Summary of an update of the Mori-Butterworth (2006) model of the krill-predator dynamics of the Antarctic ecosystem

Naseera Moosa and Doug S. Butterworth

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Abstract

The Mori-Butterworth (2006) model of the krill-predator dynamics of the Antarctic ecosystem is refined in Moosa (2017). Updates to and the revision of abundance and trend information are summarized. Key features of the updated and refined model are the inclusion of a depensatory effect for the Antarctic fur seals in the krill and predator dynamics, and the imposition of bounds on K_a (the carrying capacity of krill in Region a, in the absence of its predators); these lead to a better fit to the data overall. A particular difference in results compared to those from the Mori-Butterworth model is more oscillatory behaviour in the trajectories for krill and some of its main predators. This likely results from the different approach to modelling natural mortality for krill (which decreases the residual mortality remaining after taking account of consumption by the main predators) and warrants further investigation. That may in turn resolve a key mismatch in the model which predicts minke whale oscillations in the Indo-Pacific region to be out of phase with results from a SCAA assessment of these whales. A number of other areas for suggested future research are listed.

Introduction

The aim of the thesis submitted which is summarized here (Moosa, 2017) is to update/refine the Mori-Butterworth (2006) Antarctic ecosystem model, detailed in Mori (2005). The Mori (2005) study attempted to explain the population dynamics of major species in the Antarctic using predator-prey interactions only.

Mori (2005) concluded that it was possible to explain the observed population trends of the main Antarctic krill-predators through predator-prey interactions only. However, she highlighted that there was room for improvements to her model. She acknowledged that in order for a reliable krill-predator Antarctic ecosystem model to be developed, estimates of krill consumption by other krill-predators such as birds, fish and cephalopods, not included in her model, needed to be developed to see if they merited inclusion in her model. Furthermore, at the time of the Mori (2005) study, abundance estimate analyses from some major seal and whale sighting surveys were unfinalised.

Mori (2005) acknowledged that the Mori-Butterworth (2006) model was only a first step to producing a realistic and reliable krill-centric predator-prey Antarctic ecosystem model.

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

The objective of Moosa (2017) is to update/refine the Mori-Butterworth (2006) model by taking this new information and data into account. These updates and refinements include the following.

1) Updates to the various species' abundance and trend estimates as well as to whale catch data, and
2) The inclusion of minke whale stomach contents' weight trend data, to examine their consistency with the estimates from the model.

Framework for and data used in the model developed

This section details key aspects of and inputs to the model developed in Moosa (2017).

Species Included

In the Antarctic ecosystem, taken here to be roughly south of 60°S, the main krill-feeding baleen whales are found to be the blue, humpback, fin and minke whales. The main krill-feeding seals are the Antarctic fur seal, leopard seal and the crabeater seal. Of the fish species, the main krill-eating species are the marbled rockcod (*N. rossii*) and the mackerel icefish (*C. gunnari)*. Of the penguin species, the main krill-predators are the Adélie, chinstrap, macaroni and royal penguins. Southern right whales are also krill-predators but feed in offshore pelagic areas in sub-Antarctic waters and do not enter Antarctic waters (Kenney, 2009). Squid are also found to be a significant krill-predator. However, due to their fast growth rates and the lack of information on squid abundance and consumption rates, these species are not included in the model developed.

Moosa (2017) re-calculates the krill consumption per capita by some of the afore-mentioned krill-predators. Where applicable, updated information on the krill-predator's diet, period of feeding in the Antarctic, average weight and daily krill intake are used to determine the annual per capita consumption of krill by the krill-predators. The sources of the updated information, the annual per capita consumption of krill by these krill-predators and the total consumption of krill by weight (mt) are presented in Table 1.

The main krill-predators that merited inclusion in the ecosystem model developed are the blue whale, fin whale, humpback whale, minke whale, crabeater seal and the Antarctic fur seal. Each of these species accounts for krill consumption that has exceeded 1 million tonnes annually during recent decades.

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

Region AI = IWC Area II + IWC Area III + IWC Area IV   (60°W eastwards to 130°E)

Region PO = IWC Area V + IWC Area VI + IWC Area I   (60°W westwards to 130°E)

Region AI combines the IWC areas in the Atlantic and Indian sectors of the Southern Ocean, whilst Region PO contains the IWC areas in the Pacific sector of the Southern Ocean only. The same divisions are retained in Moosa (2017).

Catch History

A revised whale catch series (from 1900 until 2014) is used in Moosa (2017), rather than the series used in Mori-Butterworth model (from 1900 until 2000). The catch series for minke, humpback, fin and blue whales for each IWC Area was kindly provided by C. Allison of the IWC Secretariat. The IWC Area data are combined to form a catch series for Region AI and PO for each species, combining male and female numbers.

Abundance and Trend Estimates

Antarctic ship surveys

Three ship surveys have been conducted in the Antarctic, namely IDCR/SOWER, JARPA and JSV.

The IDCR/SOWER surveys have circled the Antarctic (south of 60°S) completely three times: CPI (1978/79 – 1983/84), CPII (1985/86 – 1990/91) and CPIII (1991/92 – 2003/04). At the time Mori (2005) developed her Antarctic ecosystem model, the analysis of all the CPIII surveys had not been completed. The IDCR/SOWER data are better for calculating whale abundance estimates as they provide a circumpolar estimate and their conduct is better standardised.

The JARPA surveys were a component of a long-term monitoring program in the Antarctic that operated from 1987/88 until 2004/05. During their operation, the surveys also determined estimates of minke whale abundances from sightings. JARPA alternated between the IWC Areas IIIE + IV and V + VIW during its operation, providing a time series of whale abundance estimates. JARPA II followed JARPA, taking place from 2007/08 until 2013/14.

The JSV data are compromised almost entirely of data collected by full-time scouting vessels operating in relatively high whale density areas, and cover the period from 1965/66 until 1987/88, when commercial whaling was still in operation. The JSV data are considered to be unsuitable for direct whale density estimation as they are potentially biased in terms of use for abundance estimation because the vessels were linked to whaling operations which do not cover areas in an unselective manner. However, due to the JSV's earlier more northerly coverage, the data are useful for extrapolating IDCR/SOWER survey estimates northwards, such as in Butterworth and Geromont (1995).

Results in Branch (2007) are used to calculate the abundance and trend estimate for the blue whales. The successive circumpolar abundance estimates from Branch (2007) provide a basis to determine blue whale trend estimates.

The most recent and best available consensus estimates of minke whale abundance are found in IWC (2013). These estimates are the "preferred estimates" from the Okamura and Kitakado (2012) model using the best mean dive-time estimates from Hedley (2012), and with some appropriate adjustment factors applied based on the Bravington and Hedley (2012) model approach. Key advances in these analyses compared to the earlier estimates of Branch and Butterworth (2001b) that were used in Mori (2005) are the uses of sightings from independent platforms on vessels to estimate the value of $g(0)$, and improved allowance for the spatial distribution of the whales. The CPIII surveys are used for the updated minke abundance estimates in Moosa (2017) rather than using both CPII and CPIII estimates because the overall minke trend information used in Moosa (2017) takes the CPII data into account. To avoid using the same information twice, the CPII minke abundance estimates are not used in fitting the ecosystem model to data.

Punt (2014) is used to provide the minke trend estimates. Punt (2014) applied a Statistical Catch-at-Age Analysis (SCAA) to the Southern Hemisphere minke whale data. This analysis also uses the $g(0)$-corrected abundance estimates from Hakamada and Matsuoka (2014). Two stocks are considered in Punt (2014). There is some correlation between the abundance estimates for the two stocks. As a result, the inverse variance-covariance matrix of b_{rec} (kindly provided by A. Punt) is calculated and used in the model's likelihood function.

There have been no updates to the fin whale abundance estimate based on the IDCR/SOWER surveys since those repeated in Mori (2005). Thus these estimates are retained in Moosa (2017). Mori (2005) used fin whale abundance estimates from Branch and Butterworth (2001a), which used sighting data from the CPI, CPII and the then incomplete CPIII IDCR/SOWER surveys south of 60°S. These abundance estimates were multiplied by an extrapolation factor to take into account the higher fin whale density north of 60°S. The extrapolation factors for Region AI and PO are re-calculated in Moosa (2017) and are found to be in the same range that was calculated in Mori (2005).

The fin whale trend estimate (not determined in Mori (2005)) is calculated using information in Matsuoka and Hakamada (2014). Those authors analysed the JARPA and JARPAII survey data to estimate fin whale abundance south of 60°S. Since the underlying data (JARPA and JARPAII surveys) are area-disaggregated, they are not used to update fin whale abundance estimates. The fin whale trend estimates from Matsuoka and Hakamada (2014) are statistically significantly greater than zero but are not precisely estimated. They apply roughly to the area south of 60°S whereas the current fin whale distribution is concentrated between 50°S and 60°S. These fin whale trend estimates are pooled and weighted using *Inverse Variance Weighting*, to combine two estimates of the same quantity to provide one "overall" value with a lower variance.

In Moosa (2017), both the humpback abundance and trend estimates are taken from Jackson *et al.* (2015). However that paper uses the median of the annual abundance for each population assessment to calculate the increase rates of the individual populations. Pooling the increase rates of the individual populations to calculate the increase rates for each Region of Interest would introduce bias. To address this, several authors of the Jackson *et al.* (2015) paper were contacted and asked to provide 1000 realisations of humpback whale abundance trajectories for each breeding stock and for the years 2010 and 2015 from the Bayesian estimation process used. These estimates are assumed to be approximately normally distributed and are divided amongst the IWC Management Areas (see Moosa (2017)). The median of the 1000 simulations is used as the humpback whale abundance estimate for each Region of Interest. Similarly, the humpback whale trend estimate is calculated using the same information.

There have been no updates to the Antarctic fur seal abundance and trend estimates since those repeated in Mori (2005). As a result, those estimates are retained in Moosa (2017).

The crabeater seal abundance estimates used in Moosa (2017) are from Southwell *et al.* (2012) and Gurarie *et al.* (2015). Southwell *et al.* (2012) summarized all the available abundance surveys that had been conducted for the Antarctic pack-ice seal species. The two main survey results used in Moosa (2017) from Southwell *et al.* (2012) are the earlier Erickson and later APIS surveys (see Figure 1), with only the latter considered to provide reliable estimates of abundance in absolute terms. There were IWC Management Areas that were not covered by the APIS surveys, thought these Areas were covered by the Erickson surveys. By assuming that the ratios between the APIS and Erickson survey results are location-independent, the APIS results can be extrapolated to determine a circumpolar abundance estimate for the crabeater seals (Moosa, 2017; green numbers in Figure 1).

