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The policy relevance of Southern Ocean food web structure: Implications of food web change for fisheries, conservation and carbon sequestration

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ABSTRACT

Southern Ocean food webs provide ecosystem services with significant global value including carbon sequestration, fisheries and the existence of iconic wildlife. These services are underpinned by different energetic pathways including those dominated by Antarctic krill, fishes and squids, or gelatinous zooplankton (salps). Climate change is likely to impact Southern Ocean food webs by affecting their foundations — both primary producer communities and ice habitats. However, the implications of these changes for ecosystem services – including wildlife populations, fisheries and carbon sequestration – are unclear, as are the implications for policy and management. Here, we use a generalised representation of Southern Ocean food webs and qualitative network modelling to investigate the consequences of five simple but plausible scenarios of future change for ecosystem services and the conservation of important taxa: (i) a shift in primary producer communities with decreasing large diatoms and increasing small flagellates; (ii) increasing salps; (iii) increase (recovery) of the Great whales; and unregulated and unsustainable fisheries for (iv) krill or (v) toothfish. Strikingly, our results suggest that increases in salps might not have negative consequences for ecosystem services and could enhance carbon export potential. Simulated increases in unregulated krill and toothfish fisheries affect predatory wildlife and could also reduce carbon export potential. Our results emphasise the important policy implications of understanding the structure and change of whole food webs, and highlight that improved quantitative understanding and modelling of the relative importance of different energy pathways will be important for developing robust management responses to climate change impacts.

1. Introduction

The Antarctic marine ecosystem supports services of great global value including carbon sequestration, fisheries, biodiversity and iconic wildlife [1]. Historically, the Antarctic marine ecosystem has been viewed as being dominated by the food chain from phytoplankton through Antarctic krill (*Euphausia superba*) to the great baleen whales [2,3]. This is regarded as an efficient pathway for transferring energy (hereafter termed ‘energy pathway’) from primary producers to the higher trophic levels, with the potential to sustain a large biomass of whales [4]. In addition to the archetypal krill pathway, alternative pathways exist for this transfer of energy to top predators; these pathways sustain other predators less reliant on krill, notably toothfish, toothed whales, and a number of seals, penguins and flying birds [5,6]. The diversity of energy pathways enables the maintenance of the range of ecosystem services because distinct suites of species provide unique contributions to maintaining different services [7,8].

The diversity of energy pathways and their interaction with one another is typical of consumer networks in food webs [9,10]. This means that external forcing of change in some taxa can result in a cascade of indirect interactions and feedbacks through the food web, which may make the consequences of change unpredictable [11,12]. If species at the top of the food web are directly affected by external forces then consumer pressures from the top down through the food web can cause shifts in the relative abundance of lower trophic level species (“top-down” forcing; [13]). If species at the bottom of the food web are directly affected then the supply of production from the base of the food web can cause shifts that can propagate up food chains to affect the relative abundances of higher predators (“bottom-up forcing”; [14,15]).

