



ICED

Integrating Climate and Ecosystem Dynamics

Report of the Southern Ocean Food Web Modelling Workshop

16-18 April 2008



This is the report of the ICED Southern Ocean Food Web Modelling Workshop held at the Center for Coastal and Physical Oceanography, Old Dominion University, Norfolk, Virginia, USA on April 16-18, 2008. The report was compiled and edited on behalf of the workshop participants and the ICED programme by Eugene Murphy, Rachel Cavanagh, Nadine Johnston and Eileen Hofmann. Cover design by Jamie Oliver, British Antarctic Survey. Report citation: Murphy E.J., Cavanagh R.D., Johnston N.M. and Hofmann E.E. (Eds). 2010. Integrating Climate and Ecosystem Dynamics (ICED): Report of the Southern Ocean Food Web Modelling Workshop, 16-18 April 2008, Virginia, USA.



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Preface

The *Southern Ocean Food Web Modelling Workshop* was the first in a planned series of workshops organised by the ICED programme. The three-day workshop was held in Norfolk, Virginia, USA and hosted by the Center for Coastal and Physical Oceanography, Old Dominion University.

Some of the strongest regional expressions of global climate change have occurred in the Southern Ocean. Changes to the environment have been associated with variations in ecosystems and biogeochemical processes. Understanding climate-induced changes and their consequences for ecosystem dynamics and biogeochemical cycling is integral to predicting the impacts and feedbacks of the Southern Ocean as part of the Earth System, and to developing sustainable management for the region. Fundamental to predicting how ecosystems respond to change is an understanding of food web structure and function. This in turn requires synthesis of current knowledge of Southern Ocean food webs and modelling approaches.

The main objective of the workshop was to *consider current knowledge of Southern Ocean food webs and the status of Southern Ocean food web modelling, with the goal of developing models of circumpolar food web operation*. It also aimed to facilitate coordination between the Southern Ocean modelling community and the wider scientific community, to identify available inputs and required outputs for Southern Ocean food web models, and the analyses and observational systems that are needed to underpin these models.

The workshop consisted of plenary presentations that reviewed current understanding of Southern Ocean food webs and approaches to modelling. These were followed by four discussion groups that explored:

- key issues and questions in Southern Ocean ecosystem research;
- current knowledge of the structure and dynamics of Southern Ocean food webs;
- mechanistic models of Southern Ocean food webs, and;
- generalized models of Southern Ocean food webs.

The workshop concluded with a plenary discussion summarising the knowledge gleaned from the presentations and recommendations of the discussion groups.

The Executive Summary provides a general overview of the workshop structure and outcomes. The main report details the main aspects discussed followed by a series of recommendations for Southern Ocean food web modelling. The Appendices provide background material, the workshop agenda and participants, and details on the plenary presentations that provided the basis for the discussions.

It is anticipated that this report will provide the basis for new analyses and observational, monitoring and modelling programmes through ICED and the wider community, inspiring exciting and innovative approaches to describe and quantify Southern Ocean food webs on a circumpolar scale.

Eugene Murphy, Rachel Cavanagh, Nadine Johnston and Eileen Hofmann, January 2010

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Executive summary

This report presents the discussions and recommendations from the first ICED modelling workshop, held in April 2008 at the Center for Coastal Physical Oceanography, Old Dominion University, USA. The workshop brought together a unique group of multidisciplinary experts to take the first step towards realizing a long-term goal of the ICED programme, which is to improve the reliability of predictions of ecosystem dynamics in the Southern Ocean and how they respond to change. Fundamental to such predictions is a detailed understanding of food web structure and function.

Thus, the main objective of this first ICED modelling workshop was to *consider current knowledge of Southern Ocean food webs and the status of Southern Ocean food web modelling, with the goal of developing models of circumpolar food web operation*. The workshop discussions were focused around three broad questions:

- What is the structure of Southern Ocean food webs?
- What determines the structure of Southern Ocean food webs?
- How does food web structure respond to variability and change?

Major changes are occurring in Southern Ocean ecosystems and these have direct effects on key species and indirect impacts through the food web. To understand the effects of these changes a more thorough grasp of the circumpolar food web is required. The gaps in knowledge that limit current food web models for the Southern Ocean were highlighted with particular emphasis on regional and trophic complexities and the potential effects of climate change in altering food web structures. The discussions pointed to the requirement for a concerted effort in developing quantified food web analyses, drawing on available (including historic) data as well as initiating new research and monitoring programmes.

The discussions noted that although a wide range of Southern Ocean ecosystem modelling activities are being undertaken, there has been little coordinated effort to develop integrated analyses of food webs. The available models address aspects of the growth, development and population dynamics of a range of key species. Food web studies have been undertaken for a small number of local systems. Various physical and biogeochemical models are available, but there are significant issues that need to be considered in using these in wider scale models. Issues of coupling between models and linking models operating at different scales require detailed consideration. Generalised modelling approaches are likely to be useful and will help constrain more detailed mechanistic model studies. Applying generic models to examine the overall operation of the circumpolar food web will also help to focus more detailed regional modelling.

The recommendations made by the workshop are aimed at guiding the advances in Southern Ocean food web modelling. These recommendations, together with the workshop discussions, also form the basis for a review paper on the development Southern Ocean food web models to be published in a peer-reviewed scientific journal (currently in preparation). A similar review of the operation of circumpolar Southern Ocean food webs, which highlights the gaps in understanding and data, is also needed and is something which the ICED programme will address in the near future. In addition, detailed exercises of quantification of regional food web operation will be an important step in understanding the controls on food web structure. ICED will encourage a strategy that facilitates parallel development of multiple model approaches to simulate the operation of Southern Ocean food webs, their response to change, interactions with biogeochemical cycles and the end-to-end operation of food webs. This will require a coherent multifaceted approach, linking to modelling groups associated with other ocean ecosystem programmes.

1. Introduction

1.1. The ICED Programme

In recent years some of the strongest regional expressions of global climate change have occurred in Antarctica and the Southern Ocean (Figure 1). The physical changes observed have also been associated with variations in Southern Ocean ecosystems. Given the existence of, and potential for, dramatic responses to climate change in this region, developing the ability to predict ecosystem dynamics at a range of spatial and temporal scales is crucial. However, there is added complexity in determining climate impacts in a disturbed system where harvesting has been extensive. Understanding the underlying processes driving ecosystem responses to climate change on a regional and circumpolar basis is necessary to provide a sound basis for the sustainable management of this globally important ocean. The Southern Ocean is also a key component of the carbon cycle, yet global carbon budget models are lacking detail from this region. An understanding of these processes is also necessary to predict the impacts and feedbacks of the Southern Ocean as part of the Earth System.

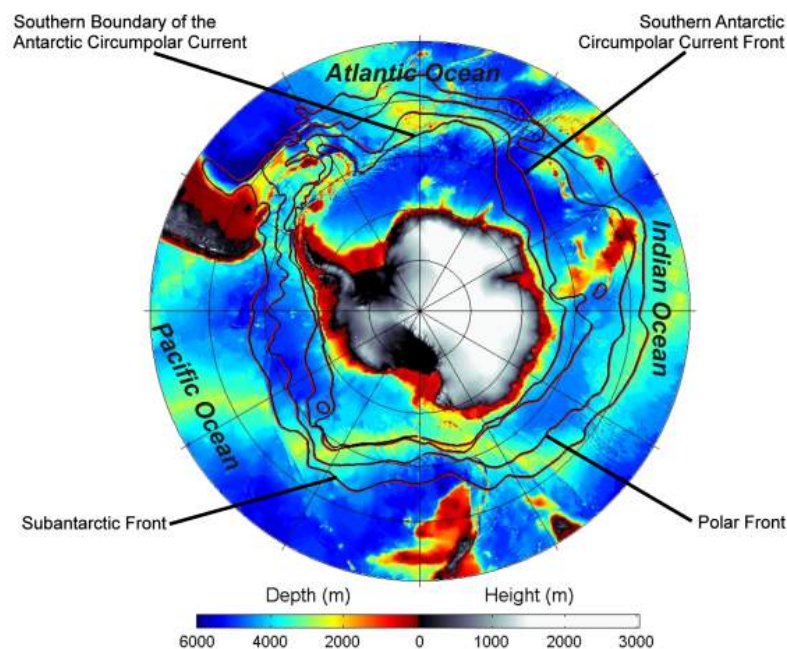


Figure 1. Map of the Southern Ocean (showing bathymetry, topography and major fronts) that links the three ocean basins of the Southern Hemisphere.

Source: M. Meredith, British Antarctic Survey

Many of the priority scientific challenges lie at the interfaces between ecosystem, climate, biogeochemistry and fisheries science. It has been recognised that addressing these challenges requires integrated circumpolar analyses of ecosystem operation and integration and coordination of international research effort. Integrating Climate and Ecosystem Dynamics in the Southern Ocean (ICED) is a decade-long international, multidisciplinary programme established primarily to deliver the scientific analyses required to address major ecological challenges arising as a result of climate and human driven changes.

The long-term goal of ICED is to:

Determine the major controls on the dynamics of Southern Ocean ecosystems and the potential for feedbacks as part of the Earth System.

To address the long-term goal ICED has three main scientific objectives:

- *To understand the structure and dynamics of ecosystems in the Southern Ocean and how they are affected by, and feedback on, climate processes;*
- *To understand how ecosystem structure and dynamics interact with biogeochemical cycles in the Southern Ocean;*
- *To determine how ecosystem structure and dynamics should be incorporated into management approaches for sustainable exploitation of living resources in the Southern Ocean.*

ICED consists of three core areas of activity: integrated ecosystem modelling, data synthesis and collation of historical data, and coordination and development of field studies, all of which will be guided by close collaboration with relevant programmes and groups operating throughout the Southern Ocean (Murphy et al. 2008).

1.2. ICED and Southern Ocean modelling

Major overarching challenges to Southern Ocean ecosystem modellers include understanding responses to variability and change, and developing a circumpolar view of ecosystem operation. Ecosystem modelling for the Southern Ocean is currently in its early stages, much of the work is restricted in geographic or trophic scope and there are considerable questions regarding appropriate model structures.

Climate change in the Southern Ocean may have rapid and significant effects on species, and has no well-studied precedent, implying that predicting ecosystem changes is likely to be difficult, posing a number of complex challenges. Food webs are complex adaptive systems and as such exhibit a range of responses (e.g. chaotic, nonlinear) to perturbations.

Coordination of the Southern Ocean ecosystem modelling community across disciplines is required to provide the multifaceted approach needed to tackle the challenges that are emerging from the wider scientific community. ICED will facilitate this coordination by organizing and supporting a series of workshops to develop models of ocean circulation, biogeochemical cycles and the end-to-end operation of food webs, within a hierarchical framework of models of different spatial, temporal and trophic resolutions (Murphy et al. 2008).

2. Workshop and report background and objectives

As noted above, changes to the Antarctic and Southern Ocean environment have been associated with variations in ecosystems and biogeochemical processes. Fundamental to predicting how ecosystems respond to such change is an understanding of food web structure and function. This requires synthesis of current knowledge of Southern Ocean food webs and modelling approaches.

Thus the primary objective of this first ICED modelling workshop was to *consider current knowledge of Southern Ocean food webs and the status of Southern Ocean food web modelling, with the goal of developing models of circumpolar food web operation*. The emphasis was on end-to-end food web models that could be used to understand the response of Southern Ocean food webs to future climate and human-induced change scenarios. The workshop achieved this by:

- Bringing together a multidisciplinary group of experts (physics, biogeochemistry, ecosystem, fisheries and modelling experts) working across a range of global marine ecosystems;
- Considering the current status of knowledge of Southern Ocean food webs (including spatial and temporal variation, alternative pathways, movement and migration, and the physical environment – particularly sea ice and physical determinants of production);
- Discussing possible influences of change on the structure and function of food webs (including historical exploitation and change, climate change, potential for regime change, interaction effects);
- Reviewing the current status of Southern Ocean food web models;
- Considering new modelling approaches (defining questions and purposes of models, main methods and structures, data requirements, predictive ability, uncertainty, sensitivity, comparisons, generic model) and issues associated with circumpolar food web models (spatial and temporal population distributions and connectivity, life cycles, physical-biological interactions, spatial/temporal scales);
- Developing a strategic basis for generating models of circumpolar operation of Southern Ocean ecosystems;
- Making recommendations for future directions in Southern Ocean ecosystem modelling.

Three broad questions were used to focus the discussion of knowledge of food web operation and modelling:

- What is the structure of Southern Ocean food webs?
- What determines the structure of Southern Ocean food webs?
- How does food web structure respond to variability and change?

These questions provided a useful starting point for discussions on quantified views of food web structure and function. In addressing these questions the workshop reviewed existing knowledge of Southern Ocean regional food web structures in terms of species, life histories, the physical environment and historical effects. Factors affecting the structure of food webs were considered, including physical processes, biogeochemistry, connectivity and productivity. Effects of environmental changes on food web structures were explored, at both broad and regional scales. Identifying gaps in information formed another key focus.

Recognition of the difficulty in resolving issues of generalising food web structure and operation versus the need to include detailed aspects of the life-cycle of key species was a common issue raised. This issue also features in the majority of model analyses which have tended to focus on either single species life-cycle studies, including linking circulation and biological models (e.g. for krill) and energy or carbon flow type studies of food webs (often based on steady-state

assumptions). This fundamental issue in food web research underpinned much of the workshop discussion.

This report presents the outcomes of the workshop, which are intended to provide a basis for coordination between the Southern Ocean modelling community and the wider scientific community to identify inputs and required outputs for Southern Ocean food web models. The report is also aimed at helping focus scientific effort to address relevant policy objectives. The structure of the report generally follows the meeting structure and provides a general overview of the major points and discussions that arose during the workshop. The first section considers what is known about Southern Ocean food webs, their structure, operation and response to change. This is followed by a section describing ongoing modelling activities with the aim of providing guidance for future work. The key points raised during the meeting are highlighted throughout the report in boxes. The Appendices provide background information on the workshop structure and participants, further detailed information on the scientific presentations and additional points of detailed discussion. The report then presents a series of recommendations for future activities aimed at developing food web modelling and a strategic capacity to enable ICED to facilitate the multiple approaches necessary to achieve circumpolar analyses of Southern Ocean ecosystems.

3. Southern Ocean food webs

3.1. What is the structure of Southern Ocean food webs?

Addressing this question began with consideration of what we know from Southern Ocean studies to date, and where the major gaps lie, in terms of describing Southern Ocean food web structures, their spatial and temporal variation, and both inter- and intra- regional/annual differences.

It became clear through workshop discussion that the lack of consensus on the extent to which the Southern Ocean ecosystem can be considered as a single food web, as opposed to a series of distinct regional food webs, highlights the lack of knowledge and data about food web structure and operation for large parts of the Southern Ocean. Detailed information is available on the structure and operation of food webs for the Scotia Sea (Figure 2 and see also Appendix III for more detail and references), Antarctic Peninsula (Ducklow *et al.* 2007) and Ross Sea (Figure 3 and see also Appendix III for more detail and references). However, even for these regions there are major gaps in our understanding of seasonal dynamics and the processes controlling responses to variability. Information exists for key rate processes, but these data are mostly based on limited studies of local regions and for short durations. Quantification of food web structures has not been completed at a level that would allow regional comparisons or to include uncertainty and variability in food web structure and operation.

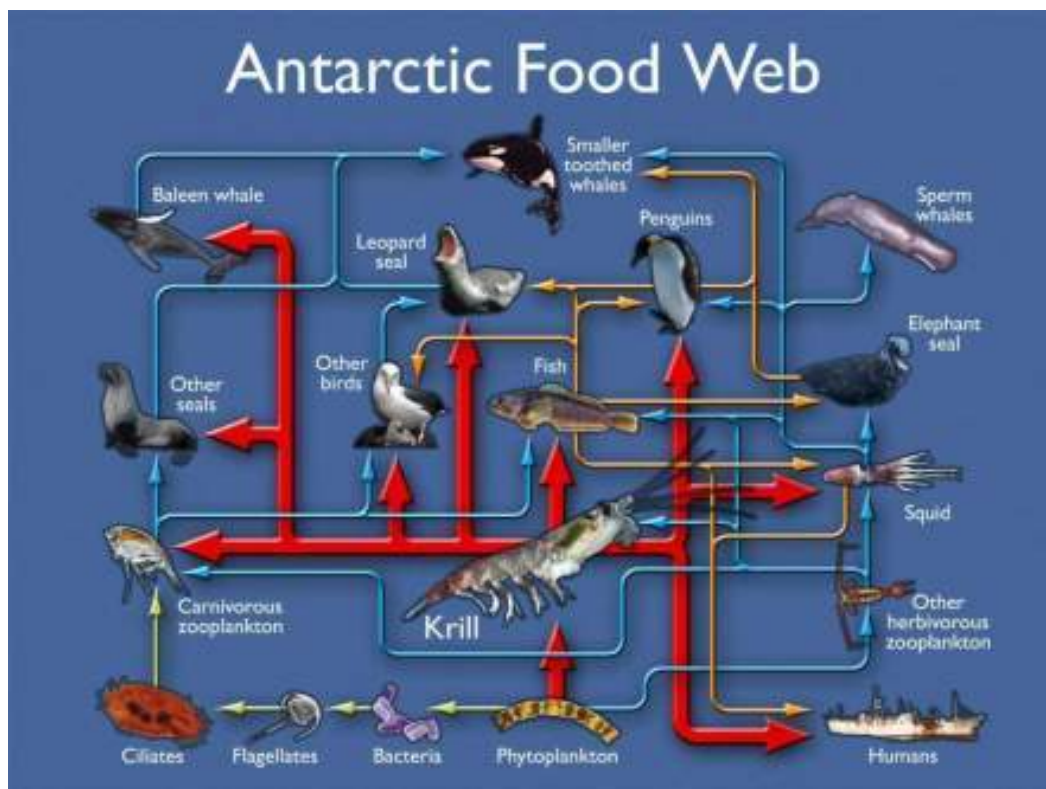


Figure 2. Schematic of the Scotia Sea food web. For more information refer to Appendix III.
Source: British Antarctic Survey

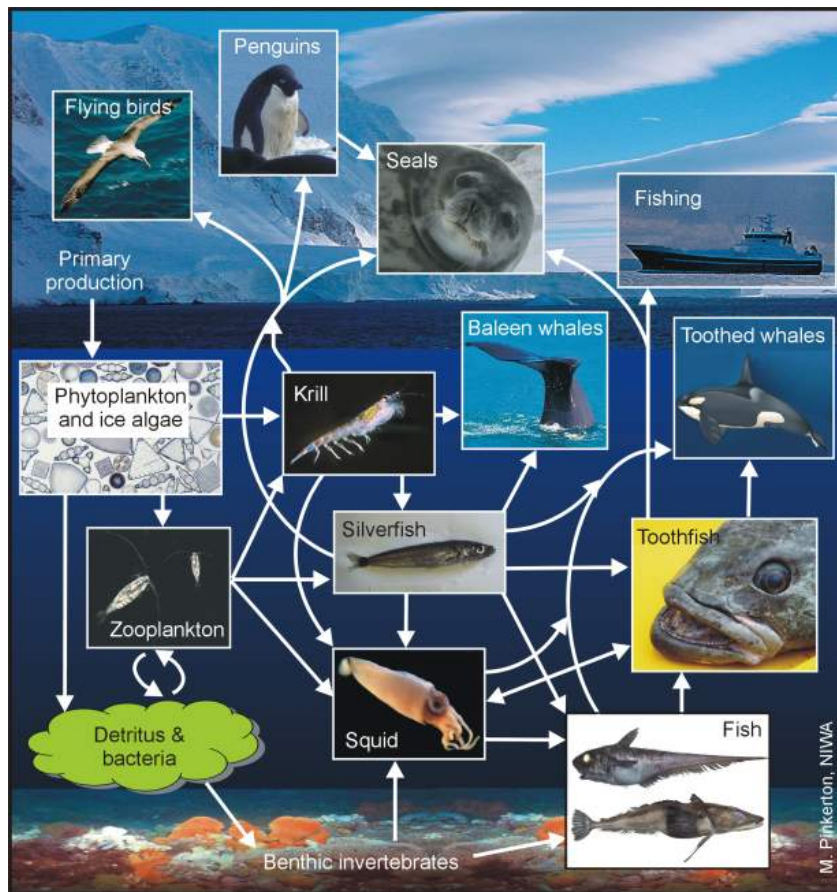


Figure 3. An example of the Ross Sea food web based on 15 groups. This has recently been extended to 50 groups (Pinkerton et al. 2008a). For more information refer to Appendix III. Source: M. Pinkerton, NIWA.

The Southern Ocean food web has often been described as a simple system dominated by Antarctic krill that link primary production to higher predators in short efficient food chains. However, recent studies are showing that this view is not correct for many regions (or seasons) across the Southern Ocean. Considerations of the Scotia Sea, Antarctic Peninsula and Ross Sea food webs highlighted some of the major differences between krill dominated systems and those dominated by other zooplankton species (e.g. copepods and ice-krill). Such considerations emphasize the importance of recognising the complexity of food webs and the role of alternative interactive pathways in the food webs (Figures 4 and 5), which vary in dominance in different regions and at different times. These alternative pathways are important in determining the structure and operation of the ecosystems and their responses to varying environmental conditions and change. Knowledge of ecosystem structure is much more limited for most other regions including the Weddell Sea, the East Antarctic and the Amundsen and Bellingshausen Seas, for which there are few or no syntheses available. In many of these regions, especially in oceanic areas, there has been no compilation of food web information to allow a comparison of structure and operation. The historical data that could be used to develop general descriptions of food web operation in these areas remain to be compiled and analysed.

§6. ecosystem variability and change

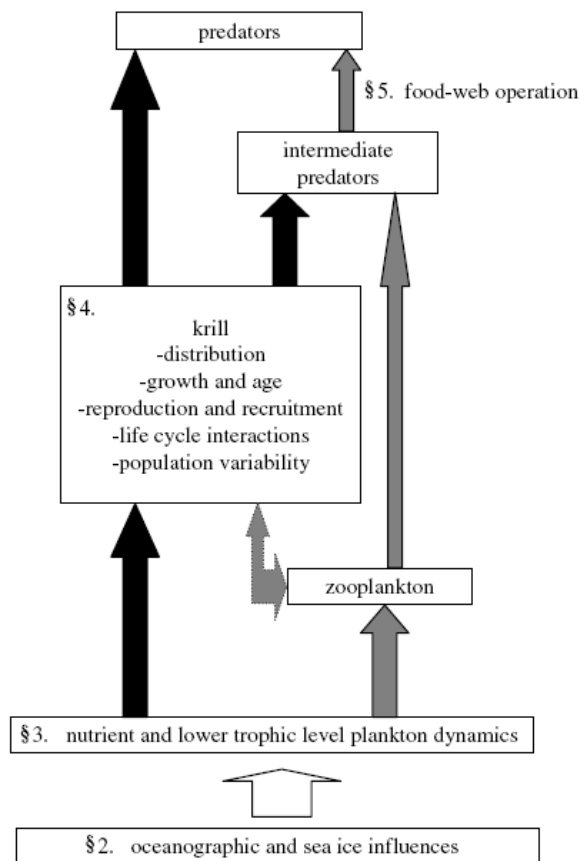


Figure 4.

Schematic of the Scotia Sea food web from Murphy et al. (2007b). Based on the 'rhomboid' approach of de Young (2004), the major focus is on krill, their life history and interactions, with reduced detail on other groups and trophic levels. Source: Murphy et al. (2007b)

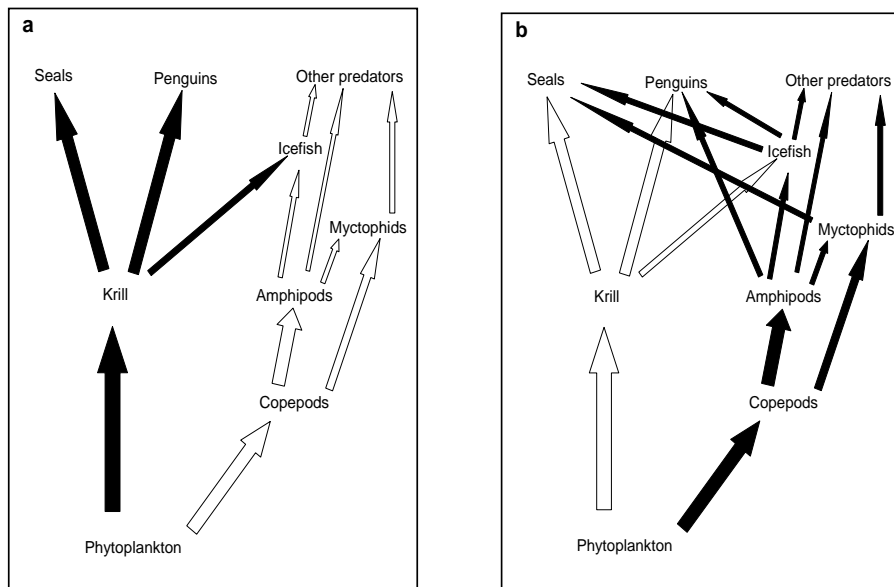


Figure 5. Schematic illustration of alternative pathways in part of the Scotia Sea food web, showing shifts between (a) years when krill are abundant across the Scotia Sea and (b) years when krill are scarce. Major pathways shown as black arrows. See also Appendix III. Source: Murphy et al. (2007b)

Major gaps remain in information for basic characteristics of many species and groups including distribution abundance and life cycle dynamics and demographics. Analyses of the main taxonomic components of Southern Ocean food webs need to focus on bridging the data gaps for a wide range of groups, including: virus distribution and activity, meso-and macro-zooplankton species composition and distribution in some regions (e.g. see Figure 6), abundance and predator-prey relationships for fish species, data on mid-trophic level fish and squid that link primary producers to top producers, information on rates of prey consumption, species partitioning and geographic variation for top predators. Of course, including all species life-history stage combinations in food web models is not practical. Models likely require more detail for the key species of interest and less detail for other trophic levels, a 'rhomboid' approach (de Young et al. 2004).

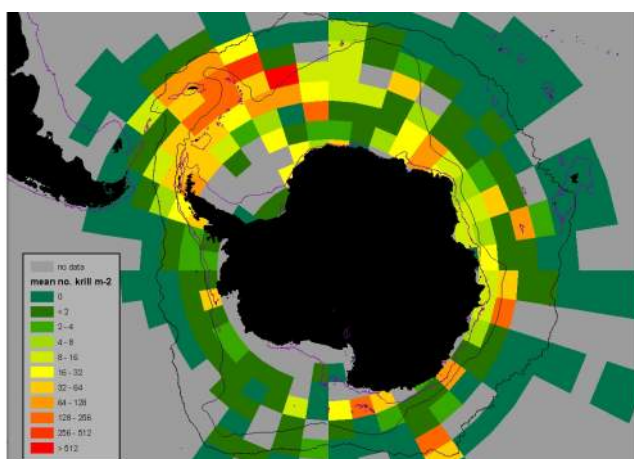


Figure 6. Circumpolar distribution of the mean density of postlarval Antarctic krill (*Euphausia superba*) in summer. This plot is based on KRILLBASE, a historical database compiling all available net sample data for 1926–2004, standardised to a common sampling method. Source Atkinson (2008).

All marine ecosystems show considerable spatial (e.g. local, regional and circumpolar) and temporal (e.g. seasonal, interannual, decadal and longer-term) variability in physical, chemical and biological properties. There are major gaps in understanding of the seasonality of Southern Ocean food webs. Difficulties with winter sampling result in few year-round monitoring programmes and relatively few process studies have been undertaken outside the summer ice-free period. However, increasing amounts of data are becoming available on winter activity and diets of some predator species. For much of the plankton and nekton information is based on a small number of local studies. There are few fully seasonal data for individual species or for major interactions in the food web. Combined process studies and monitoring efforts are needed to address the significant gaps in understanding and data availability, particularly for winter and seasonal transitions in food web operation.

More data are available on between-year variation and aspects of food web structure, which show that the biomass and abundance of individual species varies substantially between years. A number of biologically based monitoring programmes have been operating for more than 20 years and these time series are now being used to analyse interannual patterns and to infer process interactions. These analyses of interannual variability have led to major developments in understanding of the operation of regional food webs. However, these ecosystems have been disturbed by more than two centuries of harvesting and the consequences of this in determining current food web structure is unclear. There is little information available to determine whether the historical carrying capacity for a range of species differs from that of today.

