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

A. Atkinson✉*
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET
United Kingdom
Email – aat@pml.ac.uk
*New address: Plymouth Marine Laboratory
Prospect Place, The Hoe
Plymouth PL1 3DH
United Kingdom

S. Nicol and S. Kawaguchi
Australian Antarctic Division
Department of the Environment, Water, Heritage and the Arts
203 Channel Highway
Kingston, Tasmania 7050
Australia
and
Antarctic Climate and Ecosystems CRC
University of Tasmania
Private Bag 80
Hobart, Tasmania 7001
Australia

E. Pakhomov
Department of Earth and Ocean Sciences
University of British Columbia
6339 Stores Road
Vancouver, British Columbia, V6T 1Z4
Canada

L. Quetin and R. Ross
Marine Science Institute – UCSB
Santa Barbara, CA 93106-6150, USA

S. Hill
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET
United Kingdom

C. Reiss
NOAA Fisheries
Antarctic Ecosystem Research Division
8604 La Jolla Shores Drive
La Jolla, CA 92037, USA

V. Siegel
Institut für Seefischerei
Palmaille 9
22767 Hamburg, Germany

G. Tarling
British Antarctic Survey
Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET
United Kingdom

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^2)	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^2 (Miller and Hampton, 1989; Nicol et al., 2000a; Siegel, 2005) with a conservative recent estimate of 19 million km^2 (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^{-2} (i.e. biomass density) and no. m^{-2} (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^{-3}) 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 (Krakatitsa 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.

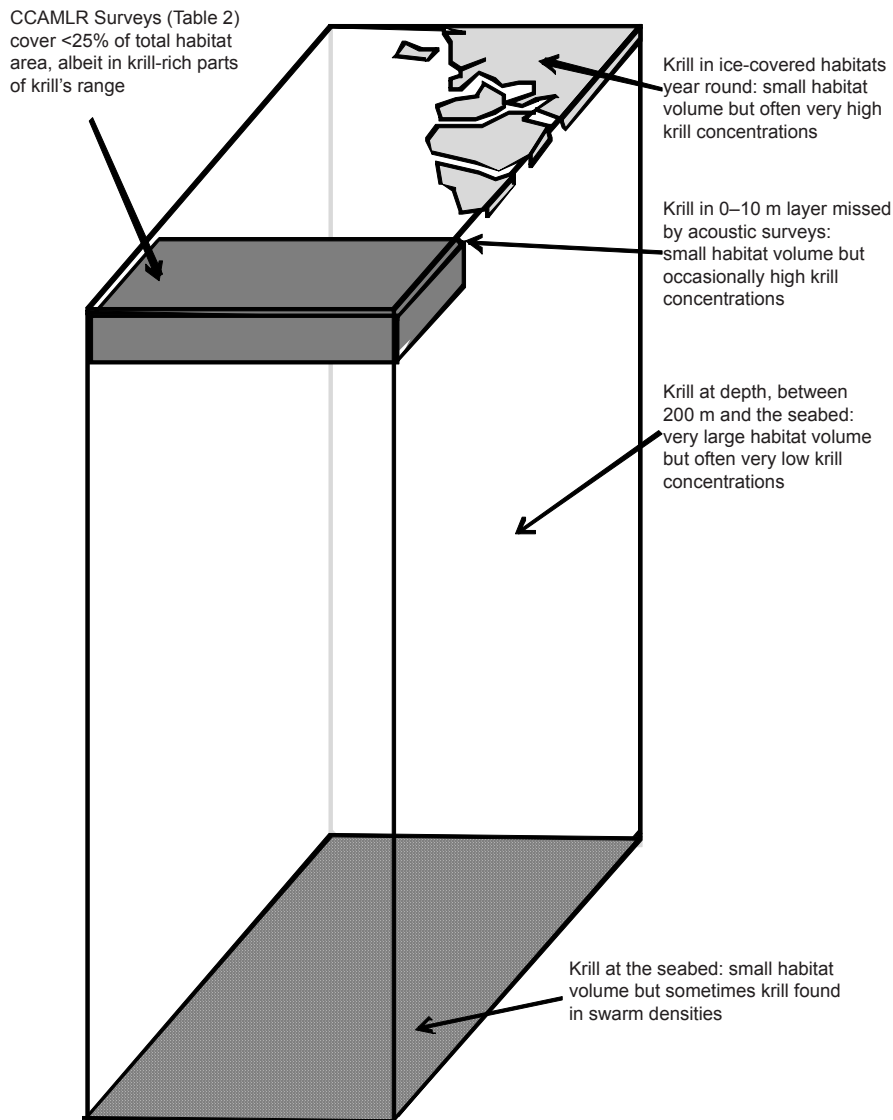| Method	Biomass estimate (million tonnes)	Reference
Nets	38.6	Siegel et al. (2004)
CCAMLR-2000 Survey acoustics	44.3	Hewitt et al. (2004a)
SDWBA method of analysing acoustic data	108–192.4	Demer and Conti (2005)
Updated SDWBA	37.29	SC-CAMLR (2007)
MaxEnt acoustic analysis	414	Heywood et al. (2006)

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^2 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), bentho-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 μm 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 unsupportable 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), 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 subpopulations (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 Nina 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 Nina; 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
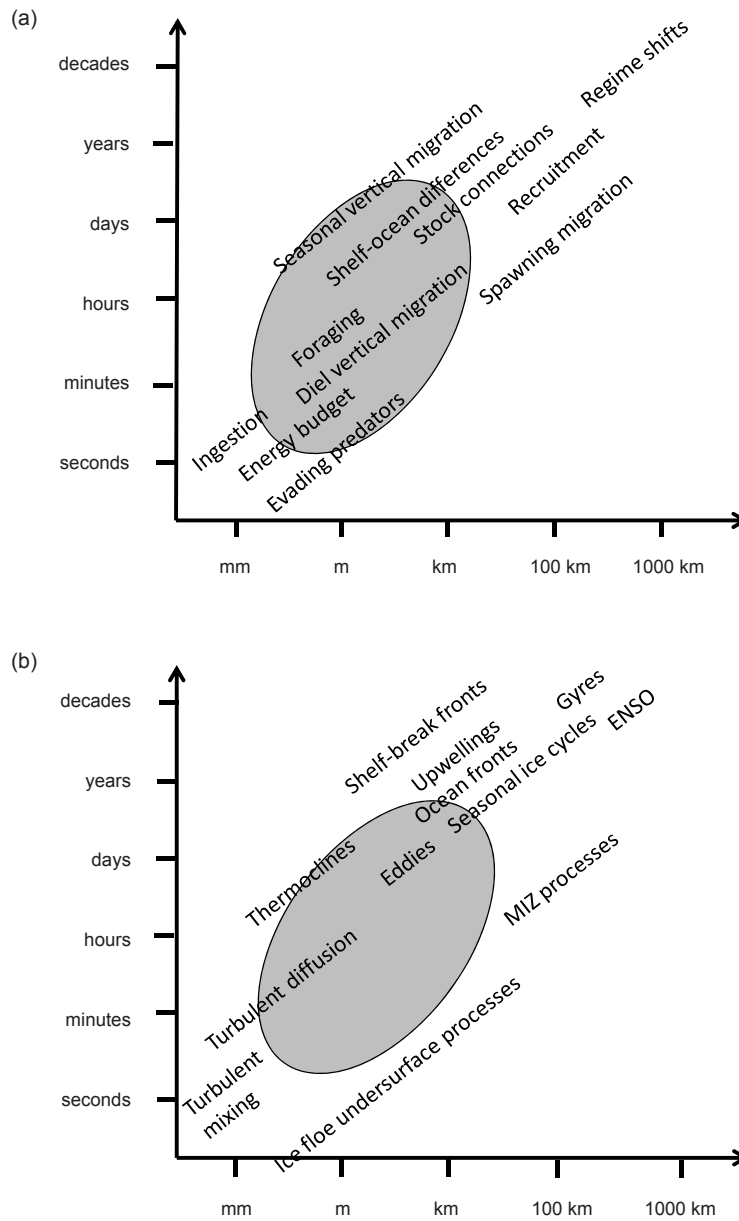
Figure 2: Conceptual time–space diagrams adapted from Murphy et al. (1988) showing (a) the characteristic scales of krill-related processes and (b) the corresponding scales of physical processes. The shaded areas represent the scales of immediate influence from krill swarms. Note, however that scales 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 though (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 Snÿder, 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}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, phytodetritus 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 ~13% of body 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 ~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^{-1} (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 Hùsrevõglu, 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 modellers 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.