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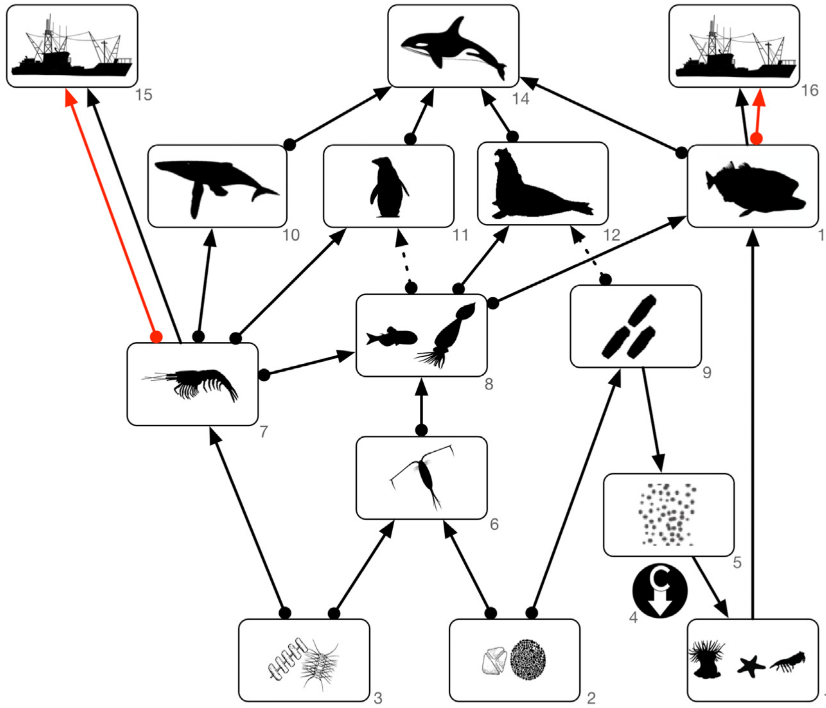

Fig. 1. A simplified and generalised representation of the Southern Ocean food web, including links to dependent fisheries and carbon sequestration. Arrows connecting two compartments can have 3 types of ends: (i) an arrow-point indicates that an increase in the compartment that the arrow is pointing from will also result in an increase in the compartment that it is pointing to; (ii) a filled circle at the base of an arrow indicates that an increase in the compartment that the arrow is pointing to will result in a decrease in the compartment it is pointing from (the one touching the filled circle). An arrow without a circle at the base implies no negative effect on the compartment the arrow points from. Fisheries in the Southern Ocean managed in accordance with CCAMLR objectives are not expected to significantly negatively impact the food web, in contrast to illegal unregulated and unreported fisheries which will be expected to negatively affect stocks (red arrows [grey in print version]). Dashed lines represent uncertain interactions. Although not pictured, all nodes have negative self-effects. [1]benthic assemblage, [2]small phytoplankton, [3]large phytoplankton, [4]enhanced carbon sequestration, [5]large sinking particles, [6]mesozooplankton (copepods etc.), [7]Antarctic krill, [8]mesopelagic fishes and squids, [9]salps, [10]baleen whales, [11]krill specialist predators, [12]fish and squid specialist predators, [13]toothfish, [14]apex predators, [15]krill fisheries, [16]toothfish fisheries.

For Antarctic marine ecosystems, common statements on likely change used by scientists and policy makers include (amongst others): changes in plankton communities arising from climate change, driven by changes in water temperature and chemistry as well as changing sea–ice conditions, including (i) declines in the production of large diatoms and increases in small flagellates and (ii) increasing gelatinous zooplankton such as salps; (iii) the recovery of the great whales; and (iv) uncontrolled fishing for krill or toothfish [6,7,15].

For scientists, an important question regards what might be the response of Antarctic marine food webs to these scenarios of change. For policy-makers, the question is extended to include what might happen to Antarctic marine ecosystem services? Moreover, policy-makers will also wish to know what information is needed to avoid inadvertently making incorrect decisions in managing human activities in the face of climate change. Specifically, we can consider whether energy pathways can be managed independently (e.g. understanding only the krill energy pathway in order to manage the krill fishery) or whether we may need to consider the interactions between pathways in order to successfully manage particular ecosystem services.

Modelling is an essential approach for addressing such questions regarding ecosystem responses to change, and implications for ecosystem services [16,17]. There has been considerable progress in the development of models for Southern Ocean food webs and ecosystems over the past two decades (reviewed in [2,18,19]) This work has yielded important insights into ecosystem structure and function. However, modelling efforts to date have mainly been centred on key species and/or localised systems (as noted by [2]), making it difficult to understand generalities. Previous and ongoing efforts to synthesise messages from modelling studies for Southern Ocean food webs and ecosystems have highlighted that simplified generalised models will be invaluable in encompassing change across a connected continuum of local and regional food web structures [2,20] and have highlighted development and analysis of such simplified generalised models as a key priority for the Southern Ocean ecosystem modelling community.

