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# Modelling Southern Ocean ecosystems: krill, the food-web, and the impacts of harvesting

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## ABSTRACT

The ecosystem approach to fisheries recognises the interdependence between harvested species and other ecosystem components. It aims to account for the propagation of the effects of harvesting through the food-web. The formulation and evaluation of ecosystem-based management strategies requires reliable models of ecosystem dynamics to predict these effects. The krill-based system in the Southern

Ocean was the focus of some of the earliest models exploring such effects. It is also a suitable example for the development of models to support the ecosystem approach to fisheries because it has a relatively simple food-web structure and progress has been made in developing models of the key species and interactions, some of which has been motivated by the need to develop ecosystem-based management. Antarctic krill, *Euphausia superba*, is the main target species for the fishery and the main prey of many top predators. It is therefore critical to capture the processes affecting the dynamics and distribution of krill in ecosystem dynamics models. These processes include environmental influences on recruitment and the spatially variable influence of advection. Models must also capture the interactions between krill and its consumers, which are mediated by the spatial structure of the environment. Various models have explored predator-prey population dynamics with simplistic representations of these interactions, while others have focused on specific details of the interactions. There is now a pressing need to develop plausible and practical models of ecosystem dynamics that link processes occurring at these different scales. Many studies have highlighted uncertainties in our understanding of the system, which indicates future priorities in terms of both data collection and developing methods to evaluate the effects of these uncertainties on model predictions. We propose a modelling approach that focuses on harvested species and their monitored consumers and that evaluates model uncertainty by using alternative structures and functional forms in a Monte Carlo framework.

Key words: ecosystem approach to fisheries, ecosystem model, Southern Ocean, *Euphausia superba*, food-web effects, model uncertainty, CCAMLR.

CONTENTS

# I. INTRODUCTION

The traditional role of fisheries scientists has been to estimate the size of fish stocks and predict their dynamic response to harvesting or, conversely, to identify acceptable harvesting strategies. The population dynamic models used in these tasks generally describe only the harvested species and do not account for their interactions with the wider ecosystem. This approach is partly responsible for the widespread failure to maintain the desired abundance of fish stocks (Hutchings, 1996), to prevent fishing operations from damaging other parts of the ecosystem (Turner *et al.*, 1999), and to control the impact of other human activities on fisheries (Bruton, 1995). It is now widely acknowledged that fisheries must be managed in a way that recognises their interdependence with the wider ecosystem. The 2002 World Summit on Sustainable Development called for this “ecosystem approach to fisheries” to be implemented in all fisheries by 2010.

Available definitions of the ecosystem approach are generally wide-ranging, recognising the socio-economic and ecological effects of fisheries and allied industries, and their interactions with other human activities (Garcia *et al.,* 2003). Fishing affects other parts of the marine food-web in various ways including the direct removal of non-target species (technical interactions) and more complex indirect effects propagated by biological interactions such as predation and competition. The ecosystem approach to fisheries will therefore need reliable models that incorporate these interactions to predict the ecosystem effects of harvesting and to identify management strategies that balance the conflicting requirements of harvesting and conservation. Several authors have discussed the role of modelling in this context (Hollowed *et al.*, 2000; Fulton, Smith & Johnson, 2003; Butterworth & Plagányi, 2004; deYoung *et al.*, 2004; Christensen & Walters, 2004). Models that incorporate food-web interactions, particularly multi-species virtual population analysis (MSVPA; Sparre, 1991) have been used in the assessment of commercially harvested fish stocks, but no models predicting the population dynamics of multiple interacting species are currently used in fisheries management (but see Livingston *et al*., 2005).

Despite the shortage of models, the management of some fisheries already takes account of known food-web interactions. For example, some species of seabirds are strongly dependent on the local availability of sandeels (family Ammodytidae), especially during the breeding season. The management of North Sea sandeel fisheries acknowledges this dependency in a decision rule that suspends fishing within 50 km of the UK North Sea coast if the breeding performance of kittiwakes, *Rissa tridactyla*, falls below a specified threshold for three consecutive years. The management of Alaskan pollock, *Theragra chalcogramma*, and mackerel, *Pleurogrammus monopterygius*, fisheries uses spatial and seasonal catch limits to minimise competition with Steller sealions, *Eumetopias jubatus*, and prohibits directed fishing for several forage species that are important prey for higher trophic levels (Witherell, Pautzke & Fluharty, 2000). The principle of controlling the food-web effects of fisheries is also incorporated into the Convention on the Conservation of Antarctic Marine Living Resources (which we will subsequently refer to as “the Convention”) which established the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) to manage Southern Ocean fisheries.

The Convention came into force in 1982, after almost two centuries of over-exploitation of Southern Ocean marine resources. This began with the near-extermination of Antarctic fur seal, *Arctocephalus gazella*, stocks in the 18th and 19th Centuries, followed by the great whales in the 20th Century and many fish stocks in the 1970-80s. From the late 1970s, catches of Antarctic krill, *Euphausia superba*, have exceeded those of all other species in the Southern Ocean. Antarctic krill is also the main prey of charismatic taxa including baleen whales, penguins and seals, and an important prey species for some albatrosses. Consequently, one of CCAMLR's priorities has been to develop an operational management approach for the krill fishery. According to Sainsbury, Punt & Smith (2000), this is currently the most advanced management approach in terms of its treatment of food-web interactions. CCAMLR attempts to manage the krill stock so that its biomass will not fall below a level considered appropriate to meet the food requirements of other species in the food-web. Although this level is precautionary, it is also arbitrary and the potential effects of the fishery on these other species are not known.

Current krill catches are around 3% of the annual catch limit but fishing pressure is likely to increase greatly in the future (Everson, Agnew & Miller, 2000; Croxall & Nicol, 2004). Consequently, there is a pressing need to assess the likely impacts of the krill fishery on the wider ecosystem, and to determine the suitability of the current management strategy or any potential alternatives.

Some of the earliest models to explore the ecosystem effects of fishing focused on the Southern Ocean (e.g. May *et al*., 1979), and numerous studies have considered food-web interactions involving krill (Sissenwine, 1983; Constable, 2001). These models were largely theoretical but there are several reasons why the krill-based system in the Southern Ocean is also particularly suitable for the development of practical models of ecosystem dynamics: (1) this system is relatively simple compared to other marine ecosystems (Everson, 1977) because the dominant primary consumer (krill) is connected to its main consumers through only one or two trophic links, and most of these consumers are top predators that have fewer trophic connections than intermediate trophic level species; (2) much work has already been done on developing models of the key species in the food-web, and on their interactions with other species; (3) CCAMLR has made considerable progress in translating the principle of managing the effects of fisheries on the food-web into operational requirements.

Herein we review the development of conceptual and mathematical models of the krill-based system in order to identify findings and approaches that are likely to be useful in developing practical models for managing fisheries in general and the krill fishery in particular. We also propose a framework for developing practical models by combining sub-models of limited parts of the system. In particular we consider how to represent uncertainty about ecosystem structure and functioning in these models.

The various models that we consider were developed to answer a range of questions, with a range of focal scales and species (Table 1). Many were not designed to describe ecosystem interactions in a management context. However we restrict our consideration to aspects of the models that are relevant to describing the ecosystem effects of krill harvesting. In the first section we describe general conceptual models of the Southern Ocean ecosystem to provide a context for the rest of the review. The second section considers the population dynamics and distributional characteristics of krill, and how physical processes influence these characteristics. The third section considers models of the interactions between krill and its predators. The fourth section considers models of energy and nutrient flow in the food-web, and those models that attempt to encapsulate interactions at multiple trophic levels. The fifth section presents models used for assessing krill yield or for modelling the dynamics of the krill fishery. Finally we consider the development of practical models of exploited marine systems, including how to deal with complexity and uncertainty.

## II. THE SOUTHERN OCEAN ECOSYSTEM

### (1) The physical environment

The Southern Ocean is a major marine system, entirely surrounding the Antarctic continent (Fig. 1). The Subtropical Front, which is characterised by steep gradients in sea surface temperature and salinity, separates the Southern Ocean from the subtropical waters of the Atlantic, Pacific and Indian Oceans. Further south, strong westerly winds drive the eastward-flowing Antarctic Circumpolar Current (ACC), which incorporates a number of fronts. Amongst these, the Antarctic Polar Front is recognised as an important physical and biological boundary and its mean position approximately defines the northern limit of the CCAMLR area. This contrasts with the arbitrary, political boundary (60ºS) of the Antarctic Treaty area. Although the various fronts limit biological exchange between the Southern Ocean and the adjoining oceans, birds (Croxall *et al*., 2005), marine mammals (Best & Schell, 1996) and some fish (Mikheev, 1965) migrate across them. The planktonic larvae of some invertebrates also survive transport across these fronts, challenging the notion of an isolated Southern-Ocean ecosystem (Clarke, Barnes & Hodgson, 2005). The Southern Ocean also exchanges waters with the adjoining oceans, and is particularly important in global thermohaline circulation as it connects to three other oceans and cold, deep waters form in the Ross and Weddell seas. South of the ACC, the subpolar regime is characterised by a westward current that combines with large cyclonic gyres in these seas and a smaller gyre near Prydz Bay. A detailed assessment of these fronts and currents is given in Orsi, Whitworth & Nowlin (1995).

Close to the Antarctic Polar Front, the Southern Ocean is between 3000 and 5000 m deep. It gradually shelves towards the Antarctic continental slope, but includes major topographic features such as the mainly submarine Scotia Ridge which runs from the Antarctic Peninsula to South Georgia, and the platforms occupied by Kerguelen and Heard Islands, and the Crozet and Prince Edward Islands. The Antarctic continental shelf is unusually deep, at between 400 and 800 m, due to the weight of the continental ice sheets. The Weddell and Ross Seas are wide bights, but otherwise the shelf is rarely more than 100 km wide. It is especially narrow on the western edge of the Antarctic Peninsula.

The Southern Ocean ecosystem is also influenced by the large-scale presence of ice, including permanent ice shelves close to the continent, and the seasonal advance and retreat of sea-ice further north. Ice cover provides a barrier between atmospheric and oceanographic processes, while melt water from retreating sea-ice affects the saline and thermal stratification of the ocean (Gordon, 1988).

## (2) Biogeography

There is considerable spatial heterogeneity in the Southern Ocean, and various authors have proposed schemes for subdividing the Ocean into zones based on physical or biological characteristics (Hart, 1942; Voronina, 1971; Longhurst, 1998). There is general agreement that the region can be divided into a permanently open ocean zone to the north, a seasonal sea-ice zone in which the annual advance and retreat of sea-ice occurs, and a coastal and continental shelf zone in which permanent ice shelves occur (Hempel, 1985; Arrigo *et al*., 1998; Longhurst, 1998). However, the relationship between these zones and the distribution and abundance of krill and its dependent species varies throughout the Southern Ocean, suggesting that models should capture local characteristics rather than attempting to generalise within these zones. For example, krill and its consumers are mostly absent from the permanently open ocean zone. However, around South Georgia a combination of high levels of krill import on ocean currents and high biological productivity, resulting from complex oceanography and possible local enhancement of nutrient flows, maintain some of the highest concentrations of both krill and its predators (Atkinson *et al.*, 2001). High concentrations of krill are also found around other subantarctic islands such as the Prince Edward Islands (Pakhomov & Froneman, 1999). Productivity is also high in the seasonal sea-ice zone where a series of phytoplankton blooms follow the retreat of ice in summer and krill is the main macroscopic component of the food-web.

Although krill represents a visible concentration of biomass in the Southern Ocean, with an estimated standing stock of 44 million tonnes in the Atlantic sector alone (Hewitt *et al*., 2004a; but see Demer & Conti, 2005), it and its consumers constitute only part of the Southern Ocean ecosystem. Indeed, Miller *et al.* (1985) estimated that krill consumed only about 3% of the daily phytoplankton production encountered during an extensive survey in summer 1981, while microorganisms consumed most of the remainder.

## III. KRILL MODELS

Effective management of exploited species requires an understanding of their life history and the factors controlling their population dynamics. For widely distributed species like Antarctic krill it is also important to understand the factors controlling their spatial and temporal distribution. This information will also be critical for predicting the ecosystem effects of harvesting. In this section we consider models that illuminate these issues. Further detail can be found in several complementary reviews on biological and population parameters  (Sahrhage, 1988; Miller & Hampton, 1989; Siegel & Nicol, 2000; Everson, 2000b) and distribution and population dynamics (Everson, 2000a; Siegel, 2005).

### (1) General characteristics

Antarctic krill is a Euphausid crustacean that can reach a maximum size of around 65 mm and has an apparent maximum lifespan of 5-7 years. It has a discrete breeding season in the Antarctic summer, it is a broadcast spawner and its early life is characterised by a strong descent-ascent cycle. Larvae become juveniles around the end of their first year, but do not begin to spawn until their third or fourth year (Ross & Quetin, 2000).

