An attempt to ecosystem modelling for species in Area IV in the Antarctic Ocean using JARPA and JARPAII data

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ABSTRACT

A development process for ecosystem modelling for species in Area IV, which is a part of the research area of JARPA and JARPAII, is introduced. Two types of modelling approaches were employed; one is a multi-species production model, and the other is the EwE, a comprehensive (whole-of-ecosystem) model. There are differences in the component species between them, but the baleen whales and krill play key roles in both. For statistical estimation in the multi-species production model, a functional response function was proposed to link the dynamics of predators (four baleen whales and crabeater seals) and prey (Antarctic krill) with between-species competitions to the prey as well as internal population competitions. The model was applied to the data on time series of the four baleen whales, crabeater seals and krill, and then a likelihood function was defined based on the data with some additional assumptions on inestimable parameters. However, the estimated population trends for the component species did not fit to the data well, which might be attributed partly to lack of spatial structure in the model and partly to lack of representativeness of assumed parameters and information on prey abundance. For the EwE approach, the authors tried to construct mass-balancing for Ecopath for 27 functional groups, which could be the basis in the next stage of analysis for projection forward using the Ecosim framework.

KEYWORDS: MODELLING; ENERGETICS; FOOD/PREY; SCIENTIFIC PERMITS; ANTARCTIC; ANTARCTIC MINKE WHALE; BLUE WHALE; FIN WHALE; HUMPBACK WHALE

INTRODUCTION

According to the stated research objectives of JARPAII, the aims relevant to the ecosystem modelling were : a) to monitor the Antarctic ecosystem (whale abundance trends and biological parameters; krill abundance and the feeding ecology of whales; effects of contaminants on cetaceans; cetacean habitat); and b) to model competition among whale species and future management objectives (constructing a model of competition among whale species; new management objectives including the restoration of the cetacean ecosystem). In this sense, the modelling is a way of expressing competition among predators like whale species for the main prey species, krill, and accounting for the dynamics of their interactions/predation, and these works are necessary steps to understand what has happened and what is going to happen in the Antarctic.

When it comes to ecosystem modelling, which is usually a substantial exercise, a broad range of approaches has been proposed (*e.g*. Plagányi 2007). One of the most comprehensive approaches (or so-called the "whole-of-ecosystem" modelling, *e.g*. Plagányi *et al*. 2012) is the one developed by the group led by Pauly, Ecopath-with-Ecosim (EwE, *e.g.* Pauly *et al*. 2000), in which a complicated system is represented by a multi-directional linkage among component species with consideration of an initial mass-balancing of the system and its subsequent dynamics afterward. This approach has been widely used for constructing marine ecosystem models, but it also requires various types of information such as the biomass levels, the diet compositions, per capita growth rates and the extent of necessary consumption with consideration of required energy, and these pieces of information are often influential with regards to the models' results. Also, predicting future dynamics demands further information and assumptions. Nevertheless, it is beneficial to try to draw a bigger picture of the ecosystem.

The dynamics of the population size of wildlife species has traditionally been expressed as a form of production models. This contains, of course, the effect of density dependence, which is usually linked with the relative depletion compared to its carrying capacity. The model is then extended to consider prey availability including competition in utilising them and the impact of predators on prey species. This can be regarded as a model of intermediate complexity of an ecosystem (*e.g*. Plagányi *et al*. 2012). Primitive but fadeless pieces of work were developed by Lotka and Volterra. Each of them derived different sets of equations, which are now called "predator-prey interactions" and "competition for food and space". Since then, the models have been further developed to take into account multiple prey and predator species simultaneously although the models have to face "the curse of dimension", especially in the presence of many species to be considered in, for example, a region of the Antarctic. Although the multiple-predators and multiple-prey system potentially possesses a large number of parameters, this could be one of the simplest ecosystem models if it is possible to confine the component species and their hierarchy.

In the Antarctic Ocean, there is no doubt that the Antarctic krill (*Euphausia superba*) is the main prey species and plays a crucial role in influencing the ecosystem surrounding large predatory baleen whales like blue (*Balaenoptera musculus*), fin (*B. physalus*), humpback (*Megaptera novaeangliae*) and Antarctic minke whales (*B. bonaerensis*) and other krill predators like seals and sea birds. When considering that sort of simple hierarchical structure, the extended production model might work well without encountering the difficulty of over-parameterization. Hence we re-visit a modelling approach in a preceding study conducted by Mori and Butterworth (2006), in which the whole Antarctic was considered, and also extend the model by considering competition among predators and so on.

We therefore have attempted to ecosystem modelling in the Indian Ocean sector of the Antarctic Ocean (IWC management area: Area IV), where the yearly changes in the environmental conditions are less than Area V, based on the following two different approaches.

MULTI-SPECIES PRODUCTION MODEL

This exercise was intended to refine the earlier approach by Mori and Butterworth (2006), but some twists were added into their basic system of equations for multiple predators (some baleen whales and seals) and single prey species (krill). Although the multi-species production model is simpler than the approach of whole-of-ecosystem modelling, it still has many unknown parameters. To reduce the number of parameters to be estimated, some bioenergetic and allometric reasoning by Yodzis and Innes (1992) were incorporated for the predator species. The maximum consumption is linked to the body weight of the predators.