Here, we use a simplified, generalised representation of the Antarctic pelagic food web to help facilitate policy discussions of the ecosystem implications of climate change, fishing and the recovery of depleted species, which are important considerations for the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR; [21]). We simplify the Southern Ocean food web into functional attributes of the energy pathways, based on recent reviews of Southern Ocean food web structure and function [2,12,20]. Each of the players in our generalised food web (Fig. 1) represent a particular functional group, which may comprise one or more species (and different species in different regions). We explore what the consequences are likely to be for different consumer groups and ecosystem services if the food web changes according to the five commonly discussed scenarios described above. Lastly, we describe the scientific strategies that could be employed to help account for these scenarios in achieving the conservation of Antarctic marine ecosystems, and in meeting associated national and international policy goals.

2. Material and methods

2.1. A simplified, generalised Antarctic marine food web

We constructed a simplified and generalised representation of the Antarctic marine food web as a signed network digraph (Fig. 1; see caption and Section 2.3 for an explanation of signed network digraphs). The food web comprises approximately five pelagic trophic levels [2–4] as well as the role of bottom-dwelling (benthic) biological assemblages that store carbon exported from the pelagic system [22,23] and also make it available through various benthic pathways for consumption by toothfish. The generalised food web is intended to be broadly representative across possible region-specific variations in food web structure.

The pelagic component of the food web comprises: primary producers (phytoplankton) that convert sunlight and make its energy accessible to the rest of the food web; grazers that feed on phytoplankton; mid-trophic level fishes and squids feeding on the grazers; higher predators including large fish (toothfish; which are bottom-associated but forage both at the sea floor and in the water column [24,25]); most whales, seals, penguins and flying birds; and the top predators such as orca and leopard seals, which feed on taxa in the mid and higher trophic levels [2,3,7]. Antarctic krill are grazers that feed predominantly on large phytoplankton, diatoms [26]. Other grazers tend to feed predominantly on phytoplankton that are smaller than diatoms [27,28]. The latter grazers include copepods, which are consumed by small fishes and squids, and salps, for which the predators are not well known but include some flying birds [29–31]. Notably, salps are the primary exporters of particulate matter to the benthic food web, as they produce large, rapidly fecal pellets and occur in high abundances [30,32–34]. While vertically migrating mesopelagic fishes may also play a major role in carbon export, our results were not sensitive to whether this link was represented in the model (Figure S2) so we have omitted it for simplicity here. Jellyfish (cnidarians) are mid-trophic level species but their role is not well understood and not included here.

Higher trophic level species can be grouped into four types of consumers. The first comprises the baleen whales, which have a clear preference for Antarctic krill [35]. The second group comprises other smaller predators that also preferentially target kirll (“krill specialists”), including taxa such as Adelie penguins and pack-ice seals; These species feed mainly on Antarctic krill but may feed on fishes and squids in some places or times [2,36]. The third group is predators that are fish/squid specialists, and includes Emperor penguins, southern elephant seals and sperm whales [2,36]. Toothfish are the fourth group of consumers, and predominantly prey on mesopelagic fishes and squids, and to a lesser extent on benthic-associated fauna [24,25].

