



# Robust model-based indicators of regional differences in food-web structure in the Southern Ocean

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## ABSTRACT

Efforts to model marine food-webs are generally undertaken by small teams working separately on specific regions (<10<sup>6</sup> km<sup>2</sup>) and making independent decisions about how to deal with data gaps and uncertainties. Differences in these largely arbitrary decisions (which we call ‘model personality’) can potentially obscure true differences between regional food-webs or lead to spurious differences. Here we explore the influence of model personality on a comparison of four Southern Ocean regional food-web models. We construct alternative model versions which sequentially remove aspects of personality (alternative model ‘currencies’, schemes for aggregating organisms into functional groups, and energetic parameter values). These alternative versions preserve regional differences in biomass and feeding relationships. Variation in a set of model metrics that are insensitive to absolute biomass and production identifies multiple regional contrasts, a subset of which are robust to differences in model personality. These contrasts imply real differences in ecosystem structure which, in conjunction with differences in primary production and consumer biomass (spanning two and four orders of magnitude respectively), underpin differences in function. Existing regional models are therefore a useful resource for comparing ecosystem structure, function and response to change if comparative studies assess and report the influence of model personality.

## 1. Introduction

The Southern Ocean, south of the Antarctic Polar Front, represents approximately 10% of the global marine area. It is a major carbon sink (Takahashi et al., 2012) and is home to a distinctive group of organisms including physiologically unique channichthyid fish (Kock and Everson, 1997), commercially important toothfish (Grilly et al., 2015) and perhaps the Earth's most plentiful free living metazoan, Antarctic krill (Meyer et al., 2020). It was heavily perturbed by the removal of around two million whales in the 20th century (Rocha et al., 2014) and it includes one of the world's marine warming hotspots (Hobday and Pecl, 2014). Critical questions about this ecosystem include how it changes in

response to these perturbations and whether its unique ecosystem characteristics can be maintained (Xavier et al., 2016).

Models that integrate biogeochemical and trophic interactions are recognized as valuable for addressing these questions and it is important that such models represent the regional characteristics of Southern Ocean ecosystems (Cavan et al., 2019; Murphy et al., 2012). Although Southern Ocean biodiversity is poorly characterised, it is known to vary spatially and to include high levels of endemism and areas of high diversity, especially amongst benthic and shallow water assemblages (Griffiths, 2010). Other environmental and biological characteristics of the Southern Ocean also vary with latitude, longitude and depth, as do the rate of warming and the degree of past perturbation (Griffiths, 2010;

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McCormack et al., 2020; Sallée, 2018; Xavier et al., 2016). Consequently, an understanding of the structural and functional differences between regions is a key requirement for understanding past dynamics and projecting future change at the circumpolar scale (Murphy et al., 2012).

Ecological research in the Southern Ocean has, to date, been largely focused on a few specific regions (scale  $<10^6$  km<sup>2</sup>), including the Antarctic Peninsula, Scotia Sea, Ross Sea and Kerguelen Plateau with individual nations tending to operate largely within a limited area (Griffiths, 2010). Circumpolar surveys, such as the Discovery investigations of the 1920s and 1930s (Deacon, 1955) and the CHINARE 2013/14 circum-Antarctic expedition (Yang et al., 2021) are the exception rather than the rule. The regionally-focused effort has nonetheless amassed considerable understanding and developed synthesis products including a suite of at least fifteen models of regional food-webs (McCormack et al., 2021). These models are therefore a resource for addressing calls to compare food-webs across the Southern Ocean as a basis for understanding regional differences in ecosystem structure and function, and ultimately developing dynamic models to explore ecosystem change at the regional and circumpolar scales (Gurney et al., 2014; Newman et al., 2019; McCormack et al., 2021; Murphy et al., 2012, 2013, 2016).

One consequence of the regionally-focused research effort is that each model has been constructed by a separate research team, often with different objectives. Many of the models share common features, including widespread use of the Ecopath framework and its underlying identities (Christensen and Walters, 2004). The popularity of Ecopath has led to the publication of several best practice guides (Christensen and Walters, 2004; Christensen et al., 2005; Heymans et al., 2016; Link, 2010) which, when followed, provide a degree of comparability between models. Nonetheless modelling teams are generally confronted with incomplete datasets and an array of choices to make in converting incomplete information to models. Thus any regional food-web model is a combination of: (1) data with its associated errors; (2) a defined model framework with its associated assumptions; and (3) the additional choices made by the modelers to fit the data to the framework. Some of the additional assumptions and choices are necessary to meet the constraints of the model framework (e.g. flows into and out of each compartment must balance), or because data are inadequate (as is often the case for energetic parameter estimates). Some are arbitrary (e.g. the model currency, such as organic carbon versus wet mass). Finally, some depend on the purpose of the model (e.g. the number and type of functional groups in the model). We henceforth refer to these assumptions and choices as 'model personality'. The accumulated model personality could have a significant impact on model outputs and therefore comparisons of models constructed by different teams (Heymans et al., 2016; Pinnegar et al., 2005), but this impact is poorly understood and has not been evaluated for Southern Ocean food-web models.

In this study we use four previously published Southern Ocean regional food-web models as the basis for exploring the influence of model personality on a comparison of model outputs. First we characterise model personality by identifying the key differences in the way the four models were constructed. We then progressively reduce personality by rendering all models in a common currency, and producing alternative versions of each model using a standard set of functional groups and a standard set of energetic parameters. We calculate a suite of metrics for each model version and assess the relative importance of between-model and between-version differences in these metrics. We also identify apparent contrasts between regions and evaluate which of these contrasts are robust to differences in functional group construction and energetic parameters. Our chosen suite of metrics is intentionally independent of absolute biomass, which is known to vary between regions (Ardyna et al., 2017; Siegel and Watkins, 2016) and is key driver of regional contrasts in various metrics (Gaichas et al., 2009; Heymans et al., 2014). We nonetheless investigate regional differences in productivity and biomass using a combination of model-based and independent estimates. We identify the between-model differences that are

influenced by functional group construction and energetic parameters, leaving a set of fifteen robust regional contrasts driven by differences in modelled feeding relationships and the relative biomass of organisms within each model.

## 2. Methods

### 2.1. Original models

The issue of model construction varying between modelling teams and therefore modelled regions affects the whole field of marine ecosystem modelling and limits the ability to compare food-web structure across regions (but see Gaichas et al. (2009), Heymans et al. (2014)). We explored how this issue impacts the comparison of Southern Ocean regions using four existing food-web models (scale  $4 \times 10^4$  to  $4 \times 10^5$  m<sup>2</sup>) that were developed by separate teams and had differing model personalities. Each team was led by one of the co-authors of the current study who were able to provide detailed information about the personalities of the individual models. While these regional models are a subset of those available for the Southern Ocean (McCormack et al., 2021) they capture a range of ecological conditions and variations in approach to constructing Ecopath-type models. The models are for the following locations (listed in descending order of primary production per unit area per year): South Georgia (Hill et al., 2012), Marguerite Bay and adjacent shelf areas on the West Antarctic Peninsula coast (Ballerini et al., 2014), the Ross Sea (Pinkerton et al., 2010) and the Prince Edward Islands (Gurney et al., 2014), (Fig. 1, Table 1). Each of the models was constructed using the standard Ecopath identities and was balanced to obey the key constraints that use of any prey group within the system (predation and associated waste) cannot exceed production by that group, and that respiration in each group must be positive (Christensen and Walters, 2004). Each model was expressed in terms of the following parameters for each functional group: biomass per unit area (B), consumption per unit biomass (Q/B), production per unit biomass (P/B), assimilation efficiency (AE: the proportion of ingested food that is used in respiration and biomass production and maintenance), ecotrophic efficiency (EE, the proportion of biomass production that is consumed within the system) and a diet vector (D) indicating the proportional contribution of each prey group to the biomass consumed by the predator. Some models also included non-trophic transfer parameters, e.g. for growth or spawning.

