

## A BALANCED MODEL OF THE FOOD WEB OF THE ROSS SEA, ANTARCTICA

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### Abstract

A quantitative food web of the Ross Sea is presented here as a step towards investigating ecosystem effects of the fishery for Antarctic toothfish (*Dissostichus mawsoni*). The model consolidates quantitative information on trophic links across all the major biota of the Ross Sea and tests for data consistency. The model has 38 trophic groups and is balanced in terms of annual flows of organic carbon in an average recent year (1990–2000). The focus of the model is on the role of Antarctic toothfish in the food web which means that the model has greater taxonomic resolution towards the top of the food web than the base. A survey of the available literature and both published and unpublished data provided an initial set of parameters describing the annual average abundance, imports, exports, energetics (growth, reproduction, consumption) and trophic linkages (diets, key predators) for each model group. The relative level of uncertainty on these parameters was also estimated. This set of parameters was not self consistent, and a method is described to adjust the initial parameter set to give a balanced model, taking into account the estimates of parameter uncertainty and the large range of magnitude (>6 orders of magnitude) in trophic flows between groups. Parameters for biomass, production rate, growth efficiency, diet fractions and other transfers of biomass between groups were adjusted simultaneously. It was found that changes to the initial set of parameters needed to obtain balance were reasonably small for most groups and most parameters. The mean absolute change for all key parameters (biomass, production rate, growth efficiency) and all groups together was 1.7%, and for diet fractions was 0.6%. Large but not implausible changes in biomass, production/biomass and production/consumption parameters were needed to balance the microzooplankton (34–47%), ice bacteria (61–72%), and ice protozoa (24–54%), components of the model. Trophic levels are in close agreement with those derived from isotope and other ecosystems. In the balanced model, there is only enough large (>100 cm) toothfish production to satisfy 6.5% of the diet of Weddell seals, 5.6% of the diet of orca and 2.6% of the diet of sperm whales. The model does not support the hypothesis that depletion of Antarctic toothfish by fishing would change the diet of predators of toothfish (Weddell seals, orca, sperm whales) by large amounts throughout the Ross Sea, though the importance of toothfish as prey items to these predators is not tested and requires further investigation. The model shows that large toothfish consume 61% of the annual production of medium-sized demersal fishes and 14% of the annual production of small demersal fishes, implying a potential for the fishery to affect these prey through trophic cascades. There is a need to establish monitoring of medium and small demersal fishes in the Ross Sea, and to model potential changes to these groups due to the fishery.

### Résumé

Un réseau trophique quantitatif de la mer de Ross est présenté ici en vue de l'étude des effets sur l'écosystème de la pêche de légine antarctique (*Dissostichus mawsoni*). Les informations quantitatives sur les liens trophiques de tous les principaux types de biote de la mer de Ross sont consolidées dans le modèle qui teste la cohérence des données. Le modèle porte sur 38 groupes trophiques et est équilibré en ce qui concerne les flux de carbone organique en une année moyenne récente (1990–2000). L'accent y est mis sur le rôle de la légine antarctique dans le réseau trophique, ce qui explique pourquoi le modèle a une plus grande résolution taxonomique vers le sommet du réseau trophique qu'à la base. Un examen de la littérature disponible et des données tant publiées qu'inédites a permis d'obtenir une première série de paramètres décrivant la moyenne annuelle de l'abondance, des importations, des exportations, de l'énergétique (croissance, reproduction,

consommation) et des liens trophiques (régime alimentaire, prédateurs clés) pour chaque groupe du modèle. Le niveau d'incertitude relative de ces paramètres est également estimé. Ce jeu de paramètres n'étant pas autocohérent, une méthode est décrite pour ajuster la série initiale de paramètres afin de donner un modèle équilibré qui tienne compte des estimations de l'incertitude des paramètres et de la magnitude considérable (>6 ordres de magnitude) des flux trophiques d'un groupe à l'autre. Les paramètres de biomasse, taux de production, efficacité de la croissance, proportions du régime alimentaire et autres transferts de biomasse entre les groupes ont été ajustés simultanément. Il est apparu que les changements apportés à la série initiale de paramètres, nécessaires pour obtenir un équilibre, étaient raisonnablement faibles pour la plupart des groupes et des paramètres. Le changement absolu moyen pour tous les paramètres clés (biomasse, taux de production, efficacité de la croissance) et tous les groupes réunis était de 1,7%, et pour les proportions du régime alimentaire, il était de 0,6%. Des changements importants mais pas impossibles des paramètres de biomasse, production/biomasse et production/consommation étaient nécessaires pour équilibrer diverses composantes du modèle : le micro-zooplancton (34–47%), les bactéries des glaces (61–72%) et les protozoaires des glaces (24–54%). Les niveaux trophiques présentent une bonne concordance avec ceux dérivés des isotopes et d'autres écosystèmes. Selon le modèle équilibré, la production de légine de grande taille (>100 cm) suffit tout juste à satisfaire 6,5% du régime alimentaire du phoque de Weddell, 5,6% de celui de l'orque et 2,6% de celui du cachalot. Le modèle ne corrobore pas l'hypothèse selon laquelle l'épuisement de la légine antarctique par la pêche modifierait grandement le régime alimentaire des prédateurs de légine (phoques de Weddell, orques, cachalots) dans l'ensemble de la mer de Ross, mais l'importance de la légine en tant que proie de ces prédateurs n'a pas été testée et demande toujours à être étudiée. Selon le modèle, les légines de grande taille consomment 61% de la production annuelle des poissons démersaux de taille moyenne et 14% de celle des poissons démersaux de petite taille. Il n'est donc pas impossible que la pêche affecte ces proies par effet de cascade sur le réseau trophique. Il est nécessaire de mettre en place un suivi des poissons démersaux de taille moyenne et de petite taille dans la mer de Ross et de modéliser les changements que la pêche pourrait provoquer sur ces groupes.

#### Резюме

Здесь представлена количественная модель трофической сети моря Росса, которая является шагом вперед в исследовании экосистемных последствий промысла антарктического клыкача (*Dissostichus mawsoni*). Эта модель объединяет количественную информацию о трофических связях между всеми основными организмами моря Росса и проверяет данные на согласованность. Модель включает 38 трофических групп и сбалансирована в плане годовых потоков органического углерода за средний год в последнее время (1990–2000 гг.). Модель концентрируется на роли антарктического клыкача в трофической системе, что означает ее более высокое таксономическое разрешение ближе к вершине трофической сети, чем к основанию. В результате обзора имеющейся литературы и опубликованных и неопубликованных данных был получен изначальный набор параметров, описывающих среднюю годовую численность, импорт, экспорт, энергетику (рост, воспроизводство, потребление) и трофические связи (рацион, основные хищники), для каждой модельной группы. Был также оценен относительный уровень неопределенности этих параметров. Этот набор параметров не был самосогласованным, поэтому описывается метод по корректировке изначального набора параметров для получения сбалансированной модели с учетом оценок неопределенности параметров и большого диапазона величин (>6 порядков величин) трофических перемещений между группами. Параметры биомассы, продуктивности, эффективности роста, компонентов рациона и других видов перемещения биомассы между группами были откорректированы одновременно. Оказалось, что изменения к изначальному набору параметров, необходимому для достижения баланса, были сравнительно небольшими для большинства групп и большинства параметров. Среднее абсолютное изменение для всех ключевых параметров (биомассы, продуктивности, эффективности роста) и всех групп вместе взятых равнялось 1,7%, а для компонентов рациона – 0,6%. Большие, но не невозможные изменения параметров биомассы, продукции/биомассы и продукции/потребления потребовались для уравновешивания таких компонентов модели, как микрзоопланктон (34–47%), ледовые бактерии (61–72%) и ледовые

простейшие (24–54%). Трофические уровни близко соответствуют тем, которые были получены по изотопам и по другим экосистемам. В сбалансированной модели производство крупных особей клыкача (>100 см) обеспечивает только 6.5% рациона тюленей Уэдделла, 5.6% рациона косаток и 2.6% рациона кашалотов. Модель не подтверждает гипотезу о том, что истощение запасов антарктического клыкача в результате промысла в значительной степени изменит рацион питающихся клыкачом хищников (тюленей Уэдделла, косаток, кашалотов) в море Росса, хотя значимость клыкача как добычи для этих хищников не проверялась и необходимы дальнейшие исследования. Модель показывает, что крупный клыкач потребляет 61% годовой продукции демерсальных рыб среднего размера и 14% годовой продукции мелких демерсальных рыб, давая основания полагать, что промысел может воздействовать на эти виды добычи через трофические каскады. Необходимо вести мониторинг средних и мелких демерсальных рыб в море Росса и моделировать потенциальные изменения в этих группах, вызванные промыслом.

#### Resumen

Se presenta un modelo cuantitativo de la red alimenticia del Mar de Ross, con el fin de avanzar en el estudio de los efectos de la pesquería de austromerluza antártica (*Dissostichus mawsoni*) en el ecosistema. El modelo consolida la información cuantitativa sobre los enlaces tróficos entre todos los principales componentes de la biota del Mar de Ross y pone a prueba la coherencia de los datos. El modelo consta de 38 grupos tróficos y es balanceado en términos del flujo anual de carbono orgánico en un año promedio reciente (1990–2000). El foco del modelo es el papel de la austromerluza antártica en la red alimenticia, y esto significa que el modelo tiene mayor resolución taxonómica hacia el tope de la red que en su base. La revisión de la literatura disponible y de los datos tanto publicados como inéditos proporcionó un conjunto inicial de parámetros que describen la abundancia anual promedio, importaciones, exportaciones, energética (crecimiento, reproducción, consumo) y enlaces tróficos (dietas, depredadores tope) para cada grupo del modelo. Asimismo, se estimó el nivel relativo de incertidumbre de dichos parámetros. Los parámetros del conjunto inicial no concordaban, y se describe un método para ajustarlo y producir un modelo balanceado, tomando en cuenta las estimaciones de la incertidumbre de los parámetros y la amplia gama de magnitudes (>6 órdenes de magnitud) de los flujos tróficos entre los grupos. Los parámetros para la biomasa, tasa de producción, eficiencia del crecimiento, porciones de la dieta y otras transferencias de biomasa entre los grupos fueron ajustados simultáneamente. Se encontró que los cambios requeridos al conjunto inicial de parámetros para balancear el modelo fueron razonablemente pequeños para la mayoría de los grupos y de los parámetros. El cambio absoluto promedio de todos los parámetros principales (biomasa, tasa de producción, eficiencia del crecimiento) y de todos los grupos combinados fue de 1.7%, y de 0.6% para las porciones de la dieta. El balance de ciertos componentes del modelo requirió grandes (pero no inverosímiles) cambios de los parámetros representativos de biomasa, producción/biomasa y producción/consumo: 34–47% para el microzooplancton, 61–72% para las bacterias del hielo y 24–54% para los protozoos del hielo. Los niveles tróficos concuerdan estrechamente con los niveles derivados de isótopos y de otros ecosistemas. En el modelo en equilibrio, la producción de ejemplares grandes de austromerluzas (>100 cm) sólo es suficiente para satisfacer el 6.5% de la dieta de las focas de Weddell, 5.6% de la dieta de las orcas y 2.6% de la dieta de cachalotes. El modelo no concuerda con la hipótesis de que la reducción de austromerluza antártica debido a la pesca cambiaría la dieta de los depredadores de este pez (focas de Weddell, orcas, cachalotes) en cantidades considerables en todo el a través del Mar de Ross; no obstante, aún cuando la importancia de la austromerluza como especie presa de estos depredadores no ha sido probada y requiere de estudios adicionales. El modelo muestra que las austromerluzas grandes consumen 61% de la producción anual de peces demersales de tamaño mediano y 14% de la producción anual de peces demersales pequeños, lo que sugiere que la pesquería tiene el potencial de afectar estas presas a través de las cascadas tróficas. Es necesario establecer el seguimiento de peces demersales de tamaño mediano y pequeño en el Mar de Ross, y modelar los cambios potenciales de estos grupos ocasionados por la pesquería.

Keywords: Ross Sea, trophic model, food web, Antarctic toothfish, mass balance, inverse modelling, ecosystem model, CCAMLR

## Introduction

A huge amount of research has been conducted on the fauna of the Ross Sea leading to complex qualitative descriptions of food-web structure (Smith et al., 2007). The development of a quantitative, balanced trophic ecosystem model of the Ross Sea shelf and slope is reported here which formalises the understanding of food-web structure and tests data consistency. The food-web model presented is a revised version of Pinkerton et al. (2007a, 2008a) and includes several key apex predators, including Weddell seals (*Leptonychotes weddelli*), orca/killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*), as separate model groups. The model is an important step towards understanding the potential effects of the fishery for Antarctic toothfish (*Dissostichus mawsoni*) on the Ross Sea ecosystem. It is known that fisheries impact other parts of the ecosystem as well as the target species, both directly from by-catches, and indirectly by altering the species composition and inter-specific relationships within the ecosystem through trophic effects, that is, by one species feeding on another (Myers et al., 2007; Daskalov et al., 2007; Heithaus et al., 2008; Casini et al., 2009). Long-term sustainable use of the Ross Sea toothfish fishery resource requires an understanding of the effects of fishing on species that are directly impacted (target species and by-catch species), and on other species through indirect effects of fishing (Pinkerton, 2007b). As a first step in investigating the indirect ecosystem effects of the fishery, it is fundamental to describe quantitatively the structure of the food web before commercial fishing could have affected it. The longline fishery in the Ross Sea began in summer 1996/97, but total removals of toothfish before January 2000 were relatively small (<350 tonnes; Hanchet et al., 2007). The aim of the present study is to model an average or typical year, representative of the state of the Ross Sea food web during the period 1990–2000. Research carried out in the Ross Sea outside this period was also used to estimate parameters for the model where appropriate. A recent stock assessment model (Dunn and Hanchet, 2009) estimated the 2009 biomass of sexually mature Antarctic toothfish in the Ross Sea stock to be 79.9% (95% confidence intervals: 77.7–82.2%) of the virgin (unfished) biomass, so that changes from the unfished state may be relatively small as yet.

