EXPLORING THE EFFECTS OF CHANGES IN THE FALKLAND ISLANDS MARINE ECOSYSTEM STRUCTURE AND FUNCTIONING

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04/2/2025 VERSION 2

VERSION CONTROL

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Acknowledgements:

DPLUS168 is a collaborative project with the Falkland Islands Fishing Companies Association (FIFCA) and Falkland Islands Government Fisheries Department. It was funded by the UK Government through Darwin Plus scheme.

Citation:

van der Grient, JMA, Riaz, J., Baylis, A.M.M. 2025. Exploring the effects of changes in the Falkland Islands marine ecosystem structure and functioning. Report for the South Atlantic Environmental Research Institute under the DPLUS168 project.

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1. ABSTRACT

This study investigates changes in ecosystem functioning and structure in the Falkland Islands marine food web by comparing current and historical biomass models. Notable differences in biomass pools, energy flows, and trophic dynamics suggest a shift in ecosystem structure, including widespread biomass losses across various trophic levels—such as rock cod, hoki, myctophids, and skates—and biomass increases in species like common hake and small demersal fishes. These changes, alongside reduced food-web connectance and omnivory, may reflect declining ecosystem stability and increasing vulnerability to disturbance. Simulations involving the doubling or halving of key species' biomass, particularly Patagonian squid, revealed strong model sensitivity and potential cascading effects throughout the food web. In contrast, changes in fur seal biomass had limited impact. Doubling or halving fur seal biomass primarily influenced epipelagic fishes and, to a lesser extent, large demersal fishes—effects that were more pronounced in the current model. These results suggest that fur seals may play a relatively minor direct role in structuring the broader food web, and that recent trends in finfish and squid abundance are more likely driven by commercial fishing pressure and environmental variability than by pinniped recovery. Fishery scenarios further emphasized food-web imbalance and underscored the outsized role of fishing in driving ecosystem changes. Uncertainty remains due to data limitations, particularly for poorly studied species and groups, and the use of static dietary matrices. Overall, the study highlights the need for improved population trend data for fur seals and other pinnipeds, along with more comprehensive and temporally resolved dietary information, to refine ecosystem models and support ecosystem-based management in the region.

2. INTRODUCTION

The Falkland Islands, an archipelago located on the eastern part of the Patagonian Shelf in the southwest Atlantic Ocean, harbours a rich biodiverse marine ecosystem, with high biomasses of ecologically and commercially important species (van der Grient et al., 2023).

Upwelling created by the Falkland Current onto the Patagonian Shelf brings nutrients to the surface and stimulates high primary productivity, making the Falkland Islands marine environment one of the most productive areas in the western South Atlantic (Palma et al., 2021; Romero et al., 2006). Indeed, this area supports the largest breeding population of black-browed albatross, southern rockhopper penguins, and South American fur seals (Baylis et al., 2013, 2019; Wolfaardt, 2013). In addition, the waters support numerous fisheries, and the revenue generated by the fisheries operating in the Falklands national waters make up much of the Falkland Islands GDP (Arkhipkin et al., 2021).

The Falkland Islands food web is an example of a wasp-waist food-web, where mobile zooplanktivorous species have top-down effects on zooplankton and other lower trophic levels, and bottom-up effects on higher predators at higher trophic levels. This type of food-web system is often present in upwelling areas (Bakun, 2006). Species that are known or suspected to be wasp-waist species in the Falklands marine environment include the Patagonian squid, southern blue whiting, Patagonian rock cod, Falkland herring, lobster krill and possibly an hyperiid amphipod *Themisto gaudichaudii* (Büring et al., 2024; Laptikhovsky et al., 2013; Padovani et al., 2012; Riccialdelli et al., 2020). However, many components of the Falkland Islands food web are still understudied (van der Grient et al., 2023). As such, it can be difficult to understand if and how species may affect the food web and potentially the marine resources available to the Falkland Islands economy.

The Falkland Islands fisheries target both finfish and squid. Broadly, finish can be separated into a trawl (Finfish fishery) and a longline fishery for Patagonian toothfish (*Dissostichus eleginoides*) (Toothfish fishery). The finfish fishery has seen large changes in their target species, shifting from southern blue whiting (*Micromesistius australis)* to rock cod (*Patagonotothen ramsayi*) to hake (*Merluccius hubbsi*) because of stock collapses (Falkland Islands Government, 2023; Laptikhovsky et al., 2013). There are two Falkland Islands squid fisheries, one that targets the Argentine squid *Illex argentinus* (Illex fishery), and one that targets the two annual cohorts of Patagonian squid *Doryteuthis gahi* (Loligo fishery). The cancellation of the 2024 second Loligo fishing season (second cohort), highlights the recent variability in Loligo biomass, related to environmental variability and possibly changes in predation pressure. The Loligo fishery had historically few seal-fishery interactions, but since 2017 these interactions have increased dramatically (Iriarte et al., 2020). It is possible that the increase in interactions is a consequence of the changes and reductions in finfish community biomasses (Riaz et al., 2024). In addition, the Falkland Islands pinniped populations have increased since historical sealing was stopped (Baylis et al., 2014). In particular, the Falkland Islands are now the largest breeding of South American fur seals in the world (approx. 36,000 pups born annually) and are still increasing.

The change in the finfish community, recovering pinniped populations, and potentially more variable and lower biomass of Loligo can have implications for the food web as a whole, especially as *D. gahi* is a wasp-waist species (Büring et al., 2024). To understand whether the changes in the ecosystem have resulted in changes in the ecosystem functioning and structure, we compare two ecosystem models based on historical and current data. Specifically, by comparing the historical and current models, we interrogate three separate questions:

1. Assuming energy requirements of species in the ecosystem have stayed constant (as measured via vital rates), are there any alterations to ecosystem functioning and structure? We address this by investigating changes in energy flow, ecosystem structure and biomass estimates between the two models via ecosystem properties such as trophic level, energy requirements, omnivory, connectedness, and keystone index. Omnivory is a measure that quantifies the distribution of feeding interactions across the food web; that is, the complexity of the food web. Omnivory interactions can improve the stability of a food web (Libralato, 2013), and changes therein can thus provide an indication of changes in the stability of the food web. Connectedness is a measure of the number of links in a food web, with higher linkages often indicating more stable food webs that are less sensitive to disturbance (Estrada, 2007). Keystone species are species with a structuring role in the food web, even if they have relatively low biomass (Libralato et al., 2006).
2. To understand the sensitivity of the ecosystem to changes in the two focal groups (*D. gahi*, pinnipeds (fur seals, sea lions)) and to changes in fisheries pressure (as measured in catches), we examine two different sets of simulations: (i) if the biomass of *D. gahi* or

the pinnipeds were doubled or halved, how does this affect historical or current model estimates, and (ii) if the fisheries catches were doubled or halved, how does this affect historical or current model estimates?

3. If the biomass data for *D. gahi* was removed, do the historical and current model estimate similar biomasses for this squid?

3. METHODS

Model domain

The model domain is defined by the Falkland Islands national waters (Figure 1), covering an area of approximately 455,500 km^2. Two different models were developed, a historical model that used data from 2001-2005 to initialise the model, and a current model that used data from 2017-2021 to initialise the model. To make the models comparable, the same number of functional groups, the same vital rates (P/B, Q/B), and the same dietary matrix were used to initialise the model.

Ecopath

Ecopath is a widely used ecosystem model framework that represents the food web as functional groups which are based on similarities in diets and behaviours (Christensen and Walters, 2004; Pauly et al., 2000). The groups are described in terms of biomass, consumption and production, and the groups are linked via trophic interactions. Two master equations describe the mass-balanced food web. The first equation describes the production term P_i within each functional group i:

$$P_i = Y_i + M2_i \times B_i + E_i + BA_i + M0_i \times B_i \qquad [1]$$

where Y_i is the total fishery catch of group i, $M2_i$ is the instantaneous predation rate for group i, B_i is the biomass of group i, E_i is the net migration rate (emigration – immigration), BA_i is the biomass accumulation of group i, and $M0_i$ is 'other' mortality which is a catch-all rate that includes all mortality that is not accounted for elsewhere.

Energy balance within each group is ensured as it is required in Ecopath that the consumption of any group is equal or less than its production. The second equation describes the energy balance for each functional group i:

$$Consumption = production + respiration + unassimilated\ food \qquad [2]$$

Advice from Link (2010) and Heymans et al. (2016) were followed in the building and balancing of the EwE model. Ecopath version 6.6.7 was used to create a balanced model.

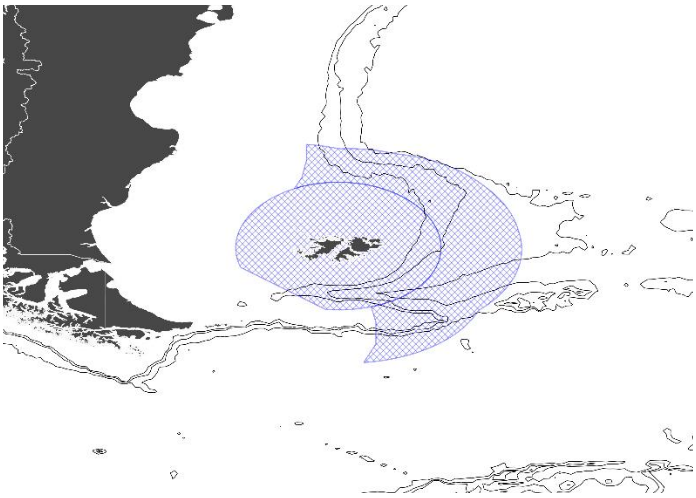

Figure 1. *The Falkland Islands national waters are indicated in blue. Black lines are 600 m depth contour.*

Functional groups

The food webs consisted of 35 single- and multispecies groups. Each model included two detrital (detritus, discards & carrion) and one primary producer (phytoplankton) group. Benthic invertebrates were divided into small and large benthic fauna. Various zooplankton groups were categorized by feeding guilds: grazers/suspension feeders, omnivores/predators, and gelatinous zooplankton. Krill (Euphausiaceae), and lobster krill (*Grimothea gregaria*) were classified separately because of their (suspected) roles in the food web (van der Grient et al., 2023). Several species in the food web are wasp-waist species, including lobster krill (*G. gregaria*), rock cod (predominately *Patagonotothen ramsayi*), southern blue whiting (*Micromesistius australis australis*), and Patagonian longfin squid (*Doryteuthis gahi*). These species were defined separately in the models based on available data. The resident Patagonian squid was defined as two separate groups in each model, because it has two major spawning peaks around the Falkland Islands in the year: an autumn spawning cohort (ASC) and a spring spawning cohort (SSC), and the cohorts are known to differ in their trophic ecology (Büring et al., 2023, 2021). The Argentine shortfin squid (*Illex argentinus*) is another abundant squid in the Falklands waters, but it is a seasonal migrator, and thus it has been defined here separately. Remaining cephalopod species were divided into small (≤40 cm adult mantle length) and large (>40 cm adult mantle length) groups. Several fish groups were defined, either as single- or multispecies group depending on data availability, including small (≤ 35 cm total adult length) and large (>35 cm total adult length) demersal fish, myctophids, deep pelagic fishes, rock cod, southern blue whiting, Patagonian toothfish, hoki, hakes, skates (Rajidae), sharks, and epipelagic fishes. Myctophids were separated from other deep pelagic species because of their potential trophic role in the food web (van der Grient et al., 2023). Hakes are seasonal visitors to the Falkland Islands and separated into two species: common hake (*Merluccius hubbsi*) and southern hake (*M. australis*). The biomass of common hake is two orders of magnitude larger than the biomass of southern hake, hence why they were split, to capture their different roles in the energy flow of the food webs. Apex predators, represented by penguins, birds, cetaceans, and pinnipeds were included. Gentoo penguins (*Pygoscelis papua*) are distinguished from other penguins (southern rockhopper penguins (*Eudyptes chrysocome*) and Magellanic penguins (*Spheniscus magellanicus*)) because of differences in diet and migration patterns. Gentoo penguins reside in the Falkland Islands year-round, whereas other species visit seasonally for breeding. A seabird group was also included to account for the various shorebirds and seabirds found in the Falklands. Two pinniped groups were included, comprised of South American fur seals (*Arctocephalus australis*) and southern sea lions (*Otara flavescens*). Toothed whales and dolphins are assumed to be in the Falklands the whole year via the presence and abundance of dolphins, while baleen whales are seasonal visitors.

