

Document [to be completed by the Secretariat]
Date submitted [to be completed by the Secretariat]
Language [to be completed by the Secretariat]
Meeting: WG-EMM 2012

WG-EMM-12/53
18 June 2012
Original: English
Agenda Item No(s): tba

Title **Network characterisation of the food-web of the Ross Sea, Antarctica**

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Published or accepted for publication elsewhere? Yes No

If published, give details

To be considered for publication in CCAMLR Science? Yes No

ABSTRACT

A balanced ecosystem model is used to explore the system-level characteristics of the food-web of the Ross Sea shelf and slope before the advent of commercial fishing for Antarctic toothfish (*Dissostichus mawsoni*) in the region. We evaluate: (1) biomass and flow of organic matter by trophic level; (2) mixed trophic impact; and (3) ecological importance. Note that the analysis considers food-web structure and function at the spatial, temporal and ecological scale of the ecosystem model, i.e. the whole Ross Sea shelf and slope area, averaged over a typical year, and in 35 trophic groups. Effects at smaller spatial and temporal scales, and effects concerning only parts of trophic groups, are not resolved by this analysis. The Ross Sea food-web is a partially inverted biomass pyramid with a pronounced peak in biomass in the lower-middle part of the food-web, a result of high biomass of mesozooplankton and benthic invertebrates. The biomass of top predators (trophic levels > 4.5) is only 0.5% of the total living biomass in the Ross Sea (bacteria excluded). The six groups with the highest 'indices of ecological importance' in the food-web of the Ross Sea are phytoplankton, mesozooplankton, Antarctic silverfish (*Pleuragramma antarcticum*), small demersal fishes, Antarctic krill (*Euphausia superba*) and cephalopods. Pelagic fishes and crystal krill (*E. crystallorophias*) are also likely to have high importance in the Ross Sea food-web. These eight groups should be the priorities for monitoring for large-scale ecosystem change in the region, for example due to climate change, trophic cascades or regime shift. The analysis presented here does not support the hypothesis that changes to the abundance of toothfish in the Ross Sea will propagate through the food-web; it appears that Antarctic toothfish only have a moderate index of ecological importance in the food-web of the Ross Sea shelf and slope. Changing the biomass of Antarctic toothfish on the Ross Sea shelf and slope is likely to have the greatest effect on the demersal fish community there.

SUMMARY OF FINDINGS AS RELATED TO NOMINATED AGENDA ITEMS

Agenda Item	Findings
3	Insights developed from large-area food-web characterisation are useful for consideration of ecosystem risks arising from the synergistic effects of fishing and/or climate change, and for determining priorities for research and monitoring.

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1. INTRODUCTION

Although subject to sealing and whaling in the 1960s to early 1980s (Ainley 2009), the ecosystem of the Ross Sea, Antarctica has been affected by human activity probably less than any other ocean in the world (Halpern et al. 2008; Ainley 2004). In particular, commercial fishing in the region only began in 1997, with the advent of an exploratory longline fishery for Antarctic toothfish, (*Dissostichus mawsoni*). The Ross Sea hence represents one of the only opportunities to study a continental shelf ecosystem with its full complement of top piscine predators (Ainley 2009). It is also clear that humans have not displaced any of the main air-breathing predators from the Ross Sea ecosystem as has occurred in many shelf sea marine ecosystems (e.g Schipper et al. 2008). The scientific study of the fauna and oceanography of the Ross Sea began with the first discovery of the region by Sir James Clark Ross in 1842. Since then, the Ross Sea has become one of the best studied regions of the high Antarctic, and is home to research bases of US, New Zealand, Italy, and by 2014/15, the Republic of Korea. Research on the structure of the food-web of the Ross Sea has culminated in complex qualitative descriptions (e.g. Smith et al 2007, Smith et al. 2010) and a quantitative model (Pinkerton et al. 2010). The model of Pinkerton et al. (2010) is an end-to-end, mass-balance model, in that it represents the flow of organic carbon (a proxy for energy) through all parts of the food-web, including bacteria and whales. The food-web model of Pinkerton et al. (2010) describes flow through the food-web in a typical year during the period 1990–2000, when cumulative removal of toothfish was close to zero (Dunn & Hanchet 2007).

The aim of the current study is to explore the system-level characteristics of the Ross Sea food-web before the advent of commercial fishing. We use the Ross Sea food-web model of Pinkerton et al. (2010) to characterise the network properties of the ecosystem by evaluating a suite of ecosystem metrics, namely: (1) biomass and flow of organic matter by trophic level; (2) mixed trophic impact; and (3) ecological importance. Insights developed from the characterisation of the food-web are useful for consideration of ecosystem vulnerabilities to pressure imposed by the synergistic effects of fishing and climate change, and for determining priorities for research and monitoring. Ecosystem characterisation of the Ross Sea is hence relevant to Article II of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which explicitly requires management of fishing in the study region to protect the relationships between all species in the food-web.

2. METHODS

2.1 Ross Sea food-web model

The Ross Sea study region defined for this work is bounded to the north by the 3000 m depth contour and by 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 area of this region is 637 000 km², with 29% of the region shallower than 500 m, 41% depths 500–1000 m, and 30% deeper than 1000 m (Davey 2004).

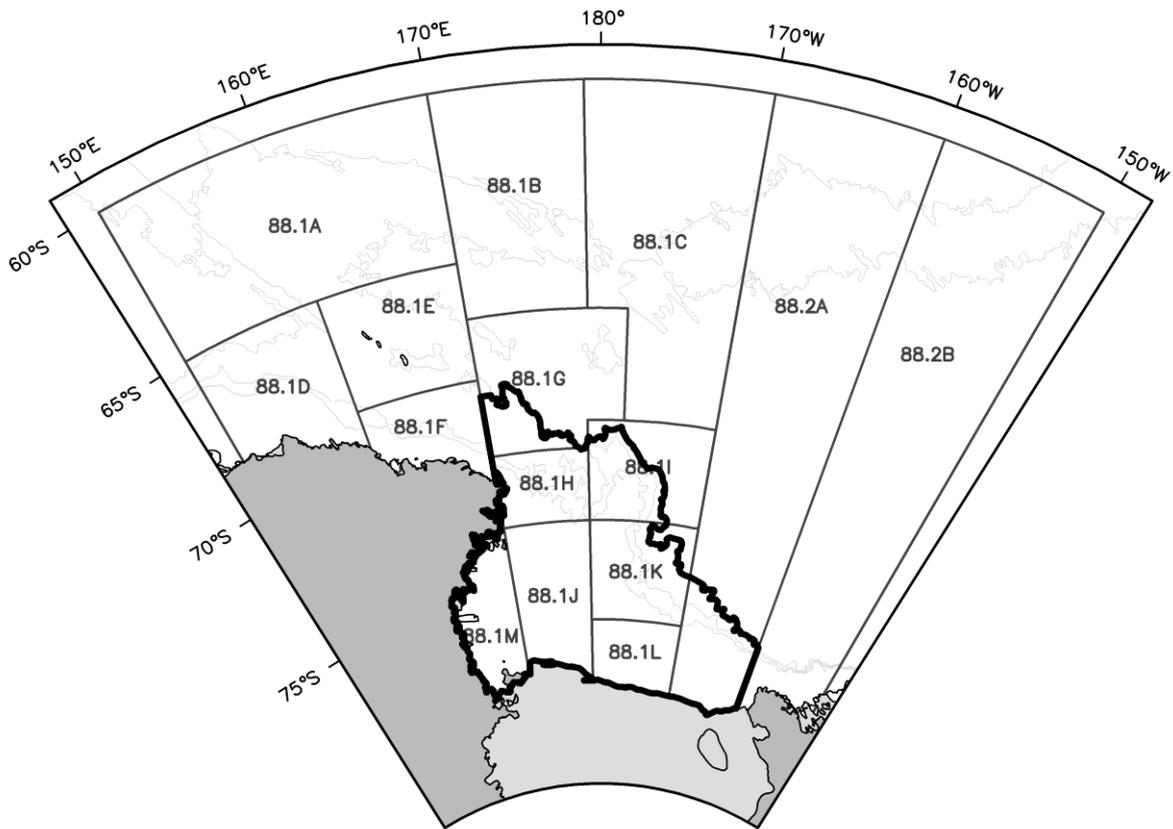


Figure 1: Ross Sea study region defined for the purposes of this work, showing Subarea 88.1, SSRU 88.2A, and SSRU 88.2B. Depth contours shown at 1000, 2000 and 3000 m. The model study area is shown in dark and encompasses the Ross Sea shelf and slope; the study area is bounded by the 3000 m depth contour, by 69°S, by the permanent ice shelf, land, and the 170°E and 160°W meridians.

The modelling approach used to develop the Ross Sea food-web model used here (Pinkerton et al. 2010) is similar to that of Ecopath with Ecosim (Christensen et al. 2008), but was independently formulated. The model has 35 trophic groups (Figure 2), with two primary producers (phytoplankton and ice algae), three groups of bacteria (water column, sea-ice and benthic), and a single detrital group made by combining carcasses, water-column detritus, ice detritus, and benthic detritus from Pinkerton et al. (2010). There are three groups of benthic invertebrates (megabenthos, macrobenthos, meiobenthos), six zooplankton groups (heterotrophic flagellates, microzooplankton, mesozooplankton, Antarctic krill, crystal krill, other macrozooplankton), cephalopods (squid and octopods combined), five groups of fishes (large demersal fishes which are exclusively Antarctic toothfish, medium demersal fishes, small demersal fishes, Antarctic silverfish, and pelagic fishes), five cetacean groups (minke whale, other baleen whales, orca, sperm whale, other toothed whales), four seal groups (crabeater seal, Weddell seal, leopard seal, Ross seal), and three bird groups (Emperor penguins, Adélie penguins, flying birds). Biomass was presented in units of organic carbon density (gC m^{-2}) and trophic flows in units of $\text{gC m}^{-2} \text{y}^{-1}$. The Ross Sea model (Pinkerton et al. 2010) had 342 parameters and 67 constraints. Estimating these 342 parameters for the Ross Sea model used over 700 published and non-published data sources. Detailed information on the estimation of the parameters is online from the CCAMLR Science journal website (www.ccamlr.org/pu/e/e_pubs/cs/Vol17SuppDocs.htm). We also estimated the relative level of uncertainty on these parameters. The initial set of parameters was not self consistent, and Pinkerton et al. (2010) describes the method used to adjust parameters 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. Pinkerton et al. (2010) 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. Initial and balanced model parameters are given in Pinkerton et al. (2010).