Siegel & Nicol's (2000) compilation of parameter estimates illustrates the high degree of spatial and temporal variability in such fundamental characteristics as the rate of natural mortality, maximum age and growth rate.  Models that incorporate natural variability have generally succeeded in replicating observed patterns of size structure. For example, Murphy & Reid (2001) reproduced monthly changes in the size distribution of krill at South Georgia using a model that incorporated seasonal variability in natural mortality and growth rate. Also, Hofmann & Lascara (2000) found that it was necessary to include a seasonal change in respiration rates in order for their bioenergetic model to replicate observed patterns of growth and shrinkage. The instantaneous growth rate is known to vary with both temperature and food availability (e.g. Atkinson *et al.*, 2006), which themselves vary over a range of spatial and temporal scales. Spatial differences in growth rate and natural mortality might lead to differences in size structure (Reid *et al*., 2002), with consequences for the interpretation of these data. In particular, attempts to establish the maximum age of krill depend on the decomposition of length-frequency distributions into apparent age classes. Mackintosh (1974) identified two to three modes in length-frequency distributions for krill at South Georgia whereas Siegel (1987) identified at least five modes in a similar size range of krill from the Antarctic Peninsula region. This discrepancy is probably due to differences in growth rate rather than differences in the maximum age.

The complex patterns of variation observed in the biological characteristics of Antarctic krill suggest that models of ecosystem dynamics will need to capture this spatial and temporal variability. In particular, the spatial scale of models should allow adequate representation of variability between areas. It is encouraging that modelling studies have generally been effective in describing patterns of variability, and it is likely that these studies will be useful in identifying appropriate parameter distributions for specific regions. However, considerable uncertainty surrounds many of these parameter estimates, due to natural variation, observation error and uncertainty about the underlying processes.

## (2) Distribution and transport

Marr (1962) described the broad-scale distribution of Antarctic krill, which extends from the Antarctic continental shelf to the Antarctic Polar Frontal Zone, with heterogeneous but large-scale concentrations of biomass, particularly in the Antarctic Peninsula – Scotia Sea region. Other than confirming the presence of Antarctic krill in the Ross Sea (Sala, Azzali & Russo, 2002), recent studies have not substantially altered this view. However, it is now clear that the spatial distribution of krill biomass can vary considerably between years (Atkinson *et al.,* 2004).

In some areas, such as the Scotia Sea, aggregations of krill occur predictably in shelf and shelf-break areas (e.g. BIOMASS, 1977; Everson & Goss, 1991; Murphy *et al.*, 1997; Trathan *et al.*, 1998). They are also often associated with oceanic fronts including the Southern Antarctic Circumpolar Current Front (SACCF) at South Georgia (Witek, Kalinowski & Grelowski, 1988; Miller & Hampton, 1989, Hofmann *et al.*, 1998; Trathan *et al.*, 2003). Everson (1976, 1977) suggested that enhanced primary productivity in regions of upwelling could be a key factor in krill distribution. By contrast, Witek, *et al.* (1988) suggested that behavioural reactions to water velocity gradients tended to concentrate krill in quiescent areas to the side of strong flow fields (see also Macaulay, English & Mathisen, 1984) where plankton abundance is often high, possibly as a consequence of the stable water conditions. Atkinson *et al.*

(2004) have shown that krill abundance in the Southern Ocean is spatially correlated with summer phytoplankton concentrations at a coarse scale.

The advection of krill in ocean currents has been the subject of a number of modelling studies. Models using a predicted circulation field for the Scotia Sea and the output from the Fine Resolution Antarctic Model (Webb *et al.*, 1991) show that passive transport could carry krill from the West Antarctic Peninsula region across to South Georgia in about three to four months (Hofmann *et al.,* 1998; Murphy *et al.,* 1998). Hofmann *et al.* (1998) indicated that Ekman drift concentrates particles in the SACCF, and concluded that the southern portion of the ACC is the primary mechanism transporting krill from the Antarctic Peninsula to South Georgia. Murphy *et al.* (1998) also considered the effects of sea-ice variation and showed that winter sea-ice sometimes covers the main transport pathways and therefore potentially affects the wider distribution of krill.

Fach, Hofmann & Murphy (2002) used estimated food availability from Coastal Zone Colour Scanner data, along with ocean temperature data, to estimate the growth of krill when transported in the ACC in the Southwest Atlantic. They found that the winter open ocean concentrations of phytoplankton were unlikely to provide sufficient food to maintain the krill as they travel from the Antarctic Peninsula region to South Georgia. The analyses also showed that the tracks of krill across the region coincide with the advancing ice-edge, suggesting that sea-ice algae could provide an alternative food-source during transport in winter.

More recently Murphy *et al.* (2004a) have examined the origin and fate of krill in the Scotia Sea using Lagrangian particle tracking and the output from the OCCAM circulation and climate model (Saunders, Coward & De Cuevas, 1999). The results showed that passive transport would have carried particles into areas of high biomass observed during extensive surveys in summer 2000. They also indicated that much of the biomass of krill observed across the Scotia Sea, including the South Georgia region, during the summer would have been associated with the winter sea-ice less than two to three months previously. The young krill that emerge from under the sea-ice during spring could have originated in a wide range of possible areas in the northern Weddell Sea and southern Scotia Arc region, and both the East and West Antarctic Peninsula. Particles that occurred in eastern regions of the central Scotia Sea were transported east around the north of the South Sandwich Islands, while particles that occurred slightly further east would pass around South Georgia. Although this study suggests transport trajectories for a specific period, Thorpe *et al.* (2002) have shown that temporal and spatial variability in ocean circulation will cause variation in the transport trajectories of particles in the Scotia Sea.

Huntley & Niiler (1995) argue that, because the life cycle of Antarctic krill is relatively long and advective features change over relatively small spatial scales, large-scale dispersion of larval cohorts is likely to be common. Consequently it might be appropriate to think of krill as forming temporary aggregations dictated by advective processes rather than self-sustaining populations at regional scales. Nevertheless, it is clear that adult krill are able to maintain discrete aggregations despite advection. Krill are able to modify their distribution locally by swimming, which will affect retention processes in shelf areas (Murphy, 1995; Murphy *et al.*, 2004b). Vertical migration will modify the pathways of transport and, as Hardy (1956) suggested, this will be important in some regions of complex circulation (Murphy *et al.*, 2004a). There is, however, no evidence that krill undertake directed large-scale migrations (Marr, 1962).

The structure of krill stocks is a particularly important consideration for fisheries management. There have been a number of genetic studies, which have found no evidence for discrete stocks (Siegel, 2005). This supports the idea of a continuous exchange of genetic material throughout the Southern Ocean. CCAMLR has pragmatically restricted its synoptic surveys of krill biomass to the Southwest Atlantic sector, where biomass and fishing activity are strongly concentrated. However, there are gaps in our understanding of the interdependence between krill populations both within this area and throughout the Southern Ocean.

The distribution of krill is complex and heterogeneous as a result of interactions between advection and krill behaviour, which vary over both time and space (Murphy *et al.,* 2004a). Large-scale numerical ocean models do not resolve well the sub-mesoscale processes that will be important for understanding the behavioural interactions of krill with ocean currents and eddies. Therefore the development of high-resolution shelf models is a high priority, especially for areas with high krill concentrations. There is a also a need to incorporate krill behaviour into these models. Nonetheless, existing models highlight the importance of advection and suggest upper bounds for its influence on krill distribution.

## (3) Population dynamics and recruitment

No relationship between adult stock size and recruitment success has been found for Antarctic krill (Siegel & Loeb, 1995). Rather, various empirical and modelling studies have suggested that recruitment success might be linked to physical environmental factors.

The models of Hofmann *et al*. (1992) and Hofmann & Hùsrevõglu (2003) focused on mechanisms that might affect the successful recruitment of young krill to the adult population. Krill eggs are released in the upper water column, from where they sink and hatch at depth. The larvae then swim back to the surface to feed. In the models, the sinking rate was governed by water density, and the development and ascent rate of embryos and larvae were governed by temperature (Hofmann *et al.*, 1992). With data inputs of water temperature and density, and bottom topography, the model indicated that, on the continental shelf, successful completion of the descent-ascent cycle will occur only in limited areas that are sufficiently deep and where warm Circumpolar Deep Water penetrates onto the shelf at depth (Hofmann & Hùsrevõglu, 2003).

Temporal variability in krill recruitment has been linked to various environmental influences (see Miller & Hampton, 1989; Sahrhage, 1988; Constable, Nicol & Strutton, 2003 for reviews), especially the presence of sea-ice, which is thought to provide a feeding habitat for larval krill (Kawaguchi & Satake, 1994; Loeb *et al.*, 1997; Fraser & Hofmann, 2003). These studies analysed the relationship between recruitment, adult distribution and seasonal sea-ice extent, suggesting that greater numbers of small krill enter the adult population after winters with extensive sea-ice coverage. After analysing seven decades of net haul data Atkinson *et al.* (2004) concluded that krill abundance in the Southwest Atlantic was correlated with winter sea-ice extent, and that krill abundance has declined progressively since the 1970s. Loeb *et al*. (1997) also found that the frequency of high krill population densities near the Antarctic Peninsula had declined since the mid-1970s, and there had been a decline in the frequency of winters with extensive sea-ice over five decades. However, despite the relationships in the Scotia Sea area, Constable *et al*. (2003)

found no environmental factors that were reliable covariates of recruitment, distribution or abundance at the Southern Ocean scale. This might be partly because recruitment indices are difficult to derive and are therefore potentially inconsistent between studies and regions.

Recent analyses of physical variability in sea-ice and oceanography (Murphy *et al.*, 1995; Fedulov, Murphy & Shulgovsky, 1996; White & Peterson, 1996; Naganobu *et al.*, 1999; Trathan & Murphy, 2002) have suggested links between large-scale atmospheric processes (indicated by the Southern Oscillation Index) and factors affecting variability in krill populations (Siegel & Loeb, 1995; Murphy *et al.*, 1998; Constable *et al.*, 2003; Trathan *et al.*, 2003). Constable *et al.* (2003) explored ways in which the physical system can affect primary and secondary productivity. They found that a loss of sea-ice over the last two decades might result in greater recruitment variability and lower abundance of krill in the Southwest Atlantic whereas recruitment might have been much less variable before the 1980s.

Inter-annual variability in recruitment success might also be an important factor determining the size structure of krill populations. Murphy & Reid (2001) modelled population structure using revised estimates of key demographic parameters (Miller & Hampton, 1989; Pakhomov, 1995) and found that observed inter-annual changes in length-frequency distribution at South Georgia were consistent with a reduction in biomass associated with the failure of a single year class to recruit into the population.

Most of the detailed analysis of krill population dynamics has focused on the Southwest Atlantic, where large inter-annual variations in abundance have been observed (e.g. Sushin & Shulgovsky, 1999). Brierley *et al*. (1999) found that inter-annual changes in abundance at South Georgia mirrored those at Elephant Island, suggesting large-scale connections between the krill found throughout the Scotia Sea. Recent work examining krill in the diets of predators at South Georgia, the Antarctic Peninsula, South Orkney and South Shetland Islands also suggests large-scale concordance in the population dynamics of krill in this region (Reid *et al.* 2002; Fraser & Hofmann, 2003; Lynnes, Reid & Croxall, 2004; Osman *et al.*, 2004).

These studies have identified some useful empirical and process models that may be helpful in predicting krill recruitment, which is of fundamental importance in the dynamics of the ecosystem. However there is a great deal of variability in this process and no definitive predictive model. These studies suggest that recruitment is largely independent of the adult population size but might be autocorrelated and linked to environmental factors in some regions. Recruitment could therefore be modelled as a stochastic process that includes autocorrelation or is informed by environmental factors. Logically, there will be some threshold adult population size below which krill recruitment is affected. The current krill management strategy recognises this and attempts to control the risk of the population size falling below an arbitrary level.

## IV. PREDATOR-PREY MODELS

Models of the interactions linking exploited species to other species will be needed to manage the impact of fisheries on other parts of the food-web. The population dynamics of many Southern Ocean species have shown dramatic changes, many of which are directly linked to harvesting, especially in the Southwest Atlantic sector. There have been major declines in the populations of baleen whales (Laws, 1977) and

Antarctic fur seals. Fur seals were apparently completely absent from South Georgia following the harvest of more than a million animals in the 1800s. However, the fur seal population increased from tens of animals in the 1930s to hundreds in the 1950s (Bonner, 1964) to an estimated 1.5 million in 1991 when the rate of population increase was still around 10% per year (Boyd, 1993). There have also been major declines in the populations of other seal and fish species. For example, the catch of the fish *Notothenia rossii* around South Georgia reportedly exceeded 500,000 tonnes in just two seasons between 1969 and 1971, but since then the estimated stock size has remained below 10% of this catch (Kock, 1992, but see Kock, Belchier & Jones 2004).

