

## FITTING *EUPHAUSIA SUPERBA* INTO SOUTHERN OCEAN FOOD-WEB MODELS: A REVIEW OF DATA SOURCES AND THEIR LIMITATIONS

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### Abstract

This paper aims to provide the overview needed to include krill in food-web models and to guide modellers to key sources of data. It describes the strengths of each method of sampling krill, i.e. with nets (for historical time series, demographic information and live krill), acoustics (distribution, time series, biomass and swarm-scale information), the fishery (sustained sampling in one place and wide area and time coverage) and via predators (long time series, demographic indices). Each data source has caveats and more efforts to combine them are recommended. Observations that krill occupy the under-ice layer, the 0–10 m layer, the deeper water column and the benthos have fundamental implications, both for assessing biomass and for modelling the food web. Temporally, the intense (order of magnitude) interannual variability in krill population size within the southwest (SW) Atlantic sector is a major scale of variability, driven by sea-ice and climate effects on recruitment. This variability masks top-down predation controls that may operate over multi-decadal scales. Growth in spring, summer and autumn is now fairly well quantified, but mortality remains an enigma. We are still not yet confident which are the major predators of krill but studies increasingly suggest that they are not currently birds or mammals. Krill feed across three trophic levels and can control food populations through locally high grazing impact and nutrient regeneration. They also have fundamental regional differences in overwintering strategies, on-shelf/off-shelf distributions, relationships with sea-ice and diet. Whether this reflects ‘subpopulations’ with regionally specific life cycles is still unclear. However, caution is urged when scaling-up food-web models and their parameterisations, either from individual to schooling krill, or from one region to another.

### Introduction

Few species of pelagic animals have received as much research attention as Antarctic krill (*Euphausia superba*). This is because (i) they have an important role in the food web of parts of the Southern Ocean (Croxall et al., 1999; Hopkins et al., 1993a, 1993b; Stowasser et al., 2012); (ii) the species is a potentially valuable resource (Nicol et al., 2011); and (iii) the species is associated with sea-ice for its early life cycle (Daly and Macaulay, 1991; Siegel and Loeb, 1995), and reductions in sea-ice have prompted concerns over what might happen to these populations in future (Atkinson et al., 2004; Flores et al., 2012).

Antarctic krill (hereafter simply referred to as krill) are micronekton (up to 65 mm in length) and relatively long lived (up to 7 years), can swim fast and maintain their position in the ocean, unlike zooplankton. They have schooling behaviour that gives rise to very large swarms and a patchy distribution. Difficulties in sampling krill across their

full habitat and in experimentation mean that significant uncertainties remain over their biology, biomass, sources of mortality, population structure, and movement/migration. These uncertainties impact on the ability to make informed predictions on population changes that might be occurring as a result of natural variability, past or current harvesting, or climate change.

This review aims firstly to help identify key references and sources of data that will help food-web modellers represent post-larval krill in their models. Many aspects of krill biology have been reviewed (e.g. Marr, 1962; Miller and Hampton, 1989; Quetin et al., 1994; Everson, 2000; Croxall and Nicol, 2004; Hofmann and Murphy, 2004; Siegel, 2005) so there is a strong focus on new developments and the recent literature. Secondly, it provides an overview of the strengths, caveats and uncertainties in the data used to parameterise these models. This paper focuses on post-larval krill; larval stages are included in the accompanying paper

Table 1: The major surveys conducted for CCAMLR, specifically for management purposes. Three recent large-scale krill surveys (BROKE, CCAMLR-2000 and BROKE-West) have been conducted to provide biomass estimates to CCAMLR so that precautionary catch limits can be set for the krill fishery (Nicol et al., 2000a, 2010; Hewitt et al., 2004a). All three used similar (although not identical) survey designs and used modern scientific echosounders and adopted some form of stratification of effort so that the geographic extent of krill habitat in the respective areas was covered. It is thus possible to compare these surveys to examine regional differences in krill distribution, density and biomass – although they occurred over the course of a decade. Note that the biomass estimate presented here for Area 48 is at the lower end of a wide range of estimates for this area (see Table 2).

Survey	CCAMLR Area (see Figure 1)	Area surveyed (million km <sup>2</sup> )	Catch limit in 2007 (million tonnes)	Biomass (million tonnes)	Reference
BROKE (1996)	Division 58.4.1	0.873	0.44	4.83*	Nicol et al. (2000b)
CCAMLR-2000	Area 48	2.065	3.47	37.3	SC-CAMLR (2007)
BROKE-West	Division 58.4.2	1.500	2.53	28.81	Nicol et al. (2010)
Total		4.438	6.44	71.0	

\* uses outdated method for estimation of krill biomass

on zooplankton (Atkinson et al., 2012b). A general caveat that applies to many aspects of krill ecology is that much of our understanding is based on a small number of observations or time series. Thus, theories, hypotheses and conceptual models have been constructed to explain or group our observations and these are necessarily based on incomplete knowledge.

### Sampling krill to provide robust abundance estimates

Sampling the full habitat volume of krill

Estimates of the geographic range of krill are from 8 to 32 million km<sup>2</sup> (Miller and Hampton, 1989; Nicol et al., 2000a; Siegel, 2005) with a conservative recent estimate of 19 million km<sup>2</sup> (Atkinson et al., 2009). Table 1 shows that modern acoustic and net surveys have covered <25% of the range. Sampling an unevenly distributed species across a vast habitat area poses obvious logistical challenges for estimating biomass.

Typically, the density of krill is estimated and then scaled to a volume of water. Figure 1 illustrates schematically the extent of habitat volume of krill and how to sample it. The key units of survey estimation for krill are the wet mass m<sup>-2</sup> (i.e. biomass density) and no. m<sup>-2</sup> (numerical density). The current paradigm is that krill are a species that primarily live in the top 200 m and this forms the

depth boundary of the estimation volume, due to the concentrations (no. m<sup>-3</sup>) here being orders of magnitude higher than those in deeper water layers. Thus, acoustic and net surveys for CCAMLR stock assessment (Table 2) sample from the near surface (typically ~10 m depth for acoustics) down to ~200 m and in areas not affected by sea-ice.

This survey design misses four additional components of krill habitat. The first is the underside of sea-ice – an important habitat for krill year-round (Brierley et al., 2002; Flores et al., 2012b). The second is the 0–10 m layer of the open ocean/sea-ice, which is ‘invisible’ to acoustics and often not properly sampled by nets either. Large-scale analyses of length-frequency distribution reveal that there is widespread undersampling of juvenile krill ~20 mm long (Atkinson et al., 2009; Kawaguchi et al., 2010), perhaps due to undersampling of the surface layer because of net mesh selection and avoidance (Kratkatsa et al., 1993; Pakhomov, 2000).