The abundance estimates for the leopard seal, Adélie penguin, marbled rockcod and the mackerel icefish are also calculated. More recent analyses on krill abundance and trend estimates have become available in 2014 and 2015 – these are discussed in Moosa (2017).

Tables 2 and 3 summarise the observed abundance and trends estimates for the main krill-predators that are used in Mori and Butterworth (2006) and Moosa (2017) respectively.

Outline of the model developed

Model Equations

In Moosa (2017), the equations in Mori and Butterworth (2006) have been amended to include a "depensatory effect" due to initial issues in fitting to the fur seal abundance estimates. The amended equations are in Table 4 (Equations 1.1 – 1.3).

The data available indicates that the fur seals decreased substantially in abundance around 1800 and remained at low numbers for a considerable period of time (about 100 years). The fur seals presumably increased again only when more krill became available, once whaling began reducing the number of the larger baleen whales in the Antarctic. Under such circumstances,

many models are likely to be very unstable, with small changes in the starting estimate for the fur seal abundance in the model causing the population either to go extinct or to increase well before the increase actually occurred. The modifications in Equations 1.1 and 1.3 introduce a "depensatory effect" which has the consequence that once a population drops to a low abundance; it tends to stay low and needs a substantial change in circumstances before it could increase to higher levels again.

When this depensatory effect was included, the krill carrying capacities for the two Regions (K_a) needed to satisfy the following conditions:

$$K_{PO} > (10 \times 10^6), K_{AI} > (10 \times 10^6), \text{ and } K_{PO} < K_{AI}$$

This is because when the depensatory effect was included, it tended to push K_{PO} to very high negative values. These conditions are included in order to "force" K_{PO} to be positive and not to exceed K_{AI}. Although there have not been any circumpolar krill surveys, the highest concentrations of krill appear to be in Region AI, close to the Antarctic Peninsula. As a result, it seemed reasonable to assume that the ("unexploited") krill biomass would not be as high in Region PO as it is in Region AI. For the depensatory effect in Equation 1.1 and 1.3, d = N#/3 where N# is a value similar to the lowest size to which fur seals decreased to during the 1800s. This value was found to be 10 (Moosa, 2017).

Likelihood Function

The complete negative log-likelihood function that is minimized in Moosa (2017) in order to estimate the parameters M^j, λ^j, μ^j and $N_{1780}^{j,a}$ for the predator species j and r^a for krill is Equation 1.4 in Table 4. In Equation 1.4, LL_{abund}^j is the component that compares the observed abundance to the model estimated abundance for each predator species j; it assumes lognormal error distributions. LL_{trend}^j is a similar component relevant to abundance trends; it assumes normal error distributions. *MS* is the component that compares the time series of the average minke whale stomach contents estimated from observations to a model estimated term that is assumed to be proportional to the minke whale krill consumption rate. For each of the likelihood components (Equations 1.5 – 1.15 in Table 4), $\sigma_y^{j,a}$ is the CV of the observed abundance (or abundance trend) of species j in Region a in year(s) y, $N_y^{j,a}$ is the observed abundance of species j in Region a for the year y; similarly $\widehat{N}_y^{j,a}$ is the model-estimated abundance, $R_{y_1-y_2}^{j,a}$ is the observed ROI of species in Region a from year y_1 to y_2; similarly $R_{y_1-y_2}^{j,a}$ is the model-estimated ROI where

$$R_{y_1-y_2}^{j,a} = \left(\frac{N_{y_2}^{j,a}}{N_{y_1}^{j,a}}\right)^{\frac{1}{y_2-y_1}} - 1 \qquad (\text{similarly for } \widehat{R}_{y_1-y_2}^{j,a})$$

For Equations 1.16 – 1.17 in Table 4, the term $\dfrac{\left(B_y^a\right)^2}{(B^{m,a})^2 + \left(B_y^a\right)^2}$ is a modifier of how much of a whale's daily desired amount of krill it consumes, depending on how much krill is available,

following the form of Equation 1.1. This term is assumed to be proportional to Q_y^a, the weight of prey contents in the stomachs of minke whales for the available years in Region a, q^a is a constant of proportionality, and w^a is a weighting factor inversely proportional to the variance of the data about the relationship assumed (see Moosa, 2017).

Estimable Parameters and their Bounds

Chapter Eight of Moosa (2017) details how the initial parameter values and the bounds on the values for the estimable parameters were calculated or chosen. The primary parameters that are estimated when fitting to the data and the input parameters of the model are detailed in Table 5. Table 5 also describes some of the parameters calculated in the model fit using these estimated parameters. Another parameter that is calculated using the estimated parameters (and not discussed in Table 5) is the scaling factor q_a, which relates the average annual weight of prey contents in the stomachs of minke whales for the years for which such data (kindly provided by Dr. K. Konishi and Prof. L. Walløe) are available in Region a (Q_y^a) to the density-dependent growth term in the predator's dynamics equation (Equation 1.2).

Of the estimable parameters, the one that changes appreciably to that reported in Mori (2005) is the intrinsic krill growth rate (r^a). A modified version of the age-structured population krill model (Model 2) described in Butterworth *et al.* (1994) is used in Moosa (2017) to calculate the intrinsic growth rate. Another important change is in the specification of *M*, the effective annual natural mortality rate for krill (effective throughout the year). The *M* included in the Butterworth *et al.* (1994b) krill model was estimated from the age distribution of the krill population and incorporated the predation of krill by its predators. Mori (2005) treated the krill harvested by its main predators in the same way as the krill fishery. She assumed implicitly that none of the six main krill-predators that are modelled explicitly in her ecosystem model (which caused much of the natural predation on krill) are included in the 'predation' attributed to the krill's natural mortality.

However this is not that realistic as the predators that are being modelled explicitly would have contributed a large proportion to the natural mortality of krill. The krill dynamics equation (Equation 1.1) in the ecosystem model explicitly took predation by the six main krill-predators into account. As a result, Moosa (2017) assumes that a large proportion of the krill's natural mortality is from the consumption of krill by the main predators. Thus *M* is reduced to 0.2 from the one that is estimated from the age-structure of krill. The value of 0.2 is chosen as it is used frequently in multi-species models as a basal mortality. This is done in order to take into account the natural mortality of krill arising only from the predation of krill from the other krill-predators not considered in the ecosystem model.

Initially, all of the above estimable parameters were fixed to their calculated initial values. However, the model was unable to fit the data satisfactorily, so these parameters were all made estimable. Two parameters are fixed in order to assist with the model fit, namely M_h and λ_h.

Results

This section discusses the results of the model developed in Moosa (2017).

Base Case

Figures 2 and 3 compare the Region AI and Region PO population trajectories from the Base Case of Moosa (2017) and the Mori-Butterworth (2006) Reference Case respectively. There are some similarities between both models but also a number of differences. The most notable differences between the two sets of results are the absence of oscillations (especially in the krill biomass and minke population trajectory) and the much larger increase in krill abundance for the Mori-Butterworth Reference Case. The oscillations in the Base Case could be a result of setting the effective annual natural mortality rate of krill to a lower value compared to the approach adopted in Mori and Butterworth (2006). For Region AI (Figure 2) the main differences between both sets of results as estimated by the Base Case are the smaller "krill surplus" between 1920 and 2000 and the oscillations in the krill population trajectory, the larger initial equilibrium level for the fin whale population, the lower humpback whale abundance between 1910 and 1930, the faster increase rate in the humpback whale population from 1960 onwards, and the smaller crabeater seal abundance between 1960 and 2000. Mori (2005) stated that her model could be using the crabeater seals as a surrogate for other bird and fish species not included explicitly in her model. This is likely not the case as Moosa (2017) shows that krill-eating bird and fish species do not consume as much krill as the six species considered in the ecosystem model (except perhaps for squid, for which there is, unfortunately, a paucity of data). The effect of including the depensatory effect can be seen clearly in the fur seal population trajectory. For Region PO (Figure 3) the main differences between both sets of results as estimated by the Base Case are the oscillations in the krill biomass trajectory, the larger initial equilibrium level for both the fin and blue whale populations, the faster increase rate for blue whales from 1960 onwards, oscillations in the minke whale population trajectory, the larger abundance for the humpback whale population from 1960 onwards, and the larger initial equilibrium level and oscillations in the crabeater population trajectory. Both the Base Case and the Mori-Butterworth Reference Case estimate delays in the minke population trends for Region PO compared to Region AI. This is probably an effect of the heavy whaling being focused initially in Region AI.

Possible explanations for the differences between the two sets of results are discussed in Moosa (2017).

Figure 4 compares the humpback whale population trajectories from the Base Case to those from the IWC models. Overall, the Base Case mirrors the IWC trajectories reasonably although it estimates a lower initial equilibrium value, an overall lower abundance between 1915 and 1940, and a faster increase rate from 1960 onwards. Figure 5 compares the minke whale population trajectories from the Base Case to the results from the SCAA model in Punt (2014). Overall, both models show an increase in abundance followed by a decrease with the Base Case estimating a larger minke abundance, and reaching its maximum abundance later, though there are also some not insubstantial differences between the pairs of trajectories in absolute terms.

Figure 6 shows the Base Case's fit to the minke stomach data (Q_y^a) determined from observations. For Region AI, the model matches an overall decrease in the weight of prey in the minke stomach contents. However, for Region PO, the model fit shows a delay – the model only matches a decrease in the weight of prey in the stomach contents from 2005 onwards. This could be because the minke oscillations in Region PO are starting too late in the Base Case. Declines in the weight of prey in the stomach contents are plausibly reactions to less food being available for minke whales as other previously heavily exploited whale populations recover. The weight of prey in the minke stomach contents is predicted to oscillate until 2200 for Region AI and until 2100 for Region PO. This behavior is similar to the krill and minke whale projected trajectories under zero catch, as shown in Figure 7.

The future projections for krill and its main predators are shown in Figure 7. Figure 7 reflects large amplitude oscillations in the krill, minke, fur seal and crabeater populations. In contrast, the fin and blue whale population exhibit steady recovery behaviour i.e. no oscillations. However, the blue whale population in Region AI is predicted to reach only two-thirds of its initial equilibrium level by the year 2500. Oscillations are also reflected in the humpback population but they are of much smaller amplitudes compared to those in the krill, minke, fur seal and crabeater projected trajectories. The fur seal population is predicted to reach a maximum abundance of 18 million. This is unrealistically as there are space limitations on the beaches which fur seals use for breeding, which have not been taken into account in the model.

