

A mass-balanced ecosystem model for the Kerguelen Plateau

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Abstract

Ecosystem models are useful tools for making informed management decisions regarding the potential effects of environmental change and fishing activity on Southern Ocean ecosystems. Recent work has successfully updated an existing Ecopath model for the Kerguelen exclusive economic zone from an unbalanced to a balanced model state (where energy inputs equal outputs). This balanced model details food-web dynamics in the Kerguelen Island region using species biomass and diet information. In this paper we present this balanced model as well as an evaluation of food-web structure and function using tools found in Ecopath. Energy flows in the model suggest that the Kerguelen Island food web is smaller and more mature than other sub-Antarctic food webs and the impacts of direct and indirect interactions on functional groups highlighted the importance of cephalopods in the food web. This model is currently undergoing an expansion to include the entire northern region of the Kerguelen Plateau.

Modèle d'équilibre de masse de l'écosystème du plateau de Kerguelen

Résumé

Les modèles écosystémiques sont des outils utiles pour prendre des décisions éclairées en matière de gestion des effets potentiels des changements environnementaux et de l'activité de pêche sur les écosystèmes de l'océan Austral. De récents travaux ont permis d'actualiser un modèle Ecopath existant de la zone économique exclusive de Kerguelen en l'amenant à l'état d'équilibre (c.-à-d. que les flux énergétiques entrant sont égaux aux flux énergétiques sortant). Ce modèle équilibré décrit la dynamique du réseau trophique de la région des îles Kerguelen à partir d'informations sur la biomasse et le régime alimentaire des espèces. Dans cet article, nous présentons ce modèle équilibré, ainsi qu'une évaluation de la structure et de la fonction du réseau trophique effectuée grâce aux outils d'Ecopath. Les flux d'énergie dans le modèle semblent indiquer que le réseau trophique des îles Kerguelen est plus simple et plus mature que les autres réseaux trophiques subantarctiques. D'autre part, les impacts des interactions directes et indirectes sur les groupes fonctionnels ont souligné l'importance des céphalopodes dans le réseau trophique. Un élargissement du modèle à l'ensemble de la région nord du plateau de Kerguelen est par ailleurs en cours.

Keywords: Kerguelen Plateau, Ecopath, ecosystem model, food web, fishing

Introduction

The ability to make predictions about the effects of environmental change, shifts in productivity and fishing on marine ecosystems requires an understanding of food-web dynamics. This in turn relies on ecosystem models as a tool to evaluate food-web structure and function. The ecosystem on the Kerguelen Plateau supports valuable French and Australian fisheries that target Patagonian toothfish (*Dissostichus eleginoides*) and mackerel icefish (*Champsocephalus gunnari*). The fishery interacts with the food web through the removal of target species, by-catch, and by providing an easy food source for apex predators (Guinet et al., 2015). The Kerguelen Plateau is a breeding ground for flying seabirds, penguins and seals, all of which consume large quantities of fish and squid as part of their diet. Despite the high occurrence of biological activity on the plateau, food-web dynamics are still poorly understood.

Ecopath with Ecosim is a widely used software platform for developing ecosystem models (Christensen and Walters, 2004). This study is confined to the Ecopath module of Ecopath with Ecosim. Ecopath provides a static view of the food web averaged over a known time period. Ecopath uses 4 parameters to describe species in the ecosystem: biomass (B), consumption/biomass (Q/B), production/biomass (P/B), and ecotrophic efficiency (EE). The model is balanced by adjusting parameters (biomass, consumption/biomass, production/biomass) until the EE of each group (the proportion of production that is used within the system) is less than one. Note that detritus groups do not require any additional parameters except for biomass. The EEs for detritus groups are defined as the ratio between flows into and out of the group. Under steady-state assumption, this ratio should be equal to 1 (Christensen and Walters, 2004). Full details on balancing Ecopath models can be found in Christensen and Walters (2004).

Pruvost et al. (2005) presented a preliminary Ecopath model to describe food-web dynamics on the Kerguelen exclusive economic zone (EEZ), however, the energy inputs and outputs of the model were unbalanced. Balancing the energy in an Ecopath (or Ecopath with Ecosim) model is crucial to obtaining interpretable estimates of energy flow in the food web.

This study presents a balanced version of that model and a basic evaluation of model parameters. We aimed to provide a balanced version of the model that is as close as possible to the original model and therefore have not included fisheries data. Our balanced model represents the mean state of the ecosystem in the absence of fishing. This model domain is currently being extended to include the entire northern region of the Kerguelen Plateau.

Methods

Ecopath model parameters were taken from Table 19 in Pruvost et al. (2005) and modified prior to balancing. Patagonian toothfish were split into two separate functional groups based on the segregation seen in the water column. We have maintained this separation in our model, one group represented juvenile toothfish and the other represented adult toothfish. Following Pruvost et al. (2005), we have also opted not to use the multistanza option for entering juvenile and adult groups of the same species to reproduce the model as closely as possible to the original.

