Trophic-based analyses of the Scotia Sea ecosystem with an examination of the effects of some data limitations and uncertainties

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Abstract

The Scotia Sea is a sub-region of the Southern Ocean with a unique biological operation, including high rates of primary production, high abundances of Antarctic krill, and a diverse community of land-breeding predators. Trophic interactions link all species in an ecosystem into a network known as the food web. Theoretical analyses of trophic food webs, which are parameterised using diet composition data, offer useful tools to explore food web structure and operation. However, limitations in diet data can cause uncertainty in subsequent food web analyses. Therefore, this thesis had two aims: (i) to provide ecological insight into the Scotia Sea food web using theoretical analyses; and (ii) to identify, explore and ameliorate for the effects of some data limitations on these analyses. Therefore, in Chapter 2, I collated a set of diet composition data for consumers in the Scotia Sea, and highlighted its strengths and limitations. In Chapters 3 and 4, I constructed food web analyses to draw ecological insight into the Scotia Sea food web. I indicated the robustness of these conclusions to some of the assumptions I used to construct them. Finally, in Chapter 5, I constructed a probabilistic model of a penguin encountering prey to investigate changes in trophic interactions caused by the spatial and temporal variability of their prey. I show that natural variabilities, such as the spatial aggregation of prey into swarms, can explain observed foraging outcomes for this predator. Pressures caused by anthropogenically-driven changes to the earth's climate may alter the community structure in the Scotia Sea. Furthermore, activities by commercial fisheries who operate in the Scotia Sea are increasing, which may impact on the food web. This thesis offers a baseline analysis of the Scotia Sea food web, which will be useful to assess changes to the ecosystem caused by future, external pressures.

Contents

List of tables

List of figures

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Authors declaration

I hereby declare that this submission is my own work except where due acknowledgement is given. This work has not previously been presented for an award at this, or any other, University.

1 Introduction

1.1 Placing the research in the wider context

Global temperatures are predicted to increase due to human enhanced atmospheric carbon affecting the earth's climate [338]. Whilst there are regional differences in temperature trends in the Southern Ocean over the last half of a century, areas in the South West Atlantic sector of the Southern Ocean are the fastest warming areas in the Southern Ocean [236, 320]. Warming is associated with a decrease in winter sea-ice extent, thickness, and duration, with an estimated 7% decade^{-1} decline in sea-ice extent at the Western Antarctic Peninsula [236, 422].

The Scotia Sea in the South West Atlantic sector is a unique ecosystem within the Southern Ocean due to multiple climatic, commercial and ecological factors. This includes a high abundance of the important macro zooplankton, Antarctic krill. If sea-ice reduction continues, this is predicted to have a negative impact on krill populations in the Scotia Sea (and other areas of the Southern Ocean) as the foraging success, breeding success, and distribution of krill are closely linked with winter sea-ice [236]. This could have cascading effects to many higher predators whose diet mostly comprises of krill [236, 262, 436]. Further pressures which may impact on the future of krill populations include their restricted temperature tolerances in a warming ocean, ocean acidification affecting the growth of young krill, unresolved effects of increased UV, and an altered distribution of krill due to changing ocean circulation patterns [236].

Aside from a decrease in krill abundance, predator populations may be affected by habitat changes altering the availability of suitable breeding habitats [243]. Warming is also likely to affect the community structure of phytoplankton which could have knock on effects to the composition of the zooplankton community [236].

Historic activities in the Southern Ocean by commercial fisheries harvesting marine resources including species of baleen whales, seals, penguins and finfish, severely depleted the stocks of many of these species [285]. There is uncertainty as to the extent of species depletion and subsequent recovery of targeted species due to the paucity of pre-exploitation abundance data [285]. This makes it difficult to resolve whether observed changes to Southern Ocean species communities are due to recovery from historic fishing or changes due current climatic factors. Currently, Antarctic krill, mackerel ice fish and the Patagonian toothfish are targeted by commercial fisheries in the Scotia Sea [285]. Demand for these resources is likely to rise due to enhanced fishing techniques, the development of new products which incorporate these species, and to help sustain a growing human population [439, 236].

It is appropriate to study the Scotia Sea ecosystem due to its important and unique biological operation. To assess how the biological community in the Scotia Sea may respond to increasing climatic stresses and resource utilisation, it is first necessary to establish the current structure of the biological component of the Scotia Sea ecosystem. This thesis offers valuable contributions to this aim.

1.2 Introduction to the Scotia Sea

A major feature of the Southern Ocean is the eastward flowing Antarctic Circumpolar Current (ACC). The Southern Ocean is often sub-divided into three segments: the South Atlantic, South Indian and South Pacific sectors. On the westward boundary of the South Atlantic sector, the Antarctic Circumpolar Current is constricted as it flows between Patagonia and the Antarctic Peninsula, an area known as the Drake Passage, see Figure 1.1. The resulting strong flows emerge into the Scotia Sea, where they encounter rugged bathymetry caused by the Scotia Arc [320]. The Scotia Arc includes three archipelagos that approximate the bounds of the Scotia Sea: to the north is the South Georgia archipelago; to the east is the South Sandwich Islands, and on the southern boundary lies the South Orkney archipelago.

The ACC has four associated fronts which are, from north to south, the Sub Antarctic Front, the Polar Front, the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary [335], see Figure 1.1. An important feature of the Scotia Sea is seasonal sea-ice, which greatly influences biological processes. The seasonal sea-ice develops northward from the Weddell Sea (Figure 1.1) during autumn, and shows marked seasonal and inter-annual variation in extent and duration; in some years it can extend as far north as the South Georgia archipelago [320].

1.3 Trophic interactions and food webs

Marine biota are important components of an ecosystem and can alter the physical environment through a complex set of biological, biogeochemical, and physical interactions [278]. One important interaction is formed when an individual consumes another individual, usu-

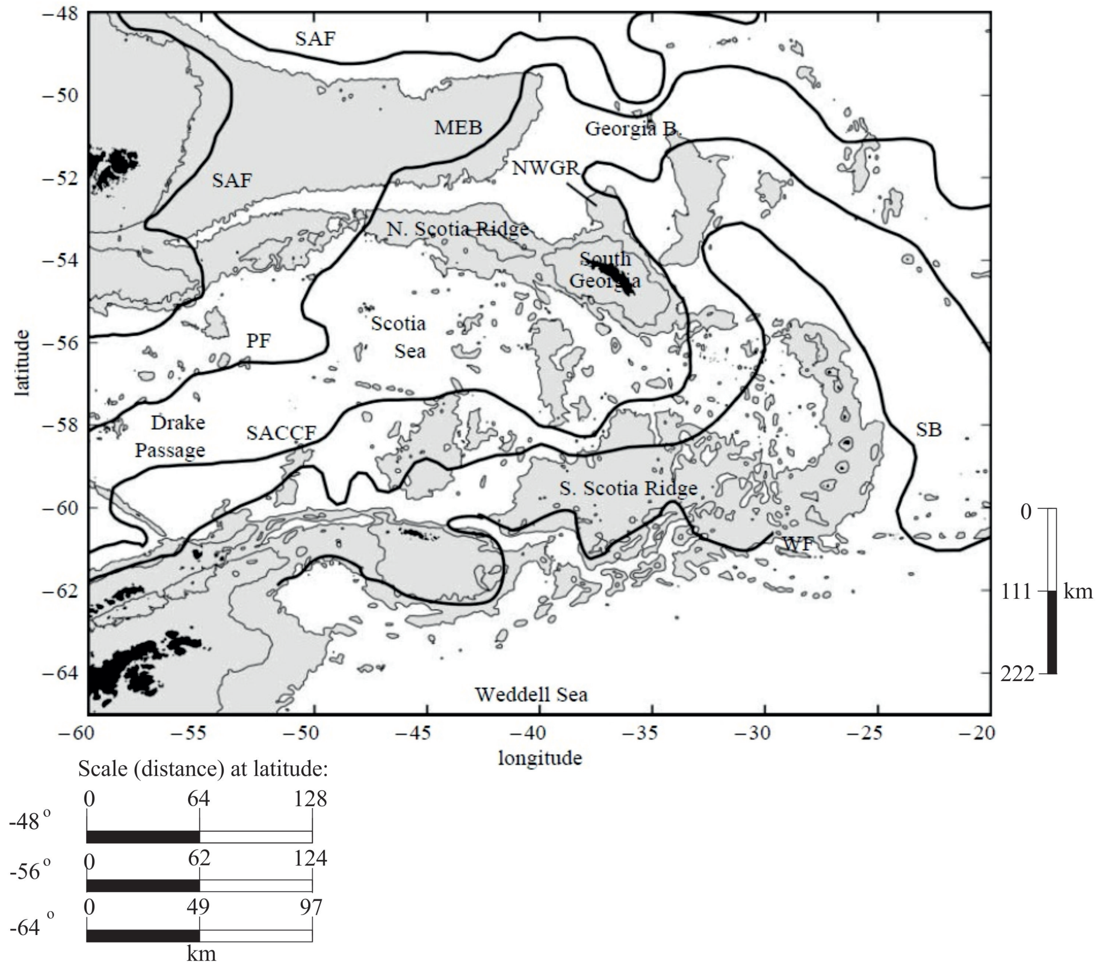

Figure 1.1: Figure adapted from Murphy et al. (2007) [320]. The Scotia Sea and surrounding areas showing the general position of the major frontal systems in relation to bottom topography. Thick black lines refer to the positions of frontal positions identified using the following acronyms: SAF, Sub-Antarctic Front; PF, Polar Front; SACCF, Southern Antarctic Circumpolar Front; SB, Southern ACC Boundary; WF, Weddell Front; MEB, Maurice Ewing Bank; NWGR, North West Georgia Rise. (see Murphy et al. (2012) [320] for references; depth contours shown for 1000 and 2000m.)

ally of a different species to its own, known as a trophic interaction. A trophic view of a food web, here after referred to as a food web, considers the ecosystem as a network made of trophic interactions connecting groups of individuals. As a minimum, groups of individuals in food web analyses are of the same species but can also include individuals from multiple species.

Trophic interactions are important as they can influence the behaviour, condition, and reproductive success of a species, which can ultimately determine community dynamics [149]. Considering the whole food web allows us to examine the direct and indirect influence of one species on all other species within the ecosystem.

1.4 The Scotia Sea food web

Historically, Southern Ocean food webs are thought to be characterized by short trophic pathways from primary producers to higher predators, with Antarctic krill forming an intermediate link between these two groups [320]. Antarctic krill are dominant macro zooplankton consumers in the Southern Ocean and over 50% of krill abundance is estimated to be in the South Atlantic sector of the Southern Ocean [132]. They form important prey for land-breeding predators, cetaceans, fish, and cephalopods.

The abundance of Antarctic krill in the Scotia Sea shows considerable spatial and interannual variation [235]. The mechanisms which drive changes in the abundance and distribution of Antarctic krill in the Scotia Sea are difficult to assess. There are only a few areas thought to be suitable for their successful spawning and recruitment, namely the Western Antarctic Peninsula and the southern Scotia Arc [320]. However, the abundance of Antarctic krill can be high in other areas, particularly the northern Scotia Sea [320, 385, 433]. Their presence in these areas is thought to be a function of the timing and success of spawning events, and favourable conditions for transporting Antarctic krill from their seed population [233, 320, 385]. If Antarctic krill are at low abundance, other zooplankton and fish become more important in the diets of higher predators [320, 445]. Figure 1.2 gives an illustrative example of possible trophic interactions formed at different krill abundances. This evidence has highlighted the complexity and variability of the trophic interactions in the Scotia Sea food web, challenging the very simple krill-centred view [320].

High latitude food webs are highly seasonal; phytoplankton blooms in the Scotia Sea can last between three and five months and, in southern areas, may be associated with the retreat of winter sea-ice [320]. Much less is known about the structure and operation of the Scotia Sea food web in the winter, particularly below the sea-ice. However, for zooplankton species, such as juvenile Antarctic krill, the sea-ice is thought to be an important source of food in the form of sea-ice algae, during the winter months. Additionally winter sea-ice may provide protection for juvenile Antarctic krill from its predators. [320].

Aside from Antarctic krill, other dominant macro zooplankton found in the Scotia Sea are the copepod *Rhincalanus gigas*, species of salp, other krill species in the genus *Thysanoessa*, and Chaetognaths (arrow worms) [301]. The meso zooplankton community is dominated by copepods [447], and the Scotia Sea also has a high abundance of myctophid fish [448, 353].

The pelagic ecosystem is linked to benthic environments through direct trophic interactions, made possible because of the vertical migration of some pelagic species such as Antarctic krill [409], and indirect input into benthic environments by the pelagic community via their contributions to detritus, which sinks to the sea bed [411].

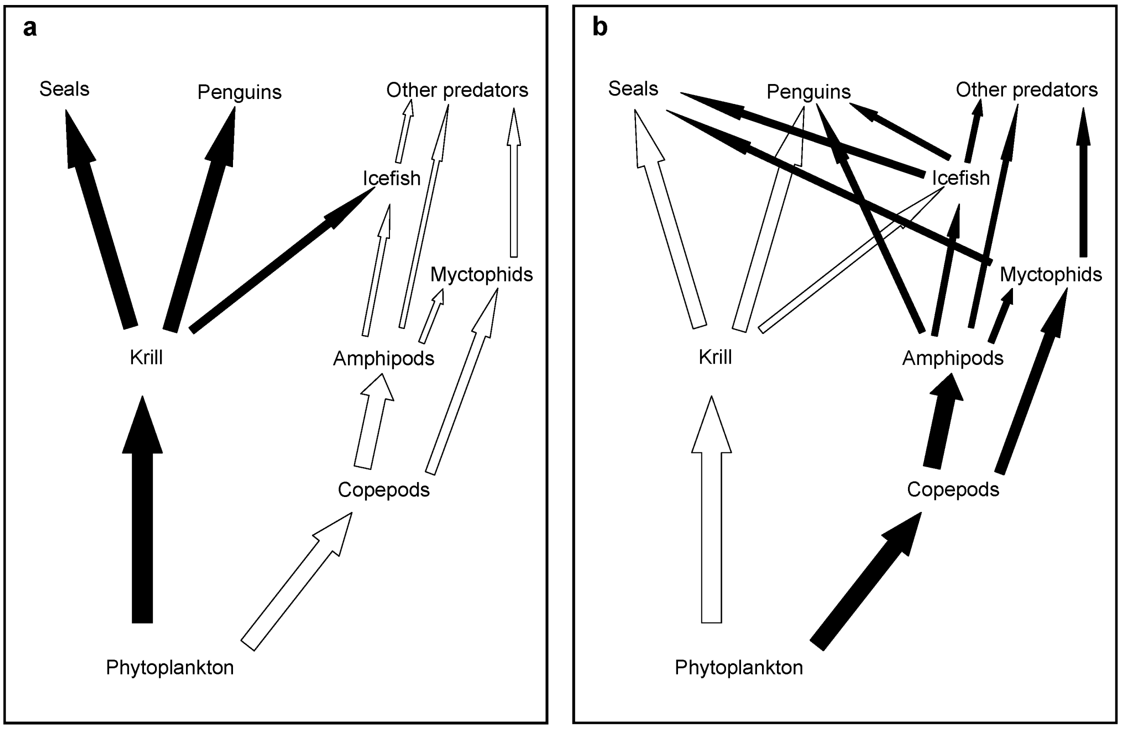

Figure 1.2: Figure from Murphy et al. (2007) [320]. Schematic illustration of alternate pathways in part of the Scotia Sea food web, showing shifts between (a) years when krill are abundant across the Scotia Sea and (b) years when krill are scarce. Major pathways shown as black arrows.

Three important features of the Scotia Sea distinguish it from other Southern Ocean ecosystems:

1. Unlike many areas of the Southern Ocean, which include high concentrations of nutrients but low chlorophyll concentrations, the Scotia Sea includes regions of high nutrients and high chlorophyll concentrations [287, 452];

2. High rates of primary production in the Scotia Sea, supports the largest densities of Antarctic krill found in the Southern Ocean [133, 132];

3. The enhanced pelagic biological activity supports one of the most diverse communities of land-breeding predators in the world, including species of penguin, seal, albatross, and other flying sea birds [320].

Therefore, understanding the trophic dependencies of species in the Scotia Sea ecosystem separate from the Southern Ocean as a whole is appropriate due to its unique biological operation. Furthermore, the Scotia Sea holds stocks of species targeted by commercial fisheries and is an important catch area for these fisheries. The three major species targeted by commercial fisheries are: mackerel icefish (*Champsocephalus gunnari*), the Patagonian toothfish (*Dissostichus eleginoides*), and Antarctic krill (*Euphausia superba*) [285, 323]. The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) manage commercial fisheries in the Antarctic. They are committed to an approach to management which reduces the direct and indirect effects of targeted fishing on the wider ecosystem [196, 285]. To assess the possible impacts caused by fisheries, we must first understand and, where possible, quantify the structure and function of the food web without these external influences.

Furthermore, biological systems are not independent of earth's climate systems [402]. Primary producers use carbon for photosynthesis. The resulting biological production is transferred to non-photosynthetic and heterotrophic organisms via trophic interactions. All living groups can release carbon across a range of oceanic depths through respiration and contributions to detritus, effectively sequestering atmospheric carbon in the ocean [182]. Furthermore, the food web can influence other processes such as nutrient recycling. For example, excretion by whales can increase local iron availability, which is an important element stimulating primary production [292].

1.5 Uncertainties in food web analysis

Food web analyses provide insight into the structure and complexity of trophic interactions between groups of individuals. They have been successfully used to compare ecosystems based on their structure, e.g. de Santana et al. (2013) [401]; to relate features of a food web's structure and diversity to its robustness to change, see Bersier et al. (2007) [281, ch. 11]; to provide insight into the production, biomass and consumption of biota which are difficult to observe, e.g. Ballerini et al. (2014) [141], Hill et al. (2012) [259], and Pinkerton et al. (2010) [358]; to assess how an ecosystem may change under future scenarios such as changes to the availability of important species, e.g. Hill et al. (2012) [259]; to assist with the management of commercial fisheries, e.g. Pinkerton et al. (2010) [358]; and to estimate primary production, e.g. Priddle et al (1998) [364].

Uncertainties can affect the results from food web analyses, and can be introduced from many sources. Figure 1.3 summarises many of the potential sources of uncertainty in the food web analyses relevant in this thesis. However other uncertainties will be unique to an ecosystem and analysis type. Figure 1.3 identifies three levels by which uncertainty can be introduced into food web models, which are all linked.

First, the natural variability in an ecosystem makes it difficult to discern universal patterns in food web structure. Some important natural variabilities in the Scotia Sea food web are: the spatial aggregations of some species into swarms, schools or colonies; regional differences in community composition, temperature, proximity to land etc.; unpredictable climate patterns caused by storm events, El Niño Southern Oscillation (ENSO) and the Southern Annular Mode (SAM); strong seasonality in solar irradiance, temperature, sea-ice cover, and community composition; and strong inter-annual variability in temperature, sea-ice extent and retreat, krill abundance etc.

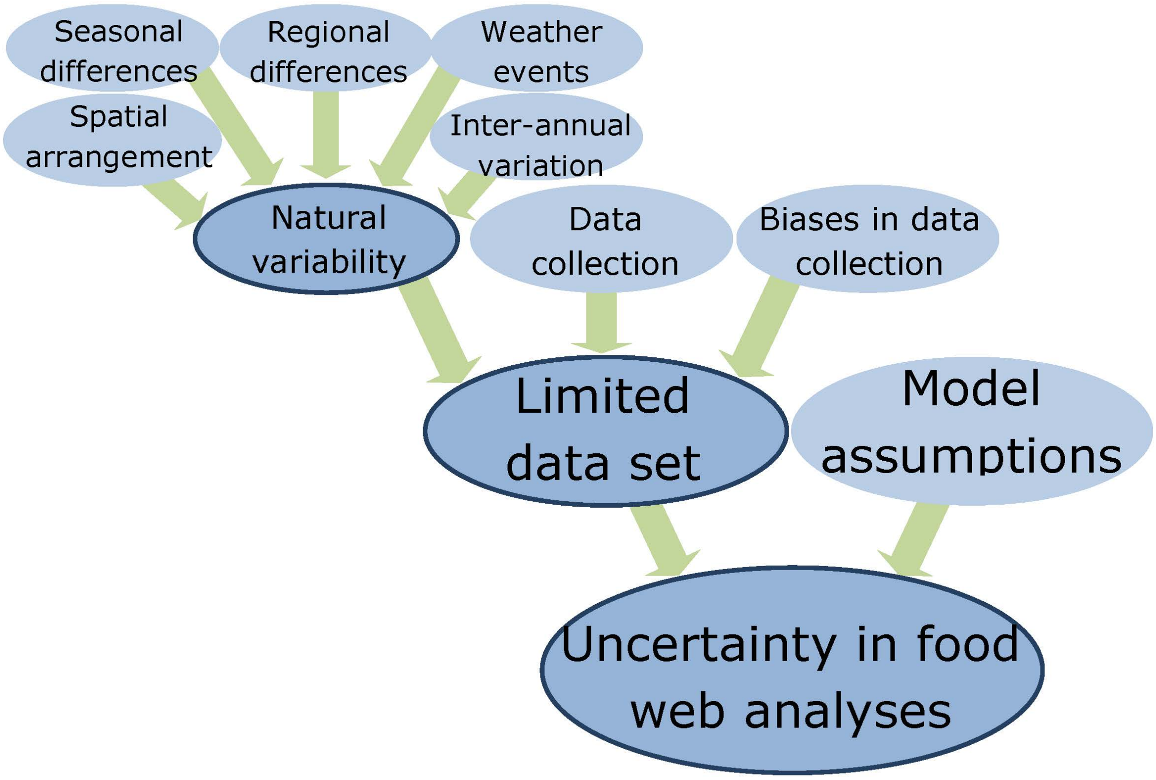

Figure 1.3: Three levels at which uncertainties are introduced into food web analyses.

Second, the empirical data quantifying biological processes in a food web are inconsistent and incomplete. Natural variability contributes to this because it would be unfeasible to collect quantitative data on trophic interactions over all realisations of food web structure. Furthermore, data sets for a food web are often skewed spatially due to practical factors, such as the ease of access to a location. In addition, food web data sets are often biased, with a high number of data for some species that are of greater interest for specific ecological studies or other reasons (e.g. species which are targetted by fisheries), or practical limitations to observing some species. Food web data sets for large marine ecosystems must be synthesised from disparate ecological studies, which use different methods to collect data and different metrics to record data. Therefore, inconsistencies are introduced into food web data, such as different taxonomic resolutions of prey in trophic interaction data.

Third, uncertainties can be introduced into food web analyses due to the pragmatic set of decisions that are used to construct the analyses. A different set of decisions could lead to different results. One such decision is how to use limited data sets to construct ecosystem analyses. For example, how should one combine data where prey are resolved to different taxonomic levels? Furthermore, decisions must be made as to the processes which are considered important to include in an analysis, to capture features of a food web pertinent to that analysis.

It is important to consider the implication of these three inter-linked levels of uncertainty on how we understand an ecosystem. Such a consideration should include understanding the importance of natural variabilities on trophic interactions, directing future data collection to fill data gaps for ecologically important species, and assessing the robustness of results arising from network analyses.

1.6 Thesis structure and aims

In this thesis I aimed to synthesise understanding on the strengths and limitations of data on trophic interactions in the Scotia Sea. From available food web data, I developed food web analyses to provide ecological insight into the structure of the Scotia Sea food web, and production of its constituent species. Importantly, I investigated how elements of uncertainty caused by natural variability, limited data, or modeller's assumptions could alter these results.

In Chapter 2, I collated predator diet samples for consumers in the Scotia Sea. A predator diet sample provides quantitative data on the diet composition of a consumer from an unpublished or published source. As such, I developed the most comprehensive data set of diet composition data available for consumers in the Scotia Sea. This is a valuable resource as these data are integral to parameterising food web analyses. In Chapter 2, I summarised the inter-annual and spatial spread of predator diet samples to highlight the extent to which the data set covered spatial and inter-annual heterogeneities in trophic interactions. A summary of the number of predator diet samples for each consumer, and the metrics which these data are given (fraction by weight, fraction by number, or fraction occurrence, defined in Section 2.2.2), are also provided. This information highlighted biases in sampling effort across consumers, and indicated where data were missing.

In Chapter 3, I used the Scotia Sea data set to develop system-level analyses of the food web based on topological network properties. Topological properties are summary statistics calculated from the food web matrix: data on trophic interactions condensed into tabular form. Topological analyses provide insight into the structure and diversity of a food web. Network properties have been linked to ecosystem robustness to change through experimental manipulation and theoretical models, see Bersier et al. (2007) [281, ch. 11]. Network properties have also been used to compare ecosystems of different types, e.g. [171, 230], and to assess possible changes to ecosystem structure over time, e.g. [162, 289].

In Chapter 3 I reported a set of binary and quantitative versions of topological network properties for the Scotia Sea. Quantitative topological properties provide a comparable alternative to their binary counterparts, but unlike binary properties, incorporate data on the strength of trophic interactions between species [157]. This is appropriate as interaction strengths are highly skewed in food webs [153, 397], and this is known to affect food web stability [321, 359].

Topological analyses rely on well resolved trophic data, and therefore the accuracy of some property estimates are reduced when data sets are limited. One solution that can be applied when only limited data are available is to aggregate species into a smaller number of groups. However this can affect property estimates [248, 305, 306, 425, 467]. I developed a novel and simple technique to mitigate for some biases caused by identifiable missing data in the Scotia Sea data set. I assessed the effects of reducing the taxonomic resolution of species in the Scotia Sea food web data set by using quantitative techniques to stepwise aggregate species into a smaller number of groups. By considering biases caused by the resolution of the food web, I assessed how robust property estimates were for the Scotia Sea. As such, Chapter 3 addressed how the choice of food web resolution affected the outcomes of a food web analysis. It also provided the first insight into how the quantitative versions of topological properties [157] may be affected by food web resolution, and how these sensitivities compare to binary properties, which do not incorporate the strength of a trophic interaction.

In Chapter 4, I developed a new food web model framework based on the widely used Ecopath model [183, 346]. Ecopath models summarise an ecosystem over a window of time, by the standing biomass and production (growth) of groups of species, known as functional groups, along with the fates of this production (consumption by predators, losses to detritus etc.). I developed a simplified version of an Ecopath model, which I called the Reduced Production Model (RPM). The RPM bypasses detail on the standing biomasses of functional groups by representing the food web through the fate of total production of each functional group. In Ecopath models and the RPM, a proportion of production is 'lost' to the detrital pool through mechanisms such as disease related mortality and messy eating. Furthermore, production by a predator is limited through its respiration and excretion. Two efficiency terms govern these processes in the RPM, which I refer to collectively as the efficiency terms, as explained in more detail in Section 4.2.1. The RPM model uses efficiency terms and trophic data for all functional groups, along with an estimate for total production of one functional group as inputs, to estimate total production of the remaining food web.

I parameterised the RPM using diet composition data collected in Chapter 2, along with estimates for efficiency terms extracted from existing ecosystem models for Southern Ocean ecosystems [141, 259, 343, 358], to estimate total production of the Scotia Sea food web. As previously discussed, production is important for carbon sequestration and for fisheries considerations. The model also provides estimates of production by functional groups that are difficult to measure empirically. I also used the RPM to assess the potential importance of each functional group in the Scotia Sea food web, by calculating the percent change in total production, to a small perturbation in each input efficiency term. An additional benefit to this analysis was that, by constructing the RPM for the Scotia Sea, I demonstrated one possible way to synthesise diet data where prey are resolved to different taxonomic levels in the Scotia Sea data set.

I also assessed the relative uncertainties in production estimates to uncertainties in efficiency terms by allowing all input efficiency terms to vary simultaneously within a plausible range for each value. As such, I assessed how uncertainty in ecological data affected the model outputs, and highlight which model outputs were least robust to these uncertainties.

Food web data sets rarely provide detail on changing diets on an intra-annual scale. Therefore, it is not possible to assess changes in trophic interactions due to natural variability at this temporal scale using empirical data. At South Georgia, there is high intra and inter-annual variability in krill density. A suggested cause of intra-annual variability is the variable timing and success of allochthonous recruitment of krill from their seed populations [385]. This variability is likely to affect the structure of trophic interactions in a food web.

In Chapter 5, I developed an analytical probabilistic encounter model, supported by numerical simulations, of a predator on one foraging trip searching for two prey types (Antarctic krill and alternate prey). I parameterised this model based on a foraging macaroni penguin, for which Antarctic krill often form the dominant prey component [445]. The probabilistic model provided information on foraging outcomes, namely the probability mass functions of each prey type, and the probability density function for forage trip duration. Using this model, I assessed the effects of the spatial aggregation of Antarctic krill into swarms on foraging outcomes.

Using model simulations, I temporally 'scaled up' the model to represent a predator foraging over a period of its breeding season. The 'scaled up' model was used to assess the relative effects of two forms of natural variability: the abundance of prey and the timing of allochthonous recruitment during the breeding season. By comparing trophic outcomes for one foraging trip and the breeding season, I provided insight into how trophic interactions can change over different time scales. The 'scaled up' model in Chapter 5 provided useful insight into penguin foraging success over a period of time pertinent to chick growth. This is important as the presence of krill in a predator's diet can relate to the reproductive success of that predator [214, 270, 445].

In summary, Chapter 5 provided a model framework in which it was possible to test variabilities in trophic interactions for a predator due to natural variabilities in their prey field. This model provided theoretical evidence as to the mechanisms which could drive the composition of a predator's diet and the energetic costs of foraging in relation to prey-type. This information is useful as it allows better interpretation of some food web data and analyses.

2 Diet composition of Scotia Sea consumers: a new data set to facilitate food web analyses

Abstract

The Scotia Sea in the Antarctic holds stocks of species which are important to commercial fisheries, provides an important habitat and foraging grounds for land-breeding predators, and is one of the most productive regions of the Southern Ocean. It is important to understand the ecosystem through the complex network of predator-prey interactions between species to facilitate ecosystem analyses. Therefore, in this chapter, we collated diet composition data for predators and consumers in order to build a food web data set for the Scotia Sea. Similar to many food web data sets which rely on data collected from disparate ecological studies, the resulting data set is biased in space, time, taxonomic coverage, and resolution of prey. Additionally, diet composition data from different sources are provided using a variety of metrics. The Scotia Sea data set included diet data collected over six decades and so covers inter-annual variabilities in the Scotia Sea as well as potential longer-term change. We highlighted other strengths of the Scotia Sea data set and where uncertainties could be introduced into food web analyses due to biases in the data set. For example, the data set contains diet composition data for only one cephalopod species, while there are many species of cephalopod in the Scotia Sea and each species consumes a different set of prey. Strengths of the data set include a large number of diet data for many species of land breeding predators and for important macro zooplankton species, Antarctic krill and *Themisto gaudichaudii*. This chapter facilitates food web analyses of a commercially and ecologically important ecosystem.

2.1 Introduction

Trophic interactions include predator-prey interactions and link all species in a food web. Trophic interactions are important as they can influence the behaviour, condition, and reproductive success of a species, which can ultimately determine community dynamics [149]. Empirical data on trophic interactions between species are primarily given by diet composition data, which can be used to quantify trophic interaction strength [153].

The Scotia Sea is an important ecosystem within the Southern Ocean for several reasons:

1. it includes areas of high primary production [134, 268, 287, 320];
2. along with areas on the Western Antarctic Peninsula, it holds an estimated 28% of the Southern Ocean Antarctic krill population [133];
3. it is an important foraging ground for one of the most diverse communities of sea-birds and marine mammals in the world [320];
4. it holds stocks of species which are exploited by commercial fisheries, including Antarctic krill, mackerel icefish and the Patagonian toothfish [319, 1].

Quantifying trophic interactions allows us to understand the structure of a food web and build models of ecosystems, for example [157, 183, 346, 397]. Three key metrics, commonly used to provide quantitative diet-composition data are the fraction of a predator's diet by wet weight, fraction of their diet by number of items, and the proportion of individuals sampled in which a prey item was found, known as fraction occurrence. Hereafter we refer to fraction by wet weight as simply fraction by weight. Data provided as fraction by weight is the most useful metric in food web models which represent the flow of carbon or biomass through the food web, for example [183, 346]; whilst fraction by number does indicate relative importance of prey in a predator's diet, it can overestimate the importance of abundant, small prey relative to less-abundant large prey [274]; finally fraction occurrence provides only information on the relative frequency with which predators consume prey, but no information on the amount which they consume. As such, data given as fraction by number is less useful in constructing food web models than data given as fraction by weight, and data provided as fraction occurrence is the least useful.

The Scotia Sea food web is highly variable in space and time [320]. Daylight hours are long in the summer compared to the winter. Phytoplankton blooms are seasonal, and last for approximately three to five months of the year [320]. The timing and strength of krill influx into the Scotia Sea from their breeding grounds in adjacent waters varies between years [385]. Antarctic krill (*Euphausia superba*) are important prey for many pelagic and land-breeding predators, and their presence or absence in the Scotia Sea can influence the diet-composition of predators [445]. Krill abundance and distribution in the Scotia Sea and the resulting trophic interactions formed between predators and krill, are affected by connected climatic and physical elements such as sea surface temperature, the position of frontal systems in the Antarctic Polar Current, and the extent of winter sea-ice cover. These elements are influenced by patterns of climate variability e.g. associated with the El Niño Southern Oscillation, (ENSO) and the Southern Annular Mode, (SAM) [312, 235, 468].

Diet-composition data for large marine ecosystems must be collated from ecological studies. The sample size used, the timing of data collection, methods used to collect data, and the effort in resolving prey to species-level varies across studies which are conducted for other purposes, for example to find relationships between diet composition and breeding success [445] or to link foraging behaviour to prey-type [205]. Thus, a food web data set is often skewed in space and time and towards a higher number of samples for some predators and consumers due to factors such as the ease of data collection and a higher interest in some species [339, 355]. Therefore, food web data sets rarely provide information on trophic interactions for all species and across all natural variabilities of the food web [339].

In this chapter, we collated diet-composition data for consumers and predators in the Scotia Sea, referring to this as the Scotia Sea data set. We collated data from published and unpublished sources. In the Southern Ocean, diet data is predominantly collected during the summer ice-free period when most field studies occur. We gave a summary of the Scotia Sea data set including its spatial and inter-annual spread. We partitioned diet data into 33 groups, representing a species or a group of species forming similar trophic interactions, and provided detail on the number of studies and the proportions of data for which the most useful diet metric provided was fraction by weight, fraction by number, or fraction occurrence. We divided data in this way to make the summary of the data set more accessible, and directly relevant to a food web model developed from the Scotia Sea data set in Chapter 4. The Scotia Sea data set provides a useful resource for parameterising food web models and can be used to understand food web structure. The summary provided here gives information on biases in the data set across species, space, and time, which highlights where possible uncertainties could be introduced into food web studies of the Scotia Sea.

2.2 Methods

2.2.1 Data set format

We adopted a format for the Scotia Sea data set which closely mirrors that of an existing diet-composition database for the Southern Ocean [370]. One set of diet-composition data provided for a predator in the Scotia Sea data set is known as a predator diet sample, and the number of individuals sampled to obtain these data is the predator sample size. Each row of the data set contains information on one trophic interaction for one predator diet sample. Table 2.1 provides a description of the important columns used to describe diet data in the Scotia Sea data set.

Table 2.1: Important columns used to record data in the Scotia Sea data set.

Name	Description
ID	Unique identifier for a row in the data set.
Source ID	An identifier for the published or unpublished source of data.
Predator diet sample ID	Predator diet sample ID identifies one, or a group of individuals within a Source ID, for which a set of diet-composition data is provided. Thus the combination of Source ID and Predator diet sample ID provides a unique reference to a predator diet sample within the data set.
Location	The name of the location where the data were collected.
West	The western-most longitude of the sampling region, in decimal degrees.
East	The eastern-most longitude of the sampling region, in decimal degrees.
South	The southern-most latitude of the sampling region, in decimal degrees.
North	The northern-most latitude of the sampling region, in decimal degrees.
Observation start date	The start date of the sampling period (DD/MM/YYYY).

Observation end date	The end date of the sampling period (DD/MM/YYYY).
Predator name original	The name of the predator as it appeared in the original source.
Predator name	The scientific name of the predator according to the WoRMS taxonomic register [377].
Predator common name	The common name (if any) of the predator according to the WoRMS taxonomic register [377].
Predator aphia ID	The identity number of a predator according to the WoRMS taxonomic register [377].
Predator sample count	The number of predators for which diet data are given.
Prey name original	The name of the prey item, as it appeared in the original source.
Prey name	The scientific name of the prey item according to the WoRMS taxonomic register [377].
Prey common name	The common name (if any) of the prey item according to the WoRMS taxonomic register [377].
Prey aphia ID	The numeric identifier of the prey item according to the WoRMS taxonomic register [377].
Prey is aggregate	If diet datum for a row (trophic interaction) provide quantification on the proportion of a group of prey (e.g. total cephalopods) in a predator's diet, but in subsequent rows provides information on subsets of this prey (e.g. cephalopod species), then a 'Y' appears in this row, otherwise the value 'N' appears.

Fraction diet by weight	The fraction by mass of a stomach sample which was this particular prey. See Section 2.2.2 for a full description.
Fraction diet by number	The fraction of total prey items which were of this particular prey. See Section 2.2.2 for a full description.
Fraction occurrence	The fraction of individuals in a predator sample in which a prey was detected. See Section 2.2.2 for a full description.
Changes to SDS	Description of any changes made to data extracted from the Southern Ocean diet database [370]. Changes were typically made: (i) to rectify an identified mistake; (ii) to approximate the longitudinal and latitudinal coordinates of data collection from location name; and (iii) to set a blank predator sample size to one.

We collated information on the diet composition of predators from ecological studies conducted within the Scotia Sea or on the South Georgia, South Sandwich Islands, or South Orkney archipelagos. We collated data from three resources:

1. We extracted diet data from a published compilation of predator diet samples collected in the Southern Ocean and sub-Antarctic waters, which we refer to as the Southern Ocean diet database [370]. We used the average of the longitudinal and latitudinal coordinates provided for collection location for each predator diet sample to represent the location of data collection. For the purposes of data extraction, we extracted data collected within longitudinal western and eastern boundaries of 58^oW and 21.5^oW and latitudinal southern and northern boundaries of 63.6^oS and 51.4^oS. The boundary of the area used to extract data was larger than the official definition of the Scotia Sea [4] by three degrees latitude south and north, three degrees west, and five degrees east so as to include predator diet samples collected within the ambits of consumers normally resident in the Scotia Sea. If a predator diet sample did not provide coordinates for its collection location, we referred to the location name provided, and used the relevant reference coordinates from an Antarctic gazetteer [4] (See appendix A for details).

Pertinent Scotia Sea predator diet samples were extracted from the Southern Ocean diet data set [370] using ArcGIS (v.10.1, Redlands, CA: Environmental Systems Research Institute). For any predator diet sample where a sample size was not provided, we assumed this was equal to one.

2. We consulted two available Ecopath (ecosystem) models for sub-regions of the Scotia Sea [170, 259]. We used references therein to identify further pertinent published diet composition data which we added to the Scotia Sea data set.

3. We used British Antarctic Survey Long-term Monitoring Diet Data (BLMDD) for the composition of black browed albatross (*Thalassarche melanophris*), grey headed albatross (*Thalassarche chrysostoma*), Adélie penguin (*Pygoscelis adeliae*), chinstrap penguin (*Pygoscelis antarcticus*), macaroni penguins (*Eudyptes chrysolophus*), and gentoo penguin (*Pygoscelis papua*) diets [125, 126]. Each predator diet sample in BLMDD had a predator diet sample size of one. Data for all albatross species were assigned a single Source ID; similarly data for all penguin species from BLMDD were assigned to a single Source ID.

2.2.2 Summary of the data

We displayed the spatial spread of predator diet samples in the Scotia Sea data set by plotting the collection location for each predator diet sample on a map of the Scotia Sea, generated using ArcGIS v.10.1. We summarised the inter-annual spread of predator diet samples using a histogram with bar width of one year. As all predator diet samples in BLMDD have a sample size of one, we generated this histogram for BLMDD separately from the remaining diet data so that BLMDD did not obscure temporal patterns in the remaining data.

We partitioned diet data into 33 species or groups of species, and provided a summary on the number of predator diet samples and the total number of sampled individuals these represent for each species/species group. We defined these 33 groups as an iterative process based on expert advice, diet composition of predators, and the availability of published diet data (the list of experts consulted can be found in the acknowledgements). By grouping some species, we made the summary of the data set more accessible, and directly relevant to the species-groups used to model the Scotia Sea food web developed in Chapter 4.

Diet data in the Scotia Sea data set are provided as one, or a combination of two or three, metrics:

1. Fraction By Weight (FBW) which is the proportion of the mass of stomach content which is of a particular prey. This is the most important diet metric used to develop food web models which represent biomass flow through an ecosystem e.g. Ecopath with Ecosim [183, 346]. A large proportion of data given as FBW in the Scotia Sea data set originates from the Southern Ocean diet database (71% sources providing FBW data) [370]; however, these do not specify whether dry or wet weight was used to calculate data. We examined a random sample of nine sources which report diet composition data as FBW in the Scotia Sea data set (13% of sources providing FBW data). We found that all examined sources calculated FBW data using wet weight [125, 126, 154, 156, 200, 205, 279, 293, 405], and therefore we proceed with the assumption all FBW data in the Scotia Sea data set refers to fraction by wet weight. We acknowledge that data calculated using dry weight could lead to a different set of diet fractions; however, our examination of a random sample of diet data suggests that this bias is minimal.

2. Fraction By Number (FBN) which is the proportion of the number of items found in the diet of a predator which are a particular prey. This is the second most important metric for developing food web models as it provides information on the relative importance of prey. However FBN data are less useful if: (i) prey are not discrete, such as algae; (ii) mastication makes an accurate prey count difficult; and (iii) predators consume prey with very different body sizes and masses [274].

3. Fraction Occurrence (FO) which is the proportion of sampled individuals in which a prey was found. This is the least useful for developing food web models as it only provides information on the probability that a prey may occur in a predator's diet, but no information on the amount a predator consumes.

For each species group, we provided information on the percentage of data (by number of predator diet sample and total number of sampled individuals) which have fraction by weight data, the percentage of predator diet samples which have fraction by number but no fraction by weight data, and the percentage of predator diet samples which only have fraction occurrence data. Thus we indicated the proportion of data with the most useful diet metric, the second most useful diet metric, and finally the least useful diet metric. We provided this summary separately for predator diet samples which provide the diet-composition of a sub-set of a predator's diet, such as the squid component only, which we refer to as Partial Predator diet Samples (PPS). We provided information on PPS separately from predator diet samples which provide information on full predator diets, as the former may be less useful information for food web analyses.

2.3 Results

2.3.1 Temporal and spatial spread of the data set

The Scotia Sea data set included 4857 predator diet samples originating from 116 sources. 4112 of predator diet samples (85%), each with a predator sample size of one, originated from two sources from BLMDD [125, 126].

Most predator diet samples (76%) originated from the South Georgia archipelago, with <1% from the South Sandwich Islands, and 22% from the South Orkney archipelago. The remaining data (2%) were collected from pelagic waters. These statistics are skewed by the large number of predator diet samples for BLMDD, for which 77% are sampled from Bird Island, South Georgia and 23% are from Signy Island, South Orkneys. If BLMDD are excluded, 69% of predator diet samples were collected from the South Georgia archipelago, 3% from the South Sandwich Islands, 15% from the South Orkney archipelago, and 13% are from other areas of the Scotia Sea. Figure 2.1 shows the spatial spread of predator diet samples in the Scotia Sea data set.

The Scotia Sea data set spans 52 years from 1961 to 2013 (Figure 2.2a, b). BLMDD provided information on diet data for black-browed albatross and grey-headed albatross continuously from 1996 to 2012, and additionally for the years 1986 and 1994. BLMDD also provided information on the diet of macaroni penguins continuously from 1990-2013, Adélie and chinstrap penguins from 2002-2013, and gentoo penguins from 1989 to 2010. A summary of BLMDD data for macaroni penguins can be found in Waluda et al. (2012) [445].

2.3.2 Summary of species groups

We partitioned the Scotia Sea data set into 33 groups of species. The number of predator diet samples and the number of individuals this relates are provided in Table 2.2, along with the proportions of data where FBW, FBN and FO was the most useful metric. A number of important features of these data were:

1. Land-breeding predators were well represented in the Scotia Sea data set and made up 59% of predator diet samples not including BLMDD. Most predator diet samples for land-breeding predators (>95%) were given in the preferred fraction by weight form.
2. The majority of predator diet samples for fish groups (>60%) provided data as fraction by weight. However, only 33% of predator diet samples for the Patagonian toothfish

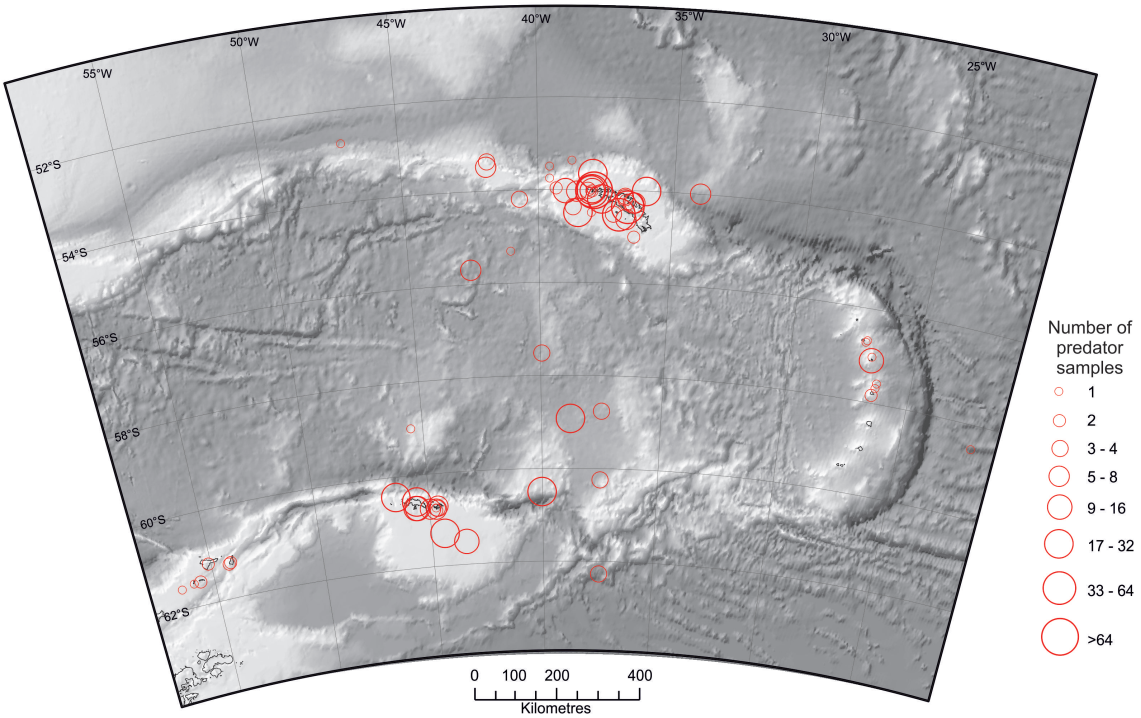

Figure 2.1: Location of data collection points for predator diet samples in the Scotia Sea data set.

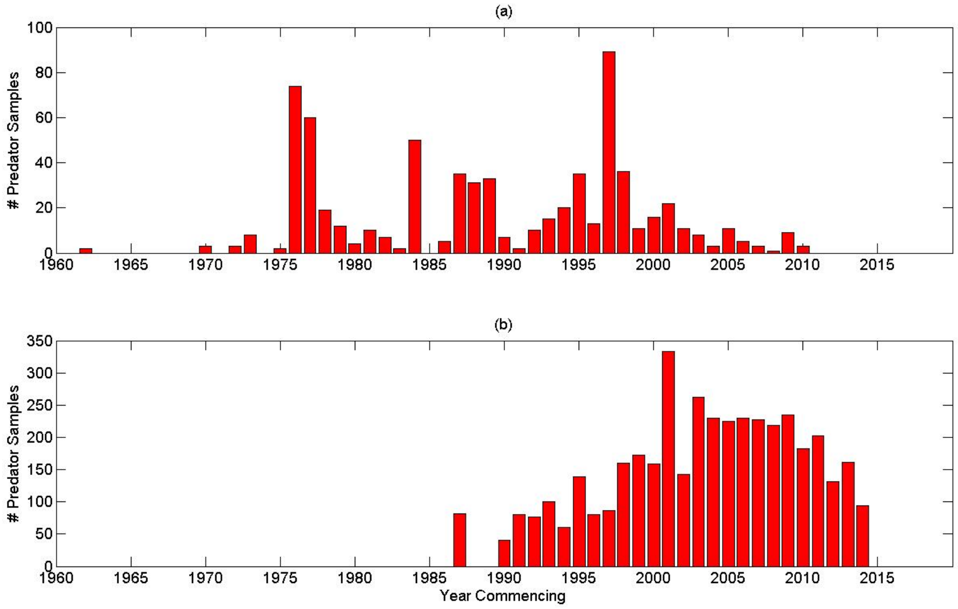

Figure 2.2: Temporal spread of predator diet samples in the Scotia Sea data set: a. for all data excluding BLMDD; b. for BLMDD.

and 0.3% for mackerel ice fish, two species important to commercial fisheries, provided data as FBW.

3. The groups named ‘skates and rays’, and ‘benthic fish, shallow, benthic diet’, were represented by three and four predator diet samples respectively and by only one species each. Similarly there was diet data for only one species of cephalopod, *Martialia hyadesi*, which provided data as fraction occurrence.

4. There were only five predator diet samples for two species of benthic fauna which, along with most predator diet samples for species of zooplankton, provided data as fraction occurrence. The exceptions to this were Antarctic krill and carnivorous macro-zooplankton, for which most predator diet samples were given as fraction by number.

5. There were seven predator diet samples for Antarctic krill and 14 predator diet samples for *Themisto gaudichaudii*.

6. The zooplankton most poorly represented in the Scotia Sea data set in terms of number of species representing the group, type of diet data, and numbers of predator diet samples were the groups named ‘salps and gelatinous zooplankton’ and ‘omnivorous macro-zooplankton’.

Table 2.2: Summary of the Scotia Sea data set divided into species 33 species groups.

Name	No. Predator diet samples (Total no. ind.)	Metric type % Predator diet samples (% ind)	Species	Reference full data	Reference PPS
Leopard seal	3 (246)	FBN: 66.7 (81.7) FO: 33.3 (18.3)	*Hydrurga leptonyx*	[240, 443]	
Antarctic fur seal	10 (996) PPS: 39 (3637)	FBW: 44.4(84.6) FBN: 11.1 (14.8) FO: 44.4 (0.6) PPS: FBW: 38.5(0.5) FBN: 5.1(10.6) FO: 56.4(88.8)	*Arctocephalus gazella*	[179, 217, 218] [225, 378] [418, p. 523-550]	[326, 325, 381] [378, 380]
Weddell seal	2 (70)	FBW: 100 (100)	*Leptonychotes weddellii*	[180]	
Chinstrap penguin	453 (759)	FBW: 100 (100)	*Pygoscelis antarctica*	[206, 211, 297] [300, 126]	

Gentoo penguin	1045 (1937) PPS: 11(422)	FBW: 91(93.6) FO 9(6.5) PPS: FO: 100(100)	*Pygoscelis papua*	[155, 159, 199] [206, 206, 205] [214, 211, 263] [280, 456, 126]	[381]
Adélie penguin	437 (674)	FBW: 100 (100)	*Pygoscelis adeliae*	[129, 293, 297] [300, 126]	
Macaroni penguin	975 (1100)	FBW: 100 (100)	*Eudyptes chrysolophus*	[206, 211, 205] [214, 126]	
King penguin	4 (116) PPS: 4(139)	FBW: 25 (<1) FO: 75 (99.1) PPS: FO: 100(100)	*Aptenodytes patagonicus*	[211, 333]	[391]
Emperor penguin	1(1)	FBW: 100(100)	*Aptenodytes forsteri*	[129]	

Wandering albatross	6 (42)	FBW: 60.0 (7.3)	*Diomedea exulans*	[186, 211, 465]	[210, 209, 463]
		FO: 40.0 (92.7)		[453, p. 285-317]	[460]
	PPS:	PPS:			
	14(698)	FBW: 92.9(61.4)			
		FO: 7.1(38.5)			
Other albatross	1412(2874)	FBW: 99.0(73.7)	*Thalassarche chrysostoma*	[198, 206, 211]	[214, 378, 384]
		FO: 1.0 (26.3)	*Thalassarche melanophris*	[212, 365, 378]	[430, 461, 462]
			Phoebetria palpebrata	[390, 430]	[460, 125]
	PPS:	PPS:	*Phoebetria fusca*		
	9(713)	FBW: 61.9(40.8)			
		FO: 38.1 (59.2)			
Scavenging seabirds	33(670)	FBW: 57.6(40.6)	*Macronectes giganteus*	[128]	[128, 195, 215]
		FBN: 18.2(38.6)	*Macronectes halli*		[206, 211, 272]
		FO: 24.4(20.8)	*Stercorarius antarcticus*		[273, 336, 351]
			Stercorarius antarcticus lonnbergi		
	PPS:	PPS:			
	1(1)	FBW 100(100)			

Diving seabirds	16(749)	FBW: 31.3(0.7)	*Pelecanoides georgicus*	[181, 215, 211]	
		FBN:31.3(56.1)	*Pelecanoides urinatrix*	[378, 379, 446]	
		FO: 37.5(43.3)	*Phalacrocorax atriceps georgianus*		
Other seabirds	78(1190)	FBW: 97.4(98.5)	*Aphrodroma brevirostris*	[128, 129, 150]	[150, 151, 163]
		FO: 2.6(1.5)	*Daption capense*	[154, 156, 161]	[331]
			Fregetta tropica	[200, 206, 215]	
	PPS:	PPS:	*Fulmarus glacialoides*	[211, 210, 209]	
	5(185)	FBW: 100(100)	*Halobaena caerulea*	[208, 216, 207]	
			Oceanites oceanicus	[212, 214, 295]	
			Pachyptila turtur	[365, 366, 379]	
			Pachyptila vittata	[453]	
			Pagodroma nivea	[211, p. 135-171]	
			Procellaria aequinoctialis		
			Sterna vittata		
			Thalassoica antarctica		

Pelagic fish	22(2714)	FBW: 40.9(67.2) FBN: 40.9(26.5) FO: 18.2(6.3)	*Bathylagus antarcticus* *Electrona antarctica* *Electrona carlsbergi* *Gymnoscopelus braueri* *Gymnoscopelus fraseri* *Gymnoscopelus nicholsi* *Krefftichthys anderssoni* *Nannobrachium achirus* *Notolepis coatsi* *Protomyctophum bolini* *Protomyctophum choriodon* *Protomyctophum tension*	[269, 399, 404] [403, 405, 415]
Benthic fish, shallow, benthic diet	4(65)	FBW: 75(35.4) FO: 25(64.6)	*Harpagifer bispinis*	[387, 427]
Skates and Rays	3(387)	FBW: 100(100)	*Amblyraja georgiana*	[302]
Benthic fish, deep, benthic diet	5(50)	FBW: 80(32) FO: 20(68)	*Pogonophryne scotti* *Notothenia coriiceps* *Artedidraco skottsbergi* *Liparidae*	[387, 427]

Benthic fish, shallow, mixed diet	40 (2888)	FBW: 61.5(59.3) FBN: 23.1(10.3) FO: 15.4(30.4)	*Notothenia rossii* *Patagonotothen guntheri* *Artedidraco mirus* *Harpagifer georgianus* *Parachaenichthys georgianus* *Champsocephalus esox* *Gobionotothen angustifrons* *Trematomus newnesi*	[175, 191, 283] [310, 327, 387] [427, 429]
Mackerel icefish	28(8159)	FBW: 0.3(14.3) FBN: 53.3(39.3) FO: 46.4(46.4)	*Champsocephalus gunnari*	[333, 283, 286] [303, 310, 328] [427]

Benthic fish, deep mixed diet	109(2146)	FBW: 79.8(77.7) FBN: 17.4(20.8) FO: 2.8(1.5)	*Dissostichus mawsoni* *Lepidonotothen squamifrons* *Trematomus hansoni* *Trematomus eulepidotus* *Muraenolepis microps* *Chaenocephalus aceratus* *Gobionotothen gibberifrons* *Cryodraco antarcticus* *Psilodraco breviceps* *Parachaenichthys charcoti* *Pseudochaenichthys georgianus* *Trematomus scotti* *Lepidonotothen larseni* *Lepidonotothen nudifrons*	[187, 283, 310] [327, 328, 387] [389, 427]
Patagonian toothfish	14(10538)	FBW: 33.3(33.3) FBN: 40.0(31.7) FO: 26.7(35.0)	*Dissostichus eleginoides*	[148, 190, 223, 310] [354, 389, 429] [464]
Cephalopod	2(127)	FO: 100(100)	*Martialia hyadesi*	[252, 394]

Carnivorous, omnivorous and detritivorous benthos	6(910)	FO: 100(100)	*Labidiaster annulatus* *Ophionotus victoriae*	[224, 244]
Salps and gelatinous zooplankton	1 (20)	FO: 100 (100)	*Salpa thompsoni*	[269]
Antarctic krill	7 (48)	FBN: 85.7 (58.3) FO: 14.2 (41.7)	*Euphausia Superba*	[269, 342]
Themisto gaudichaudii	14 (146)	FO: 100 (100)	*Themisto gaudichaudii*	[341]
Other krill	2 (44)	FO: 100 (100)	*Euphausia frigida* *Thysanoessa macrura*	[269]
Carnivorous macro-zooplankton	14 (1380)	FBN: 92.3 (98.9) FO: 7.7 (1.1)	*Paraeuchaeta antarctica* *Paraeuchaeta biloba* *Paraeuchaeta barbata* *Paraeuchaeta rasa* *Pseudosagitta gazellae*	[269, 334]
Carnivorous meso and micro-zooplankton	2 (11)	FO: 100 (100)	*Heterorhabdus austrinus* *Solidosagitta marri*	[269]

Omnivorous macrozooplankton	2(15)	FO: 100 (100)	*Eukrohnia hamata* *Vibilia stebbingi*	[269]
Omnivorous meso and microzooplankton	15 (404)	FO: 100 (100)	*Calanus propinquus* *Euchirella rostromagna* *Gaetanus tenuispinus* *Haloptilus ocellatus* *Metridia gerlachei* *Pleuromamma robusta* *Scaphocalanus farrani* *Scolecithricella cenotelis* *Spinocalanus abyssalis*	[269]
Herbivorous zooplankton	7 (184)	FO: 100 (100)	*Calanoides acutus* *Clio pyramidata* *Metridia curticauda* *Rhincalanus gigas*	[176, 269]

2.4 Discussion

2.4.1 Spatial spread of the Scotia Sea data set

The Scotia Sea data set includes predator diet samples collected on all three archipelago's in the Scotia Sea and their shelf waters as well as from off-shelf pelagic locations. However, there is a bias towards predator diet samples collected from the South Georgia archipelago in the northern Scotia Sea (see Figure 2.1). There are a high number of predator diet samples for land-breeding predators that, within the Scotia Sea, are most abundant and diverse at the South Georgia archipelago [320]. Following this, most predator diet samples originated from the South Orkney archipelago. The spatial bias of predator diet samples in the Scotia Sea data set were correlated with the location of permanent national bases, for which there are two in the South Georgia archipelago [426], two on the South Orkney archipegalo [2, 426], and none on the South Sandwich Islands. There are no diet data for land-breeding predators collected on the South Sandwich Islands. Abundant sea birds present on the South Sandwich Islands are macaroni, Adélie, and chinstrap penguins, Wilson's storm-petrel, cape petrel, and Antarctic fulmar [193]. Crabeater, Weddell, leopard, and southern elephant seals also breed on or around the South Sandwich Islands [193]. Although no data have been collected for these species at the South Sandwich Islands, there are diet data for all these species collected on the South Georgia and South Orkney archipelagos, except southern elephant seals for which there are no diet data in the Scotia Sea Data set.

A recent study of latitudinal changes in Scotia Sea biodiversity suggested that the north and south Scotia Sea have different community compositions [448]. For example, the dominant macro-zooplankton in the south Scotia Sea was Antarctic krill, and in the north Scotia Sea was the pelagic crustacean *Themisto gaudichaudii*. Proposed causes of these differences, which roughly align with the Southern Antarctic Circumpolar Current Front [448], are different temperatures, the presence/absence of winter sea-ice, and different iron and chlorophyll-a enrichment [440, 448, 447]. There is a paucity of predator diet samples collected across the Scotia Sea from off-shelf pelagic locations. This restricts the ability to make latitudinal comparison of the entire food web. However, the large number of predator diet samples for land-breeding predators collected from both the north and south Scotia Sea, means the Scotia Sea data set could be used to compare these ecosystems through differences in diets at the top of the food web, e.g. [127, 148].

