

Original Article

Characterizing foodweb structure to identify potential ecosystem effects of fishing in the Ross Sea, Antarctica

Matthew H. Pinkerton* and Janet M. Bradford-Grieve

National Institute of Water and Atmospheric Research (NIWA), Wellington 6241, New Zealand

*Corresponding author: tel: +64 4386 0369; fax: +64 4386 2153; e-mail: m.pinkerton@niwa.co.nz

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The potential ecosystem effects of fishing for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region were investigated. Mixed trophic impact analysis was applied to a model of the Ross Sea foodweb and used to calculate the relative trophic importances of species and trophic groups in the system. The trophic impact of toothfish on medium-sized demersal fish was identified as the strongest top-down interaction in the system based on multiple-step analysis. This suggests a potential for a strong predation-release effect on some piscine prey of toothfish (especially grenadiers and ice-fish on the Ross Sea slope). However, Antarctic toothfish had moderate trophic importance in the Ross Sea foodweb as a whole, and the analysis did not support the hypothesis that changes to toothfish will cascade through the ecosystem by simple trophic effects. Because of limitations of this kind of analysis, cascading effects on the Ross Sea ecosystem due to changes in the abundance of toothfish cannot be ruled out, but for such changes to occur a mechanism other than simple trophic interactions is likely to be involved. Trophic importances were highest in the middle of the foodweb where silverfish and krill are known to have a key role in ecosystem structure and function. The six groups with the highest indices of trophic importance were (in decreasing order): phytoplankton, mesozooplankton, Antarctic silverfish, small demersal fish, Antarctic krill and cephalopods. Crystal krill and small pelagic fish also had high trophic importance in some analyses. Strengths and limitations of this kind of analysis are presented. In particular, it is noted that the analysis only considers trophic interactions at the spatial, temporal and ecological scale of the whole Ross Sea shelf and slope area, averaged over a typical year and in 35 trophic groups. Interference and density-dependent effects were not included in this analysis. Effects at smaller spatial and temporal scales, and effects concerning only parts of populations, were not resolved by the analysis, and this is likely to underestimate the potential risks of fishing to Weddell seals and type-C killer whales.

Keywords: ecosystem effects of fishing, keystone, mixed trophic impact, trophic importance.

Introduction

A crucial component of an ecosystem approach to fisheries is the recognition that species in an ecosystem are linked (Ecosystem Principles Advisory Panel, 1997; Garcia and Cochrane 2005; Francis *et al.*, 2007). Commercially important species are often highly productive components of the ecosystem, and reducing their abundances can substantially affect related and dependent species and affect whole-system dynamics and resilience (Murawski, 2000; ICES, 2005). Adopting an ecosystem approach to fisheries hence implies widening of the scope of management beyond single-stock reference points (European Community, 2002; US Commission on Ocean Policy, 2004; Browman and Stergiou, 2004). Fisheries in the Southern Ocean were the first to be managed in an ecosystem context (Parkes, 1999). Coming into

force in 1982, the Convention for the Conservation of Antarctic Marine Living Resources (CAMLR), Article II, requires that fishing in the Convention Area be conducted in such a way that ecological relationships between the harvested, dependent and related species are maintained, and that the risk of ecosystem changes that are not potentially reversible in 20–30 years is minimized (CAMLR, 1979). Ecosystem impacts of fishing can take some time to occur, be difficult to detect and monitor, and can be irreversible over decadal scales (Estes and Duggins, 1995; Frank *et al.*, 2005; Daskalov *et al.*, 2007). Predicting the potential ecosystem effects of fishing in Southern Ocean systems is hence relevant to achieving CAMLR's management aims.

Species in an ecosystem are connected in many ways, but one of the main types of connection is trophic, i.e. the feeding of one organism

on another (McCann *et al.*, 1998; Pace *et al.*, 1999; Frank *et al.*, 2005). Theoretical and empirical studies show that effects of fishing on other species and on the ecosystem as a whole are dependent on the trophic characteristics of the particular ecosystem (Pace *et al.*, 1999; Brose *et al.*, 2005; Pascual and Dunne, 2006). Investigating the potential ecosystem and system-level effects of fishing needs to occur on an ecosystem-by-ecosystem basis.

A number of dynamic foodweb models have been developed to simulate responses of ecosystems to perturbations including fishing (Plagányi, 2007; Fulton, 2010). Examples of these kinds of models include Ecopath with Ecosim (EwE, Christensen and Walters, 2004; Christensen *et al.*, 2008), OSMOSE (Shin and Cury, 2004) and Atlantis (Fulton *et al.*, 2004). These models are complicated and complex, and typically require more knowledge of ecosystem behaviour than is presently available (Plagányi and Butterworth, 2004). Several measures of foodweb structure have been suggested as being relevant to assessing to what extent dependent or related species, or the resilience of the ecosystem as a whole, are put at risk by fishing (Fletcher *et al.* 2002, 2004; Hobday *et al.*, 2007). Some of these measures, such as network attack sensitivity and error sensitivity (Albert *et al.*, 2000), are based on network indices that do not take into account the fact that different links between species in ecosystems have different strengths (McCann *et al.*, 1998).

Fletcher *et al.* (2002, 2004) suggested that if the target species does not “play a keystone role” there is a lower risk of adverse ecosystem effects from fishing than if the target species has a more important role in the ecosystem. Libralato *et al.* (2006) showed how keystone species can be estimated from a mass-balance foodweb model using a method based on mixed trophic impact analysis (Ulanowicz and Puccia, 1990). Libralato *et al.* (2006) provided a method of calculating “total impact” (henceforth called “trophic importance” in this study), which is a measure of the overall effect on a foodweb due to changes in the abundance of a given species or trophic group. Trophic importance calculated in this way has been interpreted as quantifying to what extent species or trophic groups maintain the structure of a foodweb when subjected to perturbation (Libralato *et al.*, 2006).

In this study, mixed trophic impact analysis was applied to a published model of the foodweb of the Ross Sea (Pinkerton *et al.*, 2010) to study interactions between trophic groups and to calculate their trophic importances. The results are used to investigate the potential ecosystem effects of fishing for Antarctic toothfish (*Dissostichus mawsoni*) in this region, and to suggest priorities for research and monitoring.

