Krill and the Antarctic: Finding the Balance

by

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Abstract

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has a mandate to manage Southern Ocean resources using an ecosystem approach. In accordance with this, ecosystem models of the South Orkneys/South Georgia region (FAO Subareas 48.2 and 48.3, respectively) were constructed using the modelling software Ecopath with Ecosim. A model representing the region in the 1990s was used to assess the possible effects that an increased fishery for krill (*Euphausia superba*) might have on the ecosystem. The model predicted that the expanded fishery could cause small declines in the biomass of several top predators (<10%), such as Antarctic fur seals and baleen whales, and that bycatch in the krill trawl fishery could reduce some fish populations by almost 35%. Incorporating the natural annual variation in krill biomass into the model showed that predator populations could be negatively affected by years of low krill abundance, which would be further exacerbated by an increased krill fishery. The model also indicated that the traditional concept of the simple Southern Ocean food chain (i.e., primary production, krill, top predator) should be re-evaluated to consider other important intermediary species groups, such as fish and squid. Models representing the region in the past (pre-exploitation, 1900s and 1960s) were used to assess the impacts of commercial sealing, whaling and fishing in the region. Simulations suggest that the increase in Antarctic fur seals since the 1950s was not due to decreased competition for food as a result of the whaling activities in the first half of the 1900s. However, whaling may have had a positive effect on fish population sizes, especially certain commercially important species. Removing large krill predators from the simulated ecosystem, such as birds and seals, did not result in an increase in whales. Removing certain fish groups, however, had more of an acceleratory effect on whale recovery. These findings emphasize the need for a better understanding of the relative roles of species in the Southern Ocean ecosystem, as well as the natural variability of krill abundance, if management issues in the Antarctic are to be resolved.

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1. The Southern Ocean: an overview of its history, geography, biology and management

1.1 Introduction

Even before its discovery, the Antarctic was the subject of much fascination and speculation for human beings. The Greek philosophers proposed that a southern landmass known as *Terra Australis Incognita* had to exist in order to balance the weight of the lands in the northern hemisphere. Aristotle (384 – 322 B.C.) deduced that since the constellation Arktos (the bear) was found in the sky above the northern hemisphere, the land in the southern hemisphere must be Antarktikos (Berkman 2002). The lure of a southern land continued as explorers began documenting the geography of the Earth. Some of the early cartographers in the 15th and 16th centuries included a southern continent in their world maps, long before there was any concrete evidence of such a place (Berkman 2002). In fact, it wasn't until January 17, 1773 that the first people crossed the Antarctic Circle. This voyage, led by Captain James Cook (1728 – 1779), sparked an era of Antarctic exploration and exploitation that continues today.

Despite the efforts of many explorers, fishers, and scientists, there is still much about the Antarctic and its surrounding ocean that eludes us. The complex biological interactions of this rich ecosystem are not fully understood, and the impacts of human interference (in the form of scientific study or commercial fishing) are often unpredictable. However, the body responsible for the management of the Southern Ocean, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), has made a commitment to use an ecologically-based approach for the regulation of exploitation in Antarctic waters (Hofman 1993).

The objective of my research was to mathematically describe the South Orkneys/South Georgia region (Atlantic Sector of the Southern Ocean) using the software Ecopath with Ecosim and data drawn from the literature. Ecopath models can then be used to explore policy options for management, and assess potential ramifications for target species of fisheries, as well as other indirectly affected groups of organisms.

1.2 The Southern Ocean – physical characteristics

While the Antarctic continent is one of the coldest, most isolated places on earth, the ocean that surrounds it supports a productive and complex ecosystem. The Southern Ocean is a large circumpolar body of water that extends over 36 million km^2 and accounts for about a tenth of the world's ocean area (Laws 1985). To the north, the Southern Ocean is bounded by the Antarctic Polar Front, where the cold Antarctic surface water flowing northward meets the warmer sub-Antarctic water flowing southward from the Atlantic, Pacific, and Indian Oceans, forming an effective biological barrier for the organisms of the Southern Ocean (Knox 1994). Although this front is not spatially static, the mean annual position is fairly constant at about 50°S (Laws 1985). The Southern Ocean is divided into three Food and Agricultural Organization of the United Nations (FAO) statistical areas: Area 58 (Indian Ocean Antarctic), Area 88 (Pacific Antarctic), and Area 48 (Atlantic Antarctic).

The focus of my study was the area containing the South Orkney Islands and the Island of South Georgia (FAO Subareas 48.2 and 48.3, respectively, Fig. 1). This system was chosen for a number of reasons: 1) the South Orkneys/South Georgia region has been subjected to both historical and present-day exploitation, including sealing, whaling, and fishing (Berkman 2002), and is therefore of interest from a management standpoint; 2) the South Orkney Islands and the Island of South Georgia support large populations of top predators, including pinnipeds and seabirds, and the surrounding ocean is an important feeding area for these animals, as well as for populations of baleen whales (Knox 1994); 3) the area is bounded by the Antarctic Polar Front to the north and by the Weddell Sea Gyre to the south, both effective barriers to oceanic biota; 4) the exploitation and exploration that have taken place in Subareas 48.2 and 48.3 have led to extensive regional data collection compared to other areas of the Southern Ocean, such as the South Sandwich Islands to the east (Subarea 48.4); and 5) the Antarctic Peninsula region (Subarea 48.1), while relatively well studied, should be modelled separately because it has a much higher percentage of landmass and is a different type of system compared to the South Orkneys/South Georgia region.
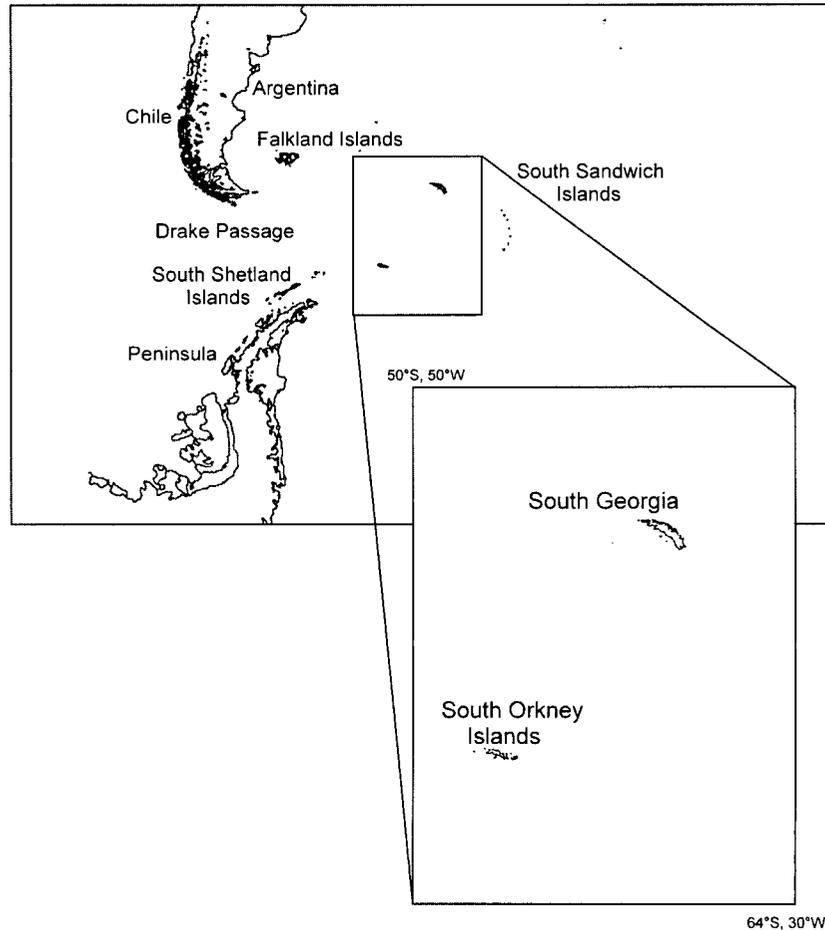
Figure 1.1 The South Orkneys/South Georgia region (FAO Subareas 48.2, 48.3).

1.2.1 Bathymetry

The bathymetry of the Southern Ocean includes three deep-water basins (the Atlantic-Indian Basin, the Indian-Antarctic Basin and the Pacific-Antarctic Basin) and a series of ridges (the Scotia Ridge and the Atlantic Indian Ridge, the Southeast Indian Ridge, and the Pacific Atlantic Ridge) that bound the basins to the north (Knox 1994). The Drake Passage separates the Antarctic Peninsula and the continent of South America and represents the narrowest point of Southern Ocean waters (1100 km wide) (Hansom and Gordon 1998). The continental shelf reaches a width of 1000 km in the Bellingshausen, Weddell and Ross Seas, but its mean width is about 200 km with a mean depth of 500 m (Anderson 1991). The large and deep nature of the Antarctic continental shelf, as well as the sloping of many areas of the shelf toward the continent

(as opposed to offshore) have been attributed to isostatic depression and glacial erosion from the ice sheets that cover the continent (Anderson 1991).

1.2.2 Winds, currents and water masses

There are two main circumpolar surface currents in the Southern Ocean. Adjacent to the continent, the East Wind Drift (Antarctic Coastal Current) is driven by easterly winds at the higher latitudes and generally flows counterclockwise with the contribution of a series of clockwise-rotating gyres (Knox 1994). Westerly winds north of about 60°S drive the West Wind Drift (Antarctic Circumpolar Current), which flows clockwise with a width of 200 – 1000 km, constricted only in the Drake Passage. At the deepest depths near the continent is a layer of water called the Antarctic Bottom Water. This layer is formed from the salt that is expressed from the sea water as it freezes under the ice shelves, resulting in cold saline water that sinks to the ocean floor and then flows northward. At the location where the East Wind Drift and the West Wind Drift meet, warmer Circumpolar Deep Water flowing southward rises over the Antarctic Bottom Water, creating an area of upwelling called the Antarctic Divergence (Laws 1985). This nutrient rich water rises to within about 100 m of the surface before diverging north and south, and mixing with the Antarctic surface water.

The other main frontal zone is the Antarctic Polar Front, which, as mentioned previously, is an area of converging and sinking water masses at the northern reaches of the Southern Ocean that acts as an effective barrier to oceanic biological resources (Laws 1985). Although the circulation of the East and West Wind Drifts is fairly symmetrical around the continent, ocean-floor geomorphology and the coastal outline influence these currents, resulting in circulatory currents called eddies and gyres. The three main gyres in the Southern Ocean are the Weddell Gyre, extending east of the Antarctic Peninsula to about 20°W and from the continent (near 70°S) to 60°S (Deacon 1979), the Ross Sea Gyre, extending north and east of the Ross Sea between about 175°E and 160°W, and the gyre east of the Kerguelen Plateau (Knox 1994).

1.2.3 Temperature and sea-ice

While 99% of the Antarctic continent is covered by ice at all times (Laws 1985), sea-ice coverage is extremely seasonal, despite fairly stable annual temperatures (Clarke 1988). In the austral summer months when the temperatures range from $-1.0°C$ near the continent to around $6°C$ further north (Knox 1994), sea-ice is confined to the coastal region, covering only about 3.5 million km^2 in February (Gloerson and Campbell 1991). In the winter, with temperatures ranging from $-1.9°C$ to $-1.0°C$, the ice cover expands over five-fold to cover 19 million km^2 in September. This seasonal sea-ice zone, defined as the area bounded by the winter maximum and summer minimum, extends up to 22000 km from the coast (between approximately 70-75°S and 55-60°S), and effectively doubles the area of the Antarctic continent from 18 to about 34 million km^2 (Laws 1985). As the sea-ice expands and contracts, its outer boundary (the Marginal Ice Zone, which comprises a 100-200 km wide complex interface between sea-ice and the open ocean) also shifts in location. This zone is an important location for biological interactions in the Southern Ocean (Hansom and Gordon 1998).

1.2.4 Nutrients

In general, nutrient concentrations in the surface waters of the Southern Ocean are higher than those found in other oceanic waters (Knox 1970). Nutrients come to the surface at the upwelling region of the Antarctic Divergence and are ultimately drawn deeper again at the downwelling region of the Antarctic Polar Front. The Southern Ocean is known as a high-nutrient, low-chlorophyll region, due to the relatively low level of primary productivity compared to the high nutrient concentrations (Priddle et al. 1998).

1.3 The Southern Ocean – exploitation

1.3.1 Pinnipeds

The first of the Southern Ocean's resources to be exploited by humans were the pinnipeds. Upon returning to England in 1775, Captain Cook told of the Island of South Georgia with its beaches teeming with Antarctic fur seals (*Arctocephalus gazella*). Sealing voyages thus ensued, and in 1822, James Weddell, a Scottish sealer, estimated that over 1.2 million skins had been taken from the area and that the species was nearly extirpated (Knox 1994). Other populations of Antarctic fur seals on the South Orkney Islands, the South Shetland Islands, and the South Sandwich Islands were also exploited extensively. As fur seal populations dwindled due to overharvesting, sealing became less economically viable and virtually ceased by the mid 1820s. By the late 1800s (more than 50 years after harvesting had stopped), fur seals did not show signs of recovering (Berkman 2002). However, in recent years the Antarctic fur seal has undergone a substantial population increase at a rate of 16.8% per year during the 1970s (Payne 1977), and 9.8% per year during the 1980s (Boyd 1993). Populations in the 1990s were thought to be at or above pre-exploitation numbers (about 2 million individuals in the study area; Bonner 1976, Boyd 2002, Knox 1994).

While the fur seals were being harvested for their pelts, southern elephant seals (*Mirounga leonina*) were being taken for their oil, although not in such large numbers (Berkman 2002). The harvesting of elephant seals continued in a controlled manner (quotas were issued in 1910 by the British government for harvests at South Georgia) until 1964 (Berkman 2002). The population on South Georgia in the 1990s was thought to be stable, with about 350 000 animals in the region (Boyd et al. 1996, Laws 1994, McCann 1985).

None of the other four Antarctic pinniped species (the crabeater seal, *Lobodon carcinophagus*, the Weddell seal, *Leptonychotes weddelli*, the leopard seal, *Hydrurga leptonyx*, and the Ross seal, *Ommatophoca rossii*) were the focus of commercial exploitation. As a result of exploratory cruises by Norway for pelagic seals in the mid 1960s, the Convention for the Conservation of Antarctic Seals was developed to provide an authoritative body to monitor and manage any seal fisheries that might develop. The convention came into force in March 1978, but to date there are no commercial seal fisheries in the Southern Ocean (Knox 1994).

1.3.2 Penguins

Penguins were also once harvested for pelts and oil. Penguin rookeries were often located in the vicinity of sealing and whaling operations, making them accessible targets. It is estimated that about 400 000 penguins (king, *Aptenodytes patagonicus*, macaroni, *Eudyptes chrysolophus*, and gentoo, *Pygoscelis papua*) were taken from South Georgia in the mid 1800s (Berkman 2002). However, with the collapse of the whaling and sealing industries, the penguin harvest also became uneconomical, and there are presently no commercial takes of penguins in the Southern Ocean.

1.3.3 Whales

Whaling has had a significant effect on cetacean populations in the Southern Ocean, just as it has in other areas of the world (Roman and Palumbi 2003). Commercial whaling in the Antarctic began in 1904, with the first whaling station at Stromness, South Georgia and a catch of 195 whales (Berkman 2002). By 1913, six land stations with 21 factory ships had captured a reported 10 760 whales, most of which were humpback whales (*Megaptera novaeangliae*) that were near the islands. As the population of humpbacks declined, whalers turned their attention to the larger blue whale (*Balaenoptera musculus*) and fin whale (*Balaenoptera physalus*). As these populations began collapsing, the fishery sought sei whales (*Balaenoptera borealis*) and sperm whales (*Physeter macrocephalus*), until 1986 when an international moratorium on all commercial whaling activities was enacted. However, the moratorium did little to discourage Japan and Norway from harvesting the smaller minke whale (*Balaenoptera acutorostrata*) during the 1990s. This pattern of shifting from larger to smaller target species as populations crashed reflects attempts to maintain the profitability of the whaling industry in the face of dwindling target species populations (Knox 1994). Antarctic whale stocks are thought to have been reduced by over 80% (May 1979), and the larger species do not seem to be recovering (Kasamatsu et al. 2000).

1.3.4 Fish

Although exploratory shore-based fishing began in conjunction with whaling in the early 20th century, commercial fishing did not begin until the late 1960s (Kock 1992). The main demersal stocks, including marbled rockcod (*Notothenia rossii*) and mackerel icefish (*Champsocephalus gunnari*), were depleted within a few years, with neither having recovered to date. Harvesting of patagonian toothfish (*Dissostichus* spp.) and mesopelagic myctophids (*Electrona* spp.) began in the late 1980s (Kock 1992). Directed fishing on rockcods has been prohibited since 1985, and until 1992 the stock at South Georgia (Subarea 48.3) was estimated to be less than 5% of its original 1969 size (Kock 1992). Present day fisheries in the South Orkneys/South Georgia region include a longline fishery for toothfish (*Dissostichus eleginoides*), trawl fisheries for mackerel icefish and myctophids (*Electrona carlsbergi*), small pot fisheries for crabs (Lithodidae) and toothfish, and a jig fishery for squid (*Martialia hyadesi*) — all within Subarea 48.3 (CCAMLR 2002a) (Table 1).