### 2.2. Model personality

The lead authors of each of the four models agreed, through discussion, a list of characteristics that capture the main details of the models and the main differences in the approaches adopted by the four modelling teams. These characteristics span readily-quantifiable details, such as model area and number of functional groups, to qualitative information such as motivation and balancing approach. We populated a table (Table 1) describing these characteristics for each of the models, drawing information from the published papers describing each model, supplemented where necessary with additional information supplied by the relevant lead author.

### 2.3. Model versions

Our main objective was to assess how the four models differ in terms of implied network properties, and to evaluate whether such differences are influenced by two key aspects of model personality, specifically aggregation of model components into functional groups and the value of energetic parameters. We assessed the relative importance of between-model and within-model differences, where 'within-model' differences relate to different versions of one of the four models. We assessed these differences using a set of sixteen ecosystem metrics (Table 2) calculated for three balanced versions of each model. These

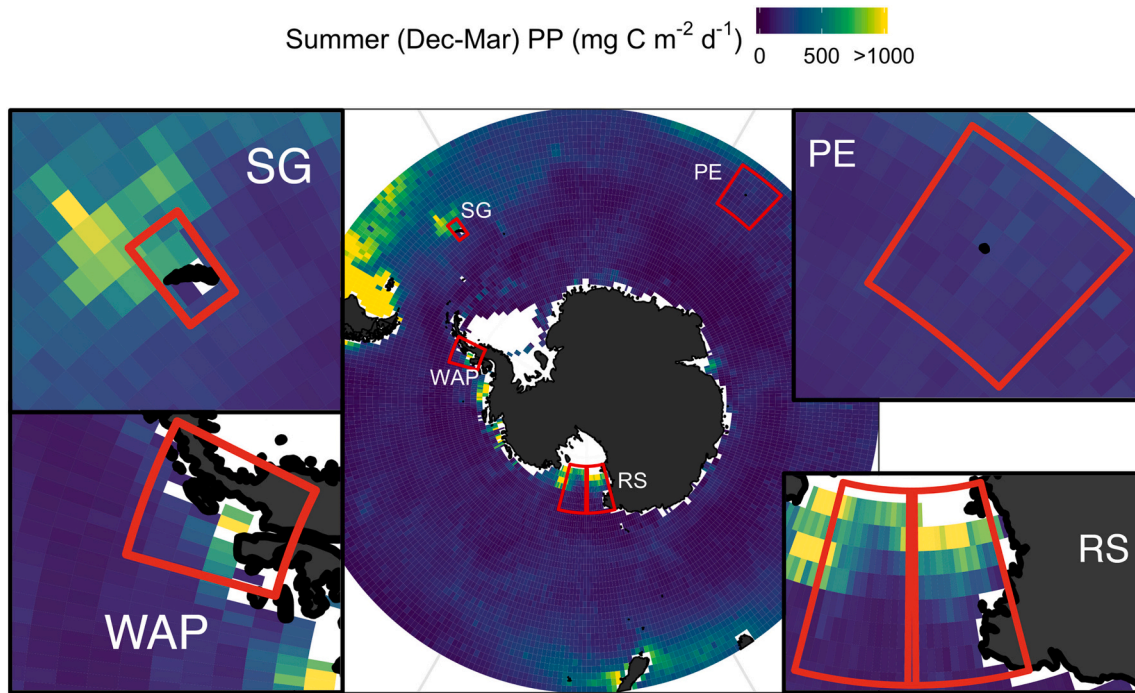


Fig. 1. The locations represented in the four Southern Ocean regional food-web models (SG = South Georgia, WAP=West Antarctic Peninsula, RS = Ross Sea, PE = Prince Edward Islands) shown in the context of mean December to March primary production for the years 2007–2015 (Arteaga et al., 2018). Polygons enclose the pixels used to calculate regional observation-based primary production estimates rather than the exact boundaries of each model.

versions were:

- (i) *original* published versions converted, where necessary, to a common currency (biomass flow in units of  $\text{g C m}^{-2} \text{yr}^{-1}$ ) and with a consistent treatment of fisheries to aid comparability.
- (ii) *aggregated* versions with a common number and type of functional groups. The groups from the original version were assigned to a set of twenty aggregate groups informed by the aggregation schemes used in the original models (Supplementary Information).
- (iii) *standardised* versions, which were the aggregated versions but with a common set of energetic parameters (P/B, Q/B and AE).

Details of steps used to convert the original models to these versions and the balancing process are given below.

### 2.3.1. Currency conversion and treatment of fishing

Two of the original models were expressed in terms of organic carbon ( $\text{g C m}^{-2} \text{yr}^{-1}$ ) and two in terms of wet mass ( $\text{g wm m}^{-2} \text{yr}^{-1}$ ). We converted the latter models (South Georgia and Prince Edward Islands) to  $\text{g C m}^{-2} \text{yr}^{-1}$  using the conversion factors (CF) in the Supplementary Information and the following equations:

$$\frac{Q}{B_{c,i}} = \frac{\sum_{z=1}^n Q_{w,i,z} \times CF_z}{B_{w,i} \times C_i} \quad (1)$$

where  $\frac{Q}{B_{c,i}}$  is the Q/B of predator  $i$  expressed in carbon currency,  $Q_{w,i,z}$  is the consumption by predator  $i$  of prey  $z$  in wet mass currency,  $B_{w,i}$  is the biomass of predator  $i$  in wet mass currency and  $CF_i$  and  $CF_z$  are the wet mass to carbon conversion factors for predators and prey respectively.

$$D_{c,i,z} = \frac{Q_{w,i,z} \times CF_z}{\sum_{z=1}^n Q_{w,i,z} \times CF_z} \quad (2)$$

where  $D_{c,i,z}$  is the contribution (proportion of carbon consumed) of prey  $z$  to the diet of predator  $i$ .  $Q_{w,i,z}$  was calculated as

$$D_{c,i,z} \times \frac{Q}{B_{w,i}} \times B_{w,i} \quad (3)$$

P/B did not require conversion and biomass was converted by scaling by the relevant conversion factor.

We also imposed a consistent treatment of fisheries on the models by omitting fisheries catches. All of the model locations include areas open to fishing but only the Prince Edward Islands model explicitly included a fishery catch in its published version. These catches ( $100 \text{ t yr}^{-1}$  of Patagonian toothfish, *Dissostichus eleginoides*) are considerably less than those that were omitted from the published South Georgia model (c.  $40,000 \text{ t yr}^{-1}$ ) but nevertheless were equivalent to 68% of the production of the fished group. However this is  $<0.001\%$  of total metazoan production, so the effect of this change was minor.

### 2.3.2. Aggregation

The original models had between 24 and 38 functional groups (Table 1) which were aggregated into a common set of 20 groups (Supplementary Information), informed by those in the set of original models. The aggregated vertebrate, cephalopod, benthos and bacteria groups represent the lowest degree of aggregation that can be achieved without disaggregating any of the original groups. It was not possible to find an appropriate set of plankton groups which match the same criterion because the original groups were based on different combinations of taxonomy, size and trophic role. We used a size-based approach for plankton but retained two important taxonomic groupings of zooplankton (euphausiids and salps) and distinguished between ice algae and phytoplankton. Seventeen of the aggregate groups were common to all of the models, meaning that each original model included at least one of the component organisms.