The third undersampled component of habitat is the seafloor. There are many direct benthic observations of krill down to 3 500 m depth (e.g. Piepenburg et al., 2002; Gutt and Siegel, 1994; Clarke and Tyler, 2008). They have also been found in the diets of benthic predators (Dearborn et al., 1991; Main and Collins, 2011) and their stomachs can contain seabed-derived material (Ligowski, 2000). However, these observations have always been assumed as exceptional, anecdotal, or winter-only and have

Table 2: Estimates of total krill biomass within the area of the CCAMLR 2000 Krill Synoptic Survey of Area 48 (CCAMLR-2000 Survey), surveyed in January–February 2000.

Method	Biomass estimate (million tonnes)	Reference
Nets	38.6	Siegel et al. (2004)
CCAMLR-2000 Survey acoustics	44.3	Hewitt et al. (2004a)
SDWBA method of analysing acoustic data	108–192.4	Demer and Conti (2005)
Updated SDWBA	37.29	SC-CAMLR (2007)
MaxEnt acoustic analysis	414	Heywood et al. (2006)

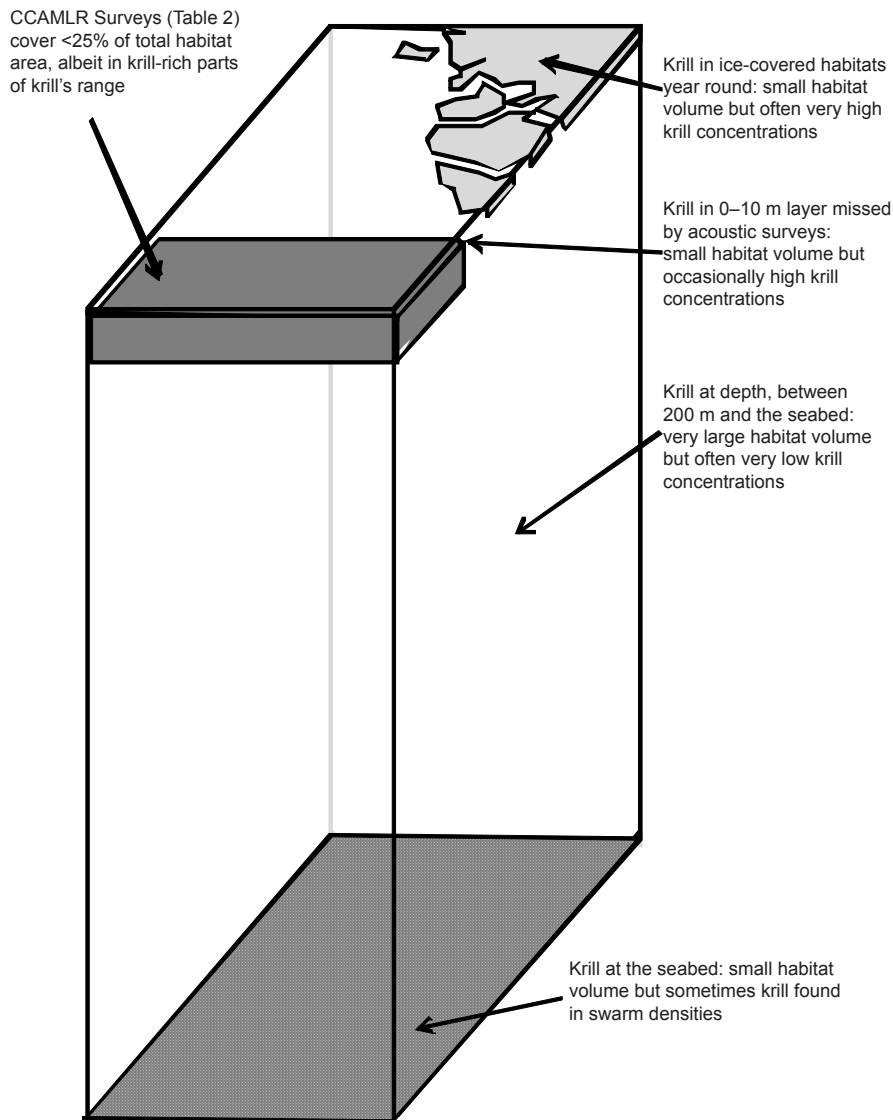


Figure 1: Schematic representation of habitat volume occupied by krill. The vertical extent of this habitat is defined here as the water column and seafloor up to 3 500 m in depth, the deepest that krill have been recorded so far (Clarke and Tyler, 2008). CCAMLR daytime acoustic biomass surveys of the 10–200 m layer (Table 2) cover 22% of the nominal 20 million km<sup>2</sup> habitat area and 5% of the total depth range of the species, defined as 0–3 500 m. This survey volume contains the highest abundances of krill, but is drawn approximately to scale with unsurveyed portions of the habitat.

never been incorporated into models. In a recent comprehensive study Schmidt et al. (2011) found that forays to feed on the benthos occurred year-round throughout Antarctica, and regularly with an estimated ~20% of the stock deeper than 200 m at any one time.

The fourth undersampled vertical habitat is the water column between 200 m and the seabed. Schmidt et al. (2011) included this habitat in the abovementioned 20% calculation. The key point here is that the numbers of krill  $m^{-2}$  is a product of the no.  $m^{-3}$  and the habitat volume (Figure 1). This means that the great habitat volume of waters deeper than 200 m partially compensates for the very low densities of krill either residing in, or transiting, these deep waters to or from the seabed.

The issue of undersampled krill has fundamental implications beyond simply determining their biomass. While benthic feeding occurs year-round (Schmidt et al., 2011), there is evidence for a seasonal vertical migration to greater depths in winter that is possibly superimposed upon these regular (probably daily) commutes to the seabed (Taki et al., 2005; Lascara et al., 1999; Fielding et al., 2012). It is uncertain whether krill occupy all components of habitat at all times. Nicol (2006) argued that there is differentiation between life stages between different components of the habitat. This may lead to undersampling particular life-history stages not found in the sampled areas, thus affecting estimates of, for example, recruitment strength.

There is now a clear need to include all four of these components of krill habitat in conceptual and numerical models involving krill. For example, foraging near ice floes, in deep water or at the seabed exposes krill to radically different food and predators than they would experience in the 10–200 m layer, and may include key aspects of their biology such as mating at depth (Kawaguchi et al., 2011), overwintering (Meyer, 2012), benthic-pelagic coupling and nutrient regeneration (Schmidt et al., 2011).

