.61E+08	5.40E+08	4.30E+08	1.03E+09	–
Bb^P	7.00E+07	7.00E+07	7.00E+07	5.00E+07	2.00E+08	7.00E+07	7.00E+07	$N^{b,P}_{1760}$	10000–100000	27463	26511	29600	26371	32212	30563	31651	K_P	1.56E+08	2.37E+08	1.55E+08	1.90E+08	2.27E+08	1.30E+08	1.64E+08	–
								$N^{m,P}_{1760}$	10000–200000	52915	200000	61348	200000	33615	27709	59128									
$\eta^{b,A}$	4.00E-08	4.00E-08	4.00E-08	2.00E-07	3.00E-08	4.00E-08	4.00E-08	$N^{b,A}_{1760}$	100000–300000	169429	300000	248718	207706	300000	300000	300000	Bm^A	1.47E+08	1.05E+08	1.41E+08	1.81E+08	5.75E+08	1.54E+08	1.98E+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	$N^{m,A}_{1760}$	10000–250000	65438	65581	65430	68311	77651	63790	62566	Bm^P	6.65E+07	5.66E+07	5.78E+07	2.77E+07	1.22E+08	5.08E+07	7.89E+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	$N^{h,P}_{1760}$	10000–100000	56412	56057	58131	35922	59702	56826	55666	Bh^A	3.21E+07	3.16E+07	3.28E+07	2.63E+08	7.61E+07	4.41E+07	6.66E+07	–
$\eta^{f,A}$	4.00E-08	4.00E-08	4.00E-08	5.00E-08	4.00E-08	4.00E-08	4.00E-08	$N^{f,A}_{1760}$	10000–400000	125736	123261	129972	197298	235957	153628	135448	Bh^P	1.63E+07	1.61E+07	1.55E+07	4.63E+07	7.89E+06	2.25E+07	3.81E+07	–
$\eta^{h,P}$	3.50E-09	3.50E-09	3.50E-09	–	1.50E-08	3.50E-09	3.50E-09	$N^{f,P}_{1760}$	10000–200000	64461	55707	76138	43418	89092	82228	81770	Bf^A	1.72E+08	1.31E+08	1.77E+08	4.23E+08	2.82E+08	1.75E+08	2.28E+08	–
$\eta^{f,A}$	7.00E-09	7.00E-09	7.00E-09	–	5.00E-10	2.00E-08	4.00E-09	$N^{f,A}_{1760}$	500000–5000000	2915890	2914040	2917080	–	2571660	2924650	3020910	Bf^P	9.61E+07	7.28E+07	1.00E+08	–	2.35E+08	1.01E+08	1.42E+08	–
$\eta^{h,P}$	1.00E-06	1.00E-06	1.00E-06	6.00E-07	1.00E-06	1.00E-06	1.00E-06	$N^{c,A}_{1760}$	100000*–10000000	277991	192755	673947	–	100000	100000	2000000	Bs^A	1.49E+08	1.43E+08	1.51E+08	–	2.44E+08	1.51E+08	1.99E+08	–
$\eta^{m,P}$	2.00E-07	1.70E-07	2.00E-07	1.70E-07	2.00E-07	2.00E-07	2.00E-07	$N^{c,P}_{1760}$	100000*–10000000	188741	100000	1520910	–	1476380	710125	2000000	Bc^A	1.34E+08	1.45E+08	8.49E+07	–	3.98E+08	1.18E+08	1.53E+08	–
$\eta^{h,P}$	1.50E-06	1.50E-06	1.50E-06	1.00E-06	1.50E-06	1.50E-06	1.50E-06										Bc^P	7.47E+07	8.01E+07	4.55E+07	–	3.18E+08	6.66E+07	9.40E+07	–
$\eta^{f,P}$	7.00E-08	7.00E-08	7.00E-08	9.00E-07	7.00E-08	7.00E-08	7.00E-08	λ^b	115.875–450.625	450.63	432.802	450.625	450.577	450.625	348.999	450.625									
$\eta^{f,P}$	6.00E-09	6.00E-09	6.00E-09	–	1.00E-09	6.00E-09	5.00E-09	λ^m	3.78–32.13	32.13	32.1299	32.13	32.11	32.13	32.13	32.13	B_{1760}	9.46E+07	9.46E+07	9.56E+07	2.85E+08	1.55E+08	9.55E+07	1.26E+08	–
								λ^h	37.8–108	108.00	108	108.00	108	108.00	108.00	107.99	B_{1760}	5.25E+07	5.17E+07	5.44E+07	4.05E+07	1.27E+08	5.47E+07	7.92E+07	–
								λ^f	27.6–110.4	[110.4]	[110.4]	[110.4]	110.4	110.40	[110.4]	[110.4]									
								λ^c	0.678–2.713	2.71	2.71	2.71	–	0.68	2.71	0.68	$N^{b,A}_{2000}$	1102	1106	1115	1104	1108	1132	1099	1104
								κ^c	3.306–5.511	5.51	5.51	5.51	–	5.51	5.51	5.51	$N^{b,P}_{2000}$	763	758	754	762	758	746	764	762
								μ^b	0.05–0.16	0.16	0.16	0.16	0.14	0.16	0.16	0.11	$N^{m,A}_{1760}$	326849	526145	325853	327244	327612	321737	325193	327369
								μ^m	0.07–0.2	0.20	0.20	0.20	0.16	0.20	0.20	0.20	$N^{m,P}_{1760}$	420493	700703	420428	420730	365288	418978	413954	420572
								μ^h	0.06–0.18	[0.18]	[0.18]	[0.18]	0.18	[0.18]	[0.18]	[0.18]	$N^{h,A}_{1760}$	5046	5045	5045	5044	5044	5057	5041	5044
								μ^f	0.05–0.16	[0.16]	[0.16]	[0.16]	[0.16]	[0.16]	[0.16]	[0.16]	$N^{h,P}_{1760}$	4861	4861	4862	4868	4863	4861	4865	4868
								μ^c	0.18–0.28	0.28	0.28	0.28	–	0.28	0.28	0.28	$N^{f,A}_{1760}$	10642	10663	10627	10591	10621	10889	10562	10591
								μ^c	0.11–0.28	0.24	0.24	0.15	–	[0.25]	0.28	0.19	$N^{f,P}_{1760}$	27281	26020	27455	27586	27692	27451	27612	27594
								M^b	0.03–0.06	0.03	0.03	0.03	0.04	0.03	0.03	[0.03]	$N^{b,A}_{1760}$	178	170	207	–	906	348	188	100
								M^m	0.04–0.1	0.04	0.04	0.04	0.07	0.04	0.05	0.04	$N^{m,A}_{1760}$	3.E+05	2.E+05	2.E+05	–	1.E+05	2.E+05	3.E+05	4.E+05
								M^h	0.03–0.08	0.08	0.08	0.08	0.04	0.08	0.07	0.06	$N^{h,A}_{1760}$	1.E+06	1.E+06	1.E+06	–	6.E+05	1.E+06	1.E+06	2.E+06
								M^f	0.03–0.05	0.03	0.05	0.03	0.04	0.05	0.03	0.03	$N^{f,A}_{2000}$	1.E+07	1.E+07	7.E+06	–	9.E+06	6.E+06	2.E+07	4.E+06
								M^f	0.07–0.3	0.07	0.07	0.07	–	0.07	0.07	0.07	$N^{f,P}_{2000}$	4.E+06	4.E+06	4.E+06	–	4.E+06	4.E+06	5.E+06	4.E+06
								M^c	0.07–0.3	0.08	0.07	0.08	–	0.07	0.11	0.07									
								λ^A	0.4–0.6	0.40	0.43	0.41	0.43	0.40	0.40	0.46	$K_{1970-2000}$	−0.016	−0.010	−0.013	0.000	0.034	0.000	−0.017	−0.024
								λ^P	0.4–0.6	0.40	0.40	0.60	0.42	[0.40]	0.57	0.60	$K_{1970-2000}$	−0.004	−0.008	−0.004	0.005	0.001	−0.004	−0.002	−0.024
																	$R_{1973-1991}$	0.093	0.094	0.094	0.114	0.075	0.105	0.103	0.11
								LI^b_{abun}		0.000	0.000	0.001	0.000	0.000	0.001	0.000	$R_{1991-1996}$	0.090	0.090	0.090	0.118	0.089	0.093	0.091	0.12
								LI^b_{struc}		−1.917	−1.957	−1.992	−2.229	−1.787	−2.099	−1.62	$R_{1996-1991}$	0.188	0.188	0.178	–	0.119	0.160	0.180	0.17
								LI^m_{abun}		0.000	4.059	0.001	0.000	0.993	0.015	0.015	$R_{1973-1991}$	0.164	0.173	0.140	–	0.119	0.154	0.156	0.10
								LI^m_{struc}		0.001	0.001	0.002	0.008	0.018	0.001	0.002	$R_{1991-2000}$	0.104	0.125	0.119	–	0.113	0.146	0.102	0.10
								LI^h_{abun}		0.000	0.000	0.000	0.000	0.000	0.000	0.000									
								LI^h_{struc}		0.101	0.100	0.101	0.001	0.127	0.095	0.086									
								LI^f_{abun}		0.000	0.007	0.000	0.000	0.000	0.002	0.000									
								LI^f_{abun}		1.028	0.993	1.644	–	14.818	4.290	1.282									
								LI^f_{struc}		0.610	1.631	0.664	–	3.318	4.272	0.509									
								LI^c_{abun}		2.381	2.475	0.499	–	1.379	0.415	4.529									
								$-\ln L$		2.205	7.310	0.920	−2.221	18.866	6.997	4.799									

* Denotes that for sensitivity scenario (vi), the lower bounds for these abundances of crabeater seals were each set to 2 million.

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Table 13.7 95% confidence intervals for the estimated parameters for the "reference case" based on likelihood profiles. All values have been rounded to three significant figures.

	Lower 95% CI	Estimate	Higher 95%CI
$N_{1780}^{b,A}$	167000	193000	207000
$N_{1780}^{b,P}$	15700	27500	33000
$N_{1780}^{m,A}$	17700	52900	193000
$N_{1780}^{m,P}$	108000	169000	299000
$N_{1780}^{h,A}$	58300	65400	66900
$N_{1780}^{h,P}$	41300	56400	59700
$N_{1780}^{f,A}$	98200	12600	175000
$N_{1780}^{f,P}$	18800	64500	104000
$N_{1780}^{s,A}$	2890000	2920000	3040000
$N_{1780}^{c,A}$	111000	278000	3630000
$N_{1780}^{c,P}$	113000	189000	2950000
λ^b	447	451	451
λ^m	28.4	32.1	32.1
λ^h	106	108	108
λ^s	1.88	2.71	2.71
λ^c	5.34	5.51	5.51
μ^b	0.125	0.160	0.160
μ^m	0.140	0.200	0.199
μ^s	0.276	0.280	0.280
μ^c	0.176	0.236	0.280
M^b	0.030	0.030	0.041
M^m	0.040	0.041	0.097
M^h	0.033	0.080	0.080
M^f	0.030	0.032	0.048
M^s	0.070	0.070	0.078
M^c	0.070	0.077	0.171
r^A	0.400	0.400	0.418
r^P	0.401	0.404	0.593

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Table 13.8 Comparison of pre-exploitation consumption of krill suggested by Laws (1977) and the estimates provided by the "reference case" model. Note that for the latter calculations are shown both for feeding rates corresponding to the krill biomass as estimated for 1920 in the model, and for maximal feeding rates (corresponding to Laws' assumptions).

	Laws (1977) estimate					This study (for 1920)							
	Numbers (thousands)	Mean weight (t)	Days feeding in the Antarctic	%weight/day	Consumption of krill/year (10^3t)	Numbers (thousands)	Mean weight (t)	Days feeding in the Antarctic	%weight/day			Consumption of krill /year (10^3t)	
									Maximum	For 1920 krill abundance		Maximum	For 1920 krill abundance
										Region A	Region P		
Blue whale	200	88	120	3.4	71702	221	103	125	3.5	1.23	2.66	99791	35435
Fin whale	400	50	120	3.4	81480	203	46	120	4	1.38	2.51	46589	7146
Humpback whale	100	27	120	3.4	11000	75	27	100	4	3.75	3.93	8316	7548
Minke whale	200	7	365	3.9	19827	238	6	90	5.1	2.14	3.97	10080	3225
Crabeater seals	-	-	-	-	-	584	0.2	335	7	3.26	5.15	12757	1391
Antarctic fur seals	-	-	-	-	-	0.11	0.2	323	7	2.88	-	0.45	0
TOTAL (whales)					184009							164775	53353
TOTAL (whales +seals)					-							177533	54745

- 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 annotation to Table 13.4.

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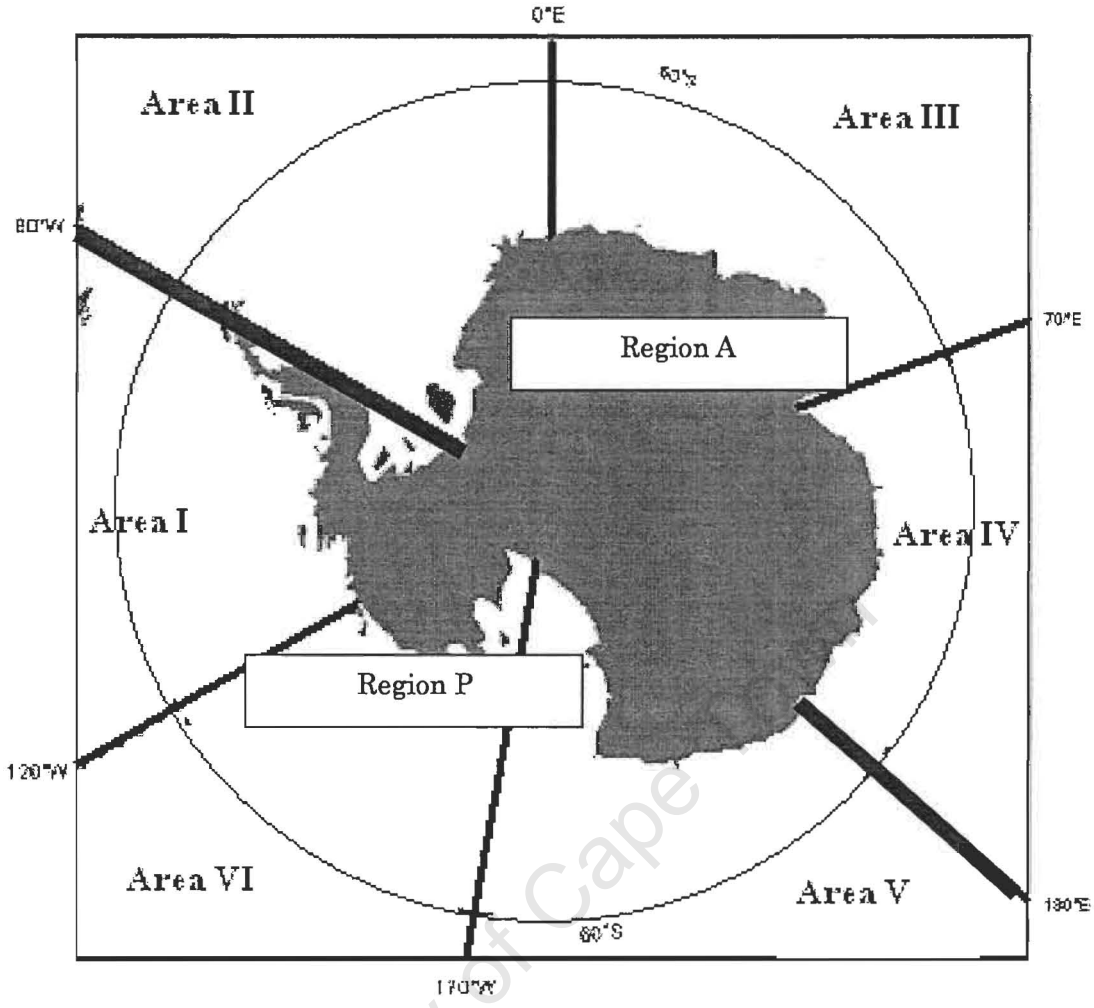


Figure 13.1 Map of IWC Management Areas (I to VI), and the two regions (Region A and Region P) considered in the model described in this Chapter.