The modelling approach used here is based on food-web modelling approaches used extensively throughout the world (e.g. Christensen and Pauly, 1992; Mendoza, 1993; Wolff, 1994; Jarre-Teichmann et al., 1997, 1998; Arreguin-Sanchez et al., 2002; Cornejo-Donoso and Antezana, 2008). Such models provide a unifying framework to bring together

varied field data and literature information to give a self-consistent picture of the trophic structure of a given ecosystem. Deficiencies in knowledge on abundances, energetics and predator–prey relationships between organisms mean that model parameters estimated from the primary literature tend not to be self consistent so that expert opinion and/or numerical techniques are used to adjust the initial set of parameters. The need for more objective adjustment of parameters has been identified (Kavanagh et al., 2004; Plagányi, 2007) and led to the development of a method to search for a balanced (feasible) mass balance model taking into account the huge differences in the magnitudes of trophic flows in the system, and respecting differences in uncertainty between parameters (Pinkerton et al., 2008c). Further developments to the method to objectively balance the model are presented here. The balanced model presented here is evaluated through comparison of the trophic levels (TLs) calculated from this model, other models and with TLs estimated from stable isotope data. Finally, the plausibility of the model overall is evaluated and it is used to investigate the role of Antarctic toothfish in the system and the potential for ecosystem effects of the fishery.

## Material and methods

### Study area

The Ross Sea defined for this work is bounded to the north by the 3 000 m depth contour and by the 69°S line of latitude; to the south by the permanent ice shelf; to the east and west by land, and the 160°W and 170°E meridians (Figure 1). The total area of the study region is c. 637 000 km<sup>2</sup>. The bathymetry in the region, taken from Davey (2004), shows that 29% of the study region is shallower than 500 m, 41% of the region has depths 500–1 000 m, and 30% is deeper than 1 000 m. This region was chosen for a number of reasons. The 3 000 m bathymetric contour approximates the location of the Antarctic Slope Front (Jacobs, 1991) which, in part at least, hydrodynamically separates the study region from the rest of the Southern Ocean (Jacobs, 1991; Langone et al., 1998; Dinniman et al., 2003). The study region covers the main fishing grounds for adult Antarctic toothfish, comprising small-scale research units (SSRUs) 881H–M, and some of SSRU 882A (Figure 1). Based on commercial catch and modelling data, it is estimated that the study area contains 86% of the biomass of toothfish in the Ross Sea stock (Dunn and Hanchet, 2009; Hanchet et al., 2007). There is no fishery take in the model as the ecosystem before fishing started is being represented. The study region encompasses the intense localised burst of primary production

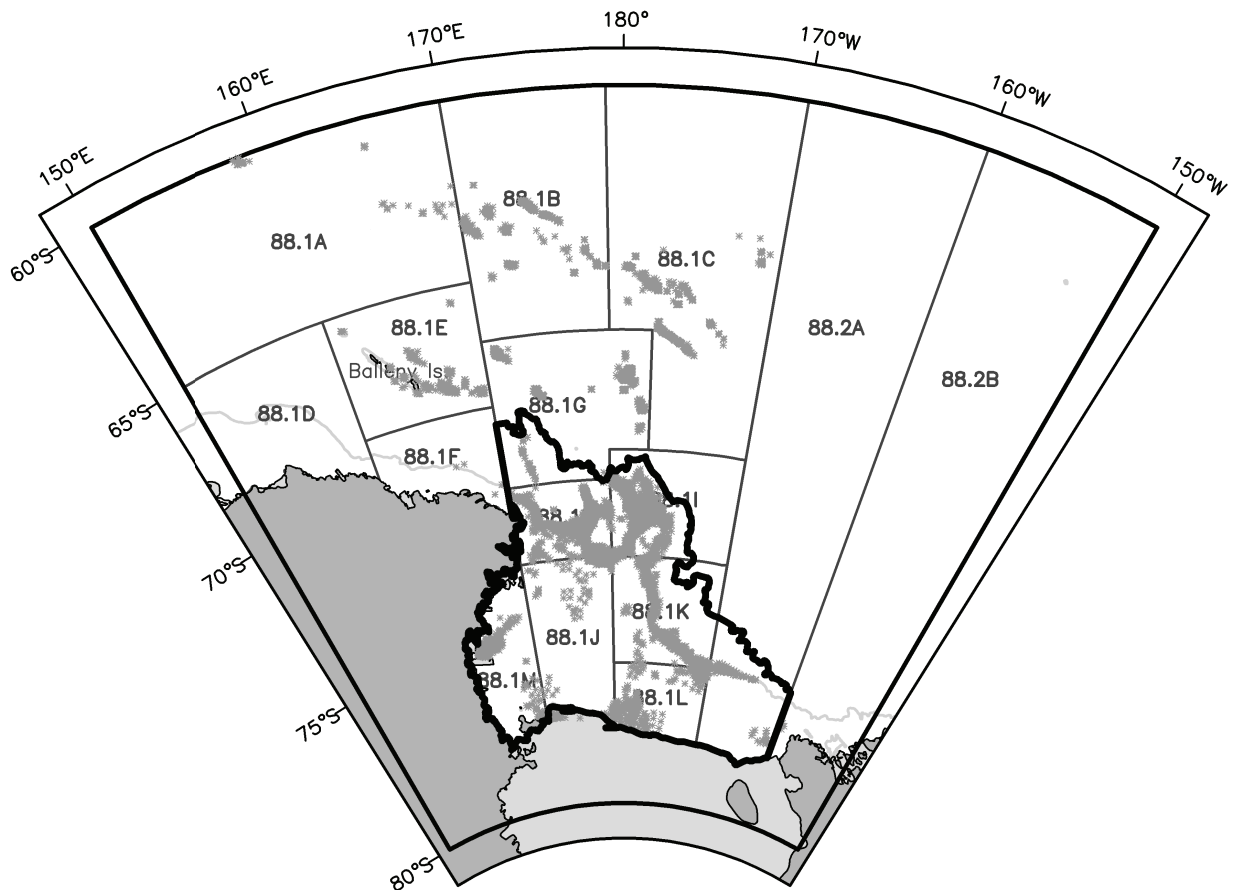


Figure 1: The model study area is shown in black. The study area is bounded by the 3 000 m depth contour, by the 69°S line of latitude, by the permanent ice shelf, land, and the 170°E and 160°W meridians. Grey stars show where Antarctic toothfish are caught by the fishery. The CCAMLR fishing areas (Subareas 88.1 and 88.2), and small-scale research units are shown.

associated with the Ross Sea polynya adjacent to the permanent ice shelf (Zwally et al., 1985; Kurtz and Bromwich, 1985; Arrigo and van Dijken, 2004). Finally, the study region is similar to that used in other Ross Sea studies (e.g. Ichii, 1990; Ichii et al., 1998; Anderson, 2000; Ainley, 2002), allowing the use of published information even when access to the base data is not available. The ecosystem below the permanent Ross ice shelf is excluded, assuming that it plays a small role in the ecosystem of the larger Ross Sea region.

### Trophic groups

The model has 38 trophic groups representing all major biota of the Ross Sea (Table 1). There are 34 non-detrital groups including two primary producers (phytoplankton and epontic algae) and four detrital groups (carcasses, water-column detritus, ice detritus, benthic detritus). Macroalgae, whilst important in some coastal regions of the Ross Sea (Norkko et al., 2004) is estimated to be unimportant

to flows of material at the scale of the model. Detailed information on biota within each group is given in the supporting documentation, and summarised under 'Discussion' (below). Trophic groups are chosen taking into account the quality and quantity of appropriate information, the purpose of the model, and the trophic similarity of the organisms. It is inevitable that the use of relatively few groups to cover the entire gamut of Ross Sea biota will make the choice of groupings somewhat of a compromise. Many of the lower and middle TL biota are grouped, whereas the upper predators tend to be treated in more taxonomic detail to maintain focus on the role of Antarctic toothfish in the food web. The divisions used include species or groups of species, function (e.g. water column primary producers), size (e.g. small, medium and large demersal fish) and sampling methodology (e.g. benthic organisms by size). Organisms grouped together always have similar energetic characteristics and, where possible, have similar prey items and predators.

## Model structure

The trophic model developed here quantifies the transfer of organic material through a food web based on the widely used mass-balance identities of the Ecopath trophic model (Christensen and Walters, 2004; Christensen et al., 2005). Biomass is presented in units of organic carbon density ( $\text{gC m}^{-2}$ ) and trophic flows in units of  $\text{gC m}^{-2} \text{y}^{-1}$ . In quantifying the trophic structure of the ecosystem, the fundamental information includes the species present, abundances in terms of weight, the energetics of species (i.e. production, consumption, growth efficiency, respiration), and trophic inter-connections between species through information on diets of predators. The model developed here also includes non-trophic transfers of organic carbon between groups. These transfers include: (i) unassimilated consumption (excreted material); (ii) loss of material through exudants (e.g. primarily phytoplankton); (iii) non-predation mortality (e.g. due to age, disease, starvation); (iv) ‘messy eating’ i.e. parts of animals that died due to predation but were not consumed at the time; (v) transfers of biota from the sea-ice habitat to the water column on melting of sea-ice in the spring; (vi) growth of biota which takes them from a smaller to a larger trophic group; (vii) vertical sinking flux of detritus from the water column to the benthos; (viii) long-term burial of organic material in the benthic sediments. Note that (ii)+(iii)+(iv) are often described by an ecotrophic efficiency parameter.

Production is defined according to equation (1). For non-detrital groups, production represents the intrinsic rate of growth of all individuals in the population. For detrital groups, production is the total net flow of organic matter into the group, including faecal material (unassimilated consumption) from consumers, dead organisms, non-consumed predation (‘messy eating’), planktonic exudants and transfers between groups. These latter transfers include, for example, the release of organic material into the water column when ice melts, and the sinking of detrital/ungrazed material to the benthos. Carbon flow through each trophic group per year is balanced according to equation (2) under the assumption that all parts of the ecosystem will be in balance in an average year. These balance equations provide 38 equality constraints to the system. Another 32 equality constraints are provided by the fact that diet fractions of each predator sum to unity.

$$P_i = B_i \left( \frac{P}{B} \right)_i$$

Non-detrital groups (1a)

$$P_j = \sum_{i=1}^n P_i \left[ T_{ij}^{1-E} + U_{ij} \left( \frac{Q}{P} \right)_i + T_{ij}^s \right]$$

Detrital groups (1b)

$$P_i \left[ 1 - \sum_{j=1}^n (T_{ij}^{1-E} + T_{ij}^g + T_{ij}^s) - X_i - A_i \right] - \sum_{j=1}^n P_j \left( \frac{Q}{P} \right)_j D_{ij} - F_i = 0$$

All groups (2)

In these and other equations in this paper, for trophic group  $i$ :

- $B_i$  annual average biomass ( $\text{gC m}^{-2}$ );
- $P_i$  annual production ( $\text{gC m}^{-2} \text{y}^{-1}$ ). Autotrophic production rate is net of respiration but assumed to include production of phytoplankton exudants and other detrital material;
- $Q_i$  annual consumption ( $\text{gC m}^{-2} \text{y}^{-1}$ ). Note that autotrophs and detritus have  $Q_i = 0$ ;
- $(P/B)_i$  production/biomass ratio ( $\text{y}^{-1}$ );
- $(Q/P)_i$  reciprocal of the growth efficiency (dimensionless);
- $D_{ij}$  average fraction of prey  $i$  in the diet of predator  $j$  by weight (dimensionless);
- $X_i$  fraction of production exported over a year due to advection and migration (dimensionless);
- $A_i$  fraction of production accumulated over a year (dimensionless);
- $F_i$  fishing removals ( $\text{gC m}^{-2} \text{y}^{-1}$ ). Note that  $F_i = 0$  for all groups in the Ross Sea model;
- $T_{ij}^{1-E}$  detrital transfer: fraction of production transferred from group  $i$  to detrital group  $j$  as non-living material, i.e. excluding direct predation but including phytoplankton exudants, parts of organisms (e.g. due to ‘messy eating’), whole dead organisms and carcasses (dimensionless);
- $T_{ij}^g$  growth transfer: fraction of production transferred from group  $i$  to group  $j$  due to growth,

i.e. as an organism gets older and/or larger it changes from one group to another (dimensionless);

|            |   |
|------------|---|
| $T_{ij}^s$ | seasonal transfer: fraction of production transferred from group $i$ to group $j$ by non-trophic, seasonal processes, e.g. due to ice melting, vertical flux of material (dimensionless); |
| $U_{ij}$   | fraction of food that has been consumed by component $i$ but which is not assimilated, instead being passed to detrital group $j$ (dimensionless);  |
| $n$        | total number of groups in the model;  |
| $R_i$      | loss of organic carbon from the system due to respiration ( $\text{gC m}^{-2} \text{y}^{-1}$ ). Respiration can be calculated as $R_i = Q_i \cdot (1 - U_i) - P_i$ .                      |

Equations (1) and (2) differ from the standard Ecopath equations (Christensen and Walters, 2004; Christensen et al. 2004) as follows. First, consumption is parameterised based on production and  $Q/P$ , the reciprocal of the growth efficiency, rather than being based on  $B$  and  $Q/B$ . This is done so that during model balancing,  $P/B$  and  $Q/B$  cannot vary independently and give unrealistic growth efficiencies. Second, the factor  $T_{ij}^{1-E}$  is used instead of the Ecopath ecotrophic efficiency parameter,  $EE_i$ , and is defined such that  $T_{ij}^{1-E} = (1 - EE_i)$ . This factor quantifies the fraction of production which is transferred from a living to detrital group(s) by processes other than unassimilated consumption. For example, it is known that a substantial part of primary organic material (i.e. phytoplankton and epontic algae) is not directly consumed but enters the detrital pool where it is decomposed by bacterial action. The proportion of net primary production undergoing these fates is given by the  $P \cdot T^{1-E}$  term for the phytoplankton group. Third, two new non-trophic transfer parameters are included: growth and seasonal transfers ( $T_{ij}^g, T_{ij}^s$ ). Growth transfer allows organisms to move between model groups as they grow (e.g. small fish becoming medium-sized fish). Seasonal transfers include physical movement of material between groups, for example, settling of water column detritus to form benthic detritus. Neither seasonal or growth transfer processes can easily be represented in standard Ecopath equations.

