

**CONSIDERATION OF MULTISPECIES INTERACTIONS IN THE ANTARCTIC:  
A PRELIMINARY MODEL OF THE MINKE WHALE – BLUE WHALE –  
KRILL INTERACTION**

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As a first step in investigating the major predator–prey interactions in the Antarctic, a model describing blue whales *Balaenoptera musculus*, minke whales *Balaenoptera acutorostrata* and krill *Euphausia superba* is developed. Blue and minke whales feed mainly on krill, and they share a similar feeding area near the Antarctic ice edge. In the early 20<sup>th</sup> century, the large baleen whales in the Antarctic were heavily harvested, some to near extinction. Blue whales were taken for almost 60 years, before being officially protected in 1964. Harvesting of the smaller minke whales commenced only in the 1970s, and the population probably increased during the mid 20<sup>th</sup> century, likely in response to increased krill abundance following the depletion of the large baleen whales. Recent studies show recoveries of some of these large baleen whale species in response to protection, and also a possible recent decrease in the stock of minke whales as the larger whales recover. This work investigates whether the abundance trends indicated by surveys and other information for these species can be explained by considering only harvesting and the predator–prey interactions between the two whale species and krill. Using historical catch data for blue and minke whales, a simple age-aggregated model including species interactions is fitted to survey abundance estimates. Uncertainties in the abundance estimates and the biological parameters are taken into account in the process by considering plausible ranges for their values. Abundance trends for the species can broadly be replicated by the model, provided the parameter values show certain features, including (i) that blue whales are able to maintain their birth and krill consumption rates until krill abundance drops to relatively low levels, and (ii) that both minke and blue whales show relatively fast rates of growth if krill is abundant, but that minke growth rate falls more rapidly as krill abundance drops. The model suggests two interesting features of the dynamics of these species. First, a substantial decrease in krill biomass from the 1970s to the 1990s as a result of the preceding rapid increase in minke whale abundance, and hence krill consumption, following the depletion of the larger baleen whales. Second, a recovery of blue whales despite the impact of minke whales on krill abundance and its resultant decrease, because blue whales are better able to tolerate decreased krill abundance. Future projections show a gradual increasing trend in blue whale abundance and a gradual decrease in minke abundance, with large amplitude oscillations superimposed. Long-term monitoring of biological parameters and abundance are essential to provide a basis for verification or otherwise of such predictions. Results presented here should be viewed qualitatively rather than quantitatively. However, for the future, refinement of the model structure and incorporation of age structure, data on some other major predator species that feed on krill and some spatial structure, is under consideration.

Key words: Antarctic, blue whale, krill, minke whale, multispecies model, predator-prey interaction

The Antarctic is a region where the largest human-induced perturbation of the marine ecosystem in the world has taken place. Since the beginning of the 20<sup>th</sup> century, large baleen whale species were depleted sequentially, some almost to extinction (Fig. 1). Blue whales *Balaenoptera musculus* were harvested legally from 1904 for almost 60 years, and humpback whales *Megaptera novaeangliae* until 1967 (though there were some illegal takes after these dates, Yablokov *et al.* 1998). Laws (1977) suggests that these two species were the most heavily harvested and were respectively reduced to about 3 and 5% of their estimated initial biomasses. The commercial harvest of minke whales *Balaenoptera acutorostrata* began in

the 1970s and ended in 1986<sup>1</sup> (when a moratorium on commercial whaling came into force), though this species was not nearly as heavily exploited as the other baleen whales. In addition to the extensive harvesting of large baleen whales, in the early 19<sup>th</sup> century at least one million fur seals *Arctocephalus gazella* were taken from South Georgia, almost rendering that population extinct (McCann and Doidge 1984),

<sup>1</sup> For convenience in this paper, the convention is adopted of referring to the austral summer (whaling) season as the latter of the two years concerned, e.g. the 1986/87 season is referred to as 1987

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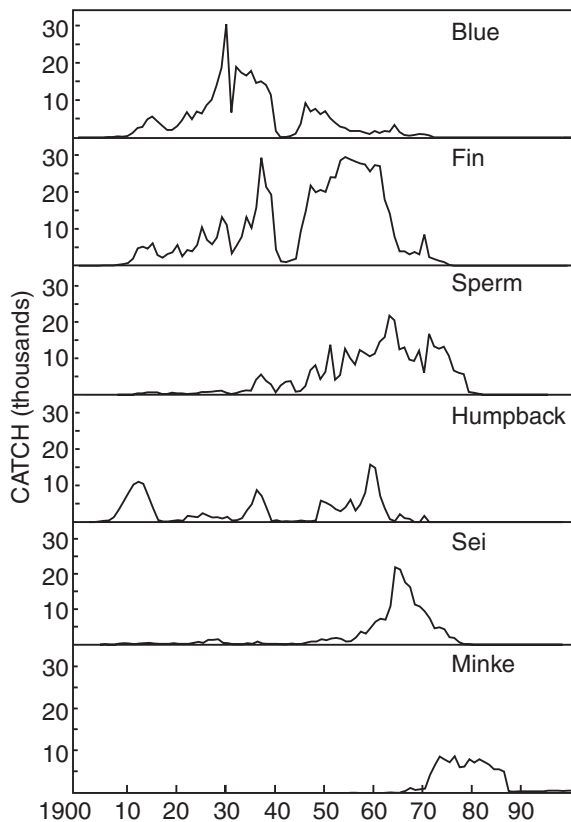


Fig. 1: Annual catches of blue, fin, sperm, humpback, sei and minke whales caught in the southern hemisphere, corrected for Soviet misreporting (source: C. Allison, International Whaling Commission, December 2002)

and Southern elephant seals *Mirounga leonina* were also substantially reduced in numbers (Laws 1984).

Figure 2 shows the major trophic interactions in the Antarctic (Miller 2002). Among the baleen whales that were heavily exploited, blue whales, fin whales *Balaenoptera physalus* and humpback whales feed mainly on krill *Euphausia superba* (Nemoto 1970, Laws 1977, 1984, Kawamura 1980, 1994, Lockyer 1981). Figure 3 shows estimates of consumption of krill by baleen whales in the Antarctic before and after exploitation (Laws 1977). From this comparison, the suggestion followed that, because of the intensive harvesting of the large baleen whales that feed mainly on krill, some 150 million tons of "surplus" annual production of krill<sup>2</sup> became available for other krill-feeding predators, such as minke whales, crabeater

seals *Lobodon carcinophagus*, fur seals, penguins and some albatrosses (Laws 1977). Ichii and Kato (1991) show that krill is the dominant food source for minke whales<sup>3</sup>, constituting 100 and 94% by weight of the stomach contents of these whales in the ice-edge and offshore zones of the Antarctic respectively. Crabeater seals eat krill almost exclusively, their diet estimated to be 94% krill, 3% fish and 2% squid (Øritsland 1977). Furthermore, fur seals take krill almost exclusively (Reid and Arnould 1996, Boyd 2002).