The following sections summarise the discussions on current knowledge of the structure of Southern Ocean food webs, controls and feedbacks on their structure and dynamics, and gaps in data that need to be filled. This section is not intended as an exhaustive review of all the components of

Southern Ocean food webs. We note that the Commission for the Conservation of Antarctic Marine Living Resources/International Whaling Commission (CCAMLR/IWC) Workshop that took place in August 2008, reviewed the components of the system in more detail. A summary of recent ecosystem modelling developments (including food web modelling) of the CCAMLR/WG-EMM can be found in CCAMLR (2004). A summary of the modelling developments and approaches of Ecosystem, productivity, ocean, climate (EPOC) modelling framework (currently being applied to CCAMLR's statistical Area 48) can also be found in Constable (2005). See also Appendix III for summaries of the presentations in this area (e.g. Constable on ecosystem modelling).

3.1.1. Key species

- What are the criteria used by modellers for key species?

The process of food web modelling itself guides the development of criteria for key species. Models are used for many different purposes (e.g. improving understanding of food web dynamics, biogeochemical cycles, and resource management). Thus, the critical species may be those key to production and biomass or species that may be indicators of change in productivity either because (i) they are rare and/or sensitive to change in the production pathway of interest; or (ii) modelling species on the periphery of their range can be good indicators of change.

Other criteria depend on the questions being addressed. For example, salps may be important in models addressing biogeochemical cycles and carbon flux as they produce large, rapidly sinking pellets; but may be less important in models addressing questions related to energy flow to top predators. Similarly, pteropods may be particularly important for questions related to both carbon flux and ocean acidification but of less importance for questions related to the maintenance of top predator populations.

- What information is available for Southern Ocean species?

Viruses and bacteria

The distribution and activity of viruses are poorly known, but they may be an important source for prokaryotic mortality (e.g. Guixa-Boixereu *et al.* 2002). Bacteria absolute abundances and activity tend to be lower in the Southern Ocean than in temperate or tropical regions and seasonal and spatial variability may lead to an uncoupling between bacteria and phytoplankton development. Nevertheless, bacteria may contribute significantly to the energy transfer in the Southern Ocean (e.g. Billen & Becquevort 1991, Delille 2004, Karl *et al.* 1996, Oliver *et al.* 2004).

Phytoplankton

Critical phytoplankton functional groups and species and the environmental factors that control phytoplankton processes are reviewed in Boyd (2002). Diatoms and the prymnesiophyte, *Phaeocystis antarctica*, are the dominant bloom-forming taxa and the major contributors to dimethyl sulphide (DMS) fluxes to the atmosphere and to carbon fluxes to deep water. The size and type of phytoplankton (flagellates, diatoms, colonial *Phaeocystis*) present influence food web pathways, e.g. krill may not feed efficiently on flagellates and few zooplankton appear to graze on colonial *Phaeocystis* (Nejstgaard *et al.* 2007). Microplankton processes in sea ice constitute another important source of primary production and food for higher trophic levels (reviewed in Palmisano & Garrison 1993).

Zooplankton

Microzooplankton seasonal abundance, distribution and control on phytoplankton are not well known. Tight coupling may occur, especially on small phytoplankton cells north of the Polar Front in the Antarctic Circumpolar Current (ACC) (e.g. Froneman 2004, Safi et al. 2007). Microzooplankton grazing, however, may not control phytoplankton in coastal regions (e.g. Calbet *et al.* 2005, Pearce *et al.* 2008). Microzooplankton are known to be a food source for mesozooplankton (e.g. Atkinson 1995).

The Southern Ocean zooplankton assemblage is essentially dominated by copepods. However, in regions where Antarctic krill or tunicates, *Salpa thompsoni*, are common (see figures in Atkinson et al. 2004) these may dominate the food web, especially in terms of biomass. Given the heterogeneous distribution of krill and salps, their role in local food webs may change over small spatial scales, across continental shelves and ice edges, and in the open ocean.

Meso- and macro-zooplankton species composition and distribution are generally well known. However, information is limited or totally lacking from some areas, including the Bellingshausen and Amundsen seas and parts of the Weddell and Ross seas. Times-series data are available for South Georgia (British Antarctic Survey, BAS) and west of the Antarctic Peninsula (e.g. US Antarctic Marine Living Resources Program and the US Long Term Ecological Research Program). Elsewhere, seasonal and interannual information are scarce. Life cycles of four major species of copepods (e.g. *Rhincalanus gigas*, *Calanus propinquus*, *Calanoides acutus*, *Metridia gerlachei*), two species of euphausiids (*Euphausia superba* and perhaps *E. crystallorophias*) are well known. Equivalent information for other zooplankton species and groups is either limited or absent.

Reviews of zooplankton species abundance and distribution, life cycle, diet, and rate measurements are given in Atkinson (1998), Conover (1991), Deibel (2007), Hempel (1985), Pakhomov (2002), Smith (1990), and Voronina (1998). Zooplankton abundances (and biomass) in coastal regions are highest in waters west of the Antarctic Peninsula, an order of magnitude less in the Ross and Weddell seas, and another order of magnitude lower in other regions (Deibel & Daly 2007). There are ongoing efforts (led by BAS) to synthesize Antarctic zooplankton data into a comprehensive database. The SCAR-Marine Biodiversity Information Network (SCAR-MarBIN) has compiled an almost-completed list of Antarctic zooplankton species (see www.scarmarbin.be).

Fish and squid

Fish species and their life histories in the Southern Ocean have been described to some extent (e.g. Kock 1992), but details such as abundances and predator-prey relationships are not well known. Two recent studies, however, have examined the diet, distribution and abundance of mesopelagic fish including *Electrona carlsbergi*, *E. antarctica*, *Protomyctophum bolini*, *Gymnoscopelus braueri*, *G. nicholsi*, *G. fraseri*, *Protomyctophum choriodon*, *Krefftichthys anderssoni* and *Nannobranchium achirus* (Collins *et al.* 2008, Shreeve *et al.* In Press). Much of the information and data on Southern Ocean fish are contained in CCAMLR reports, especially in the fish stock working group reports. CCAMLR also have considerable amounts of data on fish from commercial fishing vessels, but these data are commercially sensitive. Interested science investigators and the ICED programme may be able to access a reduced resolution set of this fish data with the required request protocols used by CCAMLR. Very little is known about squid. Some information on species and life histories is available and recently stable isotope analysis of squid beaks from the Ross Sea has been undertaken (Cherel & Hobson 2006, Thompson *et al.* 2008).

Birds and mammals

Top predators and their pelagic distributions are better known on the west side of Antarctica, less known on the east side, and with large spatial gaps between the few land-based research stations. A wide range of satellite-based tracking data has been collected on movement and migration patterns of various seabird and marine mammal species see Figure 7 and Biuw et al. (2007), Burns et al. (2004) and Shaffer & Costa (2006).

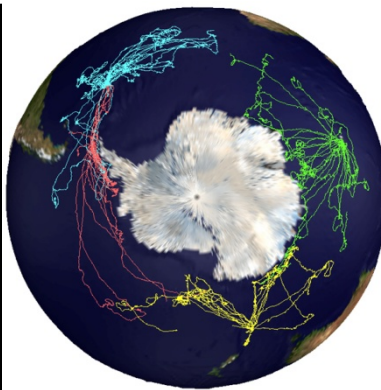
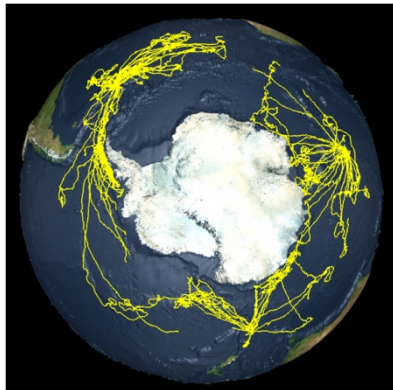


Figure 7. Tracks from SEaOS (Southern Elephant Seals as Oceanographic Samplers): an interdisciplinary programme aimed at understanding how seals interact with the physical environment. Figure redrawn from Biuw et al. (2007) by M. Fedak (who gave his permission to include this here).

This focus on the Antarctic Peninsula and Scotia Sea region is partly due to historical whale and seal exploitation activities that were concentrated in these areas (e.g. Laws 1977) and the ensuing establishment of most national research bases (a few other research bases were also established in the east (e.g. Australia). Studies centred at these research bases, including both land-based studies of seals and penguins and at-sea studies of whales, have focused efforts in areas near to the bases. Information on life histories is available, but abundance and predator-prey relationships may be poorly understood.

Breeding population estimates for a number of top predator species are reasonably well established in some areas (Croxall et al. 1985). However, many of these population estimates are known to be outdated, e.g. the population estimates of flying seabirds and crabeater seals. Of the 24 species listed in this Croxall paper, only eight of these have reliable recent population estimates (crabeater seals, macaroni penguins, whitechinned petrel, southern giant petrels, northern giant petrels, blackbrowed albatrosses, greyheaded albatrosses and wandering albatrosses).

3.1.2 Distribution, abundance, biomass and diet data

Zooplankton diet (trophic level) is summarized in Pakhomov (2000) and Deibel (2007). The most recent measurements of elemental composition of salps indicate that this group may be a more valuable food source (having a higher carbon and nitrogen content) than previously believed (Dubischar et al. 2006). Good diet data exist for birds but that for seals are less extensive. Juvenile fish as a diet source is poorly known (S. Hill pers. comm., South Georgia).

Workshop discussions then focused on cetacean diet research, first as this is where some of the expertise lay, second as this discussion highlighted many of the issues relevant to improving diet studies for inclusion in models. Good historical data exist for cetacean species that were commercially fished (i.e. from 30 - 70+ yrs ago), but little current data exist. Diet data could be updated using modern biochemical methods (Budge et al. 2008a, Budge et al. 2008b, Deagle et al.

2005, Deagle et al. 2009, Jarman et al. 2002). Compared to other ocean regions the diet of Southern Ocean baleen whales does not appear to be as diverse. The diet of Southern Ocean baleen whales is dominated by Antarctic krill *E. superba*, whereas those in the Northern Hemisphere (except blue whales) have more diverse diets that include other types of plankton and fishes. For example, the diet of right whales is dominated by *E. superba* in the Southern Ocean, but by copepods and small fish in the Northern Hemisphere. This difference has been interpreted as a response to the relatively large production and easy availability of *E. superba*. Prey-switching increases the resilience of populations, however it is currently unclear whether Southern Ocean baleen whale populations have begun to or will be able to pursue this strategy. It is not known what Southern Ocean baleen whales feed on during years when krill abundances are low.

Whether the lack of diversity in baleen whale diet will continue in the face of a changing environment is unknown. Good energy budgets are not available for any Southern Ocean whale species. Current studies of Southern Ocean killer whales have revealed the existence of three separate ecotypes, each with distinct morphology and food habits. One form specializes on fishes, primarily ice fish, a second on seals and penguins, and a third on minke whales (Krahn et al. 2008, Pitman & Ensor 2003, Pitman et al. 2007). Studies are underway to determine if these are sufficiently distinct to be called separate species (LeDuc et al. 2008).

In general, *Calanus* copepods have higher concentrations in the north Atlantic than in the Southern Ocean. Although, the average highest abundance of copepods recorded west of the Antarctic Peninsula (up to 111,565 individuals m⁻³, (see Deibel & Daly 2007, Pakhomov & Froneman 2004) is in fact the same order of magnitude as the highest abundance of *Calanus finmarchicus* (331,000 m⁻³) reported for the Great South Channel off the United States, a hot spot for right whale feeding (Wishner et al. 1995)). However, in general, copepod abundances are 1 to >3 orders of magnitude lower in the Southern Ocean, which probably would not be able to sustain whale food requirements (Deibel & Daly 2007, Pakhomov & Froneman 2004).

A more thorough understanding of the diet fractions of many Southern Ocean species would be extremely beneficial. However, these are poorly known because: diet fractions tend to be highly variable (in space, time, and between individuals in a population) and relatively few sets of data span spatial, seasonal and interannual variability; diet depends on prey availability which is usually not measured along with diet fractions, making it difficult to adjust diet between different regions/studies; stomach analysis methods can be biased towards material that is indigestible or digested more slowly, and against soft, easily digested or poorly identified prey (a differential-digestion issue); stomach analysis results are biased if only the soft-parts of a prey are consumed (a predator behaviour issue) (Pinkerton et al. 2008b); prey occurrence rather than prey proportion by mass is usually identified. Diet fractions can be adjusted in models assuming they depend on prey biomass, prey availability, and the preference of a predator for different types of prey. The 2008 CCAMLR Predator Survey Workshop planned to estimate overlap in horizontal and vertical predator-prey ranges, and this may help to determine the availability of prey species to predators.

Although there are numerous qualitative descriptions together with a limited number of numerical models of Southern Ocean food webs, there is no standardised approach for describing these systems. Many are 'snap shot' descriptions or views of food webs that do not capture temporal and spatial variability. A comprehensive review of circumpolar food web structure and existing data to highlight gaps in information and understanding is a critical next step.

Structure of Southern Ocean food webs

- Relatively comprehensive data exist for the Scotia Sea, Antarctic Peninsula and Ross Sea; however, there are still gaps in understanding of seasonal dynamics and processes controlling responses to variability;
- Basic understanding of distribution, abundance, life cycle dynamics, demographics and diet of the taxonomic components of food webs needs to be systematically improved. This needs to target the key groups: viruses, bacteria, phytoplankton, zooplankton, fish, cephalopods and top predators;
- A comprehensive review of current knowledge of the structure of circumpolar food webs (including compilation of existing data) was identified as a first key step before developing model structures;
- A standardised approach is needed for qualitative and quantitative representations of food webs;
- Energy pathways other than krill, which are important in different regions or at different times of the year, need to be characterised;
- Variations in food web structure, including inter- and intra-regional differences, seasonal and inter-annual dynamics need to be examined;

3.2 What determines the structure of Southern Ocean food webs?

Understanding what determines food web structure is fundamental in predicting how they will change over time (e.g. as illustrated by the krill-centred research depicted in Figure 8). This requires understanding of the following influences:

- Physical influences on food web structure (e.g. temperature, advection, stratification, mixing, sea ice);
- Biogeochemical influences on food web structure (including feedback effects, bottom up and top down effects);
- Biological influences on food web structure (e.g. trophic interactions, disease, competition, mobility);
- Anthropogenic influences on food web structure (e.g. harvesting, introduction of invasive species, depletion of ozone and atmospheric warming);
- The role of top down versus bottom up processes (e.g. the role of top predators in structuring marine communities).

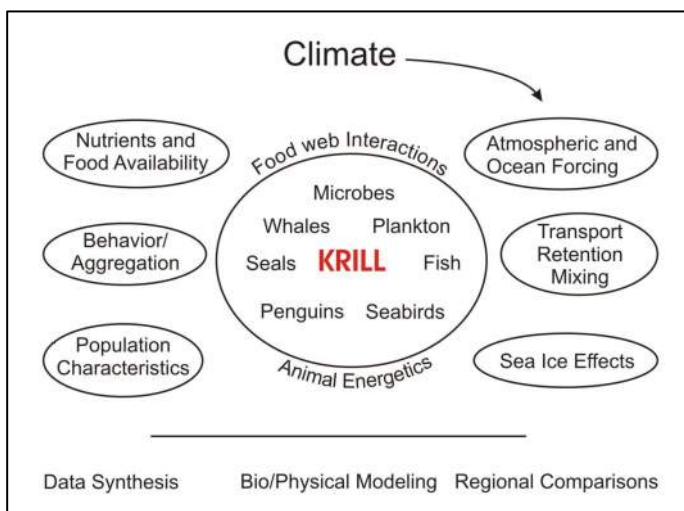


Figure 8. Summary of krill centred research conducted by the SO GLOBEC programme. This illustrates the research conducted to examine relationships between krill dynamics, their predators, the physical environment and biogeochemical cycling. Reprinted from Deep-Sea Research II, 55, Hofmann et al. (2008), Introduction to Dynamics of Plankton, Krill, and Predators in Relation to Environmental Features of the Western Antarctic Peninsular and Related Areas: SO GLOBEC Part II, 260-270., Copyright (2008), with permission from Elsevier

Food web models are dependent upon characterization and details of the physical environment, which makes it critical that the physical forcing elements be incorporated at scales that are relevant to biological processes. For much of the Southern Ocean there has been little detailed analysis of the interactions between physical and biological processes and how these determine ecosystem structure. Where available the information tends to be limited to local studies or based around a small number of species. Satellite-derived data provide a valuable resource for defining regional physical structure and variability. Analyses of physical system operation to quantify space and time variability are important to establish a dynamic basis for regional food web analyses.

Biogeographic analyses of the physical, chemical and biological factors of the circumpolar system are ongoing as part of a bioregionalisation analysis of the Southern Ocean (Grant et al. 2006). To date, this has focused on physical and chemical data, but it also provides a valuable basis for building circumpolar analyses of food web structure as it provides localised analyses of the physical controls on the dynamics of key species and food webs. However, these have not yet been considered at regional and circumpolar scales.

The spatial variation in structure of Southern Ocean food webs leads to regional differences in food webs (e.g. Figure 9), but there are important spatial connections between these that occur via advective processes (e.g. Figure 10) and biological behaviour. Workshop discussions considered how these levels of connectivity determine food web structure and highlighted the importance of defining geographic limits for food web models. However, range boundaries vary considerably by species and a single set of model boundaries would likely dissect the ranges of some, raising difficult boundary condition issues.

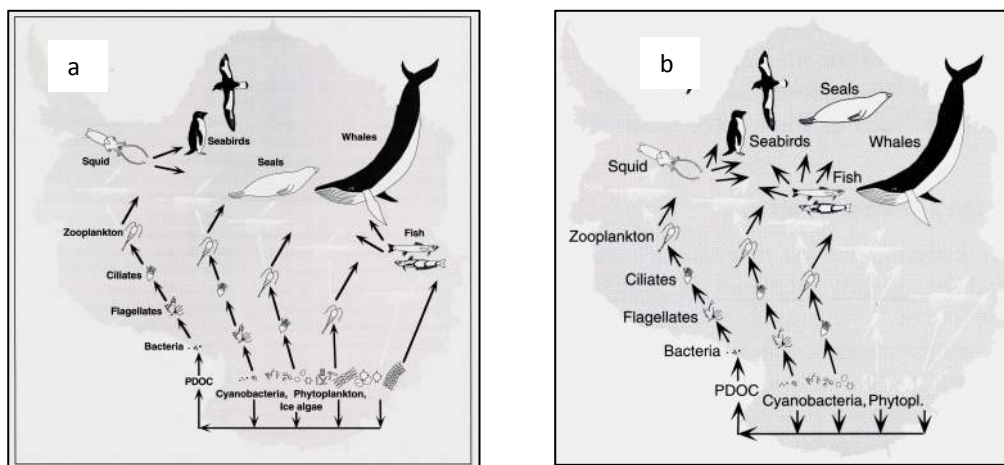


Figure 9. Food web of the a) coastal zone in summer and b) the Marginal Ice Zone in late summer and autumn (after Moloney and Ryan 1995), showing missing or minor components and linkages in white. In a) Primary producers span a range of sizes. Antarctic krill are absent. Other euphausiid species, copepods and Antarctic silverfish dominate the consumer community. Vertebrate predators such as Adélie penguins and minke whales forage in the region. In b) Primary producers are cyanobacteria and small phytoplankton. Small zooplankton dominate the community of consumers. This figure was published in *Encyclopaedia of Environmental Biology*, 1, Moloney, C.L. and Ryan, P.G. Antarctic Marine Food Webs, 53-69, Copyright Elsevier (1995).

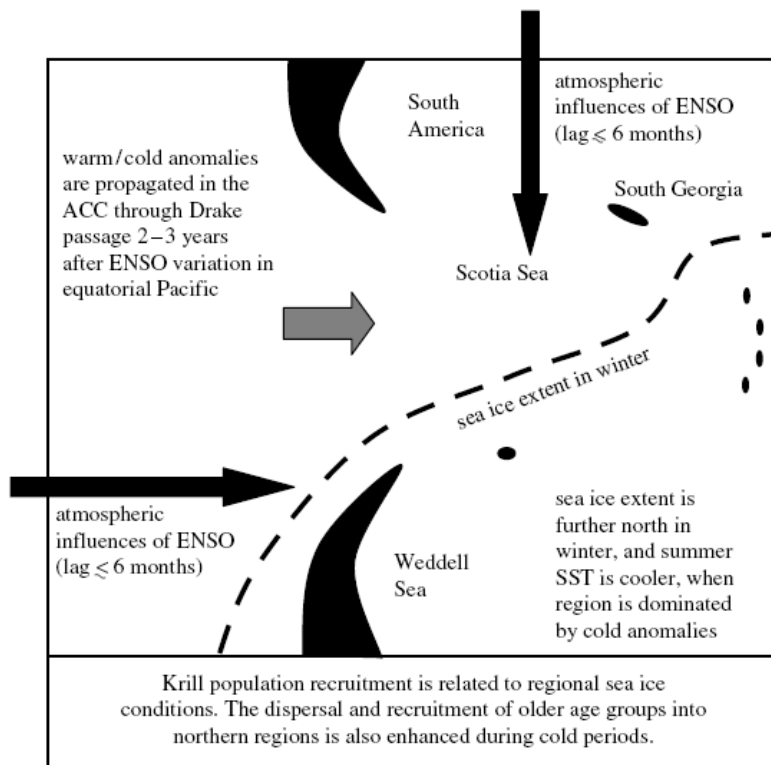


Figure 10. Schematic of the main physical processes generating variation in the Scotia Sea ecosystem as outlined in Murphy et al. (2007b). These factors also affect krill recruitment and dispersal across the region, generating observed correlations of changes in krill density and biomass and higher predator foraging and breeding performance, with sea ice and larger scale indices of oceanic and climatic variation. Source: Murphy et al. (2007b)

Discussions of the resolution of biogeochemical processes required in food web modelling noted the difficulties in combining detailed biogeochemical models with food web models. The need for better representation of food webs in current biogeochemical models was emphasized, as was the importance of food web processes and feedbacks in influencing biogeochemical cycles. For example, we need further insights into the effects of top-down influences from upper trophic level species (e.g. faecal enrichment) on biogeochemical cycles. Some detailed discussion focused on controls on primary production and the role of iron limitation. The largest primary production blooms in the Southern Ocean are typically associated with shelf areas or ice-edge areas. Discussions also raised the issue of why krill are more abundant in the Southwest Atlantic sector than elsewhere in the Southern Ocean. This led to consideration of the distribution of phytoplankton (Figure 11) and the controls on primary production. Discussions considered the different sources of iron for these blooms (e.g. island run-off, shelf sediments, glacial rock-flour, upwelled waters) and whether iron was repeatedly recycled in these locations. Other issues included variations in the solubility of iron in atmospheric dust, iron speciation and interactions with ligands, and iron scavenging.

Discussions also focused on the potential importance of different phytoplankton groups and zooplankton grazers in structuring biogeochemical cycling. For example, what would be the impacts of shifting between copepod and krill-dominated systems? How do diatom versus *Phaeocystis*-dominated phytoplankton assemblages alter food availability for zooplankton and sinking export flux? How does phytoplankton species assemblage composition affect DMS production? Other aspects discussed included the potential importance of sub-grid parameterisation of aggregation of plankton organisms in patches of different size and the importance of this in linking biogeochemical and food web models.

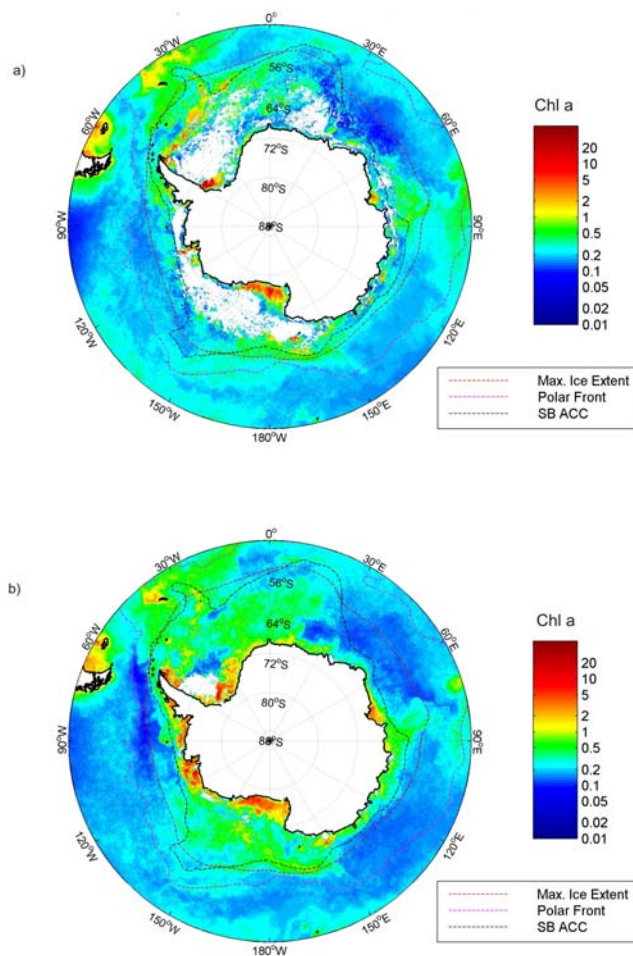


Figure 11. Large-scale surface chlorophyll *a* (Chl *a*) concentrations (mg m⁻³) around the Antarctic derived from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Project. Average concentrations are shown during a) spring (1997–2004) and b) summer (1998–2005). This type of data can be used to examine primary productivity and biogeochemistry in the Southern Ocean. SB ACC = southern boundary of the Antarctic Circumpolar Current. Source: Australian Antarctic Division.

Through considerations of how species distributions influence food web structure, workshop discussions then focused on whether Southern Ocean food webs were sufficiently similar to be represented by a generic food web model. Discussions concluded that a single adaptive model structure could be developed for the Southern Ocean, despite differences in species composition between ocean basins. Species distribution and abundance as well as regional differences in ecosystem structure would be emergent properties of the generic parameterisation. For example, a generic approach has been adopted in the CLIOTOP Modelling and Synthesis Working Group with the Apex Predators ECOSystem Model (APECOSM) (see Section 5.2 and Maury *et al.* 2007) and this approach would be worth considering for the Southern Ocean. It is also important to note that some species may influence marine community structure in a manner disproportionate to their numbers. For example, it has been proposed that endothermic top predators, due to their high metabolic rate, exert a disproportionate influence on community structure (Estes & Palmisano 1974, Estes *et al.* 1998, Springer *et al.* 2003).

Determinants of Southern Ocean food web structure

- Systematic examinations of the factors (physical, biogeochemical, biological and anthropogenic) determining the general structural and operational properties of food webs are required;
- Regional factors and spatial connections are important in shaping food web structure. It is therefore necessary consider geographic limits for the development of regional food web models;
- Biogeographical analyses of factors influencing food web structure may provide a valuable basis for identifying key regions and building circumpolar analyses;
- The development of circumpolar scale analyses of food web structure in relation to the underlying physical and chemical environment is considered a key priority (however, we need to consider whether circumpolar food webs are sufficiently similar to be represented as a generic food web);
- The role of variability and change in influencing food web structure and biogeochemical cycling and *vice versa* (through top-down and bottom up-pressure) needs to be explicitly examined;
- Understanding of the controls on primary production, including the role of iron limitation, as a basis for examining the factors determining food web structure needs to be improved;
- Grazers of phytoplankton and other microbial groups are undoubtedly important in structuring biogeochemical cycling (e.g. what are the impacts of shifting between a copepod and krill-dominated systems; are DMS effects different for different phytoplankton species compositions; what are the sources of iron; are upper trophic levels needed in biogeochemical models);
- The determinants of food web structure can be usefully examined by focusing effort on a limited number of key questions such as: why are krill more abundant in the Southwest Atlantic sector?

3.3. How does food web structure respond to variability and change

To address this we need an understanding of the following contributing factors:

- Natural variability;
- Long term natural change;
- Long term anthropogenic change.

