UNIVERSITY OF CAPE TOWN

DISSERTATION PRESENTED FOR THE DEGREE OF MASTER OF SCIENCE

An updated model of the krill-predator dynamics of the Antarctic ecosystem

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Declaration of Authorship

I, Naseera Moosa, declare that this thesis titled, 'An updated model of the krill-predator dynamics of the Antarctic ecosystem' and the work presented in it are my own. I confirm that:

- This work was done while in candidature for a research degree at the University of Cape Town.
- Where I have consulted the published work of others, this is clearly attributed.
- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.
- I have acknowledged all main sources of help.
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Signed: Signed by candidate

Date: 26/06/2017

“The future belongs to those who believe in the beauty of their dreams.”

Eleanor Roosevelt

UNIVERSITY OF CAPE TOWN

Abstract

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Dissertation presented for the degree of Master of Science in Applied Mathematics

An updated model of the krill-predator dynamics of the Antarctic ecosystem

by Naseera MOOSA

The objective of this thesis is to update the Mori-Butterworth (2006) model of the krill-predator dynamics of the Antarctic ecosystem. Their analysis aimed to determine whether predator-prey interactions alone could broadly explain the observed population trends of the species considered in their model. In this thesis, the Antarctic ecosystem is outlined briefly and details are given of the main krill-eating predators including whales, seals, fish and penguins, together with an historical record of the human harvesting in the region. The abundances and per capita krill consumption of the krill-predators are calculated and used to determine the main krill-predators to be used in the updated model developed. These predators are found to be the blue, fin, humpback and minke whales and crabeater and Antarctic fur seals. The three main ship surveys (IDCR/SOWER, JARPA and JSV) used to estimate whale abundance, and the abundance estimation method itself (called distance sampling), are summarised. Updated estimates of abundance and trends are listed for the main krill-predators. Updated estimates for the biological parameters needed for the ecosystem model are also reported, and include some differences in approaches to those adopted for the Mori-Butterworth model. The background to the hypothesis of a krill-surplus during the mid-20th century is discussed as well as the effects of environmental change in the context of possible causes of the population changes of the main krill-feeding predators over the last century. Key features of the results of the updated model are the inclusion of a depensatory effect for Antarctic fur seals in the krill and predator dynamics, and the imposition of bounds on K_a (the carrying capacity of krill in Region a, in the absence of its predators); these lead to a better fit overall. A particular difference in results compared to those from the Mori-Butterworth model is more oscillatory behaviour in the trajectories for krill and some of its main predators. This likely results from the different approach to modelling natural mortality for krill and warrants further investigation. That may in turn resolve a key mismatch in the model which predicts minke oscillations in the Indo-Pacific region to be out of phase with results from a SCAA assessment of these whales. A number of other areas for suggested future research are listed. The updated model presented in this thesis requires further development before it might be considered sufficiently reliable for providing advice for the regulation and implementation of suitable conservation and harvesting strategies in the Antarctic.

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Contents

To my grandparents

Huri Moosa	*01/02/1936 - 04/10/2007*
Essa Ismail Moosa	*06/10/1936 - 19/09/2012*
Moosa Adam Vasta	*23/08/1931 - 29/12/2004*
Zuleikha Adam Vasta	*12/09/1930 -*

Chapter 1

Introduction and overview of thesis

1.1 Background

The aim of this thesis is to update the Mori-Butterworth (2006) Antarctic ecosystem model, detailed in Mori (2005), as this model is a useful tool for understanding the dynamics of the Antartcic ecosystem and required updating in light of new information that has since become available.

The Mori (2005) study attempted to explain the population dynamics of major species in the Antarctic using predator-prey interactions only. Krill (euphausiids) is the dominant prey species in the Antarctic ecosystem with *Euphausia superba* being the main krill species - a large sustainable harvest of more than 10 million tonnes annually may well be possible from this resource (from *https://www.ccamlr.org/en/fisheries/krill-fisheries-and-sustainability* [Accessed 14/06/2017]).

Mori (2005) gives three reasons for why understanding the krill-predator dynamics in the region is important.

1) *Abundance and trend estimates of the Antarctic krill-predators*

At the time of the Mori study in 2005, roughly 50 years had passed since the large baleen whales came under protection in the Antarctic after they had been harvested extensively in the region during the early 20^{th} century. Since their protection, some studies had reported the recovery of these previously heavily exploited whale species whilst other studies had reported decreases in other krill-eating whale species that were not as extensively harvested. Mori (2005) commented that these differing trends, along with several studies consistent with Laws' (1977, 1962) "krill surplus" hypothesis (where the surplus had arisen from the near extinction of the large baleen whales in the Antarctic), strengthened the theory that the main predators of the region were competing for the same resource, krill, and were influencing krill's and each other's population dynamics.

2) *Climate change*

Mori (2005) noted that there were a number of publications, such as Kasamatsu *et al.* (2000), about the impact of climate change (in the form of melting sea-ice and sea-level rise) on the marine species in the Antarctic and their respective environments. In contrast, there was little by way of analyses which attempted to explain the population trends of these species in terms of predator-prey interactions. Given that the past whaling and sealing in the region led to the largest human-induced disturbance of any marine ecosystem, this was surprising. The respective roles of climate change and predator-prey impacts on population trends needed further clarification.

3) *Multi-species models in fisheries management*

Mori (2005) emphasised that there was a need in fisheries management to consider the impacts of fishing on the ecosystem as a whole rather than just the target species. In the development of multi-species models of marine ecosystems, the Antarctic provided a useful case study due to its relatively simple food web dominated by krill - if a multi-species model proved successful in the Antarctic, it could encourage the implementation of results from similar models elsewhere. Furthermore, with a reliable multi-species model, organisations like the International Whaling Commission (IWC; see Glossary) and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR; see Glossary) would be able to implement suitable conservation and harvesting strategies for the Antarctic ecosystem better.

Mori (2005) concluded that it **was** possible to explain the observed population trends of the main Antarctic krill-predators through predator-prey interactions only. However, she highlighted that there was room for improvement to her model. She acknowledged that in order for a reliable krill-predator Antarctic ecosystem model to be developed, estimates of the consumption of krill by the other krill-predators such as birds, fish and cephalopods not included in her model needed to be developed. This information could then be used to determine which other krill-predators merited inclusion in her ecosystem model. Furthermore, at the time of Mori (2005), abundance estimate analyses from some major seal and whale sighting surveys were unfinalised. Once available, results from these analyses could be used to improve the Mori-Butterworth (2006) model.

Mori (2005) acknowledged that the Mori-Butterworth (2006) model was only a first step to producing a realistic and reliable krill-centric predator-prey Antarctic ecosystem model, and that not all plausible variations of her model had been explored. However, with further development, she hoped that it would one day be used to provide scientific advice for suitable sustainable harvesting strategies in the Antarctic.

1.2 Objective

Roughly 10 years have passed since the Mori (2005) study. The seal and the whale sighting survey analyses have been completed. Other new analyses, information and data on the Antarctic krill-predators have become available as well.

This thesis aims to update the Mori-Butterworth (2006) model by taking this new information and data into account. The thesis also aims to examine the effect of climate change on the Antarctic ecosystem, thus broadening the understanding of the population dynamics within the region. These updates and refinements include the following.

1) Updates to the various species' abundance and trend estimates as well as to whale catch data*.

2) The inclusion of minke whale stomach contents' weight trend data, to examine their consistency with the predictions of the model*.

3) A comparison between two differently defined sets of regions to test the sensitivity of the model's results.

4) Linkage to the impact of climate change on the Antarctic ecosystem.

5) Examination of the sensitivity of the model's results to the proportion of fin whales assumed to feed in the region considered i.e. south of 60°S.

1.3 Other recent associated literature

The Mori-Butterworth (2006) model was pioneering work, a first of its kind. As a result, it garnered much interest, especially in relation to multi-species modelling. The model has been mentioned in several papers - two examples are highlighted below.

Surma *et al.* (2014) examined the ecological plausibility of a "krill surplus" hypothesis and the effects of whaling on the Southern Ocean food web using the *Ecopath with Ecosim* (mass-balance) ecosystem modelling framework. Their reasoning was based on Smetacek (2008) and Nicol *et al.* (2010) which both hypothesized that rorquals (one of the four recognized baleen whale families) recycled the iron contained in their prey (krill) and dispersed this nutrient down the water column in the form of faeces where the iron fertilized diatoms (see Glossary) and promoted primary productivity. This enhanced primary productivity implied an increase in the krill abundance which sustained the ecosystem's high carrying capacity for rorquals. Thus, with the extensive harvests of the rorquals, they argued that this positive feedback collapsed causing a decrease in primary production and krill abundance and the subsequent, rather slow, recovery of the rorquals. Some of the scenarios analysed in Surma *et al.* (2014) were in agreement with the conclusions drawn from the Mori-Butterworth (2006) model. Surma *et al.* (2014) summarised that the Mori-Butterworth (2006) model was a mathematical population modelling study which found that Laws' (1977) "krill surplus" biomass estimate was somewhat too high and that top-down predator-prey interactions alone could explain the 20^{th} century population trends in the Antarctic krill-predators, though rorqual population growth had to achieve relatively high values for this to occur.

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*The initial aim of this thesis was to consider all the objectives from 1) to 5). However, due to time constraints, only those indicated by a * were able to be examined; work on objective 3) was initiated, and the groundwork to address objective 4) was undertaken through the development of a summary of its background, which is reported in Chapter 9.

Surma *et al.* (2014) concluded that the effects of the rorqual depletion on the Southern Ocean food web were more complex than previously thought.

The Mori-Butterworth (2006) model was criticised in Willis (2014). Willis (2014) was an update of Willis (2007) where the latter hypothesized that krill could detect the presence of whales by some mechanism and as a result, respond to the possible threat. Willis (2014) surmised that the mechanism was *whale faeces odour* with the whale faeces playing a role in the iron-feedback described in Surma *et al.* (2014), though Willis (2014) mentioned that krill excrement also promoted primary production.

Willis (2014) stated that the Mori-Butterworth (2006) model failed to provide an explanation for the observed changes in krill abundance for two reasons: the Mori-Butterworth (2006) hypothesis was falsified through minke genetic studies (Ruegg *et al.*, 2010) and contemporary reports such as Marr (1962), and that the model's initialisation was implausible. Willis (2014) further stated that the Mori-Butterworth (2006) model was merely convenient for those wanting to support a krill or minke whale fishery as their current abundances were higher than their pristine abundances. Willis (2014) concluded that the hypotheses developed in his study (krill responding to the threat of whales through the smell of faeces and thus changing their daily migrations) should be tested and developed further. The Willis (2014) article is addressed in more detail in Chapter 11 which responds to a number of his criticisms.

1.4 Thesis outline

This thesis consists of two parts.

1) A review of the available data and information regarding the krill-predator dynamics in the Antarctic ecosystem.

2) Updates and refinements of the krill-predator model for the Antarctic ecosystem.

1.4.1 Section 1: Review of the data available for the Antarctic multi-species model development

A brief outline of Section 1 follows below:

Chapter Two explores the suborders *Mysticeti* (baleen whales) and the families *Phocidae* (earless seals) and *Otariidae* (eared seals). It also discusses their role in the Antarctic food web.

In Chapter Three, the history of the whale, seal and krill harvests by humans in the Antarctic ecosystem is discussed, with the main focus being on the krill-predators highlighted in Chapter Two.

Chapter Four analyses the available information on the consumption of krill by the krill-predators; this is used to determine which predators are to be included in the ecosystem model developed in this thesis.

Chapter Five reviews the existing abundance and trend estimates for the main baleen whale species in the Antarctic ecosystem, whilst Chapter Six provides a similar account for the main seal species.

In Chapter Seven, the existing abundance and trend estimates for krill and its other predators (not included in the model) are reviewed.

Chapter Eight addresses the choice of parameter values and bounds used in the ecosystem model.

1.4.2 Section 2: Development of a krill-centric Antarctic multi-species model

A brief outline of Section 2 follows below.

In Chapter Nine, the hypothesized causes of the population dynamics of the krill-feeding predators are discussed: Laws' (1977) "krill surplus" hypothesis and the impact of climate change on the Antarctic ecosystem are considered.

Chapter Ten briefly discusses the development and results of the Mori-Butterworth (2006) model.

In Chapter Eleven, the updated and refined Mori-Butterworth model and its results are presented. The criticisms of the Willis (2014) article are also addressed.

Chapter Twelve gives a brief summary of the main conclusions drawn from this thesis and suggests future work to improve the ecosystem model further.

Chapter 2

The suborder *Mysticeti* and the families *Phocidae* and *Otariidae* in the Antarctic food web

2.1 Overview of Chapter

This chapter discusses the suborder *Mysticeti* (which includes the baleen whales) and the seal families *Phocidae* and *Otariidae* with the focus being on the krill-predator species that are found in the Antarctic. Other krill-predators found in the Antarctic are also discussed. The role of these krill-predators in the Antarctic food web is reviewed at the end of the chapter. The aim of this chapter is to identify the main krill-predators (based on diet information only) within the region and to consider their role in the Antarctic food web.

2.2 General features of the suborder *Mysticeti*

The baleen whales belong to the suborder *Mysticeti*, one of the whale divisions of the Order *Cetacea*, where the whales are characterized by their baleen plates instead of teeth (the *Odontoceti*). Baleen plates are comprised of keratinized tubules typically organized into transverse cornified plates suspended from epithelial tissues of the roof of the mouth of the whale (Berta and Demèrè, 2009; see Glossary). These plates are used to filter food, mostly small marine organisms like krill (euphausiids) from the surrounding waters.

Bannister (2009) states that in general, baleen whales are larger than the toothed whales, and female baleen whales are bigger than their male counterparts. Furthermore, in general, Southern Hemisphere baleen whale species are bigger than their Northern Hemisphere equivalents. He further identifies four recognized baleen whale families, distinguished by their internal and external features. Only some of their main external features are highlighted below.

1) *Balaenidae* (known as the *right whales* and comprising of the bowhead whale and the three right whale species): Their baleen plates are black, narrow and long whilst their upper jaw is arched. Their heads are roughly one-third of their body length. In general, they lack ventral grooves and their lower lips are big and bowed.

2) *Balaenopteridae* (known as the *rorquals* and consisting of the blue, minke (common and Antarctic), fin, humpback, Bryde's, Eden's, Omura's and sei whales): Their black baleen plates are short and wide, and their upper jaw is unarched and long. Their heads are less than a quarter of their body length hence are relatively small. Most of these whales have a small dorsal fin and a number of ventral grooves.

3) *Neobalaenidae* (consisting of the pygmy right whale): They appear to have a combination of *Balaenidae* and *Balaenopteridae* features. Their heads are about a quarter of their body length and they have a dorsal fin like the *Balaenopteridae.* However, their baleen plates are yellowish-white, bordered black, but are long and narrow. Their upper jaw is arched and their lower lip is bowed like the *Balaenidae.*

4) *Eschrichtiidae* (consisting of the gray whale): They lack a dorsal fin. Their heads are short and narrow and instead of ventral grooves, they have a few "creases" near their throat. Their baleen plates are yellowish-white like the *Neobalaenidae*, and are relatively small compared to the other families.

The whale species in these families are described briefly below, focusing on their main characteristics, their diet and their main distribution regions.

2.3 *Mysticeti* whale species

The whale species in this suborder include the blue whale (*Balaenoptera musculus*), bowhead whale (*Balaena mysticetus*), Bryde's whale (*Balaenoptera edeni*, *Balaenoptera brydei*), fin whale (*Balaenoptera physalus*), gray whale (*Eschrichtius robustus*), humpback whale (*Megaptera novaeangliae*), minke whale (*Balaenoptera acutorostrata*, *Balaenoptera bonaerensis*), Omura's whale (*Balaenoptera omurai*), pygmy right whale (*Caperea marginata*), right whale (*Eubalaena glacialis*, *Eubalaena australis*, *Eubalaena japonica*) and the sei whale (*Balaenoptera borealis*).

The blue whale is the largest of the baleen whales, as well as being the "largest animal alive today" (Yochem and Leatherwood, 1985). In general, blue whales are greyish/steel-blue in colour with the undersides of their flippers being white. Blue whales in the North Atlantic and North Pacific migrate to their summer feeding grounds in the Arctic waters whilst the Southern Hemisphere blue whales feed mainly in the circumpolar belt between the Antarctic pack-ice and the Antarctic Convergence (Yochem and Leatherwood, 1985; see Figure 2.1; see Glossary). Sears and Perrin (2009) state that blue whales feed almost entirely on euphausiids.

Bowhead whales are generally black/brown in colour with occasional white-greyish areas on parts of their bodies such as their chin and lower jaw. Bowheads are closely related to right whales, except that they are a bit longer, have longer baleen plates and lack callosities (see Glossary), amongst other differences (Kenney, 2009). They generally live close to the Arctic sea-ice for much of the year and "have never occurred in the Southern Hemisphere" (Rugh and Shelden, 2009). Their diet consists mostly of copepods and euphausiids (Rugh and Shelden, 2009; see Glossary).

The Bryde's whale, often confused with the sei whale (Kato and Perrin, 2009), is bluish/black in colour with the ventral side of their body being a slight yellow. The most distinctive feature of the Bryde's whale is the three ridges that extend from the back of their snout-tip to their blowhole (Kato and Perrin, 2009; Cummings, 1985). These whales occur between 40°N and 40°S, in the tropical and temperate waters of the North and South Pacific, Indian Ocean and North and South Atlantic, and thus do not enter Antarctic waters. Additionally, they are considered to be opportunistic feeders (unlike the sei whale), with their diet consisting of pelagic fish, euphausiids, copepods and cephalopods (Kato and Perrin, 2009; see Glossary).

The fin whale is the second largest baleen whale. These whales are dark grey in colour with the ventral side of their body being white. They have an unique ridge behind the back of their dorsal fin (Gambell, 1985). During the austral summer, fin whales are distributed roughly south of 50°S but do not extend as close to the ice-edge as do blue and minke whales. The older and bigger whales penetrate further south than the younger and smaller ones. Once in Antarctic waters, fin whales feed mainly on krill (Gambell, 1985). Aguilar (2009) states that since the fin whale's food supply and distribution range coincides with some of the other *Balaenopteridae*, interspecific competition is likely to occur, especially with the blue whale.

Gray whales are the only living species of the family *Eschrichtius*. They are grey in colour with white mottling and are colonised by whale lice and barnacles (Wolman, 1985). Gray whales are the most coastal of the large baleen whales and feed on a variety of benthic, planktonic and nektonic organisms (Jones and Swartz, 2009; Wolman, 1985; see Glossary). Jones and Swartz (2009) states that they are found close to the productive neritic and estuarine waters (see Glossary) of the North Pacific Ocean and the adjacent Arctic waters.

The most prominent features of humpback whales are their long flippers, roughly one third of their entire body length, and the tubercules (see Glossary) on their head and jaw. In general, humpback whales are black in colour with the undersides of their body being either white, black or mottled (Clapham, 2009). During the austral summer, humpback whales feed exclusively on euphausiids within the Antarctic circumpolar waters (Clapham, 2009; Winn and Reichley, 1985).

Minke whales are the smallest of the *Balaenopteridae* and the second smallest of the baleen whales. In general, minke whales are black/blue/grey in colour with their ventral side being light in colour. *Balaenoptera acutorostrata*, known as the common minke whale, is found almost exclusively in the North Atlantic and the North Pacific, while *Balaenoptera bonarensis* or the Antarctic minke whale is found in the Southern Hemisphere, so the focus in this thesis will be on the latter. Antarctic minke whales have dorsal fins that are closer to their tail flukes and are more slender compared to the common minke whale (Stewart and Leatherwood, 1985). During the austral summer, these whales are found from about 60°S to the Antarctic ice-edge, sometimes occurring in polynyas (see Glossary) and in the loose pack-ice. They feed exclusively on euphausiids (Perrin and Brownell Jr., 2009).

Yamada (2009) states that the main feature of Omura's whale that distinguishes it from Bryde's whale is the absence of lateral ridges on the dorsal surface of its head. In general, this whale is black with its underside being off-white in colour. Of all the *Balaenopteridae*, it has the smallest number of baleen plates. Omura's whale does not enter Antarctic waters and little is known about its diet (Yamada, 2009).

The smallest baleen whale is the pygmy right whale which is often confused with the minke whale. These whales are medium/dark grey in colour with their underside being white/pale grey, and they have very fine bristles for their baleen. Kemper (2009) states that they are found in the Southern Hemisphere only and are known to be circumpolar, ranging between 30°S and 55°S in temperate and sub-Antarctic waters. Little information exists on their diet which is surmised to consist of copepods, euphausiids and possibly some small planktonic organisms (Kemper, 2009).

There are currently three known species of right whales: the North Atlantic right whale (*Eubalaena glacialis* which does not enter the Southern Hemisphere), the North Pacific right whale (*Eubalaena japonica* which also does not enter the Southern Hemisphere) and the southern right whale (*Eubalaena australis*) which is found in the Southern Hemisphere waters. In general, southern right whales are black in colour with occasional white patches. Their most prominent feature is the callosities on their heads which are inhabited by barnacles. Their feeding grounds are known to be offshore, pelagic areas associated with regions of high productivity between the Subtropical Convergence and the Antarctic Convergence (see Figure 2.1; see Glossary). Southern right whales do not enter Antarctic waters but rather inhabit the sub-Antarctic waters. Their diet consists mostly of krill and zooplankton (Kenney, 2009).

Finally, the sei whale is the third largest baleen whale and is found in all the oceans. In general, they are dark grey in colour with dark grey baleen plates. Laws (1977) assumed that half of the total sei population feeds south of the Antarctic Convergence (Figure 2.1) during the summer feeding months. However, Horwood (2009) states that sei whales rarely penetrate as far south as blue, fin and minke whales, and that their summer concentrations are mainly between the Subtropical and Antarctic Convergences (see Figure 2.1). This suggests that sei whales hardly enter Antarctic waters. Ohsumi *et al.* (1970) reinforce this by commenting that the highest densities of sei whales are found in the 40-50°S zone, fin whales 50-60°S, and minke and blue whales 60-70°S. The sei whale's diet includes euphausiids, copepods, the occasional fish and squid (Horwood, 2009).

In summary, as clear from the above, the main krill-feeding baleen whales within the Antarctic region are the blue, humpback, fin and minke whales.

2.4 General features of the *Phocidae*

Phocidae or the "earless/true" seals are one of the main groups in the seal superfamily *Pinnipedia*. They are distinguished from the *eared* seals (known as the *Otariidae*) by "the absence of external visible ear pinnae, ... [their] generally larger size and the inability to draw their hind (back) limbs forward under their bod[ies] when on land" (Hammill, 2009; King, 1983; see Glossary). Furthermore, their lack of tusks and jagged tongues differentiates them from the walrus family, *Odobenidae*.

In the Southern Hemisphere, there are five main species of earless seals, namely the southern elephant seal (*Mirounga leonina*), the Weddell seal (*Leptonychotes weddellii*), the Ross seal (*Ommatophoca rossii*), the leopard seal (*Hydrurga leptonyx*) and the crabeater seal (*Lobodon carcinophagus*). These seal species are described briefly below, focusing on their main characteristics, their diet and their main distribution regions.

2.5 *Phocidae* seal species

The southern elephant seal is a land breeder, found in sub-Antarctic and Antarctic waters, roughly between 16°S at St Helena to 78°S (Hammill, 2009; Ling and Bryden, 1981). These seals have dark-grey skin with silver/grey hairs that discolour with time due to dirt and excrement making their coats appear yellow/brown. They feed mainly on cephalopods and fish (Ling and Bryden, 1981).

The Weddell seal is a fast-ice breeder found within Antarctic waters (Hammill, 2009; see Glossary). They have a short snout, big brown eyes, short whiskers and are black in colour with irregular grey/silver streaks (Thomas and Terhune, 2009; Kooyman, 1981c). Their diet consists mainly of fish species (Thomas and Terhune, 2009).

Another seal inhabiting Antarctic waters is the Ross seal, a pack-ice breeder (Hammill, 2009). They have small mouths with small incisors and canines, which are bent backwards, an adaptation to their diet. Ross seals have short black fur on their backs with greyish/silver streaks on their sides. These seals feed mainly on cephalopods (roughly 47%), fish (roughly 34%), krill and invertebrates (roughly 19%) (Thomas and Rogers, 2009).

The leopard seal is another pack-ice breeder found within Antarctic waters and occasionally in sub-Antarctic waters (Hammill, 2009; Rogers, 2009). Leopard seals are dark-grey/black in colour, with their sides being almost light-grey/blue in colour. These seals are built for speed - they are slender and have long fore-flippers (Kooyman, 1981b). They prey on a variety of animals: fish, cephalopods, sea-birds and other seals (particularly juvenile crabeater seals) and krill (Rogers, 2009). Rogers (2009) states that krill makes up the largest proportion of their diet, but mainly during the winter months when other prey are scarce.

Finally, the crabeater seal is a pack-ice breeder that is found within Antarctic waters (Hammill, 2009; Bengston, 2009). Bengtson (2009) states that crabeater seals have finely divided lobed teeth, a possible adaptation to their diet, and are rather agile on ice. These seals shed their fur towards the end of summer, after which they are generally dark brown in colour. As their fur ages, its colour lightens until the seal is almost a "uniform blonde" resulting in the name "white Antarctic seal" (Kooyman, 1981a). Crabeater seals depend entirely on krill, more specifically the Antarctic krill, *Euphausia superba* for food (Bengston, 2009).

Of the *Phocidae* species, the only krill-predators within the Antarctic are the crabeater, Ross and leopard seals. However, due to the small proportion of krill in their diet, Ross seals are not considered further in this thesis.

2.6 General features of the *Otariidae*

Otariidae or the "eared" seals, consisting of the fur seals and the sea lions, are another major group in the seal superfamily *Pinnipedia*. Their main characteristics are their external ear flaps and their ability to rotate their back flippers forward and travel on all four limbs. Sea lions are covered by a single layer of hair whereas fur seals are covered by two layers - a stiff, outer layer of guard hairs and a thick, waterproof, inner layer of fine hair (Gentry, 2009). The majority of sea lions live in temperate or equatorial waters (Gentry, 2009), so that they are not considered further in this thesis.

Of the fur seals, only two species live in the Southern Hemisphere sub-polar and polar regions: the Antarctic fur seal (*Arctocephalus gazella*) and the sub-Antarctic fur seal (*Arctocephalus tropicalis*) (Gentry, 2009). These two seal species are described briefly below, with a focus on their main characteristics, their diet and their main distribution regions.

2.7 *Otariidae* seal species

Antarctic fur seals have thick bodies and long necks which make their heads appear small. Their bodies are covered by hair except for their ear tips, the "palmar surfaces" of their flippers and their snout (Forcada and Staniland, 2009). On land, Antarctic fur seals are dark brown in colour with their undersides being a pale brown (Forcada and Staniland, 2009). Bonner (1981) states that Antarctic fur seals are found on the islands south of the Antarctic Convergence and north of about 65°S, where South Georgia in the South Atlantic is their main breeding site (see Figure 2.1). Antarctic fur seals feed almost exclusively on krill, especially those at South Georgia, with the occasional fish and squid in their diet (Arnould, 2009; Bonner, 1981). Arnould (2009) states that the recent rapid recovery of the South Georgia population is thought to have been facilitated by its predominant prey, Antarctic krill (*Euphausia superba*), being found in super-abundance in the surrounding waters.

Sub-Antarctic fur seals differ from the Antarctic fur seal by their fur colour: their chest and face are pale-yellow/cream while their back and top of their head are dark-brown/grey in colour (Arnould, 2009). Bonner (1981) states that sub-Antarctic fur seals breed on the islands north of the Antarctic Convergence (in the sub-Antarctic as their name suggests) - in the Atlantic Ocean, they breed on Gough Island and occasionally on Tristan da Cunha, Nightingale and Inaccessible Islands, whilst in the Indian Ocean, they breed on Ile Amsterdam, Ile Saint Paul, Prince Edward and Marion Islands (see Figure 2.2). Bonner (1981) further states that on Marion Island, these seals prey on cephalopods and euphausiids whilst those at Ile Amsterdam prey on squid and penguins.

Thus the main krill-predator of the *Otariidae* species within the Antarctic is the Antarctic fur seal.

2.8 Other krill-predators

2.8.1 Fish

For many pelagic, mesopelagic and demersal fish (see Glossary) inhabiting Antarctic waters, euphausiids are the most abundant food organism found in their diet. As a food resource, krill in some form is eaten by all the development stages of fish, e.g. fish larvae eat krill eggs (Knox, 2007).

Regarding the deep-water fish, krill is eaten mostly by the *Notothenioidea* which include two main krill-eating families, both of which have a typical life span of 10-20 years: the *nototheniids* and the *channichthyids*, the latter being unique as they are deficient in oxygen-binding haemoglobin (Kock *et al.*, 2012; Knox, 2007). Two important species from these families are the *Notothenia rossii* (marbled rockcod) and the *Champsocephalus gunnari* (mackerel icefish) respectively.

The marbled rockcod spend their earlier years close to the shore before moving into open waters to feed on krill. Once they start feeding on krill, their growth rates begin to increase. Mackerel icefish are nocturnal krill feeders, feeding in the surface waters. During the day, these fish migrate to the bottom waters (Laws, 1985). In general, the mackerel icefish and the marbled rockcod associate with krill aggregations and/or drifting or fast-ice (Knox, 2007). In particular, they feed heavily on *Euphausia superba* in the Atlantic sector and on other euphausiids in the Indian sector of the Southern Ocean. Mackerel icefish are unable to consume other prey that have roughly the same energy content as krill. Thus, at times when krill is scarce, mackerel icefish stocks have decreased (Kock *et al.*, 2012) which indicates the importance of krill to these fish species.

Before the start of the heavy fishing of these two species off South Georgia in the 1977/78 austral summer season, the marbled rockcod and the mackerel icefish is estimated to have accounted for roughly 80% of the total krill consumption amongst seven fish species (*Champsocephalus gunnari*, *Champsocephalus aceratus*, *Pseudochaenichtjys georgianusm*, *Chionodraco rastrospinosus*, *Notothenia rossii mamorata*, *Notothenia larseni* and *Notothenia gibberifrons*) (Knox, 2007; Kock, 1985).

Amongst the mesopelagic fish species, the *myctophids*, also called lanternfish, are known to feed on krill and other euphausiids, especially the larger lanternfish species of the genera *Electrona* and *Gymnoscopelus* - Kock *et al.* (2012) state that they consume krill in large quantities.

In the summer, lanternfish move upwards in the water column, feeding in the epipelagic zone (see Glossary) to take advantage of the high plankton productivity. In the winter, they descend to just above the Circumpolar Deep Water (CDW; see Glossary) which contains planktonic crustaceans (Knox, 2007). This suggests that lanternfish feed on krill during the summer months only when krill is more readily available.

In summary, within the Antarctic, the main krill-eating demersal fish are the mackerel icefish and the marbled rockcod, whilst the main krill-eating mesopelagic fish are the lanternfish.

2.8.2 Penguins

Belonging to the order *Sphenisciformes* and to the single family *Spheniscidae*, all penguins are restricted almost entirely to the Southern Hemisphere. Six species of penguin live within the Antarctic region which is part of the CAMLR Convention Area (Ratcliffe and Trathan, 2011) - their diet and some of their main behaviour patterns are highlighted below.

Emperor penguins (*Aptenodytes forsteri*) are the heaviest and tallest of all the penguins. They feed mainly on fish, squid (particularly in the summer when shelf areas become more extensive) and crustaceans (particularly in winter, close to the shelf-edge). Juvenile emperor penguins travel further north to the Antarctic Polar Front (APF) (see Figure 2.1; see Glossary) for the duration of the summer season, possibly to take advantage of the high abundance of crustaceans and fish there.

The second largest penguin is the king penguin (*Aptenodytes patagonicus*). These penguins feed mainly on fish, more specifically on myctophids, during the summer. During the winter, chicks are often fed other fish species and squid while adult penguins continue consuming myctophids for themselves. During the summer, these penguins usually forage close to the APF or in the mesoscale eddies associated with the front. The position of the colony is often close to these oceanic features, probably because myctophid concentrations are higher and more readily available near the APF.

The smallest and the most common penguin found along the Antarctic coast is the Adélie penguin (*Pygoscelis adeliae*). Found mostly on the pack-ice (Knox, 2007), the diet of these penguins consists mostly of euphausiids and fish, varying according to the habitat surrounding the colony. Penguins over the shelf feed on both euphausiids and fish whilst the penguins in oceanic waters feed almost entirely on *Euphausia superba* (Ratcliffe and Trathan, 2011).

Chinstrap penguins (*Pygoscelis antarctica*), identified by the thin black band beneath their heads, are found mostly in the open waters around Antarctica (Knox, 2007). Their diet consists almost entirely of *Euphausia superba*, more so during their breeding season which takes place in the austral summer. The majority of chinstrap penguins inhabit the Scotia Sea (see Figure 2.1) where krill is the most abundant pelagic crustacean in the area. These penguins forage in open water and tend to avoid the pack-ice areas (Ratcliffe and Trathan, 2011).

Ratcliffe and Trathan (2011) state that the diet of gentoo penguins (*Pygoscelis papua*) consists of a wide range of crustacean fish taxa.

The macaroni penguin (*Eudyptes chrysolophus*) and the royal penguin (*Eudyptes schlegeli*) are two species of crested penguin living in the Antarctic where the royal penguin has a white face and chin while the macaroni penguin has a black face and chin. Royal penguins are found only on Macquarie Island (see Figure 2.2), whilst macaroni penguins are found on most of the Antarctic islands (Ratcliffe and Trathan, 2011). The diet of both these penguin species consists mostly of euphausiids and myctophid fish. Macaroni penguins at South Georgia feed almost entirely on *Euphausia superba*, while the penguins on the northern and eastern islands feed on the dominant crustacean in these regions, *Euphausia vallentini* and myctophids. Both macaroni and royal penguins forage around the Antarctic Convergence or shelf-edges, depending on the season (Ratcliffe and Trathan, 2011; see Glossary).

Of the penguin species, the main krill-predators within the Antarctic are the Adélie, chinstrap, macaroni and royal penguins.

2.8.3 Other

Several species of squid are known to be krill-predators. Fillippova (2002) studied the stomach contents of 325 squid specimens, taken from Antarctic expeditions between 1967 and 1987. The study suggested that there were two trophic squid groups in the Antarctic. The first group included the *Brachioteuthis* squid species. These species inhabit the surface pelagic waters of the Antarctic and feed almost entirely (roughly 98%) on crustaceans such as euphausiids (which dominate their diet, especially *Euphausia superba*), hyperiids and mysids (see Glossary). The remaining 2% of the squid diet consists of fish and other squid species. This reinforces perceptions of the important role of squid as a krill-predator. The second squid trophic group inhabits the mesopelagic and bathypelagic Antarctic zones (see Glossary), and has no direct connection to krill, so that it will not be discussed here.

Squid are typically short-lived species with fast growth rates (Nesis, 1983), making their dynamics difficult to include in a multi-species model though such a study was attempted by Mkango (2008). In general, information on squid abundance and consumption rates is scarce (Knox, 2007). As a result, squid are not included in the multi-species model developed later in this thesis despite their being important krill-predators within the Antarctic ecosystem.

2.9 The Antarctic food web

Knox (2007) states that the Southern Ocean is a rich, "highly productive plankton-pelagic system supporting (at least in the past) great populations of whales and millions of penguins, and seals, and abundant intermediate populations of fish and cephalopods, depending on the near surface productivity". Knox (2007) further highlights the main features of the Southern Ocean system or the *Antarctic ecosystem* as follows.

1) It is probably the largest oceanic ecosystem on the planet - an entire ocean surrounds a landmass, and is in connection to three other oceans (the Pacific, Atlantic and Indian Oceans) - see Figure 2.1.

2) It is a semi-enclosed ecosystem where the Antarctic Convergence, which accompanies the Antarctic Circumpolar Current (ACC), forms the northern boundary of the system whilst the Antarctic continent forms its southern boundary - see Figure 2.1 and Glossary.

3) The ecosystem is old and well-established - the major air and ocean circulation patterns are deep-rooted in the system.

4) Most animal species residing in the Antarctic are distributed circumpolarly in the region. The main difference in their distribution is related to *productivity*, with some areas being more productive than others.

5) The qualitative and quantitative characteristics of the fundamental processes in the system are driven by the distribution of *Euphausia superba*, an important species throughout the entire system as it connects the secondary consumers (krill-predators) to the primary producers (phytoplankton) within the Antarctic food web - see Figure 2.3.

A number of animals within the Antarctic feed primarily on krill. These include baleen whales, seals, penguins, seabirds, squid and fish - most of which have been discussed earlier in this chapter (see Figure 2.3).

Baleen whales are important in this ecosystem as they help determine the relative abundances of *Euphausia superba* (and consequently phytoplankton) and the other krill-consumers. Before their heavy exploitation, baleen whales were major krill-consumers. At the time they came under protection, their stocks had been reduced and other smaller baleen whales, seals, sea-birds and fish had a better chance to feed on the krill (Knox, 2007).

The distribution of penguins within the Antarctic is highly influenced by oceanographic and environmental features such as islands or ice-free grounds suitable for breeding, fronts, pack-ice zones and ice-shelves (Laws, 1985). These birds also play an important role in the Antarctic ecosystem. They act as krill- and zooplankton- predators, and they consume larval fish. Furthermore, penguins impact the terrestrial areas of the Antarctic ecosystem, more specifically, their breeding areas. Their time on land supports scavengers, releases organic matter in the form of eggs, excreta, feathers and carcasses (where the nutrients are taken in by the surrounding vegetation as the soil is nutrient-poor), and they modify the terrain through burrowing into the ground and flattening the sparse vegetation. Sometimes, penguin excrement is washed into the ocean where it acts as a fertiliser, enhancing primary production (Knox, 2007).

Myctophids are energy-rich fish so when they are available, they are preferred by the Antarctic fur seals (especially lactating fur seals) and the chinstrap penguins (especially those that are incubating) even if krill is available nearby. This emphasises the importance of fish in Antarctic food dynamics.

Overall, it can be said that the Antarctic ecosystem is a mature ecosystem, thought to be “network of dynamic systems centred around krill” (Kock *et al.*, 2012) or “a series of of interconnected ecosystems” (Knox, 2007). The feeding activities of krill or *Euphausia superba* impact the structure and functioning of the Antarctic ecosystem.

2.10 Summary

The aim of this chapter was to identify the main krill-feeding predators within the Antarctic and to consider their role in the Antarctic food web.

Considerable detail is provided in describing the differences amongst the whale and seal groups, where the main krill-feeding baleen whales are the blue, minke, humpback and fin whales and the main krill-feeding seals are the crabeater, Ross, leopard and Antarctic fur seals. Due to the small proportion of krill found in the Ross seal diet, these seals are not considered further in this thesis.

This chapter also considered the other krill-predators such as fish, penguins and squid. Of the fish species, only the marbled rockcod, mackerel icefish and lanternfish are considered as they are the main krill-feeding fish as indicated by the literature. Of the penguins, the Adélie, chinstrap, macaroni and royal penguins are considered to be the main krill-feeding penguins. Squid is another important krill-predator but information on this species is scarce. As a result, squid are not considered further in this thesis.

Finally, this chapter explored the dynamics of the Antarctic ecosystem and the role of the krill-predators within it. This served to highlight the importance of krill itself within the Antarctic ecosystem, and hopefully created a strong argument as to why understanding the krill-predator dynamics within the region is very important.

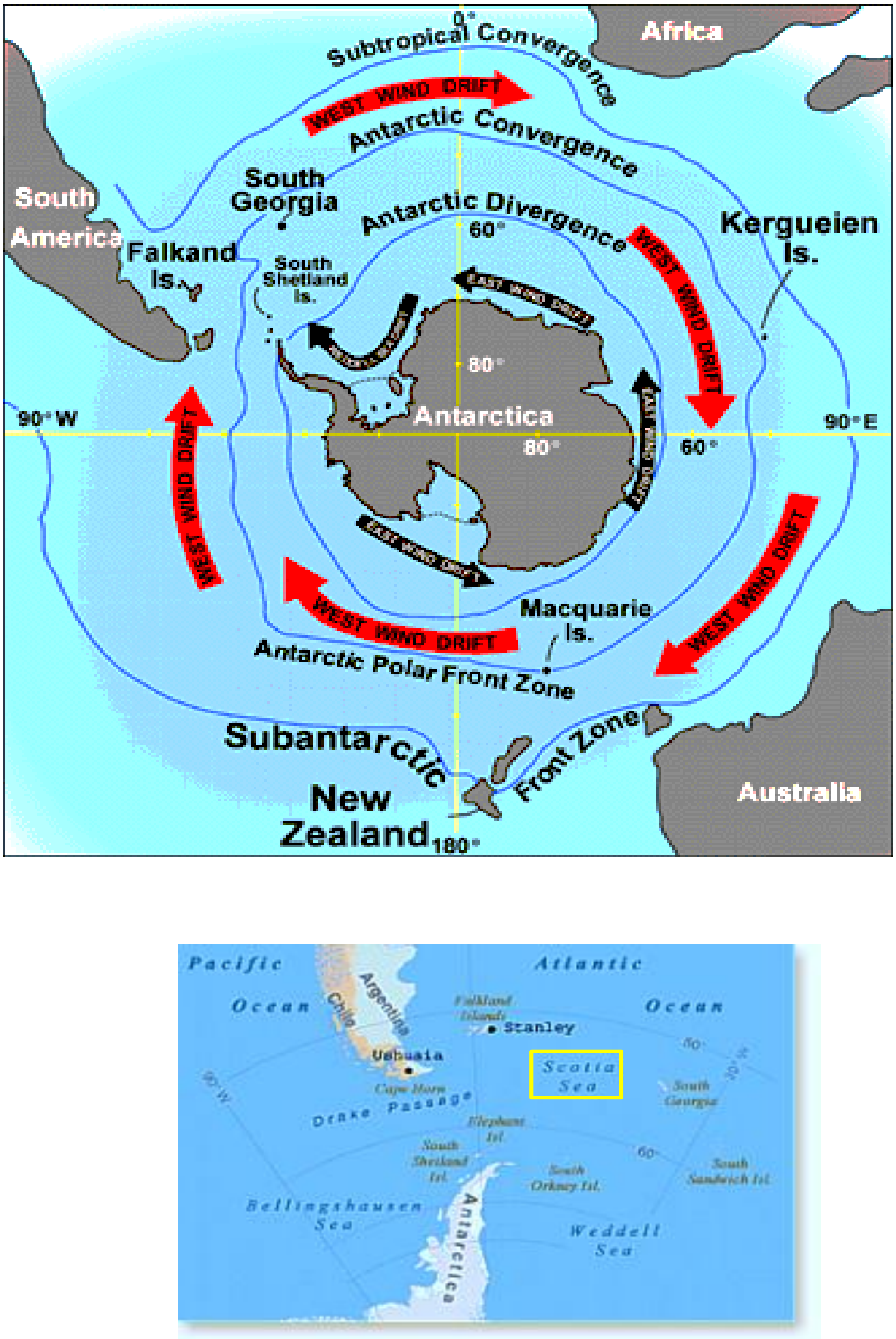

FIGURE 2.1: (Top) A map of the Antarctic Continent with its wind regimes and main fronts. Take special note of the Antarctic Convergence and the Antarctic Divergence (from *http://www.eoearth.org/view/article/150096/* [Accessed on the 29/12/2015]).

(Bottom) A map highlighting the main seas in the Atlantic and Pacific sectors of the Southern Ocean (from *http://www.goldenfleecexp.co.fk/english/expeditions_en.html* [Accessed on the 13/12/2016]).

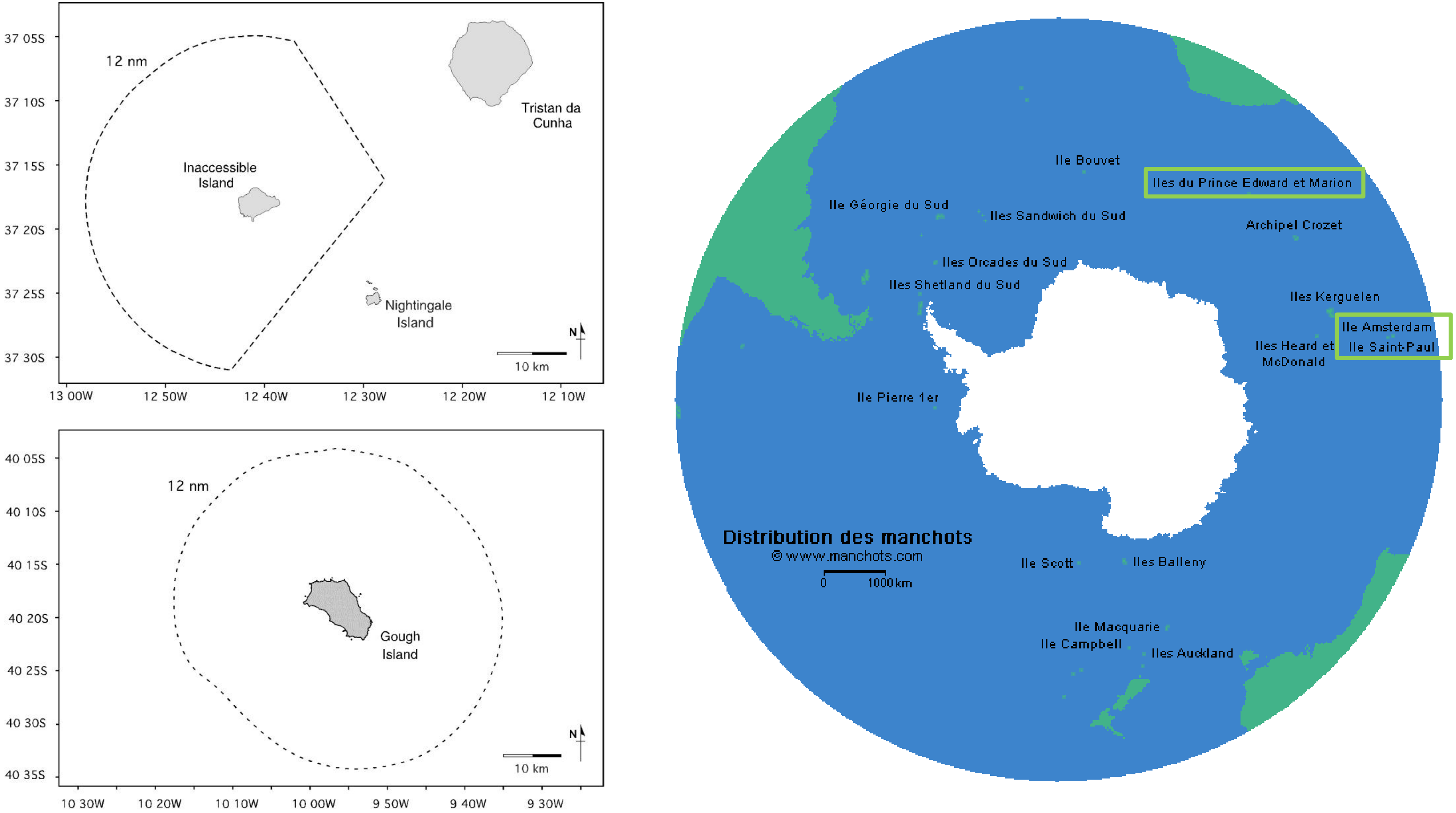

FIGURE 2.2: (Left) A diagram showing the relative positions of Gough, Nightingale, Tristan da Cunha and Inaccessible Islands (from *http://whc.unesco.org/en/list/740/multiple=1&unique_number=874* [Accessed 13/12/2016]).

(Right) A map showing the relative positions of Prince Edward and Marion Islands and the Iles of Saint Paul and Amsterdam (from *http://manchots.com/iles-subantarctiques/* [Accessed on the 13/12/2016]).

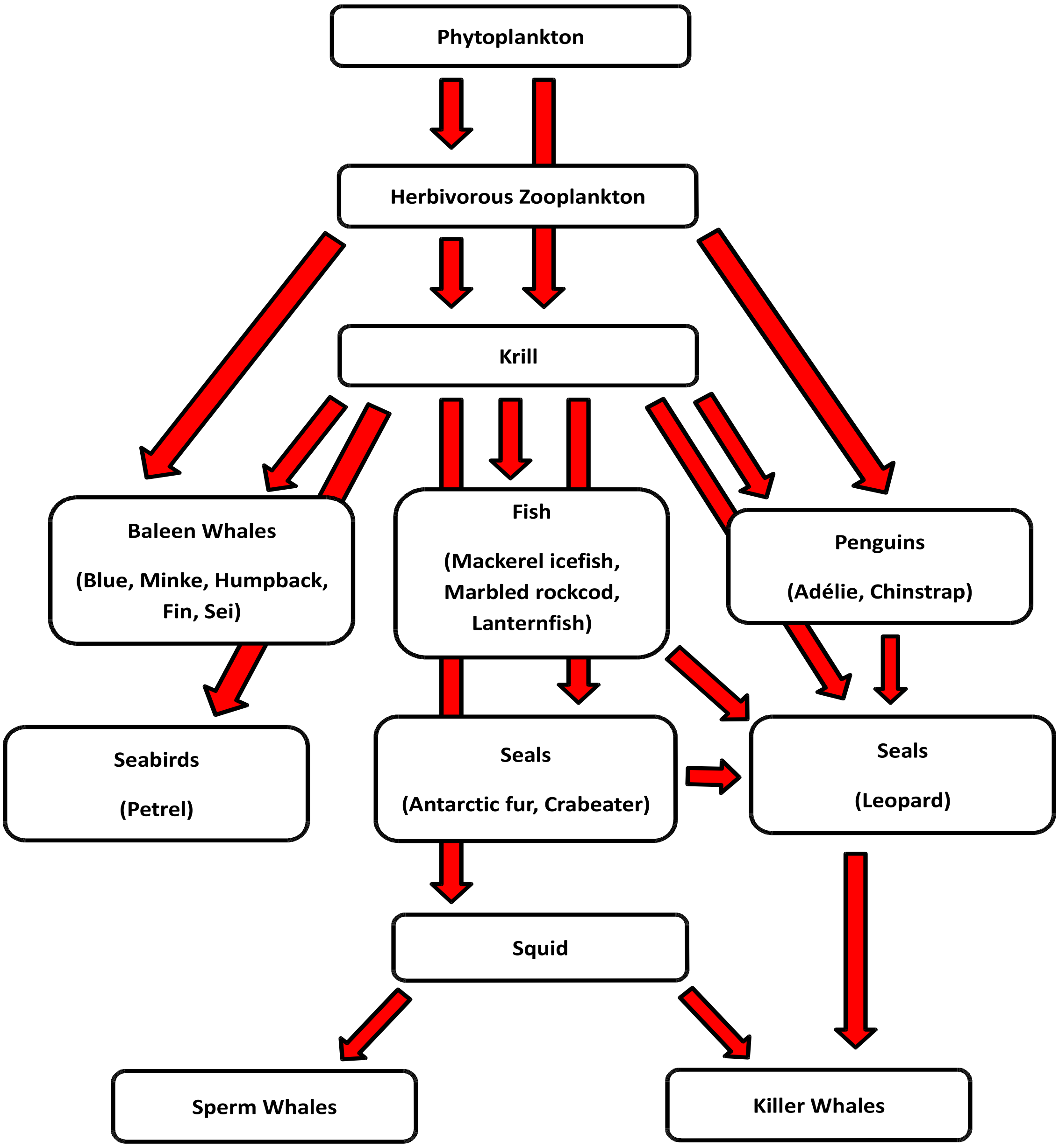

Figure 2.3: A simple representation of the Antarctic food web - after Figure 3-14 from Miller (2009). The arrows represent the flow of energy within the food web with the arrow head marking the final destination of the energy flow.

2.11 Pictures of the Antarctic

These pictures were taken during a research trip to Antarctica on the SA Agulhas II cruise ship from September 2013 until February 2014 - courtesy of Daniel Schilperoort, Masters student, Department of Oceanography, UCT.

FIGURE 2.4: View of the SA Agulhas II cruise ship from the remains of the machinery of the old whale blubber processing plant at South Georgia.

FIGURE 2.5: (Top left) Differences in size between land-ice and sea-ice; (Top right) A group of Adélie penguins about to go to sea; (Bottom left) Height of an ice-shelf in comparison to a person; (Bottom right) Two Adélie penguins courting each other on the Antarctic ice-shelf.

Chapter 3

Human harvesting in the Antarctic - historical record

3.1 Overview of Chapter

The Antarctic is a region that has experienced heavier exploitation of most of its main marine species than any other worldwide. When one harvested species came close to commercial extinction, another species became the new focus for harvesting. The extensive harvesting of seals began near the end of the 18^{th} century. At the start of the 20^{th} century, with the fur seal population level having been reduced below an economically viable level, the subsequent harvesting focused on whales. This harvesting would result in the near extirpation of some of the Antarctic whale species.

This chapter briefly outlines the history of the marine harvests in the Antarctic, focusing particularly on the krill-predators highlighted in Chapter 2. The aim of this chapter is to highlight the need to consider the impacts of human harvesting on the dynamics of the Antarctic ecosystem.

3.2 Harvesting of seals

Mori (2005) summarises that the main seal species harvested in the Antarctic were the Antarctic fur seal, sub-Antarctic fur seal and the southern elephant seal - the latter is not discussed here as it is not a krill-predator (McCann and Doidge, 1987). The Antarctic and sub-Antarctic fur seals were exploited heavily during the 18^{th} and 19^{th} centuries, mostly for their pelts.

The first known sealing expedition to South Georgia (Figure 3.2), where Antarctic fur seals - the target of the sealers - were said to be plentiful, took place between 1790 and 1792 (McCann and Doidge, 1987). Sealing at South Georgia reached its peak in 1800/01 when nearly 112 000 skins were loaded onto American and British ships. James Weddell recorded that in the year 1821, the seal population at South Georgia was near extinction. Weddell (1825) calculated that by the year 1822, nearly 1.2 million seals were harvested from South Georgia alone (McCann and Doidge, 1987). During 1838 - 1839, the 1870s and 1908, a few more seals were taken at South Georgia.

In 1819, the South Shetland Islands (Figure 3.2) became the new focus for sealers after the population numbers at South Georgia had decreased rapidly. Weddell determined that during the 1821/22 season, roughly 320 000 seals were killed (Forcada and Staniland, 2009; McCann and Doidge, 1987; Bonner, 1968). By the year 1830, the seal population at the South Shetland Islands had decreased to being close to extinction (Bonner, 1968). After this, few visits to the island occurred until 1871 when sealers from the United States began collecting seal skins for the London market. This continued until 1892, but by then the Antarctic fur seal numbers were only a tiny fraction of their previous levels (Palmer, 2004; McCann and Doidge, 1987). Today, the Antarctic fur seal population has recovered quite rapidly especially on South Georgia (Forcada and Staniland, 2009).

A similar history is evident for the sub-Antarctic fur seal. In 1790, sealers from the United States began their sealing operations around Tristan da Cunha (Figure 2.2) where around 5 600 skins were obtained. Around the year 1811, roughly 1 100 sub-Antarctic fur seal skins were collected when groups of sealers began living on Gough Island (Figure 2.2). After the year 1820, sealing decreased due to the overexploitation of the population. However, between 1860 and 1890, the revival of sealing for sub-Antarctic fur seals began on the Tristan islands (which consist of the islands Tristan da Cunha, Ascension, Saint Helena, Gough, Inaccessible and Nightingale). Between 1888 and 1890, a group staying on Gough Island obtained roughly 311 seal skins. A second group came to the Tristan islands between 1891/92 but found such a small population of sub-Antarctic fur seals that the trade ceased. The sub-Antarctic fur seal population has remained practically untouched since 1892 except for a few years before 1955/56 when up to about 400 seals were caught illegally each year (Bester, 1987).

Shaughnessy and Fletcher (1987) surmise that around the year 1810, sub-Antarctic fur seal harvesting started on Macquarie Island (Figure 3.2) and by the end of 1812, roughly over 120 000 seal pelts had been obtained. By the year 1815, sealing was no longer a financially rewarding profession although roughly 10 500 pelts had already been obtained since 1812.

Seal species like the crabeater, leopard, Ross and Weddell seals were either not exploited or not caught in appreciable numbers (Croxall *et al.*, 1992). Rogers (2009) states that historically leopard seals were never exploited commercially, but were caught in small numbers for research purposes and as pet food. Laws and Christie (1976) mention that roughly 900 crabeater seals were caught between 1970 and 1973, and that about 750 crabeater seals were caught every year from 1967 to 1977 in the Antarctic. During 1964/65 and 1986/87, crabeater seals were taken by Norway and the former Soviet Union respectively. These harvests lead to calls for preventive measures to combat the possible over-exploitation of seals. As a result, in 1978, the Convention for the Conservation of Antarctic Seals was formed. This Convention specifies management and conservation measures for the Antarctic seals at an international level (Bengtson, 2009).

3.3 Harvesting of whales

Whaling in the Antarctic began at the start of the 20^{th} century, after the substantial exploitation of seals. It resulted in the consecutive depletion of the large baleen whale species, some almost to extinction. The large baleen whales are the focus of this overview.

Due to the commercial value of the products they produced and their large size, blue whales were first to be harvested in the Antarctic from around 1904. This continued for almost 60 years (Yochem and Leatherwood, 1985). From the early 1900s, many blue whales were harvested from land-based fisheries in the Antarctic until the late 1930s when floating factory ships became the norm. Blue whale harvesting peaked around the 1930/31 season when somewhat more than 30 000 whales were killed (Yochem and Leatherwood, 1985; see Figure 3.1). The population in the Antarctic became severely depleted during the first half of the 20^{th} century as a result of some 328 000 blue whales being killed. By 1962, the Antarctic blue whale population had been reduced further to roughly 0.5% of their pristine level. They came under full protection of the IWC in 1966 (Branch *et al.*, 2004). Today, their populations are showing signs of recovery worldwide (Sears and Perrin, 2009; Branch, 2004).

Fin whales were found in large numbers in the Antarctic and were harvested from 1913 until 1976 (Gambell, 1985). Gambell (1985) states that from the start of the land-based fishery on South Georgia in 1904 to the introduction of floating factory ships in the 1920s, fin whales became an important target for whalers as blue whales started to decline. Fin whale harvests were at their largest over 1934 - 1963 when some 560 000 whales were caught - the peak being in the 1937/1938 season when 29 415 fin whales were killed (see Figure 3.1). Fin whales came under protection by the IWC in the late 1970s. Today, fin whales are taken only off Greenland by aboriginal whale fishing and off Iceland (Aguilar, 2009). A small number were recently taken in the Antarctic by the Japanese Special Permit Research Program in the Antarctic (JARPA; see Glossary).

Due to the humpback whales' coastal distribution, they were generally the first targets of whale fisheries in any given area (Clapham, 2009). Humpback whales were harvested in the Antarctic from 1904 until 1963, with catches ending officially in 1966 (Clapham, 2009). Between 1907 and 1916, some 71 000 humpback whales were killed in the region. Within the second half of the 20^{th} century, roughly 100 000 humpback whales were harvested from Antarctic waters with a peak in 1959 when some 15 800 humpback whales were killed (see Figure 3.1). Humpback whales have been under protection by the IWC since the late 1960s.

In the late 1950s, Antarctic minke whales became the target for commercial whaling, despite their small size, as the larger rorqual populations had been severely depleted (Stewart and Leatherwood, 1985). Initially, minke whales were harvested in small numbers but these increased substantially in the 1970s and continued until the 1986/87 season with some 109 000 minke whales having been taken by that time (see Figure 3.1). Land-based fisheries off the coasts of South Africa and Brazil also caught minke whales but in smaller numbers (Perrin and Brownell Jr., 2009). Minke whales came under protection by the IWC in 1986, but they had not been as heavily harvested as the larger baleen whales. After the suspension on commercial whaling was enforced in 1986, a feasibility study was proposed by Japan to the IWC (IWC, 1989) which later became the *Japanese Whale Research Programme under Special Permit in the Antarctic* or JARPA. JARPA originally caught around 400 minke whales annually (IWC, 1998). During the 2007/08 austral season, JARPAII began its operations and was completed in 2014. Currently, a new research programme is in operation, the *NEWREP-A* or the *New Scientific Whale Research Programme in the Antarctic Ocean.* Perrin and Brownell Jr. (2009) states that overall, most minke whale stocks are in better condition than most other large baleen whale stocks; however, they still need to be monitored and managed.

In 1946, the Soviet Union signed the International Convention for the Regulation of Whaling, the legal framework that is the foundation of the IWC. Thus, the Soviet Union became one of the IWC members responsible for whale conservation and whaling management. During the mid-1960s, some whale species, like the blue and humpback whales, came under protection by the IWC, i.e. their catch limits were set to zero. Only in the mid-1980s did all whales species come under protection. Thus, during the mid-1960s and the mid-1980s, catches of up to a specified limit were allowed for certain whale species. During this period, the Soviet Union continued whaling protected species such as the humpback whales, even in the Antarctic. They disguised this by mis-declaring the caught species. In 1996, Yablokov *et al.* (1998) presented the actual Soviet Union whaling statistics to the IWC. Of the Antarctic baleen whales, the most affected by these undeclared takes were the sei and humpack whales where respectively 46 094 and 33 249 whales had actually been killed compared to the 29 749 and 2 705 reported to the IWC by the Soviet Union (from *http://www.russianorca.com/Whaling/whaling_soviet_eng.htm*; *https://iwc.int/home* and *http://csiwhalesalive.org/csi97403.html* [Accessed 12/02/2016]).

Although not one of the main krill-predators in the Antarctic, the sei whales were impacted heavily after the depletion of the larger baleen whale species. Their stocks were reduced rapidly when over 60 000 sei whales were killed in the mid-1960s over four whaling seasons in the sub-Antarctic. During the 1960s, the sei whale was the main target species for the Japanese scouting vessels surveying north of 60°S. By 1972, catch limits were in place to reduce sei whale catches (de Korte *et al.*, 2008; Knox, 2007).

3.4 Harvesting of krill

In the early 1970s, the first substantial krill harvesting began. Catches peaked in 1982 with over 500 000 tonnes* of krill in total being taken (see Figure 3.1), mostly in the CCAMLR's Area 48 (Areas 48.1 - 48.6 in Figure 3.2). Catches declined substantially around 1984 due to marketing and processing issues which resulted from high fluoride levels found in the krill exoskeleton (Nicol and Endo, 1999; Nicol and de la Mare, 1993).

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*The convention, as used in this thesis, is that "tonnes" means "metric tons" (MT).

These problems were resolved and the krill harvesting resumed at increased levels until 1993 when the Soviet Union dissolved, causing a further large decline in krill catches as the former USSR members reassessed the economic feasibility of their krill fisheries in the Antarctic (Mori, 2005; *https://www.ccamlr.org/node/74620* [Accessed 23/04/2016]).

Between 1973 and 2001, roughly 6.1 million tonnes of krill were harvested in the Antarctic (Miller, 2002). The krill fishery was relatively stable between 1994 and 2007, catching less than 150 000 tonnes each year. From 2008 to 2013, roughly 200 000 tonnes of krill were caught each year, and this rose to a maximum of about 300 000 tonnes being caught in 2014 (see Figure 3.1). These catch estimates were less than the threshold precautionary catch limit of 620 000 tonnes set in 2010 for Area 48 by CCAMLR (and currently still enforced). Hewitt and Lipsky (2009) comment that as conventional fisheries elsewhere begin to decline and the demand for krill as food for aquaculture increases, fishing pressure will likely shift to *E. superba* in the Southern Hemisphere where current harvests are well below current sustainable yield estimates.

3.5 Harvesting of fish

Fish were first commercially harvested around South Georgia during the early whaling days. They were served as local food at whaling stations and sold salted in small quantities to Buenos Aires for some time after the onset of whaling. Sixty years later, these fish resources came under heavy exploitation (Kock *et al.*, 2012).

The large fish harvests began with the exploitation of finfish in the mid-1960s by the former Soviet Union and other countries in the Eastern Bloc (constituted by Poland, East Germany, Czechoslovakia, Hungary, Romania, Bulgaria and Yugoslavia). From 1969 to 1970, the marbled rockcod (*Notothenia rossii*) stocks were almost extirpated after 514 000 tons were caught around South Georgia. Marbled rockcod stocks around other islands followed a similar decline and by the end of the 1980s, the species was depleted throughout the Antarctic (Constable *et al.*, 2000). In the mid-1970s, the next target of the Soviet fleets was the mackerel icefish (*Champsocephalus gunnari*). This species has a similar exploitation history to the marbled rockcod (Constable *et al.*, 2000). The catch history of the *C. gunnari* is available at *https://www.ccamlr.org/en/fisheries/icefish-fisheries.*

Although not a krill-predator, the Patagonian toothfish began to be exploited in the 1970s, around South Georgia, as part of the mixed demersal trawl fishery. However, considerable levels of illegal, unregulated and unreported (IUU) fishing occurred around South Georgia, and the swift decrease of the toothfish stocks around Crozet and Prince Edward Islands (see Figure 3.2) in the sub-Antarctic became a major concern for management (Brandão *et al.*, 2002; Constable *et al.*, 2000).

Currently, CCAMLR controls and monitors the commercial fisheries of Antarctic krill, mackerel icefish, Antarctic toothfish and Patagonian toothfish
(from *https://www.ccamlr.org/en/fisheries/fisheries* [Accessed 12/05/2016])

3.6 Summary

The aim of this chapter was to provide a brief overview of the harvesting history of the krill-predators and krill within the Antarctic. In this region, the main targets of fisheries were seals, whales, fish and krill. This chapter also had the intent to convey how severe the reductions to many of these species were under harvesting, which would have had consequences for the Antarctic ecosystem itself, hence the need to consider the impacts of human harvesting on ecosystem dynamics in general.