Acknowledgements

References

Agnew, D.J. 1997. Review: the CCAMLR ecosystem monitoring programme. *Ant. Sci.*, 9 (3): 235–242.

Ainley, D.G., G. Ballard, S. Ackley, L.K. Blight and others. 2007. Paradigm lost, or is top-down forcing no longer significant in the Antarctic marine ecosystem? *Ant. Sci.*, 19: 283–290.

Akishin, V.V. 1988. Method for estimation of the density of krill aggregations with an account taken for the trawl selectivity. In: *Orudiya I Sposoby Rybolovstva: Voprosy Teorii I Praktiki* (Catching tools and fishery techniques: Theory and practice). VNIRO Press, Moscow: 169–176.

Alonso, F., P. Virtue, S. Nicol and P.D. Nichols. 2005. Lipids as trophic markers in Antarctic krill. III. Temporal changes in digestive gland lipid composition of *Euphausia superba* in controlled conditions. *Mar. Ecol. Prog. Ser*, 296: 81–91.

Arrigo, K.R., G.L. van Dijken and S. Bushinsky. 2008. Primary production in the Southern Ocean, 1997–2006. *J. Geophys. Res. Oceans*, 113, c8 No. C08004, doi: 10.1029/2007JC004551.

Atkinson, A. and R. Snÿder. 1997. Krill-copepod interactions at South Georgia, Antarctica, I. Omnivory by *Euphausia superba*. *Mar. Ecol. Prog. Ser.,* 160: 63–76.

Atkinson, A. and M.J. Whitehouse. 2000. Ammonium excretion by Antarctic krill *Euphausia superba* at South Georgia. *Limnol. Oceanogr.*, 45: 55–63.

Atkinson, A., P. Ward, A. Hill, A.S. Brierley and G.C. Cripps. 1999. Krill-copepod interactions at South Georgia, Antarctica, II. *Euphausia superba* as a major control on copepod abundance. *Mar. Ecol. Prog. Ser.,* 176: 63–79.

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

Atkinson, A., B. Meyer, D. Stübing, W. Hagen, K. Schmidt and U.V. Bathmann. 2002. Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter – II. Juveniles and adults. *Limnol. Oceanogr.,* 47: 953–966.

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

Atkinson, A., R.S. Shreeve, A.G. Hirst, P. Rothery, G.A. Tarling, D.W. Pond, R.E. Korb, E.J. Murphy and J.L. Watkins. 2006. Natural growth rates of Antarctic krill (*Euphusia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. *Limnol. Oceanogr.,* 51: 973–987.

Atkinson, A., V. Siegel, E.A. Pakhomov, P. Rothery, V. Loeb, R.M. Ross, L.B. Quetin, K. Schmidt, P. Fretwell, E.J. Murphy, G.A. Tarling and A.H. Fleming. 2008. Oceanic circumpolar habitats of Antarctic krill. *Mar. Ecol. Prog. Ser.,* 362: 1–23.

Atkinson, A., V. Siegel, E.A. Pakhomov, M.J. Jessopp and V. Loeb. 2009. A re-appraisal of the total biomass and annual production of Antarctic krill. *Deep-Sea Res. I*, 56 :727–740.

Atkinson, A., K. Schmidt, S. Fielding, S. Kawaguchi and P. Geissler. 2012a. Variable food processing by Antarctic krill: relationships between diet, egestion rate and the composition and sinking rates of their fecal pellets. *Deep-Sea Res. II*, 59–60: 147–158.

Atkinson, A., P. Ward, B.P.V. Hunt, E.A. Pakhomov and G.W. Hosie. 2012b. Zooplankton in Southern Ocean food web models: a critique of available data. *CCAMLR Science*, this volume.

Barkley, E. 1940. Nahrung und Filterapparat des Walkrebschens *Euphausia superba* Dana. *Z. Fisch. Beiheft,* 1: 65–156.

Beaugrand, G. 2012. Unanticipated biological changes and global warming. *Mar. Ecol. Prog. Ser.*, 445: 293–301.

Boyd, I.L. and A.W.A Murray. 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. *J. Anim. Ecol.*, 70: 747–760.

Brierley, A.S., P.G. Fernandes, M.A. Brandon, F. Armstrong, N.W. Millard, S.D. McPhail, P. Stevenson, M. Pebody, J. Perrett, M. Squires, D.B. Bone and G. Griffiths. 2002. Antarctic krill under sea ice: elevated abundance in a narrow band just south of the ice edge. *Science*, 295: 1890–1892.

Brierley, A.S., D.A. Demer, J.L. Watkins and R.P. Hewitt. 1999. Concordance of interannual fluctuations in acoustically estimated densities of Antarctic krill around South Georgia and Elephant Island: biological evidence of same-year teleconnections across the Scotia Sea. *Mar. Biol.*, 134:675–681.

Brown, M., S. Kawaguchi, S. Candy and P. Virtue. 2010. Temperature effect on the growth and maturation of Antarctic krill (*Euphausia superba*). *Deep-Sea Res. II*, 57: 672–682.

Buitenhuis, E., C. Le Quéré, O. Aumont, G. Beaugrand, A. Bunker, A. Hirst, T. Ikeda, T. O'Brien, S. Piontovski and D. Straile. 2006. Biogechemical fluxes through mesozooplankton. *Global Biogeochem. Cycles*, 20: GB2003, doi: 10.1029/2005GB002511.

Butterworth, D.S. 1988. Some aspects of the relation between Antarctic krill abundance and CPUE measures in the Japanese krill fishery. In: *Selected Scientific Papers, 1988 (SC-CAMLR-SSP/5)*, Part I. CCAMLR, Hobart, Australia: 109–125.

Butterworth, D.S. and R.B. Thomson. 1995. Possible effects of different levels of krill fishing on predators some initial modelling attempts. *CCAMLR Science*, 2: 79–97.

Butterworth, D.S., G.R. Gluckman, R.B. Thomson, S. Chalis, K. Hiramatsu and D.J. Agnew. 1994. Further computations of the consequences of setting the annual krill catch limit to a fixed fraction of the estimate of krill biomass from a survey. *CCAMLR Science*, 1: 81–106.

Candy, S.G. and S. Kawaguchi. 2006. Modelling growth of Antarctic krill. II. Novel approach to describing the growth trajectory. *Mar. Ecol. Prog. Ser.*, 306: 17–30.

Clarke, A. and P.A. Tyler. 2008. Adult krill feeding at abyssal depths. *Current Biology*, 18: 282–285.

Clarke, A., L.B. Quetin and R.M. Ross. 1988. Laboratory and field estimates of the rate of faecal pellet production by Antarctic krill, *Euphausia superba*. *Mar. Biol.,* 98: 557–563.

Constable, A.J. 2005. A possible framework in which to consider plausible models of the Antarctic marine ecosystem for evaluating krill management procedures. *CCAMLR Science*, 12: 99–117.

Constable, A. and W.K. de la Mare. 1996. A generalised model for evaluating yield and the long-term status of fish stocks under conditions of uncertainty. *CCAMLR Science*, 3: 31–54.

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

Cox, M.J., J.D. Warren and D.A. Demer. 2010. Three dimensional observations of swarms of Antarctic krill (*Euphausia superba*) made using a multi-bean echosounder. *Deep-Sea Res. II*, 57: 508–518.