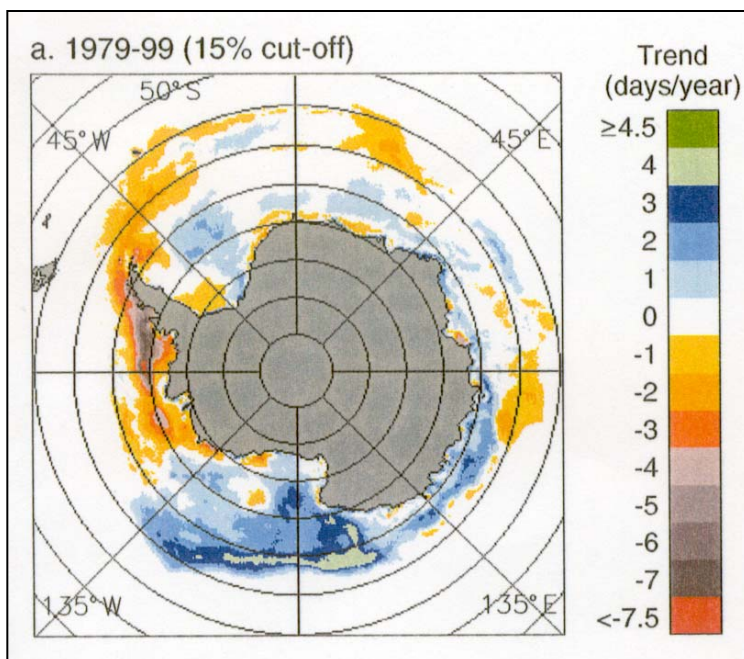
Superimposed on the natural spatial and temporal variability of Southern Ocean ecosystems is the influence of long-term change driven by both natural and anthropogenic processes. These different drivers and frequencies of change need explicit consideration. Response to change is a function of ecosystem structure and biodiversity, which affects the stability properties of the food web and hence resilience to change. The variability and frequency pattern of disturbance are also likely to be important in determining ecosystem structure, and changes in variability may be an important feature of the environmental change.

Discussions considered not just climate related change, but also the effects of historical and current harvesting. The importance of understanding and quantifying variability at seasonal, interannual and decadal time-scales was noted. There has been major progress in understanding the impacts of interannual climate-related variability throughout the Southern Ocean during the last 5 years. In addition there has been significant development of understanding of the longer-term physical

changes occurring in Southern Ocean systems. There is much less understanding of seasonality of Southern Ocean systems and their variability. The importance of analysing the effects of interannual variability to develop mechanistic understanding of the effects of large scale processes in Southern Ocean food webs was noted.

Discussions of how the broad-scale Southern Ocean marine ecosystem would respond to climate change were conducted in the context of the changes known to be occurring in the Southern Ocean (e.g. Figure 12). It was noted that recent, rapid regional warming was important and that broad-scale signals were not simple to compile, and that climate change signals are overlain by substantial interannual climate variability (e.g. Boyd *et al.* 2008). Climate change simulations from coupled ocean-atmosphere models suggest a future shift toward a more positive phase of the Southern Annular Mode (SAM), resulting in a strengthened and poleward contraction of the westerly wind maximum, a spin-up of the ACC, and an increase in upwelling of nutrient and CO₂ rich Circumpolar Deep Water. Recent studies indicate that the resultant elevated outgassing of CO₂ to the atmosphere may be decreasing the effectiveness of anthropogenic CO₂ uptake by the Southern Ocean (Le Quere *et al.* 2007, Lovenduski *et al.* 2007, Lovenduski *et al.* 2008). Ocean acidification has also become a recent focus for research as the Southern Ocean may constitute an important region for this process (McNeil & Matear 2007).

Figure 12. Trends, identified by Parkinson (2002), in the length of the Southern Ocean sea ice season between 1979–99 using a 15% ice concentration cut-off (i.e. considering a location to have sea ice if ice concentration calculations, derived from satellite passive-microwave data, show at least 15% ice coverage). Over this period most of the Ross Sea ice cover has, on average, undergone a lengthening of the sea ice season, whereas most of the Amundsen Sea ice cover and almost the entire Bellingshausen Sea ice cover have undergone a shortening of the sea ice season. Results for the Weddell Sea are mixed, with the north-western portion of the sea having experienced a shortening of the sea ice season but a substantial area in the south-central portion of the sea having experienced a lengthening of the ice season. Overall, the area of the Southern Ocean experiencing a lengthening of the sea ice season by at least 1 day per year over the period 1979–99 is $5.6 \times 10^6 \text{ km}^2$, whereas the area experiencing a shortening of the sea ice season by at least 1 day per year is 46% less than that, at $3.0 \times 10^6 \text{ km}^2$. Source: Parkinson (2002), reprinted from the *Annals of Glaciology* with permission of the International Glaciological Society.



There are already very significant signals of regional climate related changes occurring across the Southern Ocean. Around the Antarctic Peninsula oceanic warming and reductions in ice concentration and winter duration have been documented. In other regions such as the Ross Sea sea-ice concentration is increasing. Overall there is little change in sea ice at the circumpolar scale. This highlights the need to develop regional analyses of climate related change. A large number of Southern Ocean ecosystem properties could potentially change on a regional basis due to climate change. These include, *inter alia*, changes in ocean acidification, changes in seasonal stratification, altered temperature profiles, altered sea-ice dynamics and variability in the location of frontal jets within the ACC. Such changes will impact differentially upon different species and hence food webs.

There are a wide range of changes occurring in Southern Ocean ecosystems. However, the mechanisms underpinning the responses are complex and have a strong regional basis. Increases and decreases in populations of pelagic species, seabirds, and marine mammals are being observed (Barbraud et al. 2008, Barbraud & Weimerskirch 2009, Delord et al. 2004, Jenouvrier et al. 2003, 2005a, Jenouvrier et al. 2005b, Jenouvrier et al. 2006, Jenouvrier et al. 2009, Nicol et al. 2008, Trathan et al. 2007). Across the Atlantic sector krill abundance has shown a significant decline over the last 30 years (Atkinson et al. 2004, see Figure 13). Some predator populations in the region are decreasing, while others are increasing. In the West Antarctic Peninsula region, sea-ice is now less extensive and less persistent than in recent years (Ducklow et al. 2007, Fraser et al. 1992, Stammerjohn et al. 2008). These changes are thought to have produced modifications throughout the food web up to upper-trophic level species. Ice-obligate species such as Adélie penguins have experienced population decreases, while open-ocean species such as chinstrap penguins have shown population increases (Ducklow et al. 2007, Fraser et al. 1992). Similar changes in the South Orkney Islands have also been documented, though chinstrap penguin numbers now also show population declines (Forcada et al. 2006). The longest available demographic time series starting in 1952 shows that emperor penguins (*Aptenodytes forsteri*) in Terre Adélie have declined by 50% due to a decrease in adult survival that correlated with a prolonged abnormally warm period with reduced sea-ice extent (Barbraud & Weimerskirch 2001). Thus, regional climate effects are likely expressed at very local scales.

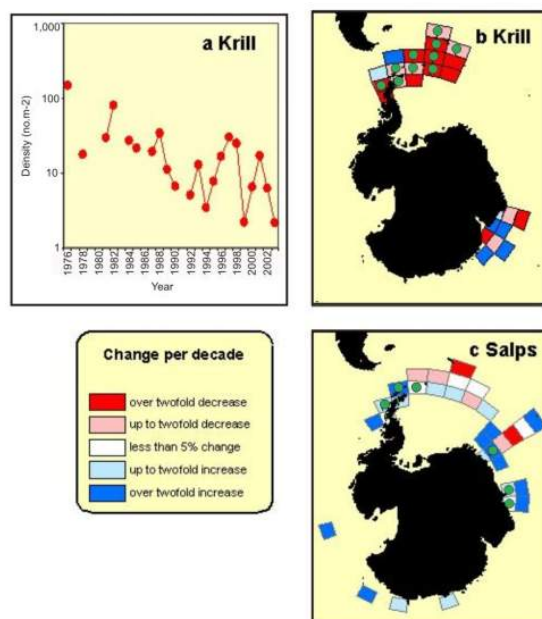


Figure 13. Spatial and temporal changes of Antarctic krill and salps. a) Krill density in the southwest Atlantic sector of the Southern Ocean (4,948 stations in years with >50 stations). Temporal trends include b) post-1976 krill data from scientific trawls; c) 1926–2003 circumpolar salp data south of the Southern Boundary (SB) of the Antarctic Circumpolar Current. Regressions of $\log_{10}(\text{mean no. m}^{-2})$ on year were calculated for cells with ≥ 3 yr of data, weighted by number of stations in that year. One-sample t-tests supported a post-1976 decrease in krill density in the southwest Atlantic (scientific trawls: $t = -3.4$, $P = 0.004$, 16 cells, smaller nets: $t = -2.5$, $P = 0.04$, 8 cells). Salp densities increased south of the SB after 1926 ($t = 3.1$, $P = 0.004$, 32 cells). Green spots denote cells usable in a spatio-temporal model of these time-trends. Reprinted by permission from Macmillan Publishers Ltd: Nature (Atkinson et al. 2004), copyright 2004

Analyses of interannual variability in the Scotia Sea have shown the importance of interactive alternative pathways of energy flow in food webs in maintaining food web structure on longer time scales (Murphy et al. 2007b). Periods of low krill availability emphasize pathways that are dependent on copepods and fish. Longer term shifts are also likely to be occurring but these are difficult to detect. The statistical detection of change in marine food webs is difficult and in most cases current monitoring data are inadequate to detect change with any certainty. Indeed, at present it is not possible to clearly identify major changes in the abundance, or the ecological role, of most Southern Ocean species. To achieve the statistical power necessary to detect such change requires carefully coordinated long-term monitoring programmes.

Match-mismatch hypotheses were considered, as were the potential consequences of changes in phenology; changes in critical rates are of importance and would likely impact upon species distribution and abundance. The analyses of such effects require greatly increased understanding of the seasonal dynamics of Southern Ocean ecosystems. As noted previously, difficulties in winter sampling in this region has resulted in a major gap in data and understanding compared to many other oceanic systems. Development of year-round biological monitoring programmes is a priority requirement on which to base the development of seasonal modelling programmes.

The importance of using models to understand the impacts of past harvesting over more than two centuries was also emphasized during discussions as this will potentially provide valuable insights for predicting future scenarios. Placing bounds on the levels of uncertainty on current and historical population trajectories is key, but available data are sparse. One of the key Southern Ocean food web questions that has still not been adequately resolved is the so-called 'krill surplus' hypothesis. This hypothesis suggests that the removal of the baleen whales during the early twentieth century released competitive effects upon other krill consumers. Consequently, penguins and seals, in particular, experienced rapid population expansion. This hypothesis remains to be validated and could usefully be addressed by the next generation of food web models.

The consequent effects of the removal of large numbers of long-lived seals and whales are still occurring. The removal of many slow growing long-lived fish species, which do not appear to be showing much sign of population recovery, even though harvesting is now at a low level or stopped, further highlights how these systems have been changed. The effects of recovery of large marine mammal populations are likely to cascade through the food web and impact lower trophic levels (Estes et al. 1998, Springer et al. 2003). Thus there is a need to include feedback impacts relating to food web structure and in particular, upper trophic level food web structure, in analyses and modelling of food web responses to change. The overall structure of the food web will be crucial in determining stability properties and resilience to change. The removal of many top predators will have greatly altered the stability properties and hence the systems resilience to change.

Robust predictions of the impacts of change on Southern Ocean food web structure are required. However, it was recognised that it would be difficult to produce robust forecasts if historical data are not adequately understood (where available). Part of such historical understanding would require analyses that help disentangle the confounding impacts of climate change and historical harvesting on population trajectories. The workshop noted that this was a key challenge and would require hindcast modelling studies to consider how the harvesting changes impacted the system in the past.

When ecosystem regime shifts occur, different processes may likely dominate and result in different 'base states'. Discussions considered whether different ecological (or model) 'rules' (e.g., relationship between temperature and primary production) should exist under such base states; should such rules remain constant, as emergent properties may change the dominance of different species under different ecosystem regime states. Developing concepts of emergence based on

ecological rules of empirically based models will be valuable. Also, comparing aspects of different systems in the context of 'vulnerability' to climate change (species level/system level) would be a valuable exercise.

Questions arising from the above discussions include;

- What is the importance of changes in ocean acidification/ seasonal stratification/ altered temperature profiles/ altered sea-ice dynamics/ or ACC variability; which species will be most affected?
- Do different base states exist under different ecosystem regime states?
- Will climate-related change result in a shift from a krill dominated to copepod/fish dominated food web?
- Are import/subsidised food webs more vulnerable to climate change?
- Do iron-replete systems result in krill dominated food webs that support large numbers of large bodied predators (i.e. iron-> big diatoms->krill-> predators)?What are the key processes and the consequences of change in these key processes?
- Could there be rapid shifts in ecosystem structure and function given the combinations of changes in key processes (i.e. is there a chance of meta-stable states and what would trigger regime shifts)?
- How do we incorporate physiology and behaviour to look at adaptation to variability?

Response of Southern Ocean food webs to climate and anthropogenic change

- Analyses of the effects of interannual variability are important in developing mechanistic understanding of the effects of large-scale processes in food webs and their response to change.
- Understanding the response of Southern Ocean food webs to climate and anthropogenic change requires consideration of the confounding impacts of natural spatial and temporal variability, long-term natural change and long-term anthropogenic change.
- The responses of different ecosystems or parts of ecosystems to climate and anthropogenic change will be variable in space and time. Integrated studies will therefore be required at different spatial (local, regional and broad/circumpolar) and temporal (seasonal, interannual and decadal) scales.
- The response of food webs to climate and anthropogenic change is a function of structure and biodiversity, which affects stability properties of the food web and hence its resilience to change. The variability and frequency of disturbance on any food web is therefore likely to be important in determining its structure. Changes in variability may thus be an important feature of the environmental change.
- Shifts in energy pathways in relation to climate change have been observed in some Southern Ocean food webs. Detection of this type of change will be enhanced by long-term monitoring programmes.
- Understanding the impacts of harvesting will help disentangle the impacts of climate change and historical harvesting on populations.
- There is a lack of information on the seasonal operation of food webs. There are indications that changes in phenology are occurring and potentially generating match-mismatch effects. To address this requires the development of focused studies on seasonal food web dynamics.
- The potential for regime shifts in Southern Ocean food webs, or even substantial long-term changes to most species distributions/abundances, requires specific consideration of data requirements to detect change.

4. Models of Southern Ocean food webs

The various modelling approaches of relevance to analyses of Southern Ocean food webs were discussed as a start towards formulating a strategy for modelling Southern Ocean food webs. It was envisaged that this would include detailed simulation/predictive models for key components/regional ecosystems in the Southern Ocean. The following sections highlight some of the key issues raised.

4.1. *Developing mechanistic models of Southern Ocean food webs*

These models could potentially integrate elements that have traditionally been dealt with in detail in ocean circulation, ocean biogeochemistry, single species, and food web models. The current status of relevant models in each category and the implications for the development of end-to-end models of Southern Ocean food web dynamics was considered, and current reviews of models for Southern Ocean krill and its predators (Hill *et al.* 2006) and Southern Ocean circulation models (Rintoul *et al.* 2001) were noted as being important resources. The key points raised during the discussion of these issues are summarized.

4.1.1. Ocean General Circulation Models (OGCM)

There are several well developed ocean general circulation models (OGCMs) which are available to any academic user and are supported with user guides or extensive user groups (a listing of models with links to model home pages is available at www.ocean-modelling.org). It is relatively straightforward to develop regional models with these modelling resources. For example, a high resolution ocean model of South Georgia has recently been developed using the Proudman Oceanographic Laboratory Coastal-Ocean Modelling System (POLCOMS) OGCM (Young *et al.* Submitted).

Most OGCMs use finite difference approaches with a structured grid. A few model codes are available that use unstructured grids (finite element and finite volume codes) which allow widely ranging grid size (e.g. Danilov *et al.* 2004). Physical process models include most physical processes that are needed to support simulation of biological and chemical properties in the ocean. For example, various turbulence submodels, advection schemes or mixed layer formulations may exist within a model code, thereby providing a range of possible dynamics for experimentation.

Biogeochemical dynamics have been the focus of major scientific development during the last decade. Almost all of the available physical models include some form of biochemical model (e.g. nutrients, phytoplankton, zooplankton and detritus - NPZD, e.g. Figure 14), which can be modified for specific applications.

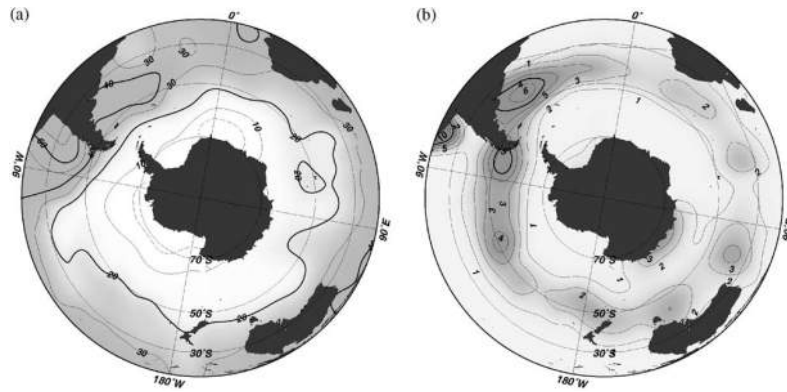


Figure 14. An ocean circulation, biogeochemical model was developed to determine rates of export production and vertical carbon fluxes in the Southern Ocean. The model exploited large sets of hydrographic, oxygen, nutrient and carbon data with information on underlying biogeochemical processes. Here, the simulated distribution of semi-labile dissolved organic carbon ($\mu\text{mol kg}^{-1}$) is shown (represented by the numbers and shading) for the Southern Hemisphere in (a) surface layer (30 m depth) and (b) 500 m depth. This shows the results from only 1 of 7 experiments that differed with respect to element ratios of particulate and dissolved organic matter, nitrification/de-nitrification processes and other factors (refer to source for details). Comparing carbon export fluxes with export production from satellite data, the model was in good agreement for low- and mid-latitudes, but for the Southern Ocean discrepancies were apparent. More direct observations are needed for a clearer understanding of the Southern Ocean's role in the carbon cycle and to fully utilise available satellite data. Reprinted from Deep Sea Research Part II: Topical Studies in Oceanography, 49, Schlitzer, R. (2002), Carbon export fluxes in the Southern Ocean: results from inverse modeling and comparison with satellite-based estimates, 1623-1644, Copyright (2002), with permission from Elsevier

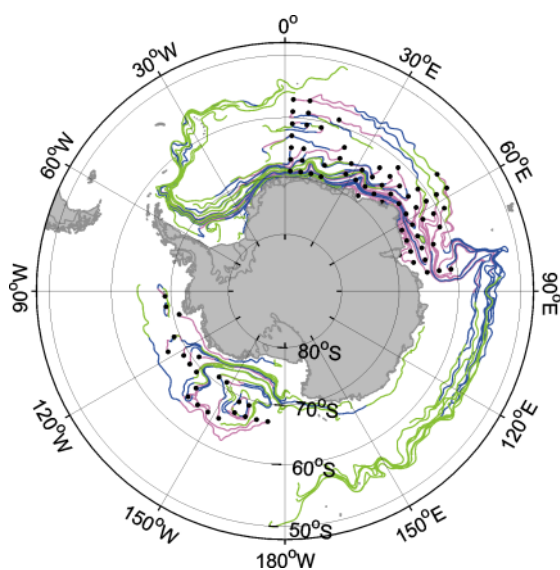


Figure 15. Lagrangian particle tracking analysis around Antarctica examining the circumpolar connection of Antarctic krill populations using OCCAM circulation model output. Particles were released into OCCAM velocity fields (marked by black dots) and tracked for 3 years in the upper 180 m of the water column. Trajectories are coloured according to time (0–1 yr: pink, 1–2 yrs: blue, 2–3 yrs: green). Reprinted from Deep Sea Research Part I: Oceanographic Research Papers, 54, Thorpe et al. (2007), Circumpolar connections between Antarctic krill (*Euphausia superba* Dana) populations: Investigating the roles of ocean and sea ice transport, 792-810, Copyright (2007), with permission from Elsevier

Lagrangian modelling is a valuable tool in analyses of biological process interactions in oceanic systems (e.g. Figure 15). Analyses of drifting particles are available in many of the publically-available models. Most particle codes are passive particles that follow the flow, or maintain a certain depth, pressure or density surface. From this basic capability, it is possible to develop biological characteristics or behaviours appropriate to certain organisms. Examples of formulations of these biological particle models with behaviours can be found in the literature e.g. Murphy et al. (2004).

Sea ice models are not as widely available but can be found (e.g., a Community Ice CodE, <http://climate.lanl.gov/Models/CICE/>). At present, none include biological processes, such as ice

algae. In some cases, the sea ice and OGCM are separate programs that communicate through an intermediate programme (a coupler). In other cases, the sea ice model is imbedded in the OGCM. Each of these structures would require different techniques to allow animals to move between ocean and ice habitats to simulate the use of sea ice as a refuge in winter.

Developing high resolution models is seen as crucial to properly represent the relevant physical and biological processes at the appropriate scales. The key to developing regional scale models is to establish the boundary conditions for the region of interest. This could be achieved through downscaling (estimating fine spatial structure from a coarser model solution) which would take global coarse ocean simulations, perhaps developed as part of a climate change analysis, and construct local conditions that are more consistent with local geometry or bottom topography. This finer scale solution may be more appropriate for biological calculations than would be the coarser solution.

There are some important limitations of OGCMs as far as the development of end-to-end models is concerned. Firstly, ocean circulation models are expensive (in terms of computer resources or sacrificed resolution) to run over the long (decadal) timescales that might be necessary for some biological components. Any long-term predictions will require climate data at appropriate scales, and it might be timely to approach groups developing climate prediction models to request such data. OGCMs are deterministic, but an ensemble could be developed to explore some uncertainties. This would also increase the 'cost' of running the models. Improvements in the skill in simulating spatial and temporal variability are realised through increasing model resolution, for example sea surface height variability tends to be underestimated in the global OGCMs (e.g. Stammer *et al.* 1996) until a sufficiently high resolution is used (Maltrud & McClean 2005). It will be important to establish the skill of the model in representing the characteristics that influence food web dynamics. It is, however, possible to tune the models to obey observed probabilities of the formation of some features (e.g. eddies). The ability of ocean circulation models to replicate fine-scale conditions is constrained by the availability of good bathymetric data. Finally, the nature of current OGCMs might lend itself to modelling bottom-up controls, but two-way-coupling could be difficult to achieve.

4.1.2. Biogeochemical Models (BGCM)

Simulation of biogeochemistry in the Southern Ocean is largely motivated by changes in past or present global climate, such as the changes that occur between glacial and interglacial periods. Some of the important questions are:

- What is the role of Southern Ocean ecosystems in the climate system?
- What is the contribution of Southern Ocean ecosystems to the uptake of anthropogenic CO₂?
- How much DMS is emitted by the Southern Ocean?
- What are the impacts of and feedbacks of the Southern Ocean to global change?
- Can we lower atmospheric CO₂ by iron fertilization?

More specific issues include:

- Can we simulate the large-scale distributions of nutrients (NO₃, PO₄, Si (OH)₄), chlorophyll, dissolved inorganic carbon (DIC) and total alkalinity (TA)?
- What is the role of iron (limiting factor; impact on stoichiometry of phytoplankton: Si:N ratios (Hutchins & Bruland 1998, Takeda 1998); switch from Si(OH)₄ to NO₃ limitation during glacials when aeolian iron input was larger (Brzezinski *et al.* 2002)?

- What are the iron sources (upwelling, shelf sediments, dust, recycling) (Tovar-Sanchez *et al.* 2007)?
- What is the chemical and physical speciation (Volker & Wolf-Gladrow 1999, Weber *et al.* 2005) and the fate of iron?

These and other questions are typically addressed using simple but appropriate models. The emphasis is usually on primary production; zooplankton is included in order to provide a non-linear loss term for phytoplankton, and higher trophic levels are neglected. At least four types of these lower trophic level models can be recognized:

- NPZD with fixed stoichiometry (canonical elemental ratios, often referred to as Redfield ratios, C:N:P; (Fasham *et al.* 1990, Franks *et al.* 1986);
- NPZD with several nutrients and variable stoichiometry (regulated models, e.g. Schartau *et al.* 2007);
- Phytoplankton functional types (PFTs), which distinguish groups such as silicifiers, calcifiers, N₂-fixers and dimethylsulphoniopropionate (DMSP) producers (Aumont *et al.* 2003, Aumont & Bopp 2006, Gregg *et al.* 2003, Gregg & Casey 2007, Le Quere *et al.* 2005, Moore *et al.* 2002);
- Size spectra models which distinguish between some groups of organisms on the basis of size (Armstrong 1999, Kriest & Oschlies 2007, Moloney *et al.* 1991).

These pelagic ecosystem models can be implemented in (or coupled with) box models (few boxes with prescribed transport and mixing) or ocean OGCMs of various resolutions (by defining an additional tracer field and adding source and sink terms). For models in regional domains (i.e. non-global) it may be a problem to provide appropriate values at open boundaries. One-way nesting is a well-established technique; two-way nesting might be possible, but is not yet in common use in the ocean modelling community.

The Southern Ocean has several special features that should be taken into account when setting up such biogeochemical models: Wind forcing drives upwelling of nutrient rich waters in the south and northward Ekman transport. The ACC transports more than 100 Sv and contains several narrow (10 km) current cores. These are the source of mesoscale eddies which lead to meridional transport of properties. Mixed layer depths vary between less than 20 m near sea ice edges to 100 m or more in the ACC. The Southern Ocean encompasses the largest of the three high nutrients low chlorophyll (HNLC) regions of the world oceans. Nutrients (NO₃, PO₄) are never used up in surface waters because of iron limitation. The phytoplankton in the Southern Ocean south of the Polar Front is dominated by a dozen or so species of diatoms. Some of these species are responsible for the formation of the opal belt in the sediment around Antarctica. Whereas large parts of the surface sediments of the opal belt are dominated by the shells/frustules of heavily silicified species *Fragilariopsis kerguelensis* the western Antarctic sector is characterized by large amounts of resting spores of weakly silicified *Chaetoceros* species. This sector is well known for its large concentration of krill (Atkinson *et al.* 2004). Up to 20 million km² around Antarctic are covered by seasonal sea ice (Smith *et al.* 1998) that hosts organisms that may provide food for certain organisms (for example, krill larvae) during winter and plankton seed populations in spring. The melting of sea ice can lead to the formation of shallow mixed layers and release of iron where intense phytoplankton blooms may develop.

The representation of the planktonic food web in biogeochemical models remains relatively simplistic. Zooplankton in NPZD models is just a closure term to provide non-linear losses of phytoplankton. There is scope for increasing the detail in the zooplankton groups, for example, to differentiate on the basis size or function or to include seasonal patterns. Behaviour of animals

(especially vertical migration) and life history stages are best simulated with Lagrangian approaches (trajectories; in contrast to the Eulerian approach for tracers). In theory, this type of model could be adapted to accommodate size-structured models of the higher food web.

Existing models have not performed well in replicating observed plankton communities, and it has often proved difficult to define appropriate parameter values from the literature. Validation is also an issue as there are few appropriate validation datasets and statistical validation methods have only recently been considered (Stow *et al.* In press). However, the priority areas for future data collection and model development are reasonably clear. More iron measurements (including speciation) are most important for the development of improved models and better data on phytoplankton assemblages are needed to validate models.

Therefore, although the development of more complex models is feasible, the performance of existing models must also be addressed. The inclusion of more organism groups or species requires a better understanding of regulation mechanisms which might be partially addressed through simulation, but will require extensive validation data. The results of the simulations (for example, phytoplankton biomass) may be used as input to models for higher trophic levels. Again, representing bottom-up control is technically more tractable than two-way coupling.

4.1.3. Models of key species- Krill

There is an active effort to develop more detailed models of krill and its ecological interactions. These include:

- Modelling of advection pathways on regional (Scotia Sea) and circumpolar scales using both Lagrangian (particle tracking) and Eulerian (grid-based advection-diffusion) modelling. This effort integrates OGCM-derived circulation fields and satellite-derived sea ice data (Hofmann *et al.* 1998, Murphy *et al.* 2004, Thorpe *et al.* 2007).
- Modelling of seasonal variation in food type and quality, and krill metabolic strategy (Fach *et al.* 2008).
- Integration of increased biological detail (including egg ascent-descent, feeding and metabolism, growth and reproduction) into advection models (e.g. Fach *et al.* 2002, 2006, Fach & Klinck 2006, Fach *et al.* 2008, Hofmann *et al.* 1992, Hofmann & Lascara 2000, Hofmann & Husrevoglu 2003, Tarling *et al.* 2007).
- Modelling the effects of temporal and regional temperature variation (around the Antarctic Peninsula and South Georgia) on the growth of krill cohorts (Wiedenmann *et al.* 2008).
- Further investigations of the statistical relationship between krill recruitment strength and various seas ice parameters (Wiedenmann *et al.* In prep).
- Modelling the potential effect of UVB at the surface, due to depletion and reconstitution of the ozone layer, on krill mortality (Mangel *et al.* In prep).