The last set of interactions in this simplified food web are for the fisheries. Antarctic krill and toothfish are the dominant target species of fisheries in the Southern Ocean at present [37]. CCAMLR uses a precautionary ecosystem approach to fisheries management, grounded by the requirement to ensure that fisheries do not have negative effects on ecosystems, with fisheries catch limits set accordingly [7,21]. Fishing by CCAMLR nations, in accordance with CCAMLR regulations and catch limits, should not therefore be expected to cause declines in stocks (below the target level for each stock). In contrast, illegal, unreported and unregulated (IUU) fishing in CCAMLR waters will be expected to have the potential to cause stock declines. IUU fishing in the Convention Area was extremely problematic in the 1990s (particularly for toothfish, with IUU toothfish catches estimated to have been over six times the catch reported by authorised fishing vessels at its peak) [38,39]. While it has been substantially reduced by concerted international effort in recent decades, it remains a serious concern for the Commission, with the potential to seriously undermine CCAMLR’s conservation objectives. Projected global shifts in global fisheries productivity may be expected to increase the incentive for IUU fishing in Antarctic waters in the future, with declines in marine ecosystem fisheries productivity expected at low and mid-latitudes [40,41]. We therefore distinguish between sustainably managed fisheries vs unsustainable IUU fisheries in our food web representation (Fig. 1).

In addition to the network links (edges), shown in Fig. 1, all groups also have negative self-effects, which, in qualitative network models, accounts for the fact that not all factors that affect each group are represented in the model (no self effect for a group implies that all things that affect the group are included in the model).

2.2. Scenarios of change and implications for ecosystem services

We explore five different scenarios of change to illustrate the consequences to ecosystem services of the expected changes in individual components of our food web. The ecosystem services that we explore are fishing (change in krill or toothfish as target species), conservation of iconic species (baleen whales, krill specialists, fish/squid specialists) and carbon export potential.

2.2.1. Climate change impacts leading to declining (i) large phytoplankton (diatoms) and increasing small phytoplankton (flagellates) or (ii) increasing gelatinous zooplankton (salps)

Climate change may cause, amongst other things, increasing sea surface temperature and acidity along with a decline in sea–ice habitat which together are expected to lead to declines in productivity of large diatoms, and an increase in productivity of small phytoplankton, as well as an increase in salps [12]. Here, we explore a decline in diatoms and an increase in small phytoplankton as one scenario, and a second scenario comprising an increase in salps.

2.2.2. (iii) Whale recovery

In the absence of any other change, baleen whales are expected to increase in abundance over the coming decades [42,43]. Understanding ecosystem recovery will be important in determining how the ecosystem will change without any other intervention or external force, hence this increase in the great whales is our third scenario.

2.2.3. Unregulated and unsustainable fisheries for (iv) krill and (v) toothfish

As noted above, the CCAMLR precautionary ecosystem management approach is expected to sustain both target species and dependent and related species, and to not cause change that cannot be recovered from within two to three decades. In the simplified food web model, we therefore assume that fisheries targeting either Antarctic krill or toothfish will not appreciably affect food web structure and function if these management controls are successful. In contrast, we assume that IUU fishing will affect food web structure and function by driving declines in target stocks. We explore two scenarios, one for krill and one for toothfish, where the target species experiences uncontrolled long-term over-fishing.

2.3. Qualitative network modelling with QPress

Using the network digraph representation of our simplified and generalised Antarctic marine food web (refer to Fig. 1 for digraph approach), we then constructed a qualitative network model, in which interactions between components are simplified to either positive or negative effects (arrows or filled circles in the network digraph). The qualitative network modelling approach is very useful for capturing feedback effects in qualitative predictions and for formulating and testing fundamental understanding of system structure and responses to perturbation, making it very well suited to this application [44,45]. It has been broadly used to evaluate food web responses to climate change and to consider possible management responses [e.g.15,46–48]. We used the *QPress* R package for qualitative network modelling [44,49] to simulate model responses our five change scenarios by considering them as press perturbations (i.e. sustained increases or declines in relevant network elements). *QPress* implements a simulation approach to sample many iterations of the community interaction matrix that corresponds with a specified signed digraph (in this case the model shown in Fig. 1). This means that, for each link, simulations sample across the range of possible strengths. Uncertain links are down-weighted by randomised exclusion from simulations. Only those iterations that are stable are maintained, and the responses are aggregated to provide a probabilistic interpretation of qualitative outcomes (as summarised in [44]), i.e. the probability of a long-term population increase or