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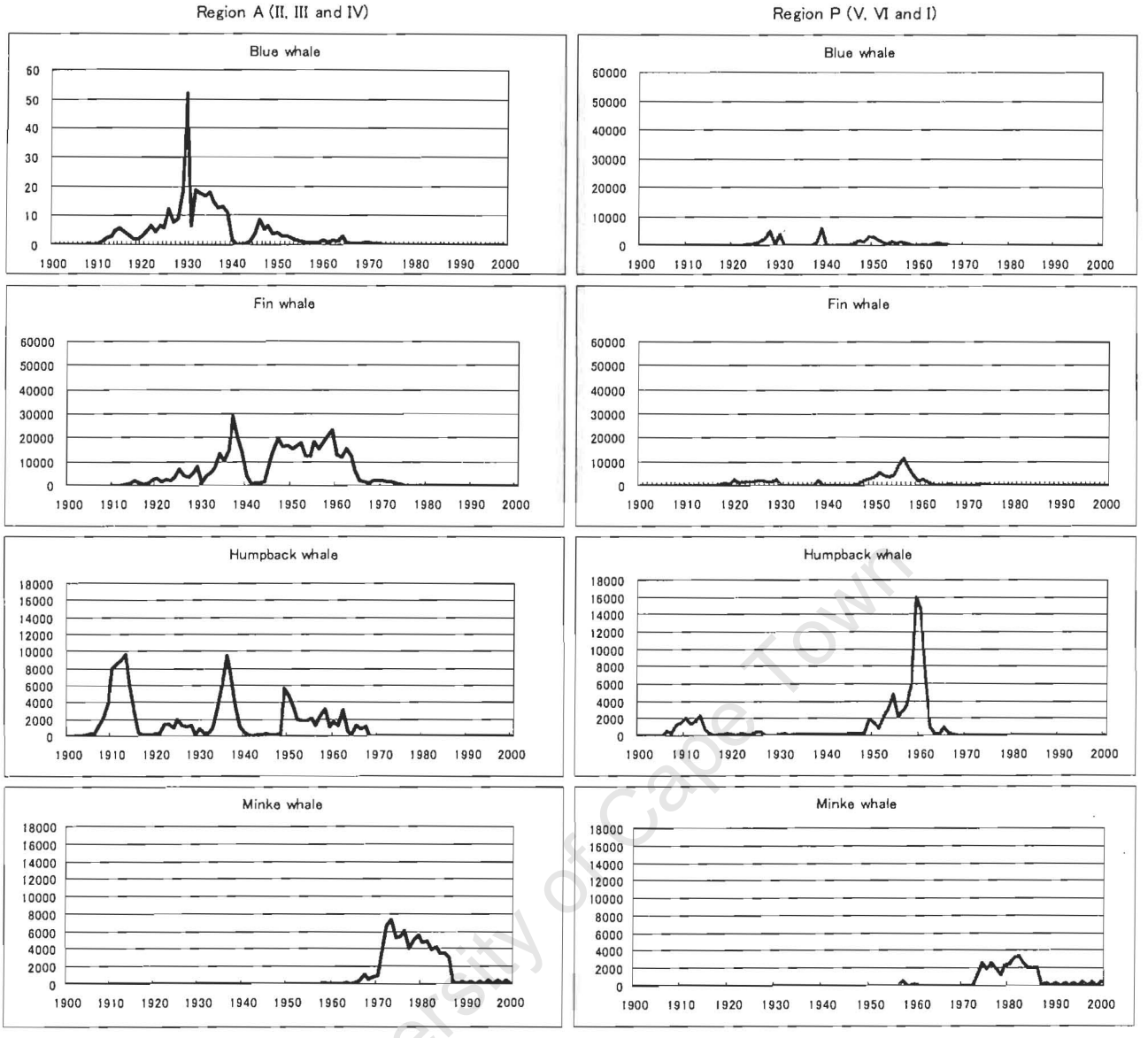
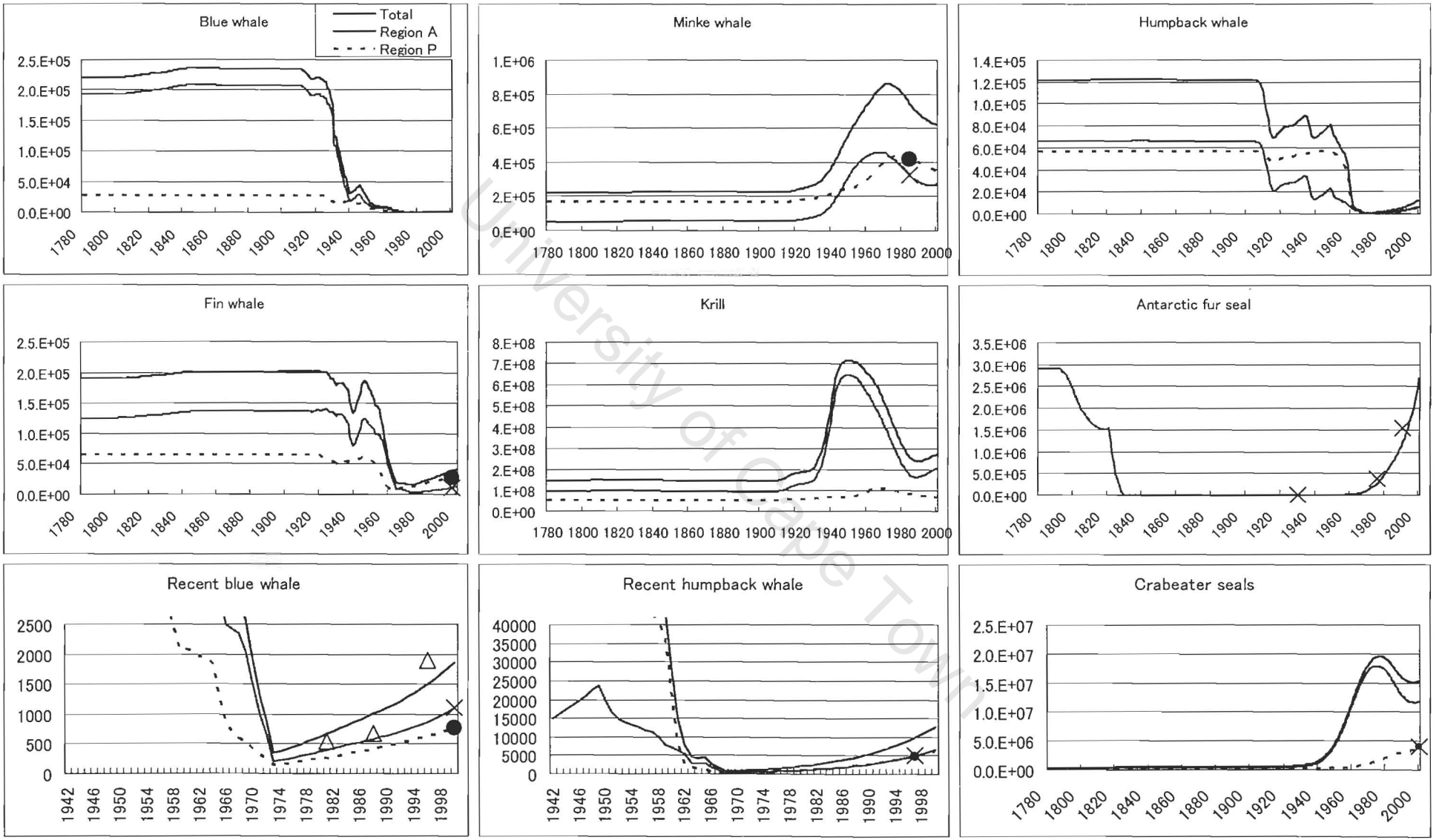


Figure 13.2 Historical catches of blue, minke, humpback and fin whales for Region A (IWC Management Areas II, III and IV) and Region P (IWC Management Areas V, VI and I). Note that the vertical scales differ between blue and fin whales in the upper plots, and humpback and minke whales in the lower.

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Figure 13.3 "Reference case" trajectories for krill and their main predators in the Antarctic. A black dot/cross shows a survey-based abundance estimate for the Pacific/Atlantic Region to which the model was fit. The open triangles shown in the recent blue whale trajectory plot are the blue whale abundance estimates from surveys for Regions A and P combined, to which the model was fit to reflect the abundance trend indicated by these estimates.

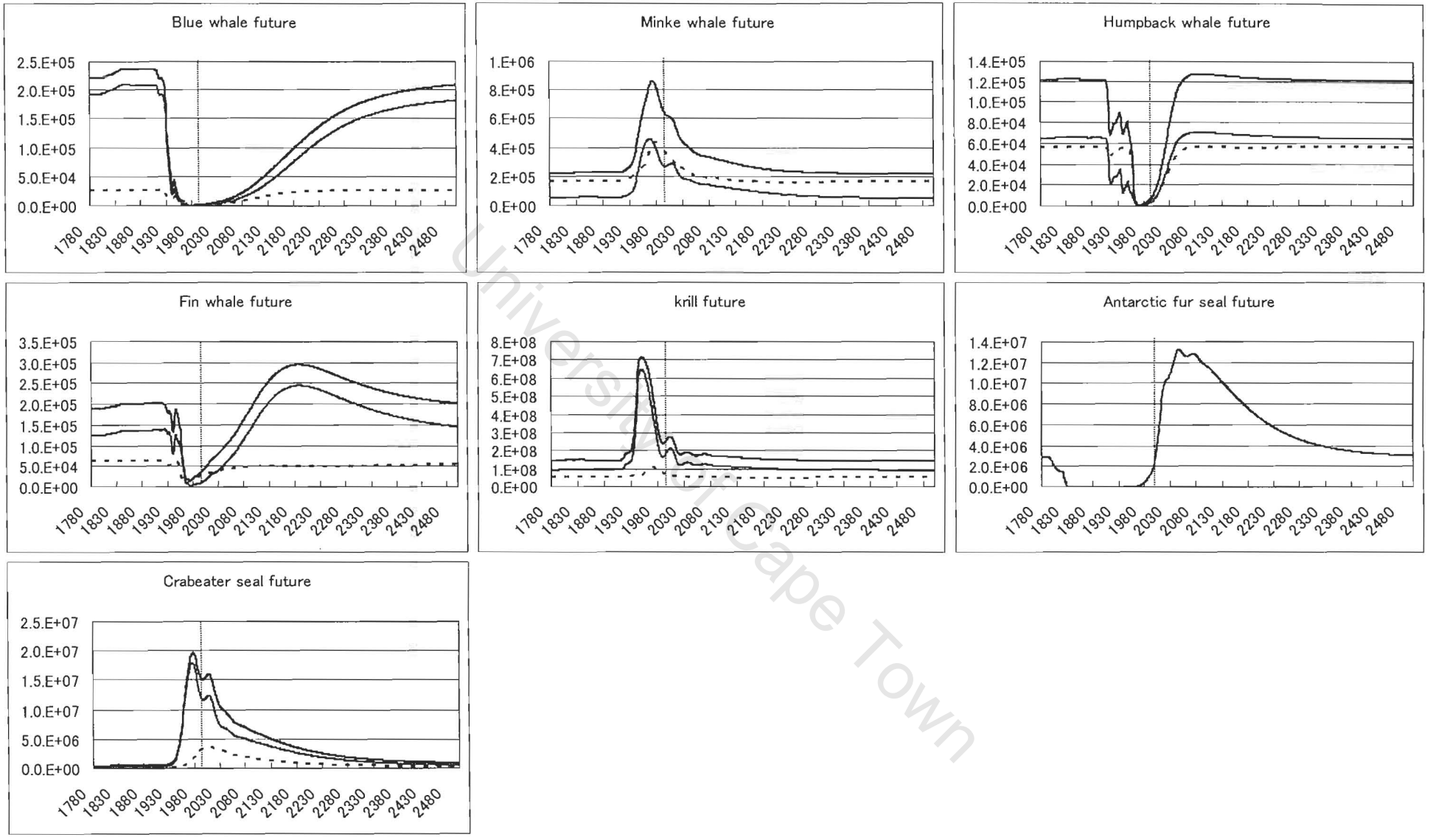


Figure 13.4 "Reference case" projections for future trajectories (up to 2500) for krill and their main predators in the Antarctic under the assumption of zero catches for all species after 2000.

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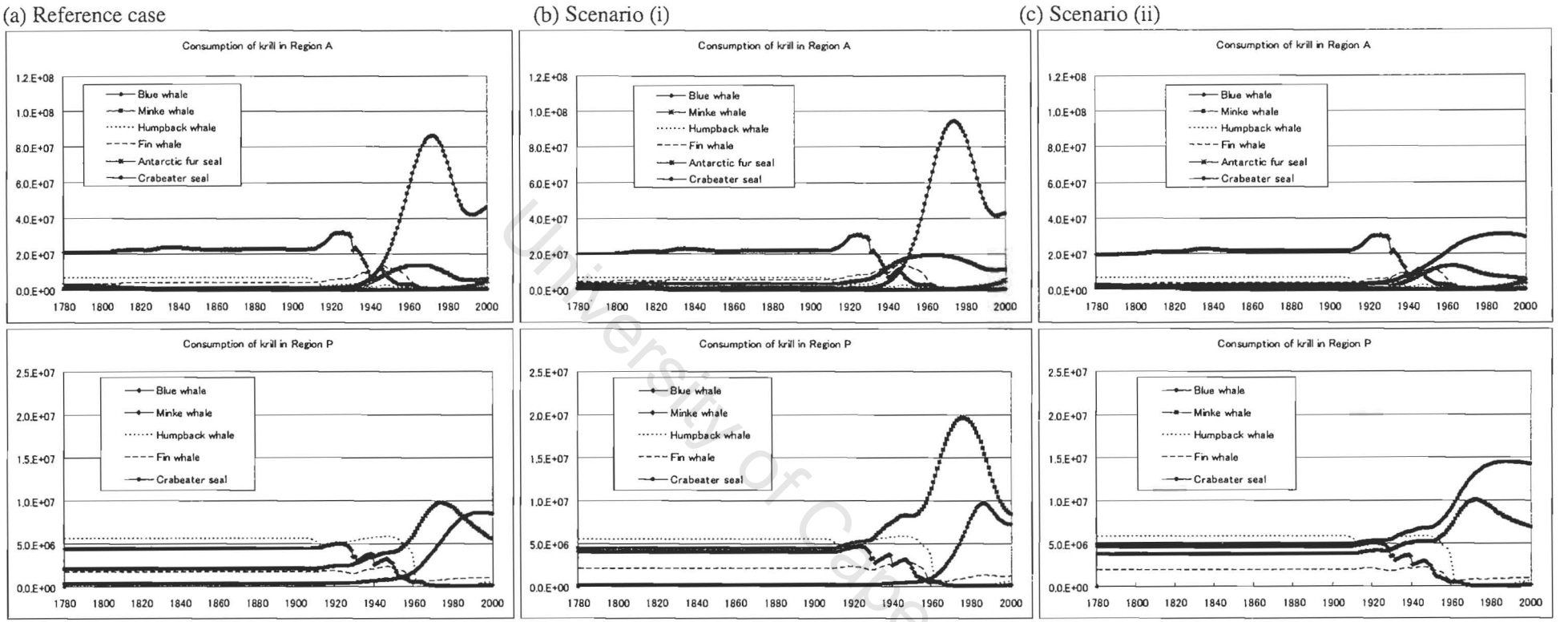


Figure 13.5 Annual consumption of krill biomass (tons) by predators considered in the model for Region A and Region P for (a) "reference case", (b) scenario (i) and (c) scenario (ii).

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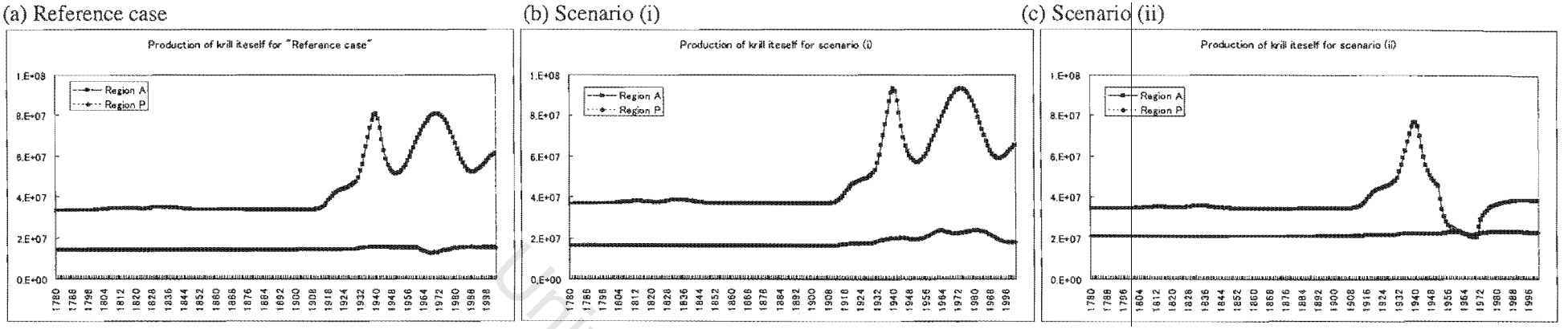


Figure 13.6 Estimated annual production of krill (tons) for Region A and Region P for (a) the "reference case", (b) scenario (i) and (c) scenario (ii).

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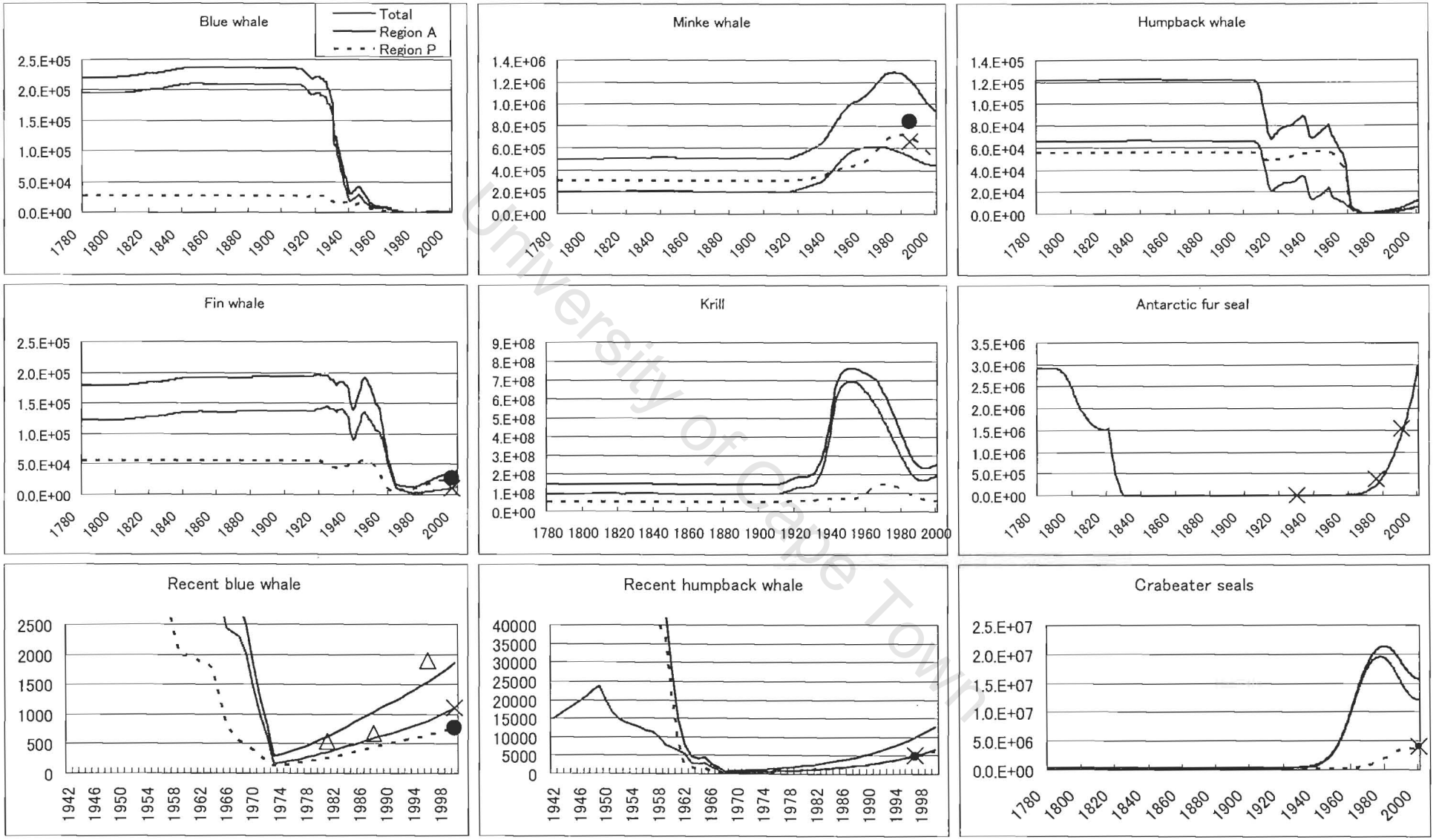
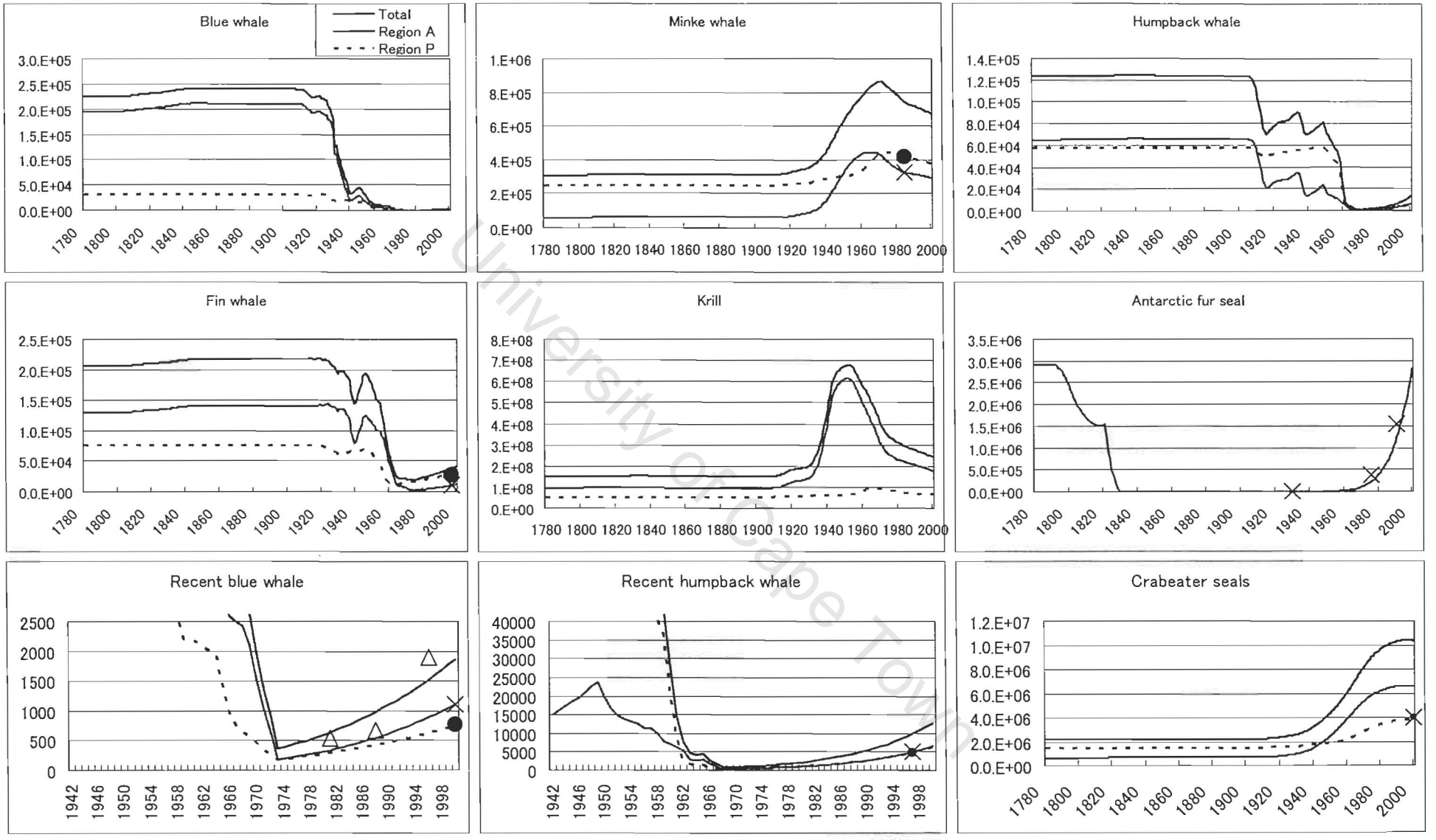