1.3.5 Krill

Several species of euphausiids have a circumpolar distribution in the Southern Ocean. Of these, the Antarctic krill (*Euphausia superba*) is the largest and most abundant, and is a key prey item for many species (Everson 2000), including birds (Croxall 1984, Prince and Morgan 1987), seals (Knox 1994), whales (Laws 1977), and fish (Kock 1992). Fishing for krill began in 1961-62 on an exploratory basis, and increased to commercial levels beginning in 1972 (Nicol and Endo 1999). The annual catch peaked in 1982 at over 500 000 tonnes, but declined in the late 1980s and early 1990s due to political and economic factors, including a decline in global demand for krill products and the break-up of the Soviet Union, which had been a dominant krill-fishing nation in the area (Nicol and Endo 1999). The Antarctic krill fishery in the 1990s took between 80 000 and 100 000 tonnes annually, and operated by pelagic trawl mainly in Area 48, around the South Shetland Islands (Subarea 48.1) and South Orkney Islands (Subarea 48.2) in summer,

Table 1.1 Nominal catches (tonnes) in FAO Subareas 48.2 and 48.3 as reported by CCAMLR (2002).

Species Group	1991/92	1992/93	1993/94	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00	2000/01
Icefish (Channichthyidae)	9		16	10			6	271	4114	966
Krill (Euphausiidae)	224 496	42 710	37 907	82 423	39 324	31 223	30 964	64 422	33 320	44 696
Crabs (Lithodidae)		299	0	0	497	1	1	0	4	13
Grandier (Macrouridae)			0	11	24	15	21	12	5	3
Jellyfish (Medusea)									5	
Deep sea cods (Moridae)				1	0	1	1	0		0
Lanternfish (Myctophidae)	51865		114					5	68	
Toothfish (Nototheniidae)	3754	3049	516	3267	3821	2389	3260	4294	4700	3347
Squid (Ommastrephidae)					52	28	53			2
Skates and Rays (Rajidae)	2		12	90	40	30	14	15	5	14

and adjacent to South Georgia (Subarea 48.3) in winter (CCAMLR 2002b). In November of 2000, the precautionary catch limit for Antarctic krill in Area 48 (Atlantic Sector) was raised from the former 1.5 million tonnes to 4.0 million tonnes (CCAMLR 2000).

Several factors impede the expansion of the krill fishery to the new precautionary limit (Nicol and Endo 1999). These include the rapid spoiling of the catch due to enzymatic action, the high fluoride concentration in the exoskeleton, and the need for a reliable and profitable product to offset the high cost of fishing. Efforts are underway to better prepare krill for human consumption, for pharmaceutical and industrial uses (Nicol and Endo 1997), and as feed for aquaculture (Anderson et al. 1997) or as a means of making other, cheaper aquaculture food more palatable (Forster 1998). Success could potentially result in increased fishing effort in the future.

1.4 Management of the Southern Ocean

It was not long after the discovery of the Antarctic continent that nations began claiming territory and the resources within those jurisdictions (Berkman 2002). Many nations wanted a piece of the proverbial pie and made claims for it during the 20th century, including England (1908 and 1917), New Zealand (1923), France (1924), Australia (1933), Norway (1939), Chile (1940), and Argentina (1943). While some of these claims overlapped (England/Chile/Argentina in the

Antarctic Peninsula region – Subarea 48.1), other countries such as the United States decided to reserve the right to make a claim at a later point in time.

The conflicting sovereignty claims over Antarctic territory, combined with the successful international scientific cooperative effort of the International Geophysical Year in 1957-1958, led to the development of the Antarctic Treaty (Hansom and Gordon 1998). The Antarctic Treaty System (ATS) includes the Antarctic Treaty itself (signed in 1959 and ratified in 1961), the Agreed Measures for the Conservation of Antarctic Fauna and Flora (1964), the Convention for the Conservation of Antarctic Seals (1972, in force since 1978), the Convention on the Conservation of Antarctic Marine Living Resources (1980, in force since 1982), the Convention on the Regulation of Antarctic Mineral Resource Activities (1988, never entered into force) and the Protocol on Environmental Protection (1991, in force since 1998). The Scientific Committee on Antarctic Research (SCAR) provides independent scientific support for the Consultative Parties to help guide the development of the Antarctic Treaty System. The objectives of the Treaty are to ensure that the Antarctic is used for peaceful purposes, with the goal of international harmony and scientific cooperation. As of December 1997, the original twelve signatories have been joined by other nations for a total of 45 adherent states (27 of whom are Consultative Parties and play an active role in the decision making process), which represent over three-quarters of the world's population.

The Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), which was enacted on the 7th of April 1982, is responsible for the management of the biological resources of the Antarctic and the surrounding Southern Ocean. The main motivation for the creation of CCAMLR came from the exploratory fishery for krill in the late 1960s and early 1970s. As distant-water fleets were being excluded from other fishing grounds due to the extension of national fisheries limits to 200 miles under the Law of the Sea Convention, other target species were being sought, of which krill was thought to be an attractive option (Hansom and Gordon 1998). The potential for an expanding krill fishery, coupled with the rapid depletion of some Southern Ocean finfish stocks provided the impetus for the drafting of the convention in the late 1970s.

CCAMLR consists of two main operational units. The Scientific Committee, which is responsible for collecting data on marine organisms and fisheries, and the Commission, which comprises 23 members (Constable et al. 2000), is charged with compiling the provided data in order to formulate, adopt and revise conservation measures (Sherman and Ryan 1988). The area for which the convention is responsible is about 8% of the world's oceans, and it applies to all types of marine life, including finfish, mollusks, crustaceans, mammals and birds in the area south of the Antarctic Polar Front (Constable et al. 2000). Decisions concerning the management of the biological resources of the Antarctic are made by consensus, however members may opt out of conservation measures to which they are opposed. Non-CCAMLR parties are not prevented from fishing in the area, but are considered to be doing so in contravention of the convention's objectives and outside of its management regime (Hansom and Gordon 1998).

The major management objectives of CCAMLR, as detailed in Article II of the convention, are threefold (Hansom and Gordon 1998):

1. Prevent harvested populations from declining below levels that ensure stable recruitment (i.e. avoid a decrease below the level that ensures the greatest net annual increment)

2. Maintain the ecological relationships between harvested, dependent and related populations, as well as restore depleted populations (to levels consistent with point 1)

3. Prevent (or minimize the risk) of changes that are not potentially reversible over two to three decades.

While the first few meetings were primarily organizational, the third meeting of the Commission in 1984 resulted in the first conservation measures for depleted stocks of finfish, while the meeting in 1987 resulted in the first setting of total allowable catches for harvested species (now set annually), as well as a reporting system for fisheries data and the establishment of open and closed seasons for various fisheries (Knox 1994). In 1991, the first precautionary catch limit for krill was set in recognition that reactive management was not a viable long-term strategy for the krill fishery (Constable et al. 2000). It was the first acknowledgement that the development of feedback management was preferred, and that precautionary measures were necessary in the interim (Nicol and de la Mare 1993).

CCAMLR's management objectives define a holistic, precautionary approach that is designed to protect and regulate the exploitation of one species while considering the impact on all other species, as well as the ecosystem's integrity as a whole. The goals of this convention surpass the traditional single-species approach to fishery management. Despite this recognition, however, the single species method has been the main management tool used by the Commission in the past, in the absence of comprehensive scientific data on all components of the ecosystem (Hansom and Gordon 1998).

2. Potential impacts of krill fishing in the Southern Ocean

2.1 Introduction

The Southern Ocean is a vast, productive ecosystem that has been exploited since the late 1770s (Berkman 2002, Knox 1994). The first to be removed as the seas and continent were being explored were the Antarctic fur seals (*Arctocephalus gazella*), which were taken for their valuable skins. This was followed by the export of meat and blubber from large whales in the early 1900s (Best 1993). A finfish fishery later developed in the 1960s, but experienced difficulties in the 1970s as populations of target species were overexploited (Kock 1992). While there is no commercial harvest of mammals in the Southern Ocean today, some fisheries exist for finfish, cephalopods and crustaceans.

One of the species that has been of interest to both fishers and managers is the Antarctic krill (*Euphausia superba*). Large populations of land breeding pinnipeds and seabirds, migrating whale populations that feed in the area, as well as a substantial krill fishery, all depend on krill for survival in the Southern Ocean. The importance of krill as prey for top predators has resulted in concern over the potential impacts of an expanded krill fishery (Nicol and de la Mare 1993). Presently, the market demand for krill products is not very great. However, technological innovations in the processing and packaging of krill, as well as the development of new uses for krill products may result in future increases in krill catches (Nicol and Endo 1999). The catch could thus rise from the present take of about 100 000 tonnes per year, to the quota (set by CCAMLR in 2000) of 4 million tonnes per year, a 40-fold increase (CCAMLR 2000).

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is the governing body of biological resources in the Southern Ocean, and has a mandate to manage the system using an ecosystem approach (Constable et al. 2000). CCAMLR's main management goals are to maintain the viability of harvested populations and to ensure that harvesting does not threaten the viability of populations of species that are dependent or related to the harvested species. CCAMLR also aims to restore depleted populations, and to prevent ecosystem changes that are not reversible in two to three decades. To meet these goals, managers require an

understanding of the role of target species in the system in order to predict the effects of fishing, not only on the target species, but also on other species. Management must therefore expand on the single species approach, moving towards a multispecies method of guiding decisions regarding the extraction of biological resources from the Southern Ocean.

The Southern Ocean food chain is thought by many to be relatively simple compared with other ocean systems (primary production, krill, top predator). In reality, however, the system is quite complex, and the relative roles of many species are poorly understood, such that it is difficult to forecast any cascading impacts that fishing might have. It is therefore necessary to develop and explore predictive models of species relationships in order to consider the possible range of ramifications of harvesting practices on ecosystem dynamics (Constable et al. 2000).

Predicting the ecosystem effects of krill fishing is further complicated by marked fluctuations in annual krill abundance, which can vary by as much as 30-fold from year to year in the South Atlantic sector (Fedoulov et al. 1996, Heywood et al. 1985, Murphy et al. 1998, Priddle et al. 1988). While there is no long-term set of comparable data for krill density (Brierley et al. 1997), fluctuations in krill biomass have been noted since the early 1900s and were thought to have played a role in the changing of the relative distribution of fin and blue whales (*Balaenoptera physalus* and *Balaenoptera musculus*, respectively) sought by whalers (Amos 1984). So-called "fin-whale years" were characterized by warmer temperatures and lower krill availability, with three such years recorded in seven seasons (Priddle et al. 1988). Scientific krill catches during the early 20th century were greater in colder years, and were consistent with the whaling data (Mackintosh 1972). Decreases in krill biomass have also been associated with decreased breeding success of several predatory species, including fur seals and penguins (Boyd et al. 1994b, Croxall et al. 1988c, Croxall et al. 1999). Changes in predator breeding success suggest that low-krill years occur in two out of every ten consecutive years (Priddle et al. 1988). In more recent years, krill abundance has been estimated using acoustic methods, and has been shown to be consistent with krill abundances inferred from predator breeding success (Brierley et al. 1997).

My goal was to explore the potential ecosystem impacts of an expanded krill fishery in the South Orkneys/South Georgia region of the Southern Ocean. The following describes an ecosystem

model, and reviews and discusses the data available for the Southern Ocean to assess ecosystem effects of management actions. The model provides insights into the possible effects of expanding the krill fishery and presents a useful framework for meeting the goals of CCAMLR.

2.2 Methods

Ecopath with Ecosim (EwE) is a modelling software package that provides a framework for creating a snapshot of biomass flow through the food web of a defined ecosystem (Polovina 1984, Christensen and Pauly 1992). Ecopath is based on two master equations (Christensen et al. 2000), the first of which traces the flow of biomass through the system:

Production = predation + fishery + other mortality + biomass accumulation + net migration   {Eq. 2.1}

And the second of which accounts for energy in the system:

Consumption = production + unassimilated food + respiration   {Eq. 2.2}

Both of these equations ensure that the model system is mass-balanced, i.e., mass and energy are neither created nor destroyed spontaneously.

Ecosim is a dynamic modelling component of the software that allows the simulation of species interactions in the system over time (Walters et al. 1997). It is useful for exploring the effects of different fishing regimes, as well as the biological responses of the species groups to environmental perturbations. Further details on EwE are contained in Appendix A.

2.2.1 Study area

I constructed an ecosystem model for the South Orkneys/South Georgia area of the South Atlantic Sector of the Southern Ocean (FAO subareas 48.2 and 48.3, respectively) for the 1990s (Fig. 1.1). This region is bounded by the Antarctic Polar Front to the north and the Weddell Sea to the south. This part of the Southern Ocean supports large populations of birds, seals and

whales, and has experienced intense exploration and exploitation (Croxall et al. 1985b). This in turn has led to an extensive database that can be used to parameterize a model.

2.2.2 Model construction

The species in the modelled system were identified and classified into 'functional groups', or assemblies of species with similar biological characteristics. The more than 200 species of fish, birds, seals and whales feeding and/or breeding in the South Orkneys/South Georgia region, as well as the lower trophic levels including phytoplankton, zooplankton and benthic invertebrates, were classified into 29 functional groups (Table 2.1). Each of the functional groups required five pieces of information, which were gleaned from the published literature:

- How much is there (biomass, B)

- Production/biomass (P/B, corresponds to mortality due to predation, fishing and other causes)

- How much they eat (consumption/biomass, Q/B)

- What they eat (diet composition, DC)

- Fisheries (catch)

A detailed description of the data sources for model parameters is contained in Appendix B.

Input parameters were adjusted to ensure that all energy and mass were accounted for in the system (i.e., that the model was balanced). The Ecopath model was then used to elucidate the overall structure of the ecosystem, while Ecosim was used to explore the systemic consequences of harvesting krill.

2.3 Results

Some of the input parameters derived from the literature were not consistent with one another and were changed to balance the model (i.e., to ensure that the lower trophic levels were present in sufficient quantities to support the upper trophic levels). In general, the published estimates

Table 2.1 Input parameters for the 1990s model of the South Orkneys/South Georgia region. Bolded values represent the parameter estimated by EwE for each functional group. Group 3 (Baleen whales) includes humpback whales, blue whales, fin whales, sei whales and southern right whales (*Eubalaena australis*). Group 12 (Penguins) includes macaroni penguins, gentoo penguins and chinstrap penguins (*Pygoscelis antarctica*).

Functional Group		B (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	E/E	Catch (t·km^{-2})
1	Killer whales	0.001	0.060	4.800	**0.000**	0.000
2	Sperm whales	0.009	0.065	4.200	**0.000**	0.000
3	Baleen whales	0.012	0.065	4.800	**0.240**	0.000
4	Minke whales	0.140	0.095	4.800	**0.023**	0.000
5	Small cetaceans	0.049	0.150	7.200	**0.008**	0.000
6	Antarctic fur seals	0.032	0.150	3.197	**0.175**	0.000
7	Elephant seals	0.083	0.150	2.656	**0.008**	0.000
8	Crabeater seals	0.005	0.110	5.798	**0.995**	0.000
9	Leopard seals	0.001	0.150	5.343	**0.500**	0.000
10	Weddell and Ross seals	0.000	0.220	11.382	**0.909**	0.000
11	King penguins	0.007	0.221	62.027	**0.113**	0.000
12	Penguins	0.020	0.240	64.236	**0.436**	0.000
13	Albatrosses	0.001	0.140	65.624	**0.791**	0.000
14	Other birds	0.008	0.260	256.419	**0.051**	0.000
15	Toothfish	0.196	0.265	1.600	**0.984**	0.032
16	Marbled rockcod	0.056	0.305	2.286	**0.991**	0.000
17	Mackerel icefish	0.060	0.570	2.912	**0.996**	0.002
18	Myctophids	16.300	0.950	7.406	**0.996**	0.000
19	Small pelagics	3.000	0.250	4.802	**0.930**	0.000
20	Large demersals	2.500	0.550	3.274	**0.989**	0.000
21	Small demersals	3.500	0.800	4.243	**0.993**	0.000
22	Large squid	1.609	2.500	12.000	**0.096**	0.000
23	Small squid	0.950	3.000	15.000	**0.980**	0.000
24	Large invertebrates	3.700	0.870	10.000	**0.996**	0.000
25	Small invertebrates	8.200	1.740	20.000	**0.998**	0.000
26	Krill	47.000	2.000	8.250	**0.995**	0.044
27	Salps	20.805	50.000	250.000	**0.005**	0.000
28	Other zooplankton	71.000	7.000	28.000	**0.993**	0.000
29	Phytoplankton	**64.772**	200.000	-	0.500	0.000
30	Detritus	-	-	-	**0.095**	

for biomass and production of the lower trophic levels were insufficient to support the organisms that have been quantified at the top of the food chain. As a result the values for biomass of the more generalized predators were reduced (i.e., leopard seals, *Hydrurga leptonyx* and killer whales, *Orcinus orca*). Several species of commercially exploited species had ecotrophic efficiencies (*EE*) greater than 1 (meaning that more production of those groups was being consumed in the system than was available). The proportion of marbled rockcod (*Notothenia rossii*) in the diets of several of its main predators was lowered, thereby reducing the simulated predation pressure on this group. The production/biomass ratio (*P/B*) was also increased slightly. In the case of mackerel icefish (*Champsocephalus gunnari*), biomass was increased and the proportion being eaten by predators was decreased. Other groups of species in lower trophic levels, namely myctophids (*Electrona* spp.), large and small demersal fish, and small pelagic fish also required increases in biomass and *P/B* to provide enough biomass and energy to support the top predators. As a result, invertebrates and zooplankton were also increased from initial estimates. Final input parameters for the balanced model are shown in Table 2.1. Other inputs and outputs of the model, as well as a model pedigree, fisheries data used for tuning the model, and settings for Ecosim runs are contained in Appendix C. The bulk of the biomass in the Southern Ocean occurs in the lower trophic levels (Fig 2.1). Top predators such as whales, seals and birds make up a relatively small portion of the total biomass.