Biomasses estimates for the historical model were based on data averaged from 2001-2005, while the current model was based on data averaged from 2017-2021. Note that for those groups for which biomasses were entered, biomass values were not always available for all these data, and in that case, the average was based on fewer years. Note that biomass estimates for birds, pinnipeds and cetaceans are low, as these populations are still recovering from historical exploitation. Stomach analyses reporting prey weight percentages were used as much as possible to create the dietary matrix and estimate prey contributions to predator groups. Studies presenting data as frequency or numerical content of prey helped further identify food web interactions. A general summary of food-web interactions in the Falkland Islands marine environment, and other characteristics, was presented in van der Grient et al. (2023). Data on mid- to higher-trophic level organisms was more readily available than data for lower-trophic level organisms, which were very limited or even absent. The models were used to estimate biomasses of these groups, while dietary information from other regions was used to inform the dietary matrix. The production/biomass ratio (P/B) and consumption/biomass ratio (Q/B) values for the different trophic groups were either obtained from literature, calculated from stock assessments, or taken from previous EwE models from the Falkland Islands or other subantarctic regions (Büring et al., 2024; Cheung and Pitcher, 2005; Dahood et al., 2019; Hill et al., 2012; Pinkerton et al., 2010; Subramaniam et al., 2020).

Catch data

Several species are fished in the Falklands, including Patagonian toothfish; southern blue whiting; hakes; hoki; rock cod (mainly *Patagonotothen ramsayi*); large demersal fish, such as red cod, kingclip, and bigeye grenadier; skates (Rajidae); Patagonian squid; and Argentine squid. The squid catches compromise the majority of fisheries in terms of number of licenses, license fees, and catches in the Falkland Islands (Falkland Islands Government, 2023). Species of commercial interest are targeted under specific fishing licenses, but for simplicity, fisheries are represented as: *Illex* fisheries, *Loligo* fisheries, *finfish* fisheries (which includes large demersal fishes, rock cod, southern blue whiting, Patagonian toothfish caught by trawling, hoki, and hakes), *skates* fisheries, and *toothfish* longline fisheries. Landing data for the species were obtained for the years 2001-2021 and averaged over the years 2001-2005 or 2017-2021 (Falkland Islands Government, 2023). Note that rock cod were not commercially targeted until 2007, although Spain recorded landings for rock cod in 2002 according to the Sea Around Us database (Dunstan et al., 2020; Palomares and Pauly, 2015), which was used to inform the catch data. See Appendix 1 table S1 for information on catch data.

Scenarios

Several scenarios were run to assess the ecosystem functioning and structure of the historical and current Falkland Islands marine food web. Firstly, the models were balanced to characterise the ecosystem functioning and structure, focusing on trophic level, energy requirements, omnivory, connectedness (the number of links in a food web), and keystone index. Secondly, to understand the influence of biomass changes on the ecosystem, the Patagonian squid and pinniped groups had their biomass halved and doubled after which the model results were inspected for change in biomass for other groups. Thirdly, to understand the influence of fishing pressure on the ecosystem, fishing fleet pressures were doubled or halved as following: all fleet (Finfish, Loligo, Skates, Illex, and Toothfish), all squid (Illex and Loligo), Loligo only, and Finfish only. After running the scenarios, model results were inspected for change in biomass for groups for which the model estimates biomass. Lastly, we removed the biomass entries for Patagonian squid in both historical and current models and used the model to estimate their biomasses and assessed the consequences in other biomass pools.

4. RESULTS

Balancing

Both models were not balanced using the initial values, with ecotrophic efficiency (EE) values above 1 for several groups (historical model: rock cod, and both Patagonian squid; historical model: skates, rock cod and Patagonian toothfish).

Historical model

Balance was obtained by making small changes in the dietary composition of groups. The rock cod EE value was lowered below 1 by reducing the predation of small demersal fishes on rock cod and increasing predation of small demersal fishes on small benthic fauna. The Patagonian squid autumn spawning cohort (ASC) EE value was lowered below 1 by reducing the predation of skates on the ASC and increasing skate predation on small demersal fishes. The Patagonian squid spring spawning cohort (SSC) EE value was lowered below 1 by reducing the predation of skates on the SSC and increasing skate predation on small demersal fishes (see Appendix 1 table S2 for final dietary composition). See figure 2 for the balanced food web of the historical model.

Current model

Balance was obtained by making small changes in the dietary composition of groups. The rock cod EE value was lowered below 1 by reducing the predation of skates on rock cod and increased skate predation on small demersal fishes, reducing predation of small demersal fishes on rock cod and increased small demersal fishes predation on small benthic fauna, and reduced common hake predation on rock cod and increased common hake predation on small demersal fishes. The skates EE value was lowered below 1 by reducing large demersal fishes predation on skates and increasing large demersal fishes predation on small demersal fishes. The Patagonian toothfish EE value was lowered below 1 by reducing toothed whale predation on toothfish and increasing toothfish predation on large demersal fishes and reducing predation of hakes on toothfish and increasing hake predation on demersal fishes (see Appendix 1 table S3 for final dietary composition). See figure 3 for the balanced food web of the current model.

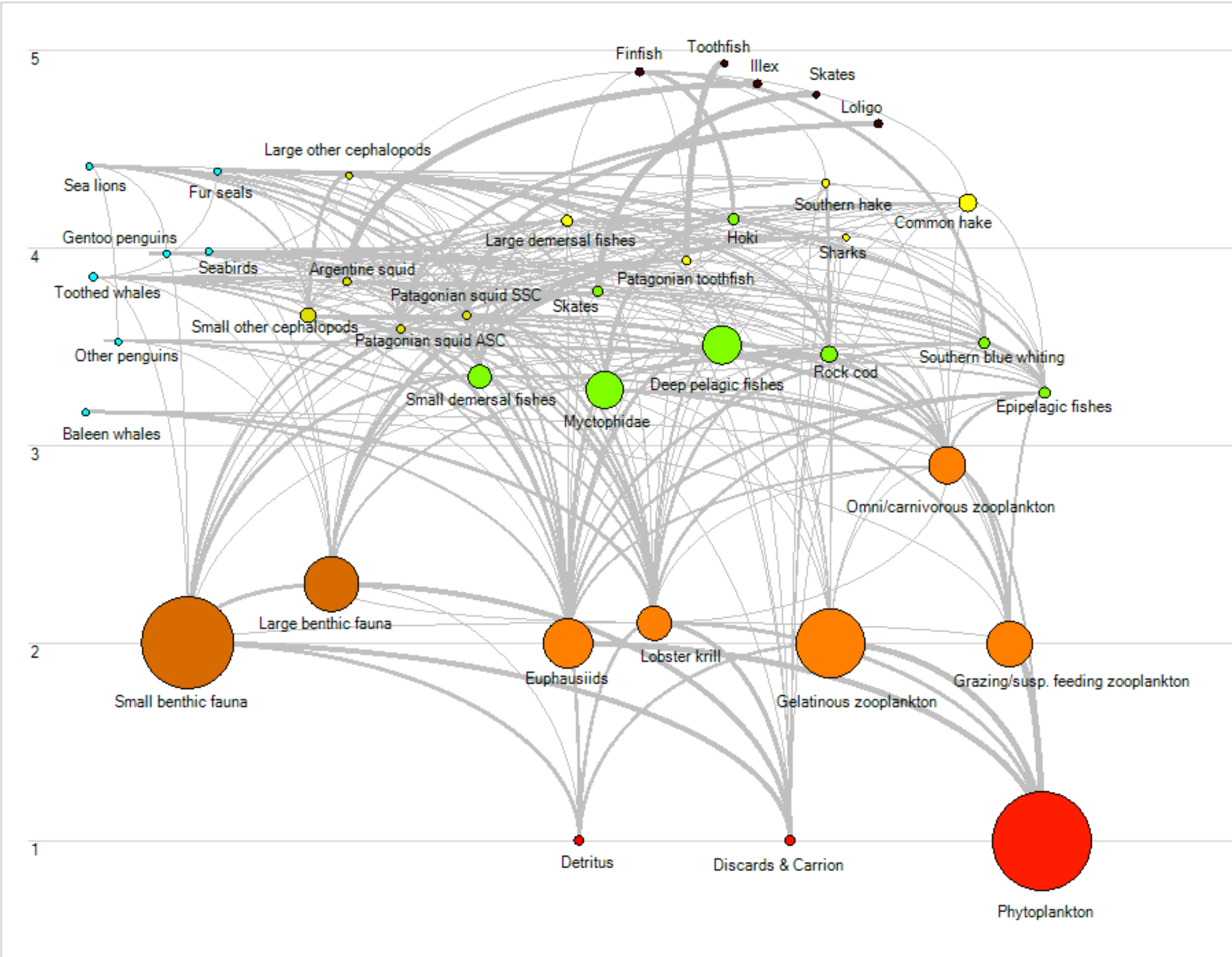

Figure 2. *The balanced historical food web model along tropic levels. The size of the coloured circles (apart from black) indicates relative biomass differences. The fisheries are presented with black circles.*

Question 1: Are there any alterations to ecosystem functioning and structure?

Biomass

Based on the available literature information, several groups are known to have increased in biomass (baleen whales, pinnipeds, penguins, seabirds, southern blue whiting, common hake and Patagonian squid), while others are known to have decreased in biomass (skates, rock cod, Patagonian toothfish, hoki, and southern hake; Table 1). For those groups that have their biomasses estimated by the models, 6 groups were predicted to have increased in biomass, while 8 groups were predicted to have decreased in biomass. The biomass increases were observed for small demersal fishes (Δ1.02 t km^{-2}), small other cephalopods (Δ0.164 t km^{-2}), small benthic fauna (Δ1.487 t km^{-2}), euphausiids (Δ0.158 t km^{-2}), lobster krill (Δ0.176 t km^{-2}) and omnivorous/carnivorous zooplankton (Δ0.036 t km^{-2}). The biomass decreases were observed for large demersal fishes (Δ-0.977 t km^{-2}), myctophids (Δ1.604 t km^{-2}), deep pelagic fishes (Δ-0.615 t km^{-2}), epipelagic fishes (Δ-0.04 t km^{-2}), Argentine squid (Δ-0.018 t km^{-2}), large benthic fauna (Δ-0.273 t km^{-2}), gelatinous zooplankton (Δ-0.444 t km^{-}

^{2}), and grazing zooplankton (Δ-0.117 t km^{-2}). Total biomass (t km^{-2}) of animals was estimated as 314.0396 t km^{-2} in the historical model and 309.4099 t km^{-2} in the current model.