Cresswell, K.A., G.A. Tarling and M.T. Burrows. 2007. Behaviour affects local-scale distributions of Antarctic krill around South Georgia. *Mar. Ecol. Prog. Ser.*, 343: 193–206.

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

Croxall, J.P. and S. Nicol. 2004. Management of Southern Ocean resources as a model for global sustainability. *Ant. Sci.*, 16: 569–584.

Croxall, J.P., C. Ricketts and P.A. Prince. 1984. The impacts of seabirds on marine resources, especially krill, at South Georgia. In: Whitto, G.C and H. Rahn (Eds). *Seabird Energetics*. Plenum, New York: 285–318.

Croxall, J.P., I. Everson, G.L. Kooyman, C. Ricketts and R.W. Davis. 1985. Fur seal diving behaviour in relation to vertical distribution of krill. *J. Anim. Ecol.*, 54: 1–8.

Croxall, J.P., R.W. Davis and M.J. O'Connell. 1988. Diving patterns in relation to diet of gentoo and macaroni penguins at South Georgia. *Condor*, 90: 157–167.

Croxall, J.P., K. Reid and P.A. Prince. 1999. Diet, provisioning and productivity responses of marine predators to differences in the availability of Antarctic krill. *Mar. Ecol. Prog. Ser.,* 177: 115–131.

Cury, P.M., I.L. Boyd, S. Bonhommeau, T. Anker-Nilssen, R.J.M. Crawford, R.W. Furness, J.A. Mills, E.J. Murphy, H. Österblom, M. Paleczny, J.F. Piatt, J.-P. Roux, L. Shannon and W.J. Sydeman. 2011. Global seabird response to forage fish depletion—one-third for the birds. *Science*, 334 (6063): 1703–1706.

Czubek, H. 1981. Studies on performance capacity and selectivity of trawls used for Antarctic krill fisheries. *Pol. Polar Res.*, 2: 131–142.

Daly, K.L. and M.C. Macaulay. 1991. Influence of physical and biological mesoscale dynamics on the seasonal distribution and behaviour of *Euphausia superba* in the Antarctic marginal ice zone. *Mar. Ecol. Prog. Ser.*, 79: 37–66.

de la Mare, W.K. and A.J. Constable. 2000. Utilising data from ecosystem monitoring for managing fisheries: development of statistical summaries of indices arising from the CCAMLR Ecosystem Monitoring Program. *CCAMLR Science*, 7: 101–117.

Dearborn, J.H., K.C. Edwards and D.B. Frat. 1991. Diet, feeding behaviour, and surface morphology of the multi-armed Antarctic sea star *Labidaster annulatus* (Echinodermata: Asteroidea). *Mar. Ecol. Prog. Ser.*, 77: 65–84.

Demer, D.A. and S.G. Conti. 2005. New target-strength model indicates more krill in the Southern Ocean. *ICES J. Mar. Sci.*, 62: 25–32.

Donnelly, J., J.J. Torres and T.L. Hopkins. 1994. Chemical composition of Antarctic zooplankton during fall and winter. *Polar Biol.,* 14: 171–183.

Everson, I. 2000. *Krill: Biology, Ecology and Fisheries*. Blackwell Science, Oxford, UK.

Everson, I. and D.G. Bone. 1986. Effectiveness of the RMT8 system for sampling krill (*Euphausia superba*) swarms Polar. Biology, 6 (2): 83–90.

Fach, B.A., B. Meyer, D. Wolf-Glarow and U. Bathmann. 2008. Biochemically-based modelling study of Antarctic krill *Euphausia superba* growth and development. *Mar. Ecol. Prog. Ser.*, 360: 147–161.

Färber-Lorda, J., G. Raymond and P. Mayzaud. 2009. Elemental composition, biochemical composition and caloric value of Antarctic krill: implications in energetic and carbon balances. *J. Mar. Sys.*, 78: 518–524.

Fevolden, S.E. and R. Schneppenheim. 1988. Genetic population structure of *Euphausia superba* Dana in the Atlantic sector of the Southern Ocean as demonstrated by different electrophoretic techniques. *Polar Biol.*, 9: 1–8.

Fevolden, S.E. and R. Schneppenheim. 1989. Genetic homogeneity of krill (*Euphausia superba* Dana) in the Southern Ocean. *Polar Biol.*, 9: 533–539.

Fielding, S., J.L. Watkins, M.A. Collins, P. Enderlein and H.J. Venables. 2012. Acoustic determination of the distribution of fish and krill across the Scotia Sea in spring 2006, summer 2008 and autumn 2009. *Deep-Sea Res. II*, 59–60: 173–188.

Flores, H., A. Atkinson, S. Kawaguchi, B.A. Krafft, G. Milinevsky, S. Nicol, C. Reiss, G.A. Tarling, R. Werner, E. Bravo Rebolledo, V. Cirelli, J. Cuzin-Roudy, S. Fielding, J.J. Groeneveld, M. Haraldsson, A. Lombana, E. Marschoff, B. Meyer, E.A. Pakhomov, E. Rombolá, K. Schmidt, V. Siegel, M. Teschke, H. Tonkes, J.Y. Toullec, P.N. Trathan, N. Tremblay, A.P. Van de Putte, J.A. van Franeker and T. Werner. 2012a. Impact of climate change on Antarctic krill. *Mar. Ecol. Prog. Ser.*, 458: 1–19, doi: 10.3354/meps09831.

Flores, H., J.A. van Franeker, V. Siegel, M. Haralsson, V. Strass, E.H. Meesters, U. Bathmann and W.J. Wolff. 2012b. The association of Antarctic krill *Euphausia superba* with the under-ice habitat. *PLoS ONE*, 7(2): e31775.

Forcada, J., P.N. Trathan, K. Reid, E.J. Murphy and J.P. Croxall. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology,* 12: 411–423.

Forcada, J., P.N. Trathan and E.J. Murphy. 2008. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*, 14: 2473–2488.

Fraser, W.R. and E.E. Hofmann. 2003. A predator's perspective of causal links between climate change, physical forcing and ecosystem response. *Mar. Ecol. Prog. Ser.*, 265: 1–15.

Fraser, W.R., W.Z. Trivelpiece, D.G. Ainley and S.G. Trivelpiece. 1992. Increases in Antarctic penguin populations-reduced competition with whales or a loss of sea ice due to environmental warming. *Polar Biol.*, 11: 525–531.

Fritsen, C.H., J.N. Kremer, S.F. Ackley and C.W. Sullivan. 1998. Flood-freeze cycles and algal dynamics in Antarctic pack ice. In: Lizotte, M.L. and K.R. Arrigo (Eds). *Antarctic Sea Ice: Biological Processes*. *Am. Geophys. Union* (*Antarc. Res. Ser.*) 73: 1–21.

Gentleman, W.C. and A.B. Neuheimer. 2008. Functional responses and ecosystem dynamics: how clearance rates explain the influence of satiation, food limitation and acclimation. *J. Plankton Res.*, 30: 1215–1231.

Gilpin, L.C., M.J. Whitehouse, J. Priddle, G. Savidge and A. Atkinson. 2002. Primary production and carbon uptake dynamics in the vicinity of South Georgia – balancing carbon fixation and removal. *Mar. Ecol. Prog. Ser.*, 242: 51–62.

Godlewska, M. 1996. Vertical migrations of krill (*Euphausia superba* Dana.) *Pol. Arch. Hydrobiol.*, 43: 9–63.

Granéli, E., W. Granéli, M. Mozzam Rabbani, N. Daugbjerg, G. Fransz, J. Cuzin-Roudy and V.A. Alder. 1993. The influence of copepod and krill grazing on the species composition of phytoplankton communities from the Scotia-Weddell Sea. *Polar Biol.,* 13: 201–213.

Gutt, J. and V. Siegel. 1994. Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctic). *Deep-Sea Res. I*, 41: 169–178.

Haberman, K.L., L.B. Quetin and R.M. Ross. 2003a. Diet of the Antarctic krill (*Euphausia superba* Dana) I. Comparisons of g razing on *Phaeocystis antarctica* (Karsten) and *Thalassiosira antarctica* (Comber). *J. Exp. Mar. Biol. Ecol.*, 283: 79–85.