Methods

Study area

Most fishing for Antarctic toothfish occurs along the continental slope of the Ross Sea, which is generally taken as lying between 150°E and 150°W, south of 60°S and shallower than 3000 m (Figure 1). Before the advent of the Ross Sea fishery in 1997, the Ross Sea was identified as the ocean region likely to have been least affected by human activity in the world (Ainley, 2004; Halpern *et al.*, 2008), and was one of the few continental shelf ecosystems with its full complement of piscine and air-breathing predators (e.g. Schipper *et al.*, 2008; Ainley, 2009).

Ross Sea foodweb model

Research into the structure of the foodweb of the Ross Sea has culminated in complex qualitative descriptions (e.g. Smith *et al.*, 2007,

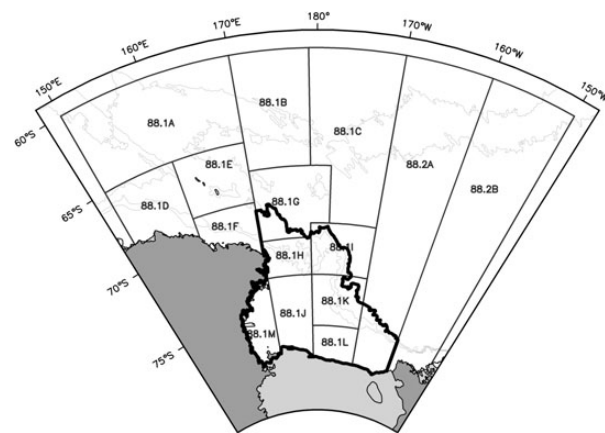


Figure 1. Ross Sea region of the Southern Ocean, showing CCAMLR small-scale research unit (SSRU) boundaries and names. Depth contours shown at 1000, 2000 and 3000 m. The Ross Sea trophic model study area is shown in dark and encompasses the Ross Sea continental shelf and slope to 3000 m depth.

2012) and a quantitative mass-balance model (Pinkerton *et al.*, 2010). The analysis presented here was based on the model of Pinkerton *et al.* (2010), henceforth referred to as the Ross Sea trophic model (RSTM, Figure 2) and described in detail in Appendix 1. The RSTM describes foodweb structure in a typical year during the period 1990–2000 when the cumulative removal of toothfish was close to zero (Dunn and Hanchet, 2007). Biomass was modelled in units of organic carbon density (gC m^{-2}) and trophic flows in units of $\text{gC m}^{-2} \text{year}^{-1}$ (a proxy for energy flow). The RSTM covered an area of 637 000 km^2 , with 29% shallower than 500 m, 41% between 500–1000 m, and 30% deeper than 1000 m (Davey, 2004).

The modelling framework for the RSTM was similar to that of Ecopath, part of the EwE package (Christensen and Walters, 2004; Christensen *et al.*, 2008), but non-trophic transfers (including release of material from sea-ice to the water column in the spring, vertical detrital flux, and spawning) were included. The RSTM had 35 trophic groups, with two primary producers (phytoplankton and ice algae), three groups of bacteria (water column, sea-ice, and benthic), and four detrital groups (carcasses, water-column detritus, ice detritus, and benthic detritus). The RSTM had three groups of benthic invertebrates (megabenthos, macrobenthos and meiobenthos), six zooplankton groups [heterotrophic flagellates, microzooplankton, mesozooplankton, Antarctic krill (*Euphausia superba*), crystal krill (*E. crystallorophias*), other macrozooplankton], cephalopods (squid and octopods combined), five groups of fish [large demersal fish which are exclusively Antarctic toothfish, medium demersal fish, small demersal fish, Antarctic silverfish (*Pleuragramma antarctica*), and pelagic fish], five cetacean groups (minke whale, other baleen whales, killer whales, sperm whale, other toothed whales), four seal groups (crabeater seal, Weddell seal, leopard seal, Ross seal), and three bird groups (Emperor penguin, Adélie penguin, flying birds).

The RSTM had 342 parameters that were estimated from over 700 published and non-published data sources. Detailed information on the estimation of the parameters is available online from the CCAMLR Science journal website (www.ccamlr.org/en/publications/science_journal/ccamlr-science-volume-17/ccamlr-science-volume-171-31, last accessed 30 January 2014). Relative uncertainties of these parameters were also estimated during model development. Using a novel approach (Pinkerton *et al.*,