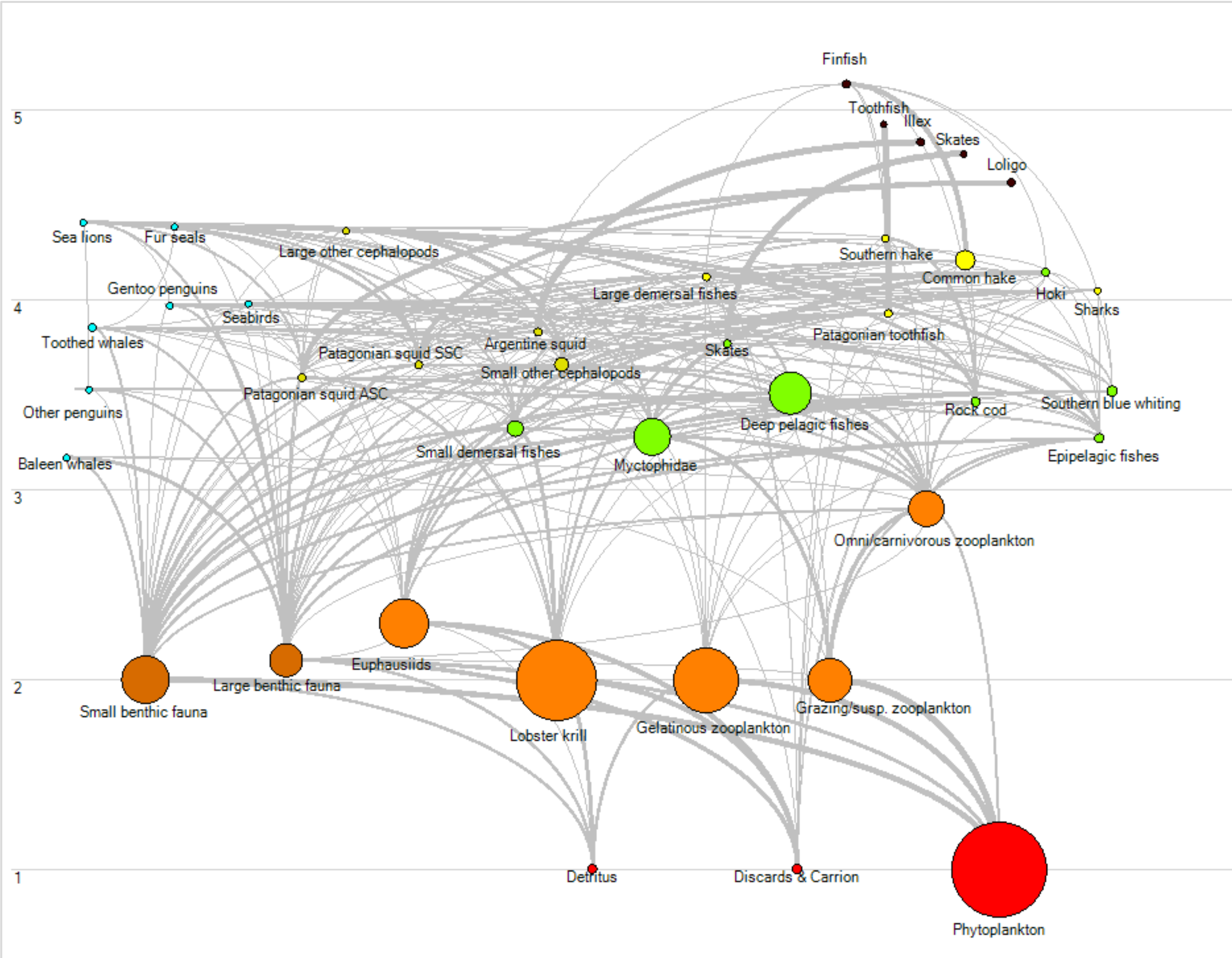

Figure 3. *The balanced current food web model along tropic levels. The size of the coloured circles (apart from black) indicates relative biomass differences. The fisheries are presented with black circles.*

Ecotrophic efficiency

Ecotrophic efficiency values estimated by the models showed changes in 15 groups, with 7 groups showing increases in ecotrophic efficiency and 8 groups showing decreasing in ecotrophic efficiency. Groups that showed increases were myctophids (Δ0.011), deep pelagic fishes (Δ0.024), rock cod (Δ0.028), hoki (Δ0.181), common hake (Δ0.017), small other cephalopods (Δ0.026) and detritus (Δ0.022). The groups that showed decreases were other penguins (Δ-0.048), gentoo penguins (Δ-0.024), skates (Δ-0.027), southern blue whiting (Δ-0.385), Patagonian toothfish (Δ-0.709), and Patagonian squid ASC (Δ-0.723) and SSC (Δ-0.75).

Energy

The energy required in the ecosystems have changed compared to the two models, with the total consumption of the historical model estimated at 9421.21 t km^{-2} year^{-1}, while the current model estimates this consumption at 9449.76 t km^{-2} year^{-1}. The sum of all exports differs between the models, with the historical model estimating it as 4852.842 t km^{-2} year^{-1} and the current model as 3925.106 t km^{-2} year^{-1}. The sum of respiratory flows also differs quite between the two time periods, with the historical model estimating it as 4827.806 t km^{-2} year^{-1} and the current model 5755.343 t km^{-2} year^{-1}. The flow of energy going into the detritus pool changes from 8033.919 t km^{-2} year^{-1} for the historical model to 7135.633 t km^{-2} year^{-1} for the current model. The total system throughput for the historical model was estimated as 27135.770 t km^{-2} year^{-1} and as 27265.84 t km^{-2} year^{-1} for the current model.

Table 1. *Balanced parameter estimates for the historical (2001-2005 averaged) and current (2017-2021 averaged) models. TL = trophic level; B = biomass; P = production; Q = consumption; EE = ecotrophic efficiency. Bolded values are estimated by the models.*

	Historical model					Current model				
Group name	TL	B (t/km^2)	P/B (/year)	Q/B (/year)	EE	TL	B (t/km^2)	P/B (/year)	Q/B (/year)	EE
Baleen whales	3.171	0	0.152	6.298	**0**	3.171	0.01	0.152	6.298	**0**
Toothed whales	3.853	0.02	0.384	8.101	**0**	3.853	0.02	0.384	8.101	**0**
Sea lions	4.416	0.0015	0.177	26.73	**0**	4.409	0.0025	0.177	26.73	**0**
Fur seals	4.391	0.0071	0.177	26.73	**0.001**	4.387	0.0072	0.177	26.73	**0.001**
Other penguins	3.529	0.000057	0.527	46.68	**0.808**	3.529	0.000101	0.527	46.68	**0.76**
Gentoo penguins	3.975	0.000309	0.527	46.68	**0.149**	3.972	0.000614	0.527	46.68	**0.125**
Seabirds	3.988	0.000079	0.33	117.5	**0**	3.982	0.000095	0.33	117.5	**0**
Skates	3.779	0.8	0.3	4.277	**0.931**	3.769	0.095	0.3	4.277	**0.904**
Sharks	4.057	0.003	0.3	7.02	**0**	4.05	0.003	0.3	7.02	**0**
Small demersal fishes	3.354	**6.133**	2.42	9.67	0.4	3.323	**7.153**	2.42	9.67	0.4
Large demersal fishes	4.139	**1.248**	0.873	3.491	0.2	4.122	**0.271**	0.873	3.491	0.2
Myctophidae	3.279	**15.857**	1.755	7.02	**0.724**	3.279	**14.253**	1.755	7.02	**0.735**
Deep pelagic fishes	3.509	**17.685**	0.965	3.862	**0.565**	3.509	**17.07**	0.965	3.862	**0.589**
Rock cod	3.463	3.418	1	2.9	**0.937**	3.46	0.531	1	2.9	**0.965**
Southern blue whiting	3.52	1.337	0.625	2.5	**0.557**	3.519	1.356	0.625	2.5	**0.172**
Patagonian toothfish	3.937	0.35	0.35	1.4	**0.706**	3.928	0.056	0.35	1.4	**0.628**
Hoki	4.146	1.569	0.525	2.1	**0.202**	4.144	0.171	0.525	2.1	**0.383**
Southern hake	4.33	0.0686	0.55	1.7	**0.957**	4.323	0.0424	0.55	1.7	**0.248**
Common hake	4.232	4.485	0.45	1.8	**0.02**	4.206	5.414	0.45	1.8	**0.037**
Epipelagic fishes	3.268	**1.457**	1.454	5.818	0.7	3.268	**1.417**	1.454	5.818	0.7
Argentine squid	3.831	**0.112**	5.764	18.85	0.7	3.831	**0.094**	5.764	18.85	0.7
Patagonian squid ASC	3.597	0.112	13	18.56	**0.975**	3.592	0.33	13	18.56	**0.252**
Patagonian squid SSC	3.661	0.18	8.5	19.14	**0.997**	3.658	0.73	8.5	19.14	**0.247**
Small other cephalopods	3.656	**2.808**	5.764	18.85	**0.8**	3.656	**2.972**	5.764	18.85	**0.826**

Large other cephalopods	4.37	**0.001**	4.605	18.42	0.7	4.366	**0.001**	4.605	18.42	0.7
Small benthic fauna	2	**97.142**	2.8	15.2	0.7	2	**98.629**	2.8	15.2	0.7
Large benthic fauna	2.3	**32.023**	1.5	15.2	0.7	2.3	**31.75**	1.5	15.2	0.7
Gelatinous zooplankton	2	**49.958**	3.8	18.7	0.5	2	**49.514**	3.8	18.7	0.5
Euphausiids	2	**26.158**	11.3	85.6	0.85	2	**26.316**	11.3	85.6	0.85
Lobster krill	2.106	**13.905**	11.3	85.6	**0.85**	2.106	**14.081**	11.3	85.6	**0.85**
Omni/carnivorous zooplankton	2.898	**15.237**	11.3	64.2	**0.851**	2.898	**15.273**	11.3	64.2	**0.851**
Grazing/susp. feeding zooplankton	2	**21.964**	26.1	80.8	0.85	2	**21.847**	26.1	80.8	0.85
Phytoplankton	1	124	78		0.5	1	124	78		0.5
Discards & Carrion	1	1				1	1			
Detritus	1	1			**0.167**	1	1			**0.189**

The energy requirements differ between the two models. The groups that consume 10% or more of the primary productivity are for the historical model: omnivorous/carnivorous zooplankton (32.85%), lobster krill (17.39%), small other cephalopods (15.7%), myctophids (13.37%), euphausiids (12.65%), deep pelagic fishes (12.47%), small demersal fishes (10.55%) and grazing zooplankton (10.02%). The current model shows the groups: omnivorous/carnivorous zooplankton (34.71%), large benthic fauna (18.56%), small other cephalopods (16.99%), small benthic fauna (13.4%), deep pelagic fishes (12.57%), myctophids (12.4%), small demersal fishes (11.83%) and grazing zooplankton (10.5%). That is, in the current model, more benthic groups are consuming more of the primary production compared to the historical model.

Structure

The two ecosystem models differ in their connectance index, with the historical model showing a slightly higher connectance value, at 0.262, compared to the current model, at 0.259. The systems omnivory index has also reduced between the two time periods, from 0.456 estimated in the historical model and 0.362 estimated in the current model.

Based on keystone index averages calculated by the models, the top five keystone species are (in order): sea lions, toothed whales, large demersal fishes, skates and hoki in the historical model, followed by Patagonian squid SSC, lobster krill, small other cephalopods, Patagonian squid ASC, and omnivorous/carnivorous zooplankton. Note that previous work proposed or identified Patagonian squid, southern blue whiting, rock cod, Falkland herring (epipelagic species), a hyperiid amphipod of the carnivorous zooplankton community (*Themisto gaudichaudii*) and lobster krill as wasp waist species. This order changes in the current model, with the top ten as follows: sea lions, toothed whales, large demersal fishes, hoki, skates, large benthic fauna, small other cephalopods, Patagonian squid SSC, omnivorous/carnivorous zooplankton and fur seals. In the top five, the change occurs between hoki and skates, who swap places compared to the historical model, but the bottom five of the top 10 places have changed quite a bit. Three groups are similar, Patagonian squid SSC, small other cephalopods, and omnivorous/carnivorous zooplankton, but at a different rank (the Patagonian squid lowered 2 places, and other small cephalopods and zooplankton both raised one place), while other groups were replaced, resulting in fewer wasp waist candidate species in the top 10 of keystone index in the current model.

The estimated trophic levels for both models show similar patterns, with the highest trophic levels estimated for sea lions and fur seals (sea lion: TL 4.416 and 4.409 for historical and current model, respectively; fur seal: TL 4.391 and 4.387 for historical and current model, respectively), followed by large demersal fishes and hakes. Species or functional groups between TL 3.4 and 3.7 show several species considered wasp-waist species in the Falkland Islands waters, including the Patagonian squid (SSC: TL 3.661 and 3.658 for historical and current model, respectively; ASC: TL 3.597 and 3.592 for historical and current model, respectively), southern blue whiting (TL 3.52 and 3.519 for historical and current model, respectively) and rock cod (TL 3.463 and 3.46 for historical and current model, respectively). Zooplankton and benthic fauna are present in the lower trophic levels. Interestingly, the trophic level estimates for several groups are slightly higher in the historical model compared to the current model. Sea lions, fur seals, gentoo penguins, seabirds, skates, sharks, small and larger demersal fishes, rock cod, southern blue whiting, Patagonian toothfish, hoki, hakes, Patagonian squid and large other cephalopods all a reduction between 0.001-0.031, with an average of 0.0085 change in trophic level. The mean trophic level of species caught in the historical model is 3.795 while in the current model it is estimated at 3.833.