Future Work

A number of proposed improvements to the model are suggested in Moosa (2017). These improvements include:

- the inclusion of a space limitation term for the fur seals in the model so as to restrict their population from increasing to unrealistically high values,
- the consideration of a set of differently defined regions as this might possibly better represent the minke abundance trends and population trajectories,
- variation of the effective annual natural mortality rate of krill, partcularly as this is likely causing the oscillations in the krill dynamics,
- variation of the bounds imposed on K_a,
- variation of the proportion of fin whales assumed to feed south of 60°S, and
- other improvements mentioned in Moosa (2017) concerning the precision, input data and technical aspects of the model.

Conclusion

The updated model presented in Moosa (2017) provides interesting advances and insights, but requires further development before it might be considered sufficiently reliable for providing advice for the regulation and implementation of suitable conservation and harvesting strategies in the Antarctic.

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Table 1: *The sources of the information, annual per capita consumption of krill (mt) and the total consumption of krill by weight (mt) by the krill-predators as used and estimated in Moosa (2017). The highlighted rows indicate the main krill-predators that merited inclusion in the ecosystem model developed in Moosa (2017).*

	Diet information	Average body weight	Duration of the feeding periods	Daily krill intake	Annual per capita consumption of krill (mt)	Year of abundance estimate	Abundance (Number)	Total krill consumption x 10³ (mt)	Total krill consumption in 1780 x 10³ (mt)
Blue whale	Nemoto (1970)	Trites and Pauly (1998)	Kasamatsu (2000)	Method suggested by T. Tamura	490.8	1997/98	2 206	1 083	97 573
Fin whale					310.4	1997/98	38 185	11 853	99 648
Humpback whale					200.7	2014/15	97 188	19 506	23 637
Minke whale	Tamura and Konishi (2014)				63.2	1997/98	469 867	29 696	23 286
Antarctic fur seal	Barlow *et al.* (2002)		McCann (1980), Laws (1984)		1.77	1990/91	1 550 000	2 744	2 265
Crabeater seal	Southwell *et al.* (2012)	Laws (1977)	Øritsland (1977), Laws (1984)		4.45	2000/01	7 719 714	34 353	21 456
Leopard seal			Knox (2007)		4.02	2000/01	35 500	143	N/A
Adélie penguin	Ratcliffe and Trathan (2011)	Nagy and Obst (1992)	Davis (1982)	Nagy and Obst (1992)	0.06	2013/14	3 655 698	216	N/A
Marbled rockcod	Kock *et al.* (2012)	see Moosa (2017)	It is assumed that they feed throughout the year	Method suggested by T. Tamura	0.03	-	1 477 111	44	N/A
Mackerel icefish					8.07 x 10⁻⁶	2014/15	32 102 million	259	N/A

Table 2: *Table comparing the observed and model-estimated abundance estimates for the main krill-predators in Mori (2005) and Moosa (2017).*

Species		Observed Estimate in Mori (2005)	Model Estimate in Mori (2005)		Observed Estimate in Moosa (2017)	Model Estimate in Moosa (2017)	% Difference between Model Estimates from Mori (2005) and Moosa (2017)
Blue whale	$N_{2000}^{b,AI}$	1 104	1 109	$N_{1997/98}^{b,AI}$	853	876	-21.09
	$N_{2000}^{b,PO}$	762	758	$N_{1997/98}^{b,PO}$	1 353	1 308	72.56
Fin whale	$N_{1997}^{f,AI}$	10 591	10 649	$N_{1997/98}^{f,AI}$	10 591	10 925	2.59
	$N_{1997}^{f,PO}$	27 594	27 361	$N_{1997/98}^{f,PO}$	27 594	24 741	-9.58
Humpback whale	$N_{1997}^{h,AI}$	5 044	5 046	$N_{2014/15}^{h,AI}$	66 182	67 117	1 230.10
	$N_{1997}^{h,PO}$	4 868	4 859	$N_{2014/15}^{h,PO}$	31 893	31 882	556.14
Minke whale	$N_{1985}^{m,AI}$	327 369	325 963	$N_{1997/98}^{m,AI}$	183 256	197 010	-39.56
	$N_{1985}^{m,PO}$	420 572	420 598	$N_{1997/98}^{m,PO}$	286 611	283 274	-32.65
Antarctic fur seal	$N_{1930}^{s,AI}$	100	175	$N_{1930/31}^{s,AI}$	100	102	-41.71
	$N_{1975}^{s,AI}$	369 000	262 422	$N_{1975/76}^{s,AI}$	369 000	379 573	44.64
	$N_{1990}^{s,AI}$	1 550 000	1 234 240	$N_{1990/91}^{s,AI}$	1 550 000	1 554 930	25.98
Crabeater seal	$N_{2000}^{c,AI}$	4 000 000	11 794 500	$N_{2000/01}^{c,AI}$	3 910 212	5 648 260	-52.11
	$N_{2000}^{c,PO}$	4 000 000	3 753 920	$N_{2000/01}^{c,PO}$	3 809 502	3 092 750	-17.61

Table 3: *Table comparing the observed and model-estimated trend estimates for the main krill-predators in Mori (2005) and Moosa (2017). Note, the blue whales are treated differently.*

Species		Observed Estimate in Mori (2005)	Model Estimate in Mori (2005)		Observed Estimate in Moosa (2017)	Model Estimate in Moosa (2017)
Blue whale	N^b_{1981}	546	N/A	$N^b_{1980/81}$	592	1 440
	N^b_{1988}	680		$N^b_{1987/88}$	686	1 640
	N^b_{1996}	1 891		$N^b_{1997/98}$	2 249	2 184
Fin whale		N/A		$R^{f,AI}_{1995/96-2007/08}$	0.116	0.026
				$R^{f,PO}_{1996/97-2008/09}$		0.027
Humpback whale	$R^{h,AI}_{1977-1991}$	0.11	0.09	$R^{h,AI}_{2010/11-2014/15}$	0.025	0.008
	$R^{h,PO}_{1981-1996}$	0.12	0.08	$R^{h,PO}_{2010/11-2014/15}$	0.058	0.034
Minke whale	$R^{m,AI}_{1970-2000}$	-0.024	-0.017	$R^{m,AI}_{1945/46-1967/68}$	0.013	0.016
				$R^{m,AI}_{1968/69-1987/88}$	-0.029	-0.030
				$R^{m,AI}_{1988/89-2003/04}$	0.010	0.006
	$R^{m,PO}_{1970-2000}$	-0.024	-0.003	$R^{m,PO}_{1945/46-1967/68}$	0.020	0.013
				$R^{m,PO}_{1968/69-1987/88}$	-0.030	-0.020
				$R^{m,PO}_{1988/89-2003/04}$	-0.003	0.006
Antarctic fur seal	$R^{s,AI}_{1957-1972}$	0.17	0.19	$R^{s,AI}_{1957/58-1971/72}$	0.168	0.170
	$R^{s,AI}_{1976-1990}$	0.1	0.17	$R^{s,AI}_{1976/77-1989/90}$	0.098	0.098
	$R^{s,AI}_{1990-1999}$	0.1	0.10	$R^{s,AI}_{1990/91-1998/99}$	0.098	0.116

Model Section	Equation	Number
Krill Dynamics	$$B_{y+1}^{a} = B_y^a + r^a B_y^a \left(1 - \left(\frac{B_y^a}{K_a}\right)\right) - \sum_j \frac{\lambda^j (B_y^a)^2 N_y^{j,a}}{(B^{j,a})^2 + (B_y^a)^2} - \frac{\lambda^s (B_y^a)^2 \left(\dfrac{N_y^{s,a}}{1 + e^{\left(-\frac{N_y^{s,a}-N\#}{d}\right)}}\right)}{(B^{s,a})^2 + (B_y^a)^2}$$	1.1
Predator Dynamics (excl. Antarctic fur seals)	$$N_{y+1}^{j,a} = N_y^{j,a} + \frac{\mu^j N_y^{j,a} (B_y^a)^2}{(B^{j,a})^2 + (B_y^a)^2} - M^j N_y^{j,a} - \eta^{j,a} (N_y^{j,a})^2 - C_y^{j,a}$$	1.2
Antarctic Fur Seal Dynamics	$$N_{y+1}^{s,a} = N_y^{s,a} + \frac{\mu^s (B_y^a)^2 \left(\dfrac{N_y^{s,a}}{1 + e^{\left(-\frac{N_y^{s,a}-N\#}{d}\right)}}\right)}{(B^{s,a})^2 + (B_y^a)^2} - M^s N_y^{s,a} - \eta^{s,a} (N_y^{s,a})^2 - C_y^{s,a}$$	1.3
Complete Negative Likelihood Function	$$-\ln L = LL_{abund}^b + LL_{trend}^b + LL_{abund}^m + LL_{trend}^m + LL_{abund}^h + LL_{trend}^h + LL_{abund}^f + LL_{trend}^f + LL_{abund}^s \\ + LL_{trend}^s + LL_{abund}^c + MS^{AI} + MS^{PO}$$	1.4
Blue Whale Likelihood Component	$$LL_{abund}^b = \frac{\left(\ln N_{1997/98}^{b,AI} - \ln \widehat{N}_{1997/98}^{b,AI}\right)^2}{2 \left(\sigma_{1997/98}^{b,AI}\right)^2} + \frac{\left(\ln N_{1997/98}^{b,PO} - \ln \widehat{N}_{1997/98}^{b,PO}\right)^2}{2 \left(\sigma_{1997/98}^{b,PO}\right)^2}$$	1.5