Names of some functional groups were changed to better describe the species in these groups. 'Filtering mammals' is now 'Baleen whales', 'Hunting mammals' is now 'Seals and dolphins', 'Surface seabirds' is now 'Flying seabirds', 'Diving seabirds' is now 'Penguins'. Note that the biomass value for filtering mammals presented in Table 19 of Pruvost et al. (2005) is incorrect (Pruvost, pers. comm.). In this model we use the correct biomass value from Table 16(b) in Pruvost et al. (2005) for filtering mammals. Two functional groups were added to the Pruvost et al. (2005) model prior to balancing: a bacteria group, and a carcass group to represent mortality from higher-trophic predators that is not consumed. If more than one detritus group is specified in Ecopath, then the detritus fate form must be completed. Following the Ecopath model for the Ross Sea, Pinkerton et al. (2010), unassimilated consumption was directed to detritus fate, and other mortality was directed to the carcass group. Fractions used to describe other mortality for functional groups were taken from Pinkerton et al. (2010). These values are presented in Table 1 and changes to the data are highlighted in bold. Parameters were adjusted in Ecopath to achieve mass-balance.

Table 1: Unbalanced parameters put into Ecopath with Ecosim for balancing. Changes made to the data to facilitate balancing are highlighted in **bold**. B – biomass, P/B – production/biomass, and Q/B – consumption/biomass, UC – unassimilated consumption, OM – other mortality. Descriptions of the species in each group is provided in (Pruvost et al., 2005).

	Group	B	P/B	Q/B	UC	OM
1	Top predators	0.036	0.05	2.0	0.3	0.5
2	Baleen whales	0.084	0.06	10.9	0.3	0.5
3	Seals and dolphins	0.015	0.1	8.46	0.3	0.5
4	Flying seabirds	0.029	0.3	36.5	0.3	0.5
5	Penguins	0.029	0.06	12	0.3	0.5
6	Sharks	0.001	0.17	1	0.3	0.5
7	Juvenile toothfish	0.038	0.2	1.4	0.3	0.5
8	Adult toothfish	0.129	0.105	0.9	0.3	0.5
9	Large pelagic fishes	0.094	0.22	2.56	0.3	0.05
10	Small pelagic fishes	4.5	0.5	6.1	0.3	0.05
11	Large benthic fishes	0.49	0.19	1.98	0.3	0.05
12	Other benthic fishes	0.286	0.502	7.33	0.3	0.05
13	Large cephalopods	0.355	0.6	2	0.3	0.05
14	Small cephalopods	1.294	1	3.333	0.3	0.05
15	Deep-benthic omnivores	30	3	1	0.3	
16	Shallow-benthic omnivores	3.1	2.1	10	0.3	
17	Shallow-benthic herbivores	8.7	2	10	0.3	
18	Euphausiids	5.828	0.95	3.8	0.3	
19	Omnivorous zooplankton	2.726	10.795	43.18	0.3	
20	Herbivorous zooplankton	11.298	24	96	0.3	
21	Benthic algae	5.9	4	0.00		
22	Phytoplankton	7	150	0.00		
23	Bacteria	10	35	100	0.3	
24	Carcass	0.00	0.00	0.000		
25	Detritus	100.0	0.00	0.000		

This balanced model was tested using previously published guidelines for assessing Ecopath parameters (Link, 2010). These guidelines, referred to as pre-balance diagnostics, provide methods for assessing Ecopath parameters prior to balancing models. One method from this guide was used to assess biomass, specifically the span and magnitude of increasing biomass with decreasing trophic level. Link (2010) suggests that biomass (on a log-scale), should span 5–7 orders of magnitude and increase 5–10% with decreasing trophic level.

Once parameters were evaluated, a preliminary look at the food-web dynamics in the model was conducted using ecosystem descriptors provided in Ecopath with Ecosim.

Results

EE was greater than 1 for detritus, indicating that primary production was insufficient to support detritus consumption. This imbalance in EE for

detritus was resolved by increasing the biomass of phytoplankton by 5%. With this modification, the model was balanced and an EE value of less than 1 was achieved for all groups (Table 2).

Pre-balance diagnostics for balanced biomass estimates show an increase in the order of 15% with decreasing trophic level (blue line in Figure 1). Groups far above or under this line included sharks, small pelagic fishes and deep-benthic omnivores (orange points in Figure 1). Biomass estimates were taken from sources not specific to the Kerguelen Island region as there are very few data for these groups on the Kerguelen Plateau. As balanced biomass estimates generally followed the guideline for trophic decomposition, we consider these estimates appropriate for use in the Ecopath model.

Summary statistics describe ecosystem size and maturity in terms of flows and can be compared with summary statistics from other Ecopath models (Table 3). Summary statistics were compared

Table 2: Parameters of the balanced model, balanced biomass value for phytoplankton highlighted in **bold**. Ecotrophic efficiencies calculated in Ecopath are shown in italics.

