FURTHER PROGRESS ON MODELLING THE KRILL-PREDATOR DYNAMICS OF THE ANTARCTIC ECOSYSTEM

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ABSTRACT

This paper addresses work conducted on the Mori-Butterworth multi-species model of the Antarctic ecosystem subsequent to the Ulsan meeting of the Scientific Committee. Points raised about the model during that meeting are addressed in turn. Results are quoted that suggest that krill is indeed unable to fully utilise the primary production available. The precision of parameters estimated when fitting the model to abundance and trend data is reported. The model is extended to include an "other predators" variable (reflecting squid, fish and seabirds) so that the crabeater seal variable does not have to act as a surrogate for these in addition to the seals themselves. This results in an improved fit of the model to available abundance estimates for crabeater seals. A list of topics for possible further work on the model is presented. The development of an improved set of abundance and trend estimates for the various krill predators is seen as a priority for improving the reliability of current models, and it is suggested that this should be a key focus of the proposed joint IWC-CCAMLR workshop on this topic.

KEYWORDS: MULTI-SPECIES MODELING, ANTARCTIC ECOSYSTEM, KRILL, BALEEN WHALES, ANTARCTIC FUR SEALS, CRABEATER SEALS

INTRODUCTION

At the 2005 meeting of the Scientific Committee in Ulsan, Mori and Butterworth (2005) presented a paper reporting the results of a multi-species model of the Antarctic including krill together with four baleen whale and two seal species, in an effort to explain the trends observed in the abundances of these species as a consequence of predator-prey dynamics. The following points were raised in the discussion of this paper at that meeting:

1) Inclusion of beaked and killer whales in the model.
2) Is primary production in the Antarctic limiting? – the large krill surplus indicated by the model in the mid-20th Century implies that primary production was not being fully utilized by krill prior to this time.
3) Pooling over the two species of krill (*Euphausia superba* and *E. crystrallorophias*).
4) Examination of likelihood profiles for the estimable parameters to infer estimation precision.
5) The effect of assuming a top-down model in contrast to a bottom-up model.
6) The interpretation that the crabeater seal variable also represents all other krill predators.

In this paper the results of further work to address these points and to refine the original model are reported. To aid the reader, the Appendix provides the basic equations of the model, and a list of the symbols used and their definitions.

ADDRESSING POINTS RAISED AT THE 57TH MEETING OF THE SCIENTIFIC COMMITTEE

1) Inclusion of beaked and killer whales in the model

The response was offered during SC57 that there was too little information available for such species to be able to include them in the model. Given the information available, the authors had tried to include the largest consumers of krill, but it was not possible to include all species and interactions (due to lack of sufficient data). Regarding killer whales, Branch and Williams (2003) roughly estimated that the Type A killer whales *Orcinus orca* (for which around 35% of the diet consists of Antarctic minke whales) may have consumed around 13,000-20,000 of Antarctic minke whales during the austral summer each year over the 1985-2000 period. This corresponds to only 2% of the estimated abundance of Antarctic minke whales of 750,000 in 1985. This 2% is not a major proportion of the VPA estimate of some 7% (Mori *et al.* 2006) for the overall minke whale natural mortality, so that failure to include killer whales in the model explicitly would not seem that serious a source of potential bias.

2) Is primary production in the Antarctic limiting? – the large krill surplus indicated by the model in the mid-20th Century implies that primary production was not being fully utilized by krill prior to this time

Primary production in the Antarctic is probably not limiting, and it is not unreasonable to assume that krill fails to make full use of the available primary productivity. This is supported by the results of Holm-Hansen and Huntley (1984) who assessed the food requirements of krill in the Scotia Sea. The mean krill biomass in the upper 200m of the water column was estimated at 10.6 mg dry wt m^{-3}, and these krill were calculated to require a food ration of 0.105-0.211 mg C m^{-3} day^{-1}. The corresponding value for krill in a super-swarm off Elephant Island was 2.4-5.4 mg C m^{-3} day^{-1}. In contrast the phytoplankton (which is the primary prey of krill) productivity for the upper 200m in the Scotia Sea and the super-swarm area was estimated to be 4.8 and 4.2 mg C m^{-3} day^{-1} respectively. This suggests that there was ample phytoplankton to provide for the food requirements of the krill. Holm-Hansen and Huntley (1984) estimated that the krill in the super-swarm were consuming between 58 and 81% of the daily production, and that the krill population in the Scotia Sea as a whole on average consumed only between 2.5 and 3.5% of the daily primary production. Miller *et al*. (1985) came to a similar conclusion for the Indian Ocean sector.

3) Pooling over the two species of krill (*Euphausia superba* and *E. crystrallorophias*)

Tamura and Konishi (2005) report that in the deep parts of the Ross Sea and Prydz Bay, minke whales feed on *E. crystallorophias*, but that the overall consumption is far less than that of krill (*E. superba*). Both D. Miller and S. Nicol (pers. commn) suspect that while there has not been any survey or assessment of the abundance of *E. crystallorophias*, this is far less than that of krill. Given the study of Tamura and Konishi (2005) and the views of Miller and Nichol, it does not seem necessary to distinguish *E. superba* and *E. crystrallorophias* at the current stage of development of the model since the abundance and consumption of *E. crystrallorophias* seem to be much less than for *E.superba*. However, if one wants to develop an area-specific model such as for the Ross Sea or Prydz Bay, it may be important to distinguish between these two krill species.

4) Examination of likelihood profiles of the parameters to infer estimation precision

This examination has been conducted. Table 1 lists 95% confidence intervals for the parameter values estimated, based on the likelihood profile method. These profiles are compared to the input ranges for each parameter in Figures 1a to 1d. To aid the reader in determining the extent to which the data used to fit the model are informative for estimating these parameter values, the comparisons are presented as if they reflected prior and posterior distributions in a Bayesian context. The priors are exact representations across the ranges specified (throughout which values are assumed to be equally likely); however, the "posteriors" are not exact representations, as they make the assumption that likelihood profiles provide close approximations to the corresponding posteriors. (Numerical convergence difficulties were encountered in attempting a Markov Chain Monte Carlo (MCMC) approach to obtain Bayesian posteriors directly.)