Satellite telemetry technology has provided insight into the intra and inter-annual differences in the dispersal of foraging predators e.g. [146, 229, 434]. For example, macaroni penguins at South Georgia were found to forage in open ocean habitats except during chick-rearing when they foraged around the shelf-break [146]. This demonstrates how shelf and open ocean habitats are connected in the Scotia Sea. Therefore, a skew towards a high number of predator diet samples collected at island archipelagos suggested in Figure 2.1, may exaggerate the spatial biases in the Scotia Sea data set, as many land-breeding predators are able to commute to open ocean habitats to forage.

2.4.2 Temporal spread of the Scotia Sea data set

The Scotia Sea data set contained diet data collected over six decades and included time series data for two albatross and four penguin species, spanning three decades [125, 126]. This could allow an examination of long-term trends in predator diets. One existing study used BLMDD for macaroni penguins, an important avian consumer [167], to examine how their diet changed inter-annually, and how these changes related to their reproductive success [445]. The Scotia Sea data are limited in their use to examine changes in the structure of the entire food web over time because multi-year diet data are not available for all species. However, the data set collectively includes data which cover years of natural variability such as low and high krill abundances [235], and climate anomalies such as the SAM [194]. The data set also includes data collected over periods of long-term change, such as a decrease in the population size of some land-breeding predators [164, 435], and a possible decrease in krill concomitant with an increase in salp abundance [132].

2.4.3 Taxonomic coverage of Scotia Sea predators

2.4.3.1 Land-breeding predators and cetaceans

As discussed in Section 2.4.1, the Scotia Sea data set contained mostly predator diet samples for land-breeding predators, and most of these data are given as fraction by weight (FBW), which is the preferred form in many food web models. However, the Scotia Sea data set does not contain diet data for crabeater seals (*Lobodon carcinophagus*), which breed on pack ice around the Antarctic Peninsula and Ross Sea but whose distribution includes Scotia Sea waters [418, p. 516-533], and southern elephant seals (*Mirounga leonina*), which are abundant in the Scotia Sea [228]. Two species of seal which occur infrequently in the Scotia Sea, and for which there are no diet data, are the sub-Antarctic fur seal (*Arctocephalus tropicalis*) and Ross seal (*Ommatophoca rossii*) [228, 348].

The Scotia Sea data set contained no predator diet samples for species of cetacean. Many cetacean species are highly transient so their presence is irregular in the Scotia Sea. Published *in situ* summer surveys of cetacean biodiversity in the Scotia Sea identified southern right (*Eubalaena australis*), minke (*Balaenoptera bonaerensis*), sei (*Balaenoptera borealis*), and humpback whales (*Megaptera novaeangliae*); and hourglass dolphins (*Lagenorhynchus cruciger*) as the most abundant species [419, 386]. Other species detected were finn (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), grays beaked (*Mesoplodon grayi*), sperm (*Physeter macrocephalus*), pilot (*Globicephala*), straptoothed (*Mesoplodon layardii*), southern bottlenose (*Hyperoodon planifrons*), and giant beaked (*Berardius*) whales; orcas (*Orcinus orca*); and, very rarely, Commerson's dolphin [419, 386]. Food web analyses for the Scotia Sea will need to infer missing information on the diet composition of cetaceans, southern elephant seals, and data missing for other seal species from alternate resources.

2.4.3.2 Cephalopods and fish

The highest number of predator diet samples per species for fish in the Scotia Sea data set were for mackerel icefish (28 predator diet samples) and the Patagonian toothfish (14 predator diet samples). These two species are exploited by commercial fisheries, and therefore this information is important to developing models which assess the conflict between fisheries and the ecosystem, which is a key objective of the Antarctic-fisheries management body CCAMLR [285]. Within the groups of fish species used to summarise the Scotia Sea data set, the groups named 'pelagic fish', 'benthic fish, shallow, mixed diet', and 'benthic fish, deep, mixed diet', were represented in the Scotia Sea data set by at least 22 predator diet samples each describing the diets of at least eight species per group. There are species from two genera of skates in the Scotia Sea [377]. The Scotia Sea data set contained predator diet samples for one species of skate, *Amblyraja georgiana*; however, this is the only species in the Scotia Sea from this genus [222]. There are up to four species of skate in the genus *Bathyraja*, which could occur in the Scotia Sea [222]. Given that there is a considerable amount to learn about this genus, for example there is still uncertainty as to the number of species in this genus due to previous misidentification [421], the better-studied *A. georgiana*, for which there was diet composition data in the Scotia Sea data set, is a good candidate species to represent all 'skates and rays' in the Scotia Sea.

There was only diet data for one species of cephalopod as a predator in the Scotia Sea data set, which was *Martialia hyadesi.* Cephalopods are important prey for many predators such as black-browed albatross [393], wandering albatross [390, 463], and king penguins [391]. A study on the distribution of juvenile cephalopods at South Georgia alone counted eight other species [392], and many more species of cephalopod appear as prey in the Scotia Sea data set. Many species of cephalopod feed on pelagic fish, particularly myctophids, while other species feed on krill [284]. Species such as *Martialia hyadesi* can consume other cephalopods [252]. This mismatch between cephalopod diversity in the Scotia Sea data set as predators compared to as prey could be problematic if these cephalopods play an important trophic role in the Scotia Sea food web. Therefore, it will be important in future work, to assess the trophic importance of cephalopods to the wider food web in the Scotia Sea.

2.4.3.3 Benthos and zooplankton

Antarctic krill and *Themisto gaudichaudii* are, depending on the time of year and location, dominant macro zooplankton in the Scotia Sea [448], and form important prey for many predators, for example macaroni penguins [445]. The diet data of these species were provided by multiple predator diet samples in the Scotia Sea data, seven for Antarctic krill and 14 for *Themisto gaudichaudii.* Other krill which can also be dominant are *Euphausia triacantha* and *Thysanoessa macrura* [353, 448]. The Scotia Sea data set did not contain diet data for *Euphausia triacantha*, however it does contain diet data for *Thysanoessa macrura.*

There was only one predator diet sample for *Salpa thompsoni* to represent the diets of salps and gelatinous zooplankton as consumers. There is one other species of Antarctic salp, *Ihlea racovitzai*, which was not represented in the data set as a consumer, and there were no data for the diet composition of species of jellyfish in the Scotia Sea data set. Salps are omnivorous and can form symbiotic feeding relationships with some species of copepod [349]. As evidence suggests that the abundance of salps is increasing in the Southern Ocean [132], it may be an important priority for future research to assess the importance of trophic interactions between salps and other species in the food web, so as to assess whether it is important to collect more empirical diet composition data for these species.

Studies on shelf biodiversity at South Georgia estimated that crustacean species richness is approximately double that of chordates [147, 266]. This does not include the contribution of deep sea (>1000m) benthic crustaceans whose biodiversity is estimated as over double that of shelf benthic crustaceans [169], or species unique to shelf ecosystems in the Scotia Sea. The Scotia Sea data set only contained diet data for two species of benthic organisms. This clearly falls short of usefully quantifying interactions of consumers living on the sea floor. This is a major source of uncertainty in the Scotia Sea data set, and food web analysis should acknowledge, and if possible explore, how these uncertainties could affect food results. Arguably more importantly, the Scotia Sea data set does not quantify interactions between microbes, and thus omits pertinent detail on nutrient recycling. Food web studies should consider the uncertainty inherent in their analyses relating to uncertainty in interactions at lower trophic levels in the food web.

2.4.4 Diet metrics

Most predator diet samples for land-breeding predators and fish in the Scotia Sea data set provided diet data in the form of FBW. The exceptions to this were diving sea birds, king penguins, Antarctic fur seals, pelagic fish, mackerel ice fish, and the Patagonian toothfish, although all three diet metrics were represented in some predator diet samples for all these groups. Some studies have suggested methods for combining different diet metrics such as the index of relative importance [303, 313, 357, 405, 406]. However, there is no clear reduction in uncertainty from combining data in this way [274], and the resulting value is not directly useable in food web models. Disregarding data which are not in the preferred FBW form is not practicable in food web data sets where available data are scarce. One possible method to resolve using FBN data in food web analyses, which we used when we constructed a food web model of the Scotia Sea in Chapter 4, would be to convert FBN to FBW data using a representative estimate for prey mass. Furthermore, one way to integrate FO data with FBW and FBN data could be to average types of diet data such that data given in the preferred metric is assigned a higher weighting than other types of data. To achieve this, it would be necessary to adjust diet data given as FO to sum to unity by diving all FO diet data by the sum of all fractions for that predator diet sample.

2.4.5 Taxonomic resolution of prey

Different prey resolution is a common feature of food web data sets. As an example, Antarctic krill were often resolved to species level in the Scotia Sea data set due to their high abundance and importance as prey in the food web [320]. However, there were fewer instances of other krill species as prey which were resolved to species level, even though *Euphausia triacantha* can be the dominant macro-zooplankton [448]. Modelling approaches must include pragmatic decisions on how to use these data, which should be clearly stated with the model. See Chapter 4 to see how we used prey resolved to different taxonomic levels in the Scotia Sea data set to construct a food web model.

2.5 Conclusion

The Scotia Sea data set included data from all three island archipelagos in the Scotia Sea and more limited diet data collected in the open ocean. It included data collected over six decades, and so covered inter-annual and decadal changes in the Scotia Sea food web. The Scotia Sea data set provided good temporal, spatial, and taxonomic cover for many species of land-breeding predator and fish, including the important avian consumer, macaroni penguins. There were also a large number of predator diet samples for important macro-zooplankton species, Antarctic krill and *Themisto gaudichaudii*. Groups which were poorly represented in terms of number of species and number of predator diet samples were benthic species, cephalopods, salps and gelatinous zooplankton, and the group ‘benthic fish, shallow, benthic diet’.

The Scotia Sea data set offers a useful resource for food web analyses. Diet composition can be used as a measure of interaction strength [397], and so the data set could be used to understand the structure of a food web using metrics such as binary or quantitative topological network properties [157]. Therefore, in Chapter 3 we completed topological network analyses of the Scotia Sea food web using the data set reported in this chapter. Furthermore, in Chapter 4 we constructed a mass-balanced model of the Scotia Sea food web where the diets of groups of species in the model were parameterised primarily by the data reported in the Scotia Sea data set. In Chapter 4, we directly addressed many of the limiting factors of the Scotia Sea data set identified in this chapter. Specifically we: (i) inferred missing diet data for species of cetacean and southern elephant seals; (ii) we assessed the importance of cephalopods, salps and gelatinous zooplankton, and all other groups of species in the Scotia Sea food web, which could be important for directing future research particularly where food web data are sparse; (iii) we synthesised data in the Scotia Sea data set which is given by different metrics, to estimate diet composition for groups of consumers in the Scotia Sea; and (iv) we assessed how sensitive model outcomes were to two scenarios for the diet composition of the microbial group in the Scotia Sea food web model (named ‘heterotrophic bacteria and chromista’). We prioritised uncertainties in the diet composition of this group as these data were absent in the Scotia Sea data set.

3 System-level properties for the Scotia Sea food web and the importance of taxonomic resolution of species

Abstract

To derive reliable projections of how an ecosystem may respond to change, it is first important to understand what factors govern its function and structure. Topological network properties are a set of summary statistics which offer system-level insight into the structure and diversity of trophic links in complex food webs. Species are often aggregated into a smaller number of groups, hereafter referred to as species aggregation. Species aggregation may be necessary when developing food web models to make it possible to use data where prey are recorded at different resolutions. However, species aggregation can obscure important trophic detail which is important in network analyses. Furthermore, network analyses may be biased by incomplete data sets arising due to under-sampled ecosystems. The Scotia Sea data set is an example of an under-sampled ecosystem, as highlighted in Chapter 2. In this chapter, we completed topological network analysis of the Scotia Sea food web. We focused on a set of classic binary topological network properties, as well as more recently developed quantitative versions of these properties. We addressed two key factors which introduce uncertainties into topological network properties. First, we applied a simple correction to prevent species in the Scotia Sea food web data from falsely appearing as apex predators (species with no predators) or basal prey (species which do not consume) due to missing data on their trophic interactions. To do this, we applied two extra ‘species’ to the food web data: one to consume false-apex predators, and one to be prey for false-basal species. We found this simple correction reduced biases caused by missing data to topological network properties which are linked to the trophic level of a species, and also reduced biases to percentage omnivory. Second, we used an aggregation algorithm to assess the range of possible network property values resulting from different degrees of species aggregation in the Scotia Sea data set. Complexity properties were very sensitive to species aggregation, whereas other properties, such as the standard deviation of vulnerability, were less sensitive, and so are relatively robust measures for the Scotia Sea. The sensitivity of network properties to species aggregation could limit their usefulness for comparing the Scotia Sea food web to other ecosystems where species are aggregated to a different extent. In this chapter, we offer the first insight into how quantitative versions of classical topological properties change with species aggregation.

3.1 Introduction

To derive reliable projections of how an ecosystem may respond to change, it is first important to understand what factors govern its function and structure [315]. A key aspect of an ecosystem is the food web: a dynamic network of organisms feeding on other organisms at varying intensities. Trophic interactions between species or groups of species within a food web, can be represented by a matrix of interactions, which, similarly to Bersier et al. (2002) [157], we refer to as the food web matrix (although other studies refer to it as the connection matrix, for example [401]). Topological network properties are summary statistics representing food web features such as the number and spread of trophic interactions, and can be calculated from the food web matrix. Many authors identify links between network properties and measures of ecosystem stability through experimental manipulation and theoretical models (see Bersier et al. (2007) [281, ch. 11] for a full review). Network properties are useful to compare real ecosystems of different types, e.g. [171, 230, 401]. Furthermore, they have been used to assess the potential structure of an ecosystem as a result of forecasted changes in species distributions due to climate change [162, 289].

There are two ways to calculate topological network properties: using either a binary or quantitative food web matrix. Properties calculated from a binary food web matrix, hereafter referred to as binary properties, are criticised for treating weak and strong trophic interactions as equal [339]. One option would be to delete weaker interactions due to their potential disproportionate influence on network properties; however the choice of deletion threshold can also influence property values [241]. Topological network properties calculated from a quantitative food web matrix, hereafter referred to as quantitative network properties, account for variable strengths of trophic interactions across species or groups of species [157]; hereafter, we refer to species or groups of species collectively as species. Quantitative network properties are advantageous over their binary counterparts as quantitative properties can identify differences between food web matrices with identical structures but different interaction strengths, and quantitative properties are less sensitive to biases introduced due to incomplete data than their binary equivalents [143].

Network properties are biased by under-sampling of food webs [251, 307] resulting in incomplete food web matrices [143, 158, 251, 307, 339, 362]. Obstacles to collecting comprehensive quantitative data to describe the diets of all organisms in an ecosystem include high spatio-temporal variability in food web structure and interaction strength, rare or transient species, restrictions on data collection due to safety issues or conservation measures, physical constraints due to the small or large size of some species, and the large magnitude of data required to describe a whole food web [339]. For food webs which include species across a large range of body sizes, such as the Scotia Sea food web, information about trophic interactions are often derived from disparate empirical studies on consumers' diets, in which the sampling intensity varies between species [339, 355]. In the extreme, this leads to consumers with no diet data causing them to falsely appear as basal prey (species with no prey) or apex predators (species with no predators) [388]; hereafter we refer to falsely basal or apex species as floating predators and floating prey, respectively. Previous studies advise that it is necessary to correct property values for under-sampled food webs [143, 307] but provide little advice on how to do this in practice.

A further limitation of topological network properties is that they may be biased by varying levels of taxonomic resolution in food web matrices. Whilst one study suggested that food web properties were sensitive to the aggregation of species in food web data sets into a smaller number of groups [305], another study found that some network properties were scale invariant [425]. Hereafter we refer to the aggregation of species in food web data into a smaller number of groups as species aggregation. Due do conflicting conclusions on the effects of species aggregation on network properties, it is important to assess the sensitivity of network properties to species aggregation for each studied ecosystem.

Species aggregation may be necessary when species are resolved to different taxonomic resolutions in diet data. However, species aggregation can obscure important trophic detail on which topological network properties rely [246] and so comparing ecosystems can be inhibited by different levels of species aggregation in food web data. Previous studies on the effects of aggregating species have focused on binary properties only e.g. [248, 305, 306], but none have yet assessed how quantitative versions of classic topological properties change with species aggregation. One binary study on the effects of species aggregation on topological network properties suggests that comparisons of food webs are possible if food web matrices have similar degrees of aggregation [248].

In this chapter, we developed a quantitative food web matrix for the Scotia Sea food web. From this we calculated binary and quantitative network properties for the Scotia Sea food web. To mitigate for biases caused by incomplete data on the trophic position of species in the Scotia Sea data set, we extended the Scotia Sea food web matrix by two rows and columns to represent two extra 'species', naming these the closure predator and closure prey group. The closure predator group consumed all species in the food web data set which falsely appear as apex predators, and closure prey acted as prey for all species falsely appearing as basal due to the paucity of diet composition data for these species. Furthermore, we assessed the range of possible values for topological network properties for the Scotia Sea, given different degrees of species aggregation. We completed the species aggregation analysis with and without closure groups to assess how sensitive our results were to errors in the trophic position of species caused by incomplete data sets. This work explored the consequences of two common limitations of topological analyses to network properties for the Scotia Sea, and proposed a simple correction to reduce biases caused by one of them. The work in this chapter provided valuable insight into the structure of the Scotia Sea food web using the newly compiled Scotia Sea data set summarised in Chapter 2.

3.2 Methodology

3.2.1 Food web matrix definition

In this study, a food web matrix with S species is defined as a square matrix $\mathbf{A}$ of size SxS, such that each element a_{ij} of $\mathbf{A}$ represents the proportion of prey i in the diet of consumer j. A value of $a_{ij} = 0$ implies that j does not consume i and if all the values in a column j of the matrix equal zero, then j is a basal species. This definition of a food web matrix is also referred to as a diet matrix.

A binary version $\mathbf{B}$ of a food web matrix has elements b_{ij}, and if b_{ij}=0 then j does not consume i, and if b_{ij}=1 then j consumes i, for all i, j.

3.2.2 Scotia Sea food web matrix

One aim of this study was to examine the effects on quantitative network properties of aggregating multiple species into one group. We call this species aggregation. To eliminate the effects of prior aggregation in this analysis, we only included interactions where both predator and prey were resolved to species level. This led to the complete removal of diet data for 36 predators (30.2% of predators). The resulting Scotia Sea food web matrix comprised of 185 species including 73 predators connected through 620 trophic interactions. This data originated from 2977 predator diet samples arising from 88 sources. Advantages of using species-resolved data were that it prevented the repetition of species which could feature in more than one taxonomic group due to variable resolution of prey across empirical studies, and it prevented poorly resolved species, for which we have no explicit records of their diet data, falsely appearing as basal.

We used fraction by weight data for a predator diet sample if available, otherwise using fraction by number data. Lastly, if neither fraction by weight nor fraction by number data were available, we used fraction occurrence data, which we rescaled so that it summed to unity to make it comparable with the two aforementioned metrics (fraction by weight, fraction by number and fraction occurrence were defined in Chapter 2, Section 2.2.2). We generated a unique list of prey from diet samples relating to each predator, and calculated the proportion each prey i in the diet of predator j as a weighted average by predator sample size across all pertinent predator diet samples. See Appendix B for a mathematical description of how we derived the food web matrix.

A yield-effort curve indicates how well the diets of sampled predators are described in food web data sets. It plots the number of species and number of trophic interactions according to the data set, against an indication of sampling effort [188]. Figure 3.1 shows the yield-effort curves for the Scotia Sea ecosystem. The number of species began to reach an asymptote. This is in contrast to the trophic interactions between these species, indicating that although most species consumed by sampled predators have been identified, not all interactions between species have.

3.2.3 Closure groups

3.2.3.1 Definition

Closure groups were two extra 'species' added to an incomplete food web matrix, to interact with floating prey and predators. In the Scotia Sea data set, we defined floating predators as all species which were not primary producers, but for which there were no diet composition data in the Scotia Sea data set. Conversely, we defined floating prey as all species which had no consumers according to the Scotia Sea data set, but were not species of marine mammals or seabirds. Closure groups were added such that a closure predator group consumed all floating prey at equal intensities i.e. for N_{fp} floating prey, the proportion of each floating prey in the diet of the closure predator was set as $\frac{1}{N_{fp}}$ in the food web matrix. A closure prey group was set to be the only prey for all floating predators. We added closure groups as a simple correction to prevent species falsely appearing as basal or apex predators. However, we do not explicitly consider them as species in the ecosystem, and so closure groups were used to calculate the trophic position of species in the matrix but were themselves excluded from calculations of network properties, explained mathematically in Section 3.2.4. We refer to a food web matrix before closure groups are applied as the original food web matrix.

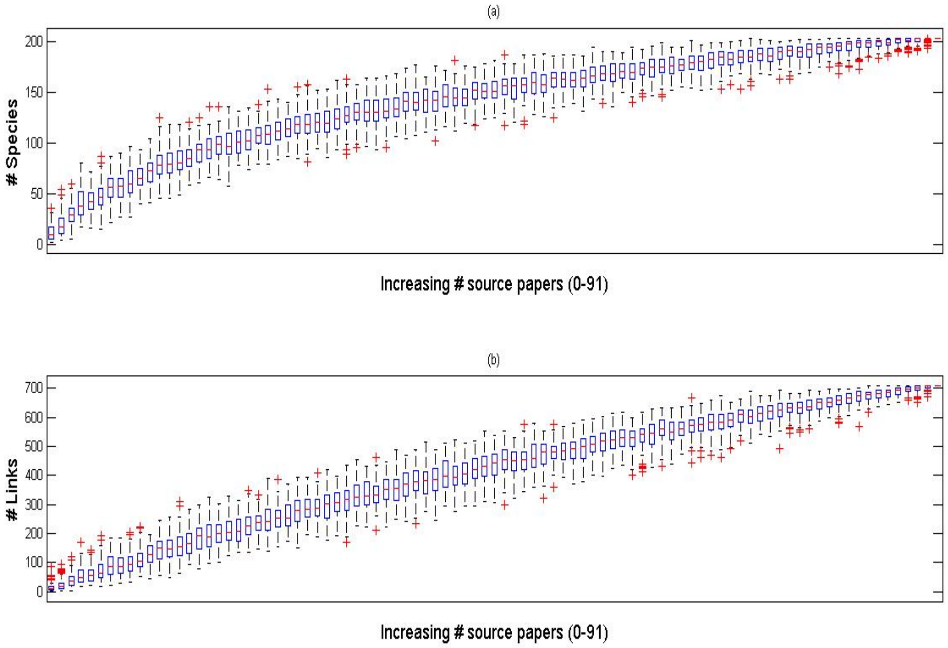

Figure 3.1: Yield-effort curve for the Scotia Sea food data set for (a) the number of species and (b) the number of trophic interactions. Sampling effort is measured by the number of source papers used to construct the food web matrix, where a source is a publication or comparable report from which a set of diet composition data originates. This was repeated 100 times at each sampling effort to produce a box and whisker plot with outliers (red crosses).

3.2.3.2 Assessing the effects of closure groups

To assess the effects of closure groups on network properties, we created degraded versions of a 'complete' food web matrix to represent food web matrices arising from incomplete data. We added closure groups to degraded matrices to see if they could result in estimates for network properties closer to the 'complete' food web matrix, than matrices without closure groups.

Gauzens et al. (2013) [248] used a binary marine food web matrix which included 74 lower trophic level marine species of which 71 were connected through trophic interactions. Whilst high trophic level species were not included, the binary matrix included taxonomically well resolved species as it was constructed from detailed literature searches, expert knowledge, and inferred data from known allometric relationships [248]. We used the 71 species connected by 224 trophic interactions [248] to represent a 'complete' food web matrix which could result from a fully sampled food web, hereafter referred to as Gauzens matrix. However, we recognise that knowledge of any food web is imperfect in practice.

To create degraded matrices we set all trophic interactions to zero in randomly selected rows and columns of the Gauzens matrix, creating floating groups. We implemented this at different intensities setting 5, 10, 15, 20, 25 or 30 rows/columns of diet data equal to zero, and repeated this 100 times at each intensity. We calculated the percentage error $\%\mathrm{err}_p$ for each network property p for degraded food web matrices as follows:

$$\%\mathrm{err}_p = 100(\frac{TN_{pd}}{TN_{pc}} - 1), \tag{3.1}$$

where TN_{pd} was the average value for property p calculated from degraded matrices, and TN_{pc} was the value for the same property calculated from the complete Gauzens matrix. We fitted a least squares linear model to estimate the slope of the relationship between the number of diet data removed and the average percent error for each network property. The slope indicated the magnitude and directional bias caused by under-sampling on each network property. We added a closure predator and a closure prey group to each degraded matrix to form trophic interactions with species whose diet data had been removed, and used the similar methods as described above to recalculate the regression-slope. We partitioned network properties into three categories according to whether adding closure groups reduced, kept the same, or increased the bias in a network property.

3.2.4 Network properties

3.2.4.1 Binary topological properties

We calculated five binary properties describing the feeding position of species in the food web (percentage of basal, intermediate and top species, the top to basal ratio and the predator to prey ratio), two binary complexity properties (connectance and linkage density, e.g. [157, 306]), and four binary properties describing the diversity of predators and prey in a food web (system generality and vulnerability [412], and the standard deviations of generality and vulnerability [454]). We calculated the mean and maximum trophic level using the short-weighted trophic level definition [455] from which we estimated system omnivory [250] and percentage of omnivorous species, e.g. [401].

For a binary food web matrix $\mathbf{B}$ with species richness S and number of trophic interactions or links L, adding a closure predator and prey group at positions $S+1$ and $S+2$ increased the species richness by two and the number of trophic interactions by N_f, where N_f is the number of floating groups. The extra two ‘species’ and trophic interactions introduced when closure groups were added to a food web matrix can bias property values; we therefore calculated properties using an approach which reduced this bias. Closure groups were used to calculate the trophic positions of species in the food web matrix, but were not included in the calculation of network properties otherwise. Table 3.1 gives the mathematical definition of how binary topological properties were calculated for the original food web matrix and a food web matrix with closure groups, which are both used in this chapter. Throughout the definitions of binary topological properties, $b_{\cdot i} = \sum_{j=1}^{s} b_{ji}$, $b_{i\cdot} = \sum_{j=1}^{s} b_{ij}$, $b'_{\cdot i} = \sum_{j=1}^{s+2} b_{ji}$ and $b'_{i\cdot} = \sum_{j=1}^{s+2} b_{ij}$.

Table 3.1: Equations for binary topological network properties as calculated from the original food web matrix, and the food web matrix with closure groups. Acronyms are as follows: S is species richness, LD is link density, C is connectance, $\%T$, $\%I$ and $\%B$ are the percentage of top, intermediate and basal species respectively, $T : B$ is the top to basal ratio, $Pred : Prey$ is the predator to prey ratio, G is system generality, V is system vulnerability, $stdG$ is standard deviation of generality, $stdV$ is standard deviation of vulnerability, $MaxTL$ is the maximum trophic level, $MeanTL$ is the mean trophic level, Omn is system omnivory and $\%Omn$ is percentage omnivory. Note that for all definitions of trophic levels, basal species were assigned a trophic level of one.

Property	Original food web matrix	Matrix with closure groups
Linkage density	$LD = \frac{L}{S}$	$LD = \frac{L}{S}$
Connectance	$C = \frac{L}{S^2}$	$C = \frac{L}{S^2}$
Percentage top	$\%T = \frac{100}{s} \sum_{\substack{b_{\cdot i}>0 \\ b_{i\cdot}=0}} 1$	$\%T' = \frac{100}{s} \sum_{\substack{b'_{\cdot i}>0 \\ b'_{i\cdot}=0 \\ i\neq s+1 \\ i\neq s+2}} 1$

Percentage intermediate	$\%I = \frac{100}{s} \sum_{\substack{b_{\cdot i} > 0 \\ b_{i \cdot} > 0}} 1$	$\%I' = \frac{100}{s} \sum_{\substack{b'_{i \cdot} > 0 \\ b'_{\cdot i} > 0 \\ i \neq s+1 \\ i \neq s+2}} 1$
Percentage basal	$\%B = \frac{100}{s} \sum_{\substack{b_{i \cdot} > 0 \\ b_{\cdot i} = 0}} 1$	$\%B' = \frac{100}{s} \sum_{\substack{b'_{i \cdot} > 0 \\ b'_{\cdot i} = 0 \\ i \neq s+1 \\ i \neq s+2}} 1$
Top to basal ratio	$T : B = \frac{\%T}{\%B}$	$T : B' = \frac{\%T'}{\%B'}$
Predator to prey ratio	$Pred : Prey = \frac{\%T + \%I}{\%B + \%I}$	$Pred : Prey\prime = \frac{\%T' + \%I'}{\%B' + \%I'}$
Generality	$G = \frac{L}{S(\%B + \%I)}$	$G' = \frac{L}{S(\%B' + \%I')}$
Vulnerability	$V = \frac{L}{S(\%T + \%I)}$	$V' = \frac{L}{S(\%T'_c + \%I')}$

Standard deviation of generality	$stdG = std(G_k)$ where, $G_k = \frac{1}{LD}\sum_{i=1}^{s} b_{ik}$	$stdG' = std(G'_k)$ where, $G'_k = \frac{1}{LD}\sum_{i=1}^{s} b'_{ik}$
Standard deviation of vulnerability	$stdV = std(V_k)$, where, $V_k = \frac{1}{LD}\sum_{i=1}^{s} b_{ki}$	$stdV' = std(V'_k)$, where, $V'_k = \frac{1}{LD}\sum_{i=1}^{s} b'_{ki}$.
Prey averaged trophic level (PTL)	$PTL_i = 1 + \frac{1}{\sum_{k=1}^{s} b_{ki}} \sum_{k_{prey}} PTL_k$	$PTL'_i = 1 + \frac{1}{\sum_{k=1}^{s+2} b'_{ki}} \sum_{k_{prey}} PTL'_k$
Short trophic level (STL)	$STL = 1+$ shortest distance between species i and a basal species	$STL' = 1+$ shortest distance between species i and a basal species
Short weighted trophic level	$TL_i = \frac{1}{2}\left(STL + PTL\right)$	$TL'_i = \frac{1}{2}\left(STL'_i + PTL'_i\right)$
Maximum trophic level	$MaxTL = \max_i TL_i$	$MaxTL = \max_{\substack{i \\ i\neq s+1 \\ i\neq s+2}} TL'_i$

Mean trophic level	$MeanTL = \frac{1}{s}\sum_{i=1}^{s} TL_i$	$MeanTL' = \frac{1}{s}\sum_{i=1}^{s} TL'_i$
Omnivory	$\begin{aligned} Omn &= \overline{O_i} \\ \text{where, } O_i &= std(TL_{prey}) \end{aligned}$	$\begin{aligned} Omn' &= \overline{O'_i}, \\ \text{where, } O'_i &= std(TL'_{prey}) \end{aligned}$
Percent omnivory	$\%Omn = \frac{100}{s}\sum_{O_i>0} 1$	$\%Omn' = \frac{100}{s}\sum_{\substack{O'_i>0 \\ i\neq s+1 \\ i\neq s+2}} 1$

3.2.4.2 Quantitative topological properties

Bersier et al. (2002) [157] proposed a set of quantitative topological network properties which use data on interaction strengths between species. They used the Shannon Index for entropy [414] for each taxon k to measure the diversity of its predators $H_{P,k}$ and prey $H_{N,k}$, see equation (3.2) and (3.3) respectively.

$$H_{P,k} = -\sum_{j=1}^{s} \frac{a_{kj}}{a_{k\cdot}} \ln \frac{a_{kj}}{a_{k\cdot}}, \tag{3.2}$$

$$H_{N,k} = -\sum_{i=1}^{s} \frac{a_{ik}}{a_{\cdot k}} \ln \frac{a_{ik}}{a_{\cdot k}}, \tag{3.3}$$

where $a_{j\cdot}$ and $a_{\cdot j}$ are defined similarly to $b_{\cdot j}$ and $b_{j\cdot}$. From these metrics, the effective number of predators and prey for each species k were calculated to represent the number of predators $n_{P,k}$ and prey $n_{N,k}$ respectively, which would be necessary to achieve the same estimates of $H_{P,k}$ and $H_{N,k}$ if all interactions between species in a food web were of the same strength [142]. The mathematical definitions of $n_{P,k}$ and $n_{N,k}$ are given in equations (3.4) and (3.5), respectively.

$$n_{P,k} = \begin{cases} \exp(H_{P,k}) & \text{if } a_{k\cdot} \neq 0 \\ 0 & \text{if } a_{k\cdot} = 0 \end{cases} \tag{3.4}$$

$$n_{N,k} = \begin{cases} \exp(H_{N,k}) & \text{if } a_{\cdot k} \neq 0 \\ 0 & \text{if } a_{\cdot k} = 0 \end{cases} \tag{3.5}$$

By adding a closure predator and prey group at positions $S+1$ and $S+2$, respectively to quantitative matrix $\mathbf{A}$ for a food web matrix with S species and L trophic interactions, then equations (3.2) and (3.3) are modified to include interactions with closure groups to yield entropy values $H'_{N,k}$ and $H'_{P,k}$ which are used to calculate $n'_{P,k}$ and $n'_{N,k}$. This prevented floating groups appearing as basal or top species where they should not. However, we did not use values for predator and prey diversity, $n_{N,s+1}$ and $n_{K,s+2}$ to calculate quantitative network properties as, similarly to binary properties, we did not want these ‘species’ to bias property values.

Using these methods, we calculated quantitative equivalents of five properties concerning the relative prevalence of species (percentage of basal, intermediate and apex species, the top to basal species ratio and the predator to prey ratio), two complexity properties (connectance and linkage density), and four properties on the diversity of predators and prey in a food web (system generality and vulnerability, and standard deviations of generality and vulnerability). We deviated from methods used by Bersier et al. (2002) [157] to calculate trophic levels as their definition relied upon a discrete definition of trophic level that did not use quantitative data. We chose a definition that integrated information on interaction strengths, resulting in continuous values for trophic level; consequently our definition for system omnivory and percentage of omnivorous species also differed, see Table 3.2 for mathematical definitions of quantitative network properties for food web matrices with and without closure groups.

Table 3.2: Equations used to calculate quantitative topological network properties for the original food web matrix, and for the food web matrix with added closure groups [157]. Acronyms for network properties are as in Table 3.1. Note that all basal species were assigned a trophic level of one.

Property	Original food web matrix	Matrix with closure groups
Linkage density	$LD_w = \frac{1}{2S}\left(\sum_{k=1}^{s} n_{P,k} + \sum_{k=1}^{s} n_{N,k}\right)$	$LD'_w = \frac{1}{2S}\left(\sum_{k=1}^{s} n'_{P,k} + \sum_{k=1}^{s} n'_{N,k}\right)$
Connectance	$C_w = \frac{LD_w}{S}$	$C'_w = \frac{LD'_w}{S}$
Distance	$d_k = \frac{n_{N,k}}{n_{N,k}+n_{P,k}}$	$d'_k = \frac{n'_{N,k}}{n'_{N,k}+n'_{P,k}}$
Percent top	$\%T_w = \frac{100}{s}\sum_{d_k=1} 1$	$\%T'_w = \frac{100}{s}\sum_{d'_k=1} 1$
Percent intermediate	$\%I_w = \frac{100}{s}\sum_{\substack{d_k\neq 1\\ d_k\neq 0}} 1$	$\%I'_w = \frac{100}{s}\sum_{\substack{d'_k\neq 1\\ d'_k\neq 0}} 1$

Percent basal	$\%B_w = \frac{100}{s} \sum_{d_k=0} 1$	$\%B'_w = \frac{100}{s} \sum_{d'_k=0} 1$
Top to basal ratio	$T : B_w = \frac{\%T_w}{\%B_w}$	$T : B'_w = \frac{\%T'_w}{\%B'_w}$
Predator to prey ratio	$Pred : Prey_w = \frac{\prod_{k=1}^{s} \left(\frac{\sum n_{P,k}}{n_{P,k}} \right)^{\frac{n_{P,k}}{\sum n_{P,k}}}}{\prod_{k=1}^{s} \left(\frac{\sum n_{N,k}}{n_{N,k}} \right)^{\frac{n_{N,k}}{\sum n_{N,k}}}}$	$Pred : Prey_w = \frac{\prod_{k=1}^{s} \left(\frac{\sum n_{P,k}}{n_{P,k}} \right)^{\frac{n_{P,k}}{\sum n_{P,k}}}}{\prod_{k=1}^{s} \left(\frac{\sum n_{N,k}}{n_{N,k}} \right)^{\frac{n_{N,k}}{\sum n_{N,k}}}}$
Generality	$G_w = \frac{1}{S(\%B+\%I)} \sum_{k=1}^{s} n_{N,k}$	$G'_w = \frac{1}{S(\%B'+\%I')} \sum_{k=1}^{s} n'_{N,k}$
Vulnerability	$V_w = \frac{1}{S(\%T+\%I)} \sum_{k=1}^{s} n_{P,k}$	$V'_w = \frac{1}{S(\%T'+\%I')} \sum_{k=1}^{s} n'_{P,k}$

Standard deviation of generality	$stdG_w = std(G_{wk})$ where, $G_{wk} = \frac{s}{\sum_{k=1}^{s} n_{N,k}} n_{N,k}$	$stdG'_w = std(G'_{wk})$ where, $G'_{wk} = \frac{s}{\sum_{k=1}^{s} n'_{N,k}} n'_{N,k}$
Standard deviation of vulnerability	$stdV_w = std(V_{wk})$ where, $V_{wk} = \frac{s}{\sum_{k=1}^{s} n_{P,k}} n_{P,k}$	$stdV'_w = std(V'_{wk})$ where, $V'_{wk} = \frac{s}{\sum_{k=1}^{s} n'_{P,k}} n'_{P,k}$
Trophic level	$TL_{wi} = 1 + \sum_{k=1}^{s} a_{ki} TL_{wk}$	$TL'_{wi} = 1 + \sum_{k=1}^{s} a_{ki} TL'_{wk}$
Maximum trophic level	$MaxTL_w = \max_i TL_{wi}$	$MaxTL'_w = \max_i TL'_{wi}$
Mean trophic level	$MeanTL_w = \frac{1}{s} \sum_{i=1}^{s} TL_{wi}$	$MeanTL_w{}' = \frac{1}{s} \sum_{i=1}^{s} TL'_{wi}$
System omnivory	$Omn = \overline{O_{wi}}$ where, $O_{wi} = std(TL_w prey)$	$Omn' = \overline{O'_{wi}}$ where, $O'_{wi} = std(TL'_w prey)$

Percent omnivory	$\%Omn = \frac{100}{s}\sum_{O_{wi}>0} 1$	$\%Omn' = \frac{100}{s}\sum_{O'_{wi}>0} 1$

3.2.5 Aggregating species in a food web matrix

We aggregated species stepwise into a smaller number of groups in the Scotia Sea food web matrix using a measure of similarity along with a hierarchical clustering scheme. To generate quantitative similarity values for pairs of species, we used the REGE algorithm [165, 442] for regular equivalence [451]. The REGE algorithm has been used in a theoretical analysis to reduce the size of food web models [313]. Aggregation using regular equivalence produced overall smaller deviation in model results from the model with disaggregate species than other similarity measures (Bray Curtis and Euclidean distance) [313]. Additionally, a different theoretical study found that the REGE algorithm resulted in higher similarity between intuitively similar species than other, structure-based similarity measures [299].

We grouped species using the aggregation algorithm as follows:

1. We generated a similarity matrix R with elements $r_{ij} = r_{ji}$, using the REGE algorithm for regular equivalence [451].
2. We selected the species with the highest similarity, e.g. α and β;
3. We updated the food web matrix by aggregating α and β to form a new group $\alpha\beta$. The consumption of $\alpha\beta$ was then set as the sum of the consumption of α and β by their predators and its diet was set as the mean diet composition of α and β. However, if α was a floating group species, the new group $\alpha\beta$ adopted the data of β only, and vice versa. If both α and β were both floating groups, then the new group $\alpha\beta$ remained connected to a closure group.
4. From the newly aggregated diet matrix, we calculated network properties and percent change of network properties compared to the disaggregate matrix, calculated similarly to % error, see Section 3.2.3.2. We measured percent aggregation as $\%Agg_t = 100(1 - \frac{S_t}{S_0})$, where S_t is species richness of the matrix at aggregation step t and S_0 is species richness for the disaggregate matrix.
5. We updated the similarity matrix R using the maximum linkage criterion [466], such that for each taxon i: $r_{[\alpha\beta]i} = r_{i[\alpha\beta]} = \max(r_{\alpha i}, r_{\beta i})$;
6. Steps 2-5 were repeated until all values of the similarity matrix equalled zero.

The Scotia Sea food web matrix is a pertinent example of an incomplete matrix arising from limited data. We performed the aggregation analysis for the Scotia Sea food web matrix with and without closure groups to test the sensitivity of the aggregation algorithm to an incomplete food web matrix. Closure groups persisted in the matrix until they were no longer connected to any species, at which point we deleted them.

Whilst there is no robust measure of an ideal aggregation, it is not desirable to aggregate species from within one food chain, for example predators with their prey, as this can obscure important trophic detail [246, 356]. Therefore, we used the formation of new feeding loops of size one, two or three to indicate when this occurs. In a one loop species α consumes α (i.e. is a cannibal), in a two loop: α consumes β and β consumes α, and in a three loop: α consumes β, β consumes γ and γ consumes α for any three species α, β and γ. Such loops can occur in real food webs, for instance as a result of older individuals feeding upon larval or juvenile individuals. The disaggregate Scotia Sea web data contained four one loops and one two loop, but no three loops. Hereafter we refer to the point where new feeding loops were formed as a matrix was aggregated, as the 'point of over-aggregation', and any matrix aggregated beyond this as 'over-aggregated'.

3.2.6 Sensitivity analysis

We tested the robustness of results from the aggregation algorithm to two possible sources of bias which could have been introduced due to the methodologies used in this chapter. First, the structural biases imposed on the Scotia Sea food web by introducing specifically two closure groups and second, the biases caused from removing non-species resolved data from the Scotia Sea data set to construct the food web matrix. We labelled each sensitivity analyses as SA1 and SA2, respectively.

3.2.6.1 SA1: Structural biases of closure groups

We compared results from the aggregation algorithm for the two closure group scheme, to those from a 28 closure group. The 28 closure group scheme consisted of a possible 14 closure predator and prey groups, one for each species type: marine mammals, sea birds, penguins, pelagic fish, demersal fish, bentho-pelagic fish, cephalopods, gelatinous animals, large benthos, small benthos, macro-zooplankton, meso zooplankton, micro zooplankton, and primary producers. We used expert advice within the British Antarctic Survey and 'functional groups' used in an existing Antarctic food web model [259] to define these species-type groups (see acknowledgements for a list of experts consulted).

3.2.6.2 SA2: Using species-resolved data only, from the Scotia Sea data set

We reran the aggregation analysis using an alternative Scotia Sea food web matrix where 15 extra groups represented all prey not resolved to species level in the data set. Fourteen of these groups were for prey falling in the categories described in SA1, and the final group represented detrital prey.

3.3 Results

3.3.1 Effects of closure groups on network properties

Adding closure groups to degraded Gauzen's matrices representing under-sampled food webs, reduced biases for estimates of the percentage of species which are top, intermediate and basal, the predator to prey ratio, the mean and maximum trophic level and percentage omnivory. As expected, the number of trophic interactions, linkage density, connectance and the standard deviation of generality and vulnerability estimates were the same for both the degraded matrices and the matrices with closure groups. The addition of closure groups to the degraded matrices increased biases in system omnivory, system generality, and system vulnerability estimates, see Figure 3.2. Table 3.3 provides binary and quantitative topological network property estimates for the original Scotia Sea food web matrix, and the matrix with closure groups applied.

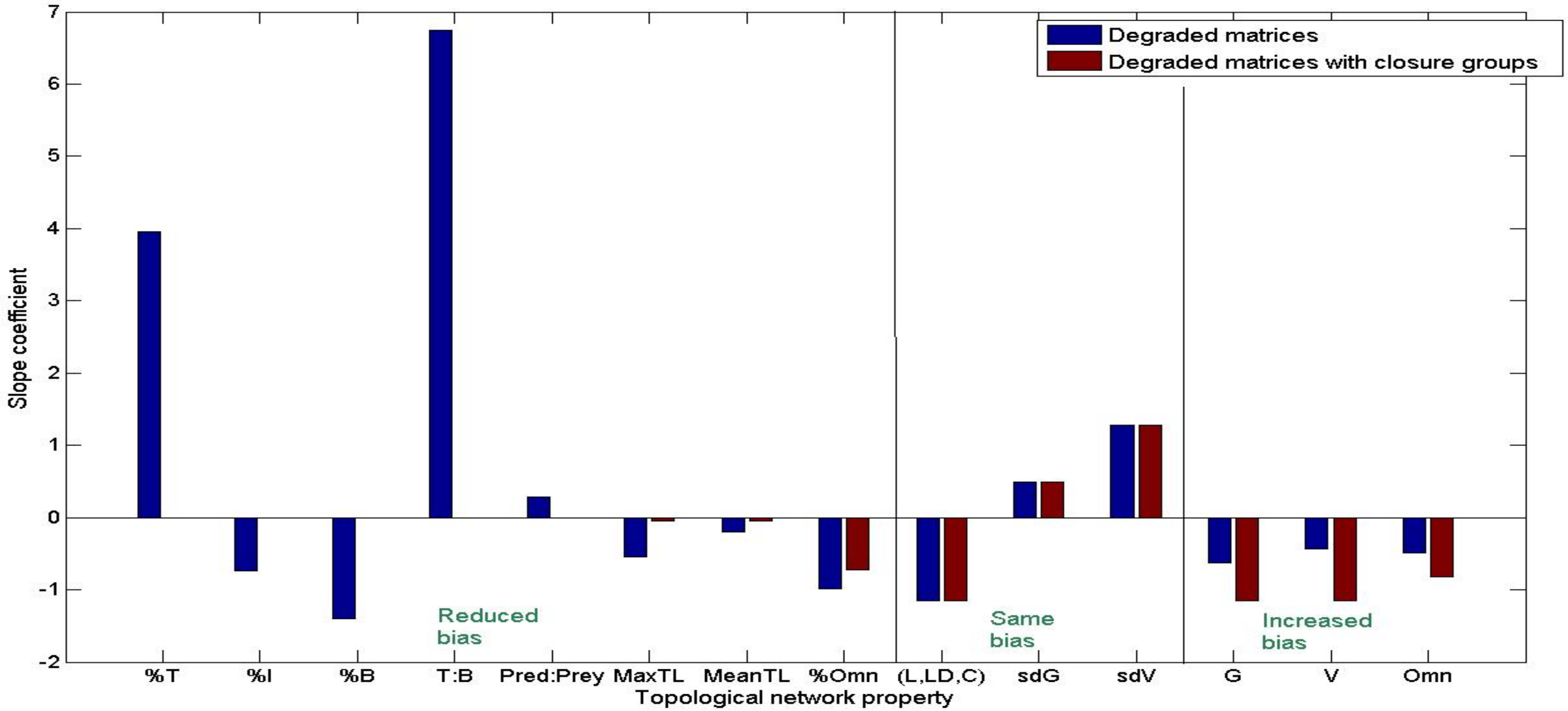

Figure 3.2: Error in binary topological network properties caused by missing diet data and the effects of adding closure groups. Y-axis shows the slope coefficient for each network property arising from a linear regression model applied to dependency of the mean percent error in network property over 100 versions of degraded Gauzens matrices on the number of diet data removed to degrade the matrix. Acronyms are as in Table 3.1. Slope coefficients were zero for %T, %I, %B, T:B, Pred:Prey for degraded matrices with closure groups.

Table 3.3: Values of binary and weighted topological network properties for the Scotia Sea food web data, before and after closure groups were added. Acronyms are as in Table 3.1.

	Binary: with closure groups	Binary: original matrix	Quantitative: with closure groups	Quantitative: original matrix
S	195	195	195	195
LD	3.4	3.4	2.0	1.6
C	0.018	0.018	0.010	0.008
$\%T$	8.2	15.4	8.2	15.4
$\%B$	5.1	61.0	5.1	61.0
$\%I$	86.7	23.6	86.7	23.6
$T:B$	1.6	0.3	1.6	0.3
$Pred:Prey$	1.0	0.5	1.1	0.5
G	3.6	8.8	2.0	3.4
V	3.7	4.0	2.2	2.3
$stdG$	2.1	2.1	1.2	1.9
$stdV$	1.7	1.7	1.6	1.7
$MaxTL$	4.4	3.7	4.8	4.5
$MeanTL$	2.4	1.6	2.5	1.7
Omn	0.13	0.16	0.14	0.19
$\%Omn$	26.2	27.7	26.4	27.7

3.3.2 Effects of aggregating species in the Scotia Sea food web matrix on network properties

The measures of similarity for pairs of species differed between the original Scotia Sea food web matrix, and the matrix with closure groups, causing different responses to network properties upon species aggregations between these matrix types (compare Figures 3.3a and 3.4 to 3.3b and 3.5).

For both types of Scotia Sea food web matrix, most network properties followed the same directional response to species aggregation up to the formation of extra feeding loops (which suggested that species had been aggregated from different trophic levels). Beyond this level of aggregation, the changes of network properties to further aggregation became erratic. For the matrix without closure groups, over aggregation occurred at 20% aggregation of the Scotia Sea food web matrix (when the food web matrix had been aggregated such that its size was reduced by 20% from the disaggregate web), but for the matrix with closure groups, this did not occur until 57% aggregation.

Most binary and quantitative network properties changed in a qualitatively similar way as species in the Scotia Sea food web matrix became more aggregated. With the exceptions of the top to basal ratio, mean trophic level and percentage omnivory, quantitative properties were less sensitive to aggregation than their binary counterparts. For the matrix with closure groups, both quantitative and binary linkage density, connectance, system omnivory, percent omniory, system generality, system vulnerability and mean trophic level increased as the matrix was aggregated up until the point of over-aggregation (see Figure 3.4).

Connectance was the most sensitive property as species were aggregated in the Scotia Sea food web matrix with closure groups. This was followed by both omnivory properties. Quantitative connectance increased by 241% before the point of over-aggregation (Figure 3.4b), system omnivory increased by 149% (Figure 3.4k) and percentage omnivory increased by 141%, (Figure 3.4l). Quantitative properties which exhibited a negative trend before over-aggregation were the percentage of intermediate species and standard deviation of generality and vulnerability (Figures 3.3b and 3.4g,h). The most invariant quantitative properties were the top to basal ratio, predator to prey ratio, standard deviation of vulnerability, maximum trophic level, and mean trophic level (Figures 3.4c,d,h,i,j). Table 3.4 provides values for binary and quantitative network properties for the Scotia Sea for the disaggregated food web matrix and for the matrix at the point of over aggregation.

3.3.3 Sensitivity analysis

3.3.3.1 SA1: Structural biases of closure groups

Network properties for both the two and 28 closure group scheme responded similarly in direction and magnitude to aggregating species in a food web matrix. Results from the aggregation algorithm for the 28 closure group scheme can be found in Appendix C. The REGE algorithm assigned high similarity between floating species assigned to the same closure group for the food web matrix with the 28 closure group scheme applied.

3.3.3.2 SA2: Using species-resolved data only, from the Scotia Sea data set

We found that the response of network properties to aggregating species in the food web matrix was not sensitive to biases imposed by using species-resolved taxa only. Properties changed similarly for the Scotia Sea diet matrix constructed from species-resolved data only, and for the matrix constructed from data where non-species resolved prey were included in

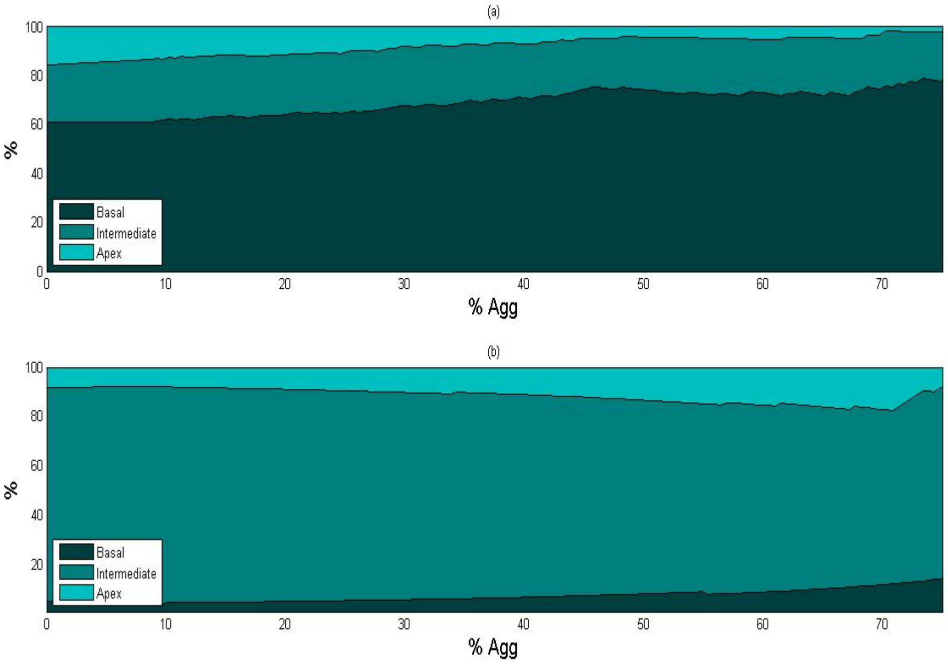

Figure 3.3: The proportion of the system which are top, intermediate and basal species at each aggregation step for (a) the original Scotia Sea food web matrix and (b) for the Scotia Sea food web matrix with closure groups.

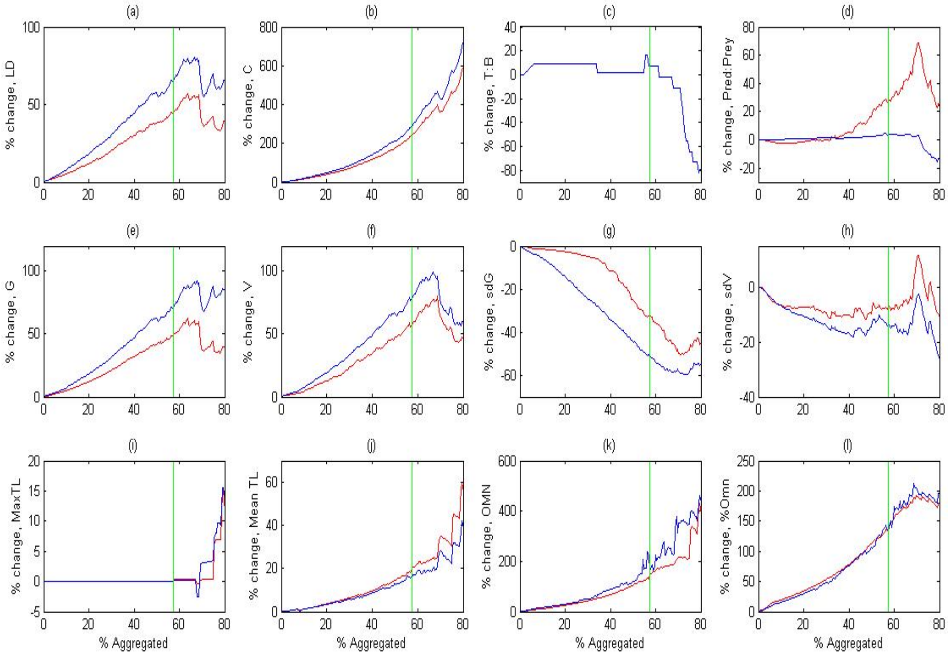

Figure 3.4: Percent change in quantitative (red) and binary (blue) network properties from the Scotia Sea food web data with closure groups at each aggregation step. The green line marks the point of over-aggregation. Acronyms for network properties are as in Table 3.1.

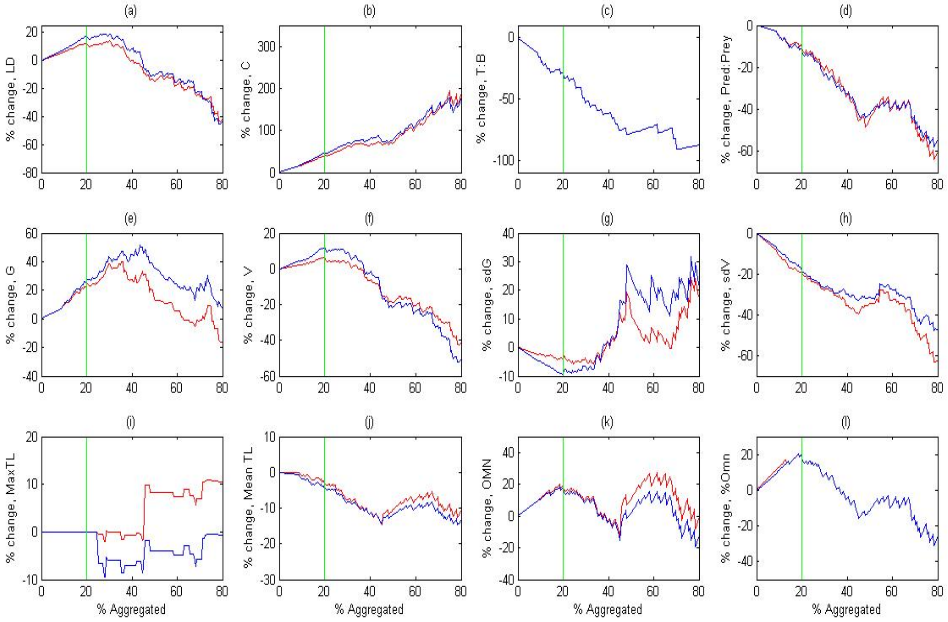

Figure 3.5: Percent change in quantitative (red) and binary (blue) network properties from the original Scotia Sea food web data (without closure groups) at each aggregation step. The green line marks the point of over-aggregation. Acronyms for network properties are as in Table 3.1.

one of 15 prey groups. Results from the aggregation analysis applied to the Scotia Sea food web matrix where non-species resolved prey were included, can be found in Appendix C.

3.4 Discussion

3.4.1 Scotia Sea network properties

In this section we discuss topological network properties calculated for the Scotia Sea from the food web matrix. We also compare the Scotia Sea to the Southern Ocean as a whole, using topological network properties calculated here to those published for the Southern Ocean in de Santana et al. (2013) [401]. De Santana et al. (2013) [401] calculated network properties using a recently published diet database for the Southern Ocean [370]. The Scotia Sea data set also used a subset of data from this database, (see Chapter 2). We acknowledge that using some of the same data could result in trivially similar network properties for the Scotia Sea and the Southern Ocean. However the chances of this are reduced as the Scotia Sea data set also contains data from sources not included in the Southern Ocean network analysis. Furthermore, comparing these two ecosystems provides useful insight into how property values change for ecosystems considered at different spatial scales.

Table 3.4: Network properties for the disaggregate Scotia Sea food web matrix with closure groups (dis.) and this matrix at the point of over-aggregation (agg.). Acronyms for network properties are as in Table 3.1.

	Quantitative		Binary	
	Dis.	Agg.	Dis.	Agg.
S	195	195	195	195
$\%T$	8.2	14.5	8.2	14.5
$\%I$	86.7	77.1	86.7	77.1
$\%B$	5.1	8.4	5.1	8.4
$T:B$	1.6	1.7	1.6	1.7
$Pred:Prey$	1.1	1.4	1.0	1.1
LD	2.0	2.8	3.4	5.7
C	0.010	0.034	0.018	0.068
G	2.0	2.9	3.6	6.2
V	2.2	3.5	3.7	6.6
$stdG$	1.2	0.8	2.1	1.0
$stdV$	1.6	1.5	1.7	1.4
Omn	0.1	0.4	0.1	0.3
$\%Omn$	26.4	63.5	26.2	61.4
$MaxTL$	4.8	4.8	4.4	4.4
$MeanTL$	2.5	3.0	2.4	2.8

We applied closure groups to the food web data used for the Southern Ocean in de Santana et al. (2013) [401] to make their network properties comparable to those for the Scotia Sea in this chapter. See Appendix D for full details on how closure groups were applied to the Southern Ocean diet matrix, and Table 3.5 for resulting network properties.

3.4.1.1 Linkage complexity

In topological network analyses, complexity of trophic links in a food web are summarised by linkage density and connectance. The range of linkage density values calculated in the aggregation analysis for the Scotia Sea food web up to the point of aggregation was overall less than linkage density for the Southern Ocean [401] (Table 3.5). This suggests that, on average, there are fewer trophic links formed per species in the Scotia Sea than in the Southern Ocean. One explanation may be that the higher abundance of krill in the Scotia Sea, compared with many other areas of the Southern Ocean [133, 257], could reduce the diversity of prey consumed by a predator in the Scotia Sea.