	Group name	Trophic level	B	P/B	Q/B	EE	P/Q
1	Top predators	4.72	0.0362	0.05	2	0	0.025
2	Baleen whales	3.36	0.084	0.06	10.9	0	0.006
3	Seals and dolphins	4.52	0.0151	0.1	8.46	0.479	0.012
4	Flying seabirds	3.59	0.0285	0.3	36.5	0.009	0.008
5	Penguins	4.05	0.0292	0.06	12	0.416	0.005
6	Sharks	4.63	0.001	0.17	1	0.426	0.17
7	Juvenile toothfish	4.29	0.0377	0.2	1.4	0.910	0.143
8	Adult toothfish	4.34	0.129	0.105	0.9	0.402	0.117
9	Large pelagic fishes	4.21	0.094	0.22	2.56	0.950	0.086
10	Small pelagic fishes	3.22	4.5	0.5	6.1	0.718	0.082
11	Large benthic fishes	3.75	0.49	0.19	1.98	0.285	0.096
12	Other benthic fishes	3.39	0.286	0.502	7.33	0.848	0.068
13	Large cephalopods	3.64	0.355	0.6	2	0.999	0.3
14	Small cephalopods	3.52	1.294	1	3.333	0.953	0.3
15	Deep-benthic omnivores	2.11	30	3	10	0.344	0.3
16	Shallow-benthic omnivores	2.33	3.1	2.1	10	0.241	0.21
17	Shallow-benthic herbivores	2.02	8.7	2	10	0.688	0.2
18	Euphausiids	2.86	5.828	0.95	3.8	0.805	0.25
19	Omnivorous zooplankton	2.70	2.726	10.795	43.18	0.571	0.25
20	Herbivorous zooplankton	2.00	11.298	24	96	0.386	0.25
21	Benthic algae	1.00	5.9	4	0	0.100	
22	Phytoplankton	1.00	7.40	150	0	0.918	
23	Bacteria	2.00	10	35	100	0	0.35
24	Carcass	1.00				0.020	
25	Detritus	1.00	100			0.985	

Table 3: Summary statistics describing the food web.

Parameter	Value	Units
Sum of all consumption	2680.92	tonnes km ⁻² y ⁻¹
Sum of all exports	31.04	tonnes km ⁻² y ⁻¹
Sum of all respiratory flows	1102.56	tonnes km ⁻² y ⁻¹
Sum of all flows into detritus	1516.81	tonnes km ⁻² y ⁻¹
Total system throughput	5331.33	tonnes km ⁻² y ⁻¹
Sum of all production	1907.68	tonnes km ⁻² y ⁻¹
Calculated total net primary production	1133.6	tonnes km ⁻² y ⁻¹
Total primary production/total respiration	1.03	
Net system production	31.04	tonnes km ⁻² y ⁻¹
Total primary production/total biomass	12.28	
Total biomass/total throughput	0.017	
Total biomass (excluding detritus)	92.33	tonnes km ⁻²
Connectance index	0.22	
System omnivory index	0.16	