Blue Whale Likelihood Component	$$LL_{trend}^b = \sum_{y=1}^{n}\left[\ln \sigma_y + \frac{1}{2\sigma_y^2}\left(\ln N_y^{b,obs} - \frac{\sum_{y=1}^{n}\frac{1}{\sigma_y^2}\left(\ln N_y^{b,obs} - \ln \widehat{N}_y^b\right)}{\sum_{y=1}^{n}\frac{1}{\sigma_y^2}} - \ln \widehat{N}_y^b\right)^2\right]$$ where the summation is over the years for which circumpolar abundance estimates are available.	1.6
Minke Whale Likelihood Component	$$LL_{abund}^m = \frac{\left(\ln N_{1997/98}^{m,AI} - \ln \widehat{N}_{1997/98}^{m,AI}\right)^2}{2\left(\sigma_{1997/98}^{m,AI}\right)^2} + \frac{\left(\ln N_{1997/98}^{m,PO} - \ln \widehat{N}_{1997/98}^{m,PO}\right)^2}{2\left(\sigma_{1997/98}^{m,PO}\right)^2}$$	1.7
	$$LL_{trend}^m = \frac{1}{2}(\vec{y}_{obs} - \vec{y}_{mod})^T V^{-1}(\vec{y}_{obs} - \vec{y}_{mod})$$ where $$\vec{y}_{obs} = \left(R_{1945/46 - 1967/68}^{m,AI}, R_{1968/69 - 1987/88}^{m,AI}, R_{1988/89 - 2003/04}^{m,AI}, R_{1945/46 - 1967/68}^{m,PO}, R_{1968/69 - 1987/88}^{m,PO}, R_{1988/89 - 2003/04}^{m,PO}\right)$$ $$\vec{y}_{mod} = \left(\widehat{R}_{1945/46 - 1967/68}^{m,AI}, \widehat{R}_{1968/69 - 1987/88}^{m,AI}, \widehat{R}_{1988/89 - 2003/04}^{m,AI}, \widehat{R}_{1945/46 - 1967/68}^{m,PO}, \widehat{R}_{1968/69 - 1987/88}^{m,PO}, \widehat{R}_{1988/89 - 2003/04}^{m,PO}\right)$$ and V^{-1} is the inverse variance-covariance matrix associated with the minke trend estimates (Punt, 2014)	1.8
Humpback Whale Likelihood Component	$$LL_{abund}^h = \frac{\left(\ln N_{2014/15}^{h,AI} - \ln \widehat{N}_{2014/15}^{h,AI}\right)^2}{2\left(\sigma_{2014/15}^{h,AI}\right)^2} + \frac{\left(\ln N_{2014/15}^{h,PO} - \ln \widehat{N}_{2014/15}^{h,PO}\right)^2}{2\left(\sigma_{2014/15}^{h,PO}\right)^2}$$	1.9
	$$LL_{trend}^h = \frac{\left(R_{2010/11 - 2014/15}^{h,AI} - \widehat{R}_{2010/11 - 2014/15}^{h,AI}\right)^2}{2\left(\sigma_{2010/11 - 2014/15}^{h,AI}\right)^2} + \frac{\left(R_{2010/11 - 2014/15}^{h,PO} - \widehat{R}_{2010/11 - 2014/15}^{h,PO}\right)^2}{2\left(\sigma_{2010/11 - 2014/15}^{h,PO}\right)^2}$$	1.10

Fin Whale Likelihood Component	$$LL_{abund}^f = \frac{\left(\ln N_{1997/98}^{f,AI} - \ln \widehat{N}_{1997/98}^{f,AI}\right)^2}{2\left(\sigma_{1997/98}^{f,AI}\right)^2} + \frac{\left(\ln N_{1997/98}^{f,PO} - \ln \widehat{N}_{1997/98}^{f,PO}\right)^2}{2\left(\sigma_{1997/98}^{f,PO}\right)^2}$$	1.11
	$$LL_{trend}^f = \frac{\left(R_{1995/96-2007/08}^{f,AI} - \widehat{R}_{1995/96-2007/08}^{f,AI}\right)^2}{2\left(\sigma_{1995/96-2007/08}^{f,AI}\right)^2} + \frac{\left(R_{1996/97-2008/09}^{f,PO} - \widehat{R}_{1996/97-2008/09}^{f,PO}\right)^2}{2\left(\sigma_{1996/97-2008/09}^{f,PO}\right)^2}$$	1.12
Crabeater Seal Likelihood Component	$$LL_{abund}^c = \frac{\left(\ln N_{2000/01}^{c,AI} - \ln \widehat{N}_{2000/01}^{c,AI}\right)^2}{2\left(\sigma_{2000/01}^{c,AI}\right)^2} + \frac{\left(\ln N_{2000/01}^{c,PO} - \ln \widehat{N}_{2000/01}^{c,PO}\right)^2}{2\left(\sigma_{2000/01}^{c,PO}\right)^2}$$	1.13
Antarctic Fur Seal Likelihood Component	$$LL_{abund}^s = \frac{\left(\ln N_{1930/31}^{s,AI} - \ln \widehat{N}_{1930/31}^{s,AI}\right)^2}{2\left(\sigma_{1930/31}^{s,AI}\right)^2} + \frac{\left(\ln N_{1975/76}^{s,AI} - \ln \widehat{N}_{1975/76}^{s,AI}\right)^2}{2\left(\sigma_{1975/76}^{s,AI}\right)^2} + \frac{\left(\ln N_{1990/91}^{s,AI} - \ln \widehat{N}_{1990/91}^{s,AI}\right)^2}{2\left(\sigma_{1990/91}^{s,AI}\right)^2}$$	1.14
	$$LL_{trend}^s = \frac{\left(R_{1957/58-1971/72}^{s,AI} - \widehat{R}_{1957/58-1971/72}^{s,AI}\right)^2}{2\left(\sigma_{1957/58-1971/72}^{s,AI}\right)^2} + \frac{\left(R_{1976/77-1989/90}^{s,AI} - \widehat{R}_{1976/77-1989/90}^{s,AI}\right)^2}{2\left(\sigma_{1976/77-1989/90}^{s,AI}\right)^2} \\ + \frac{\left(R_{1990/91-1998/99}^{s,AI} - \widehat{R}_{1990/91-1998/99}^{s,AI}\right)^2}{2\left(\sigma_{1990/91-1998/99}^{s,AI}\right)^2}$$	1.15
Minke Stomach Content Likelihood Component	$$MS^{AI} = \sum_y w^{AI} \left[Q_y^{AI} - q^{AI} \frac{\left(B_y^{AI}\right)^2}{(B^{m,AI})^2 + \left(B_y^{AI}\right)^2}\right]^2$$	1.16
	$$MS^{PO} = \sum_y w^{PO} \left[Q_y^{PO} - q^{PO} \frac{\left(B_y^{PO}\right)^2}{(B^{m,PO})^2 + \left(B_y^{PO}\right)^2}\right]^2$$	1.17

Table 5: *Table describing the some of the variables used in the model developed in Moosa (2017).Terms in square brackets were fixed to their reported value so as to assist in the model fit.*

Parameter		Description	Type in Moosa (2017)	Base-Case Estimate in Mori and Butterworth (2006)	Base-Case Estimate in Moosa (2017)
$N_{1780}^{j,a}$	$N_{1780}^{b,AI}$	Number of blue whales in Region AI in 1780	Estimated	162 332	162 532
	$N_{1780}^{b,PO}$	Number of blue whales in Region PO in 1780		26 861	36 723
	$N_{1780}^{m,AI}$	Number of minke whales in Region AI in 1780		47 155	68 422
	$N_{1780}^{m,PO}$	Number of minke whales in Region PO in 1780		271 720	300 000
	$N_{1780}^{f,AI}$	Number of fin whales in Region AI in 1780		151 505	221 724
	$N_{1780}^{f,PO}$	Number of fin whales in Region PO in 1780		87 187	99 308
	$N_{1780}^{h,AI}$	Number of humpback whales in Region AI in 1780		71 589	71 206
	$N_{1780}^{h,PO}$	Number of humpback whales in Region PO in 1780		47 095	46 567
	$N_{1780}^{s,AI}$	Number of Antarctic fur seals in Region AI in 1780		2 898 590	2 934 594
	$N_{1780}^{c,AI}$	Number of crabeater seals in Region AI in 1780		241 045	1 279 810
	$N_{1780}^{c,PO}$	Number of crabeater seals in Region PO in 1780		733 511	1 887 084
M_j	M_b	Annual mortality proportion for blue whales	Estimated	0.03	0.04
	M_m	Annual mortality proportion for minke whales		0.04	0.09
	M_f	Annual mortality proportion for fin whales		0.05	0.03
	M_h	Annual mortality proportion for humpback whales	Fixed	0.08	[0.03]
	M_s	Annual mortality proportion for Antarctic fur seals	Estimated	0.07	0.19
	M_c	Annual mortality proportion for crabeater seals		0.07	0.07
λ_j	λ_b	Max. annual per capita consumption of krill by blue whales	Estimated	450.62	165.93
	λ_m	Max. annual per capita consumption of krill by minke whales		32.13	21.06
	λ_f	Max. annual per capita consumption of krill by fin whales		[110.40]	103.60
	λ_h	Max. annual per capita consumption of krill by	Fixed	108.00	[74.35]

|					
		humpback whales			
λ_j	λ_s	Max. annual per capita consumption of krill by Antarctic fur seals		2.71	0.68
	λ_c	Max. annual per capita consumption of krill by crabeater seals		5.51	5.51
μ_j	μ_b	Max. annual female birth rate for blue whales	Estimated	0.16	0.29
	μ_m	Max. annual female birth rate for minke whales		0.20	0.31
	μ_f	Max. annual female birth rate for fin whales		[0.16]	0.25
	μ_h	Max. annual female birth rate for humpback whales		[0.18]	0.15
	μ_s	Max. annual female birth rate for Antarctic fur seals		0.28	0.87
	μ_c	Max. annual female birth rate for crabeater seals		0.24	0.20
r^a	r^{AI}	Intrinsic growth rate of krill for Region AI		0.40	0.22
	r^{PO}	Intrinsic growth rate of krill for Region PO		0.58	0.31
$B^{b,a}$	$B^{b,AI}$	Krill biomass when krill consumption by blue whales decreases to half its max. level in Region AI		1.70×10^8	1.70×10^8
	$B^{b,PO}$	Krill biomass when krill consumption by blue whales decreases to half its max. level in Region PO		7.00×10^7	7.00×10^7
$\eta_{j,a}$	$\eta_{b,AI}$	Governs density-dependence of natural mortality and/or birth rate for blue whales in Region AI	Input	4.00×10^{-8}	4.001×10^{-8}
	$\eta_{b,PO}$	Governs density-dependence of natural mortality and/or birth rate for blue whales in Region PO		1.00×10^{-6}	1.000×10^{-6}
	$\eta_{m,AI}$	Governs density-dependence of natural mortality and/or birth rate for minke whales in Region AI		3.00×10^{-7}	3.000×10^{-7}
	$\eta_{m,PO}$	Governs density-dependence of natural mortality and/or birth rate for minke whales in Region PO		2.00×10^{-7}	2.000×10^{-7}
	$\eta_{f,AI}$	Governs density-dependence of natural mortality and/or birth rate for fin whales in Region AI		4.00×10^{-8}	3.999×10^{-8}
	$\eta_{f,PO}$	Governs density-dependence of natural mortality and/or birth rate for fin whales in Region PO		7.00×10^{-8}	7.000×10^{-8}
	$\eta_{h,AI}$	Governs density-dependence of natural mortality and/or birth rate for humpback whales in Region AI		1.25×10^{-6}	1.249×10^{-6}