There are some studies that support this "surplus" krill hypothesis. The estimated trend in age at maturity of minke whales was downwards from the 1950s to the 1980s during the period of commercial whaling, indicating a likely increased abundance of minke whales in the mid 20<sup>th</sup> century, plausibly in response to increased krill abundance following the depletion of the large baleen whales (Thomson *et al.* 1999). Bengtson and Laws (1985) suggest that the mean age at maturity of crabeater seals also dropped, from 4.5 years in the 1940s to 2.5 years in the 1960s, for the same reason. Recovery of fur seals commenced around the 1940s, with a reported very large annual increase rate of 17% year<sup>-1</sup> from 1958 to 1973 at South Georgia (Payne 1977). There is anecdotal evidence of increased abundance of minke whales from observations on whaling vessels over the period 1940–1960 (Ash 1962). All these changes in biological parameters and population trends may be attributed to the krill surplus, following the depletion of the large baleen whales.

More than 30 years have now passed since the reduction and subsequent protection of the populations of large baleen whales in the Antarctic, and there are some indications of recovery of these previously heavily exploited species. A recent analysis of blue whale abundance estimates from surveys yields an 8% year<sup>-1</sup> increase (Branch *et al.* 2003). Moreover, West Australian humpback whale surveys show an 11% year<sup>-1</sup> increase (Bannister 1994) and East Australian humpback whale surveys a 12% year<sup>-1</sup> increase (International Whaling Commission 2000). Johnston and Butterworth (2002) fitted an age-aggregated production model to the historic catches and these survey abundances as well as to catch per unit effort

<sup>2</sup> The opening statement of this section rests on a comparison of this figure with recent annual removals worldwide by marine capture fisheries, which are in the vicinity of 80 million tons (FAO 2002)

<sup>3</sup> Although prey-switching behaviour in minke whales has been observed elsewhere (the Barents Sea, Haug *et al.* 2002 and north-western Pacific, Tamura and Fujise 2002), there are no other obvious and substantial alternative prey to krill for these predators at the Antarctic ice edge

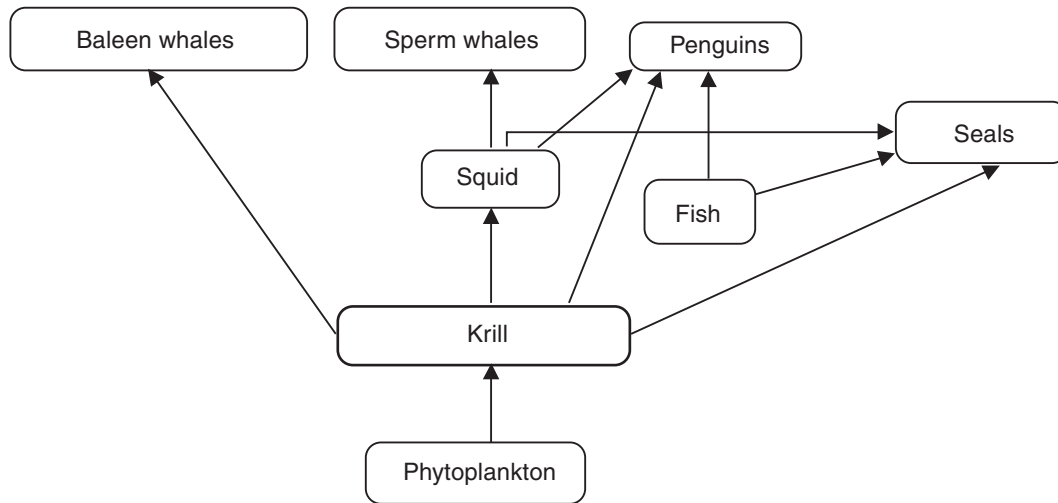


Fig. 2: A simplified representation of the Antarctic marine food chain indicating krill's central position (after Miller 2002)

(*cpue*) data and concluded that, in the absence of further whaling, stocks D (West Australia) and E (East Australia) will reach their pre-exploitation levels in the next 15–25 years.

In contrast to the recent recovery of large baleen whales in the Antarctic, there are some indications of recent declines in other predators of krill, such as minke whales, crabeater seals, fur seals and macaroni penguins *Eudyptes chrysolophus*. Butterworth *et al.* (1999, 2002), in an analysis of catch-at-age data, suggest a reduction in the minke whale population in International Whaling Commission (IWC) Management Area IV (70–130°E) from 1970 to 2000 and also that in Area V (130–170°W, though to a lesser extent; see Fig. 4). Branch and Butterworth (2001a) report that minke whale population estimates declined by about 50% from the second IWC-IDCR/SOWER circumpolar survey (1985/86–1990/91) to the third (1991/92–1997/98), although their calculations required some extrapolations because the third circumpolar survey had not yet been completed at the time their computations were carried out. A recent decline has also been indicated for crabeater seals (Gelatt and Siniff 1999). Erikson and Hanson (1990) present the latest summary of past density estimates for the major pack-ice regions of the Antarctic (Weddell Sea and the Pacific sector). A critical comparison of census data from 1969 and 1970 with those from 1984 suggests a reduction in crabeater seal density of 30–60% (after allowing for reductions in the 1969 estimate as

a result of improved analytical techniques). Studies of the age at maturity of crabeater seals provide supporting evidence for a decline in food availability for these animals, given that this age increased from 1964 to 1989 (Bengtson and Laws 1985, Hårding and Härkönen 1995). Reid and Croxall (2001) examined the relationship between the trend in krill biomass and that of its predators (fur seals, Adelle penguins *Pygoscelis adeliae* and macaroni penguins at South Georgia, and found that since 1990 the numbers of all these predators have been declining, and that the length of krill in the diets of those predators has become smaller. The authors further suggest that, for krill-dependent predators at South Georgia, the period of the “krill surplus” might now be at an end.

In this study, an initial multispecies model is developed for two species in the Antarctic that feed mainly on krill, in order to gain some insight into what could have happened in the past and might happen in the future for krill and their predators there. In this preliminary attempt, the interactions between blue whales, minke whales and krill are modelled. This is primarily because it is instructive to commence the development of a complex multispecies model at a simple level, and also because minke and blue whales share almost exactly the same habitat (Laws 1977, Kasamatsu *et al.* 1996, 2000) and the same prey (krill). Other large baleen whales, such as humpback and fin whales, are distributed farther north when in the Antarctic over summer, and are not as heavily de-