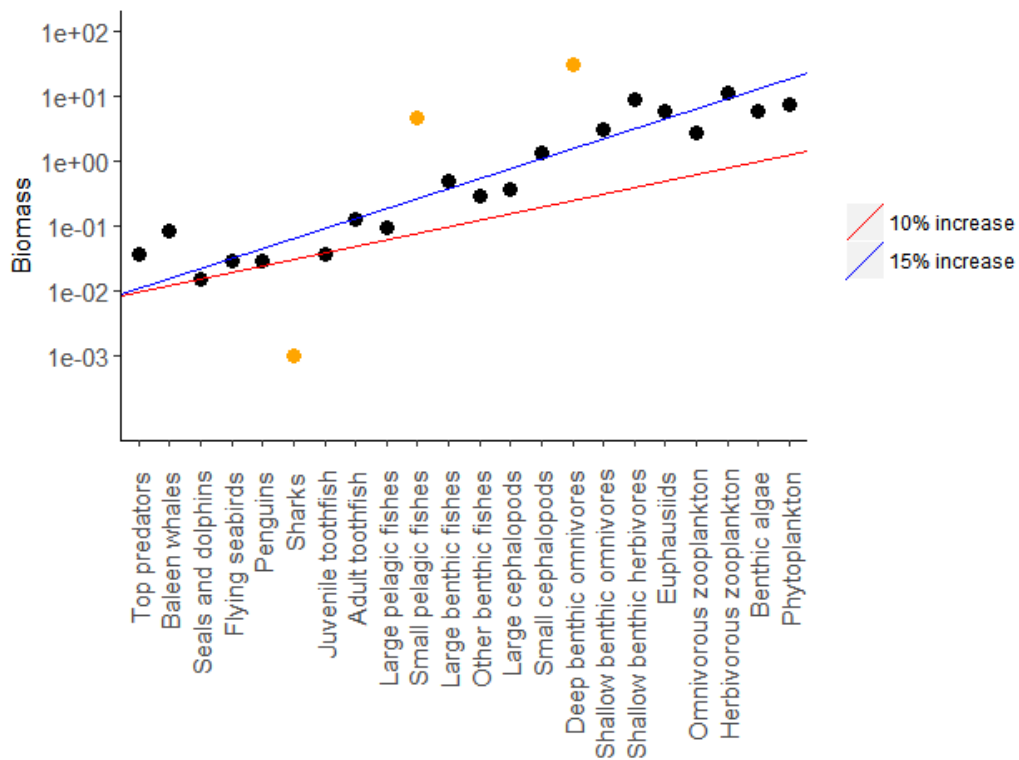


Figure 1: Pre-balance diagnostics for balanced biomass estimates. Blue – line of best fit, red – pre-balance guideline. Groups that depart far from the slope are shown as orange dots.

to Ecopath models for the Prince Edwards Islands, South Georgia, South Shetland Islands, Falkland Islands and the Antarctic Peninsula (Bredesen, 2003; Cheung and Pitcher, 2005; Erfan and Pitcher, 2005; Cornejo-Donoso and Antezana, 2008; Hill et al., 2012; Hoover, 2012; Gurney et al., 2014) (Figure 2). The size of the system was compared to other sub-Antarctic models using total system throughput and total biomass. Total system throughput in the model was 5 331 tonnes $\text{km}^{-2} \text{y}^{-1}$, and total biomass (excluding detritus) was 92 tonnes km^{-2} . Compared to the range of values reported for other sub-Antarctic models, the size of this system is smaller.

System maturity and complexity was assessed using total primary production/total respiration, net system production, total primary production/total biomass, and total biomass/total throughput. Values close to one for total primary production/total respiration and zero for net system production indicate a mature system where energy is balanced between production and respiration. Total primary production/total respiration in the balanced model was 1.03, showing energy in this system is close to being balanced. Net system production is the difference between total primary production and total respiration. In contrast to total primary production/

total respiration, our value of 31 tonnes $\text{km}^{-2} \text{y}^{-1}$ for net system production suggests that the system is still developing. However, compared to other sub-Antarctic food webs, our value is much lower (Figure 2). Low values for total primary production/total biomass indicate a mature system. Compared to other models in Figure 2, our value of 12.28 suggests that our system is more mature. Low values for total biomass/total throughput indicate a developing system. Our value of 0.017 indicates the system is still developing. However, in comparison to other models our system is more mature (Figure 2). Overall, summary statistics suggest that the food web on the plateau is smaller and more mature than other sub-Antarctic food webs.

Transfer efficiencies describe the fraction of total flows at each trophic level that are consumed at the next trophic level (Bradford-Grieve et al., 2003). On average, transfer efficiencies were 6.8% for trophic levels II–IV (Table 4). Transfer efficiency from primary producers was 8.7%, which was higher than when detritus was included (4.2%). Transfer efficiencies from primary producers were most efficient in trophic levels II and III. The most efficient transfer from detritus was to trophic levels III and IV.

Table 4: Transfer efficiencies for each trophic level.

Source	Trophic level						
	II	III	IV	V	VI	VII	VIII
Producer	9.79	13.08	5.16	6.05	2.89	1.29	
Detritus	1.52	8.72	5.61	5.18	2.84		
All flows	4.89	12.27	5.22	5.93	2.88	1.30	0.88

Proportion of total flow originating from detritus: 0.57
 Transfer efficiencies (calculated as geometric mean for TL II-IV)
 From primary producers: 8.710%
 From detritus: 4.206%
 Total: 6.792%

