9-2012

Developing Integrated Models of Southern Ocean Food Webs: Including Ecological Complexity, Accounting for Uncertainty and the Importance of Scale

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Original Publication Citation

Murphy, E.J., Cavanagh, R.D., Hofmann, E.E., Hill, S.L., Constable, A.J., Costa, D.P., . . . Doney, S.C. (2012). Developing integrated models of southern ocean food webs: Including ecological complexity, accounting for uncertainty and the importance of scale. *Progress in Oceanography*, 102, 74-92. doi: 10.1016/j.pocean.2012.03.006

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Progress in Oceanography 102 (2012) 74–92

Contents lists available at SciVerse ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Developing integrated models of Southern Ocean food webs: Including ecological complexity, accounting for uncertainty and the importance of scale

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ARTICLE INFO

Article history:
Available online 17 April 2012

ABSTRACT

The Southern Ocean supports diverse and unique ecosystems that have been impacted by more than two centuries of exploitation and are now experiencing rapid changes in ocean temperature and seasonal ice cover due to climate warming. Understanding and projecting responses of Southern Ocean marine ecosystems to changing climate conditions and direct human impacts, such as fisheries, requires integrated ecosystem analyses at scales previously unexplored. Here we consider the main ecological and modelling challenges in predicting the responses of Southern Ocean ecosystems to change, and propose three interlinked focus areas that will advance the development of integrated models for Southern Ocean ecosystems. The first focus area is development of fundamental understanding of the factors that determine the structure and function of the food webs at multiple scales. Ecological research in the Southern Ocean is often centred on key species or localised systems, a tendency which is reflected in existing food web and ecosystem models. To build on this, a systematic analysis of regional food web structure and function is required. The second focus area is development of a range of mechanistic models that vary in their resolution of ecological processes, and consider links across physical scales, biogeochemical cycles and feedbacks, and the central role of zooplankton. These two focus areas underlie the third, which is development of methodologies for scenario testing across a range of trophic levels of the effects of past and future changes, which will facilitate consideration of the underlying complexity of interactions and the associated uncertainty. The complex nature of interactions determining Southern Ocean ecosystem structure and function will require new approaches, which we propose should be developed within a scale-based framework that emphasises both physical and ecological aspects.

1. Introduction

The Antarctic marine ecosystem is a critical component of the Earth System. This unique ecosystem influences nutrient distributions and production dynamics across the global ocean (Sarmiento et al., 2007; Marinov et al., 2008; Gruber et al., 2009; Pollard et al., 2009) and has an important role in sequestration of atmospheric carbon in the deep ocean, thereby influencing future atmospheric carbon concentrations (Le Quere et al., 2007). Many species are endemic to the Antarctic, biomass of some can be large, and within-site diversity can be as high as anywhere in the world (Clarke and Crame, 1992; Clarke and Johnston, 2003). The Antarctic marine ecosystem also supports commercial finfish and zooplankton fisheries that provide protein sources for humans via direct consumption and indirectly via use in aquaculture (Constable, 2002).

The Southern Ocean is connected at the circumpolar scale by the prevailing circulation and is strongly influenced by seasonal sea ice advance and retreat (Fig. 1a and b). Chlorophyll concentrations are regionally variable (Fig. 1c) and the Southern Ocean is known for the regionally abundant Antarctic krill (*Euphausia superba*) (Fig. 1d); a species of considerable productivity and an important food item for many of the air-breathing predators (Everson, 1977, 1984; Croxall et al., 1984, 1985). Indeed, Southern Ocean food webs are often described in terms of a relatively short trophic pathway transferring primary production to top predators via krill

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0079-6611/$ - see front matter
http://dx.doi.org/10.1016/j.pocean.2012.03.006

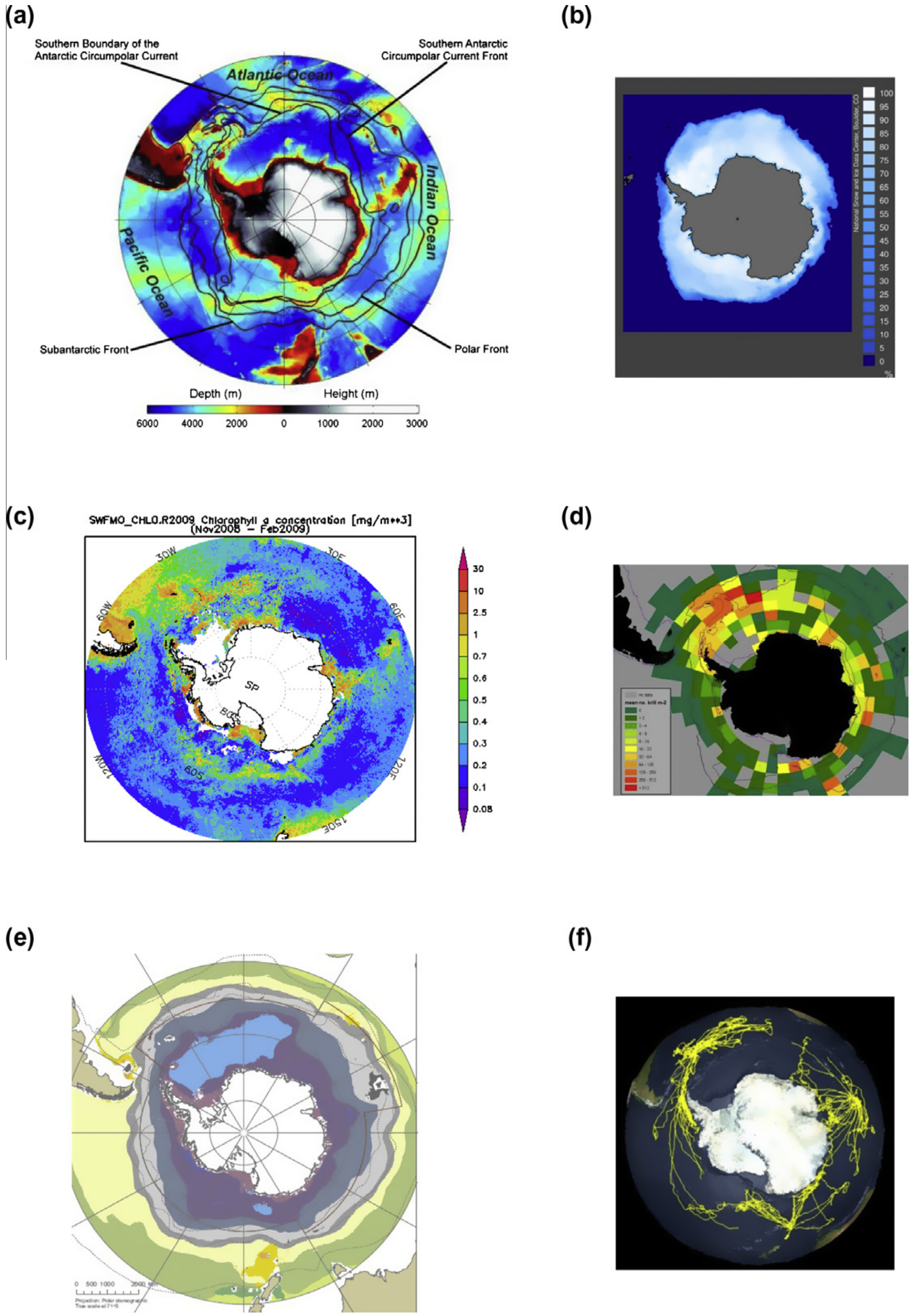

Fig. 1. Maps illustrating major circumpolar distribution features of selected physical, biological and derived variables of Southern Ocean ecosystems. (a) Circumpolar map showing the topography of the Southern Ocean region with the positions of the major ocean fronts of the ACC. (Modified after Orsi et al., 1995). (b) Circumpolar map of sea ice concentration during September 2010. Provided by the National Snow and Ice Data Centre (Fetterer et al., 2002; updated 2009). (c) SeaWiFS composite image of chlorophyll a concentration for the period from November 2008 to February 2009. Image produced with the Giovanni online data system, developed and maintained by the NASA GES DISC. (d) Circumpolar distribution of the mean density of postlarval Antarctic krill (*Euphausia superba*) in summer. This plot is based on a historical compilation of available net sample data for 1926–2004, standardised to a common sampling method (modified from Atkinson et al., 2004). (e) 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; from Grant et al., 2006). (f) 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) with permission from M. Fedak. See references for details of individual figures.