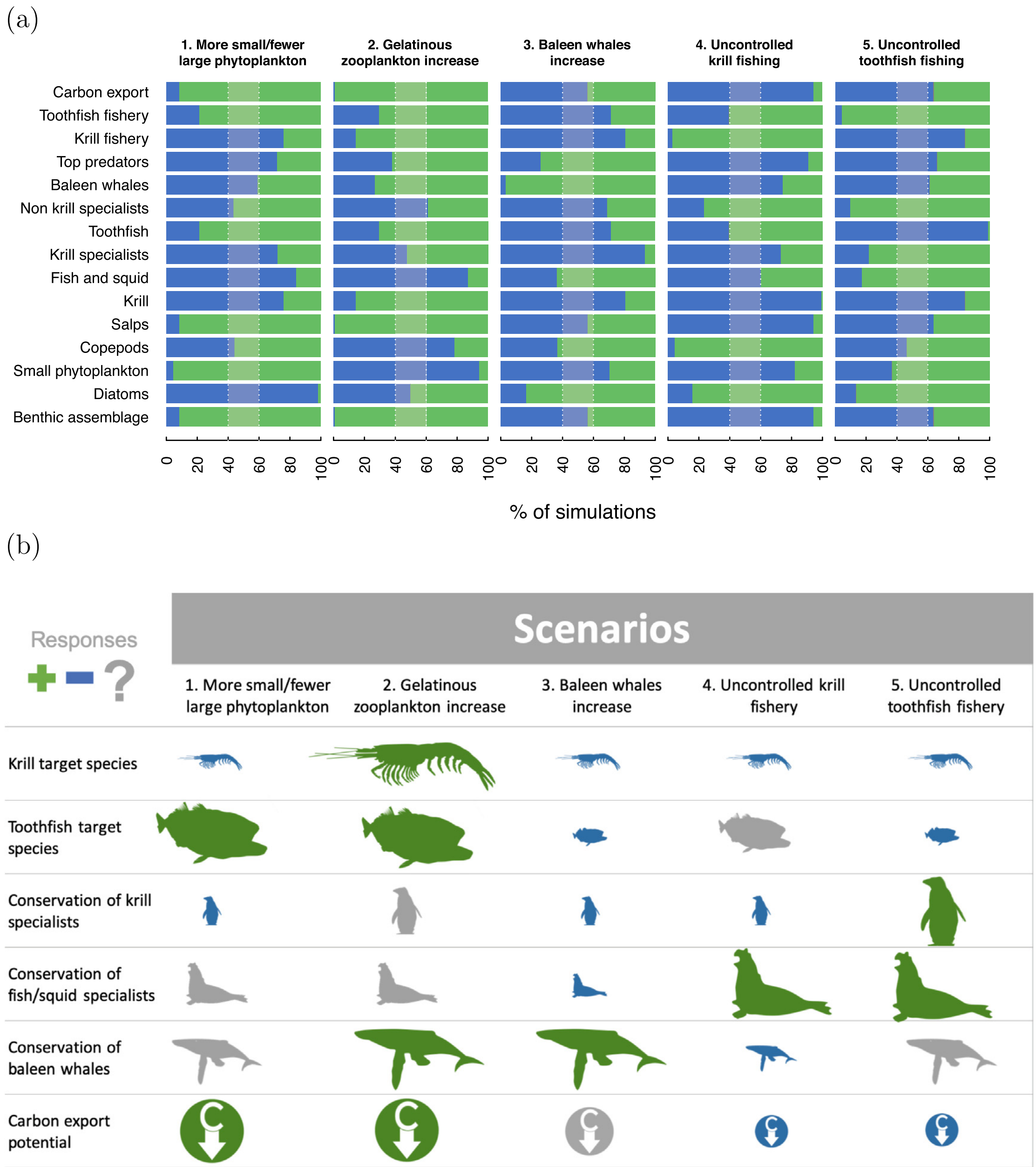

Fig. 2. Outcomes of change scenarios. Top panel (a) shows the simulation results, with 10,000 simulations for each scenario. Green [light grey in print version] shows scenarios with increases and blue [dark grey in print version] shows those with decreases. The expected change interpreted from results of the press perturbation is an overall increase or decrease when greater than 60 % of the simulations result in one or the other. The result is regarded as ambiguous when neither exceeds 60% - this region of ambiguity is indicated by the area between the dotted lines at 40% and 60% (see text in Section 2.3 for details). Bottom panel (b) provides a visual summary of the key policy-relevant components of these results: fish- eries; wildlife conservation; and carbon sequestration, with symbol size indicating whether the majority (≥ 60 %) of simulation outcomes were increases or decreases. Grey symbols indicate an ambiguous outcome.

decrease for each group in the model under a given press perturbation scenario. We considered cases where ≥ 60% of simulation outcomes were increases for a particular model component to indicate an overall predicted increase. If ≥ 60% of simulation outcomes were decreases for a particular model component then we considered this to represent an overall predicted decrease. Those cases with between 40%–60% increases or decreases were considered ambiguous. The major assumptions of the modelling approach we use here are the ecological processes represented (i.e. which network components interact with which others, and in what qualitative manner – i.e. positive or negative), and that those effects manifest at a population level. The nature of the approach means that model linkages are not directly parameterised, and that predictions for responses to change do not capture relative magnitudes of responses, only their direction. Finally, qualitative network modelling does not resolve different functional forms of predation.

3. Results and discussion

Our simulations based on a qualitative network model representation of the Southern Ocean food web (Fig. 2) indicate that changing the relative importance of key planktonic species – including either the relative balance of small vs. large primary producers, or an increase in gelatinous zooplankton (salps) – may lead to enhanced carbon export, and also indirectly enhance the toothfish fishery. Major differences between the outcomes of these scenarios are in the implications for krill, their predators, and the krill fishery, with a shift in dominance from large diatoms to small primary producers likely to have negative implications for krill that will propagate to also negatively affect their predators and the fishery.