For the estimates of the numbers of animals for the initial year considered in the model (i.e. 1780), these "posterior" distributions are somewhat narrower than the prior distributions for all the species considered, although the differences are rather small for minke whales (Figure 1a). For humpback whales and Antarctic fur seals in Region A (the Atlantic-Indian sector), the confidence intervals for the estimated initial numbers for these animals are very narrow (Figure 1a, Table 1). For humpback whales, this could be due to the low survey abundance estimate for 1997, despite the high growth rate observed for this species since 1977, which necessitates a high density dependent mortality rate parameter η and also allows little scope for the values of estimates of the initial number for this species. The low abundance estimate for Antarctic fur seals in 1930 suggests the species must have been virtually extinct when exploitation ceased in the 19th Century; this together with the relatively short period of the harvest indicates that the cumulative historic catch alone dominates any estimate of initial numbers in 1780.

For the estimates of maximum birth rates, again the "posterior" distributions are somewhat narrower than the prior distributions for all the species considered in the model; in all cases fairly high maximum birth rates are preferred. For the estimates of natural morality rates, there is not much improvement in the "posterior" distributions compared to the priors, except for blue whales and seals (Figure 1b). The narrow confidence intervals for Antarctic fur seals likely result from the steep population increase rate during the middle decades of the 20th Century that is indicated by the survey estimates of abundance of this species.

For maximum consumption rates (the λ parameters), higher values are preferred in all cases (Figure 1c). Regarding the intrinsic growth rate of krill, the model prefers a low estimate for Region A, but for Region P (the Pacific sector) the data contain insufficient information to meaningfully update the prior (Figure 1d).

5) The effect of assuming a top-down model in contrast to a bottom-up model

The authors have not yet developed any model that assumes bottom-up control effect. Note that the intention of the original Mori-Butterworth (2005) paper was to explore whether the observed trends in the abundances of krill and their main predators can be explained when top-down control effects are assumed to dominate.

6) The interpretation that the crabeater seal variable also represents all other krill predators

In this paper a further predator group termed "other-species", which is a surrogate for other species that feed mainly on krill (i.e. sea birds, fish and cephalopods) has been added. The aim of this exercise is to explore whether it is possible to obtain a better fit for the crabeater seal abundance estimate for the "reference case" model shown in Mori and Butterworth (in review) by adding such a group to the model. The "other-species" predator group were included in the model using the same form of predator-prey equations as in earlier analyses (see Appendix). For this initial analysis, this group was added only for Region A.

The input parameters were set exactly the same as for the "reference case" in Mori and Butterworth (in review) except that the density dependent parameters for crabeater seals ($\eta^{c,A}$) were modified and that for the "other-species" group was introduced. The parameter values shown in Table 2 were used for this exploratory analysis. For the density dependent parameter of the "other-species" predator group, different values were tested.

Figure 2 shows the "reference case" population model trajectories for krill and its main predators in the Antarctic extracted from Mori and Butterworth (in review), which does not include an "other-species" predator group. The recent abundance of crabeater seals in Region A is estimated by the model to be much higher than the abundance estimate from surveys of this species.

Figure 3 shows the same trajectories when the "other-species" predator group is added into the model. By adding this group it is possible to obtain a better fit to the abundance data for the crabeater seals. Figure 4 shows similar trajectories for the case where the density dependent parameter for the "other-species" predator group is set higher than for Figure 3. Figure 5 compares the estimated consumption of krill by the predator groups for the case without and within the "other-species" predator group.

From these exploratory analyses, it is evident that by including an "other-species" predator group, it is possible to obtain a better fit to crabeater seal abundance estimates, and to reflect more plausible estimates of consumption of krill by this species. However, a difficulty that remains is the choice of parameter values which are appropriate for the "other-species" predator group (e.g. if squid constitutes a large proportion of this group, should these be such that the group can manifest faster dynamics than are typical for most seals, birds and fish).

FURTHER WORK

Areas for further possible work on the model are as follows.

- Include an "other-species" predator group for Region P as well as for Region A, and investigate the consequences of forcing these and crabeater seals to have larger abundances in 1780 when the model trajectories commence.
- Input improved abundance estimates for crabeater seals.

  Earlier analyses used an initial coarse estimate provided by J. Laake (pers. commn) for the results from the APIS crabeater seal survey conducted over the 1999/2000 austral summer. Laake (pers. commn) has recently advised a refined estimate of crabeater seal abundance between 100°-150°W from this survey of 1.73 million (95%CI: 1.22-2.67 million), and C. Southwell (pers. commn) has recently estimated crabeater seal abundance from this survey between 64°-150°E to be 0.4-1.4 million. This totals about 3 million animals for about 150 degrees of longitude, which spans about 42% of the circumference of the continent. Assuming that the average density of crabeater seals is same for the remaining areas makes for an abundance estimate of around 7 million. It is difficult to compare these results with the previous study of Erickson and Hanson (1990) since the area surveyed and estimation method differ between these studies. Erickson and Hanson (1990) estimated that the number of crabeater seals is relatively high in the Weddell Sea area (20°-60°W) compared to the other areas (2.5 million in this 40 degrees sector); thus the recent abundance estimate may be higher than the extrapolation above of 7 million animals. The abundance estimate of 8 million used for the model computations reported is thus not implausible, but further work on estimating the circumpolar abundance of this species is needed (results from the part of the APIS survey that included the Weddell Sea remain to be finalised).