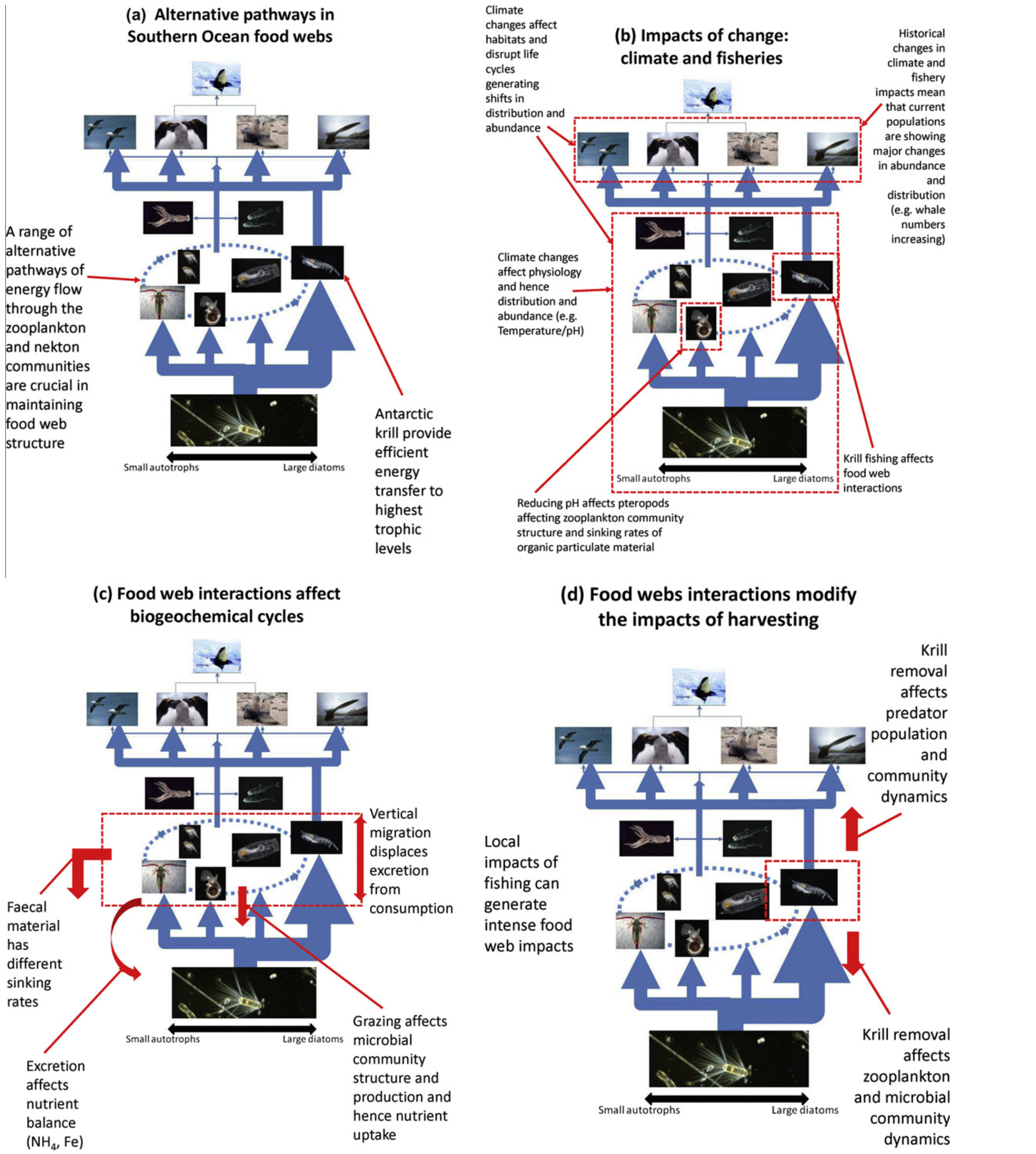

Fig. 2. Different aspects of food web structure and function are important in determining responses to change. (a) Alternative pathways of energy flow affect overall structure, function and resilience. (b) Climate change and fisheries affect different components of the food web generating interactive impacts. (c) Food web processes can affect plankton dynamics, biogeochemical processes and vertical export. (d) Harvesting impacts are modified by food web processes.

(Laws, 1984) (Fig. 2a). Increasingly, however, it is recognised that such simple views do not apply over much of the region (Ducklow et al., 2007; Murphy et al., 2007b, 2008; Smith et al., 2007; Pinkerton et al., 2010; Nicol and Raymond, 2012).

During the last few decades rapid changes have occurred across the high latitude regions of the Southern Hemisphere that have affected oceanic and cryospheric conditions (Parkinson, 2002; King et al., 2004; Meredith and King, 2005; Turner et al., 2005). There have also been significant biological changes, including an apparent reduction in the abundance of Antarctic krill in the Atlantic region over the last 30 years (Atkinson et al., 2004; Fig. 1d), and increases and decreases in the abundance of various seabird species (Fraser et al., 1992; Ainley et al., 2003; Fraser and Hofmann, 2003; Clarke et al., 2007; Ducklow et al., 2007; Jenouvrier et al., 2009). Understanding the factors responsible for these biological changes is complicated by the confounding effects of harvesting during the last two centuries, which generated extreme perturbations of Southern Ocean food webs (Murphy, 1995; Everson, 1977;

Ainley and Blight, 2009) (Fig. 2b); the effects of which are still occurring today, together with the impacts of current harvesting (Constable, 2004). Major changes associated with global climate change processes are expected to occur in atmospheric, oceanic and cryospheric conditions which will modify the current regional habitat structure (Fig. 1e) during the next century and ocean acidification may start to generate biologically significant changes in only a few decades (McNeil and Matear, 2008).

Given the critical role of the Southern Ocean ecosystem at a global scale, it is necessary to develop reliable projections of how it will respond to change. Analyses of the impacts on individual species give a degree of insight, however, complex food web interactions influence both species and system level behaviour, affecting system stability and hence resilience to change of the overall ecosystem (Martinez et al., 2006; Neutel et al., 2007; Dunne and Williams, 2009; Romanuk et al., 2009). The composition, or biodiversity, of the Southern Ocean food web is therefore important in determining the response of the system and its individual components to change.

Models that predict how oceanic ecosystems respond to change, and include the influences of food web structure, biogeochemical cycling and harvesting impacts (Fig. 2b–d), are the focus of current global research efforts (Wassmann et al., 2006; Steele et al., 2007b). These models, termed end-to-end models, pose major challenges in linking across areas of science that focus on very different questions (Collie et al., 2009; Fox et al., 2009; Libralato and Solidoro, 2009). However, development of end-to-end system-level ecosystem models is the next logical step for the marine ecological modelling community (Moloney et al., 2011).

Over the last decade integrated analyses of Southern Ocean ecosystems that allow the consideration of end-to-end food web operation have developed to a level that has not been possible for most other oceanic ecosystems (Ducklow et al., 2007; Murphy et al., 2007b, 2008; Smith et al., 2007; Hofmann et al., 2008; Nicol and Raymond, 2012). Detailed reviews of local food web structure are available for the Antarctic Peninsula (Ducklow et al., 2007) with extensive information on key components and interactions (Hofmann et al., 2008, 2011), for the Ross Sea (Smith et al., 2007), Scotia Sea (Murphy et al., 2007b) and East Antarctica (Nicol and Raymond, 2012). Consideration of the impacts of variability and change on regional food web structures have also been discussed for different areas around the Southern Ocean (e.g. Siegel and Loeb, 1995; Loeb et al., 1997, 2009; Murphy et al., 1998, 2007a; Smith et al., 1999, 2007; Fraser and Hofmann, 2003; Quetin and Ross, 2003; Hewitt et al., 2004; Massom et al., 2006; Clarke et al., 2007; Quetin et al., 2007; Meredith et al., 2008; Ross et al., 2008; Constable and Doust, 2009) and development of modelling approaches for analyses of Southern Ocean ecosystems with a particular emphasis on harvesting impacts have been reviewed (Constable, 2005b; Hill et al., 2006). Issues related to linking Southern Ocean ecological understanding with the technical aspects of system analysis and modelling have also been identified (Murphy et al., 2010). Hence, the Southern Ocean scientific community is poised to undertake data synthesis and development of new approaches that will allow integrated analyses of Southern Ocean ecosystems.

The objectives of this paper are to identify the major issues and potential solutions for development of Southern Ocean food web models that have sufficient skill to provide useful predictions of how these systems will respond to variability and change. Knowing what is needed will provide a basis for more focused food web model development, concentrating on taxonomic and food web based data analysis and synthesis. We consider the status of food web modelling, and the development of integrated models of Southern Ocean food webs. Finally, we propose a scale–based framework and identify three key foci to guide Southern Ocean food web research and model development.

2. Modelling Southern Ocean food webs: challenges and requirements

Three major scientific challenges involving Southern Ocean ecosystems have been identified (Murphy et al., 2008), which can be encapsulated under three questions:

1. How do climate processes affect the structure and dynamics of Southern Ocean ecosystems and how will they respond to future change?
2. How does the structure and dynamics of Southern Ocean ecosystems affect biogeochemical cycles in the Southern Ocean?
3. How should the structure and dynamics of Southern Ocean ecosystems be incorporated into management approaches to sustainable exploitation of Southern Ocean species?

These challenges overlap in their central requirement to examine the controls on food web structure and dynamics (Fig. 2). However, they also emphasise different aspects of food webs, requiring a focus on different trophic levels and interactions, and the degree to which wider food web processes are critical. Moreover, the connectivity of Southern Ocean ecosystems provided by the large-scale ocean circulation (Fig. 1a), presents an added circumpolar dimension for models to address these challenges.

Examination of climate driven changes (e.g. in sea ice or chlorophyll distribution) and projecting trophic responses requires consideration of spatial and temporal variability at regional to circumpolar scales (Fig. 1c–f) and seasonal to decadal scales. Similarly, differences in underlying biogeochemistry need to be considered as these affect the production regimes, plankton community composition and dynamics (Fig. 2c). However, the composition of the planktonic and nektonic communities can also affect the biogeochemistry and fate of production in the Southern Ocean (Fig. 2c). The food web structure, and in particular, the composition of the main grazing community, is therefore crucial in determining both the dynamics of the planktonic community and biogeochemical cycling. Many of the important Southern Ocean zooplankton species, such as Antarctic krill, have complex life histories that may be disrupted by climate related changes (Fig. 2b). Thus, examining how meso- and macro-zooplankton community composition affects biogeochemical cycling in Southern Ocean ecosystems is a major challenge and will require understanding of the life cycles and food web interactions of a range of species. The dependencies of the diverse Southern Ocean top predator communities on the zooplankton communities (predator–prey interactions), exploited components of the ecosystem, and climate driven food web variability requires that an ecosystem approach be central to models developed for this system (Fig. 2b and d). The following sections provide descriptions of the current state of model development to address the above challenges, and gives guidance on the next steps in this process.

3. Current views and models of Southern Ocean food webs

3.1. Analyses and models of Southern Ocean food web structure

The first step towards developing predictive ecosystem models is to understand the structure and variability of the relevant food webs. Generic views of Southern Ocean ecosystems tend to be that of a simple system dominated by Antarctic krill that link primary production to higher predators in short, efficient food chains (Everson, 1977; Laws, 1984) (Fig. 2a). However, this is not the case for many regions (or seasons) across the Southern Ocean. The food webs of the Scotia Sea (Murphy et al., 2007b), Antarctic Peninsula (Ducklow et al., 2007) and Ross Sea (Smith et al., 2007) differ in the extent to which they are dominated by Antarctic krill versus other zooplankton such as copepods and ice-krill (*Euphausia crystallorophias*) (Siegel, 2005; Murphy et al., 2007b; Smith et al., 2007; Atkinson et al., 2008; Pinkerton et al., 2010). Understanding of food web 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 (Murphy et al., 2010).