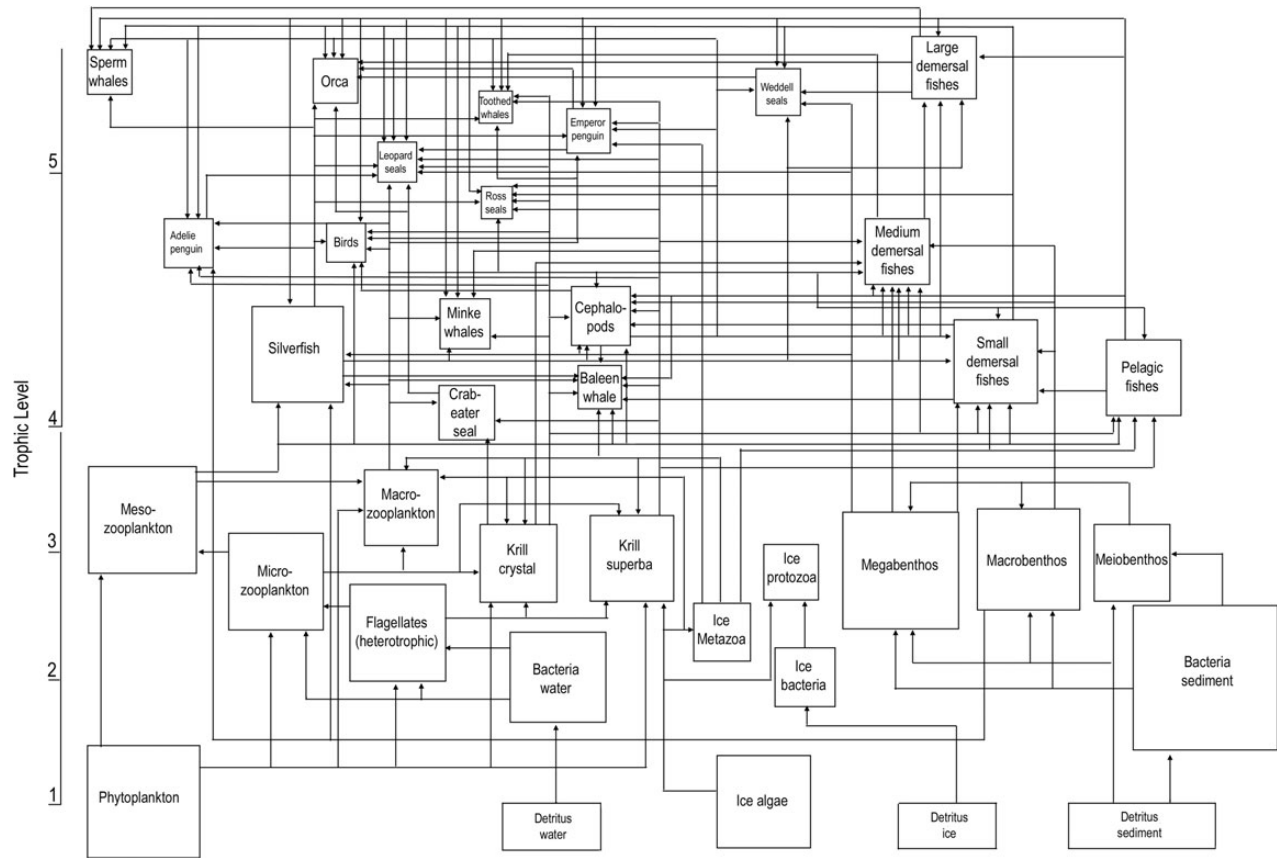


Figure 2. Ross Sea trophic model flow diagram, with arrows showing the direction of organic carbon flow. Box sizes for non-detrital groups are scaled so that the sides are proportional to biomass in that group to the power 0.1, and positioned vertically according to (approximate) trophic level. Note the change in y-axis scale at trophic level 4. Flows to detritus and respiration sinks are not shown for clarity.

2008, 2010), the entire initial set of model parameters were adjusted simultaneously to give a balanced model (i.e. one where all material is accounted for). Parameters for biomass, production rate, growth efficiency, diet fractions, and other transfers of biomass between groups were adjusted simultaneously according to the estimated parameters i.e. parameters estimated to have higher uncertainty tended to be adjusted by more than parameters with lower uncertainty. Mean absolute change during balancing across all key parameters (biomass, production rate, growth efficiency) for all groups together was 1.7%. Mean absolute change in diet fractions during balancing was 0.6%. Larger changes were needed to balance some poorly constrained groups (microzooplankton, 34–47%; ice bacteria, 61–72%; ice protozoa, 24–54%). Stable isotope data from the New Zealand International Polar Year – Census of Antarctic Marine Life (IPY–CAML) voyage in 2008 has since provided some independent validation of trophic levels in the model (Pinkerton *et al.*, 2011).

Mixed trophic impact analysis

Mixed trophic impact (MTI) analysis investigates the effect on one trophic group (the “affected” group, *j*) due to an infinitesimal change in the biomass of another group (“affecting” group, *i*; Ulanowicz and Puccia, 1990; Libralato *et al.*, 2006). The MTI matrix **M** is a square *n*-by-*n* matrix (where *n* is the number of groups in the model) calculated from a foodweb model as in equation 1. Recent work has shown good general agreement between **M**

and relative changes in biomasses from EwE perturbation analyses (Libralato *et al.*, 2006).

$$M^t = (I - Q^t)^{-1} - I \tag{1}$$

In equation 1, **I** is the identity matrix of size *n*-by-*n* where *n* is the number of groups in the model. The “*t*” superscript indicates matrix transpose. Equation 1 takes into account indirect foodweb effects by adding up the impacts of one species on another via all possible multiple steps through the foodweb (Ulanowicz and Puccia, 1990). The *n*-by-*n* matrix **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 **Q**, and defined as the difference between bottom-up (*g_{ij}*) and top-down effects (*f_{ij}*) (equation 2).

$$q_{ij} = g_{ij} - f_{ij} \tag{2}$$

In equation 2, *g_{ij}* is the proportion of prey item *i* in the diet of predator *j*, the assumption being that higher abundance of a prey item will positively affect its predators, with the amount of impact depending on how much of the diet is made up of that prey item. The element *f_{ij}* is the fraction of the net production of prey item *j* that is consumed by predator *i*. Prey species are assumed to be negatively affected by higher abundances of their predators. By “net production”, Ulanowicz and Puccia (1990) meant to exclude respiratory output.

By this definition, the denominator of f_{ij} would be equal to “production” (P_j) in EwE (Christensen and Walters, 2004). In our analysis, non-trophic transfers that increase “production” were included in the denominator of f_{ij} , as these contribute to the amount of matter in a group available for consumption by predators. We note that f_{ij} defined in this way is subtly different to that proposed by Ulanowicz and Puccia (1990), which did not include non-trophic imports but is consistent with comments by the authors in that paper in that different formulations for the denominator of f_{ij} are potentially valid and should be considered. Our definition is different again from the method implemented in EwE, 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 (Christensen et al., 2008). We suggest that the EwE formulation of f_{ij} can lead to unrealistically strong top-down factors being returned when only a part of the mortality of a group is due to direct predation. See Appendix 1, equations 21–23 for these alternative formulations for f_{ij} .

We extended the mixed trophic analysis to include detrital groups, because detrital pathways can be important to flows of energy in ecosystems (Gage, 2003; Ducklow et al., 2006). In terms of affects on detrital groups, g_{ij} represents the proportion of the flow of material into detrital group j from source group i . Flows of detritus are from three sources—unassimilated consumption by predators, mortality of trophic groups that is not due to predation, and transfers of detritus from one detrital group to another (for example, settling of particulate detritus from the water column to the benthos, and release of sea-ice detritus into the water column on melting). For detrital groups, f_{ij} is the proportion of the annual inflow of material to detrital group j that is consumed by detritivorous group i .