	$\eta_{h,PO}$	Governs density-dependence of natural mortality and/or birth rate for humpback whales in Region PO	Input	1.50×10^{-6}	1.500×10^{-6}
	$\eta_{s,AI}$	Governs density-dependence of natural mortality and/or birth rate for Antarctic fur seals in Region AI		3.50×10^{-9}	3.200×10^{-9}
	$\eta_{c,AI}$	Governs density-dependence of natural mortality and/or birth rate for crabeater seals in Region AI		7.00×10^{-9}	7.001×10^{-9}
	$\eta_{c,PO}$	Governs density-dependence of natural mortality and/or birth rate for crabeater seals in Region PO		6.00×10^{-9}	7.001×10^{-9}
B^a_{1780}	B^{AI}_{1780}	Krill biomass for Region AI for the year 1780	Calculated	9.26×10^{7}	7.90×10^{7}
	B^{PO}_{1780}	Krill biomass for Region PO for the year 1780		5.21×10^{7}	4.38×10^{7}
K_a	K_{AI}	Krill carrying capacity, in the absence of predators in Region AI		8.22×10^{8}	1.87×10^{9}
	K_{PO}	Krill carrying capacity, in the absence of predators in Region PO		1.25×10^{8}	1.86×10^{9}
$B^{m,a}$	$B^{m,AI}$	Krill biomass when krill consumption by minke whales decreases to half its max. level in Region AI		1.45×10^{8}	1.02×10^{8}
	$B^{m,PO}$	Krill biomass when krill consumption by minke whales decreases to half its max. level in Region PO		5.29×10^{7}	4.37×10^{7}
$B^{f,a}$	$B^{f,AI}$	Krill biomass when krill consumption by fin whales decreases to half its max. level in Region AI		1.28×10^{8}	1.83×10^{8}
	$B^{f,PO}$	Krill biomass when krill consumption by fin whales decreases to half its max. level in Region PO		1.79×10^{7}	1.04×10^{8}