Microbial processes play a critical role in nutrient and energy cycling (Griffiths, 2010) but heterotrophic bacteria are commonly omitted from representations of marine food-webs. Only two original models included bacterial components (Ross Sea and South Georgia) and the parameterisation of these groups was particularly uncertain. We reduced the potential influence of these differences in our versions of all original

**Table 1**

Characteristics of the four previously published models analysed in this study, showing some of the main differences between modelling teams in their approach to model construction.

Characteristic	South Georgia (Hill et al., 2012)	West Antarctic Peninsula (Ballerini et al., 2014)	Ross Sea (Pinkerton et al., 2010)	Prince Edward Islands (Gurney et al., 2014)
Study region	South Georgia shelf (~55°S, ~36°W). Shore to 1000 m	Marguerite Bay and adjacent continental shelf, West Antarctic Peninsula (66–70°S, 69–71°W).	Continental slope of the Ross Sea (150°E–150°W and south to 60°S). Shore to 3000 m.	Prince Edward Islands archipelago, (46°46'S, 37°51'E). A 200 nm radius from a point between Marion and Prince Edward islands.
Objective*	To identify inconsistencies in the data and evaluate the trophic roles of krill and copepods.	To identify the dominant trophic pathways, and to investigate the role of Antarctic krill in energy transfer and potential changes in the productivity of seabirds and marine mammals in response to potential climate-driven changes in the relative abundance of plankton groups.	To describe quantitatively the structure of the food-web after whaling/sealing but before commercial fishing could have affected it.	To identify relevant ecosystem indicators and provide a tool for fisheries and conservation management
Total area	45,530 km <sup>2</sup>	83,670 km <sup>2</sup>	637,000 km <sup>2</sup>	431,014 km <sup>2</sup>
Modelling platform*	ECOPATH	Bespoke code. Similar to ECOPATH.	Bespoke code. Similar to ECOPATH; including non-trophic transfers	ECOPATH
Alternative model versions (italics identify that used here)	Five: A general <i>base</i> model and four scenarios exploring possible changes in prey availability and predator behaviour.	One <i>food-web</i> model and 32 sensitivity analyses to analyse uncertainty around model input parameters. (Five ECOTRANS simulations also presented).	One	Three, for different decades: 1960s, 1980s, 2000s
Timing (years) of model used here*	2000–2010	2001–2002	1990–2000	2000–2010
Timing (seasons)*	Annual, based mainly on summer data. Biomass scaled by fraction of the year that species are present.	Annual. Winter data from 2002 with autumn and spring data from multiple years. Biomass scaled using monthly or seasonal abundance ratios.	Annual. Seasonal transfers of material between some groups.	Annual, based mainly on April/May data. Biomass scaled by fraction of the year that species are present.
System type* (see caption for more information)	Productive subantarctic shelf waters; ice free; T: 2.4/0.5 °C, DL: 17:38/7:04; pelagic focus; one benthic invertebrate group; open (see "Exchange of materials").	Continental shelf and bay; seasonal ice; T: -0.4/-1.8 °C, DL: 24:00/0:00; pelagic focus; one benthic invertebrate group; one ice group; no bacteria; closed.	Major bight with gyre; shelf, slope and off-shelf waters; permanent and seasonal ice; T: -0.3/-1.8 °C, DL: 24:00/0:00; pelagic and benthic; three benthic invertebrate groups; three ice groups; closed	Low productivity subantarctic island shelf and surrounding ocean; ice free; T: 7.8/5.9 °C, DL: 15:47/08:37; pelagic and coastal; two benthic invertebrate groups; includes macrophytes; no bacteria; open.
Currency*	t wet mass km <sup>-2</sup> y <sup>-1</sup>	g C m <sup>-2</sup> y <sup>-1</sup>	g C m <sup>-2</sup> y <sup>-1</sup>	t wet mass km <sup>-2</sup> y <sup>-1</sup>
Number of functional groups*	30	24	38	37
Absent functional groups (from the set of re-aggregated groups)*	Ice algae	Bacteria, toothed whales, external	External	Bacteria, ice algae, baleen whales, external
Includes fisheries?*	No	No	No	Yes (Patagonian toothfish fishery)
Balancing approach*	Manual, rule-based (Primarily through increasing prey biomass to reduce EE to 1, but allowing adjustments to energetic parameters and diet to avoid extreme biomass adjustments or violating constraints).	Manual, rule-based (Increase biomass of prey species to reduce EE to 1)	Automated (Simultaneous adjustment of all parameters to find a solution close to the original values)	Manual: only minor adjustments were required (after extensive reworking of Q/B data)
Parameters adjusted during balancing*	B, P/B, Q/B, Diet	B	B, P/B, Q/B (Q/P), AE, Diet, Export fraction, Accumulation fraction, Non-trophic transfers (through growth, to detritus and seasonal)	Diet, B
Treatment of data-poor groups*	Expert opinion, proxies from other species and areas	Use of metabolic theory for physiological parameters; expert opinion for diet composition and biomass	Proxies from other species and areas	Proxies from other species and areas, expert opinion
Treatment of parameter uncertainty	Uncertainty estimates not provided.	Uncertainty estimates not provided. Some uncertainties explored with sensitivity analysis.	Data pedigree provided. Used in model balancing.	Data pedigree provided.
Ontogeny*	No separation of life stages	Antarctic krill only, split into two groups (larvae and adults).	Demersal fish and zooplankton, with "growth transfer" between size categories.	No separation of life stages
Exchange of materials with the surrounding area*	External prey represented as additional functional groups.	NA	NA	Includes not zero migration terms
Detrital feeding*	One detrital group. Phytodetrital feeding represented as direct feeding on phytoplankton	One detrital group.	Four detrital groups, one of which was carcasses	Two detrital groups (general & macrophyte detritus)

(continued on next page)



Table 1 (continued)

Characteristic	South Georgia (Hill et al., 2012)	West Antarctic Peninsula (Ballerini et al., 2014)	Ross Sea (Pinkerton et al., 2010)	Prince Edward Islands (Gurney et al., 2014)
Estimation of energetic parameters*	Multiple methods, including some adjustments during balancing	Consistent methods used for each parameter: P/B based inlife history; AE (Assimilation Efficiency) and PE (Production Efficiency) based on organism type and diet R (Respiration) = 1-PE. Gross growth efficiency = AE*PE.	Multiple methods, including adjustments during balancing.	Multiple methods: field estimates where possible; Mammal and bird Q/B extensively refined using bioenergetics modelling.
Assimilation efficiency (AE)*	Ecopath default (0.8)	Various (range 0.70–0.93)	Various (range 0.70–0.84)	Various (range 0.76–0.90)
Primary production estimation*	Minimum PP required to support consumption.	Minimum PP required to support consumption.	Estimated from observations.	Estimated from observations.
Acknowledged issues*	Setting EE = 1 might underestimate input to detritus pool. Heterotrophic bacteria feed exclusively on detritus which is “not technically accurate”. The study identified data issues including uncertain estimates of fish biomass.	Setting EE = 1 might underestimate input to detritus pool. Intra-guild predation on benthic invertebrates and microplankton was not explicitly modelled but is accounted for by reducing their gross growth efficiency by 50%.	Limited information on seasonal presence of apex predators and their diets.	Many EEs are well below 1. Discussed as an issue perhaps relating to data. Considered appropriate as there is an important benthic-pelagic coupling occurring in this system.