- Construct models using different modelling approaches (e.g. Ecopath with Ecosim) and compare results for different modelling techniques and functional forms for species interactions.
- Update inputs given further information on the "other species" predator group (ideally these would be agreed in collaboration with the CCAMLR SC).
- Incorporate abundance estimates obtained from JARPA and JARPAII surveys.

A key consideration for refinement of this and related models is the development of an improved set of abundance estimates and trends for the various predator species for input to enhance the reliability of model outputs. We suggest that this should be a key focus for the proposed joint IWC-CCAMLR workshop on this subject.

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Table 1. 95% confidence intervals for the estimated parameters for the “reference case” of Mori and Butterworth (2005) based on likelihood profiles. All values have been rounded to three significant figures.

	Lower 95% CI	Estimate	Higher 95%CI
$N_{1780}^{b,A}$	167000	193000	207000
$N_{1780}^{b,P}$	15700	27500	33000
$N_{1780}^{m,A}$	17700	52900	193000
$N_{1780}^{m,P}$	108000	169000	299000
$N_{1780}^{h,A}$	58300	65400	66900
$N_{1780}^{h,P}$	41300	56400	59700
$N_{1780}^{f,A}$	98200	12600	175000
$N_{1780}^{f,P}$	18800	64500	104000
$N_{1780}^{s,A}$	2890000	2920000	3040000
$N_{1780}^{c,A}$	111000	278000	3630000
$N_{1780}^{c,P}$	113000	189000	2950000
λ^b	447	451	451
λ^m	28.4	32.1	32.1
λ^h	106	108	108
λ^s	1.88	2.71	2.71
λ^c	5.34	5.51	5.51
μ^b	0.125	0.160	0.160
μ^m	0.140	0.200	0.200
μ^s	0.276	0.280	0.280
μ^c	0.176	0.236	0.280
M^b	0.030	0.030	0.041
M^m	0.040	0.041	0.097
M^h	0.033	0.080	0.080
M^f	0.030	0.032	0.048
M^s	0.070	0.070	0.078
M^c	0.070	0.077	0.171
r^A	0.400	0.400	0.418
r^P	0.401	0.404	0.593

Table 2. Modified or newly added input parameters for the model which includes an “other-species” predator group.

Parameter	Value
$\eta^{c,A}$	$2\text{x}10^{-8}$
λ^o	3.5
μ^o	0.4
M^o	0.2
$\eta^{o,A}$	$1\text{x}10^{-8}$ or $2\text{x}10^{-8}$

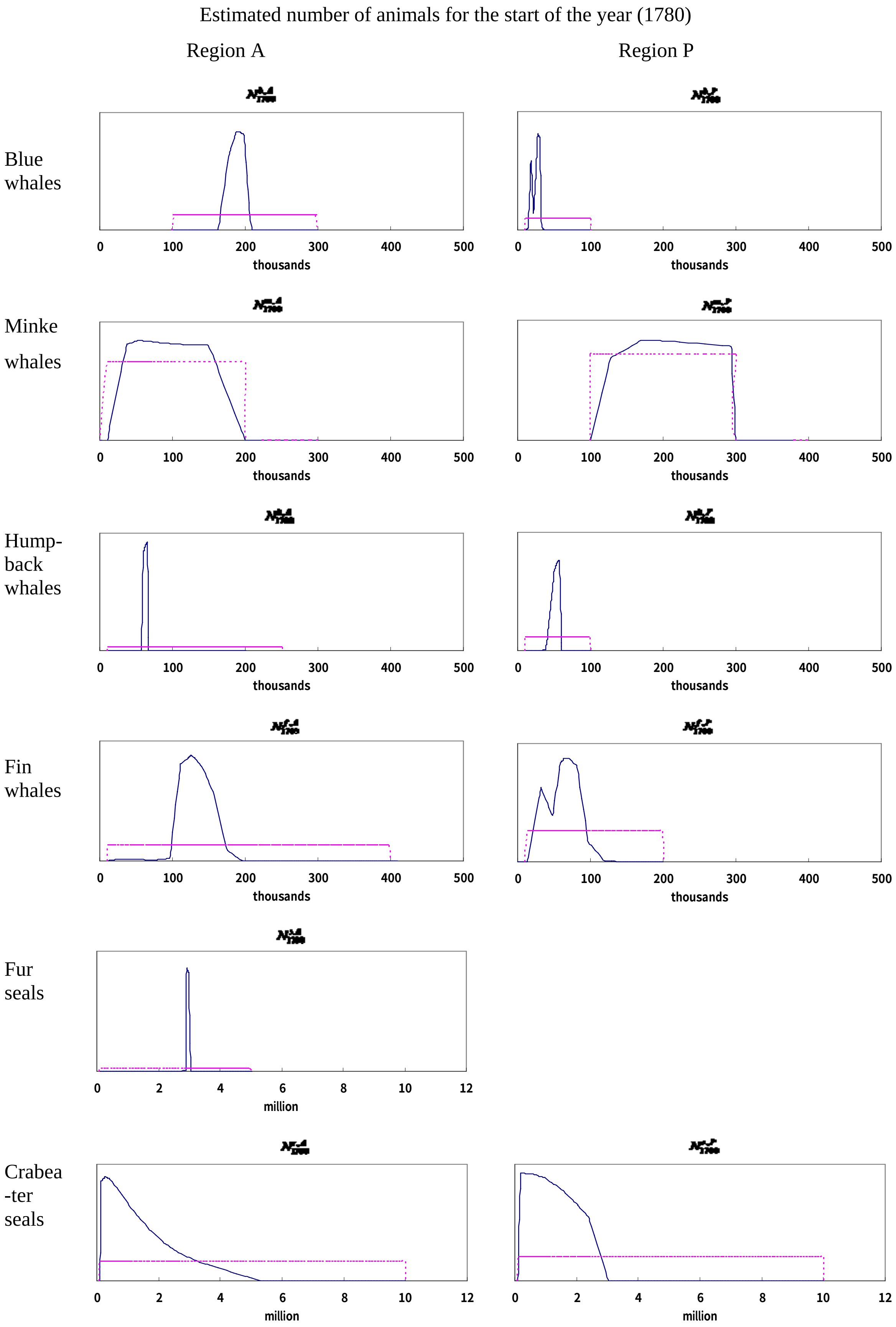


Figure 1a Probability density distributions for the initial number of animals in year 1780 for the model presented in Mori and Butterworth (2005). The solid lines are the model estimates (likelihood profiles used to approximate posteriors) and the dotted lines represent the priors.