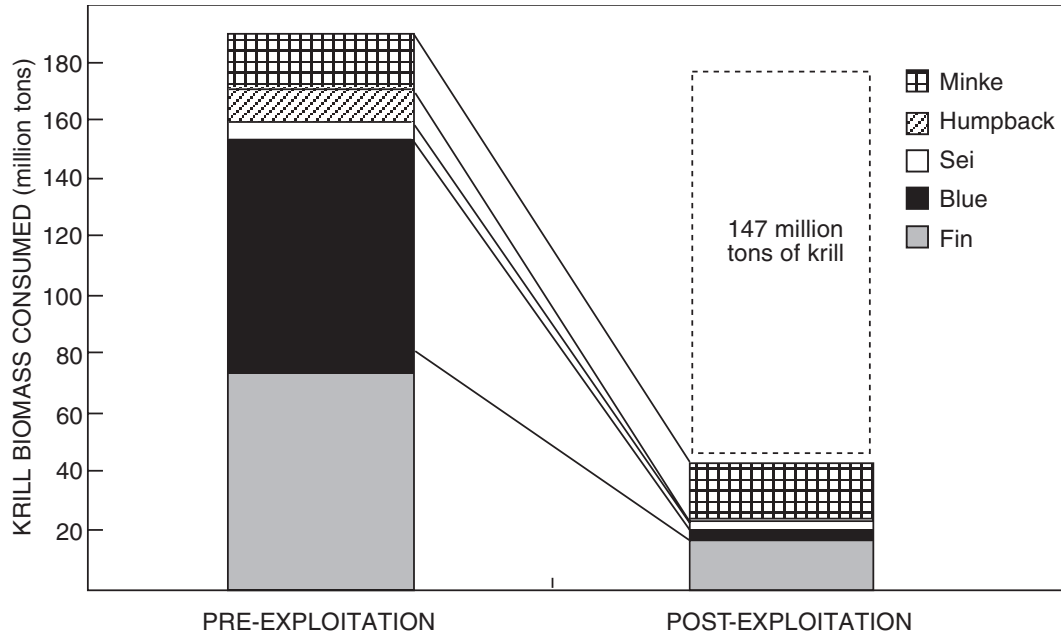


Fig. 3: Estimated consumption of krill by baleen whales in the Antarctic (after Laws 1977). The plot shows the situation "pre-exploitation" and "post-exploitation" of whales

pendent on krill as blue and minke whales, so were not considered for this initial model.

Because of the appreciable uncertainties concerning absolute estimates of krill biomass and its trends (detailed in Appendix 1), the model is fitted to the survey estimates of abundance of minke and blue whales only. The analysis first investigates whether a simple predator-prey model can reproduce past population trends suggested by the other information discussed above. Then the sensitivity of the model to different parameter values is investigated, and some future projections are developed.

In earlier work of this nature, a multispecies interaction model for whales, seals and krill was investigated by May *et al.* (1979). Thomson *et al.* (2000) and Constable (2001) investigated the effect of krill harvesting on krill-feeding predator populations. An ECOPATH with ECOSIM model (Christensen *et al.* 2000), focusing on the South Georgia region, is also in development (A. W. Trites, University of British Columbia, pers. comm.). Other than these studies, little multispecies modelling in the Antarctic seems to have been pursued. This paper constitutes the first attempt to fit, albeit coarsely, such a model to estimates of abundance for some key species that have only recently become available.

## DATA AND METHODS

### An initial illustrative model

To illustrate how the population dynamics and interactions of the three species (minke whales, blue whales and krill) might operate, the simple model shown in Equations 1–3 below was developed. A Holling Type-II functional response (Holling 1965) is assumed, for which the consumption and birthrate of the predators are dependent only on the density of prey, and not on the density of predators (Fig. 5).

For krill,

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

where, for example, the last term on the right-hand side reflects the rate at which krill is consumed by the population of minke whales. Krill harvests, which commenced in 1974, have generally been low (maximum annual take slightly above half a million tons; Thomson *et al.* 2000) in comparison with krill abun-

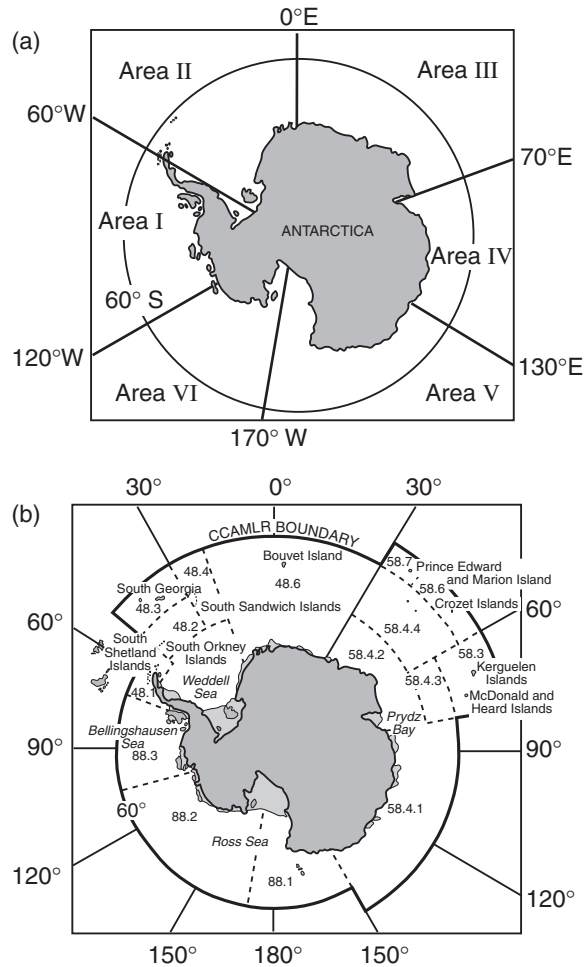


Fig. 4: Antarctic Management Areas defined by international organizations: (a) by the IWC for minke whales, (b) by CCAMLR

dance, and have therefore been ignored for this initial analysis.

For blue whales,

$$N_{y+1}^b = N_y^b + \frac{\mu^b N_y^b B_y}{B_b + B_y} - M^b N_y^b - C_y^b \quad (2)$$

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

For minke whales,

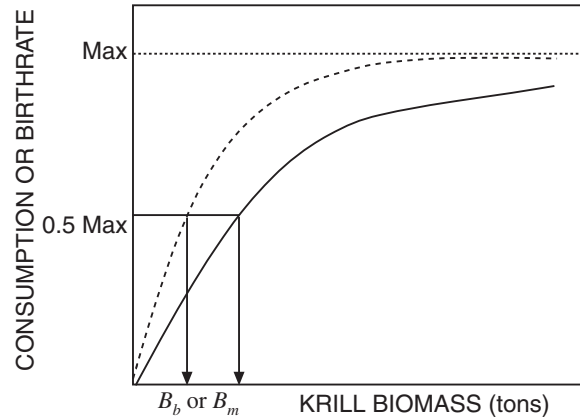


Fig. 5: Consumption and birthrate functions for blue and minke whales in terms of krill abundance. Because of uncertainties regarding appropriate values for  $B_b$  and  $B_m$ , the model is examined for different choices for these

$$N_{y+1}^m = N_y^m + \frac{\mu^m N_y^m B_y}{B_m + B_y} - M^m N_y^m - C_y^m \quad (3)$$