An early attempt to relate these dynamics to interactions between species was provided by Laws (1977) who calculated that the depletion of baleen whale stocks, from an estimated 43 million tonnes before 1930 to 7 million tonnes in the early 1970s, reduced krill consumption by 147 million tonnes per year. He also suggested that krill consumption by the remaining whales and other predators, including fur seals and various penguin species, might have increased as populations of these other predators were expanding. However, indicators of population size for predators at South Georgia showed a declining trend in the 1990s, suggesting that any ‘surplus’ krill required to sustain population increases was no longer available (Reid & Croxall, 2001).

On the basis that Laws’ (1977) estimate of the reduction in krill consumption by baleen whales exceeds the maximum recorded annual catch of global marine fisheries, Mori & Butterworth (2004) argue that this represents the biggest man-made perturbation of any marine ecosystem. Although the impacts of harvesting on target species and their prey are not directly comparable, the argument that this represents an enormous perturbation remains valid. Subsequent attempts to model the dynamics of interacting populations in the Southern Ocean have also had an important, though sometimes controversial (Yodzis, 1994), impact. Early models were largely theoretical abstractions, exploring the implications of harvesting interacting species. More recent models have explored specific influences on these interactions, and have also attempted to reconstruct the historical dynamics of some species and to establish the krill requirements of predators. Details of selected predator-prey models are given in Table 2.

### (1) Early models of long-term dynamics

The early models of long-term dynamics (May *et al*., 1979; Beddington & May, 1980; Horwood, 1981; Beddington & Cooke, 1982; Yamanaka, 1983) generally assumed logistic population growth in individual populations, but with predation subtracted from the prey population, and carrying capacity for the predator population determined by the abundance of its prey. The equations were coupled to represent simple predator-prey interactions. Variations included competition amongst predators and interactions at three trophic levels (May *et al*., 1979; Horwood, 1981; Yamanaka, 1983). These models generally assumed a steady-state environment and therefore had equilibrium solutions. Perturbation due to harvesting moves these model systems away from equilibrium and their rate of recovery after harvesting is dependent on the model structure and parameterisation, particularly the intrinsic rates of population increase.

While May *et al.* (1979) and Horwood (1981) used a linear functional response to describe prey consumption per predator, Yamanaka (1983, see description in Shimadzu, 1985) used an asymptotic function, representing the likely saturation of predation rate at high levels of prey abundance. He concluded that future harvesting of krill would reduce seal populations but that whales would recover in the long term, even with krill catches of around 100 million tonnes per year. He also considered some stochastic variability in the carrying capacity of krill, which would mask short-term population trends in krill.

The analysis of May *et al*. (1979) was instrumental in demonstrating the potential impact of harvesting one species on other parts of the food-web and, therefore, the limitations of single-species management. However, such models were never intended as realistic descriptions of the Southern Ocean ecosystem. The formulation of these models means that predator populations essentially follow changes in the prey population with some time lag, unless the predator population is artificially constrained through harvesting. When harvesting stops, these model systems return to a single (non-trivial) equilibrium. However, real systems and more complex models might have multiple potential equilibria (e.g. Harrison, 1986; Knowlton, 2004). Indeed, May *et al.* (1979) suggested that the Southern Ocean might be adjusting to new equilibria following the depletion of baleen whale populations.

Amongst the simplifications in the May *et al*. (1979) model is the assumption of a linear functional response, which, as Yodzis (1994) illustrates, is not biologically plausible and potentially exaggerates the impact of marine mammals on the standing stock of krill. Also, the simulated krill populations were governed solely by the so-called top-down effects of predation. However, there is now considerable evidence that environmental influences on recruitment can lead to changes in krill abundance, independently of predation. Also, realistic models must incorporate adequate representations of uncertainty and natural variability that are not captured in these deterministic models. The quantitative results of these simplistic models should not be regarded as reliable descriptions of the real system. Despite these limitations, these studies have provided valuable insights into the way harvested systems could behave. In particular, that any krill surplus caused by the depletion of baleen whales would be short-lived because it would allow the expansion of other, faster-growing, predator populations.

### (2) Recent models of predator-prey dynamics

More recent models of predator-prey interactions in the Southern Ocean have generally focused on predator dynamics. These models have used more detailed representations of the predator population and, often, the krill population than Lokta-Volterra-type models. In particular, these models have addressed the influence of spatial structure in krill distribution and krill harvest levels on predator populations, and the long-term dynamics of baleen whales.

Murphy (1995) modelled the response of predator populations to the input of krill into their foraging area. The model was divided into a number of spatial regions with characteristic krill input and output rates. Predator population dynamics were represented with a logistic function as in May *et al*. (1979), but different predators had different foraging radii from land and those with larger radii had greatest access to the krill as it was transported towards an island. In this scenario, the removal of whales or seals, which had greater access to the krill population, could release prey for those predators with more limited access. The form and degree of local retention could amplify the effects of changing krill abundance on predator populations.

Murphy’s (1995) study also considered the spatial demand for prey by predators at South Georgia and integrated the available data to estimate demand as a function of distance from a central predator colony. This was used to calculate the retention of krill required to meet this demand. The results indicated that retention had to be high, and krill transport slow, within 175 km of the colony, with maximum retention and slowest transport around 125 km from the land. This approximately corresponds to the shelf-break areas.

This model illustrates the potential influence of the spatial structure of the environment and the behaviour of individual species on interspecific competition and therefore population dynamics. This type of model is likely to be useful in establishing potential functional forms for competitive interactions in ecosystem dynamics models. However, more detail is required on the distribution and production of prey. For example, elaboration of coastal ocean transport would help to determine what mechanisms might contribute to concentrating or retaining krill in shelf-break areas.

Butterworth & Thomson (1995) modelled the impacts of krill fishing on krill predators. Their aim was to establish krill yields that would prevent the depletion of predator populations below reference levels. The predator model considered only reproductively mature females and had separate terms representing adult survival and recruitment. Recruitment was the product of lagged adult population size and juvenile survival, adjusted by a density-dependence term. Adult and juvenile survival were separate two-stage functions of krill abundance that were linear up to their asymptotes.  For each set of parameters considered, the models predicted a non-linear decline in the equilibrium predator population with increasing krill yields. The decline was more rapid when prey recruitment was variable than when it was constant. The asymptotic limit to the functional response means that declines in population size resulting from years of low krill availability are not necessarily compensated for by increases due to years of high availability. Although this model was parameterised with available data, the populations declined even in the absence of fishing, suggesting errors in the empirical estimates of survival rate or their assumed relationship with krill abundance, or other assumptions of the model.

Thomson *et al.* (2000) refined the approach of Butterworth & Thomson (1995) with a model of the South Georgia population of Antarctic fur seals. The central representation of the relationship between krill abundance and predator survival was replaced with a versatile function to allow the exploration of a number of functional forms (approximating to Holling types I-III). This function could potentially be parameterised for other predators as in the 1995 study. The effect of harvesting on krill abundance was modelled using stochastic population projections from the CCAMLR krill yield model (Butterworth *et al.*, 1994). Krill availability within the predators' foraging range was proportional to the regional abundance with added noise. The female part of the predator population was represented with a partially age-structured model in which offspring survival was a function of carrying capacity. The survival of each age group (pups, pre-adults and adults) had a functional relationship with krill availability that was parameterised by comparison with empirical survival data, but the shape parameter was assumed.

Thomson *et al.* (2000) attempted to correct probable bias in estimates of adult survival rate, which led to slightly higher survival rates in stochastic than in deterministic versions of the model. As a result, and by contrast with Butterworth &

Thomson (1995), the negative effects of fishing on the predator population were greater when krill recruitment was constant than when it was variable. The assumed maximum growth rate for the predator population and the shape of the relationship between krill availability and predator survival were found to produce bias in the estimated krill yield for a given target predator population. This might have been due to inaccurate representation of the predator's diet. The diet was assumed to be exclusively krill but Antarctic fur seals at South Georgia also eat substantial amounts of fish (Reid, 1995; Reid & Arnould, 1996). In addition, the relationship between krill abundance and availability to predators was assumed to be linear. However, the likelihood of a non-linear relationship between krill abundance and its exploitation rate is widely recognised as a potentially important influence on ecosystem interactions (May *et al.*, 1979; Beddington & de la Mare, 1985; Mangel, 1988; Butterworth, 1988). Consequently, there is a need to develop improved models of how the distribution and density of krill aggregations might alter with krill abundance, and the rate at which they can be exploited by both predators and the fishery.

The general approach of Butterworth & Thomson (1995) and Thomson *et al.* (2000) is a useful step towards defining predator requirements to use in establishing catch limits for the fishery. The authors appropriately analysed the implications of their results and identified problems with the model assumptions or input data. However, these models provide a very specific view of the system, namely that krill abundance influences predator population dynamics through survival rate and that this relationship is described by a simple monotonic function. There is only weak evidence for a relationship between krill availability and adult fur seal survival (Boyd *et al.*,1995). The ability to migrate long distances (Boyd *et al.*, 1998) and feed on alternative prey (Reid *et al.*, 2005) might allow adults to survive periods of low krill availability. On the other hand, offspring production is likely to be sensitive to changes in prey availability close to breeding colonies. However, it is possible that the feeding rate of individual seals will be influenced by the intensity of inter- and intraspecific competition and the availability of alternative prey, and might not be a monotonic function of krill abundance. Catch limits for krill should be robust to these uncertainties about the process by which krill availability affects predator populations. It will therefore be necessary to consider alternative models of this process to establish the potential effects of krill harvesting on predator populations.

Constable (2001) considered a more complex food-web structure in a model to illustrate the proposed development of management reference points in which predator production resulting from the consumption of fished species is used as an integrated measure of food-web function. The model was developed to explore how any number of predators might respond to variation in any number of prey when prey vary independently of predator consumption. It gives results in terms of both abundance and production trajectories with the latter responding more immediately to prey availability than the former, and therefore typically having greater variability.

Mori & Butterworth (2004) constructed a model of the dynamics of krill and two competing consumers: blue whales (*Balaenoptera musculus*) and minke whales (*B. bonaerensis*), from 1900 to 2000. Krill biomass was represented with a difference equation in which predation by whales was subtracted from logistic growth. Numbers of whales were represented by equations that included recruitment, natural mortality and catch. Recruitment to whale populations, and their predation rate on krill were asymptotic functions of krill biomass. The model estimated the carrying capacity for krill and the abundance trajectories for all three species when it was supplied with basic life history and functional response parameters and whale catch data, and was tuned to contemporary abundance estimates for the whale species. This study was potentially more realistic than that of May *et al*. (1979) because it used asymptotic functional responses, and it considered plausible ranges for many of its parameters. Not all parameter combinations gave plausible abundance trajectories, but by examining those combinations that did give plausible results, the authors were able to suggest potential characteristic functions for the whale species. This, of course, relies on the assumption that the model is a reasonable description of the interactions between its component species. These plausible dynamics involved an increase in krill biomass as harvesting depleted blue whale numbers. The increase in krill was followed by an increase in minke whales, which reduced the krill biomass to less than its original level. Minke whale populations were reduced by harvesting in the 1970s resulting in increased krill biomass in the 1990s and the first signs of a blue whale recovery. However, there is no good evidence to support the suggested recent increase in krill abundance.

This type of model is potentially useful in reconstructing the historical dynamics of the system and, indeed, predicting the future dynamics, but a lack of historical data makes it is difficult to assess whether this is a plausible view of the interactions controlling ecosystem dynamics. By simplifying the system, it is possible that the model misses important details. For example, no distinction is made between adult and juvenile whales in terms of their krill consumption or contribution to recruitment. Also, the model assumes that the dynamics result from interactions between three species, again characterised by a specific form of functional response. The dynamics of baleen whales might well have been influenced by other krill predators, such as Antarctic fur seals, which have also undergone dramatic changes in population size. It also assumes that krill abundance is controlled by the top-down effects of predators and a fixed carrying capacity. The assumption of constant natural mortality rates and carrying capacity is necessary to find an equilibrium solution. However, in reality, these parameters can be both variable and time-dependent. While identifying potential equilibrium conditions is a useful method, it might be impossible to establish whether an equilibrium ever really existed.

The models of Butterworth & Thomson (1995), Murphy (1995), Thomson *et al.* (2000) and Constable (2001) all assume that there are no top-down effects of predation on prey recruitment, although Thomson *et al.* (2000) presented, but did not evaluate, a two-way model. Mori & Butterworth (2004), in common with May *et al.* (1979), necessarily include top-down effects in order to simulate interactions between competing predators. There is strong evidence that the bottom-up effects of environmental variability have had more influence than top-down effects on the recent dynamics of both krill and its predators (Forcada *et al*., 2005). However, the depletion of top predators can increase the influence of bottom-up relative to top-down controls. Therefore it is possible that the relative importance of bottom-up and top-down controls in the krill-based system has changed over time.