2.3.1 Role of krill in the ecosystem

The number of direct links (connectance) between krill and the other groups of organisms (Fig. 2.2) shows that most groups feed directly on krill, or are eaten directly by krill. The few that are not krill predators or prey include killer whales, sperm whales (*Physeter macrocephalus*), elephant seals (*Mirounga leonina*), king penguins (*Aptenodytes patagonicus*), small invertebrates and salps (*Salpa thompsoni*). It is also apparent that the main predators of krill are fish and squid, especially myctophids, which are a group of high-lipid mesopelagic fish (Lea et al. 2002) often found in association with krill aggregations (Rembiszewski et al. 1978).
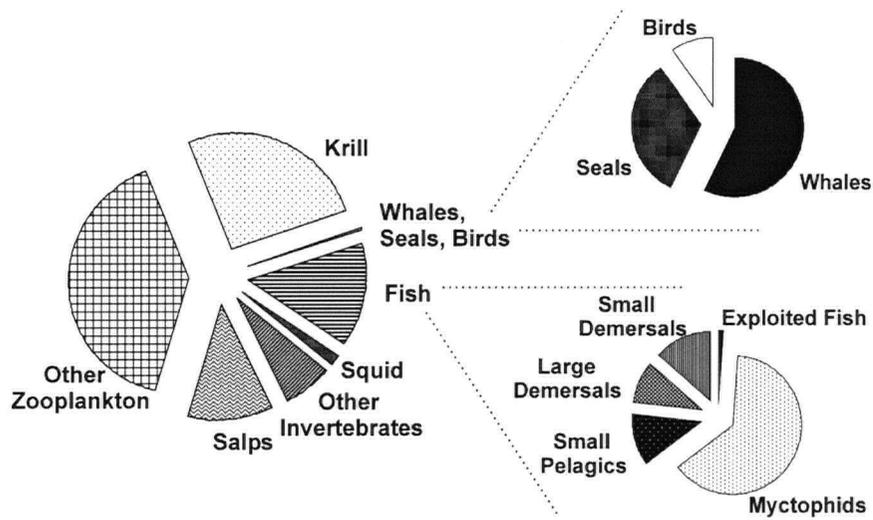
Figure 2.1 The proportion of organisms (biomass) in the South Orkneys/South Georgia ecosystem. Exploited fish refers to the three main species that have experienced intense fishing pressure in the past (i.e., marbled rockcod, mackerel icefish and toothfish, *Dissostichus eleginoides*).
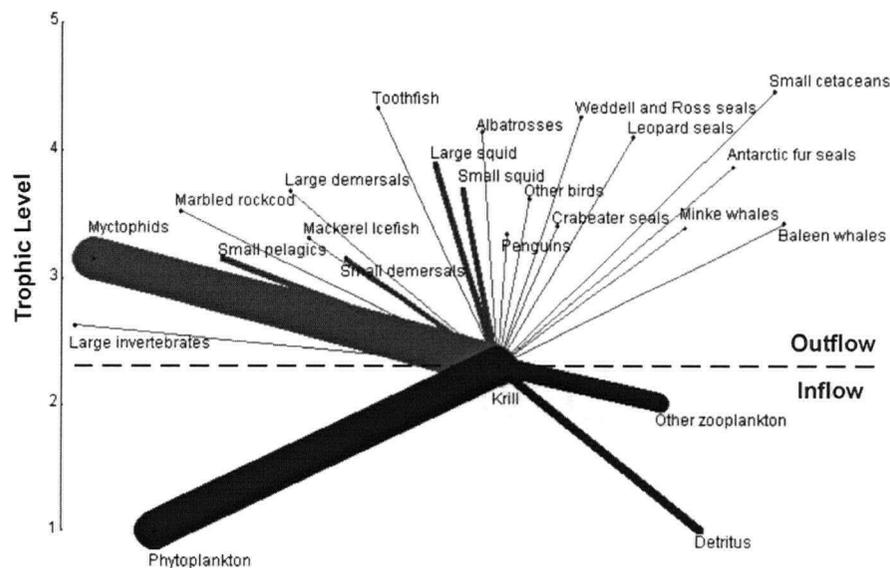
Figure 2.2 The direct role of krill in the South Orkneys/South Georgia region of the Southern Ocean. Width of connecting line represents relative predation strengths. Krill shown in the middle consume species below them (inflow) and are consumed by those above them (outflow).

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2.3.2 Krill fishery

Ecosim was used to explore the effects of the increased fishing quota for krill — 4 million tonnes/year in the South Atlantic sector, of which 2.16 million tonnes/year could be taken from the study region (CCAMLR 2000). This increased quota represents a fishing rate 26 times larger than catches in recent years. The model suggested that the majority of the functional groups would not experience a change in biomass of 5% or greater if the fishery took the new quota every year for 50 years. The only exceptions were whales and Antarctic fur seals (which all decreased less than 10%), and mackerel icefish (which declined by almost 35%) (Fig. 2.3). Mackerel icefish rely on krill for a significant proportion of their diet (Barrera-Oro et al. 1998, Kock et al. 1994), but are also caught as a bycatch species in the midwater otter trawl fishery for krill (Everson et al. 1992, Pakhomov and Pankratov 1994).

2.3.3 Krill variability

In order to introduce natural variability into the system, 11 years of acoustic estimates of krill biomass at South Georgia (Table 2.2) were used to create a 100-year time series of krill abundance using Monte Carlo simulations (median = 40 $g \cdot m^{-2}$, min. = 4 $g \cdot m^{-2}$, max. = 100 $g \cdot m^{-2}$) (Fig. 2.4). No autocorrelation was applied since strong krill cohorts can be produced even with low spawning stock levels (Siegel and Loeb 1995) (i.e., low-krill years are often followed by years of high krill availability, e.g., 1991, 1992, Table 2.2). Information on per capita breeding success of predators also shows a return to normal levels (but with smaller breeding populations) following years of low krill availability (Priddle et al. 1988).

Running Ecosim with the generated krill biomass time series (Fig. 2.4) resulted in fluctuations in the biomass of top predators that tended to track the krill biomass (Fig. 2.5). Increasing the krill fishery to the new quota had a detectable but minor effect on the overall pattern of relative biomass. Biomass changes were <10% compared with the low-krill fishing scenario for all functional groups except mackerel icefish.
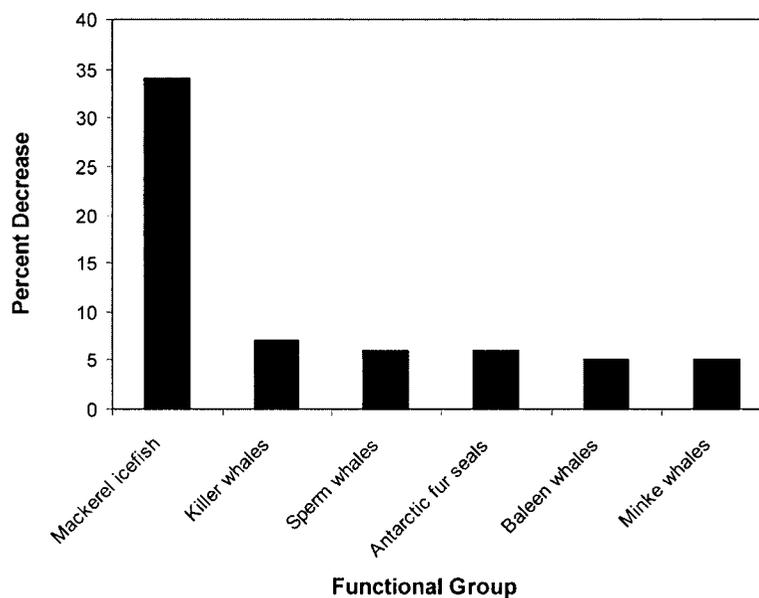
Figure 2.3 Changes in biomass due to the krill fishery (removal of target and bycatch species). The percent decrease in biomass for groups that changed by more than 5% when krill fishing was increased to the proposed quota for the South Orkneys/South Georgia region of the Southern Ocean. The simulated fishing rate began in year one (i.e. mid-1990s) and continued until the end of a 50-year simulation, at which time biomasses were recorded.

Table 2.2 Mean estimates of krill density at South Georgia from acoustic surveys (Brierley et al. 1999b).

Year	1981	1982	1986	1990	1991	1992	1993	1994	1996	1997	1998
Biomass ($g \cdot m^{-2}$)	59.7	11.7	29.7	60.1	6.4	95.0	65.8	4.7	33.7	39.9	86.2

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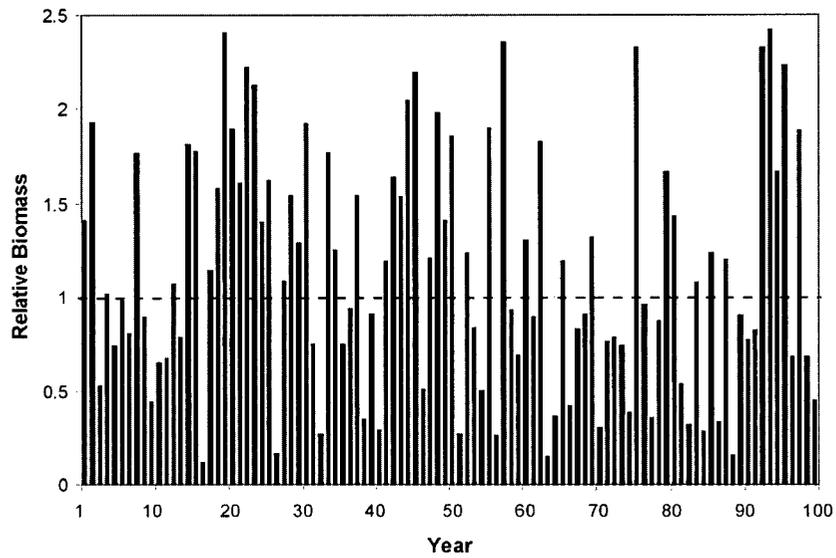
Figure 2.4 One hundred years of simulated relative krill biomass created using Monte Carlo simulations that were based on 11 years of acoustic estimates (Table 2.2, median = 40, min. = 4, max. = 100).
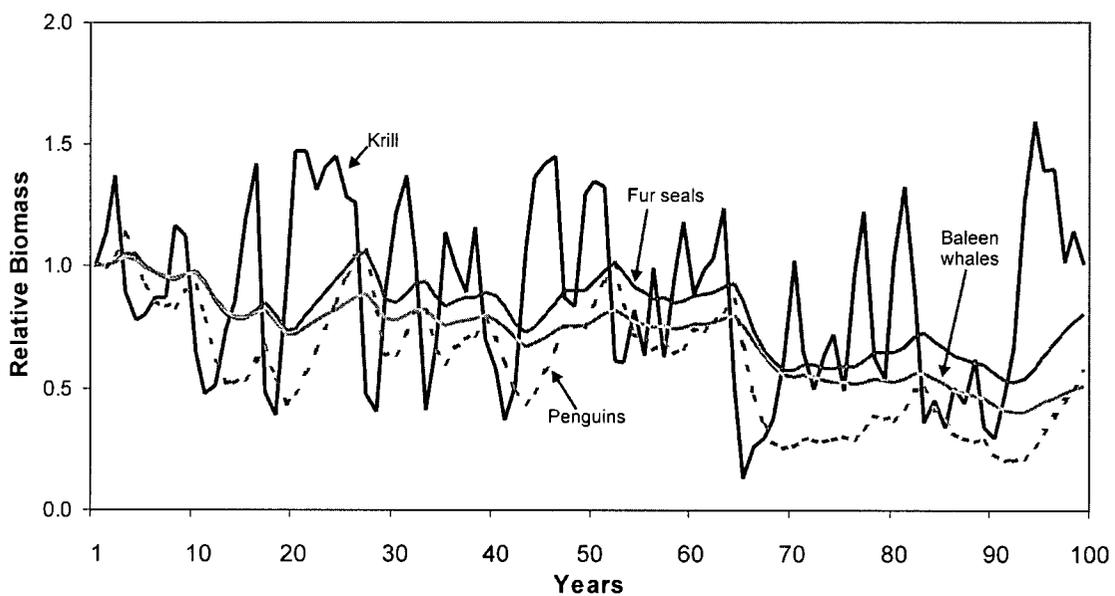
Figure 2.5 Ecosystem response to krill variability. A forward simulation of relative biomass of krill, baleen whales, Antarctic fur seals and penguins when krill variability was incorporated into the model.

2.4 Discussion

2.4.1 Ecosystem structure

Compiling the published datasets for the South Orkneys/South Georgia region model revealed that some of the estimates of consumer demand were much higher than estimates of prey production. That is, the estimated abundances of lower trophic level species were not sufficient to support the top predators. While this phenomenon has been previously observed and discussed for the Southern Ocean (e.g., Nicol et al. 2000, Pitcher and Chuenpagdee 1995), it is not limited to Antarctic waters. A feeding study of fin whales off Nova Scotia, Canada noted that average densities of euphausiids gleaned from acoustic and net sampling were insufficient to support the fin whale populations that were present (Brodie et al. 1978). Whales would have had to swim at impossible speeds of 900 km/h for 8 hours to fill their stomachs with the density of euphausiids estimated to be there.

In the case of the South Orkneys/South Georgia region, there are three possible explanations for the apparent incongruity between predator demand and prey production: 1) overestimated predator consumption, 2) undetected populations of prey, or 3) biased prey sampling techniques. With respect to the possibility that predator consumption has been overestimated, it is important to note that birds, seals and whales have long been studied in the Southern Ocean because of their interest to humans as charismatic species and as marketable products (e.g., Boyd 1999, Boyd 2002, Croxall and Prince 1987, Croxall et al. 1984b, Innes et al. 1987, Laws 1977). Basic biology, such as population sizes and consumption rates, has therefore been relatively well studied. However, little is known about the feeding behaviour of most species during winter when scientific study is difficult due to inclement conditions.

The second possible explanation for the conflict between prey availability and predator consumption is that some prey populations (particularly Antarctic krill) may not have been detected due to incomplete surveys of the region. This also seems unlikely given that the South Orkneys/South Georgia region is one of the most important krill fishing grounds in the world (Nicol and Endo 1997), and considerable research has been undertaken to understand the spatial distribution of krill in this area (e.g., Hofmann et al. 1998, Priddle et al. 1988, Siegel 2000a).

However, the area is large (over 1.86 million km^2) and difficult to cover by means of ship surveys.

The third possibility for explaining the discrepancy between predator/prey numbers relates to the accuracy of prey survey techniques. Net avoidance is one factor that could underestimate krill abundance (Everson 1988). There are also problems associated with using hydroacoustic sampling methods (Nicol et al. 2000). Krill tend to aggregate into large groups or swarms, which are detectable by acoustics. However, the presence of low densities of krill throughout the region (i.e., 'background krill') may not be evident using acoustic methods (Miller and Hampton 1989), and krill refuges, such as fast-ice and ice shelves, may shelter large aggregations of krill from net and hydroacoustic sampling efforts. Krill found at the surface would also be out of the range of downward, hull-mounted acoustic transducers (Demer and Hewitt 1995). This could be a significant bias given that krill undergo vertical migration, with the surface layer being one of the most important feeding areas for land-based predators (Boyd 1996, Croxall et al. 1985a).

To date, there has been no definitive determination of the causes of the inconsistency between predator demand and krill production (Nicol et al. 2000). This issue has also been addressed for other species of prey such as fish, for which estimated consumption by predators exceeds stock estimates (Doidge and Croxall 1985). My decision to increase abundances of lower trophic level species to support the top predators was therefore based on the relative reliability of the comprehensive body of work on predator biology. However, the issue of discrepancy between predator demand and prey availability remains one that should be further explored in future studies in the Southern Ocean.

The estimate of primary productivity in the model was high (Table 2.1) and was primarily attributed to the high biomass and rate of production of salps (Table C2). Salps have been stated as having a much higher growth rate than other groups of zooplankton (Alldredge and Madin 1982), and studies designed to improve the understanding of their role in the Southern Ocean are continuing (Loeb et al. 1997, Siegel and Loeb 1995). Their biomass may vary considerably by season and area (Everson 1984, Piatkowski et al. 1994), but this was not incorporated into the model. Thus the biomass estimate of salps used in the model may be inflated.

The estimated biomass of myctophids (Table 2.1) was increased from 5.5 tonnes/km^2 (Lubivoma et al. 1983, Sabourenkov 1991) to 16.3 tonnes/km^2 in order to balance the model (i.e., so that there were enough myctophids to meet the needs of their predators). Myctophids were an important part of the diet of many species (Table C1), but the main predator in terms of biomass consumed was squid (Table C2). Squid are not very well understood in the system (Rodhouse et al. 1993), so it is possible that their biomass was overstated in the model, or that the amount of myctophids in the diet of squid was overestimated. This does not necessarily imply that myctophids were not important in the system, but the absolute value of 16.3 tonnes/km^2 may be an amplification of their true biomass value.

2.4.2 Role of krill in the ecosystem

As previously mentioned, krill play a vital role in the Southern Ocean ecosystem. Not only are they a dominant primary consumer (Miller and Hampton 1989), but they are also a crucial source of food for many top predator species including birds, seals and whales (Croxall et al. 1988c). This is apparent from the number and magnitude of direct trophic links between krill and the other groups in the system (Fig. 2.2). In the Southern Ocean, krill are thought to fill the niche that schooling clupeid fishes occupy in other areas of the world (Verity and Smetacek 1996).

The krill population in the South Orkneys/South Georgia region is not thought to be self-sustaining since krill don't breed in the area (absence of gravid females). Local populations, therefore, rely on an influx of individuals associated with regional currents (Croxall and Pilcher 1984, Mackintosh 1972, Marr 1962, Murphy 1995, Ward et al. 1990). While genetic studies are somewhat equivocal, the krill from the Antarctic Peninsula, Weddell Sea and Scotia Sea (i.e. South Orkneys/South Georgia area) are all part of the same population (Jarman et al. 2000), with the Peninsula, and perhaps the northern Weddell Sea, acting as source regions for the krill found at South Georgia (Hofmann et al. 1998, Murphy et al. 1998). How, or if, the krill complete the loop back to the Peninsula region is not known, but it has been proposed that the South Orkneys/South Georgia region is in fact a sink for krill biomass (Ichii and Naganobu 1996, Murphy et al. 1998).