$B^{h,a}$	$B^{h,AI}$	Krill biomass when krill consumption by humpback whales decreases to half its max. level in Region AI		2.33×10^{7}	3.90×10^{7}
	$B^{h,PO}$	Krill biomass when krill consumption by humpback whales decreases to half its max. level in Region PO		2.31×10^{7}	3.02×10^{7}
$B^{s,a}$	$B^{s,AI}$	Krill biomass when krill consumption by Antarctic fur seals decreases to half its max. level in Region AI		1.46×10^{8}	1.44×10^{8}
$B^{c,a}$	$B^{c,AI}$	Krill biomass when krill consumption by crabeater seals decreases to half its max. level in Region AI		1.34×10^{8}	9.80×10^{7}
	$B^{c,PO}$	Krill biomass when krill consumption by crabeater seals decreases to half its max. level in Region PO		7.34×10^{7}	5.20×10^{7}
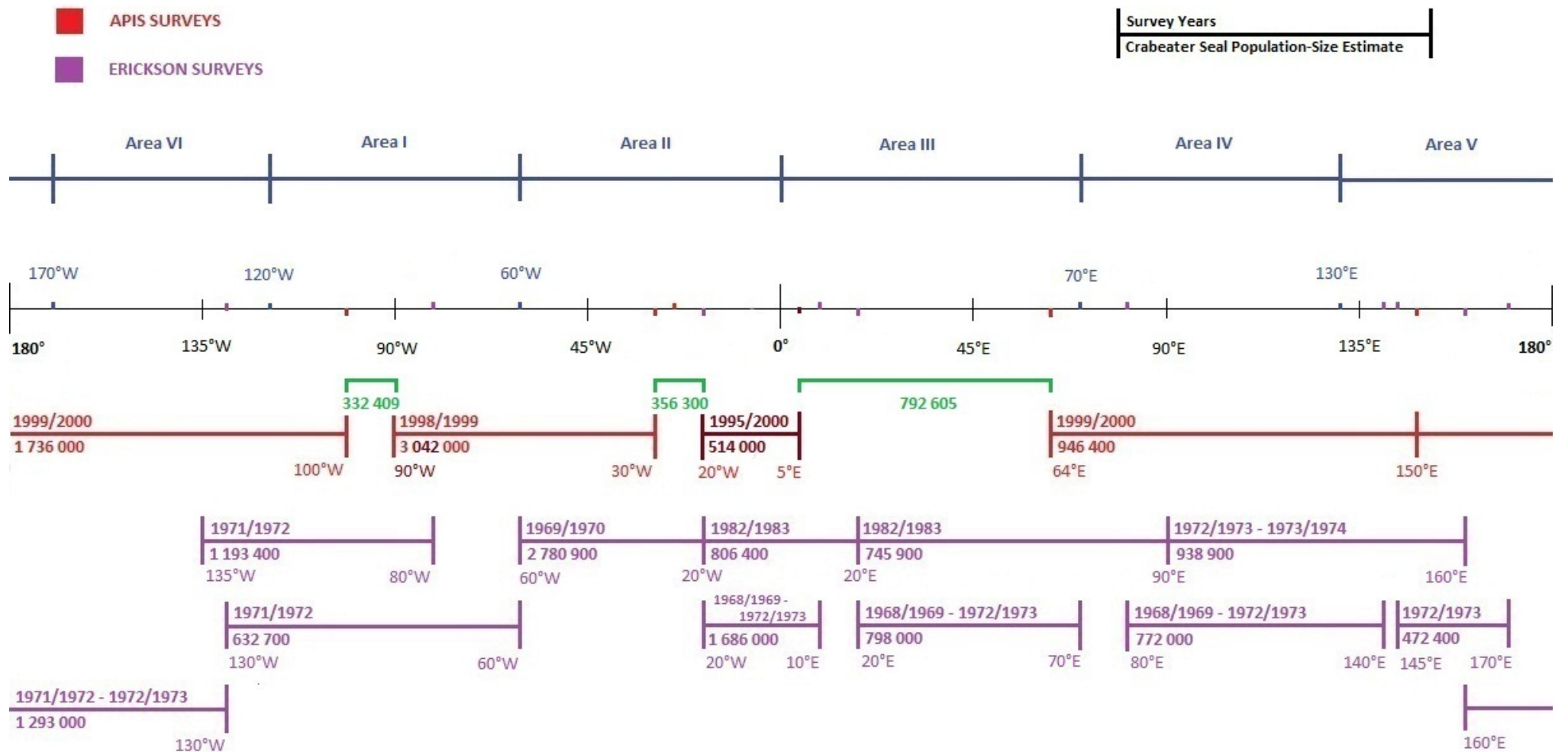
Figure 1: A **map of crabeater seal abundance estimates from the Erickson and APIS surveys, in relation to the IWC Management Areas.**
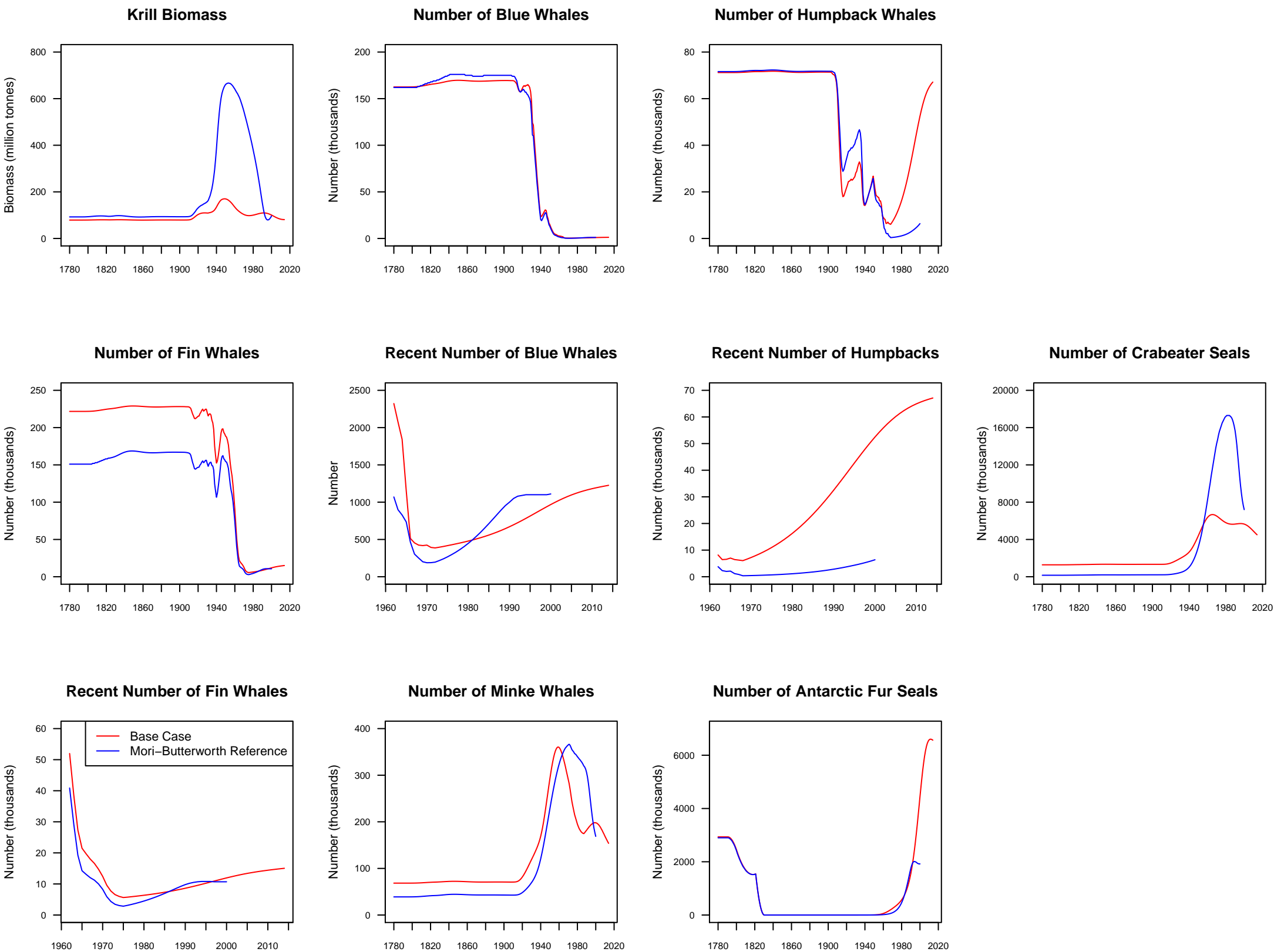
Figure 2: A comparison of the population trajectories of krill and its main predators for the Base Case and the Mori-Butterworth (2006) Reference Case for **Region AI.**
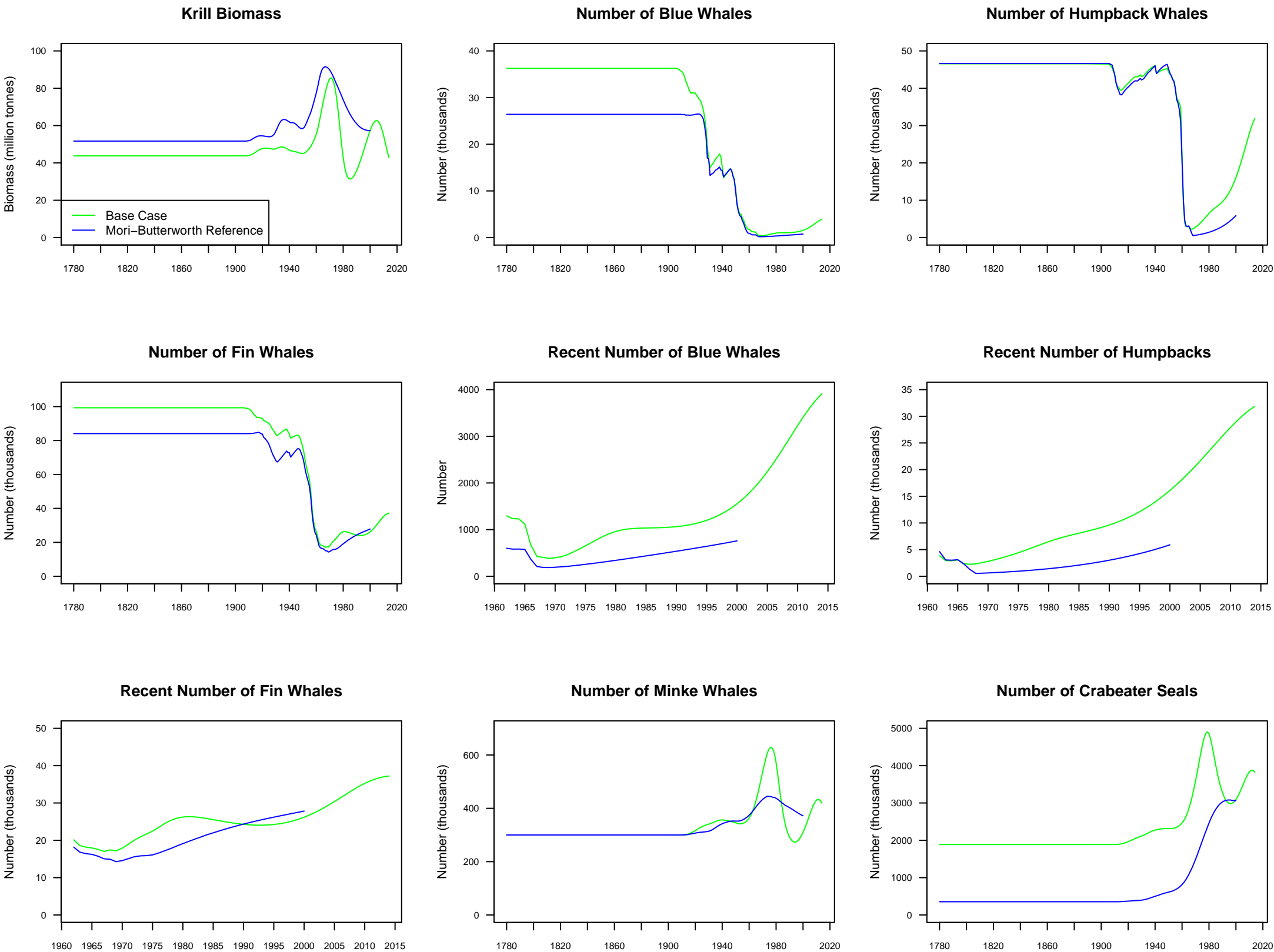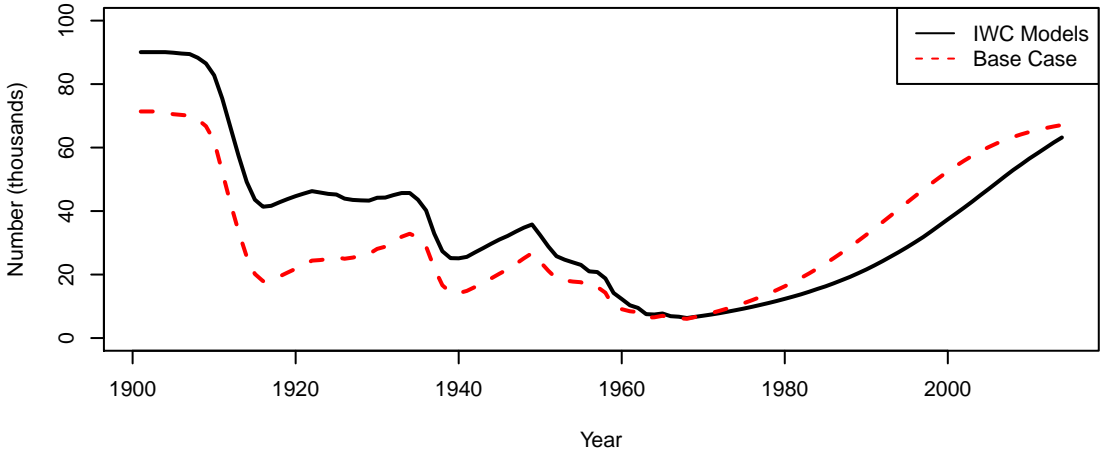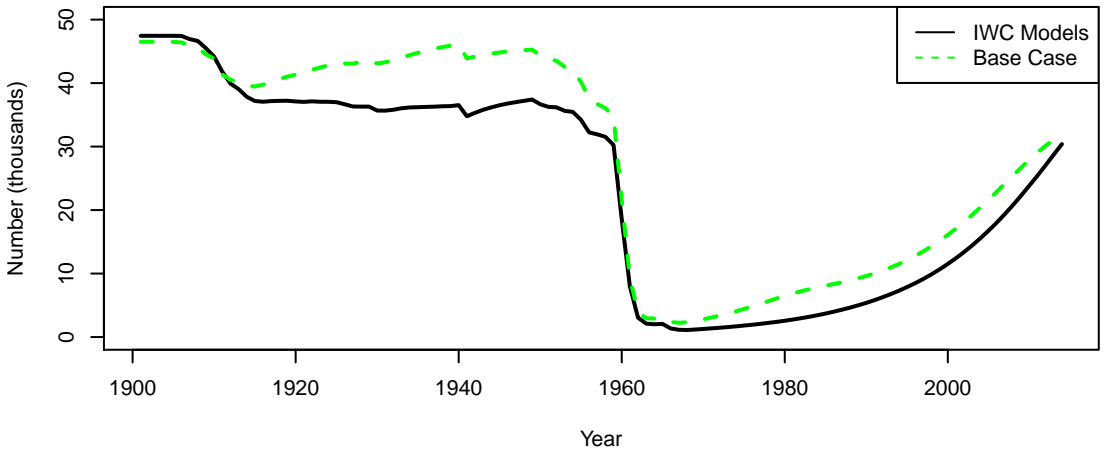
Figure 3: A comparison of the population trajectories of krill and its main predators for the Base Case and the Mori-Butterworth (2006) Reference Case for **Region PO.**