#### Approaches to estimating abundance of krill

Methods for assessing absolute krill biomass/abundance have been reviewed by Watkins (2000). They identified issues such as accuracy of estimates of krill biomass or numerical density within the defined volume of the water that is being measured,

as well as how representative the survey area is relative to the overall krill population. The strengths and weakness in the main methods of sampling krill to provide data of use in food-web models are briefly reviewed below.

#### Sampling krill using nets

The accuracy of determining density of krill using a net has been a controversial issue because of the potential for net mesh selection and avoidance of the net. Mesh sizes of modern scientific nets range up to 4.5 mm for the 8 m rectangular midwater trawl (RMT8). Siegel (1986) compared catches between the RMT8 and a 330  $\mu$ m 1 m RMT (RMT1) mounted above it and found that the former retained only ~63% of krill 20 mm long. Only when krill were >25 mm did the length frequencies from the two samplers converge, so the RMT8 seriously undersamples the 0+ juvenile cohort.

Net-avoidance by krill is well documented and believed to result in major underestimates of krill density (Hamner and Hamner, 2000; Watkins, 2000; Wiebe et al., 2004), but this view is mainly based on the use of zooplankton nets. This paper suggests that underestimates are likely to be well within an order of magnitude when larger nets, typical of modern krill surveys (RMT8), are used. Supporting evidence includes the following: (i) the only comparison using more typical krill sampling gear, an RMT8, found clear evidence of avoidance during the day but not at night (Everson and Bone, 1986); (ii) a comparison with acoustic studies during the CCAMLR 2000 Krill Synoptic Survey of Area 48 revealed broadly similar mean biomass density to that revealed by acoustics (Siegel et al., 2004; Hewitt et al., 2004a; Kasatkina et al., 2004); (iii) a calculation of circumpolar biomass based on 8 137 net hauls revealed a total biomass of 117 million tonnes (Atkinson et al., 2009), not dissimilar to estimates based on acoustics (Siegel, 2005); and (iv) simple calculations show that biomasses an order of magnitude greater than these would be unsupported from primary production (Priddle et al., 1998; Arrigo et al., 2008). A major limitation of net sampling is the tiny fraction of the total survey volume that can be sampled with any single survey (Watkins, 2000). Thus due to the patchy distribution of krill, mesoscale estimates of mean density based on nets can be very imprecise, and compare poorly to those from acoustics (Kasatkina et al., 2004; Pauly et al., 1997, 2000;



Jarvis et al., 2010; Kawaguchi et al., 2010). Analyses of large-scale composites of net data (e.g. Marr, 1962; Mackintosh, 1973; Atkinson et al., 2008) may reduce this problem, but such analyses yield climatologies rather than synoptic pictures of distribution.

#### Sampling krill using acoustics

Net sampling of krill has been increasingly replaced by acoustics for estimating biomass. This has been adopted by CCAMLR as the standard on which estimates of precautionary yield are based (Hewitt and Demer, 2000; Macaulay, 2000). While this produces an accurate measure of acoustic backscatter in the depth range from a few metres below the transducer to the attenuation depth for the frequency being used, the major challenge is to attribute the detected backscatter to specific species, and then to scale it to provide a biomass estimate. This is a technical issue that remains under current development. Some advances have resulted in significant changes in the calculation of krill target strength, a key parameter in converting backscattered energy into krill density (Table 2).

The variety of biomass estimates in Table 2 were all derived from a single survey, and illustrate the effect of the method used for scaling up the data from a series of line transects to the whole of the surveyed area. For example, the standard Jolly and Hampton (1990) method has been in use for 20 years but there have been various attempts to use other analytical methods, all of which give very different results depending on (i) assumptions about how to use the data to predict the distribution of krill in the survey area, and (ii) the acoustic target strength used for krill (Murray, 1996; Heywood et al., 2006) (Table 2). These considerations also pose the questions of how to design a survey so that known krill-rich hotspots do not cause a distorted picture (Watkins et al., 2004). Overall, comparisons between different surveys have to ensure that comparable methods have been used for data collection and analysis.

#### Sampling krill using the fishery

Information on fishing method, length frequencies, by-catch etc. is collected through the CCAMLR Scheme of International Scientific Observation ([www.ccamlr.org](http://www.ccamlr.org)), with further data also archived by fishery operators (Kawaguchi et

al., 2005). The fishery effort in recent years has been concentrated mainly in the Scotia Arc region, but this is not a reliable indicator of overall krill distribution because the fishery is also dictated by a suite of commercial and operational factors (Butterworth, 1988; Kawaguchi et al., 2005; Litvinov et al., 2004; Kawaguchi and Nicol, 2007). Information on the operational behaviour of the fishery (e.g. search effort, swarm selectivity) is needed before fisheries catch and effort data can provide a reliable index of krill density (Mangel, 1988, 1989; Butterworth, 1988). However, careful analysis yields information on where fishable concentrations of krill occur consistently and at what depth, or where they can be found when they are absent from the small areas that are surveyed scientifically (e.g. Taki et al., 2005; Kawaguchi et al., 1997, 2005).

Other problems that may arise with fisheries data include (i) potential error in catch weights arising from the method used to convert these from product weights; and (ii) catchability of krill using the different methods may range between 0.1 and 0.5 (Czubek, 1981; Akishin, 1988; Zimarev et al., 1991). While the above highlights some of the drawbacks of using fisheries-derived krill data, standardised catch-per-unit-effort (CPUE) data may have some utility in providing time series of relative abundances when the fishery operates in the same area within a season and/or between seasons and at times when other scientific activities cannot be undertaken (Kawaguchi and Nicol, 2007; Schmidt et al., 2011). Increasingly, the use of krill fishing vessels to carry out research will result in data that can be more confidently used for management.

#### Sampling krill using predators

The dynamics of the krill population has been inferred from the diet and performance of krill-dependent predators (e.g. Agnew, 1997; Croxall et al., 1999; Forcada et al., 2006, 2008; Hill et al., 2012; Boyd and Murray, 2001; Trivelpiece et al., 2011; Reid and Croxall, 2001). However, care is needed to relate these measures correctly to the spatial and temporal dynamics of the krill population. Such observations may also provide insights into krill–predator–fisheries interactions (Reid et al., 2005; Hill et al., 2007b, 2012a; de la Mare and Constable, 2000).