2.4.3 Southern Ocean food chain, re-evaluated

The Southern Ocean ecosystem has traditionally been thought of as a simple food web consisting of only about three trophic levels (i.e., primary production, krill, krill predators), with most of the research on krill predators focused on seals, whales and seabirds. Little recognition has been given to other krill predators such as fish and squid (Constable et al. 2000). Many diet studies of birds and seals have indicated that, while krill is often the main prey item, fish (especially the mesopelagic mytophids) also make up an important part of their diets (Ainley et al. 1992, Boyd et al. 1994a, Croxall et al. 1988a, Croxall and Prince 1980a, Croxall et al. 1997, Croxall et al. 1985b, Daneri and Coria 1992, Daneri and Coria 1993, Goodall and Galeazzi 1985, Green and Williams 1986, Kooyman et al. 1999, McCann and Doidge 1987, North 1996a, Oritzland 1977, Reid 1995, Reid and Arnould 1996). Studies of fish diets in the region further indicate that fish are dependent on krill as a main prey source (Agnew et al. 1998, Barrera-Oro et al. 1998, Frolkina et al. 1998, Kock 1987, Lea et al. 2002, Rowedder 1979, Targett 1981).

The relative importance of fish as krill predators is shown by the connectance diagram (Fig 2.2), suggesting that a substantial portion of the available krill biomass in consumed by fish. From this information, it is apparent that energy pathways exist in the Southern Ocean ecosystem that are more complicated than the simplest three-step food chain. Decreases in krill populations could thus have exaggerated effects on top predators, which depend both directly and indirectly on krill for survival.

Recognizing the significant role of fish as krill consumers and prey for top predators is crucial to understanding the trophic interactions within the ecosystem. At present, there is insufficient understanding of fish biology, especially in terms of abundance estimates, to evaluate the more complex trophic interactions. Additional research should therefore be focused on refining abundance and diet information of the Southern Ocean fish species.

Another area where there is a paucity of information concerns the role of squid in the Southern Ocean. Squid are thought to feed on fish (mostly myctophids) and krill (Kear 1992, Kock 1987, Rodhouse et al. 1992), possibly consuming up to 100 million tonnes of krill per year (Laws

1985). Yet, there is insufficient data to estimate the stock size of squid in the South Atlantic sector of the Southern Ocean (Rodhouse et al. 1993), making it difficult to properly quantify their role in the system. In the modelled ecosystem, squid were important krill predators, consuming more than 35 million tonnes of krill annually (Fig. 2.2). Squid were also important for higher trophic level organisms, which were estimated to consume over 1.5 million tonnes of squid each year. Squid have been a notoriously difficult group of organisms to study, and require further attention given their apparent importance in the ecosystem.

2.4.4 Krill fishery

2.4.4.1 Effects of fishery

Little change was observed in the biomasses of most functional groups (Fig. 2.3) when the midwater otter trawl fishery for krill was increased within the model to catch the new quota of 2.16 million tonnes in the South Orkneys/South Georgia region (a fishing rate 26 times larger than in the 1990s). CCAMLR arrived at this new krill quota using a single species model to identify the harvesting intensity (11.6% of krill biomass) that would result in the krill biomass being reduced to 75% of its pre-exploitation size following 20 years of harvesting (SC-CAMLR 1994, Thomson et al. 2000). Based on a krill biomass estimate derived from a near-synoptic acoustic survey of FAO Statistical Area 48 (South Atlantic Sector) in 1981, the new precautionary quota was set by CCAMLR at 4 million tonnes for Area 48 (further partitioned by subarea; SC-CAMLR 1995a). This was modified from 1.5 million tonnes due to revised target strength estimates for acoustic techniques, which changed the biomass estimate of krill and therefore the tonnage represented by the target 11.6% (Nicol et al. 2000). Relative to the estimated needs of krill consumers, the new quota is considered small (Everson 1988), thus explaining the minimal ramifications for most species in the modelled system.

2.4.4.2 Bycatch

Even though most krill predators within the modelled system did not seem to be considerably affected by the new krill quota, the potential impact of bycatch arising from the krill fishery is another factor that bears consideration. Several studies have indicated that juveniles of some fish species (mostly channichthyids and notothenids) are caught in krill trawls in sufficient numbers

to negatively affect adult breeding fish populations (Rembiszewski et al. 1978, Slosarczyk and Rembiszewski 1982). A study of bycatch in the Prydz Bay region of the Antarctic found that fish made up 4-19% of the biomass of hauls in the krill fishery (Williams·1985). Bycatch levels in the South Georgia region are similar (Slosarczyk and Rembiszewski 1982), but vary spatially, with the majority of hauls with icefish as bycatch coming from the eastern end of the island. Bycatch is also affected by depth (one haul near the seabed resulted in icefish making up about 70% by weight of the catch) (Everson et al. 1992). The smallest size class of icefish (year 0) are likely to be the most vulnerable to krill trawls during the first few months of the year, and are also the most difficult to detect in the catch because year 0 icefish are similar in size to krill, and are either transparent or translucent white (Everson et al. 1992).

The studies conducted to date cannot be used to directly infer bycatch levels in winter months when most of the krill fishing occurs around South Georgia (Everson and Goss 1991). However, studies of the life history of fish during the late winter and early summer months suggest that juveniles (especially icefish) are present in pelagic waters for most of the year (North 1991). Bycatch could therefore also be an issue during winter krill fishing around South Georgia.

The values for mackerel icefish bycatch in the modelled ecosystem were fairly conservative at about 0.3% of icefish biomass taken by the 1990s-level krill fishery. However, increasing the krill fishery to the 2000 quota of 2.16 million tonnes resulted in an increased bycatch of about 8% of the mackerel icefish biomass.

High catch rates of krill tend to be associated with low bycatch of icefish (Everson et al. 1992), suggesting that the targeting of large swarms of krill would have less of an effect on icefish populations. However, attempts to reach krill quotas may result in higher levels of icefish bycatch in years of low krill biomass when krill concentrations are difficult to locate (Croxall et al. 1988c). Thus high natural variability in icefish recruitment (de la Mare et al. 1998) combined with increased fish bycatch and increased predation pressure on icefish from Antarctic fur seals that switch prey during low krill biomass years (Agnew et al. 1998) could result in drastic reductions in icefish populations during some years.

2.4.4.3 Issue of spatial overlap

This model indicates that the new quota for the krill fishery would not greatly affect most top predators. However, this conclusion could be altered by the finer spatial elements of the real-world ecosystem that are not presently incorporated into the model. Greater spatial and temporal detail is required if the real competition between top predators and the krill fishery is to be evaluated. Land-based predators such as macaroni penguins (*Eudyptes chrysolophus*) and Antarctic fur seals that are restricted in their feeding radius during the breeding season forage in the vicinity of large krill aggregations both inshore and offshore in the South Georgia area (Hunt et al. 1992). The krill fishery also relies on large concentrations of krill for its catches, aiming to tow through swarms located using echosounders (Everson et al. 1992). This could result in increased competition between predators and fishing, where the krill resource may be much more limited to both parties than is apparent from a more spatially general depiction of the ecosystem (Everson 1988).

A key to managing the krill fishery is to ensure that fishing does not overlap spatially and temporally with spatially restricted krill predators in a way that causes serious systemic ramifications. In order to accomplish this, areas of overlap between foraging predators and fishing vessels need to be identified, and estimates of krill biomass need to be refined. If possible, the component of the krill population taken by predators and the fishery (e.g., krill size classes, depth of krill swarms, etc.) should also be detailed to assess true competition. In other words, while the overall krill biomass may be large, the effective krill population that is available to predators and fisheries may be much more limited (Zane and Patarnello 2000). Also, since krill flow into the South Orkneys/South Georgia region from other areas, the effects of fishing upstream (i.e., at the source) should also be considered (Murphy et al. 1998). Finally, while finer-scaled data on the location of krill, its predators and the fishery will improve our understanding of system interactions, the scale of the management areas (statistical areas) must also be adjusted to allow the appropriate management regimes to be applied (Nicol et al. 2000).

2.4.5 Krill variability

As previously mentioned, the krill population in the South Orkneys/South Georgia region fluctuates dramatically from year to year, with two to three years of low krill biomass occurring per decade (Priddle et al. 1988). Years of low krill abundance have been confirmed by both acoustic techniques and the breeding success of krill predators, and are often followed by years of normal to high krill abundance (Priddle et al. 1988). The biomass of krill at South Georgia appears to fluctuate in accordance with krill biomass changes in the Peninsula region (Brierley et al. 1999b), although this is somewhat controversial (Loeb et al. 1997, Murphy et al. 1998, Siegel et al. 1997, Siegel and Loeb 1995).

2.4.5.1 Factors affecting variability

Although the factors controlling krill stocks in the South Orkneys/South Georgia region are not fully understood, the short time frame of low abundance (i.e., one year) for an organism that lives for 6-7 years (Rosenberg et al. 1986) suggests that this variability is not caused solely by recruitment failure or mass mortality (Siegel 2000a). The high level of production of krill incorporated into the model (Table 2.1) was not intended to reflect the actual rate of biological reproduction of the species, but instead to represent the influx of krill into the South Orkneys/South Georgia area. The influx of krill, and thus the biomass of krill in the region, is thought to be influenced by large-scale atmospheric and oceanographic processes (Priddle et al. 1988).

The variation in abundance of krill in the South Orkneys/South Georgia region is thought to be impacted by two main factors. The first concerns the amount of krill available for import, which is dependent on the recruitment in source regions such as the Peninsula area, which is in turn affected by large-scale environmental variation, such as changes in sea-ice extent. Since the South Orkneys/South Georgia area relies on the influx of krill from other areas (e.g., Antarctic Peninsula region), changes in the pattern of recruitment in this area will affect the amount of krill available for transport (Brierley et al. 1997). Sea-ice has been linked with krill recruitment success such that years of larger sea-ice extension and longer ice-cover duration result in higher recruitment levels in the Peninsula region (Loeb et al. 1997, Siegel and Loeb 1995). This may implicate the circumpolar wave, which is a circumpolar eastward procession of anomalies in sea-

ice extent, sea surface temperature, atmospheric pressure, and wind stress that result in 4-5 year periods of environmental variation (White and Peterson 1996). The correlation of sea-ice and krill recruitment is not as straightforward as first thought (Murphy et al. 1998). While years of low krill abundance tend to be years of low ice extent, some years with less sea-ice cover have had relatively normal krill biomass levels in the South Georgia area.

The El Niño-Southern Oscillation (ENSO) has also been linked to krill abundance fluctuations. Both 1978 and 1984 were years of low krill biomass, and followed a year of strong ENSO events (Croxall et al. 1988c). However, the low krill biomass in 1991 was not associated with an ENSO event (Croxall 1992), suggesting that correlations of krill biomass with large-scale patterns of variation on longer timescales need to be interpreted with care.

The second factor affecting the abundance of krill in the South Orkneys/South Georgia region involves the processes of advection, which depend on the circulation patterns, currents and fronts (Siegel 2000a). Krill in the South Orkneys/South Georgia area are thought to be at the northern extreme of their geographical range rather than at the centre of their distribution (Siegel 2000a). Therefore, in years when weather phenomena cause the southward shifting of the Antarctic Polar Front via wind-forcing, the South Georgia region is surrounded by warmer sub-Antarctic waters, and the colder Antarctic waters containing the krill are pushed out of the area resulting in a local krill scarcity (Atkinson and Peck 1988, Heywood et al. 1985, Priddle et al. 1988).

Smaller-scale hydrodynamics also play a role in krill retention in the area, with high krill concentrations often occurring in areas of eddies (Frolkina et al. 1998). In low-krill years, long periods of strong winds have been observed to "smear" the surface layer, resulting in the weakening and eventual breakdown of the eddy system (Priddle et al. 1988). This decreases the krill residence time in the area and thus the availability of krill to predators and fisheries.

Both factors (i.e., potential krill for import, and oceanographic processes) suggest that the pattern of krill abundance in the South Orkneys/South Georgia region is part of much larger-scale processes. However, more local features, such as changes in the behaviour of krill in terms of vertical migration, swarming and dispersing, may also affect the krill biomass available to predators or detectable by survey methods such as acoustics and net sampling (Siegel 2000a).

2.4.5.2 Consequences of variability

Regardless of the uncertainty over the causes for the variation in krill abundance, it is clear that years of low krill biomass have severe consequences for krill predators. Many land-based predators experience reduced breeding success in low-krill years (Croxall et al. 1988c, Croxall et al. 1999, Fedoulov et al. 1996, Heywood et al. 1985), including Antarctic fur seals, which exhibit higher pup mortalities (Doidge et al. 1984) and longer foraging trip duration for females (McCann and Doidge 1987). Bird species, such as black-browed albatrosses (*Diomedea melanophris*), gentoo penguins (*Pygoscelis papua*) and macaroni penguins also experience reduced breeding success in low-krill years (Priddle et al. 1988). Other consequences of krill scarcity is prey switching or a shift in the diet composition of krill predators, such as an increased reliance on mackerel icefish by Antarctic fur seals (Agnew et al. 1998), and a shift from krill to the amphipod *Themisto gaudichaudii* by macaroni penguins (Croxall et al. 1999).

The simulations in which krill variability was incorporated demonstrate the degree to which fluctuations in krill biomass can affect krill predators (Fig. 2.5). The general downward trend of the relative biomasses in Figure 2.5 is not indicative of the general trend of the ecosystem when all functional groups are considered (average relative biomass at the end of the 100-year simulation is 1). Thus it appears that variation in krill abundance has greater negative consequences for top predators such as birds, seals and whales than other species further down the trophic scale. However, it seems unlikely that the overall downward trend in top predator biomass shown in Figure 2.5 is a real result of krill variability given that krill variability in the South Orkneys/South Georgia system is not a newly recorded phenomenon, and top predators still persist in the system today. In this simulation, the magnitude of the biomass fluctuations may have been too great and/or the period of the biomass shifts may have been too short for top predators to fully recover following years of low krill availability. The simulated time-series of krill biomass that I used (Fig 2.4) was based on measured estimates of krill abundance (Brierley et al. 1999b). However, these estimates may not accurately reflect patterns of krill abundance. It is possible for example that top predators rely on krill biomass that is not being detected by survey techniques during years of low krill biomass. Or perhaps top predators are better able to supplement their diet with alternative species than was simulated in the model.

Regardless of the overall downward trend of top predator biomass, years of reduced krill availability resulted in declines in top predator biomass in the modelled system. Introducing the higher simulated krill fishery resulted in a relatively small further decrease in predator biomass, which may be significant when predator biomass is already depressed due to natural krill variability.

2.5 Conclusions

The model simulations indicate that the 2000 quota for krill in the South Orkneys/South Georgia region of the Southern Ocean is unlikely to significantly affect most species in the ecosystem, except for bycatch species such as mackerel icefish. Natural annual fluctuations in krill biomass appear to have a much greater impact on the ecosystem as a whole. However, my model does not include fine spatial-scale detail, which might reveal areas where demand for krill biomass is high and competition between krill predators is much more concentrated (i.e., where krill biomass is the limiting factor for some populations). Predictive models are essential for exploring and refining our understanding of interspecific relationships if CCAMLR management goals are to be met, such that fisheries are maintained at a level that ensures the long-term sustainability of target species and the overall trophic structure of the system. While the mass-balance modelling technique employed in my study does not provide definitive answers to management dilemmas in the Southern Ocean, it does serve as a useful tool to employ in conjunction with other methods of evaluating potential impacts of fisheries. In particular, the ecosystem model is a base upon which future considerations (perhaps delving into the finer spatial detail of the system) can be explored.

2.6 Summary

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has a mandate to manage Southern Ocean resources using an ecosystem approach. In accordance with this, an ecosystem model of the South Orkneys/South Georgia region (FAO Subareas 48.2 and

48.3, respectively) was constructed using the modelling software Ecopath with Ecosim. The model was used to explore the complex interactions between Antarctic krill (*Euphausia superba*) and its predators. In particular, it was used to test what effect an increased krill fishery might have on the Antarctic ecosystem (i.e., an increase from the 1990s catch of about 100 000 tonnes of krill per year to the quota of 4 million tonnes/year that was set in 2000). The model predicts that the expanded fishery could cause small declines (<10%) in the biomass of several top predators, such as Antarctic fur seals and baleen whales, if krill recruitment remains relatively consistent from year to year. While this scenario suggests an expanded krill fishery will not significantly affect community composition, levels of fish bycatch in the krill trawl fishery may be sufficient to affect some fish populations by almost 35%. If the natural annual variation in krill biomass is incorporated, the model indicates that years of low krill abundance would have strong negative impacts on predator population sizes (as observed in field studies). The proposed krill fishery would further exacerbate these impacts. In addition to exploring the effects of krill fishing, the model indicates that the traditional concept of the simple Southern Ocean food chain (i.e., primary production, krill, top predator) may need to be re-evaluated to consider other important intermediary species groups, such as fish and squid. These findings emphasize the need for a better understanding of the relative roles of species in the Southern Ocean ecosystem, as well as the natural variability of krill abundance before expanding krill fishing in the Antarctic.

3. The impact of sealing, whaling and fishing on the Southern Ocean: insights from four ecosystem models

3.1 Introduction

The Southern Ocean is perceived by many to be a pristine ecosystem, but it has in fact experienced considerable human-induced perturbation (Berkman 2002, Knox 1994). Sealing in the late 1700s and early 1800s, along with whaling in the first half of the 1900s and fishing in the mid 1900s drastically reduced the abundance of many groups of organisms. While some species have since increased in numbers (e.g., the Antarctic fur seal, *Arctocephalus gazelle*; Bonner 1976, Boyd 2002), others, such as the large whale species, have not recovered (Kasamatsu et al. 2000).