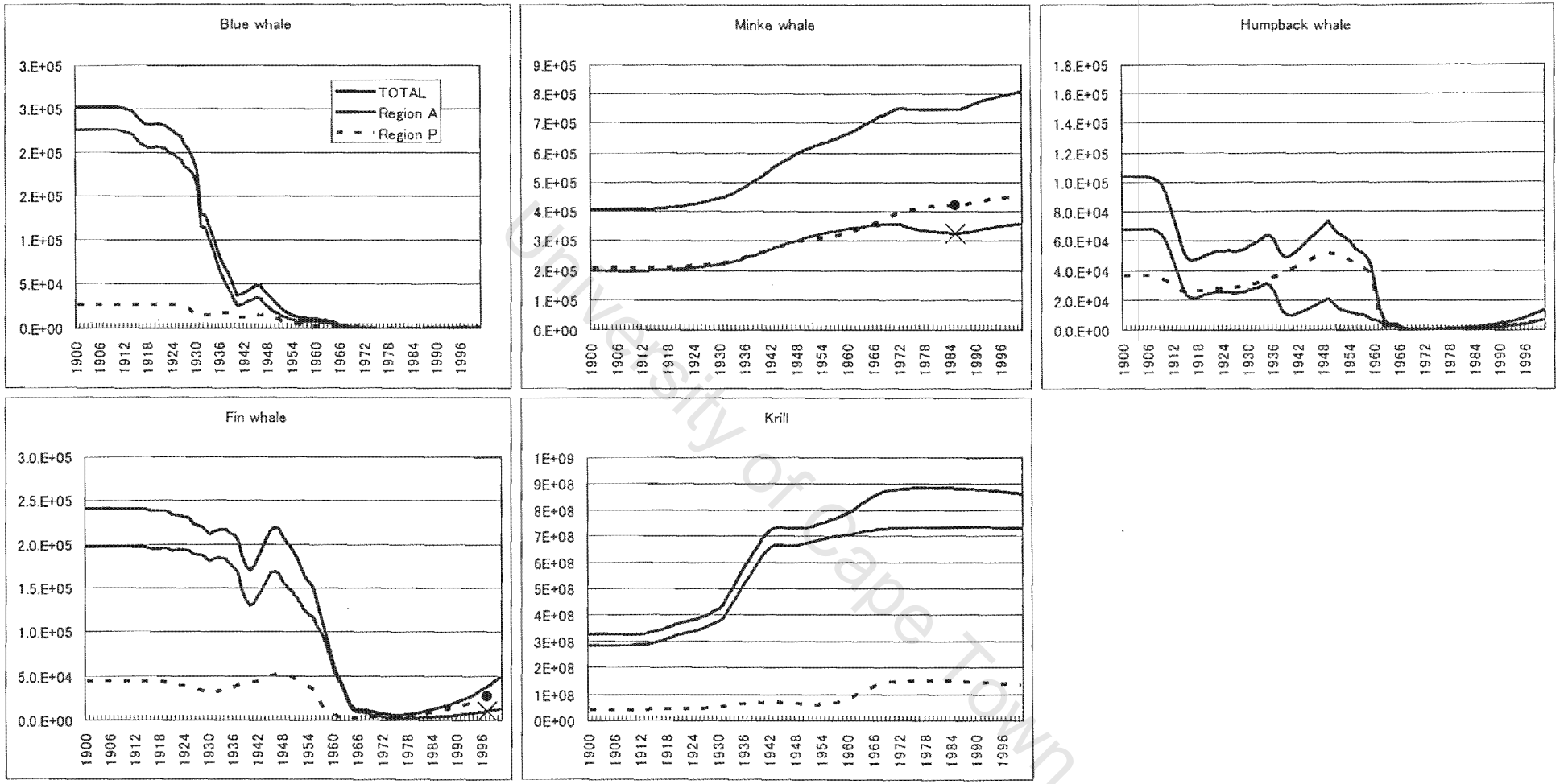
Figure 13.7 Trajectories for krill and their main predators in the Antarctic when **minke whale abundance as estimated from surveys is doubled** (scenario (i)). The meanings of the symbols are the same as in Figure 13.3.

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Figure 13.8 Trajectories for krill and their main predators in the Antarctic when **krill carrying capacity** in the Atlantic/Indian region K_A **is reduced linearly by 50% between 1950 to 1970** (scenario (ii)). The meanings of the symbols are the same as in Figure 13.3.



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Figure 13.9 Trajectories for krill and their main predators in the Antarctic when **only baleen whales are considered** in the model (a Type III functional response remains assumed) (scenario (iii)). The meanings of the symbols are the same as in Figure 13.3.

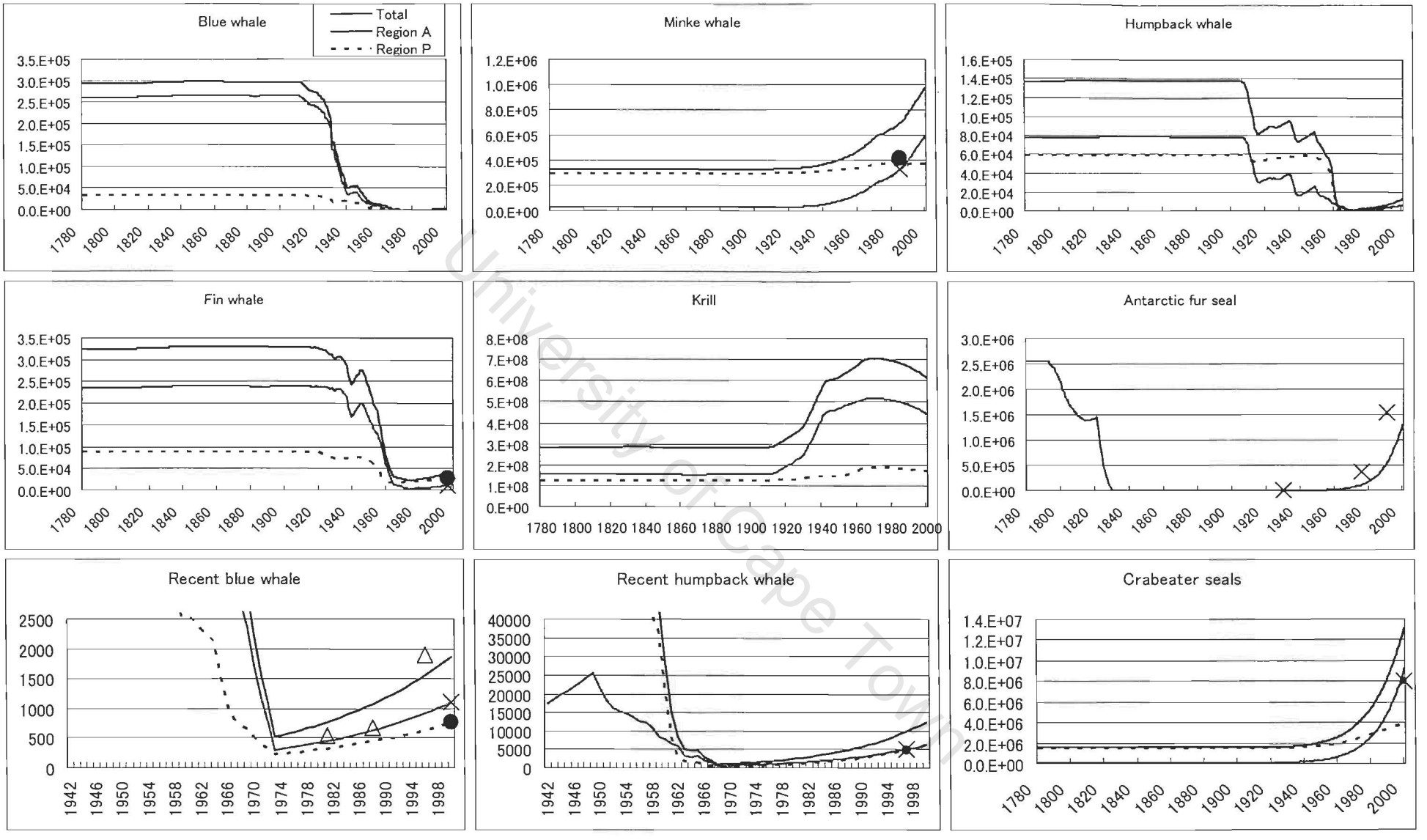
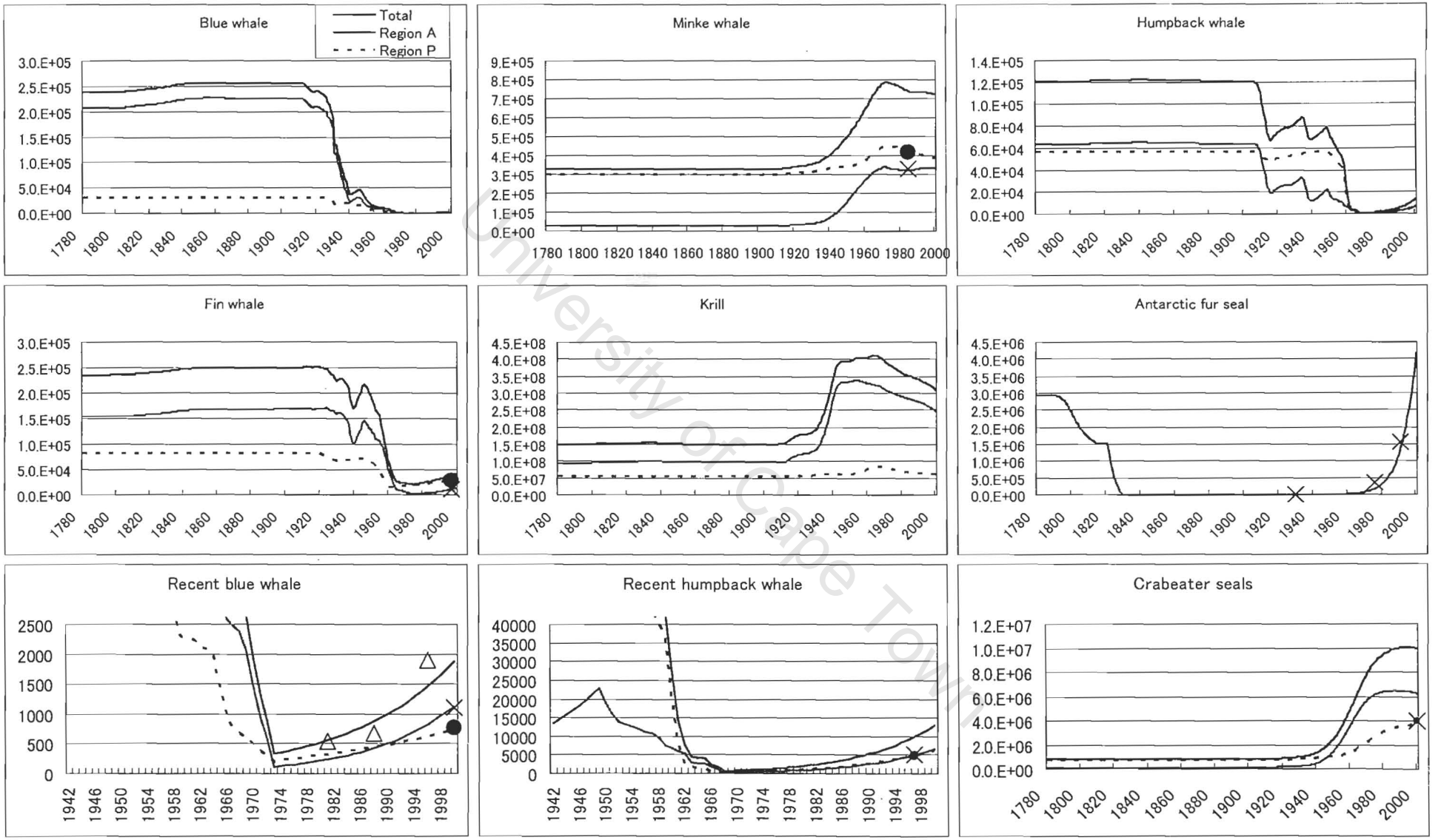


Figure 13.10 Trajectories for krill and their main predators in the Antarctic when a **Type II functional response form** is assumed (scenario (iv)). The meanings of the symbols are the same as in Figure 13.3.

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Figure 13.11 Trajectories for krill and their main predators in the Antarctic when the **density dependent mortality of crabeater seals** ($\eta^{C,A}$) **is high** compared to the "reference case" (scenario (v)). The meanings of the symbols are the same as in Figure 13.3.

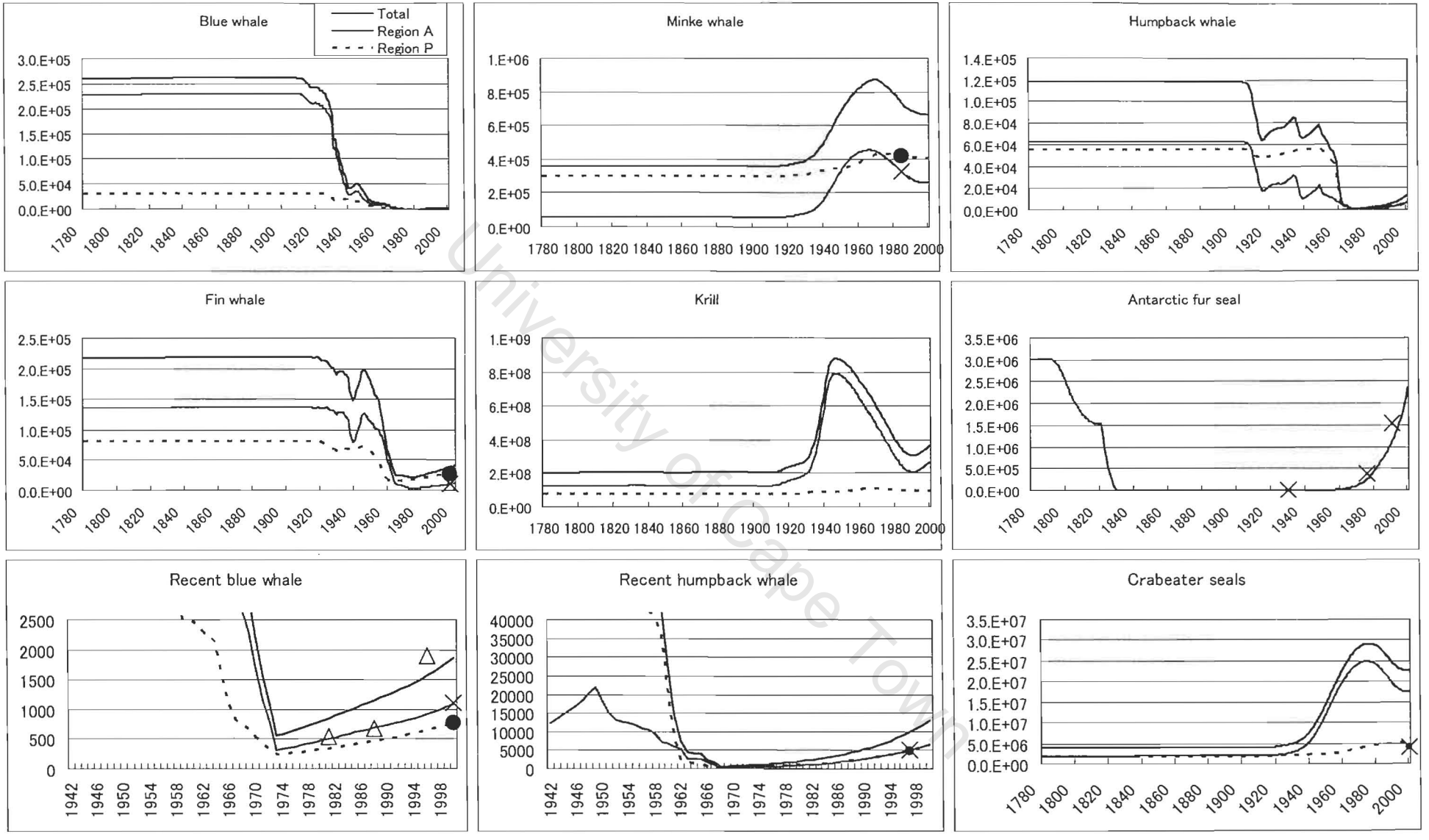
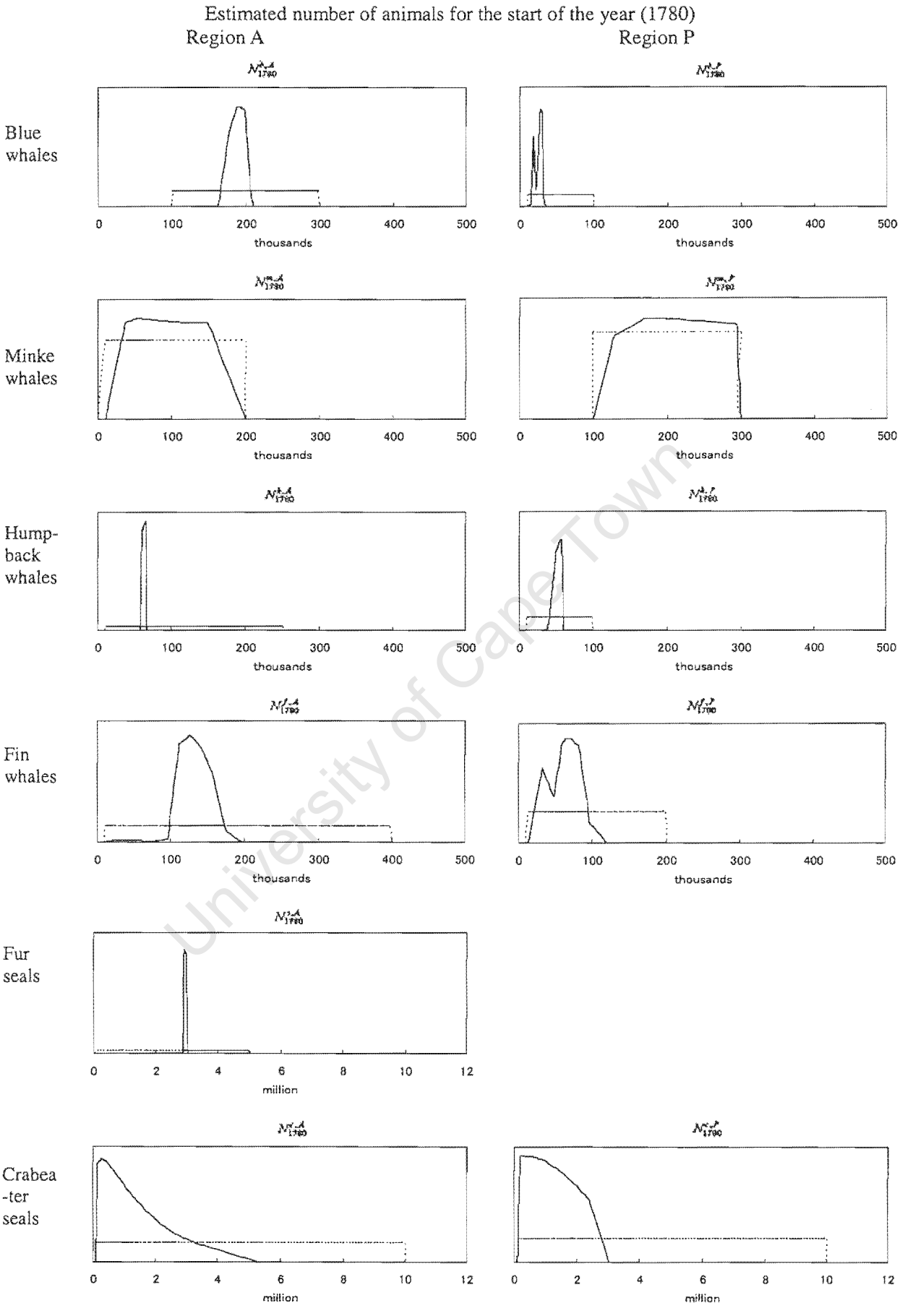