Question 2: How sensitive is the system?

Halving and doubling of squid biomasses

To understand the influence of biomass changes on the ecosystem, the Patagonian squid and pinniped groups had their biomass halved and doubled after which the model results were inspected for change in biomass for other groups. Note that in the scenarios of sea lion and fur seal doubling under both current and historical model conditions, the models were not balanced. Results are still shown.

Changes in biomass ranged from -27% decrease to 54% increases (average: 0.4%; median: -0.002). Groups that showed more than 15% decrease all occurred under current model conditions when Patagonian squid SSC was either halved (epipelagic fishes (-27%), and small demersal fishes (-18%)) or doubled (deep pelagic fishes (-21%) and myctophids (-17%)). Groups that showed more than 15% increase all occurred under current model conditions when either Patagonian squid SSC (epipelagic fishes (54%) and small demersal fishes (36%) or Patagonian squid ASC (small demersal fishes (24%)) were doubled.

Biomass change for current model conditions (regardless of target species group and their biomass change) ranged from -27% to 54% (mean: 0.7%, median: -0.002%), and historical model conditions from -7% to 13% (mean: 0.2%, median: -0.003%). The biomass change for the different groups (regardless of time period) ranged per group as follows: fur seal from -2% to 4% (mean: 0.1%, median -0.002%); sea lion from -4% to 9% (mean: 0.1%, median: -0.002%); Patagonian squid ASC from -12% to 24% (mean: 0.4%, median: 0%); and Patagonian squid SSC from -27% to 54% (mean: 1%, median -0.008%). When biomasses were doubled (regardless of species), biomass changes ranged from -21% to 54% (mean: 2%, median: 0.07%) when doubled or from -27% to 11% (mean: -0.9%, median: -0.05%) when halved.

Within the two different time periods, doubling or halving biomasses of specific species shows large variation in the resulting change in biomasses of other species that the models estimate (Figures 4-7). Generally, the current model conditions give larger changes in biomass than using historical model conditions, and generally doubling biomass result in more frequent positive changes in biomass of more than 1% than halving biomass (i.e., reducing predation pressure by the pinnipeds and squids, but also reducing prey availability in the case of the squid).

Inspecting the effects of doubling or halving Patagonian squid ASC (Figure 4) biomass showed that the largest positive change was felt by small demersal fishes (24% in current model) when the squid biomass was doubled, while the largest negative change was felt by small demersal fishes (-12% in current model) when the squid biomass was halved. A similar pattern was observed for the historical model conditions, but the range was much less (from 9% to -5%). Large positive biomass changes (5% or more) were observed for small demersal fishes, lobster krill, euphausiids (current model conditions, squid biomass doubled), and small demersal fishes (historical model conditions, squid biomass doubled). Large negative biomass changes (-5% or more) were observed for small demersal fishes (current model conditions, squid biomass halved), deep pelagic fishes, myctophids (current model conditions, squid biomass doubled).

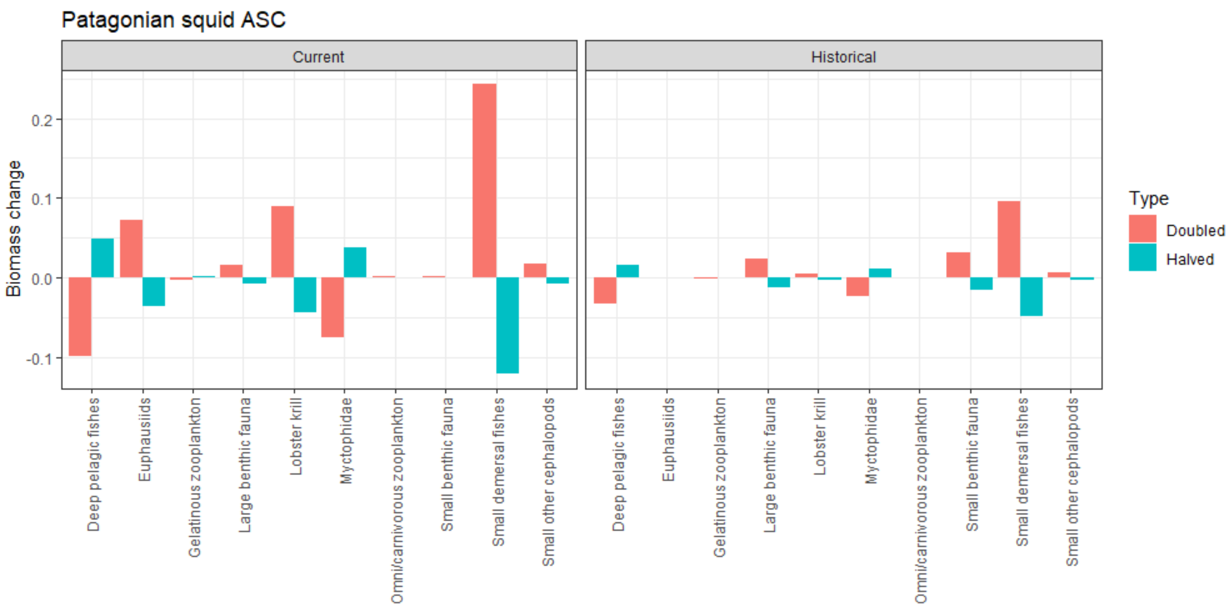

Figure 4. *Biomass change for groups whose biomass was estimated by the model, based on the doubling or halving of Patagonian squid autumn spawning cohort (ASC) biomass under current and historical model conditions.*

Inspecting the effects of doubling or halving Patagonian squid SSC (Figure 5) biomass showed that the largest positive change was felt by epipelagic fishes (54% in current model) when the squid biomass was doubled, while the largest negative change was felt by epipelagic fishes (-27% in current model) when the squid biomass was halved. A similar pattern was observed for the historical model conditions, but the range was much less (from 13% to -7%). Large positive biomass changes (5% or more) were observed for epipelagic fishes, small demersal fishes, lobster krill, euphausiids (current model conditions, squid biomass doubled), epipelagic fishes and small demersal fishes (historical model conditions, squid biomass doubled), and deep pelagic fishes and myctophids (current model conditions, squid biomass halved). Large negative biomass changes (-5% or more) were observed for epipelagic fishes, small demersal fishes, lobster krill, euphausiids (current model conditions, squid biomass halved), deep pelagic fishes, myctophids, (current model conditions, squid biomass doubled), small demersal fishes, epipelagic fishes (historical conditions, squid biomass halved), deep pelagic fishes (historical conditions, squid biomass doubled).

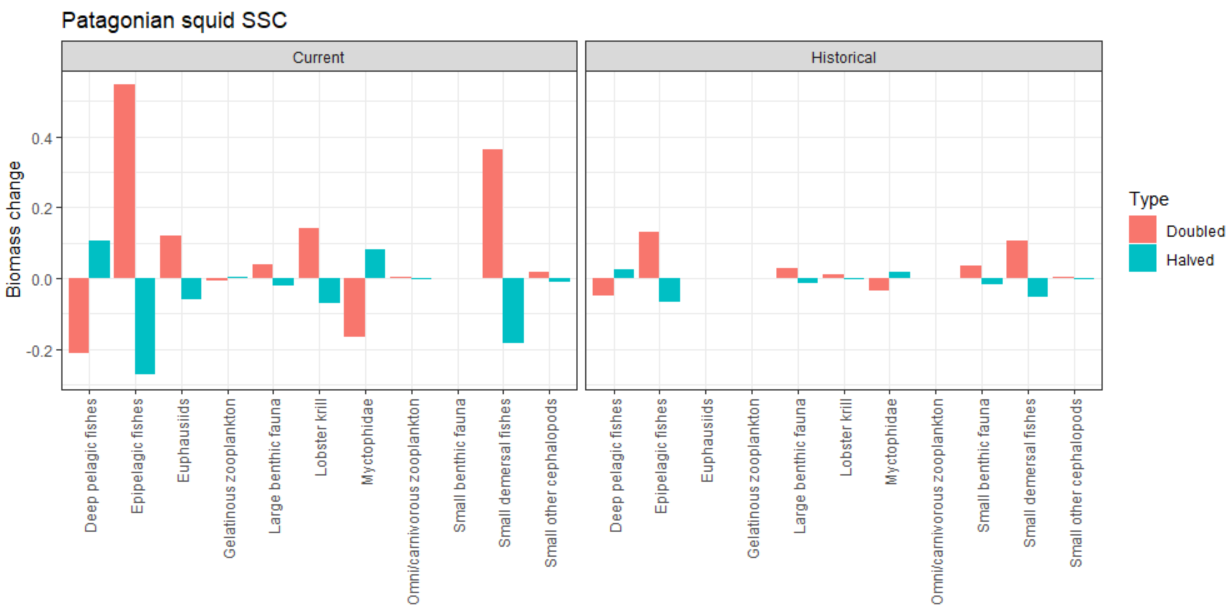

***Figure 5**. Biomass change for groups whose biomass was estimated by the model, based on the doubling or halving of Patagonian squid spring spawning cohort (SSC) biomass under current and historical model conditions.*

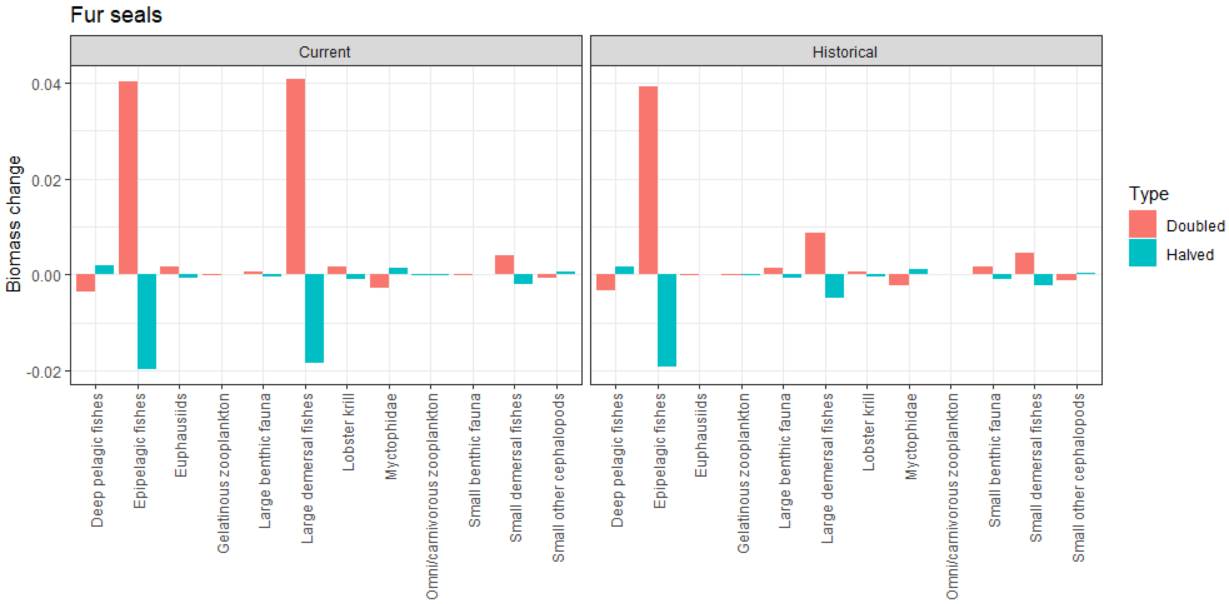

Figure 6. *Biomass change for groups whose biomass was estimated by the model, based on the doubling or halving of fur seal biomass under current and historical model conditions.*

Halving and doubling of pinniped biomasses

Inspecting the effects of doubling or halving fur seal (Figure 6) biomass showed that the largest positive change was felt by large demersal fishes (4% in current model) when the fur seal biomass was doubled, while the largest negative change was felt by epipelagic fishes (-2% in current model) when the fur seal biomass was halved. For the historical model conditions, epipelagic fishes experience the largest (4%) biomass increase when fur seal biomass is doubled, while they also suffer the largest biomass decrease (-2%) when fur seal biomass is halved. No large changes (5% or more, or -5% or more) were observed for fur seal biomass change.