Understanding how the removal of one group of organisms might affect others is important if present-day fisheries for finfish, cephalopods and crustaceans are to be managed using a precautionary ecosystem approach, as outlined in the mandate of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Constable et al. 2000). And since the current state of the Antarctic ecosystem is the product of what it was in the past, it is equally important to understand how former perturbations might have affected the structure of the system. Only then can the effects of current fisheries be distinguished from the residual outcomes of past disturbances.

For the purpose of my study, I constructed four ecosystem models of the South Orkneys/South Georgia region of the Southern Ocean representing various points in time: 1) the 1990s (i.e., present-day), 2) the 1960s (i.e., after sealing and whaling, but before the main finfish fisheries), 3) pre-exploitation (i.e., before hunting activities began), and 4) the 1900s (i.e., after sealing, but before whaling). The following briefly describes the modelling software used (Ecopath with Ecosim) and the data sets employed to construct the four models. Model simulations were used to explore hypotheses concerning the increase in Antarctic fur seal populations through the 1950s-1990s (i.e., was the increase in fur seals accelerated by the finfish fishery in the late 1960s

and early 1970s; or is it the result of whaling during the first half of the 20th century that reduced competition for food resources). The models were also used to investigate what could be limiting the recovery of large whale populations, and what management regimes might aid their recovery. Model results are shown to provide insights into the past, present and future of the Antarctic ecosystem.

3.2 Methods and Results

3.2.1 Study area

The four ecosystem models were constructed for the South Orkneys/South Georgia region of the South Atlantic Sector of the Southern Ocean (FAO subareas 48.2 and 48.3, respectively, Fig 1.1). This is a biologically important area, supporting large populations of mammals, birds, fish, and crustaceans, that has experienced intense human interference in the past (Croxall et al. 1985b, Knox 1994).

3.2.2 Tools

The modelling software package Ecopath with Ecosim was used to create an ecosystem model of the South Orkneys/South Georgia region. Ecopath is a tool that creates a snapshot of the ecosystem in time (Christensen and Pauly 1992, Christensen et al. 2000, Polovina 1984). To construct my models, biologically similar species were grouped into 'functional groups', and input parameters were gathered from the literature, including biomass, rate of production, rate of consumption, and diet composition for the groups in the system. The models were then adjusted to ensure that all mass and energy was accounted for in the system (i.e., that lower trophic levels were present in sufficient quantities to fulfill the requirements of the upper trophic levels). The models created using Ecopath described the structure and connectance of the ecosystem, and were used as the base for dynamically simulating species interactions over time using the Ecosim component of the software (Walters et al. 1997).

3.2.3 Models 1 and 2: the 1990s and 1960s

Detailed descriptions of the sources for input parameters for the 1990s model are contained in Appendix B, and other inputs and outputs of the model, as well as a model pedigree, fisheries data used for tuning the model, and settings for Ecosim runs are in Appendix C. The 1960s model was based on the 1990s model with changes made for species that were known to be different in that time period. Because the 1960s model was meant to represent the ecosystem as it was before the extensive finfish fishery in the late 1960s and early 1970s, several adjustments were made. First, the finfish fisheries that were present in the 1990s model were removed. Second, the biomass and rate of production for fish species that have since been exploited were adjusted to reflect pre-exploitation values (Barrera-Oro et al. 2000, Burchett and Ricketts 1984, Kock 1992, Kock and Kellermann 1991, North 1996b). Third, the biomass of Antarctic fur seals, which have been increasing in numbers from the 1950s to the 2000s, was decreased (Bonner 1982b, Boyd 1993, Boyd 2002, Doidge and Croxall 1985, McCann and Doidge 1987, Payne 1977). Fourth, the biomass of penguins was increased slightly, due to a decline in the population sizes of some of the more abundant species since the 1960s (Boyd 2002, Croxall et al. 1988c, Croxall and Prince 1979, Croxall et al. 1981, Croxall and Rothery 1995, Prince and Croxall 1983, Woehler and Croxall 1997).

Time series data from the beginning of fishing to the 1990s (e.g., fishing rate, relative biomass, catch, and catch per unit effort) were used to run the model forward in time from the 1960s to the 1990s. The resulting biomass values were then compared to the biomass values used in the original 1990s model (Figure 3.1).

The predicted biomass values of most of the functional groups at the end of the 30-year simulation were similar to the original input values of the 1990s model. However, some groups, such as the Antarctic fur seals and several fish groups, were either over- or under-represented by the forward simulation of the 1960s model as compared to the original 1990s model.
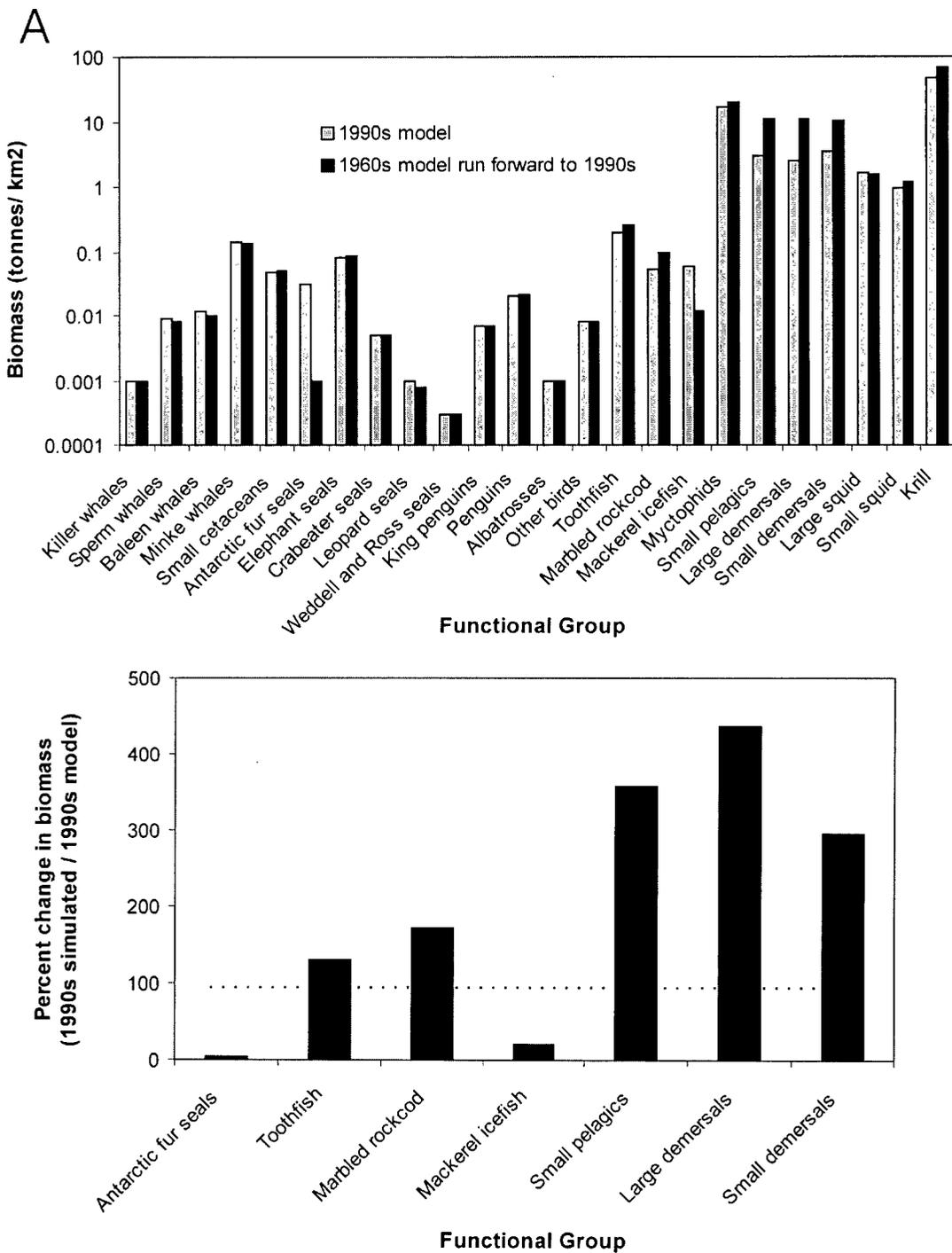
Figure 3.1 Comparison of the 1990s model and a forward simulation of the 1960s model. A) Biomass values of the functional groups as represented in the 1990s model, and in the 1960s model when run forward 30 years to the 1990s, B) Biomass values from the forward simulation of the 1960s model as percentages of the biomass values in the 1990s model.

3.2.4 Model 3: the pre-exploitation ecosystem

A pre-exploitation model was constructed to describe the South Orkneys/South Georgia ecosystem before humans began removing its biological resources. The 1990s model was again used as a base, with the following changes. First, all fishing activity was removed from the model. Second, the biomass of Antarctic fur seals was not altered, unlike the 1960s model where it was decreased, as they were thought to be at about pre-exploitation levels in the 1990s (Bonner 1976, Boyd 2002, Knox 1994). Third, the biomass and production rates of fish were taken from the 1960s model, based on the assumption that they were unlikely to have changed much prior to commercial harvesting by humans. Fourth, the biomass of penguins, crabeater seals (*Lobodon carcinophagus*), and minke whales (*Balaenoptera acutorostrata*) were decreased, as there is evidence that they increased following the onset of exploitation in the Southern Ocean (Laws 1985, Young 2000). Fifth, the biomasses of other baleen whales, as well as sperm whales (*Physeter macrocephalus*), were increased to represent populations that existed before whaling (Chapman 1988, Katona and Whitehead 1988, Knox 1994). Given these adjustments to the higher trophic levels of the system, only small increases in the lower trophic levels, such as krill (*Euphausia superba*) and phytoplankton, were required to balance energy and matter in the system (Fig. 3.2).

3.2.5 Model 4: the 1900s model

The fourth model represents the South Orkneys/South Georgia region in the early 1900s, and was adapted from the 1990s model in the same manner as the pre-exploitation model with one exception. Because the time-frame of this model falls after extensive sealing activity and before whaling and finfishing, the biomass of Antarctic fur seals was very small compared to pre-exploitation levels. Estimates of fur seals in the early part of the 20th century suggested fewer than 100 individuals (Laws 1981, Payne 1977).
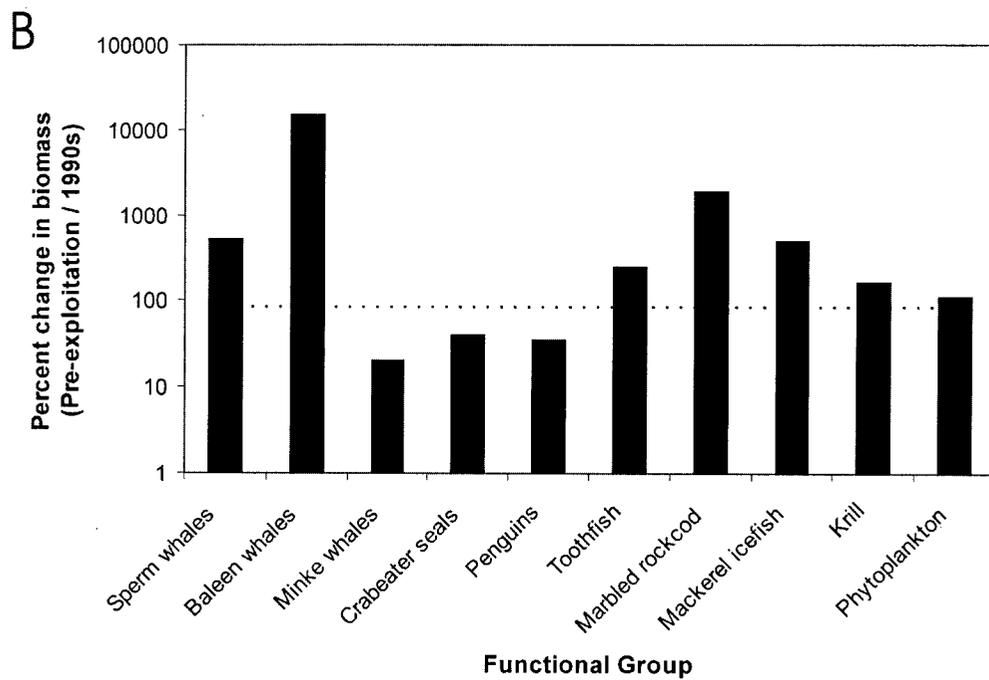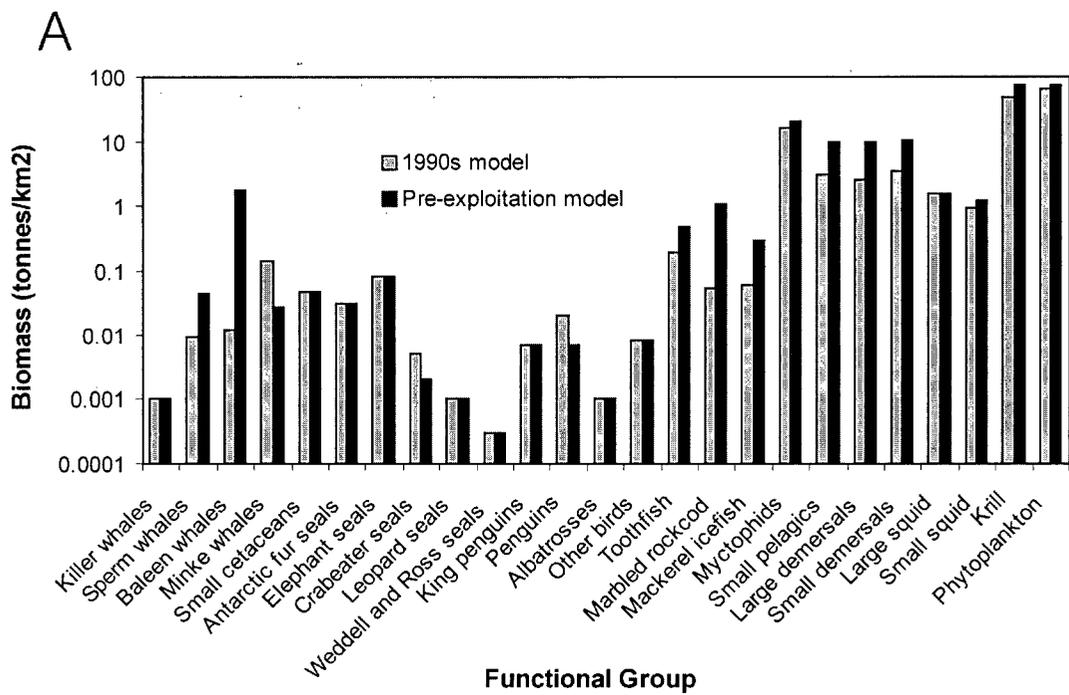
Figure 3.2 Comparison of the 1990s model and the pre-exploitation model. A) Biomass values of the functional groups in the 1990s model and the pre-exploitation model (i.e., before sealing, whaling and fishing), B) Biomass values from the pre-exploitation model as percentages of the biomass values in the 1990s model.

When the 1900s model was run forward in time, and a simulated hunt for whales was integrated, the simulated ecosystem experienced increases in the biomass of commercially important fish species, such as marbled rockcod (*Notothenia rossii*), toothfish (*Dissostichus eleginoides*) and mackerel icefish (*Champsocephalus gunnari*) (Figure 3.3). However, the biomass of Antarctic fur seals in the model simulation did not increase, in contrast to the observed trend of Antarctic fur seal populations over the last century (Boveng et al. 1998, Laws 1981, Payne 1977). Removing 10% of the baleen whale biomass each year was sufficient to reduce the biomass of the simulated whale population to about 5% of its original size in about 50 years. Ceasing whaling activity after removing 10% for 50 years resulted in whale biomass recovering to only about 10% of its original biomass at the end of 100 years of simulation.

3.2.6 Large whale recovery

The 1990s model was run forward in time with a simulated "cull" of certain species (e.g., removing 10% of the biomass annually for the duration of the 100-year simulation) to explore ways in which the recovery of the large whales in the ecosystem might be enhanced. Culling Antarctic fur seals increased penguin and crabeater seal biomass, while culling both Antarctic fur seals and crabeater seals increased penguin biomass even more. A simulated cull of penguins resulted in a positive response in baleen whale populations. But even then, the model indicated only a 10% increase in overall whale biomass after 100 years of culling. The model suggests that the greatest increase in baleen whale biomass would result from a cull of myctophids (*Electrona* spp.), which would increase whale biomass by 40% over the 100-year time period. However, reducing myctophid biomass negatively affected some species, such as Weddell seals (*Leptonychotes weddelli*) and king penguins (*Aptenodytes patagonicus*).
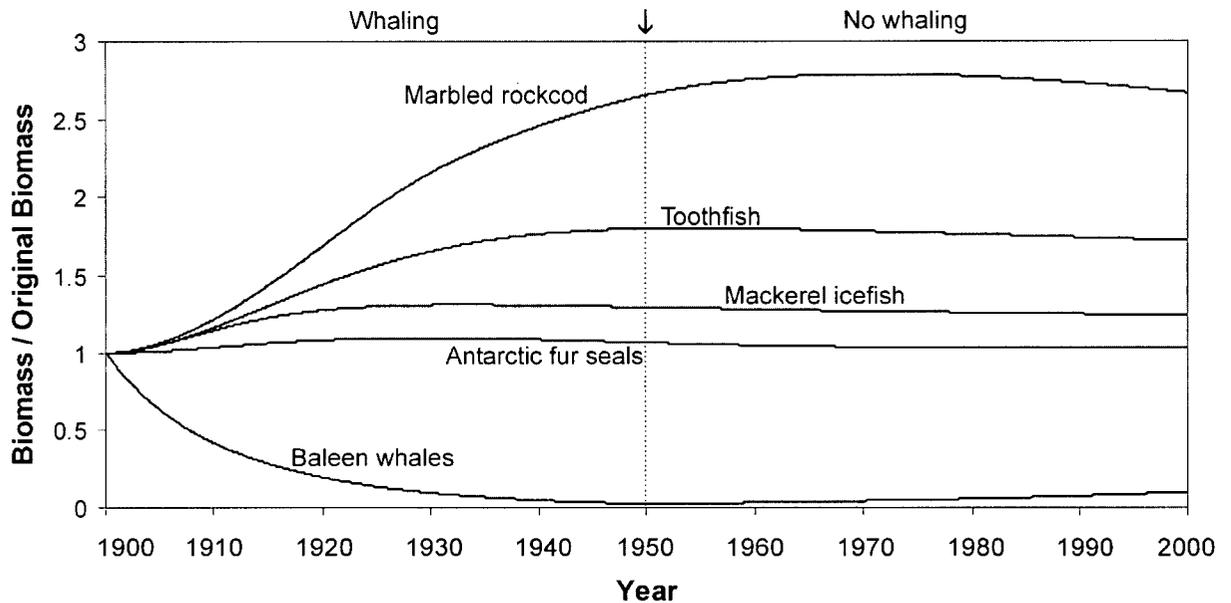
Figure 3.3 Predicted biomass changes of several species in response to simulated whaling. Ten percent of baleen whales were removed from the modelled ecosystem each year from 1900 to 1950, followed by 50 years of no whaling.