4.1.4. Models of key species- other zooplankton and fish

Relatively few life cycle models beyond krill exist for the Southern Ocean. Once such model is that of copepod life-cycles and population development (Tarling *et al.* 2004). Detailed demographic models have also been generated and parameterised for a number of commercially exploited fish species (e.g. icefish and toothfish). A number of age-structured models have been developed to aid in the management of fish stocks in the Southern Ocean. These include mackerel icefish at South Georgia (Hill *et al.* 2005), mackerel icefish fishery at Heard Island (Constable & de la Mare 1996), Antarctic toothfish in the Ross Sea (Dunn & Hanchet 2006, Hanchet *et al.* 2006), and Patagonian toothfish location (Hillary *et al.* 2006).

4.1.5. Models of key species- Predators

Demographic models and age structured-models are available for a range of seabird and marine mammal species. Analyses and models also exist for a range of marine mammals including fur seals, elephant seals and various whales. However, the data available for these models are limited, studies are often highly localised applying to relative small local colonies and for the whales are also based on data more than 30 years old. Demographic models and analyses have also been generated for penguins, albatross and other species of seabirds.

Although there are both statistical and simulation models of predator population responses to prey availability in the Southern Ocean (Forcada et al. 2005, Forcada et al. 2006, Forcada et al. 2008, Mori & Butterworth 2003, 2006a, b, Plaganyi & Butterworth 2005, 2006b, Watters et al. 2005) the processes involved in these responses are not well understood. Some ecosystem dynamic models have been used as operating models in a context that attempts to account for the major uncertainties (Hill *et al.* 2007).

Key questions for krill predators that can be addressed with modelling studies include:

- Do predators need krill in high concentrations and what happens to the 80% of krill biomass that occurs in low concentrations in oceanic areas?
- What functional responses are appropriate?
- What is the role of the ice edge in krill-predator interactions?
- How do environmental variables influence predator dynamics other than via food availability (e.g. mortality due to weather, availability of suitable habitat)?

4.1.6. Upper trophic level-focused models

Various regional food web models are now available or are under development. The majority of these make use of the mass balance approach to some degree (see Tables 1 and 2) although a dynamic model developed for the Kerguelen Plateau food web (Constable 2007) does not. These models generally focus on the upper trophic levels and, as such, reflect the trophic resolution of available data.

Generally these models have revealed gaps in the available data. Although the majority of models are mass-balanced, models that are not mass balanced are being developed because there were situations where data were insufficient to support the assumptions required to achieve mass balance (S. Hill, pers. comm.). A feasible parameter space mapping approach would help to define the range of possible values of unknown parameters. However, there are important functional groups (e.g. cephalopods) and regions (e.g. mesopelagic) whose roles as predators and prey remain unknown.

Table 1. Examples of reviews and ongoing synthesis and modelling efforts in Southern Ocean ecosystems research.

Model scope	Group/individuals
South Georgia food web models	BAS (S Hill)
New Zealand working on trophic model for Ross Sea food web model	NIWA (M Pinkerton)
CCAMLR and IWC held a joint workshop (August 2008) with input from expert groups, to compile input data for Southern Ocean modelling from the physical environment to top predators	CCAMLR/IWC (A Constable)
Foosa model (krill predator fishery forecasting and risk assessment model for FAO Sub Area 48).	US AMLR and BAS (G Watters)
Spatial Multi-species Operating Model: SMOM (krill-whale model)	E Plaganyi
Ecosystem, productivity, ocean, climate (EPOC) modelling framework (currently being applied to CCAMLR's statistical Area 48).	A Constable
Size structured ecosystem model (global)	CLIOTOP (O Maury)
Dynamic Green Ocean Model (global zooplankton synthesis)	UEA (C Le Quéré)
Global review of phytoplankton functional rates	As part of Dynamic Green Ocean Model: AWI (D Wolf-Gladrow)

*Examples of others to include: There are many existing circulation models, sea ice models, krill or other zooplankton models. For e.g. BRIOS (Bremerhaven Regional Ice Ocean Simulations), FESOM (Finite Element Southern Ocean Model), several krill models of different life stages (e.g. Fach et al. 2002, 2006, Fach & Klinck 2006, Fach et al. 2008, Hofmann et al. 1992, Hofmann & Lascara 2000, Hofmann & Husrevoglu 2003, Tarling et al. 2007).

Table 2. Recent and developing models of Southern Ocean food webs.

Region	Platform	Affiliation	Reference
Scotia Sea	Ecopath/Ecosim	UBC	(Bredesen 2003)
Kerguelen plateau and Eastern Antarctic	EPOC	AAD/ACE	(Constable 2007)
Ross Sea	Mass-balance implementation	NIWA	(Pinkerton et al. 2007)
South Georgia Shelf	Ecopath	BAS	S. Hill
Southern Ocean	Descriptive	UCT	(Moloney & Ryan 1995)
Prince Edward Island	Ecopath/Ecosim	UBC	(Gurney <i>et al.</i> 2001)

4.1.7. Specific interaction models

There is a group of models that aim to model dynamically the interactions between selected components of the Southern Ocean ecosystem, e.g. Foosa (formerly KPFM: Watters et al 2005; 2006) and SMOM (Plaganyi & Butterworth 2006b). These are 'tactical' models designed to offer quantitative information on ecosystem performance for use in management of human activities (e.g. krill fishing) in the Southern Ocean. Such models are in contrast with the more descriptive 'strategic' models that typically look at the whole ecosystem to develop our understanding of its dynamics but which are not necessarily quantitatively accurate.

4.1.8. Specific issues in developing mechanistic models

- Antarctic krill models exist, cover a range of space and time scales, and are linked with physical parameters, such as circulation. However, equivalently developed models are lacking for most other Southern Ocean species.
- Phytoplankton/zooplankton assemblages were highlighted as a crucial part of the Southern Ocean systems. More consideration is required in terms of how these should be represented in food web models rather than just assuming that the biogeochemical models adequately represent the appropriate processes.
- Higher resolution physical models are crucial for developing coupled physical-life-cycle models. Adaptive grid circulation models are needed to resolve meso-scale eddies and for Lagrangian particle simulations. Dynamic circulation models with embedded biological particles can be useful in developing plausible models of the early life stages of fish (Hanchet *et al.* 2007). Such models can be useful in identifying particular vulnerabilities of species to climate-driven environmental change (for example, changes in sea-ice cover where larval fish are likely to be found).
- Alternative pathways also need to be considered and that requires improved trophic resolution. Such pathways will not be independent, which will require new model structures to allow the importance of different pathways to be resolved.
- The species (or group) that should be included in food web models (e.g. does top-down pressure from upper trophic level species materially alter the dynamics of lower trophic level species) needs consideration.
- Foraging behaviour is likely to be particularly important as models develop to include higher trophic level species that are highly mobile, especially for individual-based models. It was noted that new methods for the spatial modelling of fish stocks driven from fisheries data using Bayesian fitting rather than from a conceptualization of fish behaviour are being developed (Dunn & Rasmussen 2008).
- In specific-interaction models the potential for interannual variability in prey mortality needs to be accounted for to allow for changes in predator or prey population size on different time scales.
- The inclusion of sea ice biological community dynamics is crucial and specific models have been developed for these systems for particular localities. Examination of ocean-sea ice system links is required and the issues of modelling the food web links require specific consideration.
- Development of climate change impacts studies will need to draw on Intergovernmental Panel on Climate Change (IPCC) analyses, including quantification of uncertainty. It will also be important to ensure that biological views of the impacts of change are developed, which will require new modelling approaches.
- Documentation of the current work in developing couplers that link models of different types and resolutions and associated issues would be useful to the ecosystem modelling community.

- Incorporation of physiology and behaviour is needed in models that examine adaptations to environmental variability. The development of new approaches to modelling key components of the food web will be required. In particular the inclusion of genomic processes of flexibility in physiological response and in adaptation will be useful to explore. Analyses of genetic basis for population dynamics will be valuable in understanding the constraints on key food web species in response to change.

4.1.9. General issues in developing mechanistic models

There are clearly a number of challenges that remain to be addressed in models of each part of the Southern Ocean system, and which will add to the uncertainties in end-to-end models. End-to-end models of marine ecosystems (which integrate diverse ecological processes from the physical operation of the system to the dynamics of upper trophic level species) are a logical goal for the ecological modelling community. Such models could be used to present integrated ideas about ecosystem structure and operation, and to predict or disentangle the effects of perturbations to any part of the system. Thus, they offer the possibility of explicit representation of controls on ecosystem dynamics, and detailed exploration of hypotheses about food web interactions. However, there are also technical challenges in linking models at various ecosystem levels. Offline coupling, which favours a bottom-up representation of ecosystem controls, appears relatively simple. Two-way coupling to allow feedbacks is much more of a challenge.

Discussions considered whether existing physical models are adequate to help force food web models, noting that many do not adequately resolve the upper water column structure for biological purposes. It was also noted that fine temporal-scale forcing was often necessary if emergent properties were to simulate reality. It is of critical importance to engage physical modellers with food web modellers throughout model development so that appropriate scale physical processes can be incorporated as food web model drivers. Discussions highlighted that existing physical models may not provide archived output at appropriate scales. For example, given that fine scale information on the impact of episodic events such as storms, mixed layer variations, cloud cover, or sea-ice break-out on biological processes is lacking, these do not tend to be adequately represented in existing models.

To develop circumpolar model analyses, global model boundaries (or at the equator) could be set so that the model domain encompasses the global ocean (or the Southern Hemisphere); under such a scenario the distributional ranges of species would be governed by interactions within the model. However, the spatial and temporal resolution of modelling such a broad domain would necessitate considerable computing power. The use of a coarse resolution large-scale domain combined with nested higher resolution sub-domains in regions of higher interest could be a solution. Alternately, a simpler approach would be to focus the geographic domain on the key species of interest, and define boundary conditions for other species where part of their life cycle falls outside these limits. A third possibility would be to model with variable space and time resolution. Under any of these approaches, the definition of regions within the geographic domain remains critical, if model predictions are to be robust. In addition, the parameterisation of species interactions or the definition of their individual boundary conditions is critical in determining the emergent food web structure.

The relative scale of models is also an important issue in this regard. It is likely that questions about upper trophic level dynamics will concern finer spatial scales and longer time scales than questions about biogeochemistry or ocean circulation. This suggests a nested model approach to spatial

scaling, where coarse scale OGCMs and BGCMs are used to define boundary conditions for fine-scale models of biological processes. However, the costs of running OGCMs and BGCMs over long time scales might also pose a problem. The scale at which biological interactions are represented is also important. Population dynamics models generalise the consequences of fine-scale processes through, for example, functional responses or mortality functions. However, it is often difficult to validate these representations. It is also likely that potentially important influences on food web dynamics, such as the influence of prey condition on its own survival and the behaviour of its predators, need to be described by fairly detailed functions.

The appropriate approach to uncertainty is likely to depend on the specific question being addressed. It is probable that uncertainties about the influences on upper trophic level dynamics can be adequately represented through the parameterisation of relatively simple, but flexible, models of the type being used by CCAMLR. However, more explicit linkages across what are currently separate model types might be needed to trace the potential response to specific perturbations.

Developing mechanistic models of Southern Ocean food webs

- Development of models of Southern Ocean food webs needs to be elevated to a major focus of effort;
- There are useful single species models available for a small number of species, but models are not available for many key species;
- High resolution regional physical models are being developed for some key regions, but a focus is required on the resolution required for biological modelling;
- Biogeochemical models are available that can be used as a base for driving food web models;
- Food web modelling has been limited to local/regional systems and there are major gaps in knowledge and data. Food web budget models provide a valuable base for comparing ecosystem structure, but concerted effort on description and quantification is required;
- Dynamic food web models have been used for study of particular predator-prey interactions. These could be a useful base for developing general analyses of impacts of change;
- Spatial variability is a major aspect of Southern Ocean food webs that will need to be explicitly considered, including regional variation in food web structure, (e.g. between sea-ice and oceanic systems) and spatial interactions across trophic levels (e.g. scales of foraging). Some spatially resolved models have been developed and these could be usefully expanded to encompass a wider domain;
- Development of methods for linking models of different scale will be required. This will need to consider physically nested models as well as models linking across different scales of biological processes (e.g. biogeochemical processes to zooplankton life-cycle processes).

4.2. Developing generalized models of Southern Ocean food webs

The discussions focused on the potential for generalized modelling of Southern Ocean food webs converged on some key points about modelling approaches, the key structures that need to be represented in models, and common processes that need to be included in a generalized model. The key points raised are summarized below.

4.2.1. Generalized models

The development of a generalized approach for modelling Southern Ocean food webs requires an approach(s) that is sufficiently flexible and robust to represent the varied structures that constitute the larger Southern Ocean ecosystem. The development of such a modelling approach assumes the existence of common processes that can be described by empirically derived relationships, generalised rules or quantified mechanisms that can be applied to the different regions, scales and times (Figure 16). Such an approach is of necessity based on fundamental ecological ideas that transcend regional differences in food web details. These rules need to be such that the model can explain/simulate the current state of the food web in different regions of the Southern Ocean. However, what is meant by food web is not always clear and is likely defined within the context of a specific question.

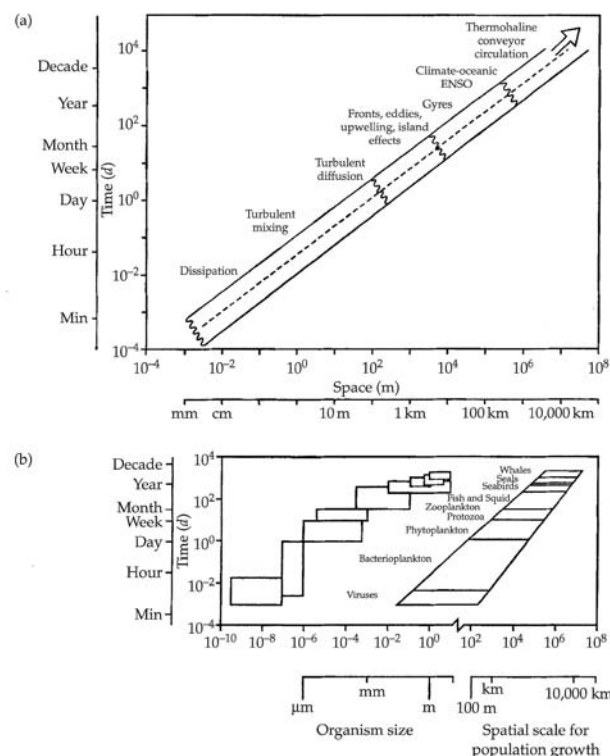


Figure 16. Dominant space and time-scales in the ocean for (a) physical motions and (b) biological scales. In (b) the left-hand overlapping boxes represent typical size ranges (on the x-axis) and typical times for population doubling (on the y-axis) for each type of organism; the right-hand boxes represent typical spatial ranges of each organism during their lifetime. Adapted from (Murphy *et al.* 1988). Source: Denman *et al.* (1995), permission granted by the IPCC.

The discussion focused on how the Southern Ocean should be viewed in terms of defining fundamental ecological rules. For example, organism size, regional processes, habitat characteristics, productivity, and connectivity between regions were discussed as frameworks for setting up generalized rules, as given below.

4.2.2. Can we use a single modelling approach to represent different ecosystem structures in the Southern Ocean?

Size-structured models have been developed for the global ocean (Figure 17 from Maury et al. (2007), see also Appendix III) and provide a valuable basis for analysing the general operation of ecosystems and linking to biogeochemically based models. Size-based approaches of Southern Ocean ecosystems were thought by some to be appropriate for many systems up to the level of mesozooplankton. The utility of this modelling approach for representing higher trophic levels was considered to be limited by the large biomass of top predators, many of which feed on a limited prey size (e.g. krill). As a result, the continuum provided by size-structured models may actually be characterized by discontinuities in Southern Ocean food webs, because the focus of large predators on limited prey size results in the same range of prey size for a wide range of predator size. Some work on size structure has been done, e.g. on the Polar Front community, however, further work is needed to develop the approach. This would require careful consideration of the spatial scale (e.g. aggregations, predator distribution) of integration required to account for spatial variability. Some consideration of the long history of perturbation of larger size classes which will have affected the current size spectrum would also be useful.

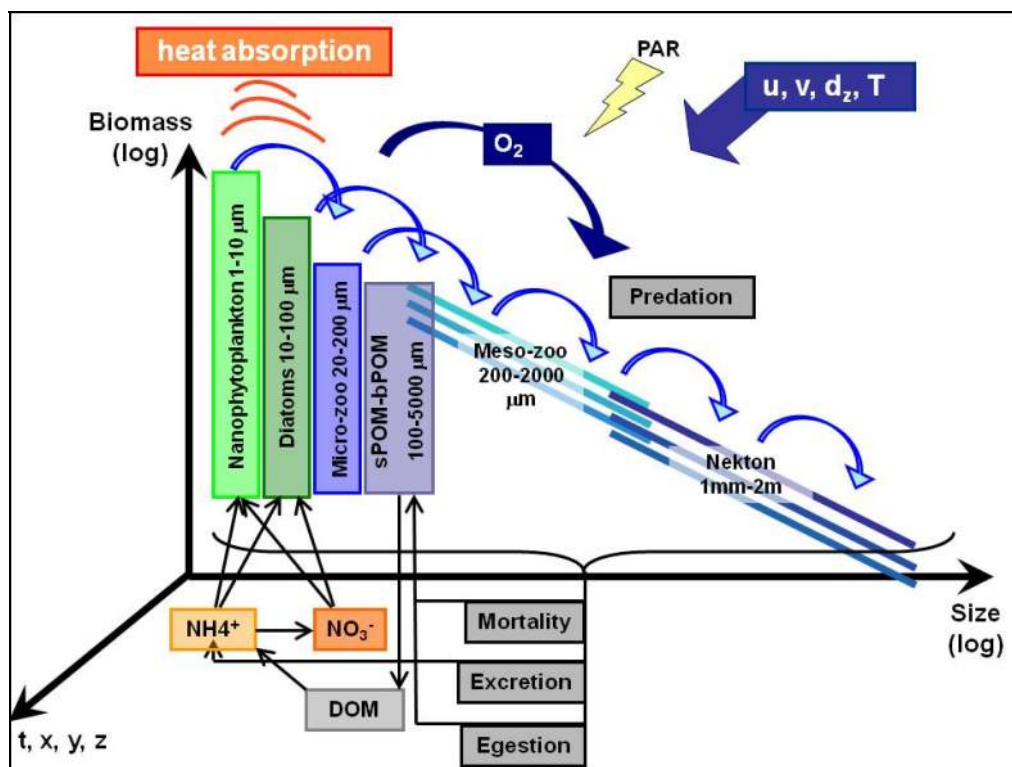


Figure 17. Generalised view of the size-based APECOSM model developed as a generic global model (Maury et al. 2007). Figure shows development of coupling with NEMO-PISCES-APECOSM (NPA), an integrated numerical model for studying 3D coupling between circulation, biogeochemistry and ecosystems. Figure by O. Maury.

The development of a generic adaptive size-based model for Southern Ocean food webs was discussed. Such a model would allow food webs to respond to regional conditions and have biological interactions as an emergent property of the model. The feasibility of this type of model remains to be determined. However, the discussions at this stage suggested that this type of

modelling structure would be valuable towards the goal of predicting responses of Southern Ocean food webs to climate change.

The discussion of common processes for models focused on whether generic ecological rules that are based on habitat, environment, productivity, or physiology can be developed for Southern Ocean food web models. Such rules are likely to be most applicable to lower trophic level components of the food web. These generic rules could then be used to predict the structure of the intermediate and higher trophic level communities. The development of generic ecological rules for larger organisms, including many of the important Southern Ocean predators, was considered to be problematic because these organisms represent a very diverse range of physiological and ecological strategies.

Various ecological modelling approaches, including NPZD models of the lower trophic levels, and Ecopath models of the higher trophic levels, routinely aggregate organisms into “functional groups” on the basis of common ecological strategies. A potentially useful goal would be to develop spatially resolved models in which local food webs are an emergent response to physical and chemical habitat characteristics. Such models could select functional groups for inclusion from a pool of candidate functional groups representing the diversity of organisms at the circumpolar scale. This idea that the spatial structure of the ecosystem should be an emergent property was one of the principles behind the development of the EPOC modelling framework model (Constable 2007).

In developing models based on functional groups, it is important to consider which characteristics will be used to group organisms. The answer is likely to be question-specific. The role of many organisms in the food web is more than just as a food source for or predator of other organisms. Other functions include mediation of biogeochemical cycling, provision of habitat structure, regulation of competitors, and facilitation of predator-prey interactions. Thus, an important issue is the need to blend the key elements that define an organism’s role, including size, taxonomy, trophic position, and possibly a range of specialised characteristics. Finding an appropriately descriptive but tractable blend is likely to be the key to allowing alternative food web pathways to emerge from a model. The key elements are likely those connected with ecosystem persistence and stability.

Blending the different food web model structures was considered to be important as well as development of approaches for comparing between ecosystems. One possibility is to use a metamodel as a general model that receives inputs from individual ecosystem models, i.e. end-to-end models for different systems. In this approach different regional models would be connected by a metamodel that passes information between the models, thereby providing connectivity between the models. This type of model would provide a framework for comparisons between different food web structures and environmental forcing conditions. This would require that the metamodel capture the main features of each system, but still remains manageable.

Developing such an adaptive generic model may be feasible for the Southern Ocean. Aspects of the system operation could be used to constrain such an approach. For example, productivity is a constraint, setting boundaries on what can be supported in the systems. This could be derived from satellite/field data or from other, biogeochemically based models. Consideration would need to be given to what metrics would be useful to characterise food web structure and hence provide not just the basis for prediction of response to change, but also the capacity to distinguish different outcomes in terms of changing food web structure.

4.2.3. Representation of key structures

The bioregionalisation (see above, Figure 18 and also Appendix III) of the Southern Ocean was discussed as a framework that could be used to define modelling structures and approaches. There are important and distinct areas of the Southern Ocean, such as high nutrient-low chlorophyll regions, permanent sea ice zones, marginal sea ice zones, regional gyre circulations, and areas directly impacted by the ACC. These regions are characterized by unique flora and fauna, many of which are endemic species. Representation of physical characteristics of these regions and their associated biological interactions may require a range of models. Such an approach would also, therefore, need to include regional and seasonal variability. Representation of this range of variability may argue against a generic modelling approach for Southern Ocean food webs.

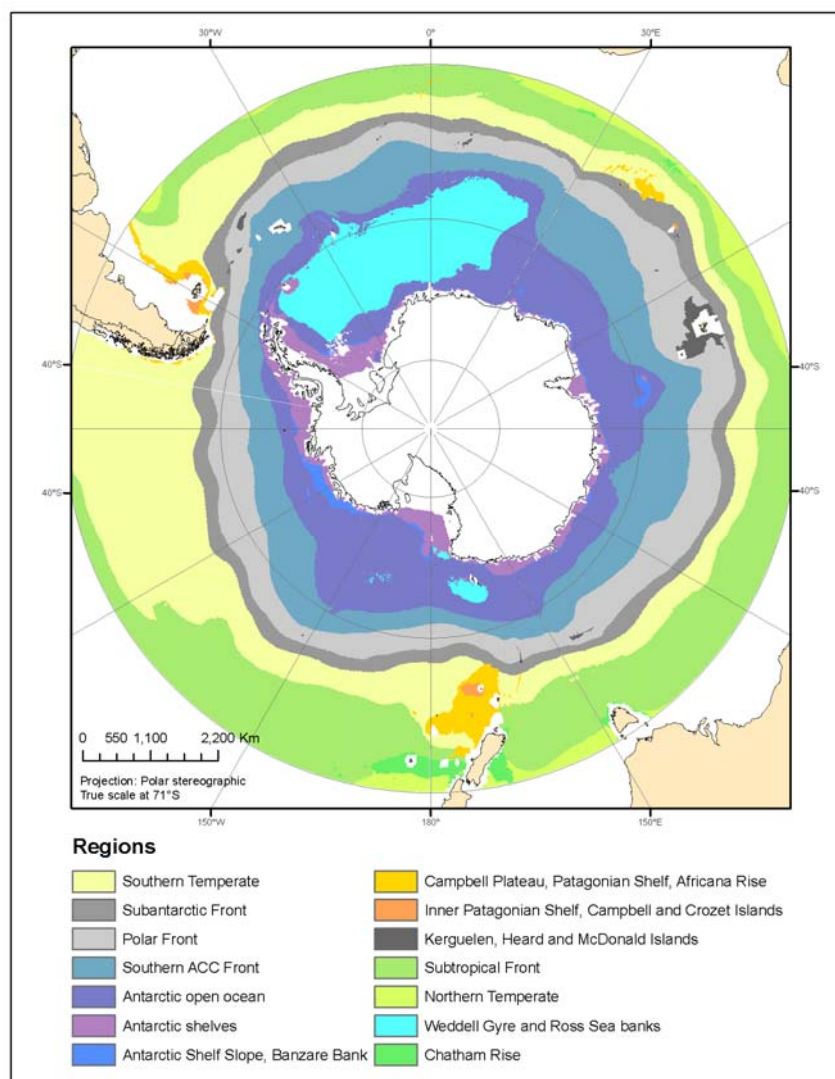


Figure 18. Primary regionalisation of the Southern Ocean based on: depth, sea surface temperature (SST), silicate (Si) and nitrate (NO_x) concentrations (14 cluster groups) (white areas represent cells with missing data that were not classified in these analyses) from Grant et al. (2006).

The circumpolar structure of the Southern Ocean generates a large degree of connectivity between regions. This connectivity has the potential to alter food web structures. Thus any circumpolar food web model must be able to account for connectivity between regions and for the potential consequences of these interactions. Development of modelling approaches and structures that allow food webs to respond to upstream/downstream conditions remain to be explored. There is also a zonal versus meridional aspect to how Southern Ocean food webs can be viewed. This is particularly important when using models to make estimates of organic material import/export, predator harvesting effects, and benthic-pelagic coupling.

It was noted that accounting for spatial variability and structure in analyses of food web structure would be crucial in the Southern Ocean. Krill distribution is patchy and predators can only access a portion of available prey. The importance of aggregations in Southern Ocean food webs was recognized and given a high priority as a key structure for inclusion in food web models. Aggregations, such as krill aggregations, map the prey field into different sized distributions and abundances for different sized predators. For example the perception of a krill aggregation by a penguin is different from that of a baleen whale. This heterogeneity in aggregation/patch sizes may be what allows a diverse predator community to exist (Murphy et al. 1988). This means that the biological and physical interactions that generate the structure and function of the food web interactions need to be considered. Different scales of variation in distribution will be important such that a range of measures of distribution may be required, for example the size of the absolute prey patch may need to be accounted for and not just the density of prey.

Understanding why organisms are where they are found was recognized as being basic to understanding the key aspects of Southern Ocean food webs. For example, why are some areas of the Southern Ocean dominated by krill and others dominated by fish? Is Circumpolar Deep Water determining phytoplankton species assemblages by controlling iron inputs? Do some food web structures sustain large numbers of predators and not others? Our current ability to develop Southern Ocean food web models is limited by a basic understanding of where, why and how species exist, coexist and persist in different regions and seasons.

4.2.4. Are there common processes across Southern Ocean food webs?

Before developing generic models it is necessary to conduct analyses to establish whether there are generic ecological rules based on habitat, environment, productivity, or physiology and whether these rules can usefully predict the structure of intermediate and higher trophic levels. These analyses should be based on appropriate scale-based views of the biological-physical interactions in ecosystems and they should consider the different biological attributes of the component organisms. They should also establish the scale of biological organisation (e.g. population, taxon, community) to which any apparent generic rules apply.

It was noted that we need to recognise the potential for evolution in Southern Ocean species. This requires the development of new methods that link genetic processes at a range of scales to ecological models. This includes the genomic basis for functional changes in process operation as part of the overall phenotypic variation through to population level changes in genetic structure.