Physical (circulation and sea ice, Fig. 1a and b) and chemical (micro and macro-nutrient supply and cycling) processes influence the structure and productivity of the food web by affecting biological processes such as primary production, zooplankton species development and community structure, krill dispersal dynamics and the spatial dynamics of predator foraging (Fraser and Hofmann, 2003; Massom et al., 2006; Murphy et al., 2007a,b; Trathan et al., 2007; Murphy et al., 2008; Ross et al., 2008) (Fig. 1c–f). As a result, Southern Ocean food webs exhibit considerable spatial and temporal variability. These differences in structure and function lead to a view that the circumpolar Southern Ocean is composed of a connected set of dynamically interacting ecosystems comprised of pelagic, benthic and (in the winter and more coastal areas) sea-ice food webs, operating within regional physical and chemical frameworks.

As mentioned above there have been attempts to describe Southern Ocean food webs, most of which provide qualitative descriptions for sub-systems such as open ocean, coastal and sea-ice areas or particular regions. For some localities quantified analyses of the structure of parts of the food web have been undertaken (Everson, 1977; Ainley et al., 1986, 1991; Hopkins, 1987; Rau et al., 1991; Hopkins et al., 1993a,b; Lancraft et al., 2004; Pinkerton et al., 2010). Few attempts have been made to develop large-scale quantified analyses, with the most comprehensive example generated over three decades ago (Everson, 1977). Recent efforts have produced detailed analysis of regional food webs that are based on mass-balance constraints (Cornejo-Donoso and Antezana, 2008; Pinkerton et al., 2010; Hill et al., 2012; Ballerini et al., submitted for publication). Inverse-model techniques have also been used to provide an integrated understanding of the material flow budgets in the Antarctic Peninsula region (Ducklow et al., 2006). Such models provide a valuable compilation of data, which helps identify key trophic groups and interactions and gaps in understanding and data. The understanding gained from analyses of the regional food webs allows development of a generalised view of Southern Ocean food webs (Fig. 3) that recognises the importance of alternate pathways (e.g. Fig. 4), variability in structure at all trophic levels, and biogeochemical cycling. Moreover, recent work on development of bioregionalisation of the Southern Ocean (Grant et al., 2006) provides large scale generalisations of current habitat structure (Fig. 1e) that in turn provides a context for circumpolar food web analysis by identifying the boundaries, and gaps in the understanding, of regional food webs.

To produce dynamic models of Southern Ocean foods requires a mechanistic view of the functional relationships that determine food web structure and function. The dependence of Southern Ocean food web structure and function on habitat structure (e.g. circulation, seasonality and sea ice) and biogeochemical cycling (e.g. iron availability) requires that mechanistic models for these systems also have links to models that describe these processes. Thus skill and accuracy of dynamic food web models is dependent at some level on the availability and performance of these other models. Here we give an overview of the current status of relevant biogeochemical and biological models for key species from the perspective of building towards more integrated dynamic models of Southern Ocean food webs.

3.2. Biogeochemical models

Biogeochemical models are available for specific regions of the Southern Ocean such as the Polar Front, sub-Antarctic islands and the Ross Sea (e.g. Arrigo et al., 2003; Hense et al., 2003; Popova et al., 2007). Each is focused on different aspects of the biogeochemistry and there is currently no standard Southern Ocean-scale

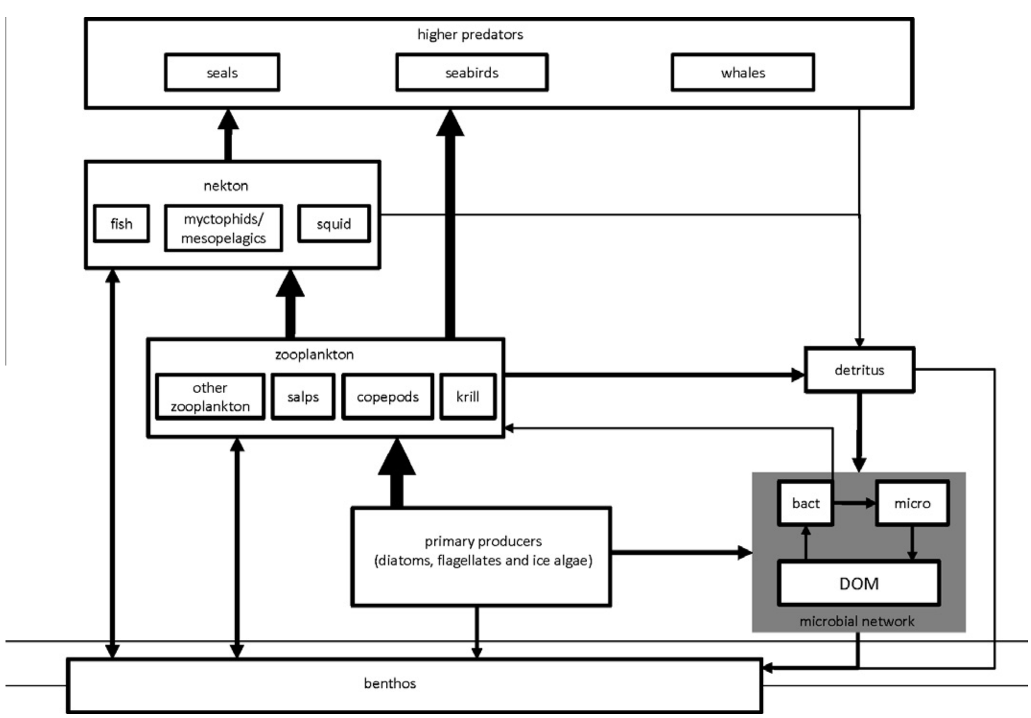

Fig. 3. Schematic illustration of the major components and pathways in the Antarctic marine food web including microbial and benthic links (bact=bacteria, micro=microbial organisms, DOM=dissolved organic matter; Developed from Clarke et al., 2007).

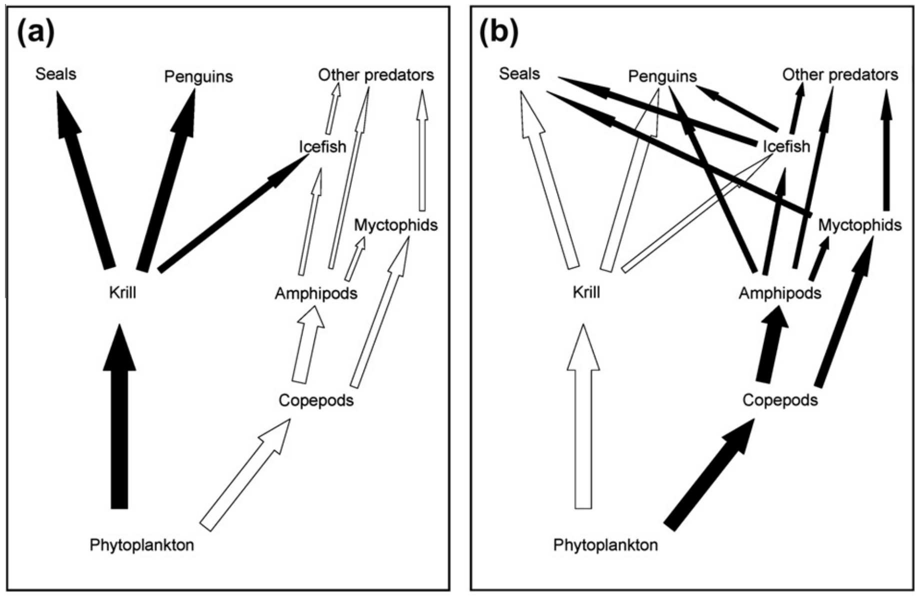

Fig. 4. Illustration of alternative pathways of major energy and material flows in part of the Scotia Sea food web, showing shifts between (a) years when krill are abundant across the Scotia Sea and (b) years when krill are scarce. Major pathways shown as black arrows (from Murphy et al., 2007b).

biogeochemical model. Biogeochemical models have been used to examine carbon dynamics and the importance of nitrogen cycling for the continental shelf off the western Antarctic Peninsula (Walsh et al., 2001; Serebrennikova et al., 2008). Additional biogeochemical models based on the dynamics of sea-ice microbial communities have been developed and applied primarily in the Ross Sea. These models focus on simulation of primary production and the controls on this production in ice and pelagic systems, with particular focus on the role of iron (Arrigo et al., 2003; Tagliabue and Arrigo, 2005). Detailed simulations of pelagic microbial and sea-ice microbial dynamics have also been the focus of a range of studies (Veth et al., 1992; Lancelot et al., 1993, 2000, 2005, 2009; Pasquer et al., 2005).

Global scale models, with a general focus on understanding primary production have been applied in the Southern Ocean but have been limited in terms of both physical (e.g. vertical resolution of mixed layers) and chemical factors (e.g. iron availability and dynamics) affecting production. These lower trophic level models typically include interactions among nutrients, phytoplankton, zooplankton and detritus. They differ in the use of fixed (Franks et al., 1986; Fasham et al., 1990) or variable (Schartau et al., 2007) stoichiometry and in the representation of phytoplankton functional types (e.g. Moore et al., 2002; Aumont et al., 2003; Gregg et al., 2003; Le Quere et al., 2005; Aumont and Bopp, 2006; Gregg and Casey, 2007; Yool et al., 2011). However, there has been little specific consideration of their performance in the Southern Ocean.