Table 3.5: Binary network properties from the original Southern Ocean food web matrix and the same matrix with added closure groups, compared to the range of possible network property values for the Scotia Sea food web with closure groups calculated from the species aggregation analysis. The first value in column four is the network property for the original Scotia Sea food web matrix, and the second is the property value at the point of over aggregation. Acronyms for network properties are as in Table 3.1.

	Southern Ocean		Scotia Sea
	Original data	With closure groups	With closure groups
% T	15	7	8.2-15
% I	40	91	87-77
% B	45	1.6	5.1-8.4
$T : B$	0.3	4.7	1.6-1.7
$Pred : Prey$	0.7	1.1	1.0-1.1
$MaxTL$	3.6	3.8	4.4-4.4
$MeanTL$	1.8	2.4	2.4-4.8
LD	5.1	5.1	3.4-5.7
C	0.027	0.027	0.018-0.068
G	9.3	5.2	3.6-6.2
V	6.0	5.5	3.7-6.6
sdG	1.8	1.8	2.1-1.0
sdV	1.5	1.5	1.7-1.4
Omn	0.3	0.2	0.1-0.3
$\%Omn$	39	40	26.2-61.4

Connectance is defined as the proportion of all potential trophic interactions in a food web (S^2), which are actually formed in the real food web. Along with linkage density, connectance is a frequently used metric of link complexity in a food web. Some studies suggest high link complexity can increase the robustness of a food web [281, ch. 11]. Although linkage density is lower, connectance is overall higher for the Scotia Sea compared to that reported for the Southern Ocean [401]. Higher connectance for the Scotia Sea compared to the Southern Ocean could be an artefact of the different spatial scale under consideration. For example, a predator's distribution in the Southern Ocean may only be a fraction of the area of the whole ecosystem. Therefore, this predator would be unable to form trophic interactions with prey with a non-overlapping distribution. At smaller spatial scales, such as the Scotia Sea, the distribution of consumers and prey are more likely to overlap, and so could, provided other biological constraints do not prevent it, form a trophic interaction. Therefore, we may expect connectance to be higher in smaller ecosystems, even if these smaller ecosystems contain fewer species.

Furthermore, connectance was the least robust network property to species aggregation in the Scotia Sea food web matrix, which makes this property less useful to compare the Scotia Sea with other ecosystems where prey and consumers are resolved to different taxonomic resolutions. Linkage density may be a more useful metric to use to compare the complexity of the Scotia Sea with other food webs as it was much less sensitive to species aggregation (Figures 3.4a,b).

3.4.1.2 The trophic positions of species

It is widely accepted that many network properties are scale dependent [281, ch. 11]. The percentage of intermediate species usually increases and the percentage of basal and top predators decreases with the increasing scale considered [308]. Differences in the percentage of top, intermediate and basal species for the Scotia Sea compared with the Southern Ocean, support this hypothesis (Table 3.5). This is further validated as the top to basal ratio and predator to prey ratio were relatively robust upon species aggregation of the Scotia Sea food web matrix. Therefore the top to basal ratio and predator to prey ratio offer robust properties with which to compare the Scotia Sea with other ecosystems.

There are a high number of intermediate species in both the Southern Ocean and the Scotia Sea food webs resulting in similar predator to prey ratios of approximately one. As discussed in Chapter 2, there are few data for some zooplankton and none for microbial species in the Scotia Sea data set. This may lead to an underestimate of the percentage of basal species. However, given that paucity of microbial data is a common limitation of food web data sets, biases caused by this limitation to the predator to prey ratio may be similar across different food web data sets.

3.4.1.3 Diversity of trophic interactions

The standard deviation of vulnerability ($stdV$) and standard deviation of generality ($stdG$) indicate the number of predators and number of prey shared per species. Thus together, they indicate the relative diversity of predators to prey, with a high $stdV$ to $stdG$ ratio indicating a high diversity of predators compared to diversity of prey [401]. The standard deviation of vulnerability for the Scotia Sea was quite robust to species aggregation (Figure 3.4), and so is a useful measure of predator diversity for the Scotia Sea.

However, the standard deviation of generality decreased with species aggregation, and furthermore, the $stdV : stdG$ ratio was greater than one for quantitative network properties but less than one for binary network properties. Conflicting conclusions arising between binary and quantitative network properties makes comparing the Scotia Sea with the Southern Ocean difficult. Binary $stdV : stdG$ for the Scotia Sea (0.8-1.4) compared to the Southern Ocean (0.8) suggests the Scotia Sea may be slightly more vulnerable to trophic cascades (predators altering species composition at lower trophic levels) than the Southern Ocean as a whole [174]; however, these results are not conclusive due to the sensitivity of these properties to some of the assumptions used to calculate them.

Omnivorous loops which include weak trophic interactions may affect food web stability [322]. High omnivory, along with high connectance, may decrease trophic cascade effects and the capacity for invasive species to establish themselves at low trophic levels [140, 166]. The robustness of the Scotia Sea to invasive species and trophic cascade effects are important to assess as it is likely that the Scotia Sea will be subjected to climatic pressures which could alter species composition [236]. Percent omnivory for the disaggregate Southern Ocean food web was in the middle of the range of $\%Omn$ estimates for the Scotia Sea at 26%. Thus we could not conclusively make inferences about the relative robustness of the two ecosystems using percentage omnivory.

The ratio of predator to prey diversity, and percentage omnivory for the Scotia Sea were sensitive to species aggregation. This led to inconsistencies when we used these properties to compare the Scotia Sea food web to the Southern Ocean. We therefore suggest that it is an important avenue of future research to assess how changes, for example to the abundance or consumption of species in the Scotia Sea, may affect other species in the ecosystem. This is particularly important to be a due to likely climatic and anthropogenic pressures on the Scotia Sea.

3.4.2 Binary versus quantitative properties

Food webs contain many weak trophic interactions [153, 397] which are argued to stabilise the ecosystem [321, 359]. Quantitative network properties improve on binary properties as they distinguish between different strengths of these trophic interactions [157]. This study found that many network properties may be less sensitive to the effects of aggregating species when building food web matrices than has been suggested by previous studies which use binary analyses. However, this result is not conclusive as we applied the species aggregation analysis to only one ecosystem. An interesting avenue for future research would apply the aggregation analysis from this chapter to a greater number of quantitative food web data sets to test the generality of our results. A similar analysis [143] which compared the effects of sampling effort on quantitative and binary properties explored in this chapter, found that quantitative properties were less sensitive to under-sampling than binary network properties.

In this chapter, we assessed for the first time, how quantitative versions of topological properties developed by Bersier et al. (2002) [157] responded to species aggregation. Our analysis supports similar analyses which concentrated on the responses of binary network properties to species aggregation [248, 305, 425]. Whilst one such study by Martinez et al. (1991) [305] concluded that most binary network properties are sensitive to species aggregation, another study by Sugihara et al. (1989) [425] found that many network properties, excluding linkage density, were robust to species aggregation. Our analysis considers a wider range of topological properties than these two studies, and we also consider how quantitative versions of topological properties respond to aggregation as well as binary properties. Our results provide evidence to support the argument of Martinez et al. (1991) [305], that network properties are sensitive to species aggregation. However, relatively insensitive network properties for the Scotia Sea are the top to basal ratio, predator to prey ratio, maximum trophic level, mean trophic level, and standard deviation of vulnerability.

3.4.3 Closure groups

We have shown that it is possible to decrease the biases caused by under-sampling by adding extra species (i.e. closure groups) to fill identifiable gaps in food web matrices. This reduces error in estimates of the trophic level of affected species, and therefore in many network properties that integrate this information including mean and maximum trophic level, percentage of top, intermediate and basal species, top to basal ratio, predator to prey ratio and percent omnivory (Figure 3.2). Furthermore, closure groups resulted in higher similarity between trophically similar species in the REGE algorithm, compared to the Scotia Sea food web matrix without closure groups as seen from a higher point of over aggregation for the former. The simplicity of closure groups is their strength: their effects on network properties are easy to understand as they reset the trophic level of falsely basal species (floating predators) from one to two; and they can be easily applied to any incomplete food web matrix.

A disadvantage of closure groups are that they increase error in some network properties, namely binary system generality, system vulnerability and system omnivory. We therefore suggest using standard deviation of generality and vulnerability and percentage omnivory in food web analyses as these are not affected by closure groups, and are also less sensitive to species aggregation than their alternatives. Furthermore, closure groups applied to incomplete food web matrices cannot improve estimates of linkage density, connectance, or the standard deviation of generality and vulnerability which can be biased by incomplete food web data [143, 251, 307]. Available empirical studies, however limited, are the only data available to build matrices of interactions in real food webs, and closure groups are a useful tool to reduce error in food web analyses which use network properties that integrate information on trophic position. We preferred the two closure group scheme to a more complex scheme, as it imposed less subjective bias on the trophic 'role' of floating species.

3.4.4 Limitations and further work

We used the REGE algorithm [165, 442] for regular equivalence [451] to assign similarity to pairs of species in the Scotia Sea food web matrix. The REGE algorithm assigns high similarity between species which occupy similar trophic roles, however these species do not necessarily have to form trophic interactions with the same predators and prey. A commonly used protocol in food web analyses is to aggregate species into groups known as trophic species [355]: groups of species which share common predators and prey. Unlike structural similarity measures such as Jaccard (used in e.g. Yodzis et al. (1999)[467]) and Bray Curtis (used in e.g. Metcalf et al. (2008) [313]), regular equivalence could allow for high similarity between floating species, and species not connected to closure groups. This is advantageous in incomplete data sets such as that for the Scotia Sea, because species which in reality share common predators and prey, but for whom there is no diet data in the food web data set, may still be aggregated with each other. Whilst we acknowledge that the REGE algorithm may result in the aggregation of some species which do not share the same predator and prey, by considering aggregation only up to the point where extra feeding-loops are formed, we reduce possible biases caused by this 'false-aggregation'. A possible extension of this work would test the sensitivity of the aggregation analysis from this chapter, to alternate similarity measures and linkage criterion which can affect species aggregation [306, 467].

Using diet fractions to measure interaction strength has the effect of treating all species' feeding rates as equal. Ideally, interaction strength would be measured as the flow of carbon between species, or feeding rates of predator on prey [143, 157, 397]. Empirical estimates of carbon flow or feeding rates are difficult to obtain [397], and so these values are often estimated from models that require a large number of parameters. This introduces new biases and uncertainties; many other measures of interaction strength, (see Wooton and Emmerson (2005) [459] for a comprehensive review of types of interaction strength), suffer from similar biases, such as the Jacobian matrix which must also be calculated from high-parameter models). Therefore, we used the diet composition of predators as a pragmatic metric on which to build quantitative food web matrices [397].

3.5 Conclusion

Topological network properties are a set of summary statistics which offer system-level insight into the structure and diversity of species and trophic links in complex food webs. In this chapter, we reported a set of binary and quantitative topological network properties for the Scotia Sea food web using a new data set summarised in Chapter 2. We addressed two common limitations which can bias network properties. First, that missing data can cause species to falsely appear as basal or apex species and second, that food web data contains species resolved to different taxonomic levels.

We applied closure groups to the Scotia Sea food web matrix to prevent species in the matrix falsely appearing as basal or apex species. This simple correction reduced biases in some network properties; namely the percentage of top, intermediate and basal species, the top to basal and predator to prey ratio, maximum and mean trophic level, and percentage omnivory.

We stepwise aggregated species in the Scotia Sea food web matrix to assess the possible range of network properties for different resolutions of species. Similar to some existing studies on the effects of species aggregation on binary network properties [305, 248], we found that most topological network properties were sensitive to species aggregation. The least sensitive properties were the top to basal ratio, predator to prey ratio, mean trophic level, maximum trophic level, and standard deviation of vulnerability, and so we conclude these are robust metrics for the Scotia Sea. The property most sensitive to species aggregation was connectance, and so we suggest that linkage density may be more useful to measure linkage complexity.

Changes of binary compared with quantitative network properties were qualitatively similar, although our results show that for the Scotia Sea food web matrix, quantitative properties were generally less sensitive to species aggregation than their binary counterparts. However, aggregation analysis applied to more quantitative food web data sets would be required to determine the generality of this result. Binary properties and quantitative network properties suggest a different ratio of predator to prey diversity. Furthermore, upon aggregation the ratio of predator to prey diversity is not consistent, and percentage omnivory is very sensitive to species aggregation. These are important properties which are linked to the robustness of a food web to invasive species and to trophic cascade effects [140, 174, 281, 321]. It will be important in future work to determine how changes to an ecosystem could propagate through the food web in the Scotia Sea, due to the likely anthropogenic and climatic stresses which could affect the abundance of some species in the Scotia Sea, for example Antarctic krill [236].

Understanding the structure of real food webs and how this relates to its function is an important goal in ecology [315]. In this chapter, we facilitate such analysis for the Scotia Sea by providing a summary of the topological structure of the Scotia Sea food web, and the sensitivity of these properties to different taxonomic resolutions of species in the food web matrix.

4 A mass-balanced model to estimate production of species in the Scotia Sea food web

Abstract

In Chapter 2, we developed a food web diet data set for the Scotia Sea ecosystem, to be primarily used to construct food web models. In Chapter 3, we used this data set to compare the Scotia Sea food web to the Southern Ocean food web using topological network properties but found we were limited in our ability to draw ecological conclusions for the Scotia Sea due to uncertainties in the data and analysis. In this chapter, we constructed a food web model for the Scotia Sea, based on the frequently used Ecopath equations, in which species within an ecosystem are represented by a set of functional groups. These mass-balanced models are useful as they: (i) provide valuable insight into how changes to one species could propagate through the food web; (ii) can provide insight into the structure of a food web at equilibrium; and (iii) quantify organic energy flow between species in an ecosystem, which can be difficult to measure empirically. We developed a version of Ecopath model framework which required fewer parameters and was always at mass-balance, which we called the Reduced Production Model (RPM). We used the RPM to identify functional groups which could be important in the Scotia Sea ecosystem by assessing how small perturbations to two ecological parameters for each group affected total primary and secondary production. Furthermore, we assessed the relative uncertainties in production estimates for each functional group by evaluating the model for 10 000 sets of input parameters, using a Latin-Hypercube Sampling-based approach to ensure the full range of uncertainty in each input parameter was evaluated. Our model highlighted species which are known to be important prey and consumers in the Scotia Sea as important in determining model outputs, specifically Antarctic krill, pelagic fish, macaroni penguins, and Antarctic fur seals. However, we also highlighted species whose importance in the ecosystem is less well known, namely salps and gelatinous zooplankton, cephalopods, and omnivorous meso and micro zooplankton. We found that uncertainties in production estimates were generally higher for the functional groups with the highest production, but that this alone could not predict uncertainty in a production estimate for all functional groups.

4.1 Introduction

The Scotia Sea food web is the most productive regime in the Southern Ocean [267, 320]. Many areas of the Southern Ocean are high nutrient, low chlorophyll ecosystems due to the limited availability of iron [320]. However, iron fertilisation from sources such as ocean upwelling resulting from the interaction of strong currents with bottom topography, dust enrichment from the Patagonian shelf, and enrichment from excretion by marine organisms, e.g. [267, 268, 292, 320] means that primary production in the Scotia Sea is high and, at times, limited by macro-nutrients [320]. This primary production supports a food web which includes a large proportion of Southern Ocean Antarctic krill biomass [132, 133], and one of the most diverse communities of land-breeding marine predators in the world [320].

Diet composition based food web models (also known as ecosystem models) quantify energy flow through an ecosystem from basal groups (groups with no prey) such as primary producers and the detrital pool, up to apex predators (species with no predators). These food web models have been produced for the South Georgia shelf ecosystem in the Scotia Sea [259], the South Georgia and South Orkney archipelago's [170], and for other Southern Ocean ecosystems such as the adjacent Western Antarctic peninsula [141]. However, a new diet-composition data set for Scotia Sea predators presented in Chapter 2, offers an opportunity to develop a food web model for the Scotia Sea which includes data collected over six decades from the South Orkney and South Georgia archipelagos, the South Sandwich Islands, and from the open ocean in the Scotia Sea.

Food web models based on diet composition are useful to produce quantified estimates of trophic interactions. A diet composition based model of the Scotia Sea would complement an existing isotope-based study [424], which provided new insight into the structure of the Scotia Sea ecosystem and the prey of some zooplankton species. It is important to understand the food web at the spatial scale of the Scotia Sea, as this spatial unit is frequently used in climate, fisheries and ecological studies, for example [192, 234, 309, 383, 452]. Furthermore, the Scotia Sea has been subjected to historic commercial exploitation of whales, seals, penguins, fish and krill populations leading to the depletion of some species including populations of higher predators [285]. The extent of the recovery of some populations remains unclear as there is a paucity of data on the state of the ecosystem pre-exploitation [285]. Food web models can be used to assess the possible impacts of change to a food web, to estimate ecosystem parameters which are difficult to measure empirically, and to provide valuable insight into how an ecosystem could be structured at equilibrium.

Ecopath is a commonly used framework for modelling the flow of organic energy through an ecosystem, and forms part of the software package Ecopath with Ecosim [183, 346]. An Ecopath model represents an ecosystem through a set of linear equations, one for each functional group, where a functional group is a collection of individual organisms with similar trophic interactions represented together in a model. In an Ecopath equation, total production (additional organic energy produced over a fixed period of time through growth or reproduction) is the sum of 'losses' of this production. These losses are, typically, to its predators and to the detrital pool. Therefore, total production by a functional group is equal to demand by other groups over a fixed period of time, usually a year. As such, the standing biomass of each functional group remains constant over long time scales (although Ecopath equations can be modified to include a change in biomass, see [183, 346]).

Usually, Ecopath is used such that estimates for consumption and production rates (per unit biomass), and biomass of each functional group are inputs into the model. Typically, this results in an unbalanced model meaning that demand for production of a functional group exceeds the input-production. An unbalanced model is represented by outputs known as ecotrophic efficiencies exceeding one. Input parameters are then adjusted using subjective judgement e.g. example [259], or objective algorithms e.g. [358], until ecotrophic efficiencies have a value between zero and one at which point the model is at mass-balance. There are uncertainties associated with each input parameter due to difficulties of sampling and data-collection, and through model balancing. It is important to investigate the sensitivities of model outputs to each input parameter, as well as assess uncertainties in model outputs [260].

In this study we developed a simplified form of the Ecopath framework which we called the Reduced Production Model (RPM). The RPM uses a reduced number of parameters compared to Ecopath, as it does not explicitly require biomass estimates for functional groups. The RPM is used to estimate the production of all but one functional group in a food web; the production estimate for the remaining functional group, ecotrophic efficiencies, and growth efficiencies (the proportion of consumption by a functional group which it converts into its own production) are model inputs. The RPM has a number of advantages over an Ecopath model framework. First, it is always at mass-balance; second, by not explicitly accounting for the biomass of each functional group, we reduced the number of dimensions for which uncertainties can be introduced; third, by using ecotrophic efficiencies and growth efficiencies as inputs into the RPM, we were able to efficiently and methodically explore the effects of uncertainty in input parameters, without the requirement of adjusting them to ensure mass-balance as would be necessary if we were using Ecopath in its typical form. This is advantageous as adjusting input parameters to ensure mass-balance introduces new uncertainties due to the multiple methodologies which can be used to complete this.

In this paper we used a new compilation of diet-composition data (see Chapter 2), to develop a mass-balanced food web model of the Scotia Sea. Each functional group in the food web model had up to two associated efficiency terms: growth and ecotrophic efficiency. Each efficiency term can determine the production and consumption estimate of the related functional group which can propagate through the food web to cause changes to the production of other functional groups. The sensitivity of the Scotia Sea food web to changes in these efficiency terms for a given functional group is, therefore, an indicator of the importance of that functional group in the food web. This is analogous to another method used in Ecopath to identify important species: mixed trophic impact analysis [294, 438]. Using our methods, we were able to see if the same groups arose as important in the Scotia Sea food web for two different ecological parameters.

We extracted estimates for efficiency terms to use as baseline input values from existing Ecopath models of Antarctic ecosystems [141, 259, 343, 358]. We used an estimate for the annual production of Antarctic krill as an input because there are published estimates of their biomass and production in the Southern Ocean e.g. [133, 257]. We identified functional groups which could be important in the Scotia Sea ecosystem, by assessing which functional groups caused the most change to total food web production when subjected to a small perturbation in each input efficiency parameter. Furthermore, we assessed the relative uncertainties in production estimates for functional groups by evaluating the model for 10 000 sets of input parameters, using a Latin-Hypercube Sampling-based approach to ensure the full range of uncertainty in each input parameter was assessed. Estimating production and consumption of predators is important for effective management of Antarctic fisheries, assessing global carbon fluxes, and providing insight into the operation of the Scotia Sea food web [231, 285, 316].

4.2 Methods

4.2.1 The Reduced Production Model

We developed an ecosystem model framework called the Reduced Production Model (RPM), based heavily on the widely used Ecopath model framework [183, 346]. In an Ecopath model, an ecosystem is represented by a set of n Functional Groups (FG) each with linear equation describing the fate of its production over a year. A simple form of an Ecopath equation for functional group i is given by equation (4.1).

$$P_i = \left(\sum_{j=1}^{n} \frac{Q_j}{B_j} B_j a_{ij} \right) + \frac{P_i}{B_i} B_i \left(1 - EE_i\right). \tag{4.1}$$

Here, P_i and $\frac{P_i}{B_i}$ are the production and production rate of functional group i, $\frac{Q_j}{B_j}$ is consumption rate by consumer j, and B_i is the biomass of functional group i. EE_i is known as the ecotrophic efficiency and $(1 - EE_i)$ is the proportional contribution of production of functional group i to detritus through mortality other than biomass ingested by its predators. This can be through messy eating by its predators (biomass not ingested by its predators), and through mortality from senescence and disease. The diet matrix $\mathbf{A}$ contains elements a_{ij}, which are the proportional contribution of i to the diet of predator j. Additional terms are sometimes included on the right hand side of equation (4.1) to account for catch by fisheries, import and export, and bio-accumulation which can be used to represent an increase in the standing biomass of a functional group if its population size is increasing. Typically, Ecopath is used such that empirical estimates for $\frac{P_i}{B_i}$, $\frac{Q_i}{B_i}$ and B_i, for all functional groups i, are inputs along with the diet matrix, and ecotrophic efficiencies are outputs.

Growth efficiency ($e_i = \frac{P_i}{Q_i}$), is the proportion of consumption by a functional group which it converts into its own growth. Thus $(1 - e_i)$ is the proportion of consumption which is used for respiration or which is not assimilated but lost in excretion. By removing explicit consideration of biomass terms and introducing growth efficiencies into equation (4.1), we derived equation (4.2).

$$P_i = \sum_{j=1}^{n-1} \frac{P_j}{e_j} a_{ij} + P_i \left(1 - EE_i\right), \tag{4.2}$$

We used a production estimate for one well observed functional group k, the diet matrix, and ecotrophic efficiency EE_i and growth efficiency e_i values for each functional group (hereafter collectively referred to as the efficiency values) as inputs into the RPM. Model outputs are then the production of the remaining functional groups. For a food web model with r apex functional groups, the RPM consists of a set of $(n - r)$ equations to calculate the $(n - 1)$ unknown production terms. If in a food web model $r = 1$ then this set of linear equations is fully determined and has a unique solution. However, if $r > 1$ then apex predators were represented by a single functional group, *apex*, with a single unknown production term, P_{apex}. We took the arithmetic average of the diet compositions and efficiency terms of apex predator functional groups to derive a new diet composition and efficiency term for the *apex* functional group.

Although the RPM does not explicitly account for respiration and unassimilated consumption, these terms are implicitly included in the growth efficiency term. Whilst this prevents the RPM from providing insight into the contribution of a functional group to the detrital pool through excretion, it reduces model complexity.

To solve this linear set of simultaneous equations using matrix algebra, all the unknown production terms were collated on one side of the equation, and all constants on the other. For any functional group $i \neq k, apex$ whose diet proportionally comprises a_{ii} itself, equation (4.2) becomes:

$$P_i\left(EE_i - \frac{a_{ii}}{e_i}\right) - \frac{a_{iapex}}{e_{apex}}P_{apex} - \sum_{\substack{j=1\\ j\neq i,k}}^{n-j} \frac{a_{ij}}{e_j}P_j = \frac{a_{ik}}{e_k}P_k. \tag{4.3}$$

The RPM cannot be solved if the diet matrix has feeding loops, for example, in a one loop, X consumes X, and in a two-loop (X consumes Y and Y consumes X). To explain why, consider cannibalism by a functional group. The production of a functional group is related to its own consumption by its growth efficiency, which is the proportion of a functional groups consumption which it turns into its own production. If cannibalism is included in the growth efficiency then consumption of its own production contributes to its own production, which is paradoxical. Thus, we removed cannibalism from the RPM and assumed that the growth efficiency was the proportion of consumption on prey other than itself which it turns into its own production, and that production is dependent on consumption by predators other than itself. For similar reasons, we remove the smallest diet fraction in all loops. As such, equation (4.3) becomes:

$$EE_iP_i - \frac{a_{iapex}}{e_{apex}}P_{apex} - \sum_{\substack{j=1\\ j\neq i,k,\mathbf{w}}}^{n-j} \frac{a_{ij}}{e_j}P_j = \frac{a_{ik}}{e_k}P_k, \tag{4.4}$$

Where $\mathbf{w}$ is the set of predators for which a_{wi} forms the weakest diet fraction in a loop. When $i = k$, equation (4.4) becomes:

$$\frac{a_{kapex}}{e_{apex}}P_{apex} + \sum_{\substack{j=1\\ j\neq k,\mathbf{w}}}^{n-j} \frac{a_{kj}}{e_j}P_j = P_k\left(1 - EE_k\right). \tag{4.5}$$

This led to an $(n - r)$ by $(n - r)$ matrix equation $\mathbf{FP} = P_k\mathbf{C}$, see equation (4.6).

$$\begin{bmatrix} EE_1 & \frac{-a_{12}}{e_2} & \dots & \frac{-a_{1\text{apex}}}{e_{\text{apex}}} \\ \frac{-a_{21}}{e_1} & EE_2 & \dots & \frac{-a_{2\text{apex}}}{e_{\text{apex}}} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{a_{k1}}{e_1} & \frac{a_{k2}}{e_2} & \dots & \frac{a_{k\text{apex}}}{e_{\text{apex}}} \end{bmatrix} \begin{bmatrix} P_1 \\ P_2 \\ \vdots \\ P_{apex} \end{bmatrix} = P_k \begin{bmatrix} \frac{a_{1k}}{e_k} \\ \frac{a_{2k}}{e_k} \\ \vdots \\ EE_k \end{bmatrix} \tag{4.6}$$

Equation (4.6) is solved for the production vector $\mathbf{P}$ by applying the inverse of matrix F to the right hand side of equation 4.6, see equation (4.7).

$$\mathbf{P} = P_k\mathbf{F}^{-1}\mathbf{C} \tag{4.7}$$

4.2.2 Scotia Sea functional groups

The Scotia Sea food web model has 42 functional groups: eight for marine mammals, five representing penguin species, five for flying seabirds, nine for fish, one for cephalopods, eleven for zooplankton, one for heterotrophic bacteria and chromista, one for primary producers, and one for detritus (see Table 4.1). We defined functional groups as an iterative process based on expert advice, diet composition of predators, and the availability of published diet data.

Table 4.1: Functional groups used to model the Scotia Sea food web. The size partitions of macro zooplankton (>six mm) used was conservative within the range (4-20mm) used in published studies on zooplankton community composition [271, 290, 291, 301, 441]. Demersal fish were partitioned into depth categories based on the boundary for the epipelagic zone at 200m.

FG	Description	Notes
101	Leopard seals	
102	Antarctic fur seals	
103	Weddell seals	
104	Crabeater seals	
105	Sub Antarctic fur seals	
106	Southern elephant seals	
107	Baleen whales	
108	Toothed whales	
201	Chinstrap penguins	
202	Gentoo penguins	
203	Adélie penguins	
204	Macaroni penguins	
205	King penguins	

301	Wandering albatross	
302	Other albatross	
303	Scavenging seabirds	
304	Diving petrels and South-Georgia shags	
305	Other seabirds	
401	Pelagic fish	
402	Benthic fish, shallow, benthic diet	Typically found at depths <200m and for which benthos constitutes >70% of predator diets.
403	Skates and rays	
404	Benthic fish, deep, benthic diet	Typically found at depths >200m and for which benthos constitutes >70% of predator diets.
405	Benthic fish, shallow, mixed diet	All other demersal fish found at depths <200m.
406	Mackerel icefish	
407	Benthic fish, deep, mixed diet	All other demersal fish found at depths >200m
408	Lamprey	
409	Patagonian toothfish	
501	Cephalopods	
601	Herbivorous benthos	
602	Carnivorous, omnivorous and detritivorous benthos	

603	Salps and gelatinous zooplankton	
604	Antarctic Krill	
605	*Themisto gaudichaudii*	
606	Other krill	
607	Carnivorous macro zooplankton	Does not consume primary producers and are >6mm in length.
608	Carnivorous meso and micro zooplankton	Does not consume primary producers and are <6mm in length.
609	Omnivorous macro zooplankton	Consumes a mixture of primary producers and other zooplankton and are >six mm in length.
610	Omnivorous meso and micro zooplankton	Consumes a mixture of primary producers and other zooplankton and are <six mm in length.
611	Herbivorous zooplankton	Consumes only primary producers
612	Heterotrophic bacteria and chromista	
701	Primary producers	
702	Detritus	

4.2.3 Parameterising the RPM

4.2.3.1 Diet matrix

We primarily used the Scotia Sea diet data set, which is a compilation of published diet composition studies for predators of the Scotia Sea (see Chapter 2), to define the diets of functional groups in the Scotia Sea food web model. In the Scotia Sea, a predator diet sample is an individual or group of individual consumers for which a list of quantified trophic interactions are given.

The Scotia Sea data set included instances of prey which: (i) were non-organic, for example 'stones'; (ii) were non-descript, for example 'other prey'; (iii) are not found in the Scotia Sea, typically these were prey found in the diets of transient predators that can forage out of the Scotia Sea ecosystem; and (iv) were parasitic, and likely bycatch from target prey. These prey did not provide useful information on organic energy flow in the Scotia Sea ecosystem, therefore we deleted predator-prey interactions between a predator and these prey from the Scotia Sea data set. There were 741 instances of these predator-prey interactions (5% of predator-prey interaction in the Scotia Sea data set), of which 80% were non-descript prey and 15% were inorganic prey.

Predator diet analyses report data as one, or a combination of three metrics. In decreasing order of usefulness for food web models, these were: fraction contribution by weight, fraction contribution by number, or fraction occurrence which is the proportion of individuals in a predator diet sample in which a prey was detected. We processed the Scotia Sea data set through an algorithm which we called the diet algorithm, to derive the fractional diet composition of each functional group. We programmed the diet algorithm in MATLAB (Release 2012a, The MathWorks, Inc., Natick, Massachusetts, United States), which ran as follows:

1. We assigned each consumer and prey in the Scotia Sea data set to a functional group. Prey in the Scotia Sea data set were given at different levels of taxonomic resolution; if we were unable to identify a functional group for a prey, we assigned it to one of five flag groups: fish, zooplankton and benthos, krill, seabirds, or marine mammals. The contribution of flag prey to a consumer's diet was later distributed amongst pertinent functional groups.

2. (a) For each functional group, we extracted the pertinent predator diet samples from the Scotia Sea data set. We did not include predator diet samples which only provided diet data for a subset of prey, for example only for the squid component

of a consumer's diet, as it was not possible to use these data to calculate a weighted average of a consumer's diet.

(b) For each predator diet sample, we normalised predator diet data to sum to unity. We did this for three reasons: first, predator diet samples report diet composition data at different degrees of accuracy and so some diet composition data did not sum to unity; second, we deleted some trophic interactions from the Scotia Sea data set (as previously discussed) and thus diet composition data no-longer summed to unity for these predator diet samples; and third, some diet data were reported as fraction occurrence, thus we normalised it to make it more comparable to diet data reported as fraction by weight or fraction by number.

(c) We used the most useful diet composition metric available for a predator diet sample (FBW, FBN or FO in decreasing order of usefulness, see Chapter 2 for an explanation). When this was fraction by number, we adjusted this value to approximate the equivalent fraction by weight value as follows: for each prey i we multiplied the fraction by number data (FbN_i), by a reference mass value for that prey (m_i). We converted each $FbN_i m_i$ to fraction by weight by dividing it by $\sum_{i=0}^{n} FbN_i m_i$, where n was the number of prey in a diet sample. The exception to this rule were if both predator and prey were fish in which case we assumed that prey mass was 1/100th of the reference mass value for the predator functional group [152]. Additionally, we did not adjust fraction by number diet data for zooplankton and benthic functional groups, because of the large orders of magnitude difference in the reference mass values of prey, for example fish versus micro/meso zooplankton, which would have resulted in unrealistic estimates of their diet composition if they were adjusted.

(d) We calculated the proportion contribution of each functional group as prey and flag prey, as a weighted average of diet data for all prey in the Scotia Sea data set pertinent to that functional group. Diet data was weighted as follows: diet data given as fraction by weight was weighted by three, (adjusted) fraction by number data was weighted by two, and fraction occurrence was weighted by one. Furthermore, data was weighted according to its sample size using a three category approach: diet data for predator diet samples with sample size one were weighted by one; samples of size two to nine were weighted by two; and samples of size greater than or equal to 10 were weighted by three. We preferred a three-category approach rather than using the size of the predator diet sample, as the latter approach could feasibly give dominance to large sized samples where data are given as fraction-occurrence or fraction by number, over smaller predator diet samples where data are given in the preferred form, fraction by weight.

(e) We distributed the contribution of flag fish prey to the diet of a consumer according to the relative proportion of fish functional groups prey in their diet (FG 401-409). If these data were not available, we inferred these proportions from other sources on a case by case basis (see Appendix E). We used similar methods to reassign the proportional contribution of flag benthos and benthos prey amongst benthos and zooplankton functional groups (FG 601-612). The proportion of flag krill in the diet of a predator was split equally between Antarctic krill' (FG 604) and 'other krill' (FG 606). We split the contribution of flag krill this way, as we found there was a higher effort at resolving Antarctic krill to species level than other species of krill. We redistributed diet data for the flag mammals and flag seabird groups on a case by case basis, which was dependent on the ecology of the consumer (see Appendix E for full details.)

3. We repeated step two for all functional groups where there was data available in the Scotia Sea data set.

For a comprehensive methodology for the derivation of the diet matrix including how predators and prey were assigned to functional groups, and how flag prey were distributed between functional groups, see Appendix E. Using these methods, we derived the diets for functional groups FG 101-103, 201-205, 301-305, 401, 402, 404-407, 409, and 603-610.

As discussed in Chapter 2, although the Scotia Sea data set is to date the best available compilation of diet composition data for predators in the Scotia Sea, there are still species for which there are little or no diet data. As such we used alternate data sources to quantify the diet composition of functional groups for which there were no or few diet data in the Scotia Sea data set, details for which are given in Table 4.2. Data for FG 104-106 and 501 were processed using the diet algorithm described above. The format of diet data used for functional groups 107, 108, 601, and 602 meant that it was not appropriate to use in the diet algorithm. Therefore, we manually processed these data.

Due to paucity of quantified information on their trophic interactions we assumed the diet of heterotrophic bacteria and chromista (FG 612) was 100% detritus, similarly to the diet of heterotrophic bacteria used in Hill et al. (2012) [259], however the diet of heterotrophic chromista could also include other zooplankton and primary producers. To test the sensitivity of our results to this assumption, we calculated production using the RPM when heterotrophic chromista consumed 50% primary producers (FG 701) and 50% detritus (FG

702). All other inputs were identical to the values used to calculate our baseline production estimates, described later.

Using the methods described above, we derived a diet matrix for the Scotia Sea food web model, which is given in Tables 4.3 and 4.4.

As discussed earlier, it was necessary to set the weakest diet fraction in a feeding loop to zero in the diet matrix. There were nine instances of cannibalism in the Scotia Sea diet matrix, five two-loops, and four three-loops. Table 4.5 gives a summary of the diet fractions which were set to zero in a feeding loop in the Scotia Sea diet matrix. When data was set to zero for a predators, we did not rescale the remaining fractions for a predator's diet to sum to zero.

Table 4.2: Sources of data used to define the diets of functional groups not represented in the Scotia Sea data set. There was only one Predator diet Sample (PS) in the Scotia Sea data set for cephalopods (FG 501). Therefore, we added the data referenced below. The number 's.XXX' given for reference [370] which is a diet composition database for consumers in the Southern Ocean, indicates the source identification number for the data. 'No. ind.' indicates the total predator sample size for data, and 'No. PS' is the number of predator diet samples.

FG	Name	Source	No. ind.	No. PS	Location
104	Crabeater seal	[370, s. 158]	56	1	Western Antarctic Peninsula
105	Sub Antarctic fur seal	[370, s. 451]	17	2	Crozet islands
106	Southern elephant seal	[370, s. 149]	126	3	South Shetland Islands
107	Baleen whales	[275, 347]			
108	Toothed whales	[347]			
501	Cephalopods	[350]	54	1	Near Macquarie and Heard Islands
601	Herbivorous benthos	[259]	-	-	-
602	Carnivorous, omnivorous and detritivorous benthos	[259]	-	-	-
612	Heterotrophic bacteria and chromista	[259]	-	-	-

Table 4.3: Diet matrix a: each column gives the proportional diet composition of a functional group.

	101	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**201**	**202**	**203**	**204**	**205**	**301**	**302**	**303**	**304**	**305**	**401**	**402**
102	0.76																			
106	0.14																			
201	0.01	0.01	0.12													0.09				
202																				
203			0.08																	
204	0.02	0.02														0.10				
205	0.01	0.01														0.04				
302																0.01				
303																0.02				
304																0.03				
305																0.14				
401	0.05	0.25		0.18	1.00	0.11	0.19	0.10			0.01	0.07	0.82	0.02	0.02			0.46		
402								0.01												
404								0.01												
405						0.02		0.02		0.01		0.01			0.01		0.09			
406		0.05						0.04		0.38		0.01		0.01	0.01					
407		0.07	0.17					0.01		0.09		0.04	0.01	0.14	0.01		0.10			

408															0.26					
409								0.01						0.14						
501		0.12	0.31	0.18		0.87	0.03	0.60					0.18	0.61	0.35	0.04	0.41	0.12		
601																				
602																			0.02	0.77
603														0.01				0.01	0.03	
604		0.46	0.32	0.64			0.74	0.08	1.00	0.51	0.99	0.66		0.01	0.17	0.11	0.35	0.23	0.32	0.23
605								0.03		0.01		0.21		0.01			0.05	0.10	0.15	
606							0.05	0.05						0.01	0.15	0.03			0.24	
607								0.03						0.01				0.02	0.02	
609								0.03												
610																			0.11	
611																		0.04	0.10	
702														0.04	0.03	0.39				

Table 4.4: Diet matrix b: each column gives the proportional diet composition of a functional group.

	403	**404**	**405**	**406**	**407**	**408**	**409**	**501**	**601**	**602**	**603**	**604**	**605**	**606**	**607**	**608**	**609**	**610**	**611**	**612**
401				0.03		1.00	0.03	0.63												
402																				
403							0.05													
404				0.02																
405	0.04		0.02		0.01		0.19													
406	0.26		0.05		0.04		0.05													
407	0.37		0.05		0.06		0.26													
408																				
409																				
501	0.01		0.03		0.01		0.35	0.23												
601		0.06								0.10										
602	0.04	0.91	0.13		0.21		0.05	0.01		0.05	0.33		0.02		0.11					
603			0.03		0.08							0.07		0.03			0.36	0.05		
604	0.27		0.60	0.75	0.57		0.02	0.10					0.03							
605			0.04	0.15	0.03			0.01												
606	0.01		0.04	0.04									0.18							
607										0.01			0.03		0.03					

608										0.01	0.12		0.33		0.02			0.03		
609			0.01							0.01			0.04							
610										0.01		0.13	0.24	0.23	0.45	1.00	0.13	0.04		
611								0.02		0.01	0.01		0.13		0.40					
612									0.72	0.69	0.36	0.27		0.33			0.21	0.20	0.05	
701		0.02							0.14	0.06	0.17	0.53		0.40			0.31	0.62	0.95	
702		0.01							0.14	0.06	0.01			0.01				0.05		1.00

Table 4.5: Diet fractions removed from the diet matrix to remove cannibalism, two-loops and three-loops. Gaps separate cannibalism (top) from two-loops (middle) and three-loops (bottom).

Predator		Prey	FG name	Proportion
303	Scavenging seabirds	303	Scavenging seabirds	0.02
401	Pelagic fish	401	Pelagic fish	0.00
405	Benthic fish, shallow, mixed diet	405	Benthic fish, shallow, mixed diet	0.02
406	Mackerel icefish	406	Mackerel icefish	0.00
407	Benthic fish, deep, mixed diet	407	Benthic fish, deep, mixed diet	0.06
501	Cephalopods	501	Cephalopods	0.23
602	Carnivorous, omnivorous and detritivorous benthos	602	Carnivorous, omnivorous and detritivorous benthos	0.05
607	Carnivorous macro zooplankton	607	Carnivorous macro zooplankton	0.03
610	Omnivorous meso and micro zooplankton	610	Omnivorous meso and micro zooplankton	0.04
407	Benthic fish, deep, mixed diet	403	Skates and rays	0.00
407	Benthic fish, deep, mixed diet	405	Benthic fish, shallow, mixed diet	0.01
406	Mackerel icefish	407	Benthic fish, deep, mixed diet	0.00

602	Carnivorous, omnivorous and detritivorous benthos	607	Carnivorous macro zooplankton	0.01
610	Omnivorous meso and micro zooplankton	608	Carnivorous meso and micro zooplankton	0.03
404	Benthic fish, deep, benthic diet	407	Benthic fish, deep, mixed diet	0.00
602	Carnivorous, omnivorous and detritivorous benthos	609	Omniovorous macro zooplankton	0.01
602	Carnivorous, omnivorous and detritivorous benthos	610	Omnivorous meso and micro zooplankton	0.01
610	Omnivorous meso and micro zooplankton	608	Carnivorous meso and micro zooplankton	0.05

4.2.3.2 Production estimate

We used an estimate for annual Antarctic krill production in the Scotia Sea as an input into the RPM. We began with an estimate for gross annual circumpolar Antarctic krill production of 439 Mt y^{-1} [133]. Gross krill production is the potential production of Antarctic krill in the absence of mortality over a period of time. This is an over estimate of actual Antarctic krill production in the presence of mortality. We multiplied the circumpolar estimate of Antarctic krill production by three scalar values:

1. **0.28:** the proportion of circumpolar Antarctic krill biomass which is found in the CCAMLR survey area [133];
2. **0.84:** the proportion area of the CCAMLR survey which is the Scotia Sea [257];
3. **0.21:** an estimate for the proportion of gross Antarctic krill production which could

still be produced given krill mortality throughout the year. We derived this value using growth and mortality models (see Appendix F).

Resultantly, we used a value of 21 Mt y^{-1}, equivalent to 14g m^{-2} y^{-1} as our krill production estimates.

4.2.3.3 Efficiency estimates

Where available we used ecotrophic efficiency and growth efficiency values adopted from an existing Ecopath model for the South Georgia shelf ecosystem as our baseline efficiency values [259]. Where an appropriate value was not available, we obtained baseline values from an ecosystem model of the Ross Sea [358]. We set ecotrophic efficiency for primary producers equal to one. Resultantly, the primary production estimate from the RPM is the minimum required primary production to support further production in the food web. We refer to these efficiency values as our baseline efficiency estimates, see Table 4.6 columns three and four for values. We derived a range of plausible values for each efficiency term by inspecting five ecosystem models for Antarctic ecosystems [141, 259, 343, 358]. We extracted the smallest and largest value which is relevant to each functional group. Minimum and maximum values for efficiency terms are given in columns six-nine in Table 4.6.

Table 4.6: Baseline values (columns three and four) and ranges (columns six to nine) for efficiency terms for each functional group in the Scotia Sea food web model.

Description	FG	e	EE	Reference	e_{min}	e_{max}	EE_{min}	EE_{max}
Leopard seal	101	6.0E-03		[259]	3.0E-03	2.7E-02		
Antarctic fur seal	102	3.5E-03	6.0E-02	[259]	3.0E-03	2.7E-02	3.0E-03	9.4E-01
Weddell seal	103	4.3E-03		[259]	3.0E-03	2.7E-02		
Crabeater seal	104	6.3E-03		[358]	3.0E-03	2.7E-02		
Sub Antarctic fur seal	105	5.3E-03		Average of FG 101-104	3.0E-03	2.7E-02		
Southern elephant seal	106	6.5E-03	3.0E-03	[259]	3.0E-03	2.7E-02	3.0E-03	9.4E-01
Baleen whale	107	5.8E-03		[259]	2.7E-03	2.5E-02		
Toothed whale	108	5.5E-03		[259]	4.3E-03	3.3E-01		
Chinstrap penguin	201	5.6E-03	1.0E+00	[259]	1.6E-03	4.2E-02	1.0E-02	9.9E-01
Gentoo penguin	202	3.3E-03	5.4E-01	[259]	1.6E-03	4.2E-02	1.0E-02	9.9E-01
Adélie penguin	203	5.3E-03	1.0E+00	[358]	1.6E-03	4.2E-02	1.0E-02	9.9E-01
Macaroni penuin	204	1.6E-03	5.1E-01	[259]	1.6E-03	4.2E-02	1.0E-02	9.9E-01
King penguin	205	3.1E-02	3.2E-01	[259]	1.6E-03	4.2E-02	1.0E-02	9.9E-01
Wandering albatross	301	1.4E-03	3.0E-01	Average of black-browed and grey-headed in [259]	4.8E-04	1.7E-02	9.0E-03	5.6E-01

Other albatross	302	1.4E-03	3.0E-01	Average of black-browed and grey-headed in [259]	4.8E-04	1.7E-02	9.0E-03	5.6E-01
Scavenging seabirds	303	2.4E-03	4.2E-01	Predatory seabirds in [259]	4.8E-04	1.7E-02	9.0E-03	5.6E-01
Diving petrels and South-Georgia shag	304	4.8E-04	4.9E-01	Other seabrids in [259]	4.8E-04	1.7E-02	9.0E-03	5.6E-01
Other seabirds	305	4.8E-04	4.9E-01	Other seabrids in [259]	4.8E-04	1.7E-02	9.0E-03	5.6E-01
Pelagic fish	401	1.0E-01	1.0E+00	Pelagic fish in [259]	9.6E-03	3.0E-01	6.8E-01	1.0E+00
Benthic fish, shallow, benthic diet	402	2.4E-01	1.0E+00	Other icefish in [259]	9.6E-03	3.0E-01	1.6E-02	1.0E+00
Skates and rays	403	1.6E-01	1.6E-02	Rays in [259]	9.6E-03	3.0E-01	1.6E-02	1.0E+00
Benthic fish, deep benthic diet	404	2.4E-01	1.0E+00	Other icefish in [259]	9.6E-03	3.0E-01	1.6E-02	1.0E+00
Benthic fish, shallow mixed diet	405	2.4E-01	1.0E+00	Other icefish in [259]	9.6E-03	3.0E-01	1.6E-02	1.0E+00
Mackerel icefish	406	2.2E-01	1.0E+00	[259]	9.6E-03	3.0E-01	1.6E-02	1.0E+00
Benthic fish, deep mixed diet	407	2.4E-01	1.0E+00	Other icefish in [259]	9.6E-03	3.0E-01	1.6E-02	1.0E+00
Lamprey	408	1.0E-01	1.0E+00	Pelagic fish in [259]	9.6E-03	3.0E-01	6.8E-01	1.0E+00
Patagonian toothfish	409	2.4E-01	1.0E+00	Other icefish in [259]	9.6E-03	3.0E-01	1.6E-02	1.0E+00

Cephalopods	501	3.7E-01	1.0E+00	[259]	1.0E-01	4.0E-01	9.5E-01	1.0E+00
Herbivorous benthos	601	2.5E-01	4.0E-01	Benthos in [259]	1.8E-02	3.4E-01	1.2E-01	9.0E-01
Carnivorous, omnivorous and detrivitous benthos	602	2.5E-01	4.0E-01	Benthos in [259]	1.8E-02	3.4E-01	1.2E-01	9.0E-01
Gelatinous stuff	603	2.5E-01	7.8E-01	Salps in [259]	1.0E-01	3.0E-01	1.0E-02	1.0E+00
Antarctic krill	604	2.5E-01	7.4E-01	[259]	1.3E-01	5.0E-01	1.2E-01	1.0E+00
Themisto gaudichaudii	605	2.5E-01	1.0E+00	Carnivorous zooplankton in [259]	1.3E-01	5.0E-01	1.2E-01	1.0E+00
Other krill	606	2.5E-01	1.0E+00	Carnivorous zooplankton in [259]	1.3E-01	5.0E-01	1.2E-01	1.0E+00
Carnivorous macro zooplankton	607	2.5E-01	1.0E+00	Carnivorous zooplankton in [259]	1.3E-01	5.0E-01	1.2E-01	1.0E+00
Carnivorous meso and micro zooplankton	608	2.5E-01	1.0E+00	Carnivorous zooplankton in [259]	1.3E-01	5.0E-01	1.2E-01	1.0E+00
Omnivorous macro zooplankton	609	2.5E-01	5.0E-01	Herbivorous and detrivorous copeopds in [259]	1.3E-01	5.0E-01	1.2E-01	1.0E+00
Omnivorous micro and meso zooplankton	610	2.5E-01	5.0E-01	Herbivorous and detrivorous copeopds in [259]	1.3E-01	5.0E-01	1.2E-01	1.0E+00
Herbivorous zooplankton	611	2.5E-01	5.3E-01	Herbivorous and detrivorous copeopds in [259]	1.3E-01	5.0E-01	1.2E-01	1.0E+00

Heterotrophic bacteria and chromista	612	2.9E-01	9.2E-01	average of two heterotrophic groups in [259]	2.7E-01	3.5E-01	8.3E-01	9.9E-01
Primary producers	701		1.0E+00		0.0E+00	0.0E+00	1.0E+00	1.0E+00
Detritus	702		1.0E+00		0.0E+00	0.0E+00	1.0E+00	1.0E+00

4.2.4 Sensitivity and uncertainty analyses

Sensitivity analyses are complemented by, but different from, uncertainty analyses. Sensitivity analyses investigate which input parameters cause change to model outputs whereas uncertainty analyses asses the uncertainty in each model output given quantified uncertainty in input parameters [400].

We approached sensitivity and uncertainty analyses using two methods. First, we completed a perturbation analysis in which each efficiency parameter was changed by plus, then minus, 5% from its baseline value. When a positive perturbation of an ecotrophic efficiency value caused it to exceed one, we set it equal to one. We evaluated the RPM with the perturbed efficiency value and then calculated total production (TP) as the sum of the production of all functional groups not including detritus. Second, we evaluated the RPM for a set of 10 000 input efficiency values which were all allowed to vary within their ranges of uncertainty. As is common practice when the shape of the distribution for a parameter is not known [304], we used a uniform distribution with boundaries e_{min} and e_{max} for growth efficiency, and EE_{min} and EE_{max} for ecotrophic efficiency, see Table 4.6.

We selected sets of efficiency values using Latin-Hypercube Sampling (LHS). In LHS, y uncertain parameters are partitioned into $X > y$ sections of equal probability, and a random value is selected from within each partition. Efficiency values were grouped, resulting in X sets of input parameters where each of the X selected values of one parameter was represented exactly once across samples. We refer to this method as our LHS based analysis. We used MATLAB (Release 2012a, The MathWorks, Inc., Natick, Massachusetts, United States) to generate a Latin Hypercube sample. LHS is advantageous as it ensures that the full range of each parameter is represented across model runs, and has been observed to give robust results even for relatively small samples [400, ch.6]. Two examples of LHS being used in biology are, to estimate the species richness of tropical arthropods [254], and to perform sensitivity analysis in a model of the spread of a fungal-pathogen in the sea fan *Gorgonia ventalina* [232].

Using these two methods, we completed our sensitivity analysis. We plotted the percent change in total production calculated as $100\left(\frac{TP^*}{TP_{bl}}-1\right)$, where TP^* is total production calculated from the RPM with a 5% perturbation to one input parameter and TP_{bl} is total production calculated from baseline efficiency values, to assess the sensitivity of system-level model outputs to each input efficiency value. Additionally, we assessed the sensitivity of production estimates for each functional group to efficiency values for each input in the LHS-based analysis, by visually inspecting scatter plots of each efficiency value plotted against production for each functional group.

We assessed the relative uncertainties in production estimates for each functional group using LHS based analysis. We inspected the distribution of production estimates for each functional group, visualised using box and whisker plots. To do this, we evaluated the RPM using 10 000 sets of efficiency values selected using LHS based analysis.

We calculated the following metrics for each functional group, to see if any could explain observed sensitivities and uncertainties in the Scotia Sea food web model:

1. The range of growth and efficiency values ($e_{max} - e_{min}$ and $EE_{max} - EE_{min}$, respectively);
2. The number of predator and prey interactions;
3. The proportional contribution of Antarctic krill in a predator's diet (a_{ki}) and the proportion of each functional group in the diet of Antarctic krill (a_{ik}).

4.3 Results

4.3.1 Baseline production estimates

Production estimates for 41 functional group in the Scotia Sea food web model are given in Table 4.7, which were calculated using the baseline efficiency values given in Table 4.6. This table gives the first estimates of production for functional groups in the Scotia Sea food web model.

Table 4.7: Production predicted by the RPM using baseline efficiency values given in Table 4.6. Column four gives the number of trophic interactions for each functional group (number of predators + number of prey).

Functional group	ID	Production (g m^{-2}y^{-1})	No. trophic interactions
Apex predators	1000	2.37E-06	28
Antarctic fur seal	102	8.20E-04	12
Southern elephant seal	106	3.00E-03	5
Chinstrap penguin	201	3.14E-03	8
Gentoo penguin	202	3.75E-04	13

Adélie penguin	203	6.02E-04	7
Macaroni penguin	204	7.62E-03	12
King penguin	205	5.15E-03	7
Other albatross	302	2.58E-06	12
Diving petrels and South-Georgia shag	304	3.49E-06	11
Other seabirds	305	1.89E-05	20
Pelagic fish	401	1.45E+00	35
Benthic fish, shallow, benthic diet	402	2.15E-03	9
Skates and rays	403	1.26E-04	14
Benthic fish, deep, benthic diet	404	1.06E-02	8
Benthic fish, shallow, mixed diet	405	6.05E-02	26
Mackerel icefish	406	1.36E-01	25
Benthic fish, deep, mixed diet	407	2.32E-01	27
Lamprey	408	4.83E-04	2
Patagonian toothfish	409	9.17E-06	14
Cephalopods	501	4.88E-01	24
Herbivrous benthos	601	2.92E+01	9
Carnivorous and omnivorous benthos	602	3.04E+01	23
Salps and gelatinous zooplankton	603	8.37E+00	16
Antarctic krill	604	1.40E+01	29
Themisto gaudichaudii	605	3.33E+00	23
Other krill	606	5.85E+00	21
Carnivorous macro-zooplankton	607	6.31E-01	14
Carnivorous meso and micro-zooplankton	608	9.50E+00	7
Omniovorous macro-zooplankton	609	1.10E+00	14
Omnivorous meso and micro-zooplankton	610	1.13E+02	14
Herbivrous zooplankton	611	1.02E+01	12
Heterotrophic bacteria and chromista	612	3.25E+02	10
Primary Producers	701	3.91E+02	11

4.3.2 Sensitivity analysis

Total production (TP) was more sensitive to perturbations in the efficiency values of benthic and zooplankton functional groups than for higher trophic level groups. In particular, of the zooplankton/benthos functional groups, total production was most sensitive to the efficiency values for salps and gelatinous organisms (FG 603), Antarctic krill (FG 604), omnivorous meso and micro zooplankton (FG 610), and *Themsito gaudichaudii* (FG 605) (Figures 4.1 and 4.2). Of the functional groups related to fish and cephalopod species, total system production was most sensitive changes in efficiency terms for pelagic fish (FG 401) and cephalopods (FG 501). Of the land-breeding predators, production was most sensitive to changes in efficiency terms for Antarctic fur seals (FG 102), Southern elephant seals (FG 106) and macaroni penguins (FG 204) (Figures 4.1 and 4.2). The strong asymmetrical response of TP to a positive versus negative perturbation of an efficiency term for some functional groups, which is most obvious in Figure 4.2, is due to a perturbation causing an efficiency term to exceed its upper limit. In these cases, the efficiency term was set equal to its upper bound and thus the perturbation in an efficiency term was less than 5%, and sometimes 0%. This explains the 0% change in total primary and secondary production resulting from a perturbation in the efficiency terms of some functional groups. From visual inspection of scatter plots, production outputs were most sensitive to the growth efficiency for pelagic fish (FG 401) and the ecotrophic efficiency for salps and gelatinous organisms (FG 603). The afore mentioned scatter plots can be viewed in Appendix G. Scatter plots for the remaining input parameters, not reported due to the large number of plots, showed weaker correlations between parameter values and production estimates.

Model outputs were generally most sensitive to the ecological parameters for functional groups which were most productive and had the most trophic interactions (see Table 4.7 and Figures 4.1 and 4.2). However, there were exceptions to this rule. As an example, herbivorous zooplankton produced more biomass than salps and gelatinous zooplankton, and had a similar number of trophic interactions (13 and 16, respectively). However TP was more sensitive to changes in efficiency terms for salps and gelatinous zooplankton than herbivorous zooplankton (Figures 4.1 and 4.2).

To test how robust our results were to the production estimate used as an input, we repeated our analysis using the production of macaroni penguins as an input into the RPM. We found our results were qualitatively robust to the choice of input production (see Appendix H for more details).

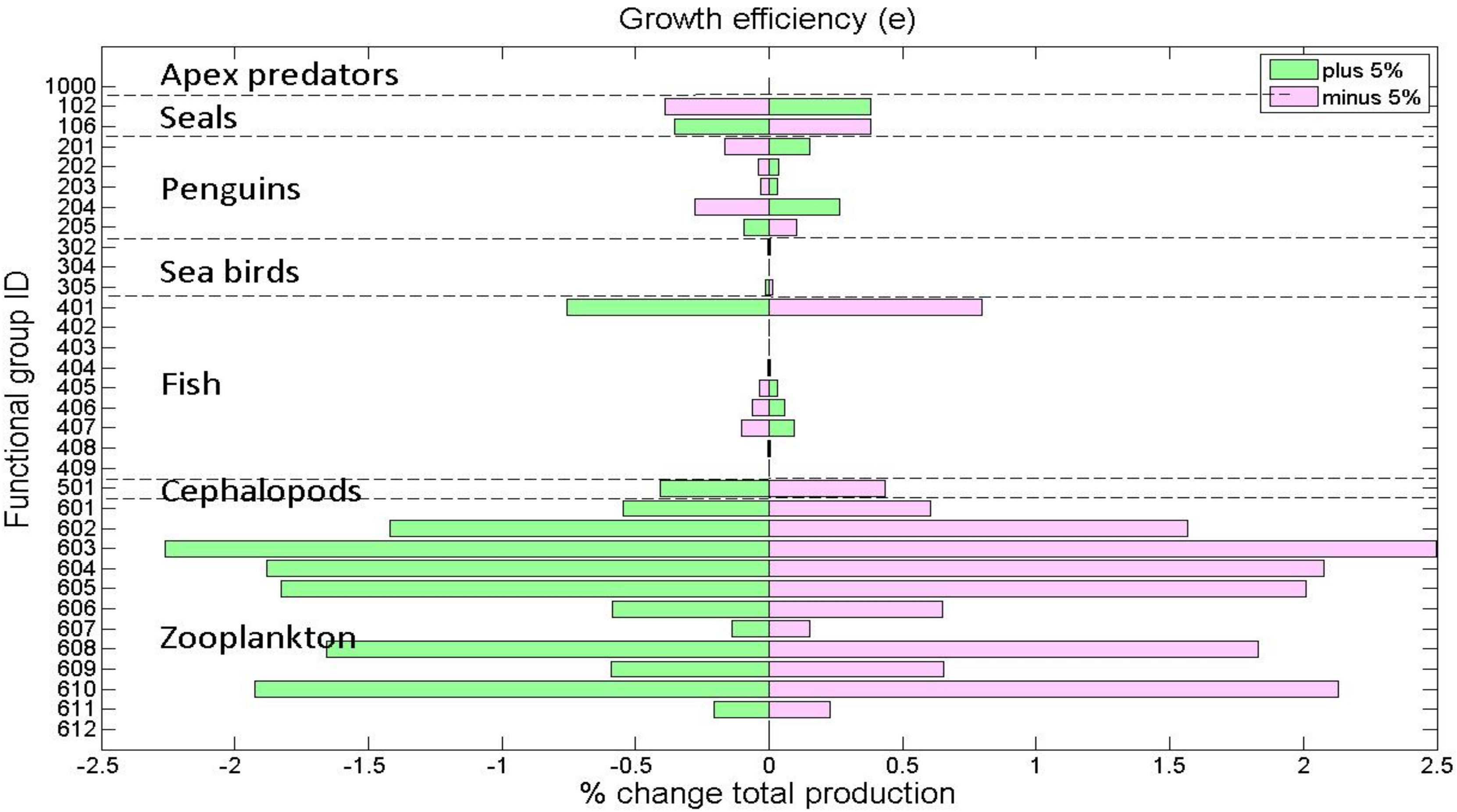

Figure 4.1: Percent change in total production to a 5% change in the growth efficiency for the functional group specified on the y-axis.