Trophic importance

Trophic importance with reference to small perturbations of the ecosystem can be estimated from the single-step trophic impact matrix, **Q** (Table 1, equations 3 and 4) or the multiple-step matrix, **M** (Table 1, equations 5 and 6). The former focuses on direct (first-order) predator–prey linkages. In contrast, **M** considers interactions arising from steps of length 1, 2, 3, . . . trophic steps in the ecosystem and may hence capture more diffuse trophic effects. It is not known which of these approaches is more realistic or appropriate, so both approaches are calculated and

Table 1. Definition of four measures of trophic 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 foodweb; uses single-step matrix, Q | $T_1(i) = \sqrt{\sum_{j=1}^n q_{ij}^2}$ [3] | $T_2(i) = \sum_{j=1}^n q_{ij} $ [4] |
| Based on multiple steps through the foodweb; uses mixed trophic impact matrix, M | $T_3(i) = \sqrt{\sum_{j=1}^n m_{ij}^2}$ [5] | $T_4(i) = \sum_{j=1}^n m_{ij} $ [6] |

compared. In addition, there are two ways of summarizing the overall importance of a species in the foodweb based on its effects on all other species. Libralato et al. (2006) suggests calculating the trophic importance of species i as the root mean square of m_{ij} calculated over all j , here denoted as $T_3(i)$ (equation 5). Using absolute values rather than squared values may give weak links higher and more appropriate importance (McCann et al., 1998; Pinnegar et al., 2005). Trophic importances calculated using mean absolute rather than RMS values are denoted as $T_2(i)$ and $T_4(i)$ based on **Q** and **M**, respectively (Table 1, equations 4 and 6, respectively). When calculating trophic importances, m_{ii} and q_{ii} were set to zero (Libralato et al., 2006).

Results

Mixed trophic impact analysis

Positive single-step impacts follow when the affected predator group obtains the majority of its prey from a single or small number of prey groups. In the RSTM, these included silverfish and pelagic fish feeding on mesozooplankton, whales feeding on squid and krill, and toothfish feeding on small demersal fish (Table 2, Figure 3). In the multiple step analysis (Table 2, Figure 4), some of these strong positive (bottom-up, prey-driven) impacts were preserved (e.g. high positive impact of mesozooplankton on silverfish), but some were weakened (e.g. positive impact of small demersal fish on toothfish). Strong negative impacts (top-down or predation impacts) given by the single-step analysis included feeding by mesozooplankton on microzooplankton, pelagic fish feeding on Antarctic krill, and toothfish feeding on medium-sized demersal fish (Table 2, Figure 3). The impact of toothfish on medium-sized demersal fish was identified as the strongest top-down interaction in the system based on multiple-step impact analysis (Table 2, Figure 3).

Trophic importance

Based on the single-step analysis, mesozooplankton, small demersal fish and Antarctic silverfish had the highest trophic importances in the Ross Sea ecosystem (Figure 5a, b). Cephalopods and Antarctic krill also had high trophic importance. The trophic importance of phytoplankton in the system was emphasized by the multiple-step analysis (Figure 5c and d), but the same five groups as before (namely, mesozooplankton, small demersal fish, Antarctic silverfish, cephalopods and Antarctic krill) also appeared within the seven most trophically important groups in the Ross Sea. Antarctic toothfish was estimated to be between the 12th and 18th most trophically important group in the Ross Sea out of the 31 groups analysed. The rank trophic importance of toothfish was negligibly affected (change of 1) by whether trophic importance was based on single-step or multiple-step analysis, but was higher when trophic importance was calculated based on the square of the individual impacts rather than the absolute values (T_1 and T_3 rather than T_2 and T_4 ; Figure 5). This is consistent with Antarctic toothfish having a small number of strong impacts on other groups rather than a larger number of relatively weak impacts.

Discussion

Much has been written in the scientific and popular press regarding the potential or actual effects of fishing for Antarctic toothfish in the Ross Sea on related or dependent species or on the ecosystem as a whole (Ainley, 2002; Ainley et al., 2007; Pinkerton et al., 2007; Ponganis and Stockard, 2007; Ainley et al., 2009; Ainley and Siniff,

Table 2. Strong positive and strong negative impacts estimated using the single-step matrix (**Q**) and the multiple-step matrix (**M**): each entry shows “Affecting group → Affected group (size of impact)”.

| Sign of impact | Elements of single-step matrix, Q | Elements of mixed trophic impact matrix, M | |
|---|--|---|--------------------------------------|
| Positive (bottom-up, prey effect) | Mesozooplank → Silverfish (0.91) | Ice algae → Ice metazoa (0.74) | |
| | Ice algae → Ice metazoa (0.88) | Cephalopods → Sperm whales (0.64) | |
| | Cephalopods → Sperm whales (0.76) | Krill superba → Baleen whales (0.57) | |
| | Bacteria sediment → Megabenthos (0.74) | Cephalopods → Toothed whales (0.50) | |
| | Krill superba → Baleen whales (0.71) | Bacteria sediment → Megabenthos (0.46) | |
| | Bacteria sediment → Meiobenthos (0.71) | Mesozoo → Silverfish (0.40) | |
| | Small dem fish → Toothfish (0.70) | Silverfish → Orca (0.36) | |
| | Silverfish → Emperor (0.67) | Silverfish → Emperor (0.35) | |
| | Mesozoo → Pelagic fish (0.67) | Krill superba → Minke whales (0.33) | |
| | Bacteria sed → Macrobenthos (0.63) | Phytoplankton → Flagellates (0.32) | |
| | Negative (top-down, predator effect) | Mesozooplank → Microzooplank (−0.82) | Toothfish → Medium dem fish (−0.47) |
| | | Flagellates → Bacteria water (−0.68) | Weddell → Toothfish (−0.45) |
| | | Small dem fish → Macrobenthos (−0.65) | Pelagic fish → Krill superba (−0.44) |
| | | Pelagic fish → Krill superba (−0.59) | Mesozooplank → Microzooplank (−0.41) |
| Toothfish → Medium dem fish (−0.53) | | Orca → Weddell (−0.36) | |
| Weddell → Toothfish (−0.51) | | Pelagic fish → Baleen whales (−0.31) | |
| Flagellates → Phytoplankton (−0.46) | | Small dem fish → Macrobenthos (−0.31) | |
| Adélie penguins → Silverfish (−0.44) | | Adélie → Silverfish (−0.28) | |
| Small dem fish → Megabenthos (−0.39) | | Leopard → Adélie (−0.27) | |
| Small dem fish → Cephalopods (−0.38) | | Flagellates → Bacteria water (−0.27) | |

The ten highest positive impacts and ten greatest negative impacts are shown (impacts of group on itself neglected). These are the largest circles in Figure 3 (left column) and Figure 4 (right column).