Developing generalized models of Southern Ocean food webs

- Developing generalised models of Southern Ocean food webs would provide a basis for comparative modelling approaches and clarifying the major issues in analysing and comparing regional food webs;
- Utilising size-based models that are being developed for global studies would be a valuable initial approach;
- There is a need to consider new approaches for linking models of different types. Analyses based on size, functional or taxonomic groups provide alternative views that could be combined to help constrain dynamics;
- Analysis of spatial structure of food webs based on bioregionalisation is a useful approach that could be applied to consider both within and between region variability.
- Analyses of spatial connectivity and spatial interactions across multiple trophic levels require new approaches that consider process interactions across scales;
- Focusing on the development of models to scale-up local/regional understanding will be a logical precursor in generating circumpolar views.

4.3. Building on current approaches to develop models of Southern Ocean food webs

Modelling of Southern Ocean food webs is not currently a major coherent research activity. The available work provides a good foundation, but further areas of work will need to be developed to generate a coherent and multifaceted approach to modelling food webs. The tendency in Southern Ocean ecosystem modelling in recent years has been fairly krill-focused in terms of simulating population dynamics, growth and controls on distribution. Within CCAMLR the emphasis has been on models for management, mainly relating to single species of fish or krill (see Figure 19, and a more detailed illustration of these processes is given in CCAMLR (2004), and see also Constable's presentation in Appendix III on CCAMLR's ecosystem modelling approaches). However, the work on krill has included consideration of dependent predators and the effects of environmental variability on krill recruitment. Specific interaction models have been developed to explore long-term impacts of harvesting, but these have been mainly used to explore general impacts. The development of mass balance (Figure 20) or energy-budget models has been undertaken for a few localities, but the issues relating to data availability and parameterisation remain extremely challenging.

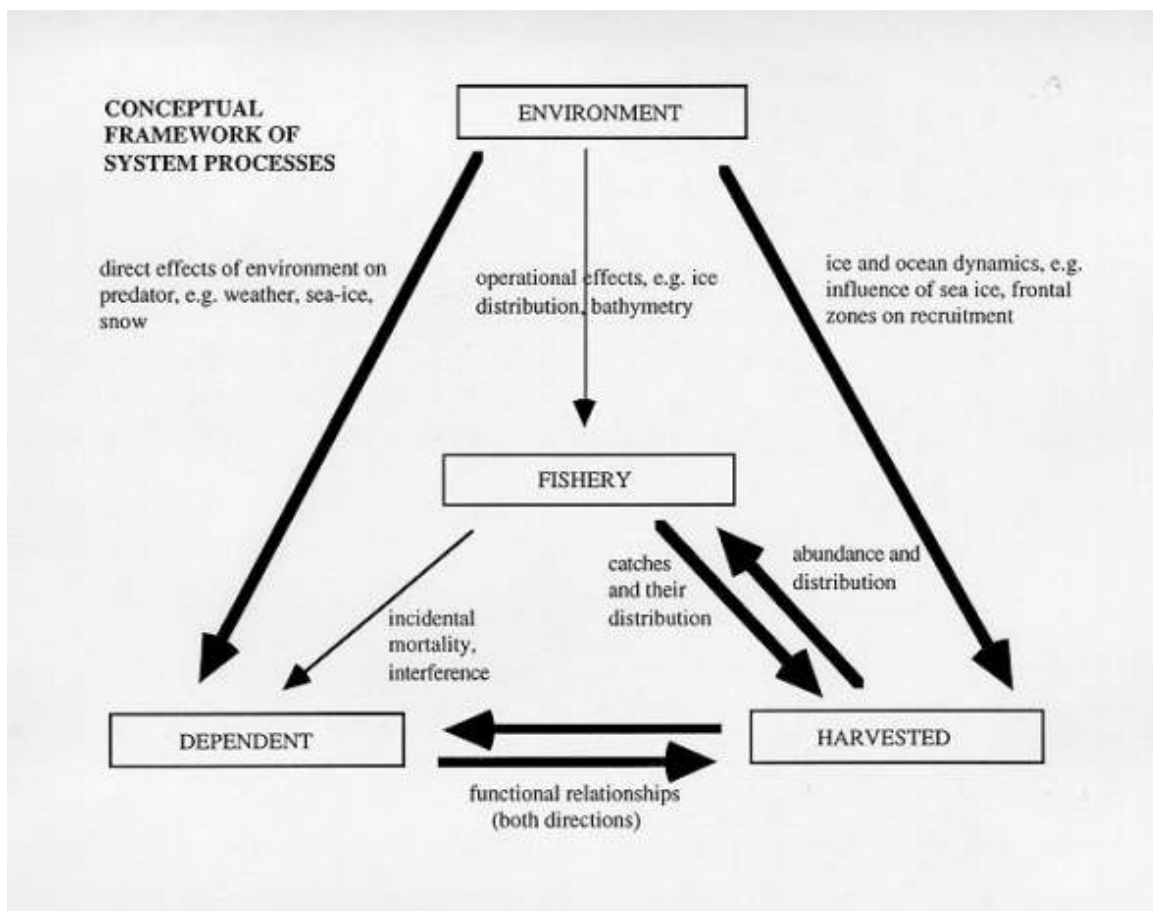


Figure 19. Schematic illustrating the basic aspects of system processes considered within CCAMLR ecosystem based analyses (CCAMLR 2000). For more information see also CCAMLR (2004).

Determining the appropriate level of biological resolution for food web modelling is highly dependent on the questions being addressed. Species-centric views can be entirely appropriate and can provide valuable ways of looking at the impacts within food webs of variability and change. Such models allow high resolution analyses of the life cycle of key species. These can be expanded to include interacting components, probably at lower biological levels of resolution (the rhomboid approach, see Figure 4). The alternative, trophocentric approaches attempt to include the major food web interactions, potentially attempting to account for all possible interactions in a mass balance approach. Such analyses provide a useful overview of the system operation and structure. The development of such approaches in the Southern Ocean requires integration across a wide range of space and time scales, and generating the appropriate data and parameterisations would be extremely challenging. Mass balance modelling can be a valuable precursor to dynamic trophic modelling. It provides a useful starting point for compiling relevant information into a consistent format and identifying components of the system that could be modelled dynamically. Indeed, both the species-centric and overall budget approaches have benefits for Southern Ocean studies. The need to link the two approaches to allow variable life cycle resolution for key components of the food web was discussed. Developing a spatially based food web model structure that resolves major regional differences but also allows for regional exchanges may also be a fruitful approach for this system which is considered to be highly open and connected in many areas.

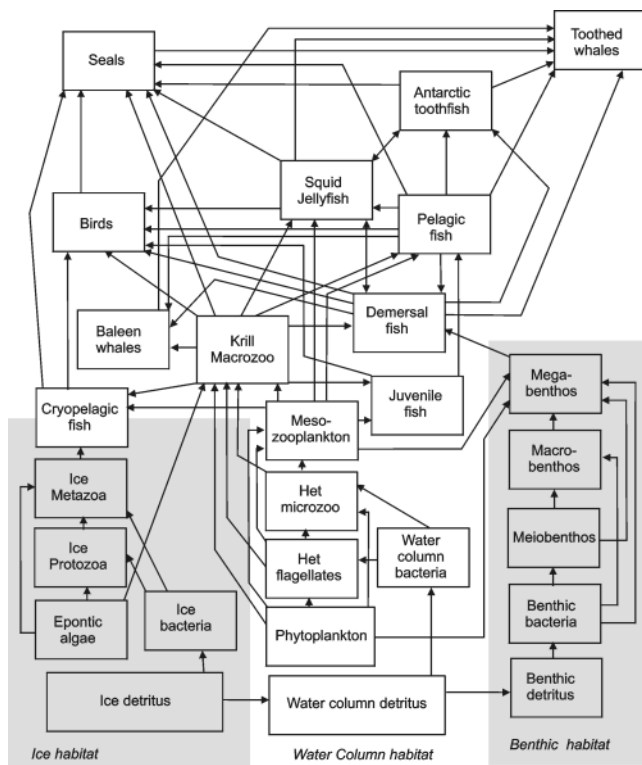


Figure 20. Mass balance model of the Ross Sea food web currently being developed by NIWA, New Zealand. Figure provided by M. Pinkerton, NIWA.

As noted above, progress is underway with the static bioregionalisation approach and appears to be promising in two regards. First, it may allow identification of ecologically distinct regions of the Southern Ocean, which could form the focus for modelling and monitoring of ecosystem dynamics. Second, methods are being developed to link the distribution of individual species to environmental characteristics. Such information may be useful for extrapolating sparse in situ biological measurements through the Southern Ocean and for highlighting important environmental-biological dependencies.

Developing coupled ecosystem models that include aspects of the complete operation of ecological systems including ocean circulation, biogeochemistry and biological processes is a logical step towards the next generation of coupled models. As discussed earlier, considerable progress has been made in incorporating particular ecological processes into circulation models. Work has also progressed with biogeochemically-based models by adding further biological complexity and also in the development of single-species models. Biogeochemically-based models have been developed and applied in Southern Ocean systems at regional levels. In addition a number of global biogeochemical models now include the Southern Ocean. However, these models have little biological realism.

A next step is to begin development of nested models of variable resolution. Many of the key processes affecting Southern Ocean pelagic species are linked to shelf regions in which the important physical processes are not well resolved in regional models. High resolution physical models are being developed for a number of regions and these include biogeochemical models. Inclusion of key species and/or linking these models to broader food web models is a logical next step. EPOC is an example of an existing framework where nested approaches could be used (see also Constable (2005)).

The issue of scaling-up analyses and models is one of the major challenges in building circumpolar views and understanding the large scale response to change. This requires scaling-up local to regional to circumpolar geographically based models. These models may be of different resolution based on nested-model structures. However, it is not possible to encompass all scales in such models, thus consideration will need to be given to how to encompass small-scale processes in model equations and parameterisations, and how to account for larger scale/longer time scale influences. Scaling analyses and models that specifically include across-scale coupling issues will be required. One possible approach is to link different models together that target different physical resolutions and biological processes. Scaling across biological processes has not received much attention but will be crucial as we develop integrated models that allow for feedbacks. This requires consideration of how genetic, physiological, adaptation, behavioural, population, community/food web, and ecosystem processes link across different levels of biological organisation. Scaling from individual-based models to population scale models is equally challenging.

Fundamental concepts such as biological versus model realism and uncertainty in models are considered vital to effective modelling approaches. The key to making reliable predictions lies in understanding the factors that need to be included in the model and those that can be excluded. Methods for dealing with uncertainties in parameter estimates are generally well developed, whereas methods for dealing with uncertainties in model structure are not. Alternative hypotheses (to capture the diversity of plausible hypotheses about the structure and operation of the real system) should be considered. It will also be important to develop more formal and rigorous approaches to structural uncertainty.

Many of the issues raised in the workshop relating to resolving food web structure, impacts of food web structure on stability properties, resilience to change the impacts of change on individual species and food web structure have not been explored in any model analyses. In addition the issues of multi-scale modelling, scaling-up and linking alternative models and developing projections of the impacts of climate change also raise major theoretical and practical issues. These require the development of the conceptual and theoretical basis for the analysis of food webs. This will benefit from the analysis of a range of models of different complexity. Particularly valuable will be the use of simple model approaches that provide more general understanding of the importance of these issues.

Developing quantified comparisons of food web structure will be a valuable exercise. Examining the basis for quantifying the structure and identifying gaps in data availability will be important. Working on methodologies and metrics for comparison will also be an important requirement.

The need for projections/predictions of the response of Southern Ocean food webs is clearly a major issue. Models considering climate change effects need to address broad and regional scale issues and address key changes such as temperature changes, sea ice dynamics, current variability and ocean acidification, and their effects on a range of species. Disentangling the effects of climate change and harvesting was a prominent issue in the discussions. Developing scenario analyses and generating projections of change with associated uncertainties attached will be important and a valuable focus.

The importance of historical harvesting impacts was stressed throughout the discussions, particularly in regard to developing future projections. Analyses of past change effects on food web structure and operation will be crucial as also will be analyses of interacting feedback effects in food webs. With the recovery of a number of great whale species from very low abundance levels, top down impacts will be occurring and will increase in importance in the coming years. Analyses of historical impacts of bottom-up and top-down impacts will be valuable in understanding current system operation and in characterising uncertainty of current dynamics. There was some discussion as to whether (or how much) historical carrying capacity need to be considered. A dynamic ecosystem model that can reproduce historical changes provides a stronger basis predicting future conditions. However, it was also noted that conditions in the future may not resemble conditions in the past so we cannot be sure the model will be able to predict future changes (i.e. past performance is no guarantee of future performance), thus ongoing monitoring is required. There may have been significant shifts in the state of the system so that it can no longer return to the pre-exploitation state. This aspect of change in state also relates to the potential for rapid regime shifts in marine ecosystems. There are suggestions that rapid physical changes associated with large-scale sea-ice reductions occurred in the last century. In addition the harvesting of the great whales and the seals will also have generated a step change in food web operation. More generalised modelling and exploration of alternative states and controls would be a useful complement to more mechanistic coupled physical-biological modelling.

Detailed model studies have been developed of the interactions of lower trophic level systems with a strong biogeochemical focus (Figure 21). The structure of lower trophic level food webs in pelagic systems was explicitly considered further during the workshop and an initial conceptual view of the major components and interactions developed (Figure 22). This included a consideration of the interactions between the deeper water and mixed layer food webs. This is a useful basis for more generalised analyses of all the trophic level interactions in Southern Ocean food webs.

Integrated data syntheses of the distribution and abundance of key species and groups across all levels of the food web will be important. This should include differentiation of the major phytoplankton groups/types, the main zooplankton groups, zooplankton community structure, nekton distribution (fish, including mesopelagic species and squid) and seabird and marine mammals. This should aim to develop seasonal views of distribution. Linking these analyses to compilations of key life history parameters will provide an extremely valuable basis for model construction and validation.

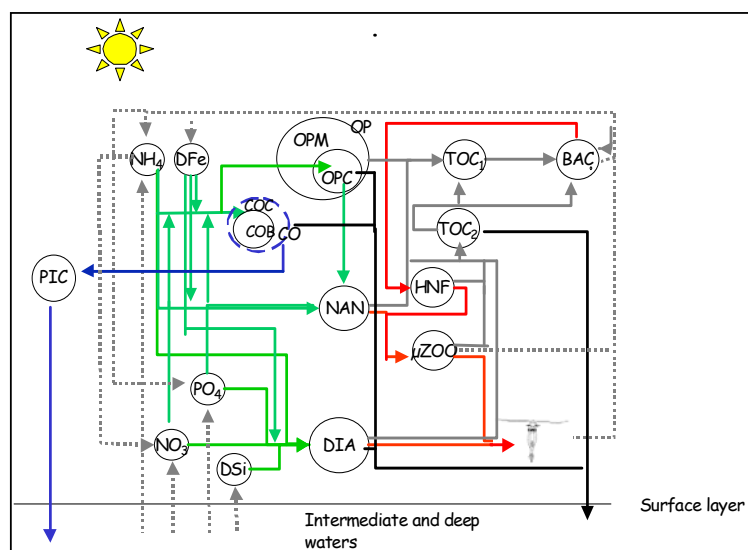


Figure 21. Structure of the ecosystem model SWAMCO-4, including processes (arrows) and state variables (including major nutrients NH_4 : ammonium; NO_3 : nitrate; PO_4 : phosphate; DSi : dissolved silica; and dissolved iron DFe). The model explicitly details the dynamics of 4 relevant phytoplankton groups: i) DIA: diatoms; ii) NAN: pico/nano phytoplankton; iii) OP, OPC, OPM: Phaeocystis colony, cell, colony polysaccharide matrix; iv) CO, COB, COC: coccolithophorid cell, biomass, attached coccoliths and PIC: COC+detached coccoliths. TOC_i : fast ($i=1$) and slowly ($i=2$) biodegradable organic matter; BAC: bacteria; HNF: heterotrophic nanoflagellate; μZOO : microzooplankton. The model integrates knowledge on mechanisms controlling biological productivity and the structure of the planktonic ecosystem. Reprinted from Journal of Sea Research, 53, Pasquer et al. (2005), Linking ocean biogeochemical cycles and ecosystem structure and function: results of the complex SWAMCO-4 model, 93-108., Copyright (2005), with permission from Elsevier

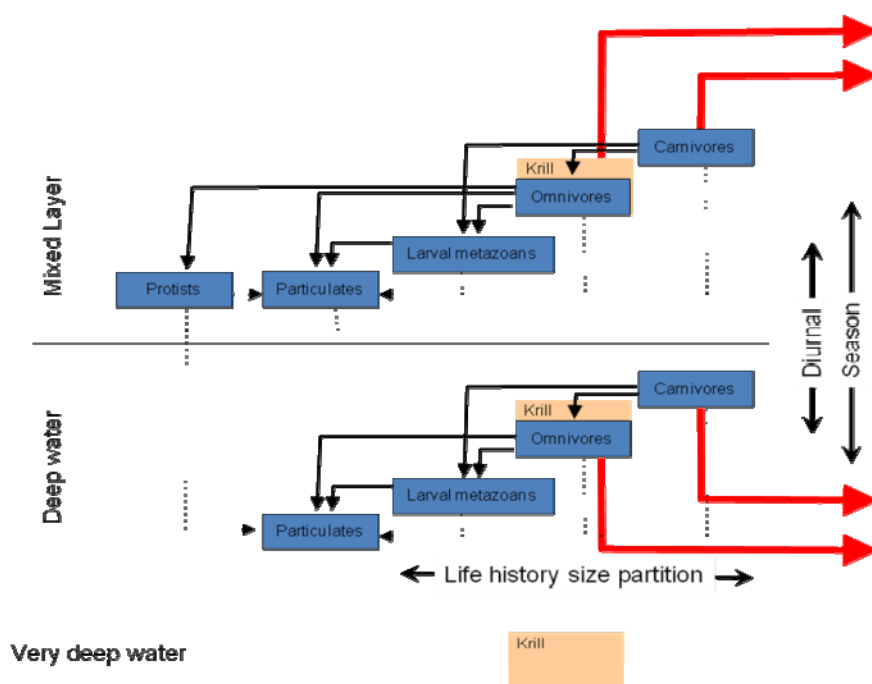


Figure 22. Conceptual simplified view of the lower trophic level major components and interactions in the upper mixed layer and mid-ocean regions of Southern Ocean food webs. Figure was produced during the workshop. Source: ICED 2008.

Time series information is critical to understanding ecosystem dynamics. Improving the available time-series base through expanded monitoring programmes will be crucial. These can build on the CCAMLR Ecosystems Monitoring Programme (CEMP) programme and link to the developing Southern Ocean Observing System (SOOS) programme. Recovery of historical time-series data through data-mining will provide further valuable information that will allow hindcast modelling of the impacts of past change. It will also provide the basis for the analysis of indicators of change.

Key simulations for Southern Ocean food web modelling were identified and include:

- i. The spatial distribution of a range of model elements, including nutrients (e.g. iron), productivity, and a range of species (e.g. diatoms, Phaeocystis, copepods, krill, penguins);
- ii. The complete life cycle of a range of species, particularly key species of interest such as krill;
- iii. The full annual cycle of a range of model elements, including physical elements such as sea-ice and biological elements such as upper-trophic level predator species including their abundance, foraging patterns and migration behaviour. Simulating the annual cycles at one example locality would be valuable.

Building on current approaches to develop models of Southern Ocean food webs

- Developing end-to-end models of ecosystem operation is a requirement for addressing the major challenges in Southern Ocean ecosystem science. To achieve this, modelling Southern Ocean food webs needs to become a coherent research activity; with coordination of multiple modelling approaches;
- There are major gaps in data availability. Historic and current data syntheses and the establishment of new monitoring programmes are essential;
- Models that consider in detail the life-cycles of key species with more generalised representation of overall food web structure will be valuable;
- Regional nested models of food web operation will be important;
- Developing methods and models for scaling-up physical and biological process models will be a major challenge. This is likely to require multi-scale models and a focus on coupling processes allowing feedback processes to be included;
- Generalised analyses and models of food web structure and operation based on analyses of the impacts of change (historical and future) is required;
- Analyses of the effects of change should explicitly consider the effects of top-down controls in determining ecosystem structure and other properties and response to change. Explicit consideration of the effects of recovery of exploited species will be important;
- A focus is required on whole ecosystem operation and new ways of analysing food webs. This should consider whole food web properties of biodiversity, network structure, complexity, stability and resilience to change.

Developing generalised approaches to modelling Southern Ocean food webs will be extremely valuable. Future modelling approaches must be sufficiently flexible to accommodate regional differences and represent interactions between regional food webs. Coordination of the modelling effort and progress towards the eventual goal of integrated circumpolar models may be best facilitated by a generalised multidisciplinary approach that is sufficiently flexible and robust to

represent different processes, scales and structures that constitute the wider Southern Ocean ecosystem. These approaches need to consider wider issues such as utilising generic versus specific models, complexity versus simplicity in representation of food webs, including analyses of the stability properties of food webs, consideration of properties that emerge from interactions and comparisons of different model approaches that link across scales.

5. The way forward in Southern Ocean food web modelling

5.1. Southern Ocean food web models

The ultimate modelling goal of ICED is to develop reliable models of Southern Ocean food webs to provide useful predictions of how they respond to variability and change. To achieve this, coordination between the Southern Ocean modelling community and the wider scientific community is needed to identify available model inputs and required model outputs, and to develop the most appropriate approaches and structures. There is also a need for scientists, policy makers and other stakeholders to work together to produce quantitative definitions of policy objectives for successful stewardship of the region. In both cases this requires timely and coordinated dialogue between modellers and relevant stakeholders.

Within the framework of developing models to represent Southern Ocean food web structures and to predict how they may respond to future change, the main questions to emerge from the workshop discussions centred around a number of key concepts that include physical (key physical processes and the consequences of changes in these), biogeochemical (e.g. the role of iron, acidification, nutrient availability) and ecological aspects (e.g. food web structure and function in different regions, life histories, behaviour):

- *Will climate related change result in significant shifts in food web structure?*
- *Do regional food webs differ in their vulnerability to climate change and harvesting?*
- *How do changes in productivity affect food web structure?*
- *What is the importance of top-down impacts in ecosystems?*

Addressing these questions forms a strategic basis for developing Southern Ocean food webs models in terms of the kind of issues we need to consider and the type of predictions we need to make.

Model development is dependent on the scientific data gathered in the region, including data from over a century of multidisciplinary research, well developed hypotheses about biological responses to environmental drivers, and a range of model structures addressing the system from the physical biogeochemical and biological perspectives. However, by no means all of the existing data have been analysed or are in useable accessible formats. The workshop identified requirements for focused efforts on data syntheses to shed more light on food web operation and identify gaps in knowledge. Existing data (e.g. from historical data sets, current national and international research programmes/efforts) can be used to improve knowledge on the life cycles of key species and on aspects of regional to circumpolar food web operation. Monitoring data (e.g. from long term scientific monitoring programmes, fisheries-based monitoring and current national and international research programmes) should be synthesised to include integration of existing predator tracking data to provide a multi-species synoptic view of a region (e.g. Tagging of Pacific Predators, or TOPP, see www.topp.org) or a complete Southern Ocean view of a single species e.g. Biuw (2007).

A comprehensive review of circumpolar food webs is required and should consider what is known about the structure of circumpolar Southern Ocean food webs. There is also a need to standardise food web descriptions across regions, seasons and years. Identification of monitoring requirements should also be documented with the aim of developing new monitoring in regions where there are few data series available, such as the Bellingshausen and Amundsen Seas and the East Antarctic. Developing the time-series studies in conjunction with SOOS will be more efficient.

ICED will need to apply a number of modelling approaches in order to characterise and model the circumpolar Southern Ocean food web. No single approach alone is likely to be sufficient to capture

the links between ecosystems and climate in Southern Ocean for the research and management purposes envisaged. Whilst it is recognised that there are many gaps in knowledge, it is envisaged that these will be addressed in parallel with appropriate model developments (Murphy et al. 2008).

There is a need to develop both mechanistic and generalised food web models for the Southern Ocean. Mechanistic models should focus on the development of simulation or predictive models for key components or regional ecosystems in the Southern Ocean. Such models would offer the possibility of explicit representation of controls on ecosystem dynamics and detailed exploration of hypotheses about food web interactions. The current status of relevant ocean circulation, biogeochemical, single species and food web models was briefly reviewed (with literature sources provided for more details). Integrating these elements into end-to-end models of Southern Ocean food web dynamics was considered and specific priorities, challenges and limitations were highlighted for further exploration as ICED modelling activities progress.

Despite the different conditions and structures in different ocean basins, the potential for developing a generic food web model for the Southern Ocean is worthy of exploration. Concerted efforts to compile food web studies already undertaken, together with data collation and a series of useful model simulations, would form valuable steps at this stage. In order to develop generalised modelling of Southern Ocean food webs there is a need to identify a set of common processes (by defining a set of fundamental ecological rules) that can be applied to different regions, scales and times. There is a need to blend size, functional group and taxonomic approaches to modelling. There is also a potential for a meta-model to be built to receive inputs from different regions. This type of model would provide a framework for comparisons between different food web structures and environmental forcing conditions. The possibility that the Southern Ocean may not be particularly amenable to generalised models is something that ICED will explore in detail.

Existing modelling efforts, though useful, are compartmentalised in terms of the processes, scales and regions they consider; the role of natural variability has not been adequately addressed; and there are still a lot of unknowns about the Southern Ocean system. Therefore we need to aim towards a modelling approach that will allow continued exploration of important processes at relevant scales, allow comparison of regional food webs yet still retain detail about locally important features, integrate knowledge about physics, biogeochemistry, biology and human activities, link across scales to model regional and circumpolar effects, allow potentially bi-directional linkages across processes and scales, deal sensibly with natural variability, accommodate multiple hypotheses about any individual processes, and be parsimonious (i.e. focus on what is relevant to model users and the processes that affect these things) (Figure 23).

The development of a range of modelling approaches therefore needs to be coordinated and considered in parallel to develop comparative studies. To do this requires:

- Definition of objectives to inform development of models from the outset;
- Standardisation of food web descriptions;
- Specification of specific life cycle models;
- Food web budget and network analyses;
- Dynamic models of interactions and simplified food webs;
- Coupled models of species and simplified food webs;
- Generic modelling of large scale food web operation;
- Generalised modelling of ecosystem operation and analyses of issues of scale;
- Scenario testing to consider past and future change.

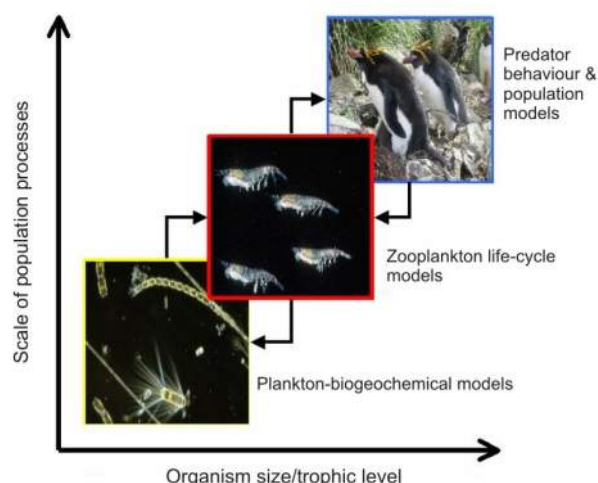


Figure 23. Producing coupled models of ecosystem operation requires the development of models encompassing different temporal and spatial scales. At different scales the biological processes and trophic resolution included will vary and depend on the main scientific issues being addressed. A major challenge is to develop the appropriate links between different types of models that resolve different biological processes, and apply these at different scales.
Source: E. J. Murphy, British Antarctic Survey.

The workshop considered that both historical hindcast model analyses of past change effects and future change scenario analyses would be valuable. The future scenarios analyses should aim to develop IPCC-like projections of change for key components of the Southern Ocean ecosystem and for the food web of which they are a part. This will require methods for dealing with and communicating uncertainty. To identify available inputs and required outputs for the development of Southern Ocean food web models, it is imperative that ICED promotes effective coordination between the Southern Ocean modelling community and the wider scientific community. Valuable insight will be gained through links with programmes such as ESSAS (comparisons with the Arctic and

Sub-Arctic marine ecosystems), CLIOTOP (Apex Predators Ecosystem Model), CCAMLR, IWC and many physical and biogeochemically-focused modelling groups through IMBER and the global community.