Inspecting the effects of doubling or halving sea lion (Figure 7) biomass showed that the largest positive change was felt by large demersal fishes (9% in current model) when the sea lion biomass was doubled, while the largest negative change was felt by large demersal fishes (-4% in current model) when the sea lion biomass was halved. A similar pattern was observed for the historical model conditions, but the range was much less (from 1% to -1%). Large positive biomass changes (5% or more) were observed for large demersal fishes (current model conditions, sea lion biomass doubled). No large decreases in biomasses (-5% or more) were observed.

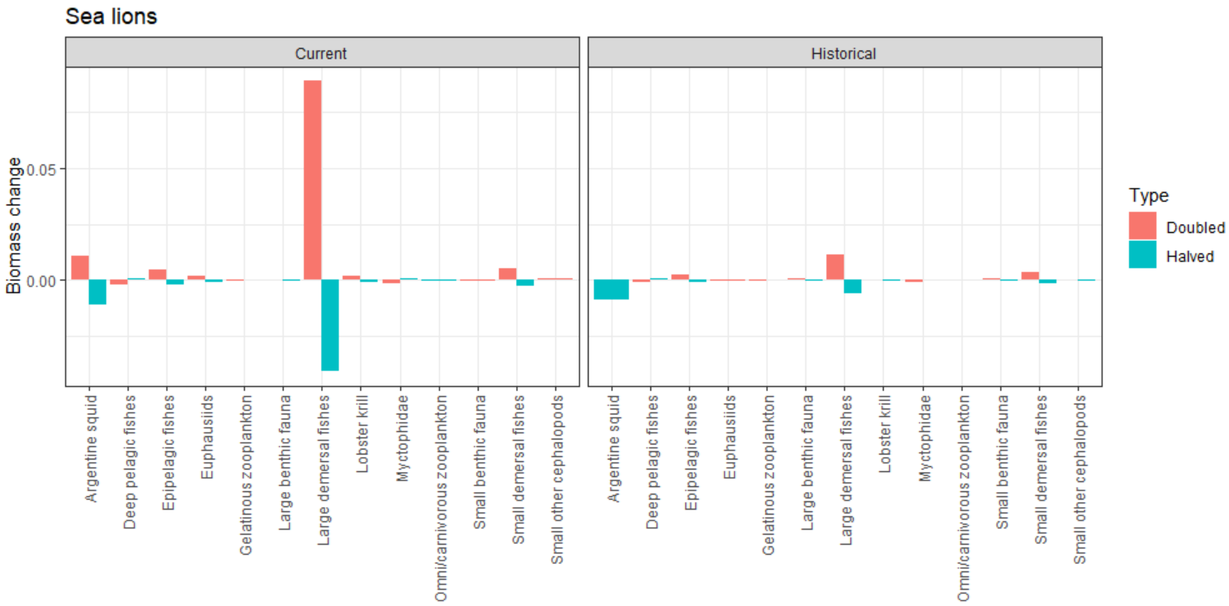

***Figure 7**. Biomass change for groups whose biomass was estimated by the model, based on the doubling or halving of sea lion biomass under current and historical model conditions.*

Halving and doubling fishing pressure

To understand the influence of fishing pressure on the ecosystem, fishing fleet pressures were doubled or halved as following: all fleet (Finfish, Loligo, Skates, Illex, and Toothfish), all squid (Illex and Loligo), Loligo only, and Finfish only. After running the scenarios, model results were inspected for change in biomass for groups for which the model estimates biomass. Note that in the scenarios of All fishing and Finfish fishing pressure doubling under current model conditions, All, Finfish, Squid fishing and Loligo pressure doubling in historical model conditions, the models were not balanced. Results are still shown. Note that the doubling or halving of Loligo under historical model conditions did not result in any change, and therefore it is not included in the analyses below.

Changes in biomass under historical or current model conditions (regardless of fleet doubling or halving) ranged from -80% decrease to 33% increases (average: -3%; median: -8). Groups that increased more than 25% in biomass occurred all for Argentine squid when fishing pressure was doubled either in All or Squid fleets for both historical and current model conditions. Groups that decreased more than 25% in biomass occurred for large demersal fishes when fishing pressure was either halved or doubled for all fleets, and for Argentine squid when All or Squid fishing pressure was halved; all under current model conditions.

Biomass change for current model conditions (regardless of Fleet) ranged from -80% to 30% (mean: -6%, median: -0.5%), and historical model conditions from -17% to 33% (mean: 0.5%, median: -0.004%). The biomass change for when the pressures of the different fleets (regardless of time period) were changed ranged as follows: All from -80% to 33% (mean: -2%, median: 0.004%), Finfish from -80% to 17% (mean: -3%, median: -0.009%), Loligo from -78% to 17% (mean: -6%, median: -0.7%), and Squid from -78% to 30% (mean: -3%, median: -0.005%). When fishing pressures were doubled (regardless of time period or fleet), biomass change ranged from -78% to 33% (mean: -2%, median: 0.009%) and when they were halved ranged from -80% to 17% (mean: -5%, median: -0.1%).

Within the two different time periods, doubling or halving fishing pressures in the different fleets or combinations thereof showed large variation in the resulting change in biomasses of species that the models estimate biomass for (Figures 8-11). Generally, the current model conditions give larger changes in biomass than using historical model conditions.

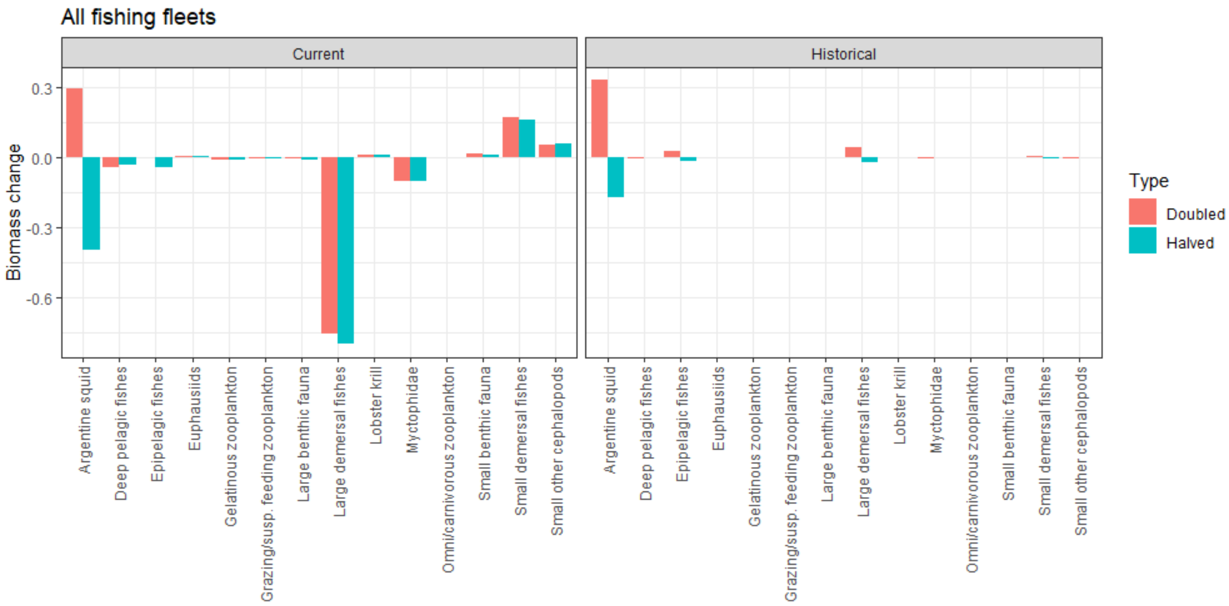

Figure 8. *Biomass change for groups whose biomass was estimated by the model, based on the doubling or halving of All fishing fleets pressures under current and historical model conditions.*

Inspecting the effects of doubling or halving All fishing fleet pressures (Figure 8) showed that the largest positive change was felt by Argentine squid (33% in historical model) when the fishing pressure was doubled, while the largest negative change was felt by large demersal fishes (-80% in current model) when the fishing pressure was halved. Large positive biomass changes (10% or more) were observed for Argentine squid with All fishing pressure was doubled in current and historical model conditions, and for small demersal fishes when fishing pressure was doubled or halved under current model conditions. Large negative biomass changes (-10% or more) were observed for large demersal fishes when fishing pressures were doubled or halved under current model conditions, Argentine squid when fishing pressure was halved under historical and current model conditions, and myctophids when fishing pressure was halved or doubled under current model conditions.

Inspecting the effects of doubling or halving Squid fishing pressure (Figure 9) showed that the largest positive change was felt by Argentine squid (30% in historical model) when the Squid fishing pressure was doubled, while the largest negative change was felt by large demersal fishes (-78% in current model) when the fishing pressure was halved. Large positive biomass changes (10% or more) were observed for Argentine squid when Squid fishing pressure was doubled under both historical and current model conditions, and for small demersal fishes when fishing pressure was halved or doubled. Large negative biomass changes (-10% or more) were observed for large demersal fishes when fishing pressure was halved or doubled under current model conditions, Argentine squid when fishing pressure was halved for historical and current model conditions, and myctophids when fishing pressure was doubled or halved under current conditions.

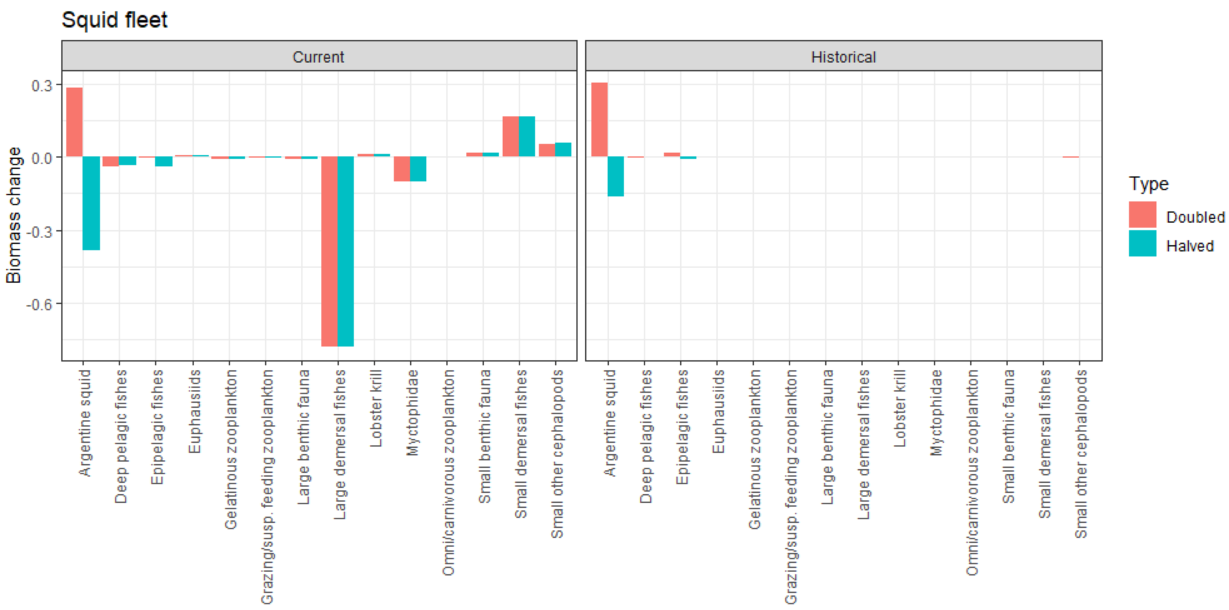

Figure 9. *Biomass change for groups whose biomass was estimated by the model, based on the doubling or halving of all Squid fishing fleets pressures under current and historical model conditions.*

Inspecting the effects of doubling or halving Loligo fishing pressure (Figure 10), which only showed changes under current model conditions, showed that the largest positive change was felt by small demersal fishes (17%) when the Loligo fishing pressure was doubled, while the largest negative change was felt by large demersal fishes (-78%) when the fishing pressure was halved. Large positive biomass changes (10% or more) were observed for small demersal fishes when Loligo fishing pressure was doubled or halved. Large negative biomass changes (-10% or more) were observed for large demersal fishes, Argentine squid, and myctophids when fishing pressure was halved or doubled.