These models involve different representations of the dynamic interactions between species, which are difficult to verify. It is unlikely that the representations of predator population structure, or the necessarily simplistic treatment of top-down and bottom-up controls used in these models will capture all of the important aspects of the system’s dynamics. However, these studies have suggested ways of linking the dynamics of predator and prey populations, which are transferable to more complex models. They have also explored the consequences of different forms in these interaction functions. It is not clear however which interactions are necessary to include in models and which functional forms are most realistic. A modelling approach that compares the effects of different assumptions about these interactions will be necessary to make informed decisions about harvesting.

### (3) Inclusion of small-scale processes in models of predator-prey-fishery interactions

Population dynamics are the result of smaller scale processes such as individual behaviour. The relationship between these scales has been explored in a set of models based on dynamic programming methods (Mangel & Switzer, 1998; Alonzo & Mangel, 2001; Alonzo, Switzer & Mangel, 2003a,b). Mangel & Switzer (1998) considered the spatial distribution of krill relative to a penguin colony, which was affected by diffusion and advection, and depleted by fishing and foraging. The model incorporated fishing fleet behaviour, a number of penguin breeding strategies, penguin foraging behaviour, and mortality risk to foraging penguins. The effects on penguins of krill harvesting were assessed in terms of reproductive success and parental survival, both of which showed a negative linear response to the total krill catch.

Alonzo & Mangel's (2001) dynamic state model suggests that the body size of krill shrinks under a range of influences including thermal stress, food deprivation and predation pressure, and that the fine-scale distribution of krill is driven by the behaviour of individuals. The authors suggest that the influence of predators is particularly strong, such that the spatial distribution and size structure of krill populations represents a trade-off between growth (which is a function of food availability and temperature) and survival (which is a function of predation pressure).

However, Ritz (2002) observes that krill can adjust their swarm size in response to predation pressure and suggests that it is unnecessary to postulate shrinkage as a survival strategy.

Alonzo *et al*. (2003a,b) further developed the habitat selection model of Alonzo & Mangel (2001) to examine the reciprocal effects of penguins and krill on the behavioural strategies of the two taxa and interactions between them, and to assess the indirect effects of krill harvesting on penguin behaviour and foraging success. In this approach, penguin behaviour influenced krill survival in offshore and onshore habitats, affecting the distribution of krill between the two habitats. Food availability to penguins was influenced by habitat selection in krill, the foraging strategy of the penguins, and water temperature, which affected krill growth and therefore habitat choice.

In the absence of harvesting, the model of Alonzo *et al*. (2003a,b) suggests that penguin foraging decisions could be a major influence on both taxa. Modelled krill avoided predation by feeding at the surface at night only, and descending during the day. However, smaller krill must spend more time feeding at the surface than larger krill. Penguins that minimise their time spent foraging will not travel offshore whereas penguins that maximise their consumption of prey will also forage offshore, with a greater effect on the prey population and a greater susceptibility to the influence of fluctuations in prey abundance. Also, the environmental conditions that best suit krill growth might allow them to evade capture by penguins and therefore reduce the predators’ food intake.

When fishing was included in the model, the behaviour of krill was found to amplify the negative effects of the fishery on the penguin population. This approach could provide insights into population-level interactions that are difficult to capture without incorporating individual behaviour. Alonzo *et al*. (2003a) suggest that the impact of fisheries could be assessed through monitoring specific aspects of the foraging behaviour of predators.

Population-level responses are the product of both the behavioural and physiological responses of individuals. Individual-based modelling might therefore help to inform data collection on the links between processes at these two scales. This type of model could also be used to identify and test appropriate functional relationships (for example between exploitation rate and predator survival) that may be useful in constructing models to manage the fishery. These relationships might not be possible to determine empirically, so individual-based models are useful in both suggesting plausible forms of these relationships, and determining whether they are compatible with our understanding of the underlying processes. Individual-level responses, such as behaviour or offspring production are often easier to monitor than population-level responses, so it might be necessary to include these effects in practical models. However, individual-based models should be used with caution as incorrect assumptions about small-scale processes may lead to serious errors at the population level.

## V. FOOD-WEB AND ECOSYSTEM MODELS

The ecosystem approach to fisheries will need models that capture critical processes at the community level. It will be particularly important to understand the structure of the food-web and the food requirements of different trophic levels in order to represent the flow of energy or mass between them. Various authors have attempted to elaborate Southern Ocean food-webs and several studies have estimated the food requirements of predators. Furthermore, a few complex ecosystem models, incorporating higher trophic levels, have been developed for parts of the Southern Ocean, and various large-scale biogeochemical models, incorporating planktonic ecology, have also been developed.

### (1) Estimates of consumption

Everson (1977) used available data to quantify production and consumption in a simplified representation of the Southern Ocean food-web with the intention of identifying gaps in the available data. He calculated krill production based on estimates of primary production and conversion efficiencies. The problems encountered were general for this type of study. Firstly, it is difficult to account for changing food availability, so the resulting view of energy flows was, at best, a snapshot of a single situation. Secondly, data are often patchy, as highlighted by a paucity of information on consumption by fish and squid.

Hempel (1985) noted that, because survival is energetically expensive in the cold and turbulent environment of the Southern Ocean, krill-based food-webs are inefficient converters of primary production into animal biomass. Subsequent attempts to model energy flow have generally focussed on consumption by higher predators. Croxall, Ricketts & Prince (1984), Croxall, Prince & Ricketts (1985) and Croxall, Ricketts & Wood (1990) modelled the consumption of krill and other prey by birds and mammals. They based their calculations on estimates of the energetic costs of the daily activities performed by sections of the population at each stage in the breeding cycle. These were then converted to food requirements of the predators using data on diet composition, the energy content of prey and conversion efficiency. Although the latter was measured for macaroni penguins (*Eudyptes chrysolophus*) and Antarctic fur seals, it had to be assumed for other predators. Impacts on prey populations in specific locations were then inferred based on estimates of foraging range and distribution of foraging effort.

Other authors have used a similar approach in scaling up prey consumption estimates from diet data or energetics calculations (Kock, 1985, Croll & Tershy, 1998; Everson *et al.*, 1999, Boyd, 2002), to calculate the consumption of prey species (krill and icefish) by predator populations. Boyd (2002) used an algorithm incorporating metabolism, growth, diet, life history and activity budgets to estimate prey consumption by fur seals and macaroni penguins at South Georgia in 1991. The model was sensitive to life-history characteristics, which affect the age structure of the predator population, while other variables contributed <0.1% of the overall variance in the output. Not surprisingly, it was most sensitive to estimates of abundance of the predator populations. With an appropriate predator population model, this approach can be used to illustrate seasonal changes in demand and identify the life stages that are most susceptible to competition from the fishery.

The method’s shortcomings inevitably arise from inaccuracies in the input data and its assumptions (Boyd, 2002). Overall estimates of consumption of specific prey generally suffer from a lack of good data for all predators. For example, Croxall *et al.* (1990) were able to estimate daily consumption for the breeding part of seabird populations and fur seals, which could be monitored at land-based colonies, but only annual estimates were possible for other seals.

These approaches have been applied to predator communities at South Georgia and the Scotia Sea, where seals and seabirds were estimated to have roughly equal prey requirements. Croxall *et al.* (1990) estimated that krill comprise 70% of the diet of the predator assemblage considered, and identified crabeater seals (*Lobodon carcinophagus*) and macaroni and chinstrap (*Pygoscelis antarctica*) penguins as the main krill consumers. As in many studies that followed, the estimated standing stocks of krill and fish were often low compared to estimates of consumption by predators (Croxall *et al.*, 1985). Although these standing stock estimates do not indicate the production available for consumption, it is likely that either consumption was overestimated or krill abundance was underestimated (Nicol, Constable & Pauly, 2000). Identifying the cause of these discrepancies could improve the methods and models used to estimate both consumption and prey availability.

Estimating the food requirements of consumers is a particularly important step in understanding the operation of food-webs. These estimates will be useful in parameterising more complex models of ecosystem dynamics. These models are also potentially useful in assessing the prey requirements of predator populations based on their size and demographic structure, and therefore in defining the limiting effects of prey availability. The ability to relate the status of a predator population to its prey consumption implies a way to construct functional responses and to estimate local prey abundance from studies of predator populations.  However, the apparent mismatch between krill supply and predator demand suggests uncertainty in our understanding of the system, which must be either resolved or quantified.

## (2) Food-web models

Early conceptual models of the Antarctic marine ecosystem, in the form of qualitative descriptions of the food-web, were produced by Hart (1942), Holdgate (1967), Knox (1970), and Everson (1977). There have also been three simulation studies that attempted to model multi-species interactions in the Southern Ocean ecosystem (Green, 1975, summarised in Green Hammond, 1981; Doi, 1979, summarised in Shimadzu, 1985; Bredesen, 2003).

Green (1975) developed a Ross Sea annual model that simulated the flows of carbon from nutrients to whales in a closed system. The model attempted to encapsulate some of the major dynamics of the ecosystem, such as the seasonal migrations of great whales into the region. The species and nutrients in the system were grouped into thirteen broad compartments that included the major constituents represented in the ecosystem models that proliferated two decades later. The approach also recognised the multiple and often two-way energy transfer pathways that occur in natural food-webs. However, the shortage of data meant that it was not testable as a simulation model.

Doi (1979) employed a network model consisting of 14 biological compartments and four trophic levels. Most species were harvested, and most of the detail was in the upper trophic level (which included nine of the biological compartments). This was a complex model with 137 variables and parameters, in which interactions among species were represented in terms of the energy flow from lower to higher trophic levels. For the equilibrium state, 12 of these energy flow terms were parameterised from empirical data and the remaining nine were solved for in a process similar to the later “mass balance” approach (Polovina, 1984). Some standing stock and mortality estimates as well as catches were also obtained from the literature. Other terms were either given arbitrary values or estimated in the model. In simulations, the phytoplankton standing stock and the predation rate upon it by krill and zooplankton were kept constant, so variations in krill abundance were due to the top-down effects of harvesting and predation. With whale exploitation at 1975 levels (which were well below peak levels) but no krill harvesting, the model predicted a recovery of whale populations and a consequent decline in krill due to increased consumption. With krill harvesting at 10 million tonnes per year, the model predicted recovery in most whale populations. Both scenarios resulted in a decline in fish stocks due to predation by increasing numbers of seals and penguins. The study again suffered from the lack of empirical knowledge of the system.  For example, squid were modelled as important krill predators even though few data were available.

Over the last two decades the mass balance approach has been widely used for constructing models of aquatic ecosystems (Christensen & Pauly, 2004). These have generally used the Ecopath with Ecosim (EwE) software suite (Christensen & Walters, 2004), in which a series of linear equations are solved such that the overall consumption of prey biomass is balanced with the production of biomass within each predator group plus respiration and biomass lost from the system. The assumption that the system has a single balance point allows this method to estimate missing values when only some of the required parameters have been measured for each trophic group.

Plagányi & Butterworth (2004) considered the suitability of EwE for addressing the management of krill and its predators in the Southern Ocean. They found the inclusion of Ecospace, which implements spatially resolved dynamic models, useful for addressing the issues of krill schooling and the different foraging ranges of land-based and pelagic predators. They also suggest that EwE will be useful for investigating complex interactions, such as competition between krill and salps for phytoplankton. Ecosim divides prey populations into those that are vulnerable and those that are not vulnerable to predation by each predator. This is a potential weakness in assessing the effects of changes in krill abundance, as it is effectively an *a priori* specification of the relative competitive abilities of the predators. While the vulnerability settings are also potentially useful in representing differences between land-based and pelagic predators in access to prey, the manner in which functional feeding relationships can be established is not clear at present. The current specification of EwE would not capture physical influences on krill population dynamics, changes in predator life-history traits in response to changing prey availability, the apparent density-independent preference of many predators for krill as a prey, the abrupt switching between prey types that has been suggested for some predators, or the disproportionate effects of prey shortages on early life stages. Each of these issues is potentially surmountable in future versions of EwE. However, the necessary assumption of a contemporary equilibrium is problematic for an ecosystem that is both naturally variable and probably changing states. The constraint of this assumption might prevent EwE from capturing the processes that drive the system away from equilibrium (Hollowed *et al.*, 2000).

In addition to the possibility that a system might be in a “transient phase” rather than at equilibrium, there are two further reasons why the assumption of a single balance point might be inappropriate. The first is the practical issue of parameterising the model with data collected at different times and different places that may represent different states in the system or different extremes of natural variation. The second is the related issue that uncertainty about these parameter values might imply multiple potential balance points, and therefore require a model that identifies all possible balance points.