A striking result from our model is evidence that an increase in salps (gelatinous zooplankton) may enhance most ecosystem services, including the krill and toothfish fisheries, conservation of baleen whales, and carbon export, and with uncertain (not clearly negative or positive) implications for other seals, penguins, seabirds and other top predators. In this model, this is likely a result of feedbacks that mediate negative pressure on krill from fishes and squids, and also arises from the differentiation between the feeding preferences of krill and salps for large vs. small phytoplankton respectively. Direct food competition between krill and salps would result in decreases in krill and krill-dependent predators with an increase in salps (Figure S3; [50,51]).

Our simple model indicates that an increase in baleen whales, in the absence of any other change, would have negative implications for krill and all predators, including both those that mainly feed on krill, and those that mainly target fishes and squids. It is, however, important to note that our model configuration does not account for the potentially important role that whales play in enhancing surface primary production, because the scale and ecosystem-level importance of this effects is still to be established [52]. This may be expected to partly offset their potential negative impact on krill (and indirect impacts on other krill-specialist predators), and evidence from quantitative food web modelling suggests that the bottom-up effects of changing patterns of primary production on krill may outweigh top-down forcing from recovering predator populations [53].

Our results indicate that uncontrolled fisheries, both for krill and toothfish, would have negative implications for both the target species and carbon export, and that both may indirectly benefit populations of those predators whose diets are not dominated by krill, but instead mainly feed on fishes and squids. This would include, amongst others, species such as Emperor penguins, southern elephant seals and sperm whales. Un-controlled krill fishing would also have strong negative implications for krill-dependent predators (baleen whales along with Adelie penguins and pack-ice seals) in our simulations.