The Pinkerton et al. (2010) model of the Ross Sea ecosystem has to be seen as preliminary because, although a surprising amount of data is available for the Ross Sea ecosystem (Smith et al. 2000; Pinkerton et al. 2010), a number of parameters were based on incomplete information. Many plausible models are likely to be obtainable from the initial parameter set because this type of model is highly under-constrained and because the system varies from year to year. Nevertheless, the food-web model of Pinkerton et al. (2010) represents a plausible, self-consistent, quantitative, semi-validated view of the structure of the Ross Sea ecosystem.

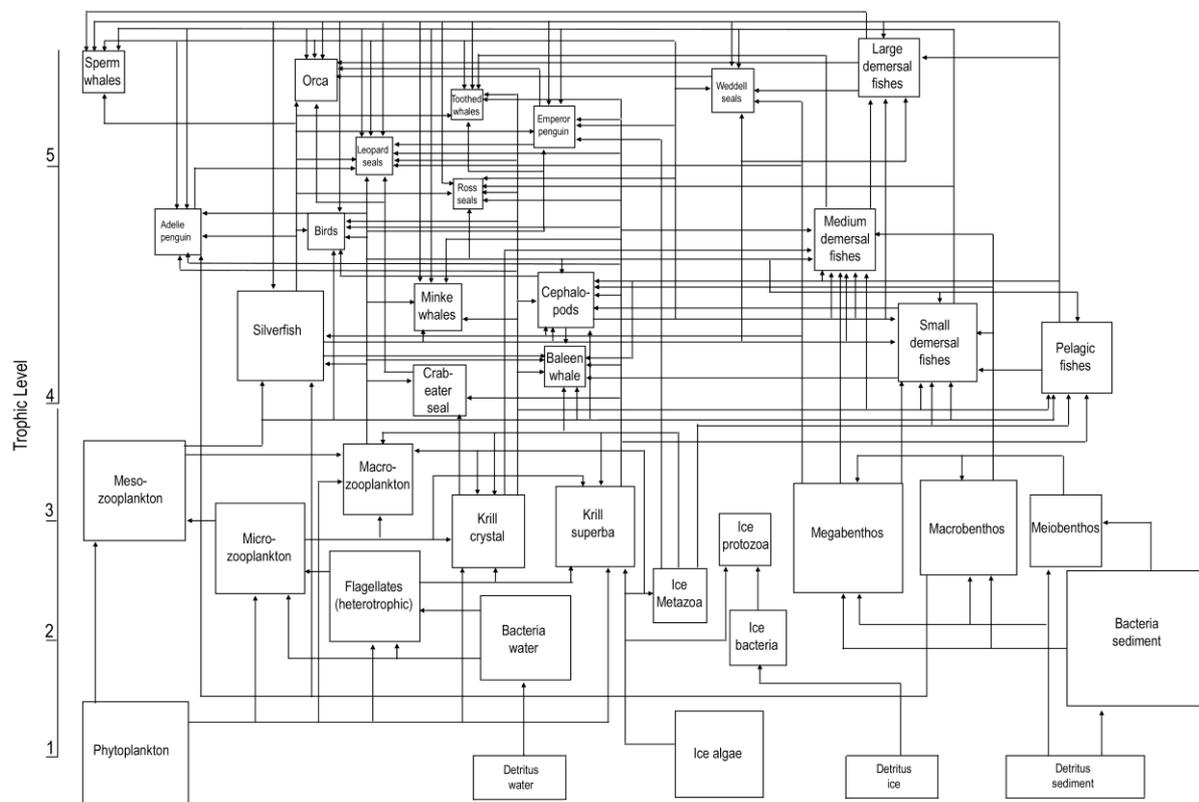


Figure 2: Model food-web of the Ross Sea. Boxes sizes for non-detrital groups are scaled so that the sides are proportional to biomass in that group to the power 0.1, and positioned vertically according to (approximate) trophic level. Note the change in y-axis scale at trophic level 4. Arrows show the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

2.2 Network characterisation

2.2.1 Biomass and energy flow by trophic level

Biomass and productivity of all groups of organisms in the Ross Sea food-web model were grouped by trophic level: trophic level <1.5 (primary producers), 1.5-2.5 (lower food-web), 2.5-3.5

(lower/middle trophic level groups), 3.5-4.5 (upper/middle trophic level groups), and >4.5 (top predators). In addition, non-fractional trophic levels were calculated using trophic level decomposition (Christensen et al. 2008) to give the “Lindeman-spine” (*sensu* Lindeman 1942). In trophic level decomposition, a proportion of the biomass of each group in the trophic model is assigned to integer trophic levels, written I, II, III, IV etc. The allocation is carried out to maintain the average trophic level of the group, and to maintain pathways of energy flow through the food-web. The Lindeman spine shows the flow of organic carbon into and out of each integer trophic level, as well as the amount of carbon leaving through respiration, import, export, transfer to detritus, and other non-trophic transfers due to spawning and growth. The detrital pathway is also represented in the Lindeman spine decomposition. In effect, the Lindeman spine decomposition conceptually translates an interlinked food-web into a linear series of integer trophic level bins and a parallel detrital pathway and allows an alternative visualisation of energy flow through the food-web.

2.2.2 Mixed trophic impact analysis

Mixed trophic impact (MTI) analysis investigates the effect on one organism or group of organisms (the “impacted” group) due to a small change in the biomass of another (the “impacting” group) (e.g. Ulanowicz & Puccia 1990; Libralato et al. 2006). The MTI matrix \mathbf{M} is calculated from a balanced food-web diagram as equation 1. The MTI matrix, \mathbf{M} , is a square n -by- n matrix where n is the number of the number of groups in the model. The matrix has elements m_{ij} that are often interpreted (e.g. Libralato et al. 2006) as the change in biomass of one group (the “impacted” group, j) due to a small change in the biomass in another group (the “impacting” group, i). Recent work has shown good general agreement between the MTI matrix \mathbf{M} and relative changes in biomasses from perturbation analyses using Ecosim simulations (Libralato et al. 2006) which supports the interpretation of \mathbf{M} as the change in biomass of one group due to a small change in the biomass in another.

$$\mathbf{M}^t = (\mathbf{I} - \mathbf{Q}^t)^{-1} - \mathbf{I} \quad [1]$$

Here, \mathbf{I} is the identity matrix of size n -by- n where n is the number of groups in the model. Equation 1 takes into account indirect food-web effects, that is, impacts of one species on another via multiple steps through the food-web (Ulanowicz & Puccia 1990). The n -by- n matrix \mathbf{Q} gives a measure of the direct (one-step) trophic impact of one species on another. The trophic impact of species i on species j is written as element q_{ij} in the matrix \mathbf{Q} , and defined as the difference between bottom-up (g_{ij}) and top-down effects (f_{ij}) (equation 2, Ulanowicz & Puccia 1990).

$$q_{ij} = g_{ij} - f_{ij} \quad [2]$$

Here, g_{ij} is the proportion of prey item i in the diet of predator j , and f_{ij} is the fraction of the net production of prey item j that is consumed by predator i (Ulanowicz & Puccia 1990). By “net production”, Ulanowicz & Puccia (1990) meant to exclude respiratory output. By this definition, the denominator of f would be equal to “production” (P) in Ecopath models (Christensen & Walters, 2004; Christensen et al. 2008). Here, we also include non-trophic net imports in the denominator of f to allow the importance of detrital pathways to be considered. Note that f defined in this way is subtly different to that proposed by Ulanowicz & Puccia (1990), which did not include non-trophic imports, but consistent with comments by the authors in that paper that different formulations for the denominator of f are potentially valid and should be considered. Our definition is different again from the method implemented in Ecopath, where the denominator of f_{ij} is taken as the total consumption of j by all its predators, i.e. excluding production of j that is not consumed. We feel that the Ecopath formulation of f can lead to unrealistically strong top-down factors being returned by in those cases where only a part of

the mortality of a group is by direct predation. We note that MTI analysis is typically based on food-web models such as Ecopath, and, as such, only considers trophic effects at the spatial and temporal scale of the underlying model. MTI analysis does not consider non-trophic interactions between species (e.g. provision of habitat), “behavioural” interactions between species (e.g. Preisser et al. 2005), threshold or compensatory effects, or non-linearity in ecosystem response to perturbation.

2.2.3 Ecological importance

We define ecological importance (*sensu* Libralato et al. 2006) as a measure of the overall effect on food-web structure of changes to the abundance of a species or group. Ecological importance as defined here aims to quantify how important an organism or group of organisms are in maintaining the structure and function of a food-web subjected to perturbation. Ecological importance is preferred over “keystoneness” since the meaning of the latter strictly refers to the amount by which the importance of a species in an ecosystem exceeds that “expected on the basis of abundance alone” (Power et al. 1996). Unfortunately, there is no accepted measure of ecological importance expected based on abundance alone. In any case, we argue that ecological importance is the relevant measure in terms of assessing by how much changes in the abundances of one species or group are likely to affect the food-web, irrespective of whether those species have high or low biomass in the ecosystem.

Ecological importance with reference to small perturbations of the ecosystem can be estimated from the single-step trophic impact matrix, \mathbf{Q} (equations 3 and 4) or the multiple-step matrix, \mathbf{M} (equations 5 and 6; Table 1). The former focuses on direct (first order) predator-prey linkages and does not consider how these effects may propagate through the food-web. In contrast, \mathbf{M} considers multiple interactions in the ecosystem and hence may capture more diffuse or higher-order effects. It is not known which of these approaches is more realistic or appropriate, so here, we calculate and compare both approaches. In addition, there are two ways of summarizing the overall importance of a species in the food-web based on its effects on all other species. Libralato et al. (2006) suggests calculating the ecological importance of species i as the root mean square of the squared value of m_{ij} calculated over all j here denoted as EI3 _{i} (equation 5). We also define EI4 _{i} based on the sum of the absolute values of m_{ij} calculated over all j (equation 6). It is possible that using absolute values rather than squared values gives weak links (*sensu* McCann et al. 1998; Pinnegar et al. 2005) higher and more appropriate importance. The measures are denoted as EI1 and EI2 based on \mathbf{Q} and \mathbf{M} respectively. Note that in all cases, m_{ii} and q_{ii} are set to zero before calculating ecological importance; we do not allow a group to affect itself in this analysis.