where

- $N_y^b$  is the number of blue whales at the start of year  $y$ ,
- $N_y^m$  the number of minke whales at the start of year  $y$ ,
- $B_y$  the biomass of krill at the start of year  $y$ ,
- $r$  the intrinsic growth rate of krill,
- $K$  the carrying capacity of krill in tons,
- $\lambda^b$  the maximum *per capita* rate of krill consumption (tons per year) by blue whales,
- $B_b$  the level of krill biomass at which the *per capita* blue whale consumption rate drops by 50%,
- $\lambda^m$  the maximum *per capita* rate of krill consumption (tons per year) by minke whales,
- $B_m$  the level of krill biomass at which the *per capita* minke whale consumption drops by 50%,
- $\mu^b$  the maximum *per capita* birth rate for blue whales,
- $M^b$  the annual rate of natural mortality of blue whales,
- $\mu^m$  the maximum *per capita* birth rate for minke whales,
- $M^m$  the annual rate of natural mortality of minke whales, and
- $C_y^{b/m}$  is the catch in year  $y$  of blue/minke whales from the Antarctic (and other parts of the southern hemisphere).

**Data**

Annual catches of blue whales ( $C_y^b$ ) and minke whales

Table I: Catch statistics for blue and minke whales in the southern hemisphere (including the Antarctic; 1900–2000). Source: C. Allison, International Whaling Commission, 2002. A moratorium on commercial whaling came into force in 1987; catches of minke whales from that time have been under a scientific research programme

Year	Blue whale	Minke whale	Year	Blue whale	Minke whale
1900	0	0	1951	5 147	9
1901	0	0	1952	4 002	0
1902	0	0	1953	2 888	12
1903	0	0	1954	2 544	0
1904	11	0	1955	1 749	45
1905	51	0	1956	1 715	46
1906	68	0	1957	1 769	493
1907	106	0	1958	1 250	103
1908	245	0	1959	936	206
1909	212	0	1960	1 743	162
1910	387	0	1961	1 143	2
1911	1 235	0	1962	1 748	21
1912	2 505	0	1963	1 508	104
1913	2 774	0	1964	3 347	51
1914	4 888	0	1965	1 477	79
1915	5 636	0	1966	665	374
1916	4 387	0	1967	462	1 099
1917	3 173	0	1968	674	618
1918	2 046	0	1969	920	764
1919	2 009	0	1970	834	917
1920	3 002	0	1971	538	4 155
1921	4 521	0	1972	7	6 583
1922	6 774	1	1973	1	8 541
1923	4 918	0	1974	0	7 884
1924	6 966	0	1975	0	7 185
1925	6 422	0	1976	0	8 676
1926	8 665	0	1977	0	6 000
1927	10 108	0	1978	0	6 156
1928	13 898	0	1979	0	7 897
1929	18 726	0	1980	0	7 142
1930	30 457	0	1981	0	7 903
1931	6 659	0	1982	0	7 301
1932	18 983	0	1983	0	6 680
1933	17 432	0	1984	0	5 568
1934	16 612	0	1985	0	5 567
1935	17 870	0	1986	0	4 969
1936	14 598	0	1987	0	273
1937	15 119	0	1988	0	241
1938	14 127	0	1989	0	330
1939	11 518	0	1990	0	327
1940	1 754	0	1991	0	288
1941	51	0	1992	0	330
1942	127	0	1993	0	330
1943	349	0	1994	0	330
1944	1 050	0	1995	0	440
1945	3 646	0	1996	0	440
1946	9 237	0	1997	0	438
1947	6 968	0	1998	0	389
1948	7 731	0	1999	0	439
1949	6 240	1	2000	0	440
1950	7 035	0			

( $C_y^m$ ) from 1900 onwards are shown in Table I. These figures have been corrected from earlier Soviet misreporting (Yablokov *et al.* 1998). Branch and Butterworth (2001a, b) calculated abundance estimates for

minke whales and blue whales using the IWC–IDCR/SOWER survey sighting data. The abundance estimates used in this analysis and associated plausible ranges are listed in Table II.

Because of the uncertainties concerning values for these parameters, plausible ranges are considered in all cases and are shown in Table II. Each parameter is chosen randomly in the simulations by selecting from the minimum, middle or maximum value for its range. The value of  $u$  in Equation (1) was set to 0.2, based upon the behaviour of the age-structured krill dynamics model developed by Butterworth *et al.* (1994), which is that used by CCAMLR to provide a basis for setting krill catch limitations (see Appendix 1).

**Model-fitting procedure and parameter estimation**

In order to estimate the yearly abundances of krill, blue whales and minke whales using Equations (1)–(3), the starting value (abundance) for each species in the year 1900, before human exploitation, which corresponds to the co-existence equilibrium level for these species, needs to be estimated. The condition that all three species were in equilibrium (balance) in the year 1900 provides relationships between the parameter values. Thus, by setting  $B_{y+1} = B_y$  in Equation (1), it follows that:

$$r \left( 1 - \left( \frac{B_{1900}}{K} \right)^u \right) (B_b + B_{1900})(B_m + B_{1900}) = \lambda^b N_{1900}^b (B_m + B_{1900}) + \lambda^m N_{1900}^m (B_b + B_{1900}) \quad (4)$$

Similarly, setting  $N_{y+1}^b = N_y^b$  in Equation (2), and  $N_{y+1}^m = N_y^m$  in Equation (3), yields:

$$\mu^b B_{1900} = M^b B_b + M^b B_{1900} \quad , \quad (5)$$

$$\mu^m B_{1900} = M^m B_m + M^m B_{1900} \quad . \quad (6)$$

From Equations (5) and (6), it follows that:

$$B_{1900} = \frac{M^b B_b}{\mu^b - M^b} = \frac{M^m B_m}{\mu^m - M^m} \quad . \quad (7)$$

Equation (7) indicates that given values for  $r$ ,  $\mu^b$ ,  $M^b$ ,  $\mu^m$  and  $M^m$ , once  $B_b$  is specified, the value of  $B_m$  follows, as does the value of  $B_{1900}$ . That leaves only one quantity “free” in Equation (4): the value of  $K$ , which follows once values for  $N_{1900}^b$  and  $N_{1900}^m$  are obtained.

$N_{1900}^b$  and  $N_{1900}^m$  are estimated by minimizing the difference between the estimated abundance indicated by the population models of Equations (1)–(3), and the survey abundance estimates shown in Table II. The function minimized ( $SS$ ) is as follows:

$$SS = (N_{2000}^b - \hat{N}_{2000}^b)^2 + (N_{1985}^m - \hat{N}_{1985}^m)^2, \quad (8)$$

where

- $N_{2000}^b$  is the survey estimate of the abundance of blue whales in 2000,  
 $\hat{N}_{2000}^b$  the model estimate of the abundance of blue whales in 2000,  
 $N_{1985}^m$  the survey estimate of the abundance of minke whales in 1985, and  
 $\hat{N}_{1985}^m$  is the model estimate of the abundance of minke whales in 1985.