## Parameter estimation

There is a huge amount of information on the physical environment of the Ross Sea, and its flora and fauna, including physiology, life histories, energetics and ecology. Estimating the 225 non-zero biomass, energetic and transfer parameters and 195 non-zero diet fractions constitutes a major part of the work presented here. Initial information on the estimation of the biomass, energetic parameters, and diets for each trophic group is given in Pinkerton et al. (2006) which lists over 700 references. Since this report was completed, several sections have been revised and the current set of documentation applicable to the model presented here is available online from the *CCAMLR Science* website<sup>1</sup> and from the NIWA website<sup>2</sup>. Results from research on various parts of the Ross Sea ecosystem become available constantly and no trophic model should ever be considered final. Specifically, new information from the IPY-CAML voyage to the Ross Sea (Hanchet et al., 2008) will provide data requiring parameters in the model to be revised. Nevertheless, the authors feel that the parameters obtained here represent a detailed up-to-date and appropriate summary of the state of available information to date. The initial parameter estimates are summarised in Tables 1 and 2.

## Balancing methodology

Each of the model parameters initially estimated has an associated uncertainty because the values are imperfectly and incompletely observed, and because the parameters vary between years and hence differ from the average recent year modelled here. Hence the preliminary estimates of all parameters were adjusted to obtain a model where all the equality constraints are fulfilled. Such solutions are henceforth referred to as balance points. All parameters were allowed to vary except fishing take ( $F$ ) which is fixed at zero. Models such as this are highly under-constrained, with >3 times more parameters to fit than constraints (Pinkerton et al., 2008c), so there is a large family of possible solutions, all of which are feasible according to the conceptual model. This study aims to find the solution that is 'closest' to the initial set of estimated parameters as defined below. The problem at this stage is non-linear and an iterative approach to search for this solution by simultaneously adjusting all parameters was adopted. The system is first linearised and then singular value decomposition (SVD) (Press et al., 1992) is applied to find the adjustment vector which minimises the cost

<sup>1</sup> [www.ccamlr.org/ccamlr\\_science/Vol17SuppDocs.htm](http://www.ccamlr.org/ccamlr_science/Vol17SuppDocs.htm)

<sup>2</sup> [www.niwa.co.nz/our-science/oceans/research-projects/all/the-ross-sea-trophic-model](http://www.niwa.co.nz/our-science/oceans/research-projects/all/the-ross-sea-trophic-model)

function,  $\Delta$  (equation 3). This balance point is the closest one to the initial parameter set taking into account relative uncertainties between parameters and ensuring even adjustment across groups in the model.

$$\Delta^2 = \sum_{\text{all } i} \left[ \delta B_i^2 + \delta \left( \frac{P}{B} \right)_i^2 + \delta \left( \frac{Q}{P} \right)_i^2 + \delta X_i^2 + \delta A_i^2 + \delta U_{ij}^2 \right] + \sum_{\text{all } i,j} \left[ \delta D_{ij}^2 + \left( \delta T_{ij}^{1-E} \right)^2 + \left( \delta T_{ij}^{g2} \right)^2 + \left( \delta T_{ij}^{s2} \right)^2 \right] \quad (3)$$

Where the parameters  $\delta B_i$ ,  $\delta(P/B)_i$  etc. represent the changes to the parameter needed to achieve model balance. These changes are assumed to be small, and defined below. In equations (4) to (13), using export as an example,  $X_i'$  is the value of export that causes the model to balance, and  $X_i$  is the starting value (initial estimate of value from the literature and data). The family of dimensionless  $K$  parameters represents the relative uncertainty between parameters, with high  $K$  values representing greater uncertainty.

Biomass

$$B_i' = B_i + B_i^s \cdot K_i^B \cdot \delta B_i \quad (4)$$

Production

$$\left( \frac{P}{B} \right)_i' = \left( \frac{P}{B} \right)_i + \left( \frac{P}{B} \right)_i^s \cdot K_i^P \cdot \delta \left( \frac{P}{B} \right)_i \quad (5)$$

Growth efficiency<sup>-1</sup>

$$\left( \frac{Q}{P} \right)_i' = \left( \frac{Q}{P} \right)_i + \left( \frac{Q}{P} \right)_i^s \cdot K_i^{QP} \cdot \delta \left( \frac{Q}{P} \right)_i \quad (6)$$

Export fraction

$$X_i' = X_i + K_i^X \cdot \delta X_i \quad (7)$$

Accumulation fraction

$$A_i' = A_i + K_i^A \cdot \delta A_i \quad (8)$$

Unassimilated consumption

$$U_{ij}' = U_{ij} + K_{ij}^U \cdot \delta U_{ij} \quad (9)$$

Diet fraction

$$D_{ij}' = D_{ij} + K_{ij}^D \cdot \delta D_{ij} \quad (10)$$

Transfer to detritus

$$T_{ij}^{1-E}' = T_{ij}^{1-E} + K_{ij}^{1-E} \cdot \delta T_{ij}^{1-E} \quad (11)$$

Transfer by growth

$$T_{ij}^{g2}' = T_{ij}^{g2} + K_{ij}^{g2} \cdot \delta T_{ij}^{g2} \quad (12)$$

Seasonal transfer

$$T_{ij}^{s2}' = T_{ij}^{s2} + K_{ij}^{s2} \cdot \delta T_{ij}^{s2} \quad (13)$$

For changes to three model parameters ( $B$ ,  $P/B$ ,  $Q/P$ ), the changes were applied relative to scale values  $B^s$ ,  $(P/B)^s$ ,  $(Q/P)^s$  which are initially set to the estimated starting parameter values. Using the parameter values themselves to scale the adjustments appropriately handles the large range in magnitudes of these parameters across the food web. The parameter changes were not scaled for diet and transfer fractions because these parameters are of similar magnitudes (between 0 and 1) as they are scaled by  $P$  to obtain the actual flows of carbon (equation 2).

After adjustment in this way by SVD, the set of equality constraints will not be satisfied exactly because the minimisation works on a linearised version of the constraints assuming small changes. Hence, iterations were performed until the equality constraints were satisfied with an error within computational accuracy (8 iterations for within 0.0001% of true balance). On each iteration, the three scale parameters  $B^s$ ,  $(P/B)^s$ ,  $(Q/P)^s$  were updated by setting each to the lower of the current estimate or the initial estimate of that parameter. Updating scale values in this way means that logarithmically equal increases and decreases of parameters over multiple iterations will lead to the same change to the cost function. For example,  $K \cdot \delta = +1$  will represent a doubling of the parameter and  $K \cdot \delta = -1$  will represent a halving of the parameter.

#### Parameter uncertainty

In order to use an objective balancing method, it is necessary to assign relative magnitudes to the uncertainties of all parameters in the model. The absolute magnitudes of  $K$  across all groups are not important, but their relative values will affect the balanced model obtained. Whereas it is possible to assign uncertainties to some parameters by using information on the variability associated with various parts of the data used in their derivations, an entirely objective approach is not possible for all parameters for all groups. As a solution to the problem of assigning uncertainties to parameters consistently, Kavanagh et al. (2004) suggested that a 'data pedigree' approach was useful where parameters were assigned indices representing their relative uncertainties and these pedigree indices then mapped onto numerical uncertainty factors. A similar method was used here. Pedigree values of 1–9 were assigned for each key parameter ( $B$ ,  $P/B$ ,  $Q/P$ ,  $D$ ), and these mapped onto  $K$  values representing relative uncertainties (Table 3). For example, being metabolically constrained, it was assumed that intrinsic growth efficiencies for organisms ( $P/Q$ ) are likely to be less variable than biomass, productivities or diets, so  $K^{QP}$  values are generally lower than  $K^B$ ,  $K^P$  and  $K^D$  for the same data pedigree index. Note that the uncertainty values in



Table 3 do not imply absolute limits on plausible parameters as actual changes are determined by  $K$  values and the required  $\delta$  values for balance.

Diet uncertainty factors ( $K_{ij}^D$ ) were estimated by a two-stage process. First, a base value of was assigned to all diet fractions of a given predator based on an estimate of the quality of the available diet information for that predator in the Ross Sea. This predator-wise  $K$  value is denoted as  $K_0^D$ . These base values were then adjusted for each prey item in the diet of the predator, based on the actual values of the estimated diet fractions, as equation (14).

Diet fraction uncertainties

$$K_{ij}^D = K_0^D \cdot [a - b \cdot \exp(-c \cdot D_{ij})] \quad (14)$$

where the constants  $a = 1.114$ ,  $b = 0.9143$ ,  $c = 4.159$  were chosen so that  $K_{ij}^D/K_0^D = 1$  at  $D_{ij} = 0.5$ . For diet fractions of  $D_{ij} \rightarrow 0$  and  $D_{ij} = 1$ ,  $K_{ij}^D/K_0^D = 0.2$  and  $K_{ij}^D/K_0^D = 1.1$  respectively. This means that changes to diet fractions will tend to be smaller for prey species that make up lower proportions of the diet, to prevent these minor prey fractions being overinflated during the balancing procedure.

Similarly,  $K$  factors were estimated for transfer fractions ( $K_0^{1-E}, K_0^S, K_0^g, K_0^A, K_0^X$ ) using a two-step methodology. First, base transfer parameter uncertainties were set for all groups in the model ( $K_0^{1-E}, K_0^S, K_0^g, K_0^A, K_0^X$ ) and then adjusted according to estimates of the actual values of the parameters (equations 15 to 19).

Accumulation

$$K_i^A = K_0^A \cdot (a \cdot A_i^2 + b \cdot A_i + c) \quad (15)$$

Export

$$K_i^X = K_0^X \cdot (a \cdot X_i^2 + b \cdot X_i + c) \quad (16)$$

Transfer to detritus

$$K_{ij}^{1-E} = K_0^{1-E} \cdot [a \cdot (T_{ij}^{1-E})^2 + b \cdot T_{ij}^{1-E} + c] \quad (17)$$

Transfer by growth

$$K_{ij}^g = K_0^g \cdot [a \cdot (T_{ij}^g)^2 + b \cdot T_{ij}^g + c] \quad (18)$$

Seasonal transfer

$$K_{ij}^S = K_0^S \cdot [a \cdot (T_{ij}^S)^2 + b \cdot T_{ij}^S + c] \quad (19)$$

Constants of  $a = -2.8$ ,  $b = 2.8$ ,  $c = 0.3$  were used in equations (15) to (19). This formulation gives

$K_{ij}/K_0 = 1$  for  $T_{ij} = 0.5$ , and  $K_{ij}/K_0 = 0.3$  for  $T_{ij} \rightarrow 0$  and  $T_{ij} = 1$ . This approach prevents excessive changes occurring during balancing when initial estimates are towards an extreme of the possible range. Base values of  $K_0^A = 0.3$ ,  $K_0^{1-E} = 0.3$ ,  $K_0^S = 0.5$  and  $K_0^g = 0.1$  were used for all groups in the model.  $K_0^X = 0.1$  was set where the parameter was estimated from a model (penguins, cetaceans), and  $K_0^X = 0.2$  otherwise (flying birds, seals, large demersal fishes).  $K_{ij}^U = 0.1$  was used for all unassimilated transfers from all groups.

The final uncertainty ( $K$ ) parameters for all groups are given in Table 4. Although still more arbitrary than the authors would like, this method of assigning relative uncertainties is certainly an improvement on other methods currently available, and leads to a plausible balanced model. The sensitivity of the balanced model to different  $K$  factors is an important issue and is discussed later.

## Trophic levels

Trophic levels (Lindeman, 1942; Odum and Heald, 1975; Christensen and Pauly, 1992) of groups were calculated in the balanced model based on three rules: (i) primary producers and non-carcass detritus groups are defined as having a trophic level of 1; (ii) consumers trophic level is the sum of the trophic levels of their prey items, weighted by diet fraction, plus one; (iii) the carcass group takes the average trophic levels of material flowing into it, weighted by their respective flows. Unlike most trophic models, bacteria and detritus were separated as separate groups so here bacteria are treated as normal consumers. Stable isotope data will be a valuable independent cross-check on trophic levels calculated from the model. Stable isotope data for many Ross Sea organisms are available now, either in the primary literature (e.g. Burns et al., 1998; Zhao et al., 2004) or in reports and working papers (e.g. Bury et al., 2008; Thompson et al., 2008; Pinkerton et al., 2009), as well as typical changes in  $\delta^{15}\text{N}$  per trophic level (e.g. Post, 2002). Additional stable isotope data, including for benthic invertebrates, will become available soon; tissue from many organisms relevant to the current trophic model were sampled for stable isotope composition on the recent New Zealand IPY-CAML survey of the Ross Sea and processing is under way at the time of writing (Hanchet et al., 2008).