Table 1: Definition of four measures of ecological importance used in this study.

	Weak links (lower values of q and m) are of low importance	Weak links (lower values of q and m) have greater importance
Based on direct (single step) effects in the food-web; uses single step matrix, \mathbf{Q}	$EI1(i) = \sqrt{\sum_{j=1}^n q_{ij}^2}$ [3]	$EI2(i) = \sum_{j=1}^n q_{ij} $ [4]
Based on multiple steps through the food-web; used mixed trophic impact matrix, \mathbf{M}	$EI3(i) = \sqrt{\sum_{j=1}^n m_{ij}^2}$ [5]	$EI4(i) = \sum_{j=1}^n m_{ij} $ [6]

3. RESULTS & DISCUSSION

3.1 Description of the Ross Sea food-web

Primary production in the Ross Sea occurs mostly in the intense localised burst of primary production in the Ross Sea polynya adjacent to the permanent ice shelf (Zwally et al. 1985; Kurtz & Bromwich 1985; Arrigo & van Dijken 2004). Phytoplankton blooms in the Ross Sea form a bimodal distribution: blooms of the prymnesiophyte *Phaeocystis antarctica* in late October/early November in unstratified waters, followed by diatom dominated blooms in December/January as the water stratifies (DiTullio & Smith 1997; Arrigo & van Dijken 2004; Reddy & Arrigo 2006). 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 (>96%) of primary production in the Ross Sea is by phytoplankton in the water column. Although sea ice plays a key structural role in forcing the ecology of the Ross Sea (Thomas & Dieckmann 2002; Arrigo & Thomas 2004), ice algae are estimated to produce only 3.5% of total primary production of the Ross Sea. The proportion of primary production in the Ross Sea that is grazed is poorly known. 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 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 enters the detrital pool and is eventually decomposed by bacterial action in the water column or transferred to the benthos by settling. 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 & Thomas 2002; Arrigo & 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 productivity is estimated to be nearly a hundred 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. The vertical flux to the sea-bed corresponds to 26% of total detrital input, 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 is a notable concentration of predators in the Ross Sea in summer, including large demersal fishes (Antarctic toothfish, *Dissostichus mawsoni*), birds, seals and whales. Consumption by these predators in the model is in the ratio 5%, 55%, 29%, and 11%, respectively. Bird biomass in the Ross Sea is dominated by penguins, with a total of about 1 million breeding pairs of Adélie penguins (*Pygoscelis adeliae*), and more than 30,000 pairs of emperor penguins (*Aptenodytes forsteri*) (Young

1981; Harper et al. 1984; Ainley et al. 1984). Antarctic petrels (*Thallassoica 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 12%.

Seals are the most common marine mammals in the Ross Sea, but the numbers of seals present in the study area are poorly known because of their cryptic nature and the difficulty of research in pack-ice. It is estimated that there are more than 200,000 crabeater seals (*Lobodon carcinophagus*) present in the Ross Sea in summer. Weddell seals (*Leptonychotes weddelli*) 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 (*Hydrurga leptonyx*) and Ross seals (*Ommatophoca rossi*) are also present. There is debate over whether or not Weddell seals are migratory, and on the dispersion patterns of all seal species in the winter. In the model, we estimate that seal consumption is made up from crabeater seals 75%, Weddell seals 18%, leopard seals 5% and Ross seals 2%.

The abundances and movements of minke (*Balaenoptera bonarensis*, *Balaenoptera acuturostrata*) and other baleen whales (blue, fin, sei, humpback) in the Ross Sea region are poorly known. It appears that, with the exception of minke whales, baleen whales tend to remain on the periphery of our study area. All baleen whales are absent from the region in other seasons. The main toothed whales present in the study area in summer are sperm whales (*Physeter macrocephalus*) and orca/killer whales (*Orcinus orca*). Information on the seasonal abundances of toothed whales is limited, coming primarily from surveys of their distribution and numbers carried out by systematic surveys (e.g., Bassett & Wilson 1983; Ainley 1985; Kasamatsu & Joyce 1995). The high encounter rate of sperm whales along the Ross Sea slope in some reports is notable (Kasamatsu & Joyce 1995). Recent work has shown that three different types of orca may occur in the Ross Sea (Pitman et al. 2001; Pitman & 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%.

There are two species of krill in the study area, crystal krill (*Euphausia crystallorophias*) over the shelf, and Antarctic krill (*E. superba*) 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*, *Metridia gerlachei* and *Paraeuchaeta* sp.) (Voronina 1998; Tarling 2004). Other smaller copepod species such as *Ctenocalanus citer*, *Microcalanus pygmaeus*, and *Oithona* spp. are numerically very important. Pteropods (*Clione limacina* and *Limacina helicina antarctica*) provide a significant but poorly quantified contribution to the mesozooplankton biomass and productivity of the Ross Sea. In the model, Antarctic krill dominate the macrozooplankton in terms of biomass and production (55%, 42% respectively), with crystal krill and the “other macrozooplankton” group making up the remainder approximately equally. “Other macrozooplankton” in the Ross Sea includes species that, in fact, span the nominal size-ranges for meso- and macrozooplankton. Species included in this trophic group were, *inter alia*, Coelenterata (*Dipulmaris antarctica*, *Calycopsis borchgrevinki*), Amphipoda (*Hyperiella dilatata*, *H. macronyx*, *Cylopus lucasii*), Euphausiacea (*Thysanaessa macrura*), Chaetognatha (*Sagitta gazellae*, *Eukrohnia hamata*), and Salpidae (*Salpa gerlachei*).

Antarctic silverfish (*Pleuragramma antarcticum*) 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* *T. scotti*, *T. eulepidotus*, *T. lepidorhinus*), icefish (especially *Chinobathyscus dewitti*, *Chionodraco hamatus*, *Cryodraco myersi*), dragonfishes (especially *Bathydraco marri*), deepsea smelts (*Bathylagus antarcticus*), deepsea cods (especially *Antimora rostrata*), eel cods (Muraenolepidae), macrourids (*Macrourus whitsoni*, *M. caml*), and skates (*Bathyraja eatonii*, *Raja georgiana*) (La Mesa et al. 2004; Clarke et al. 2010). Abundances 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%).

The abundance and ecological role of cephalopods in the Ross Sea is poorly known. It is likely that pelagic squids are more numerous over the continental slope than shelf including *Bathyteuthis abyssicola*, *Galiteuthis glacialis*, *Kondakovia longimana*, *Mesonychoteuthis hamiltoni*, *Psychroteuthis glacialis* and *Slosarczykovia circumantarctica*. Many small benthic octopods occur over the Ross Sea shelf, including *Adelieledone* sp., *Cirroctopus mawsoni*, *Graneledone antarctica*, *Megaleledone setebos*, a number of species of *Pareledone* sp., and *Thaumeledone peninsulae*. Production within these middle-trophic level 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%), medium-sized demersal fishes (0.5%). The two species of krill together are responsible for more than twice the secondary production of silverfish, but are less important as a prey-source to air-breathing predators.

Large benthic invertebrates (mega- and macrobenthos) have high biomass in the food-web model, but the highly-aggregated representation of the benthic community in Pinkerton et al. (2010) is otherwise 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 IPY-CAML (International Polar Year–Census of Antarctic Marine Life) survey (Hanchet et al. 2008), including stable isotope data on benthic invertebrates, may allow us to disaggregate the megabenthic compartment in the future. It appears for now, that benthic invertebrates are a high biomass and significant component of the Ross Sea food-web, but their ecological importance is hard to determine from the trophic model of Pinkerton et al. (2010). Benthic invertebrates are also likely to be important ecologically as providers of biogenic habitat but that is not tested by trophic models.

3.2 Flow decomposition by trophic level

Based on trophic levels from the food-web model of Pinkerton et al. (2010), upper level predators with trophic levels >4.5 were flying birds, Weddell, leopard and Ross seals, toothed whales, large demersal fishes, and medium demersal fishes. Middle level pelagic groups with trophic level 3.5–4.5 were crabeater seals, baleen whales, small demersal fishes, silverfish, pelagic fishes and cephalopods. Pelagic groups with trophic level 1.5–3.5 were 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 (equivalent to only 2.4% of total primary production) comes from mesozooplankton (59%), benthic invertebrates (19%), krill and macrozooplankton (14%), other medium trophic level pelagic biota (6%), with small (<1%) contributions from ice biota and carcasses. Antarctic silverfish are the major prey item of the

top predators (trophic levels >4.5). Consumption by upper level predators (equivalent to 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; *P. antarcticum* 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).

Biomass and productivity of all groups of organisms in the Ross Sea food-web model, grouped by their fractional trophic levels, is shown in Figure 3a. Bacteria are not included in this analysis as their biomass and productivity is so high they would mask other features of interest. The decomposition of the food-web of the Ross Sea to integer trophic levels via the Lindeman spine transformation is given in Table 2. This decomposition provides a complementary description of the flow of organic matter through the food-web (Figure 3b). It is clear that productivity declines with increasing trophic level, as is always the case. In terms of biomass, the Ross Sea food-web is a partially inverted pyramid (Jackson 2006), with a pronounced peak in biomass in the lower-middle part of the food-web (trophic level 2.5-3.5, or integer trophic level III). In the Ross Sea, this is a result of high biomass of mesozooplankton and large biomass of benthic organisms (mega and macrobenthos). Partially inverted food-web pyramids (i.e. ones with higher biomass in the middle of the food-web than at the base) are often found in open-ocean communities while upright biomass pyramids tend to be the norm in terrestrial and coastal ecosystems (Odum, 1971: p. 81). Jackson (2006) suggested that partially inverted food-web pyramids were the historical norm in all systems, and upright pyramids were the result of loss of large predators, especially large herbivores, from many of the world's ecosystems. This conclusion is corroborated by observations in pristine coral reefs (Wang et al. 2009 and references therein) although other features such as immigration of prey and prey refuges have been associated with inverted biomass pyramids. In the Ross Sea, as in other marine systems, biomass decreases rapidly with trophic level above about 3.5 (or IV). According to Pinkerton et al. (2010), the biomass of top-predators (those with trophic levels greater than 4.5) is only 0.5% of the total living biomass in the Ross Sea (excluding bacteria).