2009). However, to date, critical analysis of these risks has been lacking.

The research described here used a quantitative foodweb model of the Ross Sea to evaluate the relative trophic importance of species and trophic groups in the region, and hence examined the potential effects of a change in biomass of Antarctic toothfish on other species in the ecosystem. The term “trophic importance” was preferred over “total impact” (Libralato *et al.*, 2006), because non-trophic interactions (e.g. provision of habitat, and “behavioural” interactions, Preisser *et al.*, 2005) were not considered by this analysis. “Trophic importance” was 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 the trophic importance expected based on abundance alone. Keystoneness may be a useful concept because low biomass components in an ecosystem may often be more vulnerable to human impacts than high biomass components. However, trophic importance is the relevant measure for assessing to what extent changes to one species or group may affect the foodweb as a whole, irrespective of whether the group initially had high or low biomass.

MTI analysis (Ulanowicz and Puccia, 1990) was used here to estimate trophic importance. The MTI approach relies on two premises: (i) that increasing the availability of prey positively affects its predators, with the size of the effect being dependent on the predator diet; and (ii) that increasing the amount of predation on a prey population will negatively affect the abundance of the prey, especially if the predator is the main consumer of that prey. These are reasonable assumptions, but a number of important caveats are required. First, MTI analysis is relevant only for small (strictly infinitesimal) changes from the current state of the system, and longer-term compensatory, density-dependent or other non-linear adjustment mechanisms are not considered. Second, the MTI method only considers trophic effects and ignores non-trophic interactions between

species, such as the provision of habitat or behavioural/interference interactions between species (e.g. Preisser *et al.*, 2005). Third, MTI provides information only at the scale of the underlying foodweb model. In this case, the spatial scale is the whole Ross Sea shelf and slope area, the time-scale is a typical annual period, and the biotic resolution is 35 trophic groups. Effects at smaller spatial and temporal scales, and effects concerning only parts of populations, cannot be resolved by MTI analysis. Fourth, the conclusions are dependent entirely on the validity of the underlying foodweb model, in this case the balanced RSTM (Pinkerton *et al.*, 2010), so limitations and errors in the RSTM may invalidate the conclusions presented here.

Although a considerable amount of data is available on the Ross Sea ecosystem (Smith *et al.*, 2007; Pinkerton *et al.*, 2010; Smith *et al.*, 2012), our knowledge is incomplete for all groups. In particular, higher modifications were required during balancing to microzooplankton, ice bacteria and ice protozoa, indicating relatively poor information on these groups. Lack of sampling outside the summer is also problematic for building models that represent average ecosystem properties over an annual period. It is well known that such models are highly underconstrained (Kavanagh *et al.*, 2004), and that comprehensive investigation of the effects of parameter uncertainty in models such as these is not possible (Fulton, 2010). Nevertheless, the RSTM represents the best available self-consistent, quantitative, semi-validated view of the structure of the Ross Sea ecosystem with which to develop “working hypotheses” of ecosystem structure and function. Consistent with best practice in ecosystem modelling (Fulton, 2010), the analysis presented here should be seen as being strategic (identifying priorities for research and management), rather than being tactical (determining what level of harvesting will achieve management aims). Three pieces of evidence suggest that the conclusions of this study are likely to be robust enough to account for parameter uncertainty. First, only small changes to most parameters were required to balance the model (mean changes were <2%). Second, the groups that required