This sort of model has the potential to estimate the extent of competition between the baleen whales. For example, since the population sizes of other larger baleen whales such as blue, fin and humpback whales declined through commercial harvesting, there may have been a state of krill surplus in the Antarctic. This surplus could be utilized by the Antarctic minke whales, and since that time the minke whales may be still above their pre-exploitation level.

Basic model

This is a sort of update of the former approach by Mori and Butterworth (2006), but some twists have been added. A basic system of equations for multiple predators (some baleen whales and seals) and a single prey species (krill) is given as follows:

$$
\begin{aligned}
&P_{t+1,i} = P_{t,i} - M_i\, P_{t,i} + E_i\, f_i(B_t) P_{t,i} - \alpha_i\, P_{t,i}^2 - C_{t,i}, \ \ (i = 1, 2, \ldots, n) \\
&f_i(B_t) = c_{\max,i}\, \frac{B_t^{\theta}}{H_i^{\theta} + B_t^{\theta}}, \\
&B_{t+1} = B_t + r\, B_t \left(1 - \frac{B_t}{K}\right) - \sum_{i=1}^{n} f_i(B_t) P_{t,i},
\end{aligned}
\tag{1}
$$

where $P_{t,i}$ and B_t are respectively the population sizes for predators and prey species, and M_i, E_i and α_i are the natural mortality rate, the energy conversion factor and a parameter for the density dependence for predator species *i*, respectively. The function "*f*" is a so-called functional response, which is used to link the predator with prey. The parameters, $c_{\max,i}$ and H_i, are respectively a maximum consumption per the *i*-th predator in the feeding season and the prey biomass when the consumption of the *i*-th predator drops to a half of $c_{\max,i}$. These become the Type II and Type III functional responses for cases of $\theta = 1$ and 2, respectively. The parameters *r* and *K* in the prey dynamics are the ones used in the usual logistic production model.

As shown above, Mori and Butterworth (2006) assumed a density-dependence within each species, but there may be some other density dependence by other predator species. It may not be a useful way to simply include all other predators' effects in each species dynamics. Instead, one possible way is to modify the available prey abundance by considering a food competition among the predators as follows:

$$
\begin{aligned}
&P_{t+1,i} = P_{t,i} - M_i P_{t,i} + E_i c_{\max,i} \frac{(\omega_{t,i} B_t)^\theta}{H_i^\theta + (\omega_{t,i} B_t)^\theta} P_{t,i} - \alpha_i P_{t,i}^2 - C_{t,i}, \\
&B_{t+1} = B_t + r B_t \left(1 - \frac{B_t}{K}\right) - \sum_{i=1}^{n} c_{\max,i} \frac{(\omega_{t,i} B_t)^\theta}{H_i^\theta + (\omega_{t,i} B_t)^\theta} P_{t,i}, \\
&\text{where } \omega_{t,i} = \frac{s_i P_{t,i} W_i^{0.75}}{\sum_j s_j P_{t,j} W_j^{0.75}}.
\end{aligned}
\tag{2}
$$

Here, s_i is a selectivity of the *i*-th predator to the prey species, and it is assumed to be 1 for all the predators in this application.

This model is further developed to incorporate the species-internal completion (density dependence) into the functional response itself as in the following formula:

$$
P_{t+1,i} = P_{t,i} - M_i P_{t,i} + E_i c_{\max,i} \frac{(\omega_{t,i} B_t)^\theta}{H_i^\theta + (\omega_{t,i} B_t)^\theta + \phi_i P_{t,i}} P_{t,i} - C_{t,i}. \tag{3}
$$

This model can be regarded as an extension of Beddington (1975)'s model. The carrying capacity for the krill and the parameters for the density dependence for the predators are solved through an assumption of an equilibrium condition to reduce the number of parameters to be estimated.

Using the model, the following hypotheses can be tested;

i) Does direct competition among predators in food availability happen?

ii) Can an indirect effect through different *H* parameters among predators explain ecosystem dynamics?

These issues can be addressed in the functional response in Equation (3).

Bioenergetic and allometric reasoning

Though the multi-species production model is simpler than other ecosystem modelling approaches like whole-of-ecosystem modelling, it still has lots of unknown parameters. To reduce the number of parameters to be estimated, some bioenergetic and allometric reasoning by Yodzis and Innes (1992) was incorporated over predator species. The maximum consumption and the rate of increase are linked with the masses of predators (W) as

$$c_{\max,i} = \beta W_i^{0.75},$$
$$\mu_i = \gamma W_i^{-0.25}. \tag{4}$$

Then the energy conversion factor was calculated as

$$E_i = \frac{\mu_i}{c_{\max,i}} = \frac{\gamma W_i^{-0.25}}{\beta W_i^{0.75}} = \delta W_i^{-1}. \tag{5}$$

Note that the exponent in the rate of increase "-0.25" may not be suitable for marine mammals (Duncan *et al*. 2007). Using a dataset of Duncan *et al*. 2007, the exponent for cetaceans is roughly estimated as -0.0315 and this was used as a proxy value for predators.

Data

The following data set was used in this analysis.