## Results

### Model balancing

The model had 342 variables and 67 constraints, implying a highly under-constrained system as expected. The balancing procedure applied SVD to the linearised system over eight iterations to give a steady solution within 0.0001% of true balance for all groups. The balanced model values are given in Tables 5 and 6. The balancing procedure changed many biomass and energetic parameters but the changes were generally small; the median biomass change during balancing was 1.7%. The biomasses of 12 groups were changed by more than 5% relative to the original estimate of the parameter. In descending order of magnitude, the biomass changes were: ice bacteria (−72%), ice protozoa (−54%), microzooplankton (−47%), benthic bacteria (−29%), mesozooplankton (−26%), ice algae (−17%), water column bacteria (−15%), heterotrophic flagellates (−13%), pelagic fishes (−13%), cephalopods (−7%), crabeater seals (*Lobodon carcinophagus*) (−7%), and Antarctic krill (*Euphausia superba*) (+6%). The balancing process adjusted 10 values of  $P/B$  by more than 5%, generally decreasing productivities to find a model balance point. The largest changes were: ice bacteria (−61%), microzooplankton (−34%), ice protozoa (−24%), benthic bacteria (−24%), mesozooplankton (−19%), ice algae (−12%), water column bacteria (+12%), heterotrophic flagellates (−10%), cephalopods (−6%) and pelagic fishes (−9%). The balancing process adjusted seven growth efficiencies ( $P/Q$ ) by more than 5%: Adélie penguins (*Pygoscelis adeliae*) (+20%), ice bacteria (+10%), ice protozoa (+9%), crabeater seals (+9%), benthic bacteria (−7%), pelagic fishes (+6%) and emperor penguins (*Aptenodytes forsteri*) (+5%).

Twenty-five diet fractions were changed by more than 5% (in absolute terms) during the balancing procedure. The largest changes were for the diet of pelagic fishes, where the balancing suggested that they consumed more mesozooplankton (+25%) and less Antarctic krill (−25%) than originally estimated. The diet of Antarctic silverfish (*Pleuragramma antarcticum*) was changed substantially from the initial estimates, with less consumption of crystal krill (*E. crystallorophias*) (−11%), and more consumption of mesozooplankton (+15%). Cephalopod consumption of Antarctic krill was also reduced (−12%) and compensated for by mesozooplankton (+11%). The only other change >5% in the diet of a fish group was an increase in the proportion of megabenthos consumed by small demersal fishes (+10%). Crabeater seals consumed less Antarctic krill (−7%) than originally predicted (compensated by slightly more consumption of

crystal krill and macrozooplankton). No other diet fraction of any apex predator group changed by more than 5%.

Zooplankton diet proportions were highly modified during balancing. Mesozooplankton in the balanced model had reduced consumption of phytoplankton (−15%) and heterotrophic flagellates (−11%) and increased consumption of mesozooplankton (+15%) and microzooplankton (+12%). Microzooplankton consumed more heterotrophic flagellates (+11%) and less phytoplankton (−9%) in the balanced model than anticipated. The proportion of heterotrophic flagellates in the diet of heterotrophic flagellates themselves also increased during balancing (+13%), at the expense of phytoplankton (−16%). No diet components of either krill species changed by more than 5% during balancing. An increase in the consumption of mesozooplankton (+7%) was the only major change to the diet of macrozooplankton. Both ice metazoa and ice protozoa consumed more ice algae than expected (+24%, +25% respectively), which reduced consumption of ice protozoa (−21%) and ice bacteria (−24%) respectively. Within the benthic habitat, the balancing procedure reduced consumption of benthic detritus by meiobenthos and megabenthos (−7% and −6% respectively), compensated for by increased consumption of meiobenthos (+6%) and benthic bacteria (+4%) respectively. Macrobenthos consumed more meiobenthos than anticipated (+5%).

Other model parameters had generally small changes to achieve balance. Four detrital transfer  $T_{ij}^{1-E}$  parameters were changed by more than 5% (in absolute terms): sediment bacteria (−12%), ice algae (−9%), ice bacteria (+8%) and phytoplankton (+7%). Four seasonal transfer parameters ( $T_{ij}^S$ ) were changed by more than 5%: ice algae to phytoplankton on ice melt (+22%), ice bacteria to water column detritus on ice melt (−20%), ice detritus to water column detritus on ice melt (−9%), water column detritus to benthic detritus due to vertical settling (−9%). No export ( $X_i$ ), unassimilated ( $U_i$ ), accumulation ( $A_i$ ), or growth ( $T_{ij}^g$ ) parameters were changed by more than 2%.

### Trophic levels

TLs were calculated for the final model (Table 5). TLs of predators from the model are (in descending order): sperm whales (5.44), orca (5.42), Weddell seals (5.37), Antarctic toothfish (5.35), toothed whales (5.31), emperor penguins (5.21), leopard seals (*Hydrurga leptonyx*) (5.17), Ross seals (*Ommatophoca rossi*) (4.94), Adélie penguins (4.74), flying birds (4.76), minke whales (*Balaenoptera*

*bonarensis*, *B. acuturostrata*) (4.43), baleen whales (4.20) and crabeater seals (4.10). Information on the stable isotopes of nitrogen in Antarctic seals to the east of the Ross Sea are available (Zhao et al., 2004). Using nitrogen fractionation factors from Post (2002), these data agree well with model TLs for seals. Isotope data suggests that Weddell seals occupy the highest trophic level of seals, with leopard seals <0.1 TL lower (here 0.20), Ross Seals 0.6 lower (here 0.42), and crabeater seals 1.2 lower (here 1.27) than Weddell seals. Krahn et al. (2006) gave stable isotope data for orca which suggested a TL 0.09 greater than that of Weddell seals assuming nitrogen fractionation factors from Post (2002); in the model the difference is 0.06. Mesozooplankton in the model has a higher TL (3.35) than Antarctic krill (2.99) or crystal krill (3.00) because mesozooplankton in the model consume greater proportions of mesozooplankton and microzooplankton than krill, and lower proportions of heterotrophic flagellates and phytoplankton. This result is consistent with preliminary stable isotope data from the region (Pinkerton et al., 2009) which shows a higher average  $\delta^{15}\text{N}$  (and hence trophic level) for mesozooplankton compared to krill, and shows a slightly higher average  $\delta^{15}\text{N}$  for crystal krill and non-krill macrozooplankton than Antarctic krill.

The hypothesis that TLs of particular organisms should be similar between different ecosystems is only partially borne out by the current results. The flying birds group at 4.8 compares well with 4.5 (Jarre-Teichmann et al., 1998) but less well with 3.8 (Arreguin-Sanchez et al., 2002) and 3.8 (Cornejo-Donoso and Antezana, 2008), probably to do with differences between the species of birds in the different areas. Flying birds in the Ross Sea are capable of taking larger prey than those in the Gulf of California where the Arreguin-Sanchez work was based. Species names are not given for the bird group in Cornejo-Donoso and Antezana (2008). Values for pelagic fishes and silverfish at TL = 4.2–4.3 are higher than values for similar fishes in other systems: 3.3 (Jarre-Teichmann et al., 1998), 2.7–3.5 (Wolff, 1994), 3.2 (Cornejo-Donoso and Antezana, 2008) and 3.2–3.9 (Mendoza, 1993). The relatively high trophic position of these small fish in the Ross Sea is plausible as it agrees with high  $\delta^{15}\text{N}$  values for Antarctic silverfish ( $N = 100$ ), five species of myctophids (*Electrona carlsbergi*, *E. antarctica*, *Gymnoscopelus nicholsi*, *G. opisthopterus*, *G. braueri*;  $N = 208$ ), and eight species of small demersal fishes ( $N = 234$ ) measured in the region (Pinkerton et al., 2009). The high TL of cephalopods in the model (4.4) is also in agreement with preliminary local stable isotope data (Thompson et al., 2008; Pinkerton et al., 2009), though their trophic position is higher than TL = 3.7 given for cephalopods

on the Antarctic Peninsula by Cornejo-Donoso and Antezana (2008). Megabenthos and macrobenthos at TL = 2.9–3.0 compares reasonably well with values for crabs and predatory invertebrates in other models (e.g. 2.4: Arreguin-Sanchez et al., 2002; 3.3–3.4: Wolff, 1994) even though benthic species do not overlap.

## Discussion

### Model validity

The present study carried out an extensive search of literature and data to obtain initial estimates of parameters required to produce a plausible food-web model of the Ross Sea. The relatively small number of groups and simple conceptual structure used in this model is appropriate given the inconsistency in available data across organisms, seasons and years. The trophic groups used in the model are also designed to be appropriate to the specific aim of the study, namely to investigate potential trophic impacts of the fishery for Antarctic toothfish in the Ross Sea. For example, whereas it is known that primary production in the water column in the Ross Sea is bimodal (DiTullio et al., 2000; Smith et al., 2000, 2003), different phytoplankton groups are not distinguished between in this model as the primary concern of this study is middle and upper TL groups.

The initial set of parameters was not self-consistent within the model conceptual framework, and an automated procedure adjusted these parameters to obtain model balance, with changes of only a few percent generally needed for balance. There were large, but not unreasonable, changes in the biomass and productivity estimates of some groups, especially ice bacteria, ice protozoa, microzooplankton, mesozooplankton and sediment bacteria. The relatively large changes needed to balance the sea-ice biota compartments in the model suggests that information on sea-ice biota at the scale of the Ross Sea annual cycle is poor – perhaps not surprising given the heterogeneity of the habitat and lack of large-area estimation methods. The quite large changes to the initial estimates of the biomass and productivity of benthic bacteria to achieve balance also probably reflect the fact that large area and seasonally resolved information on these parts of the system is sparse. Given that bacterial biomass and detrital flows are highly variable spatially and temporally, have been measured only in some seasons for relatively short periods, and the fraction of bacteria that are viable (actively consuming and producing) tends not to be measured, large changes to parameters for benthic bacteria are not implausible. This may be one reason why

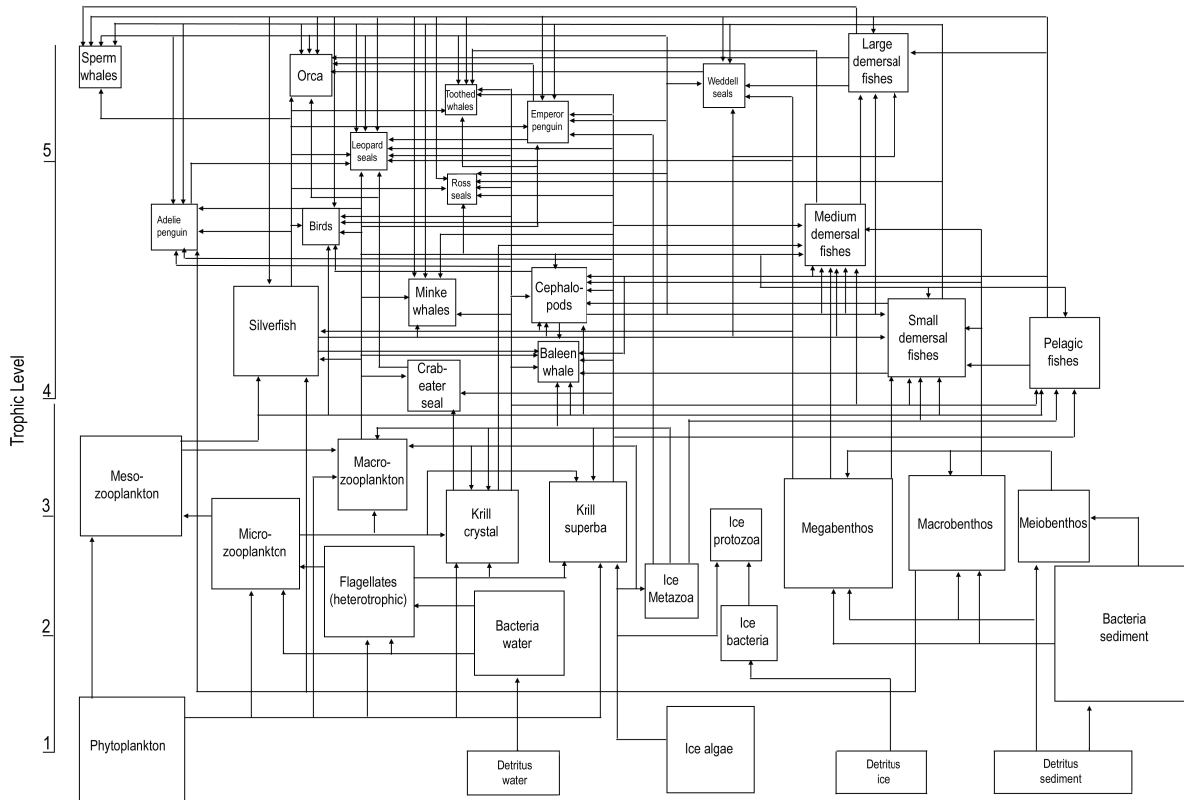


Figure 2: Model food web of the Ross Sea. Box sizes for non-detrital groups are scaled so that the sides are proportional to biomass in that group to the power 0.1, and positioned vertically according to (approximate) trophic level. Note the change in y-axis scale at trophic level 4. Arrows show the direction of organic carbon flow. Carcasses, flows to detritus, and respiration sinks are not shown for clarity.

few trophic models attempt to quantify the detrital pathways. Similarly, the paucity of data on micro and mesozooplankton biomasses and productivities over large areas and through the winter means that larger changes in biomass and productivity parameters for these groups are within the bounds of uncertainty associated with their estimates. Most diet fraction changes were <5% and larger changes were plausible. For example, the replacement of krill in the diet of silverfish by mesozooplankton is explicable, given that most studies show that copepods dominate the diet of silverfish and that most euphausiids found in the stomachs of silverfish are developmental stages (Williams, 1985; Hubold and Hagen, 1997; Granata et al., 2009). Field data to investigate the proportion of mesozooplankton in the diets of Antarctic silverfish and pelagic fishes will become available from the New Zealand IPY-CAML survey of the Ross Sea in due course (Hanchet et al., 2008) and will be valuable to improve the model.