3.3 Discussion

3.3.1 Models 1 and 2: the 1990s and 1960s

Running the 1960s model forward to the mid 1990s with 30 years of historic fishing data yielded differences between predicted and reported biomass of several species groups for the 1990s. The most notable of these discrepancies was the Antarctic fur seal, which was under-represented by the forward simulation (Figure 3.1). This suggests that the extensive increase observed in fur seal populations in South Georgia from the 1950s to the 2000s (Boyd 1993, McCann and Doidge 1987, Thomson et al. 2000) was unlikely to have been aided by the finfish fishery. The exploitation of other krill predators in the region may have reduced competition for prey, resulting in more food availability and an increase in fur seal biomass (the 'krill surplus' theory, (Croxall 1992, Laws 1977, Laws 1985, Murphy et al. 1988, Payne 1977, Sladen 1964). The rise in fur seal numbers may also be the result of recovery from extensive exploitation (Knox 1994).

The forward 1960s to 1990s simulation predicted that marbled rockcod and toothfish biomass should have increased (Figure 3.1). However, this prediction is questionable if catches were underreported during this time. Since catches were incorporated into the forward simulation, under-representing the amount of fish removed from the system would have resulted in the predicted biomasses being higher at the end of the simulation. Biomass estimates based on fish stock assessments indicate that there have been significant levels of unreported catches of toothfish in the South Georgia area (Parkes et al. 1996, SC-CAMLR 1995b). The apparent discrepancy in the biomass for mackerel icefish may be due to their highly variable recruitment patterns (de la Mare et al. 1998, Everson et al. 1999, Parkes 2000), which were not incorporated into the model. Years of very low mackerel icefish biomass since the early 1990s do not appear to have occurred in conjunction with fishing (Parkes 2000). The biomass used in the 1990s model was in the upper range of published estimates, which may not reflect their overall average biomass.

The biomasses for some of the lower trophic groups had to be increased to balance the 1960s model (i.e., to ensure there was enough matter at each trophic level to support the higher levels). Otherwise, it was not possible to support the relatively larger estimated populations of penguins and commercially important fish species. Simulating forward to the 1990s resulted in the larger initial biomasses of these groups being maintained (i.e., small pelagics, large demersals, small demersals), which is at odds with the biomass estimates used in the 1990s model (Figure 3.1). The additional biomass of these groups that was required to support the system in the 1960s may still be present in the 1990s, but is not strictly necessary to support the higher trophic levels present in the 1990s model. This has implications for species they consume, such as krill, and should be considered when assessing the viability and ramifications of a krill fishery.

3.3.2 Model 3: the pre-exploitation ecosystem

The model of the South Orkneys/South Georgia ecosystem demonstrates that the ecosystem could have simultaneously supported large pre-exploitation populations of whales, seals and fish (Fig. 3.2). Although the biomass of krill had to be increased slightly to sustain the upper trophic levels, the higher krill biomass was still within the range of biomasses observed today (Brierley

et al. 1999a). This is an important point to consider when contemplating the recovery, or lack thereof, of large whale populations in the Antarctic, and suggests that other factors besides food limitations might be impeding their recovery.

3.3.3 Model 4: the 1900s model

Running the 1900s ecosystem model 100 years forward from the post-sealing-pre-whaling era in conjunction with a removal of whales over the first 50 years of the simulation (i.e., representing the whaling industry of the last century, Fig. 3.3), resulted in an increase in commercially important fish species, such as marbled rockcod, toothfish and mackerel icefish. This suggests that fish stocks might have been unusually high in the late 1960s and early 1970s when finfishing became commercially valuable. Antarctic fur seals, on the other hand, failed to increase in the model simulation as whale biomass was decreased. This implies that the observed increase in fur seal populations over the last several decades (Boyd 1993, Boyd 2002, Payne 1977) is unlikely to have been caused solely by reduced competition for food resources (the 'krill surplus' model; Croxall et al. 1988c, Laws 1984, Payne 1977, Sladen 1964). Other confounding factors, such as the recovery of Antarctic fur seal populations from exploitation, or a reduction in predation pressure, may also have influenced their population dynamics.

3.3.4 Large whale recovery

The simulated slow recovery of baleen whales following the complete cessation of whaling activity (Fig. 3.3) was relatively consistent with reported trends in whale biomass (Kasamatsu et al. 2000). Simulated culling regimes of groups of organisms traditionally thought to compete with baleen whales for food resources (i.e., Antarctic fur seals, crabeater seals and penguins) did little to facilitate baleen whale recovery. However, culling myctophids over the 100-year simulation resulted in a 40% increase in baleen whale biomass, but reduced the biomass of other species, including fish-eating seals and penguins. This potential trade-off should be taken into account if a fishery for myctophids is to be considered as a potential management tool to aid

baleen whale recovery. Such findings emphasize the need for further investigation and understanding of the role of fish and other lower trophic level species in the ecosystem, which have been customarily ignored when discussing the Southern Ocean.

A more detailed resource-partitioning model needs to be developed to further explore how competition for food resources might be affecting the recovery of large whales in the Southern Ocean (i.e., a model that delves beyond the simple prey species categories represented by my models). This might include aspects of krill that are not currently captured by these EwE models, such as krill body size, depth in the water column, swarm size, and smaller-scale horizontal distribution that influence foraging efficiency and success of the major krill predators.

3.4 Conclusions

The present-day South Orkneys/South Georgia ecosystem is largely the product of a long history of exploitation. The four models I constructed to gain insights into the past suggest that the increase in Antarctic fur seals beginning in the late 1950s cannot be explained by the subsequent 30-40 years of finfishing alone. Nor can it be explained solely by a decrease in competition for prey as a result of the removal of the large whales. Instead, these two factors are likely confounded with each other, as well as with other long-term factors, such as the recovery of the species from exploitation. The high landings of finfish in the 1960s and 1970s may have been inflated by larger fish populations that benefited from the competitive release of prey following commercial whaling during the earlier part of the 20th century. Based on our understanding of biological interactions of species within the Antarctic ecosystem (i.e., who eats whom and how much) the removal of large krill predators such as birds and seals has little effect on the recovery rate of large whales. Instead, management actions should be focused on other krill predators in the system such as fish, being mindful of subsequent ecosystem changes that could occur as a result of such actions. Increased attention should be spent on elucidating the factors that affect true competition for prey resources to understand the role that prey availability plays in the population dynamics of the Southern Ocean.

3.5 Summary

A series of ecosystem models representing the South Orkneys/South Georgia region of the Southern Ocean at different time periods were built using Ecopath with Ecosim to assess the impacts that commercial sealing, whaling and fishing may have had on the Antarctic ecosystem. The models suggest that the increase in Antarctic fur seals in recent history is not due solely to decreased competition for food as a result of the whaling activities in the first half of the 1900s. However, whaling may have had a positive effect on fish population sizes, especially commercially important species such as marbled rockcod, mackerel icefish and toothfish. Simulations were explored to determine whether direct or indirect competitive interactions were impeding the recovery of large whales. Removing large krill predators (i.e., birds and seals) from the modelled ecosystem only resulted in minimal responses in whale population sizes, while removing certain fish groups had more of an acceleratory effect on whale recovery. Unreported catches of some fish species and a poor understanding of biomass values of several of the lower trophic level species complicate the assessment of the viability of different fishing regimes for species of commercial interest, such as krill.

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Appendix A: Ecopath with Ecosim

Ecopath with Ecosim (EwE) is a modelling software package that allows for the consideration of multispecies interactions within a system. The mass-balance approach to tracing biomass flow through a food web (Ecopath) has been under development since the late 1980s (Christensen and Pauly 1992) and is derived from work on biomass flow in aquatic systems during the mid 1980s (Polovina 1984). In 1995, Ecosim was introduced as a component of the software, allowing for dynamic simulations of ecosystem interactions through time (Walters et al. 1997). And in 1998, a spatial component called Ecospace was launched to incorporate the smaller-scale spatial interactions of the system for the exploration of policies such as marine protected areas (Walters et al. 1999).

The process for developing an ecosystem model using the EwE software begins with defining the ecosystem to be modelled (i.e., the South Orkneys/South Georgia region of the South Atlantic sector of the Southern Ocean, see section 1.2). The next step is to group the species that live within the ecosystem into functional groups of ecologically similar organisms due to the unrealistic task of considering each individual species independently in the model (due to issues of model complexity as well as data availability). Grouping independent parameter estimates may result in more reliable model predictions since deviations of estimates from true values tend to be randomly distributed and therefore act to cancel each other out when estimates of several populations are pooled (Brey et al. 1996). The process of grouping species depends on the biological characteristics of the organisms, as well as on the purpose or aim of the model. Model input parameter values are compiled for the species groupings from the published literature.

There are two master equations that provide the foundation for Ecopath models (Christensen et al. 2000). The first (Eq. 1.1) breaks the production of a given group into the following components, tracking and accounting for the fate of all matter in the system:

Production = predation + fishery + other mortality + biomass accumulation + net migration   {Eq. 1.1}

'Production' is defined as the product of the biomass (B) and the production/biomass (P/B) ratio of the functional group, where the P/B rate usually corresponds to the total mortality rate (Z) (Allen 1971). 'Predation' refers to the portion of production that is consumed by all predators of the group, which is calculated using the biomass (B), consumption per biomass ratio (Q/B) and diet composition (DC) for the predatory species. 'Fishery' refers to the fraction of production removed from the system by humans, while 'other mortality' includes all mortality not addressed elsewhere in the model, including mortality due to causes such as old age or disease. Other mortality is calculated using:

*Other mortality = Production * (1 – Ecotrophic Efficiency)* {Eq. 1.2}

where 'ecotrophic efficiency' (EE) is defined as the proportion of the production that is used in the system. In most systems, phytoplankton tends to have a very high EE unless in a bloom situation, while top predators that are not being heavily exploited by humans tend to have a lower EE.

The last two terms in the production equation (Eq. 1.1) are 'biomass accumulation', which represents any increasing or decreasing trend in biomass of the functional group, and 'net migration' (emigration – immigration), which takes into account the movement of the organisms into and out of the system.

The second master equation traces the flow of energy through the system (Eq. 1.3), ensuring that any energy flowing into a group also flows out of the group, preventing any spontaneous creation or destruction of energy:

Consumption = production + unassimilated food + respiration {Eq. 1.3}

Along with values for catch rate, net migration rate, biomass accumulation rate, assimilation rate, and diet compositions, which must be entered for all functional groups, there are four main parameters necessary to construct an Ecopath model:

- Biomass (B)   (how much is there, $t \cdot km^{-2}$)
- Production/biomass (P/B)   (corresponding to total mortality, $t \cdot km^{-2} \cdot year^{-1}$)
- Consumption/biomass (Q/B) (how much they eat, $t \cdot km^{-2} \cdot year^{-1}$)
- Ecotrophic efficiency (EE)   (proportion of production used in the system for predation or export)

Due to the nature of the equations and model structure, only three of the four parameters need to be entered, and the software can estimate the fourth. In most cases, *EE* is the parameter left for Ecopath to estimate. However, if data are not available for one of the other three parameters, then a value for *EE* can be entered allowing the missing parameter to be estimated by the model.

While Ecopath provides a snapshot of the ecosystem structure at a certain point in time, Ecosim allows for the simulation of the interspecific interactions over time. Models can be run with different fishing regimes or under different environmental regimes in order to explore the reactions of the functional groups over time.

Appendix B: Sources for 1990s model input parameters

Input data for the 29 functional groups of species in the 1990s Ecopath model was compiled from the following sources:

1. **Killer whales**: body mass (Trites and Pauly 1998), population size (International Whaling Commission (IWC) 1995), production (Evans and Stirling 2001), consumption (Laws 1977, Lockyer 1981b), diet (Goodall and Galeazzi 1985, Kasamatsu et al. 2000, Pauly et al. 1998)

2. **Sperm whales**: body mass (Trites and Pauly 1998), population size (Whitehead 2002), production (Evans and Stirling 2001), consumption (Lockyer 1981a), diet (Knox 1994, Nemoto et al. 1988, Pauly et al. 1998), only large males in the area (Lockyer and Brown 1981)

3. **Baleen whales**: (includes blue whales, fin whales, humpback whales, sei whales, and southern right whales): body mass (Trites and Pauly 1998), population size (Chapman 1988, International Whaling Commission (IWC) 1990, International Whaling Commission (IWC) 2003), production (Evans and Stirling 2001), consumption (Laws 1977, Lockyer 1981b), diet (Mackintosh 1972, Nemoto 1959, Pauly et al. 1998, Tamura and Ohsumi 2000)

4. **Minke whales**: body mass (Trites and Pauly 1998), population size (International Whaling Commission (IWC) 2003), production (Evans and Stirling 2001), consumption (Laws 1977, Lockyer 1981b, Ohsumi 1979), diet (Ichii and Kato 1991, Kawamura 1994, Pauly et al. 1998)

5. **Small cetaceans**: body mass (Trites and Pauly 1998), population size (Brown and Lockyer 1984, International Whaling Commission (IWC) 1995, Kasamatsu and Joyce 1995, Leatherwood et al. 1988, Tamura and Ohsumi 2000), production (Evans and Stirling 2001), consumption (Kasamatsu and Joyce 1995, Sergeant 1969)), diet (Goodall and Galeazzi 1985, Pauly et al. 1998)

6. **Antarctic fur seals**: body mass (Trites and Pauly 1998), population size (Boyd 2002), production (Croxall 1987), consumption (Innes et al. 1987, Trites et al. 1999), diet (Bonner and Hunter 1982, Daneri and Coria 1992, Daneri and Coria 1993, Doidge and Croxall 1985, Laws 1977, North et al. 1983, Pauly et al. 1998, Reid and Arnould 1996)

7. **Elephant seals**: body mass (Trites and Pauly 1998), population size (Boyd et al. 1996, Laws 1994, McCann 1985, McCann and Rothery 1988), production (Croxall 1987), consumption (Innes et al. 1987, Trites et al. 1999), diet (Boyd et al. 1994a, Laws 1977, Pauly et al. 1998, Reid and Nevitt 1998)

8. **Crabeater seals**: body mass (Trites and Pauly 1998), population size (Erickson and Hanson 1990), production (Croxall 1987), consumption (Innes et al. 1987, Trites et al. 1999), diet (Bonner 1982a, Croxall et al. 1985b, Lowry et al. 1988, Oritzland 1977, Pauly et al. 1998)

9. **Leopard seals**: body mass (Trites and Pauly 1998), population size (Siniff and Stone 1985), production (Croxall 1987), consumption (Innes et al. 1987, Trites et al. 1999), diet (Bengtson and Laws 1985, Croxall et al. 1985b, Lowry et al. 1988, Oritzland 1977, Pauly et al. 1998, Siniff and Stone 1985, Stone and Meier 1981, Walker et al. 1998)

10. **Weddell and Ross seals**: body mass (Trites and Pauly 1998), population sizes (Gilbert and Erickson 1977), production (Croxall 1987), consumption (Innes et al. 1987, Trites et al. 1999), diet (Croxall et al. 1985b, Harwood and Croxall 1988, Oritzland 1977, Pauly et al. 1998, Plotz et al. 2001, Plotz et al. 1991)

11. **King penguins**: body mass (Williams 1995), population size (Croxall et al. 1984a, Prince and Croxall 1996), production (Croxall and Prince 1983), consumption (Croxall et al. 1985b), diet (Croxall et al. 1985b, Croxall et al. 1984b)

12. **Penguins**: body mass (Williams 1995), population size (Croxall et al. 1984a, Prince and Croxall 1996), production (Croxall and Prince 1983), consumption (Croxall et al. 1985b), diet (Croxall and Davis 1999, Croxall et al. 1988a, Croxall and Prince 1980b, Croxall et al. 1997,

Croxall et al. 1985b, Croxall et al. 1999, Croxall et al. 1984b, Croxall and Rothery 1995, Kooyman et al. 1999, Lishman 1985, Williams 1991)

13. **Albatrosses**: body mass (Croxall 1984), population size (Croxall et al. 1984a, Prince and Croxall 1996), production (Croxall and Prince 1983), consumption (Croxall et al. 1985b), diet (Croxall et al. 1988d, Croxall et al. 1997, Croxall et al. 1985b, Croxall et al. 1984b, Nishikawa and Tsuda 2001, Pages et al. 1996, Reid et al. 1996a, Thomas 1983)