Characteristics labelled \* contribute to model personality. The “System type” summarises key model features and ecological information including surface temperature (T) in January/July (2000–2010 mean) and day length (DL) on 1st January/1st July.

models by applying a consistent approach to inclusion and parameterisation of bacteria. We used the energetic and ecotrophic efficiency parameters (P/B, P/Q, EE) from water column bacteria in the published Ross Sea model as the starting point for this parameterisation. Bacteria were specified as detritus feeders but we did not add any new consumption of bacteria to models where none was specified (West Antarctic Peninsula and Prince Edward Islands). Initial bacteria biomass was estimated from production, and consumption where available. All bacteria parameters in the original model versions were adjusted for balance simultaneously with other parameters (Section 2.3.4). These balanced bacteria parameters were then propagated into the aggregated models, and the balanced bacterial biomass propagated into the standardised models.

The original and aggregated versions of each model grouped air-breathing vertebrates on the basis of taxonomy and fish on the basis of either taxonomy or habitat. Therefore all vertebrate groups from the original models were either preserved, or combined to form the re-aggregated groups. It was necessary to split the biomass of some of the original plankton groups between two of the aggregated groups. The proportions assigned to each group were decided by the lead authors of the original models based on their knowledge of the initial parameter calculations (e.g. the large crustacean group in the original Prince Edward Islands model was divided 88:12 between euphausiids and macrozooplankton in the aggregated model versions. See Supplementary Information).

Unlike the other three models, the South Georgia model included feeding on prey species outside the modelled arena. This prey biomass and the predator biomass that it supports was not supported by primary production in the modelled arena. In our aggregated and standardised versions of the South Georgia model this prey biomass was represented using an “External” group. This group was presented as a primary producer to allow the models to balance, although it was excluded from model-based estimates of primary production. The Ross Sea model also included the net export of material using non-zero values for net migration rate (Christensen and Walters, 2004). These exports were represented in all of our versions of the Ross Sea model.

The two high latitude models (West Antarctic Peninsula and Ross Sea) included ice algae while the South Georgia and Prince Edward Islands models did not. The original West Antarctic Peninsula model did not include toothed whales and the original Prince Edward Islands model did not include baleen whales. These contrasts were retained in the aggregated and standardised versions. We performed a series of tests to evaluate the influence of these differences in the number of functional groups and the treatment of external feeding on our results (see Section

2.4).

Aggregation into a smaller number of comparable functional groups removes one of the key elements of model personality, but at the cost of reduced detail in some models. Such lost detail includes the structure of the sea-ice community from the Ross Sea model (Bradford-Grieve, 2014; Pinkerton et al., 2010) and macrophytes and associated detritus from the Prince Edward Islands model (Gurney et al., 2014). Guidelines for aggregation of groups include guarding against aggregation of serially linked groups (Fulton et al., 2003). In the case of detrital groups such aggregation was unavoidable. Although detrital groups in the original Ross Sea model were linked by the non-trophic transfer of material between groups, the removal of these non-trophic connections increases comparability with the other models and is consistent with the Ecopath framework (Christensen et al., 2005).

The input parameters for the aggregated versions of the models were calculated from the input parameters of the original versions (converted to Carbon currency where necessary). The biomass of each aggregated group was the summed product of the biomass of its components. The P/B, Q/B and AE of each aggregated group was the biomass-weighted mean of the values of its components. The diet of each aggregated group was calculated by first expressing the diet of each component predator in terms of the aggregated prey groups, second calculating the consumption-weighted mean contribution of each prey item and third rescaling these consumption-weighted mean contributions to sum to 1 (see Supplementary Information for equations).

### 2.3.3. Standardisation of energetic parameters

In the standardised versions of each model we assume that the energetic parameters (P/B, Q/B and AE) for each aggregate functional group do not vary between regions. For example, the annual prey consumption (as a proportion of body mass) by a large demersal fish is the same whether it feeds in the Ross Sea or at South Georgia. The standardised value for each parameter was the average of values for the relevant functional group across the set of aggregated versions of the models (see Section 3.2). These values are plausible given that the component model-specific values are also plausible, but they are not definitive.

Regional differences in these parameters are certainly possible due, for example, to differences in water temperature, food type, behaviour or average size. However, these actual differences are likely to be smaller than the disparities between the published models, which result more from scarce information and which publications the modelers consulted. The key exception is potentially the P/B for primary producers which can vary with temperature, nutrient supply, ice cover and

**Table 2**  
The metrics used to compare models.

Metric	Name	Description	Reference
TE	System-level Transfer Efficiency	Geometric means of transfer efficiency across (decomposed) trophic levels II, III and IV.	Ulanowicz (1995); Christensen and Walters (2004)
SOI	System Omnivory Index	Average omnivory index (OI) of consumers, weighted by the zero-inflated logarithm of each consumer's food intake as a fraction of all consumption.	Adapted from Christensen and Walters (2004)
NAsc	Normalised Ascendency	'System development' index which combines total system throughput with the link structure and is linked to maturity of the system. Here Normalised Ascendency is calculated using flows normalised by Total System Throughput (Fath and Borrett, 2006)	Adapted from Ulanowicz and Norden (1990); Ulanowicz (1997); Ulanowicz (2004)
Con	Connectance	The proportion of direct connections present = $L/n^2$	Basic measure
LD	Link Density	Average number of links per node = $L/n$	Basic measure
PPR	Pathway Proliferation Rate	Measures how fast the number of links between two groups increases with the length of the paths	Fath and Borrett (2006)
FCI	Finn Cycling Index	Cycling index for throughflow which represents whether the flow exiting a compartment will return again.	Finn (1976), Finn (1978)
APL	Average Path Length	Measures the tendency for material to cycle within the system (network aggradation)	Fath and Borrett (2006)
IFI	Indirect Flow Intensity	Quantifies whether indirect effects have greater importance than direct effects.	Higashi and Patten (1989)
HMGO	Output-oriented Network Homogenization Ratio	Ratio of variation in the direct and indirect flows to measure the extent to which flows are more 'even' after accounting for indirect flows.	Fath and Patten (1999)
AMPO	Output-Oriented Network Amplification Ratio	Measures the degree to which indirect flows lead to stronger interactions than direct flows.	Fath and Borrett (2006)
synF	Flow-based network Synergism	Tests whether net positive interactions ('utility') between groups outweigh net negative interactions in terms of total flow affected.	Patten (1991), Fath and Patten (1998)
mutF	Flow-based network Mutualism	Measures whether there are more positive interactions ('utility') than negative in terms of number of interactions.	Fath and Borrett (2006)
AscCap	Ascendency-to-Capacity Ratio	System development expressed as a proportion of capacity (potential for further system development).	Ulanowicz and Norden (1990), Ulanowicz (2004)
AMI	Average Mutual Information	Measures the average amount of 'constraint' exerted upon flow passing from any one compartment to the next.	Ulanowicz (1997), Latham and Scully (2002), Canning and Death (2018)
PP	Model-based primary production estimate	Sum of production and for all primary producers	

$L$  = number of links;  $n$  = number of nodes (functional groups);  $A$  = adjacency matrix (Fath and Borrett, 2006).

water clarity. For the purposes of the current study we standardised P/B for this functional group as well as all the others. This potentially exaggerates between-version differences in primary production compared to the alternative of maintaining regionally distinct P/B values. Increased between-version differences might reduce the number of regional contrasts that appear robust to model personality (i.e. they might increase the number of false negatives but not of false positives).