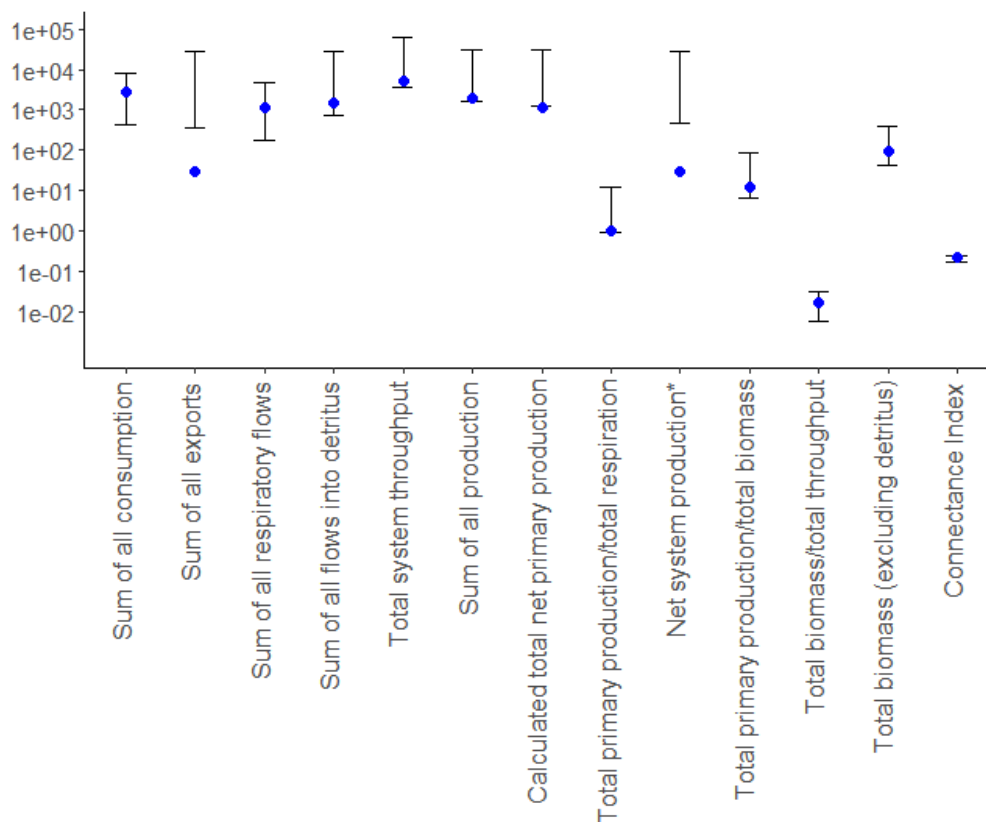


Figure 2: Summary statistics for the balanced model (blue points) in comparison with sub-Antarctic models (error bars). *negative value for Hill et al. (2012) omitted.

The mixed trophic impact plot highlighted the impacts of direct and indirect interactions on functional groups in the balanced model (Figure 3). This section focusses on the more pronounced positive and negative impacts (the deeper shades in Figure 3) and unexpected impacts highlighted in the plot. In the balanced model, an increase in the biomass of top predators negatively affected seals and dolphins, flying seabirds, penguins and sharks (Figure 3). This is expected, as top predators are one of the few predators preying on these groups (see diet matrix, Table 5). An increase in

the biomass of top predators has positive effects on large pelagic fishes (Figure 3). This is in line with expectations as the predators of this group are the seabirds. An increase in the biomass of top predators would increase their consumption of seabirds, and reduce seabirds consuming large pelagic fishes. An increase in the biomass of cephalopod groups negatively affects seals and dolphins, flying seabirds, penguins and sharks. This result is unexpected and could be a result of competition with fish groups for food as they consume the same prey. Fish are a major component in the diet of these groups and