- Catch series for each species (Fig. 1)
- Baleen whales abundance estimates (blue, fin, humpback and Antarctic minke whales) (Fig. 2):
  - IDCR/SOWER absolute estimates
    - Blue whales (Branch, 2007)
    - Fin whales (No estimate specific to Area IV)
    - Humpback whales (Branch, 2011)
    - Minke whales (Okamura and Kitakado, 2012; IWC, 2013)
  - JARPA and JARPAII estimates
    - Blue whales (Matsuoka and Hakamada, 2014)
    - Fin whales (Matsuoka and Hakamada, 2014)
    - Humpback whales (Matsuoka *et al*., 2011; Hakamada and Matsuoka, 2014a)
    - Antarctic minke whales (Hakamada and Matsuoka, 2014b)
- Crabeater seal estimate (Southwell *et al*., 2008a) (Fig. 2)
- Krill abundance estimate (Wada and Tamura, 2014) (Fig. 2)
- Stomach contents for the Antarctic minke whales (time series of nominal average contents weight, in this study) (Fig. 3)

Statistical estimation

Both the data sets on abundance and stomach contents contributed to the likelihood for the estimation as follows:

loglike (time series of abundance estimates) + loglike(time series of the stomach contents for minke) (6)

The first term is derived from the following usual assumption:

$$\log \hat{N}_t = \log N_t + \varepsilon_t, \quad \varepsilon_t \sim N(0, c\hat{v}_t^2). \tag{7}$$

The average stomach contents of a minke whale (assumed as per day) is decreasing, which might be caused by a recent dramatic increase in humpback populations, but the current model can explain only the decrease of krill abundance (but it is not so obvious). An alternative possible model might be possible by linking the functional response with other predators' effects (but this is not considering any niche overlap or spatial manner).

$$\log\left(\text{average stomach contents}\right)_t = \log a + \log f_{Minke}(B_t) + v_t, \quad v_t \sim N(0,\sigma^2) \qquad (8)$$

There are a number of parameters in the model (as shown in the Table 1). To reduce the number of parameters to be estimated without assuming specific values as much as possible, we assume

i) Some structural relationships between the bioenergetics parameters and body mass as shown in previous formulas;

ii) A system of simultaneous equations derived by an equilibrium condition before starting exploitation;

iii) A fixed proxy value for the maximum krill consumption by the Antarctic minke whale, $c_{\max,Minke}$,which was given by twice of the per capita consumption shown in Tamura and Konishi (2014).

As shown in Table 1, some parameters are fixed in the model because of the limited abundance information. For example, only one abundance estimate is available for the krill, and therefore it is impossible to estimate both the rate of increase and initial population size. We use a value of r=0.5 and try to estimate the initial biomass in 1900/91 (B_0). Similarly, for the crabeater seals, for which the abundance estimate is available only in 1999/00, we fix a ratio of the abundance estimate in 1999/00 to the initial population size (P_0) at 0.05 and try to estimate the parameter in the function response, H. The parameter β in the maximum consumption $c_{\max}$ is computed by assuming the current consumption level for the Antarctic minke whales is a half of its maximum. In nature, these fixed parameters are subject to sensitivity tests although a full examination has not been finished.

Results

The model was applied to the data on time series of four baleen whales, crabeater seals and krill, and then a likelihood function was defined based on the data with some additional assumptions on inestimable parameters. However, the estimated population trends for the component species did not fit to the data well.

During the fitting process, we tried to change the weights of data to the likelihood function for better fitting. The issue of weighting has often been discussed when the analysis uses multiple sources of data in the stock assessment (*e.g*. CPUE and size composition data from multiple fleets in tuna fisheries). The change of weighting was helpful to some extent in this exercise, but it did not improve the fitness reasonably. So, further modification of the model or use of additional data especially on the krill abundance to capture a better relationship between predators and prey. The lack of fit might also be attributed partly to lack of spatial structure in the model and partly to lack of representativeness of assumed parameters and information on prey abundance.

Work plan and Recommendation for future works

1) Find a better set of fixed values if available
2) Use random effects to ease the parameter constraints by the allometric and bioenergetics reasoning
3) Add additional information on krill abundance (*e.g.* JARPA surveys)
4) Invent other sources of data on prey availability (*e.g.* time series of consumption in the commercial whaling period)
5) Modify the current models, especially the component of the functional response
6) Extend the study area to the whole of JARPA and JARPAII survey areas
7) Extend the model to incorporate spatial nature of prey and predators distribution patterns

COMPREHENSIVE (WHOLE-of-ECOSYSTEM) MODELLING via EwE FRAMEWORK

Mass-balancing

An initial step of the EwE approach is to take a mass-balance of component species (Ecopath), which also includes some key processes of 1) selection of the component functional groups, 2) collection and estimation of basic parameters such as biomass and production and consumption per unit biomass of each species, and 3) adjustment of input parameters by monitoring some indices so that the system can achieve a mass-balance.

For our exercise of ecosystem modelling for the Indian Ocean sector of the Antarctic Ocean (IWC management area: Area IV), we chose 27 functional groups, which consist of species from toothed and baleen whales to zoo- and phyto-planktons (see Table 2). We summarized the basic information for the mass-balance in Tables 2-6. The initial year of JARPA period (1989/90 season) is assumed to be the year when the mass-balance holds.

One notable feature in the model is that the Antarctic minke whale is classified into four functional groups depending on sex and maturity status (2-by-2 of mature/immature and male/female) to use information on the consumption by sex and maturity in addition to the natural whaling mortalities although some of the information could be revised based on the statistical catch-at-age (SCAA) analysis by Punt. Note that the information on the diet composition of minke and fin whales was obtained through JARPAII.