Preliminary stable isotope data are consistent with trophic levels estimated from the model as an initial independent check on model validity. Even so, it is recognised that the model presented

here is but one solution amongst many; the model is too under-constrained for this to be otherwise. Also, the model represents conditions for a typical year (e.g. typical sea-ice, primary production etc.) and does not capture interannual variability. Nevertheless, the model represents a plausible, self-consistent, quantitative, semi-validated view of the structure of the Ross Sea food web and, as such, is a useful baseline description of ecosystem state.

#### The Ross Sea food web in the balanced model

The Ross Sea food web in the balanced model is shown in Figure 2. Total non-macroalgal primary production in the balanced model is estimated to be  $56.3 \text{ gC m}^{-2} \text{ y}^{-1}$ , the vast majority of which is from phytoplankton in the water column (>96%). Although sea-ice plays a key structural role in forcing the ecology of the Ross Sea (Thomas and Dieckmann, 2002; Arrigo and Thomas, 2004), epontic algae are estimated to produce only 3.5% of total primary production of the Ross Sea. In the model, only 57% of all primary production in the water column is directly consumed, consistent with the

inverse modelling of Ducklow et al. (2006) which suggested that half the primary production in the Ross Sea is ungrazed. The majority of phytoplankton production consumed in the water column is taken by heterotrophic flagellates (83%), with lesser consumption by microzooplankton (8%), mesozooplankton (7%) and macrozooplankton including krill (2%). A diverse mesozooplankton community is present, including large and small copepods (77% biomass, 53% production), pteropods and developmental stages of euphausiids. The non-consumed fraction of primary production in the water column, equivalent to  $24.4 \text{ gC m}^{-2} \text{ y}^{-1}$  enters the detrital pool and is eventually decomposed by bacterial action in the water column or transferred to the benthos by settling. All but 19% of the epontic algal production is also ungrazed. In the model,  $1.1 \text{ gC m}^{-2} \text{ y}^{-1}$  of algae is transferred from sea-ice to the water column on ice melt in the spring, equivalent to 52% of total annual epontic algal production. A further 29% of epontic production becomes detritus in sea-ice. Although not as productive as the water column on the scale of the whole Ross Sea, the lower part of sea-ice constitutes a unique habitat for microalgae and bacteria which provide a food source for associated protozoa and metazoa and the cryopelagic fauna of the surface water layer immediate below the ice (Garrison, 1991; Brierley and Thomas, 2002; Arrigo and Thomas, 2004). Consumption of sea-ice metazoa in the model is by a variety of predators, in proportions: 4% birds, 4% small cryopelagic fishes (included in the small demersal fishes group), 6% small pelagic fishes, 33% crystal krill, 27% Antarctic krill, 6% other macrozooplankton and 11% ice metazoa. The remaining 10% of production by ice metazoa is transferred to the water column when ice melts.

Benthic bacteria are the largest bacterial group in terms of biomass in the model, making up 99% of total bacteria biomass. However, benthic bacteria are responsible for only 58% of total bacterial productivity in the model, with water column bacteria responsible for 41% and sea-ice bacteria 1%. The disparity between biomass and productivity between the bacterial groups arises because water column bacteria annual  $P/B$  is estimated to be 74 times higher than that of bacteria in the sediments, consistent with field measurements. The vast majority of detrital material, in whatever habitat, is decomposed by bacterial action in the model: 83% in the sea-ice habitat, 74% in the water column and 93% in the sediments. Non-consumed organic detritus is transferred from the sea-ice to the water column on ice melt in the spring ( $1.3 \text{ gC m}^{-2} \text{ y}^{-1}$ ), from the water column to the benthos by vertical settling ( $12.6 \text{ gC m}^{-2} \text{ y}^{-1}$ ), or is buried in the sediments ( $2.5 \text{ gC m}^{-2} \text{ y}^{-1}$ ). The vertical flux to the

seabed is 26% of total input to water column detritus, and the annual burial is 7% of the input to the benthic detritus pool. The latter is close to the burial proportion of 4.9% estimated by Nelson et al. (1996).

There are a number of apex predators in the Ross Sea in summer, including large demersal fishes (entirely Antarctic toothfish), birds, seals and whales. Consumption by these groups in the model is in the ratio 5, 55, 29 and 11% of the total consumption by apex predators respectively. Bird biomass in the Ross Sea is dominated by penguins, with a total of about 1 million breeding pairs of Adélie penguins and more than 30 000 pairs of emperor penguins (Young, 1981; Harper et al., 1984; Ainley et al., 1984). Antarctic petrels (*Thalassoica antarctica*) and snow petrels (*Pagodroma nivea nivea*, *Pagodroma nivea major*) are the most common flying birds in the region, with a smaller number of albatrosses and south polar skuas (*Catharacta maccormicki*). Overall, Adélie penguins are responsible for 70% of bird consumption, with emperor penguins responsible for 18%, and flying birds for 12%. It is estimated that a net 15% of secondary bird production occurring within the study area is exported as a result of the population leaving the study area in autumn being greater than that re-entering it the following year. In the model, non-predation mortality (e.g. starvation) accounts for 43, 47 and 85% of the mortality of Adélie penguins, emperor penguins, and flying birds respectively, and these are consumed as carcasses.

Seals are the most common marine mammals in the Ross Sea, with more than 200 000 crabeater seals estimated to be present in summer. Weddell seals are likely to be the second-most common seal in the Ross Sea, with estimates for the larger Ross Sea region of 32 000 individuals (Stirling, 1969; Ainley, 1985; Stewart et al., 2003), or about 45% of the entire Pacific sector population. Leopard seals and Ross seals are also present. There is debate over whether or not Weddell seals are migratory, and on the dispersion patterns of all seal species in winter. In the model, it is estimated that seal consumption is made up from crabeater seals 75%, Weddell seals 18%, leopard seals 5% and Ross seals 2%. There is a net export of biomass from the Ross Sea due to seasonal seal movements, amounting to c. 25% of the annual production of these species within the study area. It is estimated that 37–75% of the mortality of seals in the study area is not due to direct predation, and this material is transferred to the carcasses group in the model.

The abundances and movements of minke and other baleen whales (blue (*B. musculus*), fin

(*B. physalus*), sei (*B. borealis*), humpback (*Megaptera novaeangliae*) in the Ross Sea region are poorly understood. It appears that, with the exception of minke whales, baleen whales tend to remain on the periphery of this study area. All baleen whales are absent from the region outside summer. The main toothed whales present in the study area in summer are sperm whales and orca/killer whales, and again information on their seasonal abundance is rather limited, coming primarily from surveys of their distribution and numbers, carried out by systematic surveys (e.g. Bassett and Wilson, 1983; Ainley, 1985; Kasamatsu and Joyce, 1995). The high encounter rate of sperm whales along the Ross Sea slope is notable (Kasamatsu and Joyce, 1995). Recent work has shown that three different types of orca may occur in the Ross Sea (Pitman et al., 2001; Pitman and Ensor, 2003; Pitman, 2003). Type-C (fish-eating) orca are considered to be by far the most common form in the McMurdo Sound region, but the migration and feeding characteristics of this type are poorly known. Consumption by these species (as a proportion of consumption by all cetaceans) are minke (49%), other baleen (15%), orca (19%), sperm whale (16%) and other toothed whales (1%). Because of the elevated feeding rates of whales while in the study area (factor of 1.05–2.5 greater than annual average), virtually the entire secondary production of cetaceans (95%) is exported from the region, with the remainder being consumed in the study region as carcasses.

There are two species of krill in the study area, crystal krill over the shelf, and Antarctic krill over the deeper slope and to the north. Although crystal and Antarctic krill form an important link between the water column, sea-ice and larger predators in the Ross Sea, they are less productive (slower turnover rates) than the large epipelagic copepods (*Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas* and *Metridia gerlachei*) (Voronina, 1998; Tarling et al., 2004). Other macrozooplankton biota in the Ross Sea are grouped into a single compartment and include large mysids, amphipods, salps and pteropods. In the model, Antarctic krill dominate the macrozooplankton in terms of biomass and production (55 and 42% respectively), with crystal krill and the 'other macrozooplankton' group making up the remainder approximately equally. Antarctic silverfish have a life history that is thought to take in the whole Ross Sea shelf and slope (Hubold, 1985; Granata et al., 2002, 2009; Vacchi et al., 1999, 2004), and their juveniles dominate the Ross Sea shelf ichthyoplankton. Myctophids are not present over the Ross Sea shelf, but the myctophid genera *Electrona* and *Gymnoscopelus* are common over the deeper Ross Sea slope. The small (<40 cm length) and medium-sized (40–100 cm) demersal fish community on the Ross Sea shelf and slope is diverse, and dominated by notothenids (especially

*Trematomus* sp.), icefish (especially *Chinobathyscus dewitti*, *Chionodraco hamatus*), dragonfishes (especially *Bathyraco marri*), deepsea cods (especially *Antimora rostrata*), eel cods (especially *Muraenolepis* spp.), macrourids (especially *Macrourus whitsoni*) and skates (*Bathyraco* cf. *eatonii*, *Raja georgiana*) (La Mesa et al., 2004). Abundance of small and medium-sized demersal fishes is poorly known, but is thought to be dominated in terms of biomass by macrourids (c. 70%), skates (c. 10%) and icefish (c. 7%). Cephalopods appear to be relatively minor components of the Ross Sea nekton, with few pelagic, usually juvenile, squids but many small benthic octopods occur over the Ross Sea shelf. Production within these trophic groups in the Ross Sea in the model is spread quite evenly: Antarctic krill (24%), silverfish (19%), crystal krill (16%), other macrozooplankton (16%), small demersal fishes (10%), pelagic fishes (9%), cephalopods (6%) and medium-sized demersal fishes (0.5%). The two species of krill together are responsible for more than twice the secondary production of silverfish.

In order to discuss transfers of material between the lower, middle and upper pelagic biota, upper level predators were here defined as having TLs >4.5 (flying birds, Weddell, leopard and Ross seals, toothed whales, large and medium demersal fishes), middle level pelagic groups as having TL 3.5–4.5 (crabeater seals, baleen whales, small demersal fishes, silverfish, pelagic fishes and cephalopods), and lower level pelagic groups as having TL 2–3.5 (krill, other macrozooplankton, mesozooplankton, microzooplankton and heterotrophic flagellates). The model suggests that the input of primary production to the middle pelagic trophic levels together is channelled mainly through the mesozooplankton. The total overall consumption by the middle pelagic trophic groups of 1.4 gC m<sup>-2</sup> y<sup>-1</sup> (2.4% primary production) comes from mesozooplankton (59%), benthic invertebrates (19%), krill and macrozooplankton (14%), other medium TL pelagic biota (6%), with small (<1%) contributions from ice biota and carcasses. Antarctic silverfish are the major prey item of the top predators (TLs >4.5). Consumption by upper level predators in the model of 0.17 gC m<sup>-2</sup> y<sup>-1</sup> (0.3% of primary production) is satisfied by silverfish (42%), crystal krill (16%), small demersal fishes (14%), Antarctic krill (7%), cephalopods (7%), benthic invertebrates (4%), pelagic fishes (3%), other macrozooplankton (2%) and all else 4% combined. This result is consistent with current understanding; Antarctic silverfish are known to be ubiquitous in the diet of all large animals (seabirds, seals, toothed and baleen whales, toothfish, many other species of fish, squid) in the Ross Sea, with krill also important prey items (DeWitt, 1970; Laws, 1984).

The model representation of the macrobenthic and megabenthic communities is not very informative. These two groups appear to have similar energetic parameters and diets in the balanced trophic model. Information on the benthic assemblage of the Ross Sea from the recent survey (Hanchet et al., 2008), including large amounts of stable isotope data on benthic invertebrates (Pinkerton et al., 2009) may allow the disaggregation of the megabenthic compartment in the future. Separation of the megabenthos into grazers, filter feeders, detritivores and predators may be useful. It appears, however, that benthic invertebrates are a minor but significant component of the Ross Sea food web. Benthic invertebrates are also likely to be important ecologically as providers of biogenic habitat, but that is not tested by the model.

#### Effects of fishing on the Ross Sea food web

The model is used to consider the first-order trophic links of large toothfish to assess the potential impact of the fishery for Antarctic toothfish on its prey and predators. The entire large demersal fishes group is made up of large Antarctic toothfish (>100 cm), whereas only 15% of the biomass of the medium demersal fishes group (40–100 cm) is toothfish. As toothfish >100 cm make up the vast majority of the fishery catch (>90% by weight), the abundance of the large demersal fishes group is likely to be most affected by the toothfish fishery, and this study focuses on the trophic links to this group.

The prey items of large toothfish in the model are medium demersal fishes (14%), small demersal fishes (71%), pelagic fishes (1%), carcasses (1%) and cephalopods (13%). These balanced diet proportions are consistent with measurements of stomach contents of toothfish from the Ross Sea (Fenaughty et al., 2003; Stevens, 2004), and with stable isotope analyses on the Ross Sea slope (Bury et al., 2008). In the model, the proportion of the annual production of each of these prey groups consumed by toothfish is estimated to be 61% (medium demersal fishes), 14% (small demersal fishes), 0.3% (pelagic fish), and 5% (cephalopods). The model hence suggests that some of the largest impacts of the fishery on the Ross Sea ecosystem are likely to be on medium and small demersal fishes in that order. The proportion of the medium demersal fish (*M. whitsoni*, *A. rostrata*) component made up of fish known to be consumed by Antarctic toothfish rather than skates or smaller toothfish is 67% in terms of biomass and 78% in terms of production, so the model predicts that the majority (79%) of the mortality of individuals >40 cm in length of these two species is likely to be due to Antarctic toothfish predation. As there

is no reliable information available on the abundances of small and medium demersal fishes in the Ross Sea, the exact figures are uncertain, though the conclusions are likely to be robust. Key small demersal fish species in the toothfish diet include icefish (*C. dewitti*) and moray (eel) cod, but their proportions in the small fish assemblage are not known. The model developed here hence implies that these four species of demersal fishes should be a high priority for further research and that monitoring of the species should be established as soon as possible while changes to large Antarctic toothfish abundance due to fishing are still likely to be relatively small.