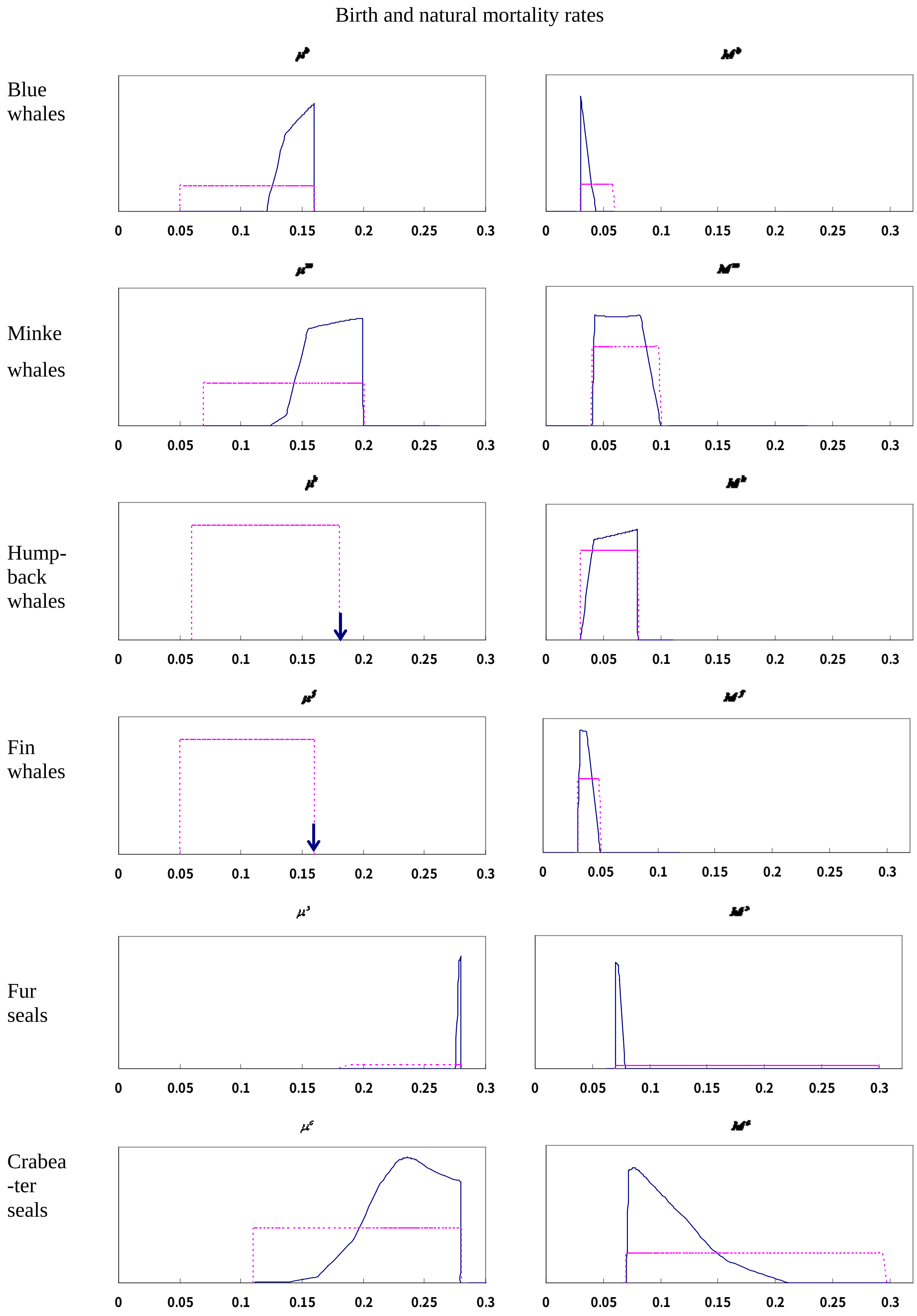


Figure 1b Probability density distributions for birth and natural mortality rates for the model presented in Mori and Butterworth (2005). The solid lines are the model estimates (likelihood profiles used to approximate posteriors) and the dotted lines represent the priors. The μ^h and μ^f parameters were fixed at the maximum of their ranges (see arrows), rather than estimated.