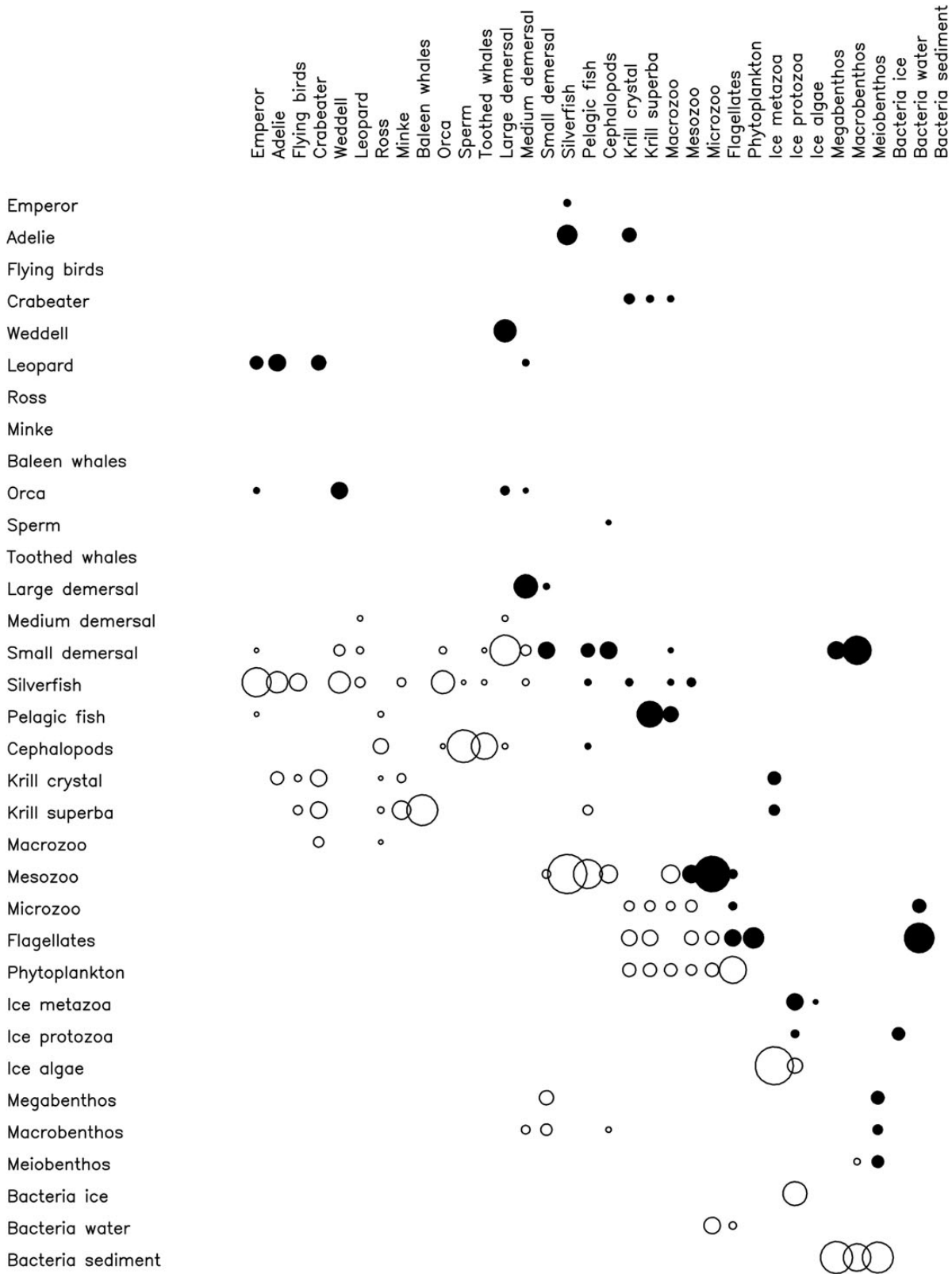


Figure 3. Single-step trophic impact matrix, Q , for the Ross Sea trophic model. Positive impacts are shown in white and negative in black, and the size of the circle shows the magnitude of the impact. “Impact” is interpreted as the effect that a small increase in the biomass of the affecting group (shown on the left of the diagram) has on the biomass of the affected group (shown across the top), based on steps of length 1.

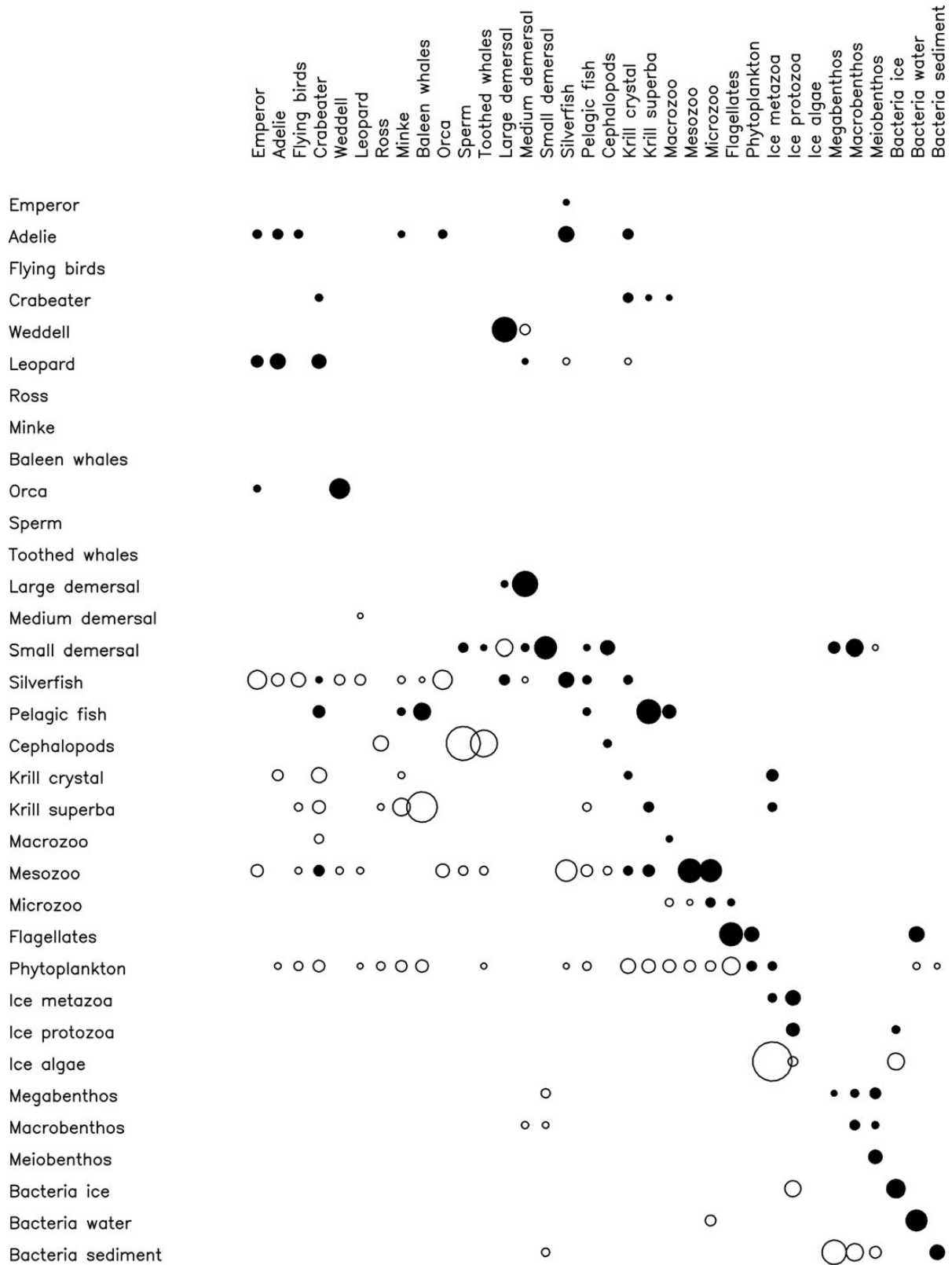


Figure 4. Mixed trophic impact matrix, M , for the Ross Sea trophic model. Positive impacts are shown in white and negative in black, and the size of the circle shows the magnitude of the impact. "Impact" is usually interpreted as the effect that a small increase in the biomass of the affecting group (shown on the left of the diagram) may have on the biomass of the affected group (shown across the top), taking into account multiple steps in the foodweb.