The representation of the planktonic food web in the Southern Ocean-specific biogeochemical models is often relatively simplistic with inclusion of zooplankton only as a non-linear loss term for phytoplankton, and no inclusion of higher trophic levels. However, these models were designed to address questions of bottom-up regulation of nutrient and carbon cycling and their structure is consistent with this objective. Methods for linking these bottom-up biogeochemical models to broader food web models are beginning to be developed (Steele, 2009; Steele and Ruzicka, 2011), which will allow current understanding of the importance of the structure of the grazer community on nutrient and carbon cycling in Southern Ocean ecosystems to be explicitly included in these models. For example, the different major macro-zooplankton grazer species in Southern Ocean ecosystems (e.g. krill, salps or copepods) produce faecal material that has different rates of sedimentation affecting vertical carbon flux (Perissinotto and Pakhomov, 1998; Dubischar and Bathmann, 2002; Pakhomov et al., 2002; Schnack-Schiel and Isla, 2005). Although the development of more complex models is feasible, the inclusion of more species or groups requires a better understanding of mechanisms of regulation of production, zooplankton feeding and population dynamics. These can be partially addressed through simulation, but will also require extensive data for model development and validation (Stow et al., 2009). Priority areas for data collection include measurements of micro and macro-nutrient controls on primary production concurrent with measurements of the phytoplankton and grazer community assemblages and associated rates of consumption and export (Murphy et al., 2010). Macro-zooplankton species and other organisms that are larger than the microbial species usually encompassed in biogeochemically based models of plankton dynamics have complex behaviours and life-histories. These complexities generate spatial and temporal differences in interactions in Southern Ocean food webs that affect their structure and function, which requires the development of specific models for key species.

3.3. Models of key species

Krill are an important component of Southern Ocean food webs (Figs. 2 and 3) and considerable effort has been directed into detailed modelling of this species and its ecological interactions. Initial models focused on understanding advection pathways of krill at regional (Scotia Sea, western Antarctic Peninsula) and circumpolar scales as a basis for understanding circulation controls on its distribution (Fig. 1d). These models used Lagrangian (particle tracking) and Eulerian (grid-based advection–diffusion) approaches that were based upon simulated and data-derived circulation and sea ice distributions (Murphy et al., 1998, 2004; Hofmann et al., 1998; Fach et al., 2002; Fach and Klinck, 2006; Thorpe et al., 2007). The addition of details of the embryo-larva ascent-descent cycle, feeding and metabolism, growth and reproduction provides biological realism to the particles tracked in these Lagrangian models (e.g. Hofmann et al., 1992; Hofmann and

Lascara, 2000; Fach et al., 2002, 2006, 2008; Hofmann and Husrevoglu, 2003; Fach and Klinck, 2006; Tarling et al., 2007).

Deterministic and empirical models of krill growth have been generated, which have allowed the large-scale impacts of variation in temperature and food availability to be explored (Murphy et al., 2007b). Modelling of seasonal variation in food type and quality, and krill metabolic strategy provides the ability to test the effect of different diets on krill growth (Fach et al., 2008). Statistical models of the relationship between krill recruitment strength and sea-surface temperature and sea ice parameters have been developed (Murphy and Reid, 2001; Constable et al., 2003; Murphy et al., 2007a,b; Wiedenmann et al., 2009). These have included modelling the effects of temporal and regional temperature variation (around the Antarctic Peninsula and South Georgia) on magnitude and growth of krill cohorts, which have been used to explore the impacts of climate related change (Reid et al., 2002; Atkinson et al., 2006; Tarling et al., 2006; Murphy et al., 2007a).

These various models of krill growth, metabolism and dispersal contribute to the development of coupled physical–biological models of the complete krill life-cycle which are needed to investigate controls on large-scale distribution and abundance of this species and how this may be altered by climate change. These models also provide a strong basis for building species-centric views of food web operation, for example, examining the detailed interactions in food webs involving krill of different life stages and ages. However, krill represent only one of many possible energy pathways in Southern Ocean food webs (Figs. 2 and 3) and there has been much less of a focus on development of models for other zooplankton species (Tarling et al., 2004).

Models have been developed for some components of the upper trophic levels of the food web. Detailed demographic models exist for a number of commercially exploited fish species, such as mackerel icefish (Constable and de la Mare, 1996; Hill et al., 2005), Antarctic toothfish in the Ross Sea (Dunn and Hanchet, 2006; Hanchet et al., 2006) and Patagonian toothfish (Hillary et al., 2006). Demographic models and age-structured models are also available for a range of seabird and marine mammal species (Tuck et al., 2001; Jenouvrier et al., 2003, 2005, 2006, 2009). However, the data available for these models are limited, studies are often highly localised and, in the case of the whales, are based on data more than 30 years old. Demographic models have also been used with diet information to calculate consumption values (Croxall et al., 1984; Boyd, 2002) and to examine the changes in prey demand by species between seasons, but the methods have not been widely applied. A number of statistical and simulation models of predator population responses to prey availability exist for the Southern Ocean (e.g. Constable, 2001, 2005a,b, 2006, 2008, submitted for publication; Forcada et al., 2005, 2006, 2008; Mori and Butterworth, 2006; Constable and Candy, 2008). However, the processes involved in these responses are not well understood.

The role of individual higher predators in Southern Ocean food webs has been studied and operation of the planktonic food web, in terms of functional groups, is relatively well understood. Yet there is no single modelling framework within which these studies have been conducted, and coordination between studies of the planktonic food web and higher trophic levels is rare. Assessing the relative importance of different biological interactions on any particular aspect of food web structure is therefore often difficult. Statistical models of interaction effects focused on key species can provide a useful basis for general understanding of specific interactions within food webs (Barbraud et al., 2008; Forcada et al., 2008; Forcada and Trathan, 2009). There have also been focused modelling studies considering system operation and change based on a small number of interactions (May, 1979; May et al., 1979; Murphy, 1995). Much of the emphasis of dynamic modelling has been on models for management, mainly relating to single species of fish or krill. However, in the context of the ecosystem approach to management (Constable, 2001, 2002, 2004, 2005b), work on krill has incorporated dependent predators and effects of environmental variability on krill recruitment (e.g. Constable, 2005a,b, 2006, 2008, submitted for publication; Hill et al., 2007; Constable and Candy, 2008). A further important direction utilises dynamic models to simulate the impacts of changing prey field on penguin chick growth and on foraging success (Cresswell et al., 2008).

3.4. Developing mechanistic coupled physical–biological models of food webs

Coupling individual sub-model components models (Sections 3.1–3.3) offers a promising direction for Southern Ocean food web analyses. These models could be linked together to examine issues relating to whole ecosystem operation, thus offering a more comprehensive picture to surpass current, often disjointed, efforts. The tendency of current modelling efforts is to focus on bottom-up pathways from physics to biogeochemistry to food webs. Top-down effects are important yet neglected factors in modelling and two-way interactions between regional food webs should also be considered. However two-way coupling to allow feedbacks, such as the influence of macro-zooplankton life histories on biogeochemical processes, or the seasonal dispersal dynamics of whales, seals or seabirds on demand for prey, poses challenges that will require innovative theoretical and technical advances. Developing the methods for appropriate coupling between models of varying resolution is an area requiring dedicated focus and coordination of efforts, with the resolution required to resolve biological processes posing particular challenges.

Zooplankton dynamics and interactions should be a major consideration in the development of appropriate mechanistic models because of their central importance in Southern Ocean food webs, as consumers of primary production and as prey for higher trophic levels organisms (Figs. 2 and 3). Representation of a suite of zooplankton grazers in food webs will allow assessment of alternative pathways and the effects of changing species assemblages. As noted, numerous Antarctic krill models exist, covering a range of space and time scales, and are linked with physical parameters, such as circulation. However, equivalent models are lacking for most other Southern Ocean zooplankton species such as salps, copepods and amphipods.

There are other potentially important influences on food web dynamics, such as the influence of prey condition on its survival and its predators (Constable, 2005b) or the relative value of different prey items for different predators, that need consideration in mechanistically based food web models. However, including full detail of the biology of every species and its life-history stage combinations in food web models is not practical. To focus effort, models may require more detail for the key species of interest and less detail for other trophic levels, termed the 'rhomboid' approach (deYoung et al., 2004). Such a focused approach is likely to be particularly important in coupled models, such as linked food web-biogeochemical models or linked harvesting-ecosystem models. Linking biogeochemical and food web models can provide insights into top-down influences from upper trophic levels (e.g. faecal enrichment) on biogeochemical cycles that have recently been highlighted for Southern Ocean ecosystems (Nicol et al., 2010). Under such scenarios, the choice of species-centric versus more trophic-centric model elements will be critical.

Progress is being made in this area and several studies of larger scale systems have highlighted multi-scale processes and some have applied models of different resolution based on nested structures (e.g. Brind'Amour et al., 2005; Dong et al., 2009; Samuelsen et al., 2009; Skliris and Beckers, 2009; Tang et al., 2009), but such models have not been applied to Southern Ocean systems. Models are also being developed that target different physical resolutions and biological processes (Constable, 2005a, 2006, submitted for publication; Hengeveld et al., 2009; Koniak and Noy-Meir, 2009; Le Fur and Simon, 2009). However, the availability of data for specifying boundary conditions and for model evaluation limits the development and application of these models.

4. Developing models of Southern Ocean food webs

Much of the discussion based around Southern Ocean ecosystem modelling has parallels in general marine food web modelling (Allen and Somerfield, 2009; Allen and Fulton, 2010; Rose et al., 2010). Most food web modelling tends to be based on the concept of a network based budget analysis of energy, carbon or mass flow (Plaganyi and Butterworth, 2008; Christensen et al., 2009; Freon et al., 2009; Gascuel and Pauly, 2009; Libralato and Solidoro, 2009; Travers et al., 2010). These models are useful for producing general patterns of overall food web structure. They are also valuable for developing quantified descriptions of food webs, which provide a useful basis for comparative analyses of food web structure and function (Steele et al., 2007a). These in turn will be important in understanding the determinants of food web structure at global scales, but require standardisation of parameterisation and approach. Indeed, the development of quantified descriptions of Southern Ocean food webs will be important not only for Antarctic focused studies but will also contribute to analyses at the global scale.