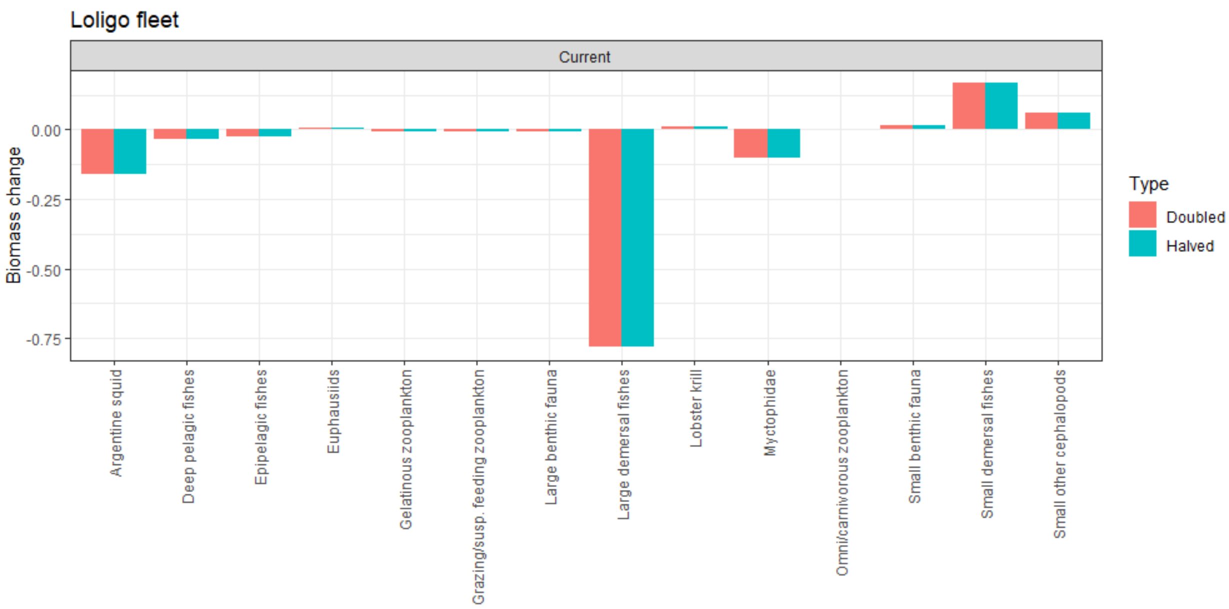

Figure 10. *Biomass change for groups whose biomass was estimated by the model, based on the doubling or halving of Loligo fishing fleets pressures under current model conditions.*

Inspecting the effects of doubling or halving Finfish fishing pressure (Figure 11) showed that the largest positive change was felt by small demersal fishes (17% in current model) when the fishing pressure was doubled, while the largest negative change was felt by large demersal fishes (-80% in current model) when the fishing pressure was halved. Large positive biomass changes (10% or more) were observed for small demersal fishes when Finfish fishing pressure was doubled under current model conditions. Large negative biomass changes (-10% or more) were observed for large demersal fishes, Argentine squid, and myctophids when fishing pressure was halved or doubled under current model conditions.

Question 3: Model estimates of Patagonian squid biomass

When the biomass values entered for the two Patagonian squid cohorts in the historical model are removed (0.112 t km^{-2} for the ASC and 0.18 t km^{-2} for the SSC), the model estimates the squid biomasses as 0.162 t km^{-2} for ASC and 0.273 t km^{-2} for SSC, or in other words, 52% (SSC) and 45% (ASC) more biomass. When the biomass values entered for the two Patagonian squid cohorts in the current model are removed (0.33 t km^{-2} for the ASC and 0.73 t km^{-2} for the SSC), the model estimates the squid biomasses as 0.092 t km^{-2} for

ASC and 0.153 t km^{-2} for SSC, or in other words, -79% (SSC) and -72% (ASC) less biomass. Large positive biomass changes (10% or more) are observed for deep pelagic fishes (24%) and myctophids (19%) under current model conditions (Figure 12). Large negative biomass changes (-10% or more) are observed for small demersal fishes (-46%), epipelagic fishes (-43%), small benthic fauna (-18%) and large benthic fauna (-15%), all under current model conditions (Figure 12).

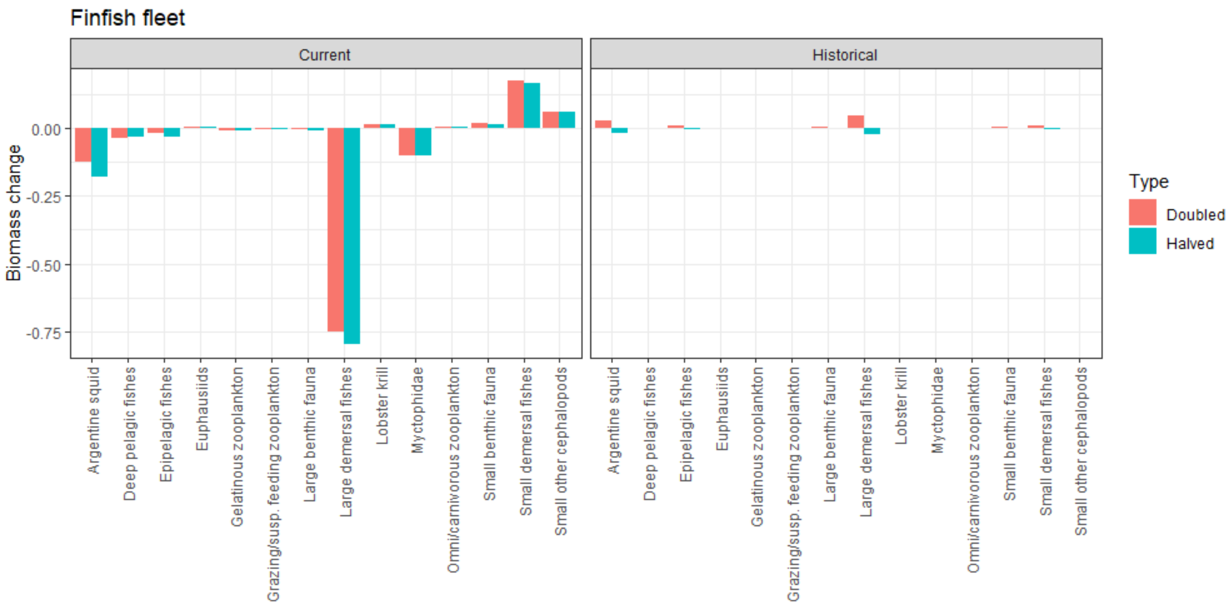

Figure 11. Biomass change for groups whose biomass was estimated by the model, based on the doubling or halving of all Finfish fishing fleets pressures under current and historical model conditions.

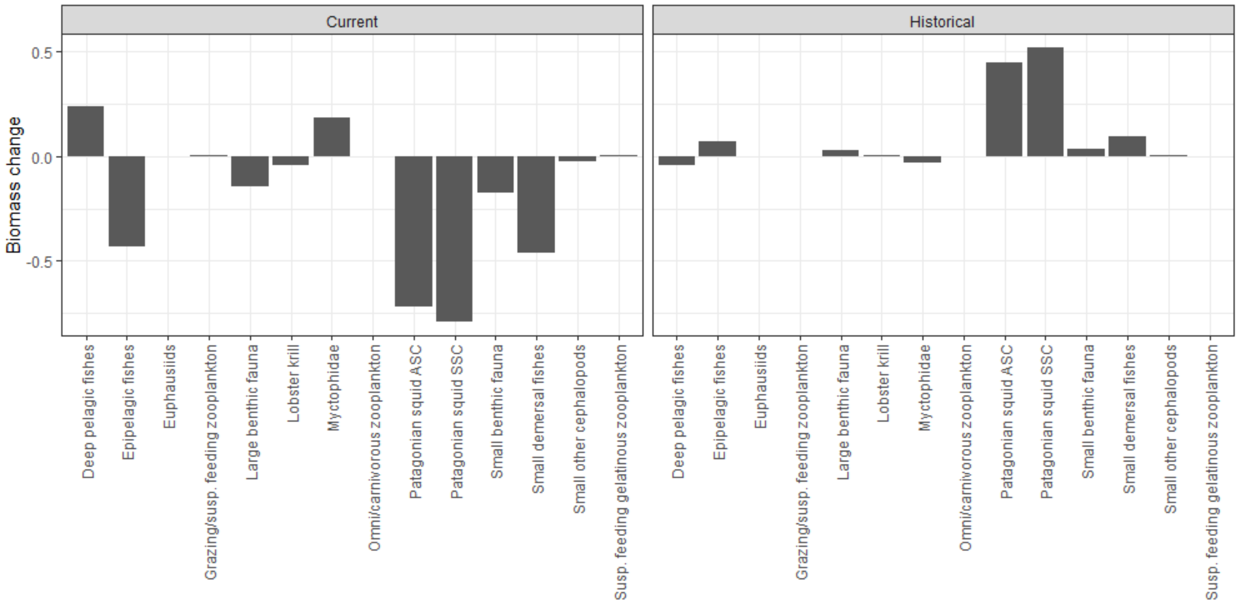

Figure 12. *Biomass change for groups whose biomass was estimated by the model, based on including Patagonian squid ASC and SSC as groups to estimate biomass for under current and historical model conditions.*

5. DISCUSSION

The current and historical models demonstrate differences in ecosystem functioning, highlighted by the differences in specific biomass pools, structural differences, and changes in energy flows. The change in biomass occurs across the food chain with no specific pattern (mean trophic level for groups increasing in biomass = 3.40 ($\pm$ 0.78 standard deviation); mean trophic level for groups decreasing in biomass = 3.38 ($\pm$0.79 standard deviation). The largest loss was registered for rock cod with a loss of 2.887 t km^{-2} (Falkland Islands Government, 2023) and which is a species with a known stock collapse (Laptikhovsky et al., 2013). Another species with a known stock collapse is hoki, which also had a large loss in biomass (1.398 t km^{-2}) (Falkland Islands Government, 2023; Ramos and Winter, 2021). The model predicted a large biomass loss for myctophids (-1.604 t km^{-2}) and deep pelagic fishes (-0.615 t km^{-2}); these groups of species are poorly studied in the Falkland Islands waters (van der Grient et al. 2023). Their roles in the food web are poorly understood, although they frequently appear in stomach analyses as prey items. Two other groups with large biomass losses were large demersal fishes (-0.977 t km^{-2}) and skates (-0.705 t km^{-2}). The biomass of large demersal fishes was estimated by the model; while several large demersal fishes are fished, and therefore have some information on their population biomass, many other species have been poorly studied (van der Grient et al. 2023). It is possible that this group was not well characterized because of the limited data, and thus this change in biomass is uncertain. Likewise, while skate biomass data were obtained from fishery reports (Winter, 2018), these estimates come from a smaller area as this species is not fished everywhere, and the biomass estimates are therefore uncertain. Large biomass increases were predicted for small demersal fishes (1.02 t km^{-2}), and small benthic fauna (1.487 t km^{-2}); two highly aggregated groups with little information on them (van der Grient et al. 2023), making these estimates somewhat uncertain. The largest known increase in biomass comes from common hake (0.929 t km^{-2}), a known increase which has already seen the Falkland Islands finfish fishery focusing on this species (Falkland Islands Government, 2023). The models estimate an overall loss in biomass for the Falkland Islands waters (3.14.0396 (historical) vs 309.4099 (current) t km^{-2}), but based on the discussion above, this may be uncertain whether this difference is indeed this large or perhaps even larger.