Haberman, K.L., R.M. Ross and L.B. Quetin. 2003b. Diet of the Antarctic krill (*Euphausia superba* Dana) II. Selective grazing in mixed phytoplankton assemblages. *J. Exp. Mar. Biol. Ecol.*, 283: 97–113.

Hagen, W., G. Katner, A. Terbrüggen and E.S. van Vleet. 2001. Lipid metabolism of the Antarctic krill (*Euphausia superba*) and its ecological implications. *Mar. Biol.,* 139: 95–104.

Hamner, W.M. and P.P. Hamner. 2000. Behavior of Antarctic krill (*Euphausia superba*); schooling, foraging and antipredator behaviour. *Can. J. Fish. Aquat. Sci.*, 57: 192–202.

Hernández-Leon, S., A. Portillo-Hahnefeld, C. Almeida, P. Becognee and I. Moreno. 2001. Diel feeding behaviour of krill in the Gerlache Strait, Antarctica. *Mar. Ecol. Prog. Ser.*, 223: 235–242.

Hewitt, R.P. and D.A. Demer. 2000. The use of acoustic sampling to estimate the dispersion and abundance of euphausiids, with an emphasis on Antarctic krill, *Euphausia superba*. *Fish. Res.*, 47: 215–229.

Hewitt, R.P., J. Watkins, M. Naganobu, V. Sushin, A.S. Brierley, D. Demer, S. Kasatkina, Y. Takao, C. Goss, A. Malyshko, M. Brandon, S. Kawaguchi, V. Siegel, P. Trathan, J. Emery, I. Everson and D. Miller. 2004a. Biomass of Antarctic krill in the Scotia Sea in January/February 2000 and its use in revising an estimate of precautionary yield. *Deep-Sea Res. II*, 51: 1215–1236.

Hewitt, R.P., G. Watters, P.N. Trathan, J.P. Croxall, M. Goebel, D. Ramm, K. Reid, W.Z. Trivelpiece and J.L. Watkins. 2004b. Options for allocating the precautionary catch limit of krill among small-scale management units in the Scotia Sea. *CCAMLR Science*, 11: 81–97.

Heywood, B.G., A.S. Brierley and S.F. Gull. 2006. A quantified Bayesian Maximum Entropy estimate of Antarctic krill abundance across the Scotia Sea and in small-scale management units from the CCAMLR-2000 Survey. *CCAMLR Science*, 13: 97–116.

Hill, H.J., P.N. Trathan, J.P. Croxall and J.L. Watkins. 1996. A comparison of Antarctic krill, *Euphausia superba,* caught in nets and taken by macaroni penguins, *Eudyptes chrysolophus:* evidence for selection? *Mar. Ecol. Prog. Ser.*, 140: 1–11.

Hill, S.L., K. Reid and A.W. North. 2005. Recruitment of mackerel icefish (*Champsocephalus gunnari*) at South Georgia indicated by predator diets and its relationship with sea surface temperature. *Can. J. Fish. Aquat. Sci.*, 62: 2530–2537.

Hill, S.L., E.J. Murphy, K. Reid, P.N. Trathan and A.J. Constable. 2006. Modelling Southern Ocean ecosystems: krill, the food-web, and the impacts of fishing. *Biological Reviews*, 81: 581–608.

Hill, S.L., G.M. Watters, A.E. Punt, M.K. McAllister, C. LeQuere and J. Turner. 2007a. Model uncertainty in the ecosystem approach to fisheries. *Fish and Fisheries*, 8: 315–333.

Hill, S.L., K. Reid, S.E. Thorpe, J. Hinke and G.M. Watters. 2007b. A compilation of parameters for ecosystem dynamics models of the Scotia Sea – Antarctic Peninsula region. *CCAMLR Science*, 14: 1–25.

Hill, S.L., P.N. Trathan and D.J. Agnew. 2009. The risk to fishery performance associated with spatially resolved management of Antarctic krill (*Euphausia superba*) harvesting. *ICES J. Mar. Sci.*, 66 (10): 2148–2154.

Hill, S.L., C.M. Waluda, S. Fielding and H. Peat. 2012a. Two decades of variability in krill predators at Bird Island, South Georgia and their potential as ecosystem indicators. Document *WG-EMM-12/16*. CCAMLR, Hobart, Australia.

Hill, S.L., K. Keeble, A. Atkinson and E.J. Murphy. 2012b. A foodweb model to explore uncertainties in the South Georgia shelf pelagic ecosystem. *Deep-Sea Res. II*, 59–60: 237–252.

Hofmann, E.E. and Y.S. Hùsrevõglu. 2003. A circumpolar modelling study of habitat control of Antarctic krill (*Euphausia superba*) reproductive success. *Deep-Sea Res. II*, 50: 3121–3142.

Hofmann, E.E. and E.J. Murphy. 2004. Advection, krill and Antarctic Marine Ecosystems. *Ant. Sci.*, 16: 487–499.

Hopkins, T.L., D.G. Ainley, J.J. Torres and T.M. Lancraft. 1993a. Trophic structure in open waters of the Marginal Ice Zone in the Scotia-Weddell Confluence region during spring (1983). *Polar Biol.,* 13: 389–397.

Hopkins, T.L., T.M. Lancraft, J.J. Torres and J. Donnelly. 1993b. Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice-zone in winter (1988). *Deep-Sea Res. I*, 40: 81–105.

Hosie, G.W. and T.G. Cochran. 1994. Mesoscale distribution patterns of macrozooplankton communities in Prydz Bay, Antarctica – January to February 1991. *Mar. Ecol. Prog. Ser.*, 106: 21–39.

Huntley, M.E., W. Nordhausen and M.D.G. Lopez. 1994. Elemental composition, metabolic activity and growth of Antarctic krill *Euphausia superba* during winter. *Mar. Ecol. Prog. Ser.,* 107: 23–40.

Jarman, S.N. and S. Nicol. 2002. Sources of variance in studies of krill population genetics. *CCAMLR Science*, 9: 107–116.

Jarvis, T., N. Kelly, S. Kawaguchi, E. vanWijk and S. Nicol. 2010. Acoustic characterisation of the broad scale distribution and abundance of Antarctic krill (*Euphausia superba*) off East Antarctica (30–80°E) in January–March 2006. *Deep-Sea Res. II*, 57: 916–933.

Jolly, G.M. and I. Hampton. 1990. A stratified random transect design for acoustic surveys of fish stocks. *Can. J. Fish. Aquat. Sci.*, 47: 1282–1291.

Kasatkina, S.M., C. Goss, J.H. Emery, Y. Takao, F.F. Litvinov, A.P. Malyshko, V.N. Shnar and O.A. Berezhinsky. 2004. A comparison of net and acoustic estimates of krill density in the Scotia Sea during the CCAMLR 2000 Survey. *Deep-Sea Res. II*, 51: 1289–1300.

Kawaguchi, S. and S. Nicol. 2007. Learning about krill from the fishery. *Ant. Sci.*, 19: 219–230.

Kawaguchi, S., T. Ichii and M. Naganobu. 1997. Catch per unit effort and proportional recruitment indices from Japanese krill fishery data in Subarea 48.1. *CCAMLR Science*, 4: 47–63.

Kawaguchi, S., S. Candy, S. Nicol, K. Taki and M. Naganobu. 2005. Analysis of trends in Japanese krill fishery CPUE data, and its possible use as a krill abundance index. *CCAMLR Science*, 12: 1–28.

Kawaguchi, S., S.G. Candy, R. King, M. Naganobu and S. Nicol. 2006. Modelling growth of Antarctic krill. I. Growth trends with sex, length, season, and region. *Mar. Ecol. Prog. Ser.,* 306: 1–15.