We did not standardise ecotrophic efficiency (EE) which is adjusted during model balancing (see Pinkerton et al., 2010) and could be regarded as an emergent property indicating the 'tightness' of ecological coupling. However, information on EE is particularly uncertain and EE values are also subject to the preferences of different modelling teams. While our approach is tenable, we suggest that future work should consider whether to standardise EE across models as a pre-balancing step.

### 2.3.4. Model balancing

Each version of each model was balanced using the method of Pinkerton et al. (2010) which simultaneously adjusts all parameters (i.e. biomass, energetic parameters, diet and EE). This approach takes into account the uncertainty in each parameter (akin to the Ecopath 'pedigree' approach; (Christensen and Walters, 2004; Kavanagh et al., 2004)) and the large range of trophic flows (>6 orders of magnitude). The relative uncertainty factors (K), which control the degree of adjustment permitted to each parameter, were made consistent across all models to eliminate the effects of pedigree uncertainty between models. The values used for all model versions were: B ( $K_B = 1.2$ ), P/B ( $K_{PB} = 1.0$ ), P/Q ( $K_{PQ} = 0.3$ ), EE ( $K_{PB} = 0.3$ ) and diet ( $K_D = 1.0$ ), which are the same as the values used for parameters based on "poor information" in the original Ross Sea model (Pinkerton et al., 2010). Other parameters, controlling non-trophic transfers (growth and export) were held constant during balancing. For the standardised models, we used these same values for  $K_B$  and  $K_D$  but set  $K_{PB} = 0$  and  $K_{PQ} = 0$  so that energetic parameters were held constant.

### 2.3.5. Model metrics

A large range of metrics are available to describe the structure and flows of energy through ecosystems. We selected a set of 16 such metrics to compare models. We included the 12 key 'Network Environ Analysis' metrics identified by Fath and Patten (1999) to characterise the complex structure and behaviour of ecological systems. We also included three network metrics that have been recognized as key descriptors of marine food-webs since the work of Fath and Patten (1999) (Fulton et al., 2005; Heymans et al., 2014; Eddy et al., 2020; Armengol et al., 2019). These were: (1) Transfer Efficiency; (2) a modified System Omnivory Index (Christensen and Walters, 2004) and; (3) A normalised version of Ascendency (Ulanowicz, 1997, 2004; Ulanowicz and Norden, 1990). Finally, we included modelled Primary Production as an indicator of productivity and biomass.

Our calculation of System Omnivory Index was modified from Christensen and Walters (2004) who defined it as the Average Omnivory Index (OI) of all consumers when each is weighted by the logarithm of the consumer's food intake. Weighting in this way depends on the absolute values of consumption and so is arbitrary. Instead, we weighted the individual OI by  $\ln(1 + Q_i)$ , where  $Q_i$  is the consumption by group  $i$  divided by the total consumption by all groups. This means all weightings are independent of the absolute consumption values and is true to the intention of Christensen et al. (2005).

Our Normalised Ascendency is calculated after normalizing all flows by Total System Throughput, a measure of the overall energy flow (Fath and Borrett, 2006), to remove the influence of absolute production.

Our primary interest was in the distribution and structure of energy flows between groups of organisms so we used mainly throughflow-based metrics. The relative biomass of organisms within a model affects some of our metrics but, with the exception of Primary Production, they are not influenced by between-model differences in absolute biomass or production. Nonetheless, differences in absolute production and biomass are an important influence on ecosystem function (Heymans et al., 2014). We examined these differences by including modelled Primary Production in our set of metrics, and exploring its relationship with modelled consumer biomass and independent

observation-based estimates of primary production.

### 2.3.6. Primary production data

We used observation-based estimates of summer and autumn (December to March) net primary production (NPP) (Arteaga et al., 2018) for the period 2007–2015 (the period for which these data are available) to provide an independent indicator of biomass and production in each model location. These estimates are based on monthly chlorophyll data from two sources resolved to a spatial scale of  $1^\circ$  by  $1^\circ$ . The sources are level 3 MODIS products and phytoplankton carbon biomass data from the Cloud-Aerosol Lidar with Orthogonal Polarization sensor (Hunt et al., 2009; Winker et al., 2009), converted using the Chl:C ratio  $0.01 \text{ g g}^{-1}$  (Arteaga et al., 2018). We mapped the domain of each model onto the data grid and calculated a monthly climatology for each grid cell as the average monthly NPP over all years. We then calculated the December to March climatology for the model domain as the mean of all relevant grid-cell specific monthly climatologies, ignoring missing data which indicate ice cover or land mass.

December to March represents a period of increased primary productivity in all four model locations. Our index is largely independent of data used to parameterize the models, except for 2 years of overlap (2007 and 2008) with the data used to parameterize the Prince Edward Islands model. The index therefore provides a general measure of ecosystem productivity that is not tied to the specific status during the period represented by any model.

### 2.4. Analysis

We applied two-way analysis of variance with post hoc Tukey tests to examine the relative importance of between-model and within-model differences in each network metric. We also examined changes in the rank order of the models for each metric across the set of versions to determine how each of our treatments affects model comparison based on these metrics.

To test whether the representation of external feeding in the South Georgia model affects conclusions about between-model and between-version differences, we repeated the analysis of variance excluding the metrics from the South Georgia model. To test whether between model differences in the number of functional groups affects conclusions, we examined the correlation between the value of each metric and the number of functional groups per model in each of the versions.

## 3. Results

### 3.1. Model personality

Table 1 describes the four original published models in terms of the twenty one characteristics identified by the respective lead authors as capturing the main differences in their approaches. All models use the Ecopath identities to provide an annualised snapshot of a regional food-web. However they vary in terms of every listed characteristic including model scale, focal time frame and number and type of functional groups. Other differences include the process for estimating energetic parameters, the range of parameters affected by the balancing process, and the treatment of primary production. Each of these has important implications for model interpretation.

### 3.2. Biomass differences

The rank order of models in terms of both consumer (protozoans to whales) biomass (per unit area) and primary production was consistent across all model versions with South Georgia having the highest biomass and production, followed by the West Antarctic Peninsula, the Ross Sea and finally the Prince Edward Islands (Fig. 2). Consumer biomass spanned four orders of magnitude across the models in each version and primary production spanned two orders of magnitude. Consumer

biomass and primary production were strongly correlated across models within each version ( $r > 0.98$ ,  $p < 0.01$ ). The ratio of consumer biomass to primary production varied between versions and models from 2.67% in the original Prince Edward Islands model to 6.31% in the original South Georgia model.

Modelled consumer biomass and primary production were both significantly correlated with new observation-based estimates of primary production within each of the versions. None of the network metrics were significantly correlated with either observation-based or model-based estimates of primary production in any of the versions (recalling that our Normalised Ascendency is deliberately independent of primary production). However, with a low sample size (4), the power of these tests was also low. Four of the tests resulted in (absolute) correlation coefficients between 0.80 and 0.87, for which power was 0.28–0.36.

Modelled primary production in the South Georgia and West Antarctic Peninsula models exceeded the relevant new observation-based estimates. Conversely, modelled primary production was lower than the new observation-based estimates in the Ross Sea and Prince Edward Islands models, which were informed by chlorophyll observations.