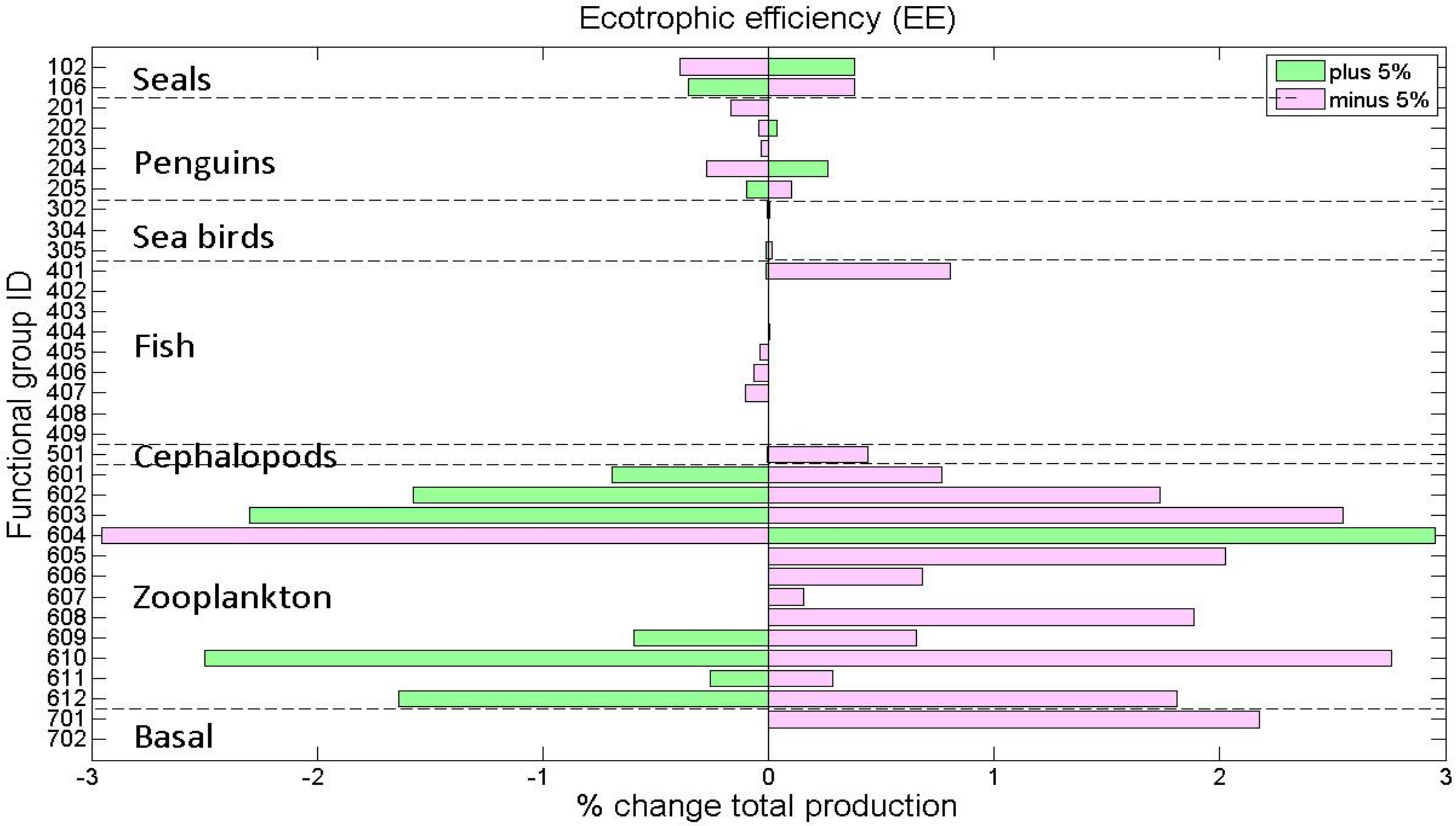

Figure 4.2: Percent change in total production to a 5% change in the ecotrophic efficiency for the functional group specified on the y-axis.

4.3.3 Uncertainty analysis

Production estimates resulting from the LHS approach to uncertainty analysis are given in Figures 4.3, 4.4, 4.5 and 4.6; note the different scales of the x-axis on each figure. Generally, uncertainty was higher for production estimates of functional groups with lower trophic levels.

Many functional groups which we identified as important for determining TP in the sensitivity analysis were also the functional groups for which there was high uncertainty associated with their production estimates. For example, of the penguin functional groups, ecological parameters for macaroni (FG 204), chinstrap (FG 201), and king penguins (FG 205) were most important in determining TP, in decreasing order. These were also the penguins for which production estimates were most uncertain (Figure 4.6). Similarly, production for pelagic fish (FG 401) was the most uncertain of the fish functional groups (Figure 4.5). Production of omnivorous meso and micro-zooplankton (FG 610) was the most uncertain of zooplankton and benthos (Figure 4.4), and ecological parameters for these functional groups were also highlighted in the sensitivity analysis as important for determining TP. However, the production of other functional groups highlighted in the sensitivity analysis, were relatively robust to uncertainties in ecological input parameters. Such groups include salps and gelatinous zooplankton (FG 603), *Themisto gaudichaudii* (FG 605), and cephalopods (FG 501) (Figures 4.5 and 4.4). This could be explained for cephalopods (FG 501), by the small range of their ecotrophic efficiency values, see Table 4.6.

We found that there was no universal correlation between the number of trophic interactions formed by a functional group, the strength of a trophic interaction with krill, magnitude of production estimate, or the range of uncertainty in efficiency parameters, which could alone explain the magnitude in uncertainty of a functional group. It is likely that a combination of these and other factors not explored here, such as the diversity of diet, fully explain these results.

Of the zooplankton and benthos functional groups, production estimates were most robust for the four macro zooplankton: other krill, *Themisto gaudichaudii*, carnivorous macro zooplankton and omnivorous macro zooplankton. For fish and squid functional groups, the most robust production estimates were for skates and rays, Patagonian toothfish, lamprey and benthic fish, shallow, benthic diet. Of the land-breeding predators and cetaceans, estimates were most robust for other albatross, and diving petrels and South-Georgia shag. Production estimates for primary producers (FG 701) and heterotrophic bacteria and chromista

(FG 612) had the most uncertainty (Figure 4.3).

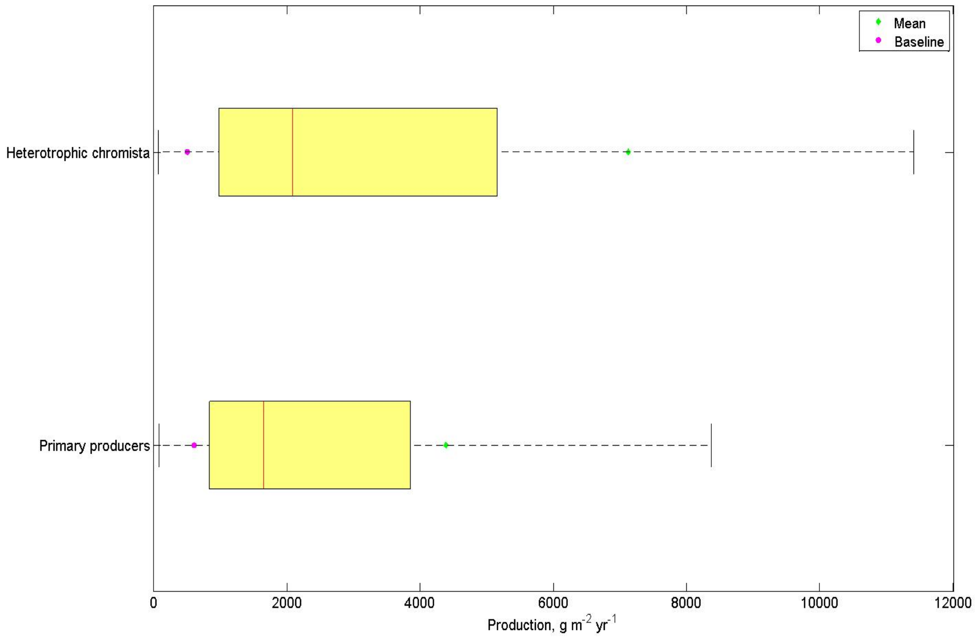

Figure 4.3: Box and whisker plots for production estimate calculated from 10 000 evaluations of the RPM for heterotrophic chromista and primary producers. Combinations of efficiency parameters were selected using Latin-Hypercube Sampling. Outliers are not shown.

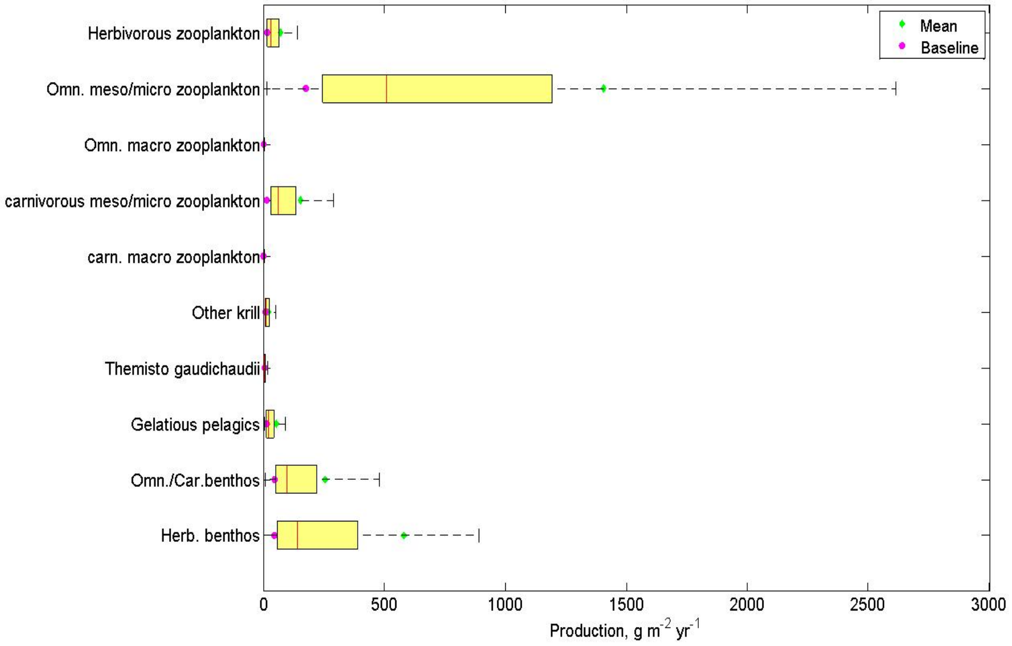

Figure 4.4: Box and whisker plots for production estimate calculated from 10 000 evaluations of the RPM for benthos and zooplankton. Combinations of efficiency parameters were selected using Latin-Hypercube Sampling. Outliers are not shown.

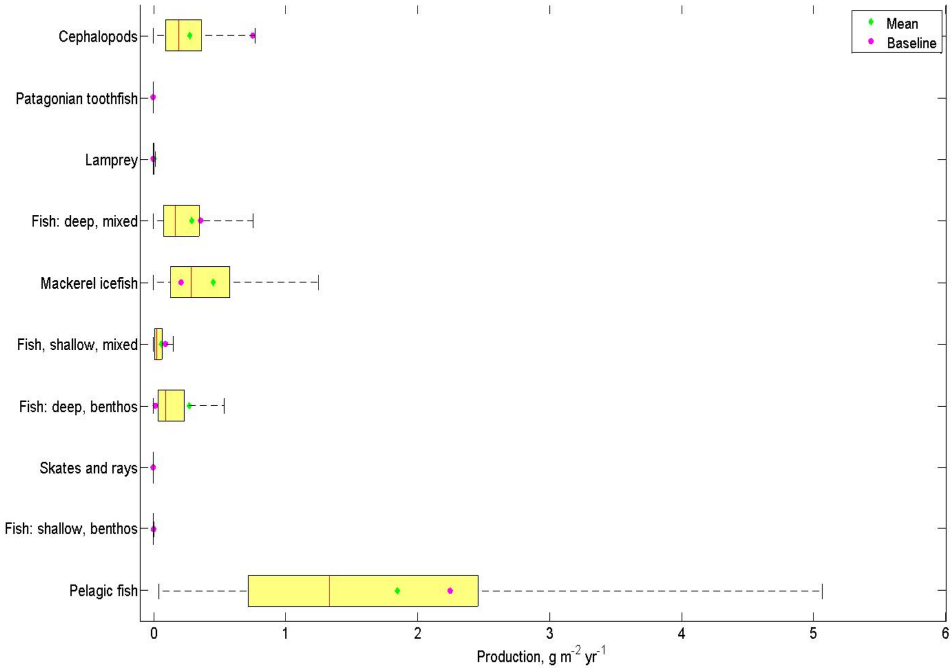

Figure 4.5: Box and whisker plots for production estimate calculated from 10 000 evaluations of the RPM for fish and cephalopod. Combinations of efficiency parameters were selected using Latin-Hypercube Sampling. Outliers are not shown.

4.4 Discussion

4.4.1 Summary of the sensitivity and uncertainty analyses

In this chapter we conducted two complementary analyses, sensitivity and uncertainty analyses [400]. We assessed which functional groups could be important in the Scotia Sea food web using the sensitivity analysis. In the sensitivity analysis we changed ecotrophic or growth efficiency for a functional group by 5% from a baseline value. These efficiency terms are ecological parameters of a food web model which affect a functional groups production or consumption. The effects of change to the production or consumption of one functional group can propagate through the food web causing changes in production estimates of other functional groups. The sensitivity of the Scotia Sea food web to changes in these efficiency terms for a given functional group is, therefore, an indicator of the importance of that functional group in the food web. In the uncertainty analysis we assessed the robustness of production estimates for each functional group to uncertainties in efficiency input terms.

The results from the sensitivity analysis suggested that, in general, groups with high production estimates and which form many trophic interactions are the most important in the

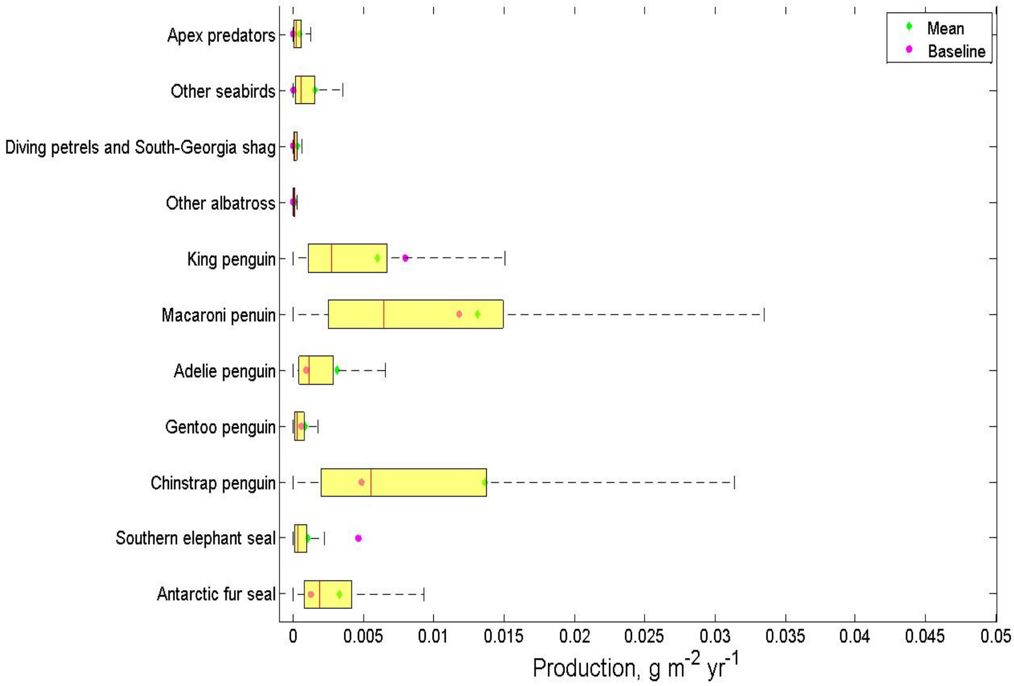

Figure 4.6: Box and whisker plots for production estimate calculated from 10 000 evaluations of the RPM for land-breeding predators and cetaceans. Combinations of efficiency parameters were selected using Latin-Hypercube Sampling. Outliers are not shown.

Scotia Sea food web. However, there were also large uncertainties in production estimates for some functional groups with the largest production estimates. In the following sections, we discuss functional groups which are highlighted as important in the sensitivity analysis, and the groups for which production estimates are most uncertain. We do this in turn for primary producers, zooplankton and benthos, fish and cephalopods, and land-breeding predators and cetaceans, and suggest where future theoretical and empirical analyses could improve our understanding of the Scotia Sea food web.

4.4.2 Primary production

In this paper we derived a mass-balanced model of the Scotia Sea ecosystem. Minimum required primary production estimated by the RPM ($391\text{gm}^{-2}\text{y}^{-1}$) were within the current range, 91.25-1907 $\text{gm}^{-2}\text{y}^{-1}$ of primary production for areas within the Scotia Sea [287, 288, 309] (estimates from published literature were scaled from carbon to wet weight using a factor of ten [296] and projected to yearly values assuming a three month production period in a year [320]). Note, the RPM estimates the minimum required primary production to support the food web. However, this may be an underestimate of actual primary production as the Scotia Sea model does not account for primary production demand by heterotrophic bacteria and chromista, or direct losses through, for example, sedimentation.

We aggregated all heterotrophic bacteria and chromista into a single functional group (FG 612) which fed solely on detritus. In some temperate and tropical food webs up to 50% of net primary production is thought to be processed by heterotrophs, however this is unlikely to be the case in Antarctic waters where feeding on detritus could be their main source of food [136]. Therefore our assumption that heterotrophic microbes, which include chromista and bacteria, consume detritus, is a plausible scenario. The primary production estimate provides validity to our food web model of the Scotia Sea, as predicted minimum required primary production is low within the existing range of estimates for primary production [287, 288, 309].

We propose two avenues of research, to strengthen future food web models of the Scotia Sea. First, to quantify trophic interactions of microbial species including heterotrophic bacteria and chromista, which includes feeding on other microbes, detritus, imported and exported organic material, and directly on primary producers and dissolved organic matter [135, 136]; Second, to integrate these into food web models in a meaningful way which accounts for the different time scales at which microbial processes function compared with processes relating to larger organisms. Microbial processes are important in the Scotia Sea as delays in microbial processes could increase food availability in winter months, where primary production is low [136, 320]. Additionally, microbial sea-ice communities are an important food source for many zooplankton species [320]. Understanding these processes are also pertinent to understand global climate models as delays caused by the microbial loop are important in the carbon cycle [131]. As shown here, food web models can be most sensitive to microbial processes, which highlights the importance of understanding these interactions.

4.4.3 Zooplankton and benthos

Salps can be the numerically dominant zooplankton in parts of the southern Scotia Sea, particularly in the autumn [448]. Salps, along with small copepods, are important in biogeochemical cycles [320] and could influence the composition of the microbial community [420]. For these reasons Murphy et al. (2007) [320] identified salps and their role in the Scotia Sea ecosystem as a priority for further research. We support this proposition as our results suggested that salps and other gelatinous pelagic organisms (FG 603) were influential components of the Scotia Sea food web. We additionally identified omnivorous micro and meso zooplankton (FG 610), which include many species of small copepod, and Antarctic krill (FG 604), as important organisms in the Scotia Sea food web. Whilst the importance of Antarctic krill is well known, we suggest that future research should determine the trophic importance of omnivorous zooplankton whose diets are not as well studied. This could also reduce high uncertainty in the production estimate for omnivorous meso and micro-zooplankton.

4.4.4 Fish and cephalopods

Pelagic fish form a major constituent of the pelagic community in the Scotia Sea [353], and the Scotia Sea food web model developed in this chapter, estimated high production for pelagic fish (1.5 g m^{-2} y^{-1}). Pelagic fish are important prey for many higher predators and constitute more than 25% of the diets of king penguins, other flying sea birds, fur seals, and cephalopods, see Tables 4.3 and 4.4. Their importance in the diets of these, and other functional groups, may increase in years where Antarctic krill abundance is low [383, 445]. Pelagic fish diet includes species which can be primary consumers, such as Antarctic krill species. Thus, pelagic fish form an important link between primary consumers and higher predators. Our results highlight pelagic fish and Antarctic krill as important species in the Scotia Sea food web. This could be because many higher predators who feed on pelagic fish, also feed on Antarctic krill, and so form a type of three-species omnivorous loop, which can be important in determining food web stability [322]. In support of this hypothesis, land-breeding predators for which total production calculated by the Scotia Sea food web model was most sensitive included macaroni penguins and Antarctic fur seals, which are major consumers of Antarctic krill in the Scotia Sea and who both also consume pelagic fish [167, 445].

Our uncertainty analysis also highlighted production estimates for pelagic fish as the least robust of the fish and cephalopod functional groups. High uncertainty in the production of a functional group which was also identified as ecologically important, highlights the necessity to resolve ecological information on these groups. Pelagic fish are important prey of many cephalopod species [284], which we also identify as important in the Scotia Sea food web (Figures 4.1 and 4.2). However, and as discussed in more detail later in Section 4.4.6, there are only data for one species of cephalopod in the Scotia Sea. King penguins and southern elephant seals consume mostly cephalopods and pelagic fish. High uncertainty in the production estimate for pelagic fish could explain the relatively high uncertainty for land-breeding predators whose diets are dominated by pelagic fish compared to other land-breeding predators (Figure 4.6).

We highlight two priorities to improve food web models of the Scotia Sea: First, to quantify the importance of pelagic fish in the diet of a variety of cephalopod species; and second, to reduce uncertainty in the growth efficiency of pelagic fish species. Species on which to focus could be the dominant mesopelagic species such as the myctophids: *Electrona antarctica, Gymnoscopelus braueri, Krefftichthys anderssoni, Electrona calsbergi, Protomyctophum bolini*, as well as *Bathylagus* and *Cylothone* species [192]. This could help reduce uncertainty in the production estimate of pelagic fish and their predators.

Production estimates for two commercially important species, the Patagonian toothfish and the mackerel icefish, were estimated at 14 and 209 885 tonnes, respectively; note, data was scaled to tonnes using an estimated area of 1 543 272 km^{-2} for the Scotia Sea [257]. Whilst catch of mackerel icefish by commercial fisheries in 2014 (33 tonnes) [237] is less than the annual production estimate as predicted by the RPM, catch of the Patagonian toothfish in 2014 (2 244 tonnes) [238, 239] exceeds estimated production. The baseline ecotrophic efficiency estimate for the Patagonian toothfish was set at one, which implies all toothfish production is consumed by their predators during a year. However, few species are recorded as having toothfish as a large part of their diet [58]. Therefore, our model suggests that the ecotrophic efficiency value of one is highly likely to be a large overestimate of its true value, and that much of the Patagonian toothfish production is not consumed by its predators.

4.4.5 Apex and land-breeding predators

Along with macaroni penguins and Antarctic fur seal, southern elephant seals were the most influential on total primary and secondary production. For Antarctic fur seals and macaroni penguins this may be due to the large sizes of these populations and their importance as consumers of krill [144, 167, 213]. It is thought that two of the largest populations of both species compete for the same population of krill at South Georgia [144]. There is also potential for competition of Antarctic fur seals with commercial fisheries for mackerel icefish [213] which should be carefully considered in fisheries management, given the high sensitivity of system-level properties of the Scotia Sea food web model to Antarctic fur seals.

According to the results of our baseline model, Antarctic fur seal production was lower than production by southern elephant seals (8.2E^{-4} g m^{-2} y^{-1} for Antarctic fur seals and 3.0E^{-3} g m^{-2} y^{-1} for southern elephant seals). Antarctic fur seals are the most abundant seal species in the Scotia Sea, and are approximately four times more abundant than Southern elephant seals [285]. The difference in production estimates can be explained predominantly by the large weight difference between the two species, which is 12 fold for females and 1.5 fold for males [88, 265]. However, southern elephant production estimates may be skewed by the paucity of information on the diet composition for most cephalopod species in the Scotia Sea, and uncertainty in the production estimate for cephalopods. Additionally, there is high uncertainty in pelagic fish production, which is prey of southern elephant and Antarctic fur seals. Abundance of both species were reduced greatly following hunting for Antarctic fur seal pelts during the eighteen to twentieth centuries, and for oil from elephant seals in the early-mid twentieth century [285]. The extent of the depletion of Antarctic fur seals remains unknown. It has been suggested that the populations are now largely stable and that Antarctic fur seals may have even exceeded pre-exploitation numbers [285]. To assess if seal populations have recovered from historical exploitation it will be important to assess current population sizes from in-situ surveys. Our results suggest that, if recovered, Antarctic fur seal production should be approximately one quarter of that of southern elephant seals.

4.4.6 Caveats and future work

As discussed in the methodology, it was necessary to remove some trophic interactions to prevent loops so that we were able to evaluate the RPM. This removal may have resulted in an underestimate for the production of some functional groups as our model calculates production as demand by predators other than itself or groups which it forms the weakest interaction in a feeding loop (by proportional contribution to its diet). However, in most cases, the trophic interaction removed formed a minor component of a predators diet (<7%). The exception to this was cephalopods which, according to the diet algorithm, had a diet of which 23% was other cephalopods. Many species of cephalopod feed on pelagic fish particularly myctophids, and some cephalopods feed on krill [284]. However other species such as *Martialia hyadesi* consume other cephalopods, see [252] and Chapter 2. In this study, and similar to most other Antarctic-focused Ecopath models e.g. [141, 259, 343, 358], we represented all species of cephalopods by a single functional group. Although this simplification is likely to have obscured important trophic interactions, it was necessary as we found diet composition data for one species of cephalopod in the Scotia Sea, and two in the Antarctic [252, 350].

We suggest an avenue for future research would be to investigate how simplifying possible complexities in the trophic interactions of cephalopods could affect production estimates in the RPM. One way to do this could be to increase the number of functional groups representing cephalopod species, and evaluate these for a range of scenarios for their diet composition. Another functional group for which there is a paucity of diet data, and so would benefit from this kind of sensitivity analysis is the carnivorous, omnivorous, and detritivorous benthos.

The RPM required all apex predators to be aggregated into a single functional group to create a fully determined set of equations. This simplification may have obscured trophic detail which prevented full evaluation of the sensitivity of the Scotia Sea food web to these species. One possible alternative method would be to increase the number of production estimates required as input into the RPM, to the number of apex functional groups, so that aggregating all apex predators into a single group is not necessary. We did not adopt this approach as it would have introduced additional uncertainties associated with each input production parameter and would undermine the purpose of the RPM, which is to predict production. Our perturbation analysis suggested that system level properties were relatively insensitive to changes in input parameters for the apex functional group compared to other functional groups; however we acknowledge that our model cannot fully assess the importance of apex predator functional groups and uncertainty in production estimates for apex predator species.

In our Latin Hypercube Sampling approach to uncertainty analysis, many sets of input parameters resulted in production estimates which were unrealistic, such as for primary production which exceeded experimental and model-derived estimates for primary production in the Scotia Sea [287, 288, 309]. We do not claim that all production values calculated from the LHS based analysis were realistic. However, we used the LHS based approach to provide useful insight into the relative uncertainties in production estimates. One possible avenue for future research using the RPM could be to reduce uncertainty in efficiency inputs using a Bayesian approach in which the RPM is evaluated using the LHS generated efficiency values, and then sets of parameters eliminated by applying a set of criterion to validate model outputs such as an upper and lower bound for primary production estimates.

4.5 Conclusion

In this chapter we used a new diet-composition data set of predators in the Scotia Sea (see Chapter 2). We used this data set to parameterise a quantified model of the Scotia Sea food web, and conducted a comprehensive sensitivity analysis to indicate which functional groups were most important in the Scotia Sea. Our results suggested that important species in the Scotia Sea were generally those with the highest production estimates and which formed the most trophic interactions. Important species highlighted in the sensitivity analysis included species of land-breeding predators, Antarctic fur seals, and macaroni penguins, agreeing with previous studies who have highlighted these species as important consumers in the Scotia Sea [144, 167, 213]. We additionally highlighted southern elephant seals as an important land-breeding predator. Antarctic krill and pelagic fish are two dominant prey of many large-bodied predators. This is reflected by the large amount of research dedicated to understanding the ecology of these species and their role in the ecosystem, for example [192, 234, 235, 428]. Our model also highlighted Antarctic krill and pelagic fish as important groups in the Scotia Sea food web, but also suggested that salps and gelatinous zooplankton, and omnivorous micro and meso zooplankton were important. The role of these groups in the Scotia Sea food web are less studied and we suggest that it would be prudent to focus on understanding and quantifying the trophic importance of species in these groups.

In this chapter, we also undertook an uncertainty analysis to indicate which production estimates were most robust to uncertainties in input efficiency parameters, by evaluating the RPM for 10 000 sets of input efficiency parameters. The most robust zooplankton production estimates were for macro zooplankton; for fish were skates and rays, Patagonian toothfish, lamprey and benthic fish, shallow, benthic diet. For land-breeding predators and cetaceans, production estimates for albatross functional groups, and the diving petrels and South Georgia shag, were most robust. Two functional groups to which Scotia Sea food web model outputs were sensitive, but also had high uncertainty in production estimates, were pelagic fish and omnivorous meso and micro-zooplankton. Pelagic fish are important prey for many predators including king penguins, Antarctic fur seals and cephalopod species.

There is paucity in data on the diets of cephalopod species, and food web model outputs were sensitive to ecological parameters for cephalopods, and similarly for salps and gelatinous zooplankton. We identify three avenues for future research which could reduce uncertainty in the Scotia Sea food web model: first, narrowing estimates for the growth efficiency of pelagic fish; second, collecting diet data for more species of cephalopod in the Scotia Sea; and third, understanding and quantifying the ecological role of omnivorous meso and micro-zooplankton, and salps and gelatinous zooplankton in the Scotia Sea food web.

Lastly, we suggest that quantifying energy transfer by heterotrophic microbes and bacteria, and integrating these into food web models such as the one presented here, would greatly strengthen these models and enhance our ability to estimate primary production from predator demand.

5 The importance of swarming prey and their intra-annual variability for the foraging outcomes of a predator

Abstract

To be able to interpret the significance of model outputs from food web models, we must understand the mechanisms which determine trophic interactions such as natural variabilities in the spatial structure and availability of prey and how trophic interactions affect predator survival. Detailed models of a foraging predator can provide valuable insight into the mechanisms driving its foraging outcomes. Antarctic krill are a dominant prey for many predators in the Scotia Sea, and form large, dense, monospecific swarms. At South Georgia, one major source of natural variability is the timing of allochthonous recruitment of krill into the region. Therefore, in this chapter we developed a probabilistic encounter model of a penguin foraging (i) over one foraging trip, and (ii) over the part of its breeding season when chick mortality is at its highest. Macaroni penguins were a good candidate species for this analysis because there are annual time-series data on their diet composition (see Chapter 2), and we highlighted them as an important land-breeding predator in the sensitivity analysis of the Scotia Sea food web (see Chapter 4). We found that the spatial aggregation of its dominant prey, Antarctic krill, into swarms generates foraging outcomes comparable to empirical diet composition data. Furthermore, we found evidence that swarming prey had a lower energetic cost to foraging than non-swarming prey with implications for the potential energy provisioned to its chick. The foraging success of a predator during the breeding season was very sensitive to a small change in the timing in the allochonous recruitment of swarming-prey during the breeding season. Understanding the mechanisms which govern predator foraging during the breeding season is important given the rapid climatic changes in the Western Scotia Sea which are likely to affect the availability of Antarctic krill to its predators across the Scotia Sea.

5.1 Introduction

5.1.1 Chapter motivation: the importance of detailed interactions

Food web models, such as the one developed in Chapter 4 for the Scotia Sea food web, consider the flow of energy between species or groups or species. To be able to interpret the significance of outputs from food web models, we must understand the mechanisms which determine predator diet composition, such as natural variabilities in the spatial structure and availability of prey types, and the energetic costs of different prey to a predator. Furthermore, to build effective marine conservation plans and ecosystem-based management measures for commercial fisheries [196], and to provide ecological insight into food web structure and operation, one must first establish a detailed understanding of the trophic interactions between species in an ecosystem. The strength of these interactions varies between conspecifics e.g. [445], and across different temporal [154, 199, 217, 379, 445] and spatial scales [148, 383, 405, 406]. Factors that are likely to influence the availability of prey to its predator and cause observed natural variability in trophic interactions include the spatial and temporal heterogeneities in the abundance and spatial distribution of prey [242, 385].

In this chapter, we developed a model of a predator during one foraging trip in the breeding season. Outcomes of the foraging model were the probability distributions for the relative amounts of prey types caught and trip duration. Furthermore, we modelled a succession of foraging trips to represent a predator foraging over a longer period of time during its breeding season. This model was used to provide theoretical evidence as to the mechanisms by which natural variability in the spatial aggregation of prey, the timing at which prey become available, and prey abundance, could affect foraging outcomes which are linked to reproductive success [445].

We parameterised our model based on a foraging macaroni penguin (*Eudyptes chrysolophus*). Macaroni penguins were a good candidate species for this analysis because, (i) as highlighted in Chapter 2 they are one of the best represented species in the Scotia Sea data set; (ii) as shown in Chapter 4, small changes to ecological parameters for macaroni penguins had a relatively large influence on model outputs compared to most other land-breeding predators, highlighting them as important predators in the Scotia Sea; and (iii) a recent empirical study of macaroni penguins has linked their diet composition to reproductive success [445].

The South Georgia archipelago in the northern Scotia Sea hosts a diverse community of breeding sea birds and marine mammals [320]. Many of these predators consume Antarctic krill (*Euphausia superba*), and the presence of krill in the diet of some predator's has been shown to increase the probability of survival of their offspring [206, 445]. Macaroni penguins are a pertinent example of a predator whose diet is dominated by Antarctic krill; however they also eat other crustaceans, fish and cephalopods [205, 206, 212, 445]. During one foraging trip, individual macaroni penguins will predominantly feed on one prey type, typically Antarctic krill, and as a result, composition of prey in predator diet samples for an individual is often bimodal, composed of all/almost all or no krill [445]. Krill-derived energy in a macaroni penguin's diet, rather than total energy, is correlated with mass of chick at fledging [445], which may affect a chick's survival into the next year [270]. Additionally, provisioning during the breeding season can also affect within year survival of penguin chicks [145].

5.1.2 Overview of macaroni penguin ecology

Macaroni penguins form monogamous pairs. After the chick hatches in late December, the female macaroni penguin forages until chick fledging at approximately 59 days [220]. The three weeks following chick hatch in late December, are known as the brood phase. During the brood phase, the female provisions alone whilst the male broods the chick [145, 220]. The female penguin makes frequent visits back to its nest to feed its chick, with most foraging trips lasting less than two days [145, 205, 253, 434]. The period following this is known as the créche phase during which chicks from within a colony form créches. During the créche phase, males frequently join provisioning duties but must first replenish their own reserves following a 40 day fast [220]. However, in some instances, chick-provisioning by the male ceases altogether [145]. On average, females provide approximately 70% of a chick's meals [145].

At South Georgia, the foraging grounds of many macaroni penguins are north-west of Bird Island towards the shelf-break [434], where their prey occurs in high abundance [444]. One such prey is Antarctic krill, which form large, dense, monospecific swarms [235, 428]. Their abundance around South Georgia fluctuates greatly between years [235]. At South Georgia, Antarctic krill density is likely to be a function of successful spawning events at seed populations at the Western Antarctic Peninsula, southern Scotia Sea, and Weddell Sea; transport of juvenile Antarctic krill from their spawning grounds into the Scotia Sea; and movement of Antarctic krill on and off the South Georgia shelf [318, 431, 468]. The magnitude and timing of allochthonous recruitment, hereafter referred to as recruitment, into predator foraging grounds at South Georgia, is highly variable between years [385].

5.1.3 Individual-based stochastic encounter modelling

Probabilistic encounter models based on Poisson processes are useful to understand trophic interactions between a predator and their prey. A Poisson process is a stochastic counting process in which, in their simplest form, events occur at a fixed rate α [160]. They have been successfully modified to model individual predators foraging for spatially aggregated prey e.g. [160, 360, 361]. In these models, an event is a predator encountering a spatial aggregation of prey, or encountering and consuming individual prey. The probability of encountering any prey is $\frac{1}{\alpha}\delta t + O(\delta t^2)$, over a small time interval δt, and the probability of encountering two prey in time δt, is of order $O(\delta t^2)$, and is considered negligible.

In this chapter, we built two Poisson process based models of a foraging female macaroni penguin breeding on Bird Island, South Georgia. We developed parsimonious models of a penguin encountering two prey types, Antarctic krill and alternate prey, during one foraging trip. We calculated a set of foraging metrics as model output: the distribution of each prey type, total prey, and trip duration. In Model 1, a predator randomly encountered individuals of both prey types, and in Model 2, a predator randomly encountered individual alternate prey or monospecific swarms of Antarctic krill. We assumed that when a predator encountered prey, it consumed it with a 100% success rate, and when it encountered a swarm, it was able to eat until satiation.

Concomitantly, we programmed numeric simulations of a foraging predator to validate the analytical model and to allow us to efficiently and accurately assess the effects of some elements of biological complexity which were omitted from Model 2. We also calculated foraging outcomes over the brood phase using a succession of simulations of Model 2. On these timescales we examined foraging outcomes over the period of time when chick mortality is at its highest. By using Poisson process based models, we could examine how the spatial aggregation of prey affected foraging outcomes, separate from active foraging behaviours, such as prey preference or a predator adjusting its swimming speed. Furthermore, the probabilistic nature of these models allowed us to investigate the relative likelihood of different foraging outcomes which could arise under one set of environmental conditions.

5.1.4 Aims

We used Models 1 and 2 to investigate: (i) whether the spatial aggregation of Antarctic krill into swarms could explain the observed bimodal distribution of Antarctic krill in predator diets during one foraging trip; (ii) what the effects of some elements of biological complexity (whether the macaroni penguin leaves a krill swarm before satiation, prey handling time, and spatial aggregation of alternate prey) are on foraging outcomes; (iii) whether prey which formed swarms had different energetic costs to a foraging predator than non-swarming prey during one foraging trip and over the brood phase; and (iv) what the relative impacts of the timing and magnitude of krill recruitment events could be on foraging success over the brood phase.

Possible mechanisms driving variation in trophic interactions and breeding success have been widely discussed [214, 385, 445]. By using a simple model of a foraging predator, we explored how the spatial arrangement of prey into swarms and availability of swarming prey during the breeding season, could affect foraging outcomes. This would not be possible using empirical data because detailed information on prey abundance and distribution are difficult to obtain. Understanding the mechanisms which govern predator foraging, which can impact on survival, is important given the rapid climatic changes in the western Scotia Sea which are likely to affect the availability of Antarctic krill to its predators [236].

5.2 Methods

In Section 5.2.1 we introduce the key assumptions which we apply in our model of a foraging penguin. In Section 5.2.2, we provide details of two analytical model frameworks. In Model 1, both prey were randomly distributed, and in Model 2, Antarctic krill formed large monospecific swarms. In Section 5.2.3 we provide details of how we developed simulations of Models 1 and 2, and in Section 5.2.4, we explain how we temporally ‘scaled-up’ Model 2 using simulations, to represent foraging by a macaroni penguin throughout the brood phase of the breeding season. In the subsequent sections (sections 5.2.5-5.2.8), we explain how we used the models described in sections 5.2.1-5.2.4 to investigate the aims listed in Section 5.1.4.

5.2.1 Macaroni penguin (*Eudyptes chrysolophus*): biology and model constraints

We parameterised our model based on a breeding female macaroni penguin on Bird Island, South Georgia. We modelled the penguin whilst in its foraging grounds, and made the following simplifying assumptions:

1. predator foraging was not affected by its condition, weather events, competition from conspecifics or other predator species, or by its predators;

2. a predator foraged alone, and moved randomly in its environment at a constant speed throughout a foraging trip;
3. a predator consumed two types of prey: Antarctic krill and alternate prey;
4. when the predator encountered prey it consumed it with a 100% success rate;
5. time taken to capture and consume encountered prey (handling time) was small in comparison to search time and was therefore considered negligible;
6. a foraging trip ended when a predator was satiated, i.e. had consumed a maximum number of prey N_m, or a maximum time limit, $T_m =$ two days, had elapsed, whichever occured first.

5.2.2 Modelling a penguin's foraging trip

We modelled a penguin encountering prey as a Poisson process: the predator (penguin) encountered targets (krill, patches of krill, or alternate prey) stochastically [160, 360, 361]. In a Poisson process with rate α per unit time, the time taken to encounter one target follows an exponential distribution with mean $\frac{1}{\alpha}$ and probability density function as given in equation (5.1).

$$P_{T_1}(t) = \alpha e^{-\alpha t}. \tag{5.1}$$

When no time constraints were applied to trip duration, the probability density function for the n^{th} encounter occurring at exactly time t was given by equation (5.2), and the distribution of number of prey caught by time t, given by $\mathbf{Q_t}$, was a simple Poisson random variable with distribution function given in equation (5.3).

$$P_{T_n}(t) = \frac{\alpha^n t^{n-1} e^{\alpha t}}{(n-1)!}. \tag{5.2}$$

$$P(\mathbf{Q_t} = n) = \int_0^t \frac{\alpha^n t_1^{n-1} e^{-\alpha t_1}}{(n-1)!} \left(1 - \int_0^{t-t_1} \alpha e^{-\alpha t_2}\right) dt_2 dt_1 = \frac{(\alpha t)^n e^{-\alpha t}}{n!}. \tag{5.3}$$

This mathematically simple and tractable framework formed the basis for our consideration of foraging for different resources, of which krill were subject to different spatial heterogeneities.

5.2.2.1 Model 1: both prey are randomly distributed

In Model 1 we assumed that there were two prey types, each randomly distributed in space. A penguin encountered individual Antarctic krill and alternate prey with rates α_1 and α_2, respectively. We used a definition for encounter rate developed by Gerritsen and

Strickler (1977) [249]; we assumed that prey swimming speeds were negligible in comparison to predator swimming speeds, and predators were unaffected by turbulent motion. The resultant equation used to calculate encounter rates with individual prey is given in equation (5.4).

$$\alpha_i = \pi v_p^2 s_p d_i, \; i = 1, 2, \tag{5.4}$$

where $\pi v_p^2 s_p$ is the rate at which a penguin with visual range v_p and swimming speed s_p can search a unit volume of water, and d_i is the density of prey type i per unit volume. Here $i = 1$ is Antarctic krill and $i = 2$ is alternate prey.

Using equations (5.2) and (5.3), we calculated forage trip duration $\mathbf{T_1}$ with probability density function $P_{\mathbf{T_1}}(t)$, and the number of all prey $\mathbf{N_1}$, krill prey $\mathbf{K_1}$, and alternate prey $\mathbf{G_1}$ caught during one forage trip. The probability density function for trip duration and probability mass functions for $\mathbf{N_1}$, $\mathbf{K_1}$, and $\mathbf{G_1}$, are given in equations (5.5)-(5.8). Note, in equations (5.5)-(5.8), we defined $\alpha = \alpha_1 + \alpha_2$.

$$P_{\mathbf{T_1}}(t) = \begin{cases} e^{-\alpha T_m} \sum_{j=0}^{N_m-1} \frac{(\alpha T_m)^j}{j!} & \text{if } t = T_m; \\ e^{-\alpha t} \frac{\alpha^{N_m} t^{(N_m-1)}}{(N_{max}-1)!} & \text{if } t < T_m; \end{cases} \tag{5.5}$$

$$P(\mathbf{N_1} = n) = \begin{cases} e^{-\alpha T_m} \frac{(\alpha T_m)^n}{(n)!} & \text{if } n < N_m; \\ 1 - e^{-\alpha T_m} \sum_{j=1}^{N_m-1} \frac{(\alpha T_m)^j}{j!} & \text{if } n = N_m; \end{cases} \tag{5.6}$$

$$P(\mathbf{K_1} = k) = \begin{cases} \begin{bmatrix} k \\ N_m \end{bmatrix} \dfrac{\alpha_2^{N_m-k} \alpha_1^k}{\alpha^{N_m}} \left(1 - e^{-\alpha T_m} \displaystyle\sum_{i=0}^{N_m-1} \frac{(\alpha T_m)^i}{i!}\right) \\ \qquad + e^{-\alpha T_m} \displaystyle\sum_{i=k}^{N_m-1} \begin{bmatrix} k \\ i \end{bmatrix} \frac{\alpha_2^{i-k} a_1^k (\alpha T_m)^i}{\alpha^i i!} & , \quad \text{if } k < N_m; \\ \left(\frac{\alpha_1}{\alpha}\right)^{N_m} \left(1 - e^{-\alpha T_m} \sum_{i=0}^{N_m-1} \frac{(\alpha T_m)^i}{i!}\right), & \quad \text{if } k = N_m; \end{cases} \tag{5.7}$$

$$P(\mathbf{G}_{\mathbf{1}=}g) = \begin{cases} \begin{bmatrix} g \\ N_m \end{bmatrix} \dfrac{\alpha_1^{N_m-g} \alpha_2^g}{\alpha^{N_m}} \left(1 - e^{-\alpha T_m} \displaystyle\sum_{i=0}^{N_m=1} \frac{(\alpha T_m)^i}{i!}\right) \\ \qquad + e^{-\alpha T_m} \displaystyle\sum_{i=g}^{N_m-1} \begin{bmatrix} g \\ i \end{bmatrix} \frac{\alpha_1^{i-g} \alpha_2^g (\alpha T_m)^i}{\alpha^i i!} & , \quad \text{if } g < N_m \\ \left(\frac{\alpha_2}{\alpha}\right)^{N_m} \left(1 - e^{-\alpha T_m} \sum_{i=0}^{N_m-1} \frac{(\alpha T_m)^i}{i!}\right), & \quad \text{if } g = N_m; \end{cases} \tag{5.8}$$

For a verbal description of the analytical Model 1, see Appendix J.

5.2.2.2 Model 2: krill form swarms

In Model 2, krill formed dense, spherical, spatial aggregations known as swarms, of radius r_s. Similar to existing models of foraging predators e.g. [360], we assumed that the visual range of a penguin was small in comparison to the size of the swarm. Additionally, we assumed that the predator was unaffected by turbulence, and thus we calculated encounter rate of a penguin with a krill swarm according to equation (5.9) [360, 398].

$$\alpha_{1s} = \pi r_s^2 s_p d_s, \tag{5.9}$$

where $d_s = \frac{d_1}{\frac{4}{3}\pi r_s^3 d_{ks}}$ is the density of krill swarms (per m^3) and is a function of r_s, d_1: the density of krill if they were homogenously distributed, and d_{ks}: the density of krill within a swarm. We calculated encounter rate with alternate prey α_2 using equation (5.4), as in Model 1.

Krill swarms are frequently large and dense [428]. Therefore, in Model 2, we assumed that krill swarms were sufficiently large and dense that encounter rate with individual krill within a swarm was large compared to the rate at which a randomly moving penguin could leave a swarm. Therefore, we assumed a predator was always able to eat until it was satiated, i.e. had consumed N_m prey, when it encountered a swarm. We calculated the forage trip duration $\mathbf{T_2}$ with probability density function $P_{\mathbf{T_2}}(t)$, and the number of all prey $\mathbf{N_2}$, krill prey $\mathbf{K_2}$ and alternate prey $\mathbf{G_2}$ caught during one forage trip. Probability density function for trip duration and probability mass functions for $\mathbf{N_2}$, $\mathbf{K_2}$, and $\mathbf{G_2}$, are given in (5.10)-(5.13). Note, in (5.10)-(5.13), we defined $\alpha = \alpha_{1s} + \alpha_2$.

$$P_{\mathbf{T_2}}(t) = \begin{cases} \frac{\alpha_2^{N_m} t^{N_m-1} e^{-\alpha t}}{(N_m-1)!} + \alpha_1 e^{-\alpha t} \sum_{j=0}^{N_m-1} \frac{(\alpha_2 t)^j}{j!}, & \text{if } t < T_m; \\ e^{-\alpha T_m} \sum_{j=0}^{N_m-1} \frac{(\alpha_2 t)^j}{j!}, & \text{if } t = T_m; \end{cases} \tag{5.10}$$

$$P(\mathbf{N_2} = n) = \begin{cases} e^{-\alpha T_m} \frac{(\alpha_2 T_m)^n}{n!}, & \text{if } n < N_m; \\ 1 - e^{-\alpha T_m} \left(\sum_{j=0}^{N_m-1} \frac{(\alpha_2 T_m)^j}{j!} \right), & \text{if } n = N_m; \end{cases} \tag{5.11}$$

$$P(\mathbf{K_2} = k) = \begin{cases} \left(\frac{\alpha_2}{\alpha}\right)^{N_m} + e^{-\alpha T_m} \sum_{i=0}^{N_m-1} \frac{(T_m \alpha_2)^i}{i!} - \left(\frac{\alpha_2}{\alpha}\right)^{N_m} \frac{(T_m \alpha)^i}{i!}, & \text{if } k = 0; \\ \frac{\alpha_1 \alpha_2^{N_m-k}}{\alpha^{N_m-k+1}} \left(1 - \exp^{-\alpha T_m} \sum_{j=0}^{N_m-k} \frac{(\alpha T_m)^j}{j!}\right), & \text{if } 0 < k \leq N_m; \end{cases} \tag{5.12}$$

$$P(\mathbf{G_{2}}_{=g}) = \begin{cases} \frac{(\alpha_2 T_m)^g e^{-\alpha T_m}}{g!} + \frac{\alpha_2^g \alpha_1}{\alpha^{g+1}} \left(1 - e^{-\alpha T_m} \sum_{j=0}^{N_m-1} \frac{(\alpha T_m)^i}{i!}\right), & \text{if } g < N_m \\ \frac{\alpha_2^{N_m}}{\alpha} \left(1 - e^{-\alpha T_m} \sum_{i=0}^{N_m-1} \frac{(\alpha T_m)^i}{i!}\right), & \text{if } g = N_m; \end{cases} \tag{5.13}$$

Table 5.1: Parameter values and references for Models 1 and 2.

	Description	Value	Reference and comments
s_p	Swimming speed of a penguin (m h^{-1})	5.00E+03	[204], and references therein.
v_p	Visual range of a penguin (m)	1.00E-01	Most prey of macaroni penguins are zooplankton species. Thus we assumed that randomly distributed prey are difficult to detect and chose a short visual range.
d_{ks}	Density of krill within a swarm (krill m^{-3})	6.50E+01	Mean packing concentration of large krill swarms, in [428].
T_m	Maximum duration of forage trip (h)	4.80E+01	[145, 205, 253, 434].
R_s	Radius of swarm (m)	5.00E+01	Approximately half of the length of a large swarm, in [428].
L_k	Length of krill (mm)	4.55E+01	Mean of inter-annual minimum and maximum krill length, in [235].
M_k	Average mass of krill (g)	6.98E-01	Using the length-mass relationship for krill of length, in [257].
E_k	Energetic value of one prey (KJ)	3.24E+00	$M_k \times 4.65$ Kj g^{-1}: mean of male and female energetic value of Antarctic krill from South Georgia, in [184].

5.2.2.3 Parameter values

Parameter values for the swimming speed, visual range, and maximum trip duration of a penguin are given in Table 5.1 along with parameter values for the length, mass, and energetic value of a krill, and in-swarm density and dimensions of a krill swarm. Using a meal mass of 524g (maximum inter-annual meal mass, reported in Waluda et al. (2012) [445]) we estimated the maximum number of prey that a penguin can consume, N_m, to be 785, for average prey of mass 0.7g. The analytical model was not computationally tractable for large values of N_m due to the use of the factorial function resulting in unmanageably large numbers. We therefore decreased N_m to 80, and mitigated for the biases caused by this by adjusting density estimates for prey. We did this by multiplying prey density by $\sigma = \frac{80}{785}$ in equation (5.4). It was not necessary to adjust encounter rates with a swarm in equation (5.9), as our assumption affected in-swarm density d_{ks}, rather than the density of swarms d_s. By reducing N_m to 80, we were able to estimate model outcomes within 99% accuracy of n_m=785 (see Appendix K).

Using the values given in Table 5.1, we calculated α_1, α_{1s} at low, medium, and high densities of krill, based on inter-annual krill density estimates collected from within the predator's foraging range at South Georgia [235]. For alternate prey, we used density estimates for *Themisto gaudichaudii* collected during January at South Georgia [450], and defined these as normal alternate prey density levels. Table 5.2 provides values for low, medium, high krill densities and normal alternate prey density.

5.2.3 Forage trip simulations

We numerically calculated the probability density of trip duration and probability mass function of prey types through simulation of M foraging trips. We used MATLAB (Release 2012a, The MathWorks, Inc., Natick, Massachusetts, United States), to execute our simulations. Simulations for Model 1 ran as follows:

1. Step 1, we initiated a penguin at the start of the foraging trip time with cumulative trip duration $t = 0$, and cumulative number of prey consumed $n = 0$, krill consumed $k = 0$, and alternate prey consumed $g = 0$.

2. Step 2, while $n < N_m$ and $t < T_m$:

    (a) $t = t + s$, where s was time taken to encounter the next prey and was extracted at random from an exponential distribution with mean $\frac{1}{\alpha_1+\alpha_2}$;

Table 5.2: Density values for prey types used to parameterise the penguin foraging model. Where necessary, density estimates were converted from value 1 (g wet weight m^{-2}) to value 2 (ind. m^{-3}) by multiplying by depth (240m: [235]) and dividing by wet weight of one krill (assumed to be 0.7g, see Table 5.1).

	Value 1 (g m^{-3})	Value 2 (ind. m^{-2})	Reference	α_i	α_{1s}
Low krill	2.74	0.02	Minimum inter-annual krill density, in [235].	0.26	0.02
Medium krill	55.74	0.33	Average of inter-annual krill densities, in [235].	5.32	0.38
High krill	137.03	0.82	Maximum inter-annual krill density, in [235].	13.1	0.94
Alternate prey	-	0.1	*Themisto gaudichaudii* density is at, or below, 0.1 individuals m^{-3}, in [450].	1.6	-

(b) i. If $t < T_m$, we selected a value v from a Bernoulli random variable with probability parameter $\frac{\alpha_1}{\alpha_1+\alpha_2}$. If $v = 1$, we set $k = k + 1$ and $n = n + 1$, else $g = g + 1$ and $n = n + 1$;

   ii. If $t > T_m$, then we set $t = T_m$;

3. Step 3, we recorded the final values for t, n, k and g;

4. Step 4, we repeated steps 1-3, $M - 1$ times.

We modified the above simulations to numerically estimate outcomes of Model 2. First, we changed Step 2a such that we extracted a random number from an exponential distribution with mean $\frac{1}{\alpha_{1s}+\alpha_2}$; second, we changed Step 2b such that the probability parameter for the Bernoulli random variable was $\frac{\alpha_1 s}{\alpha_1 s+\alpha_2}$; and third, we altered Step 2b so that if $v = 1$, then $n = N_m$, $k = N_m - g$, else $n = n + 1$ and $g = g + 1$. Numerical simulations allowed us to verify the accuracy of calculations used to derive our analytical models. Additionally, we used simulations to estimate the probability that, following a foraging trip, a penguin had a diet dominated by krill. We calculated this as the number of simulated forage trips where a penguin consumed $\geq 90\%$ krill, divided by the total number of simulated forage trips. We calculated the probability of a penguin having a diet dominated by alternate prey similarly.

5.2.4 Krill recruitment and penguin breeding success

We temporally 'scaled up' our simulations of Model 2, to represent a penguin foraging over the brood phase of the breeding season. In this model of a penguin foraging over the brood phase, a penguin foraged to reach a quota of prey X_b, which represented the number of prey a penguin must consume to fulfil its own and its chick's energetic requirements over the brood phase. We focused on the brood phase, as it is the period when only the female forages and when chick mortality is at its highest (up to 25%) [145]. We assumed that a penguin spent 68% of its time during the breeding season foraging [253], and thus had 375 hours to reach brood prey quota. The remaining 32% of the brood phase, a penguin spends at the nest site, or commuting from the nest to the shore line which takes approximately 30 minutes [145]. For simplicity, we assumed that the energetic contents of both prey types were the same and equal to the energetic content of one krill E_k =3.24 Kj, see Table 5.1. A penguin with average mass 3.65Kg requires 8.22 W Kg^{-1} [253], and therefore we calculated the brood phase prey quota to be X_b =1.84E+04 prey.

We generated a succession of foraging trips using steps 1-3, described for simulations of Model 2 in Section 5.2.3. After each foraging trip, we recorded the cumulative number of each prey type consumed and the cumulative time spent foraging. We terminated simulations for foraging over the brood phase as soon as the cumulative number of prey consumed was exactly X_b. This often required the final foraging trip to be terminated early. We recorded cumulative time spent foraging as the total elapsed time when a penguin consumed the X_b^{th} prey. We recorded foraging success for the brood as, (i) failed if a penguin did not reach the brood quota within 375 hours, (ii) successful if a penguin reached the brood prey quota in 375 hours. Lastly, we applied an assimilation rate of 0.15 h prey^{-1} (based on the assumption that a penguin consumes a maximum of 80 prey during one foraging trip, and on the observation that a penguin makes a maximum of two trips in one day [205]). By applying an assimilation rate, we implicity account for time spent by a penguin on land and commuting to its foraging grounds.

5.2.5 Can the spatial aggregations of krill into swarms explain observed patterns in the diet composition of macaroni penguins?

The diet composition of macaroni penguins is often composed of a bimodal distribution of krill and alternate prey i.e. the proportion of diet of a macaroni penguin is often composed of all/almost all, or none of each prey type [445]. We used our analytical Models 1 and 2 to compare foraging outcomes for two scenarios of prey distribution: when both prey were randomly distributed, and when Antarctic krill formed large dense swarms and the alternate prey were randomly distributed. Specifically, we generated distributions for G_i, K_i, N_i and T_i for $i = 1, 2$ at low, medium and high densities of krill; alternate prey density was set at normal for all three scenarios of krill density (see Table 5.2). Furthermore, we compared probability of the penguin having a krill dominated diet for krill densities from 0 to 0.85 individuals m^{-3} increasing in steps of 0.005 individuals m^{-3}, using simulations of 1000 forage trips (see Section 5.2.3), referring to this as our stepwise analysis.

5.2.6 How does biological complexity affect foraging?

We used modified versions of the simulation for Model 2 to add three elements of biological complexity into the predator foraging model. Below, we describe each element added into the model, prefixed by ABC #, and describe how we altered simulations of Model 2 to add in each element of biological complexity.

5.2.6.1 ABC1: A predator encountering a krill swarm may leave the swarm before satiation

In these simulations, we removed the assumption that a penguin is always able to eat until satiation when it encountered a swarm from our simulations of Model 2, by introducing two new Poisson processes-based encounters which began once a penguin encountered a swarm. Once in a swarm, a penguin either encountered individual prey within a swarm at rate $\beta_1 = \pi \upsilon_p^2 s_p \sigma d_{ks}$ or left the swarm at rate γ. We calculated β_1 using values given in Table 5.1. We extracted the time taken for an in-swarm event to occur r, from an exponential distribution with mean $\frac{1}{\gamma_1+\beta_1}$. If the sum of r and the cumulative trip duration before this event exceeded T_m, we terminated the foraging trip, set trip duration to T_m and the number of prey as the number caught before the final event. Otherwise, we added r to the cumulative trip duration. We identified event type by extracting a random value from a Bernoulli distribution with parameter $\frac{\gamma_1}{\gamma_1+\beta_1}$. A value of 1 signified a penguin left the swarm, in which case it continued foraging out of the swarm with events occurring at rate $\alpha_{1s} + \alpha_2$. A value of 0 signified an encounter with an individual krill, at which point it consumed it with a 100% success rate and continued foraging within the swarm with events occurring at rate $\gamma_1 + \beta_1$.