EwE was used to model the krill-based food-web around South Georgia, represented by 29 compartments (Bredesen, 2003). The main predators of krill were found to be squid and fish, especially myctophids. Simulation of increased krill fishing suggested that mackerel icefish, *Champsocephalus gunnari*, would be the dependent species worst affected by the fishery, mainly because it is a by-catch species, and that whales and fur seals would also suffer declines. The ecology of the South Georgia area is strongly affected by the apparently variable transport of krill as well as the seasonal migration of predators, so it is inappropriate to regard the area as a self-contained ecosystem. Adequately accounting for interactions with other areas is a major challenge in developing complex models at this scale.

These whole-ecosystem models reinforce the comment of Everson (1977) that the krill-based ecosystem is simple only by comparison with other aquatic systems. Pathways that do not include krill, and consumers that are not well studied, are also likely to be important to the functioning of the ecosystem. In general, attempts to parameterise complex food-web models have been useful exercises in compiling available information that inevitably identify the lack of available data on food-web interactions, particularly the various rate processes.

The mass balance approach is potentially useful in solving for unknown parameters, such as biomass, in partially observed systems, subject to the caveats above. EwE in particular has promoted widespread interest in modelling the ecosystem dynamics of harvested marine systems. Carefully constructed EwE models could be used to predict the potential consequences of management strategies, but should not be accepted as the definitive predictions. The drawbacks of this approach are the high data requirements, including for parts of the system that are not well studied, and inability to estimate the uncertainty associated with model structure (both internal functions and assumed trophic relationships). The important dynamics in a given system might be adequately represented by models of partial food-webs focusing on key species. However, these will need to be specifically constructed, with approaches appropriate to the system and its component species.

## (3) Large-scale models of the Southern Ocean ecosystem

A range of models, with varying complexity, of lower trophic level interactions in the Southern Ocean have been developed. Recent models of note include the three-dimensional coupled model of Hense *et al.* (2003), which studied phytoplankton dynamics in the Antarctic Circumpolar Current and Antarctic Polar Front; Arrigo, Worthen & Robinson's (2003) model of nutrient and plankton dynamics in the Ross Sea; and Lancelot *et al.*'s (2000) model of primary production in the Atlantic sector of the Southern Ocean. These models focus on the biogeochemical and microbial components of the ecosystem and have little or no representation of the larger zooplankton species or any of the higher trophic level species.

Walsh, Dieterle & Lenes (2001) developed a detailed simulation of planktonic processes and their interaction with the physical environment. Plankton interactions include protozoan grazing on flagellates, which promotes diatom growth by reducing competition. Diatoms are the major food for larval krill, and may have a negative impact on salps, a potential competitor of krill (Loeb *et al*., 1997), through clogging their feeding apparatus. This illustrates the potential for complex feedback in the planktonic part of the food-web, so the consequences of a change in the physical environment are not easy to predict.

Huntley, Lopez & Karl (1991) used a simple compartmental design to model carbon flux in the Southern Ocean food-web, to explore the idea that artificial enhancement of primary production could cause the ecosystem to sequester atmospheric carbon dioxide (Martin, Fitzwater & Gordon, 1990). This model suggested that the ecosystem is an inefficient carbon sink because much of the carbon fixed in primary production is returned to the atmosphere via respiration from predators. However, Priddle *et al.* (1998) calculated that the carbon respired by endotherm predators in the Southern Ocean would be a fraction of that implied by Huntley *et al*. (1991). Moloney (1992) also challenged Huntley *et al.* (1991) on the basis of observations from the subtropical Benguela ecosystem, which suggest that the model was an oversimplification and that less carbon would be returned to the atmosphere.

Each of these models gives potential insight into processes that could ultimately affect the krill-based system. It is notable that the models exploring the effects of fisheries rarely consider the influence of trophic levels below krill, and it would be useful to examine the likely interactions between the upper and lower trophic levels. Currently, these lower trophic level models are not formulated to answer questions relating to the management of the fishery. Adapting them to do so will mean linking them to models at very different scales.

## VI. ASSESSMENT AND FISHERY MODELS

## (1) Estimating krill yield

Catch limits for the Southern Ocean krill fishery are set using a population projection model to determine the probability distributions of krill spawning stock biomass before and after the removal of a given annual catch (Butterworth *et al*., 1994). This is used to find the highest long-term annual catch that meets a three-part decision rule (see Constable *et al.*, 2000 for a detailed discussion). To produce these probability distributions the projection model is run thousands of times for each catch scenario, with parameter values for most variables drawn at random from distributions estimated from empirical data. The aim of this approach is to integrate across uncertainties in an estimate of krill biomass from an acoustic survey, and estimates of population processes, particularly recruitment, natural mortality, age at maturity and vulnerability to the fishery.

The decision rule allows for the escapement of a stock considered sufficient to maintain recruitment, and it makes provision for the requirements of predators by ensuring that the fishery does not deplete the krill stock to less than 75% of its unexploited size. 75% escapement is the midpoint between no fishery (100% escapement) and the 50% level that results in maximum sustainable yield in the Schaeffer surplus production model because logistic population growth is highest at half the asymptotic population size. However, this is not suggested as a realistic view of the system, rather an arbitrary but conservative level that has been adopted until a more appropriate estimate can be found. The models of Butterworth & Thomson (1995) and Thomson *et al.* (2000) were specifically designed to address this issue. The decision rule also requires that the krill stock is maintained above 20% of its median unexploited biomass to ensure future recruitment, but again this reference level is arbitrary.

The general approach used in the krill yield model is useful in evaluating uncertainty in krill population dynamics without explicit reference to interactions with other trophic levels. It therefore makes pragmatic simplifications, especially about recruitment, and should not be interpreted as a definitive description of krill population processes. However, improved understanding of these processes could allow the development of a more realistic population model, and allow input values to be constrained to a narrower range, potentially reducing uncertainty in the output. There are also some uncertainties that are not accounted for, including the interpretation of acoustic data on which the estimate of krill biomass is based (Demer & Conti, 2005).

This is a single-species approach that identifies an appropriate krill yield based on a decision rule that can be refined as our understanding of predator requirements and krill recruitment dynamics improves. However, the management advice resulting from this approach must be evaluated in order to be confident that objectives for the krill and its dependent species will be met despite uncertainties in knowledge (de la Mare, 1998; Cooke, 1999; Smith, Sainsbury & Stevens, 1999, Constable, 2002, 2004; Yodzis, 1994). We consider the use of multispecies models to evaluate management strategies in section VII.

### (2) Models of the krill fishery

Mangel (1988) & Butterworth (1988) developed models of the interaction between krill aggregations and harvesting operations to assess the utility of catch rate data as a proxy for krill abundance. The studies concentrated on the Japanese (Butterworth, 1988) and Soviet (Mangel, 1988) krill fisheries, which had different fishing strategies. In the Soviet system, a separate research vessel would search for concentrations, in conjunction with the fishing fleet, but individual fishing vessels would search for swarms within concentrations (Mangel, 1988). In the model of the Japanese system, fishing vessels worked independently to locate concentrations and find swarms within them (Butterworth, 1988).

A fundamental feature of these models was the representation of krill aggregations in both space and time (Murphy *et al.*, 1988). Spatially, both studies used a hierarchy of “patches within patches”. That is, krill form swarms that are in turn aggregated into larger concentrations. Both Butterworth (1988) and Mangel (1988) represented swarms as (initially) circular patches with characteristic radius (around 50 m) and krill density. The swarms themselves were randomly placed in a concentration that was also circular with characteristic radius (around 5 to 11 nautical miles). At a larger scale, the habitat was divided into strata with characteristic concentration densities. Although krill aggregations have a third spatial dimension (depth), the models were effectively reduced to two dimensions. In Mangel (1988), concentrations were moved each day to represent the temporal variability of krill aggregations.

These studies found that catch rate is a poor index of krill density as vessels relocate to unexploited patches to maintain high catch rates despite declines in the overall abundance of krill. There is therefore a need to distinguish between time spent fishing and time spent searching, although there may be practical difficulties in distinguishing between searching for concentrations and searching for swarms.

May *et al.* (1979) commented that krill distribution may be an important modifier of predator-fishery interactions, and these studies highlighted the need to improve the spatial model of krill distribution. The methods used by Butterworth (1988) and Mangel (1988) are potentially useful in simulating krill distribution to derive functional relationships for these interactions. However, this level of spatial resolution is impractical and impossible to initialise in models of ecosystem dynamics to guide management decisions.

Several of the models described in this review have considered the general issue of competition between krill predators and the fishery. However, because the distributions of krill, its predators and fishing effort are highly heterogeneous, the intensity of this competition will be spatially variable. Krill fisheries tend to operate close to land, in areas that are extensively used by krill predators such as seals and penguins, especially during the breeding season. The potential for overlap between these fisheries and predator foraging grounds is widely recognised (Agnew & Phegan, 1995; Croll & Tershy, 1998). Models exploring this overlap show that the fishery could have localised impacts on predator populations, even with a precautionary overall catch limit (Agnew & Marin, 1994; Marin & Delgado, 2001). Reid *et al.* (2004) showed that although they operate at different spatial scales, there was near-complete overlap between fisheries and predators in the Scotia Sea.

## VII. DISCUSSION

The modelling effort described in this review has used a variety of approaches to address various questions at a range of scales. Many of these studies have explicitly focused on the Scotia Sea area where there is a concentration of krill biomass, fishing operations and scientific activity. It is not possible to extrapolate specific results to the Southern Ocean as a whole because of the scale and variability of the system. However, results concerning the applicability of existing models and the requirements of future models are more generally relevant.

The future management of the Scotia Sea krill fishery, and of other fisheries worldwide, will need reliable models to predict the future state of the system. This state in any location, at any time is the result of interacting biological and physical processes that are highly variable in space and time. The modelling effort has generally focused on specific processes or theoretical explorations of ecosystem dynamics. It is now important to consider how these studies can contribute to the development of models that make quantitative predictions about the food-web effects of harvesting.

Our understanding of krill recruitment dynamics remains vague, with few process models to predict recruitment. However, empirical models suggest strong environmental influences. There are consistent patterns of recruitment variation throughout the Scotia Sea. These patterns are correlated with sea-ice extent, which in turn has apparent decadal-scale pseudo-cycles in its variability. This suggests the possibility of forecasting krill recruitment based on predicted ice cover. It also suggests that autocorrelation in krill recruitment should be considered in population dynamics models.

It will be more problematic to model spawning stock effects on krill recruitment. Logically, successful recruitment must depend on the presence of a critical biomass in a suitable area. The methods of Hofmann & Hùsrevõglu (2003) may be useful for identifying this area, especially if they are used with a transport model to predict the fate of krill larvae. However, current information on stock structure and stock-recruitment relationships is not sufficient to revise CCAMLR's assumption that the Scotia Sea krill stock should be maintained above 20% of its median unexploited biomass.

The spatial distribution of krill will affect its interactions with predators and the fishery. These processes will be scale dependent, with advection driving the coarse-scale distribution and behaviour becoming more important at finer scales. Output from numerical ocean models such as OCCAM will be useful in predicting krill transport at a coarse scale (e.g. Murphy *et al*., 2004a) but there are no process models describing the local retention of krill. There are, however, empirical relationships with oceanographic features, and the approach of Murphy (1995) could be used to identify plausible bounds for retention based on predator demand.

The size structure of krill populations will affect their attractiveness to fisheries, and their interactions with predators and physical processes. It is clearly important to capture this size structure in models. The influences on size structure include recruitment, growth, and the potential size-specific effects of transport and mortality. According to Alonzo & Mangel (2001), size could also be a function of an individual krill's survival strategy. Models of small-scale processes, including behaviour and growth, have generally proved useful in developing theory and guiding research. However, their assumptions have not been verified, and they can only make predictions when supplied with detailed data on interacting ecosystem components. These data are generally unavailable. In particular, there are no models to predict the distribution and abundance of lower trophic levels at relevant scales. Consequently, detailed models of fine-scale processes are not suitable for predicting ecosystem dynamics. Nonetheless, such models could be used to suggest functional relationships between ecosystem components, which will be necessary for constructing ecosystem dynamics models.

Most models used to explore predator-prey dynamics in the Southern Ocean, with the exception of Butterworth & Thomson (1995) and Thomson *et al.* (2000) do not consider the demographic structure of the predator population and most, with the exception of Murphy (1995), have no spatial structure. These models either assume a “closed loop” in which the system’s dynamics are driven entirely by harvesting and interactions between the modelled species, or they assume that krill dynamics are not influenced by predator abundance. Furthermore, the interaction between species is reduced to a single functional response. This degree of simplification is unlikely to capture the local dynamics of predator populations or the impact of predation on krill populations.

There is a contrast between the level of detail in these predator-prey models and those used to estimate prey consumption by predators. These consumption models compile information on the energy requirements, diets, activities and population structure of predators. They should be useful for identifying the characteristics that contribute to changes in local demand for prey and that ecosystem dynamics models will need to incorporate.