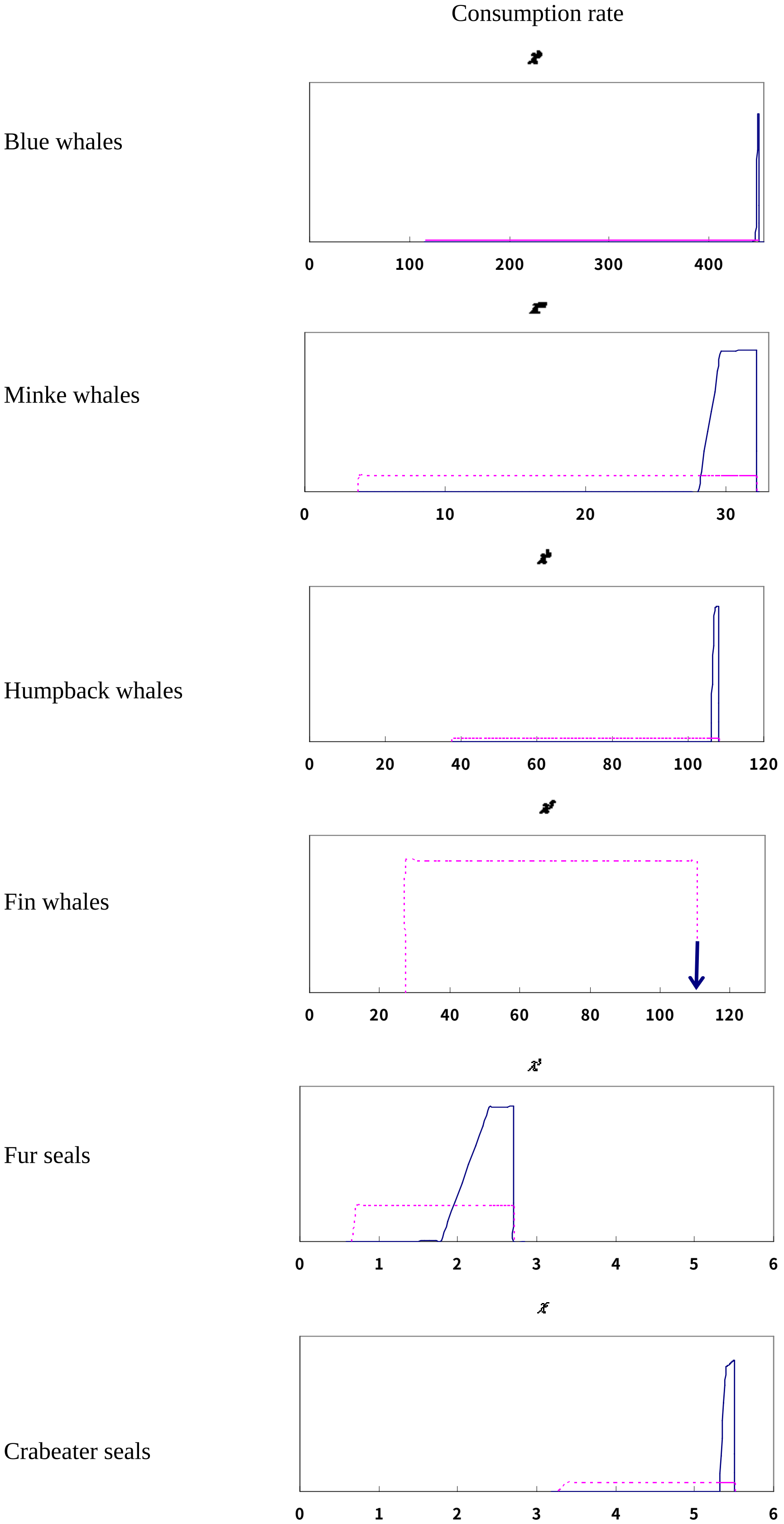


Figure 1c Probability density distributions for consumption rates for the model presented in Mori and Butterworth (2005). The solid line is the model estimate (likelihood profiles used to approximate posteriors) and the dotted line represents the prior. λ^f was fixed at the maximum of its range (see arrow), rather than estimated.

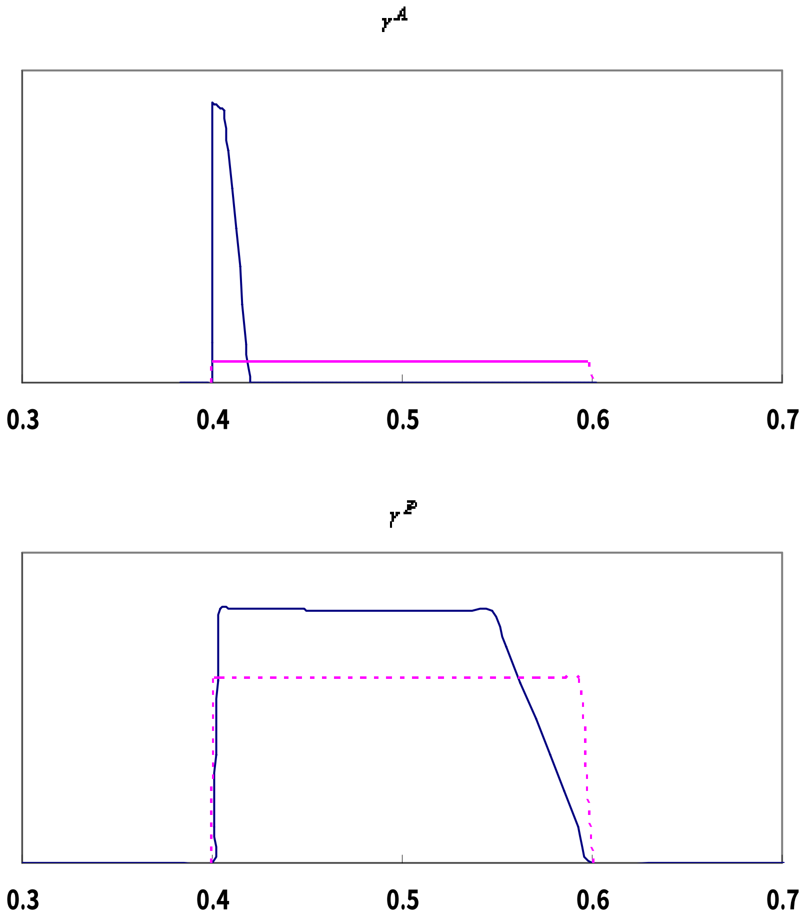


Figure 1d Probability density distributions for the intrinsic growth rate of krill for the model presented in Mori and Butterworth (2005). The solid line is the model estimate (likelihood profiles used to approximate posteriors) and the dotted line represents the prior.