The discussions held at the workshop and the compilation of this report have provided a firm and thorough basis for reviewing these issues so it is also timely that the major conclusions of this report be developed for scientific publication.

The way forward: key issues in the development of Southern Ocean food web models

- Aim to conduct a series of simulations, including the full annual cycle of a range of key model elements; the complete life cycle of a range of key species and the spatial distribution of a range of key model elements;
- Consider issues of coupling, feedbacks, uncertainty, scales and bioregionalisation in detail;
- Further evaluate existing modelling approaches and prepare a set of 'hind-cast' test cases to use to compare the results of various modelling approaches;
- Identify key indicators for ecosystem modelling (link with SOOS);
- Develop scenario testing and model projections on the impacts of change in Southern Ocean food webs to feed into IPCC activities;
- Assess and develop modelling approaches in collaboration with the wider modelling community (biogeochemical, physical, other regions, global);
- Consider generic modelling approaches and generalised models of Southern Ocean food webs.

5.2. Recommendations

The workshop recommended a number of scientific and strategic priorities in the development of Southern Ocean food web models, including:

Scientific priorities

- Prepare a manuscript on modelling Southern Ocean food webs based on the concepts initiated in this workshop that will be published in the peer-reviewed science literature;
- Compile key datasets on Southern Ocean ecosystems; including making key data from the grey/unpublished literature available to the ICED modelling community. Link this to other data retrieval exercises being conducted on Southern Ocean food webs (e.g. CCAMLR/IWC and European efforts through the EUR-OCEANS Consortium). Compile and integrate available Southern Ocean predator tracking data sets;
- Undertake a comprehensive review of circumpolar food webs and what is known about the structure of circumpolar Southern Ocean food webs that includes:
 - Preparation of a series of conceptual diagrams representing the food webs in different regions;
 - Identification of main gaps in knowledge and ways to address/overcome these including new long-term monitoring.
- Begin quantitative analyses of Southern Ocean food webs;
- Devise a strategy for developing mechanistic and generalised models, regional and circumpolar models, recognising that no single modelling approach is likely to be sufficient to capture the links between ecosystems and climate in the Southern Ocean;
- Aim to develop food web models to simulate the operation of Southern Ocean food webs, interactions with climate and their response to climate and harvesting driven change;
- Aim to link the food web modelling work with biogeochemical and physical modelling studies to develop end-to-end analyses of the operation Southern Ocean food webs as part of the circumpolar ecosystem;

Strategic priorities

- Establish multidisciplinary ICED Modelling Working Group and refine the key priority questions for the group;
- Consider group-level integrative funding efforts towards building a Southern Ocean modelling community with global links;
- Build links with key programmes and groups to streamline modelling efforts;
- Build capacity – e.g. ICED training programmes for students to assist the next generation of the community and to generate specific outputs relating to ICED objectives;

Plan of action to follow workshop

- Develop a science-based paper for publication on modelling Southern Ocean food webs based on the concepts initiated in this workshop;

- Generate a review of the structure, operation degree of isolation of circumpolar Southern Ocean food webs;
- Establish ICED Modelling Working Group/ modelling community for Southern Ocean;
- Develop links to other groups to avoid duplicating effort/issue of individuals being on many groups. A core group with common aims might be a useful way forward;
- Explore funding and collaborative opportunities.

Possible future workshops:

- Biogeochemistry-focused – food web interactions, considering lower level food web structure, links with physics, links with global biogeochemical cycles;
- Predator-focused – complimentary to and joint with CCAMLR – focused on species comparisons in different regions with a view towards circumpolar coverage. Focus on integration of existing data sets, to allow integration and identification of gaps to guide future research;
- ICED fieldwork coordination and planning;
- Mesopelagic-focused workshop;
- Joint ICED/ESSAS (Southern Ocean/Arctic) workshop focused on modelling collaborations for comparative work.

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Appendix I. Questionnaire

Background Information

This first ICED model development workshop will bring together a group of multidisciplinary experts to begin to characterise the Southern Ocean food web. This is the first step towards a longer-term aim of ICED; that is to develop circumpolar ecosystem models and in doing so improve the reliability of predictions of ecosystem dynamics in the Southern Ocean. In this workshop we aim to identify major gaps in knowledge and data availability in developing Southern Ocean food web models, consider regional and trophic complexities, and the potential issues in bringing together the different scales and processes operating across the Southern Ocean.

These are some of the main issues and challenges as we see them:

- Can we identify an appropriate food web structure for Southern Ocean ecosystem models?
- Are there general constraints within which food web structures can be assembled?
- To what extent can regional differences be represented by a generic model structure?
- To what extent can we reflect different scales and processes?
- Can we facilitate explicit representation of important physical constraints?
- Consideration of the importance of trophic pathways other than krill.
- Consideration of the relevance to global models.

We would like the input of all workshop participants (and those who cannot make it but wish to stay involved!) to help structure the workshop agenda and discussion sessions. As such we have attached a questionnaire that we ask you to complete as far as possible and return to us by **March 3rd**. Keep in mind that the main output of the workshop will be a group peer reviewed paper on Southern Ocean ecosystem modelling. This will review where things stand and outline key science questions and priorities for the coming few years. We will compile your responses and use them to structure the workshop and the outline for the paper.

ICED Workshop Questionnaire

1. Information on workshop participants

Briefly describe your area(s) of expertise and interest. Please include (if appropriate) geographic regions of the Southern Ocean, trophic focus, modelling experience, main group(s) you work with, etc.

2. Key Challenges

What are the key challenges in Southern Ocean ecosystem model development?

Consider:

- What do you consider to be the main gaps, key questions and priorities for Southern Ocean food web model development (if they differ from the above list)?

3. Geographic focus

Consideration of geographical differences in characterising the food web structure of the Southern Ocean

Consider:

- Can you provide a brief overview of how the food web is structured in the region(s) you work in? Note the main gaps you are aware of and list the priorities as you see them (e.g. spatial, temporal, trophic).
- To what extent can the regionally different systems (e.g. Ross Sea, West Antarctic Peninsula, Scotia Sea, East Antarctic...) be represented by a generic model structure?
- How can we develop an approach to constructing functional groups that is consistent across regions? E.g. which species are we interested in? Which species do we have data for? What is the trophic resolution of our data?
- If you have (or aware of) circumpolar distribution maps e.g. krill, predator distribution, etc, please bring these to the workshop.

4. Model development

How should we go about modelling the Southern Ocean food web(s)?

Consider:

- What are the criteria we should be using to develop realistic models of Southern Ocean ecosystems? What elements should be included in an outline structure?
- How do we link trophic interactions of biological processes across spatial and temporal scales?
- What is the appropriate resolution of biological processes at different trophic levels?
- Comparing types of models from various regions: to identify what has already been developed and assess their suitability.
- Parameter requirements and model modules.

5. Future

In developing circumpolar models what direction should we be moving in?

Consider:

- What do we know? How do we get towards where we want to be?
- Taking it forward, workshop and beyond - what would you like to see developed (and why)?

6. Other

- Have we missed anything that you consider to be key questions/issues?
- Do you have any comments at this stage regarding potential aims of the group paper?
- Gather and bring other relevant information to the workshop - think about key concepts beforehand, organise information on what is known for your region, relevant literature/data sources to help build a specific bibliography (see above)
- Is there anything that has really worked in previous workshops (or not worked) in terms of general structure and running of the event?

Appendix II. Agenda

ICED Workshop on Southern Ocean Food Webs, 16-18 April 2008

Wednesday 16 April

- | | |
|------|---|
| 0830 | Welcome and local logistics (Hofmann) |
| 0840 | Workshop goals and objectives (Murphy) |
| 0900 | Summary of workshop questionnaire (Murphy/Cavanagh) |
| 0930 | Southern Ocean GLOBEC results – new ideas and directions for research (Hofmann) |
| 1000 | Overview of Southern Ocean zooplankton and mesopelagic food webs (Pakhamov) |
| 1030 | Coffee |
| 1100 | Higher trophic levels – food web linkages and directions for modelling (Costa) |
| 1130 | Latest developments in ecosystem modelling in CCAMLR; including key ecological/modelling points from earlier workshop (Constable) |
| 1200 | Open Discussion |
| 1215 | Lunch |
| 1315 | Change to break out discussion groups |
| | <i>Modelling Southern Ocean ecosystems: clarifying major issues and considerations of the structure of Southern Ocean food webs</i> |
| 1330 | Breakout group meetings |
| 1530 | Coffee |
| 1600 | Plenary reports from breakout groups |
| 1730 | Adjourn |

Thursday 17 April

- | | |
|------|---|
| 0845 | Review of previous day activities (Murphy/Hofmann) |
| 0900 | Food web models (Steele) |
| 0930 | Southern Ocean mass balance models and bioregionalization (Pinkerton) |
| 1000 | Circulation/sea ice/atmospheric models (Klinck/Dinniman) |

1030	Coffee
1100	Perspectives from the North (Hunt)
1130	Perspectives on predators (Maury)
1200	Open Discussion
1215	Lunch
1315	Change to breakout discussion groups
	<i>Modelling approaches: discussing options and identifying the way(s) forward</i>
1330	Breakout group meetings
1530	Coffee
1600	Plenary report from breakout groups
1700	Adjourn

Friday 18 April

0830	Review of previous day activities (Murphy/Hofmann)
0900	Modelling with uncertainty (Hill)
0930	Overview of biogeochemistry and lower trophic level models (Gladrow)
1000	Overview of Southern Ocean food web modelling – issues and structures
1030	Coffee
1100	Overview of Southern Ocean food web modelling – issues and structures Review of text Discussion of paper structure
1215	Lunch
1315	Plenary discussions
1530	Coffee
1600	Plenary discussions Future workshops and planning Recommendations
1700	Close

Appendix III. Southern Ocean food web modelling workshop presentations and discussion points

In order to plan the workshop a questionnaire (Appendix I) was completed by all participants ahead of the workshop. The agenda (Appendix II) was designed to provide background information, summarise the current level of understanding and stimulate discussions. A number of speakers were invited to present on key issues to set the scene and inform the subsequent discussion groups. The major points from these discussions have been included in the main report of the meeting. More detailed discussion points are included here where appropriate.

Main topics on the agenda included:

- Key issues in analysing Southern Ocean food webs;
 - Overview of Southern Ocean food webs
 - Major questions and challenges in Southern Ocean research
 - Structure and dynamics of Southern Ocean
- Modelling Southern Ocean food webs;
 - Current modelling approaches
 - Developing mechanistic models of Southern Ocean ecosystems
 - Developing generalised models of Southern Ocean ecosystems.

The following sections summarise the content and outcomes of the presentations and discussion groups. Supporting information is included in the appendices. The issues and recommendations of the workshop will be further expanded in an ensuing manuscript.

Key issues in analysing Southern Ocean food webs

Overview of Southern Ocean food webs

This section comprises summaries of presentations on some aspects of current Southern Ocean food webs research. Any specific discussion points are also summarised where relevant. As text was provided by the speakers each summary does not conform to the same format. It should also be noted that these are not intended as a comprehensive coverage of the issues involved.

Results from the Southern Ocean GLOBEC Program

Eileen Hofmann, Center for Coastal Physical Oceanography, Old Dominion University, USA

The Southern Ocean Global Ocean Ecosystem Dynamics (SO GLOBEC) programme focused on understanding physical and biological factors that contribute to enhanced Antarctic krill (*Euphausia superba*) growth, reproduction, recruitment, and survivorship. The extensive multidisciplinary data sets from SO GLOBEC are providing new and important insights and understanding of Antarctic marine ecosystems, such as 1) the role of circulation and sea ice in structuring Antarctic krill distributions, 2) understanding of the suite of overwintering mechanisms used by Antarctic krill, 3) knowledge of the importance of Circumpolar Deep Water in producing biological hot spots, 4) the effect of this biological production at all trophic levels, especially during winter, 5) the importance of alternative food webs and implications for carbon and nitrogen cycling, 6) the importance of fish as alternative food source for upper trophic level predators, and 7) the significance of climate variability at interannual and sub-decadal scales as a moderator of ecosystem processes. The recognition that larger scale processes affect regional physical and biological interactions provides a basis for the ICED program. The knowledge and lessons learned from the SO GLOBEC programme provide a strong basis for continuing into this next phase of Southern Ocean research.

Main discussion points

- From a climate perspective there is a need to merge information from both ocean and atmospheric aspects, and to achieve this, improved communication is needed between the relevant groups.

Overview of zooplankton, epi- and mesopelagic food webs in the Southern Ocean

Evgeny Pakhomov, University of British Columbia, Canada

- Major zonal biological patterns (biogeography) are the result of physical settings (e.g. major frontal systems);
- Large zonal patterns can therefore be predicted but regional specifics should be taken into consideration (spatially-explicit models?);
- Zonation of zooplankton assemblages at the large scale (circum Antarctic zonal belts) is clearly visible in the assemblage composition. Broadly, there are four major zooplankton assemblages in the Southern Ocean. These correspond to water masses north of the Sub Tropical Convergence (STC), between the STC and Subantarctic Front (SAF), between the SAF and Antarctic Polar Front (APF) and south of the APF. The SAF appears to be the most important biogeographical boundary broadly separating the temperate/subAntarctic and Antarctic assemblages (Pakhomov & McQuaid 1996, Pakhomov et al. 2000). South of the APF, four further assemblages can be found. These are similar, with some regional specifics, between various coastal regions, e.g. Bellingshausen Sea, Weddell Sea, Lazarev Sea, Cosmonaut Sea, Prydz Bay Region, Ross Sea, consisting of oceanic (copepod dominated), salp dominated, krill dominated and neritic (neritic krill *Euphausia crystallorophias* and silverfish *Pleuragramma antarcticum* dominated) assemblages (Hunt et al. 2007, Pakhomov & Froneman 2004);
- There are several zooplankton groups that are poorly represented in existing models, yet form critical links between primary productivity and higher trophic levels. Depending on the size of the phytoplankton, variety of trophic pathways may be important and this could be region and assemblage specific. In fact, the size and composition of the phytoplankton at the base of the food web could be critical in determining the complexity and the structuring of trophic pathways in the system;
- Underrepresented groups/taxa in models include: microzooplankton, small copepods, large copepods, other species of euphausiids (neritic krill, *Thysanoessa* spp.), tunicates (*Salpa thompsoni*, *Ihleia racovitzai* and appendicularians), other gelatinous zooplankton, squid and pteropods;
- Alternative trophic pathways are also important in the pelagic zone of the Southern Ocean. These include phytoplankton-copepods-fish (-squid) pathway, phytoplankton-pteropods (-fish?) pathway, phytoplankton-copepods-*Themisto gaudichaudi*-fish pathway;
- Other alternative trophic pathways according to Hopkins et al. (1993b)
 - Phytoplankton + protozoans → copepods + krill → *Electrona antarctica* → flying seabirds
 - Phytoplankton + protozoans → krill → mammals
 - Phytoplankton + protozoans → krill → cephalopods → penguins + fur seal
- The mesopelagic food web is poorly understood yet it is a critical region of the ocean. ~ 90% organic matter is remineralized between 200-1000 m, controlling carbon sequestration beyond mesopelagic layer (feedback to global warming) and marine productivity on global

scale. It appears trophically that mesopelagic species rely on epipelagic resources, and particularly on mesozooplankton/copepod resources

- There is strong seasonal input of secondary production into the mesopelagic layer due to copepod ontogenetic migration;
- Macroplankton and micronekton seem to follow this migration;
- No knowledge on the copepod mortality during this period of time available;
- Very little understanding of the mesopelagic food web structure overall;
- Detailed food web structure and major trophic pathways are unknown;
- Circum-Antarctic coverage is absent;
- Knowledge on the role of gelatinous predators is almost absent;
- Knowledge on the role of squid and mesopelagic fish is limited.

Main discussion points

- Technology is providing new methods of quantifying abundances of mesopelagic organisms over large scales (e.g. Continuous Plankton Recorder, video and optical plankton recorders, multi-frequency acoustics). An important question is to what extent can we relate distributions of mesopelagic biota to environmental parameters observable on large scales in order to extrapolate between sparse in situ measurements? Are such biology-environment relationships likely to be robust between geographic regions, and under climate variability and change?
- The role of larger (> 1 cm) organisms relative to microbial components is poorly constrained. Rate process information on the mesopelagic fauna is needed to assess their quantitative role in the entire food web.

Climate change and habitat selection of seals in the Western Antarctic Peninsula

Dan Costa, University of California, Santa Cruz, USA

The Western Antarctic Peninsula (WAP) is a region of the world undergoing one of the most dramatic increases in temperature. In an attempt to understand how climate change might impact Antarctic seals in the WAP we examined the habitat utilization of three of the most common seals in this region. Using Satellite Relay Data Loggers we examined the foraging behaviour of 42 adult female southern elephant seals, *Mirounga leonine* over four years (2005, 2006, 2007 & 2008), 43 crabeater seals, *Lobodon carcinophaga* over three years (2001, 2002 & 2007), and two Weddell seals, *Leptonychotes weddelli* (2007) foraging in the Western Antarctic Peninsula (WAP). Southern elephant seals made the deepest (357 m) and longest dives (24.3 min). Some elephant seals remained in WAP foraging along the continental slope in all years and some remained in the pack ice as it formed during the winter. During 2006 some elephant seals foraged well into the Amundsen Sea some 5400 km west. In contrast during 2007 all elephant seals remained in the WAP region or in the Drake Passage. These changes correspond to marked differences in SST between years. Crabeater seals did not show as dramatic variations in their habitat utilization. They foraged along the continental shelf and remained deep within the pack ice throughout the winter, remaining closer to shore than elephant seals. Some moved considerable distances (664 km to northeast, 1147 km to southwest), but most remained within 300 km of their tagging location. Average dive depths for crabeater seals were 61 m, and lasted 3.8 min. The Weddell seals remained within 94 km of where they were tagged and made surprisingly shallow dives 91 m that lasted 11.5 min (deepest 455 m, longest 27.5 min). Our data suggest that elephant seals forage in a greater range of habitat types and that crabeater seals are more dependent on sea ice and thus would be more impacted by climate change.

Main discussion points

- Using marine mammals as oceanographic samplers is a cost-effective means to sample the environment, but more work is necessary to establish the bias in the sampling, and the behaviour of the animals while at sea.

Ecosystem modelling in support of CCAMLR and IWC

Andrew Constable, Australian Antarctic Division and Antarctic Climate and Ecosystems Cooperative Research Centre

Modelling of Southern Ocean food webs and ecosystems, particularly related to krill, have been reviewed in Constable (2002) and Hill (2006). Early models were primarily mass balance or deterministic multi-species models. A variety of models were also developed to investigate the responses of predators to different prey dynamics (e.g. Constable 2001, Mangel & Switzer 1998, Thomson et al. 2000).

The development of ecosystem models in CCAMLR has been facilitated by the following key events:

Year	Outcome	Report
2001	Establishing programme of work in which the development of ecosystem models was a central component	SC-CAMLR-XX, WG-EMM report
2002	Spatial characterisation of krill-based food web in Area 48 (data synthesis for small-scale management units)	SC-CAMLR-XXI, Annex 4, Appendix D: WG-EMM Workshop on Small-Scale Management Units, such as predator units (in Area 48)
2004	Workshop on developing ecosystem models (with emphasis on plausible models for krill but compilation suitable for multiple purposes)	SC-CAMLR-XXIII, Annex 4, Appendix D: WG-EMM Workshop on plausible ecosystem models for testing approaches to krill management
2005-	Ecosystem model development – KPFM/FOOSA, SMOM, EPOC	SC-CAMLR-XXIV-XXV Annex 4, Appendix D: WG-EMM first and second Workshops on Management Procedures to evaluate options for subdividing the krill catch limit among small-scale management units. SC-CAMLR-XXVI, Annex 7 Report of Working Group on Statistics, Assessments and Modelling
2007	Spatial characterisation of Southern Ocean (bioregionalisation)	SC-CAMLR-XXVI, Annex 9 Workshop on Bioregionalisation of the Southern Ocean
2008	Compilation and evaluation (documenting uncertainties) of data inputs to models (with IWC)	August 2008

The concerted ecosystem modelling effort began with a workshop in 2004. Since then "operating" models have been developed to evaluate approaches for subdividing krill catch amongst small-scale management units to account for the needs of predators. Ecosystem models are also being

developed to explore the effects of finfish fisheries in some regions of the Southern Ocean and for understanding the potential effects of climate change. The “Workshop on plausible ecosystem models for testing approaches to krill management” was held in conjunction with the meeting of WG-EMM in 2004 with the following Terms of Reference:

- (i) To review the approaches used to model marine ecosystems
- (ii) To consider plausible operating models for the Antarctic marine ecosystem, including (a) models of the physical environment; (b) food-web linkages and their relative importance; (c) dynamics of the krill fishing fleet; (d) spatial and temporal characteristics of models and their potential limitations in space and time; and (e) bounding the parameters used in the models;
- (iii) To advance a programme of work to develop and implement operating models to investigate the robustness of different management approaches to underlying uncertainties in the ecological, fishery, monitoring and assessment systems,

The report of the workshop (SC-CAMLR-XXIII, Annex 3, Appendix D) covered the following items in considerable detail including tables and figures summarising each part of the ecosystem:

- 1) Desirable attributes of ecosystem models
- 2) Conceptual representation of ecosystem models, including
 - a) Physical system
 - b) Primary production
 - c) Invertebrate herbivores and carnivores
 - d) Target species
 - e) Mesopelagic species
 - f) Marine mammals and birds
 - g) Fisheries
- 3) Plausible scenarios for the antarctic marine ecosystem
- 4) Model formulation and specification

Ecosystem studies in the IWC have centred on potential competition between cetacean species as well as cetacean-fisheries interactions. This work has followed the timeline:

Year	Event
Early-mid 90s	Commission passed a series of resolutions expressing concern regarding climate change effects on whale populations and on the reliability of its management procedures in particular
Mid 90s	Revised Management Procedure (RMP) development expanded to included testing robustness to one aspect of potential carrying capacity (CC), a substantial decrease in CC of 50%; Establishment of new working group on Environmental Concerns within the IWC SC
1996	IWC convened a symposium and workshop in Hawaii to consider the potential effects of CC on whale populations and individuals
Late 90s	The workshop led to the development of a major new research effort within the IWC SC

	entitled Southern Ocean Whale Ecosystem Research (SOWER)
2000	First SOWER field programme conducted in collaboration with CCAMLR during the synoptic survey of the Atlantic sector, CCAMLR2000 (within IWC this is referred to as SOWER2000)
2000....	<ul style="list-style-type: none"> • Subsequent SOWER field sampling conducted in conjunction with SO GLOBEC and some national programmes. • Pre-existing annual research cruises conducted under IDCR (International Decade of Cetacean Research) expanded in scope to include limited environmental sampling, re-titled SOWER cruises.
2001	IWC resolution to consider predator- prey dynamics (cetacean-fishery interactions)
2002	Workshop on cetacean-fishery interactions
2003	Initial cetacean-krill model for Southern Ocean
2004-	Further development of model
2008	Compilation and evaluation (documenting uncertainties) of data inputs to models (with CCAMLR)

CCAMLR models at present vary from exploratory food web models for building general scenarios on food web dynamics to those that provide realism, relating food web dynamics to time series of physical parameters. These models are “minimum realistic models” rather than trying to capture all processes. CCAMLR has been considering the implications of uncertainties in this modelling work, including exploring the consequences to results of:

- i) Bias and precision of parameter estimates used in a model,
- ii) Natural variation/stochasticity, and
- iii) Model (mis)specification.

Uncertainty arising from model (mis)specification is one of the most important issues to address. The following uncertainties are being considered because of the need to appropriately represent cause and effects, particularly the relative strengths and timing of ecological linkages:

1. Could relative importance of trophic pathways be masked by the use of guilds & functional groups?
2. Are the predator consumption – prey mortality functions (feeding relationships) appropriate?
3. Are the dynamics of populations consistent with expected lags following consumption of resources?
4. Are parameters and model structures internally consistent such that covariation between factors is realistic?

The Scientific Committees of the Commission for the Conservation of Antarctic Marine Living Resources (SC-CAMLR) and the International Whaling Commission (SC-IWC) have agreed to hold a joint workshop to review input data required for ecosystem models being developed to provide management and conservation advice on krill predators in the Antarctic marine ecosystem (SC-CAMLR-XXIV, 2005, paragraphs 13.44-13.53; SC-IWC Report 2006, Annex K, Appendix 6). The following text is extracted from SC-CAMLR-XXVI/BG05.

The Workshop has the following terms of reference:

1. For models on the Antarctic marine ecosystem, and in particular predator-prey relationships, that could be developed for providing management and conservation advice relevant to CCAMLR and IWC, consider the types, relative importance and

uncertainties associated with input data for those models, in order to understand what is needed to reduce uncertainties and errors in their use.

2. Review the available input data from published and unpublished sources that are currently available for such models.
3. Summarise the nature of input data (e.g. abundance estimates, trend estimates, foraging scales, seasonal diet etc), based on metadata (see definition below), by describing methodology, broad levels of uncertainty, time series, spatial extent and determine the appropriate scale at which those input data are relevant to these modelling efforts.
4. Identify and prioritise the gaps in knowledge and types of analyses and field research programs needed to reduce important uncertainties in ecosystem models being developed for CCAMLR and IWC and how scientists from the two Commissions can best collaborate and share data to maximise the rate of development and scientific quality of modelling efforts and input data.

Models developed to support discussions in SC-CAMLR and SC-IWC include those of Watters *et al.* (2005, 2006), Plaganyi & Butterworth (2005, 2006a, 2006b), Mori & Butterworth (2003, 2006a, 2006b), and Constable (2005, 2006). An important difference in the current modelling for SC-CAMLR and SC-IWC is the spatial scale and taxa of interest. Models on the dynamics of cetacean populations will necessarily operate at larger scales commensurate with the ability of whales to move widely in Antarctic waters. Models of krill availability to all predators is an important issue being addressed by SC-CAMLR and at this stage are focused on krill availability and predator foraging at the scale of land-based predator colonies and of CCAMLR's small-scale management units (SSMUs); however, given the potential for appreciable increase in the krill fishery in the longer term, models at a wider spatial scale are also of interest to SC-CAMLR. An important issue for both sets of models is how to ensure that they provide results that are consistent with each other.

While these models operate at different spatial and temporal scales, they collectively incorporate knowledge on, or estimates from, the collection of estimates of parameters and variables:

Factor	Attributes
Population	biomass/numbers in different regions of the Southern Ocean, trends in abundance, population structure, including age/size/spatial structure
Habitat utilisation	movement, key habitats and environmental variables (drivers of key population processes), foraging areas
Population growth rates	growth of individuals, reproductive output, recruitment, mortality rates, carrying capacity
Foraging activities	diet, foraging success, consumption rate, competition
Catch	biomass/numbers taken and size structure in different regions over time

The degree of detail in taxonomic information remains to be decided but a number of physical and ecological parameters can impact on krill availability and food web dynamics (Murphy *et al.* 2007a, Murphy *et al.* 2007b). Expert groups are compiling ecological and environmental input data for the following main categories:

- 1) Cetaceans – toothed, baleen

- 2) Seals - pack ice seals, fur seals
- 3) Birds – penguins, flying birds
- 4) Mesopelagic and epipelagic predators - fish and squid
- 5) Krill
- 6) Other biological components – primary production & protists, zooplankton
- 7) Environmental components - sea ice, sea temperature and ocean processes.

Preparation for the workshop is continuing all expert groups compiling metadata. These are being entered into a database currently hosted at the Australian Antarctic Data Centre with the expectation that the final database will be deposited with both the CCAMLR and IWC Secretariats after the workshop.

Main discussion points

- It was noted that the work presented by Dan Costa captured many of the issues of data and uncertainty. i.e. this type of work removes much of the uncertainty;
- It was noted that a key aim of ICED is to promote and carry out work to compliment the efforts of CCAMLR and IWC;
- It was noted at many times during the ICED workshop that no single model is likely to be appropriate for the objectives given above, but that many different modelling approaches should be pursued. A useful division is between strategic models (used to understand ecosystem functioning and develop a holistic view of Southern Ocean food-webs), and tactical models (used to guide specific aspects of management).