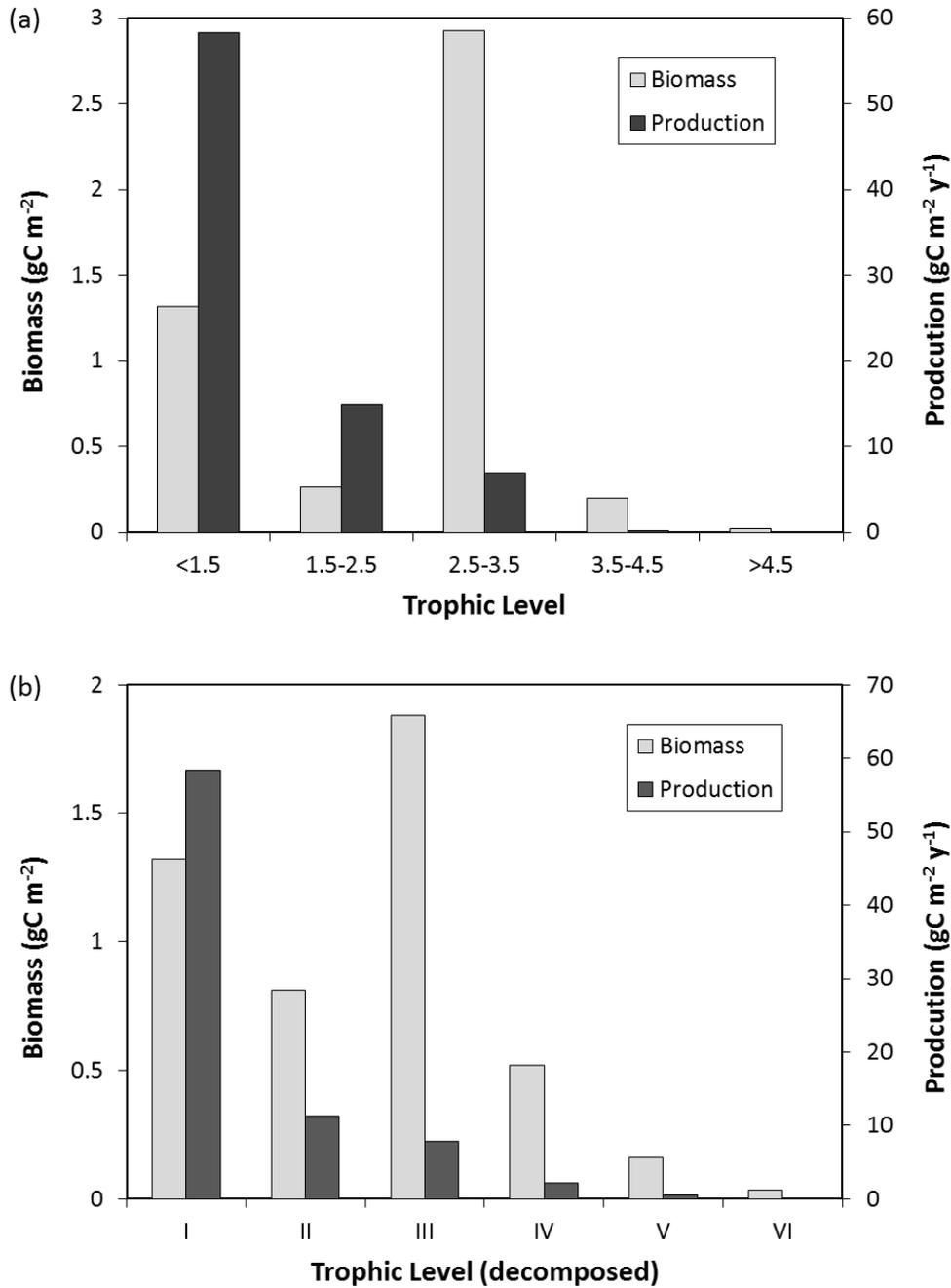


Figure 3: Biomass (gC m⁻²) and production (gC m⁻² y⁻¹) based on the food-web model of the Ross Sea (Pinkerton et al. 2010). a: Biomass and production based on fractional trophic levels in bins: <1.5 (primary producers), 1.5-2.5 (lower food-web), 2.5-3.5 (lower/middle trophic level groups), 3.5-4.5 (upper/middle trophic level groups), and >4.5 (top predators). b: Biomass and production based on integer trophic levels (referred to as I, II, III etc) after network decomposition described in the text.

Table 2: Trophic level decomposition to the Lindeman spine. Values show the allocation of biomass of a model group in Pinkerton et al. (2010) to the Lindeman spine trophic level (I, II, III etc). Groups are listed in ascending trophic level. Note that rows sum to 1.

Group name	Trophic level	I	II	III	IV	V	VI	VII	VIII	IX
Orca	5.4	0.00	0.00	0.01	0.21	0.36	0.28	0.10	0.03	0.01
Weddell	5.3	0.00	0.00	0.01	0.22	0.37	0.27	0.09	0.03	0.01
Toothed_whales	5.3	0.00	0.00	0.03	0.22	0.37	0.25	0.10	0.03	0.01
L_demersal	5.2	0.00	0.01	0.02	0.17	0.48	0.21	0.08	0.02	0.01
Sperm	5.2	0.00	0.00	0.04	0.24	0.34	0.26	0.08	0.02	0.01
Emperor	5.2	0.00	0.00	0.04	0.24	0.34	0.26	0.08	0.02	0.01
Ross	4.9	0.00	0.00	0.13	0.24	0.32	0.20	0.07	0.02	0.01
Leopard	4.8	0.00	0.11	0.06	0.22	0.30	0.20	0.08	0.02	0.01
Adélie	4.7	0.00	0.00	0.17	0.27	0.30	0.18	0.06	0.01	0.00
Flying_birds	4.7	0.00	0.01	0.17	0.26	0.29	0.18	0.06	0.02	0.00
M_demersal	4.6	0.00	0.02	0.12	0.35	0.30	0.14	0.05	0.01	0.00
Cephalopods	4.4	0.00	0.00	0.20	0.37	0.27	0.11	0.03	0.01	0.00
Minke	4.4	0.00	0.00	0.26	0.29	0.28	0.12	0.04	0.01	0.00
Silverfish	4.3	0.00	0.00	0.25	0.33	0.29	0.09	0.02	0.01	0.00
Pelagic_fish	4.3	0.00	0.00	0.29	0.31	0.28	0.09	0.02	0.01	0.00
Baleen_whales	4.2	0.00	0.00	0.32	0.30	0.26	0.08	0.02	0.01	0.00
S_demersal	4.2	0.00	0.02	0.17	0.53	0.18	0.06	0.02	0.01	0.00
Crabeater	4.1	0.00	0.00	0.37	0.29	0.25	0.07	0.02	0.00	0.00
Macrozoo	3.4	0.00	0.34	0.19	0.26	0.15	0.05	0.01	0.00	0.00
Mesozoo	3.3	0.00	0.25	0.32	0.30	0.09	0.02	0.01	0.00	0.00
Krill_crystal	3.0	0.00	0.37	0.33	0.25	0.05	0.01	0.00	0.00	0.00
Krill_superba	3.0	0.00	0.38	0.32	0.25	0.04	0.01	0.00	0.00	0.00
Macrobenthos	3.0	0.00	0.19	0.67	0.13	0.02	0.00	0.00	0.00	0.00
Meiobenthos	2.9	0.00	0.17	0.74	0.08	0.01	0.00	0.00	0.00	0.00
Megabenthos	2.9	0.00	0.18	0.76	0.06	0.01	0.00	0.00	0.00	0.00
Microzoo	2.8	0.00	0.31	0.57	0.09	0.02	0.00	0.00	0.00	0.00
Ice_protozoa	2.7	0.00	0.35	0.59	0.06	0.01	0.00	0.00	0.00	0.00
Flagellates	2.5	0.00	0.63	0.30	0.06	0.01	0.00	0.00	0.00	0.00
Ice_metazoa	2.2	0.00	0.89	0.05	0.05	0.01	0.00	0.00	0.00	0.00

Key

	>0.5
	0.2-0.5
	0.1-0.2
	<0.1
	0.00

3.3 Network characterisation

Many of the same features regarding impacts of one group on another in the Ross Sea food-web can be seen in the single-step matrix (**Q**) and multiple-step (mixed trophic impact) matrix (**M**) (Figures 4 and 5), including, for example: the negative impact of Adélie penguins on their main prey items, Antarctic silverfish and crystal krill; the negative impact of Weddell seals on large demersal fishes (toothfish); the negative impact of toothfish on medium demersal fishes; the positive impacts of key prey species silverfish, cephalopods, both species of krill and mesozooplankton on many air-breathing and piscine predators; the positive impacts of phytoplankton on herbivores and omnivores in the water column; the positive impact of ice algae on ice protozoa; and the positive impact of sediment bacteria on benthic invertebrates. These impacts follow from important predator-prey relationships. Differences between the impacts based on the single-step and multiple-step matrices tend to be subtle. For example, in the single-step framework (Figure 4), phytoplankton affects herbivores and omnivores; in the multiple-step framework (Figure 5), phytoplankton also affects air-breathing and piscine predators that rely on the prey species that, ultimately, obtain their energy from primary production by phytoplankton.