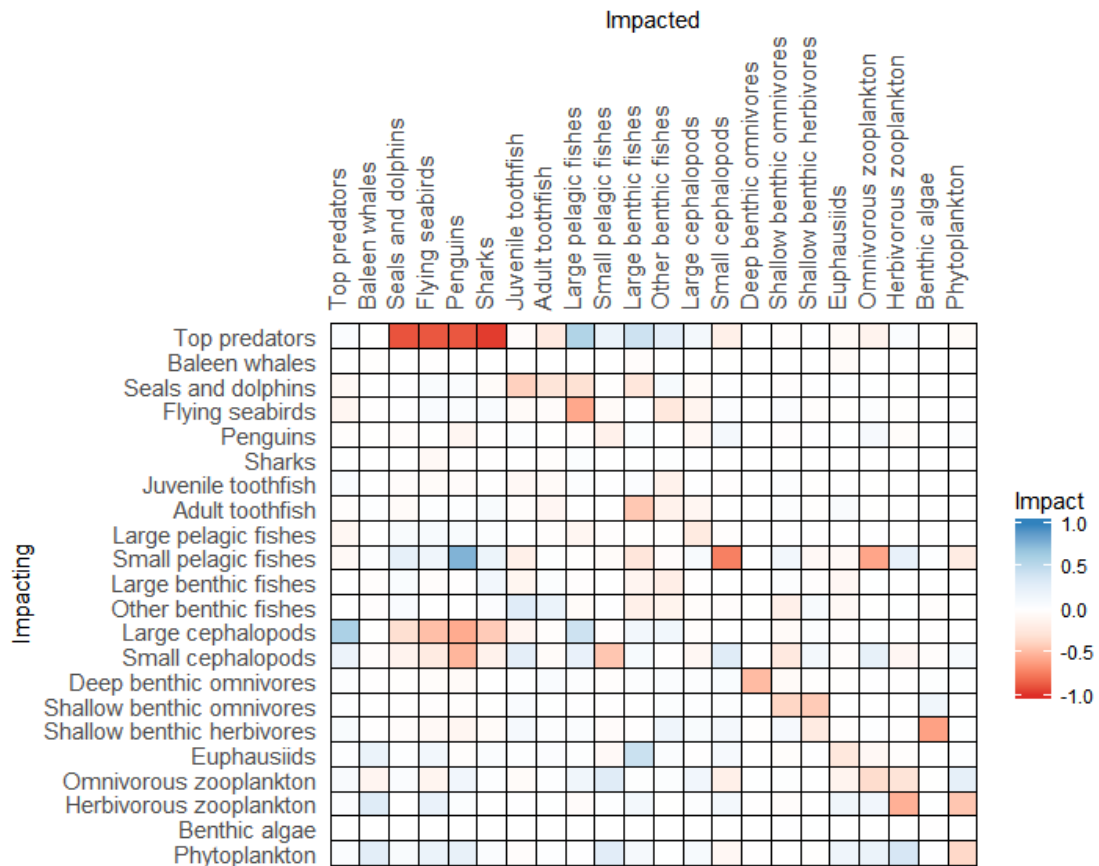


Figure 3: Mixed trophic impact plot. Diagram shows the positive (blue) or negative (red) impact of an increase in the biomass of the impacting functional group on the impacted functional group.

increasing cephalopod biomass could introduce competition for food, reducing prey availability for predator groups (Table 5).

Discussion

The increased biomass value of 7.4 tonnes km⁻² for phytoplankton is comparable to Ecopath models for sub-Antarctic islands in the Indian Ocean and in situ measurements on the plateau. A biomass of 8.51 tonnes km⁻² was used for phytoplankton in the Ecopath model for the Prince Edward Islands (Gurney et al., 2014). Average chlorophyll *a* (chl *a*) biomass for the southwest side of the Kerguelen Plateau from early spring to late summer (stations A13–A18) was 0.184 mg chl *a* m⁻³ (Becquevort et al., 2000). Assuming a chl *a* to carbon conversion of 35 (Dehairs et al., 1992; Fiala et al., 1998) and that carbon is 10% of wet weight (Dalsgaard et al., 1997), this converts to a biomass of 8.9 tonnes km⁻². Sampling at the Kerfix station on the southwest side of the plateau showed a range of 15–85 mg chl *a* m⁻², which converts to a biomass range of 5.3–29.8 tonnes km⁻² (Fiala et al.,

1998). A long-term analysis of satellite chl *a* data for the entire Kerguelen Plateau showed a range of 0.2–0.7 mg chl *a* m⁻³, converting to a biomass range of 8.4–29.4 tonnes km⁻² (Dragon et al., 2011). This suggests that the balanced value is on the lower end of the range of phytoplankton biomass estimates for the area.

The pre-balance guideline is a relatively new method that has been used in recent Ecopath models (Heymans et al., 2016 and references therein). In the balanced model, top predator biomass is lower than adult toothfish biomass, which may undermine the interpretations of model outcomes for fisheries management. The top predators group consists of orcas and sperm whales and is not the only group preying on toothfish in the model. The collective biomass of these groups (top predators, seals and dolphins, flying seabirds, and sharks) is still slightly lower than toothfish biomass however, this is also seen in the Ecopath model for the Ross Sea (Pinkerton et al., 2010). In other models where toothfish is also a separate functional group, predator biomasses are only slightly higher than toothfish

Table 5: Diet matrix for the balanced Ecopath model. Numbers refer to functional groups shown in Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	23
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0.001	0	0	0	0	0.005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0.01	0	0	0	0	0.004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0.05	0	0.025	0	0	0.047	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0.05	0	0.013	0	0	0.1582	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0.05	0	0.044	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0.025	0	0.341	0.11	0.74	0.2633	0.171	0.171	0.33	0	0.012	0	0.3	0.2	0	0	0	0	0	0	0
11	0.01	0	0.088	0	0	0.1582	0	0.124	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0.01	0	0.09	0.03	0	0.039	0.411	0.287	0	0	0.024	0	0	0	0	0	0	0	0	0	0
13	0.6	0	0.235	0.05	0.04	0.1672	0	0.216	0.2	0	0	0	0	0	0	0	0	0	0	0	0
14	0.183	0	0.164	0.02	0.01	0.1321	0.316	0.1	0.2	0.04	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0.017	0	0.102	0	0	0.119	0.155	0.1	0.1	0.1	0	0	0	0	0	0
16	0	0	0	0	0	0.009	0.082	0	0	0	0	0.21	0.1	0.1	0	0.02	0	0	0	0	0
17	0	0	0	0	0	0	0.02	0	0	0	0	0.2	0.1	0.1	0	0.3	0.02	0	0	0	0
18	0	0.3	0	0.23	0.06	0	0	0	0.15	0.04	0.646	0.264	0.1	0.1	0	0	0	0.05	0	0	0
19	0	0.14	0	0.11	0.03	0	0	0	0.08	0.47	0.195	0.1	0.2	0.2	0	0	0	0.1	0	0	0
20	0	0.56	0	0.44	0.12	0	0	0	0.03	0.25	0	0.07	0.1	0.2	0	0	0	0.6	0.7	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0.02	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0.1	0.3	0.9	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0.01	0	0.004	0.001	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9	0.66	0.96	0.15	0	0.1	1

biomass (Hill et al., 2012; Gurney et al., 2014). Additionally, as these predators are transient, their biomass is weighted by the time spent away from the model domain, resulting in a lower biomass in the model. We are therefore confident that these biomass values are reasonable.