Key research priorities for developing Southern Ocean food web energy or material flow models include: (i) better agreement on energetic rates for Southern Ocean biota, (ii) inclusion of migrating top-predator species in food-web models, (iii) constraining food web models based on available data, (iv) identifying functional groups to use if/when standardising to a generic food-web model, (v) defining measures of food-web structure, (vi) developing approaches to deal with the intense seasonality of lower food web components in a mass balance model which is balanced over a year, (vii) allowing for interannual variability in an annual mass balance model, (viii) consolidation/comparison of diets across the Southern Ocean, and (ix) developing methods of validation (e.g. using stable isotopes and other tracers).

4.1. Generalised models of Southern Ocean food webs

In complex adaptive systems such as food webs, the interactions that occur as part of a network generate system level properties. Thus, mechanistic decomposition of these systems provides incomplete analyses of their operation and dynamics. System level analyses, on the other hand, attempt to capture broader scale dynamics rather than focusing on individual components. Southern Ocean food webs are both spatially connected and highly spatially and temporally variable in species composition and interactions, which suggests that a focus on generalised modelling of overall food web structure and function will be important. To develop such generalised modelling of Southern Ocean food webs requires quantified relationships of the major determinates of food web structure and function that can be applied to the different regions, scales and times. This requires examination of food web structure in relation to regional differences in physical and chemical characteristics (e.g. Fig. 1e).

Dominant food web structures that are associated with particular regions can be identified along with their seasonal variability. For example, Antarctic krill dominate in ecosystems where large diatoms are the main autotrophs, such as around the Antarctic Peninsula and Scotia Sea regions (Atkinson et al., 2008). These krill dominated regions are where large colonies of higher predators are found during summer. In pack-ice regions ice-krill and various fish species (especially Antarctic silverfish, *Pleuogramma antarcticum*) dominate the intermediate trophic levels and characterise an alternate food web structure (Smith et al., 2012). Outside the ice covered regions the food web can be dominated by other zooplankton species such as copepods or salps. In areas where salps dominate, the energy flow pathways to higher predators are more complex and the available food does not support a large biomass of higher predators (Murphy et al., 2012).

Some Southern Ocean top predators have defined geographic distributions, whereas others move between regions, highlighting both regional differences and significant connections (e.g. Murphy et al., 2012). Although the species associated with a particular food web and region varies spatially and temporally, there is sufficient consistency to suggest that forming generalised views of Southern Ocean food webs is possible. This is most clearly illustrated by the krill dominated systems, where the species of predator exploiting the krill may vary, but the general structure of the system is similar. For example, at South Georgia macaroni penguins are the main penguin species feeding on krill, while around the Antarctic Peninsula it is Adélie penguins. These differences result from habitat preferences and life history constraints, but the fundamental food web structure does not appear to be substantially different (Murphy et al., in press).

The view that consistent regional food webs can be identified allows a generic structure for Southern Ocean food webs based on trophic levels and alternative functional groups or congeneric species to be proposed (Fig. 5a and b). This structure does not identify exact species or groups, allowing the same basic model to be applied across the Southern Ocean (Fig. 5b). Distinctions can be made between various groups that dominate the system or are considered to be important in different food webs. For example, in a krill-dominated food web (Fig. 5c), the predator assemblages may consist of those that feed predominantly on krill (e.g. macaroni and Adélie penguins) and those that feed predominantly on fish and squid (e.g. king and emperor penguins). The proposed generic structure allows the major components of the other trophic groups to be distinguished, with the level of detail in each determined by the regional habitat characteristics. The generic food web structure could potentially be expanded to the circumpolar scale, allowing the food web operation and major pathways of energy flow to emerge in different regional systems. This requires an objective functional basis for such a dynamic structure and definition and quantification of such a functional basis appears a tractable goal in Southern Ocean ecosystems.

As an alternative approach, a size-based generic model for the Southern Ocean has the potential to draw on allometric relationships to provide simplified parameterisations of key rate processes (Moloney et al., 1991; Zhou et al., 2009). Size-structured models have been developed for the global ocean (Maury et al., 2007), providing an alternative to the functional group approach, for analysing the general operation of ecosystems. A size-based view of the trophic interactions in Southern Ocean ecosystems (Fig. 6) illustrates schematically some of the potential size-based connections in which groups are scaled on the basis of relative body size.

Extension of size-based models to trophic levels higher than mesozooplankton could be particularly limited in the Southern Ocean. Over large parts of the Southern Ocean the dominate energy flow pathway to larger bodied predators (such as penguins, seals and whales) is through the krill, with much reduced flow through fish and squid (Murphy et al., 2007b, 2012). This suggests there is a major discontinuity in size structure in Southern Ocean food webs. Such a discontinuity will generate a higher level of energy flow to the largest higher predator species compared to food webs with a more continuous size spectrum of feeding relationships. The generic size-structured view also highlights the importance of sea ice and benthic systems in providing supplementary inputs into the

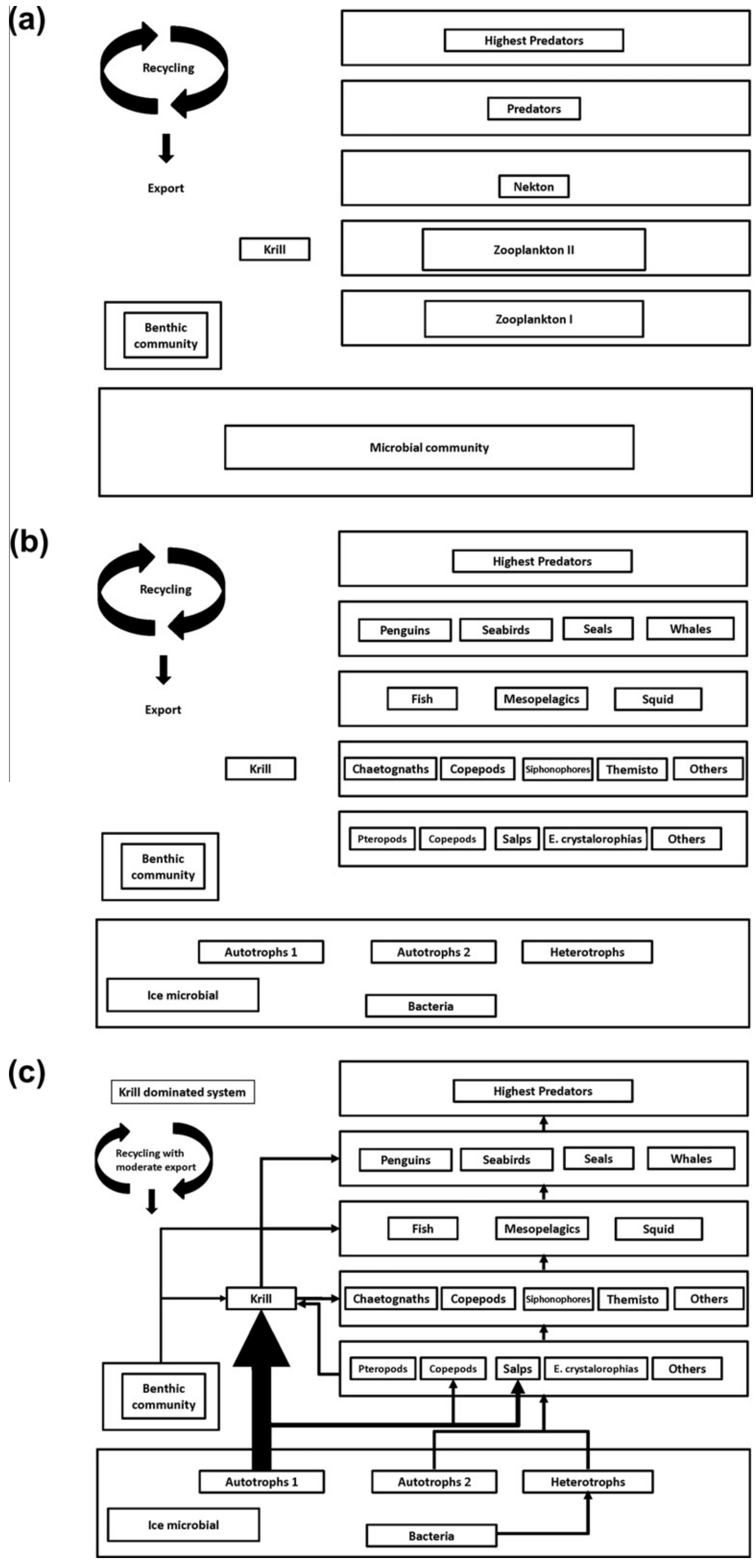

Fig. 5. Development of a generalised trophic framework for the Southern Ocean food web (focused on upper trophic level interactions). (a) General trophic framework within which the species present in the food web can vary. (b) Identification of key species, functional groups or congener groups within the trophic framework. The figure presents the major structural components of food webs in the Southern Ocean with an emphasis on the intermediate zooplankton groups. The figure highlights the potential for alternative, but interactive pathways of energy flow through the food webs. (c) Application of the generic structure to a krill dominated ecosystem during summer. The major pathways are illustrated as arrows and the thickness of the arrows indicates the magnitude of the energy/carbon flow. The level of recycling and export is indicated by the size of the arrows on the left. Autotrophs 1 = large autotrophs (e.g. diatoms), Autotrophs 2 = small autotrophs.

pelagic food web, providing further food input for the plankton and, through the demersal fish, a direct link to the higher predators. These sub-components of regional ecosystems provide supplementary or alternative pathways of energy flow that potentially help maintain larger-bodied intermediate and higher trophic level groups. Some studies of Southern Ocean ecological