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

- Blue whales: high abundance initially (1900), followed by a dramatic decrease because of exploitation. Subsequent recovery has been gradual.  
 Minke whales: start low initially (1900), rise to maximum, and then start to decrease from about 1970, as suggested by the catch-at-age analysis of Butterworth *et al.* (1999, 2002).

In addition to these features, situations were sought where the co-existence equilibrium for the three species

was stable, and where the fluctuations in krill biomass were not too large.

## RESULTS

Different sets of parameter values gave very different trajectories for the three species considered. Only some of these reflected the trends suggested by other information. Figure 6 shows some of the trajectories for minke whales, blue whales and krill that did reflect these trends reasonably (parameter values corresponding to these trajectories are listed in Table App.1). Fitting to the high and low abundance estimates for minke and blue whales in Table II did not show trajectories that differed from those in Figure 6 in qualitative terms, but the absolute abundance of all three species increased when the model was fitted to higher abundance estimates (Fig. 7). These trajectories suggest an interesting possible pattern of events over the last century in the Antarctic. Blue whale abundance decreased dramatically after 1920 as a result of excessive whaling; then following this decrease, krill abundance increased because of diminished consumption by blue whales. Minke whales were not harvested until the 1970s and the population increased dramatically until then as a result of the increase in krill biomass. However, this large increase of minke whales reduced the krill biomass to a low level. As a consequence of this reduction, minke whale biomass started to drop from the late 1970s. By the 1990s, krill biomass had increased again as a result of the minke whale

Table II: Plausible ranges assumed for the abundance estimates and biological parameter values. Parameters selected from these ranges were also required to satisfy the conditions:  $\mu^b - M^b \geq 0.02$  and  $\mu^m - M^m \geq 0.03$ , i.e. that blue and minke whales could attain *per capita* growth rates of at least 2 and 3% respectively under optimal feeding conditions

Parameter	Range	References
$M^b$ : blue whale natural mortality rate (year <sup>-1</sup> )	0.03–0.06	
$M^m$ : minke whale natural mortality rate (year <sup>-1</sup> )	0.04–0.1	
$\mu^b$ : maximum <i>per capita</i> birth rate for blue whales (year <sup>-1</sup> )	0.05–0.16	
$\mu^m$ : maximum <i>per capita</i> birth rate for minke whales (year <sup>-1</sup> )	0.07–0.2	
$\lambda^b$ : maximum <i>per capita</i> rate of consumption (tons year <sup>-1</sup> ) by blue whales	103 tons $\times$ [0.9 – 3.5%] $\times$ 125 days	Tamura (2002) Trites and Pauly (1998)
$\lambda^m$ : maximum <i>per capita</i> rate of consumption (tons year <sup>-1</sup> ) by minke whales	7 tons $\times$ [0.6 or 2.85 or 5.1%] $\times$ 90 days	Ichii and Kato (1991) Kasamatsu <i>et al.</i> (1996) Butterworth <i>et al.</i> (1994)
$r$ : intrinsic growth rate of krill (year <sup>-1</sup> )	$MSYR = 0.15, 0.2, 0.25$	
$B_b$ : level of krill biomass (tons) at which blue whale consumption drops by 50%	Consider different values: [100, 300, 500, 1000] $\times$ 10 <sup>6</sup>	
Abundance estimate	Value	
$N_{2000}^b$ : blue whale (year = 2000)	1 500, 2 000, 3 000	Branch and Butterworth (2001b)
$N_{1985}^m$ : minke whale (year = 1985)	700 000, 750 000, 1 200 000 (reflecting $g(0) < 1$ )	Branch and Butterworth (2001a)

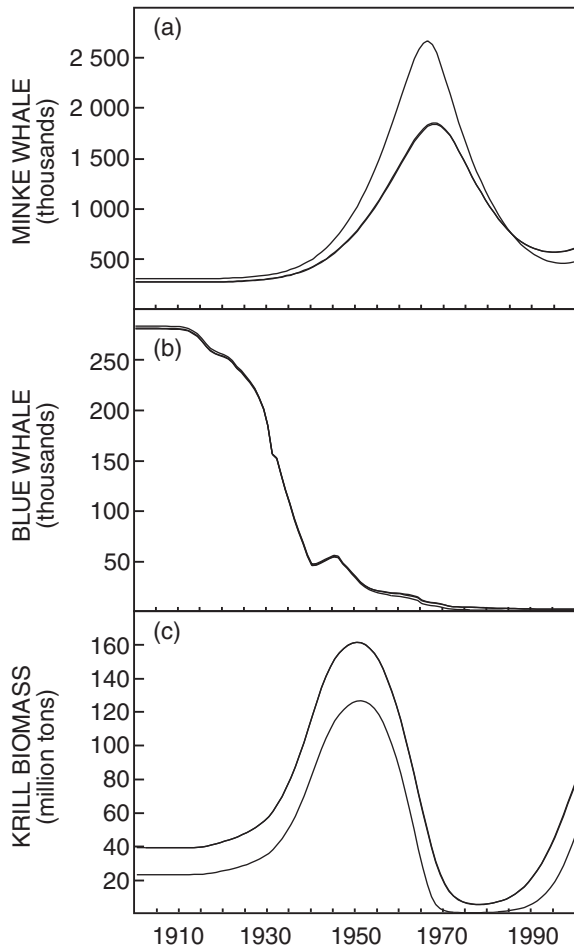


Fig. 6: Trajectories of minke whales, blue whales and krill that reflect trends suggested by surveys and related analyses. A minke whale abundance in 1985 of 750 000 is fitted in all cases. Details of scenarios are given in Table.App. 1

decline, and this allowed a blue whale recovery to start at a rate of about 1–2% year<sup>-1</sup>.

### Sensitivity of the model

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

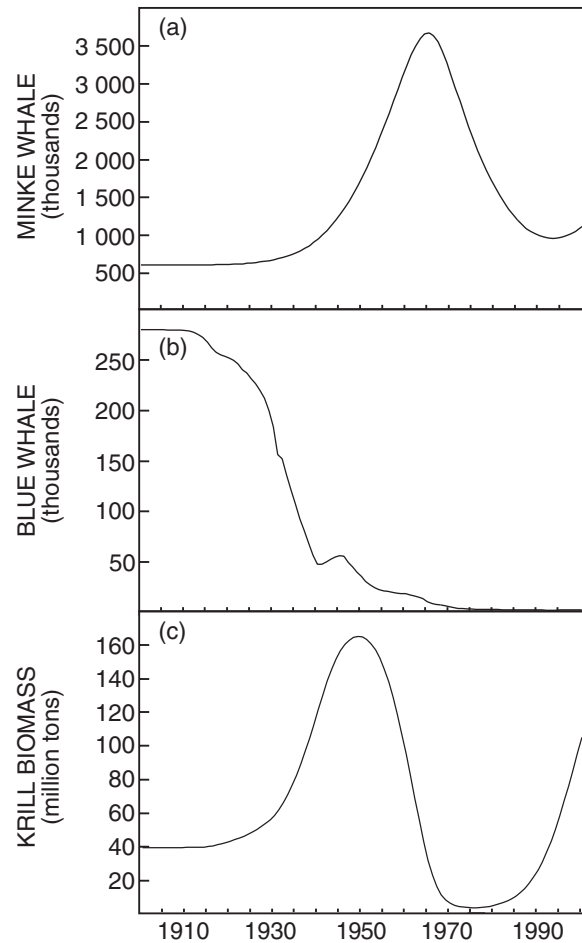


Fig. 7: Trajectories for minke whales, blue whales and krill that reflect trends suggested by surveys and related analyses. A minke whale abundance in 1985 of 1 200 000 is fitted here