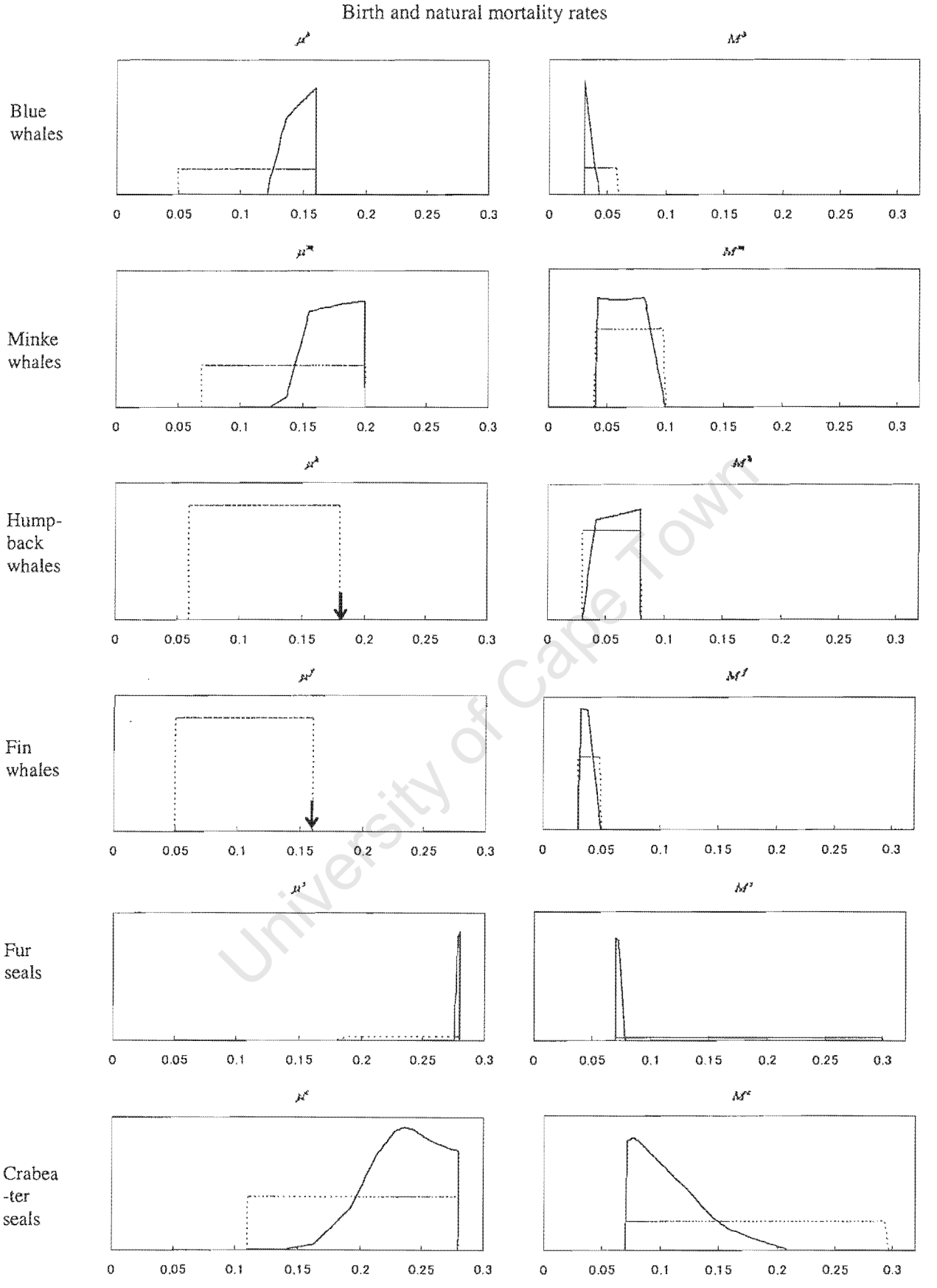
Figure 13.12 Trajectories for krill and their main predators in the Antarctic when the **lower bounds for the initial abundance of crabeater seals in each Region are set to 2 million**, rather than 10 thousand animals as in the Reference case (scenario (vi)). The meanings of the symbols are the same as in Figure 13.3.

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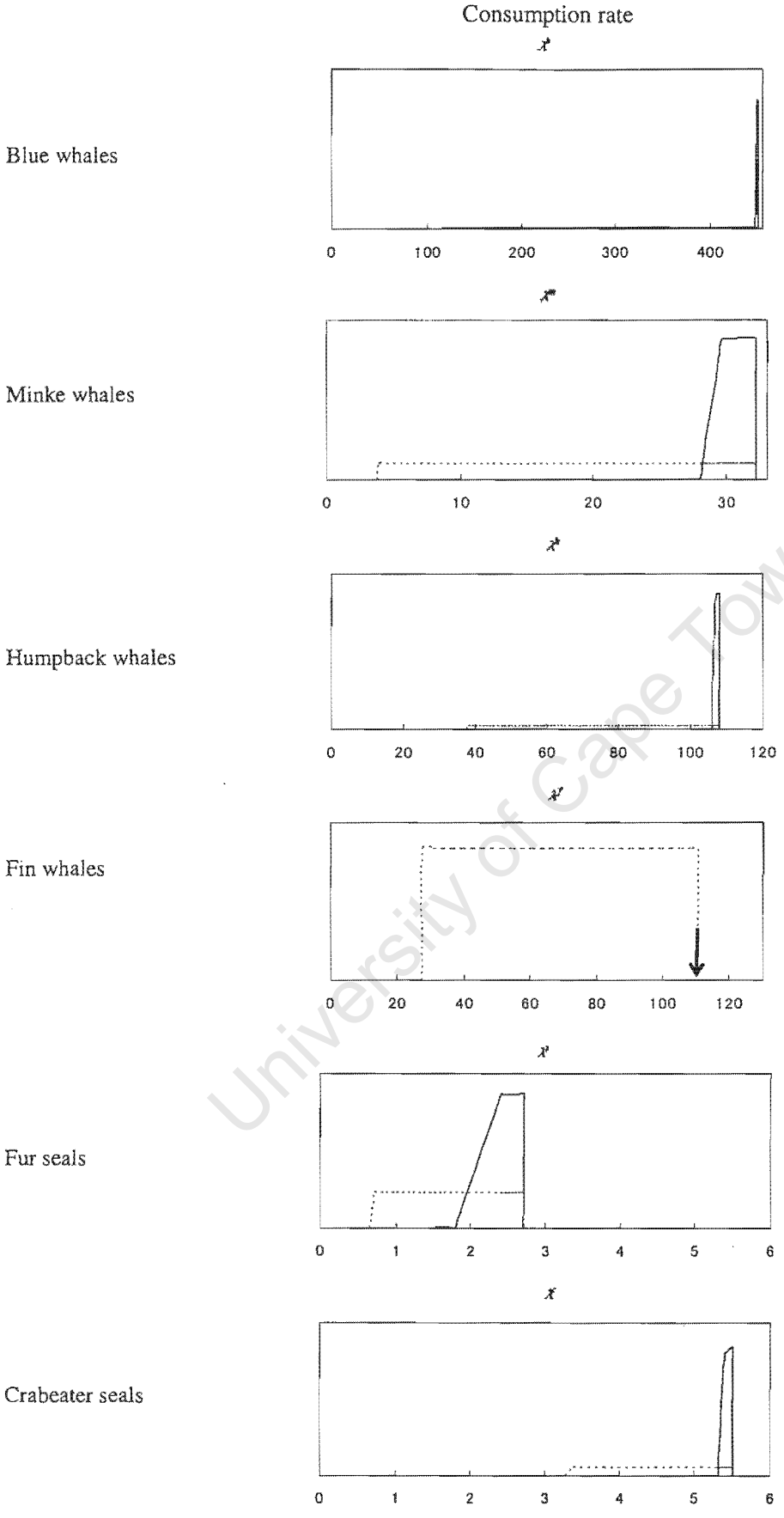
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Figure 13.13a Probability density distributions for the initial number of animals in year 1780. The solid lines are the model estimates (likelihood profiles used to approximate posteriors) and the dotted lines represent the priors.



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Figure 13.13b Probability density distributions for birth and natural mortality rates. The solid lines are the model estimates (likelihood profiles used to approximate posteriors) and the dotted lines represent the priors. For μ^h and μ^f parameters were fixed at the maximum of their ranges (see arrows), rather than estimated.



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Figure 13.13c Probability density distributions for consumption rates. The solid line is the model estimate (likelihood profiles used to approximate posteriors) and the dotted line represents the prior. λ^f which was fixed at the maximum of its range (see arrow), rather than estimated.

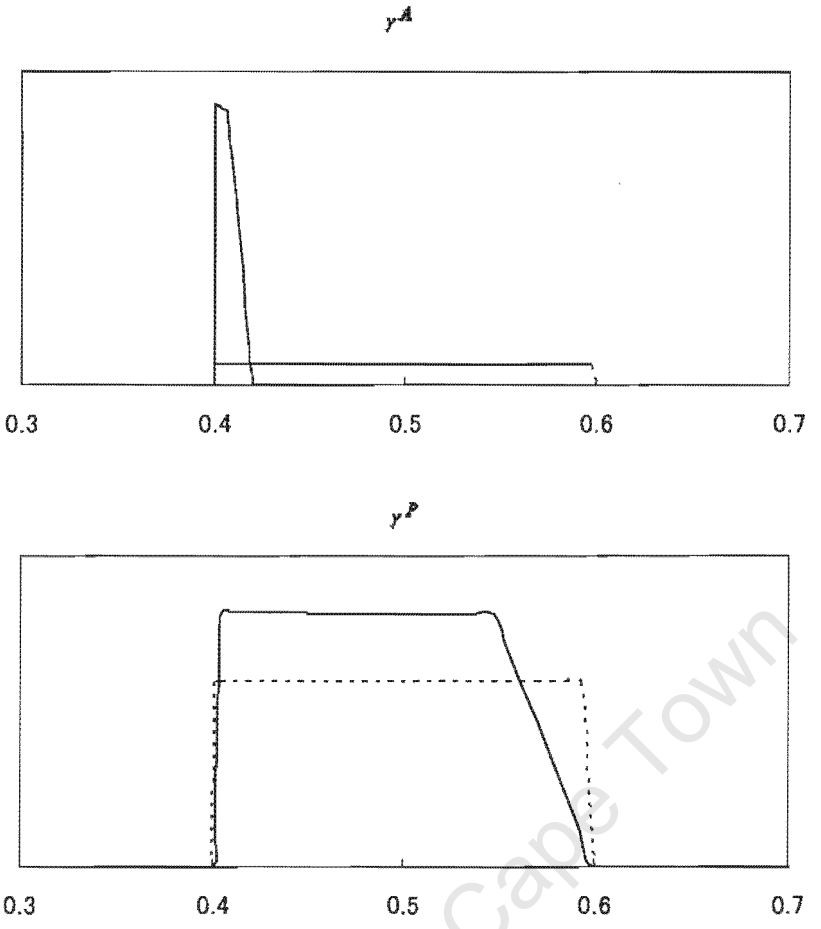
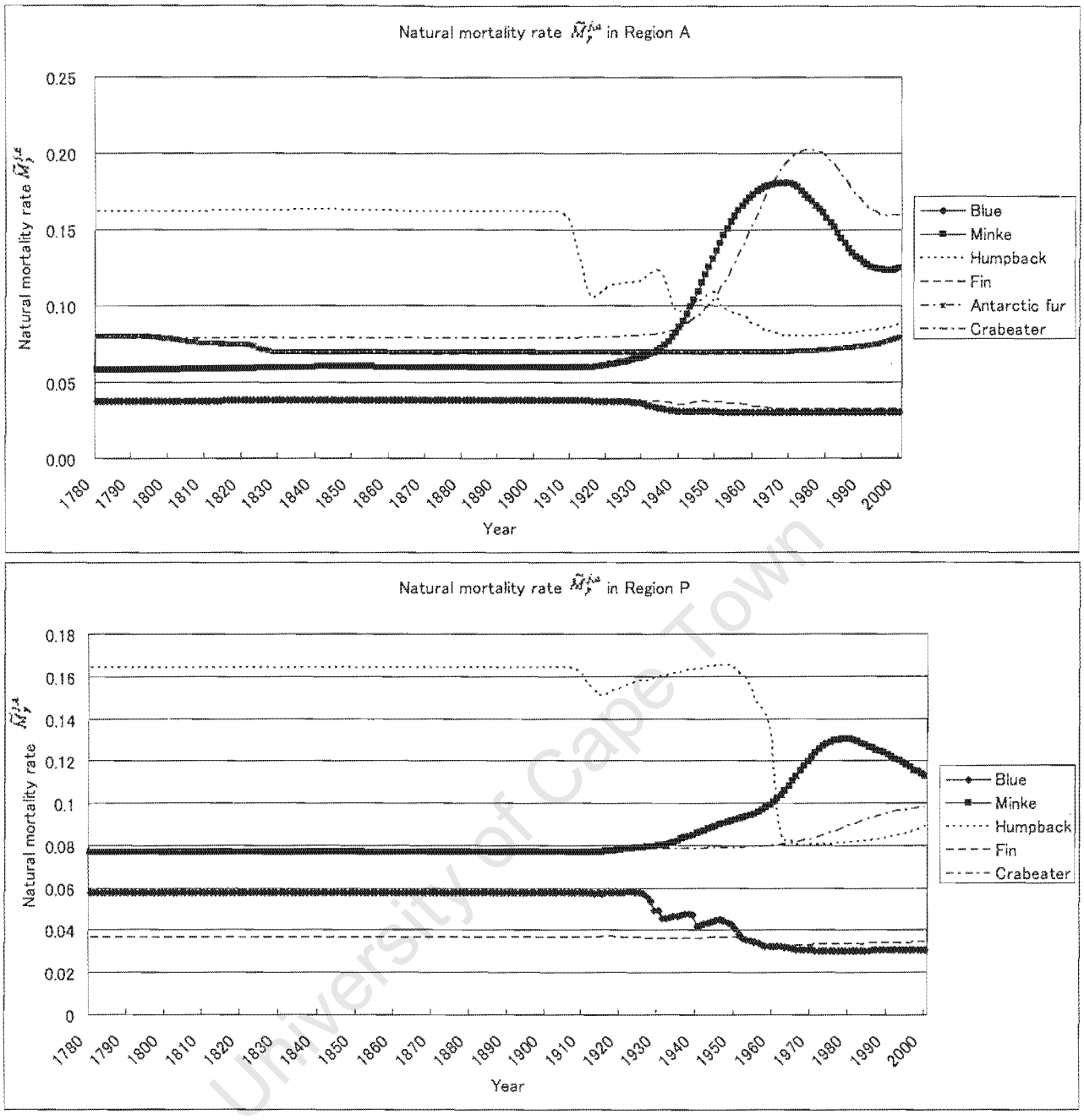


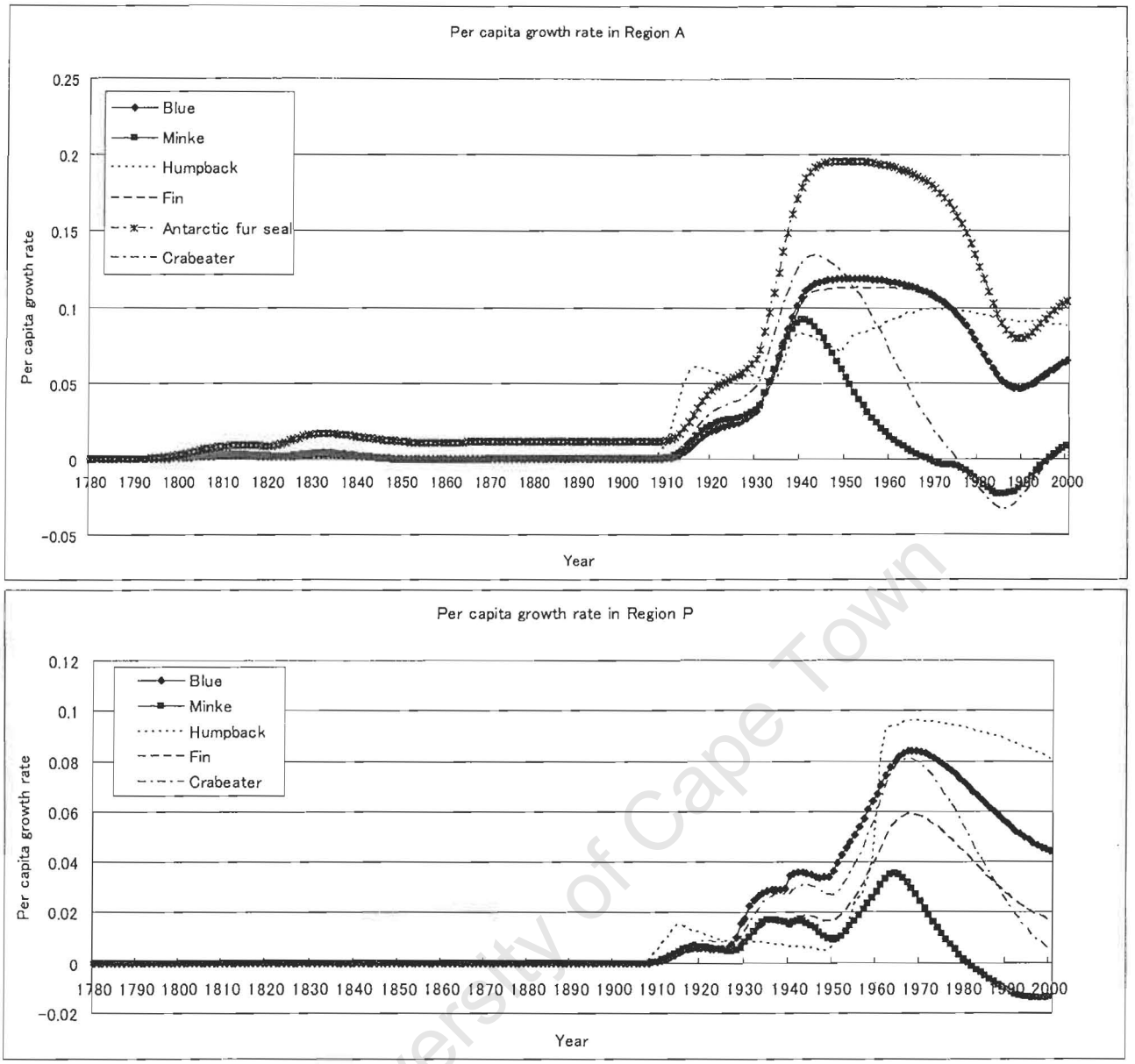
Figure 13.13d Probability density distributions for the intrinsic growth rate of krill. The solid line is the model estimate (likelihood profiles used to approximate posteriors) and the dotted line represents the prior.