The response of the model to all scenarios occurring simultaneously was a decrease in krill, toothfish and krill specialists, and increases in fish/squid specialists, baleen whales and carbon export (Fig S4). However we note that this combined scenario may not be ecologically realistic, as baleen whales populations would be unlikely to undergo sustained increases if krill decline in the long term [53,54].

Our results are broadly consistent with and complimentary to those from other studies that have used different modelling approaches to consider the implications of likely future changes for Southern Ocean food webs and ecosystems (and resulting reconfiguration of energy pathways). Mass-balance food web modelling (i.e. Ecopath [55,56]) has been the most widely-used approach to address these questions, and several previous studies have used mass-balance models to evaluate the likely implications of potential future regional declines in krill biomass (e.g. [51,57–59]). Our scenario for the uncontrolled krill fishery is analogous to these krill decline scenarios, and the resultant negative impacts on krill-specialists is congruent with the results of these studies. In one of these studies, Hill et al. [57] showed that, in the South Georgia region, the negative implications of krill declines for krill-dependent vertebrates may be lessened if they are able to switch prey, which is captured in our model by the uncertain link between krill-dependent predators and fishes and squids. The extent to which krill-dependent predators may be able to shift to alternative prey remains an important question for future trophodynamic and empirical food web studies and monitoring programs.

In another mass-balance modelling study, Ballerini et al. [51] showed that, on the continental shelf in the Antarctic Peninsula region, increased predominance of small phytoplankton led to reduced production of krill, with negative implications for krill-dependent predators. While the negative effect on krill-dependent predators in Ballerini et al. [51] is consistent with our study, a point of difference was that in Ballerini's model, production from small phytoplankton is primarily directed to salps (via microzooplankton) so no benefits of shifting composition of primary producer communities were evident at higher trophic levels. This is because the alternative energy pathway via fish was not considered to be important in this model (and squids were not directly represented). Empirical assessment of regional variation in how much production the squid/fish energy pathway is able to transfer from small phytoplankton to higher trophic levels remains an important goal for future research [7,36,59,60].

3.1. Conclusions

We have shown that Southern Ocean food web structure and change have important policy implications. Our results indicate that uncontrolled fishing, whether for krill or for toothfish, will impact ecosystem services, including climate mitigation through carbon export. We use a simple modelling approach to show that the impacts of single forces of change (our scenarios) are more complex for Southern Ocean ecosystems than commonly believed because of multiple interacting energy pathways and the feedbacks among them. While our analysis removes a lot of food web complexity, a policy-maker can place particular species in our generic representation by considering the types of prey it consumes. If a species eats predominantly krill then it will be a krill predator, relying on the krill energy pathway. If it eats fish then it will be a fish predator in the fish energy pathway. If a species eats mostly krill but switches to fish when krill are in short supply (a prey switcher) then it would be a predator that eats krill and fish, and so on. Even if a particular species is not easily placed in the food web representation we use here, our central conclusion remains the same: we need to know about the food web structure and function in order to successfully manage for the effects of change.

How the system will respond to multiple forces of change is an important and urgent question for guiding management actions in the face of climate change and expanding fisheries. This is because the conservation of Southern Ocean ecosystems, and the maintenance of their resilience and ecosystem services will require actions well in advance of when changes may be detected. Ongoing improvement of quantitative understanding and modelling capability for energy pathways in Southern Ocean food webs will be important to develop robust management responses to climate change impacts and will be a key priority for future research and investment. Strengthening linkages between ecosystem models and observations as well as between science and policy will maximise chances of achieving desirable futures for Southern Ocean food webs and the ecosystem services that they support.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Rowan Trebilco: Conceptualization, Methodology, Visualization, Writing - original draft. **Jess Melbourne-Thomas:** Conceptualization, Methodology, Visualization, Writing - review & editing. **Andrew John Constable:** Conceptualization, Writing - review & editing.

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Appendix A. Supplementary data

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