Although some attempts have been made to model complex food-webs in the Southern Ocean, there is a shortage of data on substantial parts of these food-webs. Mass or energy balance models are able to estimate missing parameters, but their assumptions cannot be verified. Further assumptions are needed to simulate ecosystem dynamics and it is impossible to assess whether these models truly reflect the structure and operation of the real system.

Models predicting the state of harvested systems will need to include more detail on population structure, food-web complexity and trophic interactions than is found in simple predator-prey models. The level of detail assigned to each ecosystem component should be defined by the purpose of the model and the availability of data. Ecosystem dynamics models designed to predict the effects of human activities on harvested species and other ecosystem attributes should include the important characteristics of the harvested species. The rest of the model should be designed around the other ecosystem attributes to be considered. CCAMLR’s conservation objectives concern harvested, “dependent” and “related” species, so relevant models must include details that are important to the dynamics of these species. Many other indicators of ecosystem status have been proposed, ranging from the performance of individual species to community characteristics like biodiversity, size spectra and mean trophic level. The appropriate model structure therefore depends on both the characteristics of the system and the metrics used to assess its state. Bespoke models designed to address specific problems, based on specialised knowledge of the focal system are likely to be more relevant than generalised models. These generalised models might not accommodate the appropriate functions or level of detail, and might be constrained by requirements to specify details for less well-understood parts of the system.

Almost every study that we have discussed has identified considerable uncertainty in the parameter, function or trophic relationship of interest. The extent of this uncertainty is unsurprising given the scale of the system and the gaps in the available data. However, the potential expansion of the krill fishery in the near future leaves little time to increase our understanding. This problem is common to most marine ecosystems: the requirement to implement ecosystem approaches to fisheries by 2010 implies a requirement to achieve this based on current levels of knowledge. It might be possible to refine our comprehension of some key processes in the short term, but we cannot postpone the development of the ecosystem approach until this task is complete. Future management of marine ecosystems should be robust to uncertainties in our understanding of these systems, and the models used to support this management must provide explicit quantification of this uncertainty.

The processes affecting the distribution and abundance of krill and its predators are subject to high degrees of spatial and temporal variation. Modelling studies have improved our understanding of these processes. It is now necessary to produce predictive models that incorporate the large-spatial-scale dynamics of krill populations, and smaller scale interactions with the fishery and local populations of land-based predators. Integrating across scales and ensuring that key processes are represented sufficiently will require attention to the level of detail at each scale. Quantifying uncertainty will require the construction of models that provide a range of forecasts representing the potential future dynamics suggested by our knowledge of the system and the uncertainties associated with this knowledge. The following sections discuss these general issues of complexity and model uncertainty in more detail before considering the requirements for an ecosystem dynamics model of the Scotia Sea.

## (1) Complexity

There is a trade-off between the complexity and utility of models. While too little detail might result in a model that fails to capture important aspects of the system, too much detail is computationally expensive, and produces high levels of uncertainty and output that might be impossible to interpret (Fulton *et al*., 2003). An obvious first step in designing a model is to define its purpose. CCAMLR will require models to predict the dynamics of krill and its predators. The models should focus on the processes driving the dynamics of these focal species. However, it is not necessary to include all of the relevant complexity in a single model. Detailed models of specific processes can be used to derive functions or parameter distributions to summarise these processes in ecosystem dynamics models, or to test the effects of different model structures. This approach allows models operating at different scales to be used together (Salvanes, 2001; Fulton *et al*., 2003; deYoung *et al.*, 2004).

Model complexity can be minimized by limiting the number of food-web interactions included. The choice of food-web components and interactions is a central issue in modelling ecosystem dynamics and output is often more sensitive to the complexity of the modelled food-web than any other factor (Punt & Butterworth, 1995; Bax, 1998). We advocate the development of "minimum realistic models" that include only species that have important interactions with the focal species (Punt & Butterworth, 1995). These models may use different approaches for different trophic levels, with most detail at the level of the focal species (deYoung *et al.*, 2004). Species other than the focal species may be aggregated into functional groups with similar characteristics, as long as these groups do not include organisms that prey on other members of the group, or organisms with rate constants that differ by more than threefold (Fulton *et al*., 2003). If the group of other consumers includes species with very different competitive abilities or levels of specialisation on a particular prey species, the performance of this group will depend on the relative abundance of its component species. However, excessive aggregation of prey species can exaggerate the level of competition amongst predators (deYoung *et al.*, 2004). It is not necessary to include all life stages of species that only interact with focal species during part of their life history. Where different life stages have different interactions with the focal species, it is necessary to represent this ontogenetic complexity (Hollowed *et al.*, 2000), for example by including the different life stages in different functional groups.

In designing a minimum realistic model it is necessary to consider what constitutes an important interaction. Minority prey species should be included if they become important when major prey species are scarce, or if they play “keystone” roles in ecosystem structure or are otherwise limiting, for example because they provide essential nutrients. Otherwise excluding interactions accounting for up to 10% of consumption of and by species in the model might have minimal effects on its predictions (Yodzis, 1998). It is also necessary to consider how to represent influences other than those explicitly included in the model. For example, a variable natural mortality rate could be used to represent the combined effects of several predators.

Some representation of spatial complexity is necessary because spatial processes influence the dynamics and stability of most systems (Hollowed *et al.*, 2000; Fulton *et al*., 2003) and fisheries target specific areas. The degree of spatial complexity needed in a model will depend on its purpose. Although biological interactions between predators and their competitors and prey will be affected by the spatial distribution and motility of each, these interactions may be adequately captured by functional relationships with no spatial resolution. These relationships might be difficult to establish empirically, but plausible functions could be derived using spatially resolved, individual-based models (Berec & Krivan, 2000).

Models do not have to be entirely process-based. That is, they can include empirical, rather than mechanistic, representations of important but poorly understood interactions. Although this approach can produce misleading results (Fulton *et al*., 2003), empirical models can be less prone to bias than incorrectly specified food-web models (Essington, 2004). This is therefore one method of minimising model uncertainty, at least within the domain specified by the data (Fulton *et al*., 2003).

Practical models of ecosystem dynamics must be possible to understand and use, and must also produce meaningful results. It is therefore necessary to minimise complexity while maintaining relevance. Parsimonious models will not make predictions about non-focal species or general ecosystem characteristics like diversity or maturity. They will however make specific and relevant predictions about the effects of harvesting if they focus on directly affected species and those indirectly affected species for which conservation objectives are specified.

## (2) Model uncertainty

The sources of uncertainty in data and models are reviewed in Francis & Shotton (1997), Butterworth & Punt (1999), Patterson *et al.* (2001) and Regan, Colyvan, & Burgman (2002). There are well-developed methods for dealing with many sources of uncertainty, particularly those relating to natural variation and observation errors, although little effort has been devoted to establishing the reliability of the resulting uncertainty estimates (Patterson *et al.*, 2001). Less attention has been devoted to the issue of model uncertainty, which is due to incomplete information about how to represent real systems in models.

In its simplest sense, model uncertainty can be due to a lack of information about the appropriate value for a particular parameter. It can also relate to different future scenarios such as regime shift and climate change, which might be represented as numerical inputs into an ecosystem dynamics model. Finally, it can relate to the structure of the model, such as the specification of functional relationships or which trophic links are included.

Uncertainty in model results can be represented by presenting these results as probability distributions. These can be generated using Monte Carlo projection in which the model is run numerous times with the elements affected by uncertainty randomly selected from a choice representing that uncertainty (Francis & Shotton, 1997). Bayesian methods also give results as probability distributions and they have been used to integrate uncertainties due to model structure in single-species models (McAllister & Kirchner, 2002).

In order to evaluate model uncertainty, it will be necessary to consider the range of plausible alternative model structures as well as parameter values in Monte Carlo projections. This does not necessarily mean that the overall model should include the explicit structures of each set of alternative sub-models. In some cases, a set of alternative sub-models could be summarised by a distribution of input values for the next stage in the model. Also, where possible, alternative structures should be represented with smooth functions that take different forms depending on parameterisation (McAllister & Kirchner, 2002). Defining all the potential models of a given biological process, let alone a complex system, would be intractable. However, most potential models are unlikely, and many will produce similar results.

The alternative models should therefore be a limited set of plausible models that includes the most divergent views of the system (McAllister & Kirchner, 2002), provided these views are consistent with the precautionary approach. Ideally the influence of any model on the results would be weighted by an objective measure of its plausibility, such as its ability to explain historical data.

In the absence of data to assess the plausibility of models, it is possible to assign semi-objective weighting by following pre-defined guidelines such as those of Butterworth, Punt & Smith (1996). The final alternative is to assign the models equal weights and to ensure that the set of alternatives is well balanced to minimise bias due to extreme views of the system. In practice there is a danger that undue weight will be given to politically or commercially motivated views, or models that unintentionally bias the results. Individual models should be carefully scrutinised and their implications evaluated before they are used in the Monte Carlo framework.

Because there may be sets of alternative sub-models at various stages in the overall model, Monte Carlo projections must be implemented in a way that ensures that only sets of logically compatible sub-models are used in each individual run. However, it is not necessary to have multiple sub-models for every process as even diverging models of a system are likely to include some structural similarities, especially for processes supported by strong empirical relationships.

Although little work has been devoted to the assessment of model uncertainty, we believe it can be taken into account in models forecasting the ecosystem effects of fishing. The approach is relatively simple, requiring a choice of alternative sub-models for individual processes in Monte Carlo projections. There are several drawbacks: the addition of alternative sub-models will increase the complexity of the overall model; objectivity in the choice of alternative sub-models and weighting regimes cannot be guaranteed; and the real system might be outside the range suggested by the chosen models. However, expert opinion on what constitutes a plausible range of alternative models will provide an explicit measure of model uncertainty whereas the use of a single “best” model will not.

## (3) Applying this approach to the Scotia Sea krill fishery

Here we describe the main characteristics of a practical ecosystem dynamics model for the Scotia Sea area (Figs 2 & 3). We do not specify the mathematical details of the model. Instead, we present a framework that can accommodate alternative specifications for each of its component processes and is intended to be used in Monte Carlo simulations to integrate uncertainty in parameter values and model structure.

The purpose of the model is to predict the effects of specified krill harvesting strategies on parts of the ecosystem that are most relevant to CCAMLR’s aims and activities:  the krill stock, selected krill predators, and the fishery. The model could be used, for example, to assess the performance of candidate management strategies in a Management Strategy Evaluation approach (Sainsbury *et al.*, 2000). The model’s main outputs concern parts of the ecosystem that are routinely monitored (the grey bubbles in Fig. 2). Its predictions are therefore made in terms of the same metrics that will be used for judging the state of the real ecosystem. This is particularly important because management cannot rely solely on predictive models, and might have to be revised if the system deviates from its predicted state.

A suite of predators are monitored at breeding sites on islands throughout the Scotia Sea, and CCAMLR has defined small-scale management units (SSMUs) around these islands, based on predator foraging ranges (Hewitt *et al.*, 2004b). The proposed model is spatially resolved to the SSMU scale. Each spatial unit would have its own set of parameter distributions to capture spatial differences in characteristics such as krill growth rate. The units would be linked, mainly through the advection of krill, but the migration of predators could also be accommodated. The temporal resolution of the model must account for seasonal differences in the behaviour of focal species, especially predators that migrate away from breeding areas outside of the breeding season.

Each spatial unit has a size-structured krill population. There is no explicit representation of interactions with lower trophic levels because there are no available models to predict phytoplankton availability at appropriate scales. The model therefore integrates uncertainty in krill recruitment and growth as in the krill yield model. However, the parameter values used for any time period can be constrained to represent the influence of the physical environment. This can be used to explore the effects of scenarios such as gradual warming. Recruitment can also be linked to the size of the spawning stock in any combination of spatial units. The effects of advection are modelled through the specification of transport rates between SSMUs derived, for example, from Murphy *et al.*'s (2004a) transport model. Finally, the krill population is reduced by size-specific mortality as a result of interactions with predators and the fishery.

CCAMLR does not routinely monitor the overall size of the krill stock due to considerable logistic and financial constraints, but the Convention specifies the need to maintain populations of harvested species at or above levels that ensure stable recruitment. Local indices of krill abundance, such as the density in key areas, are available. A survey model must therefore link monitored indices to spawning stock biomass.

The model also focuses on monitored predator species. CCAMLR selected the suite of monitored species partly for practical reasons of accessibility and continuity and partly because their collective response to krill harvesting is thought to indicate that of a broader group of krill predators. Although conservation objectives concern all predators in this broader group, the effectiveness of krill fishery management in achieving these objectives must be assessed principally through the performance of the monitored predators.