and birth rate functions for blue whales (Fig. 8). None of the trajectories reflected the suggested trends when  $B_b$  was higher than 300 million tons, which suggests that the krill biomass level ( $B_b$ ) at which the blue whale birthrate (and consumption rate) drops to half of their possible maxima is relatively low.

The second feature concerns the relationship between the growth rates of minke and blue whales. The interesting point here is that the growth rate of minke whales is higher than that of blue whales only when the krill biomass is relatively high. When the krill biomass is low, the growth rate of blue whales becomes negative, but not to the same extent as that of



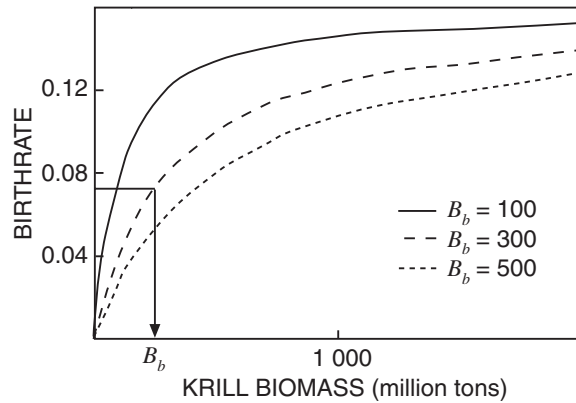


Fig. 8: Examples of birthrate functions for blue whale in terms of krill abundance. To reflect population trends suggested by other information, the krill biomass when blue whale birthrate and consumption rate drop to half of their maximum rate ( $B_b$ ) needs to be relatively low, between 100 and 300 million tons. None of the trajectories examined reflected the trends suggested by other information when  $B_b$  was higher than 300 million tons

minke whales (Fig. 9). This may underlie the gradual recovery of blue whales in recent years, blue whales being better able to cope with fluctuations in krill biomass to low levels than minke whales.

The last feature concerns various biological parameters for blue and minke whales, as summarized in Table III. These suggest that both species have a relatively high maximum birthrate; the maximum growth rate for blue whales needs to be higher than 10% year<sup>-1</sup>, and 13% year<sup>-1</sup> for minke whales. These indications do not seem unrealistic when compared with the recent estimate of a 8% year<sup>-1</sup> increase for blue whales (Branch *et al.* 2003) and of an  $MSYR_{1+}$ <sup>4</sup> of some 5–6% for minke whales (Butterworth and Punt 1999). Blue whales are indicated also to have a relatively low maximum consumption rate (1–2.2% of body mass day<sup>-1</sup>), whereas minke whales have a relatively high maximum consumption rate (3–5% of body mass day<sup>-1</sup>). This also seems plausible, given that larger mammals can survive without food for longer periods than smaller ones because of their lower metabolic rate in relation to body mass (Laws 1977).

<sup>4</sup>  $MSYR_{1+}$  is the ratio of  $MSY$  to the population level at which it is achieved ( $MSYL$ ), when harvesting selects uniformly from all whales aged 1 and above (1+). The maximum rate of increase at low population size would typically be some 50–100% larger than this

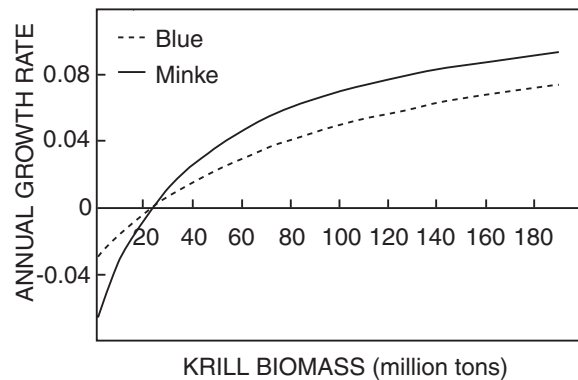


Fig. 9: *Per capita* population growth rates for minke and blue whales as a function of krill abundance that follow from Equations (2) and (3). To reflect population trends suggested by other information, the growth rate of minke whales needs to be higher than that of blue whales when krill biomass is relatively high. However, when krill biomass is relatively low, the growth rate for blue whales does not drop below zero to as appreciable extent as does that for minke whales

## Projections

To get a very broad idea of future possibilities, some deterministic projections were run under a zero catch for all species. Figure 10 shows the trajectories for the three species for the next 500 years. Although there are some very large oscillations in current population numbers, in terms of underlying trends the minke whale population decreases gradually over time, whereas the blue whale population increases gradually, both eventually returning to their original equilibrium level.

## DISCUSSION

The model has revealed some interesting possible consequences of multispecies interactions in the Antarctic:

1. There might have been an appreciable decrease in krill biomass from the 1970s to the 1990s, because of the rapid increase in abundance of minke whales (and hence of their krill consumption) following the depletion of the large baleen whales.
2. The recent recovery of blue whales, despite the decrease of minke whales, can possibly be explained by the differences in growth rate of the two species in relation to krill biomass. Minke whales maintain a higher growth rate than blue whales when krill

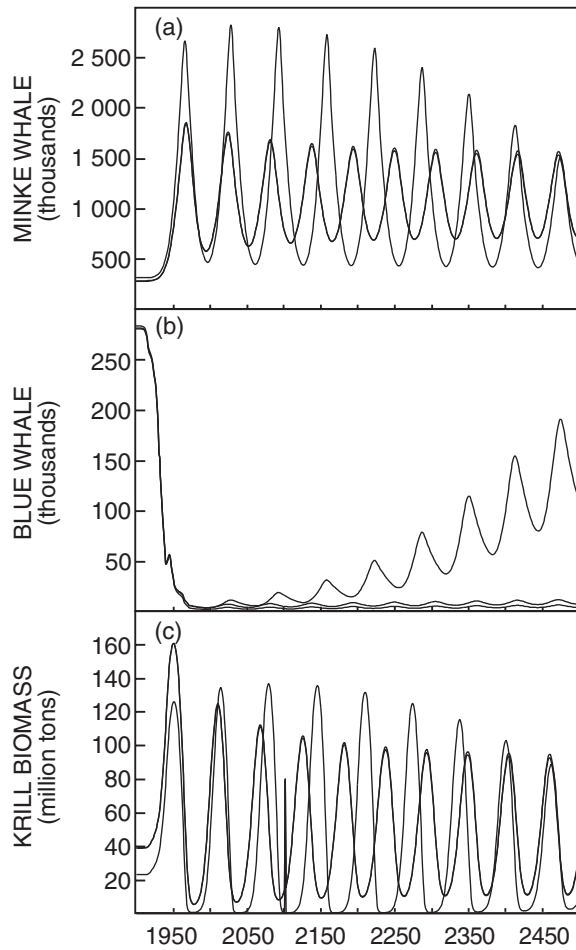


Fig. 10: Future trajectories for minke whales, blue whales and krill for the cases shown in Figure 6. These simulations assume no catch of any species after 2000

biomass is high, but blue whales are better able to cope with periods of low krill abundance.