Under this new model format, we simulated a penguin foraging over 100 000 foraging trips at medium krill and normal alternate prey densities (see Table 5.2), for each γ_1=0, 0.0001β_1, 0.0005β_1, 0.001β_1, 0.005β_1, 0.01β_1, 0.05β_1, 0.1β_1. We calculated the probability that a penguin had a krill dominated diet, the probability density function for trip duration, and probability mass functions for the number of krill in a predator's diet.

5.2.6.2 ABC2: Handling time of prey

In these simulations, we introduced a handling time to represent the time taken for a penguin to consume its prey before it was able to resume foraging. We used the simulation framework for ABC1 and set $\gamma_1 = 0$ and introduced handling times for krill and alternate prey of τ_1 and τ_2, respectively. When a predator was not in a swarm, if the next event was an encounter with alternate prey, then the time taken for this event to occur was set as $s + \tau_2$, where s was a randomly generated value from an exponential distribution with mean $\frac{1}{\alpha_{1s}+\alpha_2}$. If the sum of the elapsed time during a foraging trip and $s + \tau_2$ exceeded T_m, we terminated the foraging trip, set trip duration to T_m and the number of each prey consumed as the numbers consumed before the final event. If the next event was an encounter with a krill swarm we added s (defined above) to the total elapsed time. Subsequent in-swarm events always related to an encounter with an individual krill as γ_1=0. Thus the time taken to encounter and consume each krill within a swarm was set as $r + \tau_1$, where r was a random number extracted from an exponential distribution with mean $\frac{1}{\beta_1}$

In the first, null model we set $\tau_1 = \tau_2 = 0$. We compared this to a second parameterisation where we set $\tau_1 = \frac{1}{180}$ hours based on observations of a penguin feeding on a krill swarm [205]. Penguins are diving predators, thus must return to the surface to breath during the rapid subsequent encounters with krill in a krill swarm. This constraint does not apply for randomly distributed prey and so we set $\tau_2 = 0.5\tau_1$ to account for this. First, we compared the probability distribution for trip duration (placed into 1 hour width bins) and the probability distribution of krill resulting from the model with non-zero handling times, to the model parameterised with handling times set to zero. We calculated these at medium krill and normal alternate prey density over simulations of 100 000 forage trips. For both models, we used our stepwise analysis (see Section 5.2.5) to calculate the probability that a penguin had a diet dominated by krill across a range of krill densities.

5.2.6.3 ABC3: Alternate prey also form swarms

In these simulations we assumed both prey formed large dense swarms. A penguin encountered krill swarms at rate α_{1s}, calculated using equation (5.9), or alternate prey at rate $\alpha_{2s} = \pi r_s^2 s_p d_g$, where d_g is the density of alternate prey swarms and was calculated as $d_g = \frac{d_2}{\frac{4}{3}\pi r_s^3 d_{gs}}$. We based model simulations on that used in ABC1, but modified it as follows: (i) the time taken for an out-of-swarm event to occur was extracted from an exponential distribution with mean $\frac{1}{\alpha_{1s}+\alpha_{2s}}$; (ii) we identified the type of out-of-swarm event by extracting a random number from a Bernoulli distribution with parameter $\frac{\alpha_{1s}}{\alpha_{1s}+\alpha_{2s}}$, where a value of one or zero signified an encounter with a krill swarm or alternate prey swarm, respectively; (iii) if an encounter is with a swarm of alternate prey, a penguin either encountered individuals within the swarm at rate β_2, or left the swarm at rate γ_2, similar to simulation of in-swarm events described in ABC1.

We assumed that swarms formed by alternate prey were the same dimensions as used to model Antarctic krill ($r_s = 50$m), and calculated foraging metrics for in-swarm densities of alternate prey d_{gs}=10, 20, 30, 40, 50, 60, 70, and 80 ind. m^{-3}. We set $\gamma_1 = \gamma_2 = 0.05\beta_1$ and used normal alternate prey density and medium krill density (see Table 5.2). We calculated the probability mass function for the number of krill in a predator's diet, and probability density function for trip duration, along with the probability of having a krill dominated diet, from 100 000 simulations of a foraging predator.

5.2.7 Do prey which form swarms have different energetic costs than non-swarming prey?

Waluda et al. (2012) [445] found that years when species of krill dominated the diets of penguins, were years when the mass of chick at fledging was greater [445]. One suggested reason was that krill have lower energetic costs of foraging than other prey. Therefore, we assessed whether prey which formed swarms had different energetic cost to a predator than non-swarming prey, first, during one foraging trip, and second, throughout the brood phase of the breeding season. For one foraging trip, we used simulations for Model 2, (see Section 5.2.3), to inspect the distribution of foraging trip duration separately for penguins with krill dominated diets, diets dominated by alternate prey, and those with mixed diet where neither prey type constituted greater than 10% of total prey consumed. We completed this at low, medium and high densities of krill (see Table 5.2).

For consideration of the different energetic costs of prey over the brood phase, we inspected the time taken to reach the brood quota using simulations of the brood phase (see Section 5.2.4). We inspected the distribution of time taken to reach the brood quota separately for foraging trips where total diet over the brood phase was proportionally composed of values in the ranges of [0-0.1], (0.1-0.2], (0.2-0.3] . . . or (0.9-1] krill.

5.2.8 How does the timing and strength of krill recruitment during the brood phase affect foraging success?

Reid et al. (2010) found evidence to suggest that allochthonous krill recruitment resulted in intra-annual variation comparable to estimated inter-annual variability in krill abundance [385]. They highlighted the importance of the timing of allochthonous recruitment, as late recruitment could result in a mismatch between prey availability and important events in predators breeding cycle [177, 385]. Therefore, in this section, we assessed how the density of krill affected brood foraging success concomitantly with the availability of krill through recruitment. We used the simulations for the brood phase (see Section 5.2.4), and assumed that krill density, and therefore encounter rate, at the beginning of the brood period was low. When krill recruitment occurred at a time point T_r during the brood period, post recruitment krill density S_r, was set at a higher rate for the remainder of the brood phase, and encounter rate was recalculated accordingly.

We simulated 100 penguins provisioning during the brood period each for a recruitment event occurring from T_r from 180 to 340 hours in increasing blocks of 10 hours. We simulated foraging over 100 chick-provisioning periods at each value T_r, and for post recruitment krill densities from S_r=0.03-0.30, in increasing increments of 0.03. For each combination of S_r and T_r, we calculated the probability that a penguin had a successful brood period, as the number of simulated brood periods which were successful divided by the total number of simulated brood periods.

5.3 Results

5.3.1 Forage trip outcomes: random versus swarming krill

Both in Model 1 where krill were randomly distributed and Model 2 where krill formed large dense swarms both predators had a 100% chance of consuming N_m prey by the end of a foraging trip where krill density was set at medium, and alternate prey density was normal (Figure 5.1). At these prey densities, the probability mass functions for each prey in Model 1 suggested that alternate prey was more likely to be the most abundant prey, whereas in Model 2, krill was most likely to be the most abundant prey. Furthermore, in Model 1, the probability of having a diet dominated by either prey type was <0.01, but in Model 2 this rose to 0.81. There was a clear difference in the shape of distributions of prey in predator diets; Model 2 was more likely to result in diets dominated by krill or alternate prey than Model 1 (Figure 5.1).

In the stepwise analysis applied to Model 2, the probability of having a diet dominated by krill rose quickly from <0.05 for all krill densities at or below 0.005 krill m^3, to >0.8 for all krill densities above 0.275 krill m^3. In Model 1, the probability of having a diet dominated by krill was <0.05 for all krill densities at or below 0.47, and did not reach 0.8 for any krill density tested in the stepwise analysis. This implies that mixed diets, where neither prey constituted >10% of a predator's diet, were more likely when prey were randomly distributed, and that the chance of having a diet dominated by one prey was very high when krill formed large, monospecific swarms.

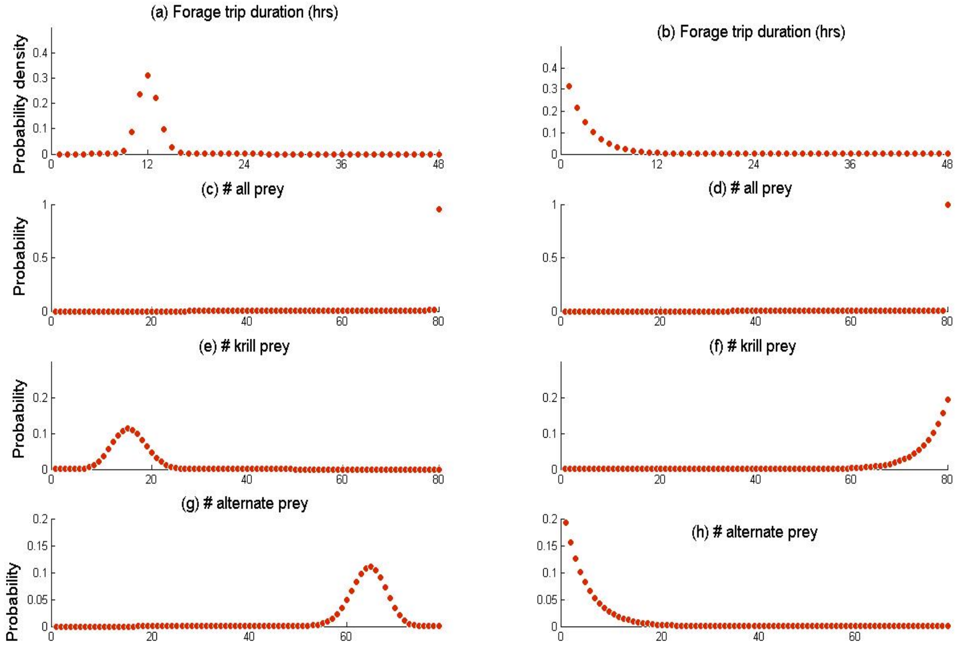

Figure 5.1: The probability density function for trip duration (a, b), and probability mass functions for all prey (c, d), krill prey (e,f), and alternate prey (g, h) for Model 1 (a,c,e,g) and Model 2 (b,d,f,h). Results are calculated from equation (5.5)-(5.13), and are for krill density set at medium, and alternate prey density set at normal.

5.3.2 How does biological complexity affect foraging?

5.3.2.1 ABC1: A penguin can leave a krill swarm before it is satiated

The probability of having a diet dominated by krill was reduced as the rate at which a penguin left a swarm increased (see Table 5.3). When the ratio of leaving a swarm to encountering an individual within a swarm was 1:20, i.e. $\gamma = 0.05\beta$, the probability of having a diet dominated by krill decreased from 0.86 to 0.53. Only when the ratio of leaving a krill swarm to encountering krill within a swarm rose to 1:10, i.e. $\gamma = 0.01\beta$, did the probability of having a krill dominated diet decrease to <0.05.

Similar to Model 2 when $\gamma = 0$, meaning that a penguin is always able to eat until satiation upon encountering a krill swarm, the distribution function for krill in predator diets showed a strong right skew for all values of γ tested. The exceptions to this were when $\gamma = 0.05\beta, 0.01\beta$, for which the probability mass function of krill in the diet of a predator, and the probability density function for trip duration, began to adopt a form similar to that when both prey were randomly distributed (compare Figure 5.1 to Figures 5.2, 5.3).

Table 5.3: Probability of having a diet dominated by krill for various rates at which a penguin leaves a krill swarm, γ in Model ABC1.

γ	Probability of krill dominated diet
0	0.86
$0.0001\ \beta$	0.86
$0.0005\ \beta$	0.86
$0.001\ \beta$	0.84
$0.005\ \beta$	0.82
$0.01\ \beta$	0.68
$0.05\ \beta$	0.53
$0.1\ \beta$	0.04

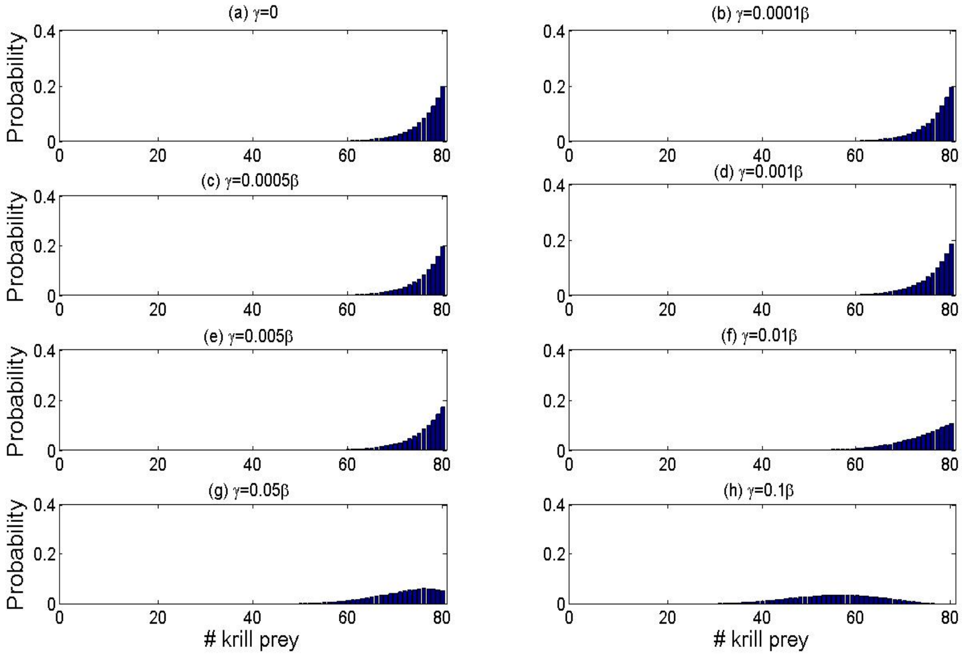

Figure 5.2: Probability mass function for the number of krill in a predator's diet for different values of γ for Model ABC1. Metrics calculated from 100 000 simulated foraging trips for medium krill density and normal alternate prey density.

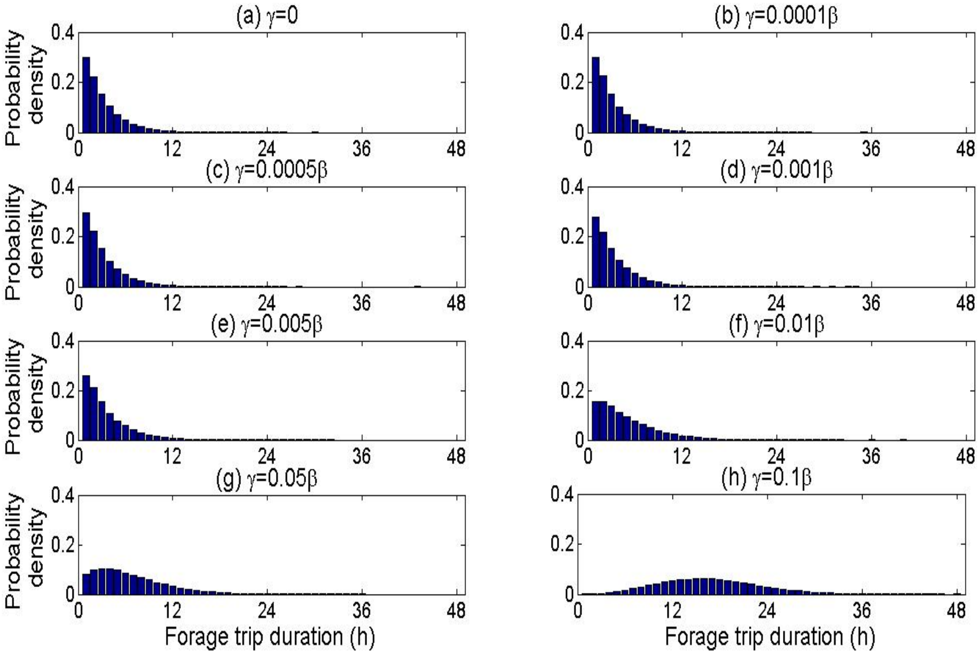

Figure 5.3: Probability density function for trip duration for different values of γ for Model ABC1. Metrics calculated from 100 000 simulated foraging trips for medium krill density and normal alternate prey density.

5.3.2.2 ABC2: Handling times of prey are non-zero

The probability mass function for the number of krill, alternate prey, and probability distribution function for trip duration exhibited less than a 4% difference to results from the simulations when handling times were set to zero (percent difference was calculated as $100|P_{\tau=0} - P_{\tau>0}|$, where $P_{\tau=0}$ is a probability calculated when $\tau_1 = \tau_2 = 0$ and $P_{\tau>0}$ is the equivalent probability when $\tau_1 = \frac{1}{180}$ and $\tau_2 = \frac{1}{360}$, respectively). The one exception to this was the probability that trip duration was between 0-1 hours, where the probability was 13% lower in the model with positive handling times to the model with no handling times (Figure 5.4). The probability of a penguin's diet being dominated by either prey type were similar for simulations where $\tau_1 = \tau_2 = 0$ and the model with positive handling times. This implies that, if handling times for each prey are small in comparison to the duration of a foraging trip, the spatial aggregation of prey is the dominant mechanism determining foraging outcomes.

5.3.2.3 ABC3: Both prey form swarms

When both prey formed swarms, the probability mass function for krill in the diet of a predator had a bimodal distribution (all/mostly all, or no krill) (Figure 5.5), similar to Model 2 where only krill formed swarms and alternate prey were randomly distributed (Figure 5.1).

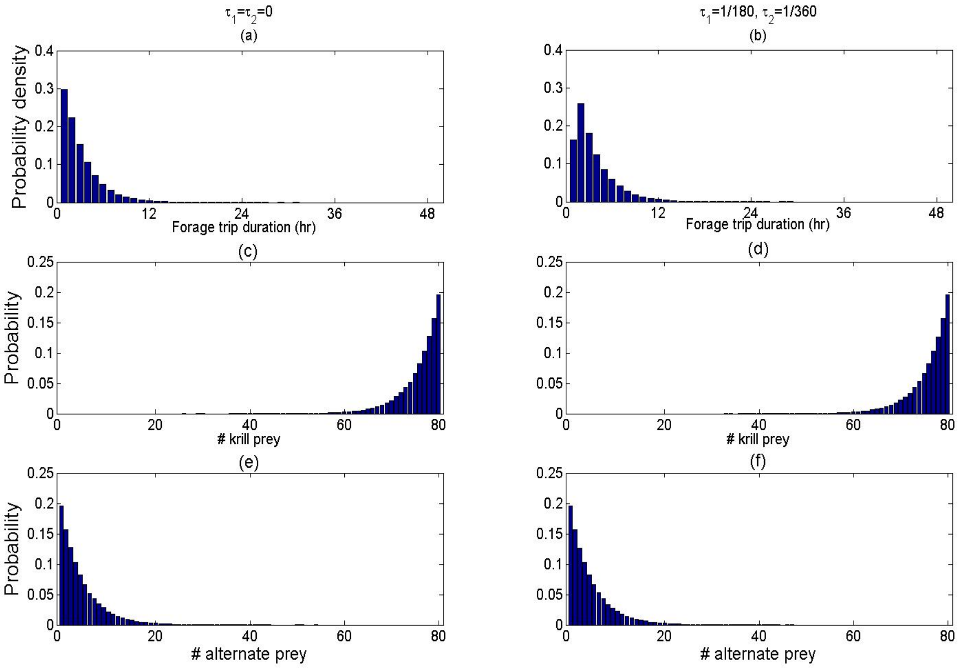

Figure 5.4: Probability density function for trip duration (a,b); probability mass function for the number of krill prey (c,d); and the probability mass function for the number of alternate prey (e,f) for Model ABC2, when handling times were set to zero (left) and when handling times were positive (right). Metrics were calculated from 100 000 simulated foraging trips at medium krill density and average alternate prey density.

In Model 2, the probability of having a diet dominated by krill was 0.8, 0.53, and <0.01 for high, medium, and low krill densities. When both prey formed swarms, this decreased for high and medium krill densities to 0.73 and 0.5, respectively, for an in-swarm alternate prey density of 0.8 ind. m^{-3}. However, the probability of having a diet dominated by krill at low krill densities increased by 0.02 in the model where both prey formed swarms, compared to Model 2.

At medium krill density, the distribution of trip duration when both prey formed swarms, was similar in shape to the distribution of trip duration for Model 1, where alternate prey were randomly distributed (compare Figure 5.1a to Figure 5.6e). However, expected trip duration was much shorter in the model when both prey formed swarms, compared to Model 1.

5.3.3 Do prey which form different spatial aggregations have different energetic costs?

A foraging trip where swarming prey dominated a predator's diet was shorter than foraging trips where the diet was mixed. Both of these were shorter than for trip durations for

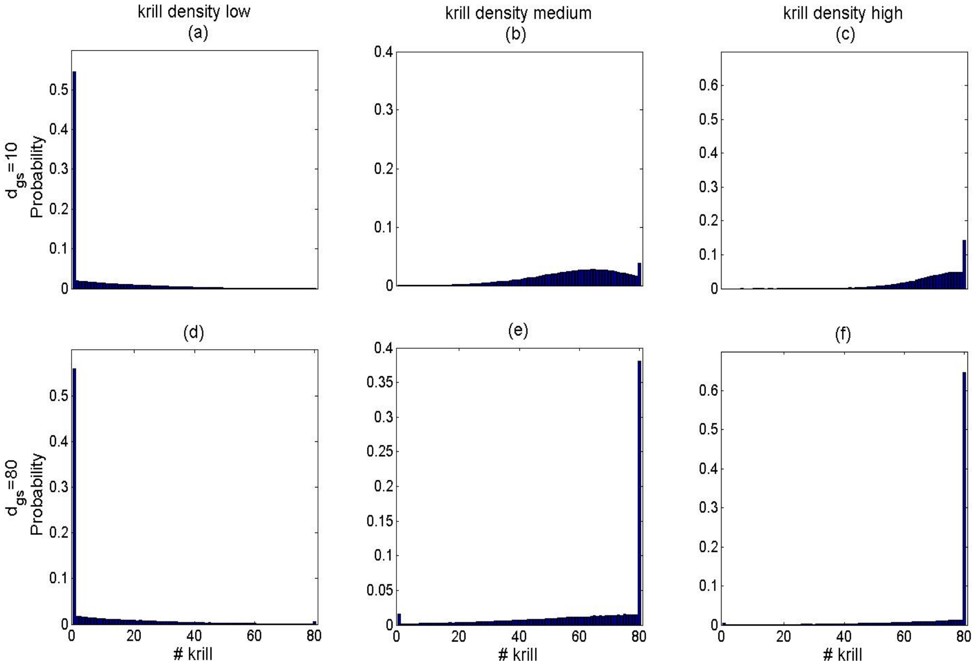

Figure 5.5: Probability mass function for the number of krill in a predator's diet when both prey types form swarms for low (a,d), medium (b,e), and high (c,f) krill densities for Model ABC3. Top graphs are for an in-swarm density of alternate prey of 10 ind. m^{-3}, and bottom are for 80 ind. m^{-3}. Metrics calculated from 100 000 simulated foraging trips.

predators whose diets were dominated by randomly distributed prey. This was true for low, medium and high krill densities (Figure 5.7).

A similar trend was seen over the brood phase of the breeding season. Penguins which frequently encountered krill swarms, reached their brood quota overall faster than those which did not. This was true over the range of tested krill densities (Figure 5.8).

As expected, as krill density decreased, the probability of brood phase foraging success decreased. There was greater variability in the duration of time taken to consume the prey quota for the brood period at lower krill densities (Figure 5.8). The shape of the distribution of krill in the diet of a penguin was also fundamentally different when considered over the brood phase compared to one foraging trip. In one foraging trip, a penguin is likely to consume all, or no krill. However, when considered over the brood phase, mixed diets become more prevalent, and the bimodal distribution of prey disappeared.

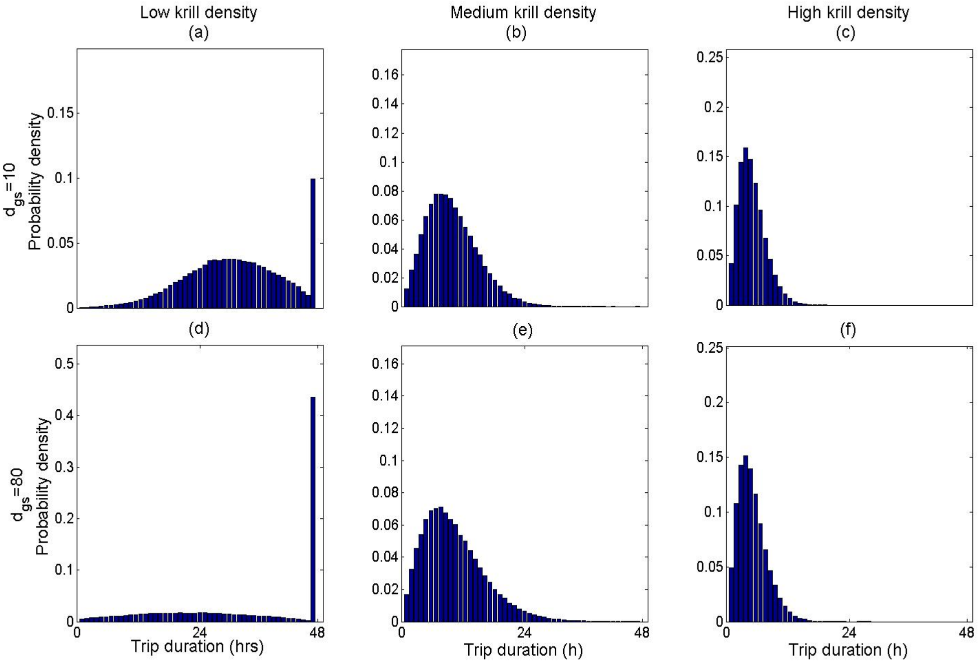

Figure 5.6: Probability density function for forage trip duration when both prey types formed swarms for low (a,d), medium (b,e) and high (c,f) krill densities for Model ABC3. Top graphs are for an in-swarm density of alternate prey of 10 ind. m^{-3}, and bottom are for 80 ind. m^{-3}. Metrics calculated from 100 000 simulated foraging trips.

5.3.4 How does the timing and strength of krill recruitment effect foraging success over the breeding season?

If the density of post-recruitment krill was above 0.12 krill m^{-3}, then the probability of successful brood phase foraging was >0.96 if recruitment occurred before 20% of the brood phase had elapsed. For post-recruitment krill densities tested above 0.12 krill m^{-3}, the probability of successful foraging over the brood phase transitioned rapidly from >0.95 to <0.05 as krill recruitment timing changed from when 20% to 50%, respectively, of the brood phase had elapsed. However, for post-recruitment krill densities below 0.09 krill m^{-3}, the foraging success over the brood phase was lower for earlier recruitment events than for higher post-recruitment krill densities (Figure 5.9), and dropped to <0.05 when the recruitment event occurred after 35% of the brood period had elapsed. For these krill densities, even when a recruitment event occurred before the beginning of the brood phase, the probability of foraging success over the brood phase was <0.55.

In our model, penguins foraging when recruitment occurred before 50% of the brood period had elapsed had a probability greater than zero of successful brood phase foraging. The relationship between the timing of recruitment events and the probability that a penguin

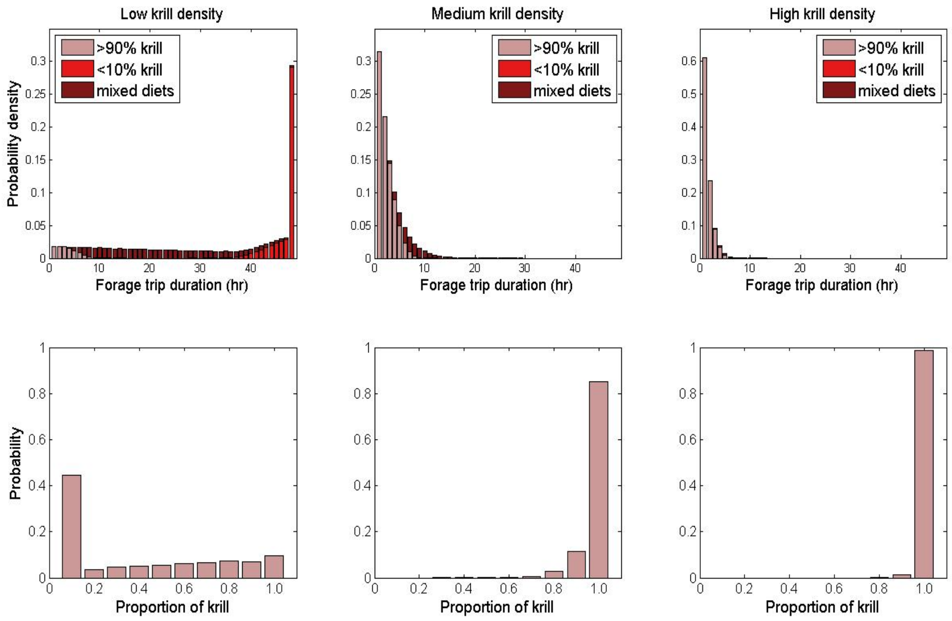

Figure 5.7: Probability density function for trip duration (top) partitioned by whether a predator's diet was dominated by krill prey, alternate prey, or had a mixed composition at the end of a foraging trip. Bottom graphs show the proportion of diet composed of krill. Metrics calculated from 100 000 simulated foraging trips each for low, medium and high krill density conditions (left-right).

foraged successfully during the brood phase, was similar for all post-krill densities of 0.12 krill m^{-3} and above. This threshold krill density is less than half of the medium krill density (Table 5.2) used in this chapter of 0.3 krill m^{-3} which was estimated from empirical data [235].

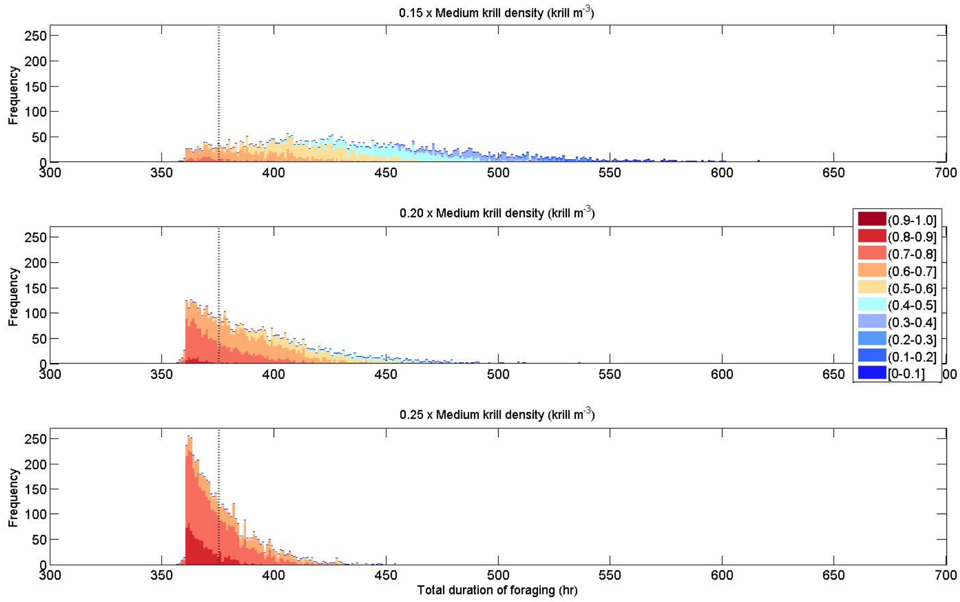

Figure 5.8: Probability distribution function for the foraging time taken to consume the target number of prey needed to sustain a chick through the brood period for 3 constant, discrete krill densities. Line shows the end of the brood period. Colours show the proportion of krill in a predator's diet. Results calculated from 5000 simulations of foraging during the breeding season.

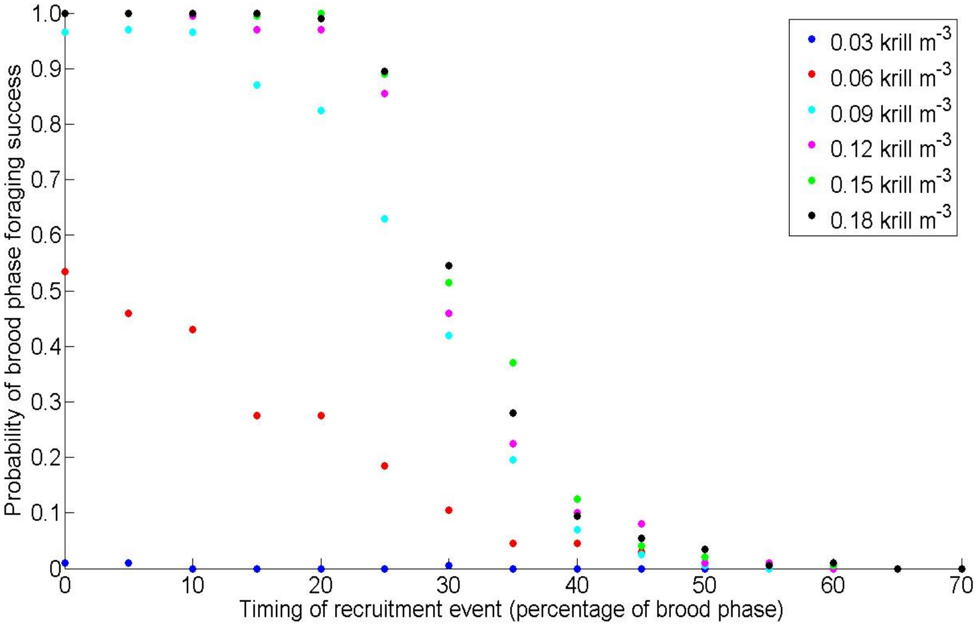

Figure 5.9: Probability of successful brood-phase foraging for different timing of krill recruitment T_r (x-axis) and for different strengths of recruitment event (colours, see legend).

5.4 Discussion

5.4.1 Aims (revisited)

In this section we review our results with reference to the four aims given in Section 5.1.4. First, we found that the spatial aggregation of krill into swarms could explain the observed bimodal pattern in predator's diet (Figures 5.1 and 5.7). Second, we found that adding handling times for prey and adding a probability below 0.05β of a penguin leaving a swarm, did not alter the qualitative pattern predicted by Model 2 (Figures 5.2, 5.3, and 5.4). This suggests that these elements of biological complexity are secondary to the spatial aggregation of krill into swarms, in predicting observed bimodal distribution of prey. If both prey formed swarms, then there was still a bimodal distribution of prey in a predator's diet (Figure 5.5). However, qualitative patterns in trip duration were altered from Model 2, when both prey formed swarms (Figure 5.6). Third, we found that prey which formed swarms had a lower energetic cost to the predator than non-swarming prey, as trip duration was shorter for penguins which encountered swarming prey (Figure 5.7). Fourth, we found that, except at very low post-recruitment krill densities (below 0.12 krill m^{-3}), foraging success over the brood phase was more sensitive to the timing of a recruitment event than post-recruitment krill density (Figure 5.9).

5.4.2 Swarming prey as a mechanism driving observed patterns in forage metrics

Our results suggest that broad patterns in foraging outcomes for macaroni penguins in the Scotia Sea can be explained by the spatial aggregation of prey, and independently of many foraging behaviours such as active prey preference or adjusting swimming speeds whilst foraging. Specifically, our parsimonious model of a foraging macaroni penguin encountering individual alternate prey, and swarms of Antarctic krill, are able to predict observed bimodal distribution i.e. all/almost all or no krill, in a predator's diet [445].

Model outcomes were robust to some of the simplifying assumptions used to develop Model 2. For example, the number of krill in the diet of a predator and trip duration were robust to the omission of handling time in Model ABC2 (Figure 5.4). Our model was still able to predict the bimodal distribution of prey in the diet of a predator when we modified our model such that both prey formed swarms in Model ABC3. This is important as other zooplankton prey of macaroni penguins, such as *Themisto gaudichaudii*, also form swarms. Although the swarming structure of Antarctic krill has been well documented and quantified, for example [202, 428], there are fewer studies on the swarming structure of other abundant zooplankton in the Scotia Sea, but see Watts and Tarling (2012) [450].

In reality, prey of macaroni penguins include swarming prey such as Antarctic krill and *Themisto gaudichaudii*, schooling prey such as *Electrona carlsbergi*, as well as prey which may not form spatial aggregations such as *Electrona antarctica* [234, 445]. Gaps in quantitative data about the spatial aggregation of some prey inhibit the predictive power of models such as the one presented here. Useful information about the spatial aggregations of prey which would strengthen our model include, in-swarm/school density of prey, their dimensions, and species composition of macro zooplankton swarms.

Observed patterns of forage trip duration for macaroni penguins during the breeding season on Bird Island found that, most frequently, foraging trips are short (<1 day), but that a small number of foraging trips last approximately two days [145, 205, 253]. At low krill densities, the three spatial aggregations of prey tested in this chapter (both prey randomly distributed, krill formed swarms, and both prey formed swarms) all predicted that most foraging trips would last two days. However, at medium and high krill densities and when one or both prey formed swarms, trip duration was more likely to be shorter and similar to observed trip durations than when both prey were randomly distributed.

Our model was able to predict observed foraging outcomes for macaroni penguins, even when many elements of biological reality were omitted from the model, but were also robust to some of these omissions. This highlights that accounting for the swarming structure of the most abundant prey, Antarctic krill, will be integral to interpreting empirical diet composition data and for predicting future scenarios of predator foraging.

5.4.3 Penguins encountering swarms can frequently eat until satiation

We developed model simulations which included the possibility that, once in a swarm, a penguin could leave it before it reached satiation (Model ABC1). In models when the rate of leaving a swarm was high, the distribution of krill in a predator's diet lost the strong right hand skew, which implied its diet consisted of all krill, at medium krill densities (Figure 5.2). Similarly, at high rates of leaving a swarm, trip duration lost its strong left hand skew and intermediate trip durations became more likely (Figure 5.3). This is similar to results from a one-prey stochastic encounter model by Pitchford et al. (2001) [360], who found that decreasing the rate at which the predator (fish larvae) left a swarm of zooplankton prey, increased their chances of growth-based recruitment through successful foraging.

As previously discussed, empirical data shows that penguin diets are typically composed of all/almost all or no krill during a single foraging trip [445], and that trip duration is either normally short (<1 day), or approximately two days [145, 253]. Our results suggest that predators are frequently able to eat until satiation on encountering a swarm. This is feasible as krill are known to form large, dense swarms of in swarm densities of 7-65 krill m^{-3} and swarm lengths of 25-1174m [428]. Furthermore, they may modify behaviour to stay within high prey density areas [360]. We reiterate that models of foraging predators will be strengthened by a quantitative understanding of aggregations of prey other than Antarctic krill in the Scotia Sea.

5.4.4 Dense, swarming prey have a lower energetic cost to a predator than randomly distributed prey

We found that the length of foraging trip was highly correlated with prey type: penguins which encountered krill swarms had short foraging trips, and those which did not, mostly lasted two days. This agrees with observed patterns in Adélie penguin diets across years, where a high abundance of krill is correlated with shorter foraging trips [242]. Shorter foraging trips are beneficial to a predator as it reduces the energetic costs which are higher for a penguin at sea rather than on land [253]. This could conceivably increase energy available for the chick as well as maintaining the parent in a good condition. Additionally, over the breeding season a penguin is able to make more forage trips if each trip is shorter. Indeed, the energetic content of Euphausiids such as Antarctic krill in the stomach of a macaroni penguin, rather than total energetic content are most correlated with its breeding success, suggesting there is a higher cost to foraging for non-Euphausiid prey [445]. Our results offer theoretical support for this hypothesis (Figures 5.7 and 5.8), and show that the mechanism driving breeding success is not only krill abundance, but also the spatial aggregation of its prey.

Does the lower energetic cost of krill mean that a penguin should not consume randomly distributed prey in favour of swarming prey such as krill? Our results suggest that at low krill densities, a penguin would risk not encountering any krill within the maximum foraging time of two days if it applied this strategy. Furthermore, some penguins were still able to achieve a successful brood phase foraging when only 50-60% of their diet was composed of Antarctic krill, (Figure 5.8). Therefore, avoiding other prey in preference for Antarctic krill would rely on *a priori* knowledge of local prey densities. Given the high intra-annual variability in krill density at South Georgia [172], we suggest that prey preference would be a riskier strategy than consuming all encountered prey.

In our models, predators move and encounter krill randomly, and ignore many more advanced foraging behaviours. However, adaptive foraging strategies can alter the foraging success of a predator. For example, increasing swimming speeds [361] and adjusting the length and frequency of movements during foraging in response to local prey density [258], can affect foraging success. Although our model omits such behaviour, we were still able to predict broad patterns in predator diets. Our results do not challenge the importance of predator behaviours; rather they highlight the importance of the spatial aggregation of prey and stochastic success in affecting foraging outcomes, which could impact on predator breeding success.

5.4.5 In a 'typical' year, recruitment timing is more important than its magnitude

Trivially, our results show that earlier, strong recruitment events result in a higher probability that a penguin successfully forages during the brood phase. Furthermore, our results suggest that there is a threshold time during the brood phase by which a recruitment event must occur, to ensure brood-phase foraging success. In our model, this was after approximately 25% of the brood phase had elapsed, however a more precise estimate of the threshold would require a more realistic estimate of the speed by which a chick can assimilate food, and would consider that penguin foraging habits are different at night [253]. Nonetheless, our model highlights the presence of a threshold beyond which the probability of successful brood phase foraging, which could affect chick survival, was reduced from >95% to <5% over a short delay in the timing of a krill recruitment event during the brood phase. We show the possible negative effects of a mismatch between biological events for prey and their predators, on the success of those predators.

In this chapter we concluded that, overall, the magnitude of a recruitment event was less important than the timing of the recruitment event. For all post-recruitment krill densities above 0.09 krill m^{-3}, the probability of successful foraging during the brood phase was similar for all timings of recruitment event. Krill density of 0.09 krill m^{-3} is low within *in situ* estimates in the Scotia Sea, where inter-annual densities range from 0.02-0.82 krill m^{-3} (estimated from [235]), suggesting that in a 'typical' year, the timing of a recruitment event will drive a predator's foraging success. Evidence suggests that oceanic factors such as winter sea surface temperatures, which affect winter sea-ice extent, could affect the movement of krill into the Scotia Sea [235, 432].

If the post-recruitment density is exceptionally low (in our model this corresponds to krill densities below 0.09 krill m^{-3}), the brood phase foraging success becomes very sensitive to the magnitude of a recruitment event (Figure 5.9). Years of weak recruitment events are likely caused by weak, growth-based recruitment of krill-larvae at seed populations such as those at the Western Antarctic Peninsula [385]. Poor growth-based recruitment events happen episodically and approximately 2-3 times a decade, sometimes lasting for more than one year [416].

Although, in a ‘typical’ year, the timing of recruitment was more important than its magnitude, it will be important to assess through empirical studies, whether weak growth-based recruitment in seed populations can lower post-allochthonous recruitment krill densities below the threshold where foraging success is affected. The management of commercial fisheries, and how we predict the response of a predator’s foraging success to changes in their prey, will depend on whether a combination of post-allochthonous and growth-based recruitment of krill affect predator foraging success, or whether it is allochthonous recruitment alone. This should be a particular priority given the rapid warming of areas in the Scotia Sea and changes to sea-ice extent, on which growth and transport of krill are dependent [236, 422].

5.4.6 Caveats and future work

Our model simplifies the prey field into two types of prey. Although many of our foraging metrics were robust to the spatial aggregation of alternate prey, we acknowledge that our results are representative of zooplankton prey only as we assumed prey swimming speeds were small and negligible compared to that of the predator. Therefore, our model does not account for highly motile prey such as fish and cephalopods [445]. Despite this omission, our model provides valid insights into macaroni penguin foraging, as zooplankton make up the majority of macaroni penguin diets [445]. However, an interesting extension to our model, which could be easily executed using model simulations, would be to include more than two prey species. This could include motile prey with different spatial aggregations. Encounter rates for motile prey must be modified to account for their swimming speed using methods, for example, described in Rothschild et al. (1988) [398]. Fish and cephalopods may have more effective escape mechanisms compared to zooplankton, which could influence catch success rate and handling time of these prey. Furthermore, an individual fish/cephalopod may have more energetic value than an individual zooplankton, which must also be accounted for if they are introduced into model simulations.

Our model provided theoretical support as to the importance of the spatial aggregation of prey in determining foraging success over the brood period. However, our numeric simulations of the brood period implicitly assumed that it was possible for a penguin to achieve successful foraging for any pattern of provisioning, provided the chick had assimilated enough food by the end of the brood phase. However, chicks may perish earlier if provisioning rate is low over a shorter period of time than considered in this chapter. Future work, that would strengthen the simulations of the brood phase developed here, would link parent provisioning to chick survival with greater biological realism; this model should include factors such as predation by giant petrels [270], egg failure [145], or death of one of the parents, and should account for the effects of individual variation in factors such as growth rate which could increase a chicks survival [177].

Macaroni penguins are air-breathing, diving predators [205], however, we do not include time spent by a penguin ascending, descending, or at the sea surface. We implicitly accounted time spent at the surface in part, when we introduced handling times: handling time was longer for krill than for alternate prey, to account for a penguin returning to the surface to breathe during feeding. We found that the addition of handling times did not substantially alter foraging outcomes for one foraging trip (Figure 5.4), although we acknowledge that introducing handling times does decrease foraging rate on prey [221]. In our models of a predator foraging over the brood phase, one could account for time spent ascending, descending, or at the surface, by decreasing the time available for a penguin to reach its brood phase quota. This would decrease the probability of foraging success over the brood phase, but would not affect the qualitative patterns in the results presented in this chapter.

We parameterise our models on a foraging macaroni penguin, however many other predators, with different biological constraints during their breeding season, also consume Antarctic krill, such as Antarctic fur seals, gentoo penguins and species of pelagic fish (see Chapter 4 for a full list of species/groups of species, which consume Antarctic krill in the Scotia Sea.) We hypothesise that the patterns observed in this study would hold for many land-breeding predators, but that the relative sensitivities and thresholds of krill densities and timings of recruitment to which foraging outcomes are sensitive, will vary between predators. An important extension to this work would parameterise our model for different land-breeding predators, to find common and unique patterns in foraging outcomes across species which forage for swarming prey.

5.5 Conclusion

In our parsimonious model of a foraging macaroni penguin, we removed many elements of predator behaviour such as active preference for any one prey type or altering swimming speeds. As such, we were able to consider the spatial aggregation of prey independently of these behavioural factors, and provided theoretical support that a major mechanism governing foraging outcomes and relatedly foraging success over the breeding season for a macaroni penguin, is the spatial aggregation of its prey into swarms. Our results were robust to some of the biological simplifications and assumptions in our parsimonious model, such as the omission of prey handling time and that alternate prey were randomly distributed.

By comparing foraging metrics predicted by our models with empirical data on predator diet composition, we found evidence that a penguin, upon encountering a krill swarm, is able to eat until satiation. We show that swarming prey are energetically advantageous to the penguins which encounter them, as foraging trips are shorter for swarming prey. If a penguin does not encounter a swarm, it is likely to forage for the maximum assigned trip duration of two days, resulting in a bimodal distribution in trip duration. The bimodality in prey type and trip duration is not present when foraging outcomes are considered over the brood period. Nonetheless, penguins that are more likely to spend less time foraging over the brood phase are those which more frequently encounter krill swarms over multiple foraging trips. As such, our model provides theoretical evidence that the presence of swarming prey can increase foraging success over the breeding season.

Lastly, we found that the timing of a recruitment event has a large impact on predator foraging success, with high sensitivity over a small change in recruitment event timing during the brood phase. We conclude that the magnitude of the event is less important as it does not affect foraging success, except at very low krill densities when predator foraging success was sensitive to both the timing and strength of the recruitment event. Therefore, it is important to assess whether poor growth-based recruitment of krill at their seed populations can weaken the post recruitment density at South Georgia sufficiently to decrease foraging success over the brood phase, as this will affect how Antarctic fisheries are managed, and how we make projections of predator response to possible climatically driven changes in their prey population [236].

6 Discussion

6.1 Thesis overview

This thesis focused on theoretical analyses of trophic-based food webs which are parameterised using empirical data. Underpinning all my analyses were two common themes: first, the ecosystem on which I built my analysis: the commercially, climatically, and ecologically important Scotia Sea ecosystem in the Southern Ocean [320]; second, the consideration of the sources and effects of uncertainty on food web data and analyses.

Uncertainties in food web analyses can originate from the limited empirical data used to construct them. One set of data which are integral in food web analyses are the collection of data on the diet composition of consumers, hereafter referred to as diet data sets. Some of the major factors which lead to limited diet data sets are: (i) different sampling efforts across species in an ecosystem; (ii) different sampling methods used to collect, and metrics used to report, diet data, each with their own advantages and limitations; (iii) variable efforts in taxonomically resolving prey; and (iv) the unfeasibly large sampling effort which would be required to collect data for all species in an ecosystem, over all natural variabilities in space and time of trophic interactions. Other types of biological data which can be required in food web analyses, such as the production/consumption rates of species and the efficiencies at which carbon is exchanged between species [183, 346], are also difficult to estimate using empirical methods.

Insight into food webs using theoretical studies is made uncertain by the pragmatic assumptions that are necessary to construct food web analyses. One set of assumptions must be made about how to synthesise limited empirical data, to be able to parameterise an analysis. Another set of assumptions must be made about which processes are important to represent in a food web analysis to capture pertinent features of that food web. Results from these analyses can be sensitive to the set of assumptions made to construct them, which introduces uncertainty in conclusions arising from these analyses.

In this thesis I highlighted uncertainties in food web data; provided resources and methods which could be useful for future assessment of the Scotia Sea; assessed the effects of uncertainty on outputs from food web analyses; used models to estimate values that are difficult to measure empirically; and quantified ecological information on the Scotia Sea food web.

This thesis contributed information and methods of practical use for food web modellers, which are listed below.

1. Chapter 2 summarised a new data set on the diet composition of predators in the Scotia Sea. The summary indicated potential biases, and the strengths and limitations of the data. Strengths of the data were a high number of predator diet samples for land-breeding predators and the important macro zooplankton, Antarctic krill and *Themisto gaudichaudii.* I identified limitations of the data set including no diet data for cetaceans, and too few predator diet samples for cephalopods.

2. In Chapter 3, I suggested adding closure groups in topological network analyses to consume, or be prey for, species with missing data on their predators or prey. Closure groups ameliorated biases caused by missing data by adjusting the trophic position of species with missing data, and so improved estimates for properties which incorporate information on trophic position.

3. Chapter 4 provided a diet matrix for 42 functional groups representing consumers, primary producers, and the detrital pool, in the Scotia Sea. In constructing the diet matrix, I synthesised diet data where prey were given at different taxonomic resolutions.

More generally, this thesis assessed the effects of some uncertainties introduced into food web analyses. Below I summarise the main conclusions arising from the uncertainty analyses.

4. Inferring ecological conclusions from topological network properties using currently available diet data for the Scotia Sea is limited by the inconsistent sensitivities of network properties to the taxonomic resolution of food web data and whether trophic interaction strength is incorporated into calculations of topological properties.

5. Production estimates calculated in Chapter 4 for functional groups in the Scotia Sea food web which are least robust to uncertainties in efficiency parameters are: heterotrophic bacteria and *chromista*, micro/meso zooplankton, benthos, pelagic fish and chinstrap penguins. Production estimates for (i) macro-zooplankton were the most robust of the zooplankton groups; (ii) the Patagonian toothfish, lamprey, skates and rays, and benthic fish, shallow, benthic diet were the most robust of the fish/cephalopod groups; and diving petrels/South-Georgian shag, and albatross which are not wandering albatross, were the most robust of the land-breeding predators and cetaceans.

Furthermore, this thesis provided ecological insight into the Scotia Sea food web using mathematical models and numeric simulations. The major conclusions from these are listed below.

6. In Chapter 4, I highlighted salps and gelatinous zooplankton, and meso/micro zooplankton as important elements of the Scotia Sea food web. Their role in the food web deserves further attention by empiricists.
7. In Chapter 5, the swarming structure of prey is found to be a major driver of foraging outcomes for a land-breeding predator.
8. In Chapter 5, I find that, unless a recruitment event of Antarctic krill is very weak, the timing of their allochthonous recruitment is more important than the post-recruitment density of Antarctic krill for ensuring that a predator can consume enough prey during the breeding season.

6.2 General discussion

In Chapters 2-5, I discussed each study in detail. Therefore, in this section I try not to repeat the sentiments of earlier chapters, but instead approach the results by concentrating on what they tell us about uncertainty in Scotia Sea data set, while also synthesising more general conclusions which are not addressed within each chapter.

6.2.1 Intra-seasonal variation in trophic interactions

Models of foraging predators can provide useful tools to predict possible trophic interactions formed by a predator under different natural variations in an ecosystem. Most data in food web data sets are insufficient to be able to investigate the effects of much natural variability on trophic interactions. One such example, pertinent for the Scotia Sea, is the swarming structure of many zooplankton prey including Antarctic krill [428]. In Chapter 5, I considered trophic interactions by a macaroni penguin over short (one foraging trip) and long (the brood phase during the breeding season) time scales. Over the short time scale, a penguin's diet was most likely to be composed of all/almost all or no krill [445]. Diet data for macaroni penguins is collected through stomach flushing [205, 214], and so data will represent diet composition from one foraging trip. However, considered over long time scales which are more comparable to time scales represented by static food web models, the bimodal pattern of prey disappears, with most predators consuming an intermediate amount of each prey type.

Two points of note arise from this, one of practical relevance for data collectors, and one important for the ecology of the penguin:

1. Data collectors should be aware that diet outcomes from one sampled penguin are not representative of that penguin's diet over a longer period of time. This will be particularly important for ecological studies which link diet composition using data collected over a small time frame, to biological processes which operate over longer periods of time, such as breeding success e.g [445]. Probabilistic models, such as the one developed in Chapter 4, could be useful tools in ecological analyses using temporally limited diet composition data, to assess what the diet composition of predators could be when considered over time scales relevant to the ecological study. Antarctic krill are strong swimmers, and can migrate vertically in the water column [203, 318]. As such, it could be feasible that penguins may not be able to predict the distribution of their prey during a foraging trip from learned information from previous foraging trips. Macaroni penguins commute to the shelf-break to forage, as this is an area of high krill abundance [337]. Provided that, once in this area, they do not have any further information on the location of their prey, and that the effects of individual variation within a population of penguins are small in comparison to the effects on foraging outcomes of the spatial aggregation of prey, then data on diet composition from a sufficiently large number of sampled individuals at one point in time, would also represent the probability distribution function of foraging outcomes for an individual.

2. Of ecological importance, our analysis showed that, over long time scales, prey other than swarming Antarctic krill, such as *Electrona Antarctica* [234], could also be important for penguin foraging success. It is possible that Antarctic krill abundance is going to decrease within the Scotia Sea in response to change in the Scotia Sea habitat, such as ocean warming and a decrease in winter sea-ice [236]. Therefore, it will be important to develop projections of krill and other prey may respond to a changing Scotia Sea, to be able to reliably predict a predator's response to ecosystem changes. It will be particularly important to assess this for other swarming prey of higher predators, such as *Themisto gaudichaudii*, as swarming prey can mean shorter foraging trips, and improved chances of successful foraging.

6.2.2 Sample resolution difficulties

In Chapter 3, I highlighted that the different taxonomic resolutions of prey in diet composition data made it difficult to use these data to draw ecological conclusions about the Scotia Sea. In many food web analyses, species are aggregated into a smaller number of groups, known as trophic species [306, 467] or functional groups. In Chapter 3, I assessed the effects of the resolution of species in food web data on a set of binary and quantitative versions of topological network analyses [157]. I found that the magnitude and direction of biases in network properties to species aggregation was not common amongst properties. Therefore, although some network properties are robust to species aggregation, analysis of the Scotia Sea, and potentially other comparably large ecosystems, using network properties are inhibited due to the inconsistent response of network properties to species aggregation.

In Chapter 4, I examined the taxonomic resolutions of predators and prey in the Scotia Sea data. I resultantly made a set of pragmatic decisions on how to partition these prey between the 42 functional groups used to represent species in the Scotia Sea food web, and detritus. The details for this are given in Chapter 4 and their related appendices. The work in this chapter could provide a valuable, time-saving resource on which to develop further multiple-species analyses of the Scotia Sea.

6.2.3 The importance of scale

In Chapters 3 and 4, I treated the Scotia Sea as temporally static (i.e. I considered interactions as an average over a window of time) and spatially homogenous. In reality, the Scotia Sea is a highly dynamic ecosystem in space and time [320]. For example the pelagic community composition is different in the northern Scotia Sea compared to the southern Scotia Sea [448, 449]. These differences are related to different biological adaptions of species to climatic and physical differences between the regions north, and south of the Antarctic Circumpolar Current Front [440, 448, 449]. Furthermore, land breeding predators are constrained to areas where there is appropriate habitat. For example, Adélie penguins must breed on ice-free land, but rely on sea-ice for foraging [164], and therefore, they are not found on or around South Georgia [222]. Furthermore, within the distributional range of a species, individuals within an area are rarely homogenously distributed as species, such as Antarctic krill, aggregate to breed, to migrate, and for protection against predators [320].

Many network analyses are scale dependent [158, 308] (but see Rossberg et al. (2011) [396]), which is highlighted in Chapter 3. In Chapter 3, I discussed how some network properties for the Scotia Sea and the Southern Ocean could be an artefact of the different distributions of species within the different spatial scales considered. Therefore, it is very important to consider the implications of the spatial scale of the ecosystem under consideration in determining outcomes of food web analyses [315].

As an example of how spatial scale matters in food web analyses, consider the production of macaroni penguins calculated for the Scotia Sea in Chapter 4 (0.008 g m^{-2} y^{-1}), to production for this species in a balanced model of the South Georgia shelf ecosystem (0.020 g m^{-2} y^{-1}) [259]. Macaroni penguins are at a much higher density on the South Georgia shelf compared to other areas of the Scotia Sea as, at South Georgia, their distribution covers the whole ecosystem under consideration [222]. The same is not true when we consider macaroni penguin production at the spatial scale of the Scotia Sea, where their distribution is skewed towards the north [222]. Furthermore, during the breeding season, they are restricted to foraging areas close to their breeding colonies [145, 337].

6.2.4 Important species in the Scotia Sea

The analysis in Chapter 4 assessed which groups could be important in the Scotia Sea food web. Of the zooplankton, model outputs were most sensitive to omnivorous micro and meso zooplankton, salps and gelatinous zooplankton, and Antarctic krill. The importance of krill in Southern Ocean ecosystems is well known, and as such there are copious studies on the ecology of krill, its role in food webs e.g. [202, 235, 320, 428], as well as a recent effort to collate known ecological parameters centred on Antarctic krill to facilitate theoretical models which include Antarctic Krill [264]. As discussed in Chapter 2, much less are known about salps and gelatinous fauna, which are represented in the Scotia Sea data set by just one predator diet sample for a single species, compared to 15 predator diet samples for omnivorous meso and micro zooplankton.

Salpa Thompsoni, has been identified as one of the most abundant metazoan filter feeders in the Southern Ocean [340], and can be an abundant zooplankton in the Scotia Sea [447]. High abundance of salps tends to coincide with low abundance of the cold-adapted Antarctic krill [340]. There is some evidence that salp abundance is increasing in the Southern Ocean, and two proposed mechanisms causing this are a decrease in krill biomass and an increase in sea temperature [132, 340]. Salps and jelly fish could potentially be important prey of pelagic and land-based predators, as shown in Chapter 4 where salps and gelatinous zooplankton were prey for nine out of 40 consumer functional groups in the diet matrix. Consumers of salps and gelatinous zooplankton in the Scotia Sea food web model were two functional groups for flying sea birds, three for fish, and four for zooplankton. However, for all but one functional group, salps constituted <10% of a predator's consumption. The exception was omnivorous macro zooplankton for which 36% of their diet constituted salps.

There is evidence of warming and sea-ice retreat in some areas of the Scotia Sea, which could change the community composition of zooplankton [320] including a potential decrease in the dominance of Antarctic krill [236]. Therefore, the trophic role of salps in the Scotia Sea food web deserves further attention, along with an assessment of how they may respond to a warming Scotia Sea.

6.3 Limitations and further work

6.3.1 Alternate structures of a food web model

The ecosystem model developed in Chapter 4 provided quantitative estimates for production of each functional group representing living organisms in the Scotia Sea. I quantified the effect of uncertainties in two ecological parameters on production estimates for functional groups using a Monte-Carlo based approach. Outputs from food web models can also be sensitive to the number of functional groups used in a model, and to the structure of the trophic interactions between them [313, 359]. Therefore, a food web model should ideally consider various food web structures [261].

In Chapter 4, I considered one alternative structure of trophic interactions formed by heterotrophic bacteria. However, I did not consider other model structures, and this could be viewed as a limitation of this study. Comprehensive consideration of alternate model structures was constrained by a small number of diet samples for some functional groups in the Scotia Sea data set. For example, there was only data for one species of cephalopod as a consumer (see Chapter 2). Where possible I parameterised species diet composition using empirical data collected in the Scotia Sea. Guided by available diet data and expert advice, I defined 42 functional groups describing living organisms and detritus in the Scotia Sea. This is the largest number of functional groups of any Ecopath model constructed for the Southern Ocean [141, 170, 201, 259, 343, 358]. This relatively high resolution means that the Scotia Sea food web may result in smaller error in results due to species aggregation than if species were aggregated to a greater extent.