While predator performance and population size may reflect the availability of krill, their diet reveals further insights into prey availability and its population structure. Thus the contribution of krill to the diets of their predators can reflect inter-annual variability in krill availability (Hill et al., 2005; Waluda et al., 2012; Hill et al., 2012a) and the median size of krill in predator diets can also be a useful proxy (Forcada et al., 2008). Data from krill predator diets have been used to identify krill recruitment pulses (Reid et al., 1999) and to make inferences about krill growth rates (Reid, 2001) and regional population dynamics (Murphy and Reid, 2001; Reid et al., 2002).

Inferences about krill populations from predator performance and diet can be prone to bias, nonlinearity and noise. A major source of bias is the fact that predators are not random samplers of the whole krill population. Predator variables should be described as *indicators* of krill availability since they are unlikely to have access to the whole population. Factors such as the vertical and horizontal distribution of krill in relation to the foraging range and diving depth of predators, the density of swarms and the presence of competitors or natural enemies of the predators may all influence this (Croxall et al., 1985, 1988; Reid et al., 1996; Nicol, 1993; Trathan et al., 2012). Predators also select krill according to size, sex, etc. (Hill et al., 1996). Such interactions (including multiple-predator interactions) are important to consider in ecosystem models (Hill et al., 2006).

A second major issue is the form of the predator's functional response, indicating how consumption rate changes relative to prey availability. Boyd and Murray (2001); Reid et al. (2005) and Cury et al. (2011) present evidence for asymptotic functional responses in many krill predators while Waluda et al. (2012) suggest that the functional response for macaroni penguins is sigmoidal. The functional response will also be modified by the availability of alternative prey (Hill et al., 2005).

In summary, krill data useable in food-web models can be provided by nets, acoustics, fisheries and predators. However, each method has its own particular sources of uncertainty and bias. A challenge is to synthesise data (a good example being on interannual variability) from each approach. Important insights can be gained, for example, by

exploring the form of relationships derived by multiple methods (e.g. Pauly et al., 2000; Hewitt et al., 2004a; Kasatkina et al., 2004).

## Krill distribution

### Circumpolar distribution

There have been many attempts to estimate the global biomass of Antarctic krill (e.g. Miller and Hampton, 1989; Nicol et al., 2000a; Siegel, 2005; Atkinson et al., 2009). Recent values range from 67 to 297 million tonnes based on acoustics (Siegel, 2005), 117 to 379 million tonnes using nets and 113 million tonnes by combining both methods (Atkinson et al., 2009). This total biomass is strongly concentrated in the southwest (SW) Atlantic sector with 75% of the population in the 0–90°W sector (Marr, 1962; Mackintosh, 1973; Siegel, 2005; Atkinson et al., 2008). How krill maintain their distribution in good habitats for growth is still unknown (Thorpe et al., 2007; Atkinson et al., 2008), but probably reflects a combination of factors that allows completion of the whole life cycle (Pakhomov, 2000; Nicol, 2006).

The SW Atlantic sector is unique in containing krill in the outer northern fringes of the Antarctic Circumpolar Current (ACC) (Krafft et al., 2010). Further east in the Lazarev Sea, there appear to be two 'populations' of krill, one in the ACC and another in the East Wind Drift, much closer to the continent. This may reflect distinct stocks or sub-populations (Mackintosh, 1973), which may even be genetically distinct. However, genetic studies on krill have yielded ambiguous results (Fevolden and Schneppenheim, 1988, 1989; Zane et al., 1998), perhaps due to the methods used (Jarman and Nicol, 2002). Genetic homogeneity may result from genetic exchange over a shorter time period, despite stock separation on the timescale of a few generations, the timescale of interest to management. Clearly, determining the degree of connectivity between subpopulations is a central issue for regionally based management within CCAMLR.

At the scale of individual sectors, relationships between krill distribution and the environment are hard to generalise. For example, right across the 80–150°E (Indian) sector there is a positive relationship between krill abundance and the average extent of winter sea-ice (Nicol et al., 2000b; Pakhomov, 2000). However, this relationship

breaks down in sectors of very extensive ice cover (e.g. the Weddell and Ross Seas) and in areas such as South Georgia where there is little or no annual sea-ice (Nicol, 2006). Circumpolar associations have been suggested between krill abundance and fronts, e.g. the Southern Boundary of the ACC (SBACC) (Tynan, 1998), but this does not hold universally. For example, in the Indian sector the north–south transition from low to high krill density is south of the SBACC (Nicol et al., 2000a, 2000b), whereas in the Scotia Sea it is near the Southern ACC Front (Ward et al., 2012).

### Regional and finer-scale distribution

Although temporally ephemeral, there are locations where high densities of krill are often found and these areas are well mapped by the fishery (Ramm et al., 2005). Both physical and biological processes appear to lead to this stability in areas of regular occurrence of krill aggregations. Large-scale recirculation (stable eddies) create physically driven retention zones that may temporarily isolate krill aggregations within them from the broader population. In these cases, patterns of abundance would more likely reflect the dominance of advection over births and deaths. Active movements by the broader krill population may also occur and may serve to maintain the population in a favourable habitat (Nicol, 2006). In this case, the residence time of the krill in these favourable habitats would be considerably longer, allowing local factors (birth and death) to dominate the temporal pattern in abundance (Siegel, 1988). Obviously, when interpreting biomass changes, it is critical to know which of these processes is dominant.

The relative importance of advection/retention and krill behaviour is a key issue in understanding krill ecology. The dominant paradigm, particularly in the South Atlantic, is that the system is dominated by advective forces and that krill populations are drifting from the west to the east and north in the ACC (Hofmann and Murphy, 2004). Thus krill data from a single location can be interpreted as the result of an influx from ‘upstream’ rather than as a result of in situ processes. As described above, there is increasing evidence that in the South Atlantic, there are areas where the population of krill has extended residence times and that in some areas there are even semi-resident stocks (Reid et al., 2010; Wiebe et al., 2011). It may also be the case that the factors affecting the distribution of

sub-adults are quite different from those affecting adults (Nicol, 2006). Thus distributions or time series need to be examined carefully to ensure that interpretations are not merely a product of the conceptual model which underlies the observations.

An important regional scale of krill distribution is their relationship to shelves. Some specific areas associated with shelves, such as canyons (Santora and Reiss, 2011), banks (Trathan et al., 1998) and shelf breaks (Warren and Demer, 2010) may attract semi-dependable concentrations of krill that are exploited by predators and fishing fleets alike. Many papers have linked high krill abundance to shelves and shelf breaks but the nature of this relationship varies regionally. For example, krill are most abundant in the inner shelf along the Western Antarctic Peninsula (Lascara et al., 1999; Ross et al., 2008), whereas in the Indian sector they are found typically in oceanic water but within 200 km of the shelf break (Hosie and Cochran, 1994; Pakhomov, 2000). However, Atkinson et al. (2008) calculated that 87% of their global population were located over oceanic water >2 000 m deep, with its great habitat area and low mean krill densities overcompensating for high densities over the much smaller habitat area of the shelf. These authors rationalised this distribution using a risk-reward model, concluding that areas of high food abundance were also high in predators, which results in this area being no better for net population growth than the lower-risk, lower-reward habitats offshore, albeit with radically different growth/mortality dynamics.