It is possible that the energy flows and ecosystem structure are changing in the Falkland Islands marine food web, with more energy being consumed by benthic fauna. Further research is required to confirm whether there is a change in the food web, via for example isotope analyses and stomach analyses (both morphological and via molecular identification for fast-digesting species). The reduction in connectance and omnivory could potentially indicate a change in food-web stability and sensitivity to disturbances (Dunne et al., 2002; Montoya et al., 2006). That is, if connectance is reduced, food-webs become more sensitive to disturbances (Estrada, 2007), may have lower stability (López-López et al., 2022), and could be more prone to secondary extinctions or less resistant to invasions (Dunne et al., 2002). However, it is not known how much loss needs to occur before such patterns become apparent. Omnivory is a measure that quantifies the distribution of feeding interactions across the food web; that is, the complexity of the food web. Omnivory interactions can improve the stability of a food web (Libralato, 2013). Important in this discussion is the strength of the interactions, as weak links improve stability (May, 1972; Van Altena et al., 2016), and this requires further study for the Falkland Islands. The keystone index indicates that several higher-trophic level groups are influential, including sea lions even with their low biomass levels. Interestingly, the number of wasp-waist species in the top ten keystone index is reduced in the current model compared to the historical model, providing another indication that there is a need to study the Falkland Islands food-web and its patterns more thoroughly, to understand if and what this may imply for the marine ecosystem.

The simulations of biomass halving or doubling indicate some large-scale changes, but also emphasize that the food web is still poorly understood. This is indicated by the scenarios that resulted in imbalanced food webs, indicating energy “missing”, the large variability in biomass estimates predicted by the model, and specifically because of similar effects of doubling or halving, for example, the Patagonian squid biomass. That is, the model is sensitive to changes, and the results of these scenarios should be interpreted with caution. Most of the large changes did, however, occur under the current model, again suggesting the change in ecosystem functioning and structure compared to historical conditions.

Largest changes were related to the doubling or halving of Patagonian squid biomass, which is unsurprising given that many species prey on this species.

The doubling or halving of fur seal or sea lion biomass resulted in little change on the food web. Fur seal biomass change appeared to affect mostly epipelagic fishes (in both historical and current models when the biomass is halved or doubled), and potentially positively large demersal fishes in the current model if fur seal biomass was doubled. Sea lion biomass appears to mostly affect large demersal fishes, with the doubling of sea lion biomass resulting in biomass increases in large demersal fishes, while the halving of sea lion biomass resulted in decreases in large demersal fishes (in both models, but with stronger effects in the current model). These changes are likely the result of changes in prey-predator strengths, either directly with the pinnipeds, or indirectly when the pinniped predation results in predation release of other species. For both squid and pinniped biomass changes, the largest changes were observed in the current model, potentially indicating again a change in stability and connectivity.

The fishery scenarios also indicated some large-scale changes, but more so here, many scenarios resulted in unbalanced ecosystems, for both the historical and current model. This again highlighted the food web is not well understood, and cation is required when interpreting the results. Larger changes in biomass under the current model compared to the historical model were also observed when fisheries catches were doubled or halved. Surprisingly, for certain groups (large demersal fishes, small demersal fishes, small other cephalopods, small benthic fauna, deep pelagic fishes, myctophids, zooplankton), the doubling or halving of fishing pressure seemed to have the same effect (but with different absolute values). It is possible that fishing has and has had a large effect on the food web in the Falkland Islands. Note that the models have not incorporated any discard information, while discards can be a food source for various species (list; van der Grient et al. 2023), and this energy link is missing.

Some of the biomass values included in the model are uncertain. The skates, for example, have already been mentioned, but rock cod, pinniped and cetacean biomass, too, have not been as well studied in the past (van der Grient et al., 2023). This increases uncertainty, but to let the models estimate more biomass pools is unlikely to provide more useful information, and there is a limit to how many unknowns can be present in these models. In addition, it is extremely difficult to estimate squid biomass. We ran an experiment of removing the Patagonian squid biomass to determine what the model would estimate for their biomass given the energy constraints and requirements of the rest of the system. The values suggest it is possible that the Patagonian squid biomasses are different from what was entered, but how likely these results are is unclear. Estimating squid population biomasses, for example, use depletion models, whereby information on catchability, natural mortality, number of squid (rather than biomass), and fishing effort are incorporated; different pieces of information that are not incorporated into ecosystem models (Winter, 2023). What is apparent, however, as was the case with the doubling or halving of the Patagonian squid biomasses, is that these changes can have quite an impact on other functional groups. One important point to note is that in the model framework used, the dietary contributions of prey to predators remains consistent. It is possible that, however, prey switching or predation intensity changed between the two time periods. For example, Büring et al. (2021) reported on interannual differences in prey consummation (between the two different spawning cohorts), indicating large changes in, for example, cannibalism and euphausiid consumption. It is likely that other groups also changed, and such changes are currently not incorporated. The dietary matrix was kept similar given the limited available data on prey information, with some data coming from very different time periods or seasons. This likely does not accurately reflect the flexibility a food web may have when biomass pools change and may potentially therefore overestimate negative consequences. A greater study towards seasonal and interannual changes in prey-predator interactions will therefore provide valuable information on the resilience of food web.

In summary, we estimated biomass of key species in the Falkland Islands marine ecosystem. We built several simulations to understand how increases and declines in key species, including fur seals, could impact the Falkland Islands ecosystem. In particular, the doubling and halving of fur seal biomass appeared to have only limited impact on the food web, implying that commercial harvesting, combined with environmental stochasticity, are more likely to be the factors driving trends in finfish and squid abundance, rather than the recovery of fur seals. However, the Falkland Islands food web remains poorly understood, and there are several uncertainties and caveats with the models used. More data on fur seal (and sea lion) population trends over time, combined with more detailed dietary data will help to improve model estimates.

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APPENDIX 1

Table S1. Catch data ($t\ km^{-2}$) for select groups in the historical and current model.

	Historical model					Current model				
Group name	Finfish	Illex	Loligo	Skates	Toothfish	Finfish	Illex	Loligo	Skates	Toothfish
Skates				0.00988					0.00424	
Large demersal fishes	0.00964					0.00682				
Rock cod	1.00E-09					0.00339				
Southern blue whiting	0.0444					0.00174				
Patagonian toothfish	0.00329				0.000635	0.00225				0.00058
Hoki	0.0496					0.0112				
Southern hake	0.000075					0.00146				
Common hake	0.00444					0.0859				
Argentine squid	0.00306	0.119				0.00786	0.168			
Patagonian squid ASC			0.0432					0.101		
Patagonian squid SSC			0.0492					0.0672		

Table S2. Dietary matrix used in the balanced historical model.

	Prey \ predator	1	2	3	4	5	6	7
1	Baleen whales							
2	Toothed whales							
3	Sea lions							
4	Fur seals		0.000011					
5	Other penguins			0.000605				
6	Gentoo penguins			0.000605				
7	Seabirds							
8	Skates							
9	Sharks							
10	Small demersal fishes		0.0528	0.121	0.05		0.0412	0.0564
11	Large demersal fishes		0.0205	0.0605	0.01			
12	Myctophidae		0.0463		0.03			0.00638
13	Deep pelagic fishes		0.0614					0.00638
14	Rock cod				0.3		0.0515	0.0128
15	Southern blue whiting				0.01		0.0103	0.0106
16	Patagonian toothfish		0.0108					
17	Hoki				0.01		0.0103	
18	Southern hake				0.002			0.00638
19	Common hake				0.002			0.00638
20	Epipelagic fishes		0.148		0.285	0.153	0.229	0.0617
21	Argentine squid		0.0366	0.00605	0.001		0.0103	0.00638
22	Patagonian squid ASC		0.0528	0.179	0.074		0.0825	0.0574
23	Patagonian squid SSC		0.0528	0.305	0.126		0.0825	0.0574
24	Small other cephalopods		0.0429	0.182	0.05		0.101	0.0314
25	Large other cephalopods		0.014					
26	Small benthic fauna		0.086				0.0619	
27	Large benthic fauna		0.0538			0.112	0.0619	0.00638
28	Susp. feeding gelatinous zooplankton							
29	Euphausiids	0.172	0.151			0.0817	0.0928	0.05
30	Lobster krill	0.293	0.171	0.145	0.05	0.122	0.134	0.0489
31	Omni/carnivorous zooplankton	0.0869				0.0204	0.0309	0.00638
32	Grazing/susp. feeding zooplankton	0.0856						
33	Phytoplankton							
34	Discards & Carrion							0.0372
35	Detritus							
	Import	0.362	0	0	0	0.511	0	0.532

Table S2. Continued.

	Prey \ predator	8	9	10	11	12	13	14

1	Baleen whales							
2	Toothed whales							
3	Sea lions							
4	Fur seals							
5	Other penguins							
6	Gentoo penguins							
7	Seabirds							
8	Skates		0.0104		0.046			
9	Sharks							
10	Small demersal fishes	0.147	0.156	0.044	0.131			0.104
11	Large demersal fishes	0.0436	0.0521					
12	Myctophidae						0.154	0.0462
13	Deep pelagic fishes					0.026		
14	Rock cod	0.0882	0.0833	0.02	0.118			
15	Southern blue whiting	0.0109			0.037			
16	Patagonian toothfish	0.0109			0.01			
17	Hoki	0.0109	0.0521		0.013			
18	Southern hake							
19	Common hake							
20	Epipelagic fishes		0.0625		0.069			0.0462
21	Argentine squid		0.0104		0.04			
22	Patagonian squid ASC	0.04	0.0833		0.12			0.0116
23	Patagonian squid SSC	0.035	0.0833		0.12			0.0116
24	Small other cephalopods	0.0545	0.0521	0.0549	0.028	0.039		0.0231
25	Large other cephalopods							
26	Small benthic fauna	0.185	0.0833	0.301	0.025			0.0578
27	Large benthic fauna	0.166	0.125	0.12	0.042			0.127
28	Susp. feeding gelatinous zooplankton		0.0104	0.044	0.05	0.0648	0.0641	0.052
29	Euphausiids	0.0109	0.0313	0.176	0.017	0.325	0.321	0.104
30	Lobster krill	0.0664	0.0833	0.0988	0.065		0.128	0.22
31	Omni/carnivorous zooplankton	0.0545		0.142	0.03	0.195	0.333	0.139
32	Grazing/susp. feeding zooplankton	0.0545				0.351		
33	Phytoplankton							
34	Discards & Carrion	0.0218	0.0208		0.04			0.0578
35	Detritus							
	Import	0	0	0	0	0	0	0

Table S2. Continued.