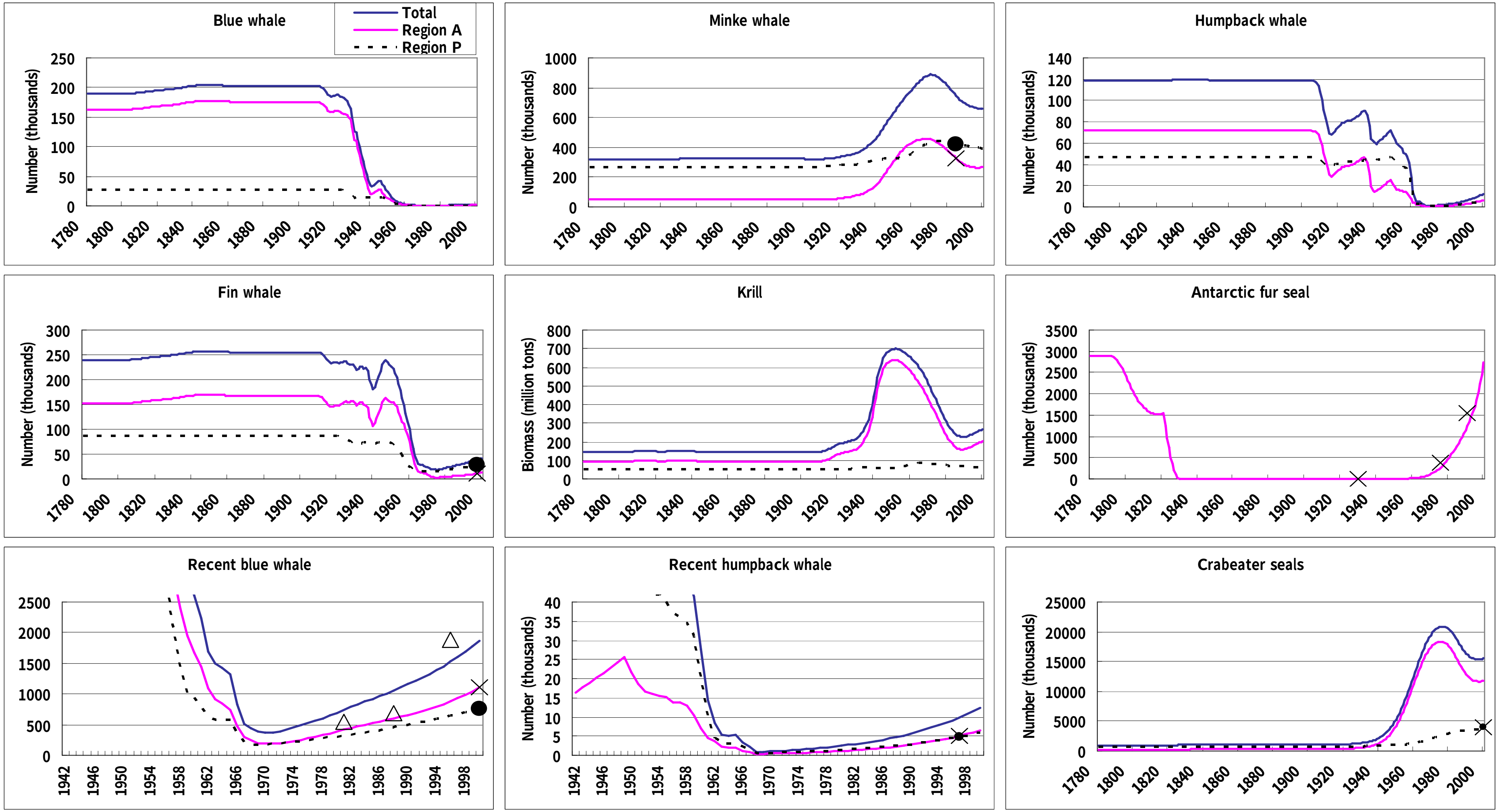


Figure 2. "Reference case" population model trajectories for krill and its main predators in the Antarctic (extracted from Figure 4 of Mori and Butterworth (in review)). In this case, no "other predator group" is included in the model. A black dot/cross shows a survey-based abundance estimate for the Pacific/Atlantic Region respectively, to which the model was fit. The open triangles shown in the recent blue whale trajectory plot are the blue whale abundance estimates from surveys for Regions A and P combined, to which the model was fit to reflect the abundance trend indicated by these estimates. Whales and seal number estimates are as indicated, and krill is in million tons.