Krill are gregarious animals, with some schools estimated at >2 million tonnes (Macaulay, 2000; Nowacek et al., 2011). Such rare but large aggregations can contain large fractions of the total regional biomass (Tarling et al., 2009), challenging our ability to sample them representatively. However, the typical length scale for swarms is much smaller, with most being tens of metres to several hundred metres across and classifiable in terms of size and relative dimensions (Tarling et al., 2009; Cox et al., 2010). Schools can also be common and large in some years but rare and more diffuse in others (Fielding et al., 2012) and they change diurnally, regionally and seasonally in size, depth and frequency of occurrence (Godlewska, 1996; Lascara et al., 1999; Klevjer et al., 2010). Schooling is a fundamental property of krill so it needs to be incorporated into models and considered when examining the ecological effect of krill.



## Temporal variation in abundance and biomass

### Interannual and decadal variability

Acoustics and net sampling monitoring surveys and indices from krill-dependent predators provide information on variability in krill numerical density and biomass across multiple timescales (Siegel et al., 1998; Ross et al., 2008; Reiss et al., 2008; Brierley et al., 1999; Atkinson et al., 2004, 2008; Croxall et al., 1999; Forcada et al., 2008). In addition to the plethora of problems of sampling krill quantitatively, factors such as the seasonal timing of the survey or irregular movement of pulses of krill into a survey area can contribute to interannual variation and reduce our ability to evaluate trends (Siegel, 1988; Saunders et al., 2007; Reiss et al., 2008; Reid et al., 2010). Despite these issues, many studies reveal significant and persistent interannual relationships between the amount of krill, their size distribution, predator performance, sea-ice extent and climatic indices (Siegel and Loeb, 1995; Pakhomov, 2000; Quetin and Ross, 2003; Atkinson et al., 2004; Murphy et al., 2007b). Just as surprising, the variability is concordant right across the Scotia sector (Brierley et al., 1999; Atkinson et al., 2004). This suggests that a combination of climate and sea-ice have strong, and possibly additive, effects on krill recruitment causing great yearly fluctuations, mainly in abundance but also in biomass.

There has been some confusion in the literature over time trends in numerical density and those of biomass density, with the two terms sometimes being used interchangeably. At an interannual scale, the two measures do not scale linearly, so interannual trends in mean biomass density are not the same as those in numerical density. This is because krill recruitment is highly episodic, with on average only a few, irregularly spaced recruitment events per decade needed to sustain the population (Siegel and Loeb, 1995; Quetin and Ross, 2003; Siegel et al., 2003). These years reflect a population greatly swelled by numerous small krill, each with an individual mass which may be only 10% of that of the larger krill.

Several studies in the SW Atlantic sector have found positive correlations between the extent of winter sea-ice and subsequent krill recruitment and population size, but the mechanisms are poorly known (Siegel and Loeb, 1995; Loeb et al., 1997,

2010; Atkinson et al., 2004; Quetin and Ross, 2003; Murphy et al., 2007a, 2007b, 2012). Recruitment is affected by a sequence of previous environmental conditions in both summer and winter that can extend back to ~2 years beforehand. This includes factors affecting spawning stock size and reproductive output per female (Quetin and Ross, 2001; Schmidt et al., 2012) plus subsequent larval survival during summer, autumn and winter.

Recruitment has been studied by a combination of field experimentation, time-series analysis and modelling. Together, these approaches show that timing of suitable conditions is crucial (Quetin and Ross, 2001, 2003; Quetin et al., 2007). For example, a recent modelling study by Lowe et al. (2012) found that the dynamics of the autumn decline in pelagic phytoplankton, the advance of winter sea-ice and its microbial communities and the late winter increase in available ice algae were all important factors governing larval condition and survival. Conditions conducive of life cycle completion are also regionally specific, for example ice cover is not regionally identical in providing conditions for growth and shelter from predators (Fritsen et al., 1998; Meyer et al., 2009). Recent work is further emphasising the light regime, both for providing a cue for seasonal behaviour of post-larvae (Meyer, 2012) and in determining the exposure of sea-ice to winter sunlight, thus generating sea-ice microbial communities. Clearly much work still needs to be done to understand this critical issue of krill recruitment.

Interannual fluctuations in krill recruitment are ultimately driven by climatic cycles that operate over a range of scales (Figure 2). Quetin and Ross (2003) showed that west of the Antarctic Peninsula, krill recruitment success was positively correlated with neutral or moderate El Niño or La Niña indices as accumulated over 15 months influencing the strength of a year class, i.e. both reproductive output and winter survival of the larvae. Failures in krill recruitment have been associated with a strong El Niño Southern Oscillation (ENSO) signal, whether El Niño or La Niña; a different effect to that observed further north near the tip of the peninsula by Loeb et al. (2010). In the Scotia Sea area Murphy et al. (2007a, 2007b) found that climatic variability, related to ENSO and the Southern Annular Mode, generated anomalies in water