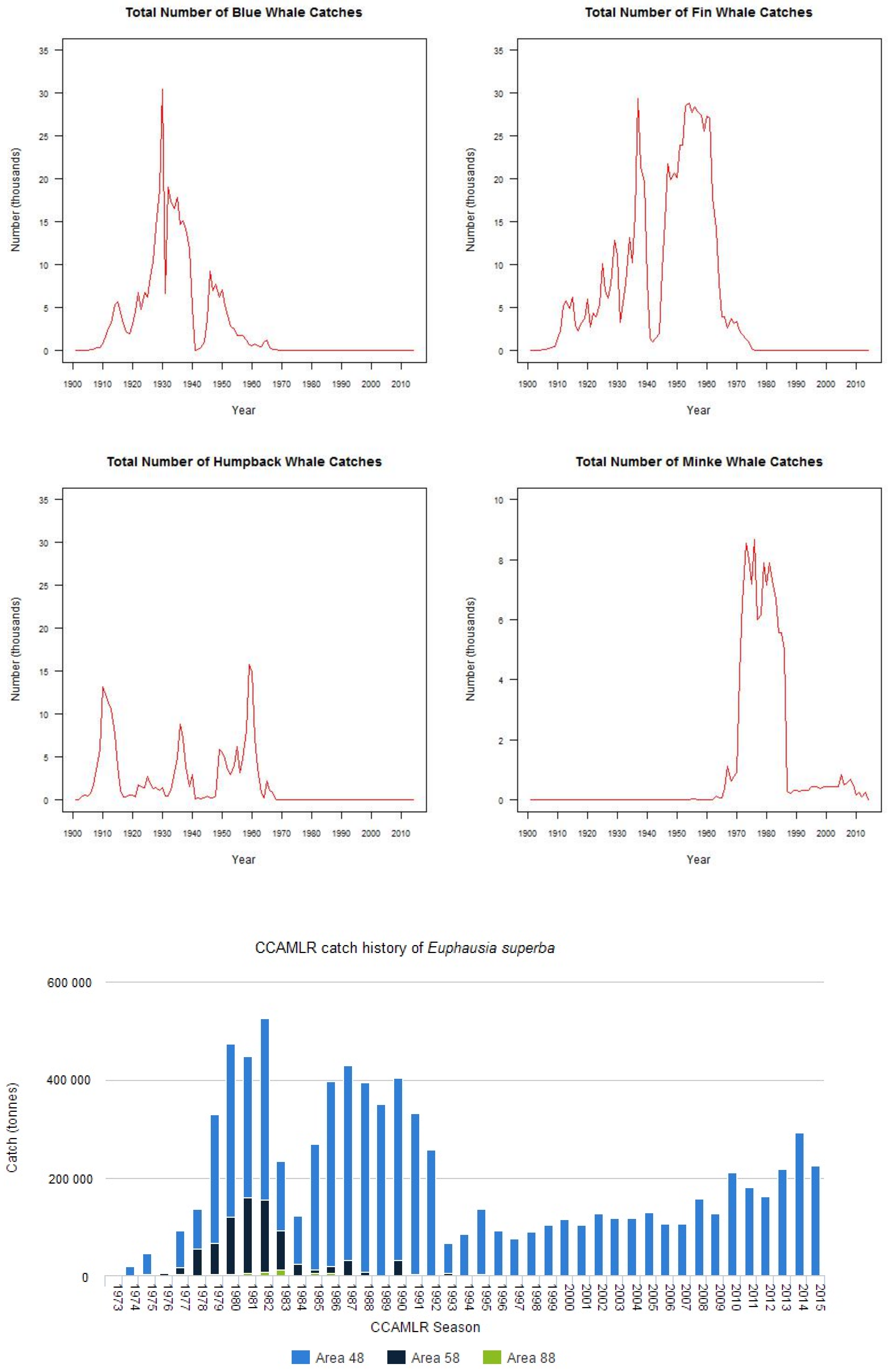

FIGURE 3.1: Total catches for blue, fin, humpback and minke whales from 1900 until 2014 and the krill catch history from 1973 until 2015 from *https://www.ccamlr.org/en/fisheries/krill-fisheries.*

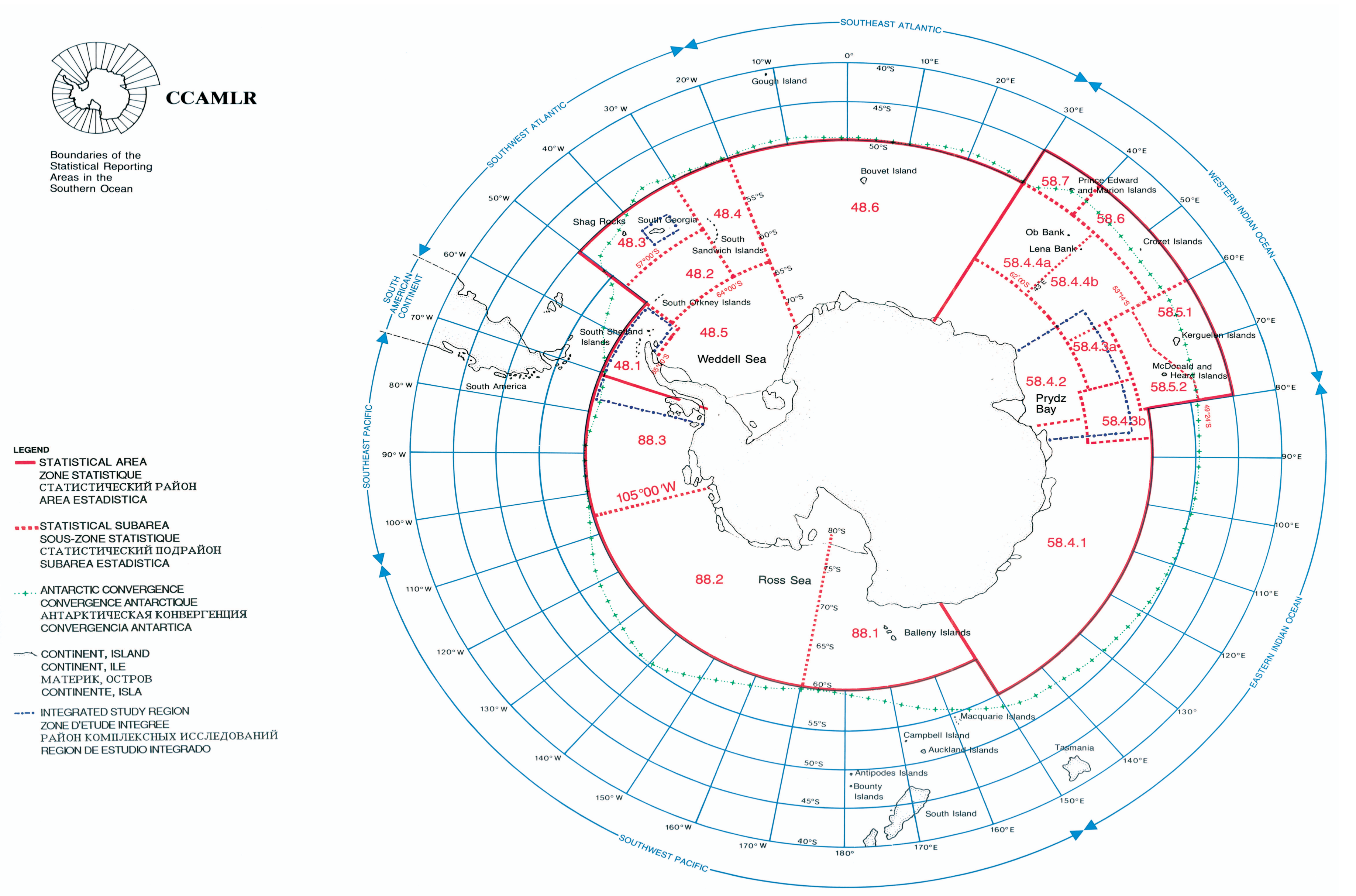

FIGURE 3.2: Map of the CCAMLR convention areas (from the CCAMLR website *https://www.ccamlr.org/en/document/organisation/map-ccamlr-convention-area* [Accessed on 18 August 2015]).

Chapter 4

Krill consumption per capita by the main krill-predators

4.1 Overview of Chapter

This chapter calculates the consumption of krill by the main krill-predators in the Antarctic. This information is used to determine which species are to be included in the model developed in Chapter 11. Information on the various krill-predators' diet, period of feeding in the Antarctic, average weight and daily krill intake, from both Mori (2005) and as used in this thesis, is discussed in this chapter in order to highlight the differences in the available information since Mori (2005). Thereafter, these values are used to determine the annual per capita consumption of krill by the krill-predators.

4.2 Krill consumption by baleen whales

4.2.1 Diet composition

Information is scarce on the diet composition of many baleen whale species following their protection since the 1960s and 1970s. The majority of the information available comes from the commercial whaling period, with much of it being qualitative - identifying only the names of the prey species found in the whales' stomachs and providing only a general idea of the amounts. Nonetheless, it is clear that most of the baleen whales satisfy a substantial proportion of their dietary needs by feeding on euphausiids (krill) while they are in the Antarctic - with some variations depending on the location and season.

Mori (2005) took her quantitative diet composition estimates (see Table 4.1) for blue, fin and humpback whales from Nemoto (1970), who had studied the stomach contents of these species from the Southern Hemisphere Japanese pelagic catches taken between 1961 and 1965. The results of his study showed that 98% of blue whale (mostly pygmy blue whales, but since pygmy blue whales have a similar diet to blue whales, these estimates were sufficient), 99% of fin whale and 100% of humpback whale stomachs (the humpback whale sample size was only nine) contained euphausiids. For her final results, Mori (2005) included amphipods and copepods, both small crustaceans, into her blue, fin and humpback whale diet estimates.

For minke whales, Mori (2005) used information from Ichii and Kato (1991) and Tamura and Konishi (2005). Ichii and Kato (1991) examined stomach contents of 273 minke whales caught during a 1987 Japanese survey. The whales were taken between the region from 105°E to 115°E and from 55°S to the ice-edge. Their study indicated that krill was the dominant food source, comprising between about 94 - 100% (by weight) of the minke stomach contents. Tamura and Konishi (2005) analysed the minke stomach contents taken from JARPA surveys during 1987-2003. The regions sampled included four IWC Management Areas (Areas III-East (35°E - 70°E), IV, V, VI-West (170°W - 145°W); see Figure 4.2). The results of their study confirmed that between 98 - 100% of the non-empty minke stomachs examined contained euphausiids only (i.e. krill, *Euphausia crystallorophias*, *Euphausia frigida* and *Thysanoessa macrura*).

There have been no recent analyses of the diet composition of the blue, fin and humpback whales. Thus, the estimates from Mori (2005) are retained; however, amphipods and copepods are excluded in this update as the focus of this thesis is only on krill. For minke whales, a more recent analysis is conducted in Tamura and Konishi (2014), which summarises the information on the Antarctic minke whale's feeding habits from data taken during the JARPA (1987/88 - 2004/05) and JARPAII (2005/06 - 2010/11) surveys. The results of their study concluded that Antarctic minke whales fed mostly on euphausiids, in particular Antarctic krill (*Euphausia superba*) which constituted 66 - 100% of the minke stomach contents by weight.

A comparison between the percentages of krill in the diet of the different whale species as used in Mori (2005) and in this thesis is presented in Table 4.2.

4.2.2 Average body weights

It is unclear from where Mori (2005) obtained average body weights of the baleen whales. Thus for coherency, these weight estimates are re-developed here.

For this thesis, information in Trites and Pauly (1998) is used to determine the average body weights for the baleen whales. These authors estimate the average masses of 30 species of marine mammals (including the baleen whales) using maximum body length measurements. This approach is used because there is a strong correlation between growth rate, survival, longevity and maximum length. Furthermore, growth curves are known for the 30 species considered. The maximum length of each species is regressed against their mean mass via the following relationship:

$$\overline{M} = aL_{max}^{b} \tag{4.1}$$

where

$\overline{M}$	is the mean mass of all individuals in the population (kg);
L_{max}	is the maximum body length of a given species (cm), i.e. the longest recorded length from a given population for which the growth curves are known; and
a,b	are the linear regression coefficients (intercept and slope respectively) that describe the relationship $ln\overline{M} = a + b\ lnL_{max}$.

The results from Trites and Pauly (1998) are summarised in Table 4.3.

The average of the male and female baleen whale mean mass, i.e:

$$\text{Average weight (mt)} = \frac{\text{female mean mass (mt)} + \text{male mean mass (mt)}}{2}$$

is used throughout this thesis.

These values and the values used in Mori (2005) are presented in Table 4.4.

4.2.3 Duration of feeding periods in the Antarctic

Mori (2005) uses information from Kasamatsu (2000) for the estimates of the durations of feeding periods of the various baleen whale species in the Antarctic. The whales considered were sighted on Japanese research vessel surveys and IWC/IDCR (International Decade of Cetacean Research; see Glossary) surveys conducted from 1976 to 1988. Kasamatsu (2000) suggests that temporal variation in the whale distribution density reveals different migratory patterns amongst the baleen whales. His book also reports a positive correlation between feeding periods and body length (see Figure 4.1). This supports the idea that whale species with a shorter body length conserve heat less efficiently compared to the larger whale species. As a result, they are unable to stay for long in an environment as cold as the Antarctic. Kasamatsu (2000) infers that, in general, blue whales spend about 125 days in the Antarctic, from about December to March, whilst minke whales typically spend a shorter period of about 90 days in the Antarctic, from about December to February - both species' feeding times coincide with the austral summer. Fin and humpback whales feed for intermediate periods in the Antarctic.

There have been no recent updates to the estimates of feeding period durations in the Antarctic; thus the results from Kasamatsu (2000) are retained in this thesis. These results are summarised in Table 4.5.

4.2.4 Daily intake of krill

Mori (2005) uses information from Tamura (2003) to determine the daily intake of krill by baleen whales. Tamura (2003) uses three alternative methods to calculate the daily prey consumption rate. These methods are summarised below.

The first method is from Innes *et al.* (1986) who put forward that the daily prey consumption of a cetacean is related to its average body weight through the following equation:

$$I = 0.42M^{0.67}$$

where

I is the daily prey consumption (kg/day); and

M is the average body weight (kg).

The second method is from Sigurjònsson and Vikingsson (1997) who estimate consumption using the following equation:

$$D = 205.25M^{0.783}$$

where

D is the daily caloric value of prey intake (kcal/day); and

M is the average body weight (kg).

The third method is from Klumov (1963) who suggests that the daily prey consumption is directly proportional to body weight:

$$I = 0.035M$$

where

I is the daily prey consumption (kg/day); and

M is the average body weight (kg).

The daily krill intake rates used in Mori (2005) took all three of these methods into account and are summarised in Table 4.6.

This thesis calculates the daily krill intake rate using a more recent and improved method suggested by T. Tamura (pers. comm.), whereby the feeding rates of marine mammals are calculated from the equation found in Perez and McAlister (1993):

$$SMR = 4.186 \cdot a \cdot M^{0.75} \tag{4.2}$$

where

SMR	is the Standard Metabolic Rate (kJ/day) which reflects the daily energy requirements which are in turn related to the daily prey consumption;
M	is the mean body mass (kg); and
a	is an estimated coefficient reflecting the feeding rate of the whale where $a = 192$ for *Mysticetes.*

The 4.186 converts from kcal/day to kJ/day as 1 kcal = 4.186kJ.

Using the *SMR* value, the Daily Prey Consumption (*DPC*) is calculated from:

$$DPC = \frac{SMR}{\text{Average energy value of } E.\ superba \cdot \text{Assimilation efficiency}} \tag{4.3}$$

where the average energy value of *E. superba* is 3 510 kJ/kg; it is measured by a bomb calorimeter and calculated using the energy density of *E. superba* samples taken from JARPA surveys (Tamura *et al.*, 2014); and

the assimilation efficiency (how efficient a species is in taking the energy from krill) is assumed to be 0.8 (80%) for all whales, as suggested by Tamura *et al.* (2014).

The DPC is then multiplied by an index H to take the higher feeding rates during the austral summer into account. As a result, an adjusted DPC value is provided, i.e.:

$$DPC_{adj} = DPC \cdot H$$

H is calculated from the following equation:

$$H = \frac{365 \cdot \text{assumed energy intake}}{\text{number of days spent in the Antarctic}} \tag{4.4}$$

where *365* reflects the total number of days in a year, the "number of days spent in the Antarctic" is as given in Table 4.5 and the "assumed energy intake" refers to the proportion of the annual energy intake consumed during the austral summer. Lockyer (1981b) assumed that 83% of the annual energy intake of the Southern Hemisphere baleen whale species is consumed during the austral summer.

Finally, the DPC_{adj} value is divided by the respective species' weight (from Table 4.4) to determine the percentage of body weight consumption per day. These values are presented in Table 4.7.

4.2.5 Consumption of krill by baleen whales

The annual per capita consumption of krill for all the krill-predators, as calculated by Mori (2005), is determined by the following equation:

$$\lambda_j = \overline{w}_j \cdot c_j \cdot d_j \cdot p_j \tag{4.5}$$

where

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

$\overline{w}_j$ is the average weight of the baleen whale species j (Table 4.4);

c_j is the consumption of prey/day, expressed as a proportion of the predator's weight, for the baleen whale species j (Table 4.6);

d_j is the number of days spent feeding in the Antarctic for the baleen whale species j (Table 4.5); and

p_j is the estimated proportion of krill in diet of the baleen whale species j (Table 4.2).

The values for λ_j, as used in Mori (2005), are summarised in Table 4.8.

This thesis also uses Equation 4.5 to calculate the *annual per capita consumption of krill* for all the krill-predators, except that c_j is taken from Table 4.7. The results are summarised in Table 4.8 and are somewhat higher than those used in Mori (2005).

Food Species	Whale Species		
	Blue whale *	Fin whale	Humpback whale
Euphausiids	517	16 158	7
Euphausiids and other species	4	18	-
Copepods	2	-	-
Amphipods	6	9	-
Fish	-	76	-
Number of empty stomachs	674	18 878	2
Total number of whales examined (including empty stomachs)	1 203	35 139	9
Percentage of euphausiids in diet (%)	97.73	99.37	100
Percentage of euphausiids and euphausiids and other species in diet (%)	98.49	99.48	100
Percentage of euphausiids, euphausiids and other species, copepods and amphipods in diet (%)	100	99.53	100

Table 4.1: Stomach contents of baleen whales (expressed first in terms of number of stomachs sampled containing the prey indicated) in Japanese pelagic catches from 1961 to 1965 in the Antarctic from Nemoto (1970).

* Includes mostly the subspecies *Balaenoptera musculus brevicanda* (the pygmy blue whale) found north of the Antarctic Convergence.

Species	Percentage of krill in diet from Mori (2005) (%)	Percentage of krill in diet, as used in this thesis (%)
Blue whale	100	98.5
Fin whale	50*	99.5
Humpback whale	100	100
Minke whale	100	100

Table 4.2: Summary of the percentages of krill in the baleen whale diet from Mori (2005) and as used in this thesis.

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[*] The current fin whale feeding distribution is located further north from the other baleen whales' feeding grounds. Mori (2005) assumed that the "krill" they eat further north belongs to a different population to the krill eaten further south. The 50% assumption attempted to take this into account.

Species	Max. Length (m)		Average Mass (mt)		Growth Curve Source
	Female	Male	Female	Male	
Blue whale	33.58	31.90	110.13	95.35	Lockyer (1981a)
Fin whale	27.00	25.00	59.82	51.36	Lockyer (1981a)
Humpback whale	18.60	17.68	32.49	28.32	Brown and Lockyer (1984)
Minke whale	10.70	9.80	7.01	6.12	Evans (1987)

Table 4.3: Results from Equation 4.1 for average mass (mt) and maximum length (m) for both male and female baleen whale species. The sources for the growth curve data as used in Trites and Pauly (1998) are included as well.

Species	Average body weight (t) from Mori (2005)	Average body weight (mt) as used in this thesis
Blue whale	103	102.74
Fin whale	46	55.59
Humpback whale	27	30.41
Minke whale	7	6.57

Table 4.4: Summary of the average body weights for the large baleen whales from Mori (2005), and as used in this thesis from Trites and Pauly (1998).

Species	Feeding duration in Antarctic (days) from Mori (2005) and as used in this thesis	Proportion of year that whales eat krill
Blue whale	125	0.34
Fin whale	120	0.33
Humpback whale	100	0.27
Minke whale	90	0.25

Table 4.5: Summary of feeding durations in the Antarctic for the large baleen whales as used in Mori (2005) and in this thesis.

Species	Daily krill intake rate (% of body weight)
Blue whale	0.9 - 3.5
Fin whale	1 - 4
Humpback whale	1.4 - 4
Minke whale	0.6 - 5.1

Table 4.6: Summary of the daily krill intake rate for the large baleen whales as used in Mori (2005).

Species	Adjusted daily prey consumption (kg/day)	Average body weight (kg)	Daily krill intake, as a proportion of body weight
Blue whale	3 981	102 737	0.039
Fin whale	2 616	55 590	0.047
Humpback whale	1 997	30 408	0.066
Minke whale	703	6 566	0.107

TABLE 4.7: Summary of the daily krill intake rate for the large baleen whales as used in this thesis.

Species	Annual per capita consumption of krill (t) λ_j from Mori (2005)	Annual per capita consumption of krill (mt) λ_j, as used in this thesis
Blue whale	115.9 - 450.6	490.8
Fin whale	27.6 - 110.4	310.4
Humpback whale	37.8 - 108.0	200.7
Minke whale	3.8 - 32.1	63.2

TABLE 4.8: Summary of the annual per capita consumption of krill for the large baleen whales as used in Mori (2005) and in this thesis.

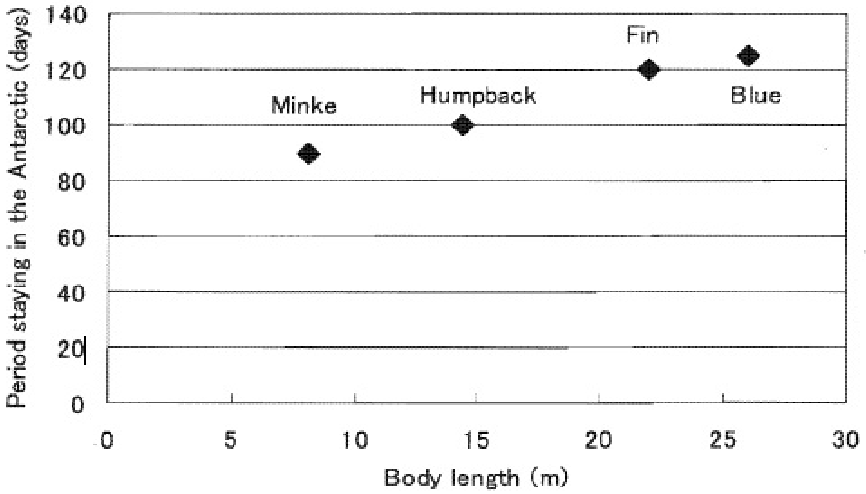

FIGURE 4.1: The relationship between feeding periods (days) in the Antarctic and body length (m) of the main baleen whale species, which feed there, taken from Mori (2005) and after Figure 2.38 in Kasamatsu (2000).

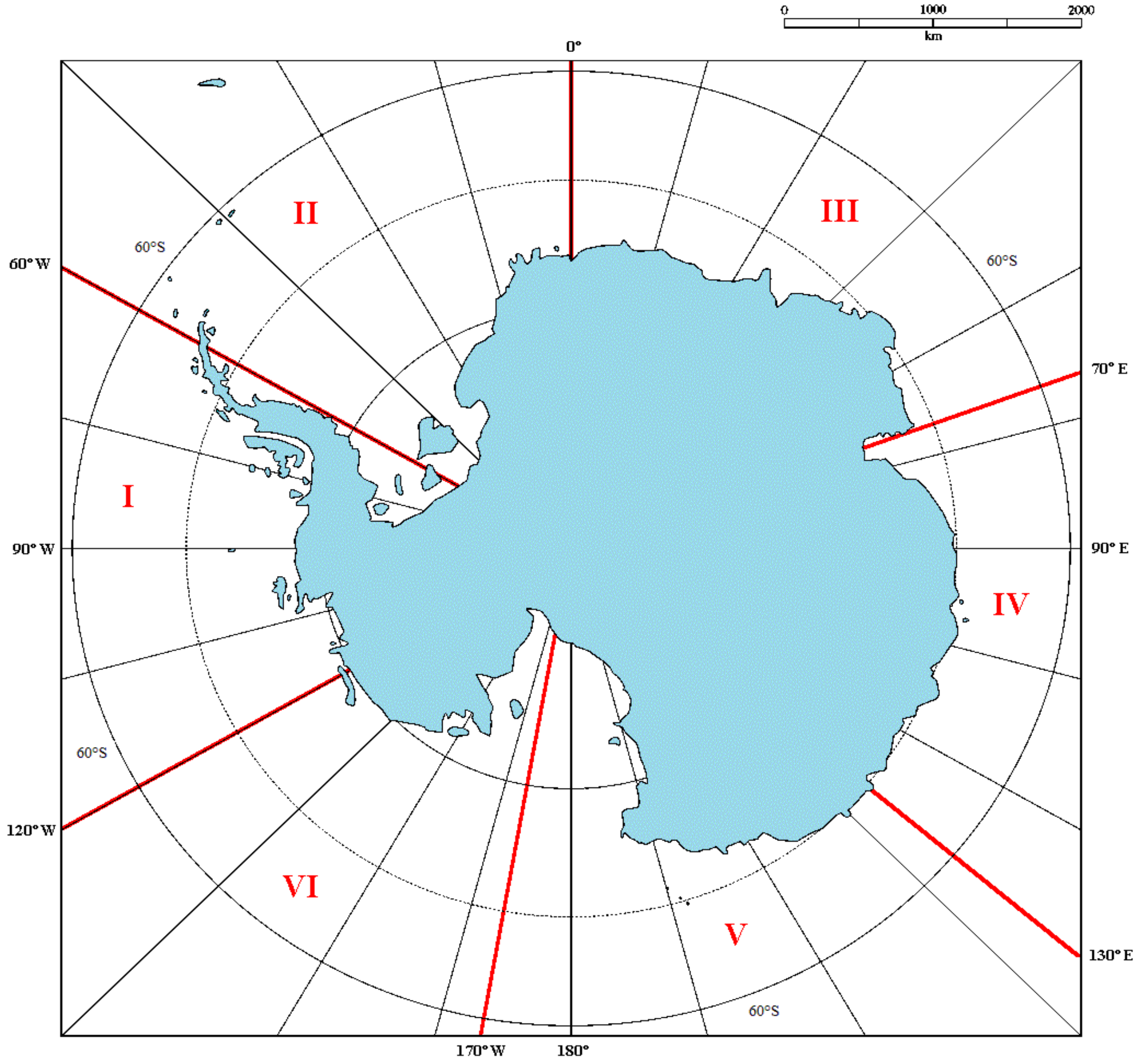

FIGURE 4.2: Map of the IWC Management areas in the Antarctic (from *http://luna.pos.to/whale/img/gen_map_ant.gif* [Accessed on 05 May 2016])

4.3 Krill consumption by seals

4.3.1 Diet composition

A number of studies such as Reid and Arnould (1996) have been conducted on the diet composition of Antarctic seals. However, the amount of information differs amongst the species - more quantitative studies have been conducted for Antarctic fur seals and leopard seals compared to crabeater seals, possibly due to the latter's limited accessibility on pack-ice (Mori, 2005).

Mori (2005) aggregated results from various sources and determined that the Antarctic fur seals' diet composition consisted of roughly 60% krill, 35% fish and 5% squid. She reasoned that 95% of the Antarctic fur seal breeding population inhabits South Georgia (Reid, 1995) where krill is available in large quantities, suggesting that krill is the prey species which is the most consumed by the South Georgian fur seal population.

Mori (2005) used Øritsland (1977) as a quantitative study for the crabeater diet composition. Øritsland (1977) used samples taken from a 1964 cruise in the pack-ice of the Weddell and Scotia Seas (see Figure 2.1). Sixty-five crabeater seals were examined and it was found that they fed almost exclusively on krill. Øritsland (1977) combined these findings with those of past cruises, and determined that the crabeater seals' diet composition consisted of roughly 94% krill, 3% fish and 2% squid.

For leopard seals, Mori (2005) states that there were diverse results concerning their diet composition so she did not provide a specific estimate.

For this thesis, the diet compositions of the crabeater and leopard seals have been determined from Southwell *et al.* (2012), as that is the most recent analysis on the diet of the Southern Hemisphere *Phocidae* seal species. For the crabeater seal, Southwell *et al.* (2012) consider stomach content and faeces analyses, which provided the quantitative diet information. Teeth and mandible morphology, observations from individuals held in captivity, diving behaviour and seal movement data allowed for indirect inferences concerning the crabeaters' diet. The average of the proportion of krill found in the crabeater seals' diet is used in this thesis.

For leopard seals, Southwell *et al.* (2012) consider stomach contents, faeces and direct observations of predatory behaviour - this provided the quantitative diet information. Diving and movement behaviour data allowed for indirect inferences concerning the leopard seals' diet. These latter data suggest that leopard seals eat a variety of prey depending on the region and the season.

Leopard seal diet consists of fish (mostly in winter and spring), cephalopods, crustaceans (especially krill in the winter months), penguins (towards the end of summer; in some regions of East Antarctica, Adélie penguins are eaten throughout the year) and other seals (especially newly weaned crabeater pups in early summer; leopard seals also prey opportunistically on Antarctic fur seals). The average of the proportion of krill found in the leopard seals' diet is used in this thesis.

The amount of krill consumed by Antarctic fur seals has been taken from Barlow *et al.* (2002). These authors examined the Antarctic fur seal diet by collecting 10 scats (seal excrement) each week between January and February during the breeding seasons of 1989 and from 1991 to 2000. The percentage of scats that contained krill in each year was used to determine the amount of krill in the fur seal diet. In the year 1994, about 70% of fur seal scats contained krill whilst in the years 1992, 1993, 1999 and 2000 nearly 100% of fur seal scats contained krill. From 1994 to 2000, Barlow *et al.* (2002) determined that the average amount of krill in the Antarctic fur seal diet was roughly 93%.

The proportions of krill in the diet of the various seal species from Mori (2005) and as used in this thesis are summarised in Table 4.9.

4.3.2 Average body weight

As was the case for the baleen whales, it is unclear from where Mori (2005) obtained the average body weights of the various seal species. For coherency, these weight estimates are re-developed here.

For this thesis, Trites and Pauly (1998) is used to provide the Antarctic fur seals' average weight (as growth curve information was available), where the methodology in that paper is the same as is described in Section 4.2.2 for baleen whales. For crabeater and leopard seals, Laws (1977) is used. Three leopard seals were sampled to give an average mass of 271.7kg and 205 crabeater seals were sampled to give a mean mass of 192.6kg (Laws, 1977; Øritsland, 1977). These results and the values from Mori (2005) are summarised in Table 4.10, where the average weight for the Antarctic fur seal is somewhat lower than what Mori (2005) used.

4.3.3 Duration of the feeding period in the Antarctic

Mori (2005) used Laws (1984) for estimates of the duration of the feeding period of the Antarctic seals. For crabeater seals, Øritsland (1977) observed that there was a marked increase in the relative frequency of empty stomachs between September and October of that year. From the 27 August until 10 October, 155 crabeater seals were examined of which 65% had empty stomachs. Between 11 - 31 October, 64 crabeater seals were examined of which 84% had empty stomachs. Laws (1984) used these observations to deduce that crabeater seals do not feed for roughly 30 days each year.

Knox (2007) states that the pack-ice seals feed for roughly 335 days of the year. This restates what was found for the crabeater seal (a pack-ice seal) and provides an estimate for the leopard seals (another pack-ice seal). Thus, leopard seals are also taken to feed for 335 days of the year.

McCann (1980) uses data from a 1976 survey in South Georgia during the Antarctic fur seal breeding season. The author states that bull seals, especially territorial bull seals, guard their territories for around 1 - 53 days (a rough average of 34 days), from late October to late December. During this period, the bulls do not feed. This fasting period depends on the seal's body size (seals with larger body sizes are able to sustain longer fasting periods), climate and the duration of the mating period. Fur seal cows suckle their pups for roughly 110 - 115 days, feed at sea for roughly 3 - 6 days and subsequently fast to suckle their pup for 2 - 5 days (Doidge and Croxall, 1985; Bonner, 1968). Laws (1984) used these observations to deduce that Antarctic fur seal bulls fast for roughly 34 days and Antarctic fur seal cows for roughly 50 days.

A summary of the feeding durations in the Antarctic for the seals considered in Mori (2005) and in this thesis is presented in Table 4.11.

4.3.4 Daily intake of krill

Mori (2005) references Laws (1984) and Øritsland (1977) for the seals' daily krill intake. These authors suggest that the average daily food intake - for crabeater, leopard and Antarctic fur seals - is roughly 7% of the seal's body weight. This estimate is based on studies regarding the daily food intake by captive seals whose daily feeding rates ranged from 4 - 10% of their total body weight. Øritsland (1977) states that although captive seals have lower energy requirements compared to wild seals, they still probably eat large amounts of food. As a result, the feeding rates of wild seals during their active feeding periods may well lie in the range recorded for captive seals.

This thesis calculates the daily krill intake using the same method as was described for the baleen whales except that in Equation 4.2, $a = 200$ for *Phocidae* and $a = 372$ for *Otariidae* from Perez and McAlister (1993), and in Equation 4.3, the assimilation efficiency for all the seal species is 0.9 (90%). Fadely *et al.* (1990) use dietary manganese (Mn^{2+}) as a stationary identifier to estimate the assimilation efficiency of captive northern fur seals (*Callorhinus ursinus*). The estimated assimilation efficiency is 90% with a standard error of 1.2%. In this thesis, it is assumed that all Antarctic seals have an assimilation efficiency of 90% as information is scarce on the assimilation efficiencies for each seal species separately. Antarctic fur seals are bigger than northern fur seals, hence consume more to retain their energy levels. Furthermore, wild seals eat slightly less compared to captive seals. Hence, a 90% assimilation efficiency seems to be a reasonable approximation. This is re-enforced by Knox (2007) who states that Lavigne *et al.* (1986; 1982) estimated that the fur seal populations at South Georgia had an assimilation efficiency of 90%. To apply Equation 4.4, it is assumed that 90% of the annual energy intake of the seal species in the Antarctic is consumed during the austral summer, i.e. the assumed energy intake of factor H is 0.9 as information on annual energy intake by seal species in the Antarctic is scarce and 90% seems to be a reasonable approximation.

This information is used to estimate the percentage of body weight to which the krill consumed per day by each seal species corresponds. These values are presented in Table 4.12.

4.3.5 Consumption of krill by seals

The annual per capita consumption of krill for all the krill-eating seal species in the Antarctic is calculated using Equation 4.5 in both Mori (2005) and this thesis. These values are summarised in Table 4.13 where $\overline{w}_j$ is from Table 4.10, c_j is from Table 4.12 (for values used in this thesis only), d_j is from Table 4.11 and p_j is from Table 4.9.

Species	Percentage of krill in diet from Mori (2005) (%)	Percentage of krill in diet as used in thesis (%)
Crabeater seal	94	94
Leopard seal	-	69
Antarctic fur seal	60	93

Table 4.9: Summary of the percentages of krill in the diet of various Antarctic seal species from Mori (2005) and as used in this thesis.

Species	Average body weight (t) used in Mori (2005)	Average body weight (mt) used in this thesis
Crabeater seal	0.15 - 0.25	0.19
Leopard seal	-	0.27
Antarctic fur seal	0.05 - 0.20	0.03

Table 4.10: Summary of the average body weights for the various Antarctic species of seals from Mori (2005) and as used in this thesis.

Species	Duration of feeding in Antarctic (days) used in this thesis (the crabeater seal and Antarctic fur seal values were also used in Mori (2005))	Source	Proportion of year that seals eat krill
Crabeater seal	335	Laws (1984), Øritsland (1977)	0.92
Leopard seal	335	Knox (2007)	0.92
Antarctic fur seal	323	Laws (1984)	0.89

Table 4.11: Summary of the feeding durations for the Antarctic seal species considered in this thesis.

Species	Adjusted daily prey consumption (kg/day)	Average body weight (kg)	Daily krill intake, as a proportion of body weight
Crabeater seal	13.46	192.6	0.07
Leopard seal	17.41	271.7	0.06
Antarctic fur seal	5.89	26.7	0.22

TABLE 4.12: Summary of the daily krill intake rates for the various Antarctic seal species as used in this thesis.

Species	Annual per capita consumption of krill (t) λ_j from Mori (2005)	Annual per capita consumption of krill (mt) λ_j used in this thesis
Crabeater seal	3.31 - 5.51	4.45
Leopard seal	-	4.02
Antarctic fur seal	0.68 - 2.71	1.77

TABLE 4.13: Summary of the annual per capita consumption of krill for the Antarctic seal species as used in Mori (2005) and in this thesis.

4.4 Krill consumption by fish

In Chapter 2, three fish species were identified as krill-predators. Of the three, only the mackerel icefish and the marbled rockcod are considered here because of the scarcity of information regarding the third (the lanternfish).

The information needed to calculate the annual per capita consumption of krill for the mackerel icefish and the marbled rockcod is summarised in Tables 4.14 and 4.15 respectively. These tables also list the sources of this information.

Information	Estimate	Source	Notes
Percentage of euphausiids in diet (%)	85	Kock *et al.* (2012)	The mean proportion by weight (%) of krill in their diet from Kock *et al.* (2012) is used.
Average weight (mt)	2.00 x 10^{-6}		The following website is the source of the average weight estimate: *http://www.eol.org/pages/206610/details#size*
Feeding duration in the Antarctic (days)	365		It is assumed that mackerel icefish feed throughout the year in the Antarctic.
Daily krill intake rate, proportion of body weight	0.013	Flores *et al.* (2004)	Flores *et al.* (2004) infer from a gastric exponential model that the average feeding rate of *Champsocephalus gunnari* is between 1.0 - 1.5 % of the fish's body weight per day, i.e. roughly 1.3 % body weight per day.
Annual per capita consumption of krill (mt)	8.07 x 10^{-6}		Using Equation 4.5

TABLE 4.14: Summary of the information used to calculate the annual per capita consumption of krill (mt) for the mackerel icefish in this thesis.

Information	Estimate	Source	Notes
Percentage of euphausiids in diet (%)	70	Kock *et al.* (2012)	The mean proportion by weight (%) of krill in their diet from Kock *et al.* (2012) is used.
Average weight (mt)	0.009		The following website is the source of the average weight estimate: *http://www.lighthouse-foundation.org/index.php?id=90&L=1*
Feeding duration in the Antarctic (days)	365		It is assumed that marbled rockcod feed throughout the year in the Antarctic.
Daily krill intake, proportion of body weight	0.013	Flores *et al.* (2004)	It is assumed to be the same as the mackerel icefish as such information appears to be lacking for the marbled rockcod.
Annual per capita consumption of krill (mt)	0.03		Using Equation 4.5

TABLE 4.15: Summary of the information used to calculate the annual per capita consumption of krill (mt) for the marbled rockcod in this thesis.

4.5 Krill consumption by penguins

In Chapter 2, four penguin species were identified as krill-predators. Of the four, only the Adélie penguin is considered here due to limited availability of information on the other three species (i.e. chinstrap, macaroni and royal).

The information needed to calculate the annual per capita consumption of krill for the Adélie penguin is summarised in Table 4.16 below.

Information	Estimate	Source	Notes
Percentage of euphausiids in diet (%)	56.16	Ratcliffe and Trathan (2011)	The latest percentage of euphausiids in the penguin's diet estimate for each of the surveyed CCAMLR subareas are averaged together.
Average weight (mt)	3.81×10^{-3}	Nagy and Obst (1992)	
Feeding duration in the Antarctic (days)	331	Davis (1982)	Davis (1982) states that during the Adélie penguin courtship, both penguins fast for roughly 12 days. After their courtship, the eggs are laid. The female penguin, whose energy reserves are depleted from the courtship fasting and from producing eggs, goes to the sea (known as the *First Foraging Trip*) leaving the male to incubate the eggs. The males will continue fasting for an extra 14 - 22 days. Once the female returns, the male goes to sea for roughly two weeks, known as *Second Foraging Trip*. If the eggs have not hatched by the time the male returns, the female goes to sea for roughly a week (*Third Foraging Trip*). In summary, it is assumed that Adélie penguins fast for roughly 34 days of the year.
Daily krill intake, proportion of body weight	0.084	Nagy and Obst (1992)	Nagy and Obst (1992) use the average value of 1 014 kJ/day for the Adélie penguin SMR. Their paper further uses a metabolizable energy efficiency $(\frac{\text{food energy}-\text{faeces and urine energy}}{\text{food energy}})$ of 0.72 for the Adélie penguin when the penguins are eating krill. This thesis assumes that 0.72 is a reasonable approximation for the penguin's assimilation efficiency of krill.
Annual per capita consumption of krill (mt)	0.06		Equation 4.5 is used with a daily prey consumption value of 0.32 kg/day.

Table 4.16: Summary of the information used to calculate the annual per capita consumption of krill (mt) for the Adélie penguin in this thesis.

4.6 Summary

The total consumption of krill by weight for each species is calculated by multiplying Equation 4.5 by the abundance estimates of each species (see Chapters 5, 6 and 7). These abundance estimates and all the annual per capita consumption of krill estimates for each species, as used in this thesis, are summarised in Table 4.17.

Species	Annual per capita consumption of krill (mt)	Year of abundance estimate	Abundance (Number)	Total krill consumption $\times 10^3$ (mt)
Blue whale	490.8	1997/98	2 206	1 083
Fin whale	310.4	1997/98	38 185	11 853
Humpback whale	200.7	2014/15	97 188	19 506
Minke whale	63.2	1997/98	469 867	29 696
Crabeater seal	4.45	2000/01	7 719 714	34 353
Leopard seal	4.02	2000/01	35 500	143
Antarctic fur seal	1.77	1990/91	1 550 000	2 744
Adélie penguin	0.06	2013/14	3 655 698	216
Mackerel icefish	$8.07 \text{ x } 10^{-6}$	2014/15	32 102 million	259
Marbled rockcod	0.03	-	1 477 111	44

Table 4.17: Summary of the annual per capita consumption of krill (mt) and the total consumption of krill by weight (mt) for all the species considered in this thesis.

By considering the total consumption of krill by weight (mt), it is quite clear from Table 4.17 that the **main** krill-predators are the blue whale, fin whale, humpback whale, minke whale, crabeater seal and the Antarctic fur seal. Each of these species accounts for a total krill consumption value that is greater than 1 million tonnes. These are the six species that will be considered in the model developed in Chapter 11 of this thesis.

Chapter 5

Abundance and trend estimation for the main krill-feeding baleen whales in model

5.1 Overview of Chapter

This chapter considers the various ship surveys that have taken place and the associated methods used to determine baleen whale abundance in the Antarctic. It then discusses in more detail how the abundance estimates, trends and respective uncertainties for the main krill-feeding whales, from both Mori (2005) and as used in this thesis, have been estimated so as to highlight the differences in the available information since Mori (2005). These survey abundance estimates and trends are used in the model-fitting process, more specifically in the negative log-likelihood function that is minimised in the model developed in Chapter 11 of this thesis.

5.2 Antarctic Ship Surveys

5.2.1 IDCR/SOWER

In 1972, in Stockholm, the United Nations Conference on the Human Environment proposed a 10 year temporary pause in commercial whaling. The Scientific Committee of the IWC, in response to this proposal, suggested that a decade of intensive research on cetaceans be conducted instead. This programme became known as the *International Decade of Cetacean Research* (IDCR). The IDCR surveys were designed as independent, systematic surveys of the Antarctic in order to assess minke whale population numbers by recording whale sightings and using these to provide unbiased abundance estimates for the minke populations by means of the line transect methodology. Using the same approach, sightings of other cetacean species were recorded, making it possible to estimate abundance for these other species in addition to minke whales. The surveys operated during the austral summer, almost entirely south of 60°S and usually within in one of the IWC Management Areas (see Figure 4.2).

The first IDCR survey took place in 1978/79 when commercial whaling was still in operation, and subsequent surveys completed circumnavigation of Antarctica by 1983/84, operating in a different IWC Management Area each year. In 1984, the IWC Scientific Committee agreed that in the context of a "comprehensive assessment" of whale stocks, there was merit to continuing the IDCR surveys. Thus a second IDCR survey series was initiated, circumnavigating Antarctica between 1985/86 and 1990/91. This followed the same approach as the first circumpolar set of IDCR surveys, except that the survey design was different and abundance was estimated using a somewhat different methodology. Starting in 1991/92, a third circumpolar survey was conducted. In 1996/97, the programme was renamed to the *Southern Ocean Whale and Ecosystem Research* (SOWER) project and included a blue whale research component. The surveys became collectively known as the *IDCR/SOWER surveys*. In total, the IDCR/-SOWER surveys have circled the Antarctic completely three times: CPI (1978/79 - 1983/84), CPII (1985/86 - 1990/91) and CPIII (1991/92 - 2003/04). At the time Mori (2005) developed her Antarctic ecosystem model, the analysis of all the CPIII surveys had not been completed (from *http://discovery.nationalarchives.gov.uk/details/r/C5885* and *https://iwc.int/sower* [Accessed 12/04/2016]; Nishiwaki, 2004). The main differences between the three survey sets are outlined below.

CPI surveyed in a rectangular turret-like pattern in the northern regions and along the ice-edge to the south, while CPII and CPIII traversed zig-zag track-lines. For both CPI and CPII, some of the region between the survey's northern boundary and 60°S was left unsurveyed (see Figure 5.1). This was not the case in the CPIII surveys which were designed to extend to 60°S. From Figure 5.1, one can see the lack of survey effort in the north near 60°S in the majority of the CPI and CPII surveys. CPIII surveyed the region from 60°S to the ice-edge completely, but had to reduce annual longitudinal coverage to achieve the extra latitudinal coverage. This resulted in some longitudinal regions being surveyed more than once and was expensive time-wise, with CPIII needing 13 years to circumnavigate the Antarctic compared to the six years taken by both CPI and CPII (Branch, 2007).

These ship surveys for whales were performed in three ways: i) closing mode, ii) passing mode and iii) independent-observer (IO) mode. In *closing mode*, the vessel leaves the track-line when a sighting is made. This is done to confirm the whale species and the school size, but introduces bias as further sightings made on such diversions cannot readily be taken into account. Thus, search effort is lost in closing mode. In *passing mode*, the vessel does not leave the track-line when a sighting is made. Instead, observers in the barrel, high on the main mast, maintain full search effort while the observers on the upper bridge work on tracking and identifying the sighting, though this can be difficult. Confirming the whale species and school size is difficult and introduces bias in passing mode. *IO* mode is exactly the same as passing mode except that an additional independent observer is placed on a separate platform (known as an *IO platform*) on the main mast, to maintain search effort and provide information that allows estimation of whale detectability on the track-line (see Figure 5.7). During IO mode, duplicate even triplicate records can be made of the same sighting. Such records (duplicate and triplicate) are either coded as “definite”, “possible” or “remote”. In general, “definite” duplicate and triplicate records are treated as a single sighting while the rest are assumed to be sightings of multiple but separate schools (Branch, 2011; Branch and Butterworth, 2001a).

For analyses on minke whales, closing and IO modes are treated separately but for analyses on other whale species where sightings are scarce (such as blue whales), these two modes are often combined. Note that CPI was conducted in closing-mode whilst CPII and CPIII alternated between closing mode and IO mode (Branch, 2011).

The differences between the three CP surveys make it difficult to compare the abundance estimates derived from them. Of the differences, Branch (2007) states that the most important one is the unsurveyed northern areas in the CPI and CPII surveys. To take these areas into account, it has been assumed that the density in the unsurveyed areas is the same as in the adjacent northern strata. This gives rise to what are termed *comparable estimates* (Branch, 2007).

5.2.2 JARPA and JARPAII

The Japanese Whale Research Program under Special Permit in the Antarctic (JARPA) surveys were a component of a long-term monitoring program in the Antarctic that operated in the austral summer from 1987/88 until 2004/05. The programme had four main objectives:

1) estimate the biological parameters of the Antarctic minke whale to improve the management of the stock;

2) explain the role of whales in the Antarctic ecosystem;

3) clarify the effect of environmental change on cetaceans in the Antarctic; and

4) explain the stock structure of the Antarctic minke whale, so as to improve stock management of the resource.

During their operation, the JARPA surveys also determined survey estimates of minke whale abundances from sightings (using line-transect sampling) that were semi-independent from their main objectives and research. Overall, the JARPA surveys conducted lethal sampling surveys, which included minke whale catches taken under special research permit, oceanographic surveys, prey species surveys and photo identification, and biopsy sampling for the large baleen whales. JARPA alternated between the IWC Areas IV and V in the same months and season during its operation, providing a time series of whale abundance estimates (from *http://www.icrwhale.org/scJARPA.html* [Accessed 12/04/2016]; Hakamada *et al.*, 2013).

JARPA II followed JARPA and began with two feasibility surveys, one in 2005/06 and the other in 2006/07. Its first full study took place during the 2007/08 austral summer where its main objectives were to:

1) monitor the Antarctic ecosystem including: whale abundance trends and biological parameters, krill abundance, whale's feeding ecology, and the effects of contaminants on cetaceans and cetacean habitat;

2) model possible competition amongst the whale species and future management objectives including the restoration of the cetacean component of the Antarctic ecosystem;

3) explain the temporal and spatial changes in whale stock structure; and

4) improve the management procedure for the Antarctic minke whale.

JARPA II ended in 2013/14 (from *http://www.icrwhale.org/scJARPA.html* [Accessed 12/04/2016]).

5.2.3 JSV

During 1965/66, when commercial whaling was still in operation, the National Research Institute of Far Seas Fisheries in Japan collected cetacean sighting records from Japanese scouting vessels as part of their whaling operations in the Antarctic. These data became known as the JSV data and are comprised almost entirely of data collected by full-time scouting vessels. The JSV data do not come from a random or systematic survey, but from whaling ships scouting in areas of relatively high whale density. As a result, these data are potentially biased in terms of use for abundance estimation. These surveys also did not have a consistent track design, only identifying species and the number of schools and animals seen in a day. They further did not classify whether sightings were primary or secondary (seen while closing on a primary sighting), and recorded only the total searching distance (n.miles) in a day and the weather as it was at noon.

Due to these aspects, the IWC Scientific Committee considers the JSV data to be unsuitable for direct whale density estimation. However, unlike the IDCR/SOWER surveys that surveyed only south of 60°S, the JSV surveyed north of 60°S in sub-Antarctic waters where the sei whale, the main target species during the 1960s, was abundant. By the 1970s, the minke whale became their next main target and as a result, the JSVs began scouting south of 60°S. Due to their earlier more northerly coverage, the JSV data are useful for studying seasonal migration patterns (de Korte *et al.*, 2008; Miyashita *et al.*, 1994) and in extrapolating IDCR/SOWER survey estimates northwards such as in Butterworth and Geromont (1995).

5.3 Regions Analysed

For her Antarctic ecosystem model, Mori (2005) divides the Antarctic into two regions, Region AI and Region PO, defined as follows:

$$\text{Region AI} = \text{Area II} + \text{Area III} + \text{Area IV} \tag{5.1}$$

$$\text{Region PO} = \text{Area V} + \text{Area VI} + \text{Area I} \tag{5.2}$$

where the *Area* refers to an IWC Management Area.

Region AI combines the IWC areas in the Atlantic and Indian sectors of the Southern Ocean, whilst Region PO contains the IWC areas in the Pacific sector of the Southern Ocean only (see Figure 5.2). Mori (2005) argues that this division is reasonable because the majority of the large baleen whale and seal commercial harvests occurred in Region AI - the harvesting in this region almost rendered some of the whale and seal stocks extinct. By comparison, large baleen whales and some seal stocks were harvested in fewer numbers in Region PO. Her divisions suggest an uneven pre-exploitation distribution of the large baleen whales and seals - with these being more abundant in Region AI and relatively fewer in Region PO.

This thesis considers a further set of *new* divisions used as a sensitivity check for the model and its results. It also divides the Antarctic into two regions, Region AO and Region PI, defined as follows:

$$\text{Region AO} = \text{Area II} + \text{Area III} \tag{5.3}$$

$$\text{Region PI} = \text{Area IV} + \text{Area V} + \text{Area VI} + \text{Area I} \tag{5.4}$$

where

Region AO contains the IWC areas in the Atlantic sector of the Southern Ocean only, whereas Region PI combines the IWC areas in both the Pacific and Indian sectors of the Southern Ocean (see Figure 5.3).

5.4 Distance Sampling

5.4.1 Introduction

Whale abundance estimates are frequently obtained using *distance sampling*, or more precisely *line transect distance sampling*: a ship travels along a randomly chosen path, known as a *line transect* or *track-line* and measures/estimates the perpendicular distance from the line to each whale or school detected. The focus of *line transect sampling* is on accurate distance measurements for all animals near the track-line. As a whale or school is detected, its perpendicular distance to the track-line whose known length is L, is measured (see Figure 5.4). These distances may be used to calculate unbiased density estimates provided that certain assumptions are met and the distances are recorded reasonably accurately. In general, several lines of length L_i are used to sample the population where $\sum L_i = L$ (see Figure 5.5). The elegance of distance sampling is the fact that not every whale needs to be seen in order to estimate the population abundance (Buckland *et al.*, 1993).

It is convenient to measure the radial sighting distance r_i and angle to the track-line θ_i rather than the perpendicular distance y_i directly for each of the school/whale detected (see Figure 5.6).

The value of y_i can be calculated using simple trigonometry:

$$y_i = r_i \sin(\theta_i)$$

5.4.2 The *detection function*

Another important aspect of distance sampling is the use of a *detectability function*, estimated robustly using the perpendicular distances for the animals that are seen. The detection function is defined as:

$$\begin{aligned} g(y) = &\ \text{the probability of detecting a whale, given that it is at perpendicular distance } y \text{ from the} \\ &\ \text{track-line} \\ = &\ prob\{\text{detection}|\text{distance } y\} \quad \text{which is often represented by} \\ = &\ key(y)[1 + series(y)] \end{aligned}$$

where the distance y is the perpendicular distance to the sighting (Figure 5.6) and $0 < g(y) \leqslant 1$.

key(y) is a simple core function, the starting point used to model $g(y)$. It is typically chosen based on visual inspection of the histogram of the sampled distances after that has been truncated to exclude outliers. The core functions used frequently are the uniform, the negative exponential, the half-normal and the hazard-rate function (see Figure 5.8). The core function alone can be used for modeling $g(y)$, especially if the sample size is small or a simple model is sufficient to describe the distribution of the perpendicular distance data.

series(y) is a series expansion, a flexible form used to adjust the core function so that the model can fit the perpendicular distance data better. The three main classes of series expansions used are the cosine series, simple polynomials and Hermite polynomials.

There is a general tendency for "detectability" to decrease with increasing perpendicular distance from the track-line so that $g(y)$ decreases with increasing y. A few models for $g(y)$ are selected before the analysis is performed, without referring to the given data set - the one that fits the data best is chosen. A flexible/robust model for $g(y)$ is imperative, and should have three properties which in the order of importance are:

1) *model robustness*: the model should be a general and flexible function that can take on a variety of likely shapes. This excludes single parameter models. Pooling robustness is an aspect of this property. Models for $g(y)$ are *pooling robust* if the data they fit can be pooled over many factors that affect detection probability.

2) *shape criterion*: the detection function should have a *shoulder* near the track-line, i.e. whale detectability remains nearly the same at small distances from the line. Mathematically speaking, this means that the derivative $g'(0) = 0$. This property excludes functions that are spiked near zero distance. In general, good models for $g(y)$ will satisfy this property near the zero perpendicular distance from the track-line.

3) *efficiency*: this is the property that the model that provides relatively precise estimates (estimates with small variance) is the most desirable model. In general, as the number of estimable parameters in the model increases, the bias decreases but the estimation variance increases (i.e. precision drops). Thus, the best model for a particular data set requires enough parameters to avoid large bias but not so many as to sacrifice precision.

5.4.3 Main assumptions

Buckland *et al.* (1993) state that for statistical inferences of population abundance to be valid:

1) the sampling survey must be competently designed and conducted; and

2) the physical setting must be idealised $\Rightarrow$ a) whales are spatially distributed in the sampling area according to some stochastic process with rate parameter D (number of whales per unit area), and b) line transects are placed randomly with respect to the distribution of the whales. These lines are surveyed and n whales/schools are detected, measured and recorded.

Random line placement ensures a representative sample of the measured distances and thus a valid density estimate.

The main assumptions for standard line-transect sampling, in order of importance, are as follows.

1) All whales directly on the line are detected always with probability of 1 or $g(0) = 1$. It is also possible that $g(0) < 1$: whales that are missed along the track-line have a $g(0) < 1$ - this would make their abundance estimates negatively biased. Minke whales are small in size and have less noticeable cues, making it difficult for an observer to detect them. Thus, it is possible that their $g(0) < 1$.

2) Whales are detected at their initial location, prior to any movement in response to the observer. Slow moving animals relative to the observer's speed, or immobile animals, cause few problems with regards to this assumption. However, animals taking evasive action prior to detection pose a problem. Thus, a jack rabbit senses the approaching observer and flushes - this evasive movement marks its initial location; however, if the jack rabbit moves away from the observer and waits under heavy cover up ahead and the observer approaches, the same rabbit will flush again. If the "new" location is thought to be its initial (original) location, then this assumption is violated. In this case, extra assumptions may be needed unless additional data are available.

3) Distances (and angles where relevant) are measured accurately or are correctly allocated to the pertinent distance category, depending on the data type and especially near the track-line itself. Rounding errors can be problematic especially close to the track-line where small sighting angles are rounded to zero, leading to the density being overestimated.

5.4.4 Important concepts

Buckland *et al.* (1993) state that when designing a line transect survey, one can denote a distance W where whales at distances $(y) > W$ can be ignored. Not every object with $y < W$ will be seen. There is some value $y = w$, where $w < W$ called the *effective search half-width* (or w_s) such that, for abundance estimation purposes, the effective area searched can be considered to be $2wL$.

Known constants and unknown parameters of interest are distinguished below - they are used in the fundamental equations of line transect sampling and abundance estimation.

Values input to analyses

A	is the sampling area, i.e. this is the area for which the abundance of the whale species of interest is to be estimated;
k	is the number of lines surveyed;
L_i	is the length of the i^{th} line transect where $i = 1, ..., \text{k}$;
L	is the total length of the line transects $= \sum L_i$ or the *distance searched*;
w	is the effective width of the area searched on each side of the line transect, often called the *effective search half-width.* For example, in the analysis by Kasamatsu *et al.* (1996), for blue whales, $w = 1.37$ n.miles whilst for minke whales, $w = 0.53$ n.miles.
n	is the number of whales/schools detected after the survey has been conducted. It depends on many factors that interact with each other such as *cue production* (an animal provides cues that leads to its detection e.g splashes, blowhole sprays; often, the probability of detecting animals based on cue production decreases as the distance increases from the observer); *observer effectiveness* (includes experience, training, acuity in vision and hearing, height and fatigue) and *environment* (includes habitat and physical conditions which can prevent detection such as wind, rain, angle of the sun, time of day). Provided $g(0) = 1$, these factors need not be taken into account explicitly in the density estimation if the distances are measured properly and an appropriate analysis is performed.
n/L	is the number of whales seen per unit of distance searched or the *encounter rate* - this can be used as a crude index of relative density.

Parameters estimated

D	is the density of the population (number whales per unit area) or the expected number of whales per unit area;
N	is the size of the population in area A;
$E(s)$	is the mean cluster size in the population often estimated by $\bar{s}$, the sample mean of the detected objects;

$f(0)$ is the probability density function of perpendicular distances from the transect line, evaluated at zero distance; and

$g(0)$ is the probability of detection on the line, usually assumed to equal one.

5.5 Abundance Estimation

The basic equation used in line transect sampling to estimate whale abundance is:

$$N = \frac{A \cdot E[s] \cdot n}{2 \cdot w_s \cdot L} \tag{5.5}$$

where

N is the abundance estimate for the whales in the region surveyed;

A is area of the region searched (typically in n.miles^2);

$E[s]$ is the mean school size;

n is the number of schools sighted during the vessel's primary search effort;

w_s is the effective search half-width for schools (typically in n.miles); and

L is the primary search effort (typically in n.miles).

The *primary search effort* relates to the time vessels spend searching for whales but excludes periods such as those used to confirm whale species and/or school size, refuelling, experiments and drifting during bad weather.

The uncertainty or *coefficient of variation (CV)* of N is based on the precision of the estimate of the encounter rate, the mean school size and the effective school search width:

$$CV(N) = \sqrt{\left[CV\left(\frac{n}{L}\right)\right]^2 + \Big[CV(E[s])\Big]^2 + \Big[CV(w_s)\Big]^2} \tag{5.6}$$

Branch (2011; 2007) states that in his analyses when estimating w_s, whale sightings are smeared using Method II of Buckland and Anganuzzi (1988) whereafter they are grouped into 0.1 n.mile bins out to the truncation distance of $w = 3.0$ n.miles. Smeared estimates are used to make allowance for the fact that angles and distances of the sightings are not known exactly but are estimated with some error. Finally, the hazard rate detection function is used to fit the smeared perpendicular distances of the sightings made on primary search effort. This function is defined as follows:

$$\begin{aligned} f(y) &= \text{the probability density function of the whale sighting distribution} \\ &\quad \text{in relation to the perpendicular distance } (y) \text{ from the track-line} \\ &= f(0)g(y) \\ &= f(0)\Big[1 - exp\Big(- \Big[\frac{y}{a}\Big]^{-b}\Big)\Big] \end{aligned}$$

where a is an estimated scale parameter subject to $a \geqslant 0.0001$ n.mile and b is an estimated shape parameter subject to $b \geqslant 1$.

Abundance estimates for blue, fin and minke whales have been obtained from surveys south of 60°S such as IDCR/SOWER and JARPA. However, for humpback whales, most of the available estimates come from their breeding grounds found in the lower latitudes of the Southern Hemisphere. Although there is some abundance information available from surveys regarding humpback whales south of 60°S, as was used in Mori (2005), the estimates used in this thesis are from models fitted to the data from their breeding grounds.

5.5.1 Potential biases associated with the survey estimates

Mori (2005) details the potential biases associated with the abundance estimates calculated using Equation 5.5. These biases are outlined below.

1) *The credibility of the assumption that* ***all*** *whales are sighted on the track-line i.e.* $g(0) = 1$.

Mori (2005) states that there is strong evidence suggesting that $g(0)$ depends on school size, observer experience and on some environmental factors. She motivated for a decrease in $g(0)$ between CPIII and CPII because less experienced observers were present in CPIII. Observer experience can affect abundance estimation - this is especially true for minke whales as they are small and have less noticeable cues. This suggests that their $g(0) < 1$.

When allowance is made for not all the whales on the track-line being detected (i.e. $g(0) < 1$), abundance estimates increase. Such an allowance has more impact for CPIII than CPII as the mean school size for CPIII is considerably smaller compared to that of CPII - smaller schools are less likely to be detected on the track-line. The IWC Scientific Committee (IWC, 2013) concluded that there is a complex relationship between $g(0)$, school size, school density and location. As a result, minke abundance estimates can vary appreciably depending on what this relationship is.

Mori (2005) further suggests that for humpback whales, $g(0)$ depends on their school size and hence could also be less than 1, especially for solitary whales. However, blue and fin whales are relatively larger (compared to minke and humpback whales) and have more noticeable cues so that they are easier to detect. This makes $g(0) = 1$ a reasonable assumption for these two whale species.

2) *The use of "comparable areas" abundance estimates*

When comparing whale abundance in the unsurveyed areas south of 60°S - *comparable areas* estimates are used. Mori (2005) and Branch (2007) state that this assumption probably introduces positive bias to the abundance estimates of minke and blue whales as the densities of these whale species tend to decrease with increasing distance away from the ice-edge. Thus, it is likely that blue and minke whale densities in the unsurveyed northern areas are lower than in the adjacent northern strata. The opposite holds true for fin whales where the fin whale sighting rate is higher in the regions north of 60°S. This suggests that *comparable areas* estimates for fin whales may be negatively biased.

3) *Abundance in the unsurveyed areas within the pack-ice*

Mori (2005) summarises several studies and concludes that there is a substantial number of minke whales present in the pack-ice. This suggests that the minke abundance estimates are negatively biased. More recently, there is a substantial difference between the latest CPIII minke abundance estimate and the CPII estimate, with the CPII estimate being bigger than the CPIII estimate (Table 5.4). A possible reason for this difference is that there were a higher proportion of minke whales in the pack-ice or polynyas (within in the pack-ice) in CPIII compared to CPII (IWC, 2013). As a result, a number of studies have been conducted to estimate the number of minke whales south of the ice-edge. Kelly *et al.* (2012) evaluate different data and methods (including aerial surveys) used to estimate minke abundance within the sea-ice* covered areas of East Antarctica (such as the Weddel Sea; see Figure 2.1). Those authors conclude that until estimates of availability bias are produced, absolute abundance estimates for minke whales in areas and over seasons in which the aerial surveys were conducted, will not be possible. Furthermore, in the case that a substantial number of minke whales are found in the sea-ice regions, more aerial surveys may need to be conducted over those regions in order to produce a truly unbiased circumpolar minke abundance estimate from any post-CPIII era survey efforts. Murase and Kitakado (2013) analyse the abundance estimates of minke whales within the sea-ice of the IWC Area IV (see Figure 4.2) from the CPIII data. They conclude that the exact relationship between minke whale abundance and sea-ice concentrations cannot be estimated using the IDCR/SOWER data but that it can be assumed that minke abundance within the sea-ice decreases as sea-ice concentration increases. It is still not known what proportion of minke whales inhabit the pack-ice (IWC, 2015).

Although blue whales are distributed close to the ice-edge, Mori (2005) reasons that they have not been detected in the pack-ice due to their current small population size. Humpback whales have also not been detected in the pack-ice. Mori (2005) deduces that if humpback whales are in the pack-ice, they would have been detected due to their "sufficiently large" population size. Lastly, fin whales have not been detected in the pack-ice, probably because their main distribution region is far to the north of the pack-ice.

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*The term *sea-ice* is used interchangeably with *pack-ice*. However, the same meaning is implied in this context, as pack-ice is simply sea-ice "packed" together.

4) *Abundance in the unsurveyed areas, north of 60° S*

Kasamatsu *et al.* (1996) analysed the relationship between the encounter rate and the baleen whales' latitudinal occurrence in the Antarctic between mid-December and mid-February from 1976 until 1988 using IDCR/SOWER and JSV data. Those authors found that the main concentration of blue and minke whales are roughly between 66°S - 70°S and south of 66°S respectively. Humpback whales are concentrated over roughly 62°S - 66°S and fin whales over roughly 54°S - 58°S. Thus, abundance estimates calculated from surveys south of 60°S (e.g. Branch (2007)) are a reasonable representation of the current minke, blue and humpback whale populations in the Southern Hemisphere. However, this does not hold true for fin whales as their main distribution during the austral summer is north of 60°S. This implies that fin whale abundance estimates calculated from surveys south of 60°S are negatively biased.

Hence, the fin whale abundance estimates used in this thesis have been extrapolated northwards using the JSV data which covered areas north of 60°S.

Mori (2005) uses Butterworth and Geromont (1995) to estimate the multiplicative extrapolation factor for fin whales. Butterworth and Geromont (1995) use the JSV sighting rate data from 1965 to 1987 as an index of relative density to extrapolate IDCR/SOWER-derived fin whale abundance estimates to areas north of 60°S. The resultant multiplicative extrapolation factor for fin whales lies within the range of about 5.5 - 7.

A similar analysis is carried out in this thesis to find the extrapolation factors for Regions AI, PO, PI and AO, using the information in Butterworth and Geromont (1995) and Butterworth *et al.* (1994a). Butterworth and Geromont (1995) extrapolate IWC/IDCR abundance estimates northwards using JSV data along certain latitudinal strata and at a half-area longitudinal level. The equation used to calculate abundance is:

$$P = \mathrm{IDCR} + \sum_{q=2}^{5} \overline{D_{1N}} \sum_{j} A_{q,j} \cdot \frac{S_{q,j}}{S_{1N}} \tag{5.7}$$

where

P is the extrapolated abundance estimate for latitudinal stratum q;

$A_{q,j}$ is the open ocean surface area of stratum q and longitudinal half-area j (for CPI);

$\overline{D_{1N}}$ is the weighted mean whale density estimate for the northern strata of the IWC/IDCR surveys, a value from Butterworth *et al.* (1994a);

$S_{q,j}$ is the total number of sightings divided by the total distance traveled during the search effort for stratum q and longitudinal half-area j from the JSV data;

$S_{1,N}$ is the whale sighting rate from the JSV data for the northern strata of the IWC/IDCR surveys, a value from Butterworth *et al.* (1994a);

$IDCR$ refers to the abundance estimate from the of the CPI IWC/IDCR surveys; and

q indexes the circumpolar latitudinal strata between the Antarctic ice-edge and 30°S:

$q = 1$ refers to the CPI IWC/IDCR surveys,

$q = 2$ refers to the area from the northern CPI IWC/IDCR survey boundary to 60°S but excludes any area between 40°W and 60°W which falls within the CPI survey area,

$q = 3$ refers to the area from 60°S to 50°S but excludes the area south of 58°S between 40°W and 60°W as it falls within the CPI survey area,

$q = 4$ refers to the area between 50°S and 40°S, and

$q = 5$ refers to the area between 40°S and 30°S.