14. **Other birds**: body mass (Croxall 1984), population size (Croxall et al. 1984a, Prince and Croxall 1996), production (Croxall 1984, Croxall 1992, Knox 1994, Pietz and Parmelee 1994), consumption (Croxall et al. 1985b), diet (Ainley et al. 1992, Berrow and Croxall 1999, Berrow et al. 2000, Bonner and Hunter 1982, Coria et al. 1997, Croxall 1987, Croxall et al. 1995, Croxall et al. 1988b, Croxall et al. 1988c, Croxall and North 1988, Croxall and Prince 1980a, Croxall and Prince 1987, Croxall et al. 1985b, Croxall et al. 1999, Croxall et al. 1984b, Favero et al. 1997, Hemmings 1984, Hunter 1983, Hunter 1984, Hunter 1985, Jablonski 1995, Osborne 1985, Prince and Copestake 1990, Reid et al. 1997a, Reid et al. 1997b, Williams et al. 1991)

15. **Toothfish**: biomass (Reid and Nevitt 1998, SC-CAMLR 1996), production (Kock et al. 1985), consumption (Kock 1992), diet (de la Rosa et al. 1997, Duhamel 1981, Fischer and Hureau 1985, Gonzalez and Rodhouse 1998, Kock 1987, McKenna Jr. 1991, Tarverdiyeva 1972)

16. **Marbled rockcod**: biomass (Barrera-Oro et al. 2000, Burchett and Ricketts 1984, Jones et al. 2000, Kock 1992), production (Tankevich 1990), consumption (Freytag 1980), diet (Burchett 1983a, Burchett 1983b, Burchett 1983c, Chechun 1984, Hureau 1970, Kock 1992, Latogurskij 1972, Linkowski et al. 1983, McKenna Jr. 1991, Tarverdiyeva 1972)

17. **Mackerel icefish**: biomass (CCAMLR 1994, Jones et al. 2000, Kock 1992), production (Kock 1992), consumption (Kock 1981), diet (Agnew et al. 1998, Kock and Everson 1997, McKenna Jr. 1991)

18. **Myctophids**: biomass (Lubivoma et al. 1983, Phleger et al. 1997, Sabourenkov 1991), production (Linkowski 1987), consumption (Hulley 1990), diet (Greely et al. 1999, Hoddell 1996, Hopkins 1985, Hopkins et al. 1993, Hopkins and Torres 1989, Kock 1987, Lancraft et al. 1991, Nishikawa and Tsuda 2001, Phleger et al. 1997, Piatkowski et al. 1994, Rowedder 1979)

19. **Small pelagics**: biomass (Kock 1992, Torres et al. 1984), production (Kunzmann 1986), consumption (Kock 1992, Kunzmann 1986), diet (Gon and Heemstra 1990, Hubold and Hagen 1997, Wohrmann et al. 1997)

20. **Large demersals**: biomass (CCAMLR 1994, Kock 1992), production (Barrera-Oro and Tomo 1988, Csirke 1987, Kock 1992), consumption (Barrera-Oro and Tomo 1988, Kock 1992), diet (Burchett et al. 1983, Croxall et al. 1988d, Croxall et al. 1985b, Everson 1981, Everson 1984, Fischer and Hureau 1985, Kock 1981, Kock 1987, Kock and Jones 2002, Reid et al. 1996b, Targett 1981)

21. **Small demersals**: biomass (CCAMLR 1994, Kock 1992), production (Daniels 1983, Kock 1992, Radtke et al. 1989, Shlibanov 1990), consumption (Kock 1981, Kock 1992, Shust and Pinskaya 1978), diet (Burchett et al. 1983, Casaux 1998, Everson 1981, McKenna Jr. 1991, Reid and Arnould 1996, Richardson 1975, Targett 1981, Vacchi and la Mesa 1995)

22. **Large squid**: biomass (Clarke 1985, Rodhouse 1997), production (Pauly and Christensen 1996), consumption (Pauly and Christensen 1996), diet (Kear 1992, Kock 1987, Laws 1985, Nemoto et al. 1988, Nemoto et al. 1985, Nicol and Endo 1997, Rodhouse and White 1995, Rodhouse et al. 1992)

23. **Small squid**: biomass (Clarke 1985, Rodhouse 1997), production (Pauly and Christensen 1996), consumption (Pauly and Christensen 1996), diet (Kear 1992, Kock 1987, Laws 1985, Nemoto et al. 1988, Nemoto et al. 1985, Nicol and Endo 1997, Rodhouse and White 1995, Rodhouse et al. 1992)

24. **Large invertebrates**: biomass (Arntz et al. 1994, Jazdzewski et al. 1986, Knox 1994), production (Brey and Clarke 1993), consumption (Pauly and Christensen 1996, Shannon and Jarre-Teichmann 1999, Trites et al. 1999), diet (Arnaud 1970, Dearborn 1967, Knox 1994)

25. **Small invertebrates**: biomass (Arntz et al. 1994, Jazdzewski et al. 1986, Knox 1994), production [Brey, 1993 #347, consumption (Pauly and Christensen 1996, Shannon and Jarre-Teichmann 1999, Trites et al. 1999), diet (Arnaud 1970, Dearborn 1967, Knox 1994)

26. **Krill**: biomass (Brierley et al. 1999b, Kasatkina et al. 1998, Nicol et al. 2000), production (Miller et al. 1985, Murphy and Reid 2001, Siegel 1992, Siegel 2000b), consumption (Clarke and Morris 1983), diet (Ackley and Sullivan 1994, Atkinson and Snyder 1997, Brierley and Watkins 2000, Buchholz and Saborowski 2000, Daly 1990, Daly and Macaulay 1991, Fach et al. 2002, Falk-Petersen et al. 2000, Kawaguchi et al. 1986, Marschall 1988, Nishikawa et al. 1995, Nordhausen et al. 1992)

27. **Salps**: biomass (Piatkowski et al. 1994), production (Alldredge and Madin 1982, Foxton 1966, Nishikawa et al. 1995), consumption (Huntley et al. 1989, Nishikawa et al. 1995), diet (Hopkins 1985, Huntley et al. 1989, Lancraft et al. 1991, Madin 1974, Nishikawa et al. 1995)

28. **Other zooplankton** biomass (Piatkowski et al. 1994, Rudjakov 1996), production (Voronina et al. 1981), consumption (Schnack 1985), diet (Atkinson 1996, Atkinson and Shreeve 1995, Atkinson et al. 1996, Atkinson et al. 1992a, Atkinson et al. 1992b, Dam et al. 1993, Jazdzewski and Konopacka 1999, Morales et al. 1993, Pakhomov et al. 1997, Tsuda and Sugisaki 1994, Ward et al. 1995)

29. **Phytoplankton**: biomass (Atkinson 1996, Pakhomov et al. 1997), production (Clarke 1985, Holm-Hansen et al. 1977)

Appendix C: Additional model information

Table C1 Diet composition data for the 1990s ecosystem model of the South Okneys/SouthGeorgia region of the Southern Ocean.

Predator → Prey ↓	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2 Sperm whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Baleen whales	0.038	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Minke whales	0.063	-	-	-	-	-	-	-	-	-	-	-	-	-
5 Small cetaceans	0.013	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Antarctic fur seals	0.050	-	-	-	-	-	-	-	0.140	-	-	-	-	-
7 Elephant seals	0.013	-	-	-	-	-	-	-	0.010	-	-	-	-	-
8 Crabeater seals	0.025	-	-	-	-	-	-	-	0.100	-	-	-	-	-
9 Leopard seals	0.013	-	-	-	-	-	-	-	-	-	-	-	-	-
10 Weddell and Ross seals	0.013	-	-	-	-	-	-	-	-	-	-	-	-	-
11 King penguins	0.025	-	-	-	-	-	-	-	0.010	-	-	-	-	-
12 Penguins	0.125	-	-	-	-	0.010	-	-	0.120	-	-	-	-	-
13 Albatrosses	0.013	-	-	-	-	-	-	-	0.010	-	-	-	-	-
14 Other birds	0.013	-	-	-	-	-	-	-	0.010	-	-	-	-	-
15 Toothfish	0.100	0.040	0.015	-	0.030	-	0.010	-	-	0.040	-	-	-	-
16 Marbled rockcod	0.050	0.040	0.015	-	0.008	-	0.010	-	-	0.040	-	0.002	-	0.002
17 Mackerel Icefish	0.050	0.040	0.015	-	0.008	0.030	0.010	-	-	0.040	-	0.007	0.046	0.002
18 Myctophids	0.100	0.025	0.030	0.060	0.058	0.160	0.100	0.030	0.070	0.050	0.850	0.010	0.035	0.158
19 Small pelagics	0.100	0.025	0.030	0.060	0.060	0.020	0.050	0.030	0.070	0.080	0.050	0.006	0.042	0.040
20 Large demersals	0.050	0.040	-	-	0.057	0.080	0.010	-	-	0.040	-	0.010	0.043	0.008
21 Small demersals	0.050	0.040	-	-	0.057	0.050	0.010	-	0.010	0.220	-	0.012	0.057	0.030
22 Large squid	0.050	0.600	-	-	0.250	0.050	0.350	-	-	0.030	-	-	-	-
23 Small squid	0.050	0.100	0.015	-	0.322	0.100	0.400	0.040	0.100	0.230	0.100	0.004	0.245	0.123
24 Large invertebrates	-	0.025	-	-	0.025	-	0.050	-	-	0.210	-	-	-	-
25 Small invertebrates	-	0.025	-	-	0.025	-	-	-	-	-	-	-	-	-
26 Krill	-	-	0.850	0.850	0.100	0.500	-	0.900	0.350	0.020	-	0.938	0.169	0.466
27 Salps	-	-	-	-	-	-	-	-	-	-	-	-	0.006	0.002
28 Other zooplankton	-	-	0.030	0.030	-	-	-	-	-	-	-	0.012	0.016	0.163
29 Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Detritus	-	-	-	-	-	-	-	-	-	-	-	-	-	0.008
Import	-	-	-	-	-	-	-	-	-	-	-	-	0.340	-
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table C1 continued.

	Predator → Prey ↓	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Sperm whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Baleen whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Minke whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Small cetaceans	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Antarctic fur seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Elephant seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Crabeater seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Leopard seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	Weddell and Ross seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	King penguins	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Penguins	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	Albatrosses	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	Other birds	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	Toothfish	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-
16	Marbled rockcod	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-
17	Mackerel Icefish	0.010	-	0.010	-	-	-	-	-	-	-	-	-	-	-
18	Myctophids	0.050	0.070	0.040	-	-	0.050	0.005	0.400	0.450	-	-	-	-	-
19	Small pelagics	0.050	0.070	-	-	-	0.050	0.005	-	-	-	-	-	-	-
20	Large demersals	0.335	0.070	-	-	-	0.050	-	0.040	-	-	-	-	-	-
21	Small demersals	0.335	0.070	-	-	-	0.200	0.010	0.040	-	-	-	-	-	-
22	Large squid	-	-	-	-	-	-	-	0.010	-	-	-	-	-	-
23	Small squid	0.100	-	-	-	-	0.020	-	0.100	0.010	-	-	-	-	-
24	Large invertebrates	0.050	0.070	-	-	-	0.250	0.050	-	-	0.010	-	-	-	-
25	Small invertebrates	-	-	-	-	-	-	0.100	-	-	0.300	0.010	-	-	-
26	Krill	0.050	0.400	0.850	0.500	0.500	0.200	0.400	0.400	0.500	0.010	-	-	-	-
27	Salps	-	-	-	0.020	0.020	-	-	-	-	0.050	0.005	-	-	-
28	Other zooplankton	-	0.250	0.100	0.480	0.480	0.180	0.400	0.010	0.040	0.200	0.100	0.300	0.050	0.010
29	Phytoplankton	-	-	-	-	-	-	0.030	-	-	0.100	0.305	0.600	0.850	0.890
	Detritus	-	-	-	-	-	-	-	-	-	0.330	0.580	0.100	0.100	0.100
	Import	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table C2 Predation mortalities from the 1990s ecosystem model of the South Okneys/SouthGeorgia region of the Southern Ocean.

	Predator → Prey ↓	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Sperm whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Baleen whales	0.016	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Minke whales	0.002	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Small cetaceans	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Antarctic fur seals	0.008	-	-	-	-	-	-	-	0.019	-	-	-	-	-
7	Elephant seals	0.001	-	-	-	-	-	-	-	0.001	-	-	-	-	-
8	Crabeater seals	0.024	-	-	-	-	-	-	-	0.085	-	-	-	-	-
9	Leopard seals	0.075	-	-	-	-	-	-	-	-	-	-	-	-	-
10	Weddell and Ross seals	0.200	-	-	-	-	-	-	-	-	-	-	-	-	-
11	King penguins	0.018	-	-	-	-	-	-	-	0.007	-	-	-	-	-
12	Penguins	0.029	-	-	-	-	0.050	-	-	0.025	-	-	-	-	-
13	Albatrosses	0.060	-	-	-	-	-	-	-	0.043	-	-	-	-	-
14	Other birds	0.008	-	-	-	-	-	-	-	0.006	-	-	-	-	-
15	Toothfish	0.002	0.008	0.004	-	0.054	-	0.011	-	-	0.001	-	-	-	-
16	Marbled rockcod	0.004	0.028	0.015	-	0.051	-	0.040	-	-	0.002	-	0.045	-	0.060
17	Mackerel Icefish	0.004	0.025	0.014	-	0.047	0.051	0.037	-	-	0.002	-	0.146	0.050	0.069
18	Myctophids	0.000	0.000	0.000	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.021	0.001	0.000	0.019
19	Small pelagics	0.000	0.000	0.001	0.013	0.007	0.001	0.004	0.000	0.000	0.000	0.007	0.002	0.001	0.027
20	Large demersals	0.000	0.001	-	-	0.008	0.003	0.001	-	-	0.000	-	0.005	0.001	0.006
21	Small demersals	0.000	0.000	-	-	0.006	0.001	0.001	-	0.000	0.000	-	0.005	0.001	0.017
22	Large squid	0.000	0.014	-	-	0.055	0.003	0.048	-	-	0.000	-	-	-	-
23	Small squid	0.000	0.004	0.001	-	0.121	0.011	0.093	0.001	0.000	0.001	0.042	0.005	0.017	0.255
24	Large invertebrates	-	0.000	-	-	0.002	-	0.003	-	-	0.000	-	-	-	-
25	Small invertebrates	-	0.000	-	-	0.001	-	-	-	-	-	-	-	-	-
26	Krill	-	-	0.001	0.012	0.001	0.001	-	0.001	0.000	0.000	-	0.026	0.000	0.020
27	Salps	-	-	-	-	-	-	-	-	-	-	-	-	0.000	0.000
28	Other zooplankton	-	-	0.000	0.000	-	-	-	-	-	-	-	0.000	0.000	0.005
29	Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table C2 continued.

	Predator → Prey ↓	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Sperm whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Baleen whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Minke whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Small cetaceans	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Antarctic fur seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Elephant seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Crabeater seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Leopard seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	Weddell and Ross seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	King penguins	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Penguins	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	Albatrosses	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	Other birds	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	Toothfish	0.016	-	-	-	-	-	-	-	-	-	-	-	-	-
16	Marbled rockcod	0.057	-	-	-	-	-	-	-	-	-	-	-	-	-
17	Mackerel Icefish	0.052	-	0.029	-	-	-	-	-	-	-	-	-	-	-
18	Myctophids	0.001	0.001	0.000	-	-	0.025	0.005	0.474	0.393	-	-	-	-	-
19	Small pelagics	0.005	0.003	-	-	-	0.136	0.025	-	-	-	-	-	-	-
20	Large demersals	0.042	0.004	-	-	-	0.164	-	0.309	-	-	-	-	-	-
21	Small demersals	0.030	0.003	-	-	-	0.468	0.042	0.221	-	-	-	-	-	-
22	Large squid	-	-	-	-	-	-	-	0.120	-	-	-	-	-	-
23	Small squid	0.033	-	-	-	-	0.172	-	2.033	0.150	-	-	-	-	-
24	Large invertebrates	0.004	0.002	-	-	-	0.553	0.201	-	-	0.100	-	-	-	-
25	Small invertebrates	-	-	-	-	-	-	0.181	-	-	1.354	0.200	-	-	-
26	Krill	0.000	0.001	0.003	1.284	0.153	0.035	0.126	0.164	0.152	0.008	-	-	-	-
27	Salps	-	-	-	0.116	0.014	-	-	-	-	0.089	0.039	-	-	-
28	Other zooplankton	-	0.000	0.000	0.816	0.097	0.021	0.084	0.003	0.008	0.104	0.231	1.638	3.663	0.280
29	Phytoplankton	-	-	-	-	-	-	0.007	-	-	0.057	0.772	3.592	68.256	27.316

Table C3 Pedigree of the 1990s model of the South Orkneys/South Georgia region. A) Evaluation of each parameter for each functional group, B) Legend (description, index and confidence interval).