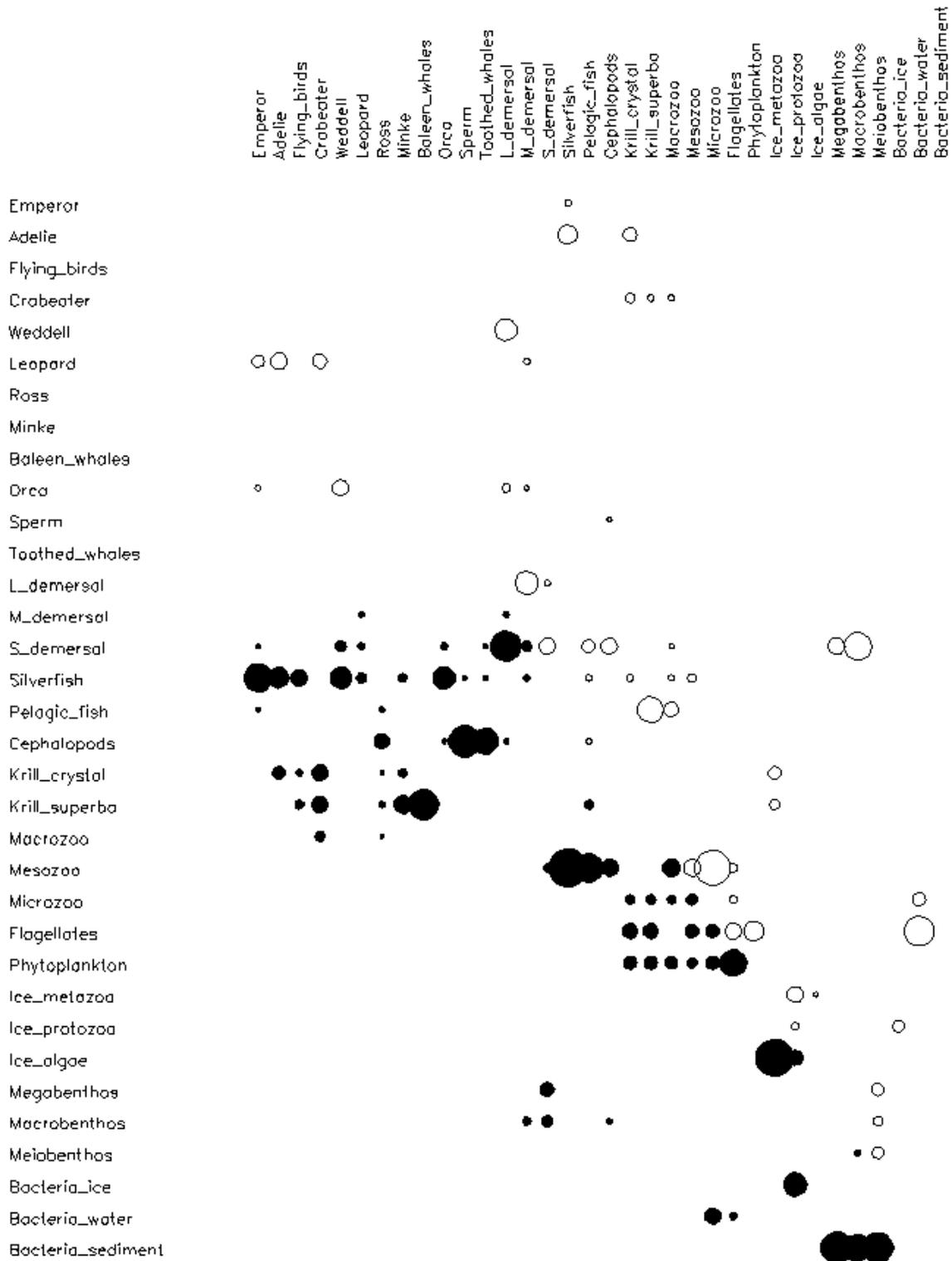


Figure 4: Single-step trophic impact matrix, Q , for the Ross Sea based on the food-web model of Pinkerton et al. (2010). Positive impacts are shown black and negative are white, with the diameter of the circle proportional to the magnitude of the effect. The “impact” is usually interpreted as the effect that a small increase in the biomass of the impacting group (shown on the left of the diagram) may have on the biomass of the impacted group (shown across the top), based on steps of length 1.

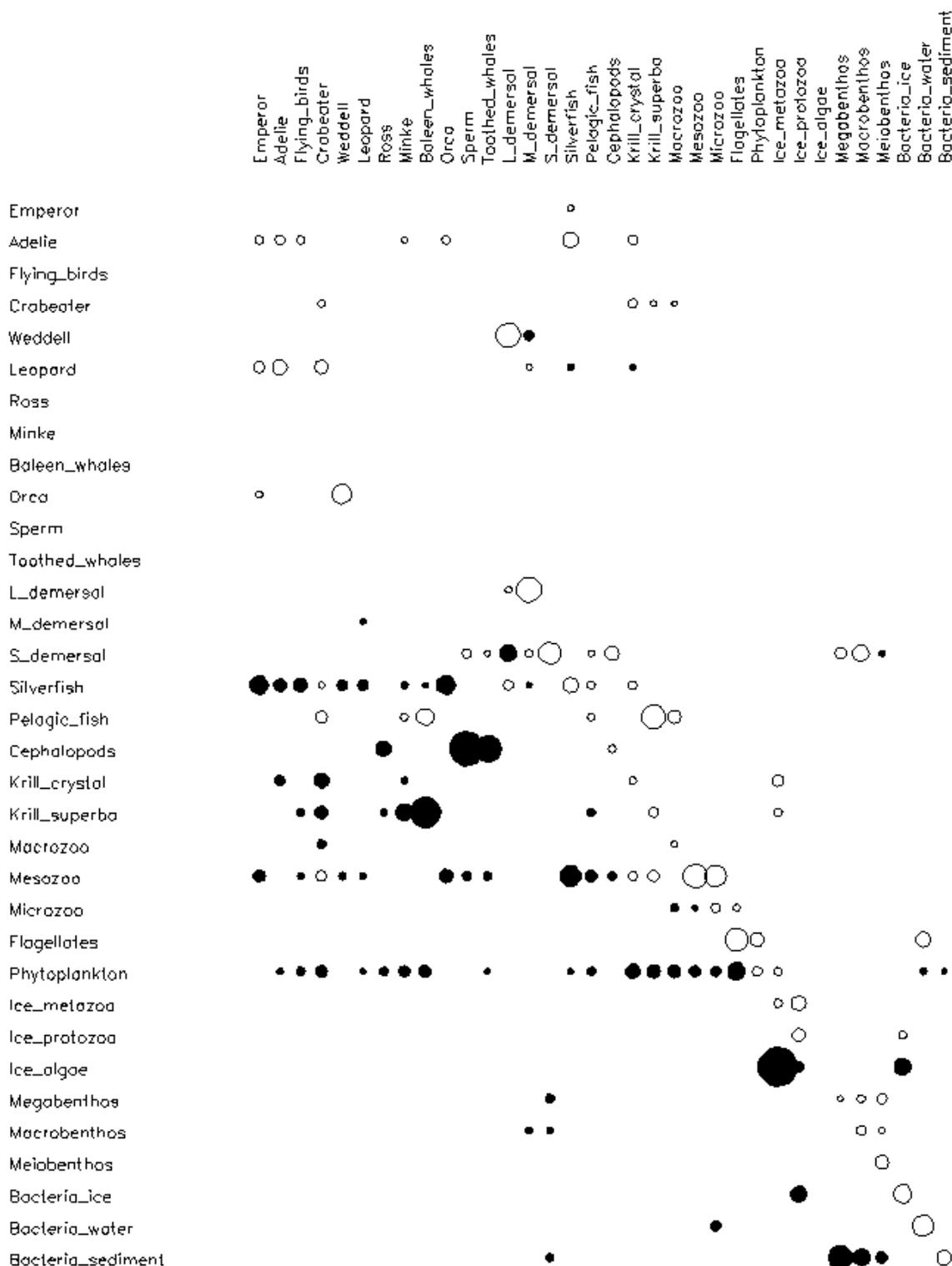


Figure 5: Mixed trophic impact matrix, M , for the Ross Sea based on the food-web model of Pinkerton et al. (2010). Positive impacts are shown black and negative are white, with the diameter of the circle proportional to the magnitude of the effect. The “impact” is usually interpreted as the effect that a small increase in the biomass of the impacting group (shown on the left of the diagram) may have on the biomass of the impacted group (shown across the top), taking into account the effect of multiple steps.

Although there are differences in the hierarchy of ecological importance determined using the single-step and multiple-step approaches, and in the relative weighting of strong and weak trophic links, the overall picture is fairly consistent (Figure 6). The six groups with the highest ecological importance in the food-web of the Ross Sea are phytoplankton, mesozooplankton, Antarctic silverfish (*Pleuragramma antarcticum*), small demersal fishes, Antarctic krill (*Euphausia superba*) and cephalopods. That phytoplankton is key to the system is clear; virtually all organisms in the Ross Sea rely on primary production by the growth of phytoplankton. Changes to the magnitude or characteristics (e.g. spatial patterns, seasonal progression or functional groups) of phytoplankton production are likely to have considerable consequences for wider ecosystem function and structure in the Ross Sea.