Next the first-order trophic links between large toothfish and its predators in the model was considered. The model summarises information on a particular space and time scale, namely the Ross Sea over a one-year period. On these scales, the balanced model suggests that Antarctic toothfish is likely to be a minor component of the diets of its predators. In the balanced model, toothfish make up 6.5% of the diet of Weddell seals, 5.6% of the diet of orca and 2.6% of the diet of sperm whales. Therefore, the model does not support the hypothesis that depletion of large Antarctic toothfish by fishing could substantially change the diet of the predators of toothfish in the Ross Sea. There is simply not enough growth by toothfish to satisfy more than a small fraction of the consumption of its predators in the study region. The robustness of this conclusion depends on the validity of the input data. Biomass and growth rates of Antarctic toothfish in the Ross Sea are relatively well known, having been specifically studied using otoliths and a tag-recapture program (Hanchet et al., 2007 and references therein). Consumption rates of mammals are generally consistent within 50% (see supporting documentation). However, biomass estimates of predators in the model, although consistent with published information (Ainley, 1985; Kasamatsu and Joyce, 1995; Stewart et al., 2003), have high uncertainties. If the biomasses of toothfish predators are substantially lower in reality compared to the model, then much larger proportions of toothfish in their diets would be possible in the model as the toothfish production would 'go further'. Knowledge of the diets of toothfish predators is uncertain and of limited help in constraining the model. For example, it is known that Weddell seals consume toothfish, but not the proportion of toothfish in their diet (Pinkerton et al., 2008b; Ainley and Siniff, 2008). Unless better estimates of the abundances or long-term diets of Weddell seals, orca and sperm whales become available, it is reasonable to conclude that Antarctic toothfish are a relatively minor component of the diets of their

predators in the Ross Sea at the scale of the model (Ross Sea shelf and slope). Note, however, that the model gives no information on whether changes to the proportions of toothfish in the diet of its predators could be ecologically important at the scale of the Ross Sea or whether consumption of toothfish in particular locations or at particular times of the year is important to its predators.

#### Future work

Mapping the whole feasible parameter space to understand the structural ambiguities of the ecosystem within this simple conceptual framework is an important next step. In particular, the sensitivity of the balanced model to the relative uncertainty ( $K$ ) factors will be further investigated in subsequent work, and the authors aim to use data on the stable isotopes of nitrogen from a range of middle trophic level biota to constrain and validate the model. It is not clear yet whether there is sufficient information to produce a quantitative model on the food web of the Ross Sea that is disaggregated seasonally. As it is important to test the similarity of conclusions as to the structure of the food web based on an annual model and a seasonally resolved model, the authors intend to investigate this issue further.

The model developed here differs fundamentally from minimum-realistic models such as fish stock assessment models, NPZD-type models of the microbial loop, or Ecosim (Christensen and Walters, 2004), in that it is descriptive rather than mechanistic. Ecosystem function and dynamics are closely, but not simply, related to ecosystem structure (e.g. Pascual and Dunne, 2006), so that knowing how the recent unexploited system may be structured does not confer an ability to predict how it may change in the future. Adding increased complexity to a model of this type in an attempt to represent biological reality better, will not make it into a predictive model. Instead, developing a dynamic (predictive) ecosystem model requires robust mechanistic insight into how the interactions of biotic and abiotic factors act to constrain population sizes. Prediction requires knowledge of the plasticity of ecological role, and on how non-trophic factors (interference competition, habitat provision, evolutionary pressure) influence ecosystem change. A quantitative descriptive model of current food-web structure, such as that developed here, is a foundation to developing such dynamic predictive models of either the whole system or, more tractably, portions of it. The present model complements qualitative work on food-web connection in the Ross Sea (Smith et al., 2007), and represents a necessary and significant step towards highlighting parts of the system on which to focus

for dynamic predictive modelling and identifying their important trophic interactions. Based on the results of this work, the authors intend to develop minimum-realistic dynamic models of toothfish and their demersal fish prey species and encourage data collection to better understand toothfish-predator interactions.

#### Conclusions

1. There is sufficient data on all major biota in the Ross Sea to set up and balance a food-web model which quantifies transfers of organic matter due to direct predation, non-predation mortality and detrital transfers, integrated over one year. The authors recognise that the balanced model is but one solution of many, consistent with the available data, and intend to further explore the effects of parameter uncertainty and seasonality on the model in the future.
2. The input of primary production to the middle trophic levels of the pelagic Ross Sea food web is channelled mainly through the mesozooplankton, with important contributions from benthic invertebrates and krill. The input of primary production to upper trophic levels is channelled mainly through Antarctic silverfish, with major contributions from krill. The sensitivities of these species to climate change should be of concern to fisheries managers as they have the potential to impact secondary production throughout the food web and hence affect sustainable fishery yield.
3. The model does not support the hypothesis that depletion of Antarctic toothfish by fishing would change the diet of predators of toothfish (Weddell seals, orca, sperm whales) by large amounts throughout the Ross Sea, though the importance of toothfish as prey items to these predators is not tested.
4. Large toothfish in the model are by far the greatest consumers of medium-sized (40–100 cm) demersal fish, consuming 61% of the annual production of this group. Toothfish are also a significant predator of smaller demersal fishes, consuming 14% of the annual production of all small demersal fishes in the Ross Sea. Medium and small demersal fish species in toothfish diet include *M. whitsoni*, *C. dewitti*, *A. rostrata*, and *Muraenolepis* spp. These results imply that demersal fish species should be a high priority for monitoring and future research, and the authors intend to develop a minimum-realistic dynamic model of toothfish interactions with these prey species.



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Table 1: Trophic group parameters for the Ross Sea model estimated from local data and literature.  $B$  – Biomass,  $P/B$  – Production,  $P/Q$  – Growth efficiency,  $E$  – Ecotrophic efficiency,  $A$  – Accumulation (as fraction of  $P$ ),  $X$  – Export (as fraction of  $P$ ),  $U$  – Unassimilated consumption,  $T^s$  – seasonal transfers (as fraction of  $P$ ),  $T^* =$  growth transfers (as fraction of  $P$ ). Fishery take,  $F = 0$  for all groups. The last four columns give the destinations for transfers out of the given row. For example, growth of medium demersal fish is routed to group 13, large demersal fishes.

| #  | Group          | $B$ (gC m <sup>-2</sup> ) | $P/B$ (y <sup>-1</sup> ) | $P/Q$   | $E$   | $A$ | $X$   | $U$   | $T^s$ | $T^*$ | $j: U_{ij}$ | $j: T_{ij}^{1-E}$ | $j: T_{ij}^s$ | $j: T_{ij}^*$ |
|----|----------------|---------------------------|--------------------------|---------|-------|-----|-------|-------|-------|-------|-------------|-------------------|---------------|---------------|
| 1  | Emperor        | 4.91E-04                  | 1.02E-01                 | 0.00232 | 0.572 | 0   | 0.145 | 0.300 | 0     | 0     | 37          | 35                |               |               |
| 2  | Adélie         | 1.25E-03                  | 3.59E-01                 | 0.00442 | 0.531 | 0   | 0.150 | 0.300 | 0     | 0     | 37          | 35                |               |               |
| 3  | Flying_birds   | 1.35E-04                  | 5.45E-01                 | 0.00473 | 0.150 | 0   | 0.150 | 0.300 | 0     | 0     | 37          | 35                |               |               |
| 4  | Crabeater      | 2.36E-03                  | 1.35E-01                 | 0.00577 | 0.625 | 0   | 0.250 | 0.200 | 0     | 0     | 37          | 35                |               |               |
| 5  | Weddell        | 4.00E-04                  | 1.19E-01                 | 0.00419 | 0.625 | 0   | 0.250 | 0.200 | 0     | 0     | 37          | 35                |               |               |
| 6  | Leopard        | 1.46E-04                  | 1.15E-01                 | 0.00489 | 0.250 | 0   | 0.250 | 0.200 | 0     | 0     | 37          | 35                |               |               |
| 7  | Ross           | 3.52E-05                  | 1.51E-01                 | 0.00455 | 0.250 | 0   | 0.250 | 0.200 | 0     | 0     | 37          | 35                |               |               |
| 8  | Minke          | 9.05E-04                  | 3.93E-02                 | 0.00259 | 0.995 | 0   | 0.995 | 0.200 | 0     | 0     | 37          | 35                |               |               |
| 9  | Baleen_whales  | 4.68E-04                  | 2.70E-02                 | 0.00320 | 0.994 | 0   | 0.994 | 0.200 | 0     | 0     | 37          | 35                |               |               |
| 10 | Orca           | 4.74E-04                  | 4.73E-02                 | 0.00441 | 0.887 | 0   | 0.887 | 0.200 | 0     | 0     | 37          | 35                |               |               |
| 11 | Sperm          | 8.48E-04                  | 2.18E-02                 | 0.00426 | 0.899 | 0   | 0.899 | 0.200 | 0     | 0     | 37          | 35                |               |               |
| 12 | Toothed_whales | 2.46E-05                  | 6.57E-02                 | 0.00549 | 0.872 | 0   | 0.872 | 0.200 | 0     | 0     | 37          | 35                |               |               |
| 13 | L_demersal     | 9.45E-03                  | 1.24E-01                 | 0.110   | 0.950 | 0   | 0.200 | 0.270 | 0     | 0     | 37          | 35                |               | 13            |
| 14 | M_demersal     | 9.60E-03                  | 2.38E-01                 | 0.126   | 0.950 | 0   | 0     | 0.270 | 0     | 0.095 | 37          | 35                |               | 13            |
| 15 | S_demersal     | 9.36E-02                  | 4.98E-01                 | 0.115   | 0.950 | 0   | 0     | 0.270 | 0     | 0.008 | 37          | 35                |               | 14            |
| 16 | Silverfish     | 6.26E-02                  | 1.35E+00                 | 0.155   | 0.950 | 0   | 0     | 0.270 | 0     | 0     | 37          | 35                |               | 15            |
| 17 | Pelagic_fish   | 4.00E-02                  | 1.37E+00                 | 0.135   | 0.950 | 0   | 0     | 0.270 | 0     | 0.215 | 37          | 35                |               | 15            |
| 18 | Cephalopods    | 4.91E-03                  | 6.70E+00                 | 0.394   | 0.950 | 0   | 0     | 0.200 | 0     | 0     | 37          | 35                |               |               |
| 19 | Krill_crystal  | 4.05E-02                  | 1.83E+00                 | 0.138   | 0.950 | 0   | 0     | 0.200 | 0     | 0     | 37          | 37                |               |               |
| 20 | Krill_superba  | 9.15E-02                  | 1.10E+00                 | 0.132   | 0.950 | 0   | 0     | 0.200 | 0     | 0     | 37          | 37                |               |               |
| 21 | Macrozoa       | 3.68E-02                  | 2.00E+00                 | 0.133   | 0.950 | 0   | 0     | 0.200 | 0     | 0     | 37          | 37                |               |               |
| 22 | Mesozoo        | 9.38E-01                  | 4.77E+00                 | 0.300   | 0.990 | 0   | 0     | 0.250 | 0     | 0     | 37          | 37                |               | 22            |
| 23 | Microzoo       | 4.01E-01                  | 2.15E+01                 | 0.350   | 0.990 | 0   | 0     | 0.300 | 0     | 0.010 | 37          | 37                |               | 22            |
| 24 | Flagellates    | 3.01E-01                  | 6.19E+01                 | 0.350   | 0.990 | 0   | 0     | 0.160 | 0     | 0     | 37          | 37                |               |               |
| 25 | Phytoplankton  | 1.10E+00                  | 5.28E+01                 | na      | 0.500 | 0   | 0     | na    | 0     | 0     | 37          | 37                |               |               |
| 26 | Ice_metazoa    | 3.14E-03                  | 2.01E+01                 | 0.273   | 0.900 | 0   | 0     | 0.200 | 0.100 | 0     | 36          | 36                | 22            |               |
| 27 | Ice_protozoa   | 2.73E-03                  | 6.00E+01                 | 0.316   | 0.900 | 0   | 0     | 0.200 | 0.200 | 0     | 36          | 36                | 37            |               |
| 28 | Ice_algae      | 2.85E-01                  | 9.93E+00                 | na      | 0.800 | 0   | 0     | na    | 0.300 | 0     | 36          | 36                | 37            |               |
| 29 | Megabenthos    | 1.42E+00                  | 2.48E-01                 | 0.200   | 0.500 | 0   | 0     | 0.300 | 0     | 0     | 38          | 38                |               |               |
| 30 | Macrobenthos   | 4.27E-01                  | 3.57E-01                 | 0.250   | 0.900 | 0   | 0     | 0.200 | 0     | 0     | 38          | 38                |               |               |
| 31 | Meiobenthos    | 4.43E-02                  | 1.00E+01                 | 0.300   | 0.900 | 0   | 0     | 0.200 | 0     | 0     | 38          | 38                |               |               |
| 32 | Bacteria_ice   | 1.79E-02                  | 1.65E+02                 | 0.300   | 0.300 | 0   | 0     | 0.300 | 0.300 | 0     | 36          | 36                |               |               |

(continued)