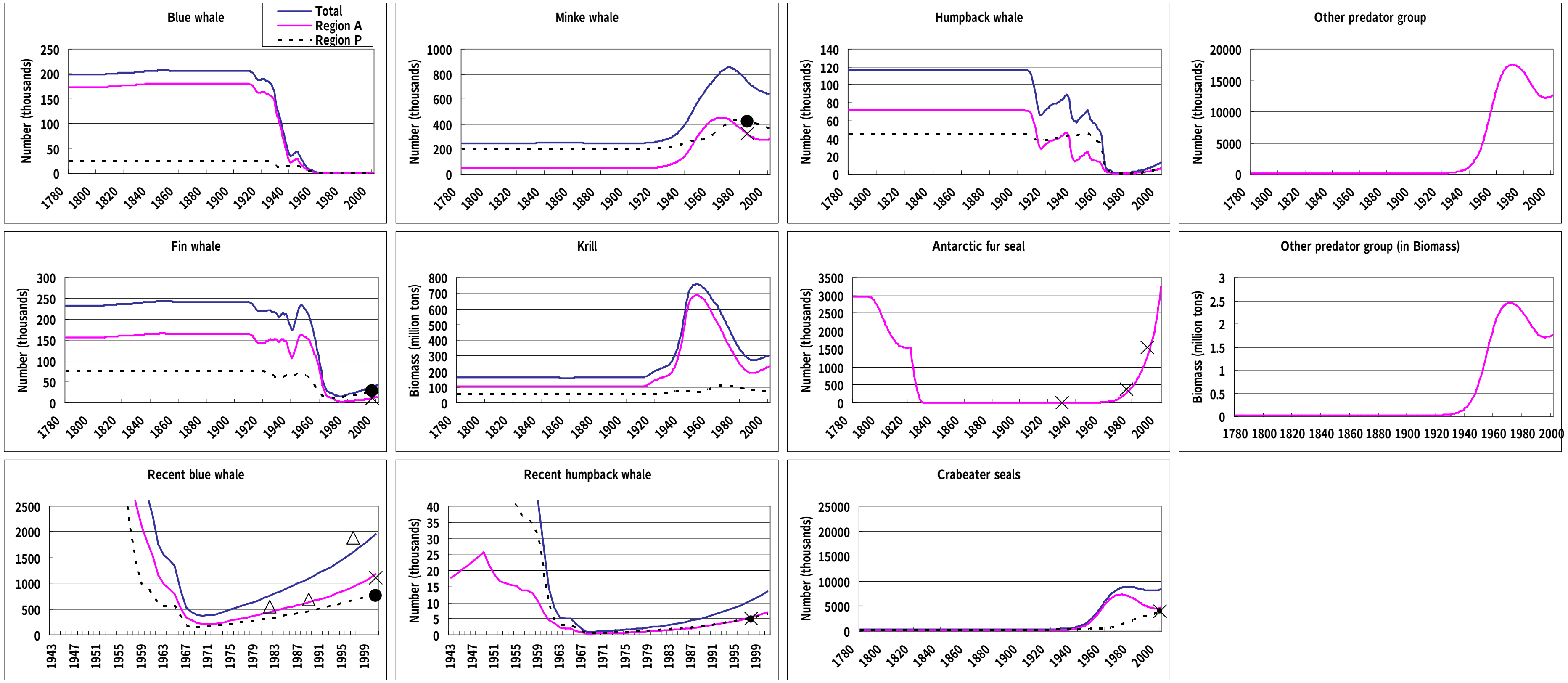


Figure 3. An example population model trajectories for krill and its main predators in the Antarctic when an “other predator group” is included in the model. In this case, density dependent parameter of the **“other predator group” ($\eta^{o,A}$) is set to 1x10^{-8}**. The meanings of the symbols are the same as in Figure 2. The biomass of the other predator group is calculated assuming that both crabeater seals and these other predators eat the same fraction of their body-weight per day (7%).

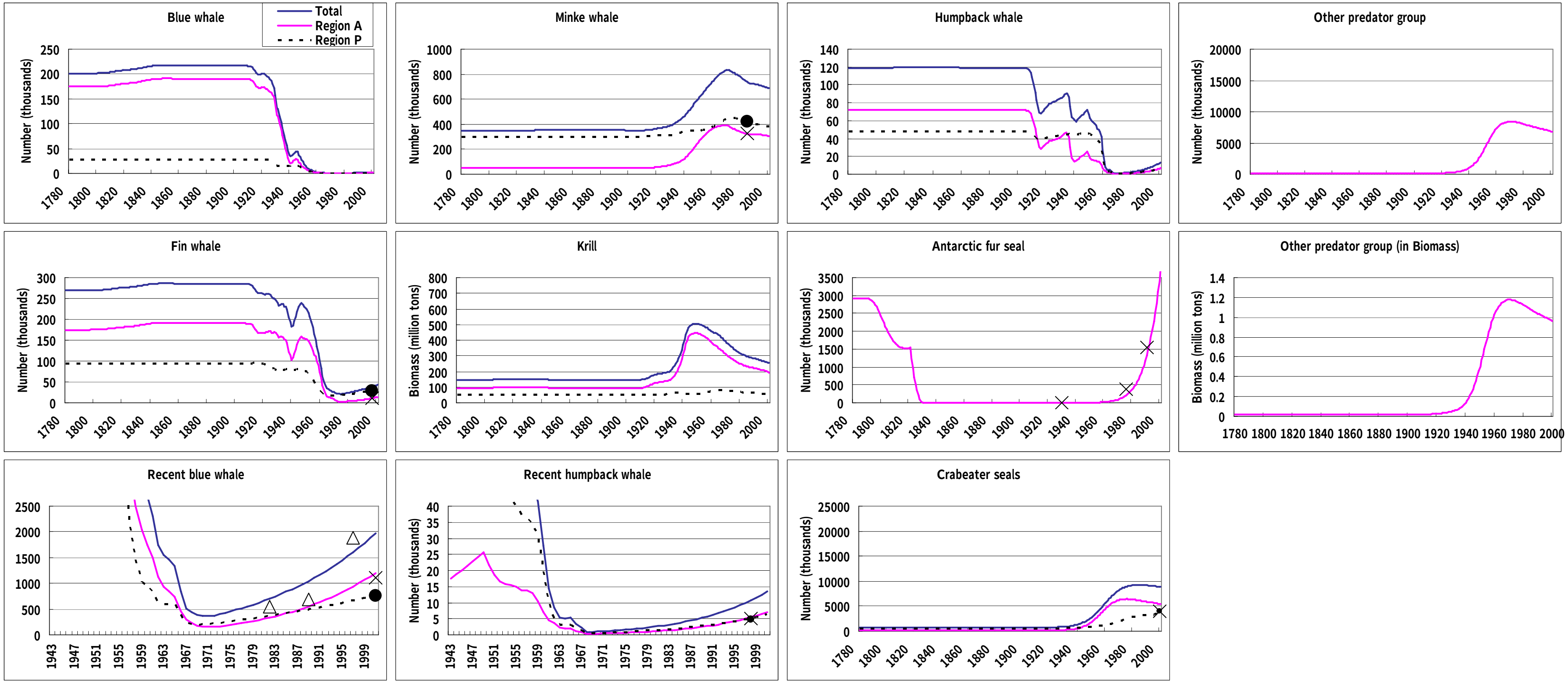
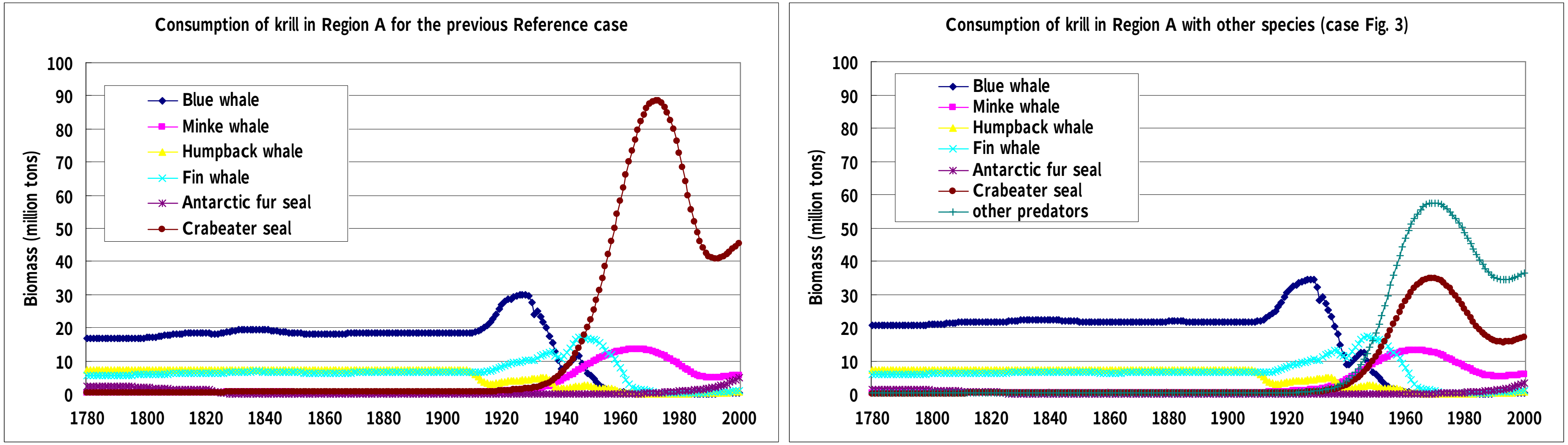