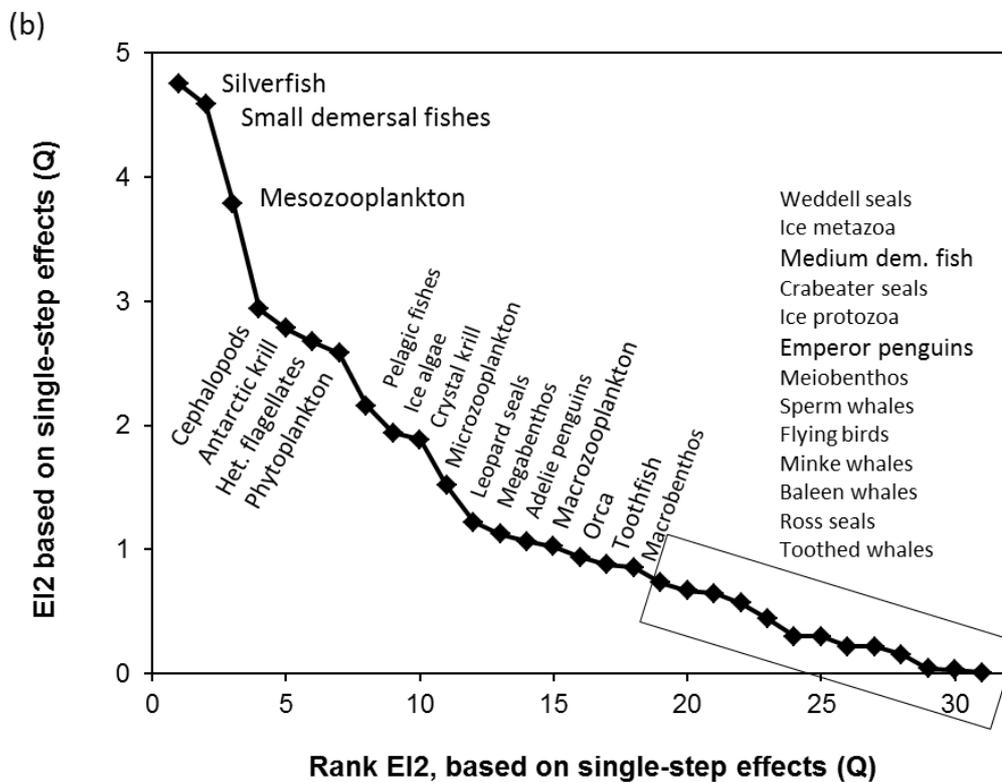
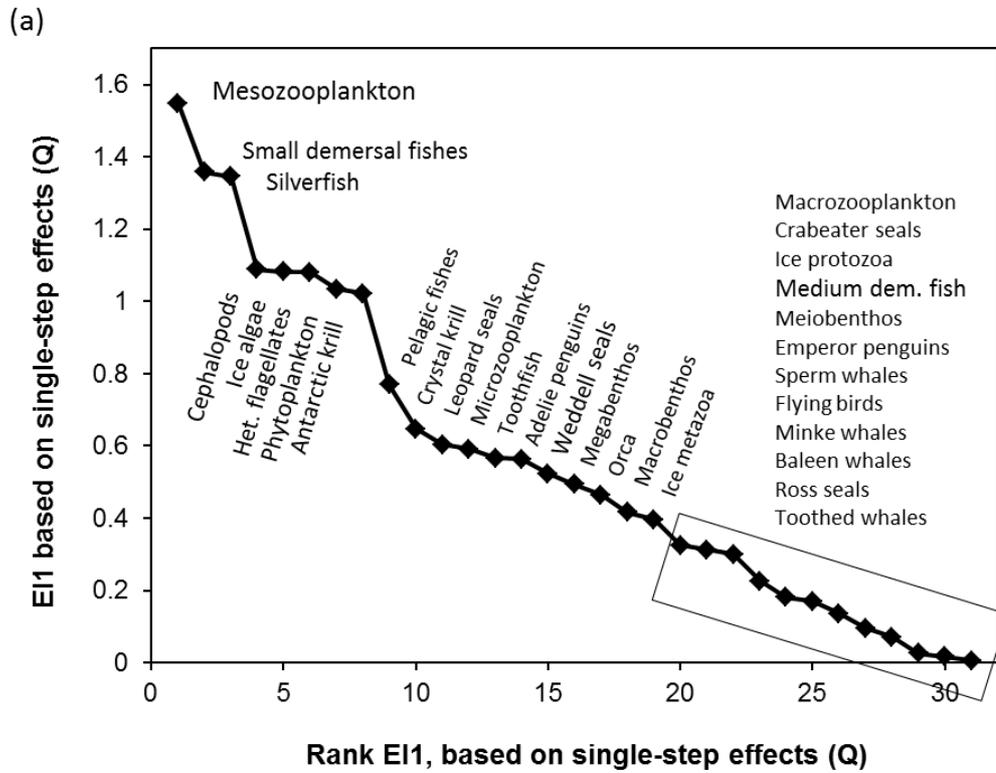
Mesozooplankton are the primary pathway by which energy is transferred from the lower food-web to middle and upper trophic levels. Mesozooplankton biomass in the Ross Sea is likely to be dominated by large copepods, with a significant but poorly quantified contribution by pteropods. Pteropods dominate the mesozooplankton assemblage of the Ross Sea in some locations at some times of the year, and can also dominate annual flux of material captured in sediment traps on the Ross Sea shelf. Different species of copepods have complex life histories that can take in the underside of sea-ice, and/or the benthos. Antarctic krill also have a well-known ecological dependence on sea-ice (Atkinson et al. 2008). Changes to sea-ice characteristics, for example due to climate variability and change, are likely to affect mesozooplankton and krill ecology and could hence have repercussions throughout the Ross Sea food-web.

Antarctic silverfish are fundamental to the food-web of the Ross Sea. It is known that Antarctic silverfish have recently disappeared from parts of the Antarctic peninsula and that this is having detrimental effects on a number of their predators (Torres, 2010). The reasons for this loss of Antarctic silverfish is not known, but may be related to changes in sea-ice in the region due to climate change (Torres, 2010). Small demersal fishes are important in the Ross Sea food-web as food for many air-breathing and piscine predators. Because the “small demersal fishes” group of Pinkerton et al. (2010) is a highly aggregated group (i.e. includes many separate species), it is likely that the information content of the Ross Sea trophic model relating to these species has not been captured well by the analysis of Pinkerton et al. (2010). Future versions of the model should investigate whether “unpacking” the small demersal fishes group into different groups would be feasible and would allow their separate ecological importances to be more usefully described.

Pelagic fishes, ice algae, heterotrophic flagellates and crystal krill are identified as either moderately or highly important depending on the approach used to calculate ecological importance. Small pelagic fishes such as *Electrona* sp. and *Gymnoscopelus* sp. are likely to be especially important to the pelagic ecosystem north of the Ross Sea proper, where they are likely to replace Antarctic silverfish as the most important fish prey for large predators. Ice algae appear in this analysis because of the self-contained nature of the ecosystem in sea-ice. In terms of overall energy flow in the Ross Sea food-web, the ecological importance of sea-ice algae is likely to be quite low. However, the sea-ice ecosystem may have an importance beyond that suggested by this kind of food-web modelling in that production by sea-ice algae may represent the major food available to mesozooplankton in the late spring and early autumn when water column phytoplankton is very low. A seasonally-resolved food-web model may be the most appropriate way to study such potential seasonal bottlenecks in energy flow in the Ross Sea ecosystem.

Indices of ecological importance for most air breathing predators tend to be low according to the analysis presented here. We estimate that air-breathing predators with the highest indices are Adélie penguins and leopard seals. The model gives higher ecological importance to these predators because

Adélie penguins are important predators of silverfish and crystal krill, and leopard seals are the main predators of Adélie and emperor penguins and of crabeater seals in the model. In terms of flows of energy alone, crabeater seals are the most important species of seal in the Ross Sea.



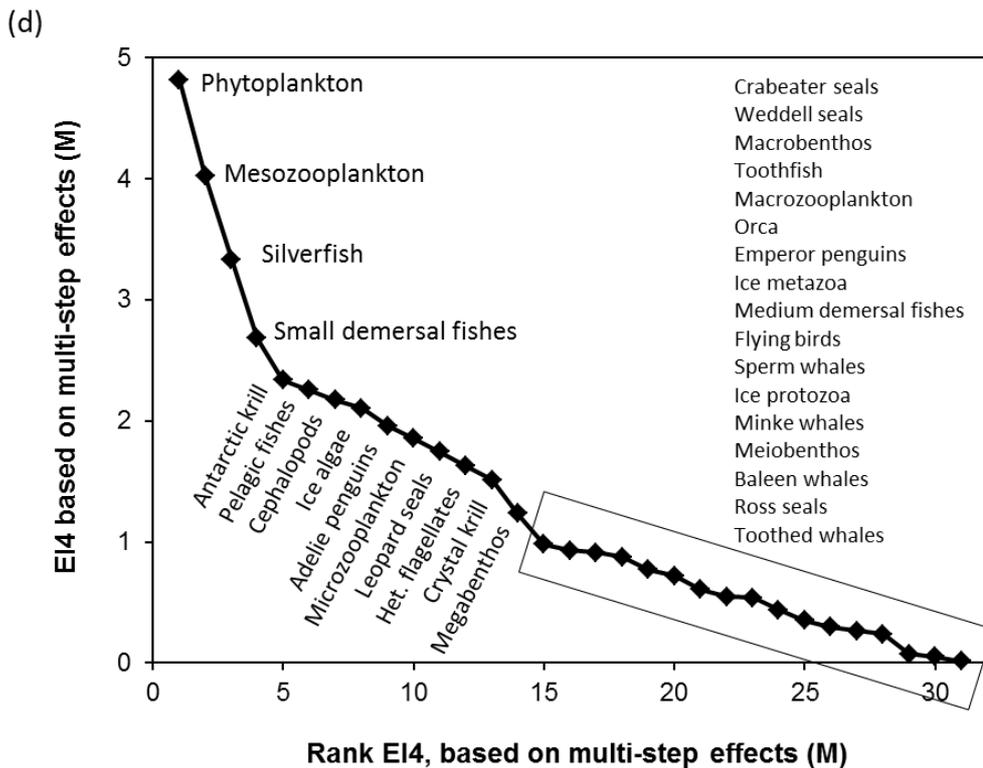
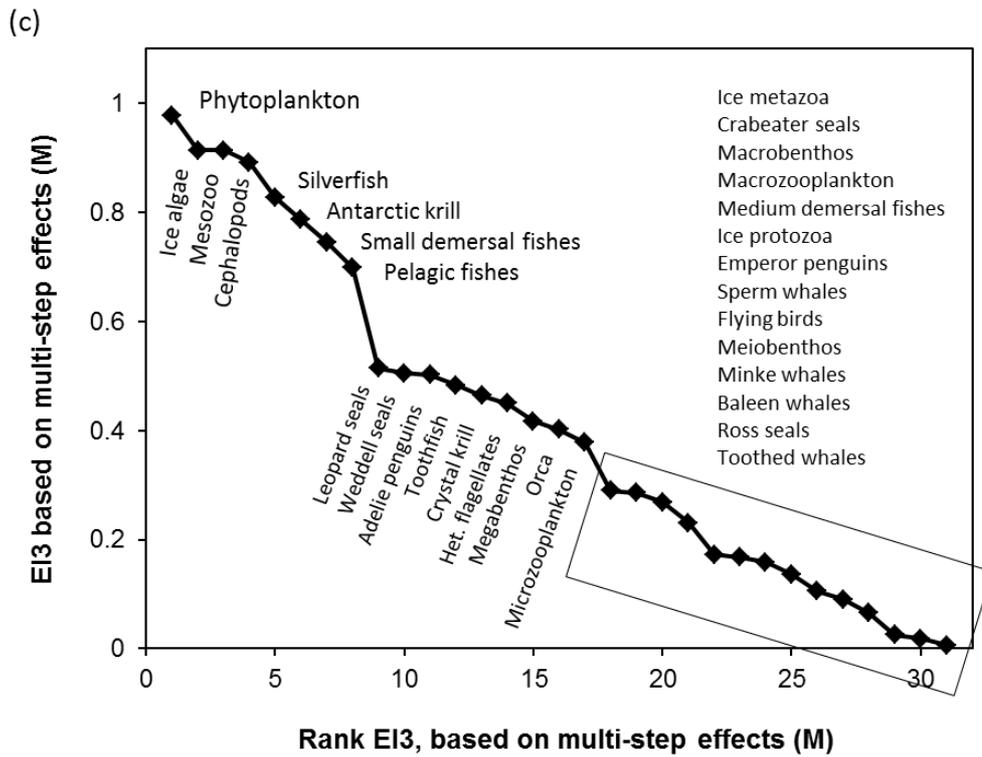


Figure 6: Ecological importance from the ecosystem model of the Ross Sea (Pinkerton et al. 2010) shown in descending order of importance. Four different measures of ecological importance are shown. EI1 and EI3 (strong links more valued) are shown in (a) and (c); EI2 and EI4 (weak links valued higher) are shown in (b) and (d). Single-step effects only (based on matrix Q) are shown in (a) and (b); multi-step effects (based on mixed trophic impact matrix M) are shown in (c) and (d).