We also incorporated the killer whales as the apex predators into our ecosystem model by taking into consideration their ecotypes for providing information on their diet composition. Three ecotypes (Types A, B and C) are now recognized in the Antarctic and the feeding behavior is different by ecotype (Pitman and Ensor, 2003). Main diets of Types A, B and C are Antarctic minke whales, seals and fish, respectively. Killer whales in the Antarctic also feed on other baleen whales and penguins. These three types are distributed in the modelling area but the information on abundance and diet composition by type has not been documented. Therefore, the following diet composition of killer whales was initially assumed; baleen whales=10%, seals=29%, penguins=1%, Antarctic toothed fish 30%, other fish=20% and cephalopods=10%. However, because this diet composition led to an unbalanced mass-balance model, it was modified as shown in Table 2. This preliminary modelling exercise revealed the possible diet composition of killer whales in the Indian sector of the Antarctic although more reliable information is needed for the biomass and feeding ecology.

We calculated the Q/B values for each functional group of whales as follows. Q/B was assessed through the following formula, log Q/B = *a* + 0.75 * log *W*, where *E* = energy requirement per day (kcal/day), *a*= coefficient, and *W* = mean body weight (kg). The value for "*a*" is 317 for toothed whales, 192 for baleen whales (Perez *et al*., 1993) were applied. It was converted into KJ as 1 kcal= 4.186KJ. The baleen whales seasonally migrate between winter breeding areas in tropical or subtropical waters and summer feeding areas in the Southern Ocean (Horwood 1990). We calculated the prey consumption during the austral summer of baleen whales. We also assumed that immature and mature males spend 90days and mature females of Antarctic minke whales spend 120days, respectively. We assumed that feeding period in the Antarctic was 120days for other baleen whales. The energy value of Antarctic krill is 3,757kJ kg^{-1} (Tamura and Konishi, 2009).

We assumed 10% of the daily prey consumption was required during the non-feeding season. The daily food consumption of baleen whales is given by the following formula: (Daily prey consumption during feeding season) = 2.53*average prey consumption per year (=365days/(120days+245days*0.1)). This depends on the accuracy of Lockyer (1981) and Armstrong and Siegfried (1991)'s conclusion that 83% and 80% of the annual required energy intake for Southern Oceans occurs during the feeding season, respectively. Our estimation of prey consumption during the feeding season is 83.2% of annual prey consumption in the Southern Oceans.

We also assumed that the feeding period in the Antarctic was 120days for toothed whales. In addition to those values, some input values were extracted from Colette *et al*. (2012), in which the EwE model was developed for the Antarctic Peninsula.

Use of those values still did not work for mass-balancing. Especially, we faced some difficulty in collecting biomass information for lower trophic level species. For example, published abundance estimates of krill (*e.g*. Pauly *et al*. 2000) were only for open waters and therefore the estimated numbers in published papers might have severe negative biases. The squid, fish species (Myctophid, Paralepidid, and Nototheniid) and cephalopods have another sort of difficulty in weighing the bodies' mass and the published estimates tend to be underestimated. Given these situations, we tried to estimate the biomasses for those species groups by assuming some values of ecotrophic efficiency (EE). We then finally reached a mass-balance using our own values (see Tables 2 (a) and (b)). However, after the completion of this work, some estimates were changed for this review meeting. These we have not reflected these changes in this work, and therefore we should update the model (and the parameters) when conducting the following future works.

Work plan and Recommendation for future works

1) Some perturbation analysis to see if the mass-balance is vulnerable or not (*e.g*. Essington, 2007)
2) Conventional "Ecosim" fitting using available time series data (by estimating some vulnerability parameters)
3) Future projection based on the current whaling level and other scenarios
4) "Retrospective-Ecosim"type analysis from 1900 to 2100 by HITTING the levels of biomass to the mass-balanced biomass in 1989 and fitting the dynamics to the time series of abundance (estimate the initial biomass in 1900)
5) Information collection on diet composition of the toothed whales

DISCUSSION

In this paper, we have introduced our attempt to ecosystem modelling for species in Area IV. As illustrated, the two types of modelling approaches were employed. Although these works are still underway, the exercises have allowed us to realize that further information is helpful. For example, in the multiple-production model, time series of krill would have helped fitting the model if available. Also, the information on diet composition for the toothed whales might also be useful in the EwE works. The curse of dimension is common in the ecosystem modelling, but continuous efforts for obtaining data including new ones are necessary.

The works on ecosystem modelling is primarily to model competition among whale species and interaction with the krill, but it would also contribute to development of management objective and procedures. In the existing RMP implementation, any species interaction is not explicitly taken into account. However, some multispecies adjustment would contribute to improvement of operating models and harvest controls to make more effective use of this resource. The multi-species production model, which development is undergoing now in the Antarctic Ocean, must be a good tool to precede such process.

For example, the model could give some information on changes in carrying capacity and provide a scenario for running "RMP" simulation to see if the current single species CLA may or may not work under the changes in carrying capacity. This was a reason for our further development of multi-species production models. The EwE approach also has potential to provide different sorts of operating models with a broad range of species components for the management strategy evaluation in the Antarctic. In this regard, it might be possible to extend the JARPAII research objective toward work for linking ecosystem modelling with management with consideration on species interaction etc.