Figure 4: Comparison between the humpback whale population trajectories for the Base Case and from the IWC models.

Number of Minke Whales in Region AI
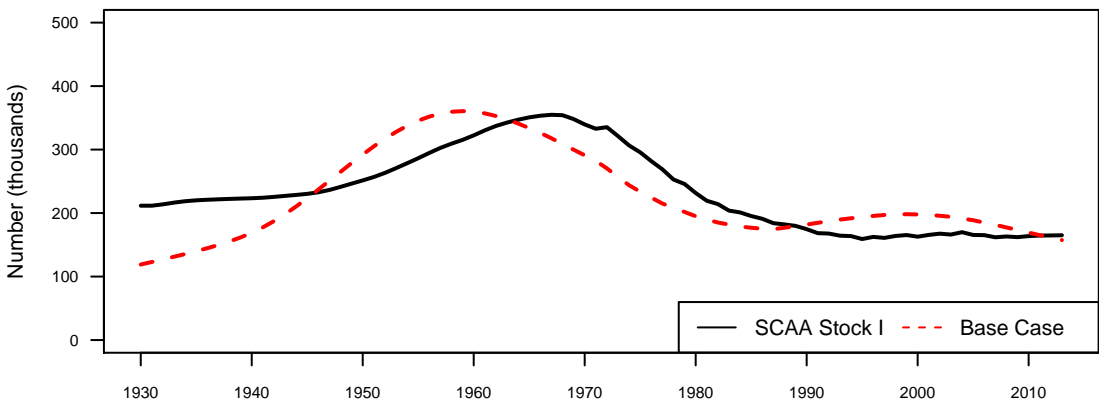
Number of Minke Whales in Region PO
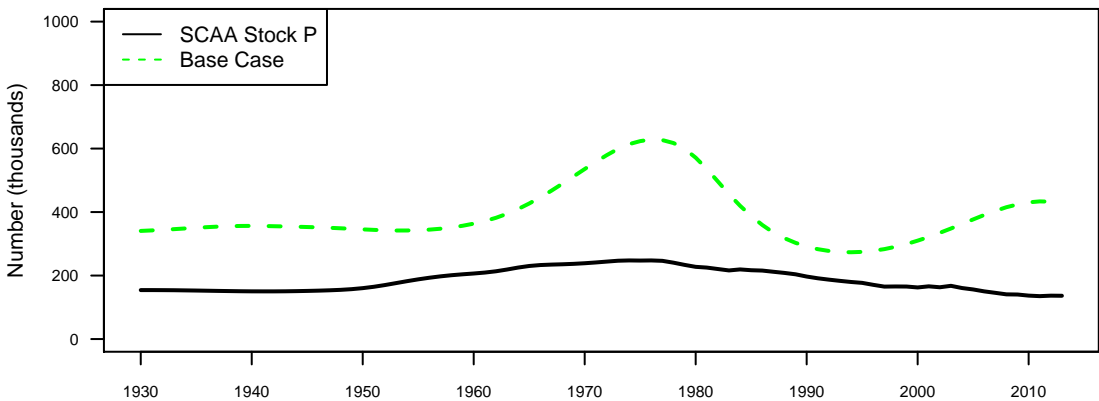
Total Number of Minke Whales
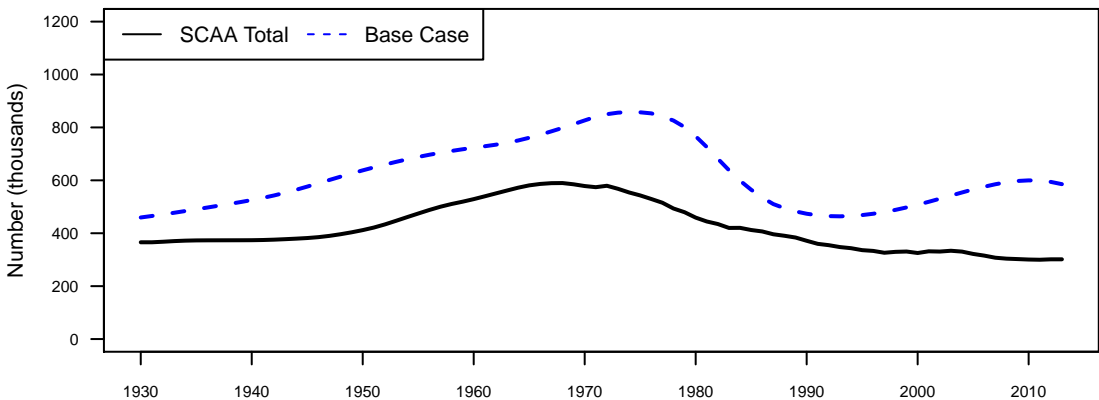
Figure 5: Comparison between the minke whale population trajectories for the Base Case and for Punt's (2014) SCAA model
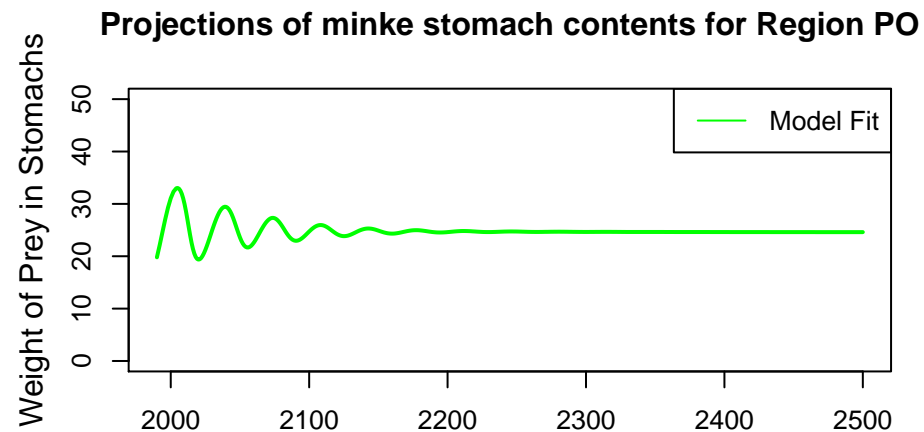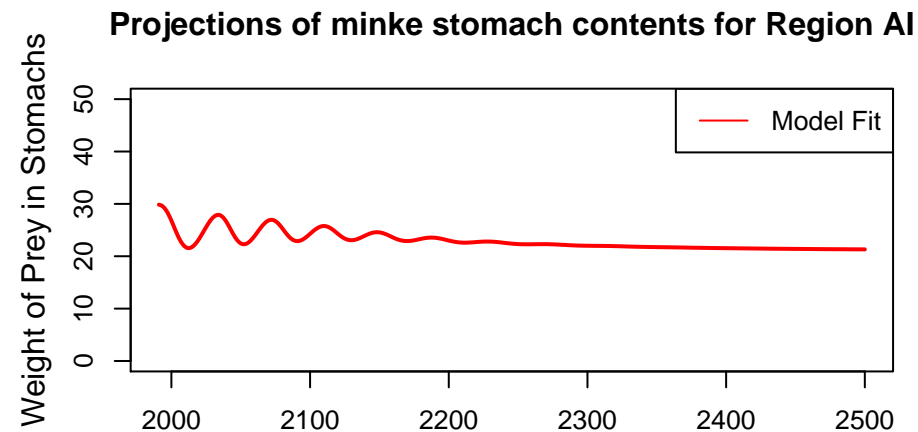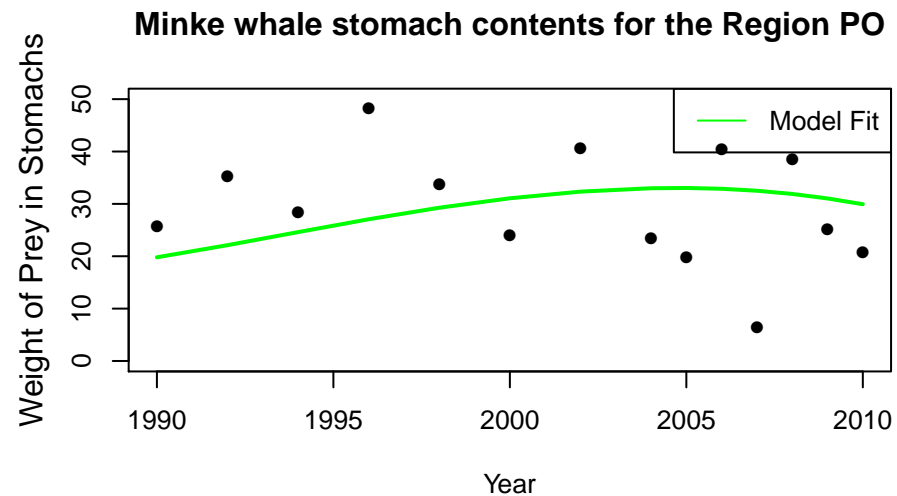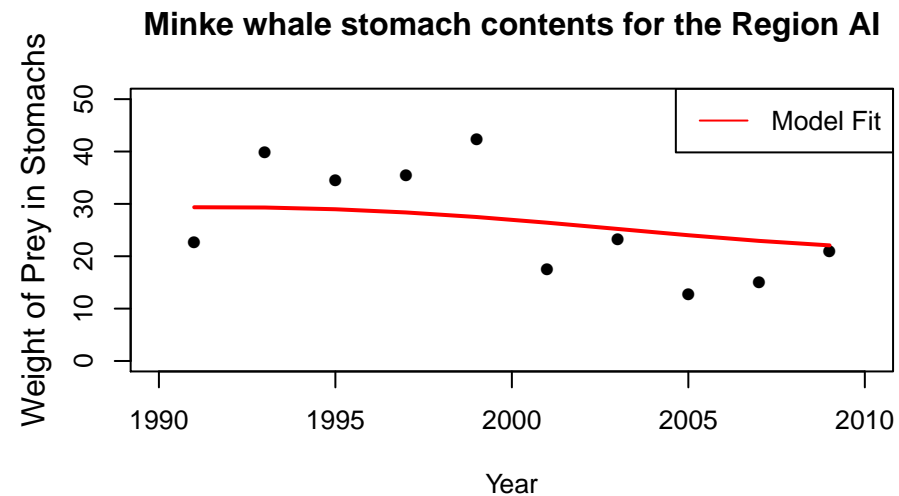
Figure 6: The Base Case model fits to the observed minke stomach content data for Regions AI and PO and their projected future trajectories (up to the year 2500), assuming zero catches for all species after the year 2014.
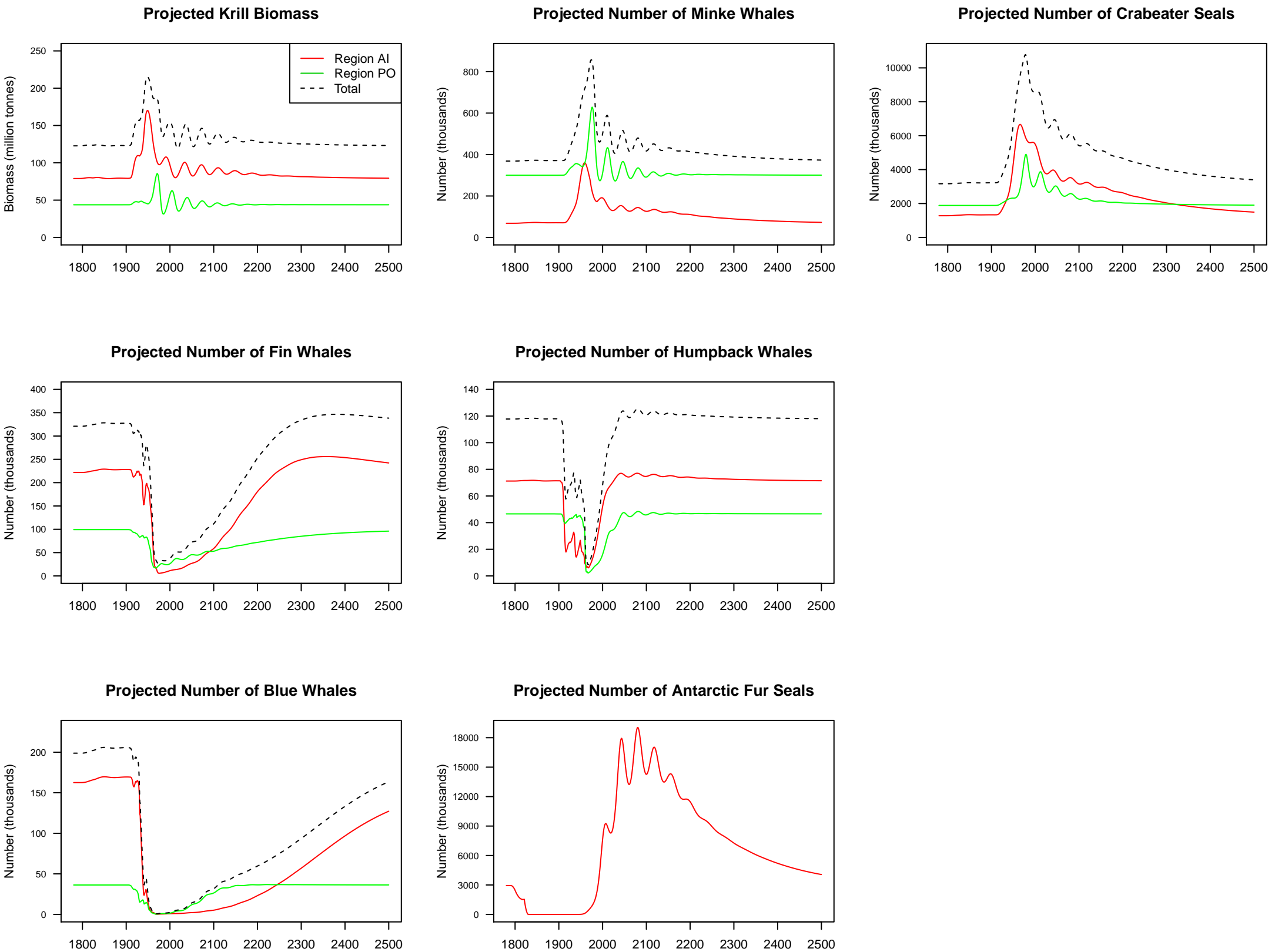
Figure 7: The Base Case population model projections for future trajectories (up to the year 2500) for krill and its main predators in the Antarctic, assuming zero catches for all species after 2014.