Equation 5.7 is adjusted slightly to take into account the further IDCR data found in Branch and Butterworth (2001a). The new abundance estimate equation for each region is:

$$P_J = \mathrm{IDCR}_J + \frac{\mathrm{IDCR}^{BB(2001)}_{total}}{\mathrm{IDCR}^{BEA(1994)}_{total}} \overline{D_{1N}} \sum_{q=2}^{5} \sum_{j \in J} A_{q,j} \cdot \frac{S_{q,j}}{S_{1N}} \tag{5.8}$$

$$= \mathrm{IDCR}_J \Big(1 + \mathrm{extrapolation}_J \Big) \tag{5.9}$$

where

$IDCR_J$ refers to the abundance estimate for Region J from the IWC/IDCR CPI surveys in Branch and Butterworth (2001a);

J refers to the Region of Interest, either Region AI, PO, AO or PI;

$IDCR^{BB(2001)}_{total}$ is the total fin whale abundance estimate from the IWC/IDCR CPI surveys from Branch and Butterworth (2001a); and

$IDCR^{BEA(1994)}_{total}$ is the total fin whale abundance estimate from the IWC/IDCR CPI surveys from Butterworth *et al.* (1994a).

Using Equations 5.8 and 5.9, the extrapolation factors for fin whales for the Regions of Interest all fall within the range found in Mori (2005) and are:

Region AI = 5.93, Region PO = 5.12, Region AO = 5.38 and Region PI = 5.50.

5) *Sightings classified as "like-species"*

Mori (2005) mentions that not all sightings of schools can be allocated to a specific whale species with certainty thus some sightings are classified as "like-species". Matsuoka *et al.* (2003) provide a general guideline of like-species identification where the cue observed is the whale blow. In most cases, the body of the whale is not observed or the view of the body is poor and insufficient to notice any determining features. As it is unclear what proportion of "like-species" sightings are of the actual species in question, abundance estimate computations are run including and excluding "like-species" sightings. It is the comparison between abundance estimates including and excluding "like-species" sightings that determine whether this aspect plays an important factor in the abundance estimation. In general, the inclusion of "like-species" sightings increases the total whale abundance estimate. Even though the abundance estimate can increase, it can decrease as well as w_s may also increase when "like-species" sightings are included.

6) *The estimation of* $E[s]$ *or the "mean school size"*

The estimation error for $E[s]$ is negligible for the blue, fin and to a lesser extent humpback whales due to their larger size (Mori, 2005). However, for minke whales, Brandão *et al.* (2001) draw attention to a positive bias in using an average of the observed school sizes as a mean school size estimate for minke whales. This is because smaller schools (by number) are less likely to be sighted than larger schools with greater distance from the track-line.

7) *Survey timing and peak in whale migration*

Matsuoka *et al.* (2003) state that from 1994 onwards, the IDCR/SOWER surveys began about two/three weeks later compared to the earlier surveys in the series. The earlier surveys began around mid-December and finished around mid-February, whilst the later surveys (after 1994) started in early January and finished towards the end of February/early March. This delay assisted in cruise track construction but raised concerns as the majority of the CPIII surveys did not coincide well with the peak migration period of minke whales. This possibly led to a decrease in minke sighting rates. The impact of survey timing for blue and fin whale is deemed small by Kasamatsu *et al.* (1996). Those authors analyse whale sighting rates in relation to seasonal occurrences using the IDCR/SOWER surveys between 1976 and 1988. They found that the peak in blue and fin whale occurrence is late January until February which falls within the periods of the CP surveys. Similarly for humpback whales, their highest densities are found throughout January and drop only in February. Thus, they are not impacted severely by survey timing.

5.6 Abundance and trend estimation for the baleen whales

General equations used in this section are:

$$\text{Abundance Estimate for Region of Interest} = \sum(\text{Abundance Estimates of IWC Areas in Region of Interest}) \tag{5.10}$$

$$\text{Calculated Variance} = (\text{Abundance Estimate})^2(\text{CV})^2 \tag{5.11}$$

where Equation 5.11 holds for the Regions of Interest and the IWC Management Areas.

$$\text{corr}_{A,B} = \frac{\text{cov}_{A,B}}{\sqrt{\text{var}_A \cdot \text{var}_B}} \tag{5.12}$$

where $corr_{A,B}$ is the correlation between quantities A and B and $cov_{A,B}$ is the covariance between A and B.

5.6.1 Blue whales

Mori (2005) used Rademeyer *et al.* (2003) for blue whale abundance estimates for the 2000/01 season. Rademeyer *et al.* (2003) note that when aggregating the IDCR/SOWER survey data to obtain composite abundance estimates, information on trend in each CP series is lost. As a result, their paper considers the IDCR/SOWER survey data at a management area level rather than a circumpolar level, where each management area is treated as containing an independent stock. These stocks are assumed not to mix with each other and to have the same intrinsic growth rate. A Schaefer model is fitted to the IDCR/SOWER survey density estimates in conjunction with Antarctic blue whale abundance indices from the JARPA surveys.

For the update in this thesis, blue whale abundance and trend estimates are both taken from Branch (2007). Branch (2007) combines closing mode and IO mode data for both CPII and CPIII due to the small number of blue whale sightings. Furthermore, all the primary search effort is included except for effort directed towards areas of expected high blue whale density. Sightings recorded as code 01 (Antarctic blue whale), code 98 (blue whale, probably Antarctic) and code 99 (blue whale, undetermined subspecies) are used when calculating the abundance estimates (Equation 5.5). Since the comparable areas assumption tends to “over-estimate” the *comparable areas* estimate for blue whales, Branch (2007) assumes that there are no blue whales in the unsurveyed northern areas.

Branch (2007) obtains estimates of blue whale school sizes from confirmed sightings in closing mode only. Since large schools are visible at larger distances (compared to small school sizes), school size estimates are corrected for bias using a regression method that is suggested in Buckland *et al.* (1993). This method takes into account the changes in the detectability of the different school sizes with respect to their distance from the track-line. Blue whale sample sizes are small in most of the CP surveys. As a result, sightings are pooled over all surveys in a CP set in order to estimate w_s and $E[s]$ following the method described in Branch and Butterworth (2001a). Furthermore, due to the scarcity of blue whale sightings, the smearing parameters cannot be estimated reliably from these data. They are set to 4.0° for angles and 0.3 n.mile for distances based on average values for other whale species and the recommended values used in Branch and Butterworth (2001a). Again, for the variance computations, each management area is assumed to contain an independent blue whale stock which does not mix with other stocks.

Table 5.1 contains the blue whale *comparable areas* estimates and their respective CVs from the CPIII IDCR/SOWER surveys for each of the IWC Areas, taken from Branch (2007). The blue whale abundance estimates for the 1997/98 season, the mid-year of the CPIII survey, are calculated for each Region of Interest (Table 5.2).

Mori (2005) used results from Branch and Rademeyer (2003) where the successive circumpolar abundance estimates provided a basis to determine blue whale trend estimates. For this update, the circumpolar estimates from Branch (2007) *adjusted simply for comparable areas* are used as a basis for the blue whale trend (Table 5.3).

5.6.2 Minke Whales

Mori (2005) used minke whale abundance estimates for the year 1985/86 from Branch and Butterworth (2001b), adjusted for potential bias factors (see Section 5.5.1). Adjustments included: comparable estimates from Branch (2003), extrapolation north of 60°S factors from Borchers (1991), school size estimates and estimates including "like minke" whales from Butterworth *et al.* (2001), and factors for the survey timing and the minimum and maximum possible effects of $g(0) < 1$ from Butterworth *et al.* (2003).

More recently, two models have been used to estimate current minke whale abundance: the Okamura and Kitakado (2012) model (the *OK* model) and the Bravington and Hedley (2012) model (the *SPLINTR* model). The most recent and best available consensus estimates of minke whale abundance are found in IWC (2013), summarised in Table 5.4. These estimates are the "preferred estimates" from the OK model using the best mean dive-time estimates from Hedley (2012), and with some appropriate adjustment factors based on the SPLINTR approach applied (IWC, 2013). Key advances in these analyses compared to the earlier estimates of Branch and Butterworth (2001b) are the use of sightings from independent platforms on vessels to estimate the value of $g(0)$, and improved allowance for the spatial distribution of the whales.

There is a substantial difference (about 33%) between the minke abundance estimate from CPIII and CPII. Possible reasons for this difference, detailed in IWC (2013), are:

1) There were more minke whales in the unsurveyed regions during CPIII than in CPII.
2) There was a higher proportion of minke whales in the pack-ice or polynyas in the pack-ice during CPIII compared to CPII. This is being investigated as mentioned in Section 5.5.1.
3) A much higher proportion of the total minke population was north of 60°S during CPIII.
4) Surveys conducted as part of CPII happened to encounter higher whale densities in certain areas due to the extensive latitudinal whale movement from year to year, compared to CPIII.
5) Intra-year movements in the open waters within the surveyed area were not adequately covered by either CP (CPIII or CPII) track-line design in space and time, with respect to environmental variables.
6) There was a genuine decrease in the minke abundance between the periods of CPII and CPIII.

For this update, the CPIII Common Northern Boundary (CNB) estimates together with the *CV internal* from Table 5.4 are used to calculate the updated minke whale abundances and CVs for the Regions of Interest (using Equations 5.10 and 5.11 where appropriate) for the 1997/98 season, this being the mid-year of the CPIII survey. The CPIII surveys are used for the updated minke abundance estimates (rather than using both CPII and CPIII estimates) because the overall minke trend information used in this update takes the CPII data into account. To avoid using the same information twice, the CPII minke abundance estimates are therefore not used in the ecosystem model fitting. The *CV internal* value is used because the Regions of Interest are very large so including the additional variance in the summations would likely lead to strong positive bias in the CV. These estimates are summarised in Table 5.5.

Mori (2005) calculated minke trend estimates using a *catch-at-age* analysis based on Butterworth *et al.* (1999). Those authors estimated trends in minke whale recruitment and abundance in the IWC Management Areas IV and V by applying an ADAPT-like version of the Virtual Population Analysis (VPA) to both commercial and research catches-at-age and abundance estimates from the IDCR/SOWER and JARPA surveys. Mori (2005) extended the Butterworth *et al.* (1999) analyses by using the most recent research catch-at-age data then available (up to the 2003/04 season) and the abundance estimates from JARPA surveys for the IWC Management Areas IV and V. Differences between the Mori (2005) and the Butterworth *et al.* (1999) analyses were:

1) use of the ADMB package (Fournier *et al.*, 2012) for the computations in Mori (2005) - ADMB has a more powerful and reliable minimisation capability when fitting the ADAPT-VPA model to data and estimating parameters;

2) with 1) and an extended data set, a 1-year-1-age analysis was implemented in contrast to the 3-year-3-age aggregation that was used in Butterworth *et al.* (1991); and

3) Mori (2005) treated the IWC Management Areas IV and V as a region that contained a single stock which was distributed into two feeding regions in such a way that there was some inter-area variability from year to year.

For this update, the minke trend estimates are calculated using the analysis conducted by Punt (2014). Punt (2014) applies a Statistical Catch-at-Age Analysis (SCAA) to the Southern Hemisphere minke whale data. This analysis is an improvement of the earlier Punt *et al.* (2013) SCAA analysis. Instead of abundance estimates that are based on the JARPA/JARPAII surveys used in Punt *et al.* (2013), the $g(0)$-corrected abundance estimates from Hakamada and Matsuoka (2014) are used (called the "New Reference Case" or *New RC*) in Punt (2014). Punt *et al.* (2013) consider two stocks: Stock I is assumed to occupy the IWC Managament Areas III-East, IV and V-West, and Stock P is assumed to occupy areas V-East and VI-West (see Figure 4.2), where this choice of boundary is based on genetic analyses. The slope of the linear regression of the estimates of the logarithms of the number of recruits (b_{rec}) over a specific time period (Punt *et al.*, 2013) is then used to provide the minke trend estimates over that period. However, there is some correlation between the two stocks as minke whales in Stock I mix with the minke whales in Stock P, and also over the different time periods as trend estimates depend on estimates of natural mortality. As a result, the inverse variance-covariance matrix of b_{rec} is calculated (using Equation 5.12 where appropriate), and is used to reflect precision when the minke trend estimates are input to the ecosystem model of Chapter 11 - see Table 5.6. The b_{rec} variance-covariance matrix and the SCAA population estimates were kindly provided by A. Punt (School of Aquatic and Fishery Sciences, University of Washington).

5.6.3 Fin Whales

There have been no fin whale abundance estimate updates based on the IDCR/SOWER surveys since those repeated in Mori (2005). Mori (2005) used fin whale abundance estimates from Branch and Butterworth (2001a) and multiplied them by an extrapolation factor to take into account the higher fin whale density north of 60°S (see Section 5.5.1, point 4). In essence, she extrapolated the IWC/IDCR survey data northwards using JSV data.

Branch and Butterworth (2001a) used sighting data from the CPI, CPII and the then incomplete CPIII IDCR/SOWER surveys south of 60°S. Fin whale abundance estimates were calculated from Equation 5.5, using the *comparable areas* abundance estimate for CPIII and using the IWC database estimation package (DESS). Using the line transect distance sampling methodology, $E[s]$ and w_s were estimated by pooling across the years and strata. Furthermore, the "like-species" sightings were not included and both "definite" and "possible" IO mode duplicates were removed. To estimate w_s, data were truncated at a certain perpendicular distance from the track-line. The rule of thumb proposed by Buckland *et al.* (1993) is to truncate roughly 5% of the data. This was implemented. Smearing parameters were obtained by pooling all the sightings within a CP survey set, irrespective of whether school size had been confirmed or not. If there were too few sightings to estimate the smearing parameters, they were set to an angle value of 4.0° and a proportional radial distance value of 0.3 - these were typical values that could have been obtained if the estimation was possible. A hazard rate function was fitted to the smeared and truncated data. Only closing mode sightings for which the school size was confirmed were used to calculate $E[s]$. If the same stratum was surveyed by two vessels, an effort-weighted average of the density estimate was used to calculate the stratum's abundance estimate.

The same fin whale abundance and CV estimates (a default value of 0.5 was used) from Mori (2005) are used for Regions AI and PO for the 1997/98 season (see Table 5.7). Given the scarcity of information, these same abundance and CV estimates are used for Regions AO and PI for the same season. This is considered reasonable as all four Regions extrapolation factors fell within the range calculated in Mori (2005) (see Section 5.5.1, point 4).

Mori (2005) did not include any fin whale trend estimate in her analysis whereas this thesis does. The fin whale trend and CV estimates use the information in Matsuoka and Hakamada (2014). Those authors analyse the 1989/90 - 2008/09 JARPA and JARPAII survey data to estimate fin whale abundance south of 60°S. Since the underlying data used was collected on the JARPA/-JARPAII surveys which are area-disaggregated, they are not used to update fin whale abundance estimates. The IDCR/SOWER surveys are better for calculating fin whale abundance estimates because they provide a circumpolar abundance estimate and their conduct is better standardised. The JARPA and JARPAII surveys were conducted mainly in IWC Management Areas III-East, IV, V and VI-West (see Figure 5.9) during the late austral summer months (January and February). Matsuoka and Hakamada (2014) use line transect distance sampling (Equation 5.5) to calculate the abundance estimates (assumed to be log-normally distributed). They further use a regression model that is recommended by the IWC Scientific Committee to calculate the annual rates of increase and CV estimates. The information in Table 5.8 comes from Matsuoka and Hakamada (2014) where the *SE* is calculated using the following equation:

$$\text{Standard Error (SE)} = \frac{\text{Upper Limit CI} - \text{Lower Limit CI}}{2 \times 1.645} \tag{5.13}$$

Strictly, Equation 5.13 is valid only for estimates from a normal distribution but is adequate for the purposes required here.

The fin whale trend estimates from Matsuoka and Hakamada (2014) are statistically significantly more than zero but are nevertheless not precisely estimated. They apply roughly to the area south of 60°S whereas the abundance estimates relate primarily to the region from 50°S to 60°S. As a result, the trend estimates (in Table 5.8) are pooled and weighted using *Inverse Variance Weighting.* This method is used to combine two estimates of the same quantity (in this case, fin whale trend estimates) and provide one "overall" value with a lower variance.

Using the values in Table 5.8, the weighted trend estimate and SE are calculated as follows:

$$\begin{aligned}\text{Weighted Trend Estimate} &= \frac{\dfrac{\text{Estimate}\left(\text{Area III-E \& IV}\right)}{\text{SE}\left(\text{Area III-E \& IV}\right)^2} + \dfrac{\text{Estimate}\left(\text{Area V \& VI-W}\right)}{\text{SE}\left(\text{Area V \& VI-W}\right)^2}}{\dfrac{1}{\text{SE}\left(\text{Area III-E \& IV}\right)^2} + \dfrac{1}{\text{SE}\left(\text{Area V \& VI-W}\right)^2}} \\ &= 0.116\end{aligned}$$

$$\begin{aligned}\text{Weighted Trend Estimate SE} &= \sqrt{\frac{1}{\frac{1}{\text{SE(Area III-E \& IV)}^2} + \frac{1}{\text{SE(Area V \& VI-W)}^2}}} \\ &= 0.053\end{aligned}$$

Using Equation 5.11, the CV of the trend estimate can be calculated. Since there is only one trend estimate and CV, they are used for all the Regions of Interest:

The weighted fin whale trend estimate is 0.116 yr^{-1} and the weighted fin whale trend CV is 0.387.

5.6.4 Humpback Whales

Müller (2011) explains that the Southern Hemisphere humpback whales are divided into seven breeding stocks, which form the basis for assessments. The breeding stocks coincide with regions that relate the high-latitude feeding grounds to the low-latitude breeding grounds. The breeding stocks and their boundaries that are adopted by the IWC Scientific Committee are summarised in Table 5.9.

The seven humpback breeding stocks are linked to the six IWC Management Areas (see Figure 5.10) as indicated in Table 5.10. This is used to calculate the humpback whale abundance in each of the management areas and subsequently the Regions of Interest.

Mori (2005) used Branch and Butterworth (2001a) to calculate humpback whale abundance and CV estimates (see Section 5.6.3 for more on the Branch and Butterworth (2001a) methodology). For the humpback trend estimate for Region AI, the rate of increase for the IWC Management Area IV from Bannister (1994) was used. For the trend estimate in Region PO, the rate of increase for the IWC Management Area V from Brown *et al.* (1997) was used. Mori (2005) stated that there was no information available on increase rates for IWC Management Areas I, II, VI at that time. There was a rate of increase for the IWC Management Area III but due to the many uncertainties in its analysis, it was not used.

For this update, both the abundance and trend estimates are taken from Jackson *et al.* (2015), which summarises a decade of research effort initiated under the IWC's "Comprehensive Assessment" on the Southern Hemisphere humpback whale. The paper uses a density-dependent sex-aggregated generalized form of the Pella-Tomlinson population model to calculate the humpback whale abundance and trend:

$$N_{t+1}^{i} = N_{t}^{i} + N_{t}^{i} \cdot R_{max}^{i} \cdot \left[1 - \left(\frac{N_{t}^{i}}{K^{i}}\right)^{z}\right] - C_{t}^{i} \tag{5.14}$$

where

N_t^i is the abundance of Stock i in year t;

K^i is the carrying capacity taken to correspond to abundance in the year 1900 for Stock i;

z is an exponent, fixed to 2.39, corresponding to a maximum sustainable yield of $0.6{\cdot}K$ (as conventionally assumed by the IWC);

R_{max}^i is the maximum population growth rate for Stock i, estimated in the model fit; and

C_t^i are the catches allocated to Stock i.

Jackson *et al.* (2015) use the median of the annual abundance from each population assessment to calculate the increase rates of the individual populations. Pooling the increase rates of the individual populations to calculate the increase rates for each Region of Interest would introduce bias. To address this, several authors of the Jackson *et al.* (2015) paper were contacted and asked to provide 1000 realisations of humpback whale abundance trajectories (using Equation 5.14) for each breeding stock and for the years 2010 and 2015 from the Bayesian estimation process used. These estimates are assumed to be approximately normally distributed. These breeding stock abundance estimates are divided amongst the IWC Management Areas on the basis indicated in Table 5.10. The median of the 1000 simulations is used as the humpback whale abundance estimate for each Region of Interest.

The SE of the humpback whale abundance estimates is calculated using the following equation which can be used because of the "normal distribution" assumption:

$$\text{SE} = \frac{95^{th} \text{ percentile estimate} - 5^{th} \text{ percentile estimate}}{2 \times 1.645} \tag{5.15}$$

With this information, the CV of the humpback whale abundance estimates can be calculated using Equation 5.11 where SE^2 provides the *Calculated Variance.* Table 5.11 provides a summary of humpback whale abundance estimates for the 2014/2015 season for each Region of Interest.

The humpback whale trend estimates for each Region of Interest are calculated as follows:

$$\text{Trend estimate} = \frac{ln\left(\frac{\text{2015 abundance estimate}}{\text{2010 abundance estimate}}\right)}{5} \tag{5.16}$$

This is calculated for every realisation i.e. there are 1000 trend estimates, and the median of these estimates is used as the humpback whale trend estimate for the Region of Interest.

The SE of the humpback whale trend estimates are calculated using Equation 5.15 and the CV is calculated using Equation 5.11. Table 5.12 provides a summary of the humpback whale trend estimates.

5.7 Summary

This chapter has reviewed the three sets of sighting surveys that were conducted in the Antarctic, namely IDCR/SOWER, JARPA and JSV. Two sets of differently defined regions termed the "Regions of Interest" (Regions AI, PO, AO, PI) were defined. Distance sampling, the main method used to calculate abundance estimates, was summarised and the potential biases associated with the results it provides were discussed. Finally, the abundance and trend estimates for the main baleen whale species, namely blue (1997/98), minke (1997/98), fin (1997/98) and humpback whales (2014/15) were calculated, where the season quoted is that to which the abundance estimate corresponds.

Notable new information in this chapter, compared to what was utilised in Mori (2005), includes:

1) Updates regarding the potential biases associated with abundances estimated in the unsurveyed areas within the pack-ice, especially with regards to minke whales.

2) The re-calculation of the extrapolation factors used to extrapolate fin whale abundance estimates north of 60°S, applying a different approach.

3) The use of the more recent analysis by Branch (2007) to provide blue whale abundance and trend estimates.

4) The use of the most recent and best available consensus estimates for minke abundance from IWC (2013).

5) The use of an improved SCAA analysis by Punt (2014) to calculate minke trend estimates. Due to the correlation between estimates for the stocks used in this analysis by Punt (2014), the inverse variance-covariance matrix of b_{rec} (the slope of the linear regression of the estimates of the logarithms of the number of recruits over a specific period of time) is calculated and used to reflect precision when the minke trend estimates are input to the ecosystem model developed in Chapter 11.

6) The calculation of a fin whale trend estimate, and its inclusion in the ecosystem model developed later in this thesis.

7) The use of IWC models to calculate abundance and trend estimates for humpback whales, as detailed in Section 5.6.4 of this chapter. With regards to the humpback whale trend estimates, this chapter adopted a more rigorous approach in its estimation compared to what was done in Mori (2005). Mori (2005) superimposed a trend estimate for one IWC Management Area to a whole Region of Interest, hence there are some uncertainties associated with her trend estimates.

With the exception of the fin whales, none of the abundance and trend estimates calculated in Mori (2005) are retained in this update. The updated abundance estimates use the same information that was used to calculate the estimates in Mori (2005), so that it would be redundant to keep the estimates from both analyses. The updated trend estimates are more recent, hence are used in the ecosystem model developed later in this thesis.

This chapter has shown how the abundance and trend estimates and their respective CVs were calculated. Chapter 11 will demonstrate how these abundance and trend estimates are used in the fitting of the Antarctic ecosystem model itself.

IWC Area	Abundance Estimate (N)	CV	SE
I (120°W - 60°W)	88	0.85	74.80
II (60°W - 0°)	268	0.58	155.44
III (0° - 70°E)	166	0.60	99.60
IV (70°E - 130°E)	419	0.51	213.69
V (130°E - 170°W)	765	0.43	328.95
VI (170°W - 120°W)	500	0.68	340.00

Table 5.1: Blue whale *comparable areas* abundance estimates with their associated CVs and SEs for the CPIII surveys for each IWC area, after Table 5 from Branch (2007).

Region	Abundance Estimate (N)	CV	SE
Region AI	853	0.33	282.39
Region PO	1 353	0.35	478.96
Region AO	434	0.43	184.61
Region PI	1 772	0.30	524.47

Table 5.2: The 1997/98 Antarctic blue whale abundance estimates, their CVs and SEs for each Region of Interest.

Circumpolar Set (Period)	Mid-year	Abundance Estimate (N)	CV
CP1 (1978/79 - 1983/84)	1981	592	0.40
CPII (1985/86 - 1990/91)	1988	686	0.47
CPIII (1991/92 - 2003/04)	1998	2249	0.36

Table 5.3: Estimates of Antarctic blue whale abundance from all three IDCR/SOWER CP surveys adjusted for comparable areas and their associated CVs, after Table 4 from Branch (2007).

		IWC Management Areas						
CP		I	II	III	IV	V	VI	Total
III	Survey Once	38 930	57 206	94 219	59 677	183 915	80 835	514 783
	CNB	34 369	58 382	68 975	55 899	180 183	72 059	469 866
	CV internal	0.20	0.19	0.15	0.34	0.11	0.14	0.09
	CV with AV	0.39	0.38	0.35	0.49	0.36	0.37	0.18
II	Survey Once	85 688	130 083	93 215	55 237	300 214	55 617	720 054
	CNB	84 978	120 025	86 804	51 241	285 559	49 885	678 493
	CV internal	0.16	0.14	0.20	0.17	0.13	0.22	0.08
	CV with AV	0.34	0.40	0.44	0.39	0.31	0.39	0.18

Table 5.4: Antarctic minke whale abundance estimates from the IDCR/SOWER CPII and CPIII surveys for each IWC Area, after Table 2 in IWC (2013).

where

Survey Once	are the estimates that cover all of the surveyed regions in the CP series, and uses the most recent/complete survey where there are duplications;
CNB	or *Common Northern Boundary* - refers to estimates that exclude certain areas of the surveyed regions in the CP series to ensure that the northern limits for both series are the same; these estimates are used to compare abundance between CPII and CPIII;
CV internal	is the uncertainty associated with the abundance estimate in the surveyed region at the time of the survey; and
CV with AV	is the uncertainty with additional variance; this is the uncertainty associated with the average number of whales in the surveyed region over the whole CP series as whales migrate in and out of a given survey area from year to year.

Region	Abundance Estimate (N)	CV	SE
Region AI	183 256	0.13	24 317
Region PO	286 611	0.08	23 278
Region AO	127 357	0.12	15 169
Region PI	342 510	0.09	30 051

Table 5.5: The 1997/98 Antarctic minke whale abundance estimates, their CVs and SEs for each Region of Interest.

Stock_{year}	$I_{1945-68}$	$I_{1968-88}$	$I_{1988-04}$	$P_{1945-68}$	$P_{1968-88}$	$P_{1988-04}$
$I_{1945-68}$	22 458.47	-91.65	-25.40	-10.56	-25.51	-9.86
$I_{1968-88}$	-91.65	24 033.01	-21.97	-8.09	-19.73	-8.24
$I_{1988-04}$	-25.40	-21.97	9 471.94	-2.61	-6.46	-6.82
$P_{1945-68}$	-10.56	-8.09	-2.61	8 194.38	-31.35	-9.85
$P_{1968-88}$	-25.51	-19.73	-6.46	-31.35	14 681.89	-14.04
$P_{1988-04}$	-9.86	-8.24	-6.82	-9.85	-14.04	8 433.85

Table 5.6: The inverse variance-covariance matrix corresponding to the trend estimates of minke whales, as reported in Punt (2014).

Region	Abundance Estimate (N)	CV
Region AI	10 591	0.5
Region PO	27 594	0.5
Region AO	10 591	0.5
Region PI	27 594	0.5

TABLE 5.7: The 1997/98 fin whale abundance estimates for each Region of Interest. The CV values are assumed.

IWC Area	Season	Trend Estimate (yr^{-1})	Upper Limit (95% CI)	Lower Limit (95% CI)	SE
III-East and IV	1995/96 - 2007/08	0.089	0.324	-0.145	0.14
V and VI-West	1996/97 - 2008/09	0.120	0.215	0.026	0.06

TABLE 5.8: The fin whale trend estimates, their 95% confidence interval limits and their SEs for the two regions analysed, from Matsuoka and Hakamada (2014).

Breeding Stock	Antarctic Longitudinal Range	Geographical Location
Breeding Stock **A**	60°W - 15°W	Brazil
Breeding Stock **B**	15°W - 20°E	Angola, West South Africa
Breeding Stock **C**	20°E - 70°E	Madagascar, Mozambique
Breeding Stock **D**	70°E - 120°E	West Australia
Breeding Stock **E**	120°E - 170°E	East Australia
Breeding Stock **O**	170°E - 110°W	Oceania
Breeding Stock **G**	110°W - 60°W	Columbia, Ecuador, Costa Rica

TABLE 5.9: The humpback whale breeding stocks, their corresponding high latitude boundaries and their geographical locations from Jackson *et al.* (2015) and Müller (pers. comm.).

IWC Area	Proportion of Breeding Stock in each IWC Area
I	$\text{BSG} + \frac{1}{8}\text{BSO}$
II	$\text{BSA} + \frac{3}{7}\text{BSB}$
III	$\text{BSC} + \frac{4}{7}\text{BSB}$
IV	$\text{BSD} + \frac{1}{6}\text{BSE}$
V	$\frac{5}{6}\text{BSE} + \frac{2}{8}\text{BSO}$
VI	$\frac{5}{8}\text{BSO}$

TABLE 5.10: Proportion of each humpback whale breeding stock linked to each of the IWC areas.

Region	Abundance Estimate (N)	CV
Region AI	66 182	0.066
Region PO	31 893	0.055
Region AO	42 356	0.086
Region PI	55 706	0.050

Table 5.11: The 2014/15 humpback whale abundance estimates and their CVs for each Region of Interest.

Region	Trend Estimate (yr^{-1})	CV
Region AI	0.025	0.200
Region PO	0.058	0.109
Region AO	0.026	0.244
Region PI	0.042	0.128

Table 5.12: Humpback whale trend (2010 - 2015) estimates and their CVs for each Region of Interest.

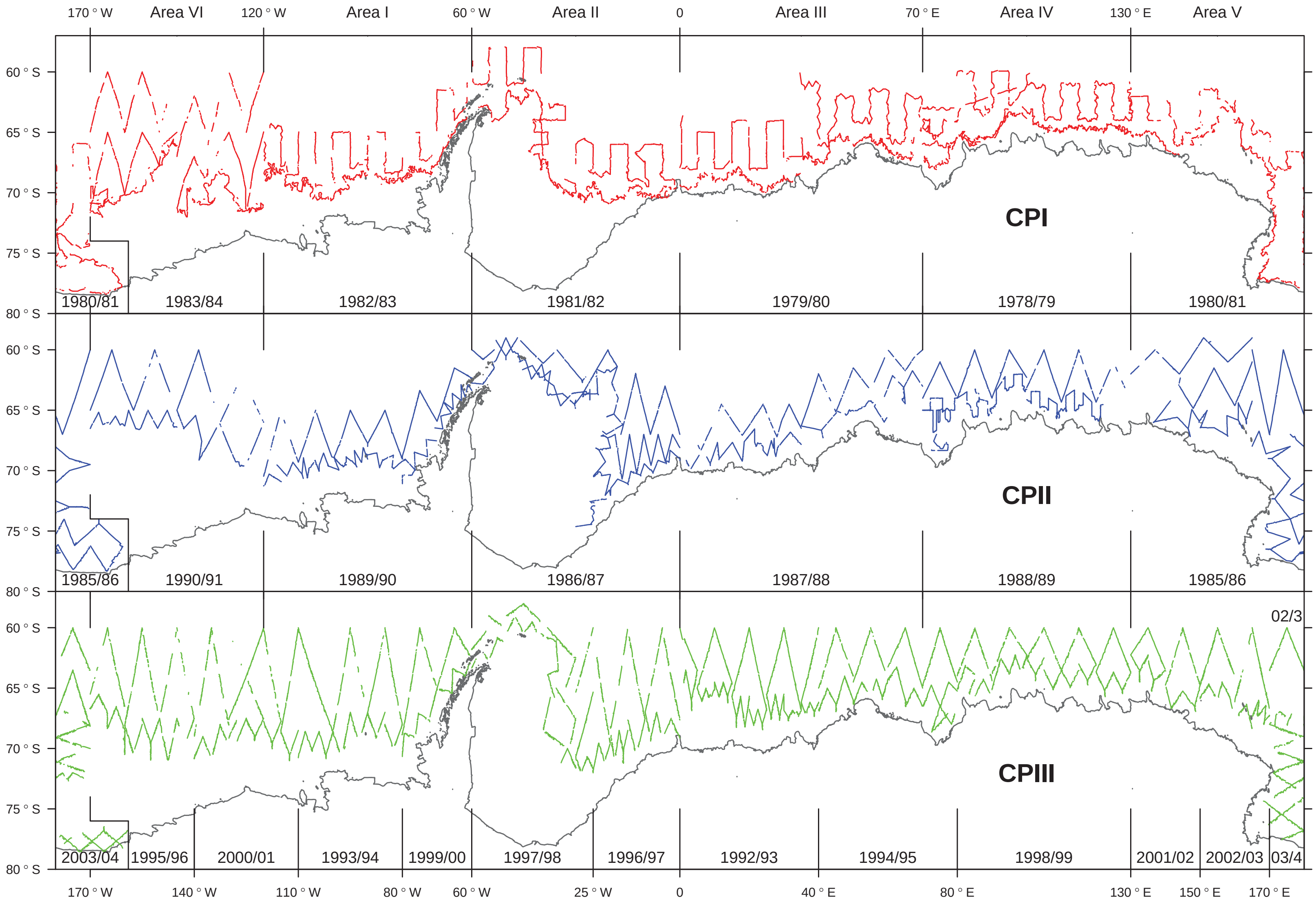

FIGURE 5.1: Comparison of the track-lines for the three IDCR/SOWER CP surveys - courtesy of T. Branch.

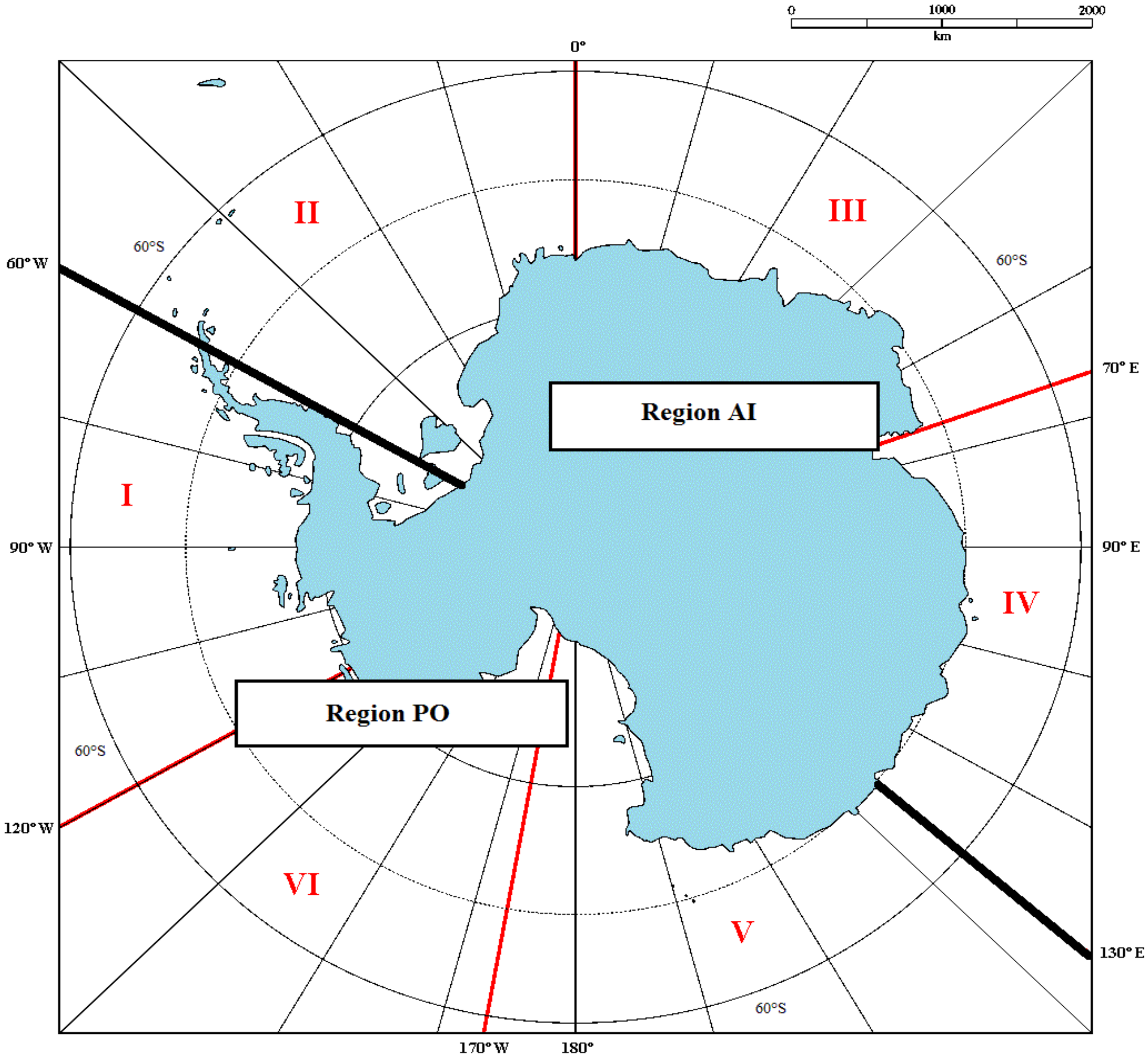

FIGURE 5.2: Map of the IWC Management areas and the two regions, Region AI and Region PO, as defined by Mori (2005) (from *http://luna.pos.to/whale/img/gen_map_ant.gif* [Accessed on 05/05/2016])

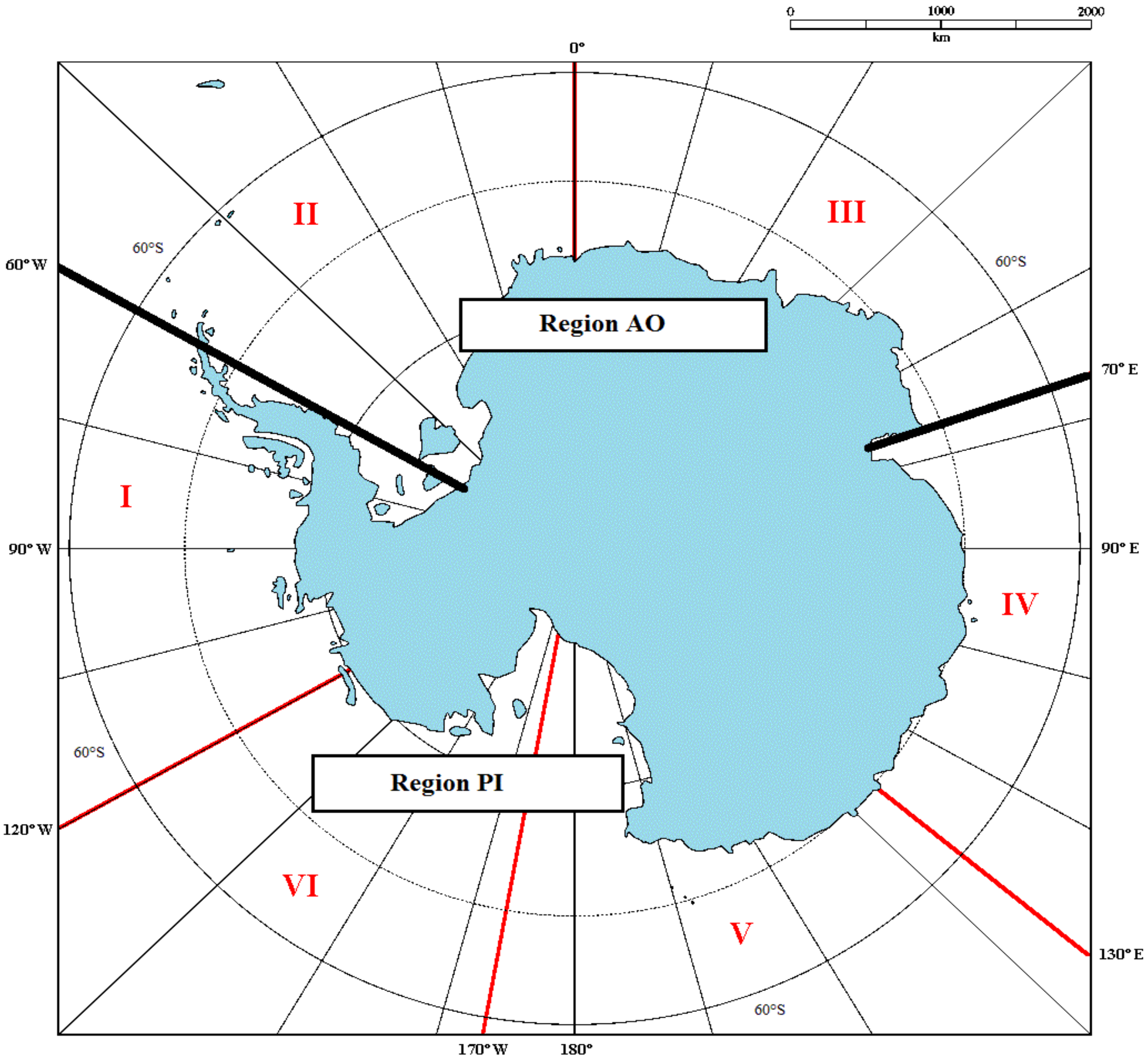

FIGURE 5.3: Map of the IWC Management areas and the two regions, Region AO and Region PI, as defined in this thesis (from *http://luna.pos.to/whale/img/gen_map_ant.gif* [Accessed on 05/05/2016])

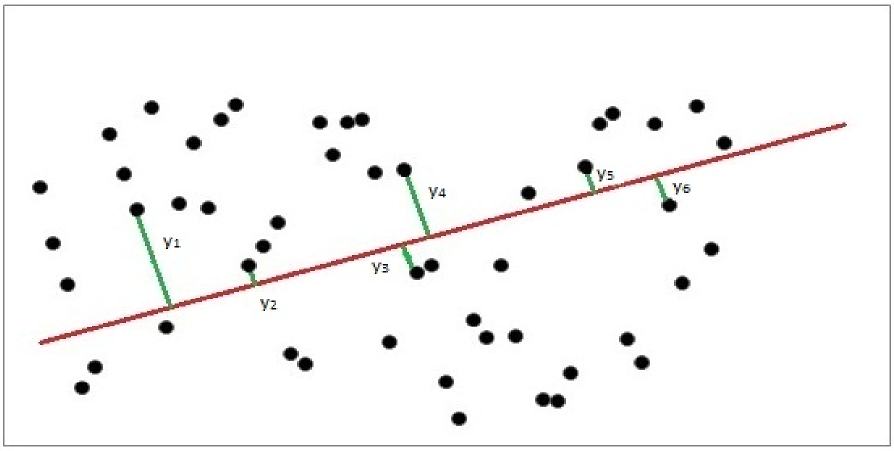

FIGURE 5.4: The line-transect sampling approach, after Figure 1.2 of Buckland *et al.* (1993) with a single, randomly placed line of length L (in red). Six objects are detected ($n = 6$) at perpendicular distances y_1 to y_6, denoted by a line showing the measured perpendicular distance (in green).

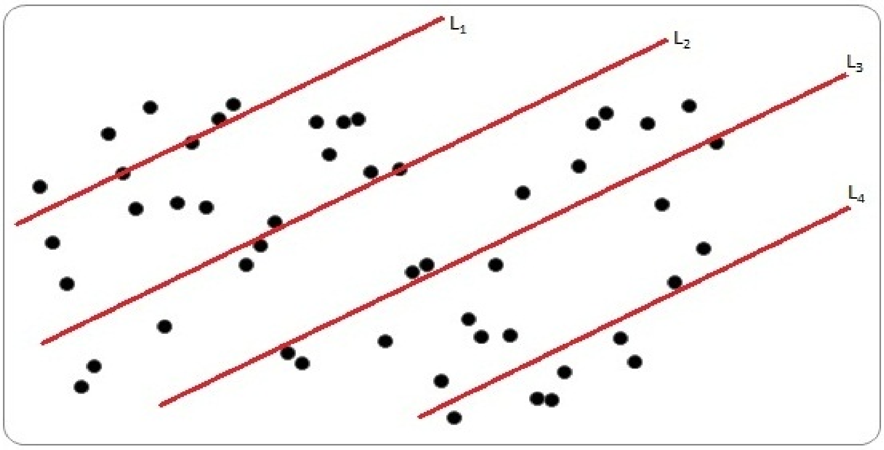

FIGURE 5.5: After Figure 1.4 of Buckland *et al.* (1993): Four lines of length L_i are used to sample the population.

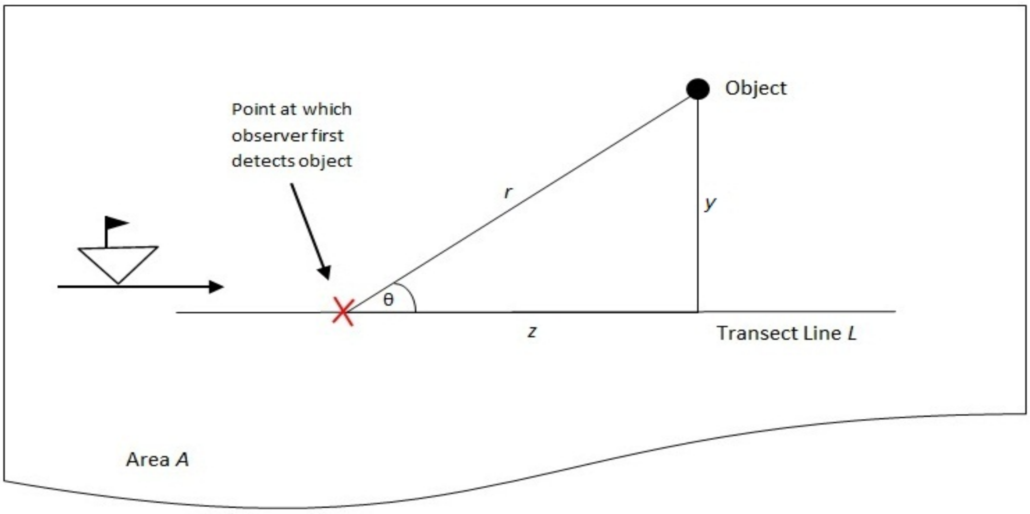

FIGURE 5.6: After Figure 1.5 of Buckland *et al.* (1993): an area of size A is sampled by a line of length L.

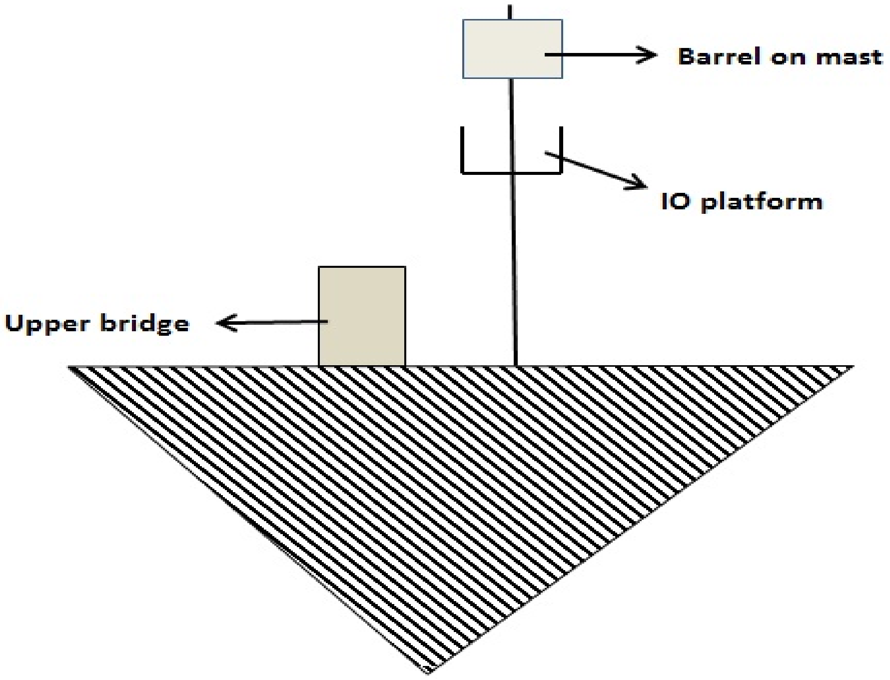

Figure 5.7: Rough sketch of the various observation points aboard an IDCR/SOWER whale survey vessel.

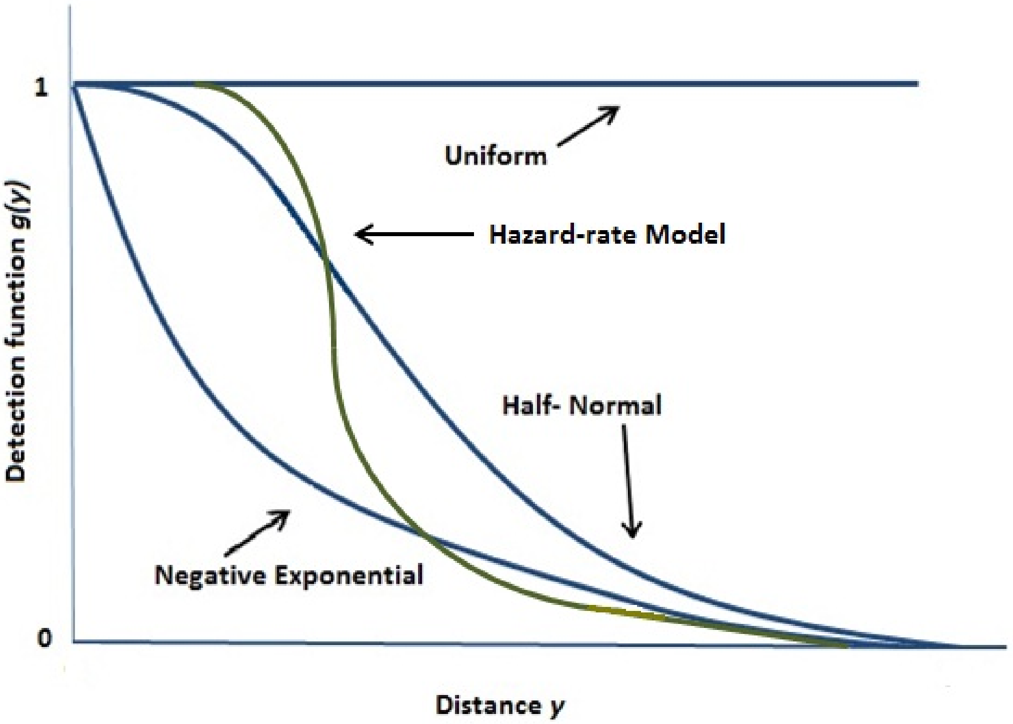

Figure 5.8: Rough sketch of the various functions used to model the detection function $g(y)$ - after Figure 2.5 of Buckland *et al.* (1993).

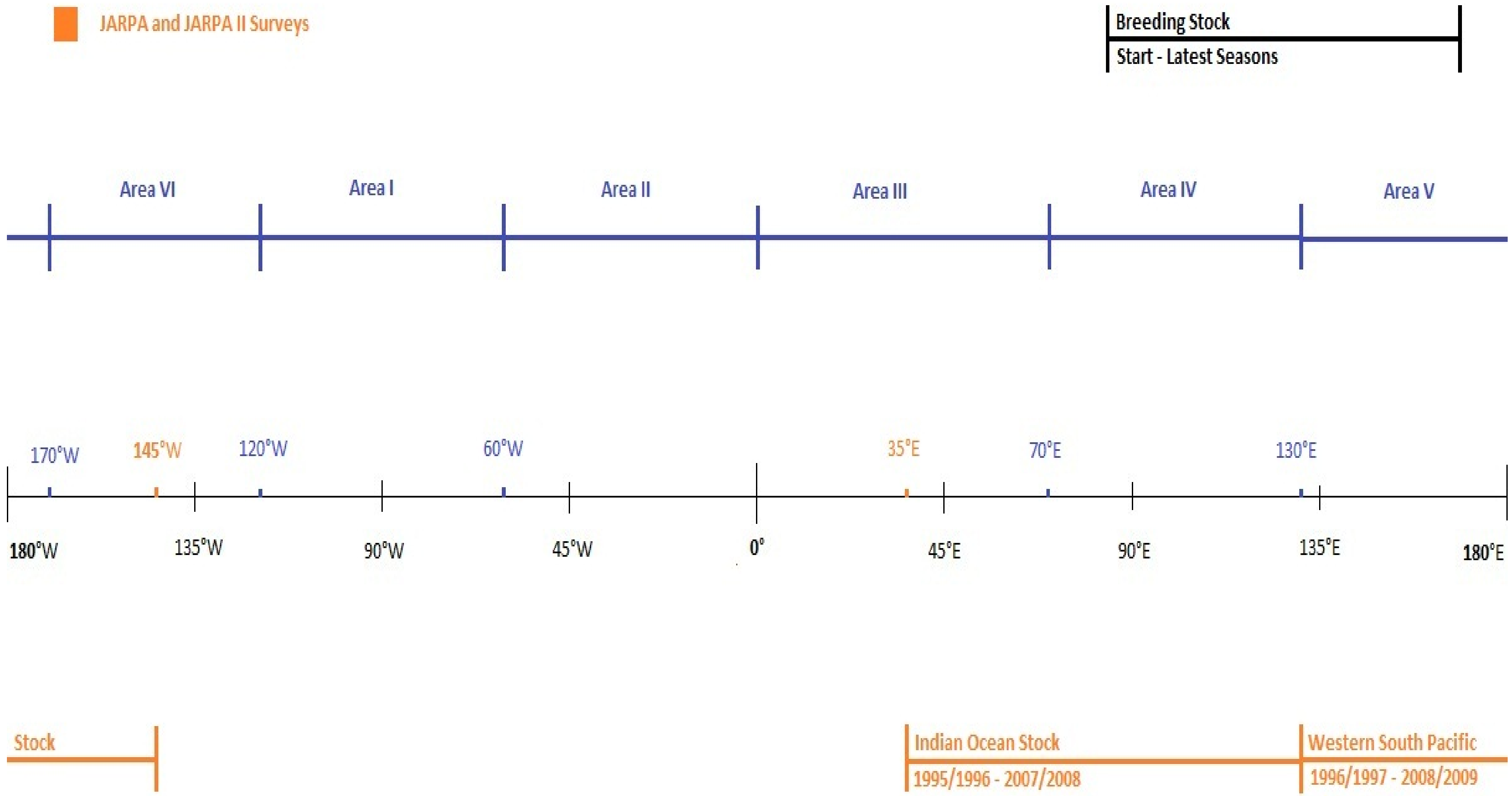

FIGURE 5.9: Map defining the two fin whale stocks that were sighted on the JARPA and JARPAII surveys in relation to the IWC Management Areas, as detailed in Matsuoka and Hakamada (2014).

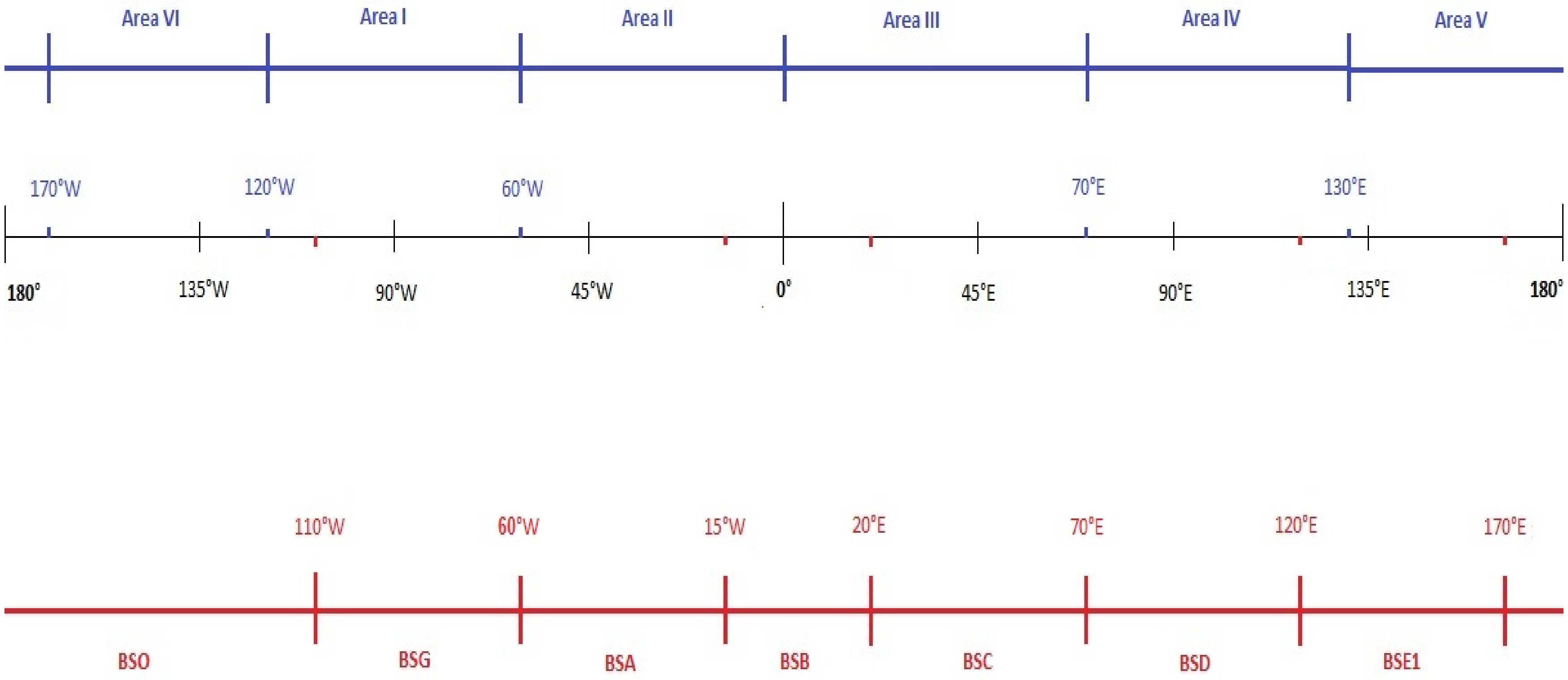

FIGURE 5.10: Map showing the boundaries of the humpback whale breeding stocks in relation to the IWC Management Areas.

Chapter 6

Abundance and trend estimation for the main krill-feeding seals in model

6.1 Overview of Chapter

This chapter is divided into three sections: Antarctic fur seals, crabeater seals and leopard seals. Each section discusses how the seal abundance and trend estimates (where available), from both Mori (2005) and as used in this thesis, have been calculated so as to highlight the differences in the available information since Mori (2005). It also discusses the methodologies that were used for the abundance surveys and the uncertainties that are associated with the resultant estimates of abundance. These survey abundance estimates and trends are used in the model-fitting process, more specifically in the negative log-likelihood function that is minimised in the model developed in Chapter 11 of this thesis.

6.2 Antarctic fur seals

6.2.1 Abundance estimates and the associated methodology

Mori (2005) states that the majority of Antarctic fur seal abundance estimates are obtained from raw counts of the seals. These include either pup or adult female counts made from land or from ships and helicopters during the fur seal breeding season, which is from mid-November to early April.

For the seal population at South Georgia (see Figure 3.2), the abundance estimation method changed as the size of the population increased (Boyd, 1993; Payne, 1977; Bonner, 1968). During the early 1930s, based on observations around South Georgia, Bonner (1968) reported that there were only about 100 fur seals on the island. From 1937 to 1955, no further detailed observations were made. Late in 1956, Bonner (1968) found a thriving fur seal population on South Georgia and the neighbouring Bird Island (see Figure 3.2). Surveys were conducted on Bird Island until 1962 in which pups were counted from a beach-situated vantage point. No further observations were made from 1964 until 1970.

In 1971, the survey at Bird Island resumed and found that the majority of the sites suitable for fur seal breeding were colonised. In 1972, the survey was extended to South Georgia where seal pups were counted from ships and helicopters. Seal pups were counted on both South Georgia and Bird Island from 1972/73 until 1975/76 (Payne, 1977). Payne (1977) reported that due to the increased density of the fur seals on the islands, undercounting of seal pups occurred. This resulted in the use of mark-recapture methods and analyses.

For the 1975/1976 season, Payne (1979) estimated the Antarctic fur seal abundance at South Georgia to be 369 000. He multiplied the total pup count or the number of pups born (which was estimated to be 90 000 if the unsurveyed mainland beaches were included) by an extrapolation factor of 4.1 to obtain an estimate of total abundance. This factor was derived as follows: information was available regarding the number of pups and the number of breeding females per age class. Estimates for the number of breeding females in each age class were divided by estimates of age-specific pregnancy rates in order to yield the total number of alive adult females. A 50:50 sex ratio was assumed for the seal pups so that only information regarding the number of one and two year old females remained unavailable. These numbers were calculated using the current number of female births adjusted for the annual increase rate of the population and the survival rate for the first two years. Estimates for the male numbers were obtained by again assuming a 50:50 sex ratio. However, after the age of seven, these estimates were subjected to an additional mortality rate. After an age of about seven, bulls start to defend territories vigorously. As a result, their survival rate drops to 0.70 (which is lower compared to a cow's survival rate) due to fighting over territory (Payne, 1979). Payne (1979) uses these mortality rates, population increase rates and sex ratios to obtain the multiplicative factor of 4.1 to convert the numbers of pups born to a total Antarctic fur seal abundance estimate.

Boyd (1993) determined that the total number of Antarctic fur seals at South Georgia for the 1990/91 season to be about 1 550 000. Adult females on the land were counted from either aboard a ship following the shoreline or from the ground overlooking the breeding sites. Boyd (1993) estimated the number of pups born using the estimated number of adult females present on South Georgia during the 1990/91 pupping season. As in Payne (1979), Boyd (1993) multiplied the number of pups born by the extrapolation factor 4.1 to determine the total abundance estimate of the Antarctic fur seal for the season considered.

Since Boyd (1993), there have been no further updates to the Antarctic fur seal abundance estimates. Thus, the abundance estimates that are used in Mori (2005) are retained in this thesis. They are summarised in Table 6.1. No CVs are available for these abundance estimates. As a result, a coarse value of 0.5 is assumed. Mori (2005) remarks that over 90% of the circumpolar Antarctic fur seal abundance is associated with South Georgia.

6.2.2 Uncertainties associated with abundance estimates

Mori (2005) details the potential biases associated with the abundance estimates of the Antarctic fur seals. These biases are outlined briefly below.

1) *Observer counting bias*

The majority of fur seal counts are recorded usually by a single observer only. As a result, there might be bias in the number of counts, depending on the observer and their judgment calls. The magnitude of this bias is quantified in Boyd (1993), who analyses the repeated counts of three study beaches by different observers. His analysis concludes that the effect of this bias is negligible for female fur seal and pup counts. However, it increases for territorial males due to the differences in opinion between observers over what constitutes a territorial male.

2) *Survey time*

Payne (1977) and Boyd (1993) mention that the Antarctic fur seal pupping season is from mid-November until the end of December, and that their breeding season is from mid-November till early April. However, Payne (1978) suggests that fur seal pups are born during a short period each year with roughly 80% of fur seal pups being born in a space of 17 days in December. The fur seal abundance estimation surveys used in Mori (2005) and in this thesis took place between December - February. Thus, the magnitude of this bias is deemed negligible.

3) *Area searched in survey*

The majority of fur seal counts are conducted by either walking around the island being surveyed or counting the seals from a vantage point (on land or aboard a ship that followed the island's coastline). Bonner (1968) notes that during his observations around South Georgia in the 1930s, the southern and western parts of the island were unsurveyed, allowing for the possibility that some seals were not counted. Thus, the abundance estimate for that period may have been negatively biased. However, Bonner (1968) suggests that the total number of seals not counted would be small as the majority of the fur seals aggregated around the north-western part of the island. For the 1990 survey at South Georgia, Boyd (1993) reports that the entire fur seal breeding range was surveyed. Thus, the impact of this bias is probably small as the majority of the areas where breeding was likely taking place were surveyed. A similar argument holds for the breeding colonies on islands other than South Georgia.

4) *Species identification*

On South Georgia, the main breeding island for Antarctic fur seals, no other similar seals are present. On islands such as Macquarie and Marion Islands (see Figure 3.2) where Antarctic fur seals and sub-Antarctic fur seals coexist, the two species can be distinguished readily. Hence the impact of this bias is negligible (Shaughnessy *et al.*, 1988).

5) *Undercounting the seals*

Mori (2005) mentions that the undercounting of fur seals tended to occur as the number of seals increased, especially at South Georgia. As a result, mark-recapture methods were used to count pups (Payne, 1977). However, in 1987, this method became impractical due to the increasingly larger number of pups (Boyd, 1993). Boyd (1993) reports that experimental censuses ashore demonstrated that female counts provided repeatable results. This method was used to obtain fur seal abundance estimates in subsequent years. A problem with this method is that seals might not be ashore at the time of the count, resulting in an undercount. This bias is taken into account by estimating the probability of a female being ashore at the time of the census (Boyd, 1993).

Mori (2005) remarks that there have been no similar attempts to correct this bias on fur seal breeding islands other than South Georgia. However, since the numbers of fur seals on the other islands are small compared to those at South Georgia, undercounting is considered to be a minor problem.

6) *Variability in pregnancy and survival rates*

Counting an entire fur seal population is possible, if the seals inhabit a small area. As the fur seal population increased however, it became near impossible to count every seal ashore. Thus, some form of calibration was necessary in order to estimate the total abundance of the population.

Payne (1979) estimated the total fur seal abundance by multiplying the number of pups counted by an extrapolation factor. This factor was derived as detailed in Section 6.2.1. Due to insufficient data at that time, those computations did not consider the implications of inter-annual variability in the pregnancy and survival rates. Boyd *et al.* (1995) estimate the annual pregnancy, survival and pup mortality rates for the Antarctic fur seals at Bird Island. These rates differ from year to year. As a result, this variability needs to be taken into account when estimating the precision of an abundance estimate.

To assess the impact this might have on the extrapolation factor, Mori (2005) recalculated the factor at the extrema of the survival and pregnancy rates' ranges (see Chapter 8 for more details on the Antarctic fur seal pregnancy and (survival) mortality rates). This gave rise to a maximum factor of 5.3 and minimum factor of 3.2, thus establishing a range for the extrapolation factor.

6.2.3 Trend estimates

Payne (1977) states that the Antarctic fur seals have experienced the most rapid population increase of all the Antarctic seal species. He determined that the annual population increase rate between 1957 and 1972 had been 16.8% at South Georgia. This estimate was based on fur seal pup counts (detailed in Section 6.2.1). Payne (1977) remarked that this value is high for a population of wild seals to maintain and suggested that it would continue for about 10 more years only.