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Table 1

Summary of estimated and fixed parameters in the model (EC: equilibrium condition)

	Parameter	**Treatment**	**#parameters to be estimated**
Predators (5 species)	Initial population size in 1900/01 (P_0)	Estimated separately for whales Fixed for crabeater seals	4
	Natural mortality (M)	Fixed (b=0.03,f=0.03,h=0.05,m=0.05,c=0.09)	0
	Energy conversion (E)	A common coefficient (δ)	1
	Density dependence	Solved by EC	0
Prey (krill)	Initial population size in 1900/01 (B_0)	Estimated	1
	Intrinsic rate of increase (r)	Fixed at 0.5	0
	Carrying capacity (K)	Solved by EC	0
Functional response	Maximum consumption (c_{max})	A common coefficient (β):fixed	0
	Prey biomass at which a half of predator consumption attains (H)	Estimated separately	5
	Exponent (θ)	Fixed at 2 (Type III)	0
Stomach contents	Constant coefficient (a)	Estimated	1
	Model errors variance	Estimated	1

Table 2

Initial and final sets of basic input values for the Ecopath. The highlighted values were those solved from the simultaneous equation of the Ecopath. All the values for EE and P/Q showed to be less than 1, which is a possible justification of successful mass-balancing.

(a) An initial set (unbalanced)

Functional group	Trophic level	Biomass (t/km^2)	P/B	Q/B	EE	P/Q
Blue_whale	3.543	0.004	0.03	3.63	3.114	0.008
Fin_whale	3.549	0.010	0.03	4.23	2.527	0.007
Antarctic_minke_whale	3.549	0.238	0.03	7.22	0.854	0.004
Humpback_whale	3.549	0.062	0.03	4.92	0.204	0.006
Sperm_whale	4.379	0.050	0.06	3.59	0.000	0.017
Southern_bottlenose_whale	4.244	0.013	0.05	7.31	0.000	0.007
Killer_whale	4.674	0.018	0.03	4.11	0.000	0.006
Crabeater_seal	3.508	0.128	0.09	15.86	2.477	0.006
Ross_seal	4.167	0.013	0.13	15.30	1.442	0.008
Leopard_seal	4.010	0.009	0.12	9.95	0.717	0.012
Resident_flying_birds	3.941	0.004	0.34	14.88	0.720	0.023
Resident_penguins	3.465	0.098	0.27	29.83	0.688	0.009
Non_resident_flying_birds	3.941	0.002	0.34	7.44	0.758	0.046
Myctophid_fishes	3.196	0.012	1.35	3.73	4.426	0.362
Paralepidid_fishes	3.196	0.003	1.35	3.73	13.597	0.362
Nototheniid_fishes	3.792	0.004	0.53	2.18	138.393	0.241
Antarctic_toothfish	4.290	0.048	0.17	0.77	5.583	0.214
Other_fish	3.130	0.138	1.31	8.77	0.600	0.150
Cephalopds	3.357	1.151	0.95	2.00	0.653	0.475
Krill_adult	2.549	5.540	1.50	33.00	1.088	0.045
Copepods	2.220	3.354	26.07	50.00	0.950	0.521
Other_zooplankton	2.099	13.341	7.40	51.34	0.950	0.144
Phytoplankton	1	50.110	45.97		0.349	
Detritus	1	3.430			0.033	

(b) The final set (mass-balanced)

Functional group	Trophic level	Biomass (t/km^2)	P/B	Q/B	EE	P/Q
Blue_whale	3.543	0.004	0.03	3.63	0.174	0.008
Fin_whale	3.549	0.010	0.03	4.23	0.062	0.007
Minke_male_J	3.549	0.017	0.12	2.59	0.789	0.046
Minke_male_A	3.549	0.082	0.06	2.41	0.850	0.025
Minke_female_J	3.549	0.018	0.12	3.29	0.821	0.036
Minke_female_A	3.549	0.092	0.06	4.83	0.712	0.012
Humpback_whale	3.549	0.062	0.03	4.92	0.518	0.006
Sperm_whale	4.379	0.050	0.06	3.59	0.025	0.017
Southern_bottlenose_whale	4.244	0.013	0.05	7.31	0.116	0.007
Killer_whale	4.718	0.018	0.03	4.11	0.000	0.006
Crabeater_seal	3.508	0.128	0.09	15.86	0.932	0.006
Ross_seal	4.167	0.013	0.13	15.30	0.646	0.008
Leopard_seal	4.010	0.009	0.12	9.95	0.127	0.012
Resident_flying_birds	3.941	0.004	0.34	14.88	0.720	0.023
Resident_penguins	3.465	0.098	0.27	29.83	0.859	0.009
Non_resident_flying_birds	3.941	0.002	0.34	7.44	0.758	0.046
Myctophid_fishes	3.196	0.307	1.35	3.73	0.850	0.362
Paralepidid_fishes	3.196	0.100	1.35	3.73	0.750	0.362
Nototheniid_fishes	3.792	2.516	0.53	2.18	0.750	0.241
Antarctic toothfish	4.290	0.494	0.17	0.77	0.650	0.214
Other_fish	3.130	2.794	1.31	8.77	0.600	0.150
Cephalopods	3.357	1.248	0.95	2.00	0.653	0.475
Krill_adult	2.549	19.027	1.50	33.00	0.703	0.045
Copepods	2.220	11.734	26.07	50.00	0.950	0.521
Other_zooplankton	2.099	49.577	7.40	51.34	0.950	0.144
Phytoplankton	1.000	74.986	45.97		0.850	
Detritus	1.000	3.430			0.157	

Table 3

A diet composition matrix used in mass-balancing for the component species.