Estimating biomass for sharks, small pelagic fish, and benthic groups is generally difficult. However, upon checking the groups identified in the biomass plot, estimates for these groups were reasonable and the best available estimate at the time. There have been no targeted studies to estimate shark biomass, as they are not common in the Southern Ocean (Cherel and Duhamel, 2004). Shark biomass in this model was assumed to be 1% of fish biomass, giving a value of 0.001 tonnes km⁻² (Pruvost et al., 2005). The biomass estimate for small pelagic fish is comparable to biomass estimates of similar fish functional groups in other Ecopath models. Hill et al. (2012) use a value of 9.2 tonnes km⁻² for pelagic fish in their balanced model and Gurney et al. (2014) use the same value as Pruvost et al. (2005) for their pelagic fish groups indicating that the value for the balanced model is sufficient. Benthic biodiversity has been recently investigated in the Kerguelen region but biomass has not been surveyed since the 1970s (Améziane et al., 2011; Féral and Poulin, 2011). One study found benthic species composition and biomass off Marion Island were similar to the Kerguelen Islands, reporting that total zoobenthic biomass ranged from 68 to 598 g m⁻² at Marion Island and 61 g m⁻² at Kerguelen Island (Beckley and Branch, 1992). This value is high but still compares to total zoobenthic biomass in the balanced model (collective biomass of benthic groups 15–17 = 41.8 tonnes km⁻²), indicating this value is reasonable.

The mixed trophic impact plot in this study illustrated its usefulness in understanding food web dynamics in the system. Most impacts were expected and easily explained by the diet matrix, however, one unexpected result from the mixed trophic impact plot was the negative impact an increase in the biomass of cephalopods had on the biomass of seals and dolphins, flying seabirds, penguins and sharks. There is a lot of overlap in the diet between cephalopod groups and these predator groups, small pelagic fish collectively make up to 25% of cephalopod diets, and up to 36% of predator diets, with 18.5% belonging to flying seabirds. Zooplankton groups make up to 45% of cephalopod diets, 78% of penguins diet and 21% of flying

seabirds diet. An increase in the biomass of cephalopods could introduce competition for resources in the model, negatively impacting predators. Especially penguins, as 95% of their diet overlaps with cephalopod diets (Table 2). One of the limitations of mixed trophic impacts is that it does not account for prey-switching in response to changes in biomass. These interactions could be further explored in Ecosim, a time dynamic module in Ecopath with Ecosim that has the capacity to accommodate prey-switching.

This work presents the first mass-balanced ecosystem model for the Kerguelen EEZ. In the next implementation of this model currently under development (Subramaniam et al., in prep), the model domain has been extended to include Heard Island and McDonald Islands. Functional groups have been reorganised to provide more resolution, the multistanza grouping has been used to define Patagonian toothfish, and specific groups have been defined for species targeted by the fishery. Fisheries catch has been added to this extended version of the model, biomass and diet data have been updated wherever possible, and data specific to the Kerguelen Plateau have been used where available. The plateau-wide version of the model is being used to evaluate the combined effects of fishing and climate change on the food web.

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References

- Améziane, N., M. Eléaume, L. Hemery, F. Monniot, A. Hemery, M. Hautecoeur and A. Dettai. 2011. Biodiversity of the benthos off Kerguelen Islands: overview and perspectives. *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d'Ichtyologie, Paris, France: 157–167.