6.3.2 Other forms of natural variability

In Chapter 5, and as discussed in Section 6.2.1, the temporal scale on which trophic interactions are considered affects how important different prey can appear in the diet of a predator. The food web analyses considered in this thesis do not account for seasonal, e.g. [288, 447], inter-annual, e.g. [235, 452] and longer term e.g. [382, 416] variability in food web dynamics. Simulation-based ecosystem models, such as Ecosim [183] and Atlantis [247], incorporate time dynamics. However, disadvantages of these models compared with static models are that they require a higher number of parameters, and are difficult to analyse and interpret.

In Chapter 5, I showed that swarming prey have a lower energetic cost than non-swarming prey. This could be incorporated into a food web model through a higher growth rate (efficiency by which a predator turns its consumption into its own production) for swarming prey. Sub-models of trophic interactions which incorporate elements of ecosystem dynamics, such as the one developed in Chapter 5, are useful for establishing the general rules as to the response of trophic interactions in food webs to ecosystem variabilities, as well as further details such as potential energetic costs to foraging. Incorporating results from these-sub models into ecosystem models could be more useful than increasing the complexity of a food web model, as a compromise between model complexity and interpretability.

6.3.3 Species based approach

The food web analyses developed in Chapters 3 and 4 are trophic based, which means all individuals of one species are represented together, and so are assumed to have identical trophic interactions. Species-based approaches do not account for variation in diet composition for individuals of different ages, and whose body sizes vary over orders of magnitude over their life span. Size based models are built on allometric feeding relationships [315]. A purely size based approach may not be appropriate for the Scotia Sea and other Southern Ocean ecosystems as: (i) many large-bodied predators such as cetaceans consume Antarctic krill suggesting a major discontinuity in allometric feeding realtionships [315]; and (ii) they are of limited use to manage targeted fisheries as they do not distinguish between species.

An interesting extension of the Scotia Sea food web model may be to incorporate size-structured elements, whilst maintaining species-resolution for commercially important species. Methods such as those used in Ballerini et al. (2014) [141] and Melbourne-Thomas (2013) [311], who used two functional groups for Antarctic krill (juveniles and adults), could be useful in the trophic based Scotia Sea food web model to introduce some size structure for pertinent species including: Antarctic krill and the Patagonian toothfish.

6.4 Concluding remarks

To successfully manage fisheries and to assess how ecosystems may respond to change, we must understand how species within an ecosystem may influence one another. This thesis has built a set of tools and analyses which further our understanding of interacting species in the Scotia Sea. These build on existing food web analyses of sub sets of the Scotia Sea e.g.

[170, 259], and an isotope based study of the Scotia Sea food web [424]. Areas of the Scotia Sea are undergoing warming [320], a loss of winter sea-ice [422], and increasing pressures from commercial fisheries [323]. These pressures are likely to increase, which may alter species composition within the ecosystem [236]. Our analysis contributes quantitative and qualitative analysis of the Scotia Sea food web using data collected over the past six decades. This is an important reference to assess changes in ecosystem structure and function of the Scotia Sea food web as it responds to future, external pressures.

Appendices

A Location references

Table A.1: Table gives the longitudinal and latitudinal coordinates used to estimate the point of data collection where the exact values were not given in the source data. Acronyms are as follows, EI is Elephant Island, SSI is South Shetland Islands, LL are the longitudinal and latitudinal coordinates.

Location	Lattitude	Longditude	Notes
Elephant Island and South Shetland Island	-56.6	-61.6	Average of EI and SSI LL
Elephant Island	-55.1	-61.1	
Gibbs Island, SSI	-55.6	-61.5	
Bird Island, South Georgia	-38.0	-54.0	
O'Brien Island	-56.0	-61.5	
South Orkney Islands	-45.5	-60.6	
Admirality Bay, King George Island	-58.4	-62.1	
Scotia Sea	-40.0	-57.5	
Pearson Point, Bird Island, South Georgia	-38.1	-54.0	
South Shetland Islands	-58.0	-62.0	
Signy Island, South Orkneys	45.6	-60.7	
South Georgia	-36.7	-54.4	
East of South Georgia	-38.2	-54.0	Used Main Island LL
Clarence Island, Chinstrap Cove	-54.2	-61.2	
Clarence Island, Cape Bowles	-54.1	-61.2	Used Clarence Island LL
South Orkney	-45.5	-60.6	
Signy	-45.6	-60.7	
Bird Island	-38.0	-54.0	

B Deriving the Scotia Sea food web matrix

In the aggregation analysis in Chapter 3, we used data from the Scotia Sea data set (see Chapter 2), which described the diets of species-resolved predators and prey only, so that the first Scotia Sea food web matrix contained no pre-aggregated species. The resulting data set consisted of data collected from 88 sources (published or unpublished material) describing 2977 predator diet samples (an individual or group of individuals for which diet composition data were reported). To make fraction occurrence data comparable to fraction by weight and fraction by number data, we normalised fraction occurrence data to sum to unity by dividing each value by the sum of all fraction occurrence values within that predator diet sample. We calculated the diet composition of each predator as follows:

1. First: We collected all predator diet samples relating to a particular predator j;
2. Second: We generated a list of unique prey for consumer j across all predator diet samples;
3. Third: If x_{cj} is the c^{th} predator diet sample for consumer j, with predator sample size ss_c then the proportion of each prey i in predator diet sample x_{cj} was reported by diet fraction, d_{ci}. We calculated a weighted average a_{ij}, weighted by predator sample size, of diet fractions across all predator diet samples for each unique prey i of consumer j according to equation (B.1).

$$a_{ij} = \sum_{c=1}^{C} \frac{ss_c d_{ci}}{\sum_{c=1}^{C} ss_c} \tag{B.1}$$

   where C was the total number of predator diet samples for consumer j, and d_{ci} was the proportion of prey i in the diet of j according to predator diet sample x_{cj}.

   For some sources, authors reported only part of a predator's diet. If x^p_{cj} refers to a predator diet sample with partial diet data and d^p_c refers to the diet fractions reported for predator diet sample x^p_{cj}, then for prey i reported in x^p_{cj}, we calculated a^p_{ij} similarly to equation (B.1). For the remaining prey of j, not in x^p_{cj} we calculated a value $a^{p\prime}_{ij}$ as in equation (B.1) but did not include $x_{cj} = x^p_{cj}$. From this a_{ij} was calculated as follows:

$$a_{ij} = \frac{a^{p\prime}_{ij}}{\sum_i a^{p\prime}_{ij} + \sum_i a^p_{ij}}, \text{ for prey } i \text{ not described in } x^p_{cj} \text{ and} \tag{B.2}$$

$$a_{ij} = \frac{a_{ij}^{p}}{\sum_i a_{ij}^{p\prime} + \sum_i a_{ij}^{p}}, \text{ for all other prey.} \tag{B.3}$$

4. Fourth: We repeated steps one to three for all j and uploaded values into food web matrix A.

C Results from the sensitivity analysis

C.1 SA1: Structural biases of closure groups

We compared how network properties changed in the aggregation analysis described in Chapter 3 for a two closure group scheme compared to a 28 closure group scheme. Figures C.1 and C.2 show the results from the 28 closure group scheme applied to the Scotia Sea food web.

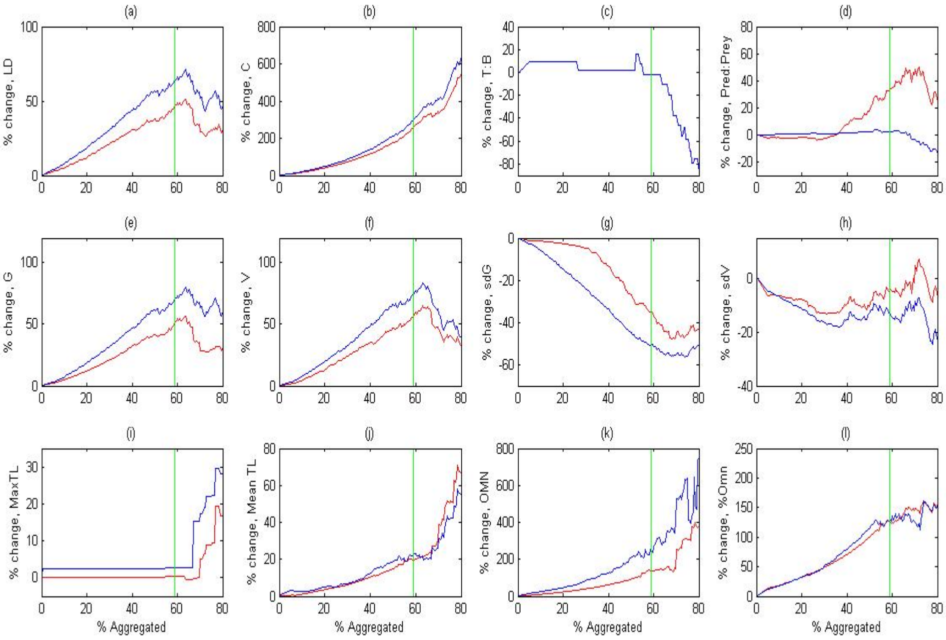

Figure C.1: Percent change in quantitative (red) and binary (blue) network properties from the Scotia Sea food web matrix with the 28 closure group scheme. The green line marks where extra feeding loops were formed. Acronyms for network properties are as in Table 3.1.

C.2 SA2: Using species-resolved data only, from the Scotia Sea data set

We ran the species aggregation analysis described in Chapter 3 for the Scotia Sea food web matrix where all data relating to prey not resolved to species level were included in one of 15 groups describing a species type. Figures C.3 and C.4 show the results of the aggregation analysis applied to this food web matrix.

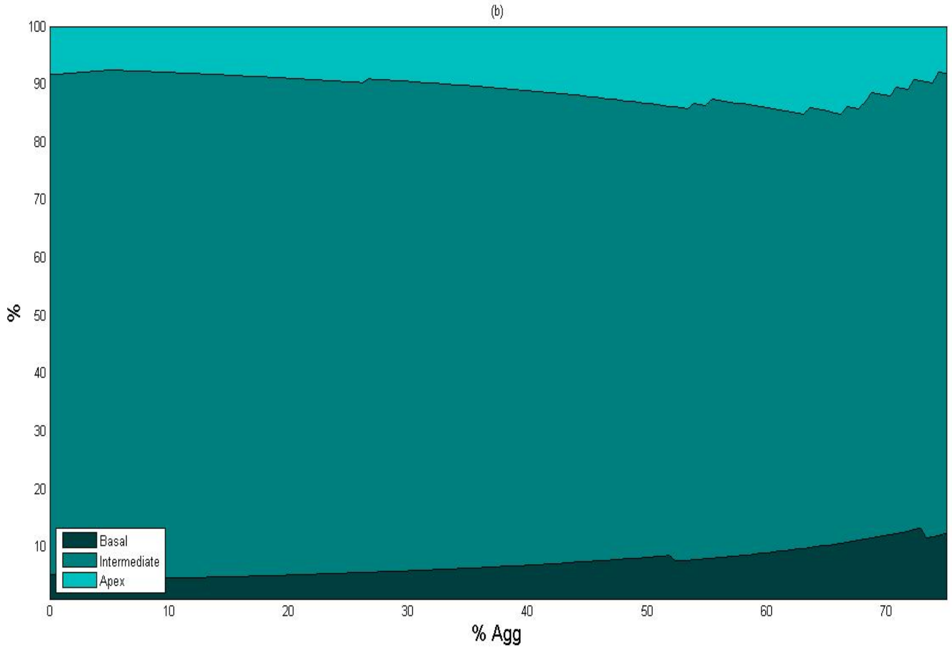

Figure C.2: The proportion of the system which are top, intermediate and basal predators at each aggregation step for the Scotia Sea food web matrix with the 28 closure group scheme applied.

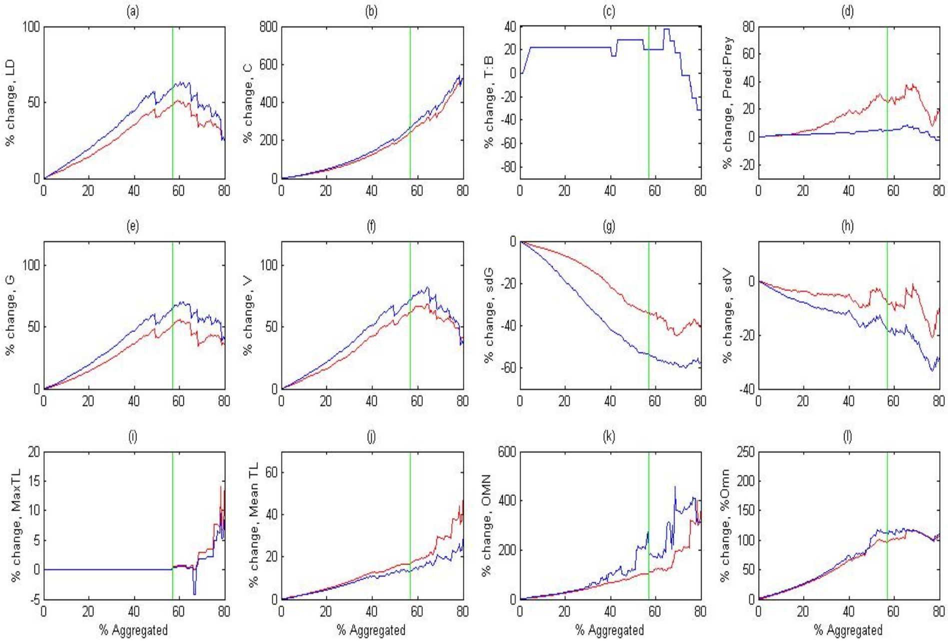

Figure C.3: Percent change in quantitative (red) and binary (blue) network properties from the Scotia Sea food web matrix with closure groups where non-species-resolved taxa were included in one of 15 prey categories. The green line marks where extra feeding loops were formed. Acronyms for network properties are as in Table 3.1.

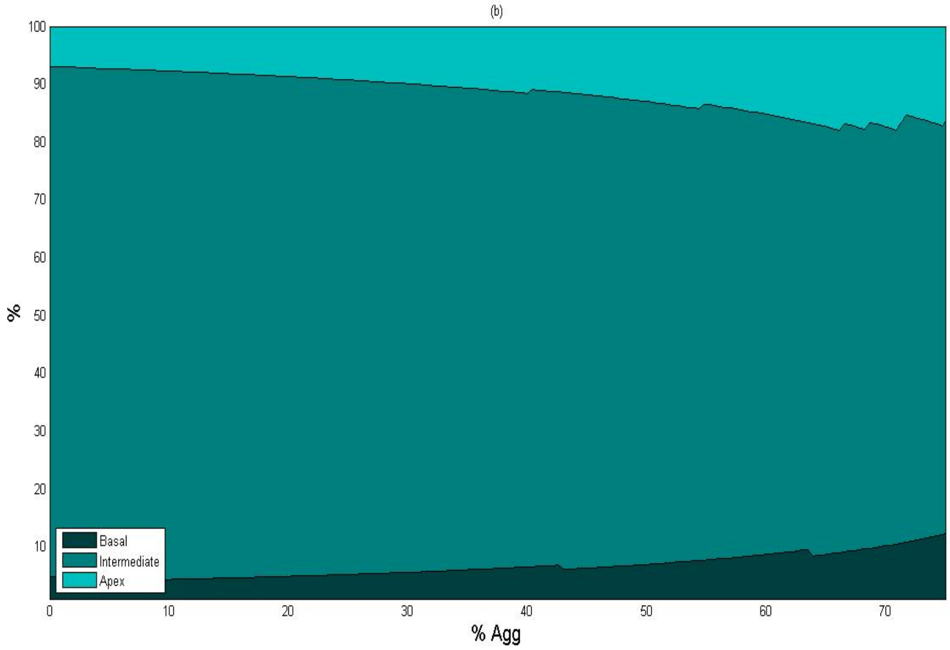

Figure C.4: The proportion of the system which are top, intermediate and basal predators at each aggregation step for the Scotia Sea food web matrix with closure groups where non-species-resolved prey were included in one of 15 prey categories.

D Example application of closure groups (methods)

We applied closure groups and recalculated binary topological properties (see Chapter 3) for the Southern Ocean food web matrix reported in a published comparison of high latitude food webs [401]. Using expert advice, we defined apex predators to be species of flying sea bird and leopard seals. As such, closure predators were set to consume all but apex species which did not have a predator according to the Southern Ocean food web matrix. A species was set to consume the closure prey group if they had no data on their diet composition, and were not primary producers. The raw diet composition data for each predator diet sample in the Antarctic food web was available as a published data set [370]. We used these data to derive a binary food matrix model for the Antarctic marine food web using methods described in the published polar comparison study [401].

E Deriving the diet matrix

Where possible, we defined the proportional composition of the functional groups used to model the Scotia Sea food web, using data from the Scotia Sea data set. To process the Scotia Sea data set using the diet algorithm, it was necessary to assign each predator and prey to a functional group (see Chapter 4 for a full explanation of the diet algorithm). Below we provide an explanation of the process we used to assign predator and prey to a functional group, and how we partitioned diet composition for flag groups amongst the relevant functional groups.

E.1 Chromista

We partitioned the 38 prey in the kingdom Chromista between heterotrophic bacteria and chromista (FG 612) or the primary producer (FG 701) functional groups; the exception to this was Ctenophora which was assigned to salps and gelatinous zooplankton (FG 603). We primarily referred to 'Biology' [369] and the online resource, the Encyclopaedia of Life, [344] to find the relevant ecological information to partition each taxa to a group. If prey contained chloroplasts, but we found no information specifying whether they were mixotrophic or photoautotrophic, then we assumed the prey were primary producers (FG 701). If we found no relevant information, then we assumed prey were heterotrophic bacteria and chromista. See Table E.1 for a list of chromista prey and the functional groups they were assigned to.

Table E.1: Chromista prey found in the Scotia Sea data set and the functional groups they were assigned to.

Chromista prey	FG	Explanation	Reference
Bacillariophyceae	701	Diatoms, member of the phylum Chrystophyta, are photosynthetic, unicellular organisms with unique double shells made of opaline silica.	[369, p. 569-573]
Thalassiosira	701	Same as above.	Same as above.
Chaetoceros	701	Same as above.	Same as above.
Nitzschia	701	Same as above.	Same as above.
Rhizosolenia	701	Same as above.	Same as above.
Guinardia striata	701	Same as above.	Same as above.
Chaetoceros decipiens	701	Same as above.	Same as above.
Pseudo-nitzschia	701	Same as above.	Same as above.
Pleurosigma	701	Same as above.	Same as above.
Grammatophora	701	Same as above.	Same as above.
Distephanus speculum	701	Same as above.	Same as above.
Hemiaulus hauckii	701	Same as above.	Same as above.
Fragilariopsis kerguelensis	701	Same as above.	Same as above.
Nitzschia bicapitata	701	Same as above.	Same as above.

Chaetoceros messanense	701	Same as above.	Same as above.
Heliozoa	612	We found no information on trophic dependence; Assume heterotrophs.	[16]
Acanthochiasma	612	Same as above.	[33]
Radiozoa	612	Same as above.	[28]
Ptychodiscus noctiluca	612	We found no detail on trophic dependence for Ptychodiscus. Ptychodiscus are in order Gymnodiniales which are heterotrophic and photoautrophic; Assume heterotrophic.	[14]
Dictyochophyceae	701	No trophic information. Many known to contain chloroplasts. Assume autotrophic.	[12]
Dictyochales	701	We found no information on the trophic dependence of Dictyochales. They are in the class: dictyochophyceae, many species of which are known to contain chloroplasts. Assume autotrophic.	[12]
Ciliophora	612	Ciliates are hetertrophic unicellular protists.	[369, p. 569-573]
Tintinnopsis acuminata	612	Same as above.	Same as above.
Stenosemella	612	Same as above.	Same as above.
Tintinnidae	612	Same as above.	Same as above.

Rhabdonella amor	612	Same as above.	Same as above.
Tintinnina	612	Same as above.	Same as above.
Foraminifera	612	Members of the phylum foraminifera are heterotrophic marine protists.	[369, p. 576-578]
Dinophyceae	612	Trophic dependence: heterotrophic and autotrophic. Assume heterotrophic.	[52]
Amphisolenia	612	Amphisolenia are heterotrophic.	[6]
Dinophysis	612	Dinophysis are heterotrophic.	[227]
Amphidinium	612	Amphidinium are heterotrophic and photoautotrophic; Assume heterotrophic.	[5]
Ceratium	701	Ceratium are photoautotrophic.	[226]
Peridinium	701	Peridinium are photoautotrophic.	[24]
Prorocentrum	612	Prorocentrum are mixotrophic and photoautotrophic; Assume heterotrophic.	[27]
Phaeophyceae	701	Multicellular algae, kelp.	[369, p. 573-576]
Ctenophora	603	Gelatinous animals ranging from 2mm-2m long. In the Scotia Sea data set they are eaten by fish predators (up to 50cm long) assign to 603.	[10]

Himantothallus	701	Genus of brown algae which is multicellular: kelp.	[369, p. 573-576]

E.2 Zooplankton and benthos

Zooplankton and benthos were assigned to a functional group using data on their habitat (benthic or pelagic), diet (carnivorous, omnivorous, or herbivorous) and, for zooplankton, on their size (micro and meso <six mm, macro: >six mm). Where available, we used information from the Scotia Sea data set to provide insight into a species' diet, but for prey which did not feature as a predator in the Scotia Sea data set, we referred to online resources and published literature. For benthic and zooplankton prey resolved to genus-level, if we were able to find the previously mentioned data for one, or a subset, of species within the genus, we inferred information from these species to the genus, to assign it to a functional group. Where possible, we used the most abundant species in the genus to represent the genus.

For prey less well taxonomically resolved, we used the Register of Antarctic Marine Species (RAMS) [3] to generate a list of species which a prey could refer to. We then used published resources to assess whether all pertinent species related to one pelagic or benthic functional group. If all Antarctic species which could relate to a poorly-taxonomically resolved prey were pelagic, and the size of species in this group fall into macro, or all into the meso and micro-zooplankton category, but information on feeding types were not available or spanned more than one functional group (e.g. omnivorous and carnivorous), we assumed meso and macro-zooplankton species were omnivorous (FG 609 and FG 610) and micro (<6 mm) were herbivorous (FG 611). If all Antarctic species within the taxonomic label of a prey group were benthic and their sizes were similar, but information on species diet composition was not found, we assumed macro and meso benthos were carnivorous, omnivorous, and detritivorous benthos (FG 602), and micro benthos were herbivorous benthos (FG 601).

We assigned prey which included species which could be pelagic or benthic to a flag-benthos and zooplankton functional group with identifier -88, and then distributed the proportion of predator diets which composed this prey group between FG 601-611 according to the proportional contribution of these as suggested by prey which we were able to assign to a functional group. For full information on the proportion of flag-benthos and zooplankton prey in the diets of each functional group, and how they were redistributed amongst benthos and zooplankton-related functional groups, see Table E.3. An additional flag-krill group with identifier -44 was used for krill prey which could refer to Antarctic krill or other krill species. We split the proportional contribution of this flag-krill equally between Antarctic krill (FG 604) and other krill (FG 606). These were treated differently to other poorly resolved zooplankton prey due to the high number of instances of prey labelled as krill in the Scotia Sea data set, and due to the importance of Antarctic krill in the Scotia Sea [320]. There were a few instances where identified prey were non-Antarctic species. We labelled such data with the identifier -101 and subsequently deleted it as it was not pertient to the analysis of the Scotia Sea.

E.3 Fish

Fish species were partitioned into functional groups using a combination of information on their habitat (pelagic or demersal), diet (mostly benthos or mixed diets), and depth range (shallow: typically found at depths <200m, or deep: typically found at depths >200m). We used the Scotia Sea data set for information on the diets of some fish, otherwise we consulted FishBase [245]. We also used FishBase for information on the depth and habitat of fish species. Where a range of depths was provided we took an arithmetic mean of its boundaries. We assigned prey resolved to genus-level, to the same functional group as all, or a representative species within that genus. Where possible this was the most abundant species within that genus found in the Scotia Sea. We also assigned prey resolved lower than genus level to a functional group if all Antarctic species represented in this taxonomic group could be assigned to the same functional group. We assigned all other poorly taxonomically resolved prey which we were unable to assign to a functional group using the above methods, to a flag-fish functional group with identifier -99 (see Table E.4). Flag-fish prey were then reassigned amongst fish functional groups (FG 401-409) according to the proportional contribution of fish functional groups calculated from data where prey were assigned to a functional group. For full information of how the proportional contribution of flag-fish prey were redistributed amongst fish functional groups (see Table E.5).

E.4 Higher predators

There were 43 references to higher predators (marine mammals and sea birds) in the Scotia Sea data set. Most (35 taxa, 81%) were resolved to species or genus level and were easily assigned to a functional group based on their taxonomy. There was one predator diet sample available for emperor penguins, however emperor penguins occur only rarely in the Scotia Sea and do not breed there, therefore we did not include them in our model. Based on expert advice (pers. comm. Richard Phillips), we assigned prey labelled as the family: *diomedeidae* (albatross) to ‘other albatross’ (FG 302), as wandering albatross are apex predators and unlikely to be prey of other predators. We assumed poorly resolved seal prey were carrion and therefore assigned them to the detritus (FG 702).

Three taxonomically vague penguin prey were assigned to a flag-penguin functional group, with identifier -66. We found that 0.04 of a leopard seals diet were flag-penguins and redistributed this at a ratio of 0.33:0.02:0.06:0.41:0.18 between FG 201-205 respectively, according to the relative abundance estimates of breeding individuals of these species in the Scotia Sea [164, Gentoo, macaroni, king and chinstrap penguins][197, 363, Adélie penguins]. We used the same methods to redistribute the 0.04 of the Antarctic fur seals diets and the 0.20 of the Weddell seal diets which were flag-penguins.

Table E.2: Zooplankton and benthos prey found in the Scotia Sea data set and the functional groups they were assigned to.

Zooplankton and benthic prey	FG	Explanation	Reference
Crustacea	-88	Broad taxonomic group which encompasses benthic and pelagic species.	
Ostracoda	-88	Same as above.	
Copepoda	-88	Same as above.	
Eumalacostraca	-88	Same as above.	
Peracarida	-88	Same as above.	
Calanoida	-88	Same as above.	
Cyclopoida	-88	Same as above.	
Harpacticoida	-88	Same as above.	
Decapoda	-88	Same as above.	
Isopoda	-88	Same as above.	
Amphipoda	-88	Same as above.	
Hyperiidea	-88	Same as above.	
Gammaridea	-88	Same as above.	

Epimeriidae	-88	Family of amphipods. No conclusive information found on whether species in family are benthic or pelagic.	[255]
Eusiridae	-88	Same as above.	[57]
Lysianassidae	-88	Same as above.	[83]
Synopiidae	-88	Same as above.	[119]
Spionidae	-88	Family in class polychaeta. Unable to find diet information. Assume same as polychaeta: flagged benthos and zooplankton.	[369, p. 660-663]
Cirratulidae	-88	Same as above.	Same as above
Maldanidae	-88	Same as above.	Same as above
Ampharetidae	-88	Same as above.	Same as above
Trichobranchidae	-88	Same as above.	Same as above
Pelagobia	-88	Same as above.	Same as above
Animalia	-88	One predator for this prey which is a copeopod. All other prey are zooplankton species. Set as flagged zooplankton.	
Mollusca	-88	Phylum includes cephalopods as well as benthic species such as bivalves. Set as flagged zooplankton.	

Nematoda	-88	Can be hunters and parasites, pelagic and benthic.	[369, p. 648-650]
Annelida	-88	Assuming prey are polychaetes (rather than leeches): polychaetes can be filter feeders and active predators. Some are gutless and can culture sulphur-oxidising bacteria. Some live in burrows or tubes in the hardened mud and others are active swimmers.	[369, p. 660-663]
Polychaeta	-88	Polychaetes can be filter feeders and active predators and some are gutless and can culture sulfer-oxidising bacteria. Some live in burrows or tubes in the hardened mud and others are active swimmers.	[369, p. 660-663]
Sipuncula	-88	Peanut worms diet. Diet composition not known.	
Hydrozoa	-88	The class Hydrozoa includes species of omnivores, predators and scavengers. In phylum Cnidaria which can benthic and pelagic.	[369, p. 640-644] [413]
Echinodermata	-88	Echinodermata include species of sea cucumbers, sea lilies, sea stars, brittle stars which are benthic.	

Hydroidolina	-88	Subclass within order, hydrozoa. No information on diet composition or habitat found. Treat similarly to hydrozoa.	[369, p. 640-644] [413]
Oedicerotidae	-88		[98]
Joubinella	-88	Genus of amphipod. No conclusive information found on haitat or diet composition.	
Dendrobranchiata	-88	Broad suborder of decapods which could include pelagic and benthic species.	
Mysidae	-88	Species in family include multiple sizes and feeding types.	
Mysida	-88	Omnivorous suspension feeders which can be pelagic or benthic. Body length 2-80mm.	[22]
Nemertea	-88	Contains benthic and pelagic species.	
Conchoeciinae	-88	Genus in family Halocyprididae. No information found on diet composition of if species within group are benthic or pelagic. Halocyprididae are carnivorous.	[15]
Zygomaera pfefferi	-88	No information found on the habitat or diet composition of species.	

Tiron antarcticus	-88	No information found on whether species is benthic or pelagic.	
Pseudericthonius gaussi	-88	No information found on whether species is benthic or pelagic.	
Chosroes decoratus	-88	Unable to find information on habitat or diet composition.	
Insecta	-101	Purely terrestrial species.	
Limnoria	-101	Does no feature in Register of Antarctic Marine Species. Assume prey out of Scotia Sea ecosystem.	
Euphausiacea	-44	Includes Antarctic krill and other krill species.	
Euphausiidae	-44	Family of krill: to be split between Antarctic krill and 'other krill' functional groups.	
Euphausia	-44	Genus of krill: to be split between Antarctic krill and 'other krill' functional groups.	
Polyplacophora	601	Most chitons are grazing herbivores that live in shallow marine habitats, but some live at depths of more than 7000m.	[369, p. 654-660]

Cirripedia	601	Barnacles and suspension feeders. Benthic. Unsure of diet compos. (particulate). Assume herbivores.	
Ascidiacea	601	*Ascidiacea* are benthic as adults. Cilia trap microscopic food particles. Assume herbivores.	[369, p. 682-683]
Oradarea	601	Information found for two species in genus, which are benthic macro herbivores. Assume these are representative of genus.	[330]
Bryozoa	601	Usually <0.5mm and live in patches on rocks, seaweed etc. Assume herbivorous benthos.	[369, p. 664-665]
Ampelisca richardsoni	601	Benthic and consumes mainly diatoms.	[329, ch.4]
Scaphopoda	602	Scaphopods include deposit feeders, omnivores, predators and scavengers.	[407]
Bivalvia	602	Most bivalves are filter feeders that live cemented to the substrate or live buried in the sediment. They extract small organisms from the water that passes through their mantle cavity.	[369, p. 654-660]

Porifera	602	'Sponges beat flagella from the coanocytes that line the inside of the sponge which draws water in through numerous small pores. Plankton and other small organisms are filtered from the water which flows through passageways.'	[369, p. 638-639]
Tanaidacea	602	Benthic. Some species are predators and detrivores whilst others are suspension feeders.	[31]
Cumacea	602	Hooded shrimps are benthic species. Feeding types unknown. Assume carnivorous benthos.	[11, 367]
Echiura	602	Benthic. Most detrital feeders. Assume carnivorous benthos.	[13]
Ampelisca	602	Species in genus are benthic. No conclusive information found their diet composition. Assume carnivorous.	[173]
Haploops	602	Genus of benthic amphipod. Includes species which can reach 22mm in size. No conclusive information found on the diet composition of species in genus. Assume carnivorous and omnivorous.	[219]

Gammaropsis	602	No conclusive information found on habitat or diet composition. Other species in genotype in Scotia Sea data set are benthic. Assume carnivorous benthos.	[59, 173]
Monoculodes	602	Information found on species in genus *M. Antarcticus* which are benthic macro fauna. No conclusive information found on their diet composition. Assume carnivorous.	[21, 89].
Oediceroides	602	Information found on subset of species in genus which are listed as macro benthos. No conclusive information found on their diet composition. Assume carnivorous benthos.	[23, 173]
Lithodidae	602	King crabs. Carnivorous macrobenthos	[20]
Echiuroidea	602	Echiuroidea are a class in the phylum Echiura. Class consists of benthic species. Echiura are mostly detitus feeders. Assume carnivrous benthos.	[13]
Munnidae	602	There were 12 species in the family munnidae according to a survey of deep Antarctic benthos. Unable to find data on their diet composition so assume carnivrous benthos.	[168, 169]

Serolidae	602	At least some species in this family are large zoobenthos. No information found on diet composition, assume carnivorous benthos.	[30]
Natatolana	602	Natatolana are in family ciroanidae which are carnivorous benthos.	[9]
Asteroidea	602	Class of benthic species including sea stars and sea daisies. Feeding types: omnivore predator scavenger suspension feeder.	[7]
Cidaroida	602	Benthic sea urchins and sand dollars. Includes species which feed on algae and encrusting animals. Some catch suspended particles. Assume carnivorous benthos.	[277]
Glyptonotus	602	Carnivorous, omnivorous, and detritivorous benthos.	[62]
Serolis	602	Omnivorous bethnos.	[185]
Metopoides	602	Benthic. No data found on diet composition. Assume carnivorous.	[173]
Paraceradocus	602	Benthic detritovores.	[189]

Cephalophoxoides	602	*C. kerguieleni* is the only Antarctic species in this genus and is benthic. We found no information on their diet composition but family, *phoxocephalidae* is carnivorous.	[25, 8]
Oediceroides lahillei	602	Benthic. No data found on diet composition. Assume carnivorous.	[173]
Gammaropsis (Gammaropsis) triodon	602	Species are macrozooplankton. Many species in the same genus are benthic. Assume carnivorous benthos.	[173, 60]
Podocerus capillimanus	602	Species is benthic. No information found on its diet composition. Assume carnivorous benthos.	[26]
Uristes gigas	602	Species is benthic and the family carnivorous are carnivorous.	[173, 32]
Rhachotropis schellenbergi	602	*Rhachotropis* are a genus in the family *Eusiridae*. *Rhachotropis* are benthic but are strong swimmers which indicates they may be partially pelagic. Diet of *Eusiridae* is carnivorous. Assume carnivorous benthos.	[298, 57]
Rhachotropis antarctica	602	Same as above.	Same as above

Notocrangon	602	Carnivorous and omnivorous benthos as determined from specimens collected in the Scotia Sea.	[423]
Notocrangon antarcticus	602	Same as above.	Same as above
Crangon (Notocrangon)	602	Same as above.	Same as above
Chorismus antarcticus	602	Benthic and carnivorous shrimp species.	[49, 368]
Siphonophorae	603	In the class *hydrozoa*, and treated similarly.	[369, p. 640-644] [413]
Appendicularia	603		
Scyphozoa	603		
Salpida	603	Salps	
Salpidae	603	Family of salp.	
Salpa	603	Genus of salp.	
Tunicata	603		
Cibacapsa gulosa	603		
Salpa thompsoni	603		
Euphausia superba	604	Antarctic krill.	
Themisto	605	Assume genus represents species *T. gaudichaudii*, which is the most abundant in the Southern Ocean. Note: there are two other species in this genus which are present in the Antarctic.	[341, 469]

Euphausia crystallorophias	606	Species of krill.	
Euphausia frigida	606	Species of krill.	
Thysanoessa macrura	606	Species of krill.	
Thysanoessa	606	Genus of krill which does not include Antarctic krill.	
Euphausia vallentini	606	Species of krill.	
Euphausia triacantha	606	Species of krill.	
Cyphocaris	607	Species in genus: *C. challengeri* are carnivorous macrozooplankton. Genus C. has mostly carnivorous diet. Assume carnivrous macrozooplantkon.	[51, 256]
Hyperia	607	Information found for two species in genus, *H.Galba* and *H. macrocephala* which are parasitic and carnivorous macrozooplankton, respectively. There are two other species in the Antarctic which are macrozooplankton but we found no conclusive information about their diet composition. Assume genus are carnivrous macrozooplankton.	[282, p.118] [17, 18]

Hyperoche	607	Data found for species in genus *Hyperoche medusarum.* Macrozooplankton which are parasitic on gelatinous organisms. Assume carnvirous zooplankton.	[19, 178]
Euchaetidae	607	Antarctic species in this family are from the genus *Euchaeta and Paraeuchaeta* which are predatory macro zooplankton.	[334]
Euchaeta	607	Predatory macrozooplankton.	[334]
Pasiphaea	607	Assume genus is represented by *P. Scotiae* which are carnivorous macrozooplankton.	[105, 106]
Pasiphaea scotiae	607	Pelagic, carnivorous macrozooplankton (decapod).	[105, 106]
Heterorhabdus	608	Carnivorous (as suggested by Scotia Sea data set for species *H. austrinus* mesozooplankton (<4mm).	[324]
Gnathophausia	608	Assume genus is represented by species *G. gigas* which are macrozooplankton. Could not find information on their diet composition so assume omnivorous.	[63, 64]
Gnathophausia gigas	608	Macrozooplankton. Could not find information on their diet composition so assume omnivorous.	[63, 64]

Vibilia	609	Information found for two species in genus, *V. Antarctica* which are particle grazers and *V. sttebbinigi* which are omnivorous. Form symbiotic relationship with salps. Assume omnivorous.	[352], Scotia Sea data set.
Gennadas	609	These is one species in genus, present in the Antarctic which is *G. Kempi* which is a macrozooplankton. Unable to find data on their diet composition. Assume omniorous.	[61]
Drepanopus forcipatus	609	Macrozooplankton (>100mm). Data on diet composition not found.	[371]
Aetideidae	610	Species could feed on diatoms or organisms in the kingdom *Animalia*. Assume omnivorous.	[34]
Calanidae	610	Family of pelagic copepods contains calanoides (herivores) and copepods which are omnivorous or carnivorous. Assume omnivrous.	[43]
Gaetanus	610	Species in genus, *G. tenuispinus* is omnivorous according to data in the SS data set	
Haloptilus	610	Pelagic meso and microzooplankton. Species in genus can consume animals and protists.	[75]

Microcalanus	610	Two species in genus are in the Antarctic which are both mesozooplankton. *M. pygmaeus* are likely to be omnivorous; no information found on the diet of *M. pusillus*. Assume genus is omnivorous.	[372]
Eucalanus	610	Found data for species *S. longiceps* in genus which is a herbivorous zooplankton.	[374]
Metridia	610	Found data for species *M. gerlachi* in genus which is omnivorous (according to the Scotia Sea data set) and are mesozooplankton (up to 2.5mm).	[470]
Pleuromamma	610	Species *P. robusta* in genus are omnivorous (according to the Scotia Sea data set) mesozooplankton (<3 mm).	[373]
Scaphocalanus	610	Information found for species *S. farrani* which are omivorous (according to the Scotia Sea data set) meso and micro zooplankton. on *S. farrani*).	[376]
Scolecithricella	610	Information found for species *S. dentate* in genus suggests they are meso/microzooplankton. The Scotia Sea data set suggests species *S. cenotelis* is omnivorous.	[375]

Haloptilus oxycephalus	610	Assume information is the same *H. ocellatus* which is omnivorous according to SS data set.	
Oithona	610	*Oithona* are pelagic copepods which can feed on heterotrophic protists and detritus. Assume omnivorous.	[437]
Oncaea	610	Omnivrorous meso zooplankton.	[314]
Calanoides	611	Assume genus is represented by species *C. acutus* which is a herbivorous zooplankton.	[410]
Candacia	611	Data for non-Antarctic species *C. bipinnata* in genus suggests it is omnivorous. Assume similar for Antarctic species.	[332]
Clausocalanus	611	Species *C. lividus* in genus consumes dinoflagelletes and algae according to a study in the Weddell Sea. Assume herbivorous.	[276]
Ctenocalanus	611	Species *C. citer*, which is dominant within genus is predominantly herbivorous.	[345]
Drepanopus	611	Based on species *D. forcipatus* in genus which is a mesozooplankton consuming mainly dinoflagelettes. Assume herbivorous zooplankton.	[130]

Halacaroidea	611	Marine mite, but no information found in diet composition. Assume herbivorous microplankton.	

Table E.3: The proportion of a functional groups diet assigned to the flag benthos and zooplankton groups (column 2) for each predator (column 1). Subsequent columns indicate how this was distributed amongst benthic and zooplankton functional groups

FG	Prop.	601	602	603	604	605	606	607	608	609	610	611
103	0.00	0.00	0.00		0.99							
201	0.02				1.00							
202	0.02				0.98	0.02						
203	0.00				1.00							
204	0.11				0.76	0.24						
301	0.01			0.34		0.34		0.31				
302	0.02				1.00							
303	0.02				1.00							
305	0.04			0.04	0.60	0.11	0.01	0.09			0.01	0.14
304	0.25				1.00							
401	0.13		0.03	0.03	0.21	0.18	0.26	0.03			0.14	0.12
402	0.90		0.77		0.23							
403	0.02		0.13		0.87							
404	0.74		0.13		0.87							
405	0.56		0.16	0.03	0.70	0.05	0.05			0.01		
407	0.53		0.25	0.09	0.63	0.03						
409	0.02		0.71		0.29							
501	0.04		0.05		0.84	0.11						

Table E.4: Fish species in the Scotia Sea data set and the functional groups they were assigned to.

Name	FG	Details	Reference
Macrouridae (family)	-99	Broad taxonomic group	
Zoarcidae (family)	-99	Broad taxonomic group	
Macrourus (genus)	-99	Broad taxonomic group	
Vertebrata (subphylum)	-99	Broad taxonomic group	
Nototheniidae (family)	-99	Broad taxonomic group	
Notothenioidei (suborder)	-99	Broad taxonomic group	
Channichthyidae (family)	-99	Broad taxonomic group	
Notothenia (genus)	-99	Broad taxonomic group	
Chionodraco (genus)	-99	Broad taxonomic group	
Fish	-99	Broad taxonomic group	
Myctophidae	401	*Myctophidae* (family). All species of myctophid in the Scotia Sea data set are pelagic. Assume family is pelagic.	
Diaphus	401	Genus of myctophid.	
Electrona	401	Genus of myctophid.	
Protomyctophum	401	Genus of myctophid.	

Bathylagus	401	All Antarctic species in the genus, *Bathylagus* are all bathypelagic.	[137, 245]
Pseudoscopelus	401	One Antarctic species in genus, *Pseudoscopelus* according to RAMS, which is bathypelagic.	[139]
Arctozenus risso	401	Bathypelagic.	[37]
Antimora rostrata	401	Bathypelagic.	[36]
Borostomias antarcticus	401	Bathypelagic.	[42]
Gymnoscopelus	401	The dominant species (*G. braueri, G. nicholsi* and *G. fraseri*, are bathypelagic).	[406]
Sardinops sagax	401	Pelagic.	[29]
Electrona antarctica	401	Pelagic.	[54]
Lampanyctus achirus	401	Pelagic.	[92]
Magnisudis prionosa	401	Bathypelagic.	[86]
Bathylagus antarcticus	401	Bathypelagic.	[41]
Electrona carlsbergi	401	Bathypelagic.	[55]
Krefftichthys anderssoni	401	Bathypelagic.	[79]
Gymnoscopelus braueri	401	Bathypelagic.	[69]
Paranotothenia magellanica	401	Pelagic, oceanic. Found at depths of 0-255m.	[104]
Nansenia antarctica	401	Bathypelagic. Found at depths of 0-4145m.	[93]
Gymnoscopelus hintonoides	401	Bathpelagic. Found at depths of 2200-2350m.	[71]

Gymnoscopelus fraseri	401	Pelagic.	[70]
Protomyctophum choriodon	401	Bathypelagic.	[111]
Sio nordenskjoldii	401	Bathypelagic. Found at depths of 2000-3000m.	[118]
Notolepis coatsi	401	Bathypelagic. Found at depths of 0-2000m.	[94]
Protomyctophum bolini	401	Bathypelagic.	[110]
Gymnoscopelus microlampas	401	Bathypelagic.	[72]
Pleuragramma antarcticum	401	Pelagic, oceanic. Found at depths of 0-728m.	[108]
Protomyctophum normani	401	High oceanic and mesopelagic. Found in the upper 104m at night.	[112]
Gymnoscopelus bolini	401	Mesopelagic, oceanic.	[68]
Gymnoscopelus opisthopterus	401	Bathypelagic.	[74]
Protomyctophum tenisoni	401	Pelagic.	[114]
Electrona subaspera	401	Bathypelagic.	[56]
Gymnoscopelus nicholsi	401	Bathypelagic.	[73]
Anotopterus vorax	401	Bathypelagic found at depths of 0-2579m.	[35]
Protomyctophum parallelum	401	Bathypelagic found at depths of 2500m.	[113]
Pseudoicichthys australis	401	Oceanic, pelagic found at depths of 0-2141m.	[116]
Harpagifer (based on H. bispinis)	402	Depth: 40-50m.	[77]
Gobionotothen marionensis	402	Depth: 100-150m. Diet: zoobenthos.	[67]

Trematomus bernacchii	402	Usually found at depths 0-200m. Diet: mainly zoobenthos.	[120]
Harpagifer antarcticus	402	Depth: 0-5m. Diet: zoobenthos.	[76]
Amblyraja georgiana	403		
Liparidae	404		
Notothenia coriiceps	404	Depth: 0-550m.	[95]
Artedidraco skottsbergi	404	Depth: 5-666m.	[39]
Pogonophryne scotti	404	Depth: 100 - 1180m.	[109]
Harpagifer georgianus	405	Mainly littoral but has been reported to occur as deep as 90m.	[78]
Artedidraco mirus	405	Depth: 8-320m.	[38]
Trematomus newnesi	405	Depth: 0-400m.	[123]
Champsocephalus esox	405	Depth: 50-250m.	[46]
Parachaenichthys georgianus	405	Depth: 5-270m.	[102]
Patagonotothen guntheri	405	Depth: 30-160m.	[107]
Notothenia rossii	405	Depth: 5-350m.	[96]
Gobionotothen angustifrons	405	Depth: 0-110m.	[65]
Champsocephalus gunnari	406		
Trematomus scotti	407	Depth: 20-793m. Diet mixed.	[124]
Parachaenichthys charcoti	407	Depth: 5-400m.	[101]

Psilodraco breviceps	407	Usually found at depths of 248-345m.	[117]
Trematomus eulepidotus	407	Depth: 70-650m.	[121]
Lindbergichthys nudifrons	407	Depth: 3-400m.	[82]
Gobionotothen gibberifrons	407	Depth: 6-429m.	[66]
Lepidonotothen squamifrons	407	Usually found at depths of 195-312m.	[81]
Lepidonotothen larseni	407	Depth: 30-750m.	[80]
Pseudochaenichthys georgianus	407	Depth: 0-475m.	[115]
Cryodraco antarcticus	407	Depth: 90-600m.	[50]
Chaenocephalus aceratus	407	Depth: 5-770m.	[44]
Muraenolepis microps	407	Depth: 10-1600m.	[91]
Trematomus hansoni	407	Depth: 6-549m.	[122]
Dissostichus mawsoni	407	Ussually found at depths of 88-1600m.	[53]
Lycenchelys	407	Depth for all Antarctic species in genus (according to occur at depths greater than 200m. No diet data. No data provided on diet composition so assume mixed.	[138]
Slender escolar	407	Depth: 368-626m. Consumes ‘nekton’.	[103]
Muraenolepis	407	Depth: 0-1600m. Based diet on *M. microps* in Scotia Sea data set.	[90]
Pagetopsis	407	Two species Depths 5-655m and 200-800m. Diet of *P. macropterus* zooplankton.	[99, 100]

Nototheniops nybelini	407	Depth: 90-400m. No data on diet. Assume mixed.	[97]
Bathydraco joannae	407	Depth: 600-1800m. No data on diet, assume mixed.	[40]
Macrourus whitsoni	407	Depth: 400-3185m. Diet: zoobenthos and plankton,	[85]
Chaenodraco wilsoni	407	Depth: 200-800m. Diet: zooplankton.	[45]
Channichthys rhinoceratus	407	Depth: 1-750m. Consumes plants and other fish.	[47]
Chionodraco rastrospinosus	407	Usually found at depths: 200-400m. Diet: mainly fish and krill.	[48]
Micromesistius australis	407	Usually found at depths: 200-400m. Diet: mainly cephalopods, small fish and copepods.	[87]
Macrourus holotrachys	407	Depth: 300-1400m. Diet includes fish, benthic and pelagic crustaceans. Assume diet is mixed.	[84]
Lampreys	408		
Geotria australis (pouched lamprey)	408		
Dissostichus eleginoides	409		

Table E.5: The proportion of a functional groups diet assigned to the flag fish group (column 2) for each predator (column 1). Subsequent columns indicate how this was distributed amongst fish functional groups.

FG	Proportion	401	402	403	404	405	406	407	408
101	0.05	1							
102	0.28	0.7				0	0.1	0.19	
201	0.00	0.94			0.06				
202	0.46					0.02	0.79	0.18	
203	0.01	1							
204	0.13	0.55				0.08	0.06	0.31	
205	0.14	1							
301	0.2					0.04	0.48	0.48	
302	0.28	0.05				0.04	0.02	0.04	0.85
303	0.01	0.05				0.04	0.02	0.04	0.85
304	0.25		0.02		0.02	0.37		0.58	
305	0.13	1							
401	0.00	1							
402	0.01					1			
403	0.09					0.06	0.39	0.55	
404	0.00							1	
405	0.11					0.16	0.4	0.44	
406	0.04	0.54			0.32		0.08	0.07	
407	0.08			0.02		0.06	0.33	0.59	
409	0.46	0.06	0	0.04		0.32	0.07	0.5	

F Krill production

Atkinson et al. (2009) [133] estimated krill gross production (growth of biomass in a year through egg production, lipid build up etc.) in the absence of mortality to be between 342-536 Mt yr^{-1}. As acknowledged by the authors, this production estimate is of gross (or potential) production as it assumes that growth of krill during a year is not curtailed by krill mortality.

Here, we integrate a simple growth model for an individual krill into a population mortality model as in Reid et al. (2002) [382], to estimate potential krill production in the absence of mortality (GP) and krill production given krill mortality (KP) and resultantly the scalar KP/GP. We use this model rather than the more complicated individual growth models used by Atkinson et al. (2009) [133] for efficiency. Note: the growth model used here [382] led to krill growth 30-47% lower than that estimated by Atkinson et al. (2009) [133], dependent on the age of the krill. We used KP/GP to indicate the proportion of gross production which could still be produced in the presence of mortality. Thus we multiplied the Atkinson et al. (2009) [133] estimate for gross krill production by the value KP/GP to approximate krill production given mortality as an input into the Scotia Sea food web model in Chapter 4.

F.1 Scotia Sea krill production

Atkinson et al. (2009) [133] estimated that 28% of Southern Ocean krill biomass was found within the CCAMLR survey area which includes the Scotia Sea as well as areas in the Antarctic Peninsula [257]. We assumed that krill production was linearly proportional to their biomass, and thus scaled the Southern Ocean production estimate given in Atkinson et al. (2009) [133] by 0.28, which is the proportion of the Southern Ocean which is the CCAMLR survey area. We multiplied this again by 0.84 to scale for the proportion of krill in the CCAMLR survey area which is found in Scotia Sea regions. We calculated the scalar value 0.84 from density estimates for krill provided for seven sub regions of the CCAMLR survey area in Hewitt et al. (2004) [257] by dividing krill density in tonnes for the five Scotia Sea regions by total krill density for all seven regions. Although the exact definition of the Scotia Sea used in this study (see Chapter 1) differs from the five sub regions of the CCAMLR survey area which relate to Scotia Sea regions, we use the CCAMLR sub-regions to approximate the proportion of krill density in the CCAMLR survey area which are in

Scotia Sea regions as they account for the skewed distribution of krill within the Scotia Sea. We used a value for krill production of (439 Mt yr^{-1}) in the middle of the range of Southern Ocean production estimates given in Atkinson et al. 2009 [133], to estimate Scotia Sea gross krill production to be 103.25 Mt yr^{-1}.

F.2 Individual growth model

We combined the growth (in length) model for post-larval krill as used in Reid et al. (2002) [382] with the length to weight relationship reported in Hewitt et al. (2004) [257] to derive a krill growth model (in mass), see equation (F.1)

$$W(t) = \alpha \left(L_{inf}^{\beta} (1 - e^{-k(t-t_0)})^{\beta} \right), \tag{F.1}$$

where $W(t)$ is the weight of krill at age t, α, β and k are growth constants and L_{inf}^{β} is the maximum length of a krill.

F.2.1 Population model

We assumed that krill population size decays exponentially with time according to the population mortality model used in Reid et al. (2002) [382], see equation (F.2).

$$N(t) = N_0 e^{-Mt}, \tag{F.2}$$

where N_t is the size of the population at time t, N_0 is initial krill population size and M is the mortality rate.

F.2.2 Krill production model

Krill production with mortality (KP) of a population over a year from an initial time point t is given by equation (F.3).

$$KP(t) = N(t+1)(W(t+1) - W(t)) + \int_0^1 \frac{N(t+s)}{dt}(W(t+s) - W(t))ds \tag{F.3}$$

We estimated potential krill production in the absence of mortality GP by setting $M = 0$ in equation (F.3), resulting in equation (F.4).

$$GP(t) = N_0 \left(\alpha L_{inf}^{\beta} (1 - e^{-k(t+1-t_0)})^{\beta} - \alpha L_{inf}^{\beta} (1 - e^{-k(t-t_0)})^{\beta} \right) \tag{F.4}$$

We used numerical simulations in Matlab R2012a, to approximate KP in equation (F.3), see equation (F.5). Note: the value used is unimportant as they cancel out when we calculate $\frac{KP}{GP}$.

Table F.1: Parameter values used in the krill growth and mortality model.

Symbol	Description	Value	Reference
α	Maximum weight (g)	2.24E-06	[257]
β	Power-factor	3.314	[257]
N_0	Initial population size (number of individuals m-2)	NA	Used an arbitrary value of 100.
k	Growth constant	0.47	[382]
t_0	Initial time (years)	0.1418	[382]
L_{inf}	Maximum length (mm)	63	[382]
M	Mortality (krill yr-1)	0.6, 0.8, 1	[382]

$$\begin{aligned}\hat{KP} &= (W(t_e) - W(t_b))N(t_e) \\ &\quad + \sum^{3} 65_{i=1} \left(N_0(t_b + \frac{i}{365}) - N(t_b + i - 1365\right)\left(W(t_b + \frac{i}{365}) - W(t_b)\right),\end{aligned} \tag{F.5}$$

where t_b and t_e are the times at the beginning and end of the year respectively.

We completed this for $t = 1, 2$, and 3. Estimates for post-larval krill mortality in the Scotia Sea range from 0.45 to greater than two, see [417] and references therein. Krill mortality estimates are dependent on proximity to predator ‘hot spots’, and thus high estimates of krill mortality are likely to be representative of predator foraging areas [317]. Murphy and Reid (2001) [317] suggest that krill mortality averaged over large areas of high and low predator foraging effort, is likely to be at the lower end of suggested mortality estimates. The Scotia Sea contains a few hot-spots of high krill abundance and predator foraging effort as well as large areas of low krill abundance and predator foraging effort. Thus we use values of krill mortality at the lower end of the krill mortality range, $M = 0.6$. However, we test the sensitivity of krill mortality to M=0.8 and 1.0. Values for parameter estimates are given in Table F.1

F.2.3 Results and discussion

We used the intermediate value of $\frac{KP}{GP} = 0.21$ and thus use a value of 21.68 Mt yr^{-1} of krill, which is equivalent to 14 gm$^{-2}yr^{-1}$ as an estimate for krill production as an input into the RPM. We converted total production estimate in Mt to gm^{-2}yr^{-1} using the area estaimte of the Scotia Sea in Hewitt et al. (20014) [257] to keep our methods consistent with those used previously to rescale the circumpolar estimate for krill density for the Scotia Sea. Uncertainty in the production estimate used as an input into the RPM, linearly scales

Table F.2: $\frac{KP}{GP}$ ratio calculated for three ages of krill at different mortality rates.

t	M	$\frac{KP}{GP}$
1	0.6	0.37
1	0.8	0.27
1	1.0	0.19
2	0.6	0.21
2	0.8	0.12
2	1.0	0.07
3	0.6	0.12
3	0.8	0.06
3	1.0	0.03

production estimates for the remaining functional groups, thus does not qualitatively alter outputs from the RPM.

G Scatter plots

The scatter plots shown in Figures G.1 and G.2 show how the growth efficiency for pelagic fish (FG 401) and ecotrophic efficiency for salps and gelatinous zooplankton (FG 603), respectively, correlated with the production of each functional group in the LHS approach to sensitivity analysis.

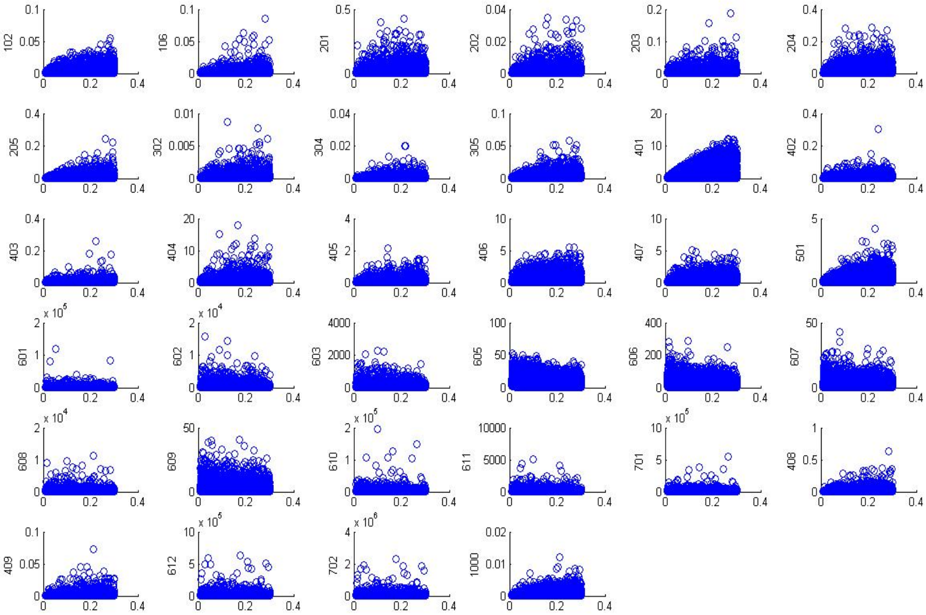

Figure G.1: Growth efficiency for functional group 401 (x-axis) used as model input to generate production estimates for each functional group (y-axis) in the LHS based analysis.

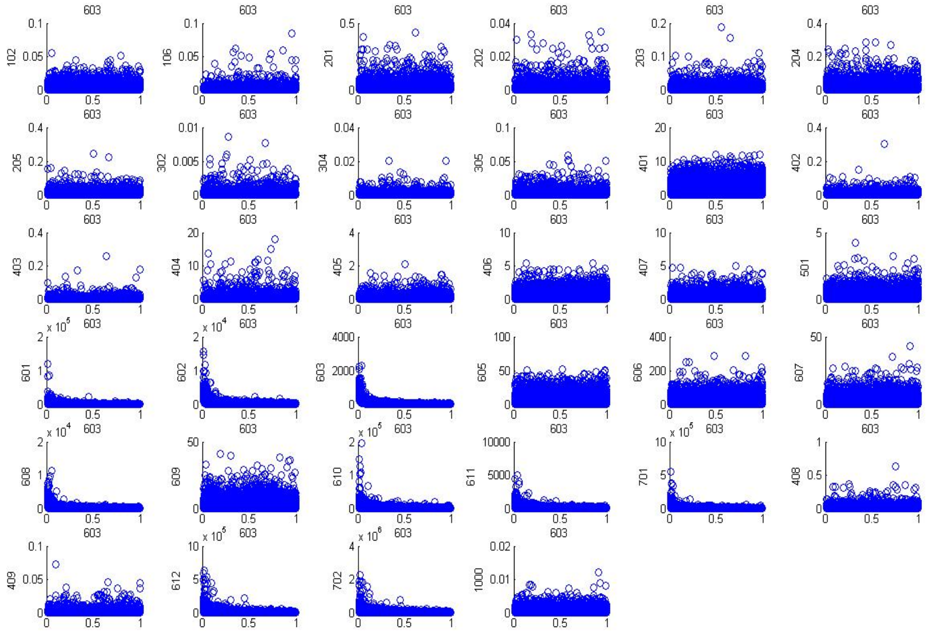

Figure G.2: Ecotrophic efficiency for functional group 603 (x-axis) used as model input to generate production estimates for each functional group (y-axis) in the LHS based analysis.