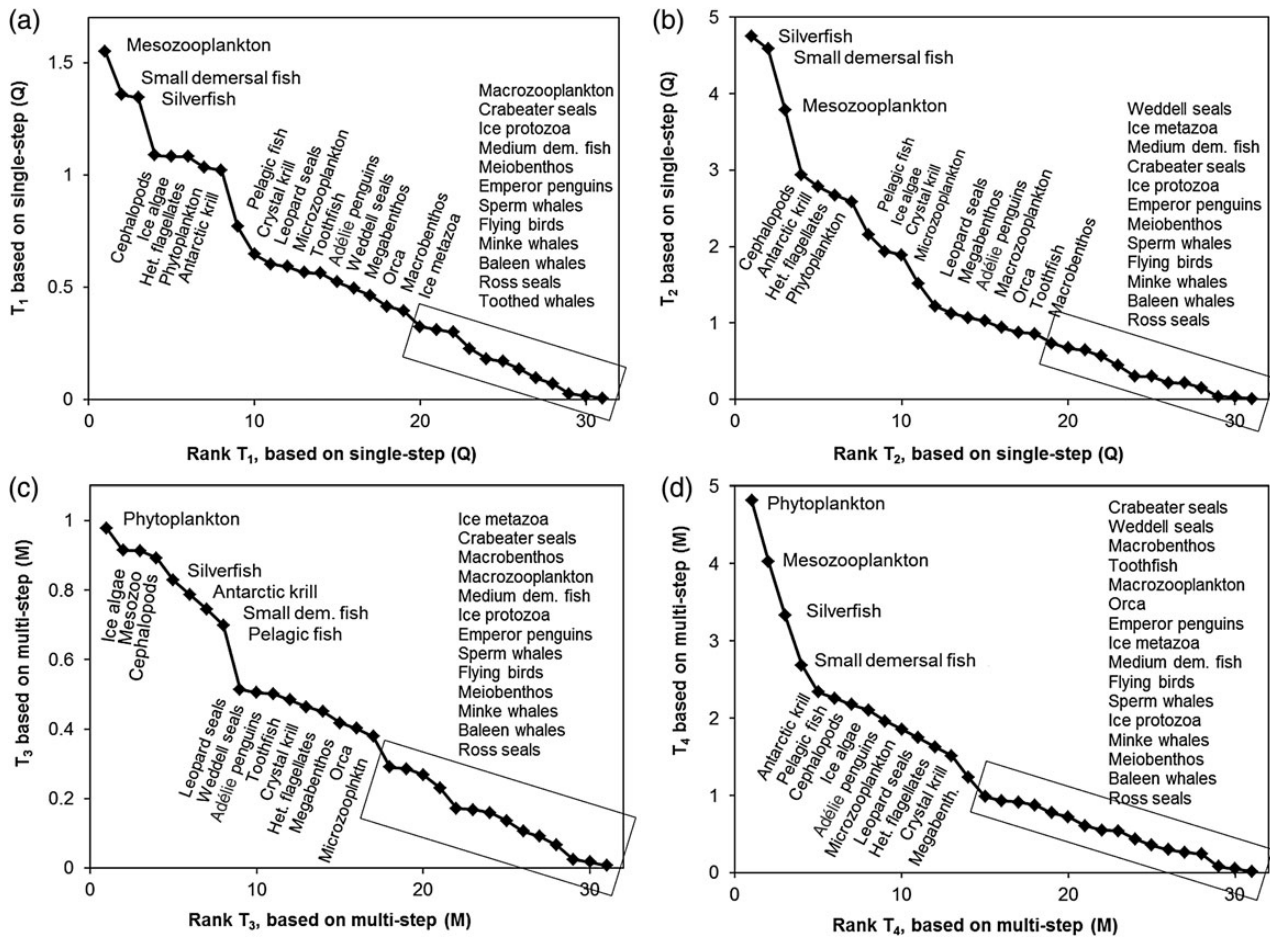


Figure 5. Four measures of trophic importance based on the Ross Sea trophic model. T₁ and T₃ (strong links more valued) are shown in (a) and (c); T₂ and T₄ (weak links valued higher) are shown in (b) and (d). Single-step effects only (based on matrix **Q**) are shown in (a) and (b); multi-step effects (based on MTI matrix **M**) are shown in (c) and (d).

larger adjustment of their parameters were not identified as having high trophic importance. Third, trophic levels in the model agreed well with those determined from stable isotope measurements in the region (Pinkerton *et al.*, 2011), giving some validation of the foodweb model.

The overall picture of trophic importance in the Ross Sea foodweb was fairly consistent between single- and multi-step approaches and when using different weightings of strong versus weak trophic links. Overall, the six groups with the highest trophic importance in the foodweb of the Ross Sea were (in decreasing order of importance): phytoplankton, mesozooplankton, Antarctic silverfish, small demersal fish, Antarctic krill and cephalopods. Pelagic fish, and crystal krill were also likely to have relatively high trophic importance in the Ross Sea foodweb. These eight groups should be the priorities for monitoring for effects of climate change or large-scale ecosystem changes, and this is now reflected in the monitoring and research plan associated with proposed spatial protection in the Ross Sea (Delegations of New Zealand and the USA, 2013).

The importance of phytoplankton in the Ross Sea is clear and changes to the magnitude or characteristics (e.g. spatial patterns, seasonal progression and/or prymnesiophyte–diatom balance) of Ross Sea phytoplankton are likely to have considerable consequences for regional ecosystem structure and function (DiTullio and Smith, 1997; Arrigo and van Dijken, 2004; Reddy and Arrigo, 2006). In the

RSTM, mesozooplankton (copepods and pteropods primarily) are the primary pathway by which energy is transferred from the lower foodweb to middle and upper trophic levels (Pinkerton *et al.*, 2010), so a high trophic importance for this group is reasonable. Antarctic silverfish have a life history that is thought to take in the whole Ross Sea shelf and slope, and their juveniles dominate the Ross Sea shelf ichthyoplankton (Hubold, 1985; Vacchi *et al.*, 1999; Granata *et al.*, 2002; Vacchi *et al.*, 2004; Granata *et al.*, 2009). Silverfish are known to be ubiquitous in the diet of predators including penguins, seals, toothed and baleen whales, fish and squid in the Ross Sea (DeWitt, 1970; Laws, 1984; La Mesa *et al.*, 2004), so their high trophic importance is not surprising. According to the RSTM, consumption by upper level predators was satisfied by silverfish (42%), crystal krill (16%), small demersal fish (14%), Antarctic krill (7%), cephalopods (7%) and other groups (<4%). Changes to silverfish abundance, as has occurred in areas close to the Antarctic Peninsula (Torres, 2010), are hence likely to have far-reaching consequences for Ross Sea ecology. Small pelagic fish 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 replace Antarctic silverfish as an important prey for predators (Croxall, 1987; Kozlov, 1995).