### Trends in krill biomass

As detailed in Appendix 2, no estimate of krill biomass in absolute terms was available before the 1980s. Therefore, it is difficult to confirm directly whether the suggested krill "surplus" following the reduction of the large baleen whales actually occurred. Moreover, there are no data monitoring trends in krill biomass before the late 1970s. Furthermore, such subsequent

data as are available (e.g. Siegel *et al.* [1998, 2002] for the vicinity of Elephant Island) pertain to small regions rather than to the Antarctic as a whole. It is tempting to cite the krill trends at Elephant Island – a decrease to low levels from the mid 1970s to early 1990s (Loeb *et al.* 1997), followed by an increase in the late 1990s (Siegel *et al.* 1998, 2002) – as qualitatively compatible with trends predicted by the model investigated here (see Fig. 6). However, Loeb *et al.* (1997) postulate regional warming as the cause of the low levels. Indeed, many other studies of krill abundance cite environmental causes (e.g. winter sea-ice conditions) for fluctuations (e.g. Siegel and Loeb 1995, Murphy *et al.* 1998, Croxall *et al.* 1999, 2002, Nicol *et al.* 2000b, Reid and Croxall 2001). A valuable insight offered by the analysis of this paper is that it is important to consider the impact that predator–prey dynamics may be having on longer-term trends in krill abundance, as well as the impact of environmental changes. In order to test model predictions, the continuation of the surveys such as CCAMLR–2000 (SC–CAMLR 2000) is very important, and would provide useful information on krill abundance and its trend in the future. Furthermore, it might be useful to develop multi-species models for a particular region, such as the vicinity of South Georgia or Elephant Island, where relatively long time-series of krill abundance are available.

### Plausibility of the model and its estimated parameters

Any basis to comment upon the plausibility of the results obtained here is limited because of a paucity of information. Other estimates of pre-exploitation abundance of blue whales (e.g. that of Laws 1977) rest upon similar calculations using historical catches, as conducted in this paper, so do not provide an independent check on the estimates of some 250 000 animals listed in Appendix 1. The recent blue whale model-predicted rates of increase listed in Appendix 1 (typically some 1–2% year<sup>-1</sup>) are not as high as the 8% estimated by Branch *et al.* (2003), although there is no necessary incompatibility because the latter estimate has a high associated standard error of 3.5%.

Certainly, the initial krill abundance estimates listed in Appendix 1 are too low, but this is a consequence of the model including only two of the major predators of krill. Inclusion of other predators would both increase krill abundance to a more realistic initial level, and also likely prevent it dropping as low over the period 1970–1990, as indicated in Figures 6 and 7. This in turn would lead to a faster predicted increase in blue whale numbers at present, and more in keeping with the point estimate of Branch *et al.* (2003).

Table III: General requirements for the biological parameters of minke whales and blue whales to reflect the population trends suggested by other information for these species

Blue whale	Minke whale
High maximum birth rate ( $\mu^b$ ) Maximum growth rate ( $\mu^b - M^b$ ): 10% year <sup>-1</sup> Low maximum consumption rate ( $\lambda^b$ ) (1–2.2% of body mass day <sup>-1</sup> )	High maximum birth rate ( $\mu^m$ ) Maximum growth rate ( $\mu^m - M^m$ ): 13% year <sup>-1</sup> High maximum consumption rate ( $\lambda^b$ ) (3–5% of body mass day <sup>-1</sup> )

### Importance of monitoring

Given the large fluctuations in the abundance of minke whales suggested by this model, one would expect some changes in biological parameters, such as an increase in age at maturity or decrease in pregnancy rate or changes in body-fat conditions corresponding to the suggested decline over recent decades. It is useful to monitor these biological parameters continuously in order to better understand the dynamics of the population. In addition, information on the functional response of whales to krill is important. For Antarctic fur seals, macaroni penguins and gentoo penguins *Pygoscelis papua* around Bird Island, Boyd and Murray (2001) demonstrate a Holling Type II functional response of an index of population status to krill biomass. However, information on the functional response of whales to krill biomass scarcely exists. The results presented here are sensitive to the shape of this functional response, and further field studies are desirable to shed light on this.

### Work in progress and future plans

Work is in progress to refine the models used for the population dynamics (Equations 1–3) in this paper. The form of these models used thus far suffers from a technical problem that amounts to a lack of robustness to parameter value variation – the joint equality of Equation (7) cannot be maintained if the value of only one parameter changes, which is unrealistic (Armstrong and McGehee 1980). This needs to be resolved by introducing terms that reflect some degree of intra- or inter-specific competition between minke and blue whales (i.e. predator per capita birth or death rates that depend on predator abundance). This was not done here in the interests of keeping the initial model as simple as possible, because at least one extra parameter whose value would have been difficult to specify would need to have been introduced. An advantage of such extra complexity, however, is that such terms can have the effect of dampening what appear to be unrealistically large amplitude oscillations in Figures 6,

7 and 10.

The results of this approach should therefore be interpreted qualitatively rather than quantitatively at this level of development. Further work will consider extensions in a number of directions for improved realism in respect of krill and its major predators, such as

- (i) adding further major predator species that feed on krill (likely humpback and fin whales, and crab-eater and fur seals);
- (ii) incorporating age structure and time-dependence in biological parameters for some species at least; and
- (iii) including spatial effects, for example by distinguishing according to the different IWC Antarctic Management Areas (Fig. 4) rather than pooling at a circumpolar level.