Boyd (1993) calculates the annual population increase rate between 1976 and 1990 at South Georgia to be 9.8%. This suggests that the Antarctic fur seal population increase rate is slowing. Boyd (1993) states that a possible explanation for this is overcrowding at the breeding beaches.

Since Mori's (2005) compilation, there have been no updates to Antarctic fur seal trend estimates. Thus, the estimates used in Mori (2005) are retained in this thesis (see Table 6.2). As with the abundance estimates, the CVs associated with the trend estimates are unavailable, so that a rough value of 0.5 is assumed.

6.3 Crabeater seals

6.3.1 Abundance estimates and their methodology

The Antarctic pack-ice is a remote and relatively inaccessible area so that few attempts to estimate the abundance of pack-ice seals have been made. Mori (2005) used rough estimates of crabeater circumpolar abundance as suggested to her by J. Laake (pers. comm.). These estimates were around 6 - 8 million crabeater seals in the area from 170°W to 125°W (corresponding to the Region PO in Figure 5.2). That region was surveyed in the 1999/2000 austral summer by the U.S. as part of the Antarctic Pack Ice Seal (APIS) programme. At the time of Mori's (2005) work, the analysis of the results from the APIS programme was incomplete. Thus, estimates from 60°E to 150°E were unavailable whilst only partial estimates for Region AI had been calculated at that time.

Erickson and Hanson (1990) remark that there is circumstantial evidence to suggest that crabeater seals occur in appreciable numbers in the ice-free waters close to the continent. Those authors also suggest that a large number of crabeater seals are found around the sub-Antarctic islands. In light of this information, Mori (2005) assumed a rough abundance of 4 million seals for both Regions PO and AI in her analysis. No CVs associated with these abundance estimates were available so that a coarse estimate of 0.5 was assumed.

For this update, the crabeater abundance estimates used in this thesis are from Southwell *et al.* (2012) and Gurarie *et al.* (2015). Southwell *et al.* (2012) summarise all the available abundance surveys that had been conducted for the Antarctic pack-ice seal species. The two main set of survey results used in this thesis from Southwell *et al.* (2012) are the Erickson and the APIS surveys (see Table 6.3 and Figure 6.2). At the time Mori (2005) wrote, the analysis of the APIS survey results was incomplete, but it has since been completed. As a result, a more reliable crabeater abundance estimate for the 2000/2001 season can be calculated which contrasts to the rough approximation used in Mori (2005).

The Erickson survey results are reported mainly in two analyses: Gilbert and Erickson (1977) and Erickson and Hanson (1990). Erickson and Hanson (1990) is considered to provide the more reliable results of the Erickson surveys (Southwell *et al.*, 2012).

Gilbert and Erickson (1977) analyse several surveys conducted from 1970 until 1974. The regions surveyed were the western Ross Sea region in 1970/71, the Amundsen-Bellingshausen Sea region in 1971/72, the Oates and George V coastal region in 1972/73, and the Dumont d'Urville Sea, the Adèlie, Claire (now known as Wilkes) and BANZARE coastal regions in 1973/74 (see Figure 6.3). Seals were counted from helicopters and from aerial photographic surveys, especially within the interior pack-ice regions. Strip transect methods were used to count seals in the outer pack-ice regions, after which the estimate was adjusted to take account of seal haul-out patterns as some seals were at sea when the surveys were conducted (Southwell *et al.*, 2012).

The main "new" features of the Erickson and Hanson (1990) analysis were the extra haul-out data available and the development (and testing) of a model that took into account the diurnal variation in the count of hauled-out seals (seals leave the sea at different times during the day). A regression analysis was applied to the crabeater seal haul-out counts. It showed a unimodal distribution, peaking around midday at all the sites surveyed. Using this information, a predictive model was developed in order to adjust counts at any time of day to those expected at the time of peak haul-out. Erickson and Hanson (1990) applied this model to all crabeater counts made during the 1967/68 - 1982/83 surveys, and calculated abundance estimates for five regions: Amundsen-Bellingshausen Seas (60°W - 130°W), Ross Sea (130°W - 160°W), south Pacific Ocean (90°E - 160°E), south Indian Ocean (20°E - 90°E) and the Weddell Sea (20°E - 60°W) (Southwell *et al.*, 2012; see Figure 6.3).

The APIS programme was an international multi-disciplinary research initiative whose aim was to understand the ecological role of the pack-ice seals. The programme has now been completed. It ran from the mid-1990s to the mid-2000s. Its primary aim was to estimate accurately the circumpolar abundance and distribution of the four pack-ice seal species considered. It also sought to provide information on the pack-ice seals' population structure, diet, movements and diving patterns.

Seals were counted along sample strips that were searched from helicopters and ships. It was assumed that these sample strips were representative of the whole area, so that estimates from the sample area could be extrapolated to the entire area. At the time, seals that were situated on the ice were counted from helicopters and ships. Seals that were at sea during the searches were taken into account by attaching satellite-linked dive recorders to the back fur of a number of seals. These instruments recorded the amount of time spent on ice and in water so as to be able to correct the seal count for those seals that were in the water at the time of the searches. The instruments fall off in the summer when the seals moult (Southwell *et al.*, 2012; *http://www.antarctica.gov.au/about-antarctica/wildlife/animals/seals-and-sea-lions/pack-ice-seals* [Accessed 07/07/2016]).

Unlike for the Erickson surveys, observers in the APIS aerial surveys counted seals from one side of the aircraft only. To take into account observers missing some seals in their count, two observers counted the same area independent of each other. They also recorded distance data to calculate density estimates of hauled-out seals using line transect methods (see Section 5.4). Line transect methods were used for the ship-based surveys as well. Although the spatial coverage of the APIS surveys was more comprehensive than that of the Erickson surveys, the constraints applying to ship and aircraft operations in the pack-ice did not allow for random line transects. To address the bias from extrapolating sampled seal densities along potentially non-representative line transects, the APIS data was analysed using spatial modeling and predictive methods. Bootstrap and jack-knife methods were used to quantify the major sources of uncertainty such as in the estimation of detection and haul-out probabilities, and in predicting abundances in a survey region using spatial models. Model uncertainty was taken into account by deriving estimates using a number of predictive models. Similarly, species identification uncertainty was taken into account by estimating abundance from both *definite only* and *definite and probable* species sightings. Since sea-ice* is dynamic, its varying distribution was taken into account by defining a survey region that portrayed the local sea-ice extent and concentration at the time of the survey (Southwell *et al.*, 2012; Bengtson *et al.*, 2011; Southwell, 2008).

Southwell *et al.* (2012) provide crabeater seal abundance estimates for:

150°E - 100°W	-	1 736 000
90°W - 30°W	-	3 187 000
64°E - 150°W	-	946 400
26°W - 7°W	-	3 564 000**

** This estimate was considered to be positively biased by the authors as it relates to a preliminary analysis.

Gurarie *et al.* (2015) provide the most recent abundance estimates for the crabeater seals (see Table 6.3 and Figure 6.2). The only changes are to the region 90°W - 30°W with an abundance estimate of 3 042 000 and extending 26°W - 7°W to 20°W - 5°E for an abundance of 514 000.

From Figure 6.2, it is quite clear that the APIS surveys did not cover the majority of IWC Area III and small parts of IWC Areas I and II (in green in Figure 6.2), whereas the Erickson surveys did. In order to calculate an abundance estimate for each Region of Interest, an abundance estimate for each IWC Area is needed.

To take into account the IWC Areas not covered by the APIS surveys, ratios between the APIS and Erickson (from the Erickson and Hanson (1990) analysis) surveys are assumed to be the location-independent. Consider Figure 6.1: the label y refers to the total abundance estimate from the Erickson survey, the label z refers to the proportion of the Erickson survey covered by the APIS survey, the label w refers to the proportion of the APIS survey covered by the Erickson survey and let x (labelled ? in Figure 6.1) be the unknown APIS equivalent estimate from an area not covered by the APIS survey. These ratios are calculated as follows:

$$\frac{w}{z} = \frac{x}{y-z}$$

$$\implies \quad x = \frac{w \cdot (y-z)}{z}$$

The numbers shown in green in Figure 6.2 have been calculated using this method.

Thus, the crabeater abundance estimates for each IWC Area for the 2000/2001 season have been obtained (Table 6.4) and consequently also for each Region of Interest (Table 6.5). As with Mori (2005), the associated CVs for the abundance estimates are assumed to be 0.5.

6.3.2 Uncertainties associated with abundance estimates

Southwell *et al.* (2012) detail the potential biases associated with the abundance estimates from the Erickson surveys. These biases are outlined briefly below, with the emphasis being on the crabeater seals.

1) *Detectability*

Southwell *et al.* (2012) explain that when using strip transects, if some seals within the strip are undetected, this would have resulted in a negatively biased abundance estimate. This is more likely to have occurred during the aerial surveys where a single observer searched the strip on both sides of the aircraft.

2) *Correction for seal haul-out*

Southwell *et al.* (2012) state that the correction of the crabeater counts to their peak haul-out is based on the number of seals hauled out only. The proportion of seals at sea at the time of the peak haul-out is not taken into account as it could not be assessed. Recent analyses using electronic diving recorders indicate that around 20% and 40% of crabeater seals are at sea around midday during the summer months (Bengtson *et al.*, 2011).

3) *Transect placement and extrapolation from sampled to unsampled areas*

Southwell *et al.* (2012) remark that an ideal survey design consists of a number of randomly placed (or regularly spaced) transects. These transects would extend from the Antarctic continent to the ice edge, in a north-south direction. In this way, certain inference methods could be used to extrapolate density estimates from the sampled transects to the the entire region. Aerial surveys use this survey design. However, there were insufficient helicopters to cover the full extent of the ice. As a result, much of the interior ice was left unsampled. The interior ice abundance estimates are based mostly on untested assumptions including those about seal distributions across the ice gradient. Shipboard surveys did not achieve this design. Southwell *et al.* (2012) comment that this bias is important for the fast-ice seal species like the Weddell seal as the fast-ice received little sampling. This suggests that the pack-ice received adequate sampling, allowing for the conclusion that this bias is small for the crabeater seals.

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[*] The term *sea-ice* is used interchangeably with *pack-ice*. However, the same meaning is implied in this context, as pack-ice is simply sea-ice “packed” together.

4) *Uncertainty or precision*

Southwell *et al.* (2012) remark that large-scale surveys like the Erickson surveys often have high uncertainty (low precision) associated with them. The Erickson survey analyses do not report any associated uncertainty.

5) *Availability*

The Erickson surveys did not take the seals in the ice-free regions around Antarctica into account. For crabeater seals, this bias is considered to be negligible as they are pack-ice mammals. However, for seal species inhabiting the fast-ice regions, this bias becomes important. Fast-ice seals need an alternative assessment method, different from the methods used in the Erickson surveys, to estimate their numbers (Erickson and Hanson, 1990).

Southwell *et al.* (2012) consider that the APIS surveys reduced or eliminated many of the biases associated with the Erickson surveys through their improved coordination, and modern survey and analytical methods. However, some biases remain inherent to the APIS estimates. The main bias relates the following concern: the availability of seals to conventional survey methods that involve counting and capture. Southwell *et al.* (2008) consider this problem to be the smallest for crabeater seals and greatest for leopard and Ross seals. This factor can result in negatively biased abundance estimates for the seal species in question.

6.3.3 Trend estimate

Mori (2005) does not include a crabeater trend estimate in her analysis but mentions that there appears to have been a recent overall decline in the crabeater population, especially within specific regions. Between 1968 and 1969, in the western Weddell Sea (see Figure 6.3), a 30% - 60% decrease in crabeater seal density estimates is suggested by Erickson and Hanson (1990). This decline is attributed to increased competition for food with the large baleen whales, which had started to recover since coming under protection. However, Green *et al.* (1995) suggest that differences in the seal counting method might have led to such a decline in crabeater seal density estimates.

Southwell *et al.* (2015) give two reasons why it is difficult to obtain reliable crabeater seal trend estimates.

1) Only a few repeat surveys have been conducted in the same/similar regions.
2) In order to compare the results from recent surveys which used newer survey and analytical methods to those from previous surveys, the data from those earlier surveys need to be re-analysed. However, it seems to be that the data collected during those earlier surveys are no longer available. Even if such data were available, other information needed like distance-to-sighting data would not have been recorded, making a comparison near impossible.

For the reasons above, this thesis also does not make use of any crabeater trend estimates.

6.4 Leopard seals

Though not one of the main krill-predators, as demonstrated in Chapter 4, this section outlines briefly how the leopard seal abundance estimate has been calculated. This is an update to what was considered in Mori (2005), as leopard seals were not investigated as part of her ecosystem model.

6.4.1 Abundance estimate and their methodology

The abundance estimates for the leopard seals, as used in this thesis, are derived from Southwell *et al.* (2012) as well. As for the crabeater seals, the two main leopard seal surveys conducted around the Antarctic pack-ice were the Erickson and APIS surveys (see Section 6.3.1 for more regarding the respective methodologies of these surveys). The leopard seal abundance estimates from these two surveys are summarised in Table 6.6.

Fewer Erickson surveys have recorded leopard seal abundance estimates compared to crabeater seals. From consideration of Figure 6.4, it is evident that roughly half of Area II and majority of Area III were not covered by the APIS surveys. Only one of the Erickson surveys was conducted in a region that included parts of both Area II and Area III. This Erickson survey neither covers the same areas as the APIS surveys, nor is it extensive enough to provide an estimate for half of Area II and the majority of Area III. As a result, ratios between the Erickson and APIS surveys, as considered for the crabeater seals, cannot be used for leopard seals.

The sum of the APIS survey estimates are used to provide an approximate leopard seal abundance estimate of 35 500 for the 2000/2001 season (see Table 6.6).

6.5 Summary

This chapter has described how the abundance and trend estimates for the Antarctic fur seals, the crabeater seals and the leopard seals (though it is not one of the main krill-predators) were obtained. It also considered the respective surveys' methodologies and their associated uncertainties.

There have been no recent updates to the Antarctic fur seal abundance estimated in 1930/1931, 1975/1976 and 1990/1991 and trend estimates since Mori's (2005) compilation. As a result, the survey estimates which she used have been retained in this analysis.

The Erickson and APIS surveys were used to calculate the crabeater seal abundance estimates, whilst APIS surveys were used to calculate a "rough" leopard seal abundance estimate.

At the time Mori (2005) wrote, the analysis of the APIS survey results was incomplete, but it has since been completed. As a result, a more reliable crabeater abundance estimate for the 2000/2001 season could be calculated which contrasts to the rough approximation made in Mori (2005). This is one of the updates of this chapter. The new crabeater seal abundance estimate utilized ratios between the Erickson and APIS surveys. No crabeater trend estimate is used in this analysis, as was the case for Mori (2005). Furthermore, Mori (2005) did not calculate an abundance estimate for leopard seals at the time she wrote - the estimation of a leopard seal abundance is a further update in this chapter.

In conclusion, this chapter has shown how the abundance and trend estimates, and their respective CVs were calculated for the main krill-feeding seal species. Chapter 11 will demonstrate how these abundance and trend estimates are used in the fitting of the Antarctic ecosystem model itself.

Year	Abundance estimate (N)	CV	Location	Reference
1930/1931	100	0.5	Bird Island, South Georgia	Bonner (1968)
1975/1976	369 000	0.5	Bird Island, South Georgia	Payne (1977)
1990/1991	1 550 000	0.5	South Georgia	Boyd (1993)

Table 6.1: Estimates of Antarctic fur seal abundance in certain years from Mori (2005). The CV values are assumed.

Year	Annual Rate Of Increase (ROI)	CV	Location	Reference
1957/1958 - 1971/1972	0.17	0.5	South Georgia	Payne (1977)
1976/1977 - 1989/1990	0.10	0.5	South Georgia	Boyd (1993)
1990/1991 - 1998/1999	0.10	0.5	South Georgia	Boyd (1993), SCAR (2000)

Table 6.2: Estimates of Antarctic fur seal trend estimates in certain years from Mori (2005). The CV values are assumed.

Survey	Region	Survey year(s)	Crabeater seal abundance estimate (N)	Reference
Erickson surveys	60°W - 20°W	1969/70	2 780 900	Erickson and Hanson (1990)
	20°W - 20°E	1982/83	806 400	Erickson and Hanson (1990)
	20°W - 10°E	1968/69 - 1972/73	1 686 000	Laws (1984)
	20°E - 70°E	1968/69 - 1972/73	798 000	Laws (1984)
	20°E - 90°E	1982/83	745 900	Erickson and Hanson (1990)
	90°E - 160°E	1972/73 - 1973/74	938 900	Erickson and Hanson (1990)
	80°E - 140°E	1968/69 - 1972/23	772 000	Laws (1984)
	145°E - 170°E	1972/73	472 400	Laws (1984), Gilbert and Erickson (1977)
	160°E - 130°W	1971/72 - 1972/73	1 293 000	Erickson and Hanson (1990)
	135°W - 80°W	1971/72	1 193 400	Laws (1984), Gilbert and Erickson (1977)

Table 6.3 – continued from the previous page

Survey	Region	Survey year(s)	Crabeater seal abundance estimate (N)	Reference
Erickson surveys	130°W - 60°W	1971/72	632 700	Erickson and Hanson (1990)
APIS surveys	150°E - 100°W	1999/00	1 736 000	Bengston *et al.* (2011)
	90°W - 30°W	1998/99	3 042 000	Forcada *et al.* (2012), Gurarie *et al.* (2015)
	64°E - 150°E	1999/00	946 400	Southwell *et al.* (2008), Gurarie *et al.* (2015)
	20°W - 5°E	1995/96 - 1999/00	514 000	Gurarie *et al.* (2015)

Table 6.3: Estimates of crabeater seal abundance estimates in certain years from the Erickson and APIS surveys, after Table 1 from Southwell *et al.* (2012) and Table 5 from Gurarie *et al.* (2015).

IWC Area	Proportion of APIS Surveyed Regions (including the *ratio estimated* regions)	Abundance estimate (N)
I	(2/11)*(150°E - 100°W) + (100°W - 90°W) + (1/2)*(90°W - 30°W)	2 169 046
II	(1/2)*(90°W - 30°W) + (30°W - 20°W) + (4/5)*(20°W - 5°E)	2 288 500
III	(1/5)*(20°W - 5°E) + (5°E - 64°E) + (3/43)*(64°E - 150°E)	961 433
IV	(30/43)*(64°E - 150°E)	660 279
V	(10/43)*(64°E - 150°E) + (4/11)*(150°E - 100°W)	851 366
VI	(5/11)*(150°E - 100°W)	789 091
Total		7 719 714

Table 6.4: Estimates of crabeater seal abundance for the 2000/2001 season for each IWC Area (see Section 6.3.1).

Region	Abundance estimate (N)	CV
Region AI	3 910 212	0.5
Region PO	3 809 502	0.5
Region AO	3 249 933	0.5
Region PI	4 469 781	0.5

Table 6.5: Estimates of crabeater seal abundance for the 2000/2001 season for each Region of Interest (see Section 6.3.1). The CV values are assumed.

Survey	Region	Survey year(s)	Leopard seal abundance estimate (N)	Reference
Erickson surveys	60°W - 20°W	1969/70	2 780 900	Erickson and Hanson (1990)
	20°W - 20°E	1982/83	28 700	Erickson and Hanson (1990)
	90°E - 160°E	1972/73 - 1973/74	68 000	Erickson and Hanson (1990)
	145°E - 170°E	1972/73	23 200	Laws (1984), Gilbert and Erickson (1977)
	160°E - 130°W	1971/72 - 1972/73	55 200	Erickson and Hanson (1990)
	135°W - 80°W	1971/72	48 600	Laws (1984), Gilbert and Erickson (1977)
	130°W - 60°W	1971/72	61 400	Erickson and Hanson (1990)
APIS surveys	150°E - 100°W	1999/00	15 000	Bengston *et al.* (2011)
	90°W - 30°W	1998/99	13 200	Forcada *et al.* (2012)
	64°E - 150°E	1999/00	7 300	Southwell *et al.* (2008)
Sum of the APIS estimates			35 500	

Table 6.6: Estimates of leopard seal abundance estimates in certain years from the Erickson and APIS surveys, after Table 1 from Southwell *et al.* (2012).

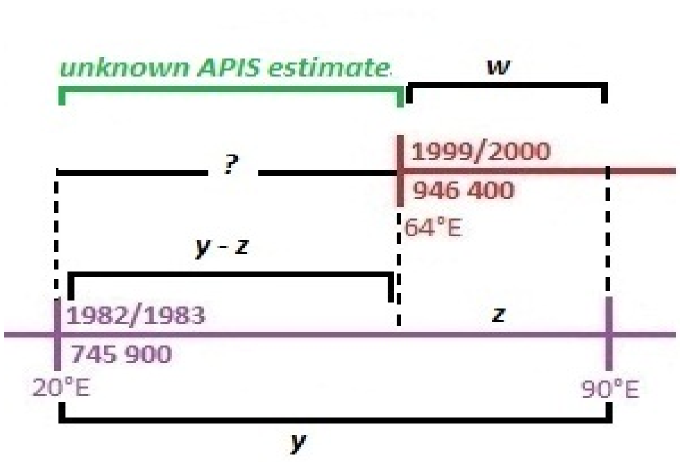

Figure 6.1: Diagram demonstrating how ratios between the two surveys are used to estimate abundances for the unknown areas not covered by the APIS surveys: y refers to the total Erickson abundance estimate, z refers to the longitudinal proportion of the Erickson survey covered by the APIS survey, w refers to the proportion of the APIS survey covered by the Erickson survey and ? is the unknown estimate of abundance from an area not covered by the APIS survey.

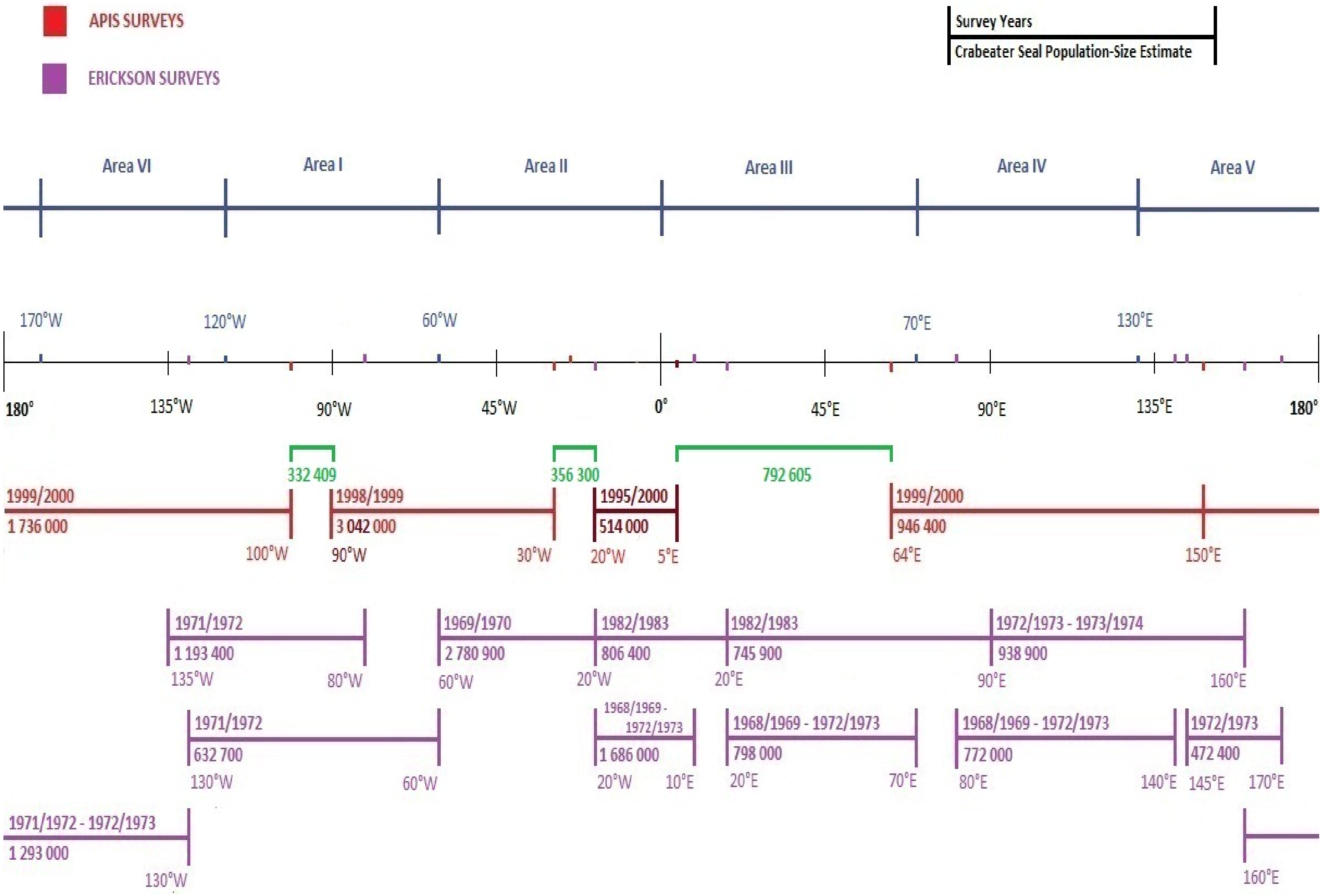

Figure 6.2: Map of the crabeater seal abundance estimates from the Erickson and APIS surveys, in relation to the IWC Management Areas.
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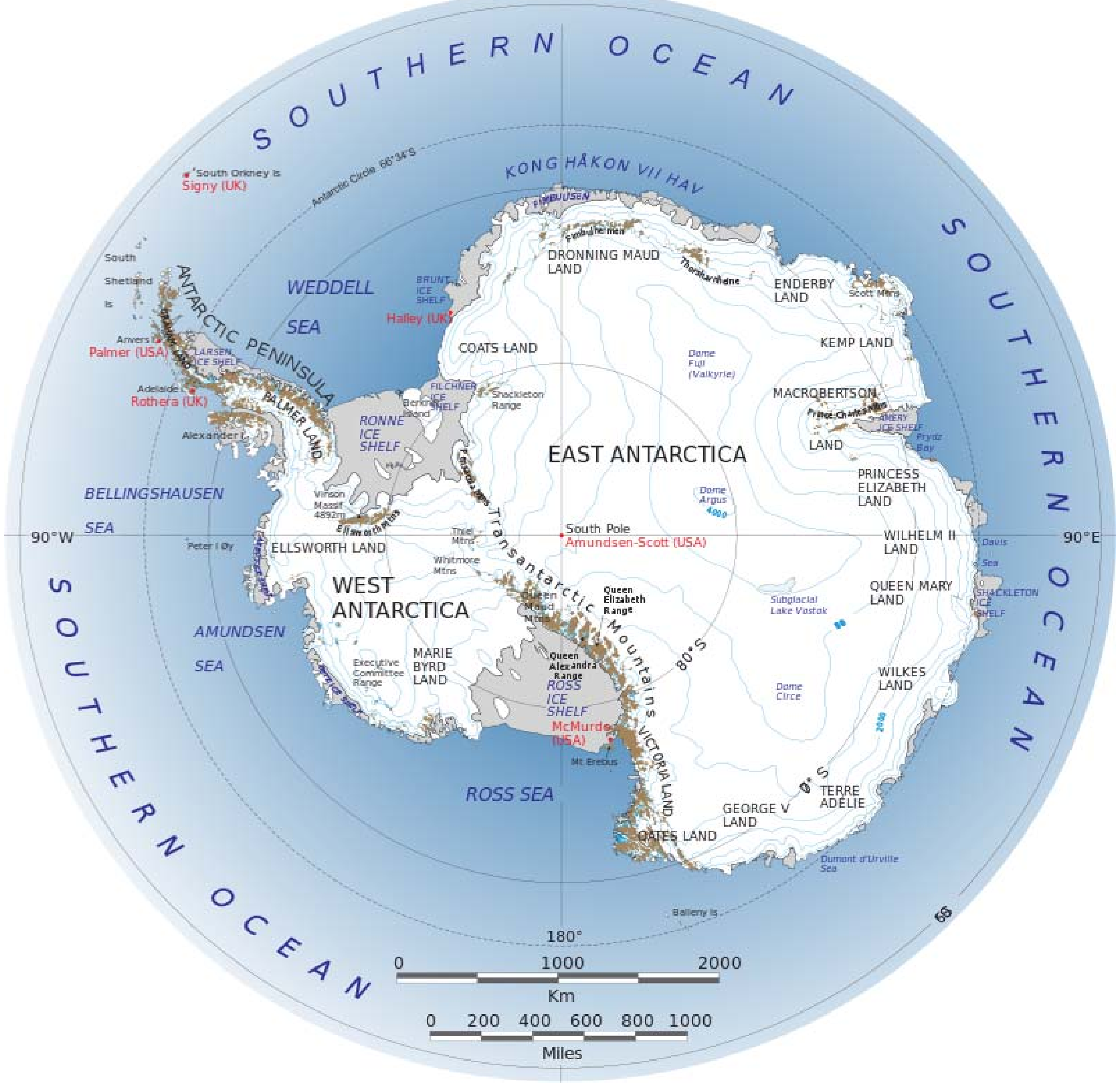

FIGURE 6.3: Map of the seas around Antarctica (from *https : //en.wikipedia.org/wiki/Geography_of_Antarctica* [Accessed 16/11/2016]).

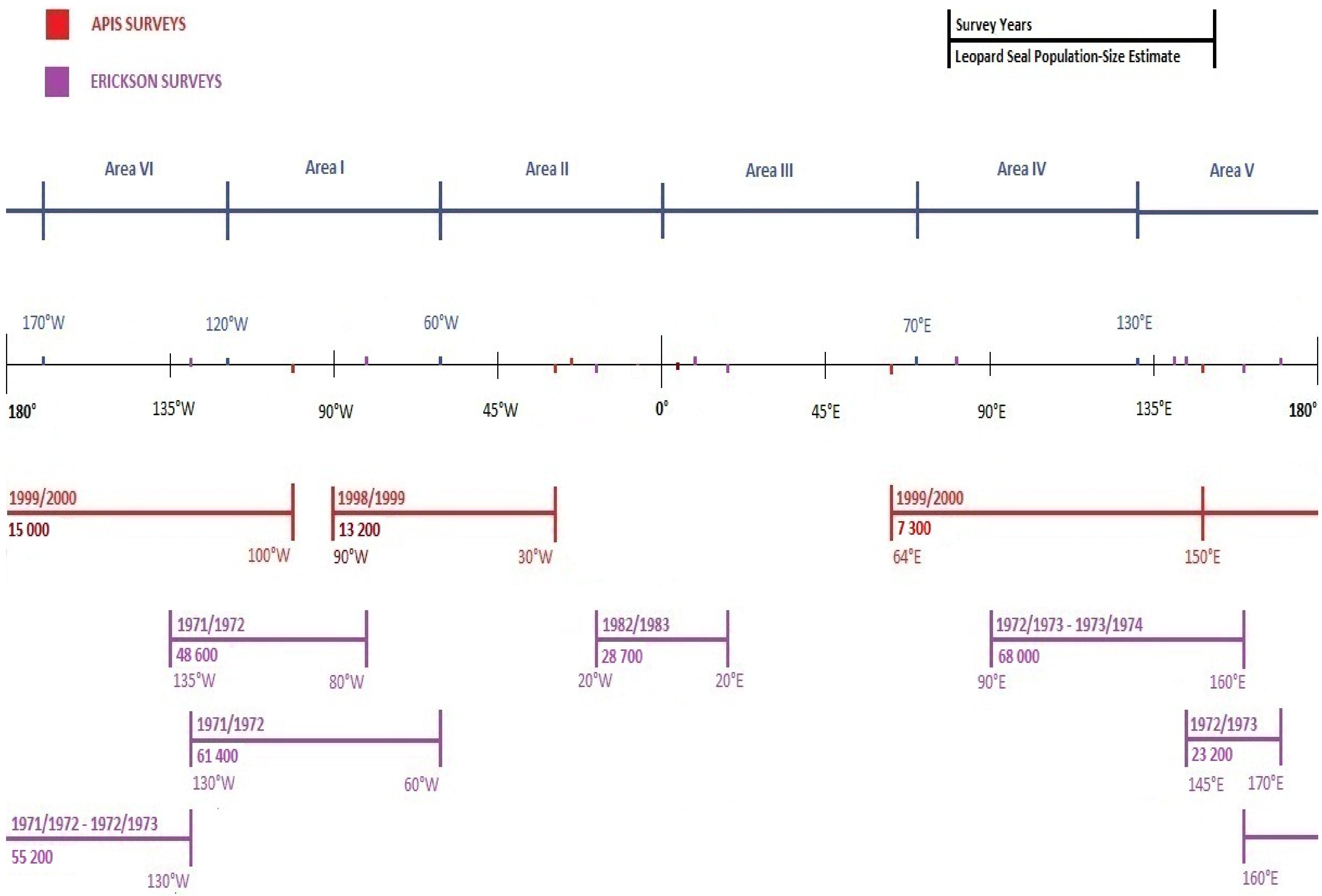

FIGURE 6.4: Map of the leopard seal abundance estimates from the Erickson and APIS surveys, in relation to the IWC Management Areas.

Chapter 7

Krill, penguins and fish: abundance and trend estimates

7.1 Overview of Chapter

This chapter reviews the main methodologies used to provide krill abundance and trend estimates. It then considers how the abundance estimates for the Adélie penguin, marbled rockcod and mackerel icefish have been calculated. The aim of this chapter is update abundance and trend estimates for krill (where possible) and to provide an abundance estimate for the Adélie penguin, marbled rockcod and mackerel icefish, which was used in calculating the total consumption of krill by weight for each of these species.

7.2 Krill *Euphausia superba*

Krill live in a remote and cold environment that is covered by ice for much of the year. This makes krill abundance estimation difficult. Krill's tendency to swim together and form thick "patches" further complicates their estimation (Cox *et al.*, 2011).

Despite these difficulties, a number of krill abundance estimates have been obtained over the years. The most reliable of these estimates come from acoustic survey data. Several techniques have been used to estimate krill abundance, and they are discussed below.

7.2.1 Acoustic Surveys

The use of echo-sounders as a measuring tool for marine stock assessments increased with the development of digital electronics, economical computing power and the Global Positioning System (GPS) (Hewitt *et al.*, 2002). Acoustic surveys allow for intensive sampling over a large area within a relatively short time-period (Brierley *et al.*, 1999). The basic principles underlying acoustic surveys of krill are summarized in Miller and Hampton (1989, p.29). The uncertainties associated with the results from such surveys are summarized in Hewitt and Demer (2000). The main uncertainties are outlined below.

1) *"Target Strength" factor*

The *target strength* (TS) is the factor that converts integrated echo energy into the absolute mass of krill, i.e. this factor is a measure of how much sound is reflected by krill (Miller and Hampton, 1989). The TS value changes with krill body shape, physical condition and orientation (Hewitt and Demer, 2000). Current TS values do not explicitly take these factors into account (Trathan *et al.*, 1992). Thus, any krill abundance estimate is sensitive to TS values which are not completely accurate.

2) *System calibration factors*

System calibration factors affect the accuracy of TS measurements (Foote and MacLennan, 1983). Calibration is carried out prior to a survey but is subject to some error.

3) *Target identification*

Nicol and de la Mare (1993) state that there is no certainty that the recorded echoes come solely from the targeted species of interest. In an attempt to account for this, direct net sampling is used to identify the target species and to assist in interpreting the acoustic contributions from krill (Hewitt and Demer, 2000).

4) *Environment*

Acoustic surveys depend on reflected sound; however echo-sounders perform poorly in noisy environments such as in rough weather or pack-ice. In the pack-ice, the sound of the ice against the ship's hull may swamp echo returns of krill at depth (Nicol and de la Mare, 1993).

5) *Transducer level*

The transducer is a device that converts one form of energy into a form that can be quantified physically. A substantial amount of krill may occur under the sea-surface above the level of the transducer on the echo-sounder. This can lead to non-detection of krill close to the sea-surface (Nicol and de la Mare, 1993).

6) *Area being surveyed*

Regional surveys that are conducted south of the Antarctic Convergence are not affected greatly by krill migrating to and from the surveyed area. However, krill abundance estimates may be biased if krill react to the approach of the survey vessel by changing either their orientation or position (Hewitt and Demer, 2000).

Although acoustic technologies have improved over the years and have assisted in the estimation of krill abundance, there are still a number of uncertainties associated with the acoustic sampling methods. Miller and Hampton (1989) and Hewitt and Demer (2000) have proposed a number of improvements to these methods.

In 2005, the Subgroup on Acoustic Survey and Analysis Methods (SG-ASAM) was formed in CCAMLR. During that year, the subgroup considered two issues relating to hydro-acoustic surveys of krill: the modeling of krill TS and the classification of volume backscattering strength (CCAMLR, 2005); both involved proposed improvements. To date, the subgroup considers the use of fishing-vessel-based acoustic data to provide quantifiable and qualitative information on the relative abundance and distribution of *Euphausia superba* (CCAMLR, 2015c). The subgroup also considers the use of acoustic data to estimate icefish abundances (CCAMLR, 2006).

7.2.2 Other Methods

Some other krill abundance estimation techniques are summarised below.

1) *Zooplankton*

Gulland (1970) estimated the standing stock of zooplankton in the Antarctic from net surveys and assumed that 50% of the herbivorous zooplankton was krill. There were several uncertainties associated with this technique, namely: the patchy distributions of krill and zooplankton, the nets used in the surveys (earlier nets were not efficient krill catchers and would have led to negatively biased estimates), and many of the technique's assumptions were untested.

2) *Predator consumption rates*

Ross and Quetin (1988) used predator consumption rates to calculate krill abundance estimates. This method is problematic as it requires reasonably precise predator consumption rates and abundance estimates of the krill-predators (whales, seals, penguins, fish and squid). Abundances for fish are especially difficult to estimate, as will be discussed in this chapter. This method also requires reasonably precise estimates for the lengths of stay of the krill-predators in the Antarctic.

These other methods are not considered to be very reliable due to their coarseness and the uncertainties associated with them.

7.2.3 Abundance estimate for krill

Mori (2005) used Nicol *et al.* (2000) to provide the krill abundance estimates for her analyses. Nicol *et al.* (2000) used krill density measurements from acoustic surveys and historical information on the overall krill distribution to calculate circumpolar krill abundance estimates. Those authors divided the overall krill distribution into eight strata. The boundaries of these strata were based on the acoustic surveys that had taken place already. The mean density of krill for each stratum, measured in the acoustic surveys, was multiplied by the stratum's ocean area to determine the stratum's krill abundance.

By aggregating the krill abundance estimates for each stratum, the overall krill abundance estimate for the Antarctic was calculated. It was between 60 - 150 million tons. Nicol *et al.* (2000) noted that these estimates were not definite values for krill abundance and had several uncertainties associated with them. These uncertainties are not discussed further in this thesis.

In 2000, a large-scale acoustic survey called the *CCAMLR-2000 Krill Synoptic Survey* (CCAMLR-2000 survey) was conducted in the south-west Atlantic (CCAMLR statistical subareas 48.1 - 48.4; see Figure 3.2) (Trathan *et al.*, 2001). The motivation for the survey, its methodology and its findings are detailed in Hewitt *et al.* (2002). The total krill biomass for the surveyed area was estimated to be 44.3 million tons (CV = 11.4%; see Table 7.1) (Hewitt *et al.*, 2002).

Mori (2005) also references Demer and Conti (2005) who re-analysed the data from Hewitt *et al.* (2002) using improved estimation techniques. This led to an overall krill biomass estimate that was roughly 2.5 fold greater than the 44.3 million tons calculated in Hewitt *et al.* (2002).

More recent analyses on krill abundance have become available in the years 2014 and 2015. The areas surveyed, which are considered in these analyses, are quite varied so that these analyses cannot be used to provide a full circumpolar abundance estimate for krill. However, they are detailed below to provide a sketch of the recent information available on krill abundance.

1) *Wada and Tamura (2014)*

During the JARPAII surveys in the austral summer of the Antarctic, krill biomass estimation surveys were conducted using a quantitative echo-sounder. Only two of the JARPAII surveys provided complete data sets: the 2007/08 season survey in Areas III-East (35°E - 70°E) and IV (70°E - 130°E) and the 2008/09 season survey in Areas V (130°E - 170°W, including the Ross Sea) and VI-West (170°W - 145°W). The echo-sounder data were recorded continuously as the vessel moved along a predetermined saw-tooth track-line. Echo-sounder data that were recorded when vessels deviated from the track-line to confirm a cetacean sighting were not used in the Wada and Tamura (2014) analysis. The methodology used to calculate the krill biomass is summarised succinctly in Wada and Tamura (2014), thus will not be addressed here. The total krill biomass estimates for the areas surveyed are summarised in Table 7.2.

Wada and Tamura (2014) list some limitations of using an echo-sounder to estimate krill abundance.

1) Low density - background krill are low in density and may not be detected by the echo-sounder.
2) Krill refuge - krill can distribute into places which a survey vessel cannot access such as under sea-ice.
3) Surface krill - krill can migrate to areas shallower than the sounder's minimum depth.

Wada and Tamura (2014) consider only one specific region in the Pacific, so their results cannot be used to provide a circumpolar estimate on krill abundance.

2) *Skaret et al. (2015)*

The Institute of Marine Research in Norway conducted annual acoustic surveys from 2011 to 2015 in order to monitor krill around the South Orkney Islands (see Figure 3.2). The surveys were conducted during the austral summer (January - February) and used two fishing vessels. Both vessels were equipped with echo-sounders; however the frequencies at which they operated varied between years and vessels. The survey coverage also varied between years due to ice. Skaret *et al.* (2015) used these five years of survey data to construct a coherent series of krill density estimates, following the CCAMLR protocol for biomass estimation as far as possible. Their analysis estimated that in the year 2014, there was about 8 million tons of krill around the South Orkney Islands (see Table 7.2).

3) *Kawaguchi et al. (2015)*

An Australian Antarctic research and resupply vessel undertook an opportunistic (due to favorable ice conditions) marine science survey off the coast of East Antarctica (Enderby Land to Prydz Bay; see Figure 6.3) from 21 February 2015 to 10 March 2015. Kawaguchi *et al.* (2015) compiled a preliminary report of this survey. The survey completed five acoustic box surveys, six demersal trawls, 131 phytoplankton samples and 214 hourly predator observations. These survey data have yet to be analysed.

4) *Cox et al. (2015)*

A transect acoustic survey was conducted at the Balleny Islands (see Figure 3.2) in February 2015. The processing of the acoustic data followed the recommendations of CCAMLR SG-ASAM. The krill biomass was estimated to be 13.75 kilotonnes (CV = 0.14) (see Table 7.2).

7.2.4 Trend estimates for krill

Mori (2005) reports that long-term consecutive surveys on krill abundance have been conducted around Elephant Island and South Georgia (see Figure 2.1) only. These two regions represent only a small percentage of the total distributional area of krill. The trend estimate for krill around Elephant Island is also problematic due to the few net samples taken during the earlier surveys and the differences in the surveyed area during the study period. As a result, calculating a circumpolar trend estimate is not possible.

Two types of data have been used to assess the trends in krill abundance: from acoustic surveys and from net sampling during cruises.

1) *Trend estimates from acoustic sampling data*

Mori (2005) analysed information from Hewitt and Demer (1994) and Brierley *et al.* (1999). She concluded that from 1981 until the mid-1990s, acoustic surveys did not show any statistically significant trends in krill abundance around Elephant Island and South Georgia (see Figure 7.1 and Figure 7.2).

2) *Trend estimates from net sampling data*

Mori (2005) reports that around Elephant Island, net sampling of krill began in 1977 and continued until the year 2000. The methods used to calculate krill density (which is used to calculate trends in krill abundance) changed over the years. Krill density estimates were first calculated using a stratified mean of standardised non-targeted net catches as suggested by Saville (1977) (Siegel and Loeb, 1995). Subsequently, the density estimates were calculated using a delta distributive approach and maximum likelihoods (the TRAWLCI method) as outlined by de la Mare (1994) (Siegel *et al.*, 1997). The TRAWLCI method is the agreed standard method used by CCAMLR to estimate densities from trawl surveys (see Figure 7.3; Siegel *et al.*, 2002). Siegel *et al.* (1998) outlines several concerns associated with these net sampling surveys.

1) Use of standardised gear and methods - these were used consistently over time thus reducing any bias in trend estimates.
2) Net avoidance behaviour - krill density estimates may be negatively biased because of this.
3) Infrequent sampling (especially in the earlier years) - this results in large coefficients of variation in the density estimates.

More recently, the study by Wada and Tamura (2014) was unable to provide a trend in krill abundance as the two surveys analysed were conducted in different areas.

Hill *et al.* (2015) used data from scientific nets in the CCAMLR subareas 48.1 to 48.4 (see Figure 3.2) from 2000 till 2011 to provide an index of krill biomass. No systematic change in the krill biomass was noticeable in the index for the analysed period.

7.3 Adélie penguin *Pygoscelis adeliae*

Results provided by Lynch and LaRue (2014) have been used to determine an Adélie penguin abundance estimate. They define a *colony* as "groups of contiguously nesting penguins" and a *breeding site* as an area of terrain that is free of snow and ice during the austral summer.

Three processes are used in developing the results of the Lynch and LaRue (2014) census.

1) Direct penguin counts of breeding pairs between December and January (when the available count data was older than four years or when satellite imaging was either insufficient or unavailable to distinguish Adélie penguins from the breeding pairs of other penguin species).
2) High resolution satellite imagery at all the known and suspected Adélie penguin colonies.
3) High resolution satellite imagery at infrequently or poorly surveyed coastlines to search for new or unreported Adélie breeding colonies.

Only 37 breeding sites had neither recent penguin counts nor imagery to estimate abundance, but 30 of these sites had been censused previously - those older estimates were used in those cases. Adélie penguin colonies were identified by the spatial and spectral distribution of their guano (see Glossary). An area of guano staining was identified as an area of nesting, which in turn was used to provide an estimate of the number of breeding pairs in the area. A Poisson regression abundance model was used to convert the nesting area into a statistical distribution that represented the predicted number of breeding pairs at each breeding site. Estimates for regionally and globally aggregated Adélie populations were calculated by repeated sampling from each of the breeding site's abundance distribution. This allowed the uncertainties associated with the individual abundance estimates to be propagated to the aggregated abundance estimates.

Lynch and LaRue (2014) conclude that the total Adélie penguin population is roughly 3.7 million breeding pairs (see Table 7.3). They report this estimate to be 53% larger than the previous estimate of 2.47 million, which was calculated in 1993. The differences are explained as follows.

1) Increased abundance at known colonies.
2) Inclusion of colonies that were not previously surveyed.
3) An increase in sea-ice extent and duration over the last 40 years, especially in East Antarctica, resulting in increased habitat availability for the penguins (Stammerjohn *et al.*, 2012).

7.4 Marbled rockcod *Notothenia rossii*

N. rossii used to be prominent in the Atlantic and Indian sectors of the Antarctic. The *N. rossii* fishery was closed by CCAMLR in the early 2000s following heavy exploitation of the resource. As a result, there is little recent abundance information available for the species.

For the Atlantic sector (South Georgia and Shag Rocks; see Figure 3.2), Everson *et al.* (1991) is used as it is one of the more "recent" assessments of the exploited Antarctic fish stocks in the region. Those authors analysed a survey that consisted of a series of randomly located trawl stations, from the surface to a depth of 500m. Altogether 78 stations were sampled, 66 at South Georgia and 12 at Shag Rocks. The *swept area* method, detailed in SC-CAMLR (1990), was used to estimate the biomass of *N. rossii* for the year 1990/91 (see Table 7.4).

For the Indian sector (Kerguelen Islands; see Figure 3.2), a bottom trawl biomass survey was conducted from September 2006 to October 2006 around the Kerguelen islands. This survey was known as *POKER 2006*. The swept area method was used to estimate abundance over a depth range from 100m to 1000m. It included 207 randomly stratified stations. All trawl catches were evaluated by identifying species, measuring fish, tagging and taking biological samples.

Duhamel and Hautecoeur (2009) analyse the data from the POKER 2006 survey to determine the biomass and abundance (by number) estimates of all the fish species found in the region. The biomass estimates for *N. rossii* are summarised in Table 7.4.

The two surveys analysed cannot be used to provide a true circumpolar biomass estimate as they do not cover the entire Antarctic region. However, they do cover the main concentrations of *N. rossii*, which is considered sufficient for present purposes.

The biomass estimates are used to calculate abundance (by number) estimates using the following equation:

$$\hat{B} = \hat{N} \cdot \bar{w} \tag{7.1}$$

where

1) $\hat{B}$ is the estimated biomass (tonnes),
2) $\hat{N}$ is the estimated abundance (number), and
3) $\bar{w}$ is the average weight of the fish species (tonnes) - see Table 4.15 for *N. rossii.*

The biomass estimates for the Atlantic and Indian sectors of the Antarctic are from surveys conducted in different years. Furthermore, the survey designs and possibly also the survey methods differed between the two analysed regions. Despite this, the biomass estimates for the two regions have been aggregated to provide a rough circumpolar biomass estimate. This is not ideal but it is the best that can be done with the information available. The abundance estimate for *N. rossii* is calculated to be 1.48 million fish, and pertains to the period of the 1990s and 2000s.

7.5 Mackerel icefish *Champsocephalus gunnari*

Unlike *N. rossii*, *C. gunnari* is targeted by licensed fisheries around South Georgia in the Atlantic sector and around Heard and McDonald Islands in the Indian sector of the Antarctic (see Figure 3.2). The icefish fishery is monitored and reviewed annually by CCAMLR (see *https://www.ccamlr.org/en/fisheries/icefish-fisheries*).

The most recent trawl survey conducted around South Georgia and Shag Rocks took place in January 2015 (Belchier *et al.*, 2015). The survey covered the entire shelf area and used 77 random and spatially stratified hauls. It covered depths from 100 to 350m (CCAMLR, 2015a).

The most recent acoustic survey that estimated the biomass of *C. gunnari* was conducted in 2004. This survey indicated that mackerel icefish of all sizes and ages spend more time mid-water. As a result, bottom trawl surveys underestimate the biomass of mackerel icefish appreciably (Agnew *et al.*, 2004). CCAMLR (2015a) states that there have been no newer standing stock estimates from acoustic surveys since that 2004 survey.

CCAMLR (2015a) also states that the overall estimated biomass for *C. gunnari* around South Georgia and Shag Rocks (see Figure 3.2) is 59 081 tonnes (Table 7.5) from Earl and Darby (2015). Earl and Darby (2015) used catch rate data from a 2015 demersal fish survey and applied a stratified bootstrap of *C. gunnari* catch density estimates to calculate the biomass.

In May 2015, a random stratified bottom trawl survey was conducted around Heard and McDonald Islands (Nowara *et al.*, 2015; see Figure 3.2). The sampled areas of the survey had high concentrations of *C. gunnari*. The bootstrap procedure outlined in Welsford (2010) was applied to the data from this survey to estimate the standing stock biomass for *C. gunnari* in the region (see Table 7.5) (CCAMLR, 2015b). CCAMLR (2015b) states that the *C. gunnari* abundance estimate from the 2015 survey for the region is roughly a third of what it had been for the survey conducted in 2014.

As was the case for the marbled rockcod, the two surveys analysed cannot be used to produce a true circumpolar biomass estimate as they do not cover the entire Antarctic region. However, they do cover the main concentrations of *C. gunnari* which is deemed sufficient for present purposes. Equation 7.1 is used to calculate a rough abundance estimate (in numbers) from the biomass estimates with $\bar{w}$ being taken from Table 4.14. The biomass estimates are all for the 2014/15 season but originate from different surveys/methods. Nonetheless, they are aggregated together to provide a rough circumpolar biomass estimate for the mackerel icefish. This is not ideal but it is the best that can be done with the information available. The resultant abundance estimate for *C. gunnari* is 32.1 billion fish in the 2014/15 season.

7.6 Summary

Over the years, krill abundance estimates have been calculated using various techniques. Acoustic surveys provide the most reliable estimates, and as a result have become the primary approach for estimating krill abundance. The most recent analyses provide krill abundance estimates of the order of several tens of million tonnes. These are much smaller than the several hundred million tonnes that was estimated from the Antarctic ecosystem model in Mori (2005). This is most likely due to the regions covered by these surveys being relatively small. Krill abundance estimates from the south-west Atlantic are listed in Mori (2005). For this thesis, abundance estimates from the Indian Ocean, Balleny and South Orkney Islands are also available. Furthermore, some of the estimates listed in this thesis come from the JARPA surveys.

Mori (2005) found no statistically significant trend in krill abundances over the 1980s and 1990s and was unable to calculate a circumpolar trend estimate. The most recent analyses on krill abundance are also unable to provide a statistically significant trend estimate.

This chapter also explained how the abundance estimates for the Adélie penguins, marbled rockcod and mackerel icefish have been calculated. A census using direct penguin counts and satellite imaging was used to calculate the abundance estimate for Adélie penguins, whilst trawl and acoustic surveys covering the main concentrations of the marbled rockcod and mackerel icefish were used to obtain their abundance estimates.

Area analysed	Mean krill density (t/km^2)	Area surveyed (million km^2)	Biomass (million tons)
Antarctic Peninsula	11.2	0.47	5.32
Scotia Sea	24.5	1.11	27.24
East Scotia Sea	11.3	0.32	3.64
South Shetland Islands	37.7	0.05	1.84
South Orkney Islands	150.4	0.02	3.67
South Georgia	39.3	0.03	0.98
Sandwich Islands	25.8	0.06	1.60
All Regions	21.4	2.06	44.29

Table 7.1: Krill density and biomass estimates for the CCAMLR-2000 Krill Synoptic Survey, after Table 1 of Hewitt *et al.* (2002).

Area analysed	Year	Biomass estimate (million tons)	Reference
IWC Area III-East	2007/08	6.6	Wada and Tamura (2014)
IWC Area IV	2007/08	12.5	Wada and Tamura (2014)
IWC Area V	2008/09	24.0	Wada and Tamura (2014)
IWC Area VI-West	2008/09	3.4	Wada and Tamura (2014)
South Orkney Islands	2014	8.0	Skaret *et al.* (2015)
Balleny Islands	2015	13.75	Cox *et al.* (2015)

Table 7.2: A summary of the various krill biomass estimates for different years and regions from various analyses.

CCAMLR Area	Abundance estimate × 10^3 (in breeding pairs)
Subarea 48.1	805.3
Subarea 48.2	191.6
Subarea 48.4	56.9
Division 58.4.1	516.0
Division 58.4.2	625.5
Subarea 88.1	1 233.8
Subarea 88.2	53.7
Subarea 88.3	172.9
Total	3 655.7

Table 7.3: The estimated abundances (in breeding pairs) of the Adélie penguin for the various CCAMLR areas, after Table 2 from Lynch and LaRue (2014).

Area	Year	Reference	Biomass estimate (tonnes)
South Georgia	1990/91	Everson *et al.* (1991)	4 295
Shag Rocks	1990/91	Everson *et al.* (1991)	0
Kerguelen Islands (northern part)	2006/07	Duhamel and Hautecoeur (2009)	8 090
Kerguelen Islands (Skiff Bank)	2006/07	Duhamel and Hautecoeur (2009)	909
Total Biomass Estimate			13 294

Table 7.4: The estimated biomasses for *N. rossii* in the Atlantic and Indian sectors of the Antarctic.

Area	Year	Reference	Biomass estimate (tonnes)
South Georgia and Shag Rocks	2014/15	Earl and Darby (2015)	59 081
McDonald and Heard Islands	2014/15	CCAMLR (2015b)	5 123
Total Biomass Estimate			64 204

Table 7.5: The estimated biomasses for *C. gunnari* in the Atlantic and Indian sectors of the Antarctic.

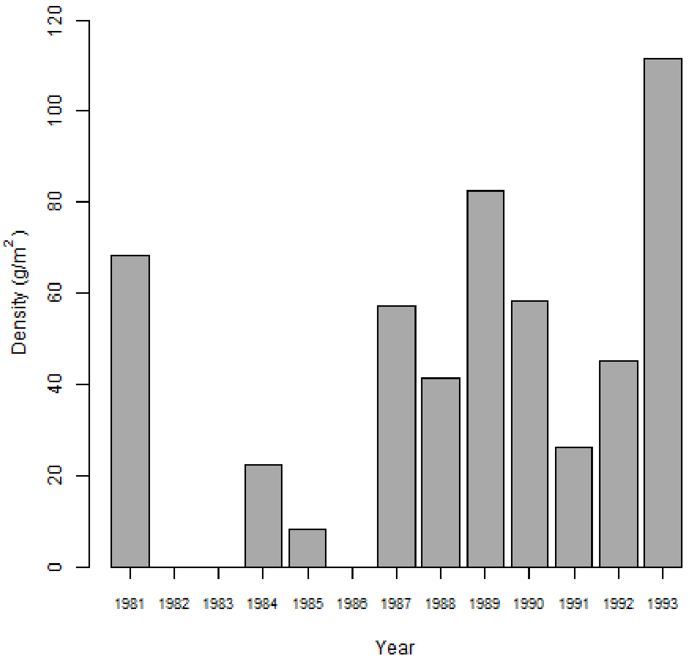

Figure 7.1: Time series of krill density estimates (g/m^2) estimated from acoustic surveys conducted from January until March around Elephant Island, after Figure 1 from Hewitt and Demer (1994).

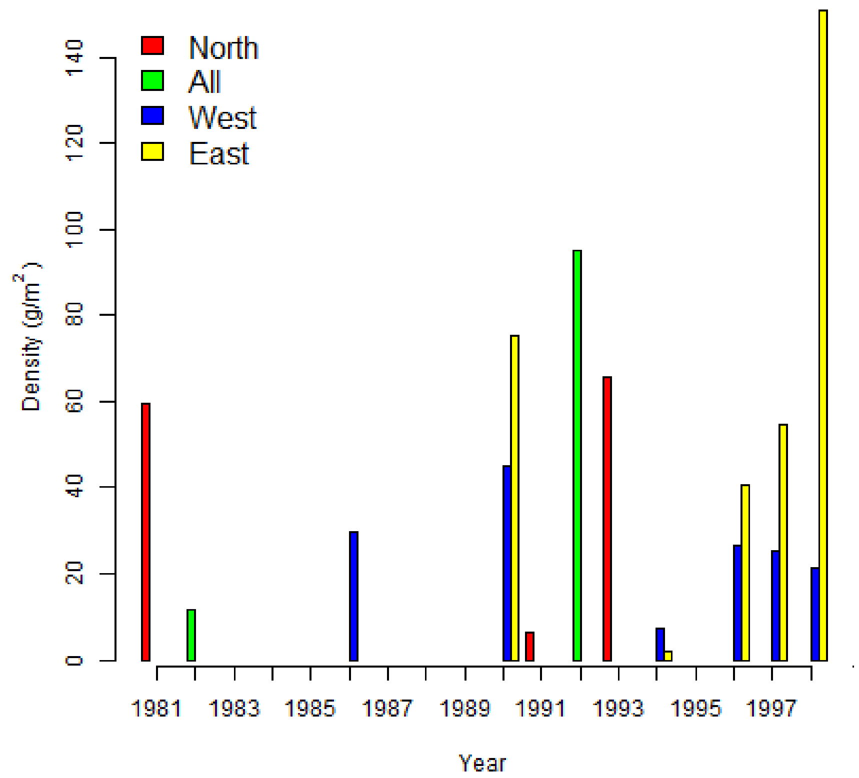

FIGURE 7.2: Krill density estimates (g/m^2) estimated from acoustic surveys conducted from 1981 until 1998 around South Georgia, after Figure 2 from Brierley *et al.* (1999).

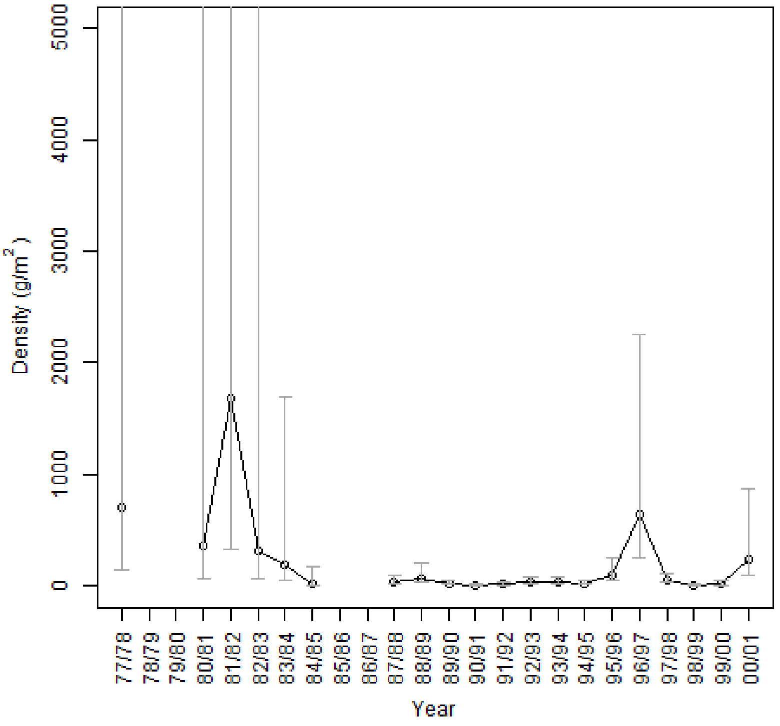

FIGURE 7.3: Krill density estimates (g/m^2) estimated using the TRAWLCI method from mid-December until mid-February around South Georgia, after Table 1 from Siegel *et al.* (2002).

Chapter 8

The selection of input parameter values and bounds on the values of the estimable parameters of the model

8.1 Overview of Chapter

This chapter discusses how the input parameter values, and bounds on the values for the estimable parameters of the model, are calculated or chosen. By placing bounds on these parameters, it assists the model during the estimation process and keeps the final estimates realistic. The primary parameters that are estimated when fitting to the data are the annual natural mortality proportions for each predator species j (M_j), the maximum product of the annual birth rate and the first-year calf-survival proportion for each predator species j (μ_j), the maximum annual per capita krill consumption rate for each predator species j (λ_j), the intrinsic growth rate of krill in Region a (r^a) and the number of each predator species j in Region a in the year 1780, which corresponds to the pristine abundance of the predator species ($N^{j,a}_{1780}$). The input parameters of the model, i.e. the parameters whose values are pre-specified, are the density-dependence of natural mortality and/or birth rate for each predator species j in Region a ($\eta_{j,a}$) and the krill biomass when the krill consumption by blue whales decreases to half of its maximum level in Region a ($B^{blue,a}$). Another parameter that is estimated in the model is the scaling factor q_a, which relates the average annual weight of prey contents in the stomachs of minke whales for the years for which such data are available in Region a (Q^a_y) to the density-dependent growth term in the equation for the predator dynamics (Equation 10.2).

8.2 Natural annual mortality estimates

The natural mortality proportion M is calculated using the following equation:

$$M = 1 - S \tag{8.1}$$

where

M is the annual proportion lost to natural mortality.
S is the annual proportion that survives.

8.2.1 Whales

Brandão *et al.* (1999) is used to provide a natural mortality estimate for humpback whales as it is the basis for the most recent estimate accepted by the IWC Scientific Committee. The article calculates the maximum possible increase rate for humpback whales as a function of the following biological parameters: the annual survival proportion after the whale's first birthday (S), the age (years) of the whale at first parturition (t_m), the annual proportion of females pregnant (p), the proportion of births that are female (q_f) and the survival proportion to the first birthday (S_j).

The steady rate of the humpback whale population's growth is then given by:

$$e^{t_m\delta} = e^{(t_m-1)\delta}S + pq_fS_jS^{t_m-1} \tag{8.2}$$

where δ is the instantaneous growth rate (yr^{-1}).

It is assumed that $q_f = 0.5$ and that $S_j \leqslant S$ because if the mother dies during the calf's first year, the calf is likely to die as well. To get the maximum possible growth rates, S_j is set to equal S in the computations. The ranges for the other biological parameters are:

$$S \text{ over } (0.91, 0.99) \qquad p \text{ over } (0.3, 0.5) \qquad t_m \text{ over } (4, 11).$$

The results of these computations indicate that the humpback population growth rates can exceed 10% per year given a two-year calving interval, provided that S is high (at least 0.96) and t_m is low (no greater than eight years). Some of these results are summarised in Table 8.1.

Annual survival proportion	Age at first parturition (years)							
	4	5	6	7	8	9	10	11
0.98	**0.128**	**0.115**	**0.105**	0.097	0.090	0.083	0.078	0.073
0.97	**0.118**	**0.105**	0.095	0.086	0.079	0.073	0.068	0.063
0.96	**0.108**	0.095	0.085	0.076	0.069	0.063	0.057	0.053

TABLE 8.1: Results from Brandão *et al.* (1999) showing the maximum instantaneous growth rates (δ) for humpback whales as a function of S, t_m and with $p = 0.5$*.

The IWC Scientific Committee (IWC, 2007) has concluded that humpback whales should have a theoretical steady maximum growth (increase) rate of 0.106 or 10.6% per year, noting also that small humpback whale populations, recovering from depletion, could show a higher increase rate for a limited period. The Committee (IWC, 2007) noted that the earliest observed age of a humpback cow giving birth was five years. From Table 8.1, a $t_m = 5$ and a growth rate of 10.6% per annum corresponds to an annual survival proportion of 0.97, i.e. to an annual mortality proportion of 0.03 (using Equation 8.1).

It is assumed that blue whales and fin whales have the same mortality proportion as humpback whales as there is a lack of information on blue and fin whale natural mortality.

The natural mortality rate for minke whales is derived from Punt (2014) whose method is outlined in Punt *et al.* (2013). This paper is used because prior to its availability, there was no solid foundation upon which to estimate minke mortality based on available data. Punt *et al.* (2013) describe a piecewise linear relationship between age and natural mortality as follows:

$$M_a^{\bar{S}} = \begin{cases} \delta M^{\bar{S}} & \text{if} \quad a \leqslant a_1 \\ M^{\bar{S}}[\delta + (1-\delta)\dfrac{a-a_1}{a_2-a_1}] & \text{if} \quad a_1 < a < a_2 \\ M^{\bar{S}} & \text{if} \quad a_2 \leqslant a \leqslant a_3 \\ M^{\bar{S}}[1 + (\gamma-1)\dfrac{a-a_3}{a_4-a_3}] & \text{if} \quad a_3 < a < a_4 \\ \gamma M^{\bar{S}} & \text{if} \quad a \geqslant a_4 \end{cases} \tag{8.3}$$

where $\bar{S}$ is the stock in question. Two stocks are defined in the paper (see Figure 4.2):

Stock I = IWC Areas III-East (35°E - 70°E), IV (70°E - 130°E) and V-West (130°E - 160°E); and

Stock P = IWC Areas V-East (160°E - 170°W) and VI-West (170°W - 145°W).

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[*] It is assumed that the calving interval is two years, so that half of the adult females become pregnant each year.

Punt (2014) sets: $a_1 = 3$, $a_2 = 10$, $a_3 = 20$ and $a_4 = 40$. The corresponding relationship of $M_a^{\bar{S}}$ to a (as described in Equation 8.3) is shown in Figure 8.1.

From Figure 8.1, very young (between ages 0 and 3) and old (ages $\geqslant 40$) minke whales have a higher probability of dying each year compared to those of intermediate age (between ages 10 and 20). However, the ecosystem model being used in this thesis requires a single value for M, independent of a and representative of the population as a whole. Thus, an average of $M_a^{\bar{S}}$ is sought, which is weighted by abundance, as the average is dependent on the number of whales found in each age group; this is to provide the average probability that any whale in the population may die each year.

This average of $M_a^{\bar{S}}$ is found using Equations 8.4 and 8.5, taking weights relative to the population size into account.