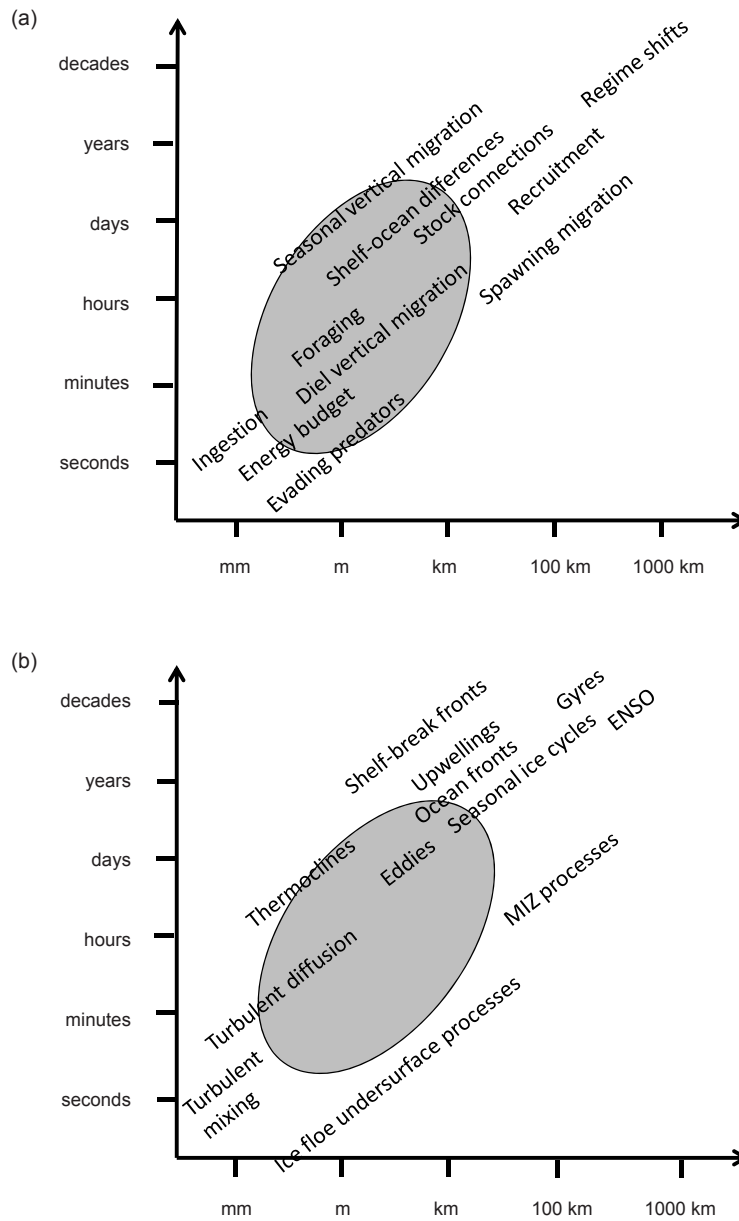


Figure 2: Conceptual time–space diagrams adapted from Murphy et al. (1988) showing (a) the characteristic scales of krill-related processes and (b) the corresponding scales of physical processes. The shaded areas represent the scales of immediate influence from krill swarms. Note, however that scales at each process propagate upwards in space and time to influence larger scale processes. The ability of krill individuals and swarms to migrate vertically and horizontally faster than purely physical transport rates means that the key krill-related processes operate over shorter timescales for a given space scale than key physical processes. Sea-ice forms an exception to this rule, affecting krill dynamics across a great range of timescales and space scales (Murphy et al., 1988).

temperature and corresponding sea-ice anomalies, leading to variation in recruitment and dispersal of krill in the Scotia Sea area.

Sub-decadal-scale periodicity in krill population dynamics has not been studied so intensively outside the SW Atlantic sector. However, around Prydz Bay (Indian sector) Pakhomov (2000) found that 3–4-year cycles with increased warm deep-water input from the north led to large numbers of salps north of the Antarctic Divergence and successful krill spawning in the region. These years have the lowest summer ice coverage and are followed by the intensive ice accumulation during the winter. This induces strong recruitment of the 1+ age group in the southern part of the Prydz Bay Region during the next summer, which in turn may promote a krill biomass increase 1–2 years later (Pakhomov, 2000).

#### Multi-decadal variability

Several studies in the SW Atlantic sector suggest longer-term trends in krill abundance or recruitment that appear to be superimposed on variability described above (Fraser and Hofmann, 2003; Loeb et al., 1997; Reid and Croxall, 2001; Atkinson et al., 2004; Trivelpiece et al., 2011). These studies tend to concur that mean krill density and recruitment strength declined in the latter decades of last century, but the magnitude, geographical extent, timing or the exact causes of this are still not properly known. A clear candidate is the warming along with winter ice loss which has affected the Bellingshausen/Amundsen Seas most strongly (Stammerjohn et al., 2008a, 2008b), but also extends across the Scotia Sea (Meredith and King, 2005; Whitehouse et al., 2008). Southwards shifts in biogeographic distribution are an expected outcome of regional warming (Pakhomov et al., 2002; Mackey et al., 2012), but have not yet been conclusively demonstrated for the krill population.

It is tempting to extrapolate past relationships (e.g. between krill and sea-ice) when modelling future scenarios, but the confidence will be low until we know more about the mechanisms of population control (Fraser et al., 1992; Reid et al., 1999; Wiedenmann et al., 2009; Murphy et al., 2007a). This problem is best illustrated in the Northern Hemisphere, where Beaugrand (2012) found a long-standing relationship between zooplankton indices and the winter North Atlantic

Oscillation (NAO) broke down suddenly around 1988. He suggested that the climate had changed the ecosystems to such an extent that the old drivers lost their importance and new factors came into play. Likewise, Loeb et al. (2010) found that the role of winter sea-ice in recruitment has been supplanted in importance by more subtle ENSO-related factors during the recent decades of more stable sea-ice and krill abundance near the tip of the Antarctic Peninsula.

Historical krill population changes may also be a product of the changes in the balance of predators caused by harvesting (Ainley et al., 2007). A variety of models suggests that superimposed longer-term trends could be linked to the major shift in balance among the higher predators due to sequential over-fishing (Mori and Butterworth, 2007; Willis, 2007; Trathan et al., 2012). However, these long-term changes would occur through complex feedbacks operating in both bottom-up and top-down modes simultaneously (Nicol et al., 2010), which emphasises the caution needed when seeking simple solutions to ecosystem problems.

#### Krill rate processes relevant to food-web modelling

Figure 2 illustrates the timescale and space-scale dependence of key aspects of krill biology, in relation to its environment. It illustrates the special characteristic of krill schooling highlighted by Murphy et al. (1988). By forming aggregations that are three orders of magnitude larger than the length of one krill, they can interact with the physics and the rest of the food web, both on the scale of the krill and on the scale of a school-sized ‘super-organism’. This is a much wider range of scales than, for example, a copepod, and suggests caution in transferring zooplankton-type modelling parameterisations directly across to krill. The benefits of schooling are poorly known (Ritz et al., 2011), but this fundamental property needs to be taken into account when modelling their food-web interactions.

This review is limited to recent developments in assessing the gain and loss terms (growth and mortality) as well as the feeding processes that may exert top-down control on their prey populations. These processes are more relevant to food-web models than detailed descriptions of the energy budget. The latter topic is covered elsewhere (e.g. Miller

and Hampton, 1989; Quetin et al., 1994; Pakhomov et al., 2002; Meyer, 2012; Atkinson et al., 2012a).