Kawaguchi, S., S. Nicol, P. Virtue, S.R. Davenport, R. Casper, K.R. Swadling and G.W. Hosie. 2010. Krill demography and large scale distribution in the Western Indian Ocean sector of the Southern Ocean (CCAMLR Division 58.4.2) in Austral summer of 2006. *Deep-Sea Res. II*, 57 (9–10): 934–947.

Kawaguchi, S., H. Kurihara, R. King, L. Hale, T. Berli, J.P. Robinson, A. Ishida, M. Wakita, P. Virtue, S. Nicol and A. Ishimatsu. 2011. Ocean bottom krill sex. *J. Plankton Res.*, 33: 1134–1138.

Kils, U. 1983. Swimming and feeding of Antarctic krill *Euphausia superba* – some outstanding energetics and dynamics – some unique morphological details. *Ber. Polarforsch. (Sonderh.)*, 4: 130–155.

Klevjer, T.A., G.A. Tarling and S. Fielding. 2010. Swarm characteristics of Antarctic krill *Euphausia superba* relative to the proximity of land during summer in the Scotia Sea. *Mar. Ecol. Prog. Ser.*, 409: 157–170.

Kopczynska, E.E. 1992. Dominance of microflag-ellates over diatoms in the Antarctic areas of deep vertical mixing and krill concentrations. *J. Plankton Res*., 14: 1031–1054.

Krafft, B.A., W. Melle, T. Knutsen, E. Bagoien, C. Broms and B. Ellertsen. 2010. Distribu-tion and demography of Antarctic krill in the southeast Atlantic sector of the Southern Ocean during the austral summer 2008. *Polar Biol*., 33: 957–968.

Krakatitsa, V.V., G.P. Karpenko and E.A. Pakhomov. 1993. Distribution peculiarities of zooplankton depending on temperature strati-fication of the 1-metre surface water layer in the Cooperation Sea. In: Voronina, N.M. (Ed.). *Pelagic Ecosystems of the Southern Ocean*. Nauka Press, Moscow: 151–157.

Lascara, C.M., E.E. Hofmann, R.M. Ross and L.B. Quetin. 1999. Seasonal variability in the distri-bution of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula. *Deep-Sea Res. I*, 46: 951–984.

Ligowski, R. 2000. Benthic feeding by krill, *Euphausia superba* Dana, in coastal waters off West Antarctica and in Admiralty Bay, South Shetland Islands. *Polar Biol.,* 23: 619–625.

Litvinov, F.F., A.Z. Sundakov. and V.I. Arkhipov. 2004. CPUE indices used in Soviet krill fishery statistics from 1997 to 1992 and their possible utility for evaluation of relative changes in krill biomass. *CCAMLR Science*, 11: 165–178.

Loeb, V., V. Siegel, O. Holm-Hansen, R. Hewitt, W. Fraser, W. Trivelpiece and S. Trivelpiece. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature,* 387: 897–900.

Loeb, V., E.E. Hofmann, J.M. Klinck and O. Holm-Hansen. 2010. Hydrographic control of the marine ecosystem in the South Shetland-Elephant Island and Bransfield Strait region. *Deep-Sea Res. II*, 57: 519–542.

Lowe, A.T., R.M. Ross, L.B. Quetin, M. Vernet and C.H. Fritsen. 2012. Simulating larval Antarctic krill growth and condition factor during fall and winter in response to environmental variability. *Mar. Ecol. Prog. Ser*., 452: 27–43.

Macaulay, M. 2000. Sampling krill – acoustic esti-mation of krill abundance. In: Everson, I. (Ed.). *Krill Biology, Ecology and Fisheries*. Blackwell Science: 20–32.

Mackey, A.P., A. Atkinson, S.L. Hill, P. Ward, N.J. Cunningham, N.M. Johnston and E.J. Murphy. 2012. Antarctic macrozooplankton of the southwest Atlantic sector and Bellingshausen Sea: baseline historical distributions (*Discovery Investigations,* 1928–1935) related to tempera-ture and food, with projections for subsequent ocean warming. *Deep-Sea Res. II*, 59–60: 130–146.

Mackintosh, N.A. 1973. Distribution of post-larval krill in the Antarctic. *Discovery Rep*., 36: 1–94.

Main, C.E. and M.A. Collins. 2011. Diet of the Antarctic starry skate *Amblyraja Georgiana* (Rajida, Chondrichthyes) at South Georgia (Southern Ocean). *Polar Biol*., 34: 389–396.

Mangel, M. 1988. Analysis and modelling of the Soviet Southern Ocean fleet. *Selected Scien-tific Papers, 1988 (SC-CAMLR-SSP/5)* Part I. CCAMLR, Hobart, Australia: 127–235.

Mangel, M. 1989. Analysis and modelling of the Soviet Southern Ocean krill fleet, II: estimat-ing the number of concentrations and analytical justification for search data. *Selected Scientific Papers, 1989 (SC-CAMLR-SSP/6)*. CCAMLR, Hobart, Australia: 283–322.

Marr, J.W.S. 1962. The natural history and geogra-phy of the Antarctic krill (*Euphausia superba* Dana). *Discovery Rep.,* 32: 33–464.

May, R.M., J.R. Beddington, C.W. Clark, S.J. Holt and R.M. Laws. 1979. Management of multi-species fisheries. *Science*, 205: 267–277.

Meredith, M.P. and J.C. King. 2005. Rapid cli-mate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys. Res. Lett*., 32 L19604, doi: 10.1029/2005GL024042.

Meyer, B. 2012. The overwintering of Antarctic krill, *Euphausia superba*, from an ecophysi-ological perspective. *Polar Biol*., 35: 15–37.

Meyer, B., A. Atkinson, B. Blume and U.V. Bathmann. 2003. Feeding and energy budgets of larval Antarctic krill *Euphausia superba* in summer. *Mar. Ecol. Prog. Ser.,* 257: 167–177.

Meyer, B., V. Fuentes, C. Guerra, K. Schmidt, A. Atkinson, S. Spahic, B. Cisewski, U. Freier, A. Olarianga and U. Bathmann. 2009. Physiology, growth, and development of larval krill *Euphausia superba* in autumn and winter in the Lazarev Sea, Antarctica. *Limnol. Oceanogr.,* 54: 1595–1614.

Miller, D.G. and I. Hampton. 1989. Biology and ecology of the Antarctic krill (*Euphausia superba* Dana): a review. *BIOMASS Scientific Series*, 9: 1–166.

Mori, M. and D.S. Butterworth. 2004. Consideration of multispecies interactions in the Antarctic: A preliminary model of the Minke whale – Blue whale – Krill interaction. *Afr. J. Mar. Sci.*, 26: 245–259.

Mori, M. and D.S. Butterworth. 2007. A first step towards modelling the krill-predator dynamics of the Antarctic ecosystem. *CCAMLR Science*, 13: 217–277.

Murphy, E.J. 1995. Spatial structure of the Southern-Ocean ecosystem – predator–prey linkages in Southern-Ocean food webs. *J. Anim. Ecol.*, 64: 333–347.

Murphy, E.J. and K. Reid. 2001. Modelling Southern Ocean krill population dynamics: biological processes generating fluctuations in the South Georgia Ecosystem. *Mar. Ecol. Prog. Ser.*, 217: 175–189.

Murphy, E.J., D.J. Morris, J.L. Watkins and J. Priddle. 1988. Scales of interaction between Antarctic krill and the environment. In: Sahrhage D. (Ed.). *Antarctic Ocean and Resources Variability*. Springer Verlag, Berlin, Germany: 120–130.

Murphy, E.J., S.E. Thorpe, J.L. Watkins and R. Hewitt. 2004. Modeling the krill transport pathways in the Scotia Sea: spatial and environmental connections generating the seasonal distribution of krill. *Deep-Sea Res. II*, 51: 1435–1456.

Murphy, E.J., P.N. Trathan, J.L. Watkins, K. Reid, M.P. Meredith, J. Forcada, S.E. Thorpe, N.M. Johnston and P. Rothery. 2007a. Climatically driven fluctuations in Southern Ocean ecosystems. *Phil. Trans. R. Soc. Lond. B*, 274: 3057–3067.