First the total number of whales in the population under steady conditions is found (Equation 8.4). The whales are assumed not to live beyond 60 years of age.

$$\begin{aligned} N &= N_o\left[1 + e^{-M_0} + e^{-(M_0+M_1)} + e^{-(M_0+M_1+M_2)} + ...\right] \\ &= N_o\left[1 + \sum_{i=0}^{60} e^{-(M_i)}\right] \\ &= \lambda N_o \end{aligned} \tag{8.4}$$

where

N_o is the number of minke whales at age 0 (calves), and

λ is the multiplier relating the total abundance to the number of calves.

A value is sought for an age-independent annual natural mortality for each stock ($M_{\bar{S}}$) which will yield the same ratio, λ. This value is found using Equation 8.5.

$$\begin{aligned} N &= N_o\left[1 + e^{-M^{\bar{S}}} + e^{-2M^{\bar{S}}} + e^{-3M^{\bar{S}}} + ... + e^{-60M^{\bar{S}}}\right] \\ &= N_o\left[1 + \sum_{i=1}^{60} e^{-iM^{\bar{S}}}\right] \\ &= N_o\left[\frac{1 - e^{-60M^{\bar{S}}}}{1 - e^{-M^{\bar{S}}}}\right] \\ &= \lambda N_o \qquad \text{so that } \lambda = \frac{1 - e^{-60M^{\bar{S}}}}{1 - e^{-M^{\bar{S}}}}. \end{aligned} \tag{8.5}$$

Figures 8.2 and 8.3 show that using a single M to approximate Punt's age-dependent M makes little difference to relative numbers-at-age for Stocks I and P respectively. Equation 8.5 is solved to find the value of $M^{\bar{S}}$. For *Stock I*, $M^I = 0.065$ and for *Stock P*, $M^P = 0.062$. The average of M^I and M^P is used. Thus, the annual natural mortality rate for minke whales used in this thesis is $M = 0.063$.

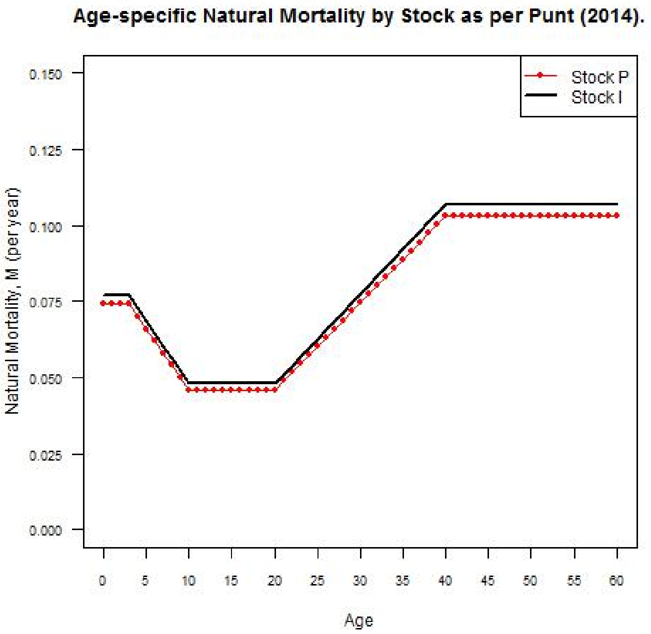

FIGURE 8.1: Graph of the natural mortalities per age for minke whales (Equation 8.3) as estimated by Punt (2014).

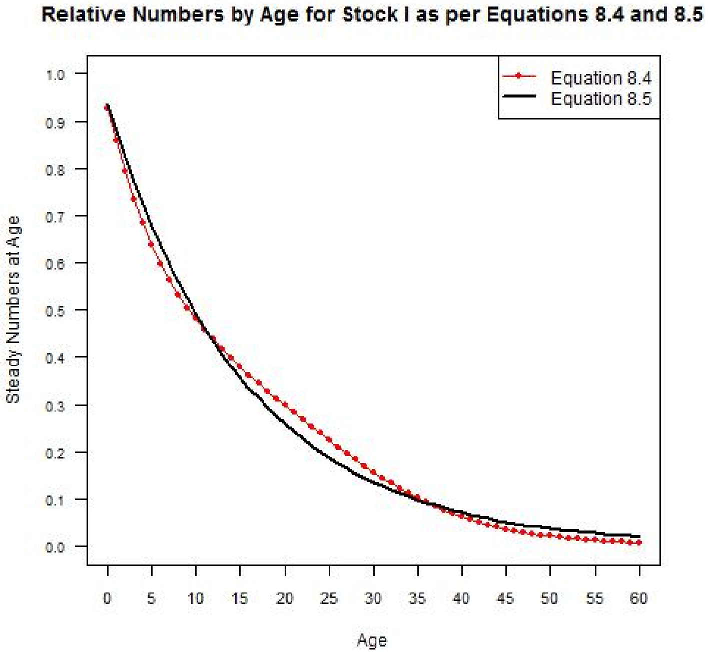

FIGURE 8.2: Plot of the relative numbers-at-age at unexploited equilibrium for Stock I for minke whales*.

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* In Figures 8.2 and 8.3, the red line shows the population structure calculated from Equation 8.4 (i.e. the age-dependent mortality rates), while the black line shows the population structure calculated from Equation 8.5 (i.e. an age-independent mortality rate).

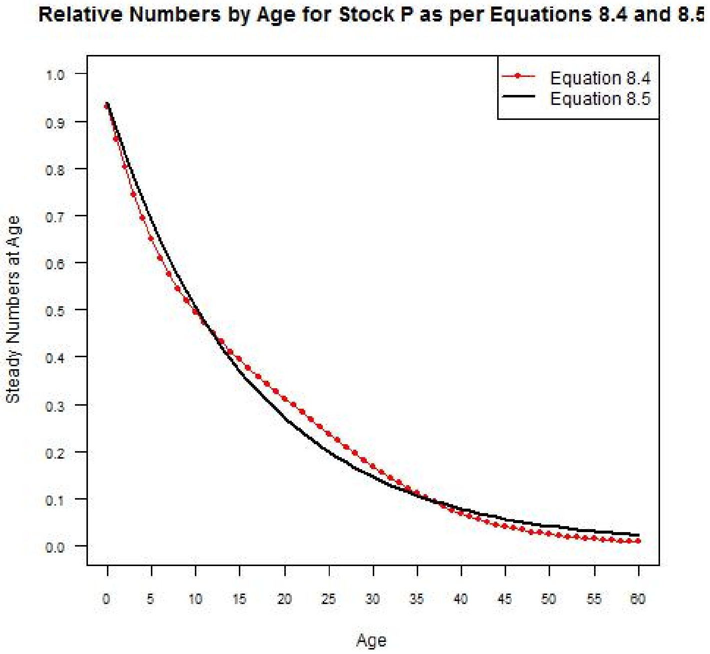

Figure 8.3: Plot of the relative numbers-at-age at unexploited equilibrium for Stock P for minke whales*.

8.2.2 Seals

Boyd *et al.* (1995) is used to determine the annual mortality proportion for Antarctic fur seals. The paper uses 11 consecutive years of mark-recapture data from a study conducted on female Antarctic fur seals at Bird Island. Adult female seals, which were tagged (on their flipper, some with two tags) as adults in previous years were monitored as either being present or absent from the specified beach used in the study - females return to this beach to give birth and to mate. The study was conducted during the austral summer between 1983/84 and 1992/93. A sample of pups (including those from tagged mothers) was caught during the birth season and numbered temporarily using peroxide hair dye. When these pups were 1-2 months old, they were tagged as adult seals. Two daily inspections (after dawn and before dusk) allowed for tag recoveries from the tagged female seals, and an elevated walkway (in place since 1978) allowed for accurate observations without unsettling the seals. Ages of captured females, returning to the study beach after sampling, were determined from their post-canine teeth.

The age-dependent annual survival proportion was approximated by the number of seals of age k known to be alive in year i and subsequently, in year $i+1$ with an age of $k+1$. Seals that were not sighted for more than one year were assumed to be dead. The survival rate also took tag loss (via abrasion and snagging against rocks and weeds) into account.

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[*] In Figures 8.2 and 8.3, the red line shows the population structure calculated from Equation 8.4 (i.e. the age-dependent mortality rates), while the black line shows the population structure calculated from Equation 8.5 (i.e. an age-independent mortality rate).

The paper states that the rate of tag loss may depend on the amount of time spent ashore, which was greater for females that were suckling. The overall estimate of the proportion of tags lost annually was 0.085 (SD 0.008) for pregnant females and 0.091 (SD 0.02) for non-pregnant females.

Survival rates in year i are corrected for tag loss using the following equation:

$$s_i^* = s_i + (s_i a_i m_1) + (s_i b_i m_2) \tag{8.6}$$

where

m_1 is the probability of losing one tag within any year (assumed to be independent of losing the other tag),
m_2 is the probability of losing the other tag,
s_i^* is the survival probability corrected for tag loss for year i,
s_i is the survival probability from year i to $i+1$,
a_i is the proportion of seals with one tag in year i, and
b_i is the proportion of seals with two tags in year i.

The study undertaken in the paper concludes that the annual survival rate is 0.79 (SD 0.092) before tag loss corrections were taken into account, and 0.83 (SD 0.099) after they were considered. The latter is used to calculate the Antarctic fur seal annual natural mortality proportion of 0.17 with a range of 0.07 - 0.35 (the range of the annual survival proportion subtracted from one), as stated in Boyd *et al.* (1995). Though the study is centred on female Antarctic fur seals, this mortality proportion is taken to be adequate as a mortality estimate which is representative of the entire Antarctic fur seal population.

It is assumed that crabeater seals have the same mortality proportion as Antarctic fur seals as there is a lack of information on adult crabeater seal natural mortality.

The estimates above for the annual natural mortality proportions for the krill-predators are summarised in Table 8.2. They are used as starting values for the M parameter which is estimated in the model fitting process.

Species	Annual natural mortality proportion, M_j
Blue whale	0.03
Fin whale	0.03
Humpback whale	0.03
Minke whale	0.063
Antarctic fur seal	0.17
Crabeater seal	0.17

TABLE 8.2: Summary of the natural annual mortality proportion estimates for the main krill-predators.

8.3 Maximum annual female birth rate estimates

The maximum annual female birth rate or μ (which includes first year survival proportion) is calculated using the following equation:

$$\mu = p \times q_f \times e^{-M} \tag{8.7}$$

p is the annual proportion of females pregnant,

q_f is the proportion of births that are female, and

e^{-M} takes the calf-survival proportion over the first year into account.

If the calf's mother dies during that year, it is likely that the calf will also die; thus the value for M is taken from Table 8.2. As stated in Section 8.2.1, q_f is assumed to be 0.5 for each krill-predator species. The next subsections detail how the estimate of the annual proportion pregnant (p) for the various krill-predators is determined.

8.3.1 Whales

Brandão *et al.* (1999) assumes that the annual humpback proportion of females pregnant is 0.5. This assumption is retained here.

Information in Gambell (1975) is used to determine the (annual) proportion of females pregnant for fin and blue whales. The paper suggests that these proportions increased during the years before World War II but subsequently decreased for some period during the war, when whaling levels dropped. These changes that were reported during the war might not be reliable - small sample sizes and catches could have affected the estimates recorded during this period. Nevertheless, fluctuations over that short period do not affect the overall trend observed in the data, and after the war, the proportion of females pregnant increased to seemingly stable levels. Estimates of the proportion of females pregnant for blue and fin whales (the ratio of the number of pregnant whales as a percentage of the total number of mature non-lactating female whales caught in the Antarctic) from Gambell (1975) are presented in Figure 8.4.

Figure 8.4 indicates that the (annual) proportion of females pregnant for blue and fin whales ranges from 0.2 to 0.6 and 0.1 to 0.6 respectively. The annual proportion of females pregnant is taken to be the median of these two sets of values. The medians of these two plots were found using WebPlotDigitizer (*http://arohatgi.info/WebPlotDigitizer/*), a web-based tool used to extract data from plots and images. For blue whales, the median is 0.48 and for fin whales, it is 0.47.

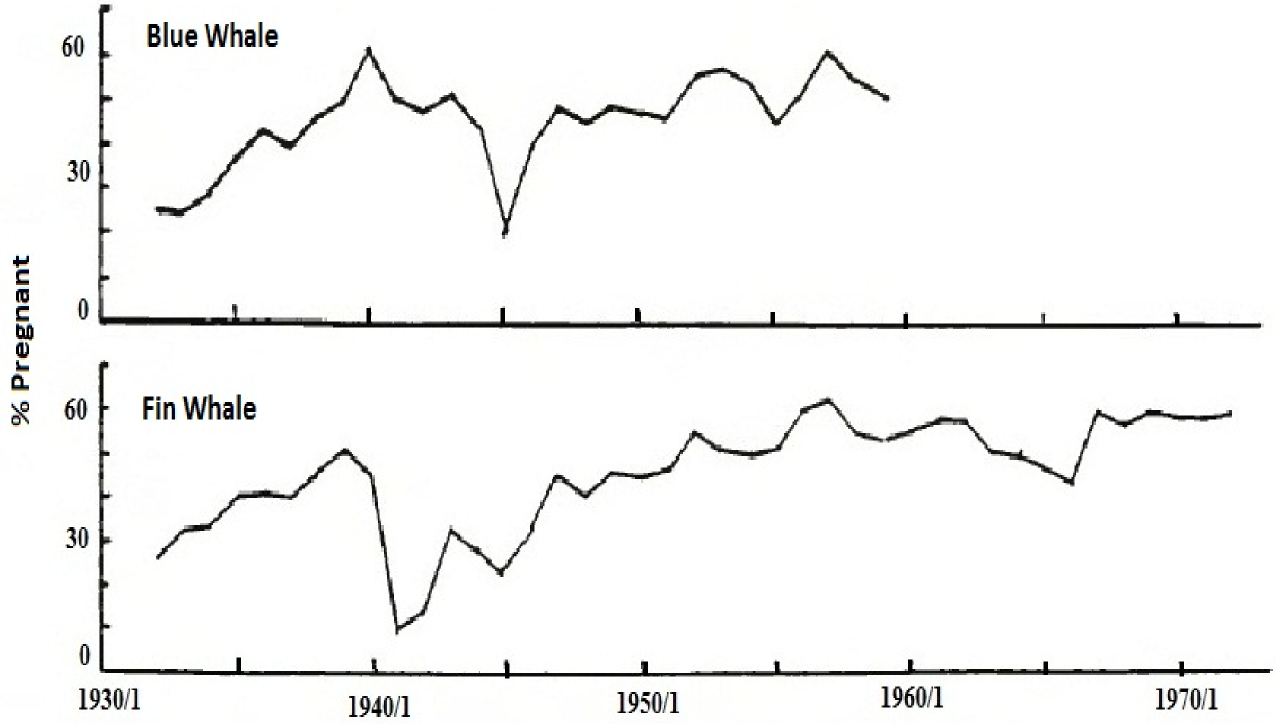

Figure 8.4: Graph of the blue and fin whale proportion of females pregnant estimates, after Figure 1 from Gambell (1975).

Bando and Hakamada (2015) is used to determine the annual proportion of females pregnant for minke whales. These authors analyse minke samples collected during the 1987/88 - 2004/05 JARPA surveys and the 2005/06 - 2010/11 JARPAII surveys. Two stocks are defined in their paper (see Figure 4.2), which match those defined previously in Punt *et al.* (2013):

Stock I = IWC Areas III-East, IV and V-West and *Stock P* = IWC Areas V-East and VI-West.

A linear regression analysis is applied to the catch year (taken from the JARPAII surveys) and the proportion of pregnant animals among mature females (PPF) (taken from Government of Japan (2005)). The PPF is used as an estimate of the annual proportion of females pregnant for minke whales.

Bando and Hakamada (2015) calculates the PPF of Stock I to be around 0.90 for the JARPAII survey period and around 0.93 when data from JARPA and JARPAII are combined. For Stock P, the PPF is calculated to be around 0.90 for the JARPAII survey period and also when data from JARPA and JARPAII are combined. Using the combined JARPA and JARPAII estimates and taking the average, the annual proportion of females pregnant for minke whales is 0.918, which is the value used in the computations following.

8.3.2 Seals

Knox (2007) uses the results from Bengston and Laws (1984) to conclude that the average proportion pregnant for mature female crabeater seals is 0.90.

Boyd *et al.* (1995) is used to determine the annual proportion of females pregnant for the Antarctic fur seal. Their study is outlined in Section 8.2.2. Boyd *et al.* (1995) assume that female seals which do not give birth or are absent from the study beach are not pregnant. Females that are absent in a particular year, and subsequently do not return to the study beach, are assumed to have died during their first year of absence, i.e. it is assumed that an absence greater than one year indicates that a female has died.

Boyd *et al.* (1995) state that on the study beach, it is possible to identify all fur seal females that are giving birth and to detect all births. The age-specific and inter-annual proportions pregnant are estimated from the number of females known to be alive in year i (or of age k) and are observed to give birth in year $i+1$, as a proportion of the total number. The normal approximation to the binomial distribution is used to provide the confidence interval for the pregnancy proportions.

In this way, Boyd *et al.* (1995) determine that the average (annual) proportion of females pregnant for Antarctic fur seals is 0.70 (SD 0.11) with an inter-annual range of 0.59 - 0.88.

The maximum annual female birth rates, calculated using Equation 8.7, for the krill-predators are summarised in Table 8.3. They are used as starting values for the μ parameter, which is estimated in the model fitting process.

Species	Maximum annual birth rate, μ_j
Blue whale	0.23
Fin whale	0.23
Humpback whale	0.24
Minke whale	0.43
Antarctic fur seal	0.30
Crabeater seal	0.38

Table 8.3: Summary of the maximum annual female birth rates for the main krill-predators.

8.4 Maximum per capita annual krill consumption estimates

To keep information on model parameters together, the results reported previously in Table 4.17 are repeated here in Table 8.4. They are used as starting values for the λ parameter which is estimated in the model fitting process.

Species	Maximum per capita annual krill consumption rate, λ_j (mt)
Blue whale	490.8
Fin whale	310.4
Humpback whale	200.7
Minke whale	63.2
Antarctic fur seal	1.54
Crabeater seal	4.45

Table 8.4: Summary of the maximum annual per capita consumption of krill (mt) for the main krill-predators.

8.5 Intrinsic krill growth rate estimates

A modified version of the age-structured population krill model (Model 2) described in Butterworth *et al.* (1994b) has been used to calculate the intrinsic krill growth rate. The algorithm for Model 2 is outlined in Appendix II in Butterworth *et al.* (1994b) and the equations used to describe the krill dynamics are detailed in Appendix I of the same paper. The model presented in this section was coded in the programming language R (Version 3.2.3). Some definitions from Butterworth *et al.* (1994b) are repeated below. The main equations used in the simulations and the common aspects for both Model 2 and its modified version are detailed in Appendix A, at the end of this chapter.

M	is the effective annual natural mortality rate (effective throughout the year).
F_y	is the effective annual fishing mortality rate.
C_y	is the catch by mass of krill from a cohort, between times t_1 and t_2 during a year, under F_y (Equation A.10).
B_a^+	is the survey estimate of biomass made mid-December and prior to any krill fishing (Equation A.9).
S_l	is the selectivity function that describes the relative likelihood of krill at age a being caught (Equation A.2).
γ	is the multiple of the biomass survey estimate. It specifies the annual catch that can be taken.

The main features of Model 2 and the modified Model 2 implemented in this thesis are outlined below.

1) Model 2

i. M is drawn randomly from a uniform distribution over a specified range.

ii. S_l is non-constant i.e. it varies with length.

iii. The upper bound for F is set to 1.5.

2) Modified model 2

i. Mori (2005) treated the krill harvested by its main predators in the same way as the krill fishery. The Butterworth *et al.* (1994b) krill model included a natural mortality (M) for krill which incorporated predation of krill by its predators. Mori (2005) assumed implicitly that none of the six main krill-predators that were modelled explicitly in her ecosystem model (and caused much of the natural predation on krill) were included in the 'predation' that was being attributed to M.

This was not realistic as the predators that were being modelled explicitly would have contributed a large proportion to the natural mortality of krill (which is estimated from the age distribution of the krill population). However, the equation of the krill dynamics in the ecosystem model explicitly takes predation by the six main predators into account (Equation 10.1). As a result, this thesis assumes that a large proportion of the natural mortality of krill is from the consumption of krill by the main krill-predators. Thus, M is reduced from the M that is estimated from the krill's age-structure to 0.2 so as to take into account only the natural mortality of krill arising from predation of krill by the other krill-predators not considered in the ecosystem model. The value of 0.2 is chosen as it is used frequently in multi-species models as a basal mortality.

ii. S_l is constant (= 1) because the krill predators consume krill of all lengths and ages; though approximate, this is more realistic than basing S_l on the commercial fishery.

iii. The upper bound of F is set to 10. This is done in order to obtain a wider range for the curve relating normalised B_a^+ and normalised C_y,

where

$$\text{Normalised } C_y = \frac{C_y}{C_y \text{ when } \gamma = 0} \qquad \text{Normalised } B_a^+ = \frac{B_a^+}{B_a^+ \text{ when } \gamma = 0} \tag{8.8}$$

The curve relating normalised B_a^+ and normalised C_y is compared to the sustainable yield curve for the Pella-Tomlinson form (see Equation 8.9 below) in Figure 8.5. The sustainable yield (SY) is the annual catch that corresponds to a population's natural growth during that year.

Since the two are equal for sustainable yield levels, the population abundance is kept constant.

$$SY = rN_B\left(1 - \left(\frac{N_B}{K}\right)^u\right) \tag{8.9}$$

where

SY is the normalised sustainable yield (i.e. expressed as a proportion of K - see below),

N_B is the normalised mid-year survey biomass i.e. normalised B_a^+; “biomass” as used here is synonymous with abundance,

r is the intrinsic growth rate of krill,

u is the “degree of compensation” parameter, and

K is the pre-exploitation biomass of krill; it corresponds to the normalised value of B_a^+ when γ equals zero i.e. $K = 1$.

By differentiating Equation 8.9, the following relationships follow:

$$\text{MSYL} = K\left[\frac{1}{1+u}\right]^{\frac{1}{u}} \tag{8.10}$$

$$\text{MSY} = rK\left[\frac{1}{1+u}\right]^{\frac{1}{u}}\left[\frac{u}{1+u}\right] \tag{8.11}$$

$$\text{MSYR} = \frac{\text{MSY}}{\text{MSYL}} = r\left[\frac{u}{1+u}\right] \tag{8.12}$$

where

MSYL is the Maximum Sustainable Yield Level, the horizontal co-ordinate of the maximum point on the N_B vs SY plot. It is the B_a^+ value corresponding to the maximum C_y value, i.e. 0.546.

MSY is the Maximum Sustainable Yield, the vertical co-ordinate of the maximum point on the N_B vs SY plot. It is the maximum value of the normalised C_y values i.e. 0.063.

MSYR is the Maximum Sustainable Rate, the ratio of MSY to MSYL i.e. 0.116.

Equation 8.10 and Equation 8.12 are solved to find u and r respectively, yielding $u = 1.545$ and $r = 0.191$. Thus, the estimate for the intrinsic growth rate of krill for all the Regions analysed is taken to be 0.191.

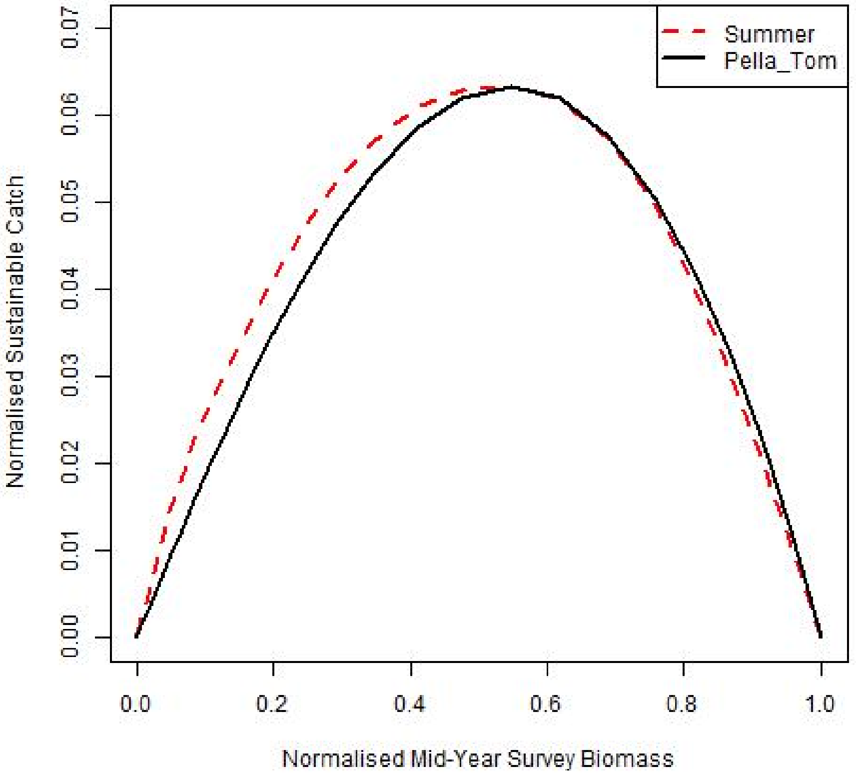

FIGURE 8.5: The normalised sustainable mid-year survey biomass vs the normalised sustainable catch of the age-structured krill model described in Butterworth *et al.* (1994) (dashed) and the sustainable yield curve of the Pella-Tomlinson form (straight) used to approximate it.

8.6 Input parameters

Mori (2005) identifies certain parameters that could not be estimated in the fitting process for the model. These parameters are $\eta^{j,a}$ for the krill-predators j in Region a and $B^{blue,a}$ for Region a (see Table 8.5). These parameters are chosen so that the resultant population trajectories reflect the patterns apparent in the data.

$B^{blue,a}$ is the krill biomass when the consumption, and as a result, the birth rate of blue whales in Region a decreases to half of its maximum level. It is used to calculate the pristine biomass of krill (Equation 10.5 in Chapter 10), which is subsequently used to calculate the $B^{j,a}$ values for the other krill-predators (Equation 10.6).

$\eta^{j,a}$ governs the intra-specific density-dependence of natural mortality and/or birth (and calf -survival) rate for the predator species j in the Region a. This parameter reflects *interference competition*, the competition between two organisms where one physically excludes the other from a region (a portion of habitat), and thus from the resources found in that region. Clapham and Brownell (1996) suggest that there is minimal interference competition between baleen whale species. From Chapter 2, there does not appear to be any interference competition between the fur and crabeater seals.

However, it is difficult to interpret η. As a result, the equations are rewritten in terms of a new parameter labeled α. Consider the mortality term of the krill-predators from Equation 10.2 in Chapter 10 (written in general terms):

$$\begin{aligned} -MN - \eta N^2 &= -MN\left[1 + \frac{\eta}{M}N\right] \\ &= -MN\left[1 + \frac{\eta \cdot N_{1780}}{M}\frac{N}{N_{1780}}\right] \\ &= -MN\left[1 + \alpha\frac{N}{N_{1780}}\right] \end{aligned}$$

where

M is the natural annual mortality proportion,

N is the population size and N_{1780} is the population size in the year 1780, and

$\alpha = \dfrac{\eta \cdot N_{1780}}{M}$

The value of α reflects the strength of interference competition. The term $\frac{N}{N_{1780}}$ is expected to lie mostly between 0 and 1. If α is small (i.e. $<< 1$) then $\alpha\frac{N}{N_{1780}}$ is negligible implying that the effect of interference competition is small. However, as α gets closer to 1, $\alpha\frac{N}{N_{1780}}$ becomes appreciable implying that the effect of interference competition is important.

Table 8.5 provides a summary of the input parameter values chosen. The η values have been chosen so that the resultant population trajectories reflect the patterns apparent in the data, as in Mori (2005). Since the corresponding α values depend on subsequent estimates of N_{1780}, these values are reported in Chapter 11.

Parameter	Region AI	Region PO
η^b (blue)	4.001×10^{-8}	1.000×10^{-6}
η^m (minke)	3.000×10^{-7}	2.000×10^{-7}
η^f (fin)	3.999×10^{-8}	7.000×10^{-8}
η^h (humpback)	1.249×10^{-6}	1.500×10^{-6}
η^s (Antarctic fur)	3.200×10^{-9}	-
η^c (crabeater)	7.001×10^{-9}	7.001×10^{-9}
B^{blue}	1.700×10^{8}	7.000×10^{7}

TABLE 8.5: Summary of the input values for η for the main krill-predators and B^{blue} for both Regions AI and PO.

8.7 Minke stomach fullness data

The values for the estimated average minke whale stomach content weights for each year used in this thesis correspond to the selected fits to the original data reported in Konishi *et al.* (2014). The analysis in that reference provides only the estimates of the slope of the regressions against year. The corresponding annual values from that analysis which are used in this thesis were kindly provided by Dr. Kenji Konishi from the Institute of Cetacean Research, Japan and Prof. Lars Walløe from the University of Oslo, Norway. These values are listed in Table 8.6 below. Chapter 11 details how these data are used in the ecosystem model developed in this thesis.

Year	Region AI	Region PO
1990	-	25.82
1991	22.64	-
1992	-	35.19
1993	39.90	-
1994	-	28.40
1995	34.55	-
1996	-	48.21
1997	35.41	-
1998	-	33.66
1999	42.26	-
2000	-	24.02
2001	17.56	-
2002	-	40.68
2003	23.22	-
2004	-	23.37
2005	12.72	19.79
2006	-	40.44
2007	15.02	6.51
2008	-	38.57
2009	20.88	25.14
2010	-	20.73

Table 8.6: List of the average weight of prey in the stomachs of minke whales (Q_y) for Regions AI and PO (see text regarding the source of these values).

8.8 Parameter bound ranges

Initially, all the above parameters were fixed to their calculated values. However, the model was unable to fit the data satisfactorily, so these parameters were all made estimable. Mori (2005) fixed some of these estimable parameters (namely λ^f, μ^h and μ^f) to assist in her model fit. The parameters fixed in this thesis so as to assist in the model fit are λ_h and M_h (see more in Chapter 11).

The bounds for the number of predator species j in Region a in the year 1780 ($N^{j,a}_{1780}$) are kept the same as in Mori (2005) as these values appear to be reasonable. Using the starting values for each of the other parameters (calculated in the sections above), if they were found to be within the parameter bounds as defined in Mori (2005), the same bounds were kept. If a parameter's starting value was found to be outside the range defined in Mori (2005), the bounds were re-calculated as follows, this being a rough approximation to ensure consistency throughout the model:

$$\frac{\text{Maximum Bound}}{\text{Starting Estimate}} = \frac{\text{Starting Estimate}}{\text{Minimum Bound}} = 3$$

The bounds for the estimated parameters are summarised in Table 8.7 below. Italicised values are from Mori (2005) and bold values are as obtained in the relevant sections above.

Estimable Parameter	Description	Estimate	Minimum bound	Maximum bound
$N^{b,AI}_{1780}$	Number of blue whales in Region AI in the year 1780	-	*100 000*	*300 000*
$N^{b,PO}_{1780}$	Number of blue whales in Region PO in the year 1780	-	*10 000*	*100 000*
$N^{f,AI}_{1780}$	Number of fin whales in Region AI in the year 1780	-	*10 000*	*400 000*
$N^{f,PO}_{1780}$	Number of fin whales in Region PO in the year 1780	-	*10 000*	*200 000*
$N^{h,AI}_{1780}$	Number of humpback whales in Region AI in the year 1780	-	*10 000*	*250 000*
$N^{h,PO}_{1780}$	Number of humpback whales in Region PO in the year 1780	-	*10 000*	*100 000*
$N^{m,AI}_{1780}$	Number of minke whales in Region AI in the year 1780	-	*10 000*	*200 000*
$N^{m,PO}_{1780}$	Number of minke whales in Region PO in the year 1780	-	*100 000*	*300 000*
$N^{s,AI}_{1780}$	Number of Antarctic fur seals in Region AI in the year 1780	-	*500 000*	*5 000 000*

Table 8.7 – continued from the previous page

Estimable Parameter	Description	Estimate	Minimum bound	Maximum bound
$N_{1780}^{c,AI}$	Number of crabeater seals in Region AI in the year 1780	-	*100 000*	*10 000 000*
$N_{1780}^{c,PO}$	Number of crabeater seals in Region PO in the year 1780	-	*100 000*	*10 000 000*
M_b	Annual mortality proportion for blue whales	0.03	*0.03*	*0.06*
M_f	Annual mortality proportion for fin whales	0.03	*0.03*	*0.05*
M_h	Annual mortality proportion for humpback whales	0.03	*0.03*	*0.08*
M_m	Annual mortality rate for minke whales	0.063	0.04	0.1
M_s	Annual mortality proportion for Antarctic fur seals	0.17	**0.07**	**0.35**
M_c	Annual mortality proportion for crabeater seals	0.17	**0.07**	**0.35**
μ_b	Maximum annual female birth rate for blue whales	0.23	**0.1**	**0.29**
μ_f	Maximum annual female birth rate for fin whales	0.23	**0.05**	**0.29**
μ_h	Maximum annual female birth rate for humpback whales	0.24	0.08	0.72
μ_m	Maximum annual female birth rate for minke whales	0.43	0.14	1.30
μ_s	Maximum annual female birth rate for Antarctic fur seals	0.295	0.10	0.89
μ_c	Maximum annual female birth rate for crabeater seals	0.38	0.13	1.14
λ_b	Maximum annual per capita consumption of krill by blue whales	490.8	163.57	1 472.4
λ_f	Maximum annual per capita consumption of krill by fin whales	310.4	103.45	931.2
λ_h	Maximum annual per capita consumption of krill by humpback whales	200.7	66.88	602.1
λ_m	Maximum annual per capita consumption of krill by minke whales	63.2	21.06	189.6
λ_s	Maximum annual per capita consumption of krill by Antarctic fur seals	1.54	*0.68*	*2.71*

Table 8.7 – continued from the previous page

Estimable Parameter	Description	Estimate	Minimum bound	Maximum bound
λ_c	Maximum annual per capita consumption of krill by crabeater seals	4.45	*3.31*	*5.51*
r^A	Intrinsic growth rate of krill in Region AI	0.19	0.06	*0.60*
r^P	Intrinsic growth rate of krill in Region PO	0.19	0.06	*0.60*

Table 8.7: Summary of the plausible bounds for the estimable parameters which are used in fitting the model.

8.9 Summary

This chapter discussed how the input parameter values, and bounds on the values for the estimable parameters of the model, were calculated or chosen.

The bound calculated for the annual natural mortality proportions (M_j) for minke whales, crabeater seals and Antarctic fur seals differs to that in Mori (2005). Different sources, methodologies and assumptions are the causes of these differences. Similarly, the bound for the maximum product of the annual birth rate and the first-year calf-survival proportion (μ_j) for all the predator species differs to that in Mori (2005). The bound for the maximum annual per capita krill consumption rate (λ_j) is different for the whale species only (blue, fin, humpback and minke whales), compared to what was calculated in Mori (2005). The parameters fixed in this thesis in order to assist in the model fit are λ_h and M_h.

Of the estimable parameters, the one that changed appreciably to that reported in Mori (2005) is the intrinsic krill growth rate (r^a). The most important change in its calculation is in the specification of M, the effective annual natural mortality rate for krill (effective throughout the year). This thesis assumes that a large proportion of the krill's natural mortality is from the consumption of krill by its main predators. Thus M is reduced to 0.2, chosen as it is used frequently in multi-species models as a basal mortality. This is done in order to take into account the natural mortality of krill arising only from the predation of krill by the other krill-predators not considered in the ecosystem model. This in turn results in a smaller lower bound compared to Mori (2005).

The average annual weight of prey contents in the stomachs of minke whales for the years for which such data are available in Region a (Q^a_y) is also introduced in this chapter.

Chapter 11 demonstrates how all of these input and estimable parameters are incorporated in the model developed in this thesis.

Appendix A

Krill Equations from Butterworth *et al.* (1994b)

For Model 2, the numbers of krill of age a years at the start of year y ($N_{y,a}$) are governed by:

$$N_{y+1,\, a+1} = N_{y,a}\, e^{-(M+S_a F_y)} \quad \text{for } 0 \leqslant a \leqslant 7 \tag{A.1}$$

where M is the natural mortality rate (effective throughout the year), F_y is the effective annual fishing mortality rate in year y, a is the (knife-edge) age-at-first-capture and S_a is the krill selectivity-at-age. It is assumed that the number of krill eight years of age and older is relatively small, and hence can be neglected.

The selectivity-at-age for krill describes the relative likelihood of krill at age a being caught:

$$S_l = \begin{cases} 0, \quad \text{for } l < l_1 = l_{50} \text{ - } \dfrac{w_r}{2} \\ \dfrac{(l-l_1)}{(l_2-l_1)}, \quad \text{for } l_1 \leqslant l \leqslant l_2 \\ 1, \quad \text{for } l > l_2 = l_{50} + \dfrac{w_r}{2} \end{cases} \tag{A.2}$$

where $l_{50} \sim$ U[38,42] and w_r = 10mm.

Krill lengths can be converted into ages using the Rosenberg *et al.* (1986) growth curves:

$$l_{a,t} = \begin{cases} L_\infty\Big[1 - e^{-\beta(a+\,4t)}\Big], \quad \text{for } 0 \leqslant t \leqslant \dfrac{3}{12} \\ L_\infty\Big[1 - e^{-\beta(a+\,1)}\Big], \quad \text{for } \dfrac{3}{12} \leqslant t \leqslant 1 \end{cases} \tag{A.3}$$

where l_∞ = 60mm, a is the age of the krill (years), t measures time after the ‘start’ of the year and $\beta = 0.45\ yr^{-1}$. It is assumed that krill grow from November till January. Thus, the ‘start’ of the year is taken to be 1st November.

The number of krill recruits at the start of year ($N_{y,0}$) is given by Equation A.4, provided that the krill spawning biomass (B^{sp}) is greater than 20% of its median value in the absence of exploitation (K^{sp}).

$$N_{y,0} = \begin{cases} N_{y,0} = R\, e^{\varepsilon_y - \frac{\sigma_R^2}{2}} & \text{for } B_y^{sp} \geqslant 0.2\ K^{sp} \\ N_{y,0} = \left[\dfrac{B_y^{sp}}{0.2K^{sp}}\right] R\, e^{\varepsilon_y - \frac{\sigma_R^2}{2}} & \text{for } B_y^{sp} < 0.2\ K^{sp} \end{cases} \tag{A.4}$$

where $\varepsilon_y \sim \mathrm{N}(0,\, \sigma_R^2)$, R is the mean recruitment and $\sigma_R \sim \mathrm{U}[0.4,\, 0.6]$ is the recruitment variability.

The krill spawning biomass is considered to be the average biomass of mature krill in the presence of an annual krill catch, over the December - March period i.e. the austral summer fishing season.

$$\begin{aligned} B_y^{sp} &= 3\alpha \sum_{a=0}^{7} N_{y,a} \\ \times &\left\{ \begin{aligned} &\bar{P}_a \sum_{\mu=0}^{3} \gamma(\mu) e^{-\mu\beta a} e^{-(M+\, 4\mu\beta)/12} \left[1 - e^{-\left(M+\, 4\bar{S}_a F_y +\, 4\mu\beta\right)(2/12)}\right] \Big/ \left[M +\, 4\bar{S}_a F_y +\, 4\mu\beta\right] \\ &+ P_{a+1}\left[1 - e^{-\beta(a+1)}\right]^3 e^{-\left(M(3/12)+\, 4\bar{S}_a F_y(2/12)\right)} \left[1 - e^{-(M+\, 4S_{a+1}F_y)/12}\right] \Big/ \left[M + 4S_{a+1}F_y\right] \\ &+ P_{a+1}\left[1 - e^{-\beta(a+1)}\right]^3 e^{-\left(M(4/12)+\, 4\bar{S}_a F_y(2/12)+\, 4S_{a+1}F_y(1/12)\right)} \left[1 - e^{-M/12}\right] \Big/ M \end{aligned} \right\} \end{aligned} \tag{A.5}$$

where $\bar{S}_a$ is assumed to equal the selectivity corresponding to the average length of krill of age a during the December - January fishing period and $\bar{P}_a$ is assumed to equal the proportion of krill aged a which matures at a length which is the average of that over the December - January spawning season.

K^{sp} or the median value of the krill spawning biomass (B_y^{sp}) in the absence of exploitation is given by the following equation:

$$\begin{aligned} K^{sp} &= 3\alpha \sum_{a=0}^{7} R\, e^{-\sigma_R^2/2}\ e^{-Ma} \\ \times &\left\{ \begin{aligned} &\bar{P}_a \sum_{\mu=0}^{3} \gamma(\mu) e^{-\mu\beta a} e^{-(M+\, 4\mu\beta)/12} \left[1 - e^{-\left(M+\, 4\mu\beta\right)(2/12)}\right] \Big/ \left[M +\, 4\mu\beta\right] \\ &+ P_{a+1}\left[1 - e^{-\beta(a+1)}\right]^3 e^{-\left(M(3/12)\right)} \left[1 - e^{-M(2/12)}\right] \Big/ M \end{aligned} \right\} \end{aligned} \tag{A.6}$$

The mass-at-age of krill is obtained from the Rosenberg *et al.* (1986) growth curves combined with the assumption that the krill's mass is proportional to its length cubed.

The mass of krill at age a at the 'start' of the year is:

$$w_a = \alpha\left[1 - e^{-\beta a}\right]^3 \quad \text{where } \beta = 0.45\ \mathrm{yr}^{-1} \tag{A.7}$$

The krill mass-at-age in the middle of the krill growth season is given by:

$$\bar{w}_a = \alpha \left[1 - e^{-\beta(a+1)} \right]^3 \tag{A.8}$$

The survey biomass estimate is estimated in the middle of the krill growth season i.e. mid-December, and before the fishing of krill has occurred. It is defined in Equation A.9.

$$B_y^{a+} = \sum_{a=a+}^{7} \bar{w}_a \; N_{y,a} \; e^{-M(1.5/12)} \quad \text{where } y \text{ is the survey year, prior to fishing.} \tag{A.9}$$

The catch by mass of krill during a year y, between fishing season times t_1 and t_2 (in this case, the summer fishing season), under annual fishing mortality F_y is given by:

$$\begin{aligned} C_y = 4F_y \; \alpha \sum_{a=0}^{7} N_{y,a} \\ \times \left\{ \begin{array}{l} \quad \bar{S}_a \displaystyle\sum_{\mu=0}^{3} \gamma(\mu) e^{-\mu\beta a} e^{-(M+\,4\mu\beta)/12} \left[1 - e^{-\left(M+\,4\bar{S}_a F_y +\,4\mu\beta\right)(2/12)} \right] \Big/ \left[M +\; 4\bar{S}_a F_y +\; 4\mu\beta \right] \\ + S_{a+1} \left[1 - e^{-\beta(a+1)} \right]^3 e^{-\left(M(3/12) +\,4\bar{S}_a F_y (2/12)\right)} \left[1 - e^{-(M+\,4S_{a+1}F_y)/12} \right] \Big/ \left[M + 4S_{a+1} F_y \right] \end{array} \right\} \end{aligned} \tag{A.10}$$

As part of the refinements outlined in SC-CAMLR (1992), a realistic limit is placed on the proportion of the recruited krill biomass which can be harvested in any year. This is implemented by placing an upper bound on F_y. If the specified fixed catch cannot be calculated by an F_y value that is less than its upper bound, then the C_y value for that year is calculated using an F_y that equals the upper bound.

The production term ($\tilde{P}$) is the sum of the increase in biomass, the catch made by the fishery and the loss of krill to its natural predators i.e:

$$\tilde{P} = B_{y+1} - B_y + C_y + P_y^r \tag{A.11}$$

The krill biomass at the "start" of year y (B_y) is given by:

$$B_y = \sum_{a=0}^{7} w_a \; N_{y,a} \tag{A.12}$$

Finally, the amount of krill lost to predation (P_y^r) over the summer fishing season is given by:

$$
\begin{aligned}
P_y^r = M\alpha \sum_{a=0}^{7} N_{y,a} \qquad\qquad\qquad\qquad (A.13)\\
\times \left\{
\begin{array}{r}
\displaystyle\sum_{\mu=0}^{3} \gamma(\mu) e^{-\mu\beta a}\left[1-e^{-\left(M+\,4\mu\beta\right)/12}\right]\Big/\left[M+\;4\mu\beta\right]\\
\displaystyle+\sum_{\mu=0}^{3} \gamma(\mu) e^{-\mu\beta a} e^{-(M+\,4\mu\beta)/12}\left[1-e^{-\left(M+\,4\bar{S}_a F_y+\,4\mu\beta\right)(2/12)}\right]\Big/\left[M+\;4\bar{S}_a F_y+\;4\mu\beta\right]\\
\displaystyle+\left[1-e^{-\beta(a+1)}\right]^{3} e^{-\left(M(3/12)+\,4\bar{S}_a F_y(2/12)\right)}\left[1-e^{-(M+\,4S_{a+1}F_y)/12}\right]\Big/\left[M+4S_{a+1}F_y\right]\\
\displaystyle+\left[1-e^{-\beta(a+1)}\right]^{3} e^{-\left(M(4/12)+\,4\bar{S}_a F_y(2/12)+\,4S_{a+1}F_y(1/12)\right)}\left[1-e^{-M(8/12)}\right]\Big/M
\end{array}
\right\} +\; w_8\; N_{y+1,8}
\end{aligned}
$$

The final term in this equation takes into account the “neglected” krill of eight years of age and older, as is implicit in Equation A.1.

Some of the common aspects for both Model 2 and its modified version used in this thesis are outlined below.

i. The krill growth season starts on the 1st November. During the February fishing period, the krill stops growing. This impacts the selectivity function and the length function.

ii. The number of krill aged eight and older are assumed to be relatively small. Thus, they can be neglected.

iii. Recruitment is independent of the spawning biomass provided that the spawning biomass is above a certain threshold i.e. $B_y^{sp} \geqslant 0.2\ K^{sp}$.

iv. A realistic limit is placed on the proportion of recruited biomass which can be harvested in any year. This was implemented by placing an upper bound on F_y. The value for F_y is found as stated in Appendix II in Butterworth *et al.* (1994b). If a value for F_y is greater than this upper bound, the value for F_y is equal to the upper bound.

v. The summer fishery operates from December till February. The winter fishery operates from April till September. The summer fishing period is used in this analysis as whales feed in the Antarctic during the austral summer.

vi. The value of γ is chosen at the start. For each new value of γ, 1000 simulations are run. The same random numbers are used for each simulation for the different γ values.

vii. The last 10 values of C_y, B_a^+, B_y^{sp}, P_y^r, B_y and $\tilde{P}$ are stored after each simulation.

Chapter 9

Hypothesized causes of the population changes of the krill-feeding predators

9.1 Overview of Chapter

By the start of the 19th century, Antarctic fur seals had been reduced close to extinction through human harvesting. In the first half of the 20th century, large baleen whales such as the blue, fin and humpbacks were harvested heavily as well, some close to extinction. Mori (2005) mentions that several studies indicated an increase in abundance in minke whales (a more recent example is Punt *et al.* (2013)), Antarctic fur seals and crabeater seals during this "large baleen whale depletion" period. The "krill-surplus" hypothesis of Laws (1977, 1962) explains this as the result of competitive release of the minke whale and seal populations through a reduction in the consumption and consequently, the increase in abundance of krill, upon which all these species depend, through the depletion of the larger baleen whale species.

During the mid-1960s to the mid-1970s, the large baleen whale species harvested previously came under protection. Some subsequent studies have indicated that more recently they show signs of recovery. Consequently, increases in minke whales (and possibly crabeater seals) may have reversed since about 1970 as suggested in Punt (2014). This is co-incident with the recovery of the large baleen whales which have been indicated by some studies (Mori, 2005).

This chapter discusses some of the hypothesised causes of these (long-term) population changes of krill and its main predators.

9.2 Laws' ***Krill Surplus*** hypothesis

Laws (1977) estimated the annual krill consumption by the baleen whales in the Antarctic before and after their heavy depletion (see Table 9.1). Following the exploitation of the large baleen whales and due to the fact that krill is essentially their only prey item, Laws (1977, 1962) calculated that roughly 150 million tonnes of "surplus" krill (surplus annual production of krill) became available to other krill-feeding predators such as minke whales, crabeater and fur seals and some penguin species. This became known as Laws' *krill surplus* hypothesis. Coarse estimates, available at that time, of the population sizes of the baleen whales and their mean body weights were used to compute the 150 million tonnes. Furthermore, Laws (1977) assumed that the krill consumption by the baleen whales was roughly 3 - 4% of their body mass per day.

Mori (2005) comments that the timing of the changes in population trends and biological parameters of minke whales, crabeater seals and Antarctic fur seals corresponds well with the "large baleen whale depletion" period. Furthermore, other krill-predators such as the Adélie and macaroni penguins also increased between the 1950s and 1970s (Croxall *et al.*, 2002; Croxall, 1992). Croxall *et al.* (2002) state that the Adélie penguins around West Antarctica, the Antarctic Peninsula and the associated island groups (see Figure 6.3) increased substantially during this period but then decreased or stabilised subsequently in the 1980s and 1990s. Croxall (1992) mentions that during the late 1970s, the macaroni penguins at South Georgia decreased by roughly 50% over five years, but have remained stable subsequently. However, macaroni penguins are less dependent on krill than Adélie penguins.

Mori (2005) concludes that since there is no obvious cause that could have led to increases in the other krill-feeding predators (minke whales, crabeater seals and Antarctic fur seals) during the early to the mid-20th century, Laws' hypothesis is certainly plausible. This is confirmed further by Surma *et al.* (2014) whose study concludes that Laws' "krill surplus" hypothesis is a plausible explanation for the biomass trends observed in some penguin and seal populations during the mid-20th century. However, their study suggests that the "krill surplus" was moderate and relatively short-lived, suggesting that the "krill surplus" period may have ended in the last quarter of the 20th century.

Reid and Croxall (2001) examined the diet of krill-feeding predators, their population sizes and reproductive success. They analysed Antarctic fur seals, gentoo penguins, macaroni penguins and black-browed albatrosses around South Georgia from 1980 until 2000. Both the population size and reproductive performance indices showed a decrease for all the species analysed. The same indices also showed an increase in the frequency of years where the species analysed were reproductively unsuccessful. By examining the krill length-frequency distributions (excluding the krill consumed by the black-browed alabatross), the authors found significant differences in the krill length-frequency distributions in the seal and penguin diet between 1980-1990 and 1991-2000. During the earlier period, the dominant modal size of krill consumed by the predators was 54-56 mm, but during the later period the mode decreased to 42-44 mm with only a small proportion of krill belonging to the larger size classes. Reid and Croxall (2001) inferred that changes in the krill's population structure and its relationship to reproductive performance suggested that the krill biomass in the larger size classes was sufficient to support predator demand in the 1980s but not in the 1990s. This suggests that the period of the "krill-surplus" may have ended by that time.

Since Mori (2005), several studies have put forward other explanations for the increase in the other krill-predators, and the later decrease in krill following the depletion of the large baleen whales. As mentioned in Chapter 1, Nicol *et al.* (2010) and Smetacek (2008) hypothesised that baleen whales recycled iron contained in krill, and dispersed this nutrient down the water column in the form of faeces. The iron fertilized diatom blooms and promoted primary productivity. This enhanced primary productivity resulted in an increase in krill abundance, which sustained the ecosystem's high carrying capacity for the large baleen whales. These authors argued that as a result of the extensive harvests of the large baleen whales, this positive feedback process collapsed, causing a decrease in primary production and krill abundance, and the subsequent slow recovery of the large baleen whales. Though not stated explicitly, their work implies that the krill available then was sufficient to allow increases in the other krill-feeding predators such as seals and penguins.

9.3 Effects of environmental change

Since Mori (2005) there have been several studies providing evidence of environmental change in the Antarctic, and discussing its impact on the species found in the region. Nicol (2006) mentions that krill have a life cycle that is closely attuned and adapted to its physical environment. The fastest rates of ocean warming and sea-ice loss are found in the southwest Atlantic sector of the Antarctic - the main nurseries and feeding grounds of krill (Flores *et al.*, 2012).

Flores *et al.* (2012) review the overall impact of climate change on the Antarctic ecosystem, particularly on krill. Krill abundance, their distribution and life cycle are impacted by sea-ice changes, ocean warming, wind circulation changes, UV radiation and ocean acidification - the main concerns that arise from environment change. These concerns are discussed below. They are the manifestations of the post 19th century human-induced carbon dioxide (CO_2) surplus, termed 'climate change' (IPCC, 2007).

9.3.1 Changes in sea-ice habitats

Over the past few decades, there has been considerable regional variability in sea-ice coverage. Between 1979 and 2008, the average monthly sea-ice extent of the western Antarctic Peninsula region (see Figure 6.3) has been decreasing at a rate of 7% per decade. However, there has also been an increase in the average monthly sea-ice extent in the Ross Sea of roughly 5% per decade over the same period (Turner *et al.*, 2009b; Stammerjohn *et al.*, 2008; see Figure 9.1).

Ecologically speaking, sea-ice duration and thickness may be of more importance than the overall sea-ice coverage. Between 1979 and 2004, the sea-ice season in the southern Bellinghausen Sea and the western Antarctic Peninsula region (see Figure 6.3) has shortened by 85 days (a rate of about 38 days per decade) - a trend consistent with increasing sea-surface temperatures and decreasing sea-ice coverage in the region (Turner *et al.*, 2009b; Stammerjohn *et al.*, 2008; Parkinson, 2004). However, in other regions such as the Ross Sea, the sea-ice season has lengthened at a rate of roughly 23 days per decade over the same time period. This has been associated with the observed overall increase of the sea-ice extent in the region (Stammerjohn *et al.*, 2008; Parkinson, 2004).

Worby *et al.* (2008) provide average Antarctic circumpolar ice thickness estimates for the period between 1981 and 2005. Their analysis reveals that the western Weddell Sea (45°W - 60°W; see Figure 6.3) has the highest average annual ice thickness and the highest ice thickness variability, when compared to other regions in the Antarctic. This region is abundant in krill and is a key krill fishing area, suggesting that the krill fishery may be impacted by changes in sea-ice coverage (Flores *et al.*, 2012). Coupled ice-ocean-atmosphere models predict a 33% decline in the overall winter sea-ice coverage by the end of the 21st century as climate change induced warming continues (Bracegirdle *et al.*, 2008); this may impact the krill fishery as detailed below.

Krill depend on sea-ice throughout their life. There is a known positive relationship between krill abundance and the winter sea-ice extent (Atkinson *et al.*, 2004). Larval and juvenile krill do not have the ability to store energy from food consumed during the pre-winter phytoplankton blooms. As a result, during winter, they use the sea-ice as a food source (Atkinson *et al.*, 2004; 2002). Ice algae congregate under the sea-ice during the winter months. They are energy-rich as they are most productive during the austral spring/summer, before the onset of winter (Daly, 2004; Meyer *et al.*, 2009; 2002). Furthermore, the sea-ice is a suitable habitat for the larval krill, protecting them from predators and providing favourable conditions for their continued growth. The breaking-off of sections of sea-ice and their consequent movement transports developing krill juveniles from the grounds where they were spawned to nutrient-rich waters such as around South Georgia (Meyer *et al.*, 2009; Thorpe *et al.*, 2007; Fach *et al.*, 2006; Fach and Klinck, 2006). Changes in the duration of the sea-ice period impact the larval krill heavily, as the timing of the sea-ice formation determines the amount of food available in the winter sea-ice. If the duration is too short, phytoplankton blooms will be affected, and as a result less food will be available for the larval krill. The areas of the fastest loss of sea-ice such as the southern Scotia and Bellingshausen Seas (see Figure 6.3) are also important krill spawning grounds (Schmidt *et al.*, 2012; Hofmann and Hüsrevoğlu, 2003). As a result, krill spawning grounds may shift southwards, bounded by the Antarctic shelf, as climate warming continues. Overall, krill recruitment is likely to be impacted heavily by the decrease in sea-ice (Flores *et al.*, 2012).

Post-larval krill are able to survive the austral winter by a number of mechanisms, namely: reducing their metabolism, shrinking in size and consuming other food sources such as zooplankton, ice algae and sea-bed detritus (Schmidt *et al.*, 2011; Meyer *et al.*, 2010; Kawaguchi *et al.*, 1986). In the summer, when the sea-ice melts, it releases ice algae and nutrients into the surrounding waters causing intense phytoplankton blooms. These blooms play an important role as a summer food source for krill, and consequently for its predators (Perissinotto *et al.*, 1997; Hempel, 1985). Due to climate change, the melting sea-ice phytoplankton blooms are likely to decrease and/or possibly shift southwards. A southward shift may reduce ice algae productivity as there is little light available close to the Antarctic shelf (Flores *et al.*, 2012).

Changes in sea-ice coverage also affect the predators of krill, and not only through the availability of krill. Some of the largest Adélie penguin colonies lie in the Ross Sea (see Figure 6.3) where sea-ice extent and duration have increased substantially over the last 40 years (Stammerjohn *et al.*, 2012). As a result, Lynch and LaRue (2014) deduce that sea-ice plays an important role in the abundance and distribution of Adélie penguins. Beekmans *et al.* (2010) infer that pack-ice* quality and quantity may affect minke whale distributions in waters close to the pack-ice edge. Antarctic minke whales may move more easily into the pack-ice in years when the pack-ice has more cracks and is diverse in quality. Similarly, the whales' movement may be restricted to the open waters near the pack-ice edge in the years when the pack-ice is more solid close to the edge (see Chapter 5, Section 5.5.1 for more on minke whales in the pack-ice). Thus, changes in sea-ice coverage can affect the distributions of the krill-predators such as Adélie penguins and minke whales.

9.3.2 Increases in sea-surface temperatures

The ocean has a greater heat capacity compared to the atmosphere and land, storing roughly 80% of the Earth's thermal energy. Due to its heat capacity and vastness, the ocean absorbs much of the increased heat caused by climate change, mitigating the effects of climate change on society (from *https://www.ipcc.ch/publications_and_data/ar4/wg1/en/ch5s5-1.html* [Accessed 18/06/2017]).

Gille (2002) states that from the 1950s to the 1980s, the Southern Ocean mid-depth waters have increased in temperature by 0.17°C. Between 1951 and 1998, surface waters west of the Antarctic Peninsula have increased by more than 1°C due to vertical mixing (Meredith and King, 2005). Furthermore, over the past 80 years, the average temperature of the top 100m surface waters at South Georgia has increased by 0.9°C and 2.3°C in January and August respectively (Whitehouse *et al.*, 2008). Turner *et al.* (2009a) predict that in 2100, sea-surface temperatures south of 60°S are likely to be 0.5°C - 1.2°C warmer than at present. Regional variability exists in the predictions for winter sea-surface temperatures, with temperatures either being around 1°C warmer or -0.25°C cooler than they are at present. Furthermore, appreciable warming (between 0.75°C - 2.0°C, regardless of season) is predicted in the surface waters of 40°S - 60°S, the core location of the Antarctic Circumpolar Current (ACC; see Glossary). Even the bottom waters along the continental margin are predicted to increase in temperature by roughly 0.25°C.

Krill are marine organisms that live in polar waters. They are stenotherms that are adapted to low stable temperatures. Changes in sea temperatures by 1 - 2°C are likely to impact krill, given that there is roughly a 7°C difference between the coldest and warmest krill habitats (Flores *et al.*, 2012). South Georgia, at present, is the "warmest" northernmost krill habitat (Schmidt *et al.*, 2011). It is possible that krill are able to tolerate temperature changes over short time scales as pertain to the El-Niño Southern Oscillation (ENSO; see Glossary), but temperatures greater than 3.5°C over a longer term might strain them physiologically, especially krill juveniles (Hirche, 1984; McWhinnie and Marciniak, 1964). As a result, krill distributions may shift further southwards

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*The term *pack-ice* is used interchangeably with *sea-ice*. However, the same meaning is implied as pack-ice is simply, sea-ice "packed" together.

to colder waters, affecting the krill fisheries (access to the more southern regions of the Antarctic will be more expensive and may prove difficult) and krill-predators i.e. having to travel further to replenish their energy levels after their winter fast.

On the other hand, ocean warming may have some positive impacts on krill. Adult krill might increase their metabolic rates, and hence might be able to take better advantage of the available food resulting in faster growth. Increases in water temperature may also affect krill behaviour; krill can avoid the warm surface waters, and feed in waters at depth and at the sea floor (Schmidt *et al.*, 2011). Behaviour like this can affect the air-breathing krill-predators that cannot penetrate that far deep.

Overall, the warming of the surface sea waters and the decline in sea-ice impacts krill negatively. In contrast, they affect the salp populations (see Glossary) positively. Salps are marine invertebrates found mostly in the Southern Ocean. They feed on phytoplankton and thus compete with krill for this resource. They have increased in number, south of the southern ACC front, over the last 80 years. This is thought to be due to the decrease in sea-ice coverage (Clarke and Harris, 2003), warmer sea-surface temperatures (Atkinson *et al.*, 2004; Pakhomov *et al.*, 2002) and the low krill abundance. Salps are not considered further in this thesis - they are discussed here only to highlight some of the ‘positive’ impacts of climate change (manifested through the increase in sea-surface temperatures).

Ocean warming affects krill both positively and negatively, depending on the region and the krill life stage (Flores *et al.*, 2012).

9.3.3 Changes in circulatory patterns

The ozone layer in the Earth’s stratosphere absorbs ultraviolet (UV) light that is discharged by the Sun, protecting all life on Earth. However, in the early 1980s, this layer began to thin, forming a “hole” over the South Pole. The “ozone hole” grew rapidly in size and depth from the 1980s until the early 1990s. Chlorofluorocarbons (CFCs) are chemicals that had been used in refrigerators and aerosol sprays since the 1930s. Since these chemicals are long-lived, they are circulated in the troposphere for decades without degrading or reacting with other chemicals. However, when they reach the upper stratosphere, beyond the protection of the ozone layer, UV light causes the CFCs to break apart and release chlorine. The chlorine acts as a catalyst and causes the destruction of the ozone molecule. After recognising the dangers of the excessive use of CFCs, the 1989 Montreal Protocol was established which banned the production of ozone-depleting chemicals (from *http://earthobservatory.nasa.gov/Features/WorldOfChange/ozone.php* [Accessed 15/12/2016]; see Glossary). The ozone depletion has been reversed to some extent. Ozone is predicted to recover to its pre-1980 levels around the year 2060 (Flores *et al.*, 2012).

The Antarctic ozone depletion has caused an increase in westerly winds. These winds contribute to a positive phase of the Southern Annular Mode (SAM) (Lovenduski and Gruber, 2008; Cai, 2006; see Glossary). This increase in the positive phase of SAM has led to an increase in poleward heat transport through the upwelling of the Circumpolar Deep Water (CDW) and the southward displacement of the fronts associated with the ACC (Gille, 2002; see Glossary). Furthermore, global climate patterns such as ENSO are influenced by this increase in westerly winds (Harangozo, 2006; Turner *et al.*, 2005). Altogether, these factors are largely responsible for the changes in circulation patterns which have an impact, both negative and positive, on krill growth, survival and recruitment.

Flores *et al.* (2012) state that the increase in westerlies and stronger ENSO events may increase the connectivity between krill populations, causing better nutrient advection and increasing krill larvae transport into krill feeding grounds. This will affect krill positively. In contrast, changes in ocean mixing and circulation due to the increased westerlies may change phytoplankton productivity and composition. This in turn will reduce the availability of food for krill, making the surrounding water conditions unfavourable for krill larvae. Changes in heat flux and eddy energy can affect the mixed layer depths and ocean stratification within the ACC (Murphy and Hofmann, 2012; Law *et al.*, 2006; 2003). This can affect the spatial distribution of phytoplankton which can affect krill abundances and distributions.

Which effect prevails is likely to vary depending on the region, local hydrography and local bathymetry. However, Flores *et al.* (2012) state that the consensus is that changes in circulatory patterns do influence the distribution and abundance of krill and their availability to the krill-predators.

9.3.4 Ocean acidification

The Southern Ocean is the most affected by ocean acidification (OA) due to the high solubilities of CO_2 and $CaCO_3$ in cold waters and the regional upwelling of hypercarbic deep waters (Doney *et al.*, 2009; Sabine *et al.*, 2004; see Glossary). The concentration of CO_2 in the atmosphere has risen from 280 ppm (in the pre-industrial era) to roughly 380 ppm today (Orr *et al.*, 2005). According to all the IPCC (2007) scenarios, atmospheric CO_2 concentrations are projected to increase throughout the 21st century. McNeil and Matear (2008) state that there will be seasonal and regional changes in surface sea-water CO_2 concentrations as climate warming continues.

Such ocean acidification (OA) is likely to have a physiological and biochemical effect on krill (Fabry *et al.*, 2008; Orr *et al.*, 2005). Kawaguchi *et al.* (2011) state that, in general, the partial pressure of CO_2 decreases with depth. As a result, animals like krill which routinely migrate vertically will spend much of their life exposed to higher and more variable levels of OA compared to surface water organisms. High levels of CO_2 (around 2000 μatm) can stop embryonic development of krill and can compromise CO_2 diffusion across gills. This can lead to increased acidity in the haemolymph resulting in physiological adjustments. These adjustments can be expensive metabolically in the long-run (Whiteley, 2011; see Glossary). Dissanayake and Ishimatsu (2011) found that elevated CO_2 concentrations and higher water temperatures compromised the respiratory performance and swimming ability of penaeid shrimps. Krill produce a new exoskeleton regularly throughout their lives. As a result, they are dependent on physiological and chemical processes that allow for the efficient uptake of calcium and other elements from the sea-water in order to form their exoskeleton - OA might interfere with this process. In terms of enzyme functioning, OA can potentially affect krill growth, moult, fitness, behaviour and reproduction.

Overall, in regions where OA is prevalent, it may affect krill embryonic development. However, the effects of OA on the Antarctic ecosystem remain unclear - more research is required.

9.3.5 Changes in UV radiation

As mentioned in Section 9.3.3, the ozone layer over the Antarctic has not recovered fully yet. As a result, UV radiation is another environmental stressor on krill and the Antarctic ecosystem.

UV-B radiation can impact krill directly through genetic damage (Dahms *et al.*, 2011; Jarman *et al.*, 1999), physiological effects (Newman *et al.*, 2000; 1999) or behavioural reactions (Newman *et al.*, 2003). Increased UV radiation can affect krill indirectly through a decrease in primary productivity and by changing the structure of the Antarctic food web(s) (Flores *et al.*, 2012).

9.4 Summary

In this chapter, two possible causes of the long-term population changes of krill and its predators have been discussed, namely: Laws' "krill surplus" hypothesis and environmental change.

Laws' hypothesis states that after the exploitation of the large baleen whales, a krill "surplus" became available to other krill-predators such as minke whales, penguins, crabeater and fur seals. This hypothesis is certainly plausible given that there are no other obvious causes that could have led to the increases in these predators during the early to the mid-20th century. However, it has been suggested in Reid and Croxall (2001) and Surma *et al.* (2014) that the period of this "krill surplus" may now have ended as there is no longer evidence of further increases in krill. Reid and Croxall (2001) argue that changes in the population structure of krill and its relationship to reproductive performance suggest that krill biomass in the larger size class (54-56 mm) was sufficient to support predator demand during the 1980s but not in the 1990s, whilst the study in Surma *et al.* (2014) suggest that the "krill surplus" was moderate and relatively short-lived.

The "iron-feedback" hypothesis, another possible explanation for the population changes in krill, was also discussed.