Examples of Regional food webs

Overview of the Ross Sea Food Web

*Matt Pinkerton, National Institute of Water and Atmospheric Research, New Zealand
(Pinkerton et al. 2008a)*

The Ross Sea is a generally considered a low primary production system, with irradiance, iron, and macronutrients (nitrate, silicate) variously limiting algal growth through the year. Primary production is highly seasonal, driven by the annual light/dark cycle and the freeze/thaw cycle of sea ice. Organisms have various strategies for survival when there is no primary production, including migrating in and out of the region, storing lipids or other high-energy products, going into a quiescent stage, increased omnivory/variety of feeding styles and adaptive breeding cycles. The mean monthly sea ice cover in the Ross Sea varies from 5% ice free in winter to 70% ice-free in January and September (Arrigo & van Dijken 2004). Ice reaches a maximum thickness around November. In contrast with most polar regions, ice extent in the Ross Sea is increasing at c. 7% per decade. The upper surface of the ice provides a habitat for a number of sea birds and mammals, while the ice itself, especially the lower part, constitutes a unique habitat for microalgae and bacteria which provide a food source for associated micro-, meio- and cryopelagic fauna of the water immediately below the ice.

The input of primary production from the water column and sea ice in the Ross Sea is channelled mainly through the copepods. The connection may not always be direct as small heterotrophic flagellates and larger heterotrophic microplankton (including dinoflagellates, tintinnids, other

ciliates, and eggs and developmental stages of metazoans) are significant grazers of primary production and are often a significant part of the diet of many copepods.

Two species of krill are found in the Ross Sea *Euphausia crystallorophias*, and *E. superba*, with *E. superba* being found primarily along the continental slope, and *E. crystallorophias* only over the shelf. Abundances of krill are probably much lower in the Ross Sea than in other parts of the Southern Ocean. Although they form an important link between the water column, sea ice and larger predators, they are believed to be less productive and have slower turnover rates than the large epipelagic copepods (*Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas* and *Metridia gerlachei*). *E. crystallorophias* replaces *E. superba* in the diet of large predators (penguins, whales) in waters over the southern Ross Sea shelf. In addition, Antarctic silverfish (*Pleuragramma antarctica*) are a major link between mesozooplankton (mainly copepods) and the larger predators. *P. antarctica* are ubiquitous in the diet of all large animals (seabirds, seals, toothed and baleen whales, toothfish, many other species of fish, squid). *P. antarcticum* have a life history that is thought to take in the whole Ross Sea shelf and slope, and their juveniles dominate the Ross Sea ichthyoplankton. Abundance of demersal fish species is poorly known, but is thought to be dominated (in terms of biomass) by the macrourid *Macrourus whitsoni*, the skate *Bathyraja eatonii*, and icefish (mainly *Chionodraco hamatus* and *C. antarcticus*). Antarctic toothfish, *Dissostichus mawsoni*, is the top piscine predator in the Ross Sea and since 1997 has been the target of an international longline fishery. The fishery is managed through the Commission for the Conservation of Antarctic Marine Living Resources, which requires that the effects of any harvesting on dependent and associated species as well as on the target species be considered. The annual catch is approximately 3000 t.

Avian biomass in the Ross Sea is dominated by penguins, with >40 000 breeding pairs of emperor penguins and about 38% of the world population of Adélie penguins (c. 1 million breeding pairs). Seals are the most common marine mammals in the Ross Sea, with more than 200 000 crabeater seals, c. 40 000 Weddell seals, 8000 leopard seals, and 5000 Ross seals. There is debate over whether or not Weddell seals remain in the Ross Sea year round. Baleen whales (minke, fin, humpback, sei, blue) tend to congregate in a feeding zone, out of the pack ice, where krill are abundant. This narrow feeding zone moves north in winter, south in summer, so that the baleen whales spend only the summer in the Ross Sea. Information on toothed whales (killer whale, sperm whale, southern bottlenose whale, Arnoux's beaked whale) in the Ross Sea is rather limited, coming primarily from surveys of their distribution and numbers carried out by systematic surveys. Recent work has shown that three different types of killer whale may exist, with the fish-eating type-C being by far the most common type in the McMurdo area (Krahn et al. 2008, LeDuc et al. 2008, Pitman & Ensor 2003, Pitman et al. 2007).

Overview of the Scotia Sea Food Web (Following Murphy et al. (2007b)

Nadine Johnston, British Antarctic Survey, Cambridge, UK

Characteristics of the Scotia sea ecosystem:

- Dominated by physics (ACC and Weddell-Scotia Confluence)
 - strong advective flow, intense eddy activity and mixing;
- Highly productive (high nutrient, high chlorophyll: 'HNHC', spring blooms can cover >0.5M km²);
- Supports large and diverse populations of seabirds and marine mammals;
- Strong seasonality

- irradiance, sea surface temp and sea ice cover (leads to shorter summers in the south);
- Interannual variability in variability in winter sea ice distribution and sea surface temperatures
 - linked to Southern Hemisphere-scale processes such as El Niño-Southern Oscillation (ENSO);
- Experienced rapid regional warming during the second half of 20th century;
- Commercially exploited for >200 yrs (seals, whales, fishes).

Structure of Scotia Sea food webs:

- Krill-centred
 - 70% of the total Antarctic krill population are found within the southwest Atlantic sector (0-90° W) of the Southern Ocean, with the Scotia Sea accounting for 26% of the total (Atkinson *et al.* 2008);
 - krill form the major link between primary production and vertebrate predators;
- Structure varies spatially and temporally
 - geographically, seasonally, interannually and over longer-time scales;
- Beginning to understand importance of krill-alternative pathways, e.g.
 - Fish (e.g. myctophids (Collins *et al.* 2008, Hopkins *et al.* 1993a, Olsson & North 1997, Reid & Arnould 1996, Rodhouse *et al.* 1992); mackerel icefish (Everson *et al.* 1999, Reid & Arnould 1996);
 - Squid (e.g. Collins & Rodhouse 2006, Rodhouse *et al.* 2001)
 - Copepods (e.g. Atkinson *et al.* 1996, Atkinson & Snyder 1997, Atkinson *et al.* 1999, Pakhomov *et al.* 1997, Reid *et al.* 1997a, Reid *et al.* 1997b, Shreeve *et al.* 2005, Ward *et al.* 1995);
 - Amphipods, mysids, euphausiids other than Antarctic krill (e.g. Bocher *et al.* 2001, Croxall *et al.* 1999, Dickson *et al.* 2004, Everson *et al.* 1999, Kock *et al.* 1994, Siegel & Muhlenhardtsiegel 1988).

Controls on the structure and dynamics of Scotia Sea food webs:

- Seasonal changes in irradiance, sea ice and foraging patterns
 - Spring blooms;
 - Seabirds and marine mammals change foraging areas/diet as sea ice advances north (e.g. Boyd *et al.* 1998, Reid & Arnould 1996);
- Regional and Southern Hemisphere-scale climate processes
 - Regional warming over the last 50 yrs;
 - ENSO;
 - Result in variations in air and sea surface temperatures
 - winter sea ice distribution;
 - affects regional primary production (and influences biogeochemical cycles); affects population dynamics and dispersal of krill (Murphy *et al.* 2007a); impacts foraging, breeding performance and population dynamics of krill predators such as seals and penguins (Murphy *et al.* 2007a, Trathan *et al.* 2007);
- Long-term variations in sea ice
 - Decline in Antarctic krill over last 30 years (Atkinson *et al.* 2004);
- Oceanography
 - Advection of Antarctic krill from more southerly areas (Thorpe *et al.* 2007);
 - Transfer of planktonic species e.g. copepods, phytoplankton (e.g. Ward *et al.* 2002);

- Influx of external production is important in maintaining food web structure
- Fisheries (historical and modern)
 - Impact on krill predators
 - Reduction in whale populations
 - Teasing apart impacts of climate change and fisheries is a challenge.

Missing data on Scotia Sea food webs:

- Lower trophic level systems (microbial and phytoplankton)
 - 2 collaborative programmes at BAS modelling phytoplankton dynamics;
- Abundance, distribution and diet data of key species
 - Diet data from marine based predators and non-krill predators;
 - Importance of mesopelagic systems, salps, squid, jelly fish, chaetognaths, pteropods, copepods, amphipods and euphausiids
 - BAS/EUR-OCEANS project synthesising data from Discovery cruises
 - Impact on larval fish and krill- effects on recruitment variability;
- Benthic-pelagic links;
- Biogeochemical controls;
- Energy fluxes between key species
 - BAS ECOPATH model of South Georgia ecosystem during summer;
- Connectivity between Scotia Sea ecosystem and other systems, e.g. advection of Antarctic krill from the south to support food webs (Thorpe et al. 2007).

Main discussion points on what are the major controls and feedbacks on structure and function of Southern Ocean food webs.

Consideration of krill-alternative food web pathways

Most of the discussion focused on alternative pathways in open ocean food webs. The krill-to-upper trophic level predators pathway may be common in some areas, such as along the Antarctic Peninsula, the Scotia Sea, and South Georgia. When krill are not present a copepod-to-myctophid-to upper trophic levels pathway is likely to occur. It was noted that these are interactive pathways that may at times act as alternatives, but at other times operate interactively. From diet studies, in some areas, even where krill are present, myctophids and/or Antarctic silverfish (*Pleuragramma antarcticum*) may serve as an alternate food source for predators in fall and winter seasons, for example, in the Ross Sea, Lazarev Sea and Prydz Bay Region. In coastal regions, a copepod pathway may dominate either over the shelf region or further to the north, away from the shelf break and continental slope, where krill concentrations are low. Near the shelf break and on shelf, *Euphausia superba* and *E. crystallorophias* may dominate, e.g. Cosmonaut, Sea, Prydz Bay region and Ross Sea. Other pathways, for which there is very little information, may have important roles in transferring carbon and energy through the food web. For example, pteropods constitute the major component of the zooplankton as well as the vertical flux of particulate carbon in the Ross Sea and other locations (Collier *et al.* 2000), yet their life cycle, rates of ingestion of organic material, size-selection abilities and rates of removal by predators are unknown or very poorly constrained. But given their large biomass and potentially critical role in localized food webs and biogeochemical cycles, understanding these (and other, poorly known organisms and pathways) is essential to an improved understanding of alternative pathways in the Southern Ocean.

Predator foraging strategies

Varying foraging and reproductive strategies of top predators was discussed based on the concept that predators adopt different strategies depending on whether they are a central-place based forager or forage over broad areas. A number of examples were highlighted:

- Elephant seals have different foraging patterns during El Nino versus La Nino periods. A single optimal foraging pattern doesn't work for the different conditions. Females show distinct foraging patterns;
- Fur seals at Cape Sheriff may have a variable diet, but may have fidelity to their particular foraging area. They appear to be krill specialists;
- South Georgia fur seals are specialists for individual foraging trips, but over a season may respond to the availability of different prey. Information is available at the population level but unfortunately, there are no data on individuals over a season.

It is important to note that the life history of top predators is adapted over the long-term. *E. superba* also are relatively long lived (about 7 years); therefore, the population can survive several years of low recruitment. The critical food threshold levels are not well defined for either krill or predators. The timing of food availability and the quality of food also may affect the health of adult populations.

Species at the edge of their range and climate change

To detect climate change, one approach is to investigate species at the periphery of their geographic range. Species at the edge of their range may respond to small changes in temperature or type and quality of food, which would provide information about the timing and extent of climate variability. Looking at species in the middle of their geographic range may not be as informative as those at edge of their range. For example, pygoscelid penguin communities are known to vary along the Antarctic Peninsula. Adélie penguin populations have contracted in recent years, whilst those of chinstrap penguins have expanded, likely in response to significant environmental changes and changes in food availability (Forcada et al. 2006).

It was noted that the type of model may depend on the questions being addressed. For example, the question how does food web structure and function control biogeochemical cycles would have a different focus. Top predators may not be important as a removal term.

To what extent can different regions of the Southern Ocean be represented by a generic food web model?

Discussions agreed that a common template model could be built using life history characteristics, behaviours, and habitat requirements of different types of taxa. Abundances of dominant species vary in different regions, seasonally, and interannually. For example, Adélie penguins occur in most regions of Antarctic above a certain latitude, but respond differently in varying environments and different seasons during which they may exploit different trophic pathways (krill versus myctophid fish). It is not known whether there are changes in lower trophic levels leading to prey switching. Models could provide insight.

General discussion points relating to operation, structure and change in Southern Ocean food webs

- It was noted that Southern Ocean food webs might vary by location (e.g., open water, ice edge, pack ice, and coastal zones) and season. The classic diatom-krill-top predator food chain likely occurs in restricted areas where krill are abundant and during the summer productive season. Food webs in most regions of the Southern Ocean and during other

seasons have longer pathways to top predators and have more complex interactions among trophic levels, which are not well known;

- We need to start by looking at SCAR-MarBIN: does this represent current knowledge? Is presence-absence data available to enable distributions to be related to environmental characteristics? Then move forwards from there with assessing and compiling data sources for models;
- Regarding the possibility of a generic model, to what extent could this be applied based on the current known characteristics of the system?
- The chinstrap penguin is an example of how food webs can change;
- Consideration of prey selection – e.g. the diet of large whales: e.g. right whales feed on copepods in the Northern Hemisphere but not in the Southern Hemisphere (krill specialists). Also the point that what is happening now may not be representative of the historical situation – i.e. that we know little about how these systems have changed over time;
- The importance of key components in the life history of species. E.g. the change in the winter diet of Adelie penguins – i.e. food web effects versus direct effects;
- It would be useful to have a series of conceptual diagrams representing the food webs of different regions. To what extent would these be representative? Are they sufficiently distinct? This would be a good aid to prompt the modelling investigations;
- Bioregionalisation – bioregions are areas with distinct ecosystem properties. The CCAMLR bioregionalisation working group is considering to what extent we can define bioregions using combinations of environmental properties rather than considering distributions of individual organisms or characteristics of food webs.

Modelling Southern Ocean food webs

Current modelling approaches

This section comprises summaries of presentations on current modelling approaches in Southern Ocean research followed by a summary of relevant discussion points where raised. As text was provided by the speakers each summary does not conform to the same format. It should also be noted that these are not intended as a comprehensive coverage of the issues involved.

Reconciling Concepts in Biological Oceanography (following Steele et al. 2007).

John H Steele, Jeremy S Collie, Dian J Gifford, Woods Hole Oceanographic Institution, USA

The inherent complexities in the structure and dynamics of marine food webs has led to two major simplifying concepts – *species centric*, focusing on physical processes affecting particular pelagic species, including the early life stages of fish – and *tropho-centric*, emphasizing energy flow through broad functional groups, from nutrient input to fish production. These two concepts are complementary. Together they embrace most food web processes and answer different questions. They can describe features of spatial distribution of individual species, and of food web structure, especially those relevant to fish communities. But they cannot provide general explanations for the factors determining changes in abundance of individual marine species. Nor can they resolve the practical problems in managing fish stocks in an ecosystem-based context. These issues remain central theoretical and practical challenges for biological oceanography and for the GLOBEC syntheses.

Mass balance model of the Ross Sea (Pinkerton et al. 2008a)

Matt Pinkerton, National Institute of Water and Atmospheric Research, New Zealand

We report on the development of a mass balanced carbon-budget trophic model of the Ross Sea as a step towards investigating ecosystem effects of the fishery for Antarctic toothfish (*Dissostichus mawsoni*). The model has 30 trophic groups representing all the major biota of the Ross Sea. Many of the lower trophic level species in the model are grouped by functional role because information is not available at greater taxonomic resolution. The model separates the following apex predators by species: Emperor penguin, Adélie penguin, crabeater seal, Weddell seal, orca, sperm whale, Antarctic toothfish. A survey of the available literature and both published and unpublished data provided an initial set of parameters describing the abundance (seasonally and spatially resolved where possible, imports, exports), energetics (growth, reproduction, consumption), and trophic linkages (diets, key predators) for each model group. We also estimated the relative level of uncertainty on these parameters. We describe the method we used to adjust the parameters to give a balanced model taking into account estimates of parameter uncertainty and the large range of magnitude (>6 orders of magnitude) in trophic flows between different groups of organisms. Biomass, production, consumption, export and diet fractions are adjusted simultaneously. We set ecotrophic efficiency to unity for all non-primary producers. Changes to the initial set of parameters needed to obtain balance were significant, especially for bacteria. Excluding bacteria, the adjustments required for balance from the parameters estimated *a priori* were <46% (biomass), <15% (production, consumption), and <28% (diet fractions). The balanced model presented here has not yet been validated and should be considered a work in progress.

On the development of Mass Balance Models and Bioregionalisation

Matt Pinkerton, National Institute of Water and Atmospheric Research, New Zealand

ICED will need to use a number of different modelling approaches in order to characterise and model the circumpolar Southern Ocean food web. No single approach alone is likely to be sufficient to capture the links between ecosystems and climate in Southern Ocean for the myriad research and management purposes envisaged.

Model types

Different types of model currently under development by the global scientific community have different strengths, weaknesses, and potential applications. The models can be grouped into three types:

1. Descriptive models, such as whole ecosystem mass balance models, and Ecopath-type models;
2. Mechanistic dynamic ecosystem models, including population models, stock models, FOOSA, SMOM, EPOC, EcoSim. These usually consider only part of an ecosystem, and use invariant rules to predict changes over time. They are generally fitted to data, and aim to provide results that are quantitatively verifiable. These models are often called tactical models for specific management purposes;
3. Stylized ecosystem models. These models are typically based on theoretical rather than empirical ecology, and have been used to investigate the characteristics of complex adaptive systems, or to investigate how organisms/ecosystems evolve over time. The models typically model part of a system, are not region or ecosystem specific, not fitted to data, and not

intended to be quantitatively verifiable. These models aim to look at general characteristics of ecological systems and are often referred to as strategic models.

Biological versus model realism

A biologically realistic model contains a substantial amount of information on the ecological and biological characteristics of a particular group with a view to systematising biological knowledge. “Model realism” means that the outputs have good quantitative or qualitative accuracy – i.e. that the model is fit for purpose, irrespective of whether the structure of the model mimics particular biological characteristics of the system being modelled. Biologically realistic models often do not provide as reliable quantitative predictions as simplified models that contain only the key factors of relevance to the prediction. The key to making reliable predictions is in understanding the factors that need to be included in the model and those that can be excluded. The emergent, system-level properties may be effectively understood without recourse to the underlying detail.

Mass balance modelling

A model that can predict ecosystem changes in the Southern Ocean will require an understanding of what controls changes in the distribution of biota in the Southern Ocean, and what controls the abundances of groups from year to year. Knowledge on this issue is lacking for many organisms (see Section 1.2 and 1.3).

Mass balance models are a valuable prerequisite to dynamic ecosystem modelling. The value of a mass balance model includes:

- Brings together information on all biota into a consistent format;
- Provides a system-level view of ecosystem characteristics;
- Provides a base for dynamic modelling, including identifying components of the system that could usefully be modelled dynamically using a minimum-realistic model.

Mass balance models for ICED should aim to quantitatively describe the current state of part of the Southern Ocean ecosystem:

- Identify all species/trophic/functional groups of biota present;
- Quantify abundances/biomasses/distribution of all groups;
- Determine interactions between trophic groups (especially trophic interactions);
- Estimate energetic and demographic characteristics (growth, production, respiration, mortality, reproduction);
- Characterise variability in factors 1-4, seasonally, spatially, and between years;
- Attempt to quantitatively estimate uncertainty in the parameters 1-5.

A mass balance trophic model of the Ross Sea is currently under development at NIWA, New Zealand. The main gaps in knowledge concern middle trophic level groups that link primary producers to top predators. These include fish (including Antarctic silverfish, other small notothenids, myctophidae), fish larvae and juveniles, cephalopods, zooplankton (including krill, salps and other gelatinous zooplankton, mesozooplankton), and the trophic role of the benthos, including habitat provision. A preliminary balanced model was presented to CCAMLR WG-EMM-08/42 in 2008 (see Appendix V for abstract).

- A method has been developed for mass balance models to simultaneously adjust biomass, diet fractions, and energetic parameters to obtain balance, taking into account variations in the estimated parameter uncertainties. The relative levels of these uncertainties can vary considerably across groups in the ecosystem;

- Many different modelling methods should be used to estimate parameters for different groups. The mass balance model then brings summary parameters from each trophic group together. Much of the complexity associated with modelling individual species is thus considered outside the trophic model, with only summary parameters brought together;
- Stable isotopes can be extremely valuable in constraining diet fractions and for validating food web models;
- Size-based (allometric) methods can be used to help estimate/constrain/validate energetics of species (production, consumption, respiration).

Bioregionalisation

Bioregionalisation aims to identify regions of Southern Ocean that are ecologically distinct (Grant *et al.* 2006). These bioregions may be consistent between seasons, consistent between years, show differences in many species/groups together, and have boundaries that are linked to large scale environmental conditions.

Bioregionalisation may be based on environment classification, typically determined as follows:

- Assemble environment data layers;
- Select data layers to use and transform these (e.g. log data);
- Cluster or classify geographic space into bioregions based on minimising differences between environmental properties;
- Display at a decided level.

Environmental data layers used for classification must be circumpolar and taken by consistent methods. E.g. bathymetry, satellite data (Chlorophyll a, sea surface temperature, ice, light, etc), and climatologies of ship data (concentration of nutrients at depth: nitrate, phosphate, silicate). The layers typically represent long-term, average conditions; however layers representing seasonal or interannual variability could be used.

The CCAMLR bioregionalisation workshop (CCAMLR 2007) adopted a primary bioregionalisation of 14 regions, based on 4 environmental variables, at 1/12 degree resolution in latitude and longitude. These agree well with expert opinion, and with historical attempts to define ecologically distinct areas of the Southern Ocean, suggesting they are likely to be robust. It is likely that biological data will be required in a second stage bioregionalisation. This should aim to identify small scale bioregions within each of the primary bioregions.

Three methods may be used to incorporate biological measurements in Southern Ocean bioregionalisation:

- use biological data to retrospectively test how well the environment classification regions discriminate biota;
- cluster regions using environmental data with explicit biological tuning e.g. using methods such as Multivariate Adaptive Regression Splines MARS (Elith & Leathwick 2007), or Generalised Dissimilarity Modelling GDM (Ferrier *et al.* 2007);
- interpolate individual species distributions (e.g. using boosted regression trees, BRT (Leathwick *et al.* 2006) and classify using biological layers directly.

The aim of BRT is to use descriptor variables (here circumpolar environment layers) to explain variance in a target variable (e.g. patchy biological data). Work in New Zealand is underway to test BRT in extrapolating measurements of zooplankton abundance in the upper Southern Ocean using

CPR (continuous plankton recorder) data. A paper will be presented to CCAMLR WG-SAM-08 in St Petersburg, Russia, July 2008 (Pinkerton et al. 2008c), and submitted to a peer reviewed journal.

If the test case of the BRT method applied to CPR data is successful, it may be useful to apply to other Southern Ocean biological datasets, including:

- Macrozooplankton abundance from net haul data, especially krill and salps;
- Pack ice seal abundance, based on a standardised sighting-at-sea methodology;
- Whale abundance based on IWC sighting data;
- Birds, based on tracking measurements;
- Fish - there are considerable amounts of data on Southern Ocean fish distributions available from both scientific and commercial vessels, and typically held by CCAMLR. Efforts will be required to gain access to these data without jeopardising commercial confidentiality (e.g. by reducing the spatial resolution of the data);
- Phytoplankton. Ocean colour satellite data provides regular and quasi-synoptic observation of biology through the Southern Ocean which may be used to test the BRT methodology.

Circulation, Sea Ice and Atmospheric Models

John Klinck and Mike Dinniman, Old Dominion University, Virginia, USA

Southern Ocean oceanographic processes can be represented with a variety of existing numerical models. Sophisticated models exist to represent circulation and water properties in response to surface fluxes of momentum, heat, light and freshwater. The existing circulation models allow a wide variety of ways to represent physical processes, such as advection, or subgrid scale processes, such as turbulence. Supporting information, such as bathymetry and surface forcing, is available to set up and run circulation models for the Southern Ocean. Open boundary conditions remain an issue of concern for regional models, both in terms of formulation and specification of conditions on the boundaries. Moderate, but widely available, computer facilities are required for regional simulations; full Southern Ocean models are possible, but will tax existing computer power in many laboratories.

Biological and ecological processes are included in many circulation models. The details of these formulations are relatively easy to change in most models. Details of how to specify ecological processes in a circulation model remain an active area of research.

Passively drifting particles are included, or are easily added, to most existing models. Biological behaviour, such as vertical migration, has been included in a number of studies. Some models include biological development which represents change in behaviour, size or capability.

Models representing the growth, melt and movement of sea ice are available and have been coupled to some circulation models. These models show some capability in representing the seasonal ice cover for the Southern Ocean. Floating ice shelves drive a vertical circulation due to basal melt and water density changes. These processes have also been added to some Antarctic regional models (Dinniman et al. 2007).

Several challenges remain, these include:

- Biological and ecological processes are a challenge to represent;
- Parameterization and rates for these processes are not well known;

- Incorporating sea ice as a habitat remains a challenge;
- A method for downscaling global climate simulations to regional scale, in particular biogeochemical processes, requires additional development and evaluation.

Ecosystem studies of Sub-Arctic Seas (ESSAS)

George Hunt, University of Washington

The goal of the GLOBEC Regional Program, Ecosystem Studies of Sub-Arctic Seas (ESSAS) is to compare, quantify and predict the impact of climate variability and global change on the productivity and sustainability of Sub-Arctic marine ecosystems (Hunt & Drinkwater 2005). The Sub-Arctic Seas support stocks of commercial fish that generate a major portion of the fish landings of the nations bordering them. They also support subsistence fishers along their coasts, and vast numbers of marine birds and mammals. Climate-forced changes in these systems, interacting with top-down removals by fisheries, will have major economic and societal impacts. Understanding the underlying processes responsible for ecosystem responses to both climate and anthropogenic forcing is the basis for providing good stewardship as these dynamic regions evolve. This task is seen as an end-to-end process that includes developing regional climate predictions, mechanistic prediction of bottom-up forcing from physics to fish, and the interaction with top-down forcing from fisheries removals. A central philosophy of ESSAS is that the use of a comparative approach will facilitate the identification of key processes and vulnerabilities of sub-arctic marine ecosystems to climate change.

To accomplish its goals, ESSAS has formed four working Groups:

- Working Group 1, Working Group on Regional Climate Prediction, has the goal of providing quantitative estimates of the magnitude and uncertainty of future climate change for the ESSAS regions, as well as and the frequency distribution of natural variability. Additionally, once regional climate predictions are developed by selection of the most appropriate IPCC models, additional work is planned to down-scale the regional climate scenarios so that they can be coupled to physical oceanographic models of system response.
- Working Group 2, Working Group on Bio-Physical Coupling, has the goal of determining how climate-driven variability in physical conditions and processes in the ocean will affect the organisms that make up marine ecosystems and thus the transfer of energy and material through sub-arctic marine ecosystems. Physical aspects of the ocean thought to be crucial to ESSAS ecosystems include sea ice cover, ocean temperature, circulation, and stratification.
- Working Group 3, Working Group on Modelling Ecosystem Response has the goal to develop conceptual, mechanistic/process, statistical/empirical, and simulation models to facilitate comparison of ESSAS ecosystems and to forecast the impacts of climate change on ecosystem structure and function in multiple ESSAS ecosystems.
- Working Group 4, Working Group 4 on Gadoid-Crustacean Interactions will assess the effects of ocean climate variation in the context of fisheries exploitation of gadoid fishes and crustaceans and their interactions by comparing their responses across multiple sub-arctic ecosystems.

The approaches of WG 3 are first to compare the results of employing a single model across a number of systems, so that the variation in results will represent difference in the systems compared, rather than difference in the structure of the models employed. It is expected that the first model to be used will be ECOPATH, as it is already running in most of the sub-arctic seas.

Subsequently, it is expected that other models may be employed similarly. Secondly, as a means of exploring what different types of models may reveal about ecosystem structure, it is planned to apply several models to each of several ecosystems.

Individual national programs affiliated with ESSAS are also conducting both major field programs and modelling efforts. It is hoped that through enhanced communication these efforts can be coordinated to enhance progress and reduce duplicative effort. To this end, ESSAS is working in close cooperation with the modelling components in the North Pacific Marine Science Organization (PICES), and it is possible that further collaborations can be developed with ICED and CLIOTOP.