The analysis presented here suggests that large demersal fishes (Antarctic toothfish) have a moderate index of ecological importance in the Ross Sea food-web as a whole; the rank ecological importance of toothfish is between 12th and 18th out of 31 groups, very close to the middle. Specifically, with regard to ecosystem effects of the fishery for Antarctic toothfish in the Ross Sea, changing the abundance of toothfish (the large demersal fish group) is likely to have the greatest effect on the medium-sized demersal fish group. The effect on the medium-sized demersal fish group is likely to be in the opposite sense to the change in toothfish group i.e. reducing the abundance of toothfish is likely to increase the abundance of medium-sized demersal fishes according to this analysis, i.e. a “predation release” effect. This result is consistent with Pinkerton et al. (2010) which concluded: “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.” Note that this analysis does not take into account the fact that the fishery also takes medium-sized demersal fishes as by-catch; only the trophic effects are considered here. The effect of changing toothfish abundance on the small demersal fishes group is much smaller than the effect on the medium-sized demersal fish group in Figures 3 and 4, because toothfish are only one of a number of important predators of small demersal fishes in the Ross Sea shelf and slope ecosystem.

The analysis presented here based on the food-web model of Pinkerton et al. (2010) does not support the hypothesis that changes to the abundance of toothfish in the Ross Sea will propagate through the food-web. Instead, the analysis suggests that the most substantial effect of changing the biomass of Antarctic toothfish on the Ross Sea shelf and slope will be most significant to the demersal fish community there.

Consistent with Pinkerton et al. (2010), we note that the results presented here are not sufficient in isolation to adequately characterise the effect of the fishery for Antarctic toothfish on the ecological viability of its predators – Weddell seals, type-C orca and possibly sperm whales – in the Ross Sea region. This is because while the model may provide meaningful results at the scale of the Ross Sea shelf and slope averaged over the year, it is still possible that toothfish predators disproportionately rely on toothfish at particular times of year or in particular locations, and if predator foraging success is of particular importance at these times and places then localized changes in toothfish abundances could have significant effects. For example, in the model of Pinkerton et al. (2010), Antarctic toothfish are a minor component of the diet of Weddell and toothfish are consequently estimated to have low mixed-trophic impacts on Weddell seals, but as in Pinkerton et al. (2008), changes to toothfish availability near Weddell seal breeding colonies in the period between pupping and weaning could plausibly affect survival of Weddell seal pups and lactating mothers, and hence have a disproportionate impact on Weddell seal populations. Risks arising from spatially- or seasonally-restricted potential impacts such as these are not addressed by the model or analysis presented here. Furthermore we note that the utility of the model to draw meaningful conclusions about ecosystem interactions involving orcas is limited by the fact that the model does not distinguish between the three distinct orca variants in the Ross Sea region (Pitman & Ensor 2003). Disaggregation of the toothed whale component of the model to account independently for the distinct feeding behaviours and different abundances of the orca variants in the Ross Sea region may be useful in this regard.

4. CONCLUSIONS

1. As in other open-ocean ecosystems, the Ross Sea food-web is a partially inverted biomass pyramid with a pronounced peak in biomass in the lower-middle part of the food-web (trophic

level 2.5-3.5, or integer trophic level III). In the Ross Sea, this is a result of high biomass of mesozooplankton and benthic invertebrates. The biomass of predators with trophic levels greater than 4.5 is only 0.5% of the total living biomass in the Ross Sea (bacteria excluded). Productivity decreases with increasing trophic level in the Ross Sea food-web as elsewhere.

2. The six groups with the highest ecological importance in the food-web of the Ross Sea are phytoplankton, mesozooplankton, Antarctic silverfish (*Pleuragramma antarcticum*), small demersal fishes, Antarctic krill (*Euphausia superba*) and cephalopods. Pelagic fishes, and crystal krill (*E. crystallophias*) are also likely to have high importance in the Ross Sea food-web. These eight groups should be the priorities for monitoring for effects of climate change or large-scale ecosystem effects of fishing, *inter alia*, trophic cascades and regime shift.
3. The analysis presented here provides information at the scale of the underlying food-web model, i.e. the whole Ross Sea shelf and slope area, averaged over a typical year, and in 35 trophic groups. Effects at smaller spatial and temporal scales, and effects concerning only subsets of trophic groups, are not resolved by this analysis. Consequently, the analysis presented here are not sufficient in isolation to test for potential indirect effects of the fishery for Antarctic toothfish on the ecological viability of toothfish predators (Weddell seals, type-C orca and possibly sperm whales) in the Ross Sea region. It is possible that indirect effects can be significant arising from interactions at smaller spatial, temporal and ecological scales (i.e. parts of populations) than are resolved by the model (Pinkerton et al. 2008).
4. The analysis presented here does not support the hypothesis that changes to the abundance of toothfish in the Ross Sea will propagate through the food-web. As the Ross Sea model of Pinkerton et al. (2010) is currently constructed, it appears that Antarctic toothfish only have a moderate index of ecological importance in the food-web of the Ross Sea shelf and slope.
5. Changing the biomass of Antarctic toothfish on the Ross Sea shelf and slope is likely to have the greatest effect on the demersal fish community there. This effect was identified as being relatively strong. Further analysis of this potential ecosystem effect of fishing is warranted.
6. The analysis presented here provides information at the scale of the underlying food-web model, i.e. the whole Ross Sea shelf and slope area, averaged over a typical year, and in 35 trophic groups. Effects at smaller spatial and temporal scales, and effects concerning only subsets of trophic groups, are not resolved by this analysis. Consequently, the analysis presented here are not sufficient in isolation to test for potential indirect effects of the fishery for Antarctic toothfish on the ecological viability of toothfish predators (Weddell seals, type-C orca and possibly sperm whales) in the Ross Sea region. It is possible that indirect effects can be significant arising from interactions at smaller spatial, temporal and ecological scales (i.e. parts of populations) than are resolved by the model (Pinkerton et al. 2008).
7. It should be investigated to what extent “unpacking” the model groups representing phytoplankton, benthic invertebrates, medium-sized demersal fishes, small demersal fishes, mesozooplankton, and orca in future versions of trophic modeling would be feasible and/or useful. In particular, separating phytoplankton into haptophytes (e.g. *Phaeocystis antarctica*) and diatoms may lead to important insights. Separating fish-eating (type C) orca from those which predate whales and seals (type A and B respectively) is likely to be important in future ecosystem modeling of the Ross Sea region.

8. There is a need to validate the trophic model of the Ross Sea (Pinkerton et al. 2010) to determine the degree to which uncertainty in parameters and model structure affects network characteristics such as those presented here. The stable isotope data collected on the New Zealand IPY-CAML voyage to the Ross Sea (Hanchet et al. 2008; Pinkerton et al. 2011) will be useful for this purpose.

5. ACKNOWLEDGEMENTS

This work was funded by the New Zealand Ministry of Science and Innovation project C01X1001 (“Protecting Ross Sea Ecosystems”). We thank the members of the New Zealand Antarctic Fisheries Working Group for helpful discussions and input into this paper.

6. REFERENCES

- Ainley, D.G. 2004. Acquiring a ‘base datum of normality’ for a marine ecosystem: the Ross Sea, Antarctica. CCAMLR document WG-EMM-04/20, Hobart, Australia.
- Ainley, D.G. 2009. A history of the exploitation of the Ross Sea, Antarctica. *Polar Record*, doi:10.1017/S003224740999009X
- Ainley, D.G. 1985. Biomass of birds and mammals in the Ross Sea. In: W.R. Siegfried, P.R. Condy, R.M. Laws (eds). *Antarctic Nutrient Cycles and Food-webs*. Springer-Verlag. Berlin: 498–515.
- Ainley, D.G.; O’Connor, E.F.; Boekelheide, R.J. 1984. The marine ecology of birds in the Ross Sea, Antarctica. *Ornithol. Monogr.* 32. Washington D.C., American Ornithologists’ Union.
- Arrigo, K.R.; Thomas, D. 2004. Large scale importance of sea ice biology in the Southern Ocean. *Antarctic Science*, 16(4), 471-486.
- Arrigo, K.R.; Van Dijken, G.L. 2004. Annual changes in sea-ice, chlorophyll a, and primary production in the Ross Sea, Antarctica. *Deep-Sea Research II* 51(1-3): 117-138.
- Atkinson, A.; V. Siegel; E.A. Pakhomov; P. Rothery; V. Loeb; R.M. Ross; L.B. Quetin; K. Schmidt; P. Fretwell; E.J. Murphy; G.A. Tarling; A.H. Fleming, 2008. Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series*, 362: 1-23.
- Bassett, J.A.; Wilson, G.J. 1983. Birds and mammals observed from the M.V. Benjamin Bowring during the New Zealand-Ross Sea cruise January/February 1981. *Transglobe Exped. Sci. Rep.*, No. 3.
- Brierley, A.S.; Thomas, D.N. 2002. Ecology of Southern Ocean pack ice. *Advances in Marine Biology*, 43, 171-277.
- Christensen, V.; Walters, C.J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modeling*, 172, 109-139.
- Christensen, V.; Walters, C.J.; Pauly, D.; Forrest, R. 2008. *Ecopath with Ecosim Version 6: user guide*. Vancouver, Canada, Fisheries Centre, University of British Columbia.
- Clark, M.R.; Dunn, M.R.; McMillan, P.J.; Pinkerton, M.H.; Stewart, A.; Hanchet, S.M. 2010. Latitudinal variation of demersal fish assemblages in the western Ross Sea. *Antarctic Science* 22(6), 782–792.
- Davey, F.J. 2004. *Ross Sea Bathymetry, 1:2 000 000, version 1.0*. Institute of Geological and Nuclear Sciences Geophysical map 16. Lower Hutt: Institute of Geological and Nuclear Sciences Limited, New Zealand.
- DeWitt, H.H. 1970. The character of the midwater fish fauna of the Ross Sea, Antarctica. In: *Antarct. Ecol.* vol 1. Holdgate, M.W. (ed). Academic Press, New York: 305-314.