	Prey \ predator	15	16	17	18	19	20	21
1	Baleen whales							
2	Toothed whales							
3	Sea lions							

4	Fur seals							
5	Other penguins							
6	Gentoo penguins							
7	Seabirds							
8	Skates		0.03					
9	Sharks							
10	Small demersal fishes	0.0226	0.24	0.0215	0.066	0.0315		
11	Large demersal fishes		0.03	0.0108				
12	Myctophidae	0.147		0.484		0.0354		0.0765
13	Deep pelagic fishes							0.0539
14	Rock cod	0.0057	0.07	0.0859	0.236	0.0962		
15	Southern blue whiting	0.0226	0.06	0.0323				0.00539
16	Patagonian toothfish							
17	Hoki		0.04					
18	Southern hake			0.0108				
19	Common hake			0.0108				
20	Epipelagic fishes			0.0215		0.0368		0.0372
21	Argentine squid					0.0113		0.0269
22	Patagonian squid ASC		0.055	0.0161	0.058	0.0453		0.00054
23	Patagonian squid SSC		0.055	0.0161	0.058	0.0453		0.0108
24	Small other cephalopods		0.01	0.0967		0.0543		0.0582
25	Large other cephalopods							
26	Small benthic fauna		0.13					
27	Large benthic fauna		0.23		0.011	0.0113		
28	Susp. feeding gelatinous zooplankton						0.0667	
29	Euphausiids	0.226		0.0859		0.0147	0.267	0.0787
30	Lobster krill			0.108		0.0113	0.267	0.0781
31	Omni/carnivorous zooplankton	0.0113			0.026	0.0199	0.267	0.035
32	Grazing/susp. feeding zooplankton						0.133	
33	Phytoplankton							
34	Discards & Carrion		0.05		0.02	0.0209		
35	Detritus							
	Import	0.565	0	0	0.526	0.566	0	0.539

Table S2. Continued

	Prey \ predator	22	23	24	25	26	27	28
1	Baleen whales							
2	Toothed whales							
3	Sea lions							
4	Fur seals							
5	Other penguins							
6	Gentoo penguins							

7	Seabirds							
8	Skates							
9	Sharks							
10	Small demersal fishes	0.154	0.101		0.09			
11	Large demersal fishes							
12	Myctophidae			0.125	0.138			
13	Deep pelagic fishes			0.125	0.159			
14	Rock cod							
15	Southern blue whiting							
16	Patagonian toothfish							
17	Hoki							
18	Southern hake							
19	Common hake							
20	Epipelagic fishes		0.0562					
21	Argentine squid							
22	Patagonian squid ASC	0.0549			0.068			
23	Patagonian squid SSC		0.0562		0.068			
24	Small other cephalopods	0.0988	0.112	0.0625	0.3			
25	Large other cephalopods				0.039			
26	Small benthic fauna	0.22	0.112				0.3	
27	Large benthic fauna							
28	Susp. feeding gelatinous zooplankton				0.01			
29	Euphausiids	0.165	0.18	0.35	0.076			
30	Lobster krill	0.176	0.213	0.125	0.021			
31	Omni/carnivorous zooplankton	0.132	0.169	0.213	0.021			
32	Grazing/susp. feeding zooplankton				0.01			
33	Phytoplankton							0.8
34	Discards & Carrion					0.7	0.66	
35	Detritus					0.3	0.04	0.2
	Import	0	0	0	0	0	0	0

Table S2. Continued.

	Prey \ predator	29	30	31	32
1	Baleen whales				
2	Toothed whales				
3	Sea lions				
4	Fur seals				
5	Other penguins				
6	Gentoo penguins				
7	Seabirds				
8	Skates				
9	Sharks				

10	Small demersal fishes				
11	Large demersal fishes				
12	Myctophidae				
13	Deep pelagic fishes				
14	Rock cod				
15	Southern blue whiting				
16	Patagonian toothfish				
17	Hoki				
18	Southern hake				
19	Common hake				
20	Epipelagic fishes				
21	Argentine squid				
22	Patagonian squid ASC				
23	Patagonian squid SSC				
24	Small other cephalopods				
25	Large other cephalopods				
26	Small benthic fauna		0.0204		
27	Large benthic fauna		0.0204		
28	Susp. feeding gelatinous zooplankton			0.0812	
29	Euphausiids			0.162	
30	Lobster krill			0.108	
31	Omni/carnivorous zooplankton		0.0204	0.0541	
32	Grazing/susp. feeding zooplankton		0.0204	0.432	
33	Phytoplankton	0.8	0.306	0.162	1
34	Discards & Carrion		0.408		
35	Detritus	0.2	0.204		
	Import	0	0	0	0

Table S3. Dietary matrix used in the balanced current model.

	Prey \ predator	1	2	3	4	5	6	7
1	Baleen whales							
2	Toothed whales							
3	Sea lions							
4	Fur seals		0.000011					
5	Other penguins			0.000605				
6	Gentoo penguin			0.000605				
7	Seabirds							
8	Skates							
9	Sharks							
10	Small demersal fish		0.0528	0.121	0.05		0.0412	0.0564
11	Large demersal fish		0.0315	0.0605	0.01			
12	Myctophidae		0.0463		0.03			0.00638

13	Deep pelagic fishes		0.0614					0.00638
14	Rock cod				0.3		0.0515	0.0128
15	Southern blue whiting				0.01		0.0103	0.0106
16	Patagonian toothfish							
17	Hoki				0.01		0.0103	
18	Southern hake				0.002			0.00638
19	Common hake				0.002			0.00638
20	Epipelagic fish		0.148		0.285	0.153	0.229	0.0617
21	Argentine squid		0.0366	0.00605	0.001		0.0103	0.00638
22	Patagonian squid ASC		0.0528	0.179	0.074		0.0825	0.0574
23	Patagonian squid SSC		0.0528	0.305	0.126		0.0825	0.0574
24	Small other cephalopods		0.0429	0.182	0.05		0.101	0.0314
25	Large other cephalopods		0.014					
26	Lobster krill		0.086				0.0619	
27	Euphausiids		0.0538			0.112	0.0619	0.00638
28	Susp. gelatinous zooplankton							
29	Small benthic fauna	0.172	0.151			0.0817	0.0928	0.05
30	Large benthic fauna	0.293	0.171	0.145	0.05	0.122	0.134	0.0489
31	Omni/carnivorous zooplankton	0.0869				0.0204	0.0309	0.00638
32	Grazing/susp. zooplankton	0.0856						
33	Phytoplankton							
34	Discards & Carrion							0.0372
35	Detritus							
	Import	0.362	0	0	0	0.511	0	0.532

Table S3. Continued.

	Prey \ predator	8	9	10	11	12	13	14
1	Baleen whales							
2	Toothed whales							
3	Sea lions							
4	Fur seals							
5	Other penguins							
6	Gentoo penguin							
7	Seabirds							
8	Skates		0.0104		0.02			
9	Sharks							
10	Small demersal fish	0.185	0.156	0.044	0.157			0.104
11	Large demersal fish	0.0546	0.0521					
12	Myctophidae						0.154	0.0462
13	Deep pelagic fishes					0.026		
14	Rock cod	0.05	0.0833		0.118			

15	Southern blue whiting	0.0109			0.037			
16	Patagonian toothfish				0.01			
17	Hoki	0.0109	0.0521		0.013			
18	Southern hake							
19	Common hake							
20	Epipelagic fish		0.0625		0.069			0.0462
21	Argentine squid		0.0104		0.04			
22	Patagonian squid ASC	0.04	0.0833		0.12			0.0116
23	Patagonian squid SSC	0.035	0.0833		0.12			0.0116
24	Small other cephalopods	0.0545	0.0521	0.0549	0.028	0.039		0.0231
25	Large other cephalopods							
26	Lobster krill	0.185	0.0833	0.301	0.025			0.0578
27	Euphausiids	0.166	0.125	0.12	0.042			0.127
28	Susp. gelatinous zooplankton		0.0104	0.044	0.05	0.0648	0.0641	0.052
29	Small benthic fauna	0.0109	0.0313	0.196	0.017	0.325	0.321	0.104
30	Large benthic fauna	0.0664	0.0833	0.0988	0.065		0.128	0.22
31	Omni/carnivorous zooplankton	0.0545		0.142	0.03	0.195	0.333	0.139
32	Grazing/susp. zooplankton	0.0545				0.351		
33	Phytoplankton							
34	Discards & Carrion	0.0218	0.0208		0.04			0.0578
35	Detritus							
	Import	0	0	0	0	0	0	0

Table S3. Continued.

	Prey \ predator	15	16	17	18	19	20	21
1	Baleen whales							
2	Toothed whales							
3	Sea lions							
4	Fur seals							
5	Other penguins							
6	Gentoo penguin							
7	Seabirds							
8	Skates		0.03					
9	Sharks							
10	Small demersal fish	0.0226	0.24	0.0215	0.066	0.103		
11	Large demersal fish		0.03	0.0108				
12	Myctophidae	0.147		0.484		0.0354		0.0765
13	Deep pelagic fishes							0.0539
14	Rock cod	0.0057	0.07	0.0859	0.236	0.025		
15	Southern blue whiting	0.0226	0.06	0.0323				0.00539
16	Patagonian toothfish							
17	Hoki		0.04					

18	Southern hake			0.0108				
19	Common hake			0.0108				
20	Epipelagic fish			0.0215		0.0368		0.0372
21	Argentine squid					0.0113		0.0269
22	Patagonian squid ASC		0.055	0.0161	0.058	0.0453		0.00054
23	Patagonian squid SSC		0.055	0.0161	0.058	0.0453		0.0108
24	Small other cephalopods		0.01	0.0967		0.0543		0.0582
25	Large other cephalopods							
26	Lobster krill		0.13					
27	Euphausiids		0.23		0.011	0.0113		
28	Susp. gelatinous zooplankton						0.0667	
29	Small benthic fauna	0.226		0.0859		0.0147	0.267	0.0787
30	Large benthic fauna			0.108		0.0113	0.267	0.0781
31	Omni/carnivorous zooplankton	0.0113			0.026	0.0199	0.267	0.035
32	Grazing/susp. zooplankton						0.133	
33	Phytoplankton							
34	Discards & Carrion		0.05		0.02	0.0209		
35	Detritus							
	Import	0.565	0	0	0.526	0.566	0	0.539

Table S3. Continued.

	Prey \ predator	22	23	24	25	26	27	28
1	Baleen whales							
2	Toothed whales							
3	Sea lions							
4	Fur seals							
5	Other penguins							
6	Gentoo penguin							
7	Seabirds							
8	Skates							
9	Sharks							
10	Small demersal fish	0.154	0.101		0.09			
11	Large demersal fish							
12	Myctophidae			0.125	0.138			
13	Deep pelagic fishes			0.125	0.159			
14	Rock cod							
15	Southern blue whiting							
16	Patagonian toothfish							
17	Hoki							
18	Southern hake							
19	Common hake							
20	Epipelagic fish		0.0562					

21	Argentine squid							
22	Patagonian squid ASC	0.0549			0.068			
23	Patagonian squid SSC		0.0562		0.068			
24	Small other cephalopods	0.0988	0.112	0.0625	0.3			
25	Large other cephalopods				0.039			
26	Lobster krill	0.22	0.112				0.3	
27	Euphausiids							
28	Susp. gelatinous zooplankton				0.01			
29	Small benthic fauna	0.165	0.18	0.35	0.076			
30	Large benthic fauna	0.176	0.213	0.125	0.021			
31	Omni/carnivorous zooplankton	0.132	0.169	0.213	0.021			
32	Grazing/susp. zooplankton				0.01			
33	Phytoplankton							0.8
34	Discards & Carrion					0.7	0.66	
35	Detritus					0.3	0.04	0.2
	Import	0	0	0	0	0	0	0

Table S3. Continued.

	Prey \ predator	29	30	31	32
1	Baleen whales				
2	Toothed whales				
3	Sea lions				
4	Fur seals				
5	Other penguins				
6	Gentoo penguin				
7	Seabirds				
8	Skates				
9	Sharks				
10	Small demersal fish				
11	Large demersal fish				
12	Myctophidae				
13	Deep pelagic fishes				
14	Rock cod				
15	Southern blue whiting				
16	Patagonian toothfish				
17	Hoki				
18	Southern hake				
19	Common hake				
20	Epipelagic fish				
21	Argentine squid				
22	Patagonian squid ASC				
23	Patagonian squid SSC				

24	Small other cephalopods				
25	Large other cephalopods				
26	Lobster krill		0.0204		
27	Euphausiids		0.0204		
28	Susp. gelatinous zooplankton			0.0812	
29	Small benthic fauna			0.162	
30	Large benthic fauna			0.108	
31	Omni/carnivorous zooplankton		0.0204	0.0541	
32	Grazing/susp. zooplankton		0.0204	0.432	
33	Phytoplankton	0.8	0.306	0.162	1
34	Discards & Carrion		0.408		
35	Detritus	0.2	0.204		
	Import	0	0	0	0

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