### 3.3. Energetic parameters

The aggregated versions of the models allow an examination of between-model differences in energetic parameters within comparable functional groups. The only parameter that was consistent across all four models was AE for macrozooplankton, which had the Ecopath default value of 0.8 (Table 3). The range of coefficients of variation (CVs) for P/B (for non-primary producers) was 0.33–1.11 and that for Q/B values was 0.23–1.61. The CVs for P/B were correlated with those for Q/B ( $r =$

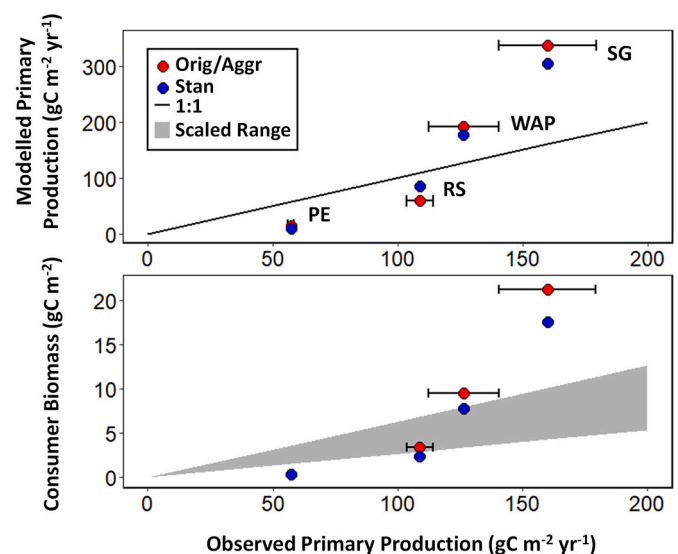


Fig. 2. Relationship between an independent observation-based estimate of primary production (mean and standard error across all pixels with valid data) and (top) modelled primary production, and (bottom) modelled consumer biomass (protozoa to whales) in each of the four regional food-web models (SG = South Georgia, WAP=West Antarctic Peninsula, RS = Ross Sea, PE = Prince Edward Islands, Orig = original, Aggr = aggregated and Stan = standardised model versions). The 1:1 line indicates equivalence between observation-based estimates and modelled primary production. The “Scaled range” envelope indicates the range of consumer biomass values that are consistent with the observation-based primary production estimate given the ratios of consumer biomass to primary production in the various models (i.e. the product of observation-based primary production and modelled consumer biomass/modelled primary production). The units of the observation-based primary production estimates have been converted to those of the model-based estimates.

**Table 3**

Mean and CV of energetic parameters by functional group in the set of aggregated models (see Supplementary Information for full details of functional groups and values by model).

Group	N	P/B		Q/B		1-AE	
		Mean	CV	Mean	CV	Mean	CV
Detritus	4						
Small phytoplankton	4	87.94	0.49				
Large phytoplankton	4	62.30	0.24				
Ice algae	2	35.19	1.06				
Bacteria	4	28.98	0.65	109.13	0.75	0.17	0.71
Microzooplankton	4	37.68	0.50	154.40	0.55	0.19	0.06
Mesozooplankton	4	7.62	0.55	44.09	0.94	0.24	0.20
Salps	4	9.19	1.11	290.38	1.41	0.22	0.22
Euphausiids	4	3.09	0.95	17.26	0.85	0.22	0.17
Macrozooplankton	4	6.21	1.01	48.17	1.24	0.20	0.00
Benthos	4	0.98	0.99	11.31	1.61	0.27	0.39
Cephalopods	4	5.28	0.46	19.09	0.43	0.20	0.00
Pelagic fish	4	0.74	0.55	4.95	0.63	0.22	0.16
Demersal fish	4	0.31	0.33	2.38	0.51	0.22	0.16
Flying seabirds	4	0.21	1.05	75.80	0.72	0.21	0.40
Penguins	4	0.19	0.34	30.10	0.70	0.23	0.25
Baleen whales	3	0.03	0.41	5.31	1.15	0.16	0.48
Toothed whales	3	0.04	0.34	5.61	0.23	0.17	0.35
Seals	4	0.13	0.63	15.32	0.70	0.16	0.30
External prey	1	3.68					

N shows the number of models contributing to each value. The means were used as the values of energetic parameters in the standardised models.

0.68,  $n = 16$ , one-tailed  $p = 0.002$ ) indicating that high between-model variability in one parameter is associated with similarly high variability in the other. The groups with the highest variability included salps, macrozooplankton, seabirds, benthic invertebrates and euphausiids. The P/B of ice algae was seven times higher in the West Antarctic Peninsula model than in the Ross Sea model.

### 3.4. Between and within-model differences

The Supplementary Information provides the full set of parameters and output metrics for three versions of each model. Our two interventions (aggregation and standardisation) made a discernible difference to most model metrics (Fig. 3). Our key concern is whether these differences affect the perceived differences between models. For five metrics (System Omnivory Index, Link Density, Finn Cycling Index, Indirect Flow Intensity and Primary Production), the rank order of models was unaffected by the interventions (i.e. the lines do not cross in Fig. 3). Aggregation changed the rank order of models in nine metrics and standardisation changed the order in seven metrics (including five that were affected by aggregation). The greatest changes occurred in the Ross Sea model for eleven metrics, the South Georgia model for three metrics and the Prince Edward Islands model for two metrics. For six of these metrics (Normalised Ascendency, Pathway Proliferation Rate, Network Homogenization Ratio, Mutualism, Ascendency to Capacity Ratio and Average Mutual Information) the rank order of the three least affected models was not changed by the interventions. Based on these qualitative results, we highlight the metrics that were unaffected by interventions because these will be more robust for comparing models with different personalities. The remaining metrics are useful for identifying where personality drives differences in model output.

Analysis of variance provides a more formal assessment of between-model differences in the context of differences in model personality. This identified that fourteen of the sixteen metrics varied significantly ( $p < 0.05$ ) between models and that five also varied significantly between versions (Table 4). Average Mutual Information and Normalised Ascendency were the only metrics that did not vary significantly between either models or versions ( $p > 0.3$ ).

For four of the metrics that varied significantly between versions (Connectance, Link Density, Mutualism and Synergism), the greatest

changes occurred on aggregation. Consequently post hoc Tukey tests identified significant differences between the original versions and both the aggregated and standardised versions. For Ascendency to Capacity Ratio *post-hoc* Tukey tests identified a more significant change associated with standardisation. *Post hoc* tests suggest that the least similar models were those for the Ross Sea and the Prince Edward Islands which showed significant contrasts ( $p < 0.05$ ) in ten of the sixteen metrics. The most similar models by this criterion were those for the two ice-free locations, South Georgia and the Prince Edward Islands. The only metric that showed significant differences in each model pair was the single biomass indicator, Primary Production.

Two models becoming more similar after intervention (i.e. converging lines in Fig. 3) indicates that the initial difference between the models was partly due to an aspect of model personality that was controlled in the intervention. Significant contrasts between such models could therefore be due, in part, to differences in model personality. Nineteen of the thirty-four significant contrasts ( $p < 0.05$ ) fall into this category. When these are excluded there are still eleven contrasts in network metrics and four in primary production (the “robust contrasts” in Table 4). The Prince Edward Islands model contrasts with the Ross Sea and West Antarctic Peninsula models in terms of four metrics (Link Density and Pathway Proliferation Rate for both, plus Ascendency-to-Capacity Ratio and Primary Production in the Ross Sea model, and Normalised Ascendency and Output-oriented Network Homogenization Ratio for the West Antarctic Peninsula model) and the South Georgia model contrasts with the Ross Sea and Prince Edward Islands models in terms of a single metric (Primary Production and Link Density respectively).

### 3.5. Potential bias effects

When the ANOVA was repeated without the South Georgia data to exclude the influence of modelled external feeding, the results were qualitatively similar to those in Table 4. However the model effect  $p$ -values were raised above 0.05 for six metrics and the version effect  $p$ -values were raised above 0.05 for three metrics. Of these, Indirect Flow Intensity was the only metric for which the effect became non-significant when the South Georgia data were excluded from the analysis but remained significant when each other model was excluded instead. Thus, it is possible that the apparent model effect for Indirect Flow Intensity is a consequence of the representation of external feeding in the South Georgia model.