- DiTullio, G.R.; Smith, W.O. 1997. Studies on dimethylsulphide in Antarctic coastal waters. In: Antarctic Communities: Species, Structures and Survival. Battaglia, B.; Valencia, J.; Walton, D.W.H. (eds.), Cambridge University Press, 93-100.
- Ducklow, H.W.; Fraser, W.; Karl, D.M.; Quetin, L.B.; Ross, R.M.; Smith, R.C.; Stammerjohn, S.E.; Vernet M.; Daniels, R.M. 2006. Water column processes in the West Antarctic Peninsula and the Ross Sea: foodweb structure and interannual variability. *Deep-Sea Research II*, 53, 834-852.
- Dunn, A.; S.M. Hanchet 2007. Assessment models for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea including data from the 2006/07 season. CCAMLR document WG-FSA-07/37, Hobart, Australia.
- Garrison, D.L. 1991. Antarctic sea ice biota. *American Zoologist*, 31, 17-33.
- Granata, A.; Zagami, G.; Vacchi, M.; Guglielmo, L. 2009. Summer and spring trophic niche of larval and juvenile *Pleuragramma antarcticum* in the western Ross Sea, Antarctica. *Polar Biol.*, 32(3): 369-382.
- Granata, A.; Cubeta, A.; Guglielmo, L.; Sidoti, O.; Greco, S.; Vacchi, M.; La Mesa, M. 2002. Ichthyoplankton abundance and distribution in the Ross Sea during 1987-1996. *Pol Biol* 25: 187-202.
- Halpern, B.S.; Walbridge, S.; Selkoe, et al. 2008. A global map of human impact on marine ecosystems. *Science*, 319, 948-951.
- Hanchet, S.M.; J. Mitchell; D. Bowden; M. Clark; J. Hall; R. O'Driscoll; M. Pinkerton; D. Robertson. 2008. Preliminary report of the New Zealand RV Tangaroa IPY-CAML survey of the Ross Sea region, Antarctica, in February–March 2008. Document *WG-EMM-08*. CCAMLR, Hobart, Australia.
- Harper, P.C.; G.A. Knox; E.B. Spurr; R.H. Taylor; G.J. Wilson; E.C. Young. 1984. The status and conservation of birds in the Ross Sea sector of Antarctica. In: *Status and conservation of the world's seabirds*. Croxall, J.P.; Evans, P.G.H.; Schreiber, R.W. (eds). International Council for Bird Preservation Technical Publication no. 2.
- Hubold, G. 1985. The early life-history of the high-Antarctic silverfish *Pleuragramma antarcticum*. In: *Antarctic nutrient cycles and food webs*. Siegfried, W.R.; Condy, P.R.; Laws, R.M. (eds), Springer-Verlag, Berlin: 445–451.
- Jackson, J.B.C. 2006. When ecological pyramids were upside down. In: Estes, J.A., Demaster, D.P., Doak, D.F., Williams, T.E., Brownell Jr, R.L. (eds). Whales, whaling and ocean ecosystems. Berkeley, CA: University of California Press, 27–37.
- Kasamatsu F.; G.G. Joyce. 1995. Current status of Odontocetes in the Antarctic. *Ant. Sci.* 7(4): 365-379.
- Kurtz, D.D.; Bromwich, D.H. 1985. A recurring, atmospherically forced polynya in Terra Nova Bay. In: *Oceanology of the Antarctic Continental Shelf*, S.S. Jacobs (ed) Antarctic Research Series 43, AGU, Washington D.C., 177-201.
- La Mesa, M.; J.T. Eastman; M. Vacchi. 2004. The role of notothenioid fish in the food web of the Ross Sea shelf waters: a review. *Polar Biol.*, 27: 321-338.
- Laws, R.M. 1984. (Ed.) *Antarctic Ecology*. Vol 2. Academic Press, London, 850 pp.
- Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23, 399-418.
- Libralato, S.; Christensen, V.; Pauly, D. 2006. A method for identifying keystone species in food web models. *Ecological Modelling*, 195, 153-171.
- McCann, K.S. 2000. The diversity-stability debate. *Nature*, 405, 228-233.
- Nelson, D.M.; DeMaster, D.J.; Dunbar, R.B.; Smith, W.O. Jr. 1996. Cycling of organic carbon and biogenic silica in the Southern Ocean: Estimates of water-column and sedimentary fluxes on the Ross Sea continental shelf, *Journal of Geophysical Research*, 101, 18,519–18,532.
- Odum, E.P. 1971. Fundamentals of ecology, 3rd edition. Philadelphia, Saunders College Publishing. 574 pp.

- Pinkerton, M.H.; Bradford-Grieve, J.M.; Hanchet, S.M. 2010. A balanced model of the food web of the Ross Sea, Antarctica. *CCAMLR Science* 17: 1–31.
- Pinkerton, M.H.; V. Cummings; J. Forman; J. Brown; S.J. Bury, 2009. Trophic connections in the Ross Sea: information from stomach contents analysis and stable isotopes of carbon and nitrogen. Final Research Report for MPI project IPY200701 Obj10. Pp 18.
- Pinkerton M.H.; Dunn, A.; Hanchet, S.M. 2008. Trophic overlap of Weddell seals (*Leptonychotes weddelli*) and Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica. CCAMLR document WG-EMM-08/43.
- Pinnegar, J.K.; J.L. Blanchard; S. Mackinson; R.D. Scott; D.E. Duplisea, 2005. Aggregation and removal of weak-links in food-web models: system stability and recovery from disturbance. *Ecological Modelling*, 184: 229–248.
- Pitman, R.L.; P. Ensor. 2003. Three different forms of killer whales in Antarctic waters. *J. Cetacean Res. Manage.*, 5(2): 131-139.
- Pitman, R.L. 2003. Good whale hunting. *Nat. Hist.* December 2003/January 2004: 24-28.
- Pitman, R.L.; L.T. Balance; S.L. Mesnick; S. Chivers. 2001. Killer whale predation on sperm whales: observations and implications. *Mar. Mamm. Sci.*, 17(3): 494-507.
- Power, M.E.; Tilman, D.; Estes, J.A.; Menge, B.A.; Bond, W.J.; Mills, L.S.; Daily, G.; Castella, J.C.; Lubchenco, J.; Paine, R.T. 1996. Challenges in the quest for keystones. *Bioscience*, 46, 609-620.
- Preisser, E.L.; Bolnick, D.; Benard, M.F. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501-509.
- Reddy, T.E.; Arrigo, K.R. 2006. Constraints on the extent of the Ross Sea phytoplankton bloom. *Journal of Geophysical Research* 111, C07005, 8 pp.
- Schipper, J.; Chanson, J.S.; Chiozza, F.; Cox, N.A. et al. 2008. The status of the World's land and marine mammals: Diversity, threat, and knowledge. *Science*, 322, 225-230.
- Smith, W.O.; Ainley, D.G.; Cattaneo-Vietti, R. 2007. Marine ecosystems: the Ross Sea. *Philosophical Transactions of the Royal Society, London B, Biological Science*, 362, 149-166.
- Smith, W.O.; J. Marra; M.R. Hiscock; R.T. Barber. 2000. The seasonal cycle of phytoplankton biomass and primary productivity in the Ross Sea, Antarctica. *Deep-Sea Res. II* 47: 3119-3140.
- Smith, W.O., Jr; Ainley, D.G.; Cattaneo-Vietti, R.; Hofmann, E.E. 2010. The Ross Sea continental shelf: Regional biogeochemical cycles, trophic interactions, and potential future changes. In: Antarctica: An extreme environment in a changing world. J. Wiley and Sons, London.
- Stewart, B.S.; P.K. Yochem; T.S. Gelatt; D.B. Siniff. 2003. The pack ice niche of Weddell seals in the western Ross Sea. In: *Antarctic Biology in a Global Context*. Huiskies, A.; Gieskes, W.W.; Rozema, J.; Schornu, R.M.L.; van der Vies, S.M.; Wolff, W.J. (eds). Backhuys Publishers, Leiden: 224–229.
- Stirling, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. *Ecology*, 50: 533–544.
- Tarling, G.A.; R.S. Shreeve; P. Ward; A. Atkinson; A.G. Hirst. 2004. Life cycle phenotypic composition and mortality of *Calanoides acutus* (Copepoda: Calonoida) in the Scotia Sea: a modelling approach. *Mar. Ecol. Prog. Ser.*, 272: 165-181.
- Thomas, D.N.; Dieckmann, G.S. 2002. Antarctic sea ice - a habitat for extremophiles. *Science*, 295, 641-644.
- Torres, J. 2010. Climate change may be to blame for disappearance of Antarctic silverfish. Antarctic Sun, available (May 2011) at antarcticsun.usap.gov/science/contenthandler.cfm?id=2192.
- Ulanowicz, R.E. & Puccia, C.J. 1990. Mixed trophic impacts in ecosystems *Coenoses*, 5, 7-16.
- Vacchi M.; M. La Mesa; M. Dalù; J. Macdonald. 2004: Early life stages in the life cycle of Antarctic silverfish, *Pleuragramma antarcticum* in Terra Nova Bay, Ross Sea. *Antarct. Sci.*, 16 (3): 299–305.
- Vacchi, M.; S. Greco; M. La Mesa. 1999. The coastal fish fauna of Terra Nova Bay, Ross Sea. In: Faranda F.; Guglielmo L.; Ianora A (eds). *Ross Sea Ecology*. Italian Antarctic Expeditions (1987–1995). Springer, Berlin Heidelberg New York, 457–468.

- Voronina, N.M. 1998. Comparative abundance and distribution of major filter-feeders in the Antarctic pelagic zone. *J. Mar. Sys.*, 17(1-4): 375-390.
- Wang, H.; Morrison, W.; Singh, A.; Weiss, H. 2009. Modeling inverted biomass pyramids and refuges in ecosystems. *Ecol. Modelling*, 220: 1376-1382.
- Young, E.C. 1981. The ornithology of the Ross Sea. *J. R. Soc. N. Z.*, 11(4): 287-315.
- Zwally, H.J.; Comiso, J.C.; Gordon, A.L. 1985. Antarctic offshore leads and polynyas and oceanographic effects. In: *Oceanology of the Antarctic Continental Shelf*, S.S. Jacobs (ed.), *Antarctic Research Series* 43, AGU, Washington D.C., 203-336.