Figure 4. Another example population model trajectories for krill and its main predators in the Antarctic when an “other predator group” is included in the model. In this case, density dependent parameter of the **“other predator group” ($\eta^{o,A}$) is set to 2x10^{-8} (higher than the case shown in Figure 3)**. The meanings of the symbols are the same as in Figure 2. The biomass of the other predator group is calculated assuming that both crabeater seals and these other predators s eat the same fraction of their body-weight per day (7%).



a) Reference case of Mori and Butterworth (in review)

b) Case with an other predator group ($\eta^{o,A}$ is set to $1*10^{-8}$)

Consumption of krill in Region A for the previous Reference case

Consumption of krill in Region A with other species (case Fig. 3)

Figure 5. Annual consumption of krill biomass (million tons) by predators in Region A for (a) the “reference case” of Mori and Butterworth (in review), and for (b) a case with an other predator group ($\eta^{o,A}$ is set to $1*10^{-8}$).

APPENDIX

Basic dynamics assumed in the model

-Dynamics of krill

$$B_{y+1}^{a} = B_{y}^{a} + r^{a} B_{y}^{a}\left(1-\left(\frac{B_{y}^{a}}{K_{a}}\right)\right) - \sum_{j}\frac{\lambda^{j}\left(B_{y}^{a}\right)^{n} N_{y}^{j,a}}{\left(B^{j,a}\right)^{n}+\left(B_{y}^{a}\right)^{n}} \tag{A.1}$$

-Dynamics of the predators

$$N_{y+1}^{j,a} = N_{y}^{j,a} + \frac{\mu^{j} N_{y}^{j,a}\left(B_{y}^{a}\right)^{n}}{\left(B^{j,a}\right)^{n}+\left(B_{y}^{a}\right)^{n}} - M^{j} N_{y}^{j,a} - \eta^{j,a}\left(N_{y}^{j,a}\right)^{2} - C_{y}^{j,a} \tag{A.2}$$

where

B_{y}^{a} is the biomass of krill in region *a* in year *y*;

r^{a} is the intrinsic growth rate of krill in region *a*;

K_{a} is the carrying capacity of krill (in the absence of predators) in region *a*;

λ^{j} is the maximum per capita annual consumption rate of krill (in tons) by predator species *j* (*j* could be either *b* (blue whale), *m* (minke whale), *h* (humpback whale), *f* (fin whale), *s* (Antarctic fur seals), *c* (crabeater seals) or *o* (other species));

$N_{y}^{j,a}$ is the number of predator species *j* in region *a* in year *y*;

$B^{j,a}$ is the krill biomass when the consumption and hence also birth rate of species *j* in region *a* drops to half of its maximum level;

μ^{j} is the maximum annual birth rate of predator species *j*;

M^{j} is the natural annual mortality rate of predator species *j* in the limit of low population size;

$\eta^{j,a}$ is a parameter governing the density dependence of natural mortality and/or birth (and calf survival) rate for predator species *j* in region *a*;

n is a parameter that controls whether a Type II or a Type III functional response is assumed (*n*=1 for Type II and *n*=2 for Type III. In this paper, *n*=2 is assumed);

$C_{y}^{j,a}$ is the catch of predator species *j* in region *a* in year *y*; and

a is either the Atlantic-Indian or the Pacific sector of the Southern Ocean around Antarctica.