Murphy, E.J., J.L.Watkins, P.N. Trathan, K. Reid, M.P. Meredith, S.E. Thorpe, N.M. Johnston, A. Clarke, G.A. Tarling, M.A. Collins, J. Forcada, R.S. Shreeve, A. Atkinson, R. Korb, M.J. Whitehouse, P. Ward, P.G. Rodhouse, P. Enderlein, A.G. Hirst, A.R. Martin, S.L. Hill, J.J. Staniland, D.W. Pond, D.R. Briggs, N.J. Cunningham and A.H. Fleming. 2007b. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill cantered food web. *Phil Trans. R. Soc. B*, 362: 113–148.

Murray, A.W.A. 1996. Comparison of geostatistical and random sample survey analyses of Antarctic krill acoustic data. *ICES J. Mar. Sci.*, 53: 415–421.

Nicol, S. 1993. A comparison of Antarctic petrel (*Thalassoica antarctica*) diets with net samples of Antarctic krill (*Euphausia superba*) taken from the Prydz Bay region. *Polar Biol.*, 13: 399–403.

Nicol, S. 2006. Krill, currents and sea ice; the life cycle of *Euphausia superba* in relation to its changing environment. *Bioscience*, 56 (2): 111–120.

Nicol, S., A.J. Constable and T. Pauly. 2000a. Estimates of circumpolar abundance of Antarctic krill based on recent acoustic density measurements. *CCAMLR Science*, 7: 87–99.

Nicol, S., T. Pauly, N. Bindoff, S. Wright, D. Thiele, G. Hosie, P. Strutton and E. Woehler. 2000b. Ocean circulation off East Antarctica affects ecosystem structure and sea-ice extent. *Nature,* 406: 504–507.

Nicol, S., A. Bowie, S. Jarman, D. Lannuzel, K. Meiners and P. Van de Merwe. 2010. Southern Ocean iron fertilization by baleen whales and Antarctic krill. *Fish and Fisheries*, 11: 203–209.

Nicol, S., J. Foster and S. Kawaguchi. 2011. The fishery for Antarctic krill – recent developments. *Fish and Fish.*, 13: 30–40.

Nowacek, D.P., A.S. Friedlaender, P.N. Halpin, E.L. Hazen, D.W. Johnston, A.J. Read, B. Espinasse, M. Zhou and Y. Zhu. 2011. Super-Aggregations of Krill and Humpback Whales in Wilhelmina Bay, Antarctic Peninsula. *PLoS ONE*, 6 (4): e19173. doi: 10.1371/journal.pone.0019173.

Oakes, S.A. 2008. Winter ecology of young Antarctic krill, *Euphausia superba*: Feeding on the sea ice microbial community with implications for growth models. Ph.D. Thesis, University of California, Santa Barbara, CA.

Pakhomov, E.A. 1995. Demographic studies of Antarctic krill (*Euphausia superba*) in the Cooperation and Cosmonaut seas (Indian sector of the Southern Ocean). *Mar. Ecol. Prog. Ser.*, 119 (1–3): 45–61.

Pakhomov, E.A. 2000. Demography and life cycle of Antarctic krill, *Euphausia superba*, in the Indian sector of the Southern Ocean: long-term comparison between coastal and open-ocean regions. *Can. J. Fish. Aquat. Sci.*, 57 (Supplement S3): 68–90.

Pakhomov, E.A., R. Perissinotto, P.W. Froneman and D.G.M. Miller. 1997. Energetics and feeding dynamics of *Euphausia superba* in the South Georgia region during the summer of 1994. *J. Plankton Res.*, 19: 399–423.

Pakhomov, E.A., P.W. Froneman and R. Perissinotto. 2002. Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. *Deep-Sea Res. II*, 49: 1881–1907.

Pakhomov, E.A., A. Atkinson, B. Meyer, B. Oettl and U. Bathmann. 2004. Daily rations and growth of larval krill *Euphausia superba* in the Eastern Bellingshausen Sea during austral autumn. *Deep-Sea Res. II*, 51: 2185–2198.

Pauly, T., S. Nicol, W.K. de la Mare, I. Higginbottom and G. Hosie. 1997. A comparison between the estimated density of krill from an acoustic survey with that obtained by scientific nets on the same survey. Document *WG-EMM-97/43*. CCAMLR, Hobart, Australia.

Pauly, T., S. Nicol, I. Higginbottom and J. Kitchener. 2000. Distribution and abundance of Antarctic krill (*Euphausia superba*) off East Antarctica (80–150°E) during the Austral summer of 1995/96. *Deep-Sea Res. II*, 47, 12/13: 2465–2488.

Perissinotto, R. and E.A. Pakhomov. 1996. Gut evacuation rates and pigment destruction in the Antarctic krill *Euphausia superba*. *Mar. Biol.*, 125: 47–54.

Perissinotto, R., E.A. Pakhomov, C.D. McQuaid and P.W. Froneman. 1997. In situ grazing rates and daily ration of the Antarctic krill *Euphausia superba* feeding on phytoplankton at the Antarctic Polar Front and the Marginal Ice Zone. *Mar. Ecol. Prog. Ser.*, 160: 77–91.

Piepenburg, D., M.K. Schmid and D. Gerdes. 2002. The benthos off King George Island (South Shetland Islands, Antarctica): Further evidence for a lack of a latitudinal biomass cline in the Southern Ocean. *Polar Biol.*, 25: 146–158.

Pinkerton, M.H., J.M. Bradford-Grieve and S.M. Hanchet. 2010. A balanced model of the food web of the Ross Sea, Antarctica. *CCAMLR Science*, 17: 1–31.

Plagányi, É.E. and D.S. Butterworth. 2012. The Scotia Sea krill fishery and its possible impacts on dependent predators – modelling localized depletion of prey. *Ecol. Appl.*, 22 (3): 748–761.

Polovina, J.J. 1984. Model of a Coral Reef Ecosystem I. The ECOPATH Model and Its Application to French Frigate Shoals. *Coral Reefs*, 3: 1–11.

Price, H.J., K.R. Boyd and C.M. Boyd. 1988. Omnivorous feeding behavior of the Antarctic krill *Euphausia superba*. *Mar. Biol.*, 97: 67–77.

Priddle J, M.J. Whitehouse, A. Atkinson, A.S. Brierley and E.J. Murphy. 1997. Diurnal changes in near-surface layer ammonium concentration-interplay between zooplankton and phytoplankton. *J. Plankton Res.*, 19: 1305–1330.

Priddle, J., I.L. Boyd, M.J. Whitehouse, E.J. Murphy and J.P. Croxall. 1998. Estimates

of Southern Ocean Primary production – constraints from predator carbon demand and nutrient drawdown. *J. Mar. Sys.*, 17: 275–288.

Quetin, L.B. and R.M. Ross. 1991. Behavioural and physiological characteristics of the Antarctic krill, *Euphausia superba*. *Am. Zool.*, 31: 49–63.

Quetin, L.B and R.M. Ross. 2001. Environmental variability and its impact on the reproductive cycle of Antarctic krill, *Euphausia superba*. *Am. Zool.,* 41: 74–89.

Quetin, L.B. and R.M. Ross. 2003. Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTER study region. *Mar. Ecol. Prog. Ser.*, 259: 185–200.

Quetin, L.B., R.M. Ross and A. Clarke. 1994. Krill energetics: seasonal and environmental aspects of the physiology of *Euphausia superba*. In: El Sayed, S.Z. (Ed.). *Southern Ocean Ecology: the BIOMASS Perspective*. Cambridge University Press, Cambridge, UK: 165–184.

Quetin, L.B., R.M. Ross, C.H. Fritsen and M. Vernet. 2007. Ecological responses of Antarctic krill to environmental variability: Can we predict the future? *Ant. Sci.*, 19 (2): 253–266.

Ramm, D., E. Appleyard, L. Millar, S. Morgan and J. Turner. 2005. Krill fishery report: 2005 update. Document *WG-EMM-05/05*. CCAMLR, Hobart, Australia.