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Figure 13.14 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" 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.



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Figure 13.15 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.

APPENDIX 13

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

App.13.1 Antarctic fur seal catch trend around South Georgia

The following four pieces of available information (McCann and Doidge 1987) regarding 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 in South Georgia is shown in Figure App.13.1. For simplicity, the two linear functions shown below were used:

$$C_y = 11000 \cdot (y - 1790) \qquad \text{for } 1790 \le y \le 1800 \qquad \text{(A13.1)}$$

$$C_y = 110000 - 5500 \cdot (y - 1800) \qquad \text{for } 1801 \le y \le 1820. \qquad \text{(A13.2)}$$

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

App.13.2 Antarctic fur seal catch trend around the South Shetland Islands

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

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

(vi) In 1821, 320000 skins had been taken.

(vii) By 1830 the stocks had been virtually exterminated.

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Assumed catch trend

The assumed catch trend for Antarctic fur seals in the South Shetland Islands is shown in Figure App.13.2. For simplicity, a linear trend was again assumed.

$$C_y = 320000 - 35556(y - 1821) \qquad \text{for } 1821 \le y \le 1829 \qquad \text{(A13.3)}$$

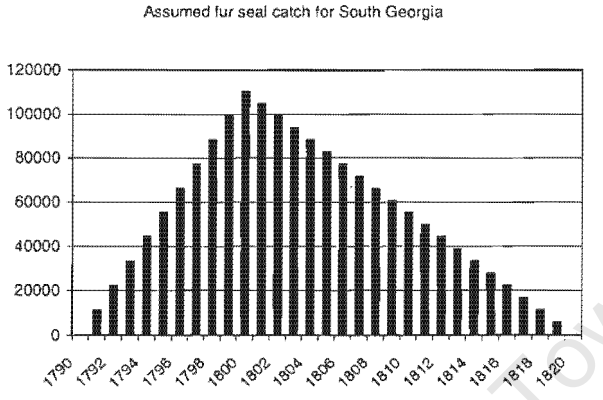


Figure App. 13.1 Assumed time series of fur seal catches around South Georgia.

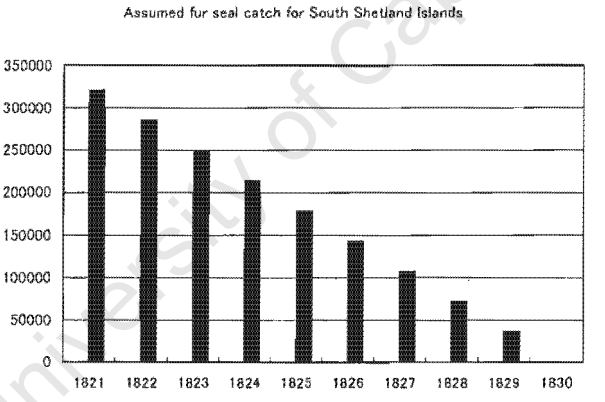


Figure App.13.2 Assumed time series of fur seal catches around the South Shetland Islands.

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CHAPTER 14

CONCLUSIONS DRAWN AND PRIORITIES FOR FUTURE WORK

14.1 Conclusions drawn

There are a number of important findings made throughout this thesis concerning the Antarctic ecosystem (especially in regard to krill and its main predators). The most important of these are summarized below.

- Among the baleen whales that feed in the Antarctic during the austral summer, blue, fin, humpback and minke whales are the main krill consumers. Among the seals, Antarctic fur seals and crabeater seals play this role. Around 1990, baleen whales could have been consuming up to 120 million tons and seals up to 70 million tons of krill each year in this region. Of the whales, minkes currently make the greatest impact on krill due to their large number at present compared to the other still depleted populations of the larger baleen whales. However, it is noteworthy that the consumption of krill by these larger baleen whales has been increasing in recent years, though likely decreasing for minke whales. Crabeater seals appear to be the seal species with the greatest current impact on krill.

- Knowledge of abundance and hence consumption of krill by birds, cephalopods and fish in the Antarctic remains very limited, and any estimates remain heavily dependent upon what are often rather sweeping assumptions. However, one cannot at present rule out the possibility that these species might be making comparable impacts on krill to those by baleen whales and seals. Hence, high priority needs to be given to improving estimates of the amount of krill consumed by these other species.

- Various biases are associated with abundance estimation of whales from sighting surveys in the Antarctic. For minke whales, the most important include the effects of failure to sight some of the whales on the trackline and animals in the unsurveyed area within the pack-ice.

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Abundance estimates corrected for these various biases would lie in the approximate ranges of 1.2-3.3 million for minke whales, 750-2300 for blue whales, 26-96 thousand for humpback whales, and 12-18 thousands for fin whales respectively for the period 1985-1990. The corresponding estimates for the period 1991-1997 are 0.33-1.1 million, 2300-3100, 25-95 thousand and 27-56 thousand respectively. Trend information suggests that the large baleen whales that were heavily depleted during the commercial whaling period are now recovering at rates in the vicinity of 10% per year, but there are some indications of a recent decrease in minke whale numbers.

- The most recent abundance estimate for the number of Antarctic fur seals, corrected for various biases, lies in the approximate range of 1-2.5 million, with that for crabeater seals in the range of about 7-12 million. (Note that the information for crabeater seals awaits an update from the results of the recent APIS programme.)

- Although Nicol *et al.* (2000a) conclude from consideration of acoustic survey results that a total krill biomass of under 155 million tons may be more realistic than one as high as 500 million tons, various uncertainties are associated with the estimate. Taking some of these into account could see the upper limit of the Nicol *et al.* estimate increased beyond even 500 million tons. Therefore, at this stage, it seems reasonable to state that the abundance estimate for krill indicated by acoustic surveys is of the order of several hundred million tons.

- Updated and refined catch-at-age analyses of minke whales in Areas IV and V suggest an increase in abundance of this species in the middle decades of the 20th Century to peak at about 1970, followed by a decline for the next three decades. This result is consistent with the previous results of Butterworth *et al.* (1999, 2001). Fitting the recruitment time trend obtained from these catch-at-age analyses to a stock-recruitment model suggests that minke whale carrying capacity first increased from about 1940 to 1960, followed by a 60% decrease over the period from the 1960s to the present. General trends in the biological parameters of this species are consistent with such a decline.

- The main objective of this thesis is to model the krill-predator dynamics of the Antarctic ecosystem so as to determine whether predator-prey interactions alone can broadly explain observed population trends of the species considered in the model without any appeal to systematic effects possibly caused by environmental change. A multi-species model developed including krill, four baleen whale and two seal species suggests that species

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interaction effects alone can account for likely trends in the abundances of these major Antarctic predator species over the past 50 or so years, though not without some difficulty. Accordingly it is not yet possible to 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, so that they 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, and hence may not originally have been as numerous as single-species models suggest.

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

- Crabeater seals appear to play a key role in the dynamics of the system (though this may in part reflect the multi-species model developed "using" them also as a surrogate for other bird, squid and fish species not explicitly included).

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14.2 Future priority work

One of the important outcomes of this thesis is that it has identified plausible ranges in abundances and consumption estimates of the main krill-feeding baleen whales and seals in the Antarctic after considering various uncertainties associated with these estimates. This information is particularly important if reliable krill-predator dynamics model in the Antarctic are to be developed. However, the development of information of similar quality for birds, cephalopods and fish is generally still in its infancy, and high priority needs to be given to improving the correct estimates of the amount of krill consumed by these other species so as to be able to judge whether they also need to be explicitly incorporated in future refinements of the multi-species model developed in this thesis. Furthermore, it would seem advisable for such further development of the model to await availability of the APIS programme results for crabeater seal abundance and the outcome of the IWC Scientific Committee's plan to provide consolidated advice on Southern Hemisphere minke whale abundance estimates and trends at its 2006 meeting.

Since the krill-predator dynamics model developed in this thesis 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, the sensitivities of the model predictions to the full range of uncertainties associated with the abundance estimates obtained from surveys has not yet been explored. However, once the information stated in the previous paragraph becomes available, more thorough sensitivity tests of the assumptions of the model and the abundance and trend information input for each species need to be explored, and also the model extended to take account of other than baleen whale and seal predators of krill in an appropriate way. With such further development, it is hoped that such a model may ultimately assist in providing scientific advice for appropriate sustainable harvesting strategies for the Antarctic marine ecosystem taking species interactions into account, as this is a matter of key importance for the IWC and for the CCAMLR.

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REFERENCES

Abe, T. and Iwami, T. 1989. Notes on fishes from the stomachs of whales in the Antarctic II: on *Dissostichus* and *Ceratias*. *Proc. NIPR Symp. Polar Biology* 2: 78-82.

Ackley, S. F., Bengtson, J. L., Boveng, P., Castellini, M., Daly, K. L., Jacobs, S., Jooyman, G. L., Laake, J., Quetin, L., Ross, R., Siniff, D. B., Stewart, B. S., Stirline, I., Torres, J. and Yochem, P. K. 2003a. A top-down multidisciplinary study of the structure and function of the pack-ice ecosystem in the eastern Ross Sea, Antarctica. *Polar Record* 39 (210): 219-230.

Ackley, S., Wadhams, P., Comiso, J. C. and Worby, A. P. 2003b. Decadal decrease of Antarctic sea ice extent inferred from whaling records revisited on the basis of historical and modern sea ice records. *Polar Research* 22 (1): 19-25.

Ainley, D. G. 1985. Biomass of birds and mammals in the Ross Sea. In: *Antarctic Nutrient Cycles and Food Webs*. Siegfried, W. R., Condy, P. R. and Laws, R. M. (Eds). SpringerVerlag, Berlin and Heidelberg: pp. 498-515.

Ainley, D. G., Clarke, E. D., Arrigo, K., Fraser, W. R., Kato, A., Barton, K. J. and Wilson, P. R. 2005. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. *Antarctic Science* 17 (2): 171-182.

Andriolo, A., Martins, C. C. A., Engel, M. H., Pizzorno, J. L., Más-Rosa, S., Freitas, A. C., Morete, M. E., Petta, C. B. and Kinas,P. G. 2002. Aerial surveys of humpback whale (*Megaptera novaeangliae*) to estimate abundance in the breeding ground, Brazil: preliminary results. *International Whaling Commission Document* SC/54/H5.

Andriolo, A., Martins, C. C. A, Engel, M. H, Pizzorno, J. L., Más-Rosa, S., Morete, M. E. and Kinas, P. G. 2003. Second year of aerial survey of humpback whale (*Megaptera novaeangliae*) in the Brazilian breeding ground, 2002. *International Whaling Commission Document* SC/55/SH1: 11 pp.

Anon. 1986. Post-FIBEX acoustic workshop. Frankfurt, Federal Republic of Germany, September 1984. *BIOMASS Rept. Ser.* 40: 106 pp.

Armstrong, R. S. and McGehee, R. A. 1980. Competitive exclusion. *Am. Nat.* 115: 151-170.

Atkinson, A., Siegel, V., Pakhomov, E. and Rothery, P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432: 100-103.

Bando, T., Zenitani, R., Fujise, Y. and Kato, H. 2005. Biological parameters of Antarctic minke whale based on materials collected by the JARPA survey in 1987/88 to 2003/04. Paper JA/J05/JR5 presented to the JARPA Review Meeting called by the Government of Japan, January 2005: 14 pp.

Bannister, J. L. 1994. Continued increase in humpback whales off Western Australia. *Rep. int. Whal. Commn* 44: 309-310.

Bannister, J. L. and Hedley, S. L. 2001. Southern Hemisphere Group IV humpback whales: their status from recent aerial survey. *Mem. Qld. Mus.* 47(2): 587-598.

University of Cape Town

Begon, M., Harper, J. L. and Townsend, C. R. 1999. *Ecology: Individuals, populations and communities*. (Third Edition) Blackwell, Oxford. 1068 pp.

Bengtson, J. L., Ferm, L. M., Härkönen, T. J. and Stewart, B. S. 1990. Abundance of Antarctic fur seal in the South Shetland islands, Antarctic, during the 1986/87 austral summer. In: *Antarctic ecosystems*. Kerry, K and Hempel, G. (Eds). Springer, Berlin Heidelberg New York: pp. 265-270.

Bengtson, J. L. and Laws, R. M. 1985. Trends in crabeater seal age at maturity: an insight into Antartic marine interactions. In: *Antarctic Nutrient Cycles and Food Webs*. Siegfried, W. R., Condy, P. R. and Laws, R. M. (Eds). SpringerVerlag, Berlin and Heidelberg: pp. 669-675.

Bengtson, J. L. and Siniff, D. B. 1981. Reproductive aspects of female crabeater seals (*Lobodon carcinophagus*) along the Antarctic Peninsula. *Canadian Journal of Zoology* 59: 92-102.

Berzin, A. A., and Vladimirov, V. L. 1983. A new species of killer whale (Cetacea, Delphinidae) from the Antarctic waters. *Zoologicheskii Zhurnal* 62: 287-295.

Best, P. B. 1981. The status of right whales (*Eubalaena glacialis*) off South Africa, 1969-1979. *Investl Rep. Sea Fish. Inst. S. Afr.* 123: 1-44.

Best, P. B. 1982. Seasonal abundance, feeding, reproduction, age and growth in minke whales off Durban (with incidental observations from the Antarctic). *Rep. int. Whal. Commn* 32: 759-786.

Best, P. B. 1984. Accuracy of shipboard estimates of the length of Antarctic minke whales. *Rep. int. Whal. Commn* 34: 323-325.

Best, P. B. 2001. Distribution and population separation of Bryde's whale *Balaenoptera edeni* off southern Africa. *Mar. Ecol. Prog. Ser.* 220: 277-289.

Best, P. B. 2005. Southern fin whales: The need for assessment and the role of a future SOWER-type cruise programme. *International Whaling Commission Document* SC/57/IA13: 7 pp.

Best, P. B., Findlay, K. P., Sekiguchi, K., Peddemors, V. M., Rakotonirina, B., Rossouw, A and Gove, D. 1998. Winter distribution and possible migration routes of humpback whales *Megaptera novaeangliae* in the southwest Indian Ocean. *Mar. Ecol. Prog. Ser.* 162: 287-299.

Best, P. B., Rademeyer, R. A., Burton, C., Ljungblad, D., Sekiguchi, K., Shimada, H., Thiele, D., Reeb, D. and Butterworth, D. S. 2003. The abundance of blue whales on the Madagascar Plateau, December 1996. *J. Cetacean. Res. Manage.* 5 (3): 253-260.

Best, P. B., Sekiguchi, K., Rakotonirina, B., and Rossouw, A. 1996. The distribution and abundance of humpback whales off Southern Madagascar, August-September 1994. *Rep. int. Whal. Commn* 46: 323-331.

Bester, M. N. 1987. Subantarctic fur seal, *Arctocephalus tropicalis*, at Gough Island (Tristan Da Cunna Groups). In: *Status, biology, and ecology of fur seals. Proceedings of an International Symposium and Wokshop, Cambridge, England, 23-27 April 1984*. Croxall, J.P and R.L. Gentry (Eds). NOAA Technical Report NMFS 51: pp. 57-60.

University of Cape Town

Bonner, W. N. 1958. Notes on the southern fur seal in South Georgia. *Proc. Zool. Soc. Lond.* 130: 241-252.

Bonner, W. N. 1968. The fur seal of South Georgia. *Br. Antarctic Surv. Sci. Rep.* 56: 1-88.

Bonner, W. N. 1981. Southern fur seals. *Arctocephalus* (Geoffroy Saint-Hilaire and Cuvier, 1826). In: *Handbook of marine mammals*. Ridgway, S. H. and Harrison, R. J. (Eds). Vol. 1. Academic Press, London and New York: pp. 161-208.

Borchers, D. L. 1991. Revised Southern Hemisphere whale abundance estimates south of 30° derived from IWC/IDCR survey and Japanese scouting vessel data (addendum to SC/42/SHMi18). *International Whaling Commission Document* SC/43/Mi34: 11 pp.

Boyd, I. L. 1993. Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarctic Science* 5: 17-24.

Boyd, I. L., Croxall, J. P., Lunn, N. J. and Reid, K. 1995. Population demography of Antarctic fur seals - the costs of reproduction and implications for life-histories. *Journal of Animal Ecology* 64 (4): 505-518.

Boyd, I. L. and Murray, A. W. A. 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. *J. Anim. Ecol.* 70: 747-760.

Bradshaw, C. J., Hindell, M. A., Best, N. J., Phillips, K. L., Wilson, G. and Nichols, P. D. 2003. You are what you eat: describing the foraging ecology of southern elephant seals (*Mirounga leonina*) using blubber fatty acids. *Proc. R. Soc. Lond.* B. 270: 1283-1292.

Branch, T. A. 2003. Updated circumpolar abundance estimates for Southern Hemisphere minke whales including results from the 1998/99 to 2000/01 IDCR-SOWER surveys. Report of the Scientific Committee, Annex G, Appendix 3. *J. Cetacean Res. Manage.* (Suppl) 5: 271-275.

Branch, T. A. 2005. Preliminary abundance estimates for Antarctic minke whales from three completed sets of IDCR/SOWER circumpolar surveys, 1978/79 to 2003/04. *International Whaling Commission Document* SC/57/IA16: 26 pp.

Branch, T. A. and Butterworth, D. S. 2001a. Southern Hemisphere minke whales: standardised abundance estimates from the 1978/79 to 1997/98 IDCR-SOWER surveys. *J. Cetacean Res. Manage.* 3 (2): 143-174.

Branch, T. A. and Butterworth, D. S. 2001b. Estimates of abundance south of 60°S for cetacean species sighted frequently on the 1978/79 to 1997/98 IWC/IDCR-SOWER sightings surveys. *J. Cetacean Res. Manage.* 3 (3): 251-270.

Branch, T. A., Matsuoka, K. and Miyashita, T. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modeling. *Mar. Mamm. Sci.* 20: 726-743.

Branch, T. A. and Rademeyer, R. A. 2003. Blue whale estimates from the IDCR-SOWER surveys: Updated comparisons including results from the 1998/99 to 2000/01 surveys. *J. Cetacean Res. Manage.* (Suppl) 5: 291-292.

University of Cape Town

Brandão, A., Butterworth, D. S and Brown, M. R. 2000. Maximum possible humpback whale increase rates as a function of biological parameter values. *J. Cetacean Res. Manage.* (Suppl) 2: 192-193.