H Alternate input production

We repeated the perturbation analysis and latin-hypercube sample-uncertainty analysis as described in Chapter 4, but used the production of macaroni penguins (FG 204) as the input production estimate. For the perturbation analysis, we used a production estimate of 1.18E-02 g $m^{-2}y^{-1}$ for macaroni penguins, which was the production estimate for this functional group as calculated by the RPM using baseline efficiency values (see Table 4.6) with Antarctic krill production as model input. Total primary and secondary production were most sensitive to the same zooplankton and benthic functional groups. Similarly out of the fish functional groups, total primary and secondary production was most sensitive to pelagic fish and of the large bodied predators, model results were most sensitive to efficiency values for macaroni penguins, fur seals, and leopard seals (Figures H.1 and H.2.)

Production estimates were most uncertain for hetertrophic chromista and primary producers (Figure H.3). Of the zooplankton and benthic functional groups there was most uncertainty associated with estimates for omnivorous meso and micro zooplankton (FG 610) and herbivorous benthos (FG 601) (Figure H.4). Of the fish functional groups, the production of pelagic fish was most uncertain (Figure H.5) and the production estimates of South Georgian shag and diving petrels (FG 303) was the most uncertain for large bodied predators (Figure H.6). These results are similar to those calculated from the RPM when the production of Antarctic krill was used as an input.

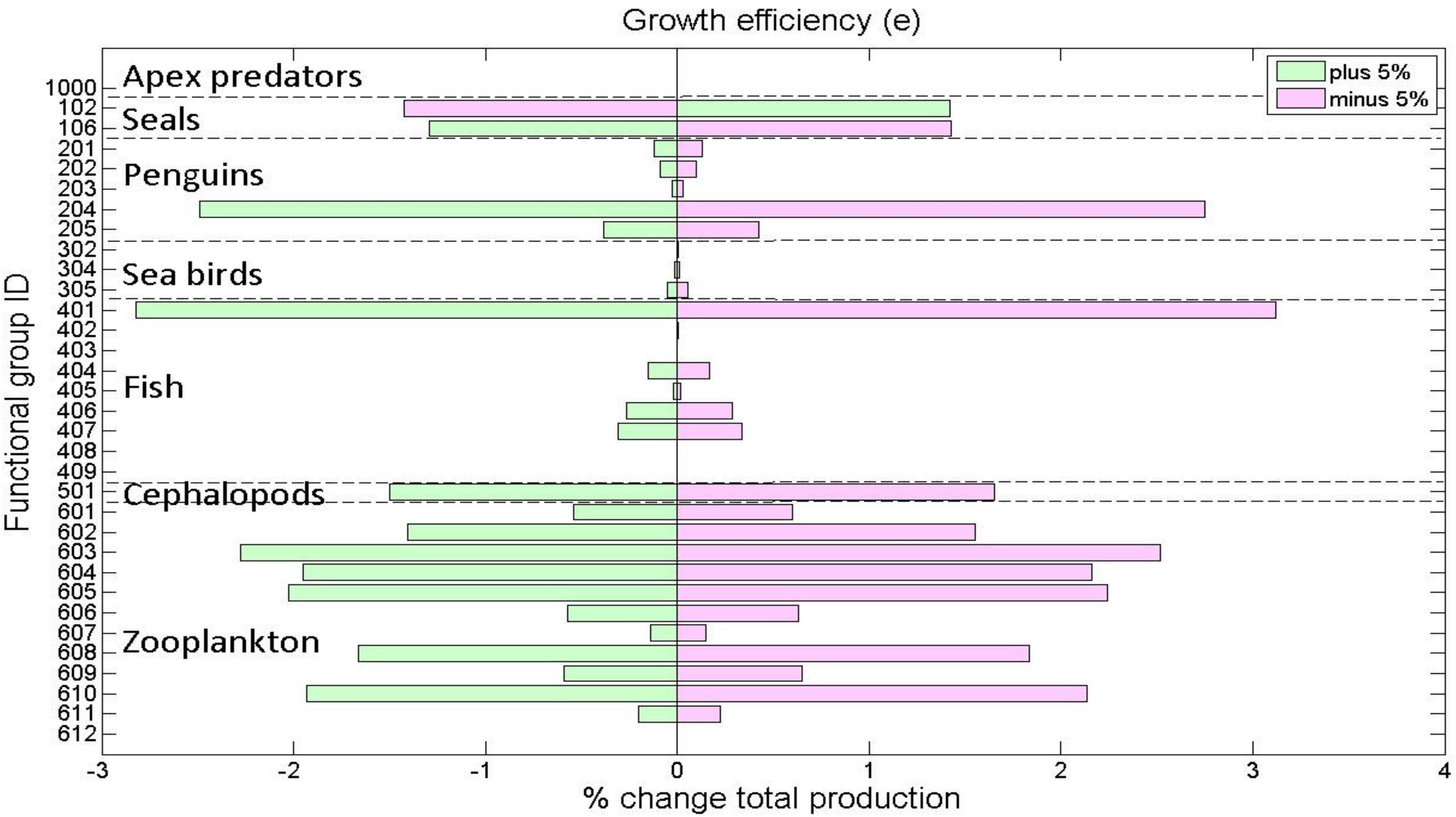

Figure H.1: Percent change in total production to a 5% change in the growth efficiency for the functional group specified on the y-axis. Input production was for macaroni penguins (FG 204).

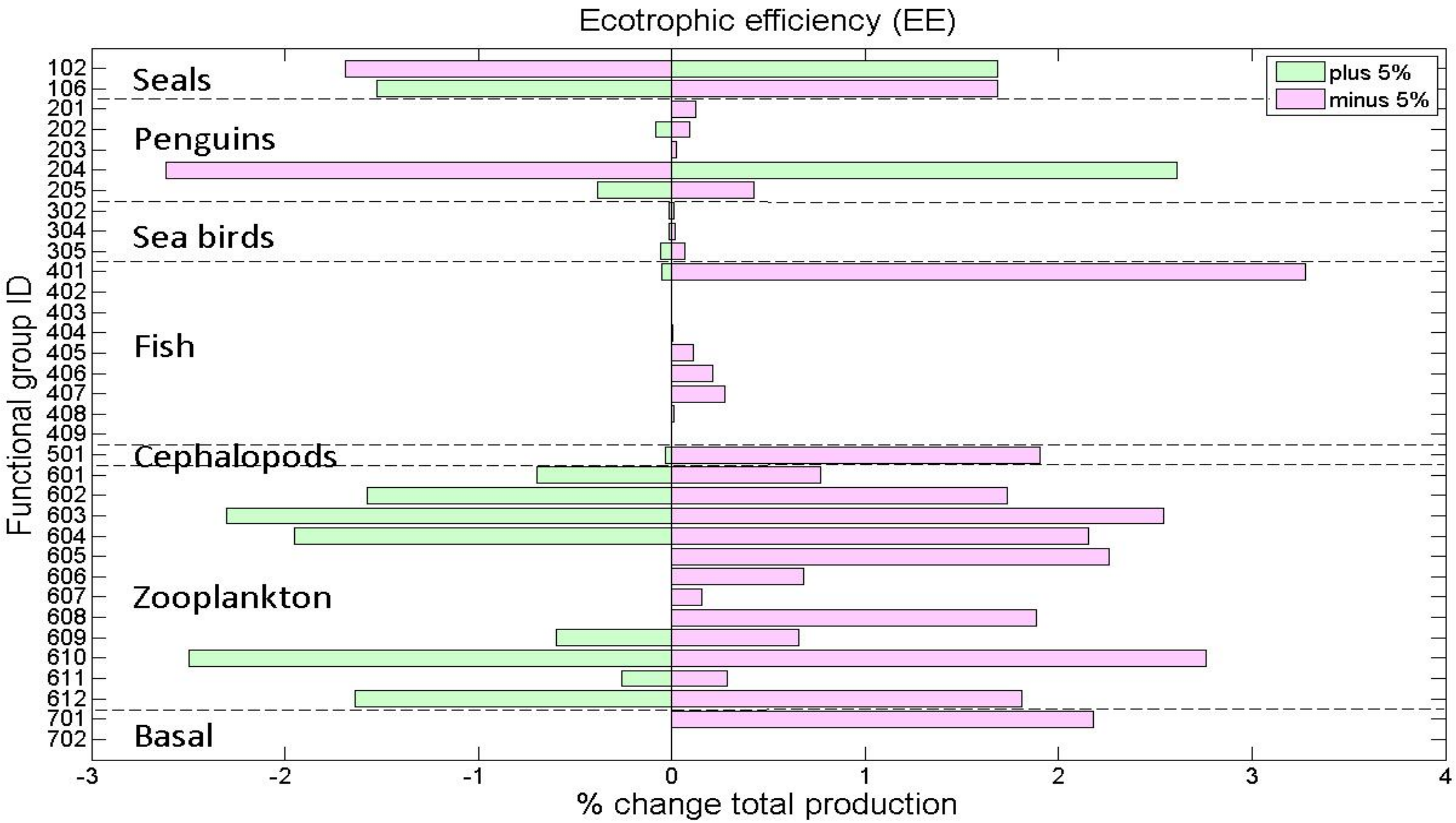

Figure H.2: Percent change in total production to a 5% change in the ecotrophic efficiency for the functional group specified on the y-axis. Input production was for macaroni penguins (FG 204).

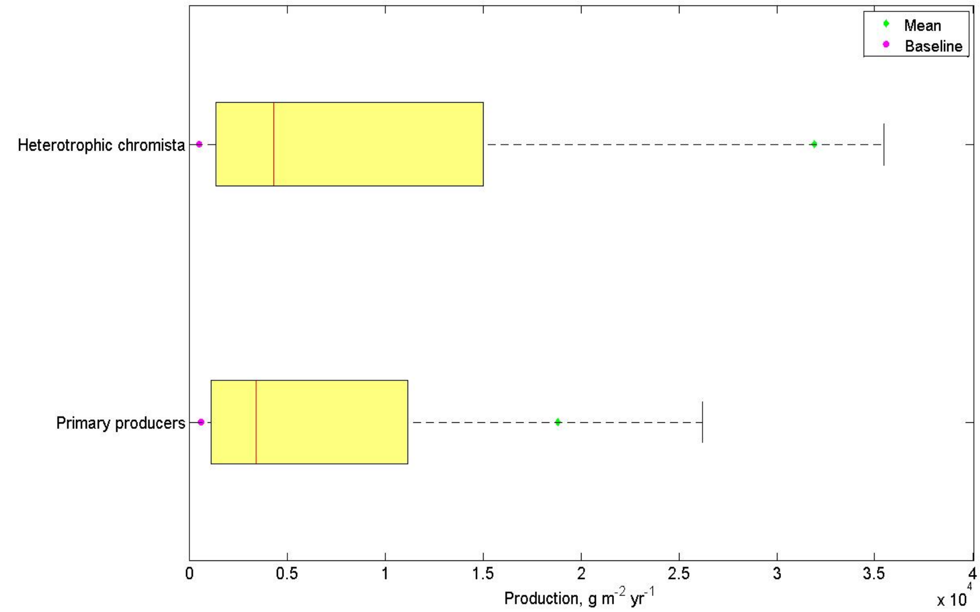

Figure H.3: Box and whisker plots for production estimate calculated from 10 000 evaluations of the RPM for heterotrophic chromista and primary producers. Combinations of efficiency parameters were selected using Latin-Hypercube Sampling. Extreme values are not shown. Input production was for macaroni penguins (FG 204).

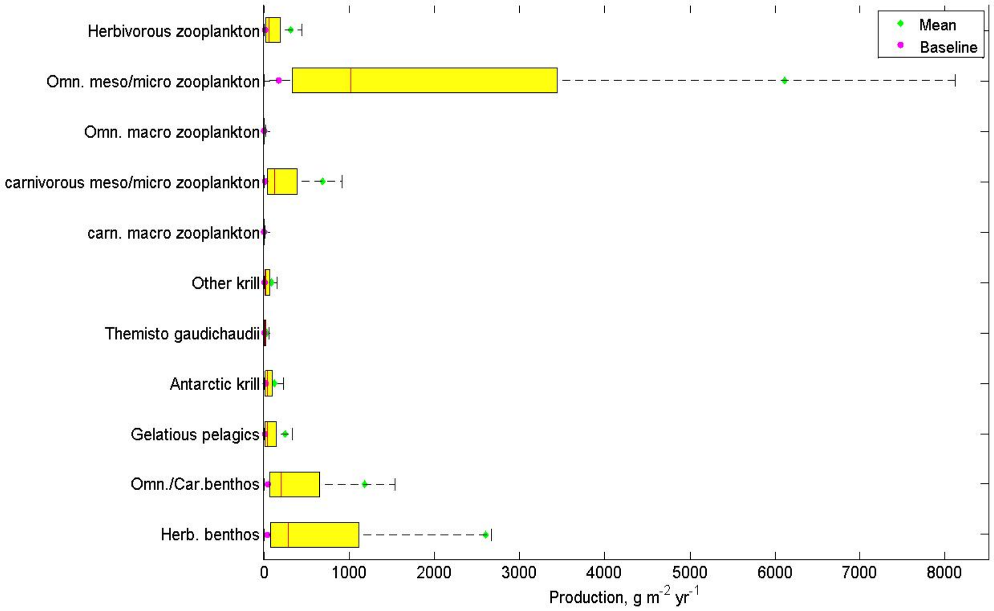

Figure H.4: Box and whisker plots for production estimate calculated from 10 000 evaluations of the RPM for benthos and zooplankton. Combinations of efficiency parameters were selected using Latin-Hypercube Sampling. Extreme values are not shown. Input production was for macaroni penguins (FG 204).

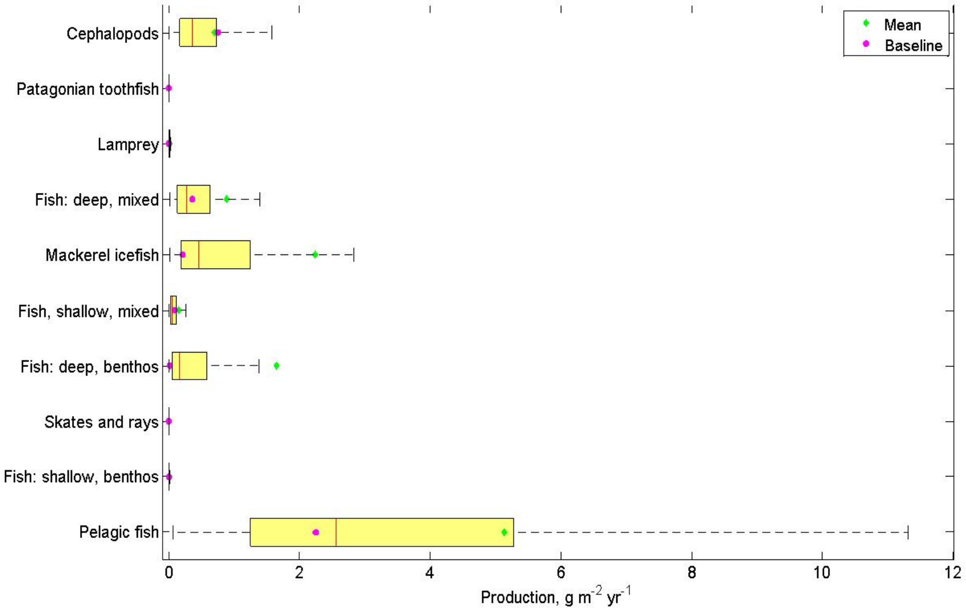

Figure H.5: Box and whisker plots for production estimate calculated from 10 000 evaluations of the RPM for fish and cephalopod. Combinations of efficiency parameters were selected using Latin-Hypercube Sampling. Extreme values are not shown. Input production was for macaroni penguins (FG 204).

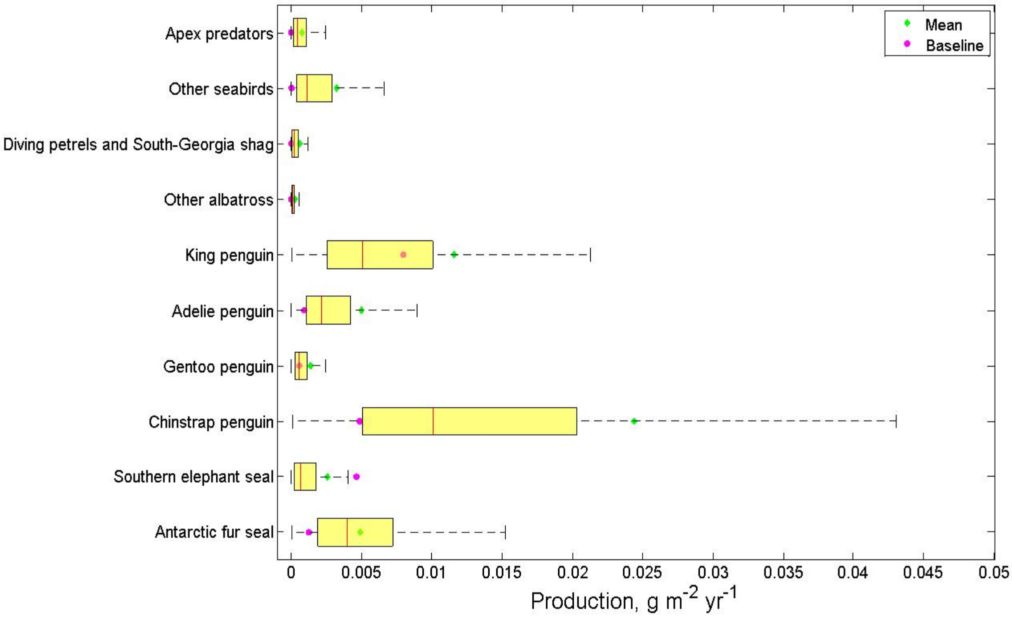

Figure H.6: Box and whisker plots for production estimate calculated from 10 000 evaluations of the RPM for land-breeding predators and cetaceans. Combinations of efficiency parameters were selected using Latin-Hypercube Sampling. Extreme values are not shown. Input production was for macaroni penguins (FG 204).

I Testing key assumptions

We calculated production for functional groups using the RPM and the methods described in Chapter 4. However, in we altered the diet composition of heterotrophic chromista to be 50% primary producers (FG 701) and 50% detritus. Production outputs for all functional groups were identical to those given in Table 4.7 except for primary production which increased by a factor of 2.4.

J Verbal description of the analytical Models

J.1 Model 1

Forage trip duration was T_m when a predator captured less than N_m prey within this time, and was $t < T_m$ if a penguin encountered N_m prey at time t. A predator encountered $n < N_m$ prey if it encountered n prey by time T_m, and encountered N_m prey if N_m^{th} encounter occurred at time t, over all possible values of $t < T_m$. For a predator to consume $k < N_m$ krill on a foraging trip, it must have encountered $N_1 \geq k$ prey, and for each possible value of N_1, k of events must be an encounter with a krill. The model was developed similarly for the number of alternate prey in a penguin's diet, G_1.

J.2 Model 2

Forage trip duration was T_m if a predator captured less than N_m alternate prey within this time and did not encounter a krill swarm by T_m. Trip duration was $t < T_m$ if the N_m^{th} encounter with alternate prey happened at exactly time t and before a predator encountered a krill swarm, or an encounter with a krill swarm happened at exactly time t and before a predator encountered N_m alternate prey. A predator encountered $n < N_m$ prey in a foraging trip if it encountered n alternate prey by time T_m and did not encounter a krill swarm by time T_m. A predator consumed N_m prey if it encountered the N_m^{th} alternate prey at exactly time t and before it encountered a krill swarm or it encountered a krill swarm at time t and before it encountered N_m other prey, over all possible values of $t < T_m$.

A penguin consumed no krill during a foraging trip if did not encounter a krill swarm by time T_m and encountered less than N_m prey during the foraging trip, or it encountered N_m other prey at exactly time t and the time taken to encounter a krill swarm took longer than this, for all values of $t < T_m$. A penguin consumed $0 < k \leq N_m$ during a foraging trip if it encountered a krill swarm at exactly time t and had encountered $N_m - k$ prey before this time over all possible values $t < T_m$. A predator consumed $g < N_m$ prey if it encountered a krill swarm at time t and had consumed g prey before this time over all $t \leq T_m$. A penguin consumed exactly N_m alternate prey during a foraging trip if it encountered the N_m^{th} alternate prey at exactly time t and the time taken to encounter a krill swarm was greater than this, over all possible $t < T_m$.

K Reducing N_m from 785 to 80

K.1 Introduction and methods

We estimated the maximum number of prey that a predator could eat during one foraging trip as 785. Our analytical foraging model (see equations (5.5)-(5.8) and (5.10)-(5.13)) included a factorial of N_m, which was not computationally tractable within Matlab R2012a for N_m=785. To overcome this limitation, we pragmatically reduce N_m to a manageable size of 80 prey. Representing multiple individuals as a single prey unit is a well-used convention in individual based models, for example [395, 408, 458, 457]. Due to our simplifying assumption that prey of one type are all identical, we simply adjustined prey density estimates by multiplying prey densities by $\sigma = \frac{N_m}{785}$.

Here, we examined how foraging metrics changed by parameterising our model with reduced N_m. We used 100 000 simulations of Model 2, see Section 5.2.3, to estimate the probability mass function for krill and alternate prey, and the probability density function for trip duration at medium krill densities and average alternate prey densities (see Table 5.2 in Chapter 5).

We repeated this for N_m=40 and 80 and readjusted prey densities by multiplying encounter rates with randomly distributed prey by $\sigma = \frac{40}{785}, \frac{80}{785}$ respectively using both simulations and analytical calculations of Model 2. Encounter rates with swarms remained the same, as the readjustment affected in-swarm prey density rather than the density of swarms. We calculated the percentage change in the probability of each event from the most biologically realistic simulations when N_m=785 using equation (K.1).

$$\%\mathit{Diff} = 100\left(\frac{P_{ijf}}{P_{785jf}} - 1\right), \tag{K.1}$$

where P_{ijf} is the probability that the random variable f has a value of j, when we reduce N_m to i.

K.2 Foraging outcomes for three values of N_m

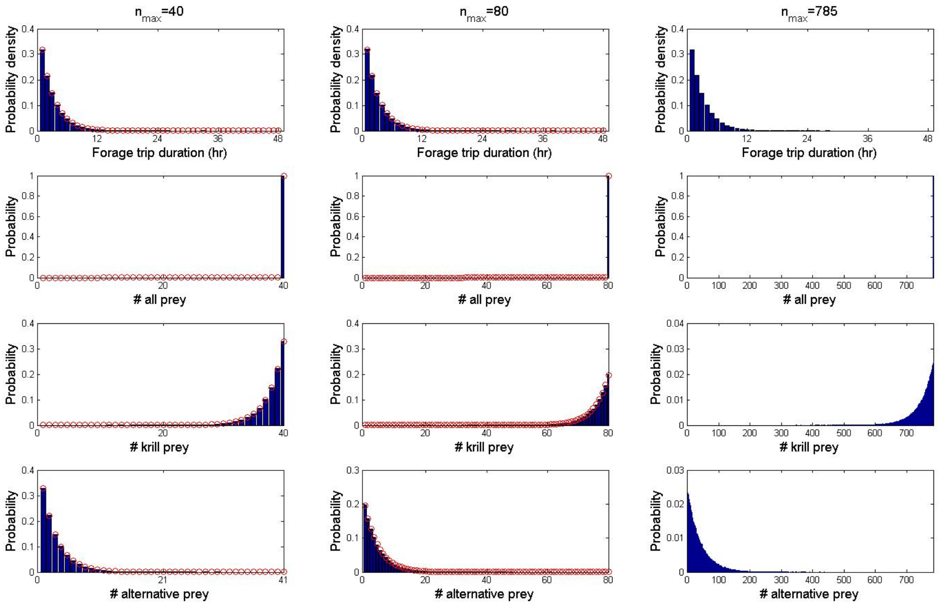

Figure K.1: Foraging metrics for medium prey densities when N_m=40 (left column), N_m=80 (centre) and N_m=785 (right column). Red dots are results from the analytical model and blue bars are probabilities estimated from binned frequency data with bin-width of one hour, over 100 000 simulated foraging trip.

Table K.1: Probability of having a full stomach, krill dominated diet, and alternate prey dominated diet for different values of N_{max}.

	N_m=785	N_m=40		N_m=80	
	Probability	Probability	% Difference from N_m=785	Probability	% Difference from N_m=785
Probability of having a full stomach	1.00E+00	1.00E+00	-6.31E-07	1.00E+00	-6.95E-07
Probability of having a krill dominated diet	8.62E-01	8.65E-01	1.90E-01	8.60E-01	-1.61E-01
Probability of having an alternate prey dominated diet	0.00E+00	5.98E-07	-	1.46E-07	-

A predator foraging for 785 prey had a 100% chance of having a full stomach, 86.2% chance of having a diet dominated by krill and 0% chance of having a diet dominated by alternate prey. These first two metrics changed by less than 1% for both values of reduced N_m and was undefined for the probability of having an alternate prey dominated diet (see Table K.1). The shape and magnitude of the probability mass function and distribution function were similar between models, taking into account that for the probability mass function of prey in the diets of a predator, one bin in the N_m=40 model is equivalent to 2 consecutive bins in the $N_m = 80$ model and $\frac{785}{40}$ consecutive bins in the simulations of $N_m = 785$.

K.3 Discussion

Models with a reduced number of N_m provided excellent approximations of foraging statistics resulting from simulations where a predator searches for a greater, and more biologically realistic, number of prey. Therefore, in Chapter 5, we used a model where a predator searches for N_m=80 prey to accurately reflect foraging metrics of the N_m=785. This made our analytical model computationally tractable, and also reduced the processing time required for simulations of foraging trips.

Bibliography

[1] Commission for the Conservation of Antarctic Marine Living Resources. 2012. Fisheries. Available from: https://www.ccamlr.org/en/fisheries/fisheries/. [Accessed 27/08/2015].

[2] Dirección Nacional del Antartico - Instituto Antártico Argentino. 2015. Argentine Antarctic stations. Available from: http://www.dna.gov.ar/INGLES/DIVULGAC/BASES.HTM/. [Accessed 27/08/2015].

[3] RAMS. De Broyer, C.; Clarke,A.; Koubbi, P.; Pakhomov, E.; Scott, F.; Vanden Berghe, E. and Danis, B. Eds., 2015. Register of Antarctic Marine Species. Available from: http://www.marinespecies.org/rams/ [Accessed 16/07/2015].

[4] Scientific Committee for Antarctic Research. The South Georgia and South Sandwich Island Place-name Map Browser. Available from: http://add.antarctica.ac.uk/public/sgssigaz/ [Accessed 27/08/2015].

[5] *Amphidinium*. Encyclopedia of Life. Available from: http://eol.org/pages/12095/overview. [Accessed 08/07/2015].

[6] *Amphisolenia*. Encyclopedia of Life. Available from: http://eol.org/pages/91081/overview. [Accessed 08/07/2015].

[7] *Asteroidea*. 2015. Accessed through: De Broyer, C.; Clarke,A.; Koubbi, P.; Pakhomov, E.; Scott, F.; Vanden Berghe, E. and Danis, B. Eds., 2015. Register of Antarctic Marine Species. Available from: http://www.marinespecies.org/rams/aphia.php?p=taxdetails&id=123080. [Accessed 16/07/2015].

[8] *Cephalophoxoides kergueleni*. Sea Life Base. Available from: http://www.sealifebase.ca/summary/Cephalophoxoides-kergueleni.html. [29/05/2015].

[9] *Cirolanidae*. Encyclopedia of Life. Available from: http://www.eol.org/pages/7264/overview [Accessed 29/05/2015].

[10] *Ctenophora*. Encyclopedia of Life. Available from: http://eol.org/pages/69/overview. [Accessed 28/05/2015].

[11] *Cumacea*. Encyclopedia of Life. Available from: http://eol.org/pages/1243/overview. [Accessed 28/05/2015].

[12] *Dictyochophyceae*. Encyclopedia of Life. Available from: http://eol.org/pages/3505/overview. [Accessed 03/02/2015].

[13] *Echiura*. Encyclopedia of Life. Available from: http://maps3.eol.org/pages/8847/overview. [Accessed 29/05/2015].

[14] *Gymnodiniales*. Encyclopedia of Life. Available from: http://eol.org/pages/4782/overview. [Accessed 03/05/2015].

[15] *Halocyprididae*. Encyclopedia of Life. Available from: http://www.eol.org/pages/1483/overview [Accessed 29/05/2015].

[16] *Heliozoa*. Encyclopedia of Life. Available from: http://eol.org/pages/4952/overview. [Accessed 03/06/2015].

[17] *Hyperia galba*. Encyclopedia of Life. Available from: http://eol.org/pages/1021725/overview [Accessed 02/06/2015].

[18] *Hyperia macrocephala*. Encyclopedia of Life. Available from: http://eol.org/pages/1019034/overview [Accessed 02/06/2015].

[19] *Hyperoche medusaram*. Marine Species Identification Portal. Available from: http://species-identification.org/species.php?species_group=zsao&id=3457 [Accessed 02/06/2015].

[20] *Lithodidae*. Encyclopedia of Life. Available from: http://www.eol.org/pages/7152/overview [Accessed 02/06/2015].

[21] *Monoculodes antarcticus*. Sea Life Base. Available from: fromhttp://www.sealifebase.org/summary/Monoculodes-antarcticus.html. [Accessed 02/06/2015].

[22] *Mysida*. Encyclopedia of Life. Available from: http://www.eol.org/pages/7365/overview [Accessed 16/07/2015].

[23] *Oediceroides*. Encyclopedia of Life. Available from: http://eol.org/pages/43828/overview [Accessed 02/06/2015].

[24] *Peridinium*. Encyclopedia of Life. Available from: http://eol.org/pages/11700/overview. [Accessed 08/05/2015].

[25] *Phoxocephaldae*. Encyclopedia of Life. Available from: http://www.eol.org/pages/1297/overview [Accessed 29/05/2015].

[26] *Podocerus capillimanus*. Sea Life Base. Available from: http://www.sealifebase.org/Summary/speciesSummary.php?ID=151717&genusname=Podocerus&speciesname=capillimanus. [16/07/2015].

[27] *Prorocentrum*. Encyclopedia of Life. Available from: http://eol.org/pages/90165/overview. [Accessed 03/05/2015].

[28] *Radiozoa*. Encyclopedia of Life. Available from: http://eol.org/pages/13073315/overview. [Accessed 03/06/2015].

[29] *Sardinops sagax*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: www.fishbase.org/summary/1477..

[30] *Serolidae*. Encyclopedia of Life. Available from: http://www.eol.org/pages/7338/overview [Accessed 01/06/2015].

[31] *Tanaidacea*. Encyclopedia of Life. Available from: http://eol.org/pages/7391/overview. [Accessed 29/05/2015].

[32] *Uristidae*. Encyclopedia of Life. Available from: http://www.eol.org/pages/1270/overview [Accessed 29/05/2015].

[33] *Acanthochiasma*. Encyclopedia of Life. Available from: http://eol.org/pages/3110664/overview. [Accessed 03/06/2015].

[34] *Aetideidae*. Encyclopedia of Life. Available from: http://eol.org/pages/1019034/overview [Accessed 02/06/2015].

[35] *Anotopterus vorax*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Anotopterus-vorax.html [Accessed 18/06/2015].

[36] *Antimora rostrata*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: www.fishbase.org/summary/2005. [Accessed 18/06/2015].

[37] *Arctozenus risso*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://fishbase.org/Country/CountrySpeciesSummary.php?c_code=032&id=6977 [Accessed 18/06/2015].

[38] *Artedidraco mirus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7065. [Accessed 18/06/2015].

[39] *Artedidraco skottsbergi*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7068. [Accessed 18/06/2015].

[40] *Bathydraco joannae*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7095 [Accessed 18/06/2015].

[41] *Bathylagus antarcticus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Bathylagus-antarcticus.html. [Accessed 18/06/2015].

[42] *Borostomias antarcticus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: www.fishbase.org/summary/5098. [Accessed 18/06/2015].

[43] *Calanidae*. Encyclopedia of Life. Available from: http://eol.org/pages/1415/overview [Accessed 29/05/2015].

[44] *Chaenocephalus aceratus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/473. [Accessed 18/06/2015].

[45] *Chaenodraco wilsoni*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/478 [Accessed 18/06/2015].

[46] *Champsocephalus esox*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/5133. [Accessed 18/06/2015].

[47] *Channichthys rhinoceratus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/477 [Accessed 18/06/2015].

[48] *Chionodraco rastrospinosus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/476 [Accessed 18/06/2015].

[49] *Chorismus antarcticus*. Encyclopedia of Life. Available from: http://eol.org/pages/330267/overview [Accessed 23/09/2015].

[50] *Cryodraco antarcticus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://fishbase.org/summary/Cryodraco-antarcticus.html. [Accessed 18/06/2015].

[51] *Cyphocaris*. Encyclopedia of Life. Available from: http://eol.org/pages/15175/overview. [Accessed 29/05/2015].

[52] *Dinophyceae*. Encyclopedia of Life. Available from: http://eol.org/pages/4758/overview. [Accessed 03/06/2015].

[53] *Dissostichus mawsoni*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7039. [Accessed 18/06/2015].

[54] *Electrona antarctica*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: www.fishbase.org/summary/6984. [Accessed 18/06/2015].

[55] *Electrona carlsbergi*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Electrona-carlsbergi.html. [Accessed 18/06/2015].

[56] *Electrona subaspera*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Electrona-subaspera.html. [Accessed 18/06/2015].

[57] *Eusiridae*. Encyclopedia of Life. Available from: http://eol.org/pages/1261/overview. [Accessed 16/07/2015].

[58] *Fish*. Accessed through, Australian Government, Department of the Environment. Available from: http://www.antarctica.gov.au/about-antarctica/wildlife/animals/fish. [Accessed 17/02/2016].

[59] *Gammaropsis*. Encyclopedia of Life. Available from: http://eol.org/pages/3063825/overview [Accessed 02/06/2015].

[60] *Gammaropsis triodon*. Encyclopedia of Life. Available from: http://www.eol.org/pages/3063825/overview [Accessed 02/06/2015].

[61] *Gennades kempi*. Sea Life Base. Available from: http://www.sealifebase.org/summary/Gennadas-kempi.html. [Accessed 23/09/2015].

[62] *Glyptonotus*. Encyclopedia of Life. Available from: http://eol.org/pages/42040/overview [Accessed 23/09/2015].

[63] *Gnathophausia gigas*. Encyclopedia of Life. Available from: http://www.eol.org/pages/342037/overview [Accessed 16/07/2015].

[64] *Gnathophausia gigas*. Sea Life Base. Available from: http://www.sealifebase.org/Summary/speciesSummary.php?ID=21175&genusname=Gnathophausia&speciesname=gigas. [Accessed 14/07/2015].

[65] *Gobionotothen angustifrons*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/59655. [Accessed 18/06/2015].

[66] *Gobionotothen gibberifrons*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7041. [Accessed 18/06/2015].

[67] *Gobionotothen marionensis*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7042 [Accessed 18/06/2015].

[68] *Gymnoscopelus bolini*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Gymnoscopelus-bolini.html. [Accessed 18/06/2015].

[69] *Gymnoscopelus braueri*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Gymnoscopelus-braueri.html. [Accessed 18/06/2015].

[70] *Gymnoscopelus fraseri*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Gymnoscopelus-fraseri.html. [Accessed 18/06/2015].

[71] *Gymnoscopelus hintonoides*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Gymnoscopelus-hintonoides.html. [Accessed 18/06/2015].

[72] *Gymnoscopelus microlampas*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Gymnoscopelus-microlampas.html. [Accessed 18/06/2015].

[73] *Gymnoscopelus nicholsi*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Gymnoscopelus-nicholsi.html. [Accessed 18/06/2015].

[74] *Gymnoscopelus opisthopterus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/6991. [Accessed 23/09/2015].

[75] *Haloptilus*. Encyclopedia of Life. Available from: http://maps3.eol.org/pages/ /overview. [Accessed 29/05/2015].

[76] *Harpagifer antarcticus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7089 [Accessed 18/06/2015].

[77] *Harpagifer bispinis*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7277. [Accessed 18/06/2015].

[78] *Harpagifer georgianus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7090. [Accessed 18/06/2015].

[79] *Krefftichthys anderssoni*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Krefftichthys-anderssoni.html. [Accessed 18/06/2015].

[80] *Lepidonotothen larseni*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7048. [Accessed 18/06/2015].

[81] *Lepidonotothen squamifrons*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7045. [Accessed 18/06/2015].

[82] *Lindbergichthys nudifrons*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7047. [Accessed 18/06/2015].

[83] *Lysianassidae*. Encyclopedia of Life. Available from: http://eol.org/pages/1161/overview [Accessed 16/07/2015].

[84] *Macrourus holotrachys*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7138 [Accessed 18/06/2015].

[85] *Macrourus whitsoni*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7139 [Accessed 18/06/2015].

[86] *Magnisudis prionosa* . Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: www.fishbase.org/summary/6978. [Accessed 23/09/2015].

[87] *Micromesistius australis*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/320 [Accessed 18/06/2015].

[88] *Mirounga leonina*. In C. Campagna. editor. The IUCN Red List of Threatened Species. Version 2015.2. Available from: http://www.iucnredlist.org. [Accessed 27/08/2015].

[89] *Monoculodes antarcticus*. Encyclopedia of Life. Available from: http://eol.org/pages/3064247/overview [Accessed 02/06/2015].

[90] *Muraenolepis*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7126. [Accessed 18/06/2015].

[91] *Muraenolepis microps*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7126. [Accessed 18/06/2015].

[92] *Nannobrachium achirus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: www.fishbase.org/summary/6998. [Accessed 18/06/2015].

[93] *Nansenia antarctica*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Nansenia-antarctica.html. [Accessed 18/06/2015].

[94] *Notolepis coatsi*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Notolepis-coatsi.html. [Accessed 18/06/2015].

[95] *Notothenia coriiceps*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/Summary/SpeciesSummary.php?id=4702. [Accessed 18/06/2015].

[96] *Notothenia rossii*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/468. [Accessed 18/06/2015].

[97] *Nototheniops nybelini*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/59654. [Accessed 18/06/2015].

[98] *Oedicerotidae*. Encyclopedia of Life. Available from: http://www.eol.org/pages/1306/overview. [Accessed 16/07/2015].

[99] *Pagetopsis macropterus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7114. [Accessed 18/06/2015].

[100] *Pagetopsis maculatus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7115 [Accessed 18/06/2015].

[101] *Parachaenichthys charcoti*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7102. [Accessed 18/06/2015].

[102] *Parachaenichthys georgianus*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7103. [Accessed 18/06/2015].

[103] *Paradiplospinus gracilis*. Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7117. [Accessed 18/06/2015].

[104] *Paranotothenia magellanica.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Paranotothenia-magellanica.html. [Accessed 18/06/2015].

[105] *Pasiphaea scotiae.* Encyclopedia of Life. Available from: http://www.eol.org/pages/3111080/overview [Accessed 29/05/2015].

[106] *Pasiphaea Scotiae.* Sea Life Base. Available from: http://www.sealifebase.org/summary/Pasiphaea-scotiae.html. [Accessed 29/05/2015].

[107] *Patagonotothen guntheri.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/54742. [Accessed 18/06/2015].

[108] *Pleuragramma antarcticum.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Pleuragramma-antarctica.html. [Accessed 18/06/2015].

[109] *Pogonophryne scotti.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7085. [Accessed 18/06/2015].

[110] *Protomyctophum bolini.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Protomyctophum-bolini.html. [Accessed 18/06/2015].

[111] *Protomyctophum choriodon.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Protomyctophum-choriodon.html. [Accessed 18/06/2015].

[112] *Protomyctophum normani.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/Protomyctophum-normani.html. [Accessed 23/09/2015].

[113] *Protomyctophum parallelum.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Protomyctophum-parallelum.html. [Accessed 18/06/2015].

[114] *Protomyctophum tenisoni.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Protomyctophum-tenisoni.html. [Accessed 18/06/2015].

[115] *Pseudochaenichthys georgianus.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/475. [Accessed 18/06/2015].

[116] *Pseudoicichthys australis.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Icichthys-australis.html. [Accessed 18/06/2015].

[117] *Psilodraco breviceps.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7105. [Accessed 18/06/2015].

[118] *Sio nordenskjoldii.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.se/summary/Sio-nordenskjoldii.html. [Accessed 18/06/2015].

[119] *Synopiidae.* Encyclopedia of Life. Available from: http://eol.org/pages/1272/overview. [Accessed 16/07/2015].

[120] *Trematomus bernacchii.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7053 [Accessed 18/06/2015].

[121] *Trematomus eulepidotus.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7054. [Accessed 18/06/2015].

[122] *Trematomus hansoni.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7055. [Accessed 18/06/2015].

[123] *Trematomus newnesi.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7058. [Accessed 18/06/2015].

[124] *Trematomus scotti.* Accessed through, R. Froese and D. Pauly. Ed, 2015. FishBase. Available from: http://www.fishbase.org/summary/7061. [Accessed 18/06/2015].

[125] Albatross: British Antarctic Survey long-term monitoring data., 2013.

[126] Penguins: British Antarctic Survey long-term monitoring data., 2013.

[127] D. G. Ainley, G. Ballard, K. J. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, and P. R. Wilson. Spatial and temporal variation of diet within a presumed metapopulation of adélie penguins. *The Condor*, 105(1):95–106, 2003.

[128] D. G. Ainley, W. R. Fraser, W. O. Smith Jr., T. L. Hopkins, and J. J. Torres. The structure of upper level pelagic food webs in the Antarctic: Effect of phytoplankton distribution. *Journal of Marine Systems*, 2:111–122, 1991.

[129] D. G. Ainley, C. A. Ribic, and W. R. Fraser. Does prey preference affect habitat choice in Antarctic seabirds? *Marine Ecology-Progress Series*, 90:207–207, 1993.

[130] J. C. Antacli, M. E. Sabatini, R. I. Silva, D. R. Hernández, A. J. Jaureguizar, and R. Akselman. Feeding and reproductive activity of the copepods *Drepanopus forcipatus* and *Calanus australis* during late summer on the southern patagonian shelf (argentina). *Brazilian Journal of Oceanography*, 62(4):295–314, 2014.

[131] K. R. Arrigo. Marine microorganisms and global nutrient cycles. *Nature*, 437(7057):349–355, 2005.

[132] A. Atkinson, V. Siegel, E. Pakhomov, and P. Rothery. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, 432(7013):100–103, 2004.

[133] A. Atkinson, V. Siegel, E. A. Pakhomov, M. J. Jessopp, and V. Loeb. A re-appraisal of the total biomass and annual production of Antarctic krill. *Deep Sea Research Part I: Oceanographic Research Papers*, 56(5):727–740, 2009.

[134] A. Atkinson, M. J. Whitehouse, J. Priddle, G. C. Cripps, P. Ward, and M. A. Brandon. South Georgia, Antarctica: a productive, cold water, pelagic ecosystem. *Mar Ecol Prog Ser*, 216:279–308, 2001.

[135] F. Azam and F. Malfatti. Microbial structuring of marine ecosystems. *Nature Reviews Microbiology*, 5(10):782–791, 2007.

[136] F. Azam, D. C. Smith, and J. T. H. The role of the microbial loop in Antarctic pelagic ecosystems. *Polar Research*, 10(1):239–244, 1991.

[137] N. Bailly. 2015. *Bathylagus.* Gill, 1884. In: R. Froese and D. Pauly. Editors. (2015) FishBase. Accessed through: De Broyer, C.; Clarke,A.; Koubbi, P.; Pakhomov, E.; Scott, F.; Vanden Berghe, E. and Danis, B. Eds., 2015. Register of Antarctic Marine Species. Available from: http://www.marinespecies.org/rams/aphia.php?p=taxdetails&id=125888. [Accessed 18/06/2015].

[138] N. Bailly. 2015. *Lycenchelys.* Gill, 1884. In: R. Froese and D. Pauly. Editors. (2015) FishBase. Accessed through: De Broyer, C.; Clarke,A.; Koubbi, P.; Pakhomov, E.; Scott, F.; Vanden Berghe, E. and Danis, B. Eds., 2015. Register of Antarctic Marine Species. Available from: http://www.marinespecies.org/rams/aphia.php?p=taxdetails&id=126103. [Accessed 16/07/2015].

[139] N. Bailly. 2015. *Pseudoscopelus.* Gill, 1884. In: R. Froese and D. Pauly. Editors. (2015) FishBase. Accessed through: De Broyer, C.; Clarke,A.; Koubbi, P.; Pakhomov, E.; Scott, F.; Vanden Berghe, E. and Danis, B. Eds., 2015. Register of Antarctic Marine Species. Available from: http://www.marinespecies.org/rams/aphia.php?p=taxdetails&id=125958. [Accessed 18/06/2015].

[140] B. Baiser, G. J. Russell, and J. L. Lockwood. Connectance determines invasion success via trophic interactions in model food webs. *Oikos*, 119(12):1970–1976, 2010.

[141] T. Ballerini, E. E. Hofmann, D. G. Ainley, K. Daly, M. Marrari, C. A. Ribic, W. O. Smith Jr., and J. H. Steele. Productivity and linkages of the food web of the southern region of the western Antarctic Peninsula continental shelf. *Progress in Oceanography*, 122:10–29, 2014.

[142] C. Banašek-Richter, M.-F. Bersier, L-F.and Cattin, R. Baltensperger, J.-P. Gabriel, Y. Merz, R.E. Ulanowicz, A.F. Tavares, D.D. Williams, P.C Ruiter, K.O. Winemiller, and R.E. Naisbit. Complexity in quantitative food webs. *Ecology*, 90(6):1470–1477, 2009.

[143] C. Banašek-Richter, M. F. Cattin, and L. F. Bersier. Sampling effects and the robustness of quantitative and qualitative food-web descriptors. *Journal of Theoretical Biology*, 226(1):23–32, 2004.

[144] K. Barlow, I. Boyd, J. P. Croxall, K. Reid, I. Staniland, and A. Brierley. Are penguins and seals in competition for Antarctic krill at South Georgia? *Marine Biology*, 140(2):205–213, 2002.

[145] K. E. Barlow and J. P. Croxall. Provisioning behaviour of Macaroni Penguins *Eudyptes chrysolophus*. *Ibis*, 144(2):248–258, 2002.

[146] K. E. Barlow and J. P. Croxall. Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Mar Ecol Prog Ser*, 232:291–304, 2002.

[147] D. K. A. Barnes. A benthic richness hotspot in the Southern Ocean: slope and shelf cryptic benthos of Shag Rocks. *Antarctic Science*, 20(Special Issue 03):263–270, 2008.

[148] E. R. Barrera-Oro, R. J. Casaux, and E. R. Marschoff. Dietary composition of juvenile *Dissostichus eleginoides* (Pisces, Nototheniidae) around Shag Rocks and South Georgia, Antarctica. *Polar Biol*, 28(8):637–641, 2005.

[149] D. A. Beauchamp, D.H. Wahl, B.M. Johnson, C. S. Guy, and M. L. Brown. Predator-prey interactions. *Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland*, pages 765–842, 2007.

[150] J. R. Beck. *Food, moult and age of first breeding in the Cape pigeon, Daption capensis Linnaeus*, volume 21. Br. Antarct. Surv. Bull., 1969.

[151] J. R. Beck and D. W. B. *The biology of Wilson's storm petrel, Oceanites oceanicus (Kuhl), at Signy Island, South Orkney Islands.* British Antarctic Survey, 1972.

[152] E. Benoit and M.J. Rochet. A continuous model of biomass size spectra governed by predation and the effects of fishing on them. *Journal of theoretical Biology*, 226(1):9–21, 2004.

[153] E. L. Berlow, A.-M. Neutel, J. E. Cohen, P. C. De Ruiter, B. Ebenman, M. Emmerson, J. W. Fox, V. A. A. Jansen, J. Iwan Jones, G. D. Kokkoris, D. O. Logofet, A. J. McKane, J. M. Montoya, and O. Petchey. Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, 73(3):585–598, 2004.

[154] S. D. Berrow and J. P. Croxall. The diet of white-chinned petrels *Procellaria aequinoctialis*, Linnaeus 1758, in years of contrasting prey availability at South Georgia. *Antarctic Science*, 11(03):283–292, 1999.

[155] S. D. Berrow, R. I. Taylor, and A. W. A. Murray. Influence of sampling protocol on diet determination of gentoo penguins *Pygoscelis papua* and Antarctic fur seals *Arctocephalus gazella. Polar Biol*, 22(3):156–163, 1999.

[156] S. D. Berrow, A. G. Wood, and P. A. Prince. Foraging Location and Range of White-Chinned Petrels *Procellaria aequinoctialis* Breeding in the South Atlantic. *Journal of Avian Biology*, 31(3):303–311, 2000.

[157] L.-F. Bersier, C. Banašek-Richter, and M-F Cattin. Quantitative descriptors of food-web matrices. *Ecology*, 83(9):2394–2407, 2002.

[158] L.-F. Bersier, P. Dixon, and G. Sugihara. Scale-invariant or scale-dependent behavior of the link density property in food webs: A matter of sampling effort? *The American Naturalist*, 153(6):676–682, 1999.

[159] R. M. Bevan, P. J. Butler, A. J. Woakes, and I. L. Boyd. The Energetics of Gentoo Penguins, *Pygoscelis papua*, during the Breeding Season. *Functional Ecology*, 16(2):175–190, 2002.

[160] J. E. Beyer and B. F. Nielsen. Predator foraging in patchy environments: the interrupted Poisson process (IPP) model unit. *DANA*, 11, 1996. 00017.

[161] W. H Bierman and K.H. Voous. *Birds observed and collected during the whaling expeditions of the Willem Barendsz in the Antarctic, 1946-1947 and 1947-1948,*. E.J. Brill, Leiden, 1950.

[162] J. L. Blanchard. Climate change: A rewired food web. *Nature*, 527(7577):173–174, November 2015.

[163] P. Bocher, Y. Cherel, J.P. Labat, P. Mayzaud, S. Razouls, and P. Jouventin. Amphipod-based food web: *Themisto gaudichaudii* caught in nets and by seabirds in Kerguelen waters, southern Indian Ocean. *Mar Ecol Prog Ser*, 223:261–276, 2001.

[164] P. G. Borboroglu and P. D. Boersma. *Penguins: Natural History and Conservation*. University of Washington Press, 2013.

[165] S. P. Borgatti and M. G. Everett. Two algorithms for computing regular equivalence. *Social Networks*, 15(4):361–376, 1993.

[166] C. Borrvall, B. Ebenman, and J. Tomas. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters*, 3(2):131–136, 2000.

[167] I. L. Boyd. Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins. *Journal of Applied Ecology*, 39(1):103 – 119, 2002.

[168] A. Brandt, S. Brix, W. Brökeland, M. Choudhury, S. Kaiser, and M. Malyutina. Deep-sea isopod biodiversity, abundance, and endemism in the Atlantic sector of the Southern Ocean-Results from the ANDEEP IIII expeditions. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(1617):1760–1775, 2007.

[169] A. Brandt, C. De Broyer, I. De Mesel, K. E. Ellingsen, A. J. Gooday, B. Hilbig, K. Linse, M. R. A. Thomson, and P. A. Tyler. The biodiversity of the deep Southern Ocean benthos. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 362(1477):39–66, 2007.

[170] E. L. Bredesen. Krill and the Antarctic : finding the balance. masters dissertation. the university of british columbia. 2003.

[171] F. Briand and J. E. Cohen. Community food webs have scale-invariant structure. *Nature*, 307(5948):264–267, 1984.

[172] A. S. Brierley, C. Goss, S. A. Grant, J. L. Watkins, K. Reid, M. Belchier, I. Everson, M. J. Jessop, V. Afanasyev, and J. P. Robst. Significant intra-annual variability in krill distribution and abundance at South Georgia revealed by multiple acoustic surveys during 2000/01. *CCAMLR Science*, 9:71–82, 2002.

[173] C. D. Broyer and M. Rauschert. Faunal diversity of the benthic amphipods (Crustacea) of the Magellan region as compared to the Antarctic (preliminary results). *Scientia Marina*, 63(1):281–293, 1999.

[174] J. Bruno and M. O'Connor. Cascading effects of predator diversity and omnivory in a marine food web. *Ecology Letters*, 8(10):1048–1056, 2005.

[175] M. S. Burchett. Food, feeding and behaviour of *Notothenia rossii* nearshore at South Georgia. *Br Antarct Surv Bull*, 61:45–51, 1983.

[176] S. E. Burghart, T. L. Hopkins, G. A. Vargo, and J. J. Torres. Effects of a rapidly receding ice edge on the abundance, age structure and feeding of three dominant calanoid copepods in the Weddell Sea, Antarctica. *Polar Biol*, 22(4):279–288, 1999.

[177] J. F. Burrow, J. W. Horwood, and J. W. Pitchford. The importance of variable timing and abundance of prey for fish larval recruitment. *J. Plankton Res.*, 33(8):1153–1162, 2011.

[178] L. B. Cahoon, C. R. Tronzo, and J. C. Howe. Notes on the Occurrence of *Hyperoche medusarum* (Kroyer) (Amphipoda, Hyperiidae) with Ctenophora off North Carolina, U.S.A. *Crustaceana*, 51(1):95–97, 1986.

[179] R. Casaux, A. Baroni, F. Arrighetti, A. Ramn, and A. Carlini. Geographical variation in the diet of the Antarctic fur seal *Arctocephalus gazella. Polar Biol*, 26(12):753–758, 2003.

[180] R. Casaux, A. Carlini, A. Corbalan, L. Bertolin, and C. Y. DiPrinzio. The diet of the Weddell seal Leptonychotes weddellii at Laurie Island, South Orkney Islands. *Polar biology*, 32(6):833–838, 2009.

[181] R. Casaux and A. Ramón. The diet of the South Georgia shag Phalacrocorax georgianus at South Orkney Islands in five consecutive years. *Polar Biol*, 25(8):557–561, 2002.

[182] E. L. Cavan, F. a. C. Le Moigne, A. J. Poulton, G. A. Tarling, P. Ward, C. J. Daniels, G. M. Fragoso, and R. J. Sanders. Attenuation of particulate organic carbon flux in the Scotia Sea, Southern Ocean, is controlled by zooplankton fecal pellets. *Geophys. Res. Lett.*, 42(3):2014GL062744, 2015.

[183] V. Christensen and C. J. Walters. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*, 172(24):109–139, 2004.

[184] A. Clarke. The biochemical composition of krill, *Euphausia superba* Dana, from South Georgia. *Journal of Experimental Marine Biology and Ecology*, 43(3):221–236, 1980.

[185] A. Clarke. Lipid content of antarctic krill, *Euphausia superba. Journal of Crustacean Biology*, 4:285–294, 1984.

[186] M. R. Clarke, J. P. Croxall, and P. A. Prince. Cephalopod remains in regurgitations of the wandering albatross *Diomedea exulans* L. at South Georgia. *Br. Antarct. Surv. Bull*, 54:9–21, 1981.

[187] S. Clarke, W.D.K. Reid, M. A. Collins, and M. Belchier. Biology and distribution of South Georgia icefish (Pseudochaenichthys georgianus) around South Georgia and Shag Rocks. *Antarctic Science*, 20(04), 2008.

[188] J. E. Cohen, R. A. Beaver, S. H. Cousins, D. L. DeAngelis, L. Goldwasser, K. L. Heong, R. D. Holt, A. J. Kohn, J. H. Lawton, N. Martinez, R. O'Malley, L. M. Page, B. C. Patten, S. L. Pimm, G. A. Polis, M. Rejmanek, T. W. Schoener, K. Schoenly, W. G. Sprules, J. M. Teal, R. E. Ulanowicz, P. H. Warren, H. M. Wilbur, and P. Yodzis. Improving Food Webs. *Ecology*, 74(1):252–258, 1993.

[189] C. O. Coleman. Burrowing, grooming, and feeding behaviour of Paraceradocus, an antarctic amphipod genus (Crustacea). *Polar Biol*, 10(1):43–48, 1989.

[190] M. A. Collins, K. A. Ross, M. Belchier, and K. Reid. Distribution and diet of juvenile Patagonian toothfish on the South Georgia and Shag Rocks shelves (Southern Ocean). *Marine Biology*, 152(1):135–147, 2007.

[191] M. A. Collins, R. S. Shreeve, S. Fielding, and M. H. Thurston. Distribution, growth, diet and foraging behaviour of the yellow-fin notothen *Patagonotothen guntheri* (Norman) on the Shag Rocks shelf (Southern Ocean). *Journal of Fish Biology*, 72(1):271–286, 2008.

[192] M. A. Collins, G. Stowasser, R. Fielding, S an.d Shreeve, J. C. Xavier, H. J. Venables, P. Enderlein, Y. Cherel, and A. Van de Putte. Latitudinal and bathymetric patterns in the distribution and abundance of mesopelagic fish in the Scotia Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 59:189–198, 2012.

[193] M. A. Collins, P. Trathan, S. Grant, D. Davidson, and K. Ross. South Georgia and the South Sandwich Islands Marine Protected Area Management Plan. Management plan 2.0, Government of South Georgia and the South Sandwich Islands, 2013.

[194] J. C. Comiso. Variability and Trends in Antarctic Surface Temperatures from In Situ and Satellite Infrared Measurements. *J. Climate*, 13(10):1674–1696, 2000.

[195] J. W. H. Conroy. *Ecological aspects of the biology of the giant petrel, Macronectes giganteus (Gmelin), in the maritime Antarctic*. British Antarctic Survey, 1972.

[196] A. J. Constable, W. K. de la Mare, David J. A., Inigo E., and D. Miller. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES J. Mar. Sci.*, 57(3):778–791, 2000.

[197] P. Convey, A. Morton, and J. Poncet. Survey of marine birds and mammals of the South Sandwich Islands. *Polar Record*, 35(193):107–124, 1999.

[198] J. T. Cooper and N. Klages. The diets and dietary segregation of sooty albatrosses (Phoebetria spp.) at subantarctic Marion Island. *Antarctic Science*, 7(01):15 – 23, 1995.

[199] N. Coria, M. Libertelli, R. Casaux, and C. Darrieu. Inter-Annual Variation in the Autumn Diet of the Gentoo Penguin at Laurie Island, Antarctica. *Waterbirds: The International Journal of Waterbird Biology*, 23(3):511–517, 2000.

[200] N. R. Coria, G. E. Soave, and D. Montalti. Diet of Cape petrel Daption capense during the post-hatching period at Laurie Island, South Orkney Islands, Antarctica. *Polar Biol*, 18(4):236–239, 1997.

[201] J. Cornejo-Donoso and T. Antezana. Preliminary trophic model of the Antarctic Peninsula Ecosystem (Sub-area CCAMLR 48.1). *Ecological Modelling*, 218(12):1–17, 2008.

[202] M. J. Cox, J. L. Watkins, K. Reid, and A. S. Brierley. Spatial and temporal variability in the structure of aggregations of Antarctic krill (*Euphausia superba*) around South Georgia, 19971999. *ICES J. Mar. Sci.*, 68(3):489–498, 2011.

[203] K. A. Cresswell, G. A. Tarling, S. E. Thorpe, M. T. Burrows, J. Wiedenmann, and M. Mangel. Diel vertical migration of Antarctic krill (*Euphausia superba*) is flexible during advection across the Scotia Sea. *J. Plankton Res.*, 31(10):1265–1281, 2009.

[204] K. A. Cresswell, J. Wiedenmann, and M. Mangel. Can macaroni penguins keep up with climate- and fishing-induced changes in krill? *Polar Biol*, 31(5):641–649, 2008.

[205] J. P. Croxall, R. W. Davis, and M. J. O'Connell. Diving Patterns in Relation to Diet of Gentoo and Macaroni Penguins at South Georgia. *The Condor*, 90(1):157–167, 1988.

[206] J. P. Croxall and J. R. Furse. Food of Chinstrap Penguins *Pygoscelzs Antarctica* and Macaroni Penguins *Eudyptes Chrysolophus* at Elephant Island Group, South Shetland Islands. *Ibis*, 122(2):237–245, 1980.

[207] J. P. Croxall, A. J. Hall, H. J. Hill, A. W. North, and P. G. Rodhouse. The food feeding ecology of the white-chinned petrel *Procellaria aequinoctialis* at South Georgia. *Journal of Zoology*, 237(1):133–150, 1995.

[208] J. P. Croxall, H. J. Hill, R. Lidstone-Scott, M. J. O'connell, and P. A. Prince. Food and feeding ecology of Wilson's storm petrel Oceanites oceanicus at South Georgia. *Journal of Zoology*, 216(1):83–102, 1988.