Appendix

The main differences between the framework for and inputs to the Tulloch *et al.* (2017) model, the Mori-Butterworth (2006) model and the Moosa (2017) model are summarized in Table A.1 below.

Table A.1: *Table showing the differences in framework and input data for Tulloch et al. (2017), Mori and Butterworth (2006) and Moosa (2017). The **bold numbers** in the information concerning the survey data sources indicate the last year of the data considered.*

	Tulloch *et al.* (2017)	**Mori-Butterworth (2006)**	**Moosa (2017)**
Years considered in model	1890 until present	1700 until 2000	1700/01 until 2014/15
Latitudinal coverage	Tropics = 0° - 40°S Polar = south of 40°S	South of 60°S	South of 60°S
Longitudinal stratification	Area A = IWC Areas II, III and IV Area P = IWC Areas V, VI and I	Region A = IWC Areas II, III and IV Region P = IWC Areas V, VI and I	Region AI = IWC Areas II, III and IV Region PO = IWC Areas V, VI and I
Species included in model	Krill, **copepods**, blue whales, fin whales, humpback whales, minke whales and **southern right whales**	Krill, **Antarctic fur seals, crabeater seals**, blue whales, fin whales, humpback whales and minke whales	Krill, **Antarctic fur seals, crabeater seals,** blue whales, fin whales, humpback whales and minke whales
Population component modeled	Females only	Males and females	Males and females
Blue whale survey data sources*	Branch and Rademeyer (2003), Reilly *et al.* (2008a), Rademeyer *et al.* (2003) ***[2000/01]***	Rademeyer *et al.* (2003) ***[2000/01]***	Branch (2007) ***[2003/04]***
Fin whale survey data sources*	IWC (1995), IWC (1996), Branch and Butterworth (2001a), Mori and Butterworth (2006) ***[1997/98]***	Branch and Butterworth (2001a), Butterworth and Geromont (1995) ***[1997/98]***	Branch and Butterworth (2001a), see Moosa (2017) ***[1997/98]***
Humpback whale survey data sources*	Branch and Butterworth (2001a), Branch (2006), Reilly *et al.* (2008b) ***[2008]***	Branch and Butterworth (2001a) ***[1997/98]***	Jackson *et al.* (2015), see Moosa (2017) ***[2014/15]***
Minke whale survey data sources*	Hakamada *et al.* (2006), Branch and Butterworth (2001b) ***[2004/05]***	IWC (1991) ***[1988/89]***	IWC (2013) ***[2012/13]***

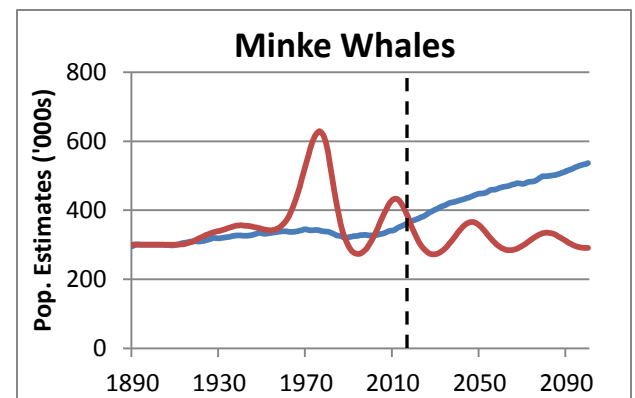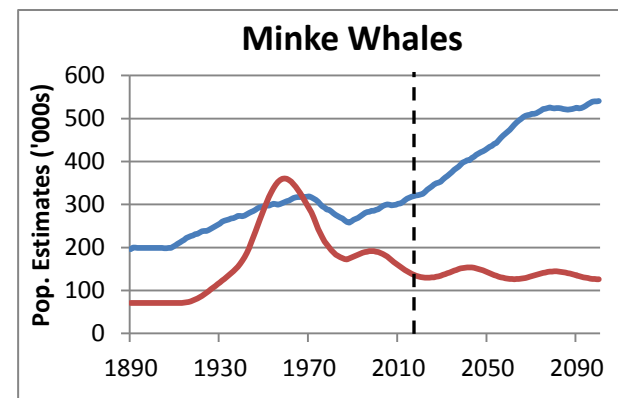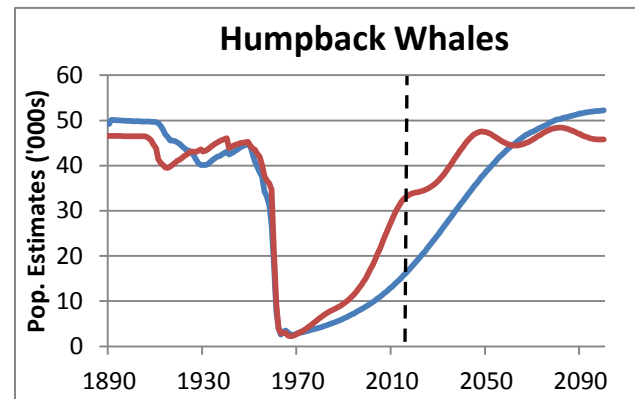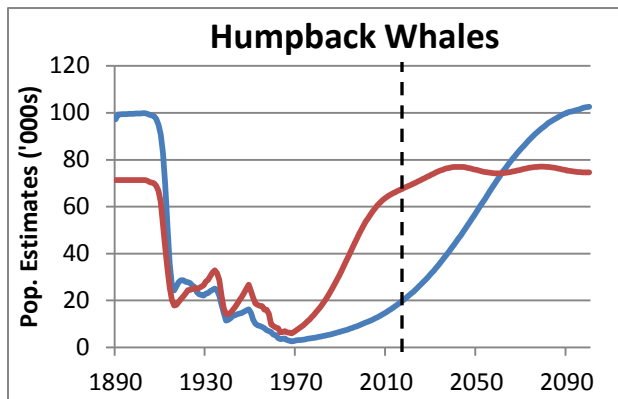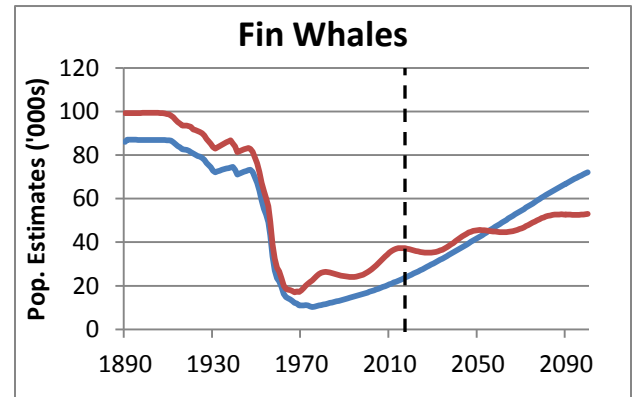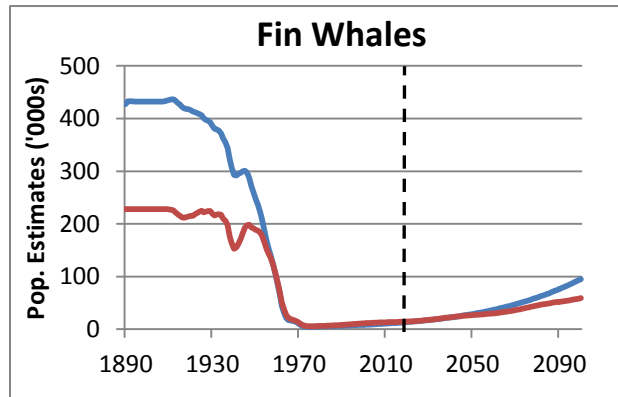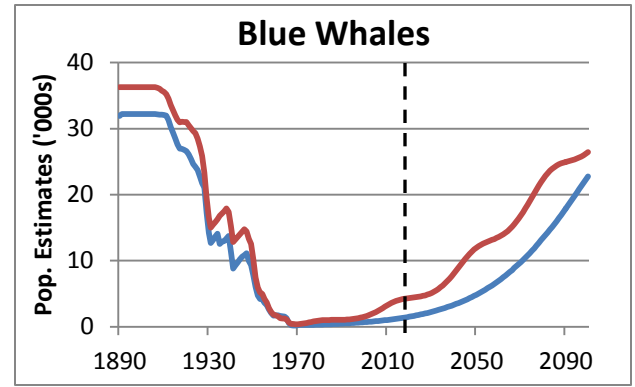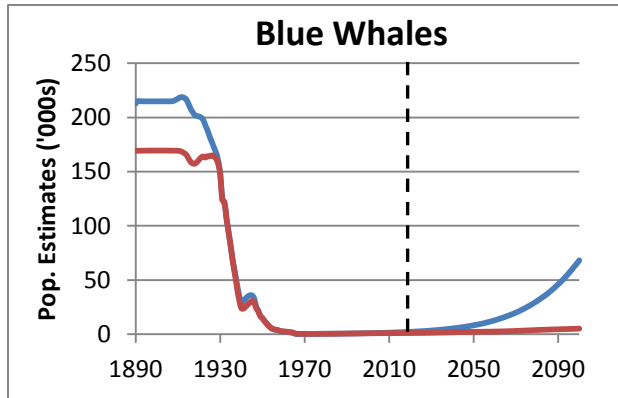 ***** Excludes sources of trend information in Moosa (2017) and Mori and Butterworth (2006).

Figure A.1. Comparison plots of the populations of four common whale species (blue, fin, humpback and minke whales) between Tulloch *et al.* (2017) (in blue) and Moosa (2017) (in red) for the Atlantic/Indian and Pacific regions. Note that, the estimates in Tulloch *et al.* (2017) are for mature females; these have been adjusted here to refer to the mature components of both sexes of the populations, which will differ somewhat from the estimates in Moosa (2017) which refer to the 1+ population. The dashed line indicates the start of the model's projections.