Table 1 (continued)

| #  | Group             | $B$ (gC m <sup>-2</sup> ) | $P/B$ (y <sup>-1</sup> ) | $P/Q$ | $E$   | $A$   | $X$ | $U$   | $T^e$ | $T^s$ | $j: U_{ij}$ | $j: T_{ij}^{1-E}$ | $j: T_{ij}^S$ | $j: T_{ij}^g$ |
|----|-------------------|---------------------------|--------------------------|-------|-------|-------|-----|-------|-------|-------|-------------|-------------------|---------------|---------------|
| 33 | Bacteria_water    | 2.34E-01                  | 3.54E+01                 | 0.300 | 0.990 | 0     | 0   | 0.300 | 0     | 0     | 37          | 37                |               |               |
| 34 | Bacteria_sediment | 3.99E+01                  | 7.07E-01                 | 0.500 | 0.300 | 0     | 0   | 0.300 | 0     | 0     | 38          | 38                |               |               |
| 35 | Carcasses         | na                        | na                       | na    | na    | 0     | 0   | na    | 0     | 0     |             |                   |               |               |
| 36 | Detritus_ice      | na                        | na                       | na    | na    | 0     | 0   | na    | 0.300 | 0     |             |                   | 37            |               |
| 37 | Detritus_water    | na                        | na                       | na    | na    | 0     | 0   | na    | 0.437 | 0     |             |                   | 38            |               |
| 38 | Detritus_sediment | na                        | na                       | na    | na    | 0.049 | 0   | na    | 0     | 0     |             |                   |               |               |

Table 2: Diet parameters for the Ross Sea model estimated from local data and literature. Values given are the proportion (by organic carbon weight) of a given prey item in the diet of predators. Predators are shown on the x-axis and prey on the y-axis.

| #  | Group             | 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   | 26   | 27   | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 |  |  |  |  |
|----|-------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|----|----|----|----|----|----|----|----|----|----|----|--|--|--|--|
| 1  | Emperor           |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 2  | Adélie            |      |      |      |      | 0.01 |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 3  | Flying_birds      |      |      |      |      | 0.05 |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 4  | Crabeater         |      |      |      |      | 0.05 |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 5  | Weddell           |      |      |      |      | 0.01 |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 6  | Leopard           |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 7  | Ross              |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 8  | Minke             |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 9  | Baleen_whales     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 10 | Orca              |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 11 | Sperm             |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 12 | Toothed_whales    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 13 | L_demersal        |      |      |      | 0.07 |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 14 | M_demersal        |      |      |      | 0.02 | 0.16 | 0.02 |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 15 | S_demersal        | 0.10 | 0.05 |      | 0.25 | 0.15 | 0.05 | 0.05 | 0.01 | 0.15 | 0.05 | 0.11 | 0.70 | 0.24 | 0.06 |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 16 | Silverfish        | 0.68 | 0.50 | 0.40 | 0.50 | 0.22 | 0.10 | 0.20 | 0.07 | 0.50 | 0.10 | 0.12 | 0.16 | 0.07 | 0.02 |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 17 | Pelagic_fish      | 0.10 | 0.05 |      | 0.05 | 0.05 | 0.13 | 0.05 | 0.01 | 0.05 | 0.05 | 0.08 | 0.01 | 0.06 | 0.02 | 0.00 |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 18 | Cephalopods       | 0.04 | 0.01 | 0.09 | 0.09 | 0.05 | 0.35 |      | 0.01 | 0.10 | 0.75 | 0.61 | 0.13 | 0.07 | 0.05 |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 19 | Krill_crystal     | 0.02 | 0.30 | 0.16 | 0.35 |      | 0.03 | 0.10 | 0.20 | 0.06 |      | 0.02 | 0.04 | 0.05 | 0.13 | 0.01 | 0.10 |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 20 | Krill_superba     | 0.02 | 0.09 | 0.23 | 0.45 |      | 0.05 | 0.15 | 0.45 | 0.72 |      | 0.03 | 0.10 | 0.03 | 0.47 | 0.15 |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 21 | Macrozoa          | 0.02 | 0.02 | 0.03 | 0.20 |      | 0.03 | 0.10 | 0.05 | 0.05 |      | 0.02 | 0.05 | 0.04 | 0.05 | 0.09 | 0.10 |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 22 | Mesozoo           |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0.16 | 0.77 | 0.42 | 0.30 |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 23 | Microzoo          |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0.21 | 0.22 | 0.20 | 0.15 |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 24 | Flagellates       |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0.35 | 0.35 | 0.03 | 0.43 | 0.20 | 0.07 |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 25 | Phytoplankton     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0.30 | 0.30 | 0.30 | 0.40 | 0.40 | 0.78 |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 26 | Ice_metazoa       | 0.02 | 0.02 | 0.02 |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0.06 | 0.05 | 0.02 |      |      |      | 0.05 |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 27 | Ice_protozoa      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0.03 | 0.02 | 0.01 |      |      |      | 0.30 | 0.10 |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 28 | Ice_algae         |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0.05 | 0.06 | 0.04 |      |      |      | 0.65 | 0.10 |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 29 | Megabenthos       |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 30 | Macrobenthos      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 31 | Meiobenthos       |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 32 | Bacteria_ice      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 33 | Bacteria_water    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 34 | Bacteria_sediment |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 35 | Carcasses         |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 36 | Detritus_ice      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 37 | Detritus_water    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |
| 38 | Detritus_sediment |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |

Table 3: Data pedigree and associated relative uncertainty factors used in this study.

| Uncertainty in parameter |                          | Biomass | Productivity | Growth efficiency <sup>-1</sup> | Diet fraction |
|--------------------------|--------------------------|---------|--------------|---------------------------------|---------------|
|                          |                          | $B$     | $P/B$        | $Q/P$                           | $D_{ij}$      |
| Pedigree                 | Comment                  | $K^B$   | $K^P$        | $K^{QP}$                        | $K_0^D$       |
| 1                        | Unknown/missing          | 9       | 9            | 3                               | 9             |
| 2                        | Guesstimate              | 4       | 4            | 1                               | 4             |
| 3                        | Very limited information | 2       | 2            | 0.5                             | 2             |
| 4                        | Poor information         | 1.2     | 1            | 0.3                             | 1             |
| 5                        | Some information         | 0.7     | 0.5          | 0.2                             | 0.5           |
| 6                        | Reasonable information   | 0.4     | 0.3          | 0.1                             | 0.3           |
| 7                        | Good information         | 0.2     | 0.2          | 0.05                            | 0.2           |
| 8                        | Extensive information    | 0.1     | 0.1          | 0.02                            | 0.1           |
| 9                        | Fixed                    | 0       | 0            | 0                               | 0             |



Table 4: Uncertainty ( $K$ ) parameters for the Ross Sea trophic model as explained in the text.

|    | Group             | $K^B$ | $K^P$ | $K^{Op}$ | $K^{I-E}$ | $K^A$ | $K^X$ | $K^U$ | $K^S$ | $K^S$ | $K_0^D$ | $K^D(\min)$ | $K^D(\max)$ |
|----|-------------------|-------|-------|----------|-----------|-------|-------|-------|-------|-------|---------|-------------|-------------|
| 1  | Emperor           | 0.2   | 0.3   | 0.05     | 0.30      | 0     | 0.06  | 0.1   | 0     | 0     | 0.5     | 0.14        | 0.53        |
| 2  | Adélie            | 0.2   | 0.3   | 0.05     | 0.30      | 0     | 0.07  | 0.1   | 0     | 0     | 0.5     | 0.12        | 0.50        |
| 3  | Flying_birds      | 0.7   | 0.3   | 0.05     | 0.20      | 0     | 0.13  | 0.1   | 0     | 0     | 1.0     | 0.24        | 0.94        |
| 4  | Crabeater         | 0.7   | 0.3   | 0.05     | 0.29      | 0     | 0.17  | 0.1   | 0     | 0     | 1.0     | 0.72        | 0.97        |
| 5  | Weddell           | 0.4   | 0.3   | 0.05     | 0.29      | 0     | 0.17  | 0.1   | 0     | 0     | 0.5     | 0.14        | 0.50        |
| 6  | Leopard           | 0.7   | 0.3   | 0.05     | 0.25      | 0     | 0.17  | 0.1   | 0     | 0     | 1.0     | 0.24        | 0.75        |
| 7  | Ross              | 0.7   | 0.3   | 0.05     | 0.25      | 0     | 0.17  | 0.1   | 0     | 0     | 1.0     | 0.27        | 0.90        |
| 8  | Minke             | 0.7   | 0.3   | 0.05     | 0.09      | 0     | 0.03  | 0.1   | 0     | 0     | 1.0     | 0.37        | 0.97        |
| 9  | Baleen_whales     | 0.7   | 0.3   | 0.05     | 0.10      | 0     | 0.03  | 0.1   | 0     | 0     | 1.0     | 0.26        | 1.07        |
| 10 | Orca              | 0.7   | 0.3   | 0.05     | 0.11      | 0     | 0.04  | 0.1   | 0     | 0     | 1.0     | 0.24        | 1.00        |
| 11 | Sperm             | 0.7   | 0.3   | 0.05     | 0.12      | 0     | 0.04  | 0.1   | 0     | 0     | 1.0     | 0.27        | 1.07        |
| 12 | Toothed_whales    | 0.7   | 0.3   | 0.05     | 0.12      | 0     | 0.04  | 0.1   | 0     | 0     | 1.0     | 0.24        | 1.04        |
| 13 | L_demersal        | 0     | 0.3   | 0.05     | 0.13      | 0     | 0.15  | 0.1   | 0     | 0     | 0.3     | 0.07        | 0.32        |
| 14 | M_demersal        | 0.4   | 0.3   | 0.10     | 0.13      | 0     | 0     | 0.1   | 0     | 0.05  | 0.5     | 0.13        | 0.39        |
| 15 | S_demersal        | 0.4   | 0.3   | 0.10     | 0.13      | 0     | 0     | 0.1   | 0     | 0.03  | 0.5     | 0.12        | 0.40        |
| 16 | Silverfish        | 0.4   | 0.3   | 0.10     | 0.13      | 0     | 0     | 0.1   | 0     | 0     | 0.5     | 0.10        | 0.54        |
| 17 | Pelagic_fish      | 0.4   | 0.3   | 0.10     | 0.13      | 0     | 0     | 0.1   | 0     | 0.08  | 0.5     | 0.11        | 0.49        |
| 18 | Cephalopods       | 1.2   | 1.0   | 0.20     | 0.13      | 0     | 0     | 0.1   | 0     | 0     | 1.0     | 0.37        | 0.85        |
| 19 | Krill_crystal     | 0.4   | 0.3   | 0.10     | 0.13      | 0     | 0     | 0.1   | 0     | 0     | 0.5     | 0.15        | 0.45        |
| 20 | Krill_superba     | 0.4   | 0.3   | 0.10     | 0.13      | 0     | 0     | 0.1   | 0     | 0     | 0.5     | 0.14        | 0.45        |
| 21 | Macrozoö          | 0.4   | 0.3   | 0.10     | 0.13      | 0     | 0     | 0.1   | 0     | 0     | 0.5     | 0.12        | 0.45        |
| 22 | Mesozö            | 0.4   | 0.3   | 0.10     | 0.10      | 0     | 0     | 0.1   | 0     | 0     | 0.5     | 0.14        | 0.48        |
| 23 | Microzö           | 0.7   | 0.5   | 0.20     | 0.10      | 0     | 0     | 0.1   | 0     | 0.03  | 1.0     | 0.72        | 0.94        |
| 24 | Flagellates       | 0.7   | 0.5   | 0.20     | 0.10      | 0     | 0     | 0.1   | 0     | 0     | 1.0     | 0.43        | 1.08        |
| 25 | Phytoplankton     | 0.2   | 0.2   | 0        | 0.30      | 0     | 0     | 0     | 0     | 0     | 0       | 0           | 0           |
| 26 | Ice_metazö        | 1.2   | 0.5   | 0.20     | 0.17      | 0     | 0     | 0.1   | 0.28  | 0     | 1.0     | 0.37        | 1.05        |
| 27 | Ice_protozö       | 1.2   | 0.5   | 0.20     | 0.17      | 0     | 0     | 0.1   | 0.37  | 0     | 1.0     | 0.51        | 1.08        |
| 28 | Ice_algae         | 0.7   | 0.5   | 0        | 0.22      | 0     | 0     | 0     | 0.44  | 0     | 0       | 0           | 0           |
| 29 | Megabenthos       | 0.7   | 0.3   | 0.10     | 0.30      | 0     | 0     | 0.1   | 0     | 0     | 1.0     | 0.24        | 1.07        |
| 30 | Macrobenthos      | 0.7   | 0.3   | 0.10     | 0.17      | 0     | 0     | 0.1   | 0     | 0     | 1.0     | 0.37        | 1.05        |
| 31 | Meiobenthos       | 0.7   | 0.5   | 0.20     | 0.17      | 0     | 0     | 0.1   | 0     | 0     | 1.0     | 0.37        | 1.07        |
| 32 | Bacteria_ice      | 1.2   | 1.0   | 0.20     | 0.27      | 0     | 0     | 0.1   | 0.44  | 0     | 0       | 0           | 0           |
| 33 | Bacteria_water    | 1.2   | 1.0   | 0.20     | 0.10      | 0     | 0     | 0.1   | 0.00  | 0     | 0       | 0           | 0           |
| 34 | Bacteria_sediment | 1.2   | 1.0   | 0.20     | 0.27      | 0     | 0     | 0.1   | 0     | 0     | 0       | 0           | 0           |
| 35 | Carcasses         | 0     | 0     | 0        | 0         | 0     | 0     | 0     | 0     | 0     | 0       | 0           | 0           |
| 36 | Detritus_ice      | 0     | 0     | 0        | 0         | 0     | 0     | 0     | 0.44  | 0     | 0       | 0           | 0           |
| 37 | Detritus_water    | 0     | 0     | 0        | 0         | 0     | 0     | 0     | 0.49  | 0     | 0       | 0           | 0           |
| 38 | Detritus_sediment | 0     | 0     | 0        | 0         | 0.13  | 0     | 0     | 0     | 0     | 0       | 0           | 0           |