Reid, K. 2001. Growth of Antarctic krill *Euphausia superba* at South Georgia. *Mar. Biol.*, 138: 57–62.

Reid, K. and J.P. Croxall. 2001. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proc. R. Soc. Lond. B,* 268: 377–384.

Reid, K., P.N. Trathan, J.P. Croxall and H.J. Hill. 1996. Krill caught by predators and nets: differences between species and techniques. *Mar. Ecol. Prog. Ser.*, 140 (1–3): 13–20.

Reid, K., K.E. Barlow, J.P. Croxall R.I. Taylor. 1999. Predicting changes in the Antarctic krill*, Euphausia superba*, population at South Georgia. Mar. Biol., 135: 647–652.

Reid, K., E.J. Murphy, V. Loeb and R.P. Hewitt. 2002. Krill population dynamics in the Scotia Sea: variability in growth and mortality within a single population. *J. Mar. Sys.*, 36: 1–10.

Reid, K., M. Sims, R.W. White and K.W. Gillon. 2004. Spatial distribution of predator/prey interactions in the Scotia Sea: implications for measuring predator/fisheries overlap. *Deep-Sea Res. II*, 51: 1383–1396.

Reid, K., J.P. Croxall, D.R. Briggs and E.J. Murphy. 2005. Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. *ICES J. Mar. Sci.,* 6: 366–373.

Reid, K., J.L. Watkins, E.J. Murphy, P.N. Trathan, S. Fielding and P. Enderlein. 2010. Krill population dynamics at South Georgia: implications for ecosystem-based fisheries management. *Mar Ecol. Prog. Ser.*, 399: 243–252.

Reiss, C.S., A.M. Cossio, V. Loeb and D.A. Demer. 2008. Variations in biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996–2006. *ICES J. Mar. Sci.*, 65 (4): 497–508, doi: 10.1093/icesjms/fsn033.

Ritz, D.A., A.J. Hobday, J.C. Montogomery and A.J.W. Ward. 2011. Social aggregation in the pelagic zone with special reference to fish and invertebrates. *Adv. Mar. Biol.*, 60: 161–227.

Rosenberg, A.A., J.R. Beddington and M. Basson. 1986. Growth and longevity of krill during the first decade of pelagic whaling. *Nature*, 324: 152–153.

Ross, R.M. and L.B. Quetin. 1986. *Euphausia superba*: A critical review of estimates of annual production. 1988. Proceedings. International Conference on the Biology of Antarctica. Ravello, Italy, Oct 1986. *J. Comp. Biochem. Physiol.*, B 90: 499–505.

Ross, R.M., L.B. Quetin and K.L. Haberman. 1998. Interannual and seasonal variability in short-term grazing impact of *Euphausia superba* in nearshore and offshore waters west of the Antarctic Peninsula. *J. Mar. Sys.*, 17: 261–273.

Ross, R.M., L.B. Quetin, K.S. Baker, M. Vernet and R.C. Smith. 2000. Growth limitation in

young *Euphausia superba* under field conditions. *Limnol. Oceanogr.*, 45: 31–43.

Ross, R.M., L.B. Quetin, D.G. Martinson, R.A. Iannuzzi, S.E. Stammerjohn and R.C. Smith. 2008. Palmer LTER: patterns of distribution of five dominant zooplankton species in the epipelagic zone west of the Antarctic Peninsula, 1993–2004. *Deep-Sea Res. II*, 55: 2086–2105.

Santora J.A. and C.S. Reiss. 2011. Geospatial variability of krill and top predators within an Antarctic submarine canyon system. *Mar. Biol.*, 158: 2527–2540.

Saunders, R.A., J.L. Watkins, K. Reid, E.J. Murphy, P. Enderlein, D.B. Bone and A.S. Brierley. 2007. Intra-annual variability in the density of Antarctic krill at South Georgia, 2002–2005: within year variation provides a new framework for interpreting previous 'annual' variation. *CCAMLR Science*, 14: 27–42.

SC-CAMLR. 2007. *Report of the Twenty-sixth Meeting of the Scientific Committee (SC-CAMLR-XXVI)*. CCAMLR, Hobart, Australia: 702 pp.

Schmidt, K., A. Atkinson, D. Stübing, J.W. McClelland, J.P. Montoya and M. Voss. 2003. Trophic relationships among Southern Ocean copepods and krill: some uses and limitations of a stable isotope approach. *Limnol. Oceanogr.,* 48: 277–289.

Schmidt K, J.W. McClelland, E. Mente, J.P. Montoya, A. Atkinson and M. Voss. 2004. Trophic level interpretation based on $\delta^{15}N$ values: implications of tissue-specific fractionation and amino acid composition. *Mar. Ecol. Prog. Ser.*, 266: 43–58.

Schmidt, K., A. Atkinson, K.-J. Petzke, M. Voss and D.W. Pond. 2006. Protozoans as a food source for Antarctic krill, *Euphausia superba*: Complementary insights from stomach content, fatty acids, and stable isotopes. *Limnol. Oceanogr.,* 51: 2409–2427.

Schmidt, K., A. Atkinson, S. Steigenberger, S. Fielding, M.C.M. Lindsay, D.W. Pond, G.A. Tarling, T.A. Klevjer, C.S. Allen, S. Nicol and E.P. Achterberg. 2011. Seabed foraging by Antarctic krill: implications for stock

assessment, bentho-pelagic coupling, and the vertical transfer of iron. *Limnol. Oceanogr.,* 56: 1411–1428.

Schmidt, K., A. Atkinson, H.J. Venables and D.W. Pond. 2012. Early spawning of Antarctic krill in the Scotia Sea is fuelled by "superfluous" feeding on non-ice associated phytoplankton blooms. *Deep-Sea Res. II*, 59–60: 159–172.

Siegel, V. 1986. Untersuchu zur Biologie des antarktischen Krill, *Euphausia superba*, im Bereich der Bransfield Strasse und angrezender Gebiete. *Mitt. Inst. Seefisch Hamburg*, 38: 1–244.

Siegel, V. 1988. A concept of seasonal variation of krill (*Euphausia superba*) distribution and abundance west of the Antarctic Peninsula. In: Sahrhage, D. (Ed.). *Antarctic Ocean and Resources Variability*. Springer-Verlag, Berlin Heidelberg: 219–230.

Siegel, V. 2005. Distribution and population dynamics of *Euphausia superba*: summary of recent findings. *Polar Biol.*, 29: 1–22.

Siegel, V. and V. Loeb. 1995. Recruitement of Antarctic krill *Euphausia superba* and possible causes for its variability. *Mar. Ecol. Prog. Ser.*, 123: 45–56.

Siegel, V and S. Nicol. 2000. Population parameters. In: Eversen, I. (Ed.). *Krill Biology, Ecology and Fisheries*. Blackwell Science, London: 103–149.

Siegel, V., V. Loeb and J. Groger. 1998. Krill (*Euphausia superba*) density, proportional and absolute recruitment and biomass in the Elephant island region (Antarctic Peninsula) during the period 1977 to 1997. *Polar Biol.*, 19: 393–398.

Siegel, V., R.M. Ross and L.B. Quetin. 2003. Krill recruitment indices from the western Antarctic Peninsula: are they representative of larger regions? *Polar Biol.*, 26: 672–679.

Siegel, V., S. Kawaguchi, P. Ward, F. Litvinov, V. Sushin, V. Loeb and J. Watkins. 2004. Krill demography and large scale distribution in the southwest Atlantic during January/February 2000. *Deep-Sea Res. II*, 51: 1253–1273.

Stammerjohn, S.E., D.G. Martinson, R.C. Smith and R.S. Iannuzzi. 2008a. Sea ice in the western Antarctic Peninsula region: spatio–temporal variability from ecological and climate change perspectives. *Deep-Sea Res. II*, 55: 2041–2058. doi: 10.1029/2007JC004269.