### Growth and production

Early work on growth rates was based on sequential sampling of the length-frequency distributions of krill from the field. Despite major assumptions required by this method, plausible-looking seasonal growth curves were obtained (Rosenberg et al., 1986; Miller and Hampton, 1989). Measuring growth rates in the laboratory has been less successful (Quetin et al., 1994) and the advent of the Instantaneous Growth Rate (IGR) method (Quetin and Ross, 1991) provided the first real cross-check on the in-situ growth curves. The IGR method has since provided empirical model predictions of growth and moulting rate based on time of year, food, temperature, krill length, sex and maturity stage (Ross et al., 2000; Kawaguchi et al., 2006; Candy and Kawaguchi, 2006; Tarling et al., 2006; Atkinson et al., 2006; Brown et al., 2010).

These growth predictions are useful because they allow krill to be ‘grown’ in models using satellite-derivable data, shortcutting the problem of having to model the entire energy budget to determine growth. Growth is a net-gain term in the energy budget so direct growth models can be used, for example to explore habitat suitability (Atkinson et al., 2008; Murphy et al., 2007b) or the effect of future climate change (Wiedenmann et al., 2008; Lowe et al., 2012). However, the unit of growth predicted from IGR is length, not mass, and this causes problems in models using mass as a currency. That is because krill stop growing in length for parts of the year and either increase their reproductive output or their overwintering energy reserves. These seasonal changes are reflected in lipid content (Hagen et al., 2001), length–mass relationships (Siegel and Nicol, 2000) and proximate, elemental and calorific composition (Donnelly et al., 1994; Färber-Lorda et al., 2009, and references therein). The second problem is that the predictive IGR models for post-larvae do not yet incorporate the long winter period. Whether krill grow or shrink, even slightly, is important because the winter period is so long. More generally, poor knowledge of the winter period is a major obstacle for all models and annual budgets involving krill.

Partly for this reason, annual production and P:B ratios of krill are difficult to estimate. These further

depend on the exact definitions of both the mass and the growth terms and whether larval growth is included. The current consensus on annual production (Miller and Hampton, 1989; Ross and Quetin, 1986; Atkinson et al., 2009) is ~100–500 million tonnes for post-larvae, and it is probably nearer the high end of this range. This value is similar to, or slightly larger than, their summer maximum biomass.

### Mortality rates and sources

Mortality rates of krill are much more poorly known than growth rates. Mortality has been estimated in a variety of ways (see Miller and Hampton, 1989; Siegel and Nicol, 2000), which follow the expectation that the lowest rates are for medium-size krill (Pakhomov, 1995, 2000). However, the main sources of this mortality are not known. The iconic krill predators in Antarctica, marine mammals and birds, are much more studied than fish or squid. The relative importance of these air-breathing predators as the primary sources of mortality has recently been challenged, with food-web analyses using Ecopath showing that fish may be much more important than originally thought (Hill et al., 2012).

The South Georgia Ecopath model also found that estimated krill production exceeded the sum of their estimated consumption rates from all known krill predators (Hill et al., 2012). This particular system is one of the most intensively studied in the Southern Ocean, with a series of ‘krill budgets’ incorporating advective supply of krill to the region, advective loss, growth and mortality (e.g. Croxall et al., 1984; Atkinson et al., 2001; Gilpin et al., 2002; Murphy et al., 2007a). While these studies have reached a variety of conclusions on the relative importance of these processes, the recent Ecopath food-web model suggests that there may be significant sources of mortality that we do not know about. These could include, among others: non-capture injury/mortality from predators, benthic mortality sources, or disease/parasites/non-predation mortality. Food-web models and budgets now face a challenge in attributing mortality sources in a meaningful way.

### Role of krill feeding

The consumption of food by krill determines the extent to which they control phytoplankton stocks



and how much of their production is transferred into the krill-based food web. Krill feeding studies have a long history, and the slowness of progress on this topic exemplifies the great difficulty in obtaining real-world data. Krill feed readily in captivity; the problem is in translating the results to the real world of swarming krill in a patchy Southern Ocean environment. The discussion below tackles critical topics that appear to be particularly sensitive terms in Nutrient–Phytoplankton–Zooplankton (NPZ) and food-web models, namely diet, prey switching, the shape of the functional response and maximum feeding rates (Buitenhuis et al., 2006; Gentleman and Neuheimer, 2008).

#### Diet, prey switching and trophic level

Krill are sufficiently large to feed across three trophic levels, namely phytoplankton, protozoans and metazoans (mainly copepods). However, the question is the extent to which they feed on each level and whether there is active switching (defined here as a behaviourally induced change in feeding method) or passive prey switching (i.e. a fixed feeding method but a diet that changes simply due to the change in composition or size of the ambient food). In the wild krill feed actively in large dense swarms so some authors suggest that there is little selection for food quality or type – particulate matter that enters a krill swarm will get consumed.

Krill were originally classed simply as filter feeders of phytoplankton, chiefly diatoms, based on mouthpart morphology, observations of feeding and the prevalence of diatoms in their guts (Barkley, 1940; Kils, 1983). However, subsequent work challenged this view. Their guts were found to contain metazoan remains (Hopkins et al., 1993a, 1993b; Huntley et al., 1994; Pakhomov et al., 1997; Perissinotto et al., 1997) and in incubations they ingested copepods at high rates (Price et al., 1988; Granéli et al., 1993; Atkinson and Snýder, 1997). Some studies went further to suggest that krill could have competitive or predator–prey interactions with copepods (Atkinson et al., 1999; Hernández-Leon et al., 2001).

The last decade, however, has seen a partial return to earlier views, and a questioning of the idea that krill switch to feeding on copepods or protozoans outside of bloom periods. Protozoans indeed appear to be an important food resource, but this is both inside and outside of bloom periods,

with fatty acids suggesting an additional role of small flagellates as well as the large thecate ciliates and dinoflagellates visible in gut contents analysis (Hopkins et al., 1993a, 1993b; Alonso et al., 2005; Schmidt et al., 2006, 2011, 2012). However, these studies have generally failed to detect large numbers of copepods in their guts. Krill have a low  $^{15}\text{N}$  ratio suggestive of a mainly herbivorous diet (Schmidt et al., 2003, 2004; Stowasser et al., 2012). Benthic feeding has been described from gut contents analysis (Ligowski, 2000; Schmidt et al., 2011) with this linked with enhanced ingestion of sediment grains, benthic diatoms, copepods, phyto-detritus and bacteria.

These seabed-surface differences represent active prey switching, as they entail behavioural responses linked to a change in diet. Active prey switching also occurs between sea-ice and the underlying water. Meyer (2012) found that feeding was an important part of krill's winter energy budget, but ice-derived sources seem more important for larval and juveniles than adults (Meyer, 2012; Atkinson et al., 2002; Quetin et al., 2007).