Brandão, A., Butterworth, D. S., Watkins, B. P. and Miller, D. G. M. 2002. A first attempt at an assessment of the Patagonian toothfish (Dissostichus eleginoides) resource in the Prince Edward Isalnds EEZ. *CCAMLR Science* 9: 11-32.

Brandão, A., Rademeyer, R. A. and Butterworth, D. S. 2001. Estimation of mean school size for minke whales from IWC/IDCR-SOWER surveys. *International Whaling Commission Document* SC/53/IA26: 21 pp.

Brierley, A. S., Goss, C., Grant, S. A., Watkins, J. L., Reid, K., Belchier, M., Everson, I., Jessop, M. J., Afanasyev, V. and Robst, J. 2002. Significant intra-annual variability in krill distribution and abundance at South Georgia revealed by multiple acoustic surveys during 2000/01. *CCAMLR Science* 9: 71-82.

Brierley, A. S., Watkins, J. L., Goss, M., Wilkinson, M. T. and Everson, I. 1999. Acoustic estimates of krill density at South Georgia, 1981 to 1998. *CCAMLR Science* 6: 47-57.

Brown, S. G. 1962. The movements of fin and blue whales within the Antarctic zone. *Discovery Reports* 33: 1-54.

Brown, M. R., Field, M. S., Clarke, E. D., Butterworth, D. S. and Bryden, M. M. 1997. Estimates of abundance and rate of increase for East Australian humpback whales from the 1996 land-based survey at Point Lookout, North Stradbroke Island, Queensland. *International Whaling Commission Document* SC/49/SH35: 15 pp.

Brown, S. G. and Lockyer, C. H. 1984. Whales. In: *Antarctic Ecology*, vol. 2. Laws, R. M. (Ed). Academic Press, London: 718-781 pp.

Bushuev, S. G. 1986. Feeding of minke whales, *Balaenoptera acutorostrata*, in the Antarctic. *Rep. int. Whal. Commn* 36: 241-245.

Butterworth, D. S. 1991. Report of the sub-committee on Southern Hemisphere minke whales, Appendix 4. The use of g(0) = 1 for Southern Hemisphere minke whale sighting surveys. *Rep. int. Whal.Commn* 41: 126.

Butterworth, D. S., Best, P.B. and Basson, M. 1982. Results of analysis of sighting experiments carried out during the 1980/81 Southern Hemisphere minke whale assessment cruise. *Rep. int. Whal. Commn* 32: 819-834.

Butterworth, D. S., Best, P.B. and Hembree, D. 1984. Analysis of experiments carried out during the 1981/82 IWC/IDCR Antarctic minke whale assessment cruise in Area II. *Rep. int. Whal. Commn* 34: 365-392.

Butterworth, D. S. and Geromont, H. F. 1995. On the consequences of longitudinal disaggregation of the Japanese scouting vessel data in the northward extrapolation of IWC/IDCR cruise estimates of abundance of some large whale species in the Southern Hemisphere. *International Whaling Commission Document* SC/47/SH20: 8 pp.

University of Cape Town

Butterworth, D. S., Gluckman, G. R., Thomson, R. B. and Chalis, S. 1994. Further computations of the consequences of setting the annual krill catch limit to a fixed fraction of the estimate of krill biomass from a survey. *CCAMLR Science* 1: 81-106.

Butterworth, D. S. and Punt, A. E. 1999. An initial examination of possible inferences concerning MSYR of Southern Hemisphere minke whales from recruitment trends estimated in catch-at-age analyses. *J. Cetacean Res. Manage.* 1: 33-39.

Butterworth, D. S., Punt, A. E., Branch, T. A., Fujise, Y., Zenitani, R. and Kato, H. 2002. Updated ADAPT VPA recruitment and abundance trend estimates for Southern Hemisphere minke whales in Areas IV and V. *International Whaling Commission Document* SC/54/IA25: 20 pp.

Butterworth, D. S., Punt, A. E., Geromont, H. F., Kato, H. and Fujise, Y. 1999. Inferences on the dynamics of Southern Hemisphere minke whales from ADAPT analyses of catch-at-age information. *J. Cetacean Res. Manage.* 1: 11-32.

Butterworth, D. S., Rademeyer, R. A. and Brandão, A. 2001. First attempts to quantify some factors that potentially confound temporal comparisons of minke whale abundance estimates from the IWC/IDCR-SOWER surveys. *International Whaling Commission Document* SC/53/IA27: 21 pp.

Butterworth, D. S., Rademeyer, R. A., Brandão, A and Mori, M. 2003. Quantification of possible effects on the changes of estimated minke whale abundance from the second to the third circumpolar IDCR-SOWER surveys of g(0) values less than 1 and dependent on school-size and of changes in the timing of the surveys. *International Whaling Commission Document* SC/55/IA 12: 15 pp.

Calambokidis, J. and Barlow, J. 2004. Abundance of blue and humpback whales in the eastern north Pacific estimated by capture-recapture and line-transect methods. *Mar. Mamm. Sci.* 20 (1): 63-85.

Casaux, R., Baroni, A. and Carlini, A. 1997. The diet of the Weddell Seal *Leptonychotes weddelli* at Harmony Point, South Shetland Islands. *Polar Biology* 18: 371-375.

Casaux, R., Baroni, A. and Carlini, A. 1998. The diet of the Antarctic fur seal *Arctocephalus gazella* at Harmony Point, Nelson Island, South Shetland Islands. *Polar Biology* 20: 424-428.

Casaux, R., Baroni, A. and Ramón, A. 2003. Diet of Antarctic fur seals *Arctocephalus gazella* at the Danco Coast, Antarctic Peninsula. *Polar Biology* 26: 49-54.

Casaux, R., Bellizia, L. and Baroni, A. 2004. The diet of the Antarctic fur seal *Arctocephalus gazellea* at Harmony Point, South Shetland Islands: evidence of opportunistic foraging on penguins? *Polar Biology* 27: 59-65.

CCAMLR [Commission for the Conservation of Antarctic Marine Living Resources] 2001. Report of the twentieth meeting of the scientific committee. Hobart, Australia, 22 to 26 October 2001. 83 pp.

CCAMLR [Commission for the Conservation of Antarctic Marine Living Resources] 2004. Report of the meeting of the working group on ecosystem monitoring and management, Siena, Italy, 12 to 23 July 2004. 87 pp.

University of Cape Town

Cherel, Y., Guinet, C. and Tremblay, Y. 1997. Fish prey of Antarctic for seals *Arctocephalus gazella* at Ile de Croy, Kerguelen. *Polar Biology* 17: 87-90.

Chittleborough, R. G. 1959. Determination of age in the humpback whale, *Megaptera nodosa* (Bonnaterre). *Aust. J. Mar. Freshw. Res.* 10 (2): 125-143.

Chittleborough, R. G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshw. Res.* 16: 33-128.

Christensen, V., Walters, C. J. and Pauly, D. 2000. *ECOPATH with ECOSIM: a User's guide, October 2000 Edition*. Fisheries Centre, University of British Columbia, Vancouver, Canada, and International Centre for Living Resources Management, Penang, Malaysia: 130 pp.

Clapham, P. J. and Brownell, Jr. R. L. 1996. The potential for interspecific competition in baleen whales. *Rep. int. Whal. Commn* 46: 361-367.

Clapham, P., Robbins, J., Brown, M., Wade, P. and Findlay, K. 2001. Appendix 5, Report of the sub-committee on the Comprehensive Assessment of Whale stocks – In-depth Assessments. *J. Cet. Res. Manag.* 3 (suppl): 196-197.

Clarke, M. R. 1980. Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Reports* 37: 1-324.

Condy, P. R. 1978. Distribution, abundance, and annual cycle of fur seals (*Arctocephalus* spp.) on the Prince Edward Islands. *S. Afr. J. Wildl. Res.* 8: 159-168.

Constable, A. J., de la Mare, W. K., Agnew, D. J., Everson, I. and Miller, D. 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES J. Mar. Sci.* 57: 778-791.

Cooke, J. G. 1985. Notes on the estimation of whale density from line transects. *Rep. int. Whal. Commn* 35: 319-23.

Cooke, J. G. and de la Mare, W. K. 1984. A note on the estimation of time trends in the age at sexual transition in baleen whales from transition layer data, with reference to the North Atlantic fin whale (*Balaenoptera physalus*). *Rep. int. Whal. Commn* 34: 701-709.

Costa, D. P., Croxall, J. P. and Duck, C. D. 1989. Foraging energetics of Antarctic Fur Seals in relation to changes in prey availability. *Ecology* 70: 596-606.

Croxall, J. P. 1984. Seabirds. In: *Antarctic Ecology*, vol. 2. Laws, R. M. (Ed). Academic Press, London: 533-616 pp.

Croxall, J. P. 1992. Southern Ocean environmental changes: effects on seabird, seal and whale populations. *Phil. Trans. R. Soc. Lon. B, Biol. Sci.* 338: 319-328.

Croxall, J. P., Reid, K. and Prince, P. A. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar. Ecol. Prog. Ser.* 177: 115-131.

University of Cape Town

Croxall, J. P. and Pilcher, M. N. 1984. Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *Br. Antarct. Surv. Bull.* 63: 117-125.

Croxall, J. P., Trathan, P. N. and Murphy, E. J. 2002. Environmental change and Antarctic seabird populations. *Science* 297: 1510-1514.

Daneri, G. A. 1996. Fish diet of the Antarctic fur seal, *Arctocephalus gazella*, in summer, at Stranger Point, King George Island, South Shetland Islands. *Polar Biology* 16: 353-355.

Daneri, G. A. and Coria, N. R. 1992. The diet of Antarctic Fur Seals, *Arctocephalus gazella*, during the Summer-Autumn period at Mossman peninsula, Laurie Island (South-Orkneys). *Polar Biology* 11: 565-566.

Daneri, G. A., Piatkowski, U., Coria, N. R. and Carlini, A. R. 1999. Predation on cephalopods by Antarctic fur seals, *Arctocephalus gazella* at two localities of the Scotia Arc, Antarctica. *Polar Biology* 21: 59-63.

de la Mare, W. K. 1994. Estimating confidence intervals for fish stock abundance estimates from trawl surveys. *CCAMLR Science* 1: 203-207.

de la Mare, W. K. 1997. Abrupt mid-twentieth-century decline in Antarctic sea-ice extent from whaling records. *Nature* 389: 57-60.

Demer, D. A. and Conti, S. G. 2005. New target-strength model indicates more krill in the Southern Ocean. *ICES Journal of Marine Science* 62: 25-32.

Demer, D. A. and Hewitt, R. P. 1995. Bias in acoustic biomass estimates of *Euphausia superba* due to diel vertical migration. *Deep-Sea Res. I.* 42 (4): 455-475.

Ensor, P. 1989. Minke whales in the pack ice zone, east Antarctica, during the period of maximum annual ice extent. *Rep. int. Whal. Commn* 39: 219-225.

Erickson, A. W., Bledsoe, L. J. and Hanson, M. B. 1989. Bootstrap correction for diurnal activity cycle in census data for Antarctic seals. *J. Mar. Mam. Sci.* 5 (1): 29-56.

Erickson, A. W. and Hanson, M. B. 1990. Continental estimates and population trends in Antarctic ice seals. In: *Antarctic ecosystems. Ecological change and conservation.* Kerry, K. R and G. Hempel (Eds). Springer-Verlag, Berlin: pp. 253-264.

Everson, I. 1977. The living resources of the Southern Ocean. FAO, Rome. GLO/SO/77/1: 1-156.

Everson, I. 1984. Fish biology. In: *Antarctic Ecology*, vol. 2. Laws, R. M. (Ed). Academic Press, London: pp. 491-532.

Félix, F. and Haase, B. 2001. The humpback whale off the coast of Ecuador, population parameters and behaviour. *Revista de Biologia Marina y Oceanografia* 36 (1): 61-74.

Filippova, J. A. 2002. Review of Soviet/Russian studies on squids in the Antarctic Ocean. *Bulletin of Marine Science* 71 (1): 255-267.

Findlay, K. P. and Best, P. B. 1996. Preliminary population estimates of humpback whales migrating past Cape Vidal, South Africa, 1988-1991. *Mar. Mammal Sci.* 12 (3): 354-370.

University of Cape Town

Findlay, K. P., Best, P. B., Peddemors, V. M. and Gove, D. 1994. The distribution and abundance of humpback whales on their Mozambique winter grounds. *Rep. int. Whal. Commn* 44: 311-320.

Findlay, K., Meÿer, M., Elwen, S., Kotze, D., Johnson, R., Truter, P., Uamusse, C., Sitoe, S., Wilke, C., Kerwath., S., Swanson, S., Staverees, L. and Westhuizen, J. V. D. 2004. Distribution and abundance of humpback whales *Megaptera novaeangliae*, off the cost of Mozambique, 2003. *International Whaling Commission Document* SC/56/SH12: 39 pp.

Foote, K. G. 1983. Use of elastic spheres as calibration targets. In: *Symposium on fisheries acoustics*. Nakken, O. and Venema, S. C. (Eds). *FAO Fish. Rep*. 300: pp. 52-58.

Free, C. A. 1983. Report of the sub-committee on minke whales, Appendix 5. Southern Hemisphere minke whales multiplicative regression analysis of Japanese CSW data. *Rep. int. Whal. Commn* 33: 111-113.

Freitas, A. C., Kinas, P. G., Martins, C. C. A and Engel, M. C. 2002. Population estimate for humpback whales from Abrolhos Bank, Brazil wintering ground in the southwestern Atlantic Ocean. *International Whaling Commission Document* SC/54/H11: 11 pp.

Fujise, Y. and Kishino, H. 1997. Further examination of segregation pattern of minke whales in Antarctic Areas IV and V as revealed by a logistic regression model. *International Whaling Commission Document* SC/M97/13: 22 pp.

Galletti, B. V. M., Carlson, C. A. and Cabrera, E. 2005. Blue whale sightings during the 2005 field season in northwestern Chiloe Island, southern Chile. *International Whaling Commission Document* SC/57/SH14: 4 pp.

Gambell, R. 1968. Seasonal cycles and reproduction in sei whales of the Southern Hemisphere. *Discovery Reports* 35: 31-134.

Gambell, R. 1985. Birds and mammals: Antarctic whales. In: *Key Environments Antarctica*. Bonner, W. N. and Walton, D. W. H. (Eds). Pergamon Press, Oxford: pp. 223-241.

Garrigue, C., Aguayo, A., Amante-Helwig, V.L.U., Baker, C.S., Caballero, P., Clapham, P., Constantine, R., Denkinger, J.,Donoghue, M., Florez-Gonzalez, L., Greaves, J., Hauser, N., Olavarria, C., Pairoa, C., Peckham, H. and Poole, M. 2002. Movements of humpback whales in Oceania, South Pacific. *J. Cetacean Res. Manage.* 4 (3): 255-60.

Garrigue, C., Baker C. S., Dodemont, R. and Steel, D. 2004. Organismal and 'gametic' capture-recapture using microsatellites genotyping confirm low abundance and reproductive autonomy of humpback whales on the wintering grounds of New Caledonia. *Mar. Ecol. Prog. Ser.* 274: 251-262.

Geraci, J. R. 1975. Pinniped nutrition. *Rapports et Procès-Verbaux des Reunions, Conseil International Pour l' Exploration de la Mer* 169: 312-323.

Gilbert, J. R. and Erickson, A. W. 1977. Distribution and abundance of seals in the pack ice of the Pacific sector of the southern ocean. In: *Adaptations within Antarctic Ecosystems, 3rd SCAR Symposium on Antarctic biology*. Llano, G. A. (Ed). Smithsonian Institution, Washington D. C: pp. 703-740.

University of Cape Town

Gille, S. T. 2002. Warming of the Southern Ocean since the 1950s. *Science* 295: 1275-1277.

Glockner-Ferrari, D. A. and Ferrari, M. J. 1984. Reproduction in the humpback whale, *Megaptera novaengliae*, occurring in Hawaiian waters. *Rep. int. Whal. Commn* (special issue) 6: 237-242.

Goldsworthy, S. D. and Shaughnessy, P. D. 1989. Counts of the Antarctic fur seal *Arctocephalus gazella* and location of colonies at Heard Island in the 1987-88 summer. *ANARE Research Notes* 72: 1-25.

Green, K., Burton, H. R. and Williams, R. 1989. The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding-season at Heard Island. *Antarctic Science* 1: 317-324.

Green, K., Burton, H. R., Wong, V., Mcfarlane, R. A., Flaherty, A. A., Pahl, B. C. and Haigh, S. A. 1995. Difficulties in assessing population status of ice seals. *Wildlife Research* 22: 193-199.

Green, K. and Williams, R. 1986. Observations on food remains in faeces of elephant, leopard and crabeater seals. *Polar Biology* 10: 179-185.

Green, K., Williams, R. and Burton, H. R. 1991. The diet of Antarctic fur seals during the late autumn and early winter around Heard Island. *Antarctic Science* 3: 359-361.

Green, K., Williams, R. and Burton, H. R. 1997. Foraging ecology of Antarctic fur seals (*Arctocephalus gazella* Peters) around Heard Island. In: *Marine mammal research in the southern hemisphere: status, ecology and medicine*. Hindell, M. A. and Kemper, C. (Eds). Surrey Beatty, Sydney: pp. 97-104.

Guinet, C., Jouventin, P. and Georges, J-Y. 1994. Long term population changes of fur seals *Arctocephalus gazella* and *A. tropicalis* on subantatctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. *Antarctic Science* 6: 473-478.

Gulland, J. A. 1970. The development of the resources of the Antarctic seas. In: *Antarctic ecology*, Vol. 1. Holdgate, M. W. (Ed). Academic Press, London: pp. 217-223.

Hakamada, T., Matsuoka, K. and Nishiwaki, S. 2005. An update of Antarctic minke whales abundance estimate based on JARPA data including comparison to IDCR/SOWER estimates. Paper JA/J05/JR4 presented to the JARPA Review Meeting called by the Government of Japan, January 2005. 33 pp.

Hamner, W. M., Stone, G. S. and Obst, B. S. 1988. Behavior of southern right whales, *Eubalaena australis*, feeding on the Antarctic krill, *Euphausia superba*. *Fishery Bulletin* 86: (1) 143-150.

Hårding, K. C. and Härkönen, T. 1995. Estimating mean age at sexual maturity in the crabeater seal (*Lobodon carcinophagus*). *Canadian Journal of Fisheries and Aquatic Sciences* 52: 2347-2352.

Harmer, S. F. 1931. Southern whaling. *Proceedings of the Linnean Society of London*. 142: 85-163.

University of Cape Town

Haug, T., Lindstorm, U. and Nilssen, K. T. 2002. Variations in minke whale (*Balaenoptera acutorostrata*) diet and body condition in response to ecosystem changes in the Barents Sea. *Sarsia* 87: 409-422.

Haw, M. D. 1991. An investigation into the differences in minke whale school density estimates from passing mode and closing mode surveys in IDCR Antarctic assessment cruises. *Rep. int. Whal. Commn* 41: 239-247.

Hewitt, R. P. and Demer, D. A. 1994. Acoustic estimates of krill biomass in the Elephant Island Area: 1981-1993. *CCAMLR Science* 1: 1-5.

Hewitt, R. P. and Demer, D. A. 2000. The use of acoustic sampling to estimate the dispersion and abundance of euphausiids, with an emphasis on Antarctic krill, *Euphausia superba*. *Fisheries Research* 47: 215-229.

Hewitt, R. P., Watkins, J. L., Naganobu, M., Tshernyshkov, P., Brierley, A. S., Demer, D. A., Kasatkina, S., Takao, Y., Goss, C., Malyshko, A., Brandon, M. A., Kawaguchi, S., Siegel, V., Trathan, P. N., Emery, J. H., Everson, I. and Miller, D. G. M. 2002. Setting a precautionary catch limit for Antarctic krill. *Oceanography* 15: 26-33.

