



ELSEVIER

Contents lists available at ScienceDirect

Deep-Sea Research I

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

A re-appraisal of the total biomass and annual production of Antarctic krill

A. Atkinson^{a,*}, V. Siegel^b, E.A. Pakhomov^c, M.J. Jessopp^{a,1}, V. Loeb^d

^a British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB30ET, UK

^b Sea Fisheries Institute, Palmaille 9, 22767 Hamburg, Germany

^c Department of Earth and Ocean Sciences, University of British Columbia, 6339 Stores Road, Vancouver, BC, Canada V6T 1Z4

^d Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039, USA

ARTICLE INFO

Article history:

Received 28 May 2008

Received in revised form

12 December 2008

Accepted 21 December 2008

Available online 25 December 2008

Keywords:

Antarctic krill

Euphausia superba

Southern Ocean

Biomass

Abundance

Range

Production

Habitat

Mortality

Growth

ABSTRACT

Despite much research on *Euphausia superba*, estimates of their total biomass and production are still very uncertain. Recently, circumpolar krill databases, combined with growth models and revisions in acoustics have made it possible to refine previous estimates. Net-based databases of density and length frequency (KRILLBASE) yield a summer distributional range of $\sim 19 \times 10^6$ km² and a mean total abundance of 8×10^{14} post-larvae with biomass of 379 million tonnes (Mt). These values are based on a standardised net sampling method but they average over the period 1926–2004, during which krill abundance has fluctuated. To estimate krill biomass at the end of last century we combined the KRILLBASE map of relative krill density around Antarctica with an acoustics-derived biomass estimate of 37.3 Mt derived for the Scotia Sea area in 2000 by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Thus the CCAMLR 2000 survey area contains 28% of the total stock, with total biomass of ~ 133 Mt in January–February 2000. Gross postlarval production is estimated conservatively at $342\text{--}536$ Mt yr⁻¹, based on three independent methods. These are high values, within the upper range of recent estimates, but consistent with the concept of high energy throughput for a species of this size. The similarity between the three production estimates reflects a broad agreement between the three growth models used, plus the fact that, for a given population size, production is relatively insensitive to the size distribution of krill at the start of the growth season. These production values lie within the envelope of what can be supported from the Southern Ocean primary production system and what is required to support an estimated predator consumption of $128\text{--}470$ Mt yr⁻¹. Given the range of recent acoustics estimates, plus the need for precautionary management of the developing krill fishery, our net-based data provide an alternative estimate of total krill biomass.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

Antarctic krill, *Euphausia superba*, are an important species in the context of fisheries (Everson, 2000), biogeochemical cycling (von Bodungen, 1986) and in the Antarctic food web (Hopkins et al., 1993; Lancraft et al., 2004). During the 80-year history of modern krill research we have learnt much about their biology, but basic questions remain over their total abundance, biomass

* Corresponding author.

E-mail address: aat@bas.ac.uk (A. Atkinson).

¹ Present address: Department of Zoology, Ecology and Plant Science, University College Cork, Distillery Fields, Enterprise Centre, North Mall, Cork, Ireland.

and production within the Southern Ocean (Ross and Quetin, 1988; Miller and Hampton, 1989; Nicol et al., 2000). These data are needed to gauge how much energy flows through krill, as compared to that through other grazers such as protozoans, copepods or salps (Voronina, 1998; Calbet and Landry, 2004; Shreeve et al., 2005). Total biomass and production are also key requirements for the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) to set a maximum annual fisheries yield, calculated as a fraction of pre-exploitation biomass (Constable et al., 2000).