Some studies suggest that adult krill do actively select specific phytoplankton taxa. Haberman et al. (2003b) found that in mixtures of diatoms and prymnesiophyte colonies of the same size, clearance rates on the latter were significantly less than those on the diatom. In natural assemblages of diatoms, prymnesiophytes and cryptophytes, krill again selected for the diatoms. Thus food size, handling time, feeding basket blockage, nutritional quality and phytoplankton composition all effect clearance rates (Haberman et al., 2003a, 2003b).

#### Maximum feeding rates and functional response

This study considers that the most realistic maximum daily ration estimate is that derived by Perissinotto et al. (1997) of  $\sim 13\%$  of body  $\text{C d}^{-1}$ . This value is lower than that derived by Clarke et al (1988), who had to make assumptions over assimilation efficiency. Assimilation and gut throughput of krill have subsequently been found to be highly variable (Perissinotto and Pakhomov, 1996; Atkinson et al., 2012a; Schmidt et al., 2012) making Clarke's original egestion-rate method less suitable to derive ingestion. However, adult summer maximum rations of about 13% fit with maximum growth rates estimated at  $\sim 25\%$  of this value,

based on energy budget calculations (Straile, 1997; Quetin et al., 1994; Atkinson et al., 2006). Maximum summer/autumn rations of larvae were ~20–25% body C d<sup>-1</sup> (Meyer et al., 2003; Pakhomov et al., 2004) so those of adults are probably lower than this.

The functional response of krill ingestion to food concentration has seldom been measured. Although the results generally show a Holling type II functional response for compression filtration (water column) with a relatively high critical concentration (Price et al., 1988; Ross et al., 1998; Oakes, 2008), the maximum ingestion rate and critical concentration are inconsistent, reflecting the great difficulty in obtaining realistic rates on a free-living swarming organism held in the laboratory. Oakes (2008) found a Holling type III functional response curve in larval and small sub-adult krill feeding in a simulated ice-scraping mode, but Holling type II in compression filtration mode.

## Discussion

Krill biomass can be sufficient to affect trophic levels below them as well as above. Areas of high krill abundance have been linked to the dominance of flagellates relative to diatoms (Kopczynska, 1992) and to reduced phytoplankton concentrations (Whitehouse et al., 2009; Wright et al., 2010), with this interpreted as a grazing effect. These areas have also been found to show elevated specific rates of nitrogen uptake by the remaining ungrazed cells (Whitehouse et al., 2011), possibly a 'conditioning effect' by krill, due to their locally intense ammonium regeneration due to excretion (Priddle et al., 1997; Atkinson and Whitehouse, 2000). Krill have also been attributed with a top-down effect in the iron cycle, either in recycling this element (Tovar-Sanchez et al., 2007; Nicol et al., 2010) or via seabed foraging and subsequent return to the surface which can import 'new' iron into surface waters (Schmidt et al., 2011). Thus krill may have diverse roles right across the food web from nutrients to whales, and we are only just starting to understand some of these.

These unique features of krill mean that they cannot be incorporated easily into existing generic food-web models. Developing 'end-to-end' food-web models involving krill is a task for the future; most 'krill food-web' models only explore the trophic links from krill upwards, while biogeochemical

models typically work upwards towards krill. In a recent review, Hill et al. (2006) identified three broad categories of model representing Antarctic krill. These comprised firstly models exploring specific aspects of krill biology such as life cycle, energetics or behaviour (e.g. Hofmann and Hüsrevöglu, 2003; Murphy et al., 2004; Fach et al., 2008; Lowe et al., 2012). The second group were multi-species population models, simulating either historic changes in the abundance of krill and its predators or the effects of harvesting on interacting species (e.g. Butterworth and Thomson, 1995; May et al., 1979; Murphy, 1995; Mori and Butterworth, 2004). The third category included single species population projection models, for example to quantify regional catch limits (Butterworth et al., 1994; Constable and de la Mare, 1996).

Since this 2006 review, several authors have used a fourth type of model: mass-balance regional food-web models incorporating krill (Cornejo-Donoso and Antezana, 2008; Pinkerton et al., 2010; Hill et al., 2012b). The mass balance constraint is that consumption of a prey group cannot exceed production by that group over an arbitrary time period (Steele, 2009; Polovina, 1984), of one year in each model. Also, several groups have recently developed spatially resolved multi-species dynamics models, which have been used to evaluate proposed management measures for the krill fishery in the Scotia and Bellingshausen Seas (Plagányi and Butterworth, 2012; Watters et al., in rev; Constable, 2005; Hill et al., 2007a).

Hill et al. (2006) suggested that the multi-species dynamics models should include a size-structured representation of the krill population; an explicit recruitment process that incorporates stock size, environmental and stochastic effects; a representation of krill transport between areas; and explicit interactions with krill predators. Both Plagányi and Butterworth (2012) and Watters et al. (in rev) represented numerical krill abundance and used a constant mass (Hill et al., 2007b) to convert this to biomass and hence fishing and predation mortality. The models also required stock recruit parameters, intrinsic population growth rates and biomass or density estimates for krill. The discussion presented here would help facilitate further development of these components of the models. In addition, Hill et al. (2007b) provided an approach for modelling krill transport at the maximum advection rate indicated by the OCCAM global circulation model

which, they suggested, represents an upper bound on the uncertainty and should therefore be contrasted with zero transport.

The interactions of both predators and the fishery with krill depend ultimately on the fine-scale spatial interactions considered above. This relationship is highly uncertain (Hill et al., 2009), and is difficult to represent well in models because of the mismatch of scales between model representation and the scales of biological processes (Hewitt et al., 2004b; Hill et al., 2007b; Plagányi and Butterworth, 2012; Watters et al., in rev). Better information is needed on the respective probabilities of the fishery and predators encountering exploitable densities of krill at the smaller scale of fishing operations (c. 3.5 nm) and foraging trips (Waluda et al., 2010; Cresswell et al., 2007, 2008).

There is a general acceptance amongst modelers that parameter estimates for krill are often highly uncertain and subject to spatial, seasonal and interannual variability, but that the extent of this uncertainty and variability is not often clear (Hill et al., 2006, 2007a, 2007b). Consequently, many models incorporate innovative methods for assessing or dealing with uncertainty (e.g. Butterworth et al., 1994; Constable and de la Mare, 1996; Plagányi and Butterworth, 2012; Watters et al., in rev; Hill et al., 2012b). The information presented in this review could be used to help refine some of these uncertainties as well as identify the critical gaps that need to be filled in delivering robust representations of krill in food-web models.

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