Table 5: Trophic group parameters for the balanced Ross Sea model.  $B$  – Biomass,  $P/B$  – Production,  $P/Q$  – Growth efficiency,  $E$  – Ecotrophic efficiency,  $A$  – Accumulation (as fraction of  $P$ ),  $X$  – Export (as fraction of  $P$ ),  $U$  – Unassimilated consumption,  $T^s$  – seasonal transfers (as fraction of  $P$ ),  $T^s$  – growth transfers (as fraction of  $P$ ), Fishery take,  $F$  – 0 for all groups.

|    | Group          | $B$ (gC m <sup>-3</sup> ) | $P/B$ (y <sup>-1</sup> ) | $Q/B$ (y <sup>-1</sup> ) | $P/Q$   | $E$   | $A$ | $X$   | $U$  | $T^s$ | $T^s$ | $R/B$ (y <sup>-1</sup> ) | Trophic level |
|----|----------------|---------------------------|--------------------------|--------------------------|---------|-------|-----|-------|------|-------|-------|--------------------------|---------------|
| 1  | Emperor        | 4.90E-04                  | 0.102                    | 41.8                     | 0.00244 | 0.573 | 0   | 0.145 | 0.30 | 0     | 0     | 29.1                     | 5.22          |
| 2  | Adélie         | 1.23E-03                  | 0.351                    | 65.9                     | 0.00533 | 0.532 | 0   | 0.150 | 0.30 | 0     | 0     | 45.8                     | 4.74          |
| 3  | Flying_birds   | 1.33E-04                  | 0.541                    | 112                      | 0.00484 | 0.150 | 0   | 0.150 | 0.30 | 0     | 0     | 77.8                     | 4.76          |
| 4  | Crabeater      | 2.21E-03                  | 0.131                    | 20.8                     | 0.00629 | 0.626 | 0   | 0.250 | 0.20 | 0     | 0     | 16.5                     | 4.10          |
| 5  | Weddell        | 3.98E-04                  | 0.119                    | 27.7                     | 0.00428 | 0.625 | 0   | 0.250 | 0.20 | 0     | 0     | 22.1                     | 5.37          |
| 6  | Leopard        | 1.44E-04                  | 0.114                    | 22.9                     | 0.00498 | 0.250 | 0   | 0.250 | 0.20 | 0     | 0     | 18.2                     | 5.17          |
| 7  | Ross           | 3.52E-05                  | 0.151                    | 33.0                     | 0.00456 | 0.250 | 0   | 0.250 | 0.20 | 0     | 0     | 26.3                     | 4.94          |
| 8  | Minke          | 8.91E-04                  | 0.039                    | 14.4                     | 0.00271 | 0.995 | 0   | 0.995 | 0.20 | 0     | 0     | 11.5                     | 4.43          |
| 9  | Baleen_whales  | 4.65E-04                  | 0.027                    | 8.32                     | 0.00323 | 0.994 | 0   | 0.994 | 0.20 | 0     | 0     | 6.63                     | 4.20          |
| 10 | Orca           | 4.67E-04                  | 0.047                    | 10.4                     | 0.00451 | 0.887 | 0   | 0.887 | 0.20 | 0     | 0     | 8.29                     | 5.42          |
| 11 | Sperm          | 8.45E-04                  | 0.022                    | 5.08                     | 0.00429 | 0.899 | 0   | 0.899 | 0.20 | 0     | 0     | 4.04                     | 5.44          |
| 12 | Toothed_whales | 2.46E-05                  | 0.066                    | 12.0                     | 0.00549 | 0.872 | 0   | 0.872 | 0.20 | 0     | 0     | 9.5                      | 5.31          |
| 13 | L_demersal     | 9.45E-03                  | 0.124                    | 1.13                     | 0.110   | 0.950 | 0   | 0.200 | 0.27 | 0     | 0     | 0.699                    | 5.35          |
| 14 | M_demersal     | 9.67E-03                  | 0.239                    | 1.89                     | 0.126   | 0.951 | 0   | 0     | 0.27 | 0     | 0.095 | 1.14                     | 4.72          |
| 15 | S_demersal     | 9.28E-02                  | 0.495                    | 4.26                     | 0.116   | 0.950 | 0   | 0     | 0.27 | 0     | 0.010 | 2.62                     | 4.26          |
| 16 | Silverfish     | 6.44E-02                  | 1.383                    | 8.92                     | 0.155   | 0.954 | 0   | 0     | 0.27 | 0     | 0     | 5.13                     | 4.34          |
| 17 | Pelagic_fish   | 3.50E-02                  | 1.24                     | 8.63                     | 0.144   | 0.949 | 0   | 0     | 0.27 | 0     | 0.216 | 5.06                     | 4.27          |
| 18 | Cephalopods    | 4.78E-03                  | 6.29                     | 15.8                     | 0.398   | 0.951 | 0   | 0     | 0.20 | 0     | 0     | 6.36                     | 4.45          |
| 19 | Krill_crystal  | 4.14E-02                  | 1.86                     | 13.4                     | 0.139   | 0.953 | 0   | 0     | 0.20 | 0     | 0     | 8.86                     | 3.00          |
| 20 | Krill_superba  | 9.70E-02                  | 1.15                     | 8.70                     | 0.132   | 0.958 | 0   | 0     | 0.20 | 0     | 0     | 5.81                     | 2.99          |
| 21 | Macrozoa       | 3.79E-02                  | 2.05                     | 15.4                     | 0.132   | 0.952 | 0   | 0     | 0.20 | 0     | 0     | 10.3                     | 3.43          |
| 22 | Mesozoo        | 6.99E-01                  | 3.85                     | 13.2                     | 0.292   | 0.966 | 0   | 0     | 0.25 | 0     | 0     | 6.06                     | 3.35          |
| 23 | Microzoa       | 2.11E-01                  | 14.1                     | 40.2                     | 0.350   | 0.982 | 0   | 0     | 0.30 | 0     | 0.006 | 14.2                     | 2.84          |
| 24 | Flagellates    | 2.63E-01                  | 56.3                     | 161                      | 0.350   | 0.989 | 0   | 0     | 0.15 | 0     | 0     | 80.0                     | 2.47          |
| 25 | Phytoplankton  | 1.08E+00                  | 52.0                     | na                       | na      | 0.567 | 0   | 0     | na   | 0     | 0     | na                       | 1.00          |
| 26 | Ice_metazoa    | 3.27E-03                  | 20.4                     | 74.6                     | 0.274   | 0.902 | 0   | 0     | 0.20 | 0.091 | 0     | 39.2                     | 2.18          |
| 27 | Ice_protozoa   | 1.25E-03                  | 45.4                     | 131.5                    | 0.346   | 0.905 | 0   | 0     | 0.20 | 0.167 | 0     | 59.6                     | 2.72          |
| 28 | Ice_algae      | 2.36E-01                  | 8.71                     | na                       | na      | 0.712 | 0   | 0     | na   | 0.518 | 0     | na                       | 1.00          |
| 29 | Megabenthos    | 1.36E+00                  | 0.243                    | 1.22                     | 0.199   | 0.453 | 0   | 0     | 0.30 | 0     | 0     | 0.615                    | 2.90          |
| 30 | Macrobenthos   | 4.39E-01                  | 0.361                    | 1.45                     | 0.249   | 0.901 | 0   | 0     | 0.20 | 0     | 0     | 0.798                    | 2.98          |
| 31 | Meiobenthos    | 4.38E-02                  | 9.9                      | 33.7                     | 0.294   | 0.895 | 0   | 0     | 0.20 | 0     | 0     | 17.1                     | 2.94          |
| 32 | Bacteria_ice   | 5.01E-03                  | 64.3                     | 195                      | 0.329   | 0.379 | 0   | 0     | 0.31 | 0.096 | 0     | 71.0                     | 2.00          |
| 33 | Bacteria_water | 2.68E-01                  | 39.7                     | 135                      | 0.293   | 0.991 | 0   | 0     | 0.30 | 0.000 | 0     | 55.6                     | 2.00          |

(continued)

Table 5 (continued)

|    | Group             | $B$ (gC m <sup>-3</sup> ) | $P/B$ (y <sup>-1</sup> ) | $Q/B$ (y <sup>-1</sup> ) | $P/Q$ | $E$   | $A$   | $X$ | $U$  | $T^s$ | $T^*$ | $R/B$ (y <sup>-1</sup> ) | Trophic level |
|----|-------------------|---------------------------|--------------------------|--------------------------|-------|-------|-------|-----|------|-------|-------|--------------------------|---------------|
| 34 | Bacteria_sediment | 2.84E+01                  | 0.537                    | 1.15                     | 0.467 | 0.177 | 0     | 0   | 0.29 | 0     | 0     | 0.280                    | 2.00          |
| 35 | Carcasses         | na                        | na                       | na                       | na    | na    | 0     | 0   | na   | 0     | 0     | na                       | 4.34          |
| 36 | Detritus_ice      | na                        | na                       | na                       | na    | na    | 0     | 0   | na   | 0.212 | 0     | na                       | 1.00          |
| 37 | Detritus_water    | na                        | na                       | na                       | na    | na    | 0     | 0   | na   | 0.349 | 0     | na                       | 1.00          |
| 38 | Detritus_sediment | na                        | na                       | na                       | na    | na    | 0.070 | 0   | na   | 0     | 0     | na                       | 1.00          |



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- Figure 1: Le secteur examiné dans le modèle est indiqué en noir. Le secteur d'étude est limité par l'isobathe 3 000 m, la latitude 69°S, la plate-forme glaciaire permanente, la côte et les méridiens 170°E et 160°W. Les étoiles grises indiquent où la légine antarctique est capturée par la pêche. Les lieux de pêche de la CCAMLR (sous-zones 88.1 et 88.2) et les unités de recherche à échelle précise sont indiqués.
- Figure 2: Réseau trophique du modèle de la mer de Ross. La taille des cases relative aux groupes non détritiques est ajustée pour que leurs côtés soient proportionnels à la biomasse de ce groupe, à la puissance 0,1, et leur position verticale correspond (approximativement) au niveau trophique. Noter le changement d'échelle de l'ordonnée au niveau trophique 4. Les flèches montrent la direction des flux de carbone organique. Pour une meilleure lisibilité, ni les carcasses, ni les flux dirigés vers les détritiques, ni les puits de respiration n'ont été indiqués.

## Список таблиц

- Табл. 1: Параметры трофических групп для модели моря Росса, полученные по локальным данным и литературе.  $B$  – Биомасса,  $P/B$  – Продукция,  $P/Q$  – Эффективность роста,  $E$  – Экотрофическая эффективность,  $A$  – Накопление (как компонент  $P$ ),  $X$  – Экспорт (как компонент  $P$ ),  $U$  – Неассимилированное потребление,  $T^S$  – Сезонные перемещения (как компонент  $P$ ),  $T^R$  – Перемещения роста (как компонент  $P$ ). Изъятие промыслом  $F = 0$  для всех групп. Последние четыре столбца указывают целевые пункты для перемещений из данного ряда. Например, рост средней демерсальной рыбы имеет целью группу 13 – крупную демерсальную рыбу.
- Табл. 2: Параметры рациона для модели моря Росса, полученные по локальным данным и литературе. Приведенные значения представляют собой долю (по весу органического углерода) данного вида добычи в рационе хищников.
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- Табл. 4: Параметры неопределенности ( $K$ ) для трофической модели моря Росса согласно пояснениям в тексте.
- Табл. 5: Параметры трофических групп для сбалансированной модели моря Росса.  $B$  – Биомасса,  $P/B$  – Продукция,  $P/Q$  – Эффективность роста,  $E$  – Экотрофическая эффективность,  $A$  – Накопление (как компонент  $P$ ),  $X$  – Экспорт (как компонент  $P$ ),  $U$  – Неассимилированное потребление,  $T^S$  – Сезонные перемещения (как компонент  $P$ ),  $T^g$  – перемещения роста (как компонент  $P$ ). Изъятие промыслом  $F = 0$  для всех групп.
- Табл. 6: Матрица рациона для сбалансированной модели моря Росса, показывающая доли добычи в рационе каждого хищника. Хищники показаны на оси  $x$ , а добыча – на оси  $y$ . Цифры "0.00" означают, что доля рациона  $>0$  и  $<0.005$ .

#### Список рисунков

- Рис. 1: Район модельных исследований показан черным. Район исследований ограничен изобатой 3 000 м, параллелью  $69^\circ$  ю.ш., постоянным шельфовым ледником, сушей и меридианами  $170^\circ$  в.д. и  $160^\circ$  з.д. Серыми звездочками показано, где ведется промысел антарктического клыкача. Показаны промысловые районы АНТКОМ (подрайоны 88.1 и 88.2) и мелкомасштабные исследовательские единицы .
- Рис. 2: Модельная трофическая сеть моря Росса. Размеры клеток для недетритных групп приведены в масштабе, так что их стороны относятся к биомассе в этих группах в степени 0.1 и размещены по вертикали в соответствии с (приблизительным) трофическим уровнем. Обратите внимание на изменение шкалы оси  $y$  на 4-м трофическом уровне. Стрелки показывают направление циркуляции органического углерода. Останки, переход в детрит и поглотители продуктов дыхания не показаны для упрощения.

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- Tabla 2: Parámetros de la dieta para el modelo del Mar de Ross estimados de datos locales y de los datos publicados. Los valores dados son la proporción (en peso de carbono orgánico) de una especie presa dada en la dieta de los depredadores.
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- Figura 2: Modelo de la red alimenticia del Mar de Ross. El tamaño de las cajas para los grupos que no son detrito ha sido ajustado de manera que los lados son proporcionales a la biomasa de ese grupo, elevado a la potencia 0.1, y han sido puestas verticalmente de acuerdo con el nivel trófico aproximado. Nótese el cambio en la escala del eje de las ordenadas (y) a nivel trófico 4. Las flechas indican la dirección del flujo de carbono orgánico. En aras de la claridad, no se incluyen cuerpos de animales muertos, el flujo a detrito, y los sumideros respiratorios.