Stammerjohn, S.E., D.G. Martinson, R.C. Smith, X. Yuan and D. Rind. 2008b. Trends in Antarctic annual sea ice retreat and advance and their relation to El-Niño-Southern Oscillation and Southern Annular Mode variability. *J. Geophys. Res.*, 113: C035S90.

Steele, J.H. 2009. Assessment of some linear food web methods. *J. Mar. Sys.*, 76: 186–194.

Stowasser, G., A. Atkinson, R.A.R. McGill, R.A. Phillips, M.A. Collins and D.W. Pond. 2012. Food web dynamics in the Scotia Sea in summer: a stable isotope study. *Deep-Sea Res. II*, 59–60: 208–221.

Straile, D. 1997. Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator–prey weight ratio, and taxonomic group. *Limnol. Oceanogr.,* 42: 1375–1385.

Taki, K., T. Hayashi and M. Naganobu. 2005. Characteristics of seasonal variation in diurnal vertical migration and aggregation of Antarctic krill (*Euphausia superba*) in the Scotia Sea, using Japanese fishery data. *CCAMLR Science*, 12: 163–172.

Tarling, G.A., R.S. Shreeve, A.G. Hirst, A. Atkinson, D. Pond, E.J. Murphy and J.L. Watkins. 2006. Natural growth rates of Antarctic krill (*Euphausia superba*): I: Factors affecting intermoult period and refinements to methodology. *Limnol. Oceanogr.*, 51: 959–972.

Tarling, G.A., T. Klevjar, S. Fielding, J.L. Watkins, A. Atkinson, E.J. Murphy, R.E. Korb, M.J. Whitehouse and R. Leaper. 2009. Variability and predictability of Antarctic krill swarm structure. *Deep-Sea Res. I*, 56: 1994–2012.

Thorpe, S.E., E.J. Murphy and J.L. Watkins. 2007. Circumpolar connections between Antarctic krill (*Euphausia superba* Dana) populations: investigating the roles of ocean and ice transport. *Deep-Sea Res. I*, 54: 792–810.

Tovar-Sanchez, A., C.M. Duarte, S. Henández-Leon and S.A. Sanudo-Wilhelmy. 2007. Krill as a central node for iron cycling in the Southern Ocean. *Geophys Res. Lett.*, 34: L11601, doi: 10.1029/2006GL029096.

Trathan, P.N., I. Everson, E.J. Murphy and G.B. Parkes. 1998. Analysis of haul data from the South Georgia krill fishery. *CCAMLR Science,* 5: 9–30.

Trathan, P.N., N. Ratcliffe and E.A. Masden. 2012. Ecological drivers of change at South Georgia: the krill surplus, or climate variability. *Ecography*, doi: 10.1111/j.1600-0587.2012.07330.x.

Trivelpiece, W.Z., J.T. Hinke, A.K. Miller, C.S. Reiss, S.G. Trivelpiece and G.M. Watters. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *PNAS*: doi: 10.1073/pnas.1016560108.

Tynan, C.T. 1998. Ecological importance of the Southern Boundary of the Antarctic circumpolar current. *Nature,* 392: 708–710.

Waluda, C.M., M.A. Collins, A.D. Black, I.J. Staniland and P.N. Trathan. 2010. Linking predator and prey behaviour: contrasts between Antarctic fur seals and macaroni penguins at South Georgia. *Mar. Biol.,* 157: 99–112.

Waluda, C.M., S.L. Hill, H.J. Peat and P.N. Trathan. 2012. Diet variability and reproductive performance of macaroni penguins *Eudyptes chrysolophus* at Bird Island, South Georgia. *Mar. Ecol. Progr. Ser.*, 466: 261–274.

Ward, P., A. Atkinson, H. Venables, G. Tarling, M. Whitehouse, S. Fielding, M. Collins, R. Korb, A. Black, G. Stowasser, K. Schmidt, S. Thorpe and P. Enderlein. 2012. Food web structure and bioregions in the Scotia Sea: a seasonal synthesis. *Deep-Sea Res. II.*, 59–60: 253–266.

Warren, J.A. and D.A. Demer. 2010. Abundance and distribution of Antarctic krill (*Euphausia superba*) nearshore of Cape Shirreff, Livingston Island, Antarctica, during six austral summers between 2000 and 2007. *Can. J. Fish. Aquat. Sci.*, 67: 1159–1170.

Watkins, J. 2000. Sampling krill – direct sampling. In: Everson, I. (Ed). *Krill Biology, Ecology and Fisheries*. Blackwell Science, Oxford: 8–19.

Watkins, J.L., R. Hewitt, M. Naganobu and V. Sushin. 2004. The CCAMLR 2000 Survey: a multinational, multi-ship biological oceanography survey of the Atlantic sector of the Southern Ocean. *Deep-Sea Res. II*, 51: 1205–1213.

Watters, G.M., S.L. Hill, J.T. Hinke, J. Matthews and K. Reid. (in rev). Decision making in the face of complexity and uncertainty: Evaluating management options for a Southern Ocean krill fishery with an ecosystem dynamics model. Unpubilished manuscript (NOAA Southwest Fisheries Science Center).

Whitehouse, M.J., M.P. Meredith, P. Rothery, A. Atkinson, P. Ward and R.E. Korb. 2008. Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: forcings, characteristics and implications for lower trophic levels. *Deep-Sea Res. I*, 55: 1218–1228.

Whitehouse, M.J., A. Atkinson, P. Ward, R.E. Korb, P. Rothery and S. Fielding. 2009. Role of krill versus bottom-up factors in controlling phytoplankton biomass in the northern Antarctic waters of South Georgia. *Mar. Ecol. Prog. Ser.*, 393: 69–82.

Whitehouse, M.J., A. Atkinson and A.P. Rees. 2011. Close coupling between ammonium uptake by phytoplankton and excretion by Antarctic krill, *Euphausia superba. Deep-Sea Res. I*, 58: 725–732.

Wiebe, P.H., C.J. Ashjian, S.M. Gallager, C.S. Davis, G.L. Lawson and N.J. Copley. 2004.

Using a high-powered strobe light to increase the catch of Antarctic krill. *Mar. Biol.*, 144: 493–502.

Wiebe, P.H., C.J. Ashjian, G.L. Lawson, A. Piñones and N.J. Copley. 2011. Horizontal and vertical distribution of euphausiid species on the Western Antarctic Peninsula. U.S. GLOBEC Southern Ocean study site. Original Research Article. *Deep-Sea Res. II*, 58 (13–16): 1630–1651.

Wiedenmann, J., K. Cresswell and M. Mangel. 2008. Temperature-dependent growth of Antarctic krill: predictions for a changing climate from a cohort model. *Mar. Ecol. Prog. Ser.,* 358: 191–202.

Wiedenmann, J., K.A. Cresswell and M. Mangel. 2009. Connecting recruitment of Antarctic krill and sea ice. *Limnol. Oceanogr.*, 54: 799–811.

Willis, J. 2007. Could whales have maintained a high abundance of krill? *Evoluitionary Ecol. Res.*, 9: 651–662.

Wright, S.W., R. van den Enden, I. Pearce, A.T. Davidson, F.J. Scott and K.J. Westwood. 2010. Phytoplankton community structure and stocks in the Southern Ocean (30–80°E) determined by CHEMTAX analysis of HPLC pigment signatures. *Deep-Sea Res. II*, 57: 758–778.

Zane, L., L. Ostellarti, L. Macatrozzo, L. Bargelloni, B. Battaglia and T. Patarnello. 1998. Molecular evidence for genetic subdivision of Antarctic krill (*Euphausia superba*) populations. *Proc. R. Soci. Lond. Ser. B*, 265 (1413): 2387–2391.

Zimarev, Y.V., S.M. Kasatkina and Y.P. Frolov. 1991. Midwater trawl catchability in relation to krill and possible ways of assessing gross catch. *Selected Scientific Papers, 1990 (SC-CAMLR-SSP/7)*. CCAMLR, Hobart, Australia: 87–113.