Population models for these species must be stage-structured to account for differences between juvenile and reproductively mature animals. The key food-web interactions are between these predators and krill. There are many potential sub-models of the process by which krill availability influences predator population size. There is strong evidence for links between krill abundance and predator offspring production (Reid *et al.*, 2005; Forcada *et al.*, 2005), but influences on survival and migration should also be considered. The availability of alternative prey and the abundance of competitor species will also influence this process. Facilitative interactions where, for example, the presence of pelagic predators benefits seabirds by driving prey to the surface, may be as important as competitive interactions. As the performance data collected in CCAMLR’s ecosystem monitoring program generally relate to offspring production, predator dynamics models must generate analogous data. Recruitment to predator populations should therefore be modelled as a two-stage process incorporating offspring production and juvenile survival.

In addition to krill and monitored predators, the models should represent other krill consumers and important alternative prey for the monitored species. The group of alternative prey should include only vulnerable life stages. Many of the other consumers could be grouped together. Uncertainties about these species might be represented by drawing their abundances from one or more distributions.

Modelling food-web interactions requires detailed information about the trophic relationships among species. There are extensive diet data for many predators at various sites on sub-Antarctic islands. These datasets reveal changes over time, which have been linked to changes in the abundance of krill (Hill, Reid & North, 2005; Reid *et al.*, 2005). They are therefore potentially useful in establishing both the key trophic interactions of these species and appropriate feeding functions. There are also data on the diets and population sizes of other krill consumers like baleen whales and some fish. However, our understanding of these other krill consumers remains severely limited.

The model must also include the spatially resolved and size-specific effects of fishing mortality on krill populations. This can be modelled as an implementation of a proposed harvesting strategy, but any potential effects of illegal, unregulated and unreported catch should also be considered. Although the fishery provides fine-scale catch data, commercial companies are likely to aim to maximise performance (catch or profit) over the whole fishing season, so annualised catch will be an appropriate output.

## (4) Concluding remarks

The utility of any modelling approach depends on the availability and quality of relevant data. There is, in fact, an abundance of data available for the Southern Ocean ecosystem, but this is subject to considerable temporal and spatial variability and uncertainty in the data and their interpretation. It is important to ensure that the data themselves are understood, and to be aware that snapshots of limited time periods or areas may introduce bias. This is another reason for developing models that focus on key species rather than attempting to model everything. However, more data collection and analysis is required to implement the model proposed above. Specifically, it is necessary to estimate the population sizes of the relevant predators and their competitors and to model the interactions between predator species, their competitors and the fishery. However, it is not necessary to establish definitive values or functions in the short term, only to define the range of plausible alternatives that can be used to assess uncertainty.

Predicting the effects of harvesting on krill and its monitored predators requires models of the dynamics within a relatively small partial food-web with direct connections between the target species and monitored predators. These models might be simpler to develop than those required for other exploited marine systems with more complex interactions between relevant species. The fact that the focal species have direct trophic connections limits the number of potentially relevant food-web structures. In systems where the focal species are separated by longer food-chains it might be necessary to consider the potential for the relative importance of different trophic pathways to vary over time

The ecosystem effects of human activities and environmental influences potentially include restructuring of the food-web and sudden shifts in the factors controlling ecosystem dynamics. For example, hypothetical scenarios in the Southern

Ocean include increased dominance of krill competitors such as salps, or disruptions to ocean stratification and circulation caused by increased freshwater run-off. The model illustrated in Fig. 3 will not predict these effects. It will be possible to adapt the model to incorporate such scenarios as they are proposed. However, an obvious limitation of most predictive models is that the range of scenarios they can predict is limited by their structure, which, in turn, is limited by what is considered plausible. The uncertainty estimate generated by such models must be viewed in this context, rather than as a definitive quantification of all possible uncertainty.

There is considerable current interest in modelling exploited resources in an ecosystem context (Shannon *et al*., 2004). This has resulted in a variety of approaches to modelling ecosystem dynamics, none of which has yet been used to inform the management of marine fisheries in the Southern Ocean or elsewhere. Quantification of uncertainty is an important feature of the single-species models employed in the current management of the Southern Ocean fishery and is recognised as a critical output of future ecosystem dynamics models (Constable, 2005). CCAMLR is currently evaluating ecosystem dynamics models that have been developed to address the allocation of allowable krill catch to SSMUs. These include a model that focuses on krill and its consumers and specifically considers the effects of uncertainty in key processes by merging results from Monte Carlo simulations using alternative forms of these functions (Watters *et al.*, 2005). Combining these results with those of entirely separate models that have also been developed to address the same problem will give a broad measure of the uncertainty associated with predictions. There is therefore a real prospect that ecosystem dynamics models focusing on relevant interactions will soon be used to help manage the impact of fisheries on clearly defined ecosystem components.

## VIII. CONCLUSIONS

(1) There is general recognition of the need to manage fisheries in a way that controls their effects on the wider ecosystem, including effects that are propagated through the food-web. This approach will need reliable models of the dynamics of interacting species to inform and evaluate management strategies.

(2) A considerable effort has been made to model the characteristics and dynamics of key species in the krill-based system of the Southern Ocean, especially in the South Atlantic. Some of these models have addressed the food-web effects of fishing, but none of the multi-species models produced is currently used in fishery management.

(3) Krill population dynamics appear to be strongly affected by recruitment which, in turn, has been linked to various environmental factors. The importance of such factors varies with area and no single factor provides a reliable predictor of krill abundance. Transport of krill on ocean currents appears to be important in some areas, but the relative influence of transport and local production is not known.

(4) The spatial structure of the environment is likely to be important in the long-term dynamics of the ecosystem, mediating the outcome of competitive interactions amongst predators. The non-linear relationships between krill abundance and its rate of exploitation by both the fishery and predators are also important determinants of ecosystem interactions.

(5) Attempts to model the system have suffered from a shortage of empirical data on trophic relations and rate parameters. Consumption estimates for predators often exceed survey estimates of prey abundance, indicating potential

problems with the data. It is therefore necessary to review these datasets together to determine whether there is a coherent interpretation.

(6) Models of ecosystem dynamics are required to predict the effects of harvesting on other parts of the food-web. It is impossible to establish with certainty the precise nature of the food-web interactions that influence these dynamics. Therefore it is necessary to develop models, and ways of using them, that are robust to this and other sources of uncertainty. Uncertainty can be represented using the Monte Carlo approach to integrate across alternative parameter values and model structures. The output can be used to assess the risk associated with candidate management options.

(7) Models must also be designed to reach a balance between utility and complexity. This can be achieved by developing models that focus on species that are harvested or monitored, and for which management objectives are set. These models simplify interactions between focal species and other components of the ecosystem. Such models will not provide predictions about parts of the ecosystem other than the focal species and it is therefore important to ensure that management objectives, models and monitoring programs are properly integrated.

(8) This approach will require data on the trophic relations and population sizes of focal species and identification of the alternative functional relationships for interactions between model components. Improved characterisation of these relationships could potentially be achieved using detailed, possibly individual based, models run separately from management models. There are good diet data sets for monitored species in the Southern Ocean, but the population sizes of major consumers should be assessed as a matter of priority.

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## FIGURE CAPTIONS

Fig. 1. The Southern Ocean, including the mean position of the Polar Front and the northern boundary of the CCAMLR area.

Fig. 2. Proposed outline for local-scale ecosystem dynamics models to predict the effects of krill fishing. The main focal species is krill, which is represented with a size-based model. Local production is determined by recruitment and growth, which

might be affected by environmental factors, predicted by larger scale climate or ocean models. The krill population will also be affected by transport into and out of the area, derived from a large-scale numerical ocean model, and links to other local-scale models. The krill population is reduced due to catches from legitimate and illegal, unregulated and unreported (IUU) fishing. The other focal species are monitored krill predators. The reproductive output and survival of these species have functional relationships with the availability of krill and other prey and the abundance of interspecific and intraspecific competitors. Specific models will be needed to derive plausible alternative forms of these functional relationships. Populations of monitored species may migrate to other areas. Grey bubbles show ecosystem characteristics that can be monitored in the real system and should be used to define performance measures.

Fig. 3. Proposed use of local-scale ecosystem dynamics models in a regional-scale model to evaluate management options. Each local-scale model would incorporate several alternative representations of important processes. Multiple realisations of the models would be used to generate probability distributions of monitored parameters for key ecosystem components and economic indicators. These would then be compared with reference points to assess the risk associated with the proposed management option.

**Table 1**. Summary of models of key Southern Ocean ecosystem components and interactions

| Reference | Topic | Taxa[†] | Scale of biological organisation | Temporal scale | Spatial scale | Spatially resolved? | Includes uncertainty? |
|---|---|---|---|---|---|---|---|
| Mackintosh (1974) | Growth | Krill | Individual | Years | <10 cm | No | No |
| Hofmann & Lascara (2000) | Growth | Krill | Individual | Years | <100 km | Yes | No |
| Hofmann *et al*. (1992) | Hatching, development | Krill | Individual | Days | <1 km (depth) | Yes | No |
| Hofmann *et al*. (1998) | Transport | Krill | Individual | Months | >1000 km | Yes | No |
| Murphy *et al*. (1998) | Transport | Krill | Individual | Months | >1000 km | Yes | No |
| Alonzo & Mangel (2001) | Habitat selection, growth | Krill | Individual | Years | <100 km | Yes | No |
| Fach *et al*. (2002) | Transport, growth | Krill | Individual | Months | >1000 km | Yes | No |
| Hofmann & Hùsrevõglu (2003) | Hatching, development | Krill | Individual | Days | >1000 km | Yes | No |
| Murphy *et al*. (2004a) | Transport | Krill | Individual | Months | >1000 km | Yes | No |
| Mangel & Switzer (1998) | Habitat selection, foraging | Krill-penguins | Individual | Years | <100 km | Yes | No |
| Alonzo *et al*. (2003a,b) | Habitat selection, foraging | Krill-penguins | Individual, Population | Years | <100 km | Yes | No |
| Butterworth (1988) | Fishery-dependent measures of abundance | Krill-fishery | Aggregations | Days | <100 km | Yes | No |
| Mangel (1988) | Fishery-dependent measures of abundance | Krill-fishery | Aggregations | Days | <100 km | Yes | No |
| Croxall *et al*. (1984) | Prey consumption | Birds | Population | Years | <1000 km | Yes | No |
| Boyd (2002) | Prey consumption | Fur seals-macaroni penguins | Population | Months | <1000 km | No | Yes |
| Butterworth *et al*. (1994) | Population dynamics, yield | Krill | Population | Decades | >1000 km | No | Yes |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Murphy & Reid (2001) | Population dynamics | Krill | Population | Years | <100 km | No | No |
| Thomson *et al*. (2000) | Harvesting impacts on predators | Krill-fur seals | Population | Decades | <1000 km | No | Yes |
| Butterworth & Thomson (1995) | Harvesting impacts on predators | Krill-fur seals/ crabeater seals/ Adélie penguins/ black-browed albatross | Population | Decades | <1000 km | No | Yes |
| Everson *et al*. (1999) | Consumption by predators | Mackerel icefish | Population | Years | <100 km | No | No |
| Kock (1985) | Prey consumption | Notothenid fish | Population | Years | <1000 km | Yes | No |
| Agnew & Phegan (1995) | Distribution of foraging effort | Penguins | Population | Months | <100 km | Yes | No |
| Agnew & Marin (1994) | Predator-fishery overlap | Penguins-fishery | Population | Months | <1000 km | Yes | No |
| Marin & Delgado (2001) | Predator-fishery overlap | Penguins-fishery | Population | Months | <1000 km | Yes | No |
| Croll & Tershy (1998) | Predator-fishery overlap | Predators | Population | Months | <1000 km | No | No |
| Constable (2001) | Production | Prey and predators | Population | Decades | <100 km | No | Yes |
| Green (1975) | Nutrient dynamics, ecosystem structure | Food web | Community | Months | >1000 km | No | No |
| Everson (1977) | Energy flow | Food web | Community | -- | >1000 km | No | No |
| Doi (1979) | Population dynamics | Food web | Community | Decades | >1000 km | No | No |
| May *et al*. (1979), Beddington & May (1982) | Population dynamics | Krill-whales-seals-cephalopods | Community | Decades | <1000 km | No | No |
| Huntley *et al*. (1991) | Carbon sequestration | Food web | Community | -- | >1000 km | No | No |
| Yamanaka (1983) | Population dynamics | Krill-seals-whales | Community | Decades | <1000 km | No | Yes |
| Murphy (1995) | Population dynamics | Krill-whales- | Community | Decades | <1000 km | Yes | No |