Hofmeyr, G. J. G., Bester, M. N. and Jonker, F. C. 1997. Changes in population sizes and distribution of fur seals at Marion Island. *Polar Biology* 17: 150-158.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45: 62 pp.

Holm-Hansen, O. and Huntley, M. 1984. Feeding requirements of krill in relation to food sources. *Journal of Crustaacean Biology* 4 (Special Issue No. 1): 156-173.

Holt, S. J. de la Mare, W. K. and van Beek, J. G. 1982. A review of information available for the assessment of minke whales in Area II. *Rep. int. Whal. Commn* 32: 717-721.

Horwood, J. 1990. Biology and exploitation of the minke whale. CRC Press, Boca Raton, Florida. 238 pp.

Hrafnkelsson, B. and Stefansson, G. 2004. Analysis of categorical length data from groundfish surveys. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1135-1142.

Hucke-Gaete, R., Osman, L. P., Moreno, C. A. and Torres, D. 2004. Examining natural population growth from near extinction: the case of the Antarctic fur seal at the South Shetlands, Antarctica. *Polar Biology* 27: 304-311.

Hunt, F. 1973. Observations on the seals of Elephant Island, South Shetland Islands 1970-71. *British Antarctic Survey Bulletin* 36: 99-104.

Hureau, J. C. 1994. The significance of fish in the marine Antarctic ecosystems. *Polar Biology* 14: 307-313.

Ichihara, T. 1964. Prenatal development of ear plug in baleen whale. *Scient. Rep. Whales Res. Inst.* 18: 29-48.

University of Cape Town

Ichii, T. and Kato, H. 1991. Food and daily food-consumption of southern minke whales in the Antarctic. *Polar Biology* 11: 479-487.

Innes, S., Lavigne, D. M., Eagle, W. M. and Kovacs, K. M. 1986. Estimating feeding rates of marine mammals from heart mass to body mass ratios. *Mar. Mamm. Sci.* 2: 227-229.

IWC [International Whaling Commission] 1988. Report of the sub-committee on Southern Hemisphere minke whales. *Rep. int. Whal. Commn* 38: 76-87.

IWC [International Whaling Commission] 1989a. Report of the Special Meeting of the Scientific Committee to consider the Japanese research permit (feasibility study). *Rep. int. Whal. Commn* 39: 159-166.

IWC [International Whaling Commission] 1989b. Report of the sub-committee on Southern Hemisphere minke whales. *Rep. int. Whal. Commn* 39: 71-93.

IWC [International Whaling Commission] 1991. Report of the sub-committee on Southern Hemisphere minke whales. *Rep. int. Whal. Commn* 41: 113-131.

IWC [International Whaling Commission] 1993. Report of the Scientific Committee, Annex E. Report of the sub-committee on Southern Hemisphere baleen whales. *Rep. int. Whal. Commn* 43: 104-114.

IWC [International Whaling Commission] 1998a. Report of the intersessional working group to review data and results from special permit research on minke whales in the Antarctic, Tokyo, 12-16 May 1997. *Rep. int. Whal. Commn* 48: 377-412.

IWC [International Whaling Commission] 1998b. Report of the Sub-Committee on comprehensive assessment of Southern Hemisphere humpback whales. *Rep. int. Whal. Commn* 48: 170-182.

IWC [International Whaling Commission] 2002. Report of the Sub-Committee on the comprehensive assessment of whale Stocks – in depth assessments . *J. Cetacean Res. Manage.* 4 (Suppl.): 192-229.

IWC [International Whaling Commission] 2003. Report of the Sub-Committee on the comprehensive assessment of whale Stocks – in depth assessments. *J. Cetacean Res. Manage.* 5 (Suppl.): 248-292.

IWC [International Whaling Commission] 2004a. Report of the Sub-Committee on other Southern Hemisphere whale stocks. *J. Cetacean Res. Manage.* 6 (Suppl.): 246-271.

IWC [International Whaling Commission] 2004b. Report of the Sub-Committee on the comprehensive assessment of whale stocks – in-depth assessment. *J. Cetacean Res. Manage.* 6 (Suppl.): 224-245.

IWC [International Whaling Commission] 2005. Report of the Sub-Committee on the comprehensive assessment of whale stocks – in-depth assessment. *J. Cetacean Res. Manage.* 7 (Suppl.): 211-234.

Jenner, K. C. S. and Jenner, M-N. 1994. A preliminary population estimate of the group IV breeding stock of humpback whales off western Australia. *Rep. int. Whal. Commn* 44: 303-307.

University of Cape Town

Johnston, S. J. and Butterworth, D. S. 2002. Further results from a preliminary assessment of Southern Hemisphere humpback whales. *International Whaling Commission Document* SC/53/IA20: 36 pp.

Johnston, S. J. and Butterworth, D. S. 2005a. A Bayesian assessment of the west and east Australian breeding populations (stocks D and E) of Southern Hemisphere humpback whales. *International Whaling Commission Document* SC/57/SH15: 25 pp.

Johnston, S. J. and Butterworth, D. S. 2005b. A Bayesian assessment of breeding stocks B, C and G of Southern Hemisphere humpback whales using a prior for growth rate from analyses for stocks D and E. *International Whaling Commission Document* SC/57/SH16: 14 pp.

Johnstone, G. W. 1982. Zoology. Expedition to the Australian territory of Heard Island and the McDonald Islands, 1980. *Division of National Mapping, Australia, Technical Report* 31: 33-39.

Jouventin, P. and Stonehouse, B. 1985. Biological survey of Ile Croy (Iles Kerguelen), 1984. *Polar Record* 22 (14): 688-691.

Kasamatsu, F. 2000. *Kujira no seitai*. Kouseishakouseikaku, Tokyo, Japan. 230 pp. [in Japanese].

Kasamatsu, F., Ensor, P., Joyce, G. G. and Kimura, N. 2000b. Distribution of minke whales in the Bellingshausen and Amundsen Seas (60°W-120°W), with special reference to environmental/physiographic variables. *Fish. Oceanogr.* 9 (3): 214-223.

Kasamatsu, F., Joyce, G. G., Ensor, P. and Mermoz, J. 1996. Current occurrence of baleen whales in Antarctic waters. *Rep. int. Whal. Commn* 46: 293-304.

Kasamatsu, F., Matsuoka, K. and Hakamada, T. 2000a. Interspecific relationships in density among the whale community in the Antarctic. *Polar Biology* 23: 466-473.

Kasamatsu, F., Nishiwaki, S. and Ishikawa, H. 1995. Breeding areas and southbound migrations of southern minke whales Balaenoptera acutorostrata. *Mar. Ecol. Prog. Ser.* 119: 1-10.

Kasamatsu, F. and Ohsumi, S. 1981. Distribution pattern of minke whales in the Antarctic with special reference to the sex ratio in the catch. *Rep. int. Whal. Commn* 31: 345-348.

Kato, H. 1983. Some considerations on the decline in age at sexual maturity of the Antarctic minke whale. *Rep. int. Whal. Commn* 33: 393-399.

Kato, H., Honno, Y., Yoshida, H., Kojima, E., Nomura, A. and Okamura, H. 2002. Further developments on morphological and behavioral key for sub-species discrimination of Southern blue whales, analyses from data through 1995/96 to 2001/02 SOWER cruises. *International Whaling Commission Document* SC/54/IA8: 16 pp.

Kato, H. and Shimadzu, Y. 1986. Feeding rate of the Southern minke whales (Abstr). Ninth NIPR Symp on Polar Biol, Tokyo, December 3-5, 1986 [in Japanese].

Kawakami, T. 1980. A review of sperm whale food. *Sci. Rep. Whales Res. Inst.* 32: 199-218.

Kawamura, A. 1978. An interim consideration on a possible interspecific relation in southern baleen whales from the viewpoint of their food habits. *Rep. int. Whal. Commn* 28: 411-419.

University of Cape Town

Kawamura, A. 1994. A review of baleen whale feeding in the Southern Ocean. *Rep. int. Whal. Commn* 44: 261-272.

Keddy, P. A. 1989. *Competition*. Chapman and Hall, London. 202 pp.

Kerley, G. I. H. 1987. *Arctocephalus tropicalis* on the Prince Edward Islands. In: *Status, biology, and ecology of fur seals. Proceedings of an International Symposium and Wokshop, Cambridge, England, 23-27 April 1984*. Croxall, J.P and R.L. Gentry (Eds). NOAA Technical Report NMFS 51: pp. 61-64.

Keyes, M. C. 1968. The nutrition of pinnipeds. In: *The behaviour and physiology of pinnipeds*. Harrison, R. J., Hubbard, R. C., Peterson, R. S., Rice, C. E. and Schusterman, R. J. (Eds). Appleton-Century-Crofts, New York. pp. 359-395.

Kinas, P. G. and Bethlem, C. B. P. 1998. Empirical Bayes abundance estimation of a close population using mark-recapture data, with application to humpback whales, *Megaptera novaeangliae*, in Abrolhos, Brazil. *Rep. int. Whal. Commn* 48: 447-450.

Kirkman, S. P., Wilson, W., Klages, N. T. W., Bester, M. N. and Isaksen, K. 2000. Diet and estimated food consumption of Antarctic fur seals at Bouvetoya during summer. *Polar Biology* 23: 745-752.

Klages, N. T. W. and Bester, M. N. 1998. Fish prey of fur seals *Arctocephalus spp.* at subantarctic Marion Island. *Marine Biology* 131: 559-566.

Klages, N. T. W., Hofmeyr, G. J. G. and Gjertz, I. 1999. Prey of Antarctic fur seals at Bouvet Island, Southern Ocean. *Polar Record*: July 255-257.

Klumov, S. K. 1963. Feeding and halminth fauna of whalebone whales (Mystacoceti). *Trudy Instituta Okeanol* 71: 94-194.

Knox, G. A. 1994. *The biology of the Southern Ocean*. Cambridge University Press, Cambridge. 444 pp.

Kock, K. H. 1985. Krill consumption by Antarctic notothenioid fish. In: *Antarctic nutrient cycles and food webs, Proc. 4th SCAR Symposium on Antarctic biology*. Siegfried, W. R., Condy, P. R. and Laws, R. M. (Eds). Springer, Berlin Heidelberg New York: pp. 437-444.

Kock, K. H. 1987. Marine consumers: fish and squid. *Environm Int.* 13: 37-45.

Kock, K. H. 1992. *Antarctic Fish and Fisheries*. Cambridge University Press, Cambridge, England, UK. 359 pp.

Kock, K. H., Purves, M. G. and Duhamel, G. 2005. Interactions between cetacean and fisheries in the Southern Ocean. *International Whaling Commission Document* SC/57/O13: 16 pp.

Konishi, K. and Tamura, T. 2005. Yearly trend of blubber thickness in the Antarctic minke whale *Balaenoptera bonaerensis* in Areas IV and V. Paper JA/J05/JR9 presented to the JARPA Review Meeting called by the Government of Japan, January 2005: 9 pp.

Korabelnikov, L. V. 1959. The diet of sperm whales in the Antarctic seas. *Priroda* 3: 103-104.

University of Cape Town

Lake, S., Burton, H. and van den Hoff, J. 2003. Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. *Mar. Ecol. Prog. Ser.* 254: 293-305.

Laws, R. M. 1956. Growth and sexual maturity in aquatic mammals. *Nature* 178: 193-194.

Laws, R. M. 1961. Southern fin whales. *Discovery Reports* 31: 327-486.

Laws, R. M. 1962. Some effects of whaling on the southern stocks of baleen whales. pp.137-58. In: *The Exploitation of Natural Animal Populations. Blackwell Scientific Publications.* Le Cren, E. D. and Holdgate, M. W. (Eds.). Oxford: xiv+399 pp.

Laws, R. M. 1973. Population increase of fur seals at South Georgia. *Polar Record* 16: 856-858.

Laws, R. M. 1977. Seals and whales of the Southern Ocean. *Phil. Trans. R. Soc. Lon. B, Biol. Sci.* 279: 81-96.

Laws, R. M. 1984. Seals. In: *Antarctic Ecology*, vol. 2. Laws, R. M. (Ed). Academic Press, London: 621-715 pp.

Laws, R. M. and Christie, E. C. 1976. Seals and birds killed or captured in the Antarctic Treaty area, 1970-73. SCAR Bulletin No. 54. *Polar Record* 18 (114): 318-320.

LeDuc, R. G., Dizon, A. E., Goto, M., Pastene, L. A., Kato, H. and Brownell, R. L., Jr. 2003. Patterns of genetic variation in southern hemisphere blue whales. *International Whaling Commission Document* SC/55/SH9: 8 pp.

Lockyer, C. 1972. The age at sexual maturity of the southern fin whale (*Balaenoptera physalus*) using annual layer counts in the ear plug. *J. Cons. Int. Explor. Mer.* 34 (2): 276-294.

Lockyer, C. 1981a. Estimation of the energy costs of growth, maintenance and reproduction in the female minke whale (*Balaenoptera acutorostrata*), from the southern hemisphere, south of 40°S. *Rep. int. Whal. Commn* 31: 337-343.

Lockyer, C. 1981b. Growth and energy budgets of large baleen whales from the Southern Hemisphere. In: *Mammals of the sea.* FAO fisheries series No.5, Vol. 3, Rome: pp. 379-487.

Lockyer, C. 1984. Review of baleen whale reproduction and implications for management. *Rep. int. Whal. Commn* (special issue) 6: 27-50.

Loeb, V. S. V., Holmhansen, O., Hewitt, R., Fraser, W., Trivelpiece, W. and Trivelpiece, S. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387: 897-900.

Lowry, L. F., Testa, J. W. and Calvert, W. 1988. Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. *Polar Biology* 8: 475-478.

Lubimova, T. G., Shust, K. V., Popkov, V. V. 1987. Ecology of mesopelagic fishes, family Myctophidae, Southern Ocean [in Russian]. In: *Biological Resources of the Arctic and Antarctic.* Nauka, Moscow: pp. 320-337.

Mackintosh, N. A. 1942. The southern stocks of whalebone whales. *Discovery Reports* 22: 197-300.

University of Cape Town

Mackintosh, N. A. 1973. Distribution of post-larvae krill in the Antarctic. *Discovery Reports* 36: 95-156.

Mackintosh, N. A. 1974. Sizes of krill eaten by whales in the Antarctic. *Discovery Reports* 36: 157-178.

Mackintosh, N. A. and Wheeler, J. F. G. 1929. Southern Blue and Fin Whales. *Discovery Reports* 1: 257-540.

Marr, J. W. S. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Reports* 32: 33-464.

Masaki, Y. 1979. Yearly change of the biological parameters for the Antarctic minke whale. *Rep. int. Whal. Commn* 29: 375-396.

Matsuoka, K., Ensor, P., Hakamada, T., Shimada, H., Nishiwaki, S., Kasamatsu, F. and Kato, H. 2003. Overview of minke whale sightings surveys conducted on IWC/IDCR and SOWER Antarctic cruises from 1978/79 to 2000/01. *J. Cetacean Res. Manage.* 5 (2): 173-201.

Matsuoka, K., Hakamada, T. and Nishiwaki, S. 2005. Distribution and abundance of humpback, fin and blue whales in the Antarctic Areas IIIE, IV, V and VIW (35°E-145°W). JA/J05/JR10 presented to the JARPA Review Meeting called by the Government of Japan, January 2005: 43 pp.

Matthews, L. H. 1937. The humpback whale, *Megaptera nodosa*. *Discovery Reports* 17: 7-92.

May, R. M., Beddington, J. R., Clark, C. W., Holt, S. J. and Laws, R. M. 1979. Management of multispecies fisheries. *Science* 205 (4403): 267-277.

McCann, T. S. 1980. Territoriality and breeding behaviour of adult male Antarctic fur seals, *Arctocephalus gazella*. *Journal of Zoology* 192: 295-310.

McCann, T. S. and Doidge, D. W. 1987. Antarctic fur seal, *Arctocephalus gazella*. In: *Status, biology, and ecology of fur seals. Proceedings of an International Symposium and Wokshop, Cambridge, England, 23-27 April 1984*. Croxall, J.P and R.L. Gentry (Eds). NOAA Technical Report NMFS 51: pp. 5-8.

McDonald, M. A., Mesnick, S. L. and Hildebrand, J. A. 2005. Biogeographic characterization of blue whale song worldwide: Using song to identify populations, *J. Cetacean Res. Manage.* in press.

Mckay, S., Širovic, A. and Thiele, D. 2005. Preliminary results of blue whale (*Balaenoptera musculus*) call detections in Eastern Antarctica. *International Whaling Commission Document* SC/57/SH4: 4 pp.

Miller, D. G. M. 2002. Antarctic krill and ecosystem management - from Seattle to Siena. *CCAMLR Science* 9: 175-212.

Miller, D. G. M and Hampton, I. 1989. Biology and ecology of the Antarctic krill. *Biomass Sci. Ser.* 9: 1-166.

University of Cape Town

Miller, D. G. M., Hampton, I, Henry, J., Abrams, R. W. and Cooper, J. 1985. The relationship between krill food requirements and phytoplankton production in a sector of the Southern Indian Ocean. In: *Antarctic Nutrient Cycles and Food Webs*. Siegfried, W. R., Condy, P. R. and Laws, R. M. (Eds). Springer-Verlag, Berlin Heidelberg: pp. 362-371.

Miyashita, T., Kato, H., and Kasuya, T. (Eds). 1995. *Worldwide map of cetacean distribution based on Japanese sighting data (Volume 1)*. Shimizu, National Research Institute of Far Seas Fisheries. 140 pp.

Mori, M. and Butterworth, D. S. 2004. Consideration of multispecies interactions in the Antarctic: a preliminary model of the minke whale – blue whale – krill interaction. *Afr. J. mar. Sci.* 26: 245-259.

Mori, M. and Butterworth, D. S. 2005. Some advances in the application of ADAPT-VPA to minke whales in Areas IV and V. *International Whaling Commission Document* SC/57/IA17: 27 pp.

Mori, M., Butterworth, D. S., Brandao, A., Rademeyer, R. A., Okamura, H. and Matsuda, H. 2003. Observer experience and Antarctic minke whale sighting ability in IWC/IDCR-SOWER surveys. *J. Cetacean Res. Manage.* 5 (1): 1-11.

Mori, M., Butterworth D, S., and Matsuda, H. 2002. Comparison of duplicate sighting rate for Southern Hemisphere whales between the 2nd and 3rd circumpolar surveys of IWC/IDCR-SOWER. *International Whaling Commission Document* SC/54/IA16: 18 pp.

Murase, H., Matsuoka, K., Ichii, T. and Nishiwaki, S. 2002. Relationship between the distribution of euphausiids and baleen whales in the Antarctic (35°E-145°W). *Polar Biology* 25: 135-145.

Murase H., Matsuoka K., Nishiwaki S., Hakamada T. and Mori M. 2004. Effect of observed covariates (school size, sighting cue, latitude and sea state) on the Antarctic minke whale abundance estimation parameters in the IWC/IDCR-SOWER surveys. *J. Cetacean Res. Manage.* 6 (3): 283-292.

Murdoch, W. W., Avery, S. and Smyth, M. E. B. 1975. Switching in predatory fish. *Ecology* 56: 1094-1105.

Murphy, E. J. 1995. Spatial structure of the Southern Ocean ecosystem: predator-prey linkages in Southern Ocean food webs. *Journal of Animal Ecology* 64: 333-347.

Murphy, E. J., Watkins, J. L., Reid, K., Trathan, P. N., Everson, I., Croxall, J. P., Priddle, J., Brandon, M. A., Brierley, A. S. and Hofmann, E. 1998. Interannual variability of the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. *Fish. Oceanogr.* 7: 381-390.