Out of 48 potential correlations between metric value and the number of functional groups, only one (with Link Density in the original model as the dependent variable) was significant at  $p < 0.05$ . This result is expected as Link Density is a function of the number of functional groups, which was not standardised in the original model versions. For the remaining metrics there is no evidence that between-model differences in the number of functional groups affected the outcome of the analysis of variance (but the power of these tests was 0.13–0.30).

## 4. Discussion

Models are imperfect representations of nature but can nevertheless be useful for understanding it. The existing set of regional scale ( $<10^6$  km<sup>2</sup>) food-web models is an important resource for exploring regional differences in the structure and function of the Southern Ocean ecosystem (Gurney et al., 2014; Murphy et al., 2012, 2013, 2016). Our Introduction identifies three key sources of uncertainty that might affect such exploration. Substantial progress has been made in methods to characterise and explore the first of these, parameter uncertainty (e.g. Guesnet et al., 2015; Steenbeek et al., 2018; Ruzicka et al., 2019). The second, model uncertainty, can be addressed by using alternative model structures (Hill et al., 2007), although studies which do so generally focus on a single region (e.g. Smith et al., 2015). The third source, model personality, has been partially addressed by various attempts to



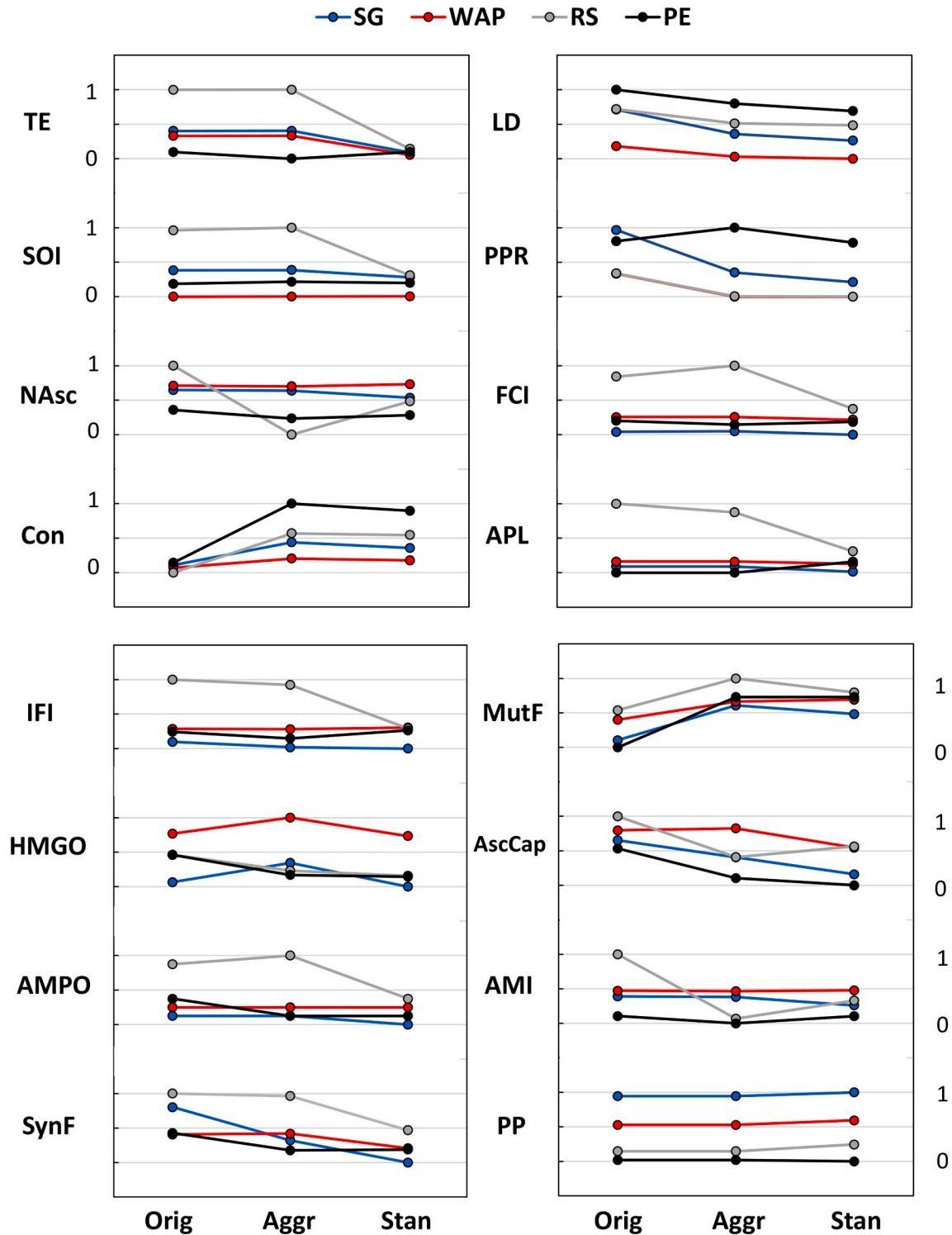


Fig. 3. Between-model (SG = South Georgia, WAP = West Antarctic Peninsula, RS = Ross Sea, PE = Prince Edward Islands) and between-version (Orig = Original with carbon currency, Aggr = Aggregated, Stan = Standardised energetic parameters) differences in sixteen model metrics (Table 2). The metrics are rescaled between 0 and 1.

standardise the practice of constructing Ecopath models (Christensen and Walters, 2004; Christensen et al., 2005; Heymans et al., 2016; Link, 2010) and by identifying network metrics that are robust to aspects of model construction (Fulton et al., 2005; Heymans et al., 2014). It is apparent that the way organisms are aggregated affects model outputs (Gaichas et al., 2009; Heymans et al., 2016; Pinnegar et al., 2005) and it follows that different approaches to selecting energetic parameters will

also have an effect. Consequently, there is a risk that any differences in model outputs might reflect these aspects of personality rather than real ecological differences between regions.

Our analysis shows that between-model differences in a suite of metrics are generally greater than between-version differences when successive versions sequentially remove aspects of personality (Fig. 3). Between-model differences are also apparent in four of five network

**Table 4**

Results of two-way analysis of variance and post hoc Tukey tests applied to fifteen network metrics and model-based primary production estimates (see Table 2 for abbreviations and details).