The ESSAS regions may provide instructive comparisons with Antarctic regions, both because of the similarity in basic processes, and because there are remarkable differences in the structure and controlling processes in the two hemispheres. For example, the consequences of differences in circulation patterns, one meridional, the other zonal, are important for the movement of heat, nutrients and plankton within the polar systems and between the polar regions and lower latitudes (see Hunt & Nettleship 1988 for a comparison of high latitude Northern and Southern Hemisphere avian biogeography). These patterns may, at least in part, be responsible for the patterns of species distributions in the two hemispheres, and for the wealth of endemic fish species in the Antarctic with specialized adaptations for dealing with cold. Similar adaptations may be lacking in temperate fish faunas that penetrate the Arctic in warm northward-flowing currents.

In the Bering Sea, the distribution of demersal fish species on the eastern Bering Sea shelf is sensitive to the size and southward extent of the pool of cold bottom water (cold pool, $<2^{\circ}\text{C}$) (Mueter & Litzow In press). Over the shelf, the water column is well mixed to the bottom in winter, with temperatures as low as -1.7°C , which affect the distributions of demersal groundfish. If bottom temperatures on the shelves in the Antarctic are mostly warmer, particularly where Antarctic Circumpolar Deep Water comes up on the narrow deep shelves of the peninsula region, conditions for fish may be more moderate than in the sub-polar seas of the Arctic. These sorts of comparisons may help to define how large-scale circulation patterns influence regional marine ecosystem structure.

Seasonal sea ice cover is a defining characteristic of the eastern Bering Sea shelf. Evidence suggests that the timing of ice retreat in spring has an important impact on the timing of the spring bloom and its fate (Hunt *et al.* 2002). Early, ice-associated blooms occur in cold water, and late, open-water blooms in relatively warm water. Early blooms have been hypothesized to result in a large portion of the production going to the benthos, whereas late blooms supply more energy to the pelagic system (Mueter *et al.* 2006).

The timing of the bloom also affects the types of copepods that will predominate. In 1999, a cold year, sea ice was present in the southeastern Bering Sea until late May, there was an early bloom, and “large” crustacean zooplankton including *Calanus marshallae* and *Thysanoessa raschii* were abundant the following summer. In contrast, 2004 was a warm year in which sea ice retreated in early March, and small shelf species dominated the summer mesozooplankton. Evidence is accumulating that *C. marshallae* requires an early bloom to feed on if it is to recruit from the nauplius stage to the first copepodite stage (Baier & Napp 2003). Simple switch mechanisms of this sort need to be built into mechanistic models, as the species-specific differences in a need for ice or a tolerance of shifts in timing of event may determine not only the size spectrum of zooplankton prey available to higher trophic levels, but whether the energy is shunted primarily to the benthos or the pelagic (Litzow & Ciannelli 2007). The differences in the sizes of copepods available on the shelf were reflected in the diets and condition of age-0 walleye pollock in 1999 and 2004 (Coyle *et al.* In Press). The lack of large zooplankton in Middle Shelf Domain waters in summer can be expected to

affect the distribution, and possibly growth, of planktivorous groundfish, such as walleye pollock (*Theragra chalcogramma*). These differences in the structure of the crustacean zooplankton community are exacerbated when there is strong summer stratification of the middle shelf region with mixing of nutrients from beneath the pycnocline suppressed. Then production is primarily based on regenerated nitrogen, and small species predominate in both the phytoplankton and the zooplankton. There are also differences in the productivity of planktivorous and piscivorous seabirds that suggest that ice cover affects the availability of these classes of prey (Hunt *et al.* In Press).

As sea seasonal ice cover is lost with global warming, there may be a major change in the structure and function of the southeastern Bering Sea ecosystem (Litzow & Ciannelli 2007). It will be instructive to use comparisons between regions to learn more about the mechanisms that will be most sensitive to climate change and how the impacts of these changes will move through the different marine ecosystems of the sub-polar regions.

APECOSM (Apex Predators ECOSystem Model): a climate driven, physiologically-structured model of ecosystem dynamics

Olivier Maury, Institut de Recherche pour le Développement, France

This talk gave an overview of the ecosystem model APECOSM (Apex Predators ECOSystem Model, Maury, 2007) which is developing within the framework of the GLOBEC-CLIO TOP Modelling and Synthesis Working Group. APECOSM uses a process based mechanistic approach, where parameterizations are derived mechanistically and are biologically, physiologically or behaviourally meaningful constants; to represent the joint effects of environmental variability and fishing on the structure and dynamics of pelagic ecosystems. The flow of energy through the ecosystem is modelled with a size-resolved mass-conservative structure in both space and time. The uptake and use of energy for growth, maintenance and reproduction by the organisms are modelled according to the DEB (dynamic energy budget) theory (Kooijman 2000) and the size-structured nature of predation is explicit. APECOSM uses a 'rhomboid' type approach as a practical way to obtain a simultaneous and interactive representation of both the non target organisms (components called OOPC for Open Ocean Pelagic Communities) and the focus species (four tuna species at present) while keeping the functional complexity limited. OOPC is divided into epipelagic and mesopelagic groups, the latter being subdivided into vertically migrant and non-migrant species. Structuring those three communities into functional groups allows alternative trophic pathways to emerge without being specified a priori. Focus species (tunas) are "extracted" from the global OOPC size-spectra without losing mass balance, and represented with more physiological and behavioural details (integrating behavioural processes acting on a variety of scales). Physical forcings (temperature and current), biogeochemical forcings (primary and secondary production, light and oxygen fields) as well as the effects of fishing are explicitly taken into account and constrain the dynamics at various levels.

Uncertainty in ecosystem models

Simeon Hill, British Antarctic Survey, Cambridge, UK

Despite rapid advances in our understanding of ecosystems, there is a lot that remains unknown. Furthermore, because models make assumptions and simplifications, it is inevitable that no model will capture the true behaviour of a real system. Methods for dealing with uncertainties in parameter estimates are generally well developed, whereas methods for dealing with uncertainties in model structure are not. Nonetheless many applications of ecological models, especially those

that make use of model-based predictions, would benefit from an evaluation of these structural uncertainties. Such evaluation must consider the results of several alternative model structures which, between them, attempt to capture the diversity of plausible hypotheses about the structure and operation of the real system. Ideally, such alternatives could be assigned weights representing their relative plausibility, and used as random variables in multiple stochastic simulations. Current approaches tend to produce the unweighted average of an ensemble of models, or an indication of the range of results. The probability distribution of potential results is likely to be more complex than either of these two approaches indicates. The alternative models used to consider structural uncertainties tend to be assembled from those that are available, and are therefore unlikely to represent the range of plausible model structures. It is appropriate to determine which alternative hypotheses should be considered in the early stages of a project. It is also important to develop more formal and rigorous approaches to structural uncertainty.

Main discussion points

- “All models are wrong. Some models are useful.” As a modelling community we should aim to develop models that provide insights, understanding or useful predictions about an ecosystem, rather than aiming for ever-increasing model complexity. More complex models are not necessarily more accurate or more useful than simpler models;
- We should also acknowledge that our capacity for prediction of ecosystem dynamics is fundamentally limited. It is important to establish management methods that are robust to inaccurate predictions of ecosystem dynamics e.g. by using feedback management systems, monitoring and precautionary behaviour.

Biogeochemistry in the Southern Ocean - Lower trophic level models

Dieter Wolf-Gladrow, Alfred Wegener Institute, Bremerhaven, Germany

This presentation was incorporated into discussion group 3 (see above). In summary, simulation of biogeochemistry in the Southern Ocean is largely motivated by changes in global climate occurring now or in the past, such as glacials and interglacials. Some of the big questions are:

- What is the role of SO ecosystems in the climate system?
- What is the contribution of Southern Ocean ecosystems to the uptake of anthropogenic CO₂?
- How much DMS is emitted by the Southern Ocean?
- What are the impacts of and feedbacks of the Southern Ocean to global change?
- Can we lower atmospheric CO₂ by iron fertilization?

Scientists try to answer these and other questions using simple but appropriate models. The emphasis is usually on primary production; zooplankton is included in order to provide a non-linear loss term for phytoplankton, and higher trophic levels are neglected. There is scope for increasing the detail in the zooplankton groups, for example, to differentiate on the basis size or function or to include seasonal patterns. Animals with behaviour (especially vertical migration) are best simulated in a Lagrangian way (trajectories; in contrast to the Eulerian approach for tracers). In theory, this type of model could be adapted to accommodate size-structured models of the higher food web.

Existing models have not performed well in replicating observed plankton communities, and it has often proved difficult to define appropriate parameter values from the literature. Validation is also an issue. However, the priority areas for future data collection and model development are

reasonably clear. More iron measurements (including speciation) are most important for the development of improved models and better data on phytoplankton assemblages are needed to validate models.

Therefore, although the development of more complex models is feasible, the performance of existing models must also be addressed. The inclusion of more organism groups or species requires a better understanding of regulation mechanisms which might be partially addressed through simulation, but will require extensive validation data. The results of the simulations (for example, phytoplankton biomass) may be used as input to models for higher trophic levels. Representing bottom-up control is technically more tractable than two-way coupling.

Main discussion points

- The potential for compounding errors was raised as an issue;
- Consider the impacts of biology on the physics of the system;
- The potential for biology to feedback into the system (e.g. iron recycling through the food web (Tovar-Sanchez et al. 2007), DMS, etc);
- Coupling between systems: is it possible to use biogeochemical models directly as input into food web models? Can they be structured such that they can be relevant to higher trophic levels?
- Note that different feedbacks become important depending on the time-scale and resolution;
- There is a need to consider differences in community structure, bloom timing/size, etc.
- There is a need to consider the physiology of phytoplankton in the models;
- We require an increased understanding of the role of the mesopelagic zone (seasonal, interannual etc.). We need to ensure strong links with the mesopelagic zone within these models. *The key point is that we need to be aware of the necessity of understanding and linking the many different components together (a key focus of IMBER);*
- How do you represent finer-scale detail at broader levels? i.e. in moving towards increasingly resolved biological systems, at some point we will have to return to less detail in order to apply detailed results into coarser scale models;
- Testing models: how well do the model outputs perform against reality e.g. estimates of primary productivity compared to satellites? We need to come up with specific hypotheses, test these in the field and test them in models;
- Long-term ecosystem effects: long-term disturbance effects and how these may impact biogeochemical processes and be accounted for in the models e.g. the effect of removal of large predators? Fisheries effects versus natural effects?

Appendix IV. ICED Modelling Workshop discussion groups

Wednesday (Day 1) Discussion Groups - Modelling Southern Ocean food webs: clarifying major issues/questions and consideration of food web structures and dynamics

Discussion Group 1: Major issues/questions in Southern Ocean ecosystems

Chair: Eileen Hofmann/Rapporteur: Phil Trathan

Goal: To discuss the major issues relating to Southern Ocean food webs and come up with a list of key questions that food web models should address

1. Why do we need to study Southern Ocean food webs?
2. What are the important issues/questions relating to Southern Ocean food webs? E.g.:
 - What is the role of physical and climate-related change (regional and hemisphere scale)?
 - What is the role of biogeochemistry?
 - What are the impacts of historical and modern fisheries?
 - What are the implications for fisheries/resource management?
3. What exactly do we need to understand about Southern Ocean food webs in order to address these major questions? E.g.:
 - We need to understand the structures of food webs in different regions of the Southern Ocean
 - Key species/pathways
 - We need to understand the controls and feedbacks on the structure and dynamics of Southern Ocean food webs
 - Role of seasonal, annual and long-term physical variation
 - Biological controls
 - Biogeochemical controls
4. Any other issues

Discussion Group 2: Southern Ocean food webs

Chair: Dan Costa/Rapporteur: Kendra Daly

Goal: To review current knowledge of the structure of Southern Ocean food webs, discuss controls and feedbacks on their structure and dynamics, and to identify any gaps in data that need to be filled

1. What are the structures of food webs in different regions of the Southern Ocean?
 - Key species, interactions and pathways
 - Distribution, abundance and biomass
2. What are the major (physical, chemical and biological) controls and feedbacks on the structure and dynamics of Southern Ocean food webs, E.g.:
 - Iron versus light limitation
 - Impact of grazing on primary production
 - Alternative trophic pathways
 - Role of top predators
 - Seasonal, annual, and long-term physical variation
3. To what extent can the regionally different food web systems (e.g. those in the Ross Sea, western Antarctic Peninsula, Scotia Sea, East Antarctic) be represented by a generic food web model?
4. What data are missing?
 - Spatial/temporal data

- Species data
5. Any other issues

Thursday (Day 2) Breakout Groups - *Modelling approaches: discussing options and identifying the way(s) forward*

Discussion Group 3: Developing mechanistic models of Southern Ocean ecosystems

Chair: Andrew Constable/Rapporteur: Simeon Hill

Goal: To discuss the development of detailed simulation/predictive models for key components/regional ecosystems in the Southern Ocean

Noting questions raised on Day 1. Could include consideration of:

1. Modelling the life cycles of key species
2. Modelling food webs – issues and data requirements
3. Models for ecosystems in key regions of the Southern Ocean
4. End-to-end models – value and challenges
5. Status of physical models for different scales
 - a. Ocean and sea-ice
 - b. Local, regional and circumpolar
 - c. Seasonality and interannual variability
6. Status of biogeochemical models for different scales
 - a. Trophic structure
 - b. Local, regional, circumpolar, global
 - c. Seasonality and interannual variability
7. Issues - linking physical and biological models
8. Issues - linking models of different biological processes/scale
9. Distinguishing best models - issues of structural variation, testing, validation and data
10. Including/parameterising sub-grid scale and large scale processes/drivers
11. Using broad scale models to define regional boundary conditions in ecosystem models.
12. Testing scenarios of change in ecosystem studies – dealing with uncertainty
13. Empirical models and use for dynamic model testing

Discussion Group 4: Developing generalised models of Southern Ocean food webs

Chair: Olivier Maury/Rapporteur: Eileen Hofmann

Goal: To discuss the potential for generalised modelling of Southern Ocean food webs.

Noting questions raised on Day 1. Could include consideration of:

1. Developing conceptual models of Southern Ocean ecosystems – issues in analyses of ecosystems – key properties of ecosystems
2. Generic models of ecosystems – potential for Southern Oceans
3. Importance of alternative pathways in food webs
4. Issues of overall structure and importance in determining response to change – stability of ecological systems
5. Feedback effects in ecosystems
6. End-to-end models – value and challenges
7. Testing scenarios of change in ecosystem studies – determining general outcomes
8. Variability and change – implications for ecosystems structure

Appendix V. Workshop participants

NAME	AREA of EXPERTISE
Julian Ashford, Old Dominion University, USA	Functioning of complex fish populations in oceanic systems; specifically how advection and physical forcing can structure these in space and time. Patagonian toothfish and ACC. Antarctic toothfish and Scotia Sea icefish. Biogeochemical response variables using the chemistry of otoliths
Rachel Cavanagh, British Antarctic Survey	ICED Programme Coordinator/Marine ecologist. Main focus is on integrating Southern Ocean and international ecosystem research towards a more coordinated approach to data collection, analyses and predictions through models.
Erik Chapman, Old Dominion University, USA	Ecological modeller. Higher trophic level.
Andrew Constable, Australian Antarctic Division and Antarctic Climate and Ecosystems Cooperative Research Centre	Mathematical and statistical ecological modelling. Developing platforms (EPOC and others) for erecting population, food web and ecosystem models. Current emphasis; developing Southern Ocean food web and ecosystem models to examine effects of climate change on ecosystems (Antarctic Climate and Ecosystems Cooperative Research Centre) and for evaluating management strategies for krill, toothfish and icefish fisheries (SC-CAMLR and its working groups) and conservation strategies for whales (SC-IWC). Outputs include consideration of krill and krill predator dynamics in CCAMLR Area 48 in relation to physical (ocean and ice) drivers. Convenor of SC-CAMLR Working Group on Statistics, Assessments and Modelling, and co-convenor of CCAMLR-IWC Workshop to review input data for Antarctic marine ecosystem models.
Dan Costa, University of California Santa Cruz	North Eastern Pacific Ocean, Southern Ocean especially WAP. Top predators: birds and mammals, energetics, foraging ecology Use of animals to sense the ocean environment. Some experience with stable isotopes as tracers of trophic relationships
Kendra Daly, University South Florida	Zooplankton ecologist. Scotia Sea, Weddell Sea, Antarctic Peninsula, and Ross Sea as part of BIOMASS (FIBEX & SIBEX), Krill Super Swarm, AMERIEZ, AMLR, WOCE/JGOFS, APIS, and GLOBEC programs.
Mike Dinniman, Old Dominion University, USA	Regional modelling of circulation, sea-ice and under ice shelf conditions for various areas (specifically Ross Sea and Antarctic Peninsula) close to Antarctica. I haven't really done any ecosystem modelling, other than some extremely simplistic nutrient uptake modelling in the Ross Sea.
Scott Doney, Woods Hole Oceanographic Institution, USA	Global focus, contrasting large-scale physical and chemical (e.g. iron, macronutrients, etc.) factors controlling ecosystem rates and structure. Modelling background on biogeochemical cycles, physics and primary producers. Work with Community Climate System Model and now with Palmer LTER
Bettina Fach, Middle East Technical University, Turkey	Krill modelling (IBM, population). Developed a biochemical krill model - how food quality influences krill growth and survival. Western Antarctic Peninsula/South Georgia region as well as Lazarev Sea. Transport of krill in different areas and how environmental conditions influence survival during transport (includes experience with large circulation and NPZ-models). Involved in SO GLOBEC and LAKRis programmes.
Simeon Hill, British Antarctic Survey	Primary interest: Fishery-ecosystem interactions; Geographical focus: South Georgia/Scotia Sea; Trophic focus: Krill, fish, mammals, birds; Modelling experience: Development of individual based and interacting population models; Collaborations: The BAS DISCOVERY 2010 programme and

	CCAMLR's WG-EMM
Eileen Hofmann, Old Dominion University, USA	Physical Oceanography Coupled physical-biological models. Research interests cover a variety of topics, ranging from mathematical modelling of marine ecosystems to descriptive physical oceanography. A main area of research involves the development of data assimilative models for investigating circulation and biological processes in coastal marine systems. The overall goal of this research is to develop a predictive capability for biological distributions in marine environments.
George Hunt, University of Washington, USA	Marine birds in the Bering, Barents seas, the north water polynya and in the Southern Ocean. Also worked in the Bering building conceptual models of the role of sea ice and its effects on energy transfer through the ecosystem.
Nadine Johnston, British Antarctic Survey	Marine Ecologist - focusing on the impacts of climate and fisheries and krill-alternative energy transfer pathways in the Scotia Sea ecosystem
John Klinck, Old Dominion University, USA	Physical Oceanography: analytical and numerical modelling of biological and physical processes in the ocean. Dynamics of a variety of oceanographic systems including the continental shelf, fjords, submarine canyons, and the Antarctic Circumpolar Current, using both analytical and numerical dynamical models. Other projects include a study of hydrography and circulation of the Antarctic Peninsula and study of circulation and krill drift in the Scotia Sea.
Olivier Maury, Institut de Recherche pour le Développement, France	Ecosystem modeller. I'm developing mechanistic numerical models of oceanic pelagic ecosystems (eg: APECOSM - running at the global scale) with a particular focus on top predator species. Including physiology using the DEB theory and behaviour into ecosystem models. Also using state-space approaches and statistical modelling for parameter estimation purpose. Involved in the CLIOTOP modelling WG.
Peter Milne, National Science Foundation, USA	NSF representative
Eugene Murphy, British Antarctic Survey	Ecological modeller, main interests are in general operation of Southern Ocean ecosystems and krill ecology.
Evgeny Pakhomov, University of British Columbia, Canada	Biological oceanographer. Wide range of interests covering epi and mesopelagic zooplankton and micronekton. Prydz Bay, Cosmonaut Sea, Lazarev Sea, Prince Edward Islands (subAntarctic). Major interest in the Lazarev Sea included research on the tunicate (<i>Salpa thompsoni</i>) ecology and research towards the elucidation of the epi and mesopelagic food web structure using stable isotopes. Currently working in close collaboration with two German groups (AWI U. Bathmann and C. Dubischar; Sea Fisheries Institute V. Siegel) and BAS group (A. Atkinson).
Andrea Pinones, Old Dominion University, USA	West Antarctic Peninsula - how physical processes such as ocean circulation, sea-ice dynamics, water masses properties may influence biological processes and the coastal ecosystem. Using a circulation model for the WAP as a tool to understand cross-shelf exchange and intrusions of Circumpolar Deep Water toward the shelf. What circulation dynamics may be responsible for the across-shelf exchange? At what extent these processes are controlling primary production on the continental shelf?

Matt Pinkerton, National Institute of Water and Atmospheric Research, New Zealand	Satellite ocean remote sensing, especially ocean colour remote sensing. Ecosystem modelling, including (1) whole ecosystem mass balance models; (2) age-structured population models; (3) coupled upper-ocean ecosystem dynamical models. Models developed/under development include trophic models for the whole Ross Sea, McMurdo Sound, Terra Nova Bay, New Zealand coastal (rocky-reef) ecosystem, New Zealand open ocean (Chatham Rise). Bioregionalisation and environment classification, including use of statistical techniques for extrapolation of biological data such as Continuous Plankton Recorder. Member of CCAMLR Ecosystem Monitoring and Management Working Group, and attendee of two "Bioregionalisation of Southern Ocean" workshops.
Steve Reilly, National Oceanic and Atmospheric Administration, USA	Cetacean population ecology; cetacean - habitat linkages; foraging ecology of baleen whales. Led IWC part of CCAMLR/IWC collaboration during the 2000 synoptic survey of the South Atlantic sector of the SO.
Cosimo Solidoro, University of Trieste, Italy	Ecological modelling: numerical analysis and modelling of aquatic ecosystems, with emphasis on coastal area (lagoon of Venice and Adriatic Sea) and Mediterranean Sea. Research interests include coupled transport biogeochemical models, food web models, bioeconomic models, sensitivity analysis and data assimilation.
John Steele, Woods Hole Oceanographic Institution, USA	Mainly North Atlantic shelf ecosystems: North Sea, Georges Bank. My work area, at one time, was 58-600 N. In 1981, I chaired an "Evaluation of Antarctic Marine Ecosystem Research" for the US NAS/NRC). My modelling experience has involved NPZ models and end-to-end food web budgets
Sally Thorpe, British Antarctic Survey	Scotia Sea and circumpolar models of Antarctic krill population dynamics, particularly physical connections between populations. Lagrangian and Eulerian models including ocean and sea ice processes. Up until now, focus has been on using ocean current data from the OCCAM model run by National Oceanography Centre, Southampton and satellite-derived sea ice motion data.
Phil Trathan, British Antarctic Survey	Scotia Sea region; predators (abundance, distribution, diets, breeding performance, foraging ecology, environmental interactions); CCAMLR; empirical ecologist.
John Wiedenmann, University of California Santa Cruz	Modelling potential impacts of climate change on Antarctic krill, and the subsequent effects that any changes in krill may have on the rorquals. To date, I have modelled the impacts that a warming Southern Ocean may have on krill growth, and how a decline in sea ice coverage may impact recruitment, and therefore biomass. The models I have worked with are single-species population models, primarily those used for fisheries assessment and rebuilding.
Dieter Wolf- Gladrow, Alfred Wegener Institute, Germany	Modelling of biogeochemistry in the Southern Ocean using an ecosystem model coupled to a global general circulation model; response of plankton to iron fertilization; grazing rates by microzooplankton; model of the seasonal variation of krill composition; pteropods and ocean acidification

Invited but unable to attend:

Uli Bathmann, Mark Mangel, Mike Meredith, Steve Nicol, Keith Reid, Walker Smith and George Watters.

Appendix VI. Glossary of terms

Scientific/modelling terms	
ACC	Antarctic Circumpolar Current
APECOSM model	Apex Predators ECOSystem Model
APF	Antarctic Polar Front
BGCM	Biogeochemical models
BRIOS model	Bremerhaven Regional Ice Ocean Simulations
BRT	Boosted Regression Trees
CC	Carrying capacity
CICE	Sea ice model: Community Ice Code
CPR	Continuous Plankton Recorder
DIC	Dissolved Inorganic Carbon
DMS	Dimethyl sulfide
DMSP	Dimethylsulphoniopropionate
Ecopath with Ecosim (EwE)	Approach and software for construction and analysis of mass-balance models and feeding interactions/nutrient flow in ecosystems
ENSO	El Niño-Southern Oscillation
EPOC model	Ecosystem, productivity, ocean, climate modelling framework
FESOM model	Finite Element Southern Ocean Model
Foosa (KPFM) model	Krill predator fishery forecasting and risk assessment model
GDM	Generalised Dissimilarity Modelling
HNHC	High–nutrient, high–chlorophyll
HNLC	High–nutrient low–chlorophyll
MARS	Multivariate Adaptive Regression Splines
NPZD model	Nutrients, Phytoplankton, Zooplankton and Detritus
OCCAM	Ocean Circulation and Climate Advanced Modelling Project
OGCM	Ocean General Circulation Models
PFT	Phytoplankton functional types
RMP	Revised Management Procedure
SAF	Subantarctic Front
SAM	Southern Annular Mode
SeaWiFS	Sea-viewing Wide Field-of-view Sensor Project
SMOM model	Spatial Multi-species Operating Model
SST	Sea Surface Temperature
STC	Sub Tropical Convergence
SWAMCO-4	A model of the marine planktonic system calculating C, N, P, Si, Fe cycling within the upper ocean, the export production and the exchange of CO ₂ between the ocean and atmosphere.

Project/Programme/Organisation abbreviations	
AAD	Australian Antarctic Division
ACE	Antarctic Climate and Ecosystems Cooperative Research Centre
AMERIEZ	Antarctic Marine Ecosystem Research at the Ice Edge Zone
APIS	Antarctic Pack Ice Seals
AWI	Alfred Wegener Institute, Germany
BAS	British Antarctic Survey, UK

BIOMASS	Biological Investigation of Marine Antarctic Species and Stocks
CCAMLR	Commission for the Conservation of Antarctic Marine Living Resources
CCAMLR-WG-EMM	Commission for the Conservation of Antarctic Marine Living Resources Working Group on Ecosystem Monitoring and Management
CLIOTOP	CLimate Impacts on Oceanic TOP Predators
ESSAS	Ecosystem Studies of Sub-Arctic Seas
EUR-OCEANS	European Network of Excellence for Ocean Ecosystems Analysis
EUR-OCEANS Consortium	Set up to ensure the continuity and further integration of Member Organisations that were involved in EUR-OCEANS (see above)
FAO	Food and Agriculture Organization of the United Nations
FIBEX	First International Biomass Experiment
GLOBEC	Global Ocean Ecosystem Dynamics
ICED	Integrating Climate and Ecosystem Dynamics in the Southern Ocean
IGBP	International Geosphere-Biosphere Program
IMBER	Integrated Marine Biogeochemistry and Ecosystem Research
IPCC	Intergovernmental Panel on Climate Change
IPY	International Polar Year
IWC	International Whaling Commission
IWC SOWER	International Whaling Commission's Southern Ocean Whale and Ecosystem Research (SOWER) programme
JGOFS	Joint Global Ocean Flux Study
LAKRis	LAzarev Sea KRill Study
NAS	National Academy of Sciences (US)
NERC	Natural Environment Research Council (UK)
NIWA	National Institute of Water & Atmospheric Research (New Zealand)
NRC	National Research Council (US)
NSF	National Science Foundation (US)
ODU/CCPO	Old Dominion University/Center for Coastal Physical Oceanography
Palmer LTER	Palmer Long Term Ecological Research
PICES	North Pacific Marine Science Organization
POLCOMS	The Proudman Oceanographic Laboratory Coastal-Ocean Modelling System
SCAR	Scientific Committee on Antarctic Research
SCAR-MarBIN	Linking, Integrating and Disseminating Marine Biodiversity Information
SC-CAMLR	Scientific Committee for the Conservation of Antarctic Marine Living Resources
SCOR	Scientific Committee on Oceanic Research
SEaOS	Southern Elephant Seals as Oceanographic Samplers
SIBEX	Second International BIOMASS Experiment
SO GLOBEC	Southern Ocean Global Ocean Ecosystem Dynamics
SOOS	Southern Ocean Observing System
TOPP	Tagging of Pacific Predators
UBC	University of British Columbia (Canada)
UCT	University of CapeTown (South Africa)
UEA	University of East Anglia (UK)
US AMLR	US Antarctic Marine Living Resources program
WOCE	World Ocean Circulation Experiment