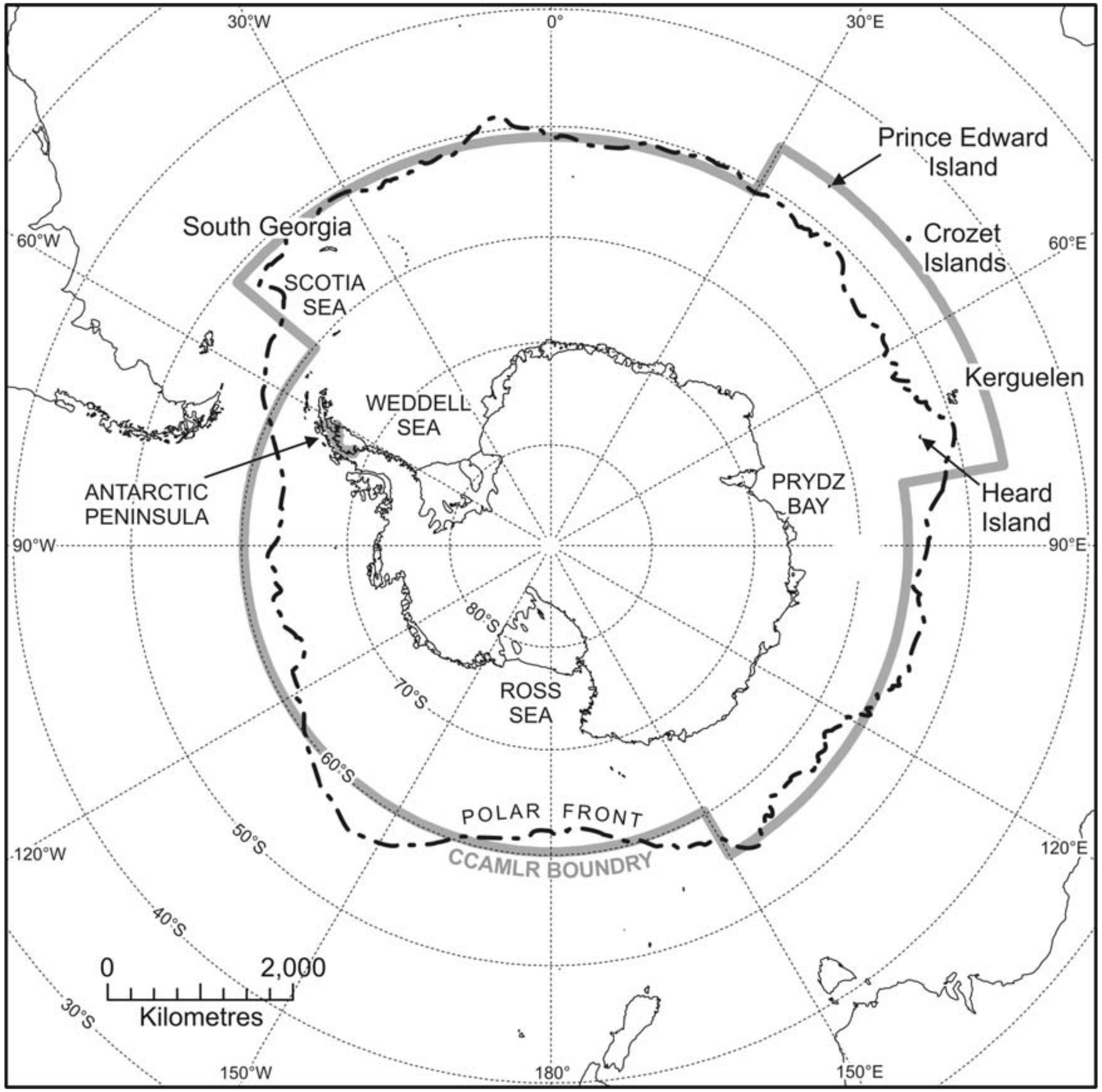
| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | penguins-seals | | | | | |
| Bredesen (2003) | Population dynamics | Food web | Community | Decades | <1000 km | Yes | Yes |
| Walsh *et al*. (2001) | Nutrient dynamics | Planktonic community | Community | Months | <1000 km | Yes | No |
| Arrigo *et al*. (2003) | Nutrient dynamics | Planktonic community | Community | Decades | >1000 km | Yes | No |
| Hense *et al*. (2003) | Nutrient dynamics | Planktonic community | Community | Months | >1000 km | Yes | No |
| Lancelot *et al*. (2000) | Nutrient dynamics | Planktonic community | Community | Months | <1000 km | Yes | No |
| Mori & Butterworth (2004) | Population dynamics | Krill-blue whales-minke whales | Community | Years | >1000 km | No | Yes |

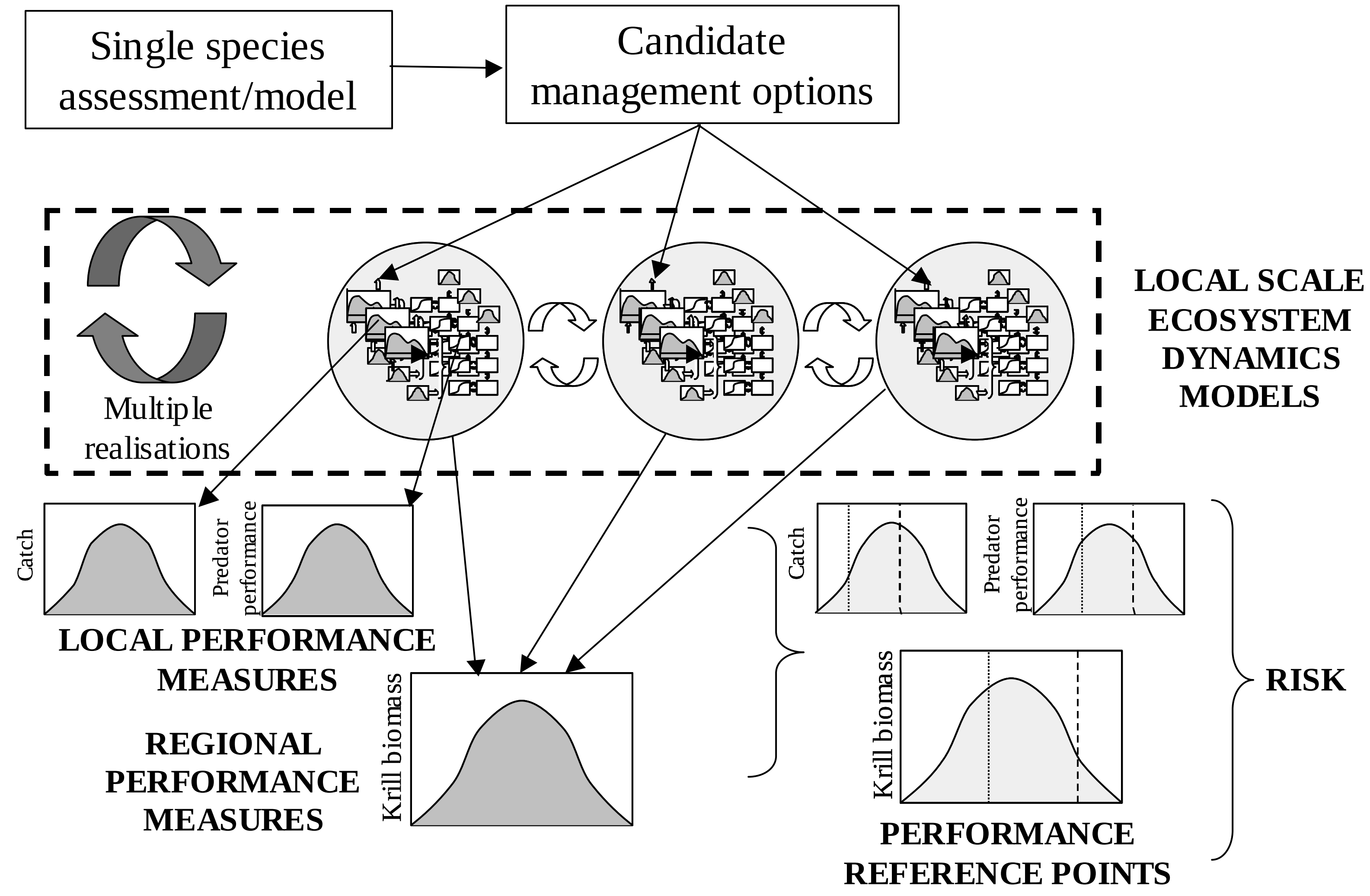
† The taxonomic names of species mentioned in this list but not in the main text are: *Pygoscelis adeliae* (Adélie penguin) and *Diomedea melanophris* (black-browed albatross).

**Table 2**. The key equations used in selected models of predator-prey interactions in the Southern Ocean. The equations are presented for one-predator-one-prey versions of the models.

| Reference | Equations | Parameters & Notes |
|---|---|---|
| May *et al.* (1979) | $\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K} - \frac{aN_2}{r_1} - F_1\right),$<br>$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{\alpha N_1} - F_2\right)$ | *N*: population size.<br>t: time<br>*r*: intrinsic rate of population growth.<br>*K*: carrying capacity for prey.<br>*a*: (maximum) per capita consumption of prey by predators.<br>*F*: harvest rate.<br>*α*: proportionality constant relating prey abundance to carrying capacity for predators.<br>Subscript 1 refers to prey and subscript 2 refers to predators. |
| Murphy (1995) | $\frac{dN_{1,i}}{dt} = \left(\frac{T_{i-1}D_i}{A_{i-1}}\right)N_{1,i-1} - \left(\frac{T_i D_i}{A_i}\right)N_{1,i} - aN_{2,i}\left(\frac{N_{1,i}}{\sum_{i'} N_{1,i'}}\right) - F_{1,i} - M_{1,i}N_{1,i},$<br>$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{aN_1}\right) - F_2 N_2$ | *T*: transport rate out of region.<br>*D*: diameter of semicircular region.<br>*A*: area of region.<br>*M*: natural mortality rate.<br>Subscripts *i* and *i'* refer to regions, where the predator forages in all regions, *i'*. |
| Butterworth & Thomson (1995) and Thomson *et al.* (2000) | $N_{2,y+1} = N_y S_A(B_{1,y}) + N_{y-L+1} S_J(B_{1,y-L+1})\left(\prod_{y'=y-L-2}^{y} S_A(B_{1,y'})\right)\left(1 - \frac{\beta N_{2,y-T+1}}{O}\right)$ | $S_A(B_1)$: survival rate of adult predators at prey biomass $B_1$.<br>*L*: age of first parturition in predators.<br>$S_J(B_1)$: Survival rate of juvenile predators at prey biomass $B_1$.<br>*O*: equilibrium number of predators.<br>*β*: constant set so that $N_2=O$ at equilibrium (to simulate a density- |

| | | |
|---|---|---|
| | | dependent constraint on recruitment).<br>Recruitment is 0 when the last term is <=0.<br>$S_A(B_1)$ and $S_J(B_1)$ are monotonic functions of $B_1$.<br>The predator model describes only the adult female part of the population.<br>Subscript $y$ refers to year. |
| Constable (2001) | $B_{1,y+1} = B_{1,y} e^{-M_1 - f_{1,y}} + r_1 B_{1,y} \left( 1 - \frac{B_{1,y}}{K} \right),$<br>$N_{2,y+1} = N_{2,y} e^{M_2} + r_2 e^{-M_2} N_{2,y} \left( 1 - \left( \frac{B_{2,y}}{P(B_{1,y})} \right)^{\zeta} \right)$ | $f$: fishing mortality rate.<br>$P(B_1)$: maximum stable biomass of predators supported by prey biomass $B_1$.<br>$\zeta$: shape parameter to adjust the degree of density dependence.<br>Recruitment is 0 when the least term in the each model is <=0.<br>The formulation of this model in Constable (2001) also includes interspecific competition at each trophic level and age structure in the predator model. |
| Mori & Butterworth (2004) | $B_{1,y+1} = B_{1,y} + r_1 B_{1,y} \left( 1 - \left( \frac{B_{1,y}}{K} \right)^{\zeta} \right) - \frac{a N_{2,y} B_{1,y}}{B_1^* + B_{1,y}},$<br>$N_{2,y+1} = N_{2,y} + \frac{\mu N_{2,y} B_{1,y}}{B_1^* + B_{1,y}} - M_2 N_2 - C_{2,y}$ | $B_1^*$ : prey biomass at which per capita consumption by predators is half of $a$.<br>$\mu$: maximum per capita birth rate for predators.<br>$C_{2,y}$: catch of predators in year $y$ |


30°W
0°
30°E
Prince Edward Island
South Georgia
Crozet Islands
60°W
60°E
SCOTIA SEA
Kerguelen
WEDDELL SEA
ANTARCTIC PENINSULA
PRYDZ BAY
Heard Island
90°W
90°E
80°S
70°S
ROSS SEA
60°S
POLAR FRONT
CCAMLR BOUNDRY
50°S
120°W
120°E
40°S
0
2,000
Kilometres
30°S
150°W
180°
150°E


Single species assessment/model
Candidate management options
Multiple realisations
LOCAL SCALE ECOSYSTEM DYNAMICS MODELS
Catch
Predator performance
LOCAL PERFORMANCE MEASURES
Krill biomass
REGIONAL PERFORMANCE MEASURES
Catch
Predator performance
Krill biomass
PERFORMANCE REFERENCE POINTS
RISK