Naito, Y. 1982. Sightings records of minke whales in the pack ice and adjacent waters off the coast of Enderby Land. *Rep. int. Whal. Commn* 32: 929-933.

Nemoto, T. 1959. Food of baleen whales with reference to whale movements. *Sci. Rep. Whales Res. Inst.* 14: 149-290.

Nemoto, T. 1970. Feeding pattern of baleen whales in the ocean. In *Marine Food Chains*. Steele, J. H. (Ed). Univ. Calif. Press, Berkeley and Los Angeles: pp. 241-252.

University of Cape Town

Nemoto, T., Okiyama, M., Iwasaki, N. and Kikuchi, T. 1988. Squid as predators on krill (*Euphausia superba*) and prey for sperm whales in the Southern ocean. In: *Antarctic ocean and resources variability*. Sahrhage, D. (Ed). Springer-Verlag, Berlin, Heidelberg: pp. 292- 296.

Nesis, K. N. 1983. *Dosdicus gigas*. In: *Cephalopod life cycles: comparative reviews*, vol. 1. Boyle, P. R. (Ed), Academic Press, London: pp. 215-231.

Nicol, S., Constable, A. J. and Pauly, T. 2000a. Estimates of circumpolar abundance of Antarctic krill based on recent acoustic density measurements. *CCAMLR Science* 7: 87-99.

Nicol, S. and de la Mare, W. 1993. Ecosystem management and the Antarctic krill. *American Scientist* 81: 36-47.

Nicol, S. and Endo, Y. 1999. Krill fisheries: development, management and ecosystem implications. *Aquatic Living Resources* 12: 105-120.

Nicol, S. and Foster, J. 2003. Recent trends in the fishery for Antarctic krill. *Aquatic Living Resources* 16: 42-45.

Nicol, S., Pauly, T., Bindoff, N. L., Wright, S., Thiele, D., Hosle, G. W., Strutton, P. G. and Woehler, E. 2000b. Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature* 406: 504-507.

Nicol, S. and Worby, A. 2005. The Antarctic sea ice ecosystem and its potential responses to global change. *International Whaling Commission Document* SC/57/E14: 34 pp.

Noad, M. J., Cato, D. H. and Paton, D. 2005. Absolute and relative abundance estimates of Australian east coast humpback whales (*Megaptera novaeangliae*). *International Whaling Commission Document* SC/57/SH12: 9 pp.

North, A., Croxall, J. and Doidge, D. 1983. Fish prey of the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *Br. Antarct. Surv. Bull.* 61: 27-37.

Ohsumi, S. 1964. Examination on age determination of the fin whale. Scient. *Rep. Whales Res. Inst.*, 12: 23-32.

Ohsumi, S. 1979. Feeding habits of the minke whale in the Antarctic. *Rep. int. Whal. Commn* 29: 473-476.

Ohsumi, S., Fujise, Y., Ishikawa, H., Hakamada, T., Zenitani, R. and Matsuoka, K. 1997. The fattyness of the Antarctic minke whale and its yearly change. *International Whaling Commission Document* SC/M97/18: 21 pp.

Ohsumi, S., Masaki, Y. and Kawamura, A. 1970. Stock of the Antarctic minke whale. *Sci. Rep. Whales Res. Inst.* 22: 75-125.

Okamura, H., Kitakado, T. and Mori, M. 2003. An improved method on line transect sampling in the Antarctic minke whales survey. *International Whaling Commission Document* SC/55/IA5: 20 pp.

University of Cape Town

Øritsland, T. 1970. Sealing and seal research in the South-west Atlantic pack ice, September-October, 1964. In: *Antarctic ecology*, Vol. 1. Holdgate, M. W. (Ed). Academic Press, London and New York: pp. 361-366.

Øritsland, T. 1977. Food consumption of seals in the Antarctic pack ice. In: *Adaptations within Antarctic Ecosystems, 3rd SCAR Symposium on Antarctic biology*. Llano, G. A. (Ed). Smithsonian Institution, Washington D. C: pp. 749-768.

Osman, L. P., Hucke-Gaete, R., Moreno, C. A. and Torres, D. 2004. Feeding ecology of Antarctic fur seals at Cape Shirreff, South Shetlands, Antarctica. *Polar Biology* 27: 92-98.

Pakhomov, E. A., Perissinotto, R. and McQuaid, C. D. 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar. Ecol. Prog. Ser.* 134: 1-14.

Palmer, S. 2004. *Far from moderate*. Ph.D. thesis, University of Portsmouth. 412 pp.

Pastene, L. A., Goto, M., Abe, H., Nishiwaki, S. and Palsboll, P. 2000. Genetic diversity of humpback whales in the Antarctic feeding ground examined by mitochondrial DNA and microsatellite. *International Whaling Commission Document* SC/52/IA4: 16 pp.

Pastene, L. A., Goto, M., Kanda, N., Bando, T., Zenitani, R., Hakamada, T., Otani, S. and Fujise, Y. 2005. A new interpretation of the stock identity in the Antarctic minke whale based on analyses of genetics and non-genetics markers. Paper JA/J05/JR3 presented to the JARPA Review Meeting called by the Government of Japan, January 2005. 31 pp.

Payne, M. R. 1977. Growth of a fur seal population. *Phil. Trans. R. Soc. Lon. B, Biol. Sci.* 279: 67-79.

Payne, M. R. 1978. Population size and age determination in the Antarctic fur seal *Arctocephalus gazella*. *Mammal Review* 8: 67-73.

Payne, M. R. 1979. Fur seals *Arctocephalus tropicalis* and *Arctocephalus gazella* crossing the Antarctic Convergence at South Georgia, South Atlantic Ocean. *Mammalia* 43: 93-98.

Pitman, R. L., and Ensor, P. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *J. Cetacean Res. Manage.* 5: 131-139.

Prince, P. A. 1980. The food and feeding ecology of blue petrel (*Halobaena caerulea*) and dove prion (*Pachyptila desolata*). *Journal of Zoology* 190: 59-76.

Punt, A. E. 1989. Bias and variance of catch-effort based model estimation procedures used in the management of the ICSEAF hake stocks - a preliminary comparative investigation. *Sel. Pap. ICSEAF int. Commn SE. Atl. Fish.* 1: 39-54.

Punt, A. E. and Polacheck, T. 2005. Application of statistical catch-at-age analysis to data for Southern Hemisphere minke whales in Antarctic Areas IV and V. *International Whaling Commission Document* SC/57/IA9: 71 pp.

Rademeyer, R. A., Brandão, A., Mori, M and Butterworth, D. S. 2003a. Trends in Antarctic blue whale populations taking acount for Area effects or: A response to Joe Horwood, 1990, RIWS 40: 47, footnote 2. *International Whaling Commission Document* SC/55/SH20: 17 pp.

University of Cape Town

Rademeyer, R., Mori, M. and Butterworth, D.S. 2003b. A Quick Examination of the Impact of Inter/Extrapolations on Comparisons of Comparable IDCR-SOWER Abundance Estimates for Minke and Killer Whales. *International Whaling Commission Document* SC/55/IA 11: 8 pp.

Reid, K. 1995. The diet of Antarctic fur seals (*Arctocephalus gazella* Peters 1875) during winter at South Georgia. *Antarctic Science* 7: 241-249.

Reid, K. and Arnould, J. P. Y. 1996. The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biology* 16: 105-114.

Reid, K. and Croxall, J. P. 2001. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proc. R. Soc. Lond. B.* 268: 377-384.

Robinson, S.A., Goldsworthy, S.G., van den Hoff, J. and Hindell, M.A. 2002. The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Marine and Freshwater Research* 53: 1071-1082.

Rosenbaum, H. C., Strindberg, S. and Ersts, P. J. 2004. Initial estimates of abundance and distribution of humpback whales on their wintering grounds in the coastal waters of Gabon (southeastern Atlantic Ocean, Area B) based on aerial surveys. *International Whaling Commission Document* SC/56/SH2: 12 pp.

Ross, R. M. and Quetin, L. B. 1988. *Euphausia superba*: a critical review of estimates of annual production. *Comp. Biochem. Pysiol.* 90 B(3): 499-505.

Roux, J. P. 1987. Subantarctic fur seal, *Arctocephalus tropicalis*, in French subantarctic territories. In: *Status, biology, and ecology of fur seals. Proceedings of an International Symposium and Wokshop, Cambridge, England, 23-27 April 1984*. Croxall, J.P and R.L. Gentry (Eds). NOAA Technical Report NMFS 51: pp. 79-81.

Sakuramoto, K. and Tanaka, S. 1985. A new multi-cohort method for estimating Southern Hemisphere minke whale populations. *Rep. int. Whal. Commn* 35: 261-271.

Saville, A. 1977. Survey methods of appraising fisheries resources. FAO *Fisheries Technical Paper* 171: 76 pp.

SC-CAMLR. 2000. *Report of the nineteenth meeting of the scientific committee* (SC-CAMLR-XIX). CCAMLR, Hobart, Australia.

Seal, U. S., Erickson, A. W., Siniff, D. B. and Cline, D. R. 1971a. Blood chemistry and protein polymorphism in three species of Antarctic seals (Lobodon carcinophagus, Leptonychotes weddelli and Mirounga leonina). In: *Antarctic pinnipedia*. Burt, W. H. (Ed). American Geophysical Union, Washington, D. S. *Antarctic Research Series* 18: 181-192.

Seal, U. S., Erickson, A. W., Siniff, D. B. and Hofman, R. J. 1971b. Biochemical, population genetic, phylogenetic and cytological studies of Antarctic seal species. In: *Symposium on Antarctic Ice an Water Masses*. Deacon, G. (Ed). Scientific Committee on Antarctic Research, Cambridge: pp. 79-95.

University of Cape Town

Sergeant, D. E. 1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. *Bulletin Fisheries Research Board of Canada* 132: 1-84.

Sergeant, D. E. 1969. Feeding rates of cetacean. *Fiskeridirektoratets Skrifter, Serie Havundersokelser* 15: 246-258.

Sergeant, D. E. 1973. Feeding, growth and productivity of northwest Atlantic harp seals (*Pagophilus groenlandicus*). *Journal of the Fisheries Research Board of Canada* 30: 17-29.

Shaughnessy, P. D. and Goldsworthy, S. D. 1990. Population size and breeding season of the Antarctic fur seal *Arctocephalus gazella* at Head Island-1987/88. *Mar. Mamm. Sci.* 6: 292-304.

Shaughnessy, P. D., Shaughnessy, G. L. and Fletcher, L. 1988. Recovery of the fur seal population at Macquarie Island. *Papers and Proceedings of the Royal Society of Tasmania* 122 (1): 177-187.

Shaughnessy, P. D. and Fletcher, L. 1987. Fur seals, *Arctocephalus* spp., at Macquarie Island. In: *Status, biology, and ecology of fur seals. Proceedings of an International Symposium and Wokshop, Cambridge, England, 23-27 April 1984*. Croxall, J.P and R.L. Gentry (Eds). NOAA Technical Report NMFS 51: pp. 177-188.

Shimada, H., Segawa, K. and Murase, H. 2001. Tentative trial for estimation of Antarctic minke whale abundance within pack ice region incorporating IDCR/SOWER data with meteorological satellites data. *International Whaling Commission Document* SC/53/IA14: 6 pp.

Shimada, H., Segawa, K. and Murase, H. 2002. A preliminary trial: estimation of the Antarctic minke whale abundance within the sea ice incorporating IDCR/SOWER data with meteorological satellites data. *International Whaling Commission Document* SC/54/IA19: 6 pp.

Siegel, V., Bergström, B., Mühlenhardt-Siegel, U. and Thomasson, M. 2002. Demography of krill in the Elephant Island area during summer 2001 and its significance for stock recruitment. *Antarctic Science* 14 (2): 162-170.

Siegel, V., de la Mare, W. K. and Loeb, V. 1997. Long-term monitoring of krill recruitment and abundance indices in the Elephant island area (Antarctic peninsula). *CCAMLR Science* 4: 19-35.

Siegel, V. and Loeb, V. 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Mar. Ecol. Prog. Ser.* 123: 45-56.

Siegel, V., Loeb, V. and Groger, J. 1998. Krill (*Euphausia superba*) density, proportional and absolute recruitment and biomass in the Elephant Island region (Antarctic Peninsula) during the period 1977 to 1997. *Polar Biology* 19: 393-398.

Sigurjónsson, J. and Víkingsson, G. A. 1997. Seasonal abundance of and estimated prey consumption by cetaceans in Icelandic and adjacent waters. *Journal of Northwest Atlantic Fish Science* 22: 271-287.

University of Cape Town

Siniff, D. B., Stirling, I., Bengtson, J. L. and Reichle, R. A. 1979. Social and reproductive behaviour of crabeater seals (*Lobodon carcinophagus*) during the austral spring. *Canadian Journal of Zoology* 57: 2243-2255.

Siniff, D. B. and Stone, S. 1985. The role of the leopard seal in the trophodynamics of the Antarctic marine ecosystem. In: *Antarctic nutrient cycles and food webs*. Siegfried, W. R., Condy, P. R. and Laws, R. M. (Eds). Springer-Verlag, Berlin: pp. 555-560.

Siniff, D. B., Stone, S., Reichle, D. and Smith, T. 1980. Aspects of leopard seals (*Hydrurga leptonyx*) in the Antarctic Peninsula pack ice. *Antarctic Journal of the United States* 15: 160 pp.

Širovic, A., Hildebrand, J.A., Wiggins, S.M., McDonald, M.A., Moore, S.E. and Thiele, D. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. *Deep Sea Research II* 51: 2327- 2344.

Smith, R. I. L. 1988. Destruction of Antarctic terrestrial ecosystem by a rapidly expanding fur seal population. *Biological Conservation* 45: 55-72.

Solomon, M. E. 1949. The natural control of animal populations. *Journal of Animal Ecology* 18: 1-35.

Solyanik, G. A. 1963. An interesting ichthyological find. *Inform Byul. Sov. Antarkt. Eksped.* 42: 62 [in Russian].

Southwell, C., Borchers, D., Paxton, C., de la Mare, B., Boveng, P., Blix, A. S. and Nordoy, E. S. 2005. Estimaing the abundance of pack-ice seals off east Antarctica. *CCAMLR document* WG-EMM-05/23: 22 pp.

SSG. 2000. Report of the meeting of the SCAR group of specialists on seals. SC-CAMLR-XIX/BG/16.

Stone, H. S. and Siniff, D. B. 1983. Leopard seal feeding and food consumption in Antarctic spring and summer. Proceedings of the Fourth Biennial Conference on the Biology of Maainr Mammals, San Francisco, December 14-18, 1981.

Tamura, T. 2003. Regional assessments of prey consumption and competition by marine cetaceans in the world. In: *Responsible Fisheries in the Marine Ecosystem*. Sinclair, M. and Valdimarsson, G. (Eds). FAO and CABI Publishing: pp. 143-170.

Tamura, T. and Konishi, K. 2005. Feeding habits and prey consumption of Antarctic minke whales, *Balaenoptera bonaerensis* in JARPA research area. Paper JA/J05/JR8 presented to the JARPA Review Meeting called by the Government of Japan, January 2005: 24 pp.

Testa, J. W., Oehlert, G., Ainley, D. G., Bengtson, J. L., Siniff, D. B., Laws, R. M. and Rounsevell, D. 1991. Temporal variability in Antarctic marine ecosystems: periodic fluctuations in the phocid seals. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 631-639.

Thiele, D. and Gill, P. C. 1999. Cetacean observations during a winter voyage into Antarctic sea ice south of Australia. *Antarctic Science* 11 (1): 48-53.

University of Cape Town

Thomson, R. B., Butterworth, D. S., Boyd, I. L. and Croxall, J. P. 2000. Modeling the consequences of Antarctic krill harvesting on Antarctic fur seals. *Ecol. Appl.* 10: 1806-1819.

Thomson, R. B., Butterworth, D. S. and Kato, H. 1999. Has the age at transition of Southern Hemisphere minke whales declined over recent decades? *Mar. Mamm. Sci* 15: 661-682.

Tomilin, A. G. 1967. *Cetacea. Mammals of the USSR and Adjacent Countries*, Vol. 9. Israel Program for Scientific Translations, Jerusalem. 756 pp.

Trathan, P. N., Agnew, D., Miller, D. G. M., Watkins, J. L., Everson, I., Thorley, M. R., Murphy, E., Murray, A. W. A. and Goss, C. 1992. Krill biomass in Area 48 and Area 58: recalculation of FIBEX data. *CCAMLR document* WG-krill-92/20: 30 pp.

Trathan, P. N., Watkins, J. L., Murray, A. W. A., Brierley, A. S., Everson, I., Goss, C., Priddle, J., Reid, K. and Ward, P. 2001. The CCAMLR-2000 krill synoptic survey: a description of the rationale and design. *CCAMLR Science* 8: 1-23.

Trites, A. W. and Pauly, D. 1998. Estimating mean body masses of marine mammals from maximum body lengths. *Can. J. Zool.* 76: 886-896.

Turchin, P. 2002. Complex population dynamics: a theoretical/empirical synthesis. *Monographs in population biology* 35. Princeton University Press: 456 pp.

Voronina, N. M. 1998. Comparative abundance and distribution of major filter feeders in the Antarctic pelagic zone. *Journal of Marine Systems* 17: 375-390.

Walker, T. R., Boyd, I. L., McCafferty, D. J., Huin, N., Taylor, R. I. and Reid, K. 1998. Seasonal occurrence and diet of leopard seals (*Hydrurga leptonyx*) at Bird Island, South Georgia. *Antarctic Science* 10 (1): 75-81.

Weddell, J. 1825. A voyage towards the South pole, performed in the years 1822-24. Longman, Hurst, Rees, Orme, Brown and Green, London. 324 pp.

Wilkinson, I. S. and Bester, M. N. 1990. Continued population increase in fur seals, *Arctocephalus tropicalis* and *A. gazella*, at the Prince Edward Islands. *S. Afr. T. Nav. Antarkt.* 20 (2): 58-63.

Woehler, E. J. 1995. Consumption of Southern Ocean marine resources by penguins. In: *The Penguins: Ecology and Management.* Dann, P., Norman, I. and Reilly, P (Eds), Surrey Beatty & Sons Pty Ltd., Australia: pp. 266-295.

Yablokov, A. V., Zemsky, V. A., Mikhalev, Y. A., Tormosov, V. V. and Berzin, A. A. 1998. Data on Soviet whaling in the Antarctic in 1947-1972 (population aspects). *Rus. J. Ecol.* 29: 38-42.

Yukhov, V. L. 1972. The range of fish of the genus *Dissostichus* (Fam Nototheniidae) in the Antarctic waters of the Indian Ocean. *Vopr. Ikthiol.* 12 (2): 384-385. Transl. as *J. Ichthyol.* 12 (2): 346-347.

Yukhov, V. L. 1982. *The Antarctic toothfish.* Nauka, Moscow. 113 pp. [in Russian].

Zenitani, R. and Kato, H. 2005. Long- term trend of age at sexual maturity of Antarctic minke whales by counting transition phase in earplugs. Paper JA/J05/JR7 presented to the JARPA Review Meeting called by the Government of Japan, January 2005. 12 pp.

University of Cape Town

Zerbini, A., Andriolo, A., da Rocha, J. M., Simões-Lopes, P. C., Siciliano, S., Pizzorno, J. L., Waite, J. M., DeMaster, D. P. and VanBlaricom, G. R. 2004. Winter distribution and abundance of humpback whales (*Megaptera novaeangliae*) off Northeastern Brazil. *J. Cetacean Res. Manage.* 6 (1): 101-107.

University of Cape Town