[209] J. P. Croxall, T. S. McCann, P. A. Prince, and P. Rothery. Reproductive Performance of Seabirds and Seals at South Georgia and Signy Island, South Orkney Islands, 19761987: Implications for Southern Ocean Monitoring Studies. In Professor Dr Dietrich Sahrhage, editor, *Antarctic Ocean and Resources Variability*, pages 261–285. Springer Berlin Heidelberg, 1988.

[210] J. P. Croxall and A. W. North. Fish prey of Wilson's storm petrel Oceanites oceanicus at South Georgia. *British Antarctic Survey Bulletin*, 78:37–42, 1988.

[211] J. P. Croxall and P. A. Prince. Seabirds as predators on marine resources, especially krill, at South Georgia. *Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge*, pages 347–368, 1987.

[212] J. P. Croxall, P. A. Prince, and K. Reid. Dietary segregation of krill-eating South Georgia seabirds. *Journal of Zoology*, 242(3):531–556, 1997.

[213] J. P. Croxall, P. A. Prince, and C. Ricketts. Relationships Between Prey Life-Cycles and the Extent, Nature and Timing of Seal and Seabird Predation in the Scotia Sea. In Prof Walter R. Siegfried, Dr Pat R. Condy, and Dr Richard M. Laws, editors, *Antarctic Nutrient Cycles and Food Webs*, pages 516–533. Springer Berlin Heidelberg, 1985.

[214] J. P. Croxall, K Reid, and P. A. Prince. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series*, 177:115–131, 1999.

[215] J. P. Croxall, C. Ricketts, and R. A. Prince. Impact of Seabirds on Marine Resources, Especially Krill, of South Georgia Waters. In G. C. Whittow and H. Rahn, editors, *Seabird Energetics*, pages 285–317. Springer US, 1984.

[216] J. P. Croxall, W. K. Steele, S. J. McInnes, and P. A. Prince. Breeding distribution of the Snow Petrel Pagodroma nivea. *Marine Ornithology*, 23(2):69–99, 1995.

[217] G. A. Daneri and N. R. Coria. The diet of Antarctic fur seals, *Arctocephalus gazella*, during the summer-autumn period at Mossman Peninsula, Laurie Island (South Orkneys). *Polar Biol*, 11(8):565–566, 1992.

[218] G. A. Daneri and N. R. Coria. Fish prey of Antarctic fur seals, Arctocephalus gazella, during the summer-autumn period at Laurie Island, South Orkney Islands. *Polar Biol*, 13(5):287–289, 1993.

[219] J-C. Dauvin and Denise Bellan-Santini. An overview of the amphipod genus Haploops (Ampeliscidae). *Journal of the Marine Biological Association of the United Kingdom*, 70(04):887 – 903, 1990.

[220] R. W. Davis, J. P. Croxall, and M. J. O'Connell. The Reproductive Energetics of Gentoo (*Pygoscelis papua*) and Macaroni (*Eudyptes chrysolophus*) Penguins at South Georgia. *Journal of Animal Ecology*, 58(1):59–74, 1989.

[221] J. H. P. Dawes and M. O. Souza. A derivation of Holling's type I, II and III functional responses in predatorprey systems. *Journal of Theoretical Biology*, 327:11–22, 2013.

[222] C. De Broyer and A. Jadewska. Biogeographic patterns of Southern Ocean benthic Amphipods. In C. De Broyer, P. Koubbi, H.J. Griffiths, B. Raymond, C. d'Udekem d'Acoz, A.P. Van de Putte, B. Danis, B. David, S. Grant, J. Gutt, C. Held, G. Hosie, F. Huettmann, A. Post, and Y. Ropert-Coudert, editors, *Biogeographic Atlas of the Southern Ocean*, pages 155–165. Scientific Committee on Antarctic Research, Cambridge UK, 2014.

[223] G. de la Rosa. Comparative feeding ecology of Patagonian toothfish (*Dissostichus eleginoides*) in the Southerwestern Atlantic. *CCAMLR Science*, 4:105–124, 1997.

[224] J. H. Dearborn, K. C. Edwards, and D. B. Fratt. *Diet, feeding behaviour, and surface morphology of the multi-armed Antarctic sea star Labidiaster annulatus (Echinodermata: Asteroidea).* 1991.

[225] D. W. Doidge and J. P. Croxall. Diet and energy budget of the Antarctic fur seal, *Arctocephalus gazella*, at South Georgia. In *Antarctic nutrient cycles and food webs*, pages 543–550. Springer, 1985.

[226] J. Dolan eds. *Ceratium*. Encyclopedia of Life. Available from: http://eol.org/pages/12149/overview. [Accessed 18/05/2015].

[227] J. Dolan eds. *Dinophysis*. Encyclopedia of Life. Available from: http://eol.org/pages/13039/overview. [Accessed 28/05/2015].

[228] G. Duhamel, P.-A Hulley, R. Causse, P. Koubbi, M. Vacchi, P. Pruvost, S. Vigetta, J.-O. Irisson, S. AU Belchier Mormde, M., J. AU Jones C.D. A. AU Detrich Dettai, H.W. AU Gutt, K.-H. Kock, L.J. Lopez Abellan, and A.P. Van de Putte. Biogeographic Patterns Of Fish. In C. De Broyer, P. Koubbi, H.J. Griffiths, B. Raymond, C. d'Udekem d'Acoz, A.P. Van de Putte, B. Danis, B. David, S. Grant, J. Gutt, C. Held, G. Hosie, F. Huettmann, A. Post, and Y. Ropert-Coudert, editors, *Biogeographic Atlas of the Southern Ocean*, pages 328–362. Scientific Committee on Antarctic Research, Cambridge UK, 2014.

[229] M. J. Dunn, J. R. D. Silk, and P. N. Trathan. Post-breeding dispersal of Adélie penguins *Pygoscelis adeliae* nesting at Signy Island, South Orkney Islands. *Polar Biol*, 34(2):205–214, 2010.

[230] J. A. Dunne, R. J. Williams, and N. D. Martinez. Network structure and robustness of marine food webs. *Mar Ecol Prog Ser*, 273:291–302, 2004.

[231] S. Z. El-Sayed. History and evolution of primary productivity studies of the Southern Ocean. *Polar Biol*, 28(6):423–438, 2005.

[232] S. P. Ellner, L. E. Jones, L. D. Mydlarz, and C. D. Harvell. WithinHost Disease Ecology in the Sea Fan Gorgonia ventalina: Modeling the Spatial Immunodynamics of a CoralPathogen Interaction. *The American Naturalist*, 170(6):E143–E161, 2007.

[233] B. A. Fach, E. E. Hofmann, and E. J. Murphy. Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea. Part II: Krill growth and survival. *Deep Sea Research Part I: Oceanographic Research Papers*, 53(6):1011–1043, 2006.

[234] S. Fielding, J. L. Watkins, M. A. Collins, P. Enderlein, and H. J. Venables. Acoustic determination of the distribution of fish and krill across the Scotia Sea in spring 2006, summer 2008 and autumn 2009. *Deep Sea Research Part II: Topical Studies in Oceanography*, 5960:173–188, 2012.

[235] S. Fielding, J. L. Watkins, P. N. Trathan, P. Enderlein, C. M. Waluda, G. Stowasser, G. A. Tarling, and E. J. Murphy. Interannual variability in Antarctic krill (*Euphausia superba*) density at South Georgia, Southern Ocean: 19972013. *ICES J. Mar. Sci.*, page fsu104, 2014.

[236] H. Flores, A. Atkinson, S. Kawaguchi, B. A. Krafft, G. Milinevsky, S. Nicol, C. Reiss, G. A. Tarling, R. Werner, E. Bravo Rebolledo, V. Cirelli, J. CuzinRoudy, S. Fielding, J. J. Groeneveld, M. Haraldsson, A. Lombana, E. Marschoff, B. Meyer, E. A. Pakhomov, E. Rombol, K. Schmidt, V. Siegel, M. Teschke, H. Tonkes, J. Y. Toullec, P. N. Trathan, N. Tremblay, A. P. Van de Putte, J. A. van Franeker, and T. Werner. Impact of climate change on Antarctic krill. *Mar Ecol Prog Ser*, 458:1–19, 2012.

[237] Commission for the Conservation of Antarctic Marine Living Resources. Fishery report 2014: Champsocephalus gunnari south georgia (subarea 48.3). *CCAMLR*, 2014.

[238] Commission for the Conservation of Antarctic Marine Living Resources. Fishery report 2014: Dissostichus eleginoides south georgia (subarea 48.3). *CCAMLR*, 2014.

[239] Commission for the Conservation of Antarctic Marine Living Resources. Fishery report 2014: Dissostichus spp. south sandwich islands (subarea 48.4). *CCAMLR*, 2014.

[240] J. Forcada, D. Malone, J. A. Royle, and I. J. Staniland. Modelling predation by transient leopard seals for an ecosystem-based management of Southern Ocean fisheries. *Ecological Modelling*, 220(12):1513–1521, 2009.

[241] D. W. Franks, G. D. Ruxton, and J. Richard. Sampling animal association networks with the gambit of the group. 64(3):493–503, 2010.

[242] W. R. Fraser and E. E. Hofmann. A predators perspective on causal links between climate change, physical forcing and ecosystem response. *Mar Ecol Prog Ser*, 265:1–15, 2003.

[243] W. R. Fraser, W. Z. Trivelpiece, D. G. Ainley, and S. G. Trivelpiece. Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biol*, 11(8):525–531, 1992.

[244] D. B. Fratt and J. H. Dearborn. Feeding biology of the Antarctic brittle star Ophionotus victoriae (Echinodermata: Ophiuroidea). *Polar Biol*, 3(3):127–139, 1984.

[245] R. Froese and 2015 D. Pauly. Ed. FishBase. Available from: WorldWideWebelectronicpublication.www.fishbase.org [Accessed 01/04/2015].

[246] E. A. Fulton, A. D. M. Smith, and C. R. Johnson. Effect of complexity on marine ecosystem models. *Marine Ecology Progress Series*, 253:1–16, 2003.

[247] E. A Fulton, A. D. M Smith, and C. R Johnson. Biogeochemical marine ecosystem models I: IGBEMa model of marine bay ecosystems. *Ecological Modelling*, 174(3):267–307, 2004.

[248] B. Gauzens, S. Legendre, X. Lazzaro, and G. Lacroix. Food-web aggregation, methodological and functional issues. *Oikos*, 122(11):1606–1615, 2013.

[249] J. Gerritsen and J. R. Strickler. Encounter Probabilities and Community Structure in Zooplankton: a Mathematical Model. *J. Fish. Res. Bd. Can.*, 34(1):73–82, 1977.

[250] L. Goldwasser and J. Roughgarden. Construction and Analysis of a Large Caribbean Food Web. *Ecology*, 74(4):1216–1233, 1993.

[251] L. Goldwasser and J. Roughgarden. Sampling Effects and the Estimation of Food-Web Properties. *Ecology*, 78(1):41–54, 1997.

[252] A. F. González and P. G. Rodhouse. Fishery biology of the seven star flying squid Martialia hyadesi at South Georgia during winter. *Polar Biol*, 19(4):231–236, 1998.

[253] J. A. Green, P. J. Butler, A. J. Woakes, and I. L. Boyd. Energy requirements of female Macaroni Penguins breeding at South Georgia. *Functional Ecology*, 16(5):671–681, 2002.

[254] A. J. Hamilton, Y. Basset, K. K. Benke, P. S. Grimbacher, S. E. Miller, V. Novotnỳ, G. A. Samuelson, N. E. Stork, G. D. Weiblen, and J. D. L. Yen. Quantifying Uncertainty in Estimation of Tropical Arthropod Species Richness. *The American Naturalist*, 176(1):90–95, 2010.

[255] J. Hammock Eds. *Epimeriidae*. Encyclopedia of Life. Available from: http://maps3.eol.org/pages/1262/overview. [Accessed 29/05/2015].

[256] M. J. Haro-Garay. Diet and Functional Morphology of the Mandible of Two Planktonic Amphipods from the Strait of Georgia, British Columbia, Parathemisto Pacifica (Stebbing, 1888) and Cyphocaris Challengeri (Stebbing, 1888). *Crustaceana*, 76(11):1291–1312, 2003.

[257] R. P. Hewitt, J. Watkins, M. Naganobu, V. Sushin, A. S. Brierley, D. Demer, S. Kasatkina, Y. Takao, C. Goss, A. Malyshko, M. Brandon, S. Kawaguchi, V. Siegel, P. Trathan, J. Emery, I. Everson, and D Miller. Biomass of Antarctic krill in the Scotia Sea in January/February 2000 and its use in revising an estimate of precautionary yield. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(1213):1215–1236, 2004.

[258] S. Hill, M. T. Burrows, and R. N. Hughes. Adaptive search in juvenile plaice foraging for aggregated and dispersed prey. *Journal of Fish Biology*, 61(5):1255–1267, 2002.

[259] S. L. Hill, K. Keeble, A. Atkinson, and E. J. Murphy. A foodweb model to explore uncertainties in the South Georgia shelf pelagic ecosystem. *Deep Sea Research Part II: Topical Studies in Oceanography*, 5960:237–252, 2012.

[260] S. L. Hill and J. Matthews. The sensitivity of multiple output statistics to input parameters in a krill-predator-fishery ecosystem dynamics model.(Report). 20:97, 2013.

[261] S. L. Hill, E. J. Murphy, K. Reid, P. N. Trathan, and A. J. Constable. Modelling Southern Ocean ecosystems: krill, the food-web, and the impacts of harvesting. *Biological Reviews*, 81(4):581–608, 2006.

[262] S. L. Hill, T. Phillips, and A. Atkinson. Potential Climate Change Effects on the Habitat of Antarctic Krill in the Weddell Quadrant of the Southern Ocean. *PLoS ONE*, 8(8):e72246, 2013.

[263] S. L Hill, K. Reid, and A. W North. Recruitment of mackerel icefish (*Champsocephalus gunnari*) at South Georgia indicated by predator diets and its relationship with sea surface temperature. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(11):2530–2537, 2005.

[264] S. L. Hill, K. Reid, S. Thorpe, J. Hinke, and G. Watters. A compilation of parameters for a krill-fishery predator model of the Scotia Sea and Antarctic Peninsula (working paper version), 2006.

[265] G. Hofmeyr. *Arctocephalus gazella*. The IUCN Red List of Threatened Species. Version 2015.2. Available from: http://www.iucnredlist.org. [Accessed 27/08/2015].

[266] O. T. Hogg, D. K. A. Barnes, and H. J. Griffiths. Highly Diverse, Poorly Studied and Uniquely Threatened by Climate Change: An Assessment of Marine Biodiversity on South Georgia's Continental Shelf. *PLoS ONE*, 6(5):e19795, 2011.

[267] O. Holm-Hansen, M. Kahru, C. D. Hewes, S. Kawaguchi, T. Kameda, V. A. Sushin, I. Krasovski, J. Priddle, R. Korb, R. P. Hewitt, and B. G. Mitchell. Temporal and spatial distribution of chlorophyll-a in surface waters of the Scotia Sea as determined by both shipboard measurements and satellite data. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(1213):1323–1331, 2004.

[268] O. Holm-Hansen, M. Naganobu, S. Kawaguchi, T. Kameda, I. Krasovski, P. Tchernyshkov, J. Priddle, R. Korb, M. Brandon, D. Demer, R. P. Hewitt, M. Kahru, and C. D. Hewes. Factors influencing the distribution, biomass, and productivity of phytoplankton in the Scotia Sea and adjoining waters. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(1213):1333–1350, 2004.

[269] T. Hopkins, D. G. Ainley, J. J. Torres, and T. M. Lancraft. Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell confluence region during spring (1983). 13(6):389–397, 1993.

[270] C. Horswill, J. Matthiopoulos, J. A. Green, M. P. Meredith, J. Forcada, H. Peat, M. Preston, P. N. Trathan, and N. Ratcliffe. Survival in macaroni penguins and the relative importance of different drivers: individual traits, predation pressure and environmental variability. *Journal of Animal Ecology*, pages n/a–n/a, 2014.

[271] G. W Hosie, M. B Schultz, J. A Kitchener, T. G Cochran, and K Richards. Macrozooplankton community structure off East Antarctica (80150E) during the Austral summer of 1995/1996. *Deep Sea Research Part II: Topical Studies in Oceanography*, 47(1213):2437–2463, 2000.

[272] S. Hunter. The food and feeding ecology of the giant petrels Macronectes halli and M. giganteus at South Georgia. *Journal of Zoology*, 200(4):521–538, 1983.

[273] S. Hunter. Breeding biology and population dynamics of giant petrels Macronectes at South Georgia (Aves: Procellariiformes). *Journal of Zoology*, 203(4):441–460, 1984.

[274] E. J. Hyslop. Stomach contents analysis–a review of methods and their application. *Journal of Fish Biology*, 17(4):411–429, 1980.

[275] T. Ichii and H. Kato. Food and daily food consumption of southern minke whales in the Antarctic. *Polar Biol*, 11(7):479–487, 1991.

[276] S. Isari and E. Saiz. Feeding performance of the copepod Clausocalanus lividus (Frost and Fleminger 1968). *J. Plankton Res.*, page fbq149, 2010.

[277] M. Jangoux and J. M. Lawrence. *Echinoderm Nutrition.* CRC Press, 1982.

[278] C. G. Jones, J. H. Lawton, and M. Shachak. Organisms as Ecosystem Engineers. *Oikos*, 69(3):373–386, 1994.

[279] C. D. Jones K.-H. Kock. The biology of the icefish Cryodraco antarcticus Dollo, 1900 (Pisces, Channichthyidae) in the southern Scotia Arc (Antarctica). *Polar Biology - POLAR BIOL*, 25(6):416–424, 2002.

[280] A. Kato, T. D. Williams, T. R. Barton, and S. Rodwell. Short-term variation in the winter diet of gentoo penguins *Pygoscelis papua* at South Georgia during July 1989. *Marine Ornithology*, 19(1):31–38, 1991.

[281] F. Képès. *Biological networks.* World Scientific, 2007.

[282] G. A. Knox. *Biology of the Southern Ocean, Second Edition.* CRC Press, 2006.

[283] K. H. Kock. Fischereibiologische Untersuchungen an drei antarktischen Fischarten: *Champsocephalus gunnari* Lonnberg, 1904. *Chaenocephalus aceratus*, 1981.

[284] K. H. Kock. Marine consumers: Fish and squid. *Environment International*, 13(1):37–45, 1987.

[285] K. H. Kock. *Understanding CCAMLR's approach to management.* CCAMLR Hobart, Australia, 2000.

[286] K. H. Kock, S. Wilhelms, I. Everson, and J. Grger. Variations in the diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* at South Georgia (Antarctic). *Marine Ecology Progress Series*, 108(1):43–58, 1994.

[287] R. E. Korb, M. J. Whitehouse, S. E. Thorpe, and M. Gordon. Primary production across the Scotia Sea in relation to the physico-chemical environment. *Journal of Marine Systems*, 57(34):231–249, 2005.

[288] R. E. Korb, M. J. Whitehouse, P. Ward, M. Gordon, H. J. Venables, and A. J. Poulton. Regional and seasonal differences in microplankton biomass, productivity, and structure across the Scotia Sea: Implications for the export of biogenic carbon. *Deep Sea Research Part II: Topical Studies in Oceanography*, 5960:67–77, 2012.

[289] Primicerio R. Fossheim M. Dolgov A. V. Kortsch, S. and M. Aschan. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proc. R. Soc. B*, 282(1814):20151546, September 2015.

[290] T. M. Lancraft, K. R. Reisenbichler, B. H. Robison, T. L. Hopkins, and J. J. Torres. A krill-dominated micronekton and macrozooplankton community in Croker Passage, Antarctica with an estimate of fish predation. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(1719):2247–2260, 2004.

[291] T. M. Lancraft, J. J. Torres, and T. L. Hopkins. Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). *Polar Biol*, 9(4):225–233, 1989.

[292] T. J. Lavery, R.B., P. Gill, J. Seymour, L. Seuront, G. Johnson, J. G. Mitchell, and V. Smetacek. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. *Proceedings of the Royal Society of London B: Biological Sciences*, 277(1699):3527–3531, 2010.

[293] M. M. Libertelli, N. Coria, and G. Marateo. Diet of the Adlie penguin during three consecutive chick rearing periods at Laurie Island. *Pol Polar Res*, 24(2):133–142, 2003.

[294] S. Libralato, V. Christensen, and D. Pauly. A method for identifying keystone species in food web models. *Ecological Modelling*, 195(34):153–171, 2006.

[295] G. M. Liddle. Interannual variation in the breeding biology of the Antarctic prion Pachyptila desolata at Bird Island, South Georgia. *Journal of Zoology*, 234(1):125–139, 1994.

[296] J. S. Link, C. A. Griswold, E. M. Methratta, and J. Gunnard. Documentation for the energy modeling and analysis eXercise (EMAX). *Northeast Fisheries Science Center Reference Document*, pages 06–15, 2006.

[297] G. S. Lishman. The food and feeding ecology of Adélie penguins (*Pygoscelis adeliae*) and Chinstrap penguins (P. antarctica) at Signy Island, South Orkney Islands. *Journal of Zoology*, 205(2):245–263, 1985.

[298] A-N. Lörz, K. Linse, P. J. Smith, and D. Steinke. First Molecular Evidence for Underestimated Biodiversity of Rhachotropis (Crustacea, Amphipoda), with Description of a New Species. *PLoS ONE*, 7(3):e32365, 2012.

[299] J. J. Luczkovich, S. P. Borgatti, J. C. Johnson, and M. G. Everett. Defining and measuring trophic role similarity in food webs using regular equivalence. *Journal of Theoretical Biology*, 220(3):303–321, 2003.

[300] A. S. Lynnes, K. Reid, and J. P. Croxall. Diet and reproductive success of Adlie and chinstrap penguins: linking response of predators to prey population dynamics. *Polar Biol*, 27(9):544–554, 2004.

[301] A. P. Mackey, A. Atkinson, S. L. Hill, P. Ward, N. J. Cunningham, N. M. Johnston, and E. J. Murphy. Antarctic macrozooplankton of the southwest Atlantic sector and Bellingshausen Sea: Baseline historical distributions (Discovery Investigations, 19281935) related to temperature and food, with projections for subsequent ocean warming. *Deep Sea Research Part II: Topical Studies in Oceanography*, 5960:130–146, 2012.

[302] C. Main and M. Collins. Diet of the Antarctic starry skate *Amblyraja georgiana* (Rajidae, Chondrichthyes) at South Georgia (Southern Ocean). *Polar Biology*, 34(3), 2011.

[303] C. E. Main, M. A. Collins, R. Mitchell, and M. Belchier. Identifying patterns in the diet of mackerel icefish (*Champsocephalus gunnari*) at South Georgia using bootstrapped confidence intervals of a dietary index. *Polar Biol*, 32(4):569–581, 2009.

[304] S. Marino, I. B. Hogue, C. J. Ray, and D. E. Kirschner. A methodology for performing global uncertainty and sensitivity analysis in systems biology. *Journal of Theoretical Biology*, 254(1):178–196, 2008.

[305] N. D. Martinez. Artifacts or Attributes? Effects of Resolution on the Little Rock Lake Food Web. *Ecological Monographs*, 61(4):367–392, 1991.

[306] N. D. Martinez. Effects of Resolution on Food Web Structure. *Oikos*, 66(3):403–412, 1993.

[307] N. D. Martinez, B. A. Hawkins, and B. P. Dawah, H. A.and Feifarek. Effects of Sampling Effort on Characterization of Food-Web Structure. *Ecology*, 80(3):1044–1055, 1999.

[308] N. D. Martinez and J. H. Lawton. Scale and Food-Web Structure: From Local to Global. *Oikos*, 73(2):148–154, 1995.

[309] S. Mathot, J-M. Dandois, and C. Lancelot. Gross and net primary production in the Scotia-Weddell Sea sector of the Southern Ocean during spring 1988. *Polar Biol*, 12(2):321–332, 1992.

[310] J. E. McKenna Jr. Trophic relationships within the Antarctic demersal fish community of South Georgia Island. *Fishery Bulletin*, 89(4):643–654, 1991.

[311] J. Melbourne-Thomas, A. Constable, S. Wotherspoon, and B. Raymond. Testing Paradigms of Ecosystem Change under Climate Warming in Antarctica. *PLoS ONE*, 8(2):e55093, 2013.

[312] M. P. Meredith, E. J. Murphy, E. J. Hawker, J. C. King, and M. I. Wallace. On the interannual variability of ocean temperatures around South Georgia, Southern Ocean: Forcing by El Nio/Southern Oscillation and the Southern Annular Mode. *Deep Sea Research Part II: Topical Studies in Oceanography*, 55(1819):2007–2022, 2008.

[313] S. J. Metcalf, J. M. Dambacher, A. J. Hobday, and J. M. Lyle. Importance of trophic information, simplification and aggregation error in ecosystem models. *Mar Ecol Prog Ser*, 360:25–36, 2008.

[314] C. Metz. Feeding of Oncaea curvata (Poecilostomatoida, Copepoda). *Mar Ecol Prog Ser*, 169:229–235, 1998.

[315] E. J. Murphy, R. D. Cavanagh, E. E. Hofmann, S. L. Hill, A. J. Constable, D. P. Costa, M. H. Pinkerton, N. M. Johnston, P. N. Trathan, J. M. Klinck, D. A. Wolf-Gladrow, K. L. Daly, O. Maury, and S. C. Doney. Developing integrated models of Southern Ocean food webs: Including ecological complexity, accounting for uncertainty and the importance of scale. *Progress in Oceanography*, 102:74–92, 2012.

[316] E. J. Murphy, E. E. Hofmann, J. L. Watkins, N. M. Johnston, A. Piones, T. Ballerini, S. L. Hill, P. N. Trathan, G. A. Tarling, R. A. Cavanagh, E. F. Young, S. E. Thorpe, and P. Fretwell. Comparison of the structure and function of Southern Ocean regional ecosystems: The Antarctic Peninsula and South Georgia. *Journal of Marine Systems*, 109110:22–42, 2013.

[317] E. J. Murphy and K Reid. Modelling Southern Ocean krill population dynamics: biological processes generating fluctuations in the South Georgia ecosystem. *Marine Ecology Progress Series*, 217:175–189, 2001.

[318] E. J. Murphy, S. E. Thorpe, J. L. Watkins, and R. Hewitt. Modeling the krill transport pathways in the Scotia Sea: spatial and environmental connections generating the seasonal distribution of krill. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(1213):1435–1456, 2004.

[319] E. J. Murphy, P. N. Trathan, I. Everson, G. Parkes, and F. Daunt. Krill fishing in the Scotia Sea in relation to bathymetry, including the detailed distribution around South Georgia. *CCAMLR Sci*, 4:1–17, 1997.

[320] E. J. Murphy, J. L. Watkins, P. N. Trathan, K. Reid, M. P. Meredith, S. E. Thorpe, N. M. Johnston, A. Clarke, G. A. Tarling, M. A. Collins, J. Forcada, R. S. Shreeve, A. Atkinson, R. Korb, M. J. Whitehouse, P. Ward, P. G. Rodhouse, P. Enderlein, A. G. Hirst, A. R. Martin, S. L. Hill, I. J. Staniland, D. W. Pond, D. R. Briggs, N. J. Cunningham, and A. H. Fleming. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. *Phil. Trans. R. Soc. B*, 362(1477):113–148, 2007.

[321] A.-M. Neutel, J. A. P. Heesterbeek, and P. C. De Ruiter. Stability in real food webs: weak links in long loops. *Science*, 296(5570):1120–1123, 2002.

[322] A.-M. Neutel, J. A. P. Heesterbeek, J. van de Koppel, G. Hoenderboom, A. Vos, C. Kaldeway, F. Berendse, and P. C. de Ruiter. Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449(7162):599–602, 2007.

[323] S. Nicol, J. Foster, and S. Kawaguchi. The fishery for Antarctic krill recent developments. *Fish and Fisheries*, 13(1):30–40, 2012.

[324] S. Nishida and S. Ohtsuka. Specialized feeding mechanism in the pelagic copepod genus Heterorhabdus (Calanoida: Heterorhabdidae), with special reference to the mandibular tooth and labral glands. *Marine Biology*, 126(4):619–632, 1996.

[325] A. W. North. Fish in the diet of Antarctic fur seals (*Arctocephalus gazella*) at South Georgia during winter and spring. *Antarctic Science*, 8(02):155–160, 1996.

[326] A. W. North, J. P. Croxall, and D. W. Doidge. Fish prey of the antarctic fur seal *Arctocephalus gazella* at south georgia. *British Antarctic Survey Bulletin*, (61):27–37, 1983.

[327] A. W. North and P. Ward. *Initial feeding by Antarctic fish larvae during winter at South Georgia.* 1989.

[328] A. W. North and P. Ward. The Feeding Ecology of Larval Fish in an Antarctic Fjord, with Emphasis on *Champsocephalus gunnari.* In Dr K. R. Kerry and Professor Dr G. Hempel, editors, *Antarctic Ecosystems*, volume 13, pages 357–364. Springer Berlin Heidelberg, 1990.

[329] F. Nyssen. *Role of benthic amphipods in Antarctic trophodynamics: a multidisciplinary study.* Ph. D. thesis, Universite de Liege, 2005.

[330] F. Nyssen, T. Brey, P. Dauby, and M. Graeve. Trophic position of Antarctic amphipods: enhanced analysis by a 2-dimensional biomarker assay. *Marine Ecology. Progress Series*, 300, 2005.

[331] B. S. Obst. Densities of Antarctic seabirds at sea and the presence of the krill *Euphausia superba. The Auk*, pages 540–549, 1985.

[332] S. Ohtsuka and T. Onbé. Evidence of selective feeding on larvaceans by the pelagic copepod Candacia bipinnata (Calanoida: Candaciidae). *J. Plankton Res.*, 11(4):869–872, 1989.

[333] O. Olsson and A. W. North. Diet of the King Penguin Aptenodytes patagonicus during three summers at South Georgia. *Ibis*, 139(3):504–512, 1997.

[334] V. Øresland and P. Ward. Summer and winter diet of four carnivorous copepod species around South Georgia. *Marine ecology progress series. Oldendorf*, 98(1):73–78, 1993.

[335] A. H. Orsi, T. Whitworth, and W. D. Nowlin Jr. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Research Part I: Oceanographic Research Papers*, 42(5):641–673, 1995.

[336] B. C. Osborne. Aspects of the breeding biology and feeding behaviour of the brown skua *Catharacta Lonnbergi* on Bird Island, South Georgia. (66), 1985.

[337] C. Green P. N. Trathan. Foraging dynamics of macaroni penguins *Eudyptes chrysolophus* at South Georgia during brood-guard. *Marine Ecology-progress Series*, 323:239–251, 2006.

[338] R. K. Pachauri, M. R. Allen, V. R. Barros, J. Broome, W. Cramer, R. Christ, J. A. Church, L. Clarke, Q. Dahe, P. Dasgupta, and others. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. 2014.

[339] R. Paine. Food Webs: road maps of interactions or grist for theoretical development? *Ecology*, 69:1648–1654, 1988.

[340] E. A. Pakhomov, P. W. Froneman, and R. Perissinotto. Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. *Deep Sea Research Part II: Topical Studies in Oceanography*, 49(910):1881–1907, 2002.

[341] E. A. Pakhomov and R. Perissinotto. Trophodynamics of the hyperiid amphipod *Themisto gaudichaudii* in the South Georgia region during late austral summer. *Marine ecology progress series. Oldendorf*, 134(1):91–100, 1996.

[342] E. A. Pakhomov, R. Perissinotto, P. W. Froneman, and D. G. M. Miller. Energetics and feeding dynamics of *Euphausia superba* in the South Georgia region during the summer of 1994. *J. Plankton Res.*, 19(4):399–423, 1997.

[343] M. L. D. Palomares, P. Provost, T. Pitcher, and D. Pauly. Modeling Antarctic marine ecosystems. *Fisheries Centre Research Report*, 13(7), 2005.

[344] N. Wilson P. Leary K. S. Schulz K. Lans L. Walley J. A. Hammock A. Goddard J. Rice M. Studer J. T. G. Holmes Parr, C. S. and Jr. R. J. Corrigan. The Encyclopedia of Life v2. Providing global access to knowledge about life on earth. Biodiversity data journal 2. e1079, doi:10.3897/bdj.2.e1079. Available from: http://eol.org/. [Accessed 27/08/2015].

[345] A. F. Pasternak and S. B. Schnack-Schiel. Feeding of Ctenocalanus citer in the eastern Weddell Sea: low in summer and spring, high in autumn and winter. *Polar Biol*, 30(4):493–501, 2006.

[346] D. Pauly, V. Christensen, and C. Walters. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES J. Mar. Sci.*, 57(3):697–706, 2000.

[347] D. Pauly, A. W. Trites, E. Capuli, and V. Christensen. Diet composition and trophic levels of marine mammals. *ICES J. Mar. Sci.*, 55(3):467–481, 1998.

[348] M. R. Payne. Fur seals textitArctocephalus tropicalis and A. gazella crossing the Antarctic Convergence at South Georgia : Mammalia. *Mammalia*, 43(1):93–98, 1979.

[349] R. Perissinotto and E. A. Pakhomov. Feeding association of the copepod Rhincalanus gigas with the tunicate salp Salpa thompsoni in the southern ocean. *Marine Biology*, 127(3):479–483, 1997.

[350] K. L. Phillips and G. D. Jackson. Predation on myctophids by the squid Moroteuthis ingens around Macquarie and Heard Islands: stomach contents and fatty acid analyses. *Marine Ecology-progress Series*, 215:179–189, 2001.

[351] R.A. Phillips, B. Phalan, and I.P. Forster. Diet and long-term changes in population size and productivity of brown skuas *Catharacta antarctica lonnbergi* at Bird Island, South Georgia. *Polar Biology*, 27(9), 2004.

[352] C. F. Phleger, M. M. Nelson, B. Mooney, and P. D. Nichols. Lipids of Antarctic salps and their commensal hyperiid amphipods. *Polar Biol*, 23(5):329–337, 2000.

[353] U. Piatkowski and P. G. Rodhouse. Nekton community of the Scotia Sea as sampled by the RMT 25 during austral summer. *Marine Ecology Progress Series*, 112(1-2):13–28, 1994.

[354] G. M. Pilling, M. G. Purves, T. M. Daw, D. A. Agnew, and J. C. Xavier. The stomach contents of Patagonian toothfish around South Georgia (South Atlantic). *Journal of Fish Biology*, 59(5):1370–1384, 2001.

[355] S. L. Pimm, J. H. Lawton, and J. E. Cohen. Food web patterns and their consequences. *Nature*, 350(6320):669–674, 1991.

[356] S. L. Pimm and J. C. Rice. The dynamics of multispecies, multi-life stage models of aquatic food webs. *Theoretical Population Ecology*, 32:303–325, 1987.

[357] L. Pinkas, M. S. Oliphant, and I. L. K. Iverson. Fish Bulletin 152. Food Habits of Albacore, Bluefin Tuna, and Bonito In California Waters. *Scripps Institution of Oceanography Library*, 1970.

[358] M. H. Pinkerton, J. M. Bradford-Grieve, and S. M. Hanchet. A balanced model of the food web of the Ross Sea, Antarctica. *CCAMLR Science*, 17:1–31, 2010.

[359] J. K. Pinnegar, J. L. Blanchard, S. Mackinson, R. D. Scott, and D. E. Duplisea. Aggregation and removal of weak-links in food-web models: system stability and recovery from disturbance. *Ecological Modelling*, 184(24):229–248, 2005.

[360] J. W. Pitchford and J. Brindley. Prey patchiness, predator survival and fish recruitment. *Bull. Math. Biol.*, 63(3):527–546, 2001.

[361] J. W. Pitchford, A. James, and J. Brindley. Optimal foraging in patchy turbulent environments. *Mar Ecol Prog Ser*, 256:99–110, 2003.

[362] G. A. Polis. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist*, 138:123–155, 1991.

[363] S. Poncet and J. Poncet. A survey of penguin breeding populations at the South Orkney Islands. *Br. Antarct. Surv. Bull*, 68:71–81, 1985.

[364] J Priddle, I. L Boyd, M. J Whitehouse, E. J Murphy, and J. P Croxall. Estimates of Southern Ocean primary productionconstraints from predator carbon demand and nutrient drawdown. *Journal of Marine Systems*, 17(14):275–288, 1998.

[365] P. A. Prince. The food and feeding ecology of blue petrel (Halobaena caerulea) and dove prion (Pachyptila desolata). *Journal of Zoology*, 190(1):59–76, 1980.

[366] P. A. Prince and P. G. Copestake. Diet and aspects of fairy prions breeding at South Georgia. *Notornis*, 37:59–69, 1990.

[367] RAMS. 2015. *Cumacea* . Watling, L.; Gerken, S. (2015) World Cumacea database. Accessed through: De Broyer, C.; Clarke,A.; Koubbi, P.; Pakhomov, E.; Scott, F.; Vanden Berghe, E. and Danis, B. Eds., 2015. Register of Antarctic Marine Species. Available from: http://www.marinespecies.org/rams/aphia.php?p=taxdetails&id=1137. [Accessed 16/07/2015].

[368] M. J. Raupach, S. Thatje, J. Dambach, P. Rehm, B. Misof, and F. Leese. Genetic homogeneity and circum-Antarctic distribution of two benthic shrimp species of the Southern Ocean, Chorismus antarcticus and Nematocarcinus lanceopes. *Marine Biology*, 157(8):1783–1797, 2010.

[369] P. Raven, G. Johnson, K. Mason, J. B. Losos, and S. S. Singer. *Biology.* Mc Graw Hill Higher Education, United State, eighth edition edition, 2008.

[370] B. Raymond, M. Marshall, G. Nevitt, C. L. Gillies, J. van den Hoff, J. S. Stark, M. Losekoot, E. J. Woehler, and A. J. Constable. A Southern Ocean dietary database. *Ecology*, 92(5):1188, 2011.

[371] C. Razouls, F. de Bovée, J. Kouwenberg, and N. et Desreumaux. 2005-1015. *Drepanopus forcipatus*. Diversity and Geographic Distribution of Marine Planktonic Copepods. Available from: http://copepodes.obs-banyuls.fr/en. [Accessed 16/07/2015].

[372] C. Razouls, F. de Bovée, J. Kouwenberg, and N. et Desreumaux. 2005-1015. *Drepanopus forcipatus*. Diversity and Geographic Distribution of Marine Planktonic Copepods. Available from: http://copepodes.obs-banyuls.fr/en. [Accessed 16/07/2015].

[373] C. Razouls, F. de Bovée, J. Kouwenberg, and N. et Desreumaux. 2005-1015. *Pleuromamma robusta*. Diversity and Geographic Distribution of Marine Planktonic Copepods. Available from: http://copepodes.obs-banyuls.fr/en. [Accessed 29/05/2015].

[374] C. Razouls, F. de Bovée, J. Kouwenberg, and N. et Desreumaux. 2005-2015. *Microcalanus longiceps*. Diversity and Geographic Distribution of Marine Planktonic Copepods. Available from: http://copepodes.obs-banyuls.fr/en. [Accessed 16/07/2015].

[375] C. Razouls, F. de Bovée, J. Kouwenberg, and N. et Desreumaux. 2005-2015. *Scaphocalanus dentata*. Diversity and Geographic Distribution of Marine Planktonic Copepods. Available from: http://copepodes.obs-banyuls.fr/en. [Accessed 29/05/2015].

[376] C. Razouls, F. de Bovée, J. Kouwenberg, and N. et Desreumaux. 2005-2015. *Scaphocalanus farrani*. Diversity and Geographic Distribution of Marine Planktonic Copepods. Available from: http://copepodes.obs-banyuls.fr/en/fichesp.php?sp=1485. [Accessed 29/05/2015].

[377] World Register of Marine Species. 2015. WoRMS Editorial Board. Available from: http://www.marinespecies.org/. [Accessed 18/08/2015].

[378] K. Reid and J. P. Y. Arnould. The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biology*, 16(2):105–114, 1996.

[379] K. Reid, J. P Croxall, and T. M. Edwards. Interannual Variation in the Diet of the Antarctic Prion Pachyptila desolata at South Georgia. *Emu*, 97(2), 1997.

[380] K. Reid, D. Davis, and I. J. Staniland. Spatial and temporal variability in the fish diet of Antarctic fur seal (<i>Arctocephalus gazella</i>) in the Atlantic sector of the Southern Ocean. *Canadian Journal of Zoology*, 84(7):1025–1037, 2006.

[381] K. Reid, S. L. Hill, T. C. D. Diniz, and M. A. Collins. Mackerel icefish *Champsocephalus gunnari* in the diet of upper trophic level predators at South Georgia: implications for fisheries management. *Mar Ecol Prog Ser*, 305:153–161, 2005.

[382] K Reid, E. J Murphy, V Loeb, and R. P Hewitt. Krill population dynamics in the Scotia Sea: variability in growth and mortality within a single population. *Journal of Marine Systems*, 36(12):1–10, 2002.

[383] K. Reid, M. Sims, R. W. White, and K. W. Gillon. Spatial distribution of predator/prey interactions in the Scotia Sea: implications for measuring predator/fisheries overlap. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(1213):1383–1396, 2004.

[384] K. Reid, P. N. Trathan, J. P. Croxall, and H. J. Hill. Krill caught by predators and nets: differences between species and techniques. *Marine Ecology Progress Series*, 140(1):13–20, 1996.

[385] K. Reid, J. L. Watkins, E. J. Murphy, P. N. Trathan, S Fielding, and P. Enderlein. Krill population dynamics at South Georgia: implications for ecosystem-based fisheries management. *Mar. Ecol.-Prog. Ser.*, 399:243–252, 2010. WOS:000274774400019.

[386] M.V. Reyes and M. Iguez. Ocurrence of cetaceans in the Scotia Sea during February-March 2013. *Paper SC/65a/SH10 presented ot the IWC scientific commitee. (Unpublished)*, 2013.

[387] M. G. Richardson. The dietary composition of some Antarctic fish. *Br Antarct Surv Bull*, 41(42):113–120, 1975.

[388] J. O. Riede, B. C. Rall, C. Banašek-Richter, S. A. Navarrete, E. A. Wieters, M. C. Emmerson, U. Jacob, and U. Brose. Scaling of food-web properties with diversity and complexity across ecosystems. *Advances in Ecological Research*, 42:139–170, 2010.

[389] J. Roberts, J. C. Xavier, and D. J. Agnew. The diet of toothfish species *Dissostichus eleginoides* and *Dissostichus mawsoni* with overlapping distributions. *Journal of Fish Biology*, 79(1):138–154, 2011.

[390] P. G. Rodhouse, M. R. Clarke, and A. W. A. Murray. Cephalopod prey of the wandering albatross textitDiomedea exulans. *Marine Biology*, 96(1):1–10, 1987.

[391] P. G. Rodhouse, O. Olsson, P. Anker-Nilssen, and A. W. A. Murray. Cephalopod predation by the king penguin Aptenodytes patagonicus from South Georgia. *Marine Ecology Progress Series*, 168:13–19, 1998.

[392] P. G. Rodhouse and U. Piatkowski. Fine-scale distribution of juvenile cephalopods in the Scotia Sea and adaptive allometry of the brachial crown. *Marine Biology*, 124(1):111–117, 1995.

[393] P. G. Rodhouse and P. A. Prince. Cephalopod prey of the black-browed albatross *Diomedea melanophrys* at South Georgia. *Polar Biol*, 13(6):373–376, 1993.

[394] P. G. Rodhouse, M. G. White, and M. R. R. Jones. Trophic relations of the cephalopod Martialia hyadesi (Teuthoidea: Ommastrephidae) at the Antarctic Polar Front, Scotia Sea. *Marine Biology*, 114(3):415–421, 1992.

[395] K. A. Rose, S. W. Christensen, and D. L. DeAngelis. Individual-based modeling of populations with high mortality: A new method based on following a fixed number of model individuals. *Ecological Modelling*, 68(34):273–292, 1993.

[396] A. G. Rossberg, K. D. Farnsworth, K. Satoh, and J. K. Pinnegar. Universal power-law diet partitioning by marine fish and squid with surprising stabilitydiversity implications. *Proc Biol Sci*, 278(1712):1617–1625, 2011.

[397] A. G. Rossberg, K. Yanagi, T. Amemiya, and K. Itoh. Estimating trophic link density from quantitative but incomplete diet data. *J. Theor. Biol.*, 243(2):261–272, 2006.

[398] B. J. Rothschild and T. R. Osborn. Small-scale turbulence and plankton contact rates. *Journal of Plankton Research*, 10(3):465–474, 1988.

[399] U. Rowedder. Feeding ecology of the myctophid-Electrona antarctica (Gunther, 1878) (Teleostei). *Meeresforschung-Reports on Marine Research*, pages 252–263, 1979.

[400] A. Saltelli, K. Chan, and E. M. Scott. *Sensitivity Analysis.* Wiley, 2000.

[401] C. N. de Santana, A. F. Rozenfeld, P. A. Marquet, and C. M. Duarte. Topological properties of polar food webs. *Mar Ecol Prog Ser*, 474:15–26, 2013.

[402] J. L. Sarmiento and M. Bender. Carbon biogeochemistry and climate change. *Photosynth Res*, 39(3):209–234, 1994.

[403] R. A. Saunders. Gymnoscopleus sp. unpublished diet data. 2014.

[404] R. A. Saunders. Protomyctophum sp. unpublished diet data., 2014.

[405] R. A. Saunders, M. A. Collins, E. Foster, R. Shreeve, G. Stowasser, P. Ward, and G. A. Tarling. The trophodynamics of Southern Ocean Electrona (Myctophidae) in the Scotia Sea. *Polar Biology*, 37(6):789–807, 2014.

[406] R. A. Saunders, M. A. Collins, P. Ward, G. Stowasser, R. Shreeve, and G. A. Tarling. Distribution, population structure and trophodynamics of Southern Ocean Gymnoscopelus (Myctophidae) in the Scotia Sea. *Polar Biol*, 38(3):287–308, 2014.

[407] S. Scarabino, V.; Gofas. 2015. *Scaphopoda.* in: Bouchet, P.; Gofas, S.; Rosenberg, G.; Bank, R.A.; Bieler, r., 2015, MolluscaBase. Accessed through: De Broyer, C.; Clarke,A.; Koubbi, P.; Pakhomov, E.; Scott, F.; Vanden Berghe, E. and Danis, B. Eds., 2015. Register of Antarctic Marine Species. Available from: http://www.marinespecies.org/rams/aphia.php?p=taxdetails&id=104. [Accessed 16/07/2015].

[408] M. Scheffer, J. M. Baveco, D. L. DeAngelis, K. A. Rose, and E. H. van Nes. Super-individuals a simple solution for modelling large populations on an individual basis. *Ecological Modelling*, 80(23):161–170, 1995.

[409] K. Schmidt, A. Atkinson, S. Steigenberger, S. Fielding, M. C. M. Lindsay, D. W. Pond, G. A. Tarling, T. A. Klevjer, C. S. Allen, S. Nicol, and E. P. Achterberg. Seabed foraging by Antarctic krill: Implications for stock assessment, bentho-pelagic coupling, and the vertical transfer of iron. *Limnol. Oceanogr.*, 56(4):1411–1428, 2011.

[410] S. B. Schnack-Schiel and W. Hagen. Life-cycle strategies of Calanoides acutus, Calanus propinquus, and Metridia gerlachei (Copepoda: Calanoida) in the eastern Weddell Sea, Antarctica. *ICES J. Mar. Sci.*, 52(3-4):541–548, 1995.

[411] S. B. Schnack-Schiel, E. Isla, and others. The role of zooplankton in the pelagic-benthic coupling of the Southern Ocean. *Scientia marina*, 69(2):39–55, 2005.

[412] T. W. Schoener. Food Webs From the Small to the Large: The Robert H. MacArthur Award Lecture. *Ecology*, 70(6):1559–1589, 1989.

[413] P. Schuchert. 2015. *Hydrozoa.* Accessed through: De Broyer, C.; Clarke,A.; Koubbi, P.; Pakhomov, E.; Scott, F.; Vanden Berghe, E. and Danis, B. Eds., 2015. Register of Antarctic Marine Species. Available from: http://www.marinespecies.org/rams/aphia.php?p=taxdetails&id=1337. [Accessed 16/07/2015].

[414] C. E. Shannon. A Mathematical Theory of Communication. *Bell System Technical Journal*, 27(3):379–423, 1948.

[415] R. S. Shreeve, G. A. Collins, M. A.and Tarling, C. E. Main, and N. M. Ward, P.and Johnston. Feeding ecology of myctophid fishes in the northern Scotia Sea. *Mar Ecol Prog Ser*, 386:221–236, 2009.

[416] V. Siegel and V. Loeb. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Marine ecology progress series. Oldendorf*, 123(1):45–56, 1995.

[417] V. Siegel and S. Nicol. Population Parameters. In Inigo Everson, editor, *Krill*, pages 103–149. Blackwell Science Ltd, 2000.

[418] W. R. Siegfried, P. R. Condy, and R. M. Laws. *Antarctic Nutrient Cycles and Food Webs*. Springer Science & Business Media, 2013.

[419] A. Sirovic, J. A. Hildebrand, and D. Thiele. Baleen whale spatial patterns in the Scotia Sea during January and February 2003. *Journal of Cetacean Reserch and Management*, 8(2), 2006.

[420] V. Smetacek, P. Assmy, and J. Henjes. The role of grazing in structuring Southern Ocean pelagic ecosystems and biogeochemical cycles. *Antarctic Science*, 16(04):541–558, 2004.

[421] P. J. Smith, D. Steinke, S. M. Mcveagh, A. L. Stewart, C. D. Struthers, and C. D. Roberts. Molecular analysis of Southern Ocean skates (Bathyraja) reveals a new species of Antarctic skate. *Journal of Fish Biology*, 73(5):1170–1182, 2008.

[422] S. E. Stammerjohn, D. G. Martinson, R. C. Smith, X. Yuan, and D. Rind. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño. Southern Oscillation and Southern Annular Mode variability. *J. Geophys. Res.*, 113(C3):C03S90, 2008.

[423] V. Storch, B. A. Bluhm, and W. E. Arntz. Microscopic anatomy and ultrastructure of the digestive system of three Antarctic shrimps (Crustacea: Decapoda: Caridea). *Polar Biol*, 24(8):604–614, 2001.

[424] G. Stowasser, A. Atkinson, R. A. R. McGill, R. A. Phillips, M. A. Collins, and D. W. Pond. Food web dynamics in the Scotia Sea in summer: A stable isotope study. *Deep Sea Research Part II: Topical Studies in Oceanography*, 5960:208–221, 2012.

[425] G. Sugihara, K. Schoenly, and A. Trombla. Scale Invariance in Food Web Properties. *Science*, 245(4913):48–52, 1989.

[426] British Antarctic Survey. Research stations. Available from: https://www.bas.ac.uk/polar-operations/sites-and-facilities/station/ [Accessed 18/06/2015].

[427] T. E. Targett. *Trophic ecology and structure of coastal Antarctic fish communities.* 1981.

[428] G. A. Tarling, T. Klevjer, S. Fielding, J. Watkins, A. Atkinson, E. Murphy, R. Korb, M. Whitehouse, and R. Leaper. Variability and predictability of Antarctic krill swarm structure. *Deep Sea Research Part I: Oceanographic Research Papers*, 56(11):1994–2012, 2009.

[429] M. I. Tarverdiyeva. *Daily food consumption and feeding pattern of the Georgian cod (Notothenia rossi marmorata Fischer) and the Patagonian toothfish (Dissostichus eleginoides Smitt) (Fam. Nototheniidae) in the South Georgia area.* 1972.

[430] G. Thomas, J. P. Croxall, and P. A. Prince. Breeding biology of the Light-mantled sooty albatross (Phoebetria palpebrata) at South Georgia. *Journal of Zoology*, 199(1):123–135, 1983.

[431] S. E. Thorpe, K. J. Heywood, D. P. Stevens, and M. A. Brandon. Tracking passive drifters in a high resolution ocean model: implications for interannual variability of larval krill transport to South Georgia. *Deep Sea Research Part I: Oceanographic Research Papers*, 51(7):909–920, 2004.

[432] S. E. Thorpe, E. J. Murphy, and J. L. Watkins. Circumpolar connections between Antarctic krill (*Euphausia superba*) populations: Investigating the roles of ocean and sea ice transport. *Deep Sea Research Part I: Oceanographic Research Papers*, 54(5):792–810, 2007.

[433] P. N. Trathan, A. S. Brierley, M. A. Brandon, D. G. Bone, C. Goss, S. A. Grant, E. J. Murphy, and J. L. Watkins. Oceanographic variability and changes in Antarctic krill (Euphausia superba) abundance at South Georgia. *Fisheries oceanography*, 12(6):569–583, 2003.

[434] P. N. Trathan, C. Green, J. Tanton, H. Peat, J. Poncet, and A. Morton. Foraging dynamics of Macaroni Penguins *Eudyptes chrysolophus* at South Georgia during brood-guard. *Marine Ecology-progress Series*, 323:239–251, 2006.

[435] P. N. Trathan, N. Ratcliffe, and E. A. Masden. Ecological drivers of change at South Georgia: the krill surplus, or climate variability. *Ecography*, 35(11):983–993, 2012.

[436] W. Z. Trivelpiece, J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, and G. M. Watters. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc Natl Acad Sci U S A*, 108(18):7625–7628, 2011.

[437] J. T. Turner. The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zool. Stud*, 43(2):255–266, 2004.

[438] R. E. Ulanowicz and C. J. Puccia. Mixed trophic impacts in ecosystems. *Coenoses*, 5(1):7–16, 1990.

[439] DeSA U.N. World population prospects: The 2012 revision. *Population Division of the Department of Economic and Social Affairs of the United Nations Secretariat, New York*, 2013.

[440] H. Venables, M. P. Meredith, A. Atkinson, and P. Ward. Fronts and habitat zones in the Scotia Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 5960:14–24, 2012.

[441] N. M. Voronina. Size structure of Antarctic metazoan plankton according to united net, trawl and water bottle data. *Russian Journal of Aquatic Ecology*, 3(2):137–142, 1994.

[442] A. Žiberna. Direct and indirect approaches to blockmodeling of valued networks in terms of regular equivalence. *Journal of Mathematical Sociology*, 32(1):57–84, 2008.

[443] T. R. Walker, I. L. Boyd, D. J. McCafferty, N. Huin, R. I. Taylor, and K. Reid. Seasonal occurrence and diet of leopard seals (Hydrurga leptonyx) at Bird Island, South Georgia. *Antarctic Science*, 10(01):75–81, 1998.

[444] C. M. Waluda, M. A. Collins, A. D. Black, I. J. Staniland, and P. N. Trathan. Linking predator and prey behaviour: contrasts between Antarctic fur seals and macaroni penguins at South Georgia. *Mar Biol*, 157(1):99–112, 2010.

[445] C. M. Waluda, S. L. Hill, H. J. Peat, and P. N. Trathan. Diet variability and reproductive performance of macaroni penguins *Eudyptes chrysolophus* at Bird Island, South Georgia. *Mar Ecol Prog Ser*, 466:261–274, 2012.

[446] S. Wanless, M. P. Harris, and J. A. Morris. Diving behaviour and diet of the blue-eyed shag at South Georgia. *Polar Biol*, 12(8):713–719, 1992.

[447] P. Ward, A. Atkinson, and G. Tarling. Mesozooplankton community structure and variability in the Scotia Sea: A seasonal comparison. *Deep Sea Research Part II: Topical Studies in Oceanography*, 5960:78–92, 2012.

[448] P. Ward, A. Atkinson, H. J. Venables, G. A. Tarling, M. J. Whitehouse, S. Fielding, M. A. Collins, R. Korb, A. Black, G. Stowasser, K. Schmidt, S. E. Thorpe, and P. Enderlein. Food web structure and bioregions in the Scotia Sea: A seasonal synthesis. *Deep Sea Research Part II: Topical Studies in Oceanography*, 59-60:253–266, 2012.

[449] P. Ward, S. Grant, M. Brandon, V. Siegel, V. Sushin, V. Loeb, and H. Griffiths. Mesozooplankton community structure in the Scotia Sea during the CCAMLR 2000 survey: JanuaryFebruary 2000. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(1213):1351–1367, 2004.

[450] J. Watts and G. A. Tarling. Population dynamics and production of *Themisto gaudichaudii* (Amphipoda, Hyperiidae) at South Georgia, Antarctica. *Deep Sea Research Part II: Topical Studies in Oceanography*, 5960:117–129, 2012.

[451] D. R. White and K. P. Reitz. Graph and semigroup homomorphisms on networks of relations. *Social Networks*, 5(2):193–234, 1983.

[452] M. J. Whitehouse, A. Atkinson, R. E. Korb, H. J. Venables, D. W. Pond, and M. Gordon. Substantial primary production in the land-remote region of the central and northern Scotia Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 5960:47–56, 2012.

[453] G. C. Whittow and American Physiological Society (1887-) Comparative Physiology Section. *Seabird energetics.* Plenum Press, 1984.

[454] R. J. Williams and N. D. Martinez. Simple rules yield complex food webs. *Nature*, 404(6774):180–183, 2000.

[455] R. J. Williams and N. D. Martinez. Limits to trophic levels and omnivory in complex food webs: theory and data. *The American Naturalist*, 163(3):458–468, 2004.

[456] T. D. Williams. Foraging ecology and diet of gentoo penguins *Pygoscelis papua* at South Georgia during winter and an assessment of their winter prey consumption. *Ibis*, 133(1):3–13, 1991.

[457] J. D. Woods. The Lagrangian Ensemble metamodel for simulating plankton ecosystems. *Progress in Oceanography*, 67(12):84–159, 2005.

[458] J. D. Woods and R. Onken. Diurnal variation and primary production in the ocean preliminary results of a Lagrangian ensemble model. *J. Plankton Res.*, 4(3):735–756, 1982.

[459] J. T. Wootton and M. Emmerson. Measurement of Interaction Strength in Nature. *Annual Review of Ecology, Evolution, and Systematics*, 36(1):419–444, 2005.

[460] J. C. Xavier and J. P. Croxall. Predatorprey interactions: why do larger albatrosses eat bigger squid? *Journal of Zoology*, 271(4):408–417, 2007.

[461] J. C. Xavier, J. P. Croxall, and K. A. Cresswell. Boluses: An Effective Method for Assessing the Proportions of Cephalopods in the Diet of Albatrosses (Les Pelotes de Réjection: Une Méthode Efficace pour valuer la Proportion de Céphalopodes dans le Régime Alimentaire chez les Albatros). *The Auk*, 122(4):1182–1190, 2005.

[462] J. C. Xavier, J. P. Croxall, and K. Reid. Interannual variation in the diets of two albatross species breeding at South Georgia: implications for breeding performance. *Ibis*, 145(4):593–610, 2003.

[463] J. C. Xavier, J.P. Croxall, P. Trathan, and P. Rodhouse. Inter-annual variation in the cephalopod component of the diet of the wandering albatross, *Diomedea exulans*, breeding at Bird Island, South Georgia. *Marine Biology*, 142(3):611–622, 2003.

[464] J. C. Xavier, P. Rodhouse, M. Purves, T. Daw, J. Arata, and G. Pilling. Distribution of cephalopods recorded in the diet of the Patagonian toothfish (*Dissostichus eleginoides*) around South Georgia. *Polar Biol*, 25(5):323–330, 2002.

[465] J. C. Xavier, P. N. Trathan, J. P. Croxall, A. G. Wood, G. Podest, and P. G. Rodhouse. Foraging ecology and interactions with fisheries of wandering albatrosses (*Diomedea exulans*) breeding at South Georgia. *Fisheries Oceanography*, 13(5):324–344, 2004.

[466] P. Yodzis. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology*, 67(4):635–658, 1998.

[467] P. Yodzis and K. Winemiller. In search of operational trophospecies in a tropical aquatic food web. *Oikos*, 87:327–340, 1999.

[468] E. F. Young, S. E. Thorpe, N. Banglawala, and E. J. Murphy. Variability in transport pathways on and around the South Georgia shelf, Southern Ocean: Implications for recruitment and retention. *J. Geophys. Res. Oceans*, 119(1):241–252, 2014.

[469] W. Zeidler. 2015. *Themisto australis* (Stebbing, 1888). Horton, T.; Lowry, j. and De Broyer, C. (2013 onwards) World Amphipoda Database. Accessed through: De Broyer, C.; Clarke,A.; Koubbi, P.; Pakhomov, E.; Scott, F.; Vanden Berghe, E. and Danis, B. Eds., 2015. Register of Antarctic Marine Species. Available from: http://www.marinespecies.org/rams/aphia.php?p=taxdetails&id=325381. [Accessed 16/07/2015].

[470] M. I. Zmijewska, J. Yen, and L. Bielecka. Size variability in two common Antarctic copepods: *Calanoides acutus* [Giesbrecht] and *Metridia gerlachei* [Giesbrecht]. *Polish Polar Research*, 4(20):325–333, 1999.