The section on environmental change also served to address the role of climate change in the Antarctic. Overall, the effects of environmental change are not uniform (Murphy and Hofmann, 2012) and have five possible manifestations, namely: sea-ice change, ocean warming, wind circulation changes, ocean acidification and UV radiation. Considerable detail has been provided regarding these manifestations and their possible impact on krill, the driver of the Antarctic ecosystem.

Krill recruitment is the factor which is most susceptible to environmental change. Changes in sea-ice coverage, thickness and duration affect krill negatively, especially their reproductive success and winter survival. As a result, changes in sea-ice might be a possible cause of a decline in krill abundance, especially if they are concentrated around the main krill recruitment and spawning grounds. Rising sea-surface temperatures may have both negative and positive effects on krill, with the balance probably more towards the negative effects. The latter could result in a southward shift in the krill distribution to colder waters. Salp populations are impacted positively by sea-ice changes and ocean warming. Salps compete with krill for food, i.e. phytoplankton. In times when krill are scarce, salps are known to flourish, especially when sea-ice coverage is less and ocean surface waters are warmer.

Krill is a species inhabiting a fluctuating environment. They can adapt their behaviour in order to remain in a particular area, particularly adult krill. Adult krill are an inherently flexible species. They can exist in different aggregation states (Schmidt *et al.*, 2011), use a wide variety of food sources (Schmidt *et al.*, 2011; Meyer *et al.*, 2010; Kawaguchi *et al.*, 1986) and possibly buffer their physiological sensitivity to small temperature increases or pH changes. With the onset of possible environmental change, the survival of adult krill may be ameliorated by these adaptive capabilities.

	Species	Food Consumption in the Antarctic (10^3 t)			Total	Percentage of Prey in Baleen Diet (%)		
		Krill	Squid	Fish		Krill	Squid	Fish
Initial Stocks, Before Whaling	Fin whale	81 480	840	1 680	84 000	0.97	0.01	0.02
	Blue whale	71 702	740	1 478	73 920			
	Humpback whale	11 000	113	227	11 340			
	Minke whale	19 827*	204	409	20 440			
	Total	184 009	1 897	3 794	189 700			
Present Stocks, After Whaling	Fin whale	16 426	169	339	16 934	0.97	0.01	0.02
	Blue whale	3 381	35	70	3 486			
	Humpback whale	322	3	7	342			
	Minke whale	19 827*	204	409	20 440			
	Total	39 956	411	825	41 202			

TABLE 9.1: Coarse estimates of the food consumption by the baleen whales in the Antarctic, before and after whaling, from Laws (1977).

* Laws (1977) assumed that minke whales feed all year round in the Antarctic at 4% body mass per day.

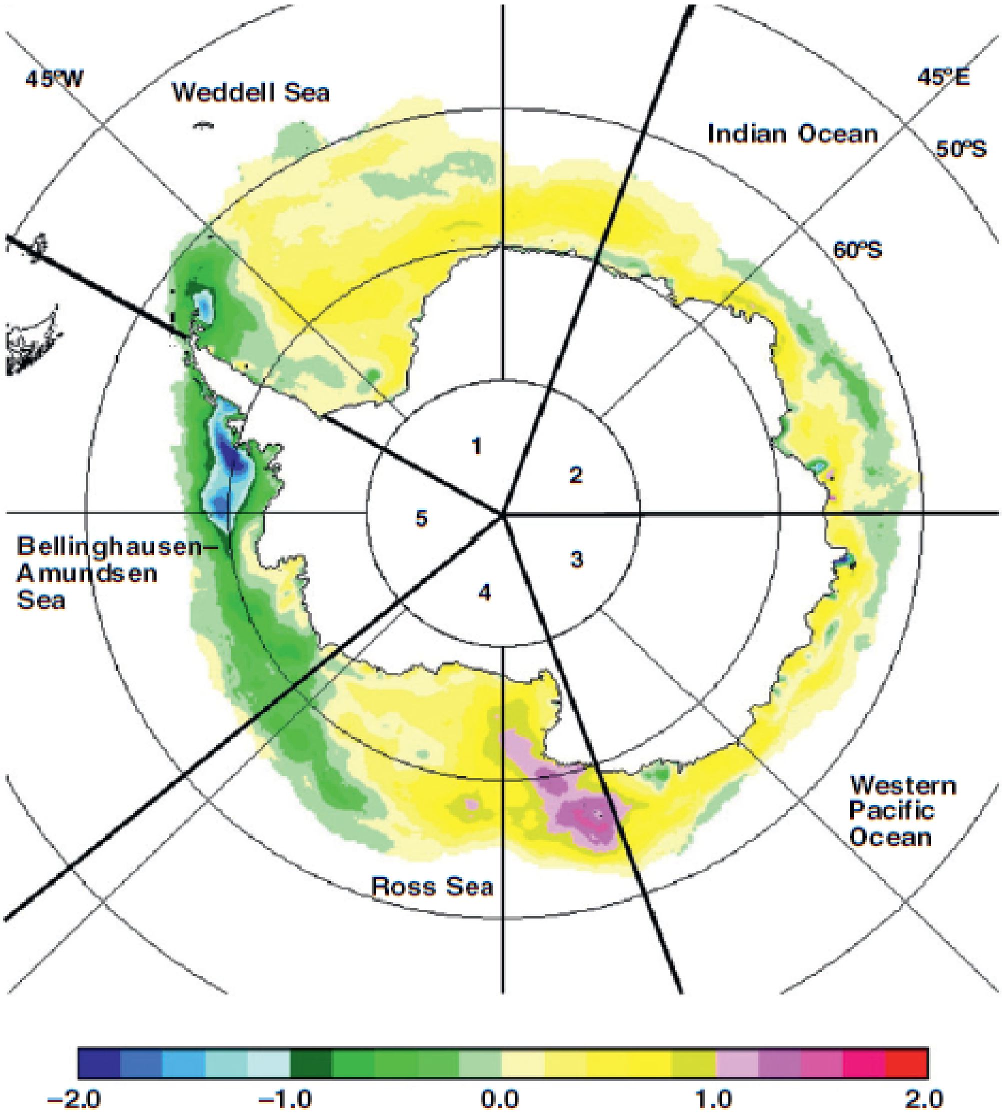

FIGURE 9.1: The spatial pattern of autumn sea-ice concentration changes from 1979 until 2007 (% ice concentration per year); areas with a decrease in ice concentration are shaded blue-green and areas with an increase in ice concentration are shaded yellow-pink - reproduced with permission from Turner *et al.*, 2009b.

Chapter 10

A summary of Mori and Butterworth (2006) and their conclusions

10.1 Overview of Chapter

The objective of the Mori and Butterworth (2006) analysis was to determine whether it was possible to evaluate, both qualitatively and quantitatively, the extent to which predator-prey interactions may be controlling the population abundances and trends of krill and its main predators.

This chapter summarises the methodology, results and conclusions drawn from the Mori and Butterworth (2006) analyses. Some aspects have been covered in previous chapters, but are repeated here to present information on the Mori-Butterworth model in a self-standing and consolidated form.

10.2 Data and methods

10.2.1 The species considered and the regional effects incorporated

Mori (2005) found the consumption of krill by the large baleen whales and seals in the Antarctic to be relatively large. As a result, both the large baleen whale (more specifically blue, minke, fin and humpback whales) and seal (Antarctic fur and crabeater seals) populations were considered in the Mori-Butterworth model. At the time the model was developed, there was a lack of information on the consumption of krill by fish and birds.

As mentioned in Chapter 5 (Section 5.3), Mori (2005) divided the Antarctic into two regions: Region AI and Region PO (see Figure 5.2). The Antarctic fur seals were included only in Region AI because, essentially, their distribution is restricted to the Atlantic sector of the Antarctic.

10.2.2 Historical catch record

In Mori (2005), the historical catch record for the blue whales was taken from Rademeyer *et al.* (2003). Some minor errors found in Rademeyer *et al.* (2003) were corrected and the revisions were used for the catch record in Mori and Butterworth (2006). The pygmy blue whales were excluded from this series as they are almost exclusively found further north.

The catch records for minke and fin whales were provided by C. Allison, from the IWC Secretariat. Some of the early catches (before the period when minke whales were taken) did not record the species caught. In such cases, the total catch of the vessel concerned was allocated to species by the same proportion as the same vessel in the same region for the closest year in which the vessel did record the species caught. This was especially necessary for fin whales. A similar basis was used to allocate catches to Region AI and PO when no catch information was provided, except that all the South Shetland fin whale catches were allocated to Region AI. Mori (2005) noted that the contributions from catch allocations (where species were not specified) totaled roughly 2% of the cumulative fin whale catch record at that time - as this was quite small, any changes in the assumptions made were unlikely to cause major changes to the fin whale catch record and the ecosystem model to which it was input.

For humpback whales, the catch records were developed by C. Allison and K. Findlay during the 2005 IWC Scientific Committee meeting. Humpback catches from breeding stocks A, B, C and D were allocated to Region AI and from stocks E, F and G to Region PI. Mori (2005) noted that the early catch records for the baleen whales and the misreporting of species by the former USSR remained under investigation.

For the Antarctic fur seals, information existed on cumulative catches, but none on yearly catches. As a result, a plausible catch series was developed based on the available knowledge of these catches (see Appendix I in Mori and Butterworth (2006)). Crabeater seals were hardly harvested during the earlier centuries, although 750 seals were caught each year in Region AI for 11 years from 1967 until 1977 (Boyd, pers. comm). Mori (2005) used this information to construct a plausible crabeater seal catch series.

The tables containing these catch series can be found in Mori and Butterworth (2006) (Tables 2a and 2b).

10.2.3 Abundance estimates and their relative trends

The absolute abundance estimates for the predator species considered and their relative trends are shown in Tables 3 and 4 of Mori and Butterworth (2006). The abundance estimates for blue, humpback and minke whales were for the region south of 60°S. As mentioned in Chapter 5.5.1 (point 4), the fin whale abundance estimate for south of 60°S was extrapolated northwards as the fin whale distribution extends further northwards during the austral summer.

Trends in abundance for fin whales and crabeater seals were not well known at the time of the Mori and Butterworth (2006) analysis, and thus were not used in fitting their population model.

10.2.4 The population dynamics

Mori (2005) states that there is almost no information on the functional response of the baleen whales to krill. Generally though, specialist predators are thought to be represented by a hyperbolic-shaped functional response, and generalist predators by a sigmoidal-shaped response (Turchin, 2002).

A CCAMLR working group had suggested that for predators whose foraging is based on interactions with individual prey species (e.g. killer whales foraging on seals), Type II functional response curves are appropriate. For predators whose foraging is based on interactions with prey organisms that aggregate to exceed a threshold density (e.g. baleen whales foraging on krill), Type III response curves are suggested (SC-CAMLR, 2004). Mori and Butterworth (2006) explored both Type II and Type III response forms.

The functional responses assumed on the krill consumption took *exploitation competition* into account. Exploitation competition is considered to be any harmful effects on a predator as a result of reduced prey levels caused by other competing predators. In order for exploitation competition to occur, the resource (prey) in question needs to be in limited supply. Laws' "krill surplus" hypothesis makes this assumption implicitly.

10.3 The model

The Mori and Butterworth (2006) model was similar to the Mori and Butterworth (2004) model but included an intra-specific density-dependent parameter (η - see Chapter 8.6) for each predator. This was necessary to allow a non-trivial co-existence equilibrium amongst the species considered. The core equations of the model were as follows.

The dynamics of krill

$$B_{y+1}^{a} = B_{y}^{a} + r^{a} B_{y}^{a} \left(1 - \left(\frac{B_{y}^{a}}{K_{a}}\right)\right) - \sum_{j} \frac{\lambda^{j} \left(B_{y}^{a}\right)^{n} N_{y}^{j,a}}{\left(B^{j,a}\right)^{n} + \left(B_{y}^{a}\right)^{n}} \tag{10.1}$$

The predator dynamics

$$N_{y+1}^{j,a} = N_{y}^{j,a} + \frac{\mu^{j}\, N_{y}^{j,a} \left(B_{y}^{a}\right)^{n}}{\left(B^{j,a}\right)^{n} + \left(B_{y}^{a}\right)^{n}} - M^{j}\, N_{y}^{j,a} - \eta^{j,a} \left(N_{y}^{j,a}\right)^{2} - C_{y}^{j,a} \tag{10.2}$$

where

B_y^a	is the krill biomass for Region a in year y;
$B^{j,a}$	is the krill biomass when the consumption (and thus also the birth rate) of species j in Region a drops to half of its maximum level; j can be either: b (blue whale), m (minke whale), f (fin whale), h (humpback whale), c (crabeater seal) or s (Antarctic fur seal);
$N_y^{j,a}$	is the abundance (by number) of predator species j in Region a for year y;
K_a	is the carrying capacity of krill, in the absence of predators, for Region a;
$C_y^{j,a}$	the catch of the predator species j for Region a in year y;
λ^j	is the maximum per capita annual krill consumption rate (in tonnes) of predator species j;
μ^j	is the maximum annual birth rate of the predator species j; this can be considered to incorporate the calf-survival rate as the net effect of these two processes together are what is measurable;
M^j	is the annual natural mortality proportion for predator species j;
r^a	is the intrinsic krill growth rate for Region a;
$\eta^{j,a}$	governs the density-dependence of natural mortality and/or birth (and calf-survival) rate for predator species j in Region a; and
n	controls whether a Type II or a Type III functional response is assumed ($n = 1$ for Type II and $n = 2$ for Type III).

Krill catch series were not considered because these catches had been small compared to krill abundance estimates (by roughly two or more orders of magnitude) at the time of Mori and Butterworth (2006) (SC-CAMLR, 2001). The krill production function in Equation 10.1 was changed from the Pella-Tomlinson form, as was used in Mori and Butterworth (2004), to the Schaefer form in order to facilitate computations. If this had not been done, then the computation of K_a (Equation 10.3) could lead to discontinuous derivatives which are not allowed by the minimisation process of the ADMB package used for these computations. Mori (2005) noted that the effect of this change was small; the krill MSY level (MSYL) increased from 40% to 50% of K_a.

Plausible bounds were imposed on the estimable parameters (Table 5 in Mori and Butterworth (2006)). Parameters selected from these ranges were also required to satisfy the following conditions: μ_b - $M_b \geq 0.02$, μ_f - $M_f \geq 0.02$, μ_h - $M_h \geq 0.02$, μ_m - $M_m \geq 0.03$, μ_s - $M_s \geq 0.03$ and μ_c - $M_c \geq 0.03$, i.e. blue, fin and humpback whales can attain per capita growth rates of at least 2% and minke whales, Antarctic fur and crabeater seal of at least 3% under optimal feeding conditions. Mori (2005) considered these constraints to be reasonable given the observed increase rates found for some baleen whale and seal species in her analysis. The range for r^a was selected following the same procedure as described in Mori and Butterworth (2004), and the ranges for the other estimable parameters were chosen based on the information available at that time. The ADMB package used treats these bounds as boundaries for uniform priors for each of the estimable parameters. As a result, the estimable parameters could be considered as either maximum likelihood estimates or modes of Bayesian posteriors.

The values for the input parameters ($B^{b,a}$ and $\eta^{j,a}$) were chosen so that the resultant population trajectories were able to reflect the patterns observed in the available data (Table 6 in Mori and Butterworth (2006)). Mori (2005) noted that the blue, fin and humpback whales had an apparent greater productivity in the Atlantic whilst minke whales had a greater productivity in the Pacific - this was a reflection of the need to choose comparatively smaller values for η for these respective regions to represent the data better.

10.3.1 Model fitting and parameter estimation

The Mori-Butterworth (2006) model made two major assumptions.

1) In the year 1780 (before commercial sealing and whaling commenced in the Antarctic), the species considered co-existed in equilibrium.
2) There is competition between **and** within the considered species.

The plausibility of these two assumptions is discussed in detail in the Mori and Butterworth (2006) paper.

To estimate the yearly abundances of krill (Equation 10.1) and its predators (Equation 10.2), the initial abundance estimate for each species for the year 1780 needed to be found.

Using assumption 1), a Type III functional response was assumed and B^a_{y+1} was set to equal B^a_y in Equation 10.1 to reflect equilibrium. This provided the following equation:

$$r^a B^a_{1780}\left(1-\left(\frac{B^a_{1780}}{K_a}\right)\right)=\sum_j \frac{\lambda^j\left(B^a_{1780}\right)^2 N^{j,a}_{1780}}{\left(B^{j,a}\right)^2+\left(B^a_{1780}\right)^2} \tag{10.3}$$

Similarly, a Type III functional response with $N^{j,a}_{y+1}=N^{j,a}_y$ and $C^{j,a}_y=0$ was assumed for Equation 10.2 which led to the following equation:

$$\frac{\mu^j\left(B^a_{1780}\right)^2}{\left(B^{j,a}\right)^2+\left(B^a_{1780}\right)^2}=M^j+\eta^{j,a}\,N^{j,a}_{1780} \tag{10.4}$$

for each predator species j.

For blue whales, Equation 10.4 can be rewritten as:

$$B^{a}_{1780} = \frac{B^{b,a}\sqrt{M^{b} + \eta^{b,a}\, N^{b,a}_{1780}}}{\sqrt{\mu^{b} - M^{b} - \eta^{b,a}\, N^{b,a}_{1780}}} \tag{10.5}$$

Equation 10.5 was used to find the initial krill biomass for Region a in the year 1780. $B^{b,a}$ and $\eta^{b,a}$ were input values and the other blue whale parameters (M^{b}, $N^{b,a}_{1780}$ and μ^{b}) were estimated in the minimisation process, their requiring initial values for the minimisation.

Similarly, by rewriting Equation 10.4 as:

$$B^{j,a} = \frac{B^{a}_{1780}\sqrt{\mu^{j} - M^{j} - \eta^{j,a}\, N^{j,a}_{1780}}}{\sqrt{M^{j} + \eta^{j,a}\, N^{j,a}_{1780}}} \tag{10.6}$$

the functional response parameter ($B^{j,a}$) for each predator species j in Region a (except for blue whales) could be found. Once all of these parameters were determined, K_{a} could be calculated from Equation 10.3. Similar equations apply for the Type II functional responses.

10.3.2 The likelihood function

The complete negative log-likelihood function minimised in Mori and Butterworth (2006) to estimate the parameters M^{j}, $N^{j,a}_{1780}$, λ^{j} and μ^{j} for the predator species j and r^{a} for krill was:

$$\begin{aligned} -\ln L = {} & LL^{b}_{abund} + LL^{b}_{trend} + LL^{m}_{abund} + LL^{m}_{trend} + LL^{h}_{abund} + LL^{h}_{trend} + LL^{f}_{abund} \\ & + LL^{s}_{abund} + LL^{s}_{trend} + LL^{c}_{abund} \end{aligned} \tag{10.7}$$

where

LL^{j}_{abund} is the component that compares the observed abundance (estimated directly from surveys) to the model estimated abundance for each predator species j. It assumed lognormal error distributions.

LL^{j}_{trend} is a similar component relevant to the abundance trends. It assumed normal error distributions.

Blue whale component

$$LL^{b}_{abund} = \frac{\left(\ln N^{b,AI}_{2000} - \ln \hat{N}^{b,AI}_{2000}\right)^{2}}{2\left(\sigma^{b,AI}_{2000}\right)^{2}} + \frac{\left(\ln N^{b,PO}_{2000} - \ln \hat{N}^{b,PO}_{2000}\right)^{2}}{2\left(\sigma^{b,PO}_{2000}\right)^{2}} \tag{10.8}$$

$$LL^{b}_{trend} = \sum_{y=1}^{n}\left[\ln \sigma_{y} + \frac{1}{2\sigma_{y}^{2}}\left(\ln N^{b,obs}_{y} - \ln q - \ln \hat{N}^{b}_{y}\right)^{2}\right] \tag{10.9}$$

where

$$\ln q = \frac{\sum_{y=1}^{n} \frac{1}{\sigma_y^2}\left(\ln N_y^{b,obs} - \ln \hat{N}_y^b\right)}{\sum_{y=1}^{n} \frac{1}{\sigma_y^2}} \tag{10.10}$$

The q in Equation 10.10 reflects a possible multiplicative bias in the abundance estimates used. The summation is over the years for which circumpolar abundance estimates are available.

Minke whale component

$$LL_{abund}^{m} = \frac{\left(\ln N_{1985}^{m,AI} - \ln \hat{N}_{1985}^{m,AI}\right)^2}{2\left(\sigma_{1985}^{m,AI}\right)^2} + \frac{\left(\ln N_{1985}^{m,PO} - \ln \hat{N}_{1985}^{m,PO}\right)^2}{2\left(\sigma_{1985}^{m,PO}\right)^2} \tag{10.11}$$

$$LL_{trend}^{m} = \frac{\left(R_{1970-2000}^{m,AI} - \hat{R}_{1970-2000}^{m,AI}\right)^2}{2\left(\sigma_{1970-2000}^{m,AI}\right)^2} + \frac{\left(R_{1970-2000}^{m,PO} - \hat{R}_{1970-2000}^{m,PO}\right)^2}{2\left(\sigma_{1970-2000}^{m,PO}\right)^2} \tag{10.12}$$

Humpback whale component

$$LL_{abund}^{h} = \frac{\left(\ln N_{1997}^{h,AI} - \ln \hat{N}_{1997}^{h,AI}\right)^2}{2\left(\sigma_{1997}^{h,AI}\right)^2} + \frac{\left(\ln N_{1997}^{h,PO} - \ln \hat{N}_{1997}^{h,PO}\right)^2}{2\left(\sigma_{1997}^{h,PO}\right)^2} \tag{10.13}$$

$$LL_{trend}^{h} = \frac{\left(R_{1977-1991}^{h,AI} - \hat{R}_{1977-1991}^{h,AI}\right)^2}{2\left(\sigma_{1977-1991}^{h,AI}\right)^2} + \frac{\left(R_{1981-1996}^{h,PO} - \hat{R}_{1981-1996}^{h,PO}\right)^2}{2\left(\sigma_{1981-1996}^{h,PO}\right)^2} \tag{10.14}$$

Fin whale component

$$LL_{abund}^{f} = \frac{\left(\ln N_{1997}^{f,AI} - \ln \hat{N}_{1997}^{f,AI}\right)^2}{2\left(\sigma_{1997}^{f,AI}\right)^2} + \frac{\left(\ln N_{1997}^{f,PO} - \ln \hat{N}_{1997}^{f,PO}\right)^2}{2\left(\sigma_{1997}^{f,PO}\right)^2} \tag{10.15}$$

Crabeater seal component

$$LL_{abund}^{c} = \frac{\left(\ln N_{2000}^{c,AI} - \ln \hat{N}_{2000}^{c,AI}\right)^2}{2\left(\sigma_{2000}^{c,AI}\right)^2} + \frac{\left(\ln N_{2000}^{c,PO} - \ln \hat{N}_{2000}^{c,PO}\right)^2}{2\left(\sigma_{2000}^{c,PO}\right)^2} \tag{10.16}$$

Antarctic fur seal component

$$LL^{a}_{abund} = \frac{\left(\ln N^{s,AI}_{1930} - \ln \hat{N}^{s,AI}_{1930}\right)^2}{2\left(\sigma^{s,AI}_{1930}\right)^2} + \frac{\left(\ln N^{s,AI}_{1975} - \ln \hat{N}^{s,AI}_{1975}\right)^2}{2\left(\sigma^{s,AI}_{1975}\right)^2} + \frac{\left(\ln N^{s,AI}_{1990} - \ln \hat{N}^{s,AI}_{1990}\right)^2}{2\left(\sigma^{s,AI}_{1990}\right)^2} \tag{10.17}$$

$$LL^{s}_{trend} = \frac{\left(R^{s,AI}_{1957-1972} - \hat{R}^{s,AI}_{1957-1972}\right)^2}{2\left(\sigma^{s,AI}_{1957-1972}\right)^2} + \frac{\left(R^{s,AI}_{1976-1990} - \hat{R}^{s,AI}_{1976-1990}\right)^2}{2\left(\sigma^{s,AI}_{1976-1990}\right)^2} + \frac{\left(R^{s,AI}_{1990-1999} - \hat{R}^{s,AI}_{1990-1999}\right)^2}{2\left(\sigma^{s,AI}_{1990-1999}\right)^2} \tag{10.18}$$

where

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

$R^{j,a}_{y_1-y_2}$ is the Rate Of Increase (ROI) of species j in Region a from year y_1 to year y_2.

$$R^{j,a}_{y_1-y_2} = \left(\frac{N^{j,a}_{y_2}}{N^{j,a}_{y_1}}\right)^{\frac{1}{y_2-y_1}} - 1 \tag{10.19}$$

10.4 Results

Mori and Butterworth (2006) investigated a reference case and six other sensitivities which are summarised below.

i) What if the observed minke abundance estimates ($N^{m,AI}_{1985}$ and $N^{m,PO}_{1985}$) were doubled?

ii) What if the carrying capacity of krill in the Atlantic (K_{AI}) was linearly reduced to half its original value between the mid-1950s and the early 1970s?

iii) What if only whales were considered in the model, i.e. no seal species were included?

iv) What if a Type II functional response form was assumed instead of a Type III?

v) For the 'reference case' scenario, what if crabeater seals in Region AI had a higher density -dependent mortality rate ($\eta^{c,AI}$) than currently assumed?

vi) What if the lower boundary limits of the initial crabeater abundance estimates ($N^{c,AI}_{1780}$ and $N^{c,PO}_{1780}$) were set higher?

The results and conclusions drawn from these sensitivities are detailed in the Mori and Butterworth (2006) paper, and thus will not be discussed here.

The trajectories of krill and its main predators for the 'reference case' of the Mori-Butterworth model when a Type III functional response form was assumed are shown in Figure 10.1*. The values of the estimable parameters for the reference case and the six sensitivities are given in Mori and Butterworth (2006) (Table 6). That paper also discusses comparisons between the prior and posterior distributions for the parameters estimated. Mori and Butterworth (2006) stated that convergence was difficult to achieve if certain parameters were estimated (namely, λ^f, μ^h, μ^f). As a result, these parameters were fixed on input.

The sequence of the primary factors (as indicated by the model results) that influenced the dynamics of krill and its main predators were considered to be as follows.

1) From roughly 1920 until 1950, krill biomass increased due to the decrease in whale predators which resulted from the extensive commercial whaling during that period. The earlier fur-seal harvests appeared to have only a limited effect on the krill biomass.
2) Due to this increase in krill biomass, minke whales, crabeater seals and Antarctic fur seals increased. Minke whales increased from roughly 1930 until 1970 with the seal species increasing a little later.
3) By about 1950, the krill biomass had almost reached its carrying capacity. However, due to the increase in krill consumption by the minke and seal populations, the krill biomass began to decline.
4) Following this decrease in krill biomass and due to the high density-dependent mortality effects, predators such as minke whales and crabeater seals (both which had benefited from the earlier krill increase) began to decrease from about 1970, while the larger baleen whale species (which were fully protected at that time) started to recover.

The plausibility of the estimates for the factors that the model suggested to be driving the dynamics in the Antarctic is discussed in Mori and Butterworth (2006). The authors concluded that the 'reference case' results passed their various plausibility tests, although the crabeater seals passed by a small margin only.

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[*] The author's code for the Mori-Butterworth model was used to generate these plots. There are a few minor discrepancies between her 'reference case' results and the Mori and Butterworth (2006) 'reference case' results but they were rather small. These discrepancies are thought to be a consequence of the improvements in the minimisation process implemented by the ADMB package since the time when Mori and Butterworth (2006) was developed.

10.5 Conclusions

A number of inferences were drawn from the Mori and Buterworth (2006) analysis - some are outlined below.

1) The effects of species interactions alone could account for the likely trends in the abundance of the main Antarctic predators over the past 50 years, although not without some difficulty. However, one could not conclude whether or not the effects of environmental change were important for explaining these observed trends.
2) The effects of species interactions affected predator dynamics in ways that differed from what would be expected from a single-species model. Thus, multi-species modelling needed to be better understood before it could be used to contribute to management decisions.
3) The interactions between the main baleen whales and krill alone were not sufficient to explain the observed abundance trends in the Antarctic. The main seal species also needed to be included.
4) There were substantial differences in the dynamics between Regions AI and PO historically. In the former, there were considerable abundance changes, while the latter had been relatively stable.
5) The heavy harvesting of the Antarctic fur seal over the turn of the 18^{th} century had less impact quantitatively compared to that of the larger baleen whales during the mid-20^{th} century.
6) In the absence of future human harvests, blue whales in Region AI were predicted to need roughly three to four centuries to reach their pre-exploitation levels. They would need time to out-compete other predators that can recover more quickly.
7) Density-dependent mortalities (η) were an important feature in the model. However, these were problematic due to the absence of independent bases to provide information on their likely values.
8) Crabeater seals played an important role in the Antarctic dynamics. Mori (2005) noted that the model could be using the crabeater seals as a surrogate for other krill-predators (such as birds and fish species) not included in her model.
9) Laws' (1977) 'krill surplus' estimate appeared to have been too high. Laws did not take into account the lower feeding rates due to the low krill abundances before the start of large-scale commercial whaling in the Antarctic.

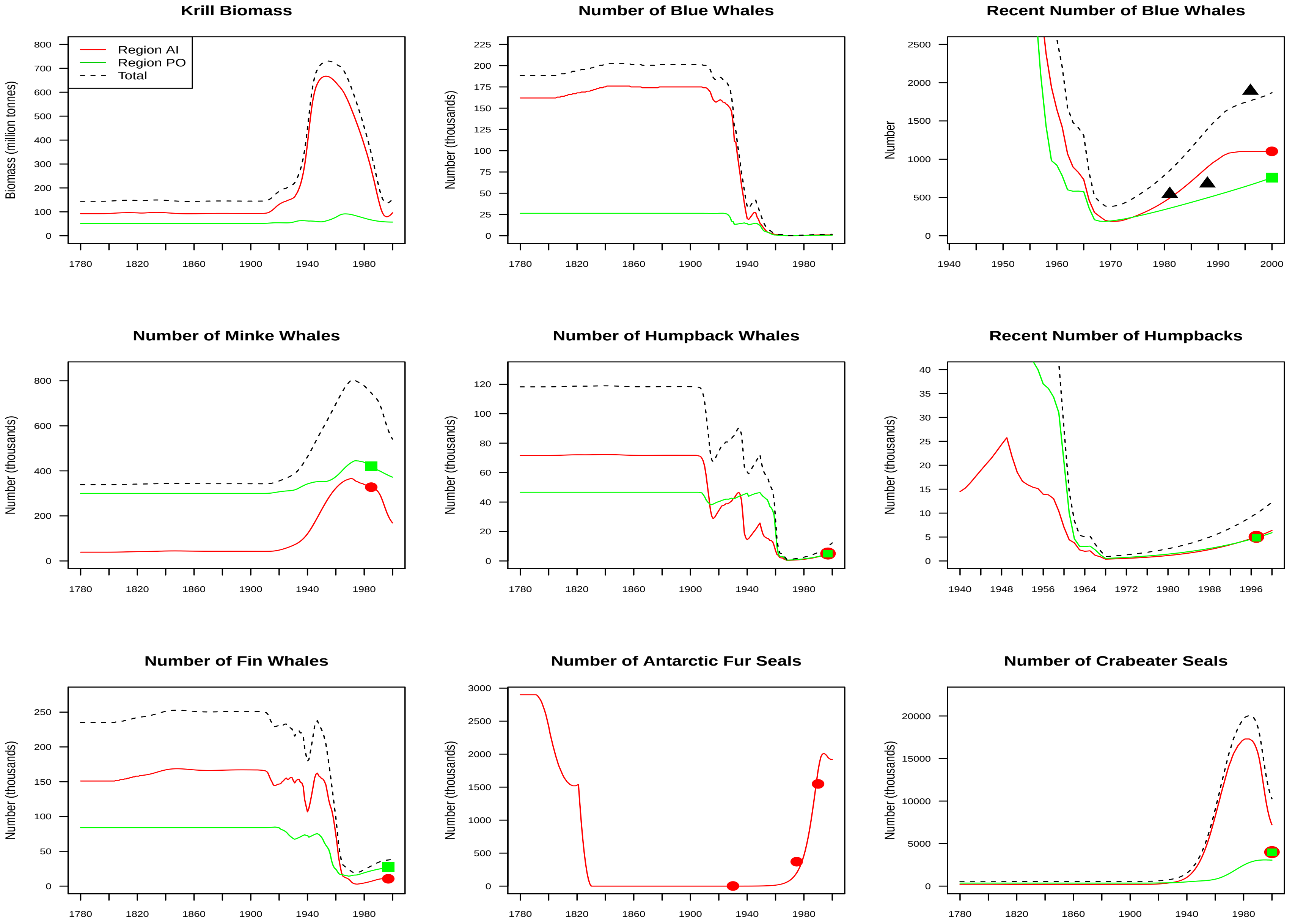


FIGURE 10.1: The ‘reference case’ population model trajectories for krill and its main predators in the Antarctic. A red circle/green square represents a survey-based abundance estimate for Regions AI/PO respectively, which has been used in the model fit. The triangles represent the blue whale abundance estimates from surveys for Regions AI and PO combined. These survey estimates were used in the model fit to reflect the blue whale abundance trend.

Chapter 11

An updated and refined predator-prey model for exploring Antarctic ecosystem dynamics

11.1 Overview of Chapter

This chapter integrates the data updates recorded earlier in this thesis together with the Mori-Butterworth methodology to develop an updated and refined predator-prey model for the Antarctic ecosystem. Some aspects of this chapter have been covered earlier, but are repeated here to present information on this refined ecosystem model in a self-standing and consolidated form. The criticisms of the Willis (2014) article are also addressed here.

11.2 Data and methods

11.2.1 Species considered in the model

In the light of the estimates of total annual consumption of krill by weight by the various Antarctic krill-predators as calculated in Chapter 4, the main krill-predators in the Antarctic ecosystem that are included in fitting the ecosystem model to the data are: blue whales, fin whales, minke whales, humpback whales, crabeater seals and Antarctic fur seals. Each of these species accounts for a total annual krill consumption value that is greater than 1 million tonnes (Table 11.1).

11.2.2 Incorporating regional effects

As mentioned in Chapter 5 (Section 5.3), the two regions analysed in Mori (2005) are used in this thesis, namely: Region AI and Region PO (see Figure 5.2).

11.2.3 Historic catch record

The humpback, minke, blue and fin whale catch records for each IWC Area (this includes regions north of 60°S) were kindly provided by C. Allison from the IWC Secretariat. These have been consolidated to form a catch series for Regions AI and PO (see Table A.1). The same Antarctic fur seal and crabeater seal catch records that were used in Mori and Butterworth (2006) (see Chapter 10, Section 10.2.2) are retained in the model developed in this chapter (see Tables A.2 and A.3 respectively).

11.2.4 Abundance estimates and their relative trends

The absolute abundance estimates for the predator species considered in this update and their relative trends are reported in Chapter 5 (for the whale species) and Chapter 6 (for the seal species). They are summarised in Tables 11.2 and 11.3 respectively. The relative trends in Table 11.3 are shown as a proportional change per year, except for the blue whales where the successive circumpolar abundance estimates listed are used to provide a basis to infer an estimate within the model-fitting process.

11.2.5 Species' population dynamics

As mentioned in Chapter 10 (Section 10.2.4), Type II functional response curves are considered to represent foraging based on interactions with individual prey species (e.g. killer whales foraging on seals), whilst Type III response curves represent foraging based on interactions with prey organisms that aggregate to exceed a threshold density (e.g. baleen whales feeding on krill) (SC-CAMLR, 2004). Thus, Type III functional response curves are assumed in this model (as was for the original Mori-Butterworth model) i.e. $n = 2$.

11.3 The model

The equations used in Mori and Butterworth (2006) are retained in this thesis (Equations 10.1 and 10.2). However, when these core equations were implemented, problems arose in fitting to the fur seal abundance estimates (see Sensitivity 2, which shows the initial issues in the model without the depensatory effect). As a result, the Antarctic fur seal component in the equations reflecting the krill dynamics (Equation 10.1) and the Antarctic fur seal predator dynamics have been amended to include a "depensatory effect" as follows (but Equation 10.2 is still retained for the other predator species):

The "depensatory effect"

$$B_{y+1}^{a} = B_{y}^{a} + r^{a} B_{y}^{a} \left(1 - \left(\frac{B_{y}^{a}}{K_{a}}\right)\right) - \sum_{j} \frac{\lambda^{j} \left(B_{y}^{a}\right)^{2} N_{y}^{j,a}}{\left(B^{j,a}\right)^{2} + \left(B_{y}^{a}\right)^{2}} - \frac{\lambda^{s} \left(B_{y}^{a}\right)^{2} \left(\frac{N_{y}^{s,a}}{1 + e^{\left(-(N_{y}^{s,a} - N\#)/d\right)}}\right)}{\left(B^{s,a}\right)^{2} + \left(B_{y}^{a}\right)^{2}} \tag{11.1}$$

$$N_{y+1}^{s,a} = N_{y}^{s,a} + \frac{\mu^{s} \left(B_{y}^{a}\right)^{2} \left(\frac{N_{y}^{s,a}}{1 + e^{\left(-(N_{y}^{s,a} - N\#)/d\right)}}\right)}{\left(B^{s,a}\right)^{2} + \left(B_{y}^{a}\right)^{2}} - M^{s} N_{y}^{s,a} - \eta^{s,a} \left(N_{y}^{s,a}\right)^{2} - C_{y}^{s,a} \tag{11.2}$$

where

B_{y}^{a}	is the krill biomass for Region a in year y;
$B^{j,a}$	is the krill biomass when the consumption (and thus also the birth rate) of species j in Region a drops to half of its maximum level; the summation over j indicates: b (blue whale), m (minke whale), f (fin whale), h (humpback whale) and c (crabeater seal), but not $j = s$ (Antarctic fur seal);
$B^{s,a}$	is the krill biomass when the consumption (and thus also the birth rate) of Antarctic fur seals in Region a drops to half of its maximum level;
$N_{y}^{j,a}$	is the abundance (by number) of predator species j in Region a for year y;
$N_{y}^{s,a}$	is the abundance (by number) of Antarctic fur seals in Region a for year y;
K_{a}	is the carrying capacity of krill, in the absence of predators, for Region a;
$C_{y}^{s,a}$	is the catch of the Antarctic fur seals for Region a in year y;
λ^{j}	is the maximum per capita annual krill consumption rate (in tonnes) of predator species j;
λ^{s}	is the maximum per capita annual krill consumption rate (in tonnes) of the Antarctic fur seals;
μ^{s}	is the maximum annual birth rate of Antarctic fur seals; this can be considered to incorporate the calf-survival rate as the net effect of these two processes together are what is measurable;
M^{s}	is the annual natural mortality proportion for the Antarctic fur seals;
r^{a}	is the intrinsic krill growth rate for Region a;
$\eta^{s,a}$	governs the density-dependence of natural mortality and/or birth (and calf-survival) rate for the Antarctic fur seals in Region a;
$N\#$	is a value that is similar to the lowest size to which fur seals decreased to during the 1800s and $d = \frac{N\#}{3}$

The data available indicate that the fur seals decreased substantially in abundance around the year 1800 and remained at low numbers for a considerable period of time (about 100 years). The fur seals presumably increased again only when more krill became available, once whaling began reducing the numbers of the large baleen whales in the Antarctic. However, under such circumstances, most models are likely to be very unstable, with small changes in the starting estimate for fur seal abundance in the model causing the population either to go extinct or to increase well before this actually occurred. The modifications in Equation 11.1 and 11.2 introduce a "depensatory effect" which has the consequence that once a population drops to a low abundance, it tends to stay low and needs a substantial change in circumstances before it can increase to higher levels again. When this depensatory effect is included, the krill carrying capacities for the two Regions (K_a) must satisfy the following conditions:

$$K_{PO} > (10 \times 10^6),\ K_{AI} > (10 \times 10^6), \text{ and } K_{PO} < K_{AI}.$$

This is because when the depensatory effect was included, it tended to push K_{PO} to very high negative values. These conditions were included in order to "force" K_{PO} to be positive and not to exceed K_{AI}. Although there have not been any circumpolar krill surveys, the highest concentrations of krill appear to be in Region AI, close to the Antarctic Peninsula. Thus it seems reasonable to assume that the ("unexploited") krill biomass would not be as high in Region PO as it is in Region AI.

Due to these issues in fitting the fur seals in the ecosystem model (see the results from Sensitivity 2 in Section 11.4.4), the dynamics of krill and fur seals alone were explored. Different values of $N\#$ corresponding to the lowest numbers to which the fur seals decreased to in the early 1800s were explored. The "best" fit, i.e. that which inhibited the fur seals from recovering too early, was achieved with $N\# = 10$.

This "depensatory effect" might also be affecting the dynamics of the other krill-predators. However, in the interests of parsimony, a "depensatory effect" is only included where such an inclusion seemed unavoidable.

As with the Mori and Butterworth (2006) analysis, krill catch series are not considered. Plausible bounds are imposed on the estimable parameters (see Table 8.7) and are chosen as detailed in Chapter 8 of this thesis. The parameters selected from these ranges are required to satisfy the same conditions as outlined in Section 10.3.

The values for the input parameters ($B^{b,a}$ and $\eta^{j,a}$) are chosen so that the resultant population trajectories are able to reflect the patterns observed in the available data (see Table 11.4).

The assumptions and model fitting procedure used in Mori and Butterworth (2006) are retained in this thesis (see Section 10.3.1).

11.3.1 The likelihood function

The complete negative log-likelihood function minimised in this thesis to estimate the parameters M^j, $N^{j,a}_{1780}$, λ^j and μ^j for the predator species j and r^a for krill is:

$$\begin{aligned}-\ln L = {} & LL^b_{abund} + LL^b_{trend} + LL^m_{abund} + LL^m_{trend} + LL^h_{abund} + LL^h_{trend} + LL^f_{abund} \\ & + LL^f_{trend} + LL^s_{abund} + LL^s_{trend} + LL^c_{abund} + MS^{AI} + MS^{PO}\end{aligned} \tag{11.3}$$

where

LL^j_{abund} is the component that compares the observed abundance (estimated directly from surveys) to the model estimated abundance for each predator species j. It assumes lognormal error distributions.

LL^j_{trend} is a similar component relevant to the abundance trends. It assumes normal error distributions.

MS is the component that compares the time series of the average minke whale stomach contents estimated from observations to a model estimated term that is assumed to be proportional to the minke whale krill consumption rate.

Blue whale component

$$LL^b_{abund} = \frac{\left(\ln N^{b,AI}_{1997/98} - \ln \hat{N}^{b,AI}_{1997/98}\right)^2}{2\left(\sigma^{b,AI}_{1997/98}\right)^2} + \frac{\left(\ln N^{b,PO}_{1997/98} - \ln \hat{N}^{b,PO}_{1997/98}\right)^2}{2\left(\sigma^{b,PO}_{1997/98}\right)^2} \tag{11.4}$$

$$LL^b_{trend} = \sum_{y=1}^{n} \left[\ln \sigma_y + \frac{1}{2\sigma^2_y} \left(\ln N^{b,obs}_y - \ln q - \ln \hat{N}^b_y \right)^2 \right] \tag{11.5}$$

where

$$\ln q = \frac{\sum_{y=1}^{n} \frac{1}{\sigma^2_y} \left(\ln N^{b,obs}_y - \ln \hat{N}^b_y \right)}{\sum_{y=1}^{n} \frac{1}{\sigma^2_y}} \tag{11.6}$$

The q in Equation 11.6 reflects a possible multiplicative bias in the abundance estimates used. The summation is over the years for which circumpolar abundance estimates are available.

Minke whale component

$$LL^m_{abund} = \frac{\left(\ln N^{m,AI}_{1997/98} - \ln \hat{N}^{m,AI}_{1997/98}\right)^2}{2\left(\sigma^{m,AI}_{1997/98}\right)^2} + \frac{\left(\ln N^{m,PO}_{1997/98} - \ln \hat{N}^{m,PO}_{1997/98}\right)^2}{2\left(\sigma^{m,PO}_{1997/98}\right)^2} \tag{11.7}$$

$$LL^{m}_{trend} = \frac{1}{2}\left(\vec{y}_{obs} - \vec{y}_{mod}\right)^{T} V^{-1}\left(\vec{y}_{obs} - \vec{y}_{mod}\right) \tag{11.8}$$

where

$\vec{y}_{obs} = \Big(R^{m,AI}_{1944/45-1967/68}, R^{m,AI}_{1968/69-1987/88}, R^{m,AI}_{1988/89-2003/04}, R^{m,PO}_{1944/45-1967/68}, R^{m,PO}_{1968/69-1987/88}, R^{m,PO}_{1988/89-2003/04}\Big)$ is the observed rates of increase for minke whales for various years and Regions.

$\vec{y}_{mod} = \Big(\hat{R}^{m,AI}_{1944/45-1967/68}, \hat{R}^{m,AI}_{1968/69-1987/88}, \hat{R}^{m,AI}_{1988/89-2003/04}, \hat{R}^{m,PO}_{1944/45-1967/68}, \hat{R}^{m,PO}_{1968/69-1987/88}, \hat{R}^{m,PO}_{1988/89-2003/04}\Big)$ is the model estimated rates of increase for minke whales for various years and Regions.

and V^{-1} is the inverse variance-covariance matrix associated with the minke trend estimates as reported in Punt (2014) (see Table 5.6).

Humpback whale component

$$LL^{h}_{abund} = \frac{\left(\ln N^{h,AI}_{2014/15} - \ln \hat{N}^{h,AI}_{2014/15}\right)^2}{2\left(\sigma^{h,AI}_{2014/15}\right)^2} + \frac{\left(\ln N^{h,PO}_{2014/15} - \ln \hat{N}^{h,PO}_{2014/15}\right)^2}{2\left(\sigma^{h,PO}_{2014/15}\right)^2} \tag{11.9}$$

$$LL^{h}_{trend} = \frac{\left(R^{h,AI}_{2010/11-2014/15} - \hat{R}^{h,AI}_{2010/11-2014/15}\right)^2}{2\left(\sigma^{h,AI}_{2010/11-2014/15}\right)^2} + \frac{\left(R^{h,PO}_{2010/11-2014/15} - \hat{R}^{h,PO}_{2010/11-2014/15}\right)^2}{2\left(\sigma^{h,PO}_{2010/11-2014/15}\right)^2} \tag{11.10}$$

Fin whale component

$$LL^{f}_{abund} = \frac{\left(\ln N^{f,AI}_{1997/98} - \ln \hat{N}^{f,AI}_{1997/98}\right)^2}{2\left(\sigma^{f,AI}_{1997/98}\right)^2} + \frac{\left(\ln N^{f,PO}_{1997/98} - \ln \hat{N}^{f,PO}_{1997/98}\right)^2}{2\left(\sigma^{f,PO}_{1997/98}\right)^2} \tag{11.11}$$

$$LL^{f}_{trend} = \frac{\left(R^{f,AI}_{1995/96-2007/08} - \hat{R}^{f,AI}_{1995/96-2007/08}\right)^2}{2\left(\sigma^{f,AI}_{1995/96-2007/08}\right)^2} + \frac{\left(R^{f,PO}_{1996/97-2008/09} - \hat{R}^{f,PO}_{1996/97-2008/09}\right)^2}{2\left(\sigma^{f,PO}_{1996/97-2008/09}\right)^2} \tag{11.12}$$

Crabeater seal component

$$LL^{c}_{abund} = \frac{\left(\ln N^{c,AI}_{2000/01} - \ln \hat{N}^{c,AI}_{2000/01}\right)^2}{2\left(\sigma^{c,AI}_{2000/01}\right)^2} + \frac{\left(\ln N^{c,PO}_{2000/01} - \ln \hat{N}^{c,PO}_{2000/01}\right)^2}{2\left(\sigma^{c,PO}_{2000/01}\right)^2} \tag{11.13}$$

Antarctic fur seal component

$$LL^{a}_{abund} = \frac{\left(\ln N^{s,AI}_{1930/31} - \ln \hat{N}^{s,AI}_{1930/31}\right)^2}{2\left(\sigma^{s,AI}_{1930/31}\right)^2} + \frac{\left(\ln N^{s,AI}_{1975/76} - \ln \hat{N}^{s,AI}_{1975/76}\right)^2}{2\left(\sigma^{s,AI}_{1975/76}\right)^2} + \frac{\left(\ln N^{s,AI}_{1990/91} - \ln \hat{N}^{s,AI}_{1990/91}\right)^2}{2\left(\sigma^{s,AI}_{1990/91}\right)^2} \tag{11.14}$$

$$LL^{s}_{trend} = \frac{\left(R^{s,AI}_{1957/58-1971/72} - \hat{R}^{s,AI}_{1957/58-1971/72}\right)^2}{2\left(\sigma^{s,AI}_{1957/58-1971/72}\right)^2} + \frac{\left(R^{s,AI}_{1976/77-1989/90} - \hat{R}^{s,AI}_{1976/77-1989/90}\right)^2}{2\left(\sigma^{s,AI}_{1976/77-1989/90}\right)^2} + \frac{\left(R^{s,AI}_{1990/91-1998/99} - \hat{R}^{s,AI}_{1990/91-1998/99}\right)^2}{2\left(\sigma^{s,AI}_{1990/91-1998/99}\right)^2} \tag{11.15}$$

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;
$N^{j,a}_{y}$	is the observed abundance of species j in Region a for the year y;
$\hat{N}^{j,a}_{y}$	is the model estimated abundance of species j in Region a for the year y;
$R^{j,a}_{y_1-y_2}$	is the observed Rate of Increase (ROI) of species j in Region a from year y_1 to year y_2;
$\hat{R}^{j,a}_{y_1-y_2}$	is the model estimated ROI of species j in Region a from year y_1 to year y_2.

$$R^{j,a}_{y_1-y_2} = \left(\frac{N^{j,a}_{y_2}}{N^{j,a}_{y_1}}\right)^{\frac{1}{y_2-y_1}} - 1 \quad \text{(similarly for } \hat{R}^{j,a}_{y_1-y_2}\text{)} \tag{11.16}$$

Minke stomach contents

$$MS^{AI} = \sum_{y} w^{AI}\left[Q^{AI}_{y} - q^{AI}\frac{(B^{AI}_{y})^2}{(B^{m,AI})^2 + (B^{AI}_{y})^2}\right]^2 \tag{11.17}$$

$$MS^{PO} = \sum_{y} w^{PO}\left[Q^{PO}_{y} - q^{PO}\frac{(B^{PO}_{y})^2}{(B^{m,PO})^2 + (B^{PO}_{y})^2}\right]^2 \tag{11.18}$$

The term $\frac{(B_y^a)^2}{(B^{m,a})^2+(B_y^a)^2}$ is a modifier of how much of a whale's daily desired amount of krill it consumes, depending on how much krill there is, following the form of Equation 11.1. This term is assumed to be proportional to Q_y^a, the weight of prey contents in the stomachs of minke whales for the available years in the Region of Interest a (see Table 8.6) and q^a is the constant of proportionality, calculated by:

$$q^a = \frac{\sum_{y=1}^{n} Q_y^a}{\sum_{y=1}^{n} \frac{(B_y^a)^2}{(B^{m,a})^2+(B_y^a)^2}}$$

$$\text{and} \qquad w^a = \frac{1}{2\sigma^2} \quad \text{is a weight where}$$

$$\sigma = \sqrt{\frac{1}{n}\sum_{y=1}^{n}\left[Q_y^a - q^a\frac{(B_y^a)^2}{(B^{m,a})^2+(B_y^a)^2}\right]^2}$$

where n excludes all years for which Q_y^a information is unavailable (see Table 8.6).

11.4 Discussion and Results

The "Base Case" solution for the updated Mori-Butterworth model minimises the objective function in Equation 11.3. The various features of this solution are discussed below.

11.4.1 Base Case

Population trajectories

The Base Case model population trajectories for krill and its main krill-predators are shown in Figure 11.1.

The krill biomass trajectories for Region AI and PO oscillate in response to the perturbations introduced by the reduced whale populations. The biomass estimates from Wada and Tamura (2014) are much lower compared to those estimated by the Base Case. This is to be expected as those krill surveys only covered a limited part of the Antarctic region under consideration.

The fin and blue whale trajectories indicate that the populations in Region PO are increasing faster (starting from the year 1960) compared to the populations in Region AI. The minke populations increase to a maximum of 600 000 (around the year 1980) from an initial equilibrium level of 300 000 in Region PO and to a maximum of 300 000 (around the year 1960) from an initial equilibrium level of roughly 100 000 in Region AI. Thus, minke whales in Region PO peak later compared to Region AI. After reaching their maxima, minke whales in both Regions decrease with Region AI decreasing until the present, whereas for Region PO there is a sharp decline in population size to roughly 300 000 (around the year 2000) before increasing again to roughly 400 000 (around the year 2011). Thereafter, minke whales in Region PO start to decrease. The most recent increase in the Region PO minke population does not appear to be realistic as the observed trend for that period is negative suggesting a decrease in population size. Furthermore, the minke oscillations in Region PO appear to be delayed compared to Region AI. This is probably because heavy whaling was focused initially in Region AI, so that krill abundance started to increase earlier in Region AI.

Humpback whales start to increase around 1960, with the population in Region AI increasing slightly faster compared to the one in Region PO. Humpbacks appear now to be close to their initial equilibrium levels (more so for Region AI than Region PO) but are still increasing relatively rapidly. This could be because the trend input data, used in the Base Case, are obtained from models that did not allow abundance to increase beyond pre-exploitation levels (see Figure 11.4). Since the fin and blue whale populations have yet to recover, there is temporarily more krill available which allows the humpback whale populations to grow further. Note that the effects of whaling can be seen in all of the humpback, blue and fin whale population trajectories.

The fur seal population decreased to very low levels in the 1830s and only around the year 1960 did the population begin to increase (slowly at first). From around the year 1980, the fur seal population increased faster reaching a maximum of roughly 6 million by the year 2000. Since then, the population starts decreasing. This more recent increase seems unrealistically high as the fur seal increase rate was thought to be slowing down by the early 1990s (Boyd, 1993; see Section 6.2.3). Due to the space limitations on the fur seal breeding beaches, some associated restrictions on the population would likely come into play, but the ecosystem model being used here does not allow for this.

The crabeater seal population shows substantial change. For Region PO, this population remained relatively stable until around 1960, following which there was an increase to a maximum of roughly 4 million (around the year 1980). The population decreased to roughly 3 million around the year 2000 and subsequently increased again. For Region AI, the crabeater population remained relatively stable until 1920 when it increased quite rapidly reaching a maximum of 6 million (around the year 1960). Since that time, this population has been decreasing slowly. The crabeater seal numbers in both Regions AI and PO do not match the observations closely. This was considered acceptable as the crabeater abundance could be underestimated (see Section 6.3.2) and the associated abundance CVs were coarsely assigned a value 0.5. Thus, one would not expect an exact fit.

Population trends

Equation 11.16 can be rewritten as:

$$ln(R^{j,a}_{y_1-y_2}+1)=\frac{ln(N^{j,a}_{y_2})-ln(N^{j,a}_{y_1})}{y_2-y_1} \tag{11.19}$$

Equation 11.19 is used to compare the observed trends to the model estimated trends visually (Figures 11.2 and 11.3 for Regions AI and PO respectively).

For Region AI, the ecosystem model appears to capture the observed minke whale linear trends for the various periods reasonably well, although the model estimated linear trend for the period 1944/45 - 1967/68 does not reflect the actual population trajectory closely. All the model estimated linear minke trends fall within the confidence intervals of the observed linear trends. Similarly, the model captures the observed fur seal linear trends and just barely captures the observed fin whale linear trend. However, the model does not capture the observed humpback whale linear trend well (it estimates an annual rate of 0.008 compared to the observed 0.025). This could be because the observed humpback trend data come from IWC models which enforce different single species dynamics. Consequently, these IWC models did not allow abundances to increase beyond their initial levels, whereas the ecosystem model used here does not impose such a restriction.

For Region PO, the ecosystem model appears to capture the observed minke whale linear trends for the periods 1944/45 - 1967/68 (0.013 compared to the observed 0.020) and 1968/69 - 1987/88 (-0.020 compared to the observed -0.030) reasonably well. However, the model fails to capture this trend for the later period (1988/89 - 2003/04), i.e. the model estimates a positive trend of 0.006 compared to the negative observed trend of -0.003. This could be a consequence of the minke oscillations in Region PO being “delayed” compared to Region AI. (Note that the “observed” minke whale trends come from Punt’s (2014) SCAA analysis (see Section 5.6.2).) The model just barely captures the observed humpback and fin whale linear abundance trends.

IWC models: humpback whales

Figure 11.4 compares the humpback whale population trajectories from the Base Case to those for the IWC models. For Region AI, the Base Case estimates a lower initial equilibrium level and a faster increase from 1970 onwards. Note that the IWC models do not allow abundances to increase beyond their initial levels. For Region PO, the Base Case estimates that there were more humpback whales between 1910 and 1960 compared to the IWC models. As for Region AI, a faster increase rate is estimated for Region PO from 1960 onwards. Overall, the Base Case mirrors the IWC trajectories reasonably although it estimates a lower initial equilibrium value, an overall lower abundance between 1915 and 1940, and a faster increase rate from the year 1960 onwards.

SCAA analysis: minke whales

Figure 11.5 compares the minke whale population trajectories from the Base Case to the results from the SCAA model in Punt (2014). In Region AI, the two trajectories are quite similar except that the Base Case starts its oscillation earlier than the SCAA model. For Region PO, the Base Case estimates the minke abundance to be considerably larger than the SCAA model. Furthermore, the Base Case fails to reflect the later negative minke abundance trend in Region PO. The minke oscillations in Region PO are delayed in the Base Case compared to Region AI - this delay is not evident for the SCAA model. Overall, both models show an increase followed by a decrease with the Base Case reaching its maximum later (around 1975 compared to 1965 for the SCAA), and estimating a larger minke abundance.

Note, Stocks I and P in the SCAA model overlap with the Regions AI and PO. Consideration of a set of differently defined regions might improve these comparisons.

Minke stomach contents

Figure 11.6 shows the Base Case's fit to the minke stomach data (Q_y) determined from observations. For Region AI, the model matches an overall decrease in the weight of prey in the minke stomach contents. However, for Region PO, the Base Case fit shows a delay compared to the observations - only from the year 2005 onwards does the ecosystem model's estimation for the weight of prey in the minke stomachs begin to decrease. This could be because the minke oscillations in Region PO are starting too late for the Base Case.

Declines in the weight of prey in the minke stomach contents are thought to be reactions to less food being available for minke whales as other (previously heavily exploited) whale populations recover. However, this picture is somewhat confused owing to oscillations (fluctuations) in the krill biomass arising from the effects of delays on the dynamics.

For the future projections, the weight of prey in the minke stomach contents is predicted to oscillate until about the year 2200 for Region AI and about the year 2100 for Region PO. This behaviour is similar to that for the krill and minke whale projected trajectories under zero future catches, which are shown in Figure 11.7.

Future projections

Figure 11.7 reflects large amplitude oscillations in the krill, minke, fur seal and crabeater populations. Krill in Region AI are predicted to oscillate for roughly 200 years before reaching their initial equilibrium levels (around the year 2200). Those in Region PO are predicted to oscillate for roughly 100 years, reaching equilibrium around the year 2100.

The fin whale population trajectory exhibits steady recovery behaviour, i.e. no oscillations. The fin population in Region PO is predicted to reach its initial equilibrium level slower compared to the population in Region AI. Around the year 2200, the population in Region AI overshoots its initial equilibrium level (of roughly 200 000) slightly before slowly decreasing to that. The blue whale population trajectory also exhibits steady recovery behaviour. The blue whale population in Region AI is predicted to reach only two-thirds of its initial equilibrium level by the year 2500. The population in Region PO is predicted to reach its initial equilibrium level of roughly 50 000 by the year 2100.

After the minke populations in both Region AI and PO reach their respective maxima, these populations are predicted to oscillate for roughly 100 years before almost stabilising near their initial equilibrium levels. For the humpback whales, those in Region AI are predicted to oscillate for roughly 200 years, compared to the 100 years predicted for Region PO, before reaching their initial equilibrium levels. These oscillations are of much smaller amplitude compared to those in the krill, minke whale, crabeater and fur seal projected trajectories.

The fur seal population is predicted to oscillate for roughly 200 years, reaching a maximum abundance of 18 million. This is unrealistically high due to the space limitations on the fur seal breeding beaches. Space limitations included as a future model refinement would change this appreciably. Around the year 2200, the fur seal population is predicted to show a decrease in population size. The crabeater population follows a similar pattern to that of minke whales, with Region PO predicted to stabilise around its initial equilibrium level around the year 2100 whilst Region AI is predicted to decrease slowly to its initial equilibrium level starting from the year 2100.

Krill consumption

The total krill consumption for all six predators for Regions AI, PO and over both Regions for this analysis are reported in Figure 11.8. As seen before, the oscillations in the annual consumption of krill are delayed in Region PO (estimated to start around 1950) compared to Region AI (estimated to start around 1920). There are more oscillations and a greater increase in annual consumption of krill in Region AI compared to Region PO. This is probably due to the initial heavy whaling that was focused in Region AI but could also be because of imposing bounds on K_a. Perhaps surprisingly, despite the whaling induced depletion of the larger whale species, krill consumption increases after only a very small drop whose duration is brief; this is the result of a combination of density dependent effects on consumption rates and the rapid increase in abundance of other predators. Both Regions AI and PO show a decrease in annual consumption of krill after the year 2000 (with the decrease in Region PO starting a bit later).

Primary events

For Region AI, krill increased around the year 1910 owing to the reductions in blue, fin and humpback whale populations as a result of heavy whaling. Owing to this increase in krill biomass, crabeater seals and minke whales increased in population size in the early 1900s (with the Antarctic fur seals increasing in population size only during the late 1900s). The crabeater seals and minke whales benefitted first from this increase in krill biomass as their populations started increasing from around 1920.

Minke whales and crabeater seals started increasing at a faster rate around the year 1940 following heavy harvests of blue whales. The fur seals started increasing from the year 1960 and increased at a faster rate from around the year 1980. Crabeater seals increased to a maximum of 6 million around the year 1960. The minke whales behaved similarly, increasing to a maximum of roughly 300 000 around the same time. The fur seals increased from 1960 to a maximum of 6 million around the year 2000.

The krill biomass started decreasing around the 1940s, possibly due to the increase in the krill consumption by the crabeater seals and minke whales. This “lowered” biomass still remained above the krill’s initial biomass level until the 1980s when the krill biomass started to increase again. The humpback whale population started to increase in the mid-1960s, following their protection. These whales recovered at a faster rate compared to the slow recovery of the blue and fin whale populations. Around the same time, minke whale and crabeater seals began to decrease.

A similar story is evident for Region PO with the exception that the increases in minke whale, crabeater seal abundance and krill biomass begin later (around the year 1950). Unlike in Region AI, the fin and blue whales are recovering "faster" in Region PO, possibly due to their initial small population sizes and the lesser extent of whaling of these species in this Region.

11.4.2 Base Case vs the Mori-Butterworth Reference Case

Figures 11.9, 11.10 and 11.11 compare the total, Region AI and Region PO population trajectories from the Base Case and the Mori-Butterworth (2006) Reference Case respectively. Considering Figure 11.9, the most notable difference between the two results is the absence of oscillations, especially in the krill biomass trajectory and the much larger increase in krill abundance for the Mori-Butterworth Reference Case. The oscillations evident for the Base Case could be a result of setting the effective annual natural mortality rate of krill to a lower value compared to the approach in Mori and Butterworth (2006) (recall the Base Case considers some of the M for krill to result from predation by the major predators in the model, unlike for the Mori-Butterworth model which treated the predation by the major krill-predators as additional to the estimated krill natural mortality M). The main differences between the two models are discussed further below, on a regional basis.

For Region AI, Figure 11.10 shows that the Mori-Butterworth Reference Case estimates a much larger "krill surplus" between the years 1920 and 2000 compared to the Base Case. Again, this could be due to setting the effective annual natural mortality rate of krill to a lower value compared to that done in Mori (2005). A future refinement would be to consider changing this "basal" krill natural mortality rate in order to see how that impacts the krill dynamics. The Base Case estimates a larger initial equilibrium level for the fin whale trajectory. However, both sets of results appear to be consistent from the year 1960 onwards. This consistency is also seen for the blue whale population trajectory, although the Base Case estimates a slower increase from the year 1960 onwards. Despite the oscillations in the Base Case minke population trajectory, both sets of results estimate (roughly) the same initial equilibrium and maximum levels. The opposite is seen for the humpback population trajectories with the Base Case estimating a lower abundance between the years 1910 and 1930, and a faster increase rate from the year 1960 onwards. The effect of including the depensatory effect (Equation 11.1) can be seen clearly in the fur seal population trajectories: the Base Case estimates that the fur seals started increasing around the year 1960 compared to 1970, as estimated by the Mori-Butterworth Reference Case. Lastly, the Mori-Butterworth Reference Case estimates a much larger crabeater abundance between the years 1960 and 2000. This appears to be unrealistic, however Mori (2005) stated that her model could be "using" the crabeater population as a surrogate for other bird and fish species not included explicitly in the model. This seems likely not to be case as this thesis has shown that the main krill-eating bird and fish species do not consume as much krill as the six species considered in this ecosystem model (see Chapter 4).

In Figure 11.11, for Region PO, the Base Case estimates a lower initial equilibrium level for the krill biomass which oscillates whereas this is not evident in the Mori-Butterworth Reference Case. The reason would be the same as suggested above. As is for Region AI, the Base Case estimates a higher initial equilibrium level for the fin whale trajectory. However, from 1960 onwards, both models estimate a similar rate of increase for the fin whale population trajectory. Similarly, the Base Case estimates a higher initial equilibrium level for the blue whale population trajectory, and a faster increase rate from 1960 onwards compared to the Mori-Butterworth Reference Case. For the minke and humpback whale population trajectories, both models are consistent until the year 1920 for minke whales and the year 1960 for humpback whales, where the Base Case estimates higher abundances for both of these whale species (it also indicates oscillations in the minke whale population). The Base Case estimates a much higher initial equilibrium level for the crabeater seal population trajectory which oscillates, whereas the crabeater trajectory for the Mori-Butterworth Reference Case does not.

Both the Mori-Butterworth Reference Case and the Base Case estimate delays in the minke population trends in Region PO compared to Region AI. This is probably an effect of the heavy whaling that was focussed initially in Region AI. While there are some consistencies between the two models, there are also a number of differences.

Possible explanations for these differences could be: the lowering of the effective annual natural mortality rate of krill, the bounds imposed on K_a (a future model refinement would be to see how lowering/increasing this bound would impact the krill dynamics), the inclusion of information on a fin whale abundance trend, humpback trends being inferred from IWC models rather than the observations used in the Mori-Butterworth Reference Case, updates to the observed abundance and trend data, differences in the α values relating to density dependence in the natural mortalities of the species considered in the model (see Table 11.4), the 'best fit' values for the estimable parameters (see Table 11.5) and different plausible bounds for the estimable parameters (Chapter 8) between the two models.

The most notable differences in the α values are for the minke whales, fin whales, humpback whales, fur seals and crabeater seals. The Base Case estimates smaller α^m values but higher α^f and α^h values for Regions AI and PO compared to the Mori-Butterworth Reference Case. This suggests that for the Base Case, interference competition is small for minke whales (possibly related to the recovery of the previously depleted blue, fin and humpback whale populations) and relatively larger for the fin and humpback populations (since the fin and blue whale populations have yet to recover, there is for the time being more krill available allowing the humpbacks to grow further).