A

	Functional Group	B	P/B	Q/B	Diet	Catch
1	Killer whales	5	4	7	5	-
2	Sperm whales	6	4	7	5	-
3	Baleen whales	6	4	7	6	-
4	Minke whales	6	4	7	6	-
5	Small cetaceans	5	4	7	3	-
6	Antarctic fur seals	6	4	7	6	-
7	Elephant seals	6	4	7	6	-
8	Crabeater seals	5	4	7	6	-
9	Leopard seals	5	4	7	6	-
10	Weddell and Ross seals	4	4	7	4	-
11	King penguins	6	4	8	6	-
12	Penguins	6	4	8	6	-
14	Other birds	6	2	8	4	-
15	Toothfish	5	4	4	6	3
16	Marbled rockcod	5	4	4	6	-
17	Mackerel Icefish	5	4	4	6	3
18	Myctophids	3	4	4	6	-
19	Small pelagics	3	4	4	5	-
20	Large demersals	4	4	4	5	-
21	Small demersals	3	4	4	5	-
22	Large squid	4	3	3	4	-
23	Small squid	4	3	3	4	3
24	Large invertebrates	4	6	3	4	-
25	Small invertebrates	3	2	3	4	-
26	Krill	6	7	7	5	3
27	Salps	5	2	2	4	-
28	Other zooplankton	5	5	5	5	-
29	Phytoplankton	1	6	-	-	-

B

	Biomass	Index	Confidence Interval (+/- %)		P/B and Q/B	Index	Confidence Interval (+/- %)
1	"Missing" parameter (estimated by Ecopath)	0.0	n/a	1	"Missing" parameter (estimated by Ecopath)	0.0	n/a
2	From other model	0.0	80	2	Guesstimate	0.1	90
3	Guesstimate	0.0	80	3	From other model	0.2	80
4	Approximate or indirect method	0.4	50-80	4	Empirical relationship	0.5	50
5	Sampling based, low precision	0.7	40	5	Similar group/species, similar system	0.6	40
6	Sampling based, high precision	1.0	10	6	Similar group/species, same system	0.7	30
				7	Same group/species, similar system	0.8	20
				8	Same group/species, same system	1.0	10

	Diet	Index	Confidence Interval (+/- %)		Catch	Index	Confidence Interval (+/- %)
1	General knowledge of related group/species	0.0	80	1	Guesstimate	0.0	>80
2	From other model	0.0	80	2	From other model	0.0	>80
3	General knowledge of same group/species	0.2	80	3	FAO statistics	0.2	80
4	Qualitative diet composition study	0.5	50	4	National statistics	0.5	50
5	Quantitative but limited diet composition study	0.7	40	5	Local study, low precision/incomplete	0.7	30
6	Quantitative, detailed diet composition study	1.0	30	6	Local study, high precision/complete	1.0	10

Table C4 Fisheries data used to run the 1960s model forward to the 1990s. Type code refers to the way the data is classified in EwE (0 = Relative biomass, 4 = Fishing rate, 6 = Catches)

Group	Marbled rockcod	Marbled rockcod	Marbled rockcod	Mackerel icefish	Mackerel icefish	Mackerel icefish	Mackerel icefish	Toothfish	Toothfish	Toothfish	Toothfish
Data Type	Biomass (tonnes)	Fishing Rate (Catch/B)	Catch (tonnes/km^2)	Biomass (tonnes)	Fishing Rate (Catch/B)	Catch (tonnes/km^2)	CPUE (tonnes/hour)	Biomass (tonnes)	Fishing Rate (Catch/B)	Catch (tonnes/km^2)	CPUE (t/hour)
Type Code	0	4	6	0	4	6	0	0	4	6	0
1965	-	-	-	-	-	-	-	-	-	-	-
1966	-	-	-	-	-	-	-	-	-	-	-
1967	-	-	-	-	-	-	-	-	-	-	-
1968	-	-	-	-	-	-	-	-	-	-	-
1969	-	-	-	-	-	-	-	-	-	-	-
1970	580000	0.6891	0.2144	-	-	-	-	-	-	-	-
1971	130000	0.7812	0.0545	50000	0.2140	0.0057	-	-	-	-	-
1972	25000	0.0400	0.0005	45000	0.0222	0.0005	-	-	-	-	-
1973	30000	0.0000	0.0000	65000	0.0308	0.0011	-	-	-	-	-
1974	40000	0.0000	0.0000	102000	0.0049	0.0003	-	-	-	-	-
1975	48000	0.0000	0.0000	153000	0.0065	0.0005	-	-	-	-	-
1976	46500	0.2312	0.0058	133000	0.0902	0.0064	-	13300	0.0000	0.0000	-
1977	49000	0.2041	0.0054	146500	0.6375	0.0501	-	-	-	0.0002	-
1978	47000	0.1277	0.0032	319500	0.4598	0.0788	-	7300	0.2637	0.0010	-
1979	49000	0.1288	0.0034	82023	0.2725	0.0120	-	-	-	0.0001	-
1980	40000	0.6224	0.0134	101646	0.1302	0.0071	-	-	-	0.0002	-
1981	10000	0.2000	0.0011	153356	0.2078	0.0171	-	-	-	0.0001	-
1982	11000	0.0787	0.0005	209100	0.2418	0.0271	-	-	-	0.0002	-
1983	13000	0.0692	0.0005	433234	0.3096	0.0720	-	-	-	0.0001	-
1984	15000	0.2015	0.0016	136100	0.6208	0.0453	-	-	-	0.0001	-
1985	13000	0.1154	0.0008	44600	0.3444	0.0082	-	8000	0.0375	0.0002	-
1986	12000	0.0167	0.0001	100800	0.1457	0.0079	-	-	-	0.0003	-
1987	10000	0.0200	0.0001	142400	0.4997	0.0382	-	-	-	0.0006	-
1988	1000	0.1000	0.0001	82600	0.4314	0.0191	-	-	-	0.0009	-
1989	1000	0.1000	0.0001	66300	0.3297	0.0117	-	-	-	0.0021	-
1990	1000	0.0000	0.0000	60800	0.1659	0.0054	3.3656	9900	0.8395	0.0045	-
1991	2000	0.0000	0.0000	67800	0.0006	0.0000	0.5792	-	-	0.0020	-
1992	-	-	0.0000	-	-	0.0000	-	-	-	0.0020	0.2860
1993	-	-	0.0000	-	-	0.0000	-	-	-	0.0016	1.2042
1994	-	-	0.0000	-	-	0.0000	-	-	-	0.0003	0.3649
1995	-	-	0.0000	-	-	0.0000	-	-	-	0.0018	0.6390
1996	-	-	0.0000	-	-	0.0000	-	-	-	0.0021	-
1997	-	-	0.0000	-	-	0.0000	-	-	-	0.0013	1.0050
1998	-	-	0.0000	-	-	0.0000	-	-	-	0.0017	1.9812
1999	-	-	0.0000	-	-	0.0001	-	-	-	0.0023	-
2000	-	-	0.0000	-	-	0.0022	6.4382	-	-	0.0025	3.7665
2001	-	-	0.0000	-	-	0.0005	1.4984	-	-	0.0018	0.7945

Table C4 continued.

Group Type Type Code	Patagonian rockcod (in Small demersals) Biomass (tonnes)	Patagonian rockcod (in Small demersals) Fishing Rate (Catch/B)	Patagonian rockcod (in Small demersals) Catch (tonnes/km^2)	Patagonian rockcod (in Small demersals) CPUE (t/day)	Large demersals Biomass (tonnes)	Large demersals Fishing Rate (Catch/B)	Large demersals Catch (tonnes/km^2)	Krill Catch (tonnes/km^2)
	0	4	6	0	0	4	6	6
1965	-	-	-	-	-	-	-	-
1966	-	-	-	-	-	-	-	-
1967	-	-	-	-	-	-	-	-
1968	-	-	-	-	-	-	-	-
1969	-	-	-	-	-	-	-	-
1970	-	-	-	-	-	-	-	-
1971	-	-	-	-	-	-	-	-
1972	-	-	-	-	-	-	-	-
1973	-	-	-	-	-	-	-	-
1974	-	-	-	-	-	-	-	0.0102
1975	-	-	-	-	-	-	-	0.0230
1976	-	-	-	-	127350	0.0369	0.0025	0.0005
1977	-	-	-	-	122700	0.1296	0.0085	0.0358
1978	-	-	-	-	112050	0.3713	0.0223	0.0424
1979	200000	0.0650	0.0070	50	81400	0.1855	0.0081	0.1431
1980	185000	0.0378	0.0038	46	89700	0.1650	0.0079	0.1395
1981	185000	0.1987	0.0197	44	79000	0.2316	0.0098	0.1053
1982	141000	0.2223	0.0168	43	69250	0.1444	0.0054	0.1650
1983	115000	0.0437	0.0027	40	71100	0.2968	0.0113	0.0731
1984	102000	0.0931	0.0051	50	61200	0.2668	0.0088	0.0393
1985	115000	0.1000	0.0062	42	50250	0.2448	0.0066	0.0920
1986	100000	0.1500	0.0080	26	36900	0.0705	0.0014	0.2069
1987	83000	0.0843	0.0047	23	42750	0.1155	0.0026	0.1481
1988	-	0.1857	0.0072	19	41250	0.3186	0.0071	0.0612
1989	-	0.2000	0.0070	37	38500	0.0616	0.0013	0.1549
1990	-	0.0029	0.0001	-	42483	0.0089	0.0002	0.1620
1991	-	-	-	-	67300	0.0004	0.0000	0.1560
1992	-	-	-	-	-	-	0.0000	0.1204
1993	-	-	-	-	-	-	0.0000	0.0229
1994	-	-	-	-	-	-	0.0000	0.0203
1995	-	-	-	-	-	-	0.0000	0.0442
1996	-	-	-	-	-	-	0.0000	0.0211
1997	-	-	-	-	-	-	0.0000	0.0168
1998	-	-	-	-	-	-	0.0000	0.0166
1999	-	-	-	-	-	-	0.0000	0.0346
2000	-	-	-	-	-	-	0.0000	0.0179
2001	-	-	-	-	-	-	0.0000	0.0240

Table C5 Vulnerability settings for the Ecosim runs of the South Orkneys/South Georgia models. Models were tuned using fisheries data (Table C4). Vulnerabilities were changed from the default values of 0.3 in order to minimize the weighted sum of squares deviations of log biomasses from log predicted biomasses (Christensen et al 2000).

Predator → Prey ↓	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2 Sperm whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Baleen whales	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Minke whales	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
5 Small cetaceans	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Antarctic fur seals	0.3	-	-	-	-	-	-	-	0.3	-	-	-	-	-
7 Elephant seals	0.3	-	-	-	-	-	-	-	0.3	-	-	-	-	-
8 Crabeater seals	0.3	-	-	-	-	-	-	-	0.3	-	-	-	-	-
9 Leopard seals	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
10 Weddell and Ross seals	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
11 King penguins	0.3	-	-	-	-	-	-	-	0.3	-	-	-	-	-
12 Penguins	0.3	-	-	-	-	0.3	-	-	0.3	-	-	-	-	-
13 Albatrosses	0.3	-	-	-	-	-	-	-	0.3	-	-	-	-	-
14 Other birds	0.3	-	-	-	-	-	-	-	0.3	-	-	-	-	-
15 Toothfish	0.3	0.3	0.3	-	0.3	-	0.3	-	-	0.3	-	-	-	-
16 Marbled rockcod	0.3	0.3	0.3	-	0.3	-	0.3	-	-	0.3	-	0.3	-	0.3
17 Mackerel Icefish	0.3	0.3	0.3	-	0.3	0.3	0.3	-	-	0.3	-	0.3	0.3	0.3
18 Myctophids	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
19 Small pelagics	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
20 Large demersals	0.3	0.3	-	-	0.3	0.3	0.3	-	-	0.3	-	0.3	0.3	0.3
21 Small demersals	0.3	0.3	-	-	0.3	0.3	0.3	-	0.3	0.3	-	0.3	0.3	0.3
22 Large squid	0.3	0.3	-	-	0.3	0.3	0.3	-	-	0.3	-	-	-	-
23 Small squid	0.3	0.3	0.3	-	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
24 Large invertebrates	-	0.3	-	-	0.3	-	0.3	-	-	0.3	-	-	-	-
25 Small invertebrates	-	0.3	-	-	0.3	-	-	-	-	-	-	-	-	-
26 Krill	-	-	0.3	0.3	0.3	0.3	-	0.3	0.3	0.3	-	0.3	0.3	0.3
27 Salps	-	-	-	-	-	-	-	-	-	-	-	-	0.3	0.3
28 Other zooplankton	-	-	0.3	0.3	-	-	-	-	-	-	-	0.3	0.3	0.3
29 Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Detritus	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3

Table C5 continued.

Predator → Prey ↓	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1 Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2 Sperm whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Baleen whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Minke whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5 Small cetaceans	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Antarctic fur seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7 Elephant seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8 Crabeater seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9 Leopard seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10 Weddell and Ross seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11 King penguins	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12 Penguins	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13 Albatrosses	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14 Other birds	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15 Toothfish	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
16 Marbled rockcod	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
17 Mackerel Icefish	0.3	-	0.1	-	-	-	-	-	-	-	-	-	-	-
18 Myctophids	0.3	0.5	0.1	-	-	0.5	0.1	0.3	0.3	-	-	-	-	-
19 Small pelagics	0.3	0.5	-	-	-	0.5	0.1	-	-	-	-	-	-	-
20 Large demersals	0.3	0.5	-	-	-	0.5	-	0.3	-	-	-	-	-	-
21 Small demersals	0.3	0.5	-	-	-	0.5	0.1	0.3	-	-	-	-	-	-
22 Large squid	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-
23 Small squid	0.3	-	-	-	-	0.5	-	0.3	0.3	-	-	-	-	-
24 Large invertebrates	0.3	0.5	-	-	-	0.5	0.1	-	-	0.3	-	-	-	-
25 Small invertebrates	-	-	-	-	-	-	0.1	-	-	0.3	0.3	-	-	-
26 Krill	0.3	0.5	0.1	0.3	0.3	0.5	0.1	0.3	0.3	0.3	-	-	-	-
27 Salps	-	-	-	0.3	0.3	-	-	-	-	0.3	0.3	-	-	-
28 Other zooplankton	-	0.5	0.1	0.3	0.3	0.5	0.1	0.3	0.3	0.3	0.3	0.3	0.3	0.3
29 Phytoplankton	-	-	-	-	-	-	0.1	-	-	0.3	0.3	0.3	0.3	0.3
Detritus	-	-	-	-	-	-	-	-	-	0.3	0.3	0.3	0.3	0.3

A

Marbled rockcod B

Mackerel icefish B

Mackerel icefish CPUE

Toothfish B

Toothfish CPUE

Patagonian rockcod B

Patagonian rockcod CPUE

Large demersals B

1965   1995 1965   1995

B

Marbled rockcod Catch

Mackerel icefish Catch

Toothfish Catch

Patagonian rockcod Catch

Large demersals Catch

Krill Catch

1965   1995 1965   1995
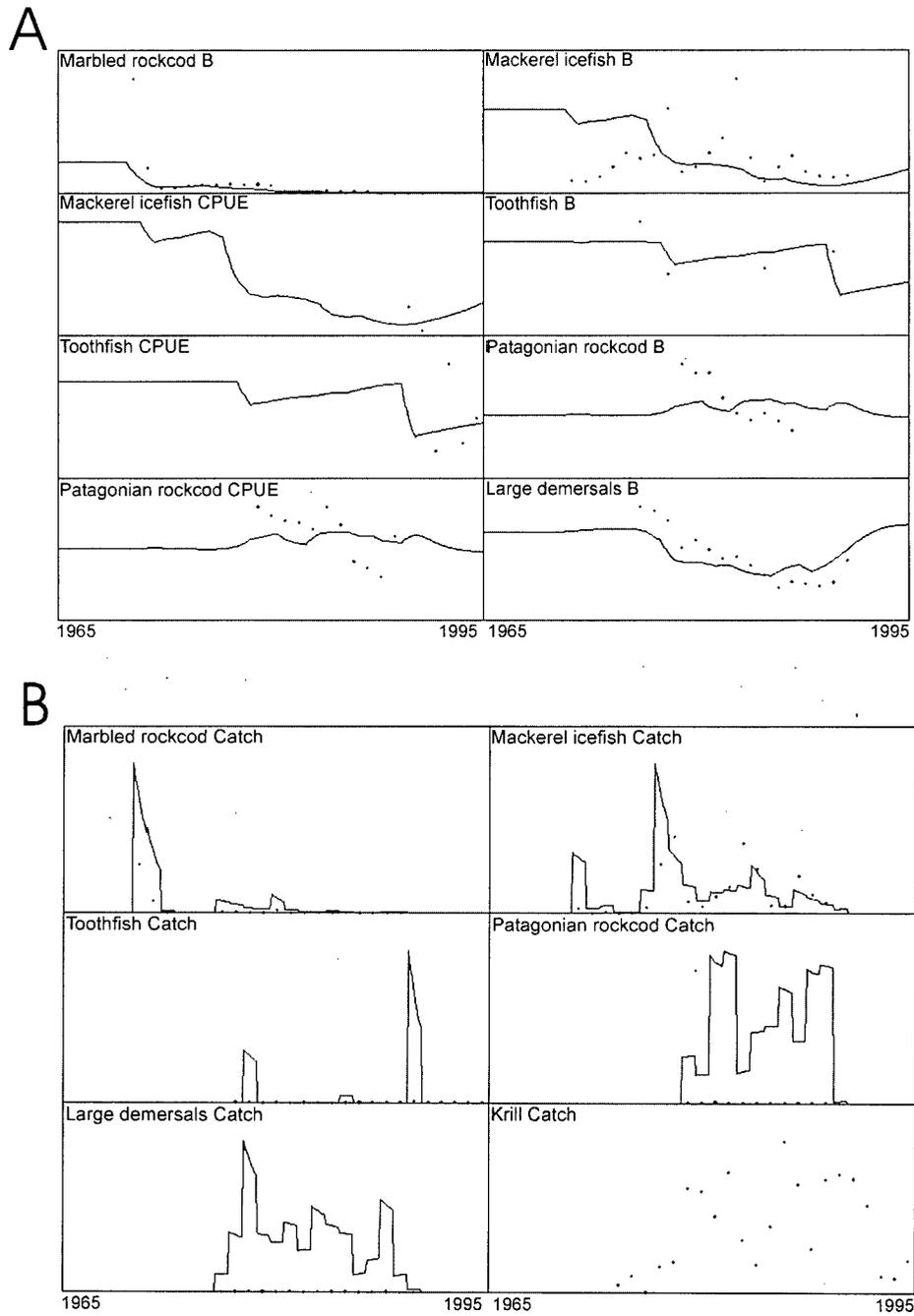
Figure C1 Simulations of A) biomass and B) mortality over time. Dots represent fisheries data, i.e., Biomass (B), Catch per unit effort (CPUE), or Catch.