- Beckley, L.E. and G.M. Branch. 1992. A quantitative scuba-diving survey of the sublittoral macrobenthos at subantarctic Marion Island. *Polar Biol.*, 11 (8): 553–563.
- Becquevort, S., P. Menon and C. Lancelot. 2000. Differences of the protozoan biomass and grazing during spring and summer in the Indian sector of the Southern Ocean. *Polar Biol.*, 23 (5): 309–320.
- Bradford-Grieve, J.M., P.K. Probert, S.D. Nodder, D. Thompson, J. Hall, S. Hanchet, P. Boyd, J. Zeldis, A.N. Baker, H.A. Best, N. Broekhuizen, S. Childerhouse, M. Clark, M. Hadfield, K. Safi and I. Wilkinson. 2003. Pilot trophic model for subantarctic water over the Southern Plateau, New Zealand : a low biomass, high transfer efficiency system. *J. Exp. Mar. Biol. Ecol.*, 289: 223–262.
- Bredesen, E.L. 2003. *Krill and the Antarctic: Finding the Balance*. Thesis.
- Cherel, Y. and G. Duhamel. 2004. Antarctic jaws: cephalopod prey of sharks in Kerguelen waters. *Deep-Sea Res. I*, 51 (1): 17–31.
- Cheung, W. and T. Pitcher. 2005. A mass-balance model of the Falkland Islands fisheries and ecosystems. In: Palomares, M.L.D., P. Pruvost, T.J. Pitcher and D. Pauly (Eds). *Modeling Antarctic Marine Ecosystems*. Fisheries Centre Research Reports, 13 (7): 65–84.
- Christensen, V. and C.J. Walters. 2004. Ecopath with Ecosim: Methods, capabilities and limitations. *Ecol. Model.*, 172: 109–139.
- Cornejo-Donoso, J. and T. Antezana. 2008. Preliminary trophic model of the Antarctic Peninsula Ecosystem (Sub-area CCAMLR 48.1). *Ecol. Model.*, 218: 1–17.
- Dalsgaard, A.J.T., D. Pauly and T.A. Okey. 1997. Preliminary mass-balance model of Prince William Sound, Alaska, for the pre-spill period, 1980–1989. *Fisheries Centre Research Reports*, 5 (2): 1–33.
- Dehairs, F., L. Goeyens, N. Stroobants and S. Mathot. 1992. Elemental composition of suspended matter in the Scotia-Weddell Confluence area during spring and summer 1988 (EPOS Leg 2). *Polar Biol.*, 12 (1): 25–33.
- Dragon, A.-C., S. MarChanD, M. Authier, C. Cotté, S. Blain and C. Guinet. 2011. Insights into the spatio-temporal productivity distribution in the Indian Sector of the Southern Ocean provided by satellite observations. *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d’Ichtyologie, Paris, France: 57–67.
- Erfan, A. and T. Pitcher. 2005. An ecosystem simulation model of the Antarctic Peninsula In: Palomares, M.L.D., P. Pruvost, T.J. Pitcher and D. Pauly (Eds). *Modeling Antarctic Marine Ecosystems*. Fisheries Centre Research Reports, 13 (7): 5–20.
- Féral, J. and E. Poulin. 2011. Kerguelen Islands: a living laboratory to understand the benthic biodiversity of the Antarctic. *The Kerguelen plateau, marine ecosystem and fisheries*. Société Française d’Ichtyologie, Paris, France: 151–156.
- Fiala, M., E.E. Kopczynska, C. Jeandel, L. Oriol, L. Arago, P. Universite and M. Curie. 1998. Seasonal and interannual variability of size-fractionated phytoplankton biomass and community structure at station Kerfix, off the Kerguelen Islands, Antarctica. *J. Plankton Res.*, 20: 1341–1356.
- Guinet, C., P. Tixier, N. Gasco and G. Duhamel. 2015. Long-term studies of Crozet Island killer whales are fundamental to understanding the economic and demographic consequences of their depredation behaviour on the Patagonian toothfish fishery. *ICES J. Mar. Sci.*, 72 (5): 1587–1597.
- Gurney, L.J., E.A. Pakhomov and V. Christensen. 2014. An ecosystem model of the Prince Edward Island archipelago. *Ecol. Model.*, 294: 117–136.
- Heymans, J.J., M. Coll, J.S. Link, S. Mackinson, J. Steenbeek, C. Walters, and V. Christensen. 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecol. Model.*, 331: 173–184.

- Hill, S.L., K. Keeble, A. Atkinson and E.J. Murphy. 2012. A foodweb model to explore uncertainties in the South Georgia shelf pelagic ecosystem. *Deep-Sea Res. II*, 59–60: 237–252.
- Hoover, C. 2012. *Effects of harvest and climate change on polar marine ecosystems: case studies from the Antarctic Peninsula and Hudson Bay*. Text thesis.
- Link, J.S. 2010. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. *Ecol. Model.*, 221 (12): 1580–1591.
- Pinkerton, M.H., J.M. Bradford-Grieve and S.M. Hanchet. 2010. A balanced model of the food web of the Ross Sea, Antarctica. *CCAMLR Science*, 17: 1–31.
- Pruvost, P., G. Duhamel, and M.L.D. Palomares. 2005. An ecosystem model of the Kerguelen Islands' EEZ. In: Palomares, M.L.D., P. Pruvost, T.J. Pitcher and D. Pauly (Eds). *Modeling Antarctic Marine Ecosystems*. Fisheries Centre Research Reports, 13 (7): 40–64.
- Subramaniam, R.C., S.P. Corney, K.M. Swadling, and J. Melbourne-Thomas. In prep. Exploring ecosystem structure and function of the northern Kerguelen Plateau using a mass-balanced food web model. *Deep-Sea Res. II*.