The Mori-Butterworth Reference Case fixed λ^f, μ^f and μ^h amongst the estimable parameters whereas the Base Case fixes λ^h and M^h. These parameters were fixed in order to assist with the model-fitting process. Furthermore, the Base Case increased the maximum function evaluations that are computed in ADMB from the default value of 1000 to 100 000. It is uncertain what was done in the fitting of the Mori-Butterworth Reference Case.

When comparing the krill consumption plots of the Base Case (Figure 11.8) and the Mori-Butterworth Reference Case, the Base Case estimates a lower annual consumption of krill biomass in Regions AI and PO overall for the krill-predators considered in the model. This is most likely due to the lower λ values estimated for the krill-predators (the exception is λ^c which is the same for both the Base Case and the Mori-Butterworth Reference Case) and the lower r^a values estimated in the Base Case (see Table 11.5). Note that, the Base Case and the Mori-Butterworth Reference Case estimate the same M, λ and (roughly) μ values for the crabeater seals. The only marked difference (in terms of crabeater seals) between the two models are the α values - this highlights the important role interference competition plays in the predictions from the Antarctic ecosystem model.

The Mori-Butterworth Reference Case did not predict any oscillations in the projected trajectories of krill and its main predators in its analysis. However, as mentioned before, the oscillations in the krill biomass of the Base Case could be due to setting the effective annual natural mortality rate of krill to a lower value compared to that done in Mori and Butterworth (2006), and this being reflected in the different dynamics of the krill-predators' system.

11.4.3 Base Case vs Sensitivity 1

For reasons of time limitations, the sensitivities explored in this thesis have been limited to key changes in the model approach compared to that of Mori and Butterworth (2006).

Sensitivity 1 is the Base Case without the minke stomach content data in the likelihood function (Equation 11.3). The comparisons between these two cases are plotted in Figures 11.12 and 11.13. There is not much difference between their results. This is not entirely surprising because there is considerable variability in the minke stomach content data (Figure 11.6), so that they do not carry much weight in the objective function.

Since Sensitivity 1 is so similar to the Base Case, the trend plots, humpback abundance comparison plot (the IWC model comparison), minke abundance comparison plot (the SCAA comparison), krill consumption plots and future projection plots are not included in this thesis. Furthermore, the analysis in Section 11.4.1 would be similar for this sensitivity case so that it is not discussed further. The values of the input data, estimated parameters, derived parameters and model estimated abundances and trends for Sensitivity 1 are reported in Tables 11.4, 11.5, 11.6 and 11.7.

11.4.4 Base Case vs Sensitivity 2

Sensitivity 2 excludes the depensatory effect from the fur seal-krill dynamics, i.e. Equations 11.1 and 11.2 are reverted back to Equations 10.1 and 10.2. As a result, the bounds on K_a are no longer imposed. Only the differences in the population trajectories between the Base Case and Sensitivity 2 are discussed.

Figure 11.14 compares the population trajectories for the Base Case and Sensitivity 2 for Region AI. The most notable differences for Sensitivity 2 are the bigger increase in the krill biomass trajectory between 1900 and 2015, the faster increase rates for the blue and fin population trajectories from the year 1960 onwards, the small response by the minke whale population (which also lies close to its observed abundance estimate), the delayed increase in the humpback trajectory with the humpback whales estimated to start recovering only around the year 1990 for Sensitivity 2 (compared to about 1960 as estimated by the Base Case), the very large (and unrealistic) increase in fur seal abundance from 1980 onwards and the smaller initial equilibrium level for the crabeater seals (which does match its observed abundance estimate).

Figure 11.15 compares the population trajectories of krill and its main predators for the Base Case and Sensitivity 2 for Region PO. The main differences for Sensitivity 2 here are as for Region AI, except for the smaller initial equilibrium levels for the fin, blue and humpback whale populations.

Sensitivity 2 estimates that most of the "krill surplus" was consumed by the fur seals and less so by the crabeater seals. Because of this, there was not much further krill for the minke whales to consume hence the small responses seen in their trajectories for Regions AI and PO.

Figure 11.16 compares the humpback whale population trajectories from Sensitivity 2 to those of the IWC models. This suggests that Sensitivity 2 underestimates the humpback whale abundance compared to the IWC models in general, more so for Region AI than Region PO. In Region PO, the humpback abundance is underestimated only from the year 1900 until 1960.

Similarly, Figure 11.17 compares the minke whale population trajectories from Sensitivity 2 to the SCAA model of Punt (2014). In essence, Sensitivity 2 is unable to duplicate the extent of variation shown in the SCAA trajectories.

This comparison illustrates the initial issues which arose with the ecosystem model, and why the depensatory effect needed to be included. By including this effect, a much better fit overall resulted.

11.5 Response to the Willis (2014) article

As mentioned in Chapter 1, Willis (2014) states that the Mori-Butterworth (2006) model failed to provide an explanation for the observed changes in krill abundance for two reasons: the Mori-Butterworth (2006) hypothesis was falsified and the model's initialisation was implausible. Each reason advanced is discussed below.

The Mori-Butterworth hypothesis was falsified

Willis (2014) states that the Mori-Butterworth model proposed that minke whales and crabeater seals increased in abundance between 1920 and 1950 due to the increased availability of krill. This then supposedly led to compensatory predatory pressure, leading to a decrease in krill abundance from 1950 while whaling further reduced whale abundances until 1970. Willis (2014) says that the Mori-Butterworth authors "confirmed" that their model would not fit with whales alone hence crabeater seals were included to drive the krill abundance down after 1950. For this to be plausible, the minke whale and crabeater seal populations would have had to increase quickly from previously low levels (before the 1950s) during the last 20 years of commercial whaling.

Willis (2014) further states that the Mori-Butterworth model "suggests" that minke whales increased from a low of roughly 300 000 to 1 200 000, whilst crabeater seals increased from a low of roughly 1 000 000 to roughly 20 000 000. He goes onto argue that since there is no evidence to support an increase in minke whale abundances, this is sufficient to falsify the Mori-Butterworth hypothesis. He suggests that this is supported further by genetic studies of minke whales (Ruegg *et al.*, 2010) and by contemporary reports on crabeater seals. Willis (2014) quotes Marr (1962) where crabeater seals were reported by every expedition passing the Antarctic pack-ice during the austral summer before 1962 or by those staying on the pack-ice during the austral winter. An example of the latter was the Belgian expedition in 1898 which estimated the crabeater seal abundance to be between 2 - 5 million. Willis (2014) states that there was no mention of a 20-fold increase in crabeater abundance before 1950 (as was indicated by the Mori-Butterworth model results) and that a 44-year time series in the Antarctic Peninsula region suggested no long-term trend in crabeater abundance after 1950 (Ballance *et al.*, 2005).

The criticisms of Willis (2014) are summarised below.

1) The Mori-Butterworth (2006) model would not fit with whales alone. As a result, crabeater seals were included to decrease krill abundance further after 1950.
2) A genetic study by Ruegg *et al.* (2010) suggests that there has not been an increase in minke whale abundance.
3) Analyses in Ballance *et al.* (2005) show no long-term trend in crabeater abundance in the Antarctic after 1950.
4) All of these factors together are sufficient to falsify the Mori-Butterworth (2006) hypothesis.

In response, it should be noted that crabeater seals were included in the Mori-Butterworth (2006) model because they are a main krill-predator (see Chapter 4 of this thesis). The Mori-Butterworth model fitted whales alone only as one of the six sensitivities conducted in their analysis.

The Ruegg *et al.* (2010) genetic study estimates a long-term population size for Antarctic minke whales, but this has a wide 95% confidence interval of 374 000 to 1 150 000 minke whales. Both the Mori-Butterworth (2006) model and the Base Case for this thesis estimate the starting population size of minke whales to be only marginally below the lower limit of this confidence interval. When one takes into account the fact that the minke whale estimates input to the ecosystem model are probably low because of failure to account for whales found in the pack-ice in particular, it seems clear that there is no real inconsistency between these various results.

Furthermore, Ballance *et al.* (2005) reference Boveng and Bengtson (1997) and state that those authors compiled a 44-year time series of crabeater seal cohort strength in the Antarctic Peninsula region. Ballance *et al.* (2005) conclude that there are obvious year-to-year variations in the abundance data with patterns of clear fluctuations that suggest longer term cycles, but that there are no apparent long term trends. However, in Boveng and Bengtson (1997), those authors state that the likelihood function for the sample age distribution (used to estimate the relative strength of cohorts) is derived **by assuming** that there is no trend in the crabeater seal population size. Hence, the claim by Willis (2014) and by Ballance *et al.* (2005) on the basis of the analyses of Boveng and Bengtson (1997) that there is no long-term trend in the crabeater seal abundance in the Antarctic is unfounded. That was an input assumption to their calculations; indeed such data by themselves cannot provide an estimate of trend.

Marr (1962) references Scheffer (1958) who estimated the crabeater seal numbers to be between 2 - 5 million. Scheffer (1958) states that "[m]inimum and maximum estimates are given for each [seal] species and subspecies. The width of the gap between minimum and maximum is an indication of the author's confidence in the estimate (the wider the less confidence)". This suggests that Scheffer's (1958) crabeater seal abundance estimates could be biased, and Scheffer does not explain how he estimated these numbers. As a result, these numbers cannot be used reliably for analyses and comparisons.

The Mori-Butterworth (2006) hypothesis and conclusion was that it is possible to explain the observed population trends of the main Antarctic krill-predators through predator-prey interactions only. The commentary above shows that none of the counter arguments offered by Willis in questioning their results are valid.

The Mori-Butterworth initialisation was implausible

Willis (2014) states that the Mori-Butterworth model assumed that too few whales consumed too few krill in the 19^{th} century. This then allowed the model to fit an enormous proportional increase in krill abundance to levels consistent with contemporary reports of the 1970s. The Mori-Butterworth estimate of krill consumed by whales that were killed through whaling was roughly 50 million tonnes compared to the 150 million tonnes estimated by Laws (1977). Willis (2014) calls this value small and implausible as whales alone had a biomass of roughly 60 - 70 million tonnes. Willis (2014) further states that Mori-Butterworth (2006) excluded all sei whales, another krill-predator and 50% of the fin whales, treating them as two separate populations. Furthermore, he comments that the Mori-Butterworth model suggested relatively high ranges of natural mortality for the larger baleen whales, which allowed the model to fit the larger whales' dynamics on the basis of a low average lifespan and as a result, a quicker turnover.

Willis (2014) comments that the pristine abundances of blue (187 000) and fin whales (235 000) as estimated by Mori-Butterworth are very small compared to estimates from other studies (327 000 and 625 000 respectively from Christensen (2006)). Furthermore, Willis (2014) claims that Mori-Butterworth model relied on whales being starved through "overfishing" of krill in the 19^{th} century. He then argues that that is falsified by contemporary reports based on stomach contents such as Hardy and Gunther (1936), where whales examined during the whaling period had stomachs full of krill. Willis (2014) states that the Mori-Butterworth model indicated that there was a high-level of inter-specific competition which suppressed the original abundances of both minke whales and crabeater seals, but that there is no independent evidence to support this.

In summary, the criticisms of Willis (2014) are as follows.

1) The Mori-Butterworth (2006) “krill surplus” estimate, which is appreciably smaller than that of Laws’ (1977), is implausibly low.
2) Mori and Butterworth (2006) excluded all the sei whales, a krill-predator and half of the fin whale population.
3) The Mori-Butterworth (2006) model estimates small pristine abundances for the blue and fin whales compared to Christensen (2006).

In response, it should be noted that Mori and Butterworth (2006) outline the main reason for the difference between their “krill surplus” of roughly 50 million tonnes compared to the 150 million tonnes calculated by Laws (1977), namely, different assumptions for predator consumption rates in relation to krill biomass. Laws (1977) assumes that the krill consumed per capita by whales are independent of the krill biomass, i.e. krill-predators each consume a certain amount of krill, but that does not take the availability of krill into account. Mori (2005) considered this assumption to be extreme as it was likely that krill-predators would find it difficult to consume the same amount of krill when the krill biomass was low (in the form of smaller krill patch sizes or fewer patches). As a result, the Mori-Butterworth (2006) model included Holling Type III functional response curves to incorporate the effects of the dependence of krill consumption on the krill biomass. Thus, the Mori-Butterworth (2006) “krill surplus” result is perfectly plausible.

As outlined in Chapter 2, although sei whales are krill-predators, they are found mostly between the Subtropical and Antarctic Convergences (Figure 2.1) during the austral summer. They are hardly found south of 60°S, and hence were not included in the Mori-Butterworth (2006) model. Furthermore, Mori and Butterworth (2006) did not exclude 50% of the fin whale population. As mentioned in Chapter 4, the current fin whale feeding distribution is located further north compared to the other baleen whales’ feeding grounds. Mori (2005) assumed that the “krill” they eat belongs to a different population to the krill eaten further south. The 50% assumption attempted to take this into account, i.e. 50% of krill consumed by fin whales is to be found further north.

Although the pristine abundances of the blue and fin whales, as calculated in Mori-Butterworth (2006), are less to those calculated in Christensen (2006), direct comparisons and inferences cannot be made as attempted by Willis (2014). Christensen (2006) uses a *Stochastic Stock Reduction Analysis* (SSRA). This is a single-species modelling approach, which ignores the species interaction effects that the Mori-Butterworth model incorporates, so it is not surprising that it arrives at different estimates.

In summary, the criticisms of the Mori-Butterworth (2006) model in Willis (2014) are generally unfounded or reflect misunderstandings.

11.6 Improvements and further sensitivities

The possible improvements and further sensitivities to the model mentioned in this chapter are as follows:

1) Including a space limitation term for the fur seals in the model.

2) Considering a set of differently defined regions for the model, e.g. Regions AO and PI (Figure 5.3) in place of Regions AI and PO (Figure 5.2). Figure A.1 shows the catch histories of the main krill-eating whale species between these four Regions to show the differences between these two sets.

3) Increasing and/or decreasing the effective annual natural mortality rate of krill.

4) Increasing and/or decreasing the bounds imposed on K_a.

The current method used in the model developed in this thesis assumes deterministic dynamics. As a result, the implications of allowing for process error, to some extent, also merit further investigation. Note also that most of the abundance and trend information available is for a limited period only (mainly near the turn of the last century). Further investigation is required to determine whether this might be leading to biases in the model estimates.

Furthermore, estimation precision needs to be evaluated further for the Base Case. However, this will not be straightforward due to the difficulty in achieving convergence at the level that a Hessian can be computed. These precision issues could be a result of some of the estimable parameters hitting their bounds.

11.7 Summary

This chapter developed and discussed the Base Case for the updated and refined Mori-Butterworth model. The Base Case population trajectories of krill and some of the krill-predators manifest oscillations. The humpback whale trajectories in the Base Case are broadly consistent with the humpback trajectories from the IWC models. This consistency is not as evident in the comparison between the Base Case minke whale trajectories to those of the SCAA model (more so for Region PO than Region AI). Furthermore, the Base Case does not fully capture the minke trends for Region PO and the humpback trend for Region AI. The Base Case also predicts oscillations in the projected trajectories of krill and some of its main predators.

The Base Case is compared to the Mori-Butterworth Reference Case; there are similarities but also many differences. These differences include the reduction of the effective annual natural mortality rate of krill, the bounds imposed on K_a, the inclusion of information on a fin whale trend, the humpback trends used to fit the ecosystem model being obtained from the IWC models, updates to the observed abundance and trend data, differences in α values (which take into account interference competition) and the differences in the 'best fit' values of the estimable parameters and in their plausible bounds.

The Base Case is also compared to two sensitivities related to new aspects of the updated model: Sensitivity 1 (a version of the Base Case that excludes minke stomach content data) and Sensitivity 2 (the model without the depensatory effect on fur seals). This chapter also reviews the criticisms made by the Willis (2014) article. In general, these were unfounded or reflected misunderstandings.

Overall, the inclusion of the minke stomach data hardly changes the predictions of the model and the inclusion of a depensatory effect leads to a much better fit. However, more sensitivities need to be performed before an Antarctic ecosystem model, more consistent with all the data, might be selected to inform management advice.

Species	Annual per capita consumption of krill (mt)	Year of abundance estimate	Abundance (Number)	Total annual krill consumption $\times 10^3$ (mt)
Blue whale	490.8	1997/98	2 206	1 083
Fin whale	310.4	1997/98	38 185	11 853
Humpback whale	200.7	2014/15	97 188	19 506
Minke whale	63.2	1997/98	469 867	29 696
Crabeater seal	4.45	2000/01	7 719 714	34 353
Leopard seal	4.02	2000/01	35 500	143
Antarctic fur seal	1.77	1990/91	1 550 000	2 744
Adélie penguin	0.06	2013/14	3 655 698	216
Mackerel icefish	8.07 x 10^{-6}	2014/15	32 102 million	259
Marbled rockcod	0.03	-	1 477 111	44

Table 11.1: Summary of the annual per capita consumption of krill (mt) and the total consumption of krill by weight (mt) for all the main krill-predators considered in this thesis.

Species		Abundance Estimate	CV	Source
Blue whale	$\mathrm{N}^{b,AI}_{1997/98}$	853	0.33	Branch (2007)
	$\mathrm{N}^{b,PO}_{1997/98}$	1 353	0.35	
Minke whale	$\mathrm{N}^{m,AI}_{1997/98}$	183 256	0.13	IWC (2013)
	$\mathrm{N}^{m,PO}_{1997/98}$	286 611	0.08	
Fin whale	$\mathrm{N}^{f,AI}_{1997/98}$	10 591	0.5	see Section 5.6.3 of this thesis
	$\mathrm{N}^{f,PO}_{1997/98}$	27 594	0.5	
Humpback whale	$\mathrm{N}^{h,AI}_{2014/15}$	66 182	0.07	see Section 5.6.4 of this thesis
	$\mathrm{N}^{h,PO}_{2014/15}$	31 893	0.06	
Antarctic Fur Seal	$\mathrm{N}^{a,AI}_{1930/31}$	100	0.5	Bonner (1968)
	$\mathrm{N}^{a,AI}_{1975/76}$	369 000	0.5	Payne (1977, 1979), McCann and Doidge (1987)
	$N^{a,AI}_{1990/91}$	1 550 000	0.5	Boyd (1993)
Crabeater Seal	$N^{c,AI}_{2000/01}$	3 910 212	0.5	Southwell *et al.* (2012), Gurarie *et al.* (2015)
	$\mathrm{N}^{c,PO}_{2000/01}$	3 809 502	0.5	

Table 11.2: Summary of the observed/inferred abundance estimates for the krill-feeding predators considered in this thesis.

Species		Fitted Trend	CV	Source
Blue whale	$\mathrm{N}^{b}_{1980/81}$	592*	0.40	Branch (2007)
	$\mathrm{N}^{b}_{1987/88}$	686*	0.47	
	$\mathrm{N}^{b}_{1997/98}$	2 249*	0.36	
Fin whale	$\mathrm{R}^{f,AI}_{1995/96-2007/08}$	0.116	0.387	see Section 5.6.3 of this thesis
	$\mathrm{R}^{f,PO}_{1996/97-2008/09}$	0.116	0.387	
Humpback whale	$\mathrm{R}^{h,AI}_{2010/11-2014/15}$	0.025	0.20	see Section 5.6.4 of this thesis
	$\mathrm{R}^{h,PO}_{2010/11-2014/15}$	0.058	0.11	
Minke whale	$\mathrm{R}^{m,AI}_{1945/46-1967/68}$	0.013	-	Punt (2014)
	$\mathrm{R}^{m,AI}_{1968/69-1987/88}$	-0.029	-	
	$\mathrm{R}^{m,AI}_{1988/89-2003/04}$	0.010	-	
	$\mathrm{R}^{m,PO}_{1945/46-1967/68}$	0.020	-	
	$\mathrm{R}^{m,PO}_{1968/69-1987/88}$	-0.030	-	
	$\mathrm{R}^{m,PO}_{1988/89-2003/04}$	-0.003	-	
Antarctic Fur Seal	$\mathrm{R}^{a,AI}_{1957/58-1971/72}$	0.168	0.5	Payne (1977)
	$\mathrm{R}^{a,AI}_{1976/77-1989/90}$	0.098	0.5	Boyd (1993)
	$\mathrm{R}^{a,AI}_{1990/91-1998/99}$	0.098	0.5	Boyd (1993), SCAR (2000)

Table 11.3: Summary of the observed abundance trend estimates for the krill-feeding predators considered in this thesis. For blue whales, estimates of abundance (*) are given; they provide information on trend to the model.

Input parameters	Mori-Butterworth Reference Case	Base Case	Sensitivity 1	Sensitivity 2
$B^{b,AI}$	1.70×10^{8}	1.700×10^{8}	1.700×10^{8}	1.700×10^{8}
$B^{b,PO}$	7.00×10^{7}	7.000×10^{7}	7.000×10^{7}	7.000×10^{7}
$\eta^{b,AI}$	4.00×10^{-8}	4.001×10^{-8}	4.001×10^{-8}	4.001×10^{-8}
$\eta^{b,PO}$	1.00×10^{-6}	1.000×10^{-6}	1.000×10^{-6}	1.000×10^{-6}
$\eta^{m,AI}$	3.00×10^{-7}	3.000×10^{-7}	3.000×10^{-7}	3.000×10^{-7}
$\eta^{m,PO}$	2.00×10^{-7}	2.000×10^{-7}	2.000×10^{-7}	2.000×10^{-7}
$\eta^{f,AI}$	4.00×10^{-8}	3.999×10^{-8}	3.999×10^{-8}	3.999×10^{-8}
$\eta^{f,PO}$	7.00×10^{-8}	7.000×10^{-8}	7.000×10^{-8}	7.000×10^{-8}
$\eta^{h,AI}$	1.25×10^{-6}	1.249×10^{-6}	1.249×10^{-6}	1.249×10^{-6}
$\eta^{h,PO}$	1.50×10^{-6}	1.500×10^{-6}	1.500×10^{-6}	1.500×10^{-6}
$\eta^{s,AI}$	3.50×10^{-9}	3.200×10^{-9}	3.200×10^{-9}	3.200×10^{-9}
$\eta^{c,AI}$	7.00×10^{-9}	7.001×10^{-9}	7.001×10^{-9}	7.001×10^{-9}
$\eta^{c,PO}$	6.00×10^{-9}	7.001×10^{-9}	7.001×10^{-9}	6.001×10^{-9}

Table 11.4 – continued from the previous page

α parameters	Mori-Butterworth (2006) Reference Case	Base Case	Sensitivity 1	Sensitivity 2
$\alpha^{b,AI}$	0.22	0.15	0.17	0.15
$\alpha^{b,PO}$	0.90	0.82	0.94	0.56
$\alpha^{m,AI}$	0.35	0.22	0.18	0.42
$\alpha^{m,PO}$	1.36	0.64	0.63	0.51
$\alpha^{f,AI}$	0.12	0.29	0.29	0.25
$\alpha^{f,PO}$	0.12	0.23	0.23	0.09
$\alpha^{h,AI}$	1.12	2.68	2.65	2.68
$\alpha^{h,PO}$	0.88	2.10	2.08	0.69
$\alpha^{s,AI}$	0.15	0.05	0.05	0.03
$\alpha^{c,AI}$	0.02	0.13	0.14	0.04
$\alpha^{c,PO}$	0.06	0.19	0.17	0.04

TABLE 11.4: Values of the input parameters η, and B^{blue}, and the α parameters for the Base Case, Sensitivity 1, Sensitivity 2 and for the Mori-Butterworth (2006) Reference Case.

Estimated parameters	Mori-Butterworth Reference Case	Base Case	Sensitivity 1	Sensitivity 2
$N^{b,AI}_{1780}$	162 332	162 532	168 095	188 826
$N^{b,PO}_{1780}$	26 861	36 273	36 475	28 968
$N^{m,AI}_{1780}$	47 155	68 442	58 141	116 934
$N^{m,PO}_{1780}$	271 720	300 000	300 000	215 331
$N^{f,AI}_{1780}$	151 505	221 724	221 753	190 558
$N^{f,PO}_{1780}$	87 187	99 308	99 093	36 433
$N^{h,AI}_{1780}$	71 589	71 206	70 555	64 359
$N^{h,PO}_{1780}$	47 095	46 567	46 189	13 703
$N^{s,AI}_{1780}$	2 898 590	2 934 594	2 914 770	2 849 673
$N^{c,AI}_{1780}$	241 045	1 279 810	1 376 922	510 653
$N^{c,PO}_{1780}$	733 511	1 887 084	1 721 576	498 953
λ^b	450.62	165.93	166.87	487.80
λ^m	32.13	21.06	21.09	22.35
λ^f	[110.40]	103.60	103.60	103.51
λ^h	108.00	[74.35]	[74.35]	73.47
λ^s	2.71	0.68	0.68	1.76
λ^c	5.51	5.51	5.51	3.32

Table 11.5 – continued from the previous page

Estimated parameters	Mori-Butterworth (2006) Reference Case	Base Case	Sensitivity 1	Sensitivity 2
μ^b	0.16	0.29	0.28	0.18
μ^m	0.20	0.31	0.33	0.15
μ^f	[0.16]	0.25	0.25	0.29
μ^h	[0.18]	0.15	0.16	0.50
μ^s	0.28	0.87	0.86	0.57
μ^c	0.24	0.20	0.20	0.13
M^b	0.03	0.04	0.04	0.05
M^m	0.04	0.09	0.10	0.08
M^f	0.05	0.03	0.03	0.03
M^h	0.08	[0.03]	[0.03]	[0.03]
M^s	0.07	0.19	0.21	0.34
M^c	0.07	0.07	0.07	0.08
r^{AI}	0.40	0.22	0.22	0.48
r^{PO}	0.58	0.31	0.29	0.26
-lnL				
LL^b_{abund}	0.000	0.008	0.005	0.000
LL^b_{trend}	-1.806	-0.827	-0.872	-2.347
LL^m_{abund}	0.001	0.159	0.104	0.438
LL^m_{trend}	0.002	1.435	1.195	9.284
LL^f_{abund}	0.000	0.026	0.026	0.001
LL^f_{trend}	-	0.054	0.056	0.009
LL^h_{abund}	0.000	0.023	0.035	0.000
LL^h_{trend}	0.186	0.028	0.030	0.131
LL^s_{abund}	0.959	0.002	0.062	1.581
LL^s_{trend}	0.692	0.001	0.002	0.033
LL^c_{abund}	2.347	0.357	0.426	0.011
MS^{AI}	-	5	-	-
MS^{PO}	-	7	-	-
$-lnL$	2.381	13.264	1.068	9.140

TABLE 11.5: Values of the estimated parameters and $-lnL$ for the Base Case, Sensitivity 1, Sensitivity 2 and for the Mori-Butterworth (2006) Reference Case. Parameters in square parenthesis were fixed rather than estimated in order to assist with the modelling fit.

Derived parameters	Mori-Butterworth Reference Case	Base Case	Sensitivity 1	Sensitivity 2
K_{AI}	8.22×10^8	1.87×10^9	4.27×10^9	3.94×10^8
K_{PO}	1.25×10^8	1.86×10^9	4.26×10^9	2.49×10^8
$B^{m,AI}$	1.45×10^8	1.02×10^8	1.04×10^8	5.91×10^7
$B^{m,PO}$	5.29×10^7	4.37×10^7	4.50×10^7	2.59×10^7
$B^{f,AI}$	1.23×10^8	1.83×10^8	1.74×10^8	3.09×10^8
$B^{f,PO}$	7.19×10^7	1.04×10^8	1.02×10^8	1.78×10^8
$B^{h,AI}$	2.33×10^7	3.90×10^7	4.11×10^7	2.24×10^8
$B^{h,PO}$	2.31×10^7	3.02×10^7	3.13×10^7	1.89×10^8
$B^{s,AI}$	1.46×10^8	1.44×10^8	1.30×10^8	9.57×10^7
$B^{c,AI}$	1.34×10^8	9.80×10^7	9.14×10^7	8.60×10^7
$B^{c,PO}$	7.34×10^7	5.20×10^7	5.05×10^7	4.61×10^7
B^{AI}_{1780}	9.26×10^7	7.90×10^7	7.52×10^7	1.19×10^8
B^{PO}_{1780}	5.21×10^7	4.38×10^7	4.27×10^7	6.34×10^7
q^{AI}	-	54.96	-	-
q^{PO}	-	49.04	-	-

TABLE 11.6: Values of derived parameters (i.e. functions of the parameters that are estimated directly) for the Base Case, Sensitivity 1, Sensitivity 2 and for the Mori-Butterworth (2006) Reference Case.

Observed quantity	Region AI	Base Case	Sensitivity 1	Sensitivity 2
$N^b_{1997/98}$	853	876	874	855
$N^m_{1997/98}$	183 256	197 010	194 507	161 834
$N^h_{2014/15}$	66 182	67 117	67 339	66 221
$N^f_{1997/98}$	10 591	10 925	10 787	10 617
$N^c_{2000/01}$	3 910 212	5 648 260	5 661 630	3 695 900
$N^s_{1930/31}$	100	102	115	120
$N^s_{1975/76}$	369 000	379 573	338 070	188 734
$N^s_{1990/91}$	1 550 000	1 554 930	1 538 760	2 855 620
$R^m_{1945/46-1967/68}$	0.013	0.016	0.016	0.009
$R^m_{1968/69-1987/88}$	-0.029	-0.030	-0.029	-0.014
$R^m_{1988/89-2003/04}$	0.010	0.006	0.006	0.012
$R^h_{2010/11-2014/15}$	0.025	0.008	0.004	0.081
$R^f_{1995/96-2007/08}$	0.116	0.026	0.025	0.113
$R^s_{1957/58-1971/72}$	0.168	0.170	0.151	0.197

Table 11.7 – continued from the previous page

Observed quantity	Region AI	Base Case	Sensitivity 1	Sensitivity 2
$R^s_{1976/77-1989/90}$	0.098	0.098	0.108	0.194
$R^s_{1990/91-1998/99}$	0.098	0.116	0.124	0.177
	Region PO			
$N^b_{1997/98}$	1 353	1 308	1 322	1 341
$N^m_{1997/98}$	286 611	283 274	284 598	287 702
$N^h_{2014/15}$	31 893	31 882	31 914	31 868
$N^f_{1997/98}$	27 594	24 741	24 684	26 994
$N^c_{2000/01}$	3 809 502	3 092 750	2 890 340	3 640 820
$R^m_{1945/46-1967/68}$	0.020	0.013	0.014	0.005
$R^m_{1968/69-1987/88}$	-0.030	-0.020	-0.021	-0.003
$R^m_{1988/89-2003/04}$	-0.003	0.006	0.006	0.002
$R^h_{2010/11-2014/15}$	0.058	0.034	0.034	0.011
$R^f_{1996/97-2008/09}$	0.116	0.027	0.025	0.065
	Blue whale trend			
$N^b_{1980/81}$	592	1 440	1 425	457
$N^b_{1987/88}$	686	1 640	1 642	884
$N^b_{1997/98}$	2 249	2 184	2 196	2 195

Table 11.7: Values of the input values for the observed abundances and trends and of the corresponding estimates for the Base Case, Sensitivity 1 and Sensitivity 2 for Regions AI and PO.

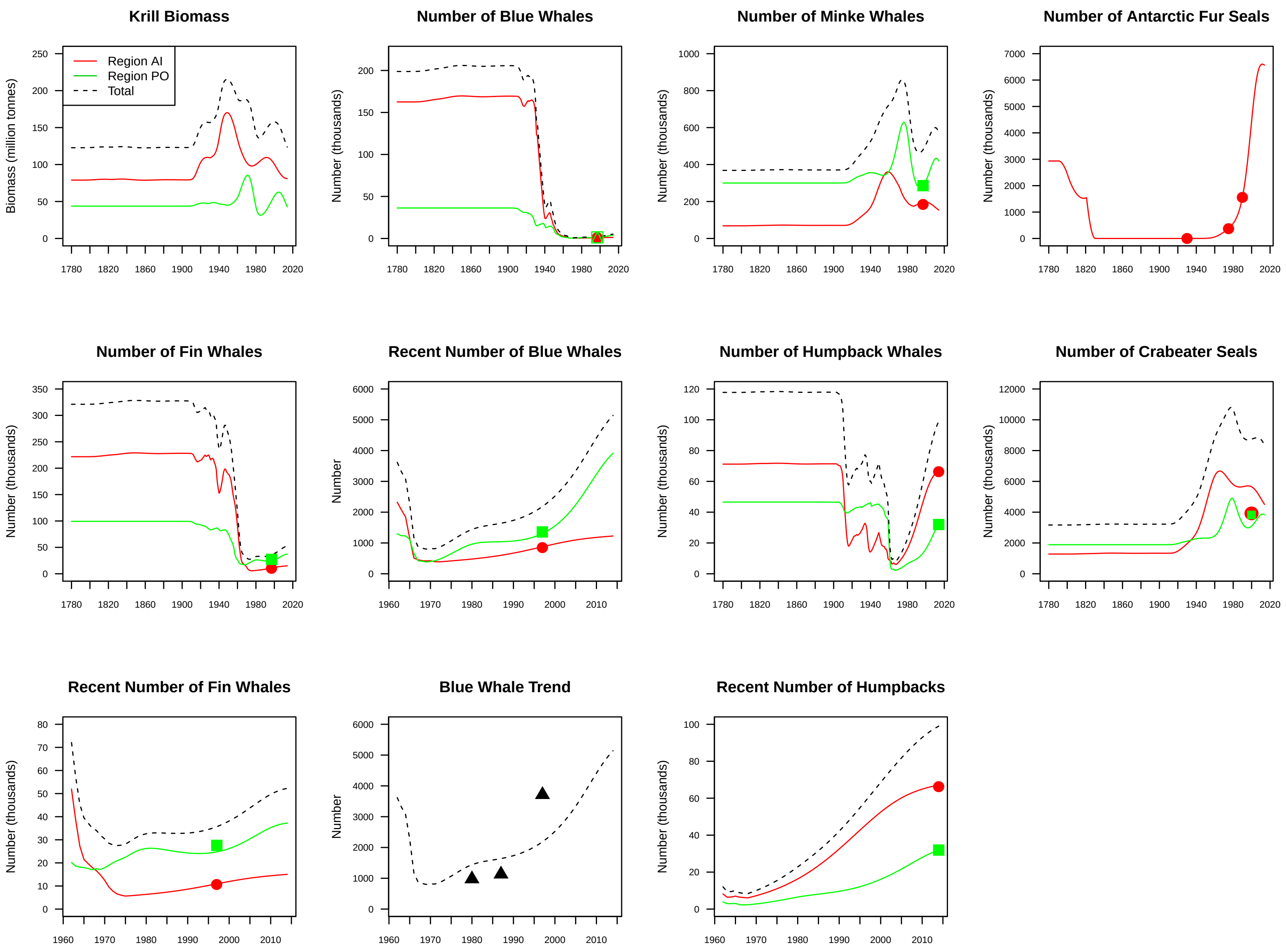


FIGURE 11.1: The Base Case population model trajectories for krill and its main predators in the Antarctic. A red circle/green square represents a survey-based abundance estimate for Region AI/PO respectively, which has been used in the model fit. The triangles represent the blue whale abundance estimates from surveys for Regions AI and PO combined. These survey estimates were used in the model fit to reflect the blue whale abundance trend.

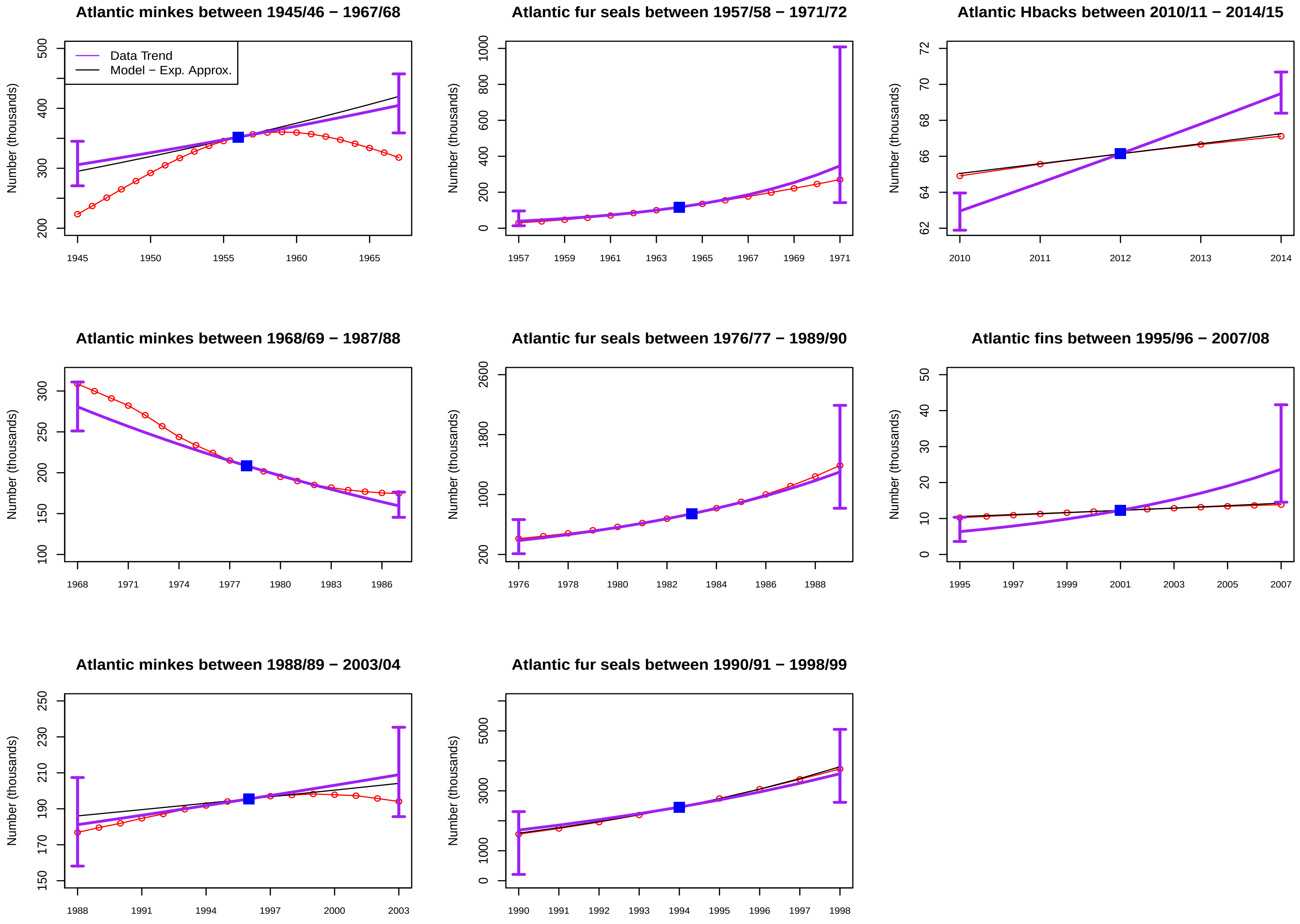


FIGURE 11.2: The Base Case abundance trajectories for **Region AI** are shown by the red dotted curves. The slope of the purple line represents the observed linear trend and the slope of the black line represents the model estimated linear trend. The 95% confidence interval about the observed trend is indicated by the bars for the initial and final years.

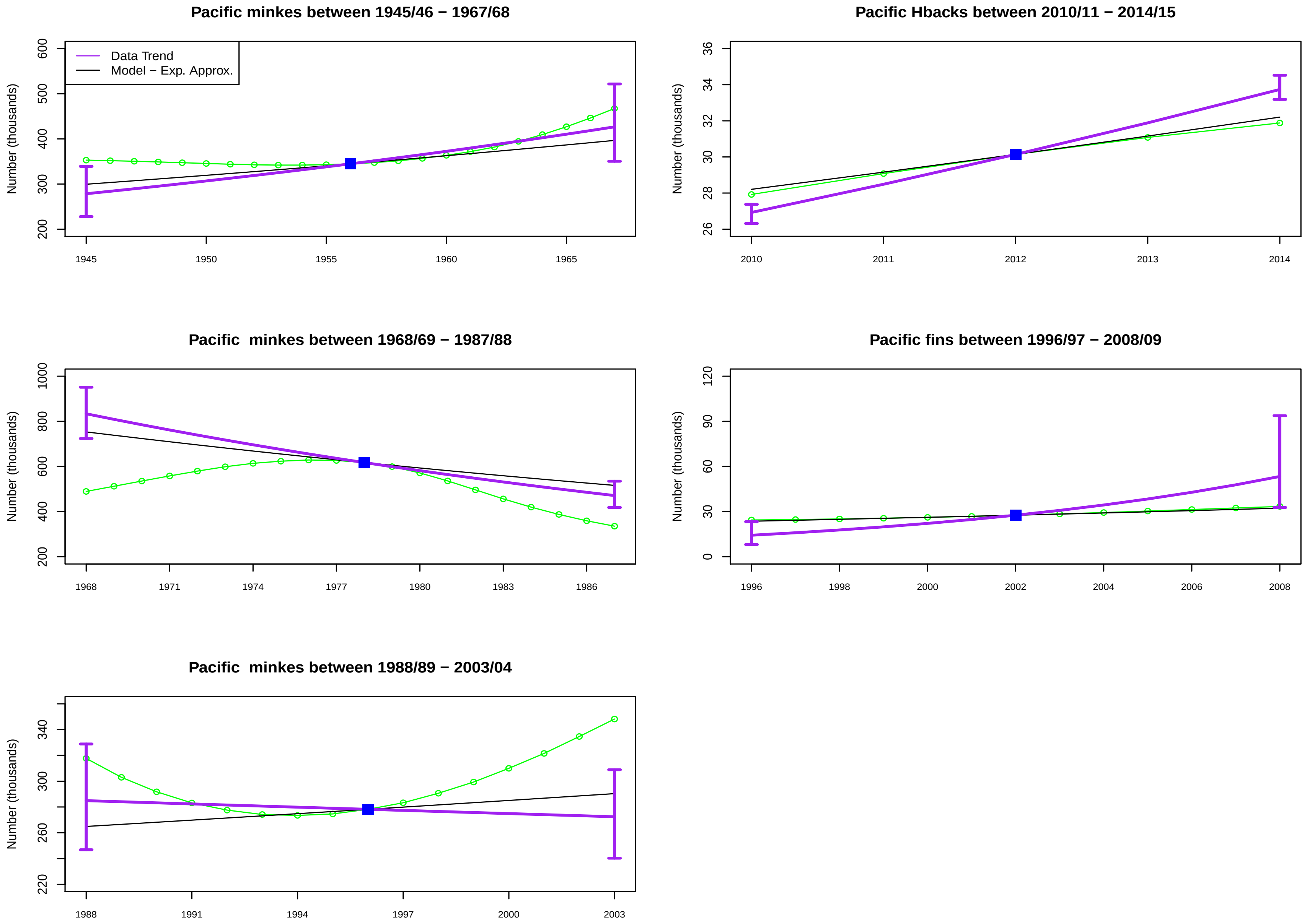


FIGURE 11.3: The Base Case abundance trajectories for **Region PO** are shown by the green dotted curves. The slope of the purple line represents the observed linear trend and the slope of the black line represents the model estimated linear trend. The 95% confidence interval about the observed trend is indicated by the bars for the initial and final years.

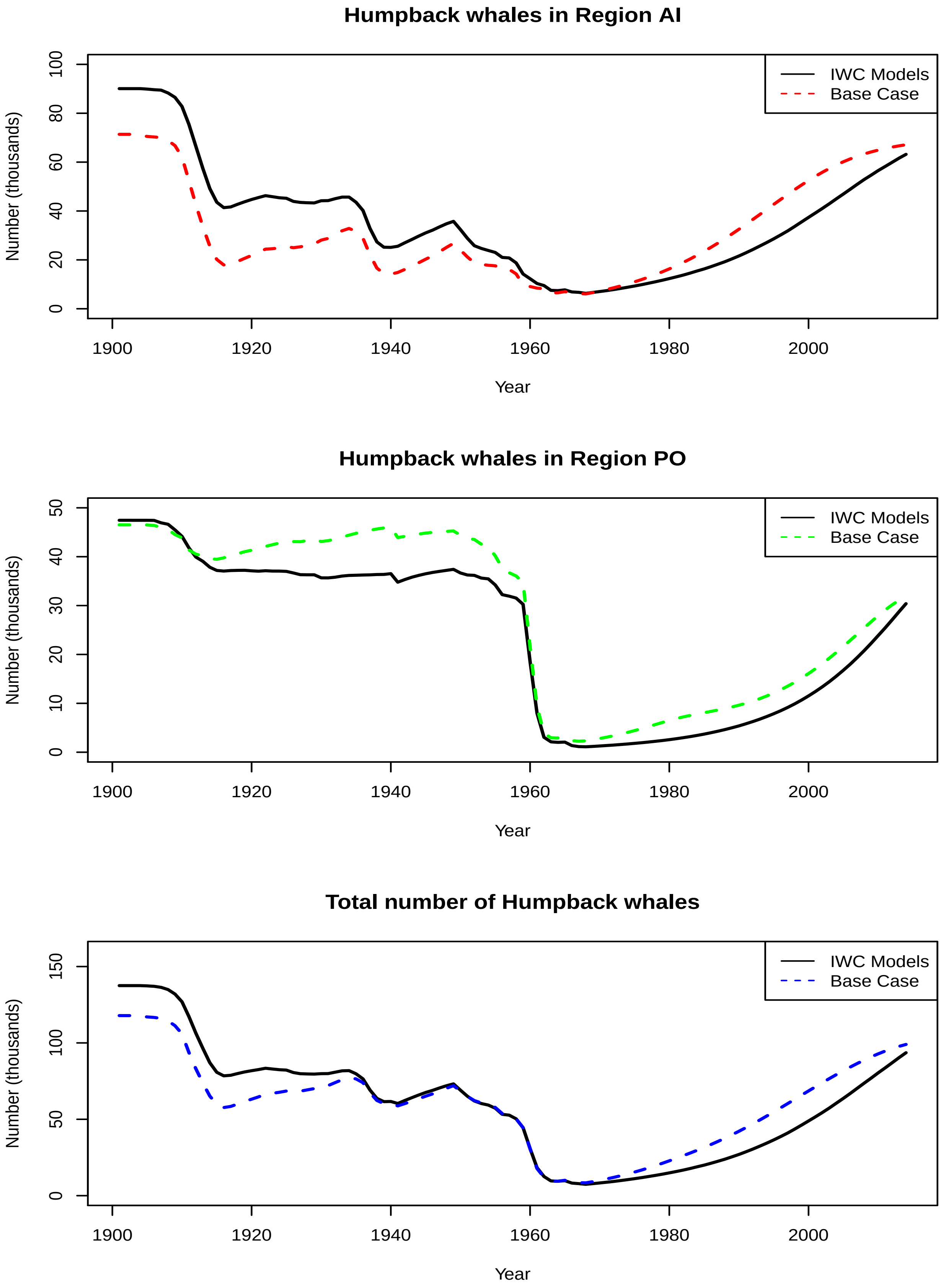


FIGURE 11.4: Comparison between the humpback whale population trajectories for the Base Case and from the IWC models.

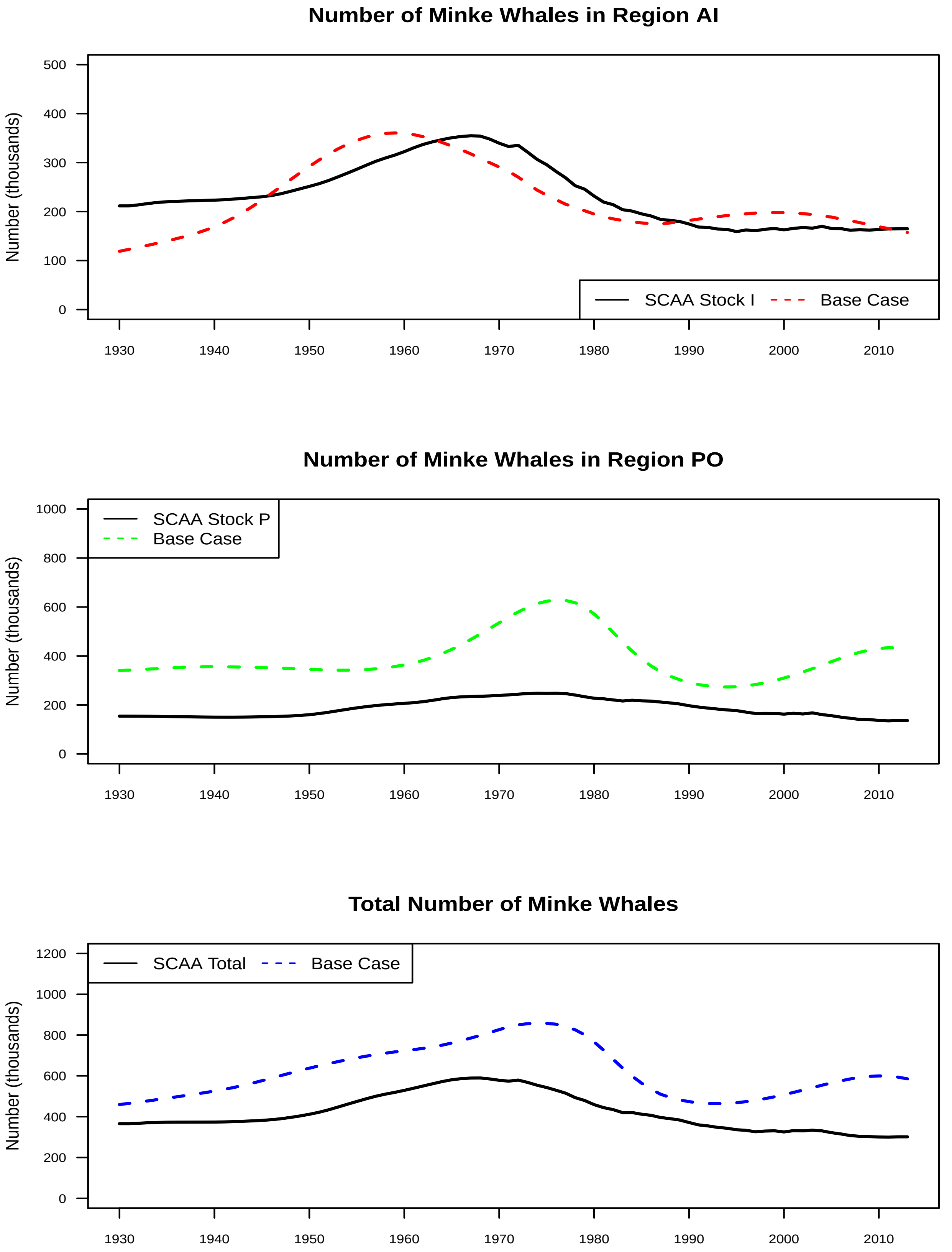


FIGURE 11.5: Comparison between the minke whale population trajectories for the Base Case and from Punt's (2014) SCAA model*.

* The results from the Base Case being entirely above that from the SCAA for Region PO may seem surprising as Figure 11.1 indicates an effectively exact fit to the observed minke abundance estimate in that Region. However, though the same observed estimate was used in fitting both the Punt (2014) model and the model of this thesis, the other information input into the Punt (2014) model led to the differences in the trajectories that can be seen here.

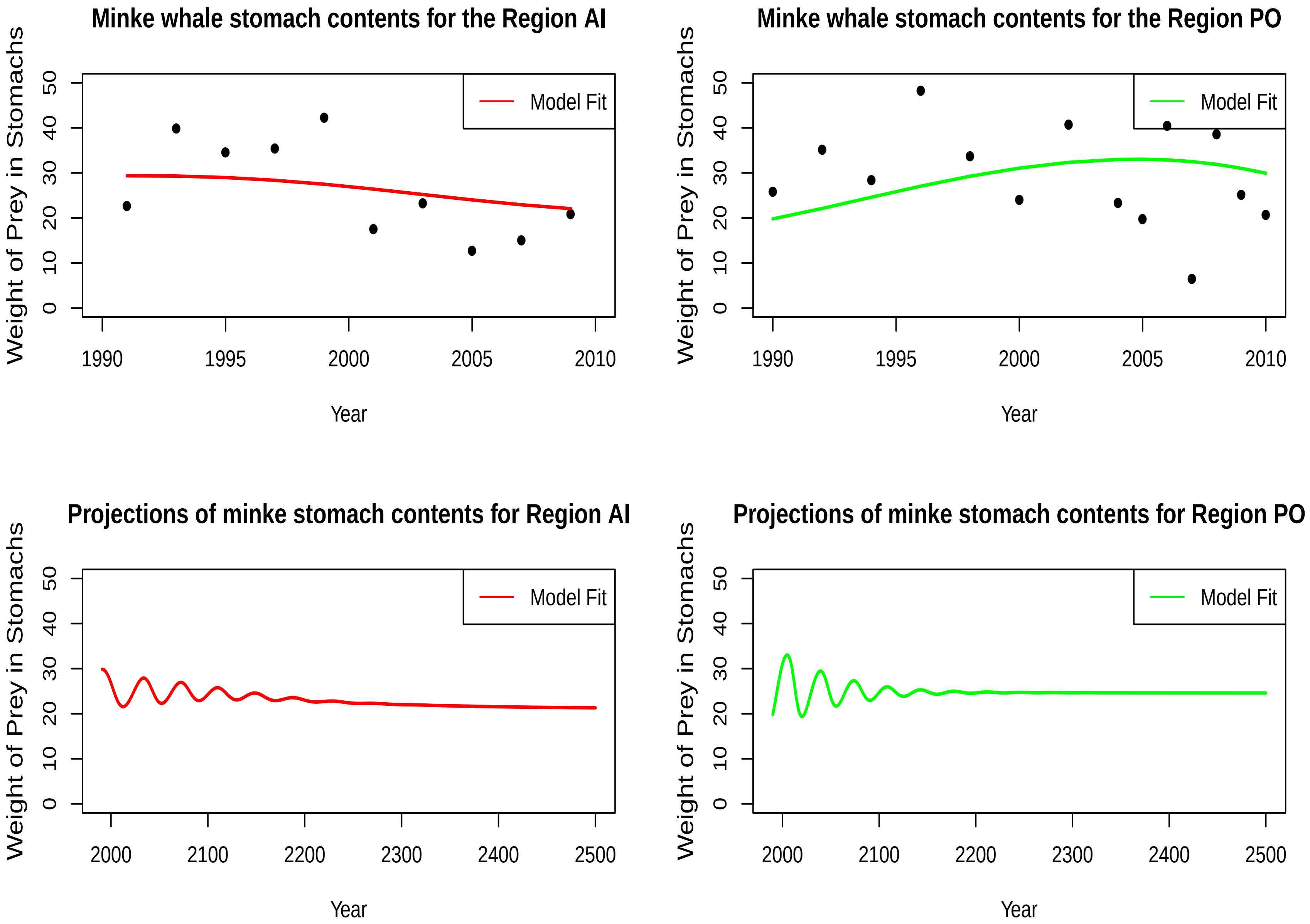


FIGURE 11.6: The Base Case model fits to the observed minke stomach content data for both Regions AI and PO and their projections for future trajectories (up to the year 2500), assuming zero catches for all the species after the year 2014.

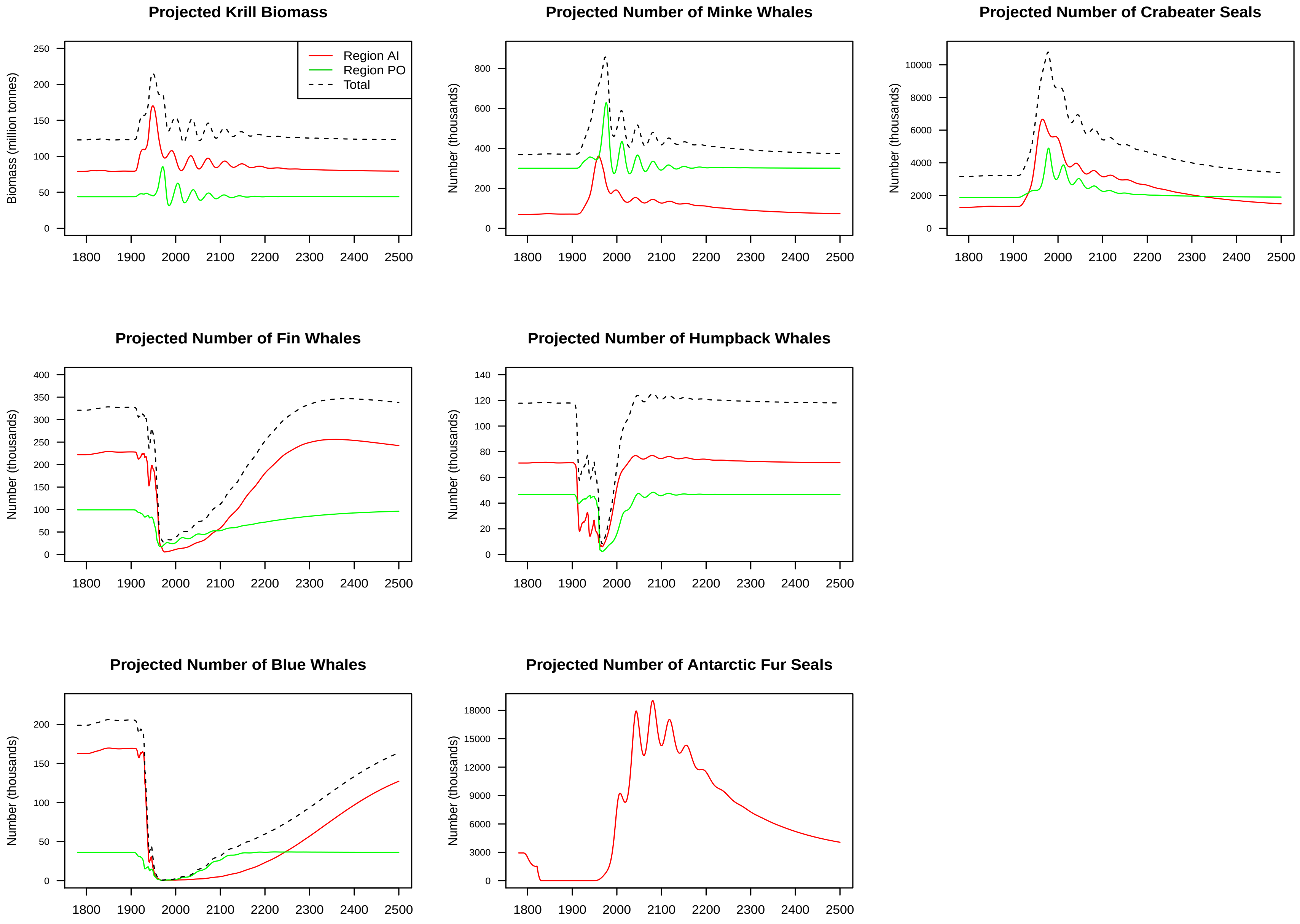


FIGURE 11.7: The Base Case population model projections for future trajectories (up to the year 2500) for krill and its main predators in the Antarctic, assuming zero catches for all species after the year 2014.

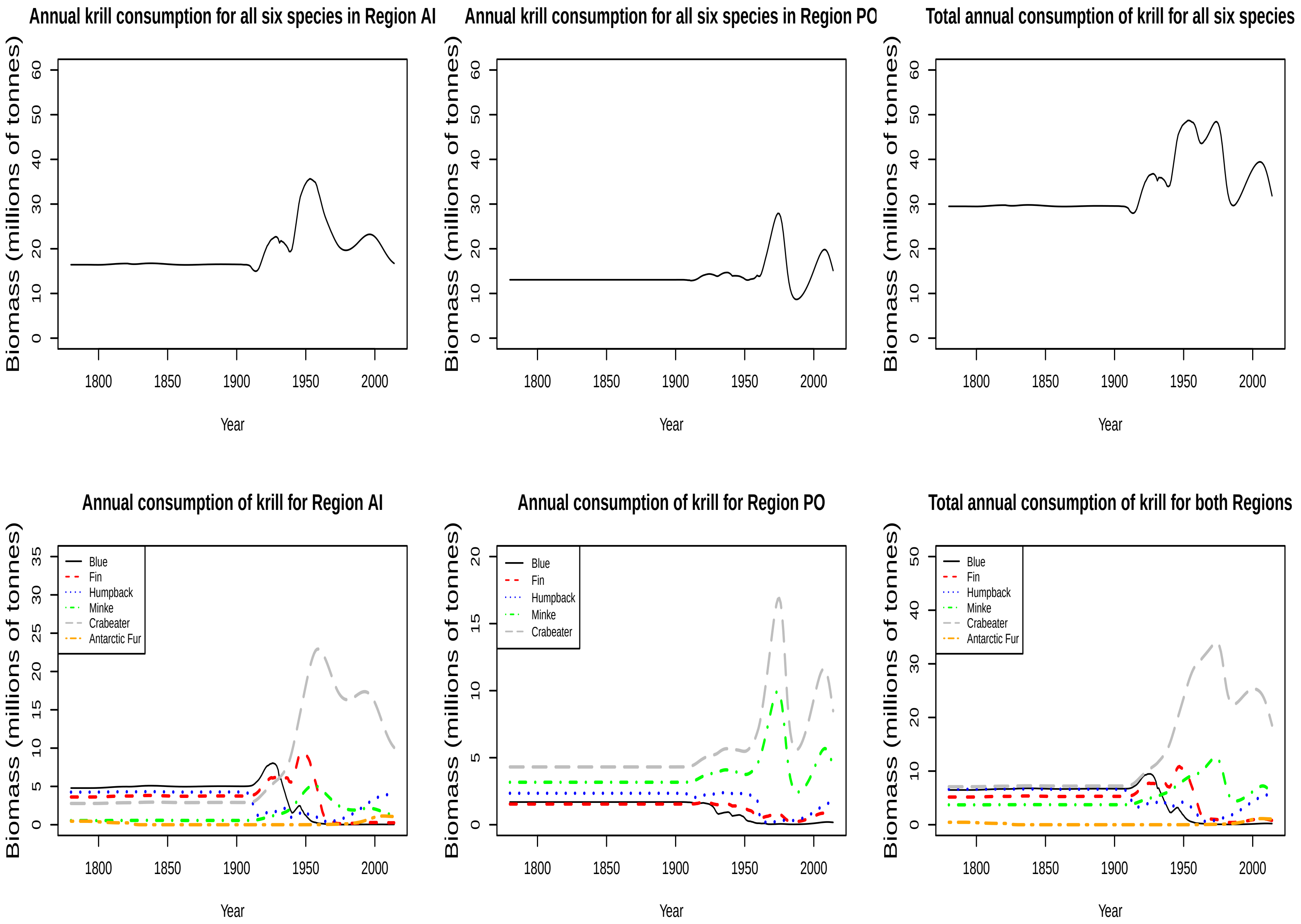


FIGURE 11.8: The total krill consumption by all six predators considered in the model for Region AI, PO and over both Regions and the annual consumption of krill biomass (millions of tonnes) by the predators for Region AI, Region PO and over both Regions.

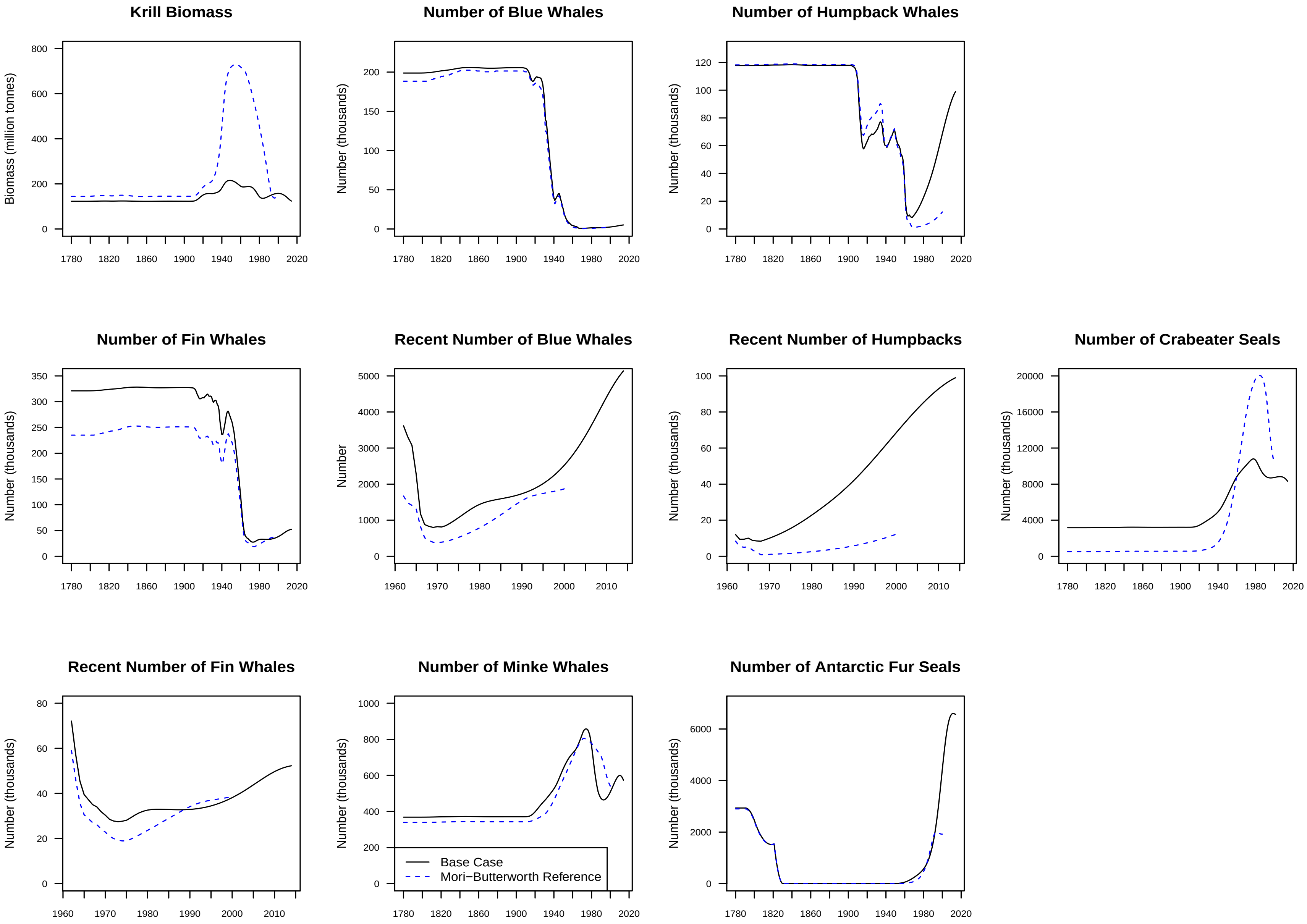


FIGURE 11.9: A comparison of the total population trajectories for krill and its main predators for the Base Case and the Mori-Butterworth Reference Case.