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APPENDIX 1

Technical details of computations

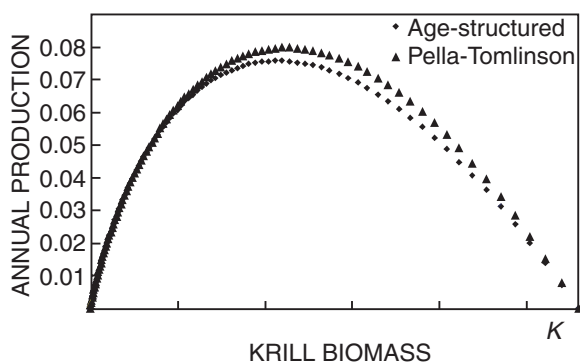


Fig. App.1: Annual krill production (expressed as a proportion of  $K$ ) for the age-structured krill model of Butterworth *et al.* (1994) and for a Pella-Tomlinson approximation to this function

Comparison of the krill dynamics model of Butterworth *et al.* (1994) with a Pella-Tomlinson form

The age-structured population model for krill developed in Butterworth *et al.* (1994) can be used to provide the curve shown in Figure App.1 relating annual equilib-

rium production ( $Y$ ) to krill abundance. The Figure also shows the Pella-Tomlinson form that is used to approximate this behaviour in Equation (1) of the main text, which models krill production:

$$Y = rB \left( 1 - \left( \frac{B}{K} \right)^u \right)$$

for which  $MSYL/K = \left( \frac{1}{1+u} \right)^{1/u}$ ,

$$MSYR = \frac{ru}{1+u}$$

The Pella-Tomlinson curve shown in Figure App.1 has  $MSYR = 0.2$  and  $u = 0.2$  (corresponding to  $MSYL/K \approx 0.4$ ).

Details of the parameter values and trends for the trajectories shown in Figures 6 and 7

The recent rates of increase ( $ROI$ ) for whales over a period from  $y_i$  to  $y_f$  are computed as

$$\frac{1}{(y_i - y_f)} \ln \left( \frac{N_{y_i}}{N_{y_f}} \right)$$

Table App.1: Parameter values for population trajectories shown in Figures 6 and 7

Parameters	Scenarios			
	Fig. 6-1	Fig. 6-2	Fig. 6-3	Fig. 7
$M^b$ (year <sup>-1</sup> )	0.03	0.045	0.045	0.045
$M^m$ (year <sup>-1</sup> )	0.07	0.07	0.07	0.07
$\mu^b$ (year <sup>-1</sup> )	0.16	0.16	0.16	0.16
$\mu^m$ (year <sup>-1</sup> )	0.2	0.2	0.2	0.2
$\lambda^b$ (tons year <sup>-1</sup> )	$103 \times 0.9\% \times 125$	$103 \times 0.9\% \times 125$	$103 \times 0.9\% \times 125$	$103 \times 0.9\% \times 125$
$\lambda^m$ (tons year <sup>-1</sup> )	$7 \times 2.85\% \times 90$	$7 \times 5.1\% \times 90$	$7 \times 5.1\% \times 90$	$7 \times 2.85\% \times 90$
$r$ (year <sup>-1</sup> ; $MSYR=0.15$ )	0.9	0.9	0.9	0.9
$B_b$ (10 <sup>6</sup> tons)	100	100	100	100
$N_{2000}^b$	3 000	1 500	3 000	2 000
$N_{1985}^m$	750 000	750 000	750 000	1 200 000
Model fit values				
$B_{1900}$ (10 <sup>6</sup> tons)	23.1	39.1	39.1	39.1
$K$ (10 <sup>6</sup> tons)	271.2	331.6	330.7	385.7
$N_{1900}^b$	283 191	280 451	281 105	279 757
$N_{1900}^m$	306 904	276 437	273 456	607 052
$ROI N_{1980-2000}^b$ (year <sup>-1</sup> )	-0.02	-0.01	-0.01	-0.01
$ROI N_{1995-2000}^b$ (year <sup>-1</sup> )	0.01	0.01	0.01	0.02
$ROI N_{1980-2000}^m$ (year <sup>-1</sup> )	-0.04	-0.02	-0.02	-0.02
$ROI N_{1995-2000}^m$ (year <sup>-1</sup> )	0.01	0.02	0.02	0.03

## APPENDIX 2

## Review of krill abundance and its trend in the Antarctic

There is considerable uncertainty about the absolute abundance of krill *Euphasia superba* in the Antarctic. Estimates made on the basis of various measurements of krill biomass span a full order of magnitude, from 135 million to 1.35 billion tons (Nicol and de la Mare 1993). Everson *et al.* (1990) suggest that indirect estimates of abundance based upon predator consumption rates give a coarsely estimated total annual production of several hundred million tons. A recent study by Nicol *et al.* (2000a) estimates the circumpolar abundance of Antarctic krill to be between 60 and 155 million tons, at the low end of the range of values that have been suggested in the past.

CCAMLR (the Convention for the Conservation of Antarctic Marine Living Resources), and the BIOMASS (Biological Investigations of Antarctic Systems and Stocks) programme that preceded it, have conducted two major biomass surveys of krill. The first survey was called the FIBEX (the First International BIOMASS Experiment) and was conducted in 1981. This survey estimated 32.7 million tons of krill in CCAMLR Management Area 48 (see Fig. 4, SC-CAMLR 2000). The second survey, called the CCAMLR 2000 krill synoptic survey (SC-CAMLR 2000), resulted in an estimate of 44.3 million tons ( $CV = 11.4\%$ ) for the same area, and 4.8 million tons for CCAMLR Management Area 58.4 (SC-CAMLR 2000). The estimates of the FIBEX survey and the CCAMLR 2000 survey are not directly comparable because of the different total areas covered by the two surveys, and different estimation techniques used in the two surveys (SC-CAMLR 2000).

Other information on long-term trends in krill biomass is scarce, except for the regions around Elephant Island and South Georgia. For Elephant Island, after a decade of low krill density and biomass, scientific net-sampling surveys have indicated a recent increase

in krill biomass. Loeb *et al.* (1997) report a decrease in krill biomass from the late 1970s to the early 1990s around Elephant Island, which they ascribe to regional warming in the Antarctic. Following this study, Siegel *et al.* (1998) note the relatively high stock size of krill in 1997, and conclude that, after almost a decade of low krill density and biomass in the area, krill density and biomass had increased. Siegel *et al.* (2002) note that the proportional recruitment index for the entire survey area for the 2000 year-class was the highest value recorded during the past 20 years around Elephant Island. Results for the 2001 season indicate above-average krill abundance and recruitment in the Elephant Island area, which is ascribed to successful spawning during 2000 (SC-CAMLR 2001). Siegel and Loeb (1995) suggest that good and poor year-classes of krill are directly and indirectly related to sea-ice conditions during the preceding winter season, the timing of krill spawning and the occurrence of dense concentrations of salps. Brierley *et al.* (1999) report the trend in krill density at South Georgia from 1981 to 1998 as estimated from acoustic surveys. They suggest that one might expect to experience seasons of poor krill abundance at South Georgia in one year out of every six or seven. However, they also note that, because of the gaps in the early part of their time-series, they were not able to assess the frequency of changes in krill abundance for the South Georgia region, and that there is no evidence of a general decline in krill abundance at South Georgia.

As detailed above, there was no absolute abundance estimate of krill biomass available before the 1980s. Therefore it is difficult to confirm the suggested krill "surplus" following the reduction of the large baleen whales in the Antarctic. Moreover, there was no monitoring of trends in krill biomass from indices of relative abundance before the late 1970s.