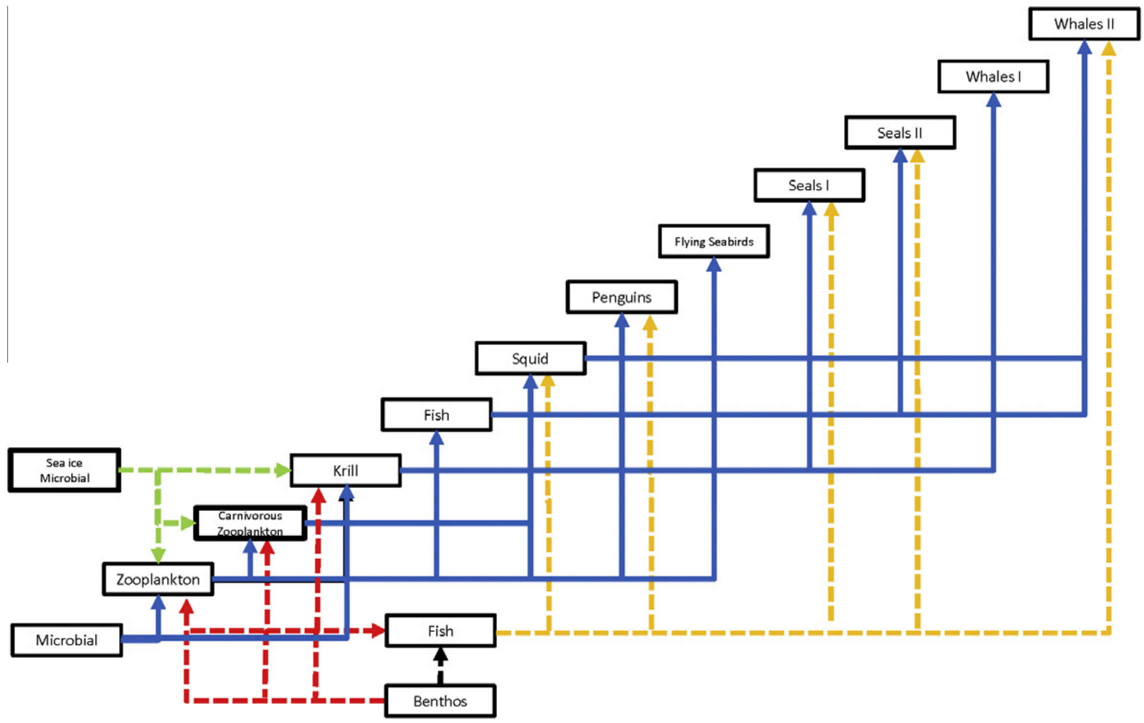

Fig. 6. A size-based view of the Southern Ocean of the food web (focused on upper trophic level interactions) based on general relative size categorisation showing the potential links in the food web. Blue lines are pelagic system links; red lines are plankton-benthic links; yellow lines are demersal fish-higher trophic level links; black dashed line links the benthic and demersal fish; green lines are sea ice microbial to pelagic community links.

size structure and food webs have been undertaken, for example on the Polar Front community (Jacques and Panouse, 1991; Rodhouse et al., 1994; Fiala et al., 1998; Froneman et al., 2004; Daniels et al., 2006; Pershing et al., 2010), but further work is needed to develop the approach.

Developing more generalised ways of modelling food webs that allow the emergence of structure based on sets of ecological rules or constraints is potentially a valuable direction to explore. Models that allow plankton assemblages to be an emergent property have been developed (Follows et al., 2007; Dutkiewicz et al., 2009; Verdy et al., 2009; Barton et al., 2010) and these potentially provide a basis for generating more objective predictions of food web structure in response to change. Extension of this modelling approach to understand and analyse higher trophic level interactions potentially provides a powerful approach for projecting changes in Southern Ocean predator communities in response to changes in lower trophic levels.

Generalised models that predict the structure of Southern Ocean food webs will require identification of metrics that characterise food web structure so that responses to change and changing food web structure can be distinguished. Identification of these metrics will also provide guidance for measurement and monitoring programs. To be useful for projections of future states, the generalised models described above require that the aspects of food web structure that allow resilience, persistence, and affect overall stability of an ecosystem are known. For Southern Ocean systems aspects of this are known but quantitative understanding is lacking. The development of general models for Southern Ocean food webs depends on the appropriate characterisation and quantification of food web structure and function and the determining factors.

4.2. Data and monitoring requirements for Southern Ocean food web models

Validating models is a crucial step in model development and requires access to appropriate data. Data sets that are adequate to assess the status of current Southern Ocean food webs or how they have changed during recent decades are limited despite over a century of multidisciplinary research. The available data tend to be biased towards the summer, with very few data on winter ecology or year-round studies. Permanently ice covered regions (including those under ice shelves) are poorly studied, yet may be lost first if the ice shelves retreat or collapse. Many of the existing data sets are not readily accessible and many remain to be analysed (Murphy et al., 2008). Analysis of food webs at the circumpolar scale will require concerted efforts to compile, validate and manage existing data (e.g. from historical data sets; current national and international research programmes; scientific and fisheries-based monitoring programmes) to build large-scale interactive data systems. Processing and making these data available will improve understanding of the consequences of variability and change, provide model tuning and validation information, and provide insights into processes that can inform development of parameterizations. A comprehensive review of current knowledge of the structure of circumpolar food webs that integrates the available data is a critical step towards developing model structures.

Monitoring is essential to indicate the state of the system and therefore the success of management efforts and the accuracy of model predictions and can be a major aspect of model development (e.g. in data assimilation methods, Brasseur et al., 2009). Development of monitoring programmes for the Southern Ocean is a major focus of current research effort (Southern Ocean Sentinel – Integrating Climate and Ecosystem Dynamics Programme, www.iced.ac.uk, Southern Ocean Observing System, www.scar.org/soos). Considerable research effort has been focused on developing indicators for monitoring changes in ecosystems, including in the Southern Ocean (e.g. Cury and Christensen, 2005; Reid et al., 2005; Cury et al., 2011), with a strong conclusion that a suite of indicators is needed to observe change in different aspects of marine ecosystems due to a combination of climate variability and change and fishing. It is important that monitoring focuses on relevant metrics. Long-term monitoring will provide time series

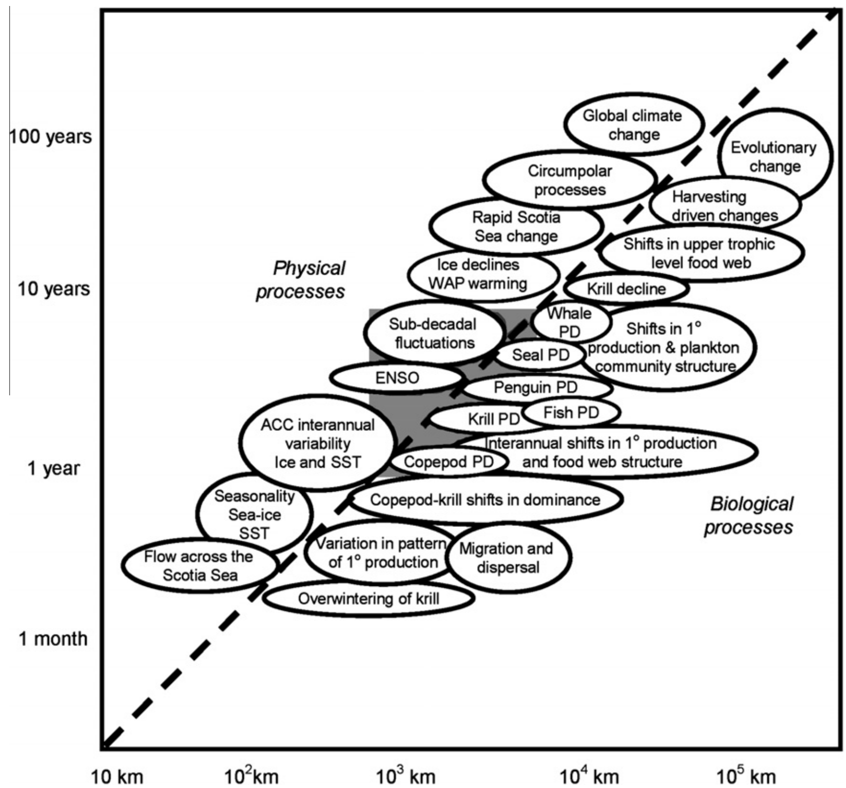

Fig. 7. Schematic of the temporal and spatial scales of the main physical and biological processes important in determining the dynamics of the Scotia Sea ecosystem. The 1: 1 relationship is based on the scales of physical mixing in the oceans. Note the physical and biological processes are illustrated offset above and below this line respectively for clarity. The shaded grey block illustrates the natural spatial and temporal scale of Scotia Sea processes. We include processes above and below this scale to approximately 10^5 km and a few hundred years and down to approximately 200 km and approximately 2–3 months. PD, population dynamics (from Murphy et al., 2007a).

data that are invaluable for determining the interrelationships between ecosystem components and for tuning and validating models. For assessment of food web models, these should not necessarily be focused on individual species or populations, but should include system level characteristics that relate to food web structure and function. For example, estimates of primary production, total carbon export from the mixed layer, higher trophic level total consumption, and pelagic size structure or dietary fluctuations of key species provide system level constraints for food web models.

4.3. The importance of scale in the development of food web models

Understanding and projecting how Southern Ocean ecosystems will respond to modifications requires models that are aimed at the food web level of biological organisation across regional and circumpolar scales. The central focus of modelling should, therefore, be at the food web level rather than on detailed mechanisms relating to individual species. Static views of food web structure that isolate the network of biological interactions from the physical and chemical systems in which they occur will be insufficient for developing models that aim to consider food web dynamics. Central to analyses of Southern Ocean ecosystems is a recognition of the importance of understanding the scales of interaction of different physical and biological processes (Murphy et al., 1988; Levin, 1990; Perry and Ommer, 2003). Changes in Southern Ocean ecosystems driven by anthropogenic processes will be superimposed on the natural variation at different scales, the dynamic consequences of which need to be captured in predictive models. The connectivity and spatial and temporal variability of Southern Ocean ecosystems indicates that models of food webs are needed that resolve different scales of processes and interactions (Fig 7). However, it is not possible to encompass all scales or levels of biological organisation in mechanistic models. Different resolution physical models can be used to identify the aspects of the physical environment that are important in particular biological processes and provide guidance on linking of local, regional and circumpolar models. This type of modelling is tractable and physically understandable and is the basis for the development of various coupled spatially explicit mechanistic models for ecosystems outside the

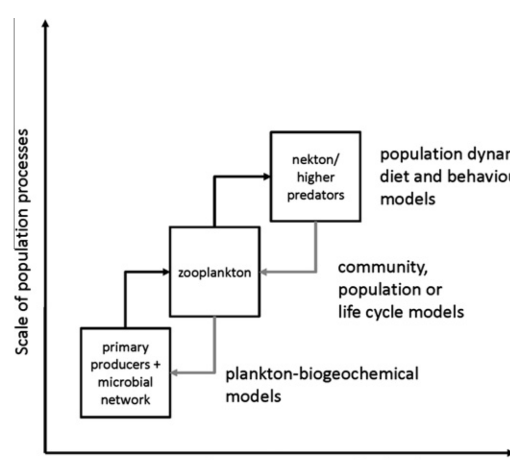

Fig. 8. Producing coupled models of ecosystem operation requires the development of models encompassing different temporal and spatial scales. At different scales the biological processes and trophic resolution included will vary and depend on the main scientific issues being addressed. A major challenge is to develop the appropriate links between models that resolve different biological processes operating over different scales.