Baleen whales: Blue and Humpback whales: Nemoto (1970), Fin and Antarctic minke whales: JARPAII data.

Toothed whales: Sperm whales: Kawakami (1980), Southern bottlenose whales: Sekiguchi *et al.*(1993), Jefferson *et al.* (1993), Pauly *et al.* (1998). *Killer whales are referred to in text.

Seals: Crabeater and Ross seals: Southwell *et al.* (2012), *Leopard seals are referred to in text.

Other components: Colette *et al*. (2012), Pinkerton *et al*.(2010) etc.

	Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	Blue_whale	0	0	0	0	0	0	0	0	0	0.00028	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Fin_whale	0	0	0	0	0	0	0	0	0	0.00025	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Minke_male_J	0	0	0	0	0	0	0	0	0	0.02108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Minke_male_A	0	0	0	0	0	0	0	0	0	0.0463	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Minke_female_J	0	0	0	0	0	0	0	0	0	0.02108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	Minke_female_A	0	0	0	0	0	0	0	0	0	0.0463	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	Humpback_whale	0	0	0	0	0	0	0	0	0	0.01272	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	Sperm_whale	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	Southern_bottlenose_whale	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	Killer_whale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	Crabeater_seal	0	0	0	0	0	0	0	0	0	0.02567	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0
12	Ross_seal	0	0	0	0	0	0	0	0	0	0.00256	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0
13	Leopard_seal	0	0	0	0	0	0	0	0	0	0.00177	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	Resident_flying_birds	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0
15	Resident_penguins	0	0	0	0	0	0	0	0	0	0.07	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0
16	Non_resident_flying_birds	0	0	0	0	0	0	0	0	0	0	0	0	0.005	0	0	0	0	0	0	0	0	0	0	0	0
17	Myctophid_fishes	0	0	0	0	0	0	0	0.01	0.025	0	0.005	0.1	0.025	0.15	0	0.15	0	0	0.05	0.02	0	0.01	0	0	0
18	Paralepidid_fishes	0	0.00015	0.00015	0.00015	0.00015	0.00015	0	0.01	0.025	0	0.005	0.1	0.025	0.15	0	0.15	0	0	0.01	0	0	0	0	0	0
19	Nototheniid_fishes	0	0.00015	0.00015	0.00015	0.00015	0.00015	0	0.01	0.05	0	0.005	0	0.025	0.15	0.005	0.15	0	0	0.1	0.45	0	0.092	0	0	0
20	Antarctic toothfish	0	0	0	0	0	0	0	0.03	0.05	0.4	0	0	0	0	0	0	0	0	0	0	0	0.005	0	0	0
21	Other_fish	0	0	0	0	0	0	0	0.03	0.05	0.25	0	0	0.01	0.1	0.015	0.1	0	0	0.37	0.17	0	0.01	0	0	0
22	Cephalopods	0	0	0	0	0	0	0	0.91	0.6	0.1	0.01	0.65	0.2	0.01	0.1	0.01	0	0	0	0.17	0	0.01	0	0	0
23	Krill_adult	0.985	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995	0	0.2	0	0.825	0.06	0.2	0.3	0.48	0.3	0.15	0.15	0.15	0.04	0.07	0.128	0	0	0.005
24	Copepods	0.004	0	0	0	0	0	0	0	0	0	0.05	0.03	0	0.07	0	0.07	0.25	0.25	0.07	0	0	0	0.36	0	0.025
25	Other_zooplankton	0.011	0.0002	0.0002	0.0002	0.0002	0.0002	0.0005	0	0	0	0.1	0.06	0.19	0.07	0.4	0.07	0.6	0.6	0.25	0.15	0.93	0.745	0.1	0.2	0.055
26	Phytoplankton	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.52	0.75	0.85
27	Detritus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0.05	0.065

Table 4

A table of biomass estimates and their references.