It has been suggested that studying the role of toothfish in the Ross Sea region may give insights into the role that top piscine predators may have had in shelf systems before the advent of

industrialized fishing and when whales, seals and seabirds were more abundant (Ainley, 2002). Although some studies certainly suggest that top marine predators had much higher trophic importance in the past than they do at present (e.g. Pinkerton, 2011), the analysis presented here did not ascribe particularly high trophic importances to groups of air-breathing predators in the Ross Sea.

Bottom-up effects of the toothfish fishery

The analysis presented here was not sufficient to test for the effects of the fishery for Antarctic toothfish on the ecological viability of the main toothfish predators in the Ross Sea region: Weddell seals and type-C (fish-eating) killer whales. Although both predators certainly consume toothfish in the Ross Sea (Ponganis and Stockard, 2007; Ainley and Ballard, 2012), the importance to these species of toothfish as a prey item is not known and is an active area of research (Torres *et al.*, 2013; Eisert *et al.*, 2013). In the RSTM, toothfish were a minor component of the diet of Weddell seals and killer whales on the scale of the Ross Sea when averaged over a year. Consequently, toothfish were estimated to have low impacts on these predators. This analysis did not take into account effects at smaller space, time- and sub-population scales, which some studies have identified as leading to increased risk of adverse effects due to fishing of toothfish (Pinkerton *et al.*, 2008; Torres *et al.*, 2013; Eisert *et al.*, 2013). For example, 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 (e.g. Pinkerton *et al.*, 2008; Eisert *et al.*, 2013). Such subtle but potentially important risks were not addressed by the model or analysis presented here.

Top-down ecosystem effects of the toothfish fishery

Single-step trophic impact analysis identified several strong, top-down impacts associated with predators consuming a large proportion of the annual production of a small number of prey groups. Most of these strong impacts were preserved in the multiple-step analysis. Of particular relevance to understanding potential fishery effects was the strong top-down impact of toothfish on medium-sized demersal fish. In the RSTM, toothfish consumed 64% of the annual production of medium-sized demersal fish. This led to the strongest, top-down impact in the whole multiple-step analysis (Table 2). We conclude that at least some piscine prey of toothfish are likely to experience a strong predation-release effect as the abundance of toothfish is reduced. We note that the fishery also takes medium-sized demersal fish as bycatch, and although this was not considered in the analysis it is likely to be too small to affect this conclusion.

Changes to prey communities due to changes in predators are predicted to be strongest where the predator is large and mobile and has a high metabolic rate, where prey species are long-lived, functional predator diversity is low, and predator intraguild predation is weak or absent (Shurin *et al.*, 2002; Borer *et al.*, 2005; Heithaus *et al.*, 2008). Many of these factors are present in the Ross Sea. On the Ross Sea continental slope, where the majority of the regional Antarctic toothfish population is likely to feed (Hanchet *et al.*, 2008), toothfish are likely to be by far the major predators of grenadiers (*Macrourus whitsoni* and *M. caml*) and icefish (*Chinobathyscus dewitti*) (Bury *et al.*, 2008; Pinkerton *et al.*, 2010; Stevens *et al.*, 2012); there are no other piscine predators of the size of Antarctic toothfish over the Ross Sea shelf and slope. Prey species of toothfish have relatively high longevity and low

productivity rates. Grenadiers in particular tend to be long-lived (Bergstad, 1995; Kelly *et al.*, 1997; van Wijk *et al.*, 2003), and in the Ross Sea region otolith ageing shows that they live in excess of 27 years (*M. whitsoni*) and 62 years (*M. caml*), and females do not become sexually mature until 16 years (Marriott *et al.*, 2006; Pinkerton *et al.*, 2013). *Chinobathyscus dewitti* in the Ross Sea region become sexually mature at ~4 years and have been measured as living in excess of 12 years (Sutton *et al.*, 2008). One mitigating factor against strong top-down changes to prey species is the relatively low consumption rate of toothfish, which is likely to be only 1–2 times its body mass per year (Pinkerton *et al.*, 2010).

Notwithstanding the caveats to MTI analysis given earlier in this discussion, MTI analysis provided information on whether changes to the Ross Sea demersal fish community are likely to “cascade” to the lower trophic levels of the ecosystem. Such trophic cascades have been shown to operate in coastal and oceanic systems, even where productivity is low (Pace *et al.*, 1999; Heithaus *et al.*, 2008). Trophic cascades may be transitory and reversible, but they can also stabilize systems in an alternative state—a biologically mediated regime shift (Estes and Duggins, 1995; Daskalov *et al.*, 2007; Casini *et al.*, 2009).

The analysis presented here suggests that Antarctic toothfish have moderate trophic importance in the Ross Sea foodweb as a whole. The rank trophic importance of toothfish was found to be close to the middle of the 31 model groups (between 12th and 18th depending on the method of analysis). We have concluded that changing the abundance of toothfish may have a substantial effect on the medium-sized demersal fish group, but the analysis presented here suggests that this effect will not cascade through the ecosystem because medium-sized demersal fish only have low trophic importance in the system (21st–23rd highest importance). Although small demersal fish have high trophic importance according to this analysis (2nd–7th highest), toothfish consume only 16% of their annual production, so the overall effect on the ecosystem of changing toothfish abundance via the effect on small demersal fish is small. Limitations to the present study given earlier mean that extensive cascading effects on the Ross Sea ecosystem due to changing the abundance of toothfish cannot be categorically ruled out. However, for such changes to occur, a mechanism other than simple trophic interactions is likely to be involved.

Final comments

Modelling the ecosystem effects of fishing remains imprecise (Plagányi, 2007; Fulton, 2010), and ecosystem monitoring is required to complement prediction (Rice, 2000; Garcia and Cochrane, 2005). Detection of the ecosystem effects of fishing in the high Southern Ocean is particularly difficult because observational data are expensive to collect and are highly limited in scope (e.g. research vessels are excluded from the region by sea-ice except in the summer). The fact that critical environmental conditions like sea-ice have high inter-annual variability and are likely to be undergoing long-term change (Parkinson, 2002; Boyd *et al.*, 2006; Stammerjohn *et al.*, 2008), means that understanding the drivers of ecosystem change in areas like the Ross Sea is especially challenging. Implementation of a comprehensive monitoring and research plan is hence crucial for early detection of any ecosystem effects of fishing in this high latitude system (Delegations of New Zealand and the USA, 2013).

Supplementary data

Supplementary data are available at the ICESJMS online version of the manuscript. These include Appendix 1 and Tables A1 and A2.

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