Southern Ocean. This approach provides a valuable framework for linking Southern Ocean ecosystem models with models from other disciplines (e.g. physical oceanography or biogeochemistry).

The second aspect that has not been as extensively considered in developing scale-based models, and is almost absent from Southern Ocean modelling, is ecological scaling across different levels of biological organisation and across very different ecological processes. For example, this can involve linking genetic to physiological processes to understand individual adaptation, or from population processes to food webs through to whole ecosystems to examine controls on structure and function. The interaction of physical and ecological processes at different scales determines how food webs are structured and function. Choosing modelling approaches that incorporate these interactions requires definition and explicit consideration of the temporal and spatial scales of the food web processes and how these vary as the focus shifts across different parts of the food web (Murphy et al., 1988). For example, sub-mesoscale physical processes are increasingly being recognised as important in biogeochemical cycles and plankton dynamics (Brentnall et al., 2003; Levy et al., 2009). Patchiness at these scales is also a major feature of the distribution of Antarctic krill as a result of both physical and behavioural interactions. This patchiness in turn is important in the relative success of predators with different foraging strategies. These processes are crucial in determining food web structure and function in local systems. A further example of the importance of cross scale ecological processes that will be important in modelling regional food webs is the major change observed in predator community assemblages as they concentrate for breeding in summer and disperse or migrate from the area in winter, resulting in very different demand for prey during summer and winter. Highlighting the scale of the question being addressed and the levels of biological organisation of interest will help make explicit the importance of cross-scale interactions and the development of quantitative methods for dealing with multiple scale processes.

A scale-based view of an end-to-end model of a Southern Ocean food web (Fig. 8) provides a focus for development of a hierarchy of models and highlights the need for physical and ecological scaling. It also emphasises that adopting more than one modelling approach will have value in constraining both model development and outcomes. The above consideration of scale also highlights that each modelling approach provides a different abstracted view of the same ecosystem. The value of the different approaches is that they are not independent views, but are abstractions of the same system, which should generate consistent views. This implies that the various models can be used as mutual constraints.

4.4. Future directions in the development of Southern Ocean food web models

Whilst analyses of food webs have become a focus for increased attention during the last 5 years, modelling of Southern Ocean food webs is a recent research area (Hill et al., 2006). Numerous modelling studies have been undertaken that provide useful building blocks towards more integrated analyses of Southern Ocean food webs. To go beyond the current, often piecemeal, approach to ecosystem modelling requires the development of new thinking, techniques and approaches. Undertaking the required integrated

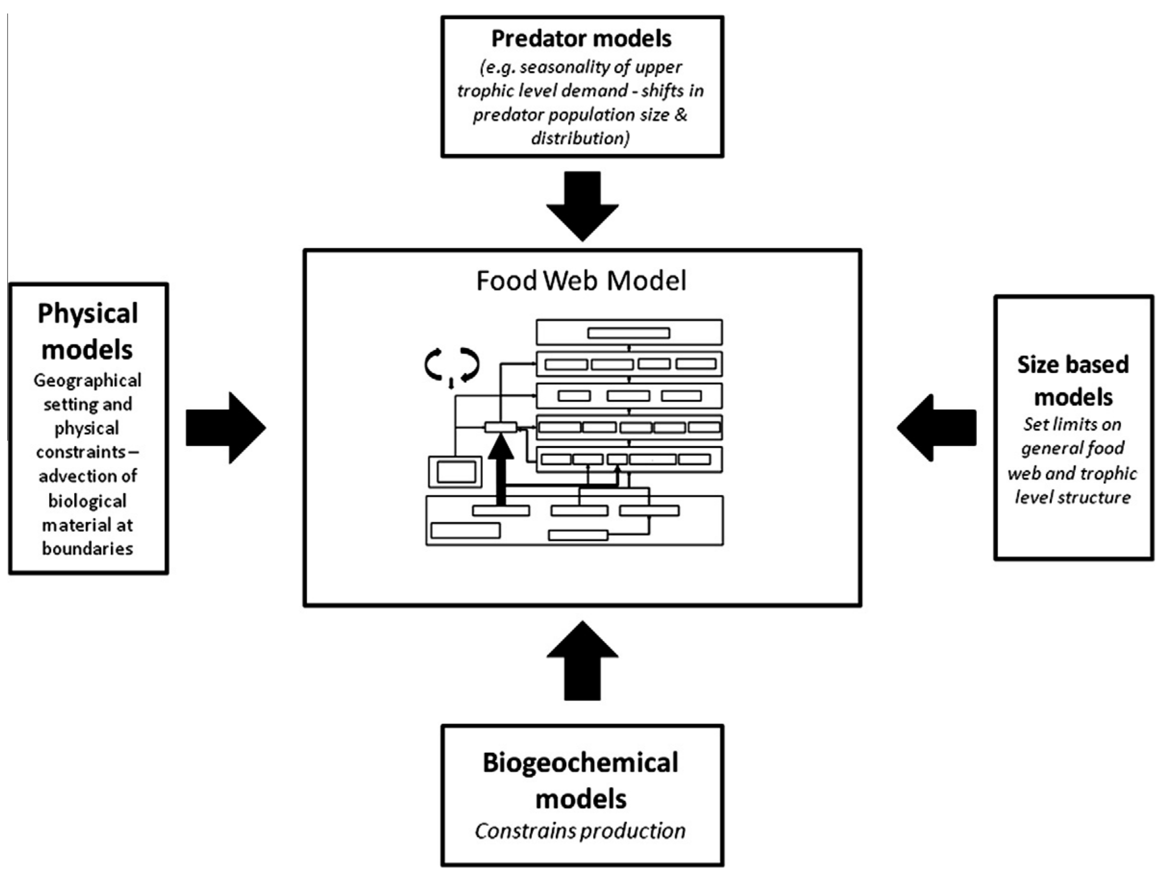

Fig. 9. Alternative models may be used to drive, constrain and provide biological boundary conditions for particular food web models. Physical models can provide fundamental information on habitat characteristics and hence constrain possible species composition; biogeochemical models can constrain production and food availability and quality at the base of the food web; size-based models provide a fundamental energetic constraint on the biomass distribution as a function of size and hence the possible biomass distribution in the food web and detailed models of predator life-cycles and behaviour potentially provide constraints on abundance and mortality functions.

Table 1
Key steps, activities and issues in the development of Southern Ocean food web models.

	Key steps	Main activities required	Issues to consider
1	Description and quantification of food web structure	(i) Compile key datasets, including making relevant data from the grey/unpublished literature available. Link to other data retrieval exercises for Southern Ocean food webs (e.g. CCAMLR/IWC and efforts through the EUR-OCEANS Consortium)	How to facilitate comparison of regional food webs yet retain detail about locally important features as necessary
	(i) Standardisation of food web descriptions	(ii) Undertake a comprehensive review of circumpolar food webs focused on what is known about the structure that includes:	Specific focus on zooplankton
	(ii) Food web budget and network analyses	– A series of conceptual diagrams representing the food webs in key regions (e.g. Ross Sea, Antarctic Peninsula, Scotia Sea, East Antarctic)	Stability and resilience properties
			Inclusion of uncertainty (data, structure and dynamic)
		– Characterisation of energy pathways	
		– Exploration of seasonality	
		– Identification of the main gaps in knowledge and ways to address these including new monitoring programmes	
		(iii) Compile and standardise standing stocks, parameters, variables and interactions	
		(iv) Undertake quantitative analyses of Southern Ocean food webs to examine the major determinants of structure and function. Consider major pathways and alternatives for energy flow	
		(v) Develop energy/carbon budgets and analyse network properties	
2	Mechanistic models that focus on:	(i) Develop biogeochemically based models of plankton dynamics at circumpolar, regional and local scales	Models may be nested or variable grid size
	Linking biogeochemical and zooplankton processes	(ii) Include a range of zooplankton species or groups that have different functional roles in food web operation and biogeochemical cycling	How to achieve appropriate resolution of physical and biological processes (many of the key regions of interest lie in areas of steep topography around island and shelf regions)? Consider fine scale processes, with tidally resolving models, role of heterogeneity, upwelling, meltwater, iron sources and cross shelf exchange processes
	Development of high resolution models for key localities	(iii) Generate a suite of species specific life cycle models	How to incorporate biogeochemical processes, such carbon flux studies and to consider importance of micronutrients (e.g. iron)?
		– Develop models of the complete life cycle of key species of interest	Develop coupled modelling approaches in collaboration with the physical and biogeochemical modelling community
		– Conduct a series of simulations including the full annual cycle and spatial distribution of a range of key species	Which plankton species will be the focus of effort? Consider a range of species or groups including smaller zooplankton (e.g. *Oithona*), mesozooplankton copepods (e.g. *Rhincalanus gigas* and *Calanoidies acutus*), krill and salps, and aim to include pteropods
		– Develop models that consider the detailed life-cycles of key species with more generalised representation of overall food web structure	
		– Develop regional nested models of food web operation	Establish the spatial distribution of a range of model elements, including nutrients (e.g. iron), productivity, and a range of species (e.g. diatoms, *Phaeocytis*, copepods, krill)
			Investigate issues of coupling, feedbacks, uncertainty and scales
		(i) Develop high resolution physical models at local scales	Allow potentially bi-directional linkages across processes and scales
		(ii) Develop biogeochemically based models of plankton dynamics at local scales	Consider model boundaries and closure
		(iii) Develop analyses of plankton life-cycle and behavioural interactions in high resolution models	Investigate cross-shelf exchange processes by which nutrients and plankton are transported onto shelf regions
		(iv) Develop predator foraging models	Examine factors generating heterogeneity of production and aggregation of zooplankton
			Investigate factors affecting the stability of hotspots of production zooplankton aggregation
			Consider how predators forage in dynamic patchy environments
3	Scenario testing to consider past and future change	(i) Dynamic models of interactions and simplified food webs	A multi-stranded strategy is required to incorporate mechanistic and generalised models, and regional and circumpolar models; no single modelling approach is likely to be sufficient to capture the links between ecosystems and climate
		(ii) Coupled models of species and simplified food webs	Identify key indicators of change (link with SOOS and Sentinel)
		(iii) Generic modelling of large scale food web operation	Consider the effects of top-down controls
		(iv) Species specific life cycle models	Consider the effects of recovery of past-exploited species
			Account for natural variability
			Simulate 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 abundance, foraging patterns and migration behaviour. Simulating the annual cycles at one example locality would be valuable
			Accommodate multiple hypotheses about any individual process or sets of processes. Be parsimonious (i.e. focus on what is relevant to model users and the processes that affect these)
			Develop scenario testing and model projections on the impacts of change in Southern Ocean food webs to feed into IPCC, CCAMLR, IWC and other relevant activities
			Further evaluate existing models and prepare a set of 'hind-cast' test cases to compare the results of various approaches;
			Consider available approaches from wider (including global) analyses
			Explore the potential for representing Southern Ocean ecosystems with a generic model from which food web structure emerges