Functional group	**Biomass (t/km^2)**	**Reference**	**Note**
Blue_whale	0.00406	Matsuoka *et al.* (2006), Trites and Pauly (1998)	JARPA 89/90
Fin_whale	0.01000	Matsuoka *et al.* (2006), Trites and Pauly (1998)	JARPA 89/90
Antarctic_minke_whale_M_juv	0.01725	Okamura and Kitakado (2012), Tamura and Konishi (2009)	IDCR/SOWER 88/89, raw weight data from JARPA
Antarctic_minke_whale_M_adul	0.08164	ditto	IDCR/SOWER 88/89
Antarctic_minke_whale_F_juv	0.01765	ditto	IDCR/SOWER 88/89
Antarctic_minke_whale_F_adul	0.09178	ditto	IDCR/SOWER 88/89
Humpback_whale	0.06200	Matsuoka *et al.* (2006), Tries and Pauly (1998)	JARPA 89/90
Sperm_whale	0.04986	Hakamada and Matsuoka (2014c), Tries and Pauly (1998)	JARPA 89/90
Southern_bottlenose_whale	0.01311	Hakamada and Matsuoka (2014c), Tries and Pauly (1998)	JARPA 89/90 - 03/04 weighted average
Killer_whale	0.01842	Hakamada and Matsuoka (2014c), Tries and Pauly (1998)	JARPA 89/90 - 03/04 weighted average
Crabeater_seal	0.12772	Southwell *et al* . (2008a)	99/00
Ross_seal	0.01276	Southwell *et al.* (2008b)	99/00
Leopard_seal	0.00881	Southwell *et al.* (2008c)	99/00
Resident_flying_birds	0.00358	Woehler (1997)	80/81 - 92/93
Resident_penguins	0.09766	Woehler (1997)	80/81 - 92/93
Non_resident_flying_birds	0.00170	Woehler (1997)	80/81 - 92/93
Myctophid_fishes	0.30742	EE: Colette *et al.* (2012)	Biomass was estimated by giving EE
Paralepidid_fishes	0.09964	EE: Colette *et al.* (2012)	Biomass was estimated by giving EE
Nototheniid_fishes	2.51635	EE: Colette *et al.* (2012)	Biomass was estimated by giving EE
Antarctic_toothfish	0.49386	EE: Colette *et al.* (2012)	Biomass was estimated by giving EE
Other_fish	2.79418	EE: Colette *et al.* (2012)	Biomass was estimated by giving EE
Cephalopds	1.24820	EE: Colette *et al.* (2012)	Biomass was estimated by giving EE
Krill_adult	19.02700	Murase *et al* . (2006)	JARPA 99/00
Copepods	11.73355	EE: Colette *et al.* (2012)	Biomass was estimated by giving EE
Other_zooplankton	49.57734	EE: Colette *et al.* (2012)	Biomass was estimated by giving EE
Phytoplankton	74.98559	EE: Colette *et al.* (2012)	Biomass was estimated by giving EE
Detritus	3.43000		Colette *et al* . (2012)

Table 5

A table of input values for P/B

Functional group	P/B	Reference	Note
Blue_whale	0.030		Assumed
Fin_whale	0.030		Assumed
Antarctic_minke_whale_M_juv	0.120	Mori and Butterworth (2006)	Referring estimate of M
Antarctic_minke_whale_M_adul	0.060	Mori and Butterworth (2006)	Referring estimate of M
Antarctic_minke_whale_F_juv	0.120	Mori and Butterworth (2006)	Referring estimate of M
Antarctic_minke_whale_F_adul	0.060	Mori and Butterworth (2006)	Referring estimate of M
Humpback_whale	0.030		Assumed
Sperm_whale	0.061	IWC (1980)	Referring estimate of M
Southern_bottlenose_whale	0.050		Assumed
Killer_whale	0.025	Colette *et al.* (2012)	
Crabeater_seal	0.090	Colette *et al.* (2012)	
Ross_seal	0.130	Colette *et al.* (2012)	
Leopard_seal	0.120	Colette *et al.* (2012)	
Resident_flying_birds	0.340	Colette *et al.* (2012)	
Resident_penguins	0.272	Colette *et al.* (2012)	
Non_resident_flying_birds	0.340		Use the value of "Resident_flying_birds"
Myctophid_fishes	1.350	Colette *et al.* (2012)	
Paralepidid_fishes	1.350		Use the value of "Myctophid_fishes"
Nototheniid_fishes	0.526	Colette *et al.* (2012)	
Antarctic_toothfish	0.165	Colette *et al.* (2012)	
Other_fish	1.312	Pinkerton *et al.* (2010)	
Cephalopds	0.950	Colette *et al.* (2012)	
Krill_adult	1.500	Colette *et al.* (2012)	
Copepods	26.066	Colette *et al.* (2012)	
Other_zooplankton	7.400	Colette *et al.* (2012)	
Phytoplankton	45.973	Wright *et al.* (2010), Strutton *et al.* (2000)	
Detritus			

Table 6

A table of input values for Q/B

Functional group	Q/B	Reference	Note
Blue_whale	3.625		See main text
Fin_whale	4.227		See main text
Antarctic_minke_whale_M_juv	2.586	Tamura and Konishi (2009)	
Antarctic_minke_whale_M_adul	2.412	Tamura and Konishi (2009)	
Antarctic_minke_whale_F_juv	3.289	Tamura and Konishi (2009)	
Antarctic_minke_whale_F_adul	4.827	Tamura and Konishi (2009)	
Humpback_whale	4.915		See main text
Sperm_whale	3.592		See main text
Southern_bottlenose_whale	7.311		See main text
Killer_whale	4.115		See main text
Crabeater_seal	15.860	Colette *et al.* (2012)	
Ross_seal	15.300	Colette *et al.* (2012)	
Leopard_seal	9.950	Colette *et al.* (2012)	
Resident_flying_birds	14.880	Colette *et al.* (2012)	
Resident_penguins	29.832	Colette *et al.* (2012)	
Non_resident_flying_birds	7.440		Use a half value of "Resident_flying_birds"
Myctophid_fishes	3.730	Colette *et al.* (2012)	
Paralepidid_fishes	3.730		Use the value of "Myctophid_fishes"
Nototheniid_fishes	2.180	Colette *et al.* (2012)	
Antarctic_toothfish	0.770	Colette *et al.* (2012)	
Other_fish	8.770	Pinkerton *et al.* (2010)	
Cephalopds	2.000	Colette *et al.* (2012)	
Krill_adult	33.000	Colette *et al.* (2012)	
Copepods	50.000	Colette *et al.* (2012)	
Other_zooplankton	51.345	Colette *et al.* (2012)	
Phytoplankton			
Detritus			