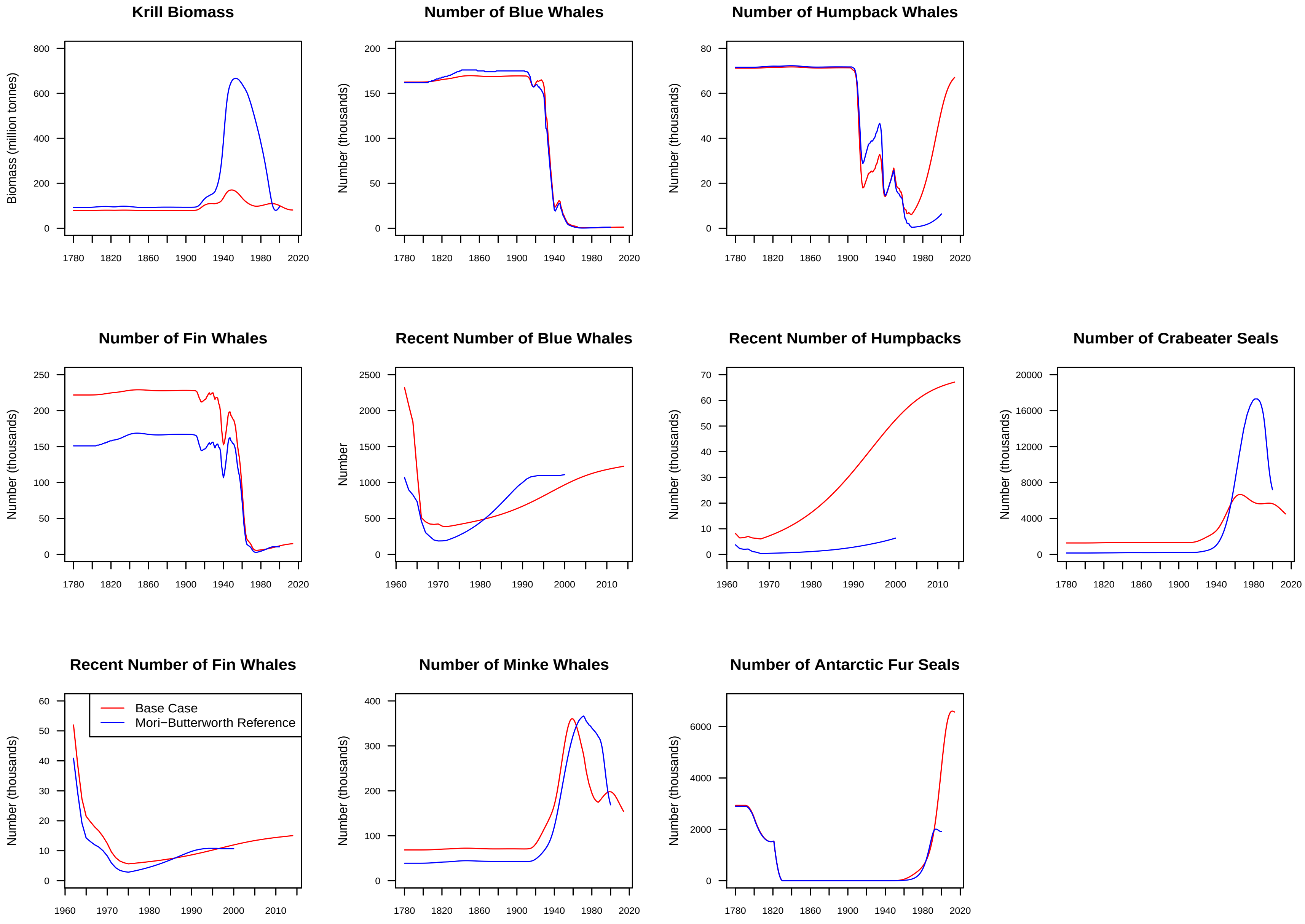


FIGURE 11.10: A comparison of the population trajectories for krill and its main predators for the Base Case and the Mori-Butterworth Reference Case in **Region AI**.

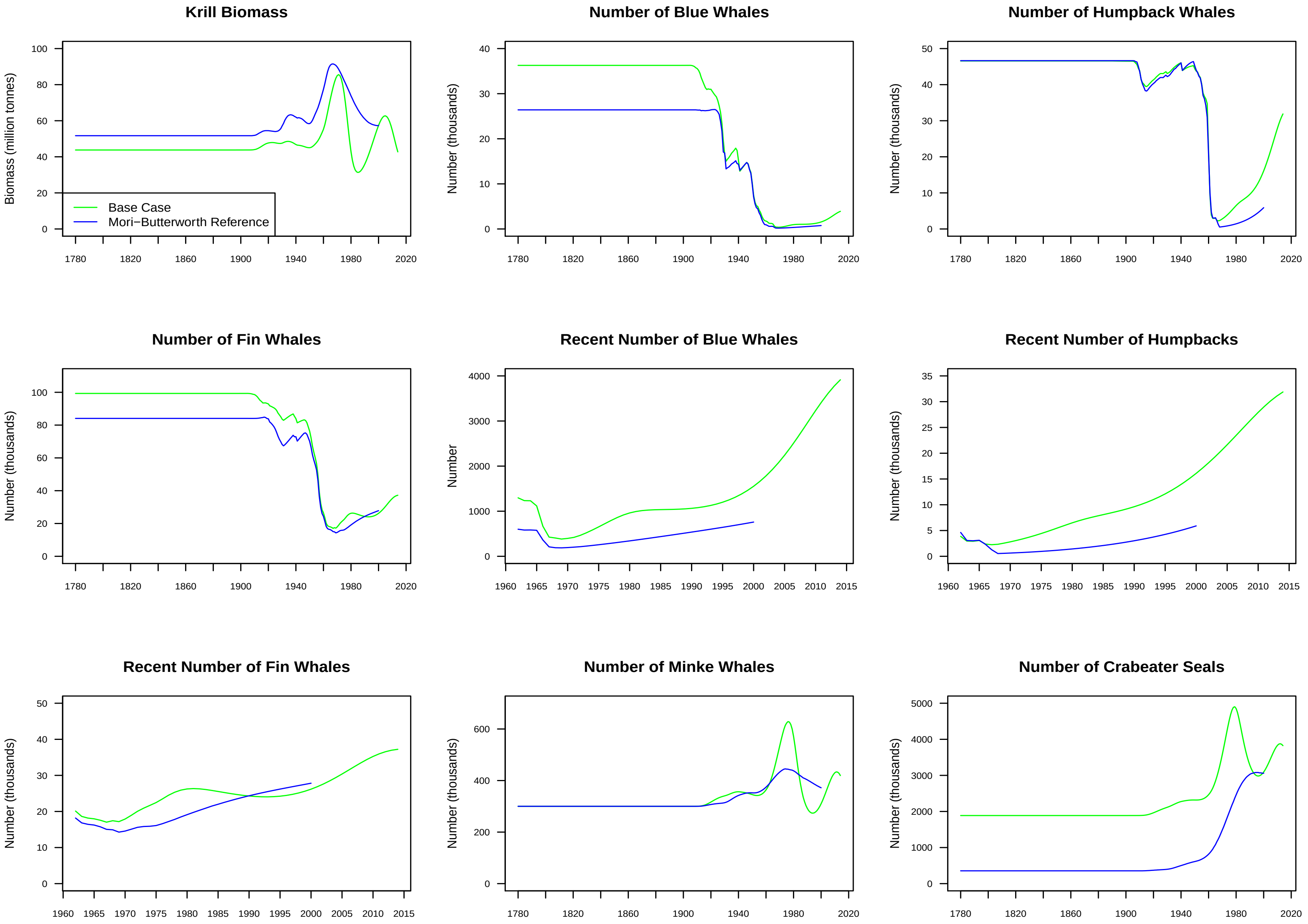


FIGURE 11.11: A comparison of the population trajectories for krill and its main predators for the Base Case and the Mori-Butterworth Reference Case in **Region PO**.

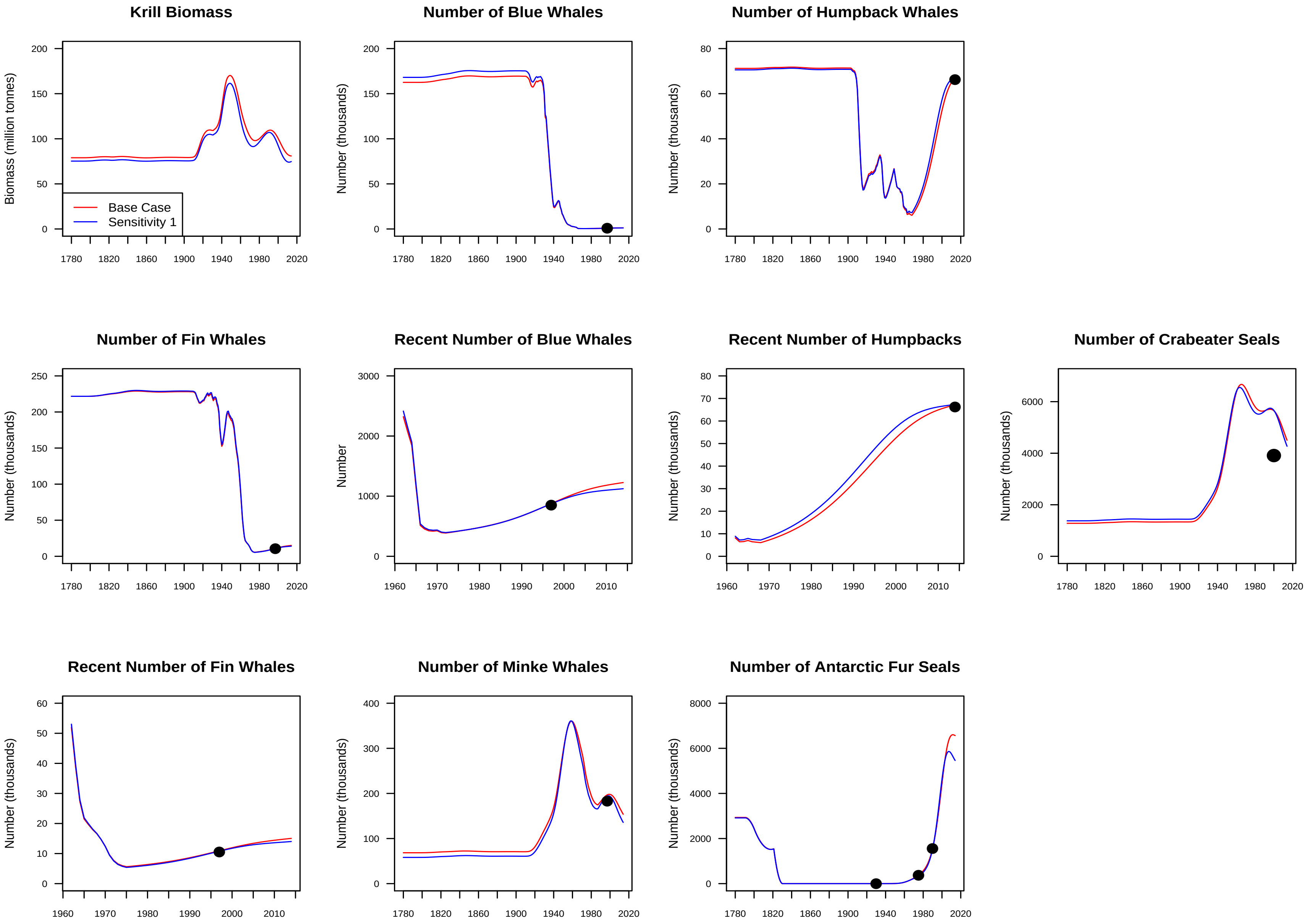


FIGURE 11.12: A comparison of the population trajectories for krill and its main predators for the Base Case and Sensitivity 1 in **Region AI**.

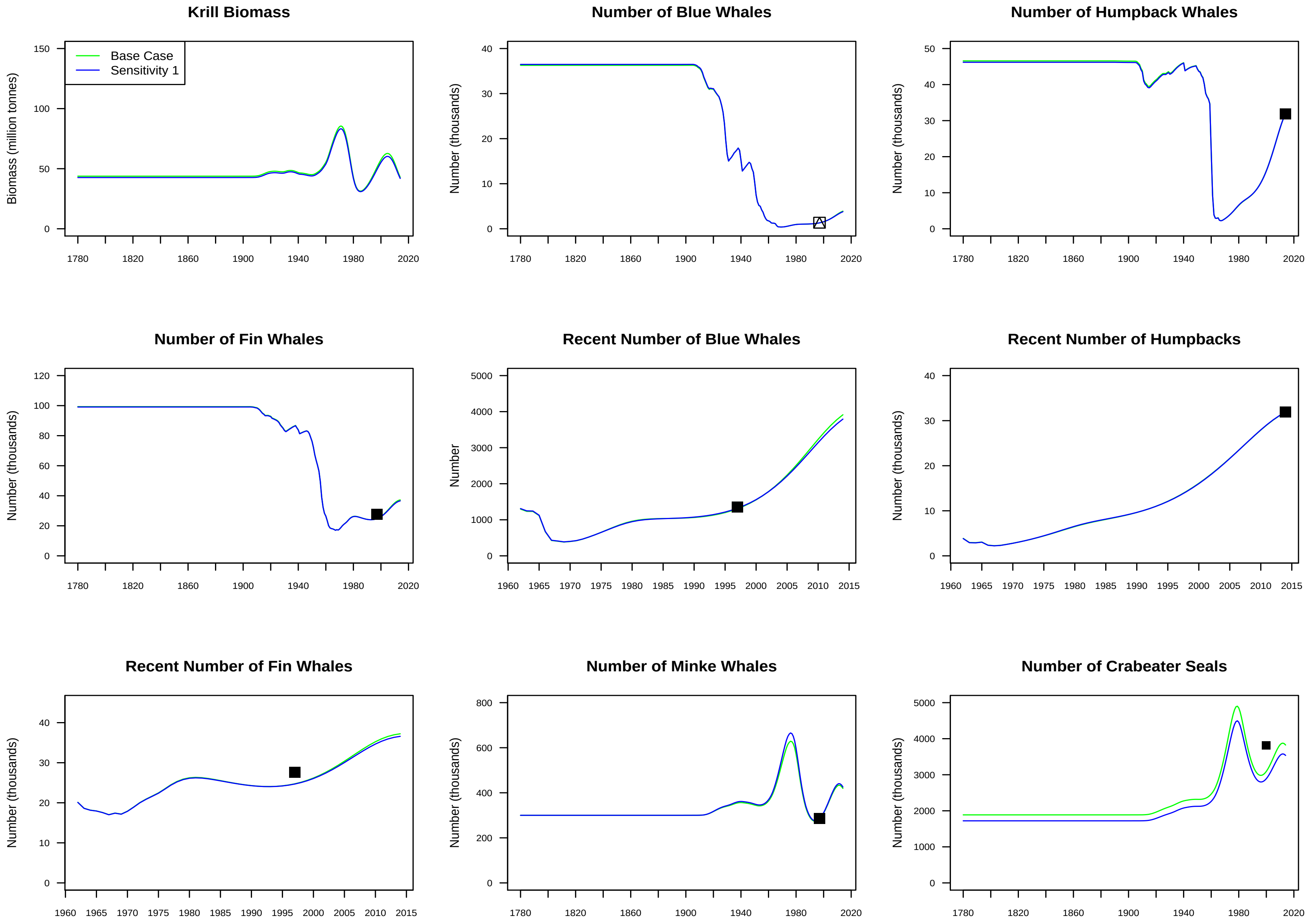


FIGURE 11.13: A comparison of the population trajectories for krill and its main predators for the Base Case and Sensitivity 1 in **Region PO**.

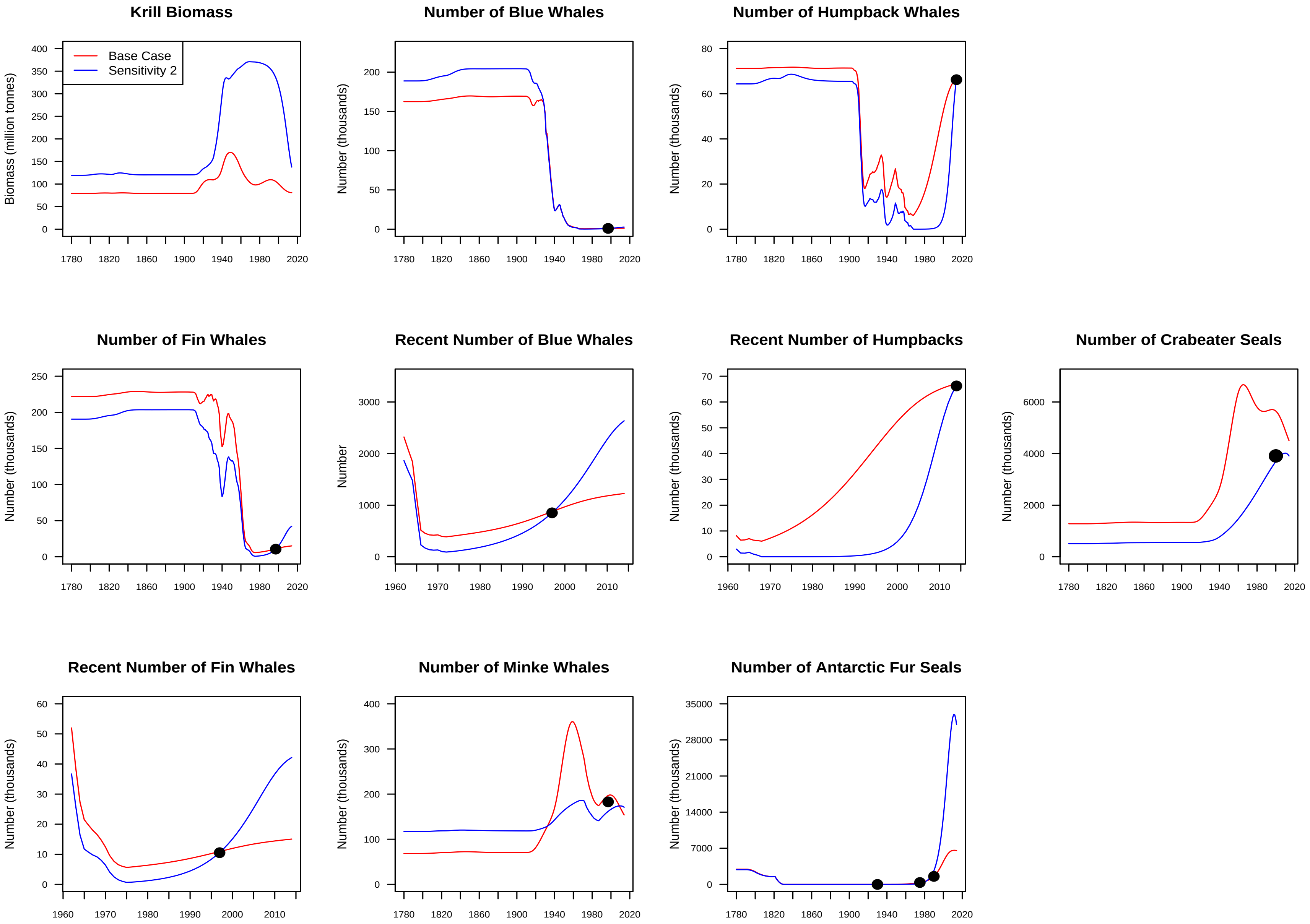


Figure 11.14: A comparison of the population trajectories for krill and its main predators for the Base Case and Sensitivity 2 in **Region AI**.

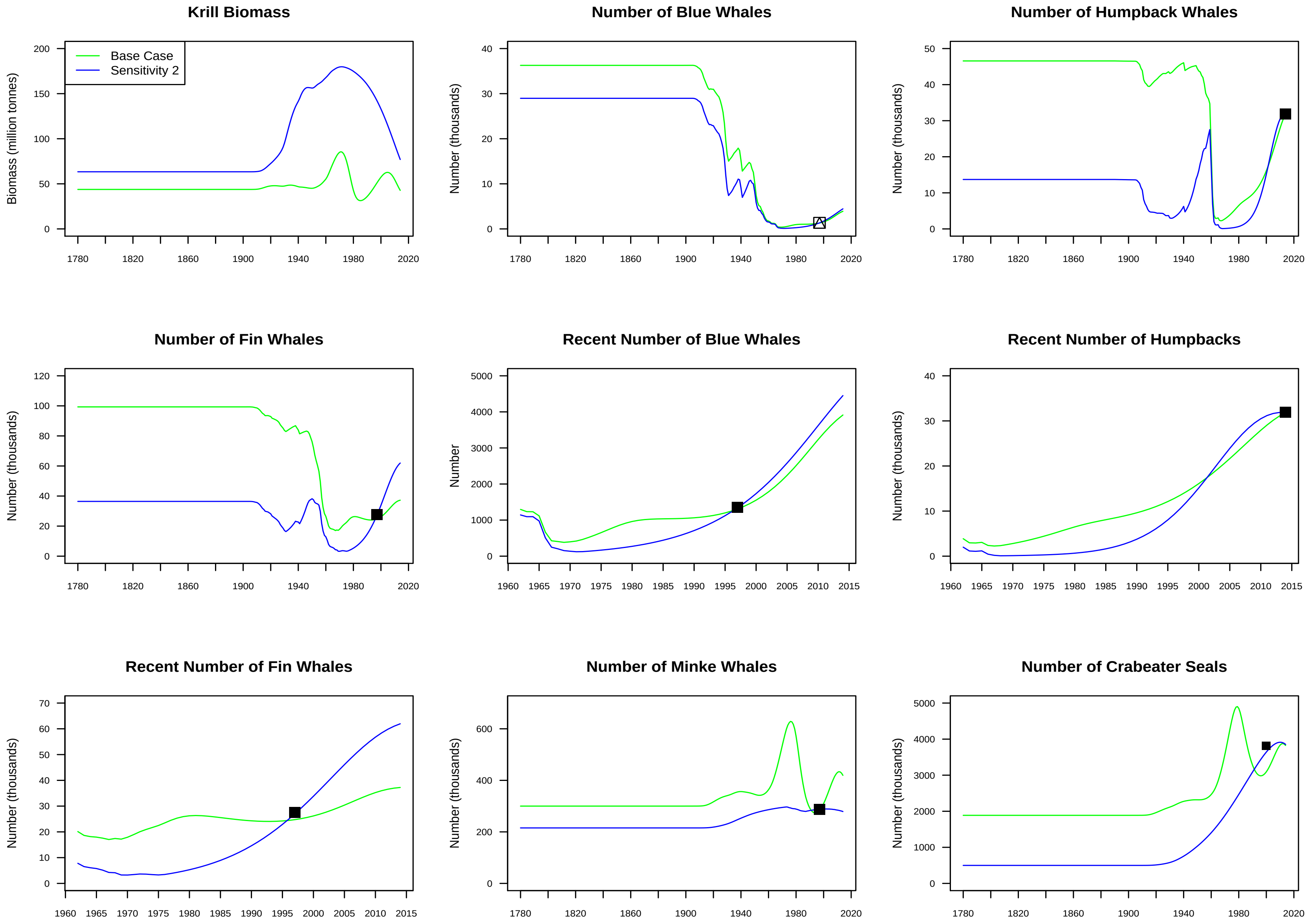
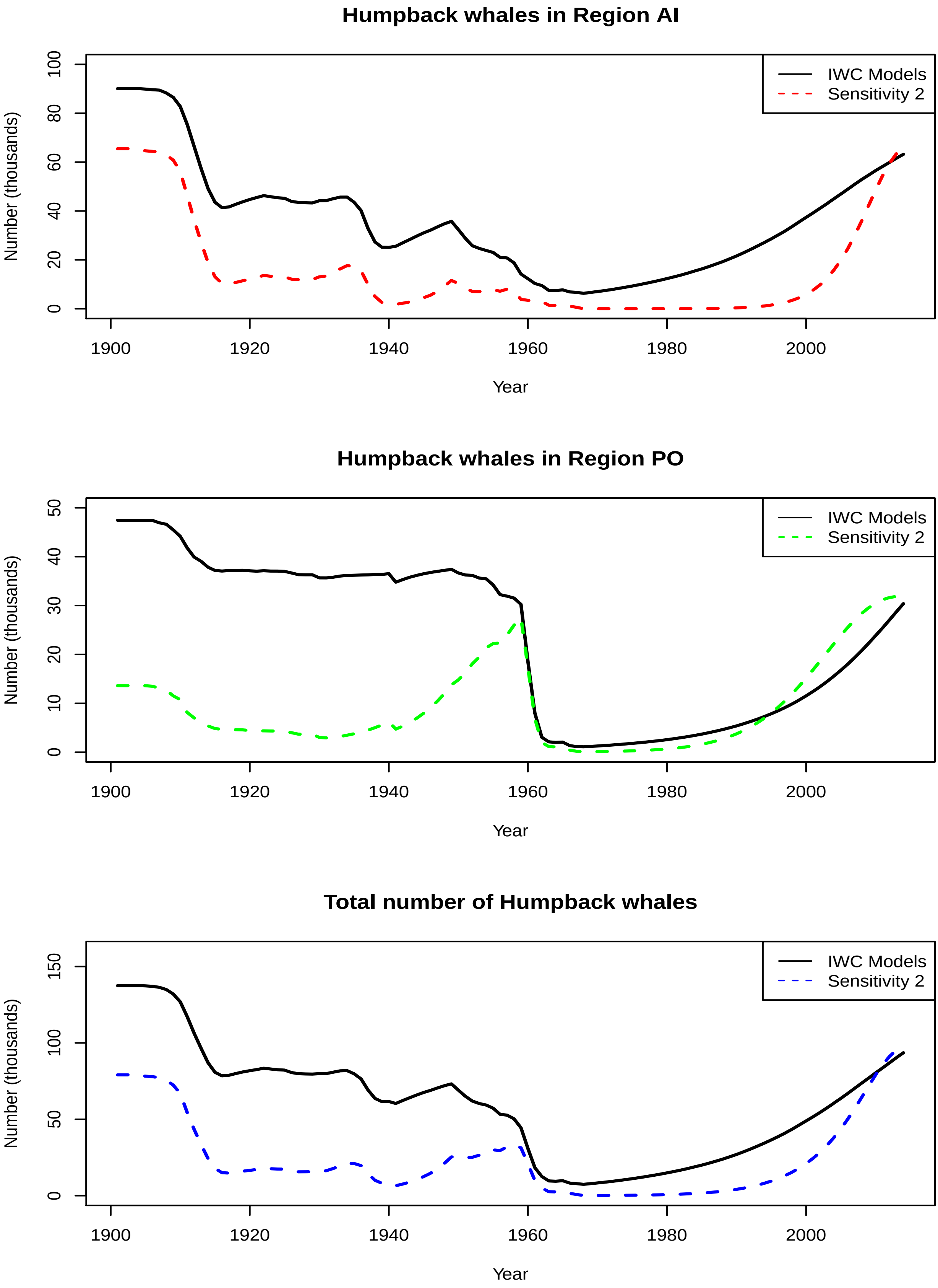


FIGURE 11.15: A comparison of the population trajectories for krill and its main predators for the Base Case and Sensitivity 2 in **Region PO**.



Humpback whales in Region AI

Humpback whales in Region PO

Total number of Humpback whales

FIGURE 11.16: A comparison between the humpback whale population trajectories for Sensitivity 2 and from the IWC models.

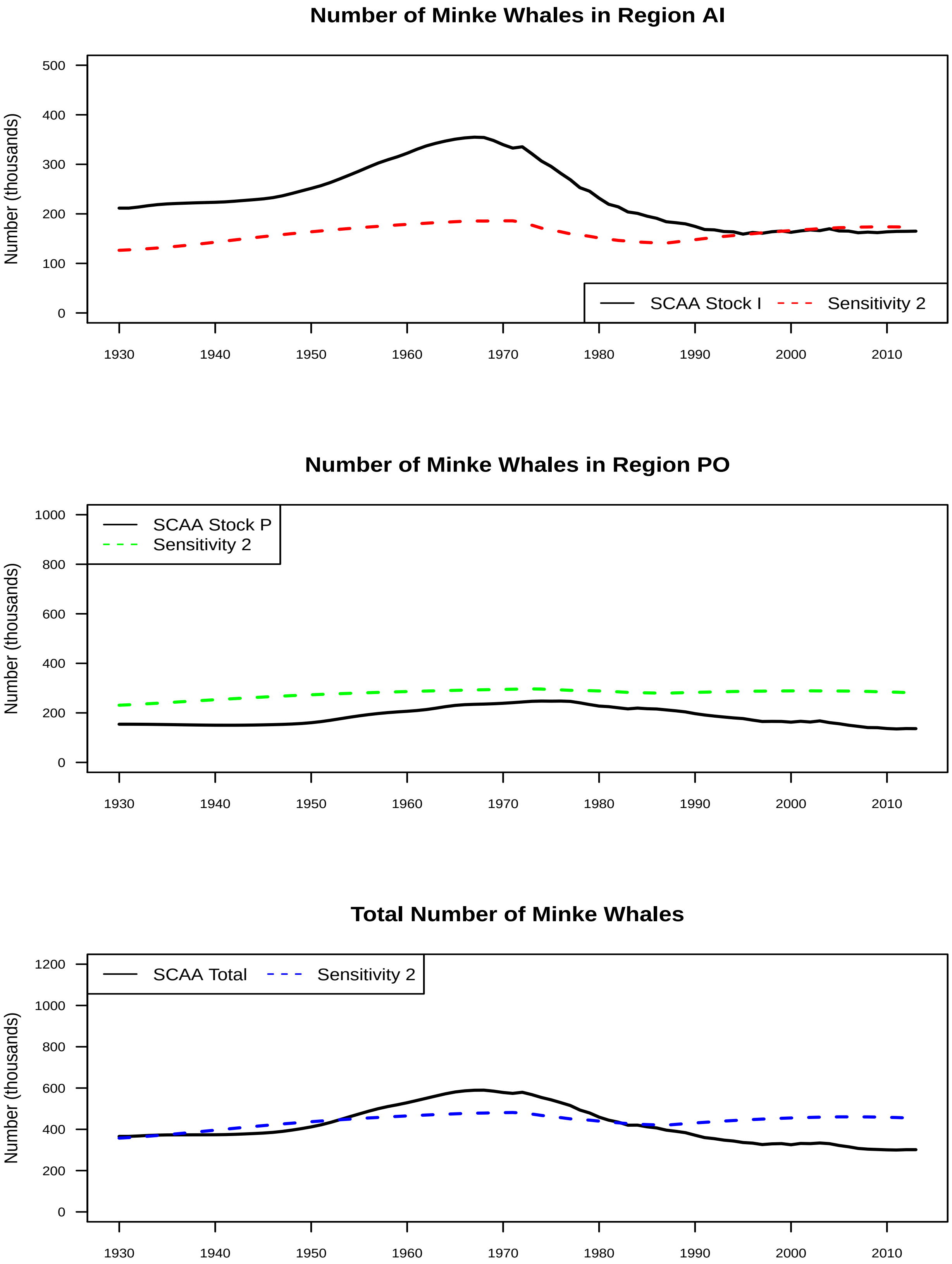


FIGURE 11.17: A comparison between the minke whale population trajectories for Sensitivity 2 and from Punt's (2014) SCAA model.

Appendix A

Catch tables for the krill-predators

Year	Blue Whale		Fin Whale		Minke Whale		Humpback Whale	
	Region AI	Region PO	Region AI	Region PO	Region AI	Region PO	Region AI	Region PO
1889/90 and before	0	0	0	0	0	0	0	0
1890/91	0	0	0	0	0	0	0	8
1891/92	0	0	0	0	0	0	0	8
1892/93	0	0	0	0	0	0	0	8
1893/94	0	0	0	0	0	0	0	8
1894/95	0	0	0	0	0	0	0	8
1895/96	0	0	0	0	0	0	0	8
1896/97	0	0	0	0	0	0	0	8
1897/98	0	0	0	0	0	0	0	8
1898/99	0	0	0	0	0	0	0	8
1899/00	0	0	0	0	0	0	0	8
1900/01	0	0	0	0	0	0	0	8
1901/02	0	0	0	0	0	0	0	8
1902/03	0	0	0	0	0	0	0	8
1903/04	0	0	0	0	0	0	338	8
1904/05	11	0	4	0	0	0	539	8
1905/06	39	29	74	50	0	0	299	113
1906/07	45	94	74	79	0	0	345	403
1907/08	22	153	23	179	0	0	1 303	468
1908/09	30	280	57	255	0	0	2 334	1 122
1909/10	111	211	254	187	0	0	5 036	825
1910/11	408	419	805	613	0	0	10 475	2 672

Table A.1 – continued from the previous page

Year	Blue Whale		Fin Whale		Minke Whale		Humpback Whale	
	Region AI	Region PO	Region AI	Region PO	Region AI	Region PO	Region AI	Region PO
1911/12	946	728	1 503	847	0	0	11 105	1 189
1912/13	1 556	1 124	4 044	1 213	0	0	10 549	796
1913/14	2 280	949	4 506	1 264	0	0	9 595	1 004
1914/15	4 382	994	4 011	887	0	0	6 989	616
1915/16	4 680	1 023	4 968	1 252	1	0	3 643	246
1916/17	3 687	754	2 620	336	0	0	1 025	108
1917/18	2 886	274	1 854	412	0	5	173	144
1918/19	1 700	520	2 406	798	0	0	186	155
1919/20	1 548	459	2 813	876	0	0	307	237
1920/21	2 075	955	4 254	1 720	0	0	395	216
1921/22	3 690	948	1 846	941	1	0	260	110
1922/23	5 859	929	3 290	1 050	0	0	1 540	171
1923/24	3 898	887	2 874	1 041	0	0	1 409	164
1924/25	5 374	1 341	4 154	1 211	0	0	1 200	221
1925/26	4 523	1 673	8 626	1 548	0	0	2 235	452
1926/27	6 683	1 980	4 843	2 176	0	0	1 396	482
1927/28	7 339	3 009	4 435	1 683	0	0	1 177	194
1928/29	9 978	4 357	6 042	1 668	0	0	1 243	164
1929/30	15 177	3 539	10 874	2 011	0	0	231	903
1930/31	28 498	1 975	9 865	1 275	0	0	1 163	275
1931/32	6 613	43	3 330	6	0	0	256	162
1932/33	18 855	148	5 511	4	0	0	467	39
1933/34	17 376	56	7 780	43	0	0	1 024	55
1934/35	16 585	18	13 097	117	0	0	3 214	65
1935/36	17 690	198	10 209	84	0	0	4 811	92
1936/37	14 495	174	15 630	235	0	0	8 719	87
1937/38	15 058	97	29 245	170	0	0	7 115	83
1938/39	13 135	1 030	19 385	2 096	0	0	3 705	105
1939/40	9 231	2 643	17 783	1 902	0	0	1 446	87
1940/41	2 097	2 878	5 167	3 001	0	0	564	2 403
1941/42	65	0	1 382	0	0	0	95	86
1942/43	127	0	980	0	0	0	156	71
1943/44	349	0	1 459	0	0	0	84	90
1944/45	1 048	2	1 892	61	0	0	175	88

Table A.1 – continued from the previous page

Year	Blue Whale		Fin Whale		Minke Whale		Humpback Whale	
	Region AI	Region PO	Region AI	Region PO	Region AI	Region PO	Region AI	Region PO
1945/46	3 605	42	9 349	80	0	0	354	107
1946/47	8 534	704	14 278	706	0	0	124	125
1947/48	5 473	1 498	20 076	1 696	0	0	133	120
1948/49	6 601	1 130	17 103	2 861	0	0	364	97
1949/50	3 564	2 677	17 738	2 898	1	0	4 811	1 058
1950/51	4 056	3 051	15 896	4 264	0	0	4 778	843
1951/52	3 441	1 764	18 643	5 277	4	0	4 258	534
1952/53	3 023	982	19 893	4 052	6	0	2 214	1 278
1953/54	2 506	382	24 880	3 689	12	0	1 964	988
1954/55	1 543	992	24 591	4 242	0	0	1 784	2 283
1955/56	1 042	697	20 267	7 468	36	0	3 019	3 149
1956/57	685	1 030	17 377	10 997	45	0	1 449	1 700
1957/58	1 027	742	20 647	7 170	12	1	3 259	1 523
1958/59	755	496	22 867	4 610	10	1	5 792	2 274
1959/60	434	195	23 193	2 390	4	1	1 609	14 167
1960/61	351	267	23 715	3 586	2	1	1 530	13 373
1961/62	339	415	23 084	3 995	3	0	1 075	6 141
1962/63	378	163	15 788	2 121	8	11	2 511	1 234
1963/64	342	110	13 047	1 163	114	6	524	293
1964/65	780	231	6 968	987	57	6	149	121
1965/66	693	564	2 664	1 267	74	7	1 226	968
1966/67	81	314	2 419	1 480	381	8	799	344
1967/68	48	69	2 004	599	1 113	5	791	137
1968/69	22	72	2 414	1 347	609	21	1	4
1969/70	8	33	2 728	403	752	18	0	1
1970/71	45	28	3 237	185	915	0	0	0
1971/72	18	10	2 139	185	4 157	5	0	3
1972/73	2	1	1 344	478	6 583	0	3	2
1973/74	1	0	750	591	7 271	1 270	1	3
1974/75	0	0	503	523	5 280	2 757	0	4
1975/76	0	0	22	211	5 350	1 835	0	8
1976/77	0	0	0	8	6 117	2 559	0	4
1977/78	0	0	0	2	4 126	1 874	0	4
1978/79	0	0	0	0	4 954	1 202	0	11

Table A.1 – continued from the previous page

Year	Blue Whale		Fin Whale		Minke Whale		Humpback Whale	
	Region AI	Region PO	Region AI	Region PO	Region AI	Region PO	Region AI	Region PO
1979/80	0	0	0	0	5 609	2 288	0	0
1980/81	0	0	0	0	4 697	2 445	0	0
1981/82	0	0	0	0	4 845	3 058	0	0
1982/83	0	0	0	0	3 935	3 366	0	0
1983/84	0	0	0	1	4 136	2 544	0	0
1984/85	0	0	0	0	3 504	2 064	0	0
1985/86	0	0	0	0	3 470	2 097	0	0
1986/87	0	0	0	0	2 935	2 034	0	0
1987/88	0	0	0	0	272	0	0	0
1988/89	0	0	0	0	0	236	0	0
1989/90	0	0	0	0	327	0	0	0
1990/91	0	0	0	0	0	323	0	0
1991/92	0	0	0	0	288	0	0	0
1992/93	0	0	0	0	0	327	0	0
1993/94	0	0	0	0	330	0	0	0
1994/95	0	0	0	0	0	330	0	0
1995/96	0	0	0	0	439	1	0	0
1996/97	0	0	0	0	0	440	0	0
1997/98	0	0	0	0	438	0	0	0
1998/99	0	0	0	0	0	389	0	0
1999/00	0	0	0	0	439	0	0	0
2000/01	0	0	0	0	0	444	0	0
2001/02	0	0	0	0	452	0	0	0
2002/03	0	0	0	0	0	441	0	0
2003/04	0	0	0	0	443	0	0	0
2004/05	0	0	0	0	0	441	0	0
2005/06	0	0	10	0	706	150	0	0
2006/07	0	0	0	3	0	508	0	0
2007/08	0	0	0	0	464	87	0	0
2008/09	0	0	0	1	0	680	0	0
2009/10	0	0	1	0	349	158	0	0
2010/11	0	0	0	2	0	171	0	0
2011/12	0	0	0	1	0	266	0	0
2012/13	0	0	0	0	102	1	0	0

Table A.1 – continued from the previous page

Year	Blue Whale		Fin Whale		Minke Whale		Humpback Whale	
	Region AI	Region PO	Region AI	Region PO	Region AI	Region PO	Region AI	Region PO
2013/14	0	0	0	0	0	251	0	0
2014/15	0	0	0	0	0	0	0	0

Table A.1: Historical catch records for the baleen whale species considered in this thesis for Regions AI and PO in the Antarctic.

Region AI	
Year	Antarctic Fur Seal
1790/91 and before	0
1791/92	11 000
1792/93	22 000
1793/94	33 000
1794/95	44 000
1795/96	55 000
1796/97	66 000
1797/98	77 000
1798/99	88 000
1799/00	99 000
1800/01	110 000
1801/02	104 500
1802/03	99 000
1803/04	93 500
1804/05	88 000
1805/06	82 500
1806/07	77 000
1807/08	71 500
1808/09	66 000
1809/10	60 500
1810/11	55 000
1811/12	49 500
1812/13	44 000
1813/14	38 500
1814/15	33 000

Table A.2 – continued from the previous page

Region AI	
Year	Antarctic Fur Seal
1815/16	27 500
1816/17	22 000
1817/18	16 500
1818/19	11 000
1819/20	5 500
1820/21	0
1821/22	320 000
1822/23	284 444
1823/24	248 888
1824/25	213 332
1825/26	177 776
1826/27	142 220
1827/28	106 664
1828/29	71 108
1829/30	35 552
1830/31 and after	0

Table A.2: Historical catch record for the Antarctic fur seals for Region AI in the Antarctic.

Region AI	
Year	Crabeater Seal
1966/67 and before	0
1967/68	750
1968/69	750
1969/70	750
1970/71	750
1971/72	750
1972/73	750
1973/74	750
1974/75	750
1975/76	750
1976/77	750
1977/78	750
1978/79 and after	0

Table A.3: Historical catch record for the crabeater seals for Region AI in the Antarctic.

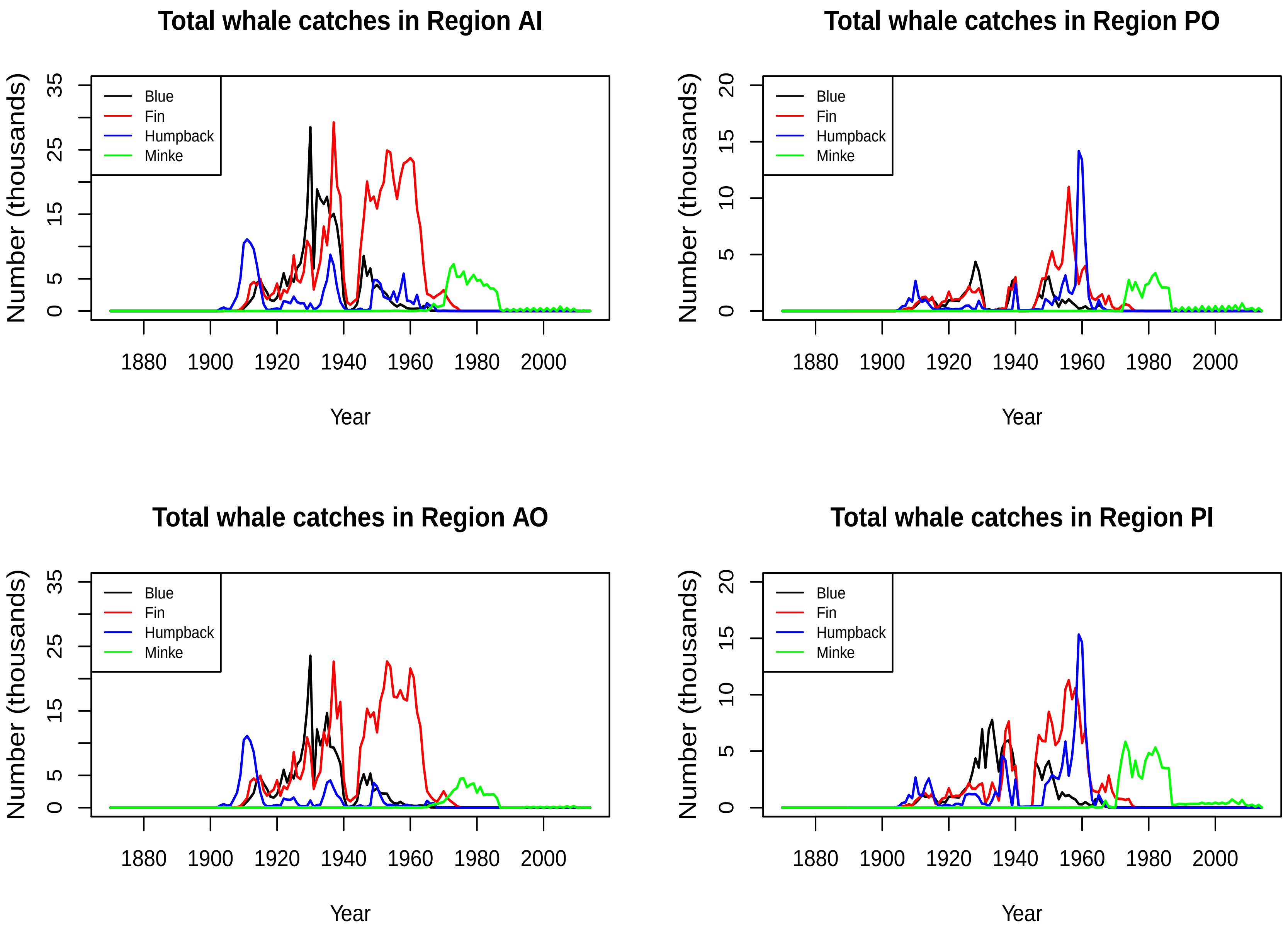


FIGURE A.1: A comparison of the catch trajectories of the main krill-eating whale species between Regions AI, PO, AO and PI.

Chapter 12

Conclusions and Future Work

12.1 Conclusions drawn

The main findings in this thesis regarding krill and its predators in the Antarctic ecosystem are highlighted below.

1) Total krill consumption estimates have been calculated for baleen whale, seal, fish and penguin species that feed in the Antarctic during the austral summer. Of the baleen whales, blue, fin, humpback and minke whales are the main krill-eating whales. Of the seal species, Antarctic fur seals and crabeater seals are the main krill-eating seal species. The fish and penguin species account for a total krill consumption of less than 1 million tonnes. As a result, they are not included in the ecosystem model developed in this thesis.

2) Updates have been made to a list of estimates of observed abundance and trends of abundance (at least, in relative terms) for krill and its main predators in the Antarctic. Since Mori (2005), the APIS results for the crabeater seal abundance and a consolidated estimate for minke abundance have become available and are used in the model developed in this thesis.

3) The biological parameters for krill and its main predators that are input to the ecosystem model have been re-assessed. Amongst these, the most important change is the lowering of the effective natural annual mortality rate of krill to 0.2, in order to take into account the removal of krill by predators other than those considered explicitly in the model. This is in contrast to the Mori and Butterworth (2006) model which considered all of the natural mortality estimate of M, drawn from a uniform distribution from 0.4 to 1.0, to relate to these other predators and not to the predators considered explicitly in the model. This is likely to be causing the oscillations seen in the krill population trajectories (in the Base Case), which in turn are being reflected in the krill-predator dynamics.

4) The literature on the impact of environmental change on krill and its predators is summarised. This is likely to impact juvenile krill negatively but adult krill positively.

5) The inclusion of a depensatory effect on the Antarctic fur seals in the krill and Antarctic fur seal dynamics of the model suppresses fur seal growth and leads to a better fit overall (the Base Case). The inclusion of estimates of annual average minke stomach weights makes little difference to the parameter estimation because these values show high inter-annual variability.

The main objective of this thesis was to update (and refine) the Mori-Butterworth (2006) Antarctic ecosystem model, where the latter showed that it was possible to explain the observed population trends of the species considered in the model through predator-prey interactions alone. Due to the difficulties during the model-fitting process, this work should be considered only as an initial update and refinement of the Mori-Butterworth model. More sensitivities need to be explored before a reliable and realistic Antarctic ecosystem model can be considered to have been developed. These sensitivities are listed in the section immediately below.

12.2 Improvements and future work

A number of proposed improvements to the model were mentioned in Chapter 11. They are repeated here along with other future work that merits consideration.

1) The inclusion of a space limitation term for the Antarctic fur seals in the model so as to restrict their population from increasing to unrealistically high values.

2) Consideration of a set of differently defined regions, e.g. Regions AO and PI (Figure 5.3) in contrast to Regions AI and PO that have been considered here (Figure 5.2). This is particularly important as the minke whale stocks as considered in the Punt (2014) SCAA analysis overlap with the Regions considered in this thesis. By considering a set differently defined regions, minke abundance trends and population trajectories may be better represented. This improvement has been initiated but due to time constraints was unable to be completed for this thesis.

3) Variation of (increasing and/or decreasing) the effective annual natural mortality rate of krill. This is likely causing oscillations in the krill dynamics and further investigation may assist matching krill trends better with the trends for minke whales in Region PO and those from the Punt (2014) SCAA model.

4) Variation of (increasing and/or decreasing) the bounds imposed on K_a. This impacts the krill dynamics, and hence sensitivity to the values assumed for these bounds needs to be explored.

5) Variation of the proportion of fin whales assumed to feed 60°S. This was unable to be initiated due to time constraints.

6) The inclusion of a term in the krill biomass equation that incorporates sea-ice concentration and sea-surface temperature data, in order to take environmental change into account.

7) Estimation of precision for the updated and refined model. This, however will not be straightforward due to the difficulty in achieving convergence at the level that a Hessian can be computed.

8) Investigation of the sensitivity to the values chosen for the η (and consequently α) parameters.

9) The use of "phases" in the ADMB framework when fitting the model, which may be converging to a local rather than the global minimum of the objective function, and increasing the number of function evaluations computed in ADMB to 1 million.

10) Weighting the objective function - this is a possible way to "force" the model to fit the abundance trend of minke and humpback whales better (though this might prove problematic for minke whales due to the inverse variance-covariance matrix used in the calculation of LL^{m}_{trend}). This provides an approach to understand what other features of the model are inhibiting a better fit to this information.

11) The application of a more systematic approach in choosing which estimable parameters should be fixed. One possible approach would be to fix parameters whose 'best-fit' values hit the bound of their respective ranges.

12) Investigation of the impact of the "depensatory effect" in the dynamics of the other krill-predators. This could be affecting the recovery rate of some of the whale species considered.

13) Investigation of the standard errors of some of the key parameters. This could not be examined due to the difficulty in achieving convergence that produces a positive definite Hessian. Gaining more insight on this is a matter that also needs to be investigated further.

14) The current method used in the model developed in this thesis assumes deterministic dynamics. As a result, the implications of allowing for process error to some extent merit further investigation.

15) Most of the abundance and trend information available is for a limited period only (mainly near the turn of the last century). Further investigation is required to determine whether this might be leading to biases in the model estimates.

16) Investigation of the potential use of random effects in the allometric relationships for the feeding ecologies.

17) Inclusion of a "ghost" population in order to assess the impact of missing component species.

Mori (2005) also recommended some further sensitivities. These include the following:

18) Exploration of the sensitivity of the model to other parameter choices (other than the ones currently used in the model).

19) Exploration of different functional responses.

20) Quantification of the uncertainties associated with the abundance estimation process so as to calculate reliable and realistic (approximate) ranges for the abundances of the krill-predators.

Mori (2005) commented that the sensitivities (18 - 20) could be implemented in theory in a Bayesian estimation approach, but that they might be difficult to compute given the high degree of non-linearity in the model. She added that this is complicated further because some of the estimable parameters hit the bounds of their respective ranges; this was also found to be the case in this thesis.

In conclusion, the Antarctic ecosystem model proposed by Mori and Butterworth (2006) has been usefully further updated and refined, but this work requires further development before the model might be used to provide scientific advice in order to regulate and implement suitable conservation and harvesting strategies in the Antarctic.

Chapter 13

Glossary

Amphipods - shrimp-like crustaceans; they do not have a carapace (the hard covering of the thorax or chest region common to crustaceans), and they are generally elongated (from *http://entnemdept.ufl.edu/creatures/misc/amphipods.htm* [Accessed 10/02/2017]).

Antarctic Circumpolar Current (ACC) - a current that originated nearly 37 million years ago when the Antarctic continent separated from Australia and South America. It is a broad current with a width of roughly 200 - 1000 km and it transports more water than any other current in the world. Its only constriction is the Drake Passage at the tip of South America (Laws, 1985).

Antarctic Convergence - also known as the Antarctic Polar Front (APF). It is a mobile front where warm sub-Antarctic waters flowing to the south (from the Atlantic, Pacific and Indian oceans) mix with cold Antarctic waters flowing to the north. The cold waters sink under the warm waters resulting in warm surface waters. The front has a fairly consistent annual average position of roughly 50°S, and consists of a number of eddies and loops. Waters south of the Antarctic Convergence are known to be nutrient rich (Laws, 1985).

Antarctic Divergence - a zone of upwelling between the East Wind Drift and West Wind Drift where deep, warmer water rise to roughly 100m of the surface, and diverges both northwards and southwards (Laws, 1985).

Antarctic Polar Front (APF) - see “Antarctic Convergence”.

Bathypelagic - relating to the deep ocean territory where the environment is cold and dark, about 1000 - 4000m at depth (from *https://australianmuseum.net.au/glossary-of-fish-terms* [Accessed 19/06/2017]).

Benthic - relating to the lowest level of a water body such as a lake or an ocean (from *http://www.nmfs.noaa.gov/pr/glossary.htm* [Accessed 19/06/2017]).

Callosities - irregular thickened patches of keratinized tissue on whales (Kenney, 2009).

CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) - an international commission, comprised of 25 member countries that manages and conserves the marine living resources and their environment in the Antarctic (from *https://www.ccamlr.org/en/organisation/about-ccamlr* [Accessed 10/02/2017]).

Cephalopods - generally consists of squid, octopus and cuttlefish
(from *http://www.thecephalopodpage.org/* [Accessed 19/06/2017]).

Circumpolar Deep Water (CDW) - the largest water mass in the Southern Ocean, constituting roughly 58% of the water in the region. Its signature properties are its *warm* temperatures (≈ 2-3°C) and its high salinity. It is derived from the North Atlantic Deep Water which gives it its high salinity trace. It flows southwards towards the Antarctic continent, rising to the surface at the Antarctic Divergence and warming the sea-surface (Tomczak and Godfrey, 2003).

Copepods - a group of small crustaceans that have bodies shaped as tear drops and large antennae (from *https://www.montereybayaquarium.org/animal-guide/invertebrates/copepod*
[Accessed 19/06/2017]).

Demersal - refers to animal species, mostly aquatic, that live close to either the ocean or sea or lake floor i.e. bottom-dwellers (Lalli and Parsons, 1997).

Diatoms - photosynthesising algae (i.e. a type of phytoplankton) that are enclosed in transparent cell walls made from silicon dioxide and water, which gives them their rigid structure (from *https://westerndiatoms.colorado.edu/about/what_are_diatoms* and *http://oceanservice.noaa.gov/facts/phyto.html* [Accessed 10/02/2017]).

Dorsal - referring to the back of an animal (from *http://www.nmfs.noaa.gov/pr/glossary.htm* [Accessed 19/06/2017]).

Eastern Bloc - a group of countries in central and eastern Europe that were once part of the former Soviet Union. These countries were: Poland, East Germany, Czechoslovakia, Hungary, Romania and Bulgaria (from *https://www.highbeam.com/topics/cold-war-formation-of-the-eastern-bloc-t10918* [Accessed 19/06/2017]).

East Wind Drift - the wind regime closest to the Antarctic continent. It moves in a westerly direction around the continent (Tomczak and Godfrey, 2003).

Eddy - a circulation system in which the water follows a closed circular/elliptic paths in either a clockwise or anti-clockwise direction (Tomczak and Godfrey, 2003; Lalli and Parsons, 1997).

El Niño - It is the warming of the surface waters of the central and eastern Pacific Ocean. It reduces the spring/winter rainfall (in extreme cases, causing drought) over much of the eastern Australia and causes heavy rainfall (in extreme cases, flooding) in western South America such as in Chile, Peru and Ecuador (from *http://www.bom.gov.au/climate/glossary/soi.shtml* [Accessed 10/02/2017]; Tomczak and Godfrey, 2003; Lalli and Parsons, 1997).

ENSO (El Niño Southern Oscillation) - a global climatic phenomenon that manifests itself through the irregular fluctuations of sea-surface temperatures, rainfall, wind patterns and ocean currents of the Pacific Ocean (Tomczak and Godfrey, 2003).

Epipelagic - refers to animal species, mostly marine, that live within the oceanic zone that receives enough sunlight for photosynthesis. This zone lies above the mesopelagic zone.
(from *http://oceanservice.noaa.gov/education/yos/resource/JetStream/ocean/layers_ocean.htm* [Accessed 19/06/2017]).

Epithelial - refers to the thin tissue that covers a body's surface and lines a body cavity, and are a major component in glands. They perform a number of functions such as protection, secretion (e.g. sweating), absorption, excretion, filtration, sensory reception and diffusion (from *https://training.seer.cancer.gov/anatomy/cells_tissues_membranes/tissues/epithelial.html* [Accessed 10/02/2017]).

Estuarine - being related to or formed in an estuary, a place where rivers (fresh water) meet the sea (salty water) (Lalli and Parsons, 1997).

Euphausiids - more commonly known as krill, are small shrimp-like marine crustaceans. They are filter-feeders that feed on both phytoplankton and zooplankton as they migrate up and down the water column. Most krill are also bioluminescent i.e. they produce their own light (from *http://www.mesa.edu.au/crustaceans/crustaceans07.asp* [Accessed 10/02/2017]).

Fast-ice - this is sea-ice that is still attached to land i.e. sea-ice that is *fastened* to the land. It does not move with winds or currents (from *https://nsidc.org/cryosphere/glossary/term/fast-ice* [Accessed 19/06/2017]).

Guano - excrement of seabirds, cave bats or seals that is sold as a fertiliser
(from *http://www.buriedtreasureguano.com/page/the-science-of-guano/* [Accessed 19/06/2017]).

Haemoglobin - the protein in red blood cells that allows for the efficient transportation of oxygen from the lungs to the rest of the body (from *http://www.medicinenet.com/hemoglobin/article.htm* [Accessed 10/02/2017]).

Haemolymph - the fluid in most invertebrates, equivalent to blood in vertebrates
(from *http://study.com/academy/lesson/hemolymph-definition-lesson-quiz.html*
[Accessed 19/06/2017]).

Hypercarbic - also known as CO_2 retention. It is a condition of abnormally elevated CO_2 levels in a fluid (Tufts and Perry, 1998).

Hyperiids - small aquatic crustaceans, found only in marine waters. They have large eyes, and most are parasites or predators of salps and jellyfish (Vinogradov *et al.*, 1996).

IDCR (International Decade of Cetacean Research) - a programme that conducted three surveys, during the austral summer from 60°S to the ice-edge that completely circumnavigated the Antarctic. The programme was renamed to the “Southern Ocean Whale and Ecosystem Research” (SOWER) project and the surveys became collectively known as the IDCR/SOWER surveys (see Chapter 5, Section 2).

Invertebrates - animals that do not have a backbone/spine e.g. corals, sea sponges, snails and molluscs (from *http://eol.org/info/443* [Accessed 19/06/2017]).

IWC (International Whaling Commission) - a global body charged with the conservation of whales and the management of whaling. It currently has 88 member governments from countries all around the world (from *https://iwc.int/home* [Accessed 10/02/2017]).

JARPA (Japanese Whale Research Program under Special Permit in the Antarctic) - a component of a long-term monitoring program in the Antarctic that operated during the austral summer from 1987/88 until 2004/05 (see Chapter 5, Section 2).

Keratin - a structural protein that protects the epithelial cells from damage. It is the same substance found in human hair and nails (from *http://marinelife.about.com/od/glossary/g/baleen.htm* [Accessed 10/02/2017]).

La Niña - It is the cooling of the surface waters of the central and eastern Pacific Ocean. It reduces the spring/winter rainfall (in extreme cases, causing drought) over much of western South America such as Chile, Peru and Ecuador and causes heavy rainfall (in extreme cases, flooding) in eastern Australia (from *http://www.bom.gov.au/climate/glossary/soi.shtml* [Accessed 10/02/2017]; Tomczak and Godfrey, 2003).

Land-ice - ice cover that is formed over land through the freezing of any form of precipitation e.g. rain, snow, hail. Examples of land-ice are icebergs, glaciers, ice sheets and ice shelves (from *https://nsidc.org/cryosphere/seaice/index.html* [Accessed 10/02/2017]).

Lateral - relating to the sides of an animal (from *https://australianmuseum.net.au/glossary-of-fish-terms* [Accessed 19/06/2017]).

Mandible - the lower jawbone in fish and mammals (from *https://australianmuseum.net.au/glossary-of-fish-terms* [Accessed 19/06/2017]).

Mesopelagic - as the name suggests, it refers to marine species that inhabit the *middle waters* of the ocean that still receives sunlight but the light is not enough to allow for photosynthesis, roughly between 200 - 1000m (Knox, 2007).

Mottling - markings with spots or smeared colours (from *http://www.nmfs.noaa.gov/pr/glossary.htm* [Accessed 19/06/2017]).

Mysids - shrimp-like crustaceans that feed on algae, detritus and zooplankton. They have a pair of stalked eyes, two pairs of antennae and the females have a brood pouch. They are sensitive to water pollution so in some cases, they are used to monitor water quality (from *http://www.reefkeeping.com/issues/2004-02/rs/* [Accessed 10/02/2017]).

Nektonic - refers to free-swimming freshwater and marine organisms that are independent of currents, and inhabit the middle depths of a lake or ocean (from *http://www.thefreedictionary.com/nektonic* [Accessed 29/03/2016]).

Neritic - also known as "the coastal waters"; it relates to the relatively shallow part of the ocean above the continental shelf drop-off, roughly 200m in depth (Lalli and Parsons, 1997).

North Atlantic Deep Water (NADW) - a deep water mass that is formed in the North Atlantic. The warm surface current known as the *Gulf Stream* moves from the Equator to the North Atlantic where it mixes with highly saline waters - its most noticeable trait - of the Mediterranean Sea. This increased salinity and the cooler temperatures causes the water to become dense and sink. As it sinks, it forms the NADW - a *cool* ($\approx$ 2-4°C) salty water mass critical to the global thermohaline circulation (Tomczak and Godfrey, 2003).

Pack-ice - a mass of sea-ice formed by smaller pieces of sea-ice freezing together i.e. it is sea-ice *packed* together (from *https://nsidc.org/cryosphere/glossary/term/pack-ice* and *http://ocean.si.edu/ocean-photos/antarctic-pack-ice* [Accessed 19/06/2017]).

Pelagic - refers to animal species, mostly marine that live above the epipelagic zone i.e. in the waters open to the air (from *https://australianmuseum.net.au/glossary-of-fish-terms* and *http://www.nmfs.noaa.gov/pr/glossary.htm* [Accessed 19/06/2017]).

Phytoplankton - microscopic photosynthesising marine plants that are part of the plankton community. There are two main classes of phytoplankton: dinoflagellates which use a tail-like structure to move through the water, and diatoms which use the ocean currents to move through the water (from *http://oceanservice.noaa.gov/facts/phyto.html* [Accessed 10/02/2017]).

Pinna - the external part of the ear in most mammals (from *http://www.asha.org/public/hearing/Outer-Ear/* [Accessed 19/06/2017]).

Planktonic - microscopic organisms (plankton-like) that inhabit the pelagic zone of fresh water bodies, seas and oceans in which they drift (Lalli and Parsons, 1997).

Polynyas - areas of persistent open water (or unfrozen sea) within the pack-ice/sea-ice i.e. an area of open water surrounded by ice (from *https://nsidc.org/cryosphere/seaice/characteristics/polynyas.html* and *https://www.niwa.co.nz/blog/what-is-a-polynya* [Accessed 10/02/2017]).

Salps - barrel-shaped and free-swimming tunicates with gelatinous bodies. As a result, they pump water through their bodies, feeding on phytoplankton and moving simultaneously as they strain the 'pumped' water through their internal filter-feeders (from *http://planktonchronicles.org/en/episode/salps-exploding-populations/* [Accessed 05/02/2017]).

SAM (Southern Annular Mode) - one of the biggest drivers of Southern Hemisphere climate. It alters the north-south movement of the westerly wind belt around Antarctica. In its positive phase, pressures are lower than normal over Antarctica causing strong westerly winds over the Southern Ocean (stormy waters). However, in the mid-latitudes, pressures are higher than normal causing relatively light winds (weaker westerlies) and settled (warm and dry) weather, on average. In its negative phase, pressures are higher than normal over Antarctica causing weak westerlies over the Southern Ocean. In contrast, the mid-latitudes experience lower pressures and stronger westerlies than normal causing wet and cool weather, on average (from *http://blog.metservice.com/Southern-Annular-Mode* [Accessed 12/10/2016]).

Scat - animal excrement or droppings (from *http://icwdm.org/inspection/scat.aspx* [Accessed 19/06/2017]).

Scientific Committee for Antarctic Research (SCAR) - an inter-disciplinary committee charged with "initiating, developing and coordinating high quality international scientific research in the Antarctic region (including the Southern Ocean), and on the role of the Antarctic region in the Earth system" (from *http://www.scar.org/about-us* [Accessed 25/03/2015]).

Sea-ice - a thin, fragile and solid layer of frozen ocean water that is formed in the Arctic and Antarctic. They are not to be confused with icebergs, which are formed from freshwater in the form of compacted snow (from *http://www.livescience.com/29654-climate-change-melting-polar-sea-ice.html* [Accessed 10/02/2017]).

Shelf-edge - refers to the "continental shelf-edge"; it is the edge of a continent that lies in the ocean (from *http://www.nationalgeographic.org/encyclopedia/continental-shelf/* [Accessed 10/02/2017]).

Spectral distribution - represents the distribution of energy that is radiated at different wavelengths in the visible part of the spectrum. Guano has no defining characteristics to the human eye but under infra-red, it does (from *http://www.schreder.com/it/learningcentre/lightingbasics/spectral-distribution-of-a-light-source* and *https://phys.org/news/2014-12-unique-spectral-signature-guano-unknown.html* [Accessed 10/02/2017]).

Southern Oscillation - the atmospheric component attached to ENSO. It is an oscillation in the surface air pressure fields between the west and east Pacific. It is measured by an index called the "Southern Oscillation Index (SOI)", which is computed from fluctuations in the surface air pressure differences between the Pacific (Tahiti) and Indian (Darwin, Austalia) Oceans. A negative SOI implies that there is a lower air pressure field over the Pacific Ocean (thus a higher air pressure field over the Indian Ocean), and is associated with El Niño. A positive SOI implies that there is a higher air pressure field over the Pacific Ocean (thus a lower air pressure field over the Indian

Ocean), and is associated with La Niña (from *http://www.bom.gov.au/climate/glossary/soi.shtml* [Accessed 10/02/2017]).

Stenotherm - an organism or species that can only live or survive within a specific temperature range (from *http://fishionary.fisheries.org/stenotherm/* [Accessed 19/06/2017]).

Stratosphere - the middle layer in the Earth's atmosphere, above the troposphere (from *https://scied.ucar.edu/shortcontent/stratosphere-overview* [Accessed 19/06/2017]).

Subtropical Convergence or Subtropical Front (STF) - the northernmost boundary of the sub-Antarctic region, separating the fresher sub-Antarctic waters from more saline subtropical waters (Tomczak and Godfrey, 2003).

Troposphere - the lowest layer of the Earth's atmosphere. Almost all weather occurs in this layer (from *http://www.windows2universe.org/earth/Atmosphere/troposphere.html* [Accessed 10/02/2017]).

Tubercules - small round protrusions on the surface of a whale's body (Clapham, 2009).

Tunicates - an invertebrate marine animal enclosed in a *tunic* with openings at each end (from *http://planktonchronicles.org/en/episode/salps-exploding-populations/* [Accessed 05/02/2017]).

Ultraviolet light (UV light) - type of electromagnetic radiation that includes radio waves, infrared radiation, x-rays and gamma rays. UV light is radiation that comes from the sun (from *http://www.livescience.com/50326-what-is-ultraviolet-light.html* [Accessed 10/02/2017]).

Upwelling - is a process where wind moves dense, cooler, nutrient-rich waters towards the ocean surface where it displaces warmer, nutrient-poor surface waters (from *http://oceanservice.noaa.gov/facts/upwelling.html* [Accessed 19/06/2017]; Tomczak and Godfrey, 2003).

Ventral - relating to the abdominal or underside of a plant or animal (from *https://australianmuseum.net.au/glossary-of-fish-terms* [Accessed 19/06/2017]).

West Wind Drift - the wind regime further from the Antarctic continent (compared to the East Wind Drift). It blows in an easterly direction, and is more consistent compared to the East Wind Drift. It is also responsible for the ACC (Tomczak and Godfrey, 2003).

Chapter 14

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