modelling requires a focus on food web specific research; together with the development of new modelling strategies given that current individual approaches do not capture the appropriate structural and dynamic constraints. Thus, modelling of Southern Ocean food webs should be developed within a scale-based framework that explicitly acknowledges the scale of the questions being addressed and identifies the scale of the modelling being undertaken. No single "grand model" or structure is likely to be capable of adequately capturing all of the aspects of change required. The value of generating alternative model approaches for modelling marine ecosystems has been highlighted previously, but not in developing models of Southern Ocean food webs. We further suggest that a suite of conceptually-different ecological models, e.g. food webs, individual species, will not only be of interest, but is a requirement for developing robust models of Southern Ocean food webs.

A hierarchy of models that vary in resolution of ecological processes can be used to examine links across physical scales, and incorporate biogeochemical cycles and feedbacks. There is potential for a meta-model hierarchical framework to be developed at the circumpolar scale to link different regionally defined systems. This type of model could provide a framework for comparisons between different food web structures and environmental forcing conditions. The challenge would be to develop a meta-model that captures the main features of each system without being overly complex. Particular attention would be required on cross-scale issues and how to link models that encompass different scales that capture both the major internal dynamics at the scale of interest, but also allow multi-scale feedback processes to be considered. This requires a focus on cross-scale bidirectional coupling to allow for feedbacks (Fig. 8). Such a model structure would be appropriate for questions centred around krill population dynamics that require linking biogeochemical, krill population, and predator behaviour and population models. This type of linked model structure will implicitly include interaction effects that encompass a wide range of scales (e.g. Lehodey et al., 2008, 2010). Developing the scientific and technical basis for cross-scale coupling of such different models will be an important step in considering how food webs, and more generally ecological systems, of the Southern Ocean will respond to change over the coming decades.

Food web operation involves aspects of size, function and taxonomy, and modelling approaches that blend all three classifications provide a useful framework for comparative analyses. Generalised models may be particularly valuable for examining how food web structure affects the stability and resilience properties and responses to variability and change. Such models are also likely to provide a useful basis for comparing different modelling approaches and clarifying the major issues in analysing and comparing regional food webs. Further, having a range of models brings the potential for these to be used as constraints or to provide biological boundary conditions for more detailed models (Fig. 9). For example, biogeochemical models can provide regional boundary conditions for nutrient inputs and also provide estimates of primary production and microbial activity as a basis for driving food web structures. Size-based models can provide a general constraint on energy transfer and trophic flows determining potential biomass possible at different trophic levels. Predator consumption or fishery yield models provide specific constraints on other components which must be balanced through the food web. Such constraints between models will help in assessing which processes are particularly important in maintaining ecosystem structure and determining responses to change. This use of alternative models as mutual constraints or biological boundary conditions provides a powerful new direction for model development and food web assessment in marine ecosystem modelling in general and Southern Ocean ecosystem modelling in particular.

Development of integrated modelling of Southern Ocean ecosystems within a scale-based view requires progress in a suite of activities (Table 1), three of which form the primary focus areas for moving model development forward. The first is to undertake a comprehensive review of current knowledge of circumpolar food webs. This should take place in parallel with efforts to compile relevant existing data. Focused descriptions and quantification of regional food webs will provide an important basis for understanding food web structure and function, for comparative analyses and for validating more mechanistic models. Emphasis should be on overall structure and function rather than on detailed mass-balance budgets.

The second is focused on development of mechanistic models that capture important food web processes and interactions. Given the central importance of zooplankton in the Southern Ocean food web, development of mechanistic models should focus on building models upwards from the physics, through the biogeochemistry, to appropriate inclusion of the zooplankton. Such models will offer the possibility of explicit representation of controls on ecosystem dynamics and detailed exploration of biogeochemical interactions and feedbacks. Innovative approaches for coupling models of different types are required for the success of this approach. Also, the importance of understanding how cross-scale processes affect food web structure emphasises the need for much higher resolution modelling of physical–biological interactions in key local regions. This requires high-resolution physical and biological models that can capture the sub-grid scale processes that allow the maintenance of local food webs (e.g. patchiness and alternate foraging strategies).

The third area is development of a series of scenario tests to consider past and future change, with a particular focus on intermediate and higher trophic levels. Such tests will be relevant to stakeholders in informing policy and management, and will provide further insight into the structure, complexity and uncertainty inherent in the system, thus forming a logical basis for fine-tuning the ongoing process of model development. As part of this process it will be useful to consider the development and application of more generalised models at circumpolar scales. Indeed, the construction of a plausible generic model structure could enable the first system level predictions of change across the whole region to be made. Key to this is developing new approaches with a scale-based view to consider explicitly how different scale physical and biological processes affect model projections.

5. Conclusions

Addressing the wide range of questions being posed about the role of Southern Ocean food webs in biogeochemical cycles, the species and food web responses to climate change, and maintaining harvesting will require the development of modelling approaches that integrate across disciplines. There is little information about the current population trajectories of many of the main components of Southern Ocean food webs or of their overall structure and function. To fully understand the impacts of variability and change requires integrated end-to-end analyses of Southern Ocean food webs, from primary production systems through to top predators. Addressing the many gaps in knowledge (through data collation, analyses and monitoring) must proceed in parallel with appropriate model development. A coordinated, multidisciplinary approach is, therefore, needed to address questions that encompass some of the most complex current issues in ecology.

No single grand model is likely to be capable of adequately capturing all the aspects of ecosystem dynamics required. Instead, a suite of conceptually-different model approaches is required that provide alternative views of ecosystems and allow comparative analyses of structure and function. Such a multiple-model approach also provides the potential basis for acknowledging and dealing with the inherent complexity and uncertainty in analyses of the structure and function of oceanic ecosystems. Advancing the capability of modelling Southern Ocean food webs will require research efforts that provide quantification of food web processes and interactions at a range of scales, development of modelling procedures and techniques that can link processes across the key scales, and training of a community that can implement these models to provide projections of future change that will inform management of policy decisions for Southern Ocean marine resources. Increasing demand for food by human communities will increase the pressure on Southern Ocean ecosystems. Understanding the interactive responses in food webs will be crucial for developing management procedures that encompass simultaneous effects of climate related and fishery driven change. Developing integrated models of Southern Ocean food webs will be an important step in developing views of how global marine systems-human community interactions should be managed in the future.

Acknowledgements

This contribution developed from discussions at the *Integrating Climate and Ecosystem Dynamics (ICED) Southern Ocean Food Web Modelling Workshop*, held at the Center for Coastal and Physical Oceanography, Old Dominion University, Virginia, USA in April 2008, and the subsequent workshop report (Murphy et al., 2010). We thank all the participants at the workshop who contributed to the discussions and the report of the meeting. The paper is also a contribution to the British Antarctic Survey Polar Science for Planet Earth – Ecosystems Programme. We also thank the following organisations and programmes for their financial and in-kind support for the modelling workshop: European Network of Excellence for Ocean Ecosystems Analysis (EUR-OCEANS, now reformed as the EUR-OCEANS Consortium), Integrated Marine Biogeochemistry and Ecosystem Research (IMBER), Global Ocean Ecosystem Dynamics (GLOBEC), the Scientific Committee on Antarctic Research (SCAR) Evolution and Biodiversity in the Antarctic (EBA) programme, the British Antarctic Survey (BAS) and Old Dominion University's Center for Coastal Physical Oceanography. In addition, we thank Woods Hole Oceanographic Institution, University of California Santa Cruz and the University of Trieste for funding the attendance of delegates from these institutions to the ICED Food Web Modelling Workshop. Aspects of the Southern Ocean ecosystem modelling approach were refined through participation in the NOAA-funded workshop on *End-to-End Modeling of Marine Food Webs*, held at the Woods Hole Oceanographic Institution in April 2010 as part of the Comparative Analysis of Marine Ecosystem Organization Program. Support for this workshop was provided by NOAA Grant No. A1000656. Individual authors acknowledge the support of the U.S. NSF Office of Polar Programs.

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