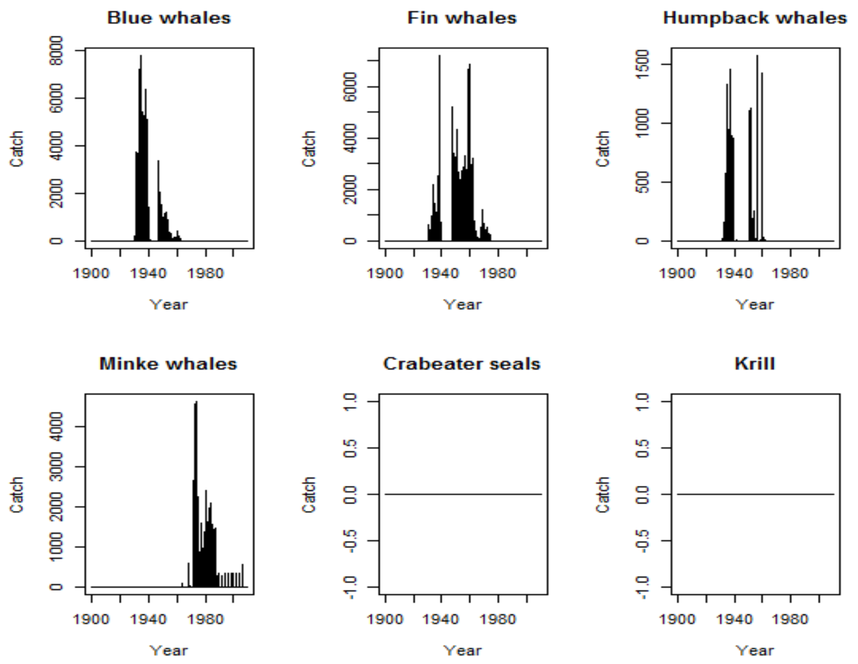

Figure 1. Catch series for component species.

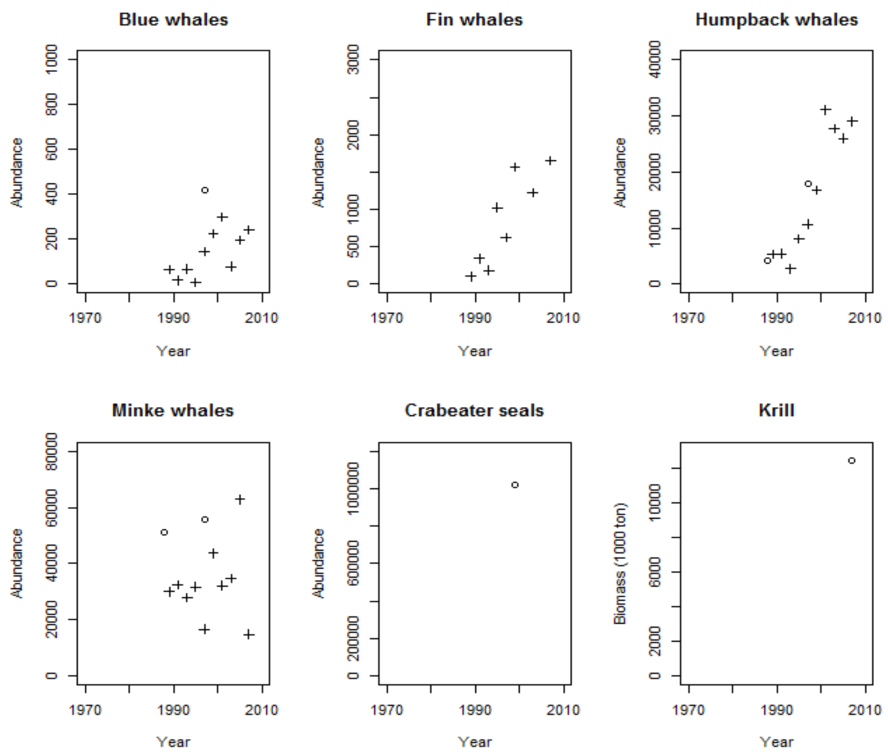

Figure 2. Time series of abunance estimates used in this analysis. The circles for the baleen whales show estimates from IDCR/SOWER surveys, and the crosses are for those from the JARPA and JARPAII surveys.

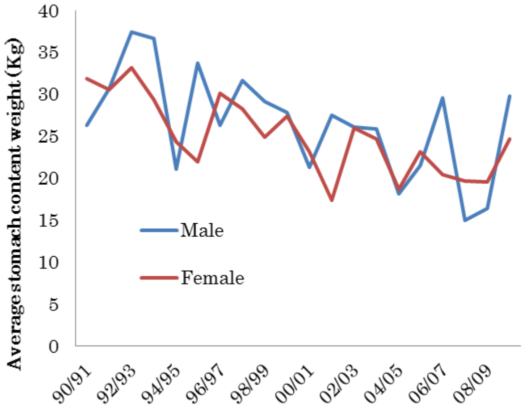

Figure 3. Time series of the average stomach contents weight of minke whales (mature individuals) in Area IV. An averaged trend was used for the fitting