Metric	MODEL			VERSION											
	F	P		SG- WAP	SG- RS	SG- PE	WAP -RS	WAP -PE	RS- PE	F	P	o-a	o-s	a-s	
TE <sup>4</sup>	4.76	0.050							*	3.43	0.102				
SOI <sup>1,4</sup>	8.83	0.013					*		*	1.44	0.309				
NAsc	1.67	0.271						*		1.42	0.313				
Con	4.87	0.048								8.63	0.017	*	*		
LD <sup>1,3,4</sup>	79.57	<0.001	**		**	**	**	**	**	25.11	0.001	**	**		
PPR	10.79	0.008						*	*	3.93	0.081				
FCI <sup>1,3,4</sup>	11.34	0.007		**			*		*	1.30	0.339				
APL <sup>3,4</sup>	7.99	0.016		*			*		*	0.74	0.518				
IFI <sup>1,2,4</sup>	6.67	0.024		*					.	0.96	0.435				
HMGO	12.78	0.005	**				*	*		1.88	0.232				
AMPO <sup>4</sup>	9.75	0.010		**			*		*	2.12	0.202				
synF <sup>4</sup>	6.22	0.028		.			.		*	6.80	0.029	*			
mutF <sup>4</sup>	5.00	0.045		*						17.44	0.003	**	**		
AscCap <sup>3</sup>	7.97	0.016						*	*	9.41	0.014	.	*		
AMI	1.95	0.224								1.38	0.322				
pp <sup>1,4</sup>	653.14	<0.001	***	***	***	***	***	***	**	4.07	0.077				
Contrasts (P<0.05)				3	6	2	7	6	10				4	4	0
Robust contrasts (P<0.05)				<u>2</u>	<u>1</u>	<u>1</u>	<u>3</u>	<u>4</u>	<u>4</u>						

Columns show the F statistic and *p*-value associated with each of two independent variables: model (SG = South Georgia, AP=West Antarctic Peninsula, RS = Ross Sea, PE = Prince Edward Islands) and version (o = original, a = aggregated, s = standardised), as well as the significance level of contrasts between models and versions identified by the Tukey tests (\*\**p* < 0.001, \*\* = *p* < 0.01, \* = *p* < 0.05, . = *p* < 0.1). Shading indicates “Robust contrasts” (i.e. those which are not affected by differences in aggregation or energetic parameters in the original model). Footnotes identify metrics that provided results that were consistent across model versions, and metrics that were sensitive to specific aspects of model personality.

<sup>1</sup>Rank order of models is consistent across model versions, indicating that the metric is useful for comparing models with different approaches to aggregation and energetic parameters.

<sup>2</sup>The significant contrasts in IFI might be influenced by the representation of external feeding in the South Georgia model.

<sup>3</sup>The significant contrasts which are not underlined are influenced in part by the different approaches to aggregation in the original model versions.

<sup>4</sup>The significant contrasts which are not underlined are influenced in part by the different approaches to energetic parameters in the original model versions.

metrics that show significant between-version differences. This suggests that, for most combinations of model and metric, neither the aggregation scheme nor the energetic parameters were the main cause of differences between models. Rather, the differences were largely due to contrasts in diet matrices and relative biomass. We also identified four network metrics (System Omnivory Index, Link Density, Finn Cycling Index, Indirect Flow Intensity) in which the rank order of models was consistent across model versions, suggesting that they are useful for comparing models assembled using different approaches to aggregation and energetic parameters.

Nonetheless, aggregation caused significant changes in four metrics. Aggregation can help to reduce the influence of differences in model topology on between-model comparisons (Gaichas et al., 2009; Heymans et al., 2016; Pinnegar et al., 2005) but our results suggest that it can also be a major influence on some model outputs. The effects on Connectance and Link Density are predictable consequences of reducing the number of functional groups, but it is noteworthy that aggregation inflated Mutualism in all models and also affected estimates of Synergism.

Sensitivity to aggregation and standardisation of energetic parameters varied between models with the Ross Sea model proving most sensitive. This indicates that the original Ross Sea model is the least typical of the set, as evidenced by the fact that it occupies an extreme position in terms of 12 of 16 metrics (Fig. 3). For example the high

Transfer Efficiency in the original Ross Sea model reflects, inter alia, high production to consumption and ecotrophic efficiency in meso-zooplankton compared to the other models.

In some cases aggregation or standardisation reduced between-model differences, indicated by converging lines in Fig. 3. This affects nineteen of the thirty-four significant between-model contrasts (Table 4) and indicates that the contrasts were influenced, in part, by different aggregation schemes or energetic parameters in the original model versions. The single example of each model-version combination precludes statistical comparison of models within versions, so it is not currently possible to quantify the impact of model personality on the significance of these contrasts. Methods which generate multiple randomized versions of a given food-web model (e.g. Guesnet et al., 2015; Steenbeek et al., 2018; Ruzicka et al., 2019) would be useful for exploring these impacts. Nonetheless the remaining “robust” contrasts, eleven in network metrics and four in primary production, are due entirely to differences in relative biomass and diet matrices. These robust contrasts include all significant contrasts in Normalised Ascendency, Pathway Proliferation Rate and Output-oriented Network Homogenization Ratio.

Given the pervasive nature of model personality it is important to ask whether any of the between-model contrasts are likely to represent real ecological differences. The spatial differences in biodiversity and feeding relationships in the Southern Ocean (Moloney and Ryan, 1995;

Griffiths, 2010; McCormack et al., 2020) inevitably influence model input data and therefore output metrics. The robust contrasts in network metrics suggest hypotheses about spatial differences in diets and relative biomass. For example, contrasts in Link Density suggest that diets are most diverse at Prince Edward Island while contrasting Output-oriented Network Homogenization Ratios suggest that trophic flows are more even at the West Antarctic Peninsula than at South Georgia. Evaluating these hypotheses requires consideration of the uncertainties in biomass and diet parameters. These uncertainties arise from multiple factors including incomplete data; taxonomic and spatial bias in sampling; seasonal, inter-annual and spatial variability in the parameter of interest; methodological differences between samples, and the effects of temporal and trophic aggregation during model construction. We cannot therefore exclude the possibility that some of the eleven contrasts are affected by assumptions made in the development of the original models. However, it is clear that understanding regional differences in relative biomasses and feeding relationships is the key to identifying genuine differences in the structure and function of regional ecosystems. This adds weight to calls for more systematic diet analysis (Newman et al., 2019) and for new approaches to surveying biomass across trophic levels (Smith et al., 2019).

Regional differences in absolute biomass also affect ecosystem structure and function (Heymans et al., 2014). The models imply regional differences in consumer biomass per unit area that span four orders of magnitude (Fig. 2). These differences are underpinned by differences in modelled primary production which are correlated with new, independent estimates (Arteaga et al., 2018). The variability in this relationship reflects differences in both model construction and ecology. For example, the estimates of primary production from the South Georgia and West Antarctic Peninsula models were based on consumption and were greater than the corresponding independent estimates, while those from the other models were based on sea colour observations and were smaller than the independent estimates. Consumer demand relative to primary production could plausibly be highest at South Georgia and the West Antarctic Peninsula since these systems have a net import of zooplankton (Murphy et al., 2013).

Our analysis suggests that while model personality is an important influence on model outputs, the influence of assumptions about aggregation and energetic parameters was generally smaller than that of relative biomass and diet matrices. Our work identifies two sets of metrics which are useful for comparing regional food-webs because either their results were consistent across model versions or because they identified robust significant differences between models (see Table 4 footnotes). Both sets of metrics include Primary Production and Link Density. Most of the metrics describe aspects of network structure and are therefore complimentary to the seven additional, mainly storage-based, metrics that Heymans et al. (2014) found to be robust to aspects of model construction. While both the current study and Heymans et al. (2014) identified Ascendency-to-Capacity Ratio as a useful metric, our results suggest that such metrics may not be completely robust to model personality. We therefore recommend that future model-based food-web comparisons should report aspects of model personality including between-model differences in aggregation schemes and energetic parameters and assess their influence as we have done here.

Murphy et al. (2012) identified the need for a systematic analysis of regional food-web structure and function using models based on, inter alia, improved agreement about energetic parameters and the construction of functional groups. This agreement remains to be reached and, in the case of functional groups, would require consistent objectives for model construction. In the meantime, we have demonstrated that informed use of the regional food-web models developed in the absence of such agreement (i.e. with inconsistent functional groups and energetic parameters) is useful for exploring regional differences in food-webs.

## Declaration of Competing Interest

Noe.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jmarsys.2021.103556>.

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