Previous estimates of krill biomass have ranged from 14 to 7000 Mt and production from 75 to 1350 Mt yr⁻¹ (Miller and Hampton, 1989). These are orders of magnitude of uncertainty. More recently, estimates have moved towards the lower end of these spectra, with biomasses of 60–420 Mt (Voronina, 1998; Nicol et al., 2000; Siegel, 2005) and production 100–500 Mt yr⁻¹ (see Ross and Quetin, 1988). However, these authors stress the great amount of uncertainty and extrapolation involved in such calculations. First the size, mobility and variable behaviour of krill present a challenge for sampling, either with acoustics or nets (Watkins et al., 2000). Secondly their vast circumpolar distribution encompasses a range of possible growth habitats—a major hurdle to extrapolation. Third, the variable recruitment success of krill leads to large inter-annual fluctuations in abundance (Mackintosh, 1973; Siegel and Loeb, 1995; Loeb et al., 1997), making it hard to generalise from single surveys.

A re-examination of the total biomass and production of krill is now timely. For example, there is a widely reported observation that, both at local scales and circumpolar scales, the biomass of krill is low compared to that estimated to be removed by predators (Miller and Hampton, 1989; Nicol et al., 2000; Constable et al., 2003; Willis, 2007). Furthermore, krill acoustics methods are currently in a phase of refinement. Thus, acoustic biomass estimates derived for the CCAMLR 2000 Synoptic survey of the Scotia Sea area (Hewitt et al., 2004) have ranged over fivefold in the last 4 years. The latest of a series of

four assessments (37 Mt; Demer et al., 2007) has also been the lowest, which does not help to resolve a reported mismatch between biomass and estimated consumption.

Several recent developments now enable us to revisit previous estimates of the total biomass and production of krill. These include “KRILLBASE”, which comprises two circumpolar databases of historical net sampling data on postlarval krill density and length frequency (Atkinson et al., 2004, 2008). A recent series of krill growth models (Ross et al., 2000; Kawaguchi et al., 2006; Candy and Kawaguchi, 2006; Tarling et al., 2006; Atkinson et al., 2006) now improve our ability to predict gross production. Here we combine acoustic data, KRILLBASE and two growth models to recalculate the total range, abundance, biomass and production of krill.

2. Methods

2.1. KRILLBASE density database

This density component of KRILLBASE comprises over 12,000 net hauls from around Antarctica, extracted from our own databases, logbooks, published reports or sent from other institutes. It contains all available net-based data on the numerical density (no. m⁻²) of postlarval *E. superba* (hereafter “krill”) spanning the years 1926–1939 and 1976–2004. To this data set we set a series of selection criteria (Table 1) to extract a subset of 8137 hauls from the spring–summer–autumn period using un-targeted sampling (Fig. 1a). Individuals < 19 mm long were deliberately excluded from the Discovery (1926–1939) portion of the database, and the predominant krill net in the modern part of the database, the RMT 8, also seriously under-samples the < 19 mm long fraction (Siegel, 1986).

A composite net-based data set on krill distribution has two main problems: first that scientific net sampling provides an underestimate of true density (no. m⁻²) distribution due to escapement (Watkins et al., 2000) and net mesh selection for the smallest post-larvae in spring

Table 1
Selection criteria of net-based krill density data from KRILLBASE for use in this study.

Net hauls included	Stations excluded	Notes
South of Antarctic Polar Front Those sampled in October–April inclusive	North of Antarctic Polar Front Those sampled in May–September	Frontal position is based on Moore et al. (1999) 66% of stations were sampled in summer (December–February)
Scientific nets whose volume filtered can be calculated Oblique or vertical hauls	Commercial or semi-commercial trawls Horizontal or near-horizontal hauls	Not possible to calculate mouth area from trawl data, and issues of net mesh selection Not possible to calculate no. krill m ⁻² from horizontal tows
Pre-fixed station positions	Hauls targeted on krill aggregations	Essential to exclude targeted hauls for realistic calculation of areal density
Topmost fishing depth either from the surface or from no more than 10 m from the surface Bottom fishing depth of at least 60 m	Top fishing depth from deeper than 10 m Bottom fishing depth shallower than 60 m	Selection made to include krill from near the surface Median bottom depth of net was 170 m, which is expected to encompass most of the summer population. Note that numbers of krill m ⁻² from stratified series of nets have been pooled over entire depth range of net series by addition

These reduced the total database of over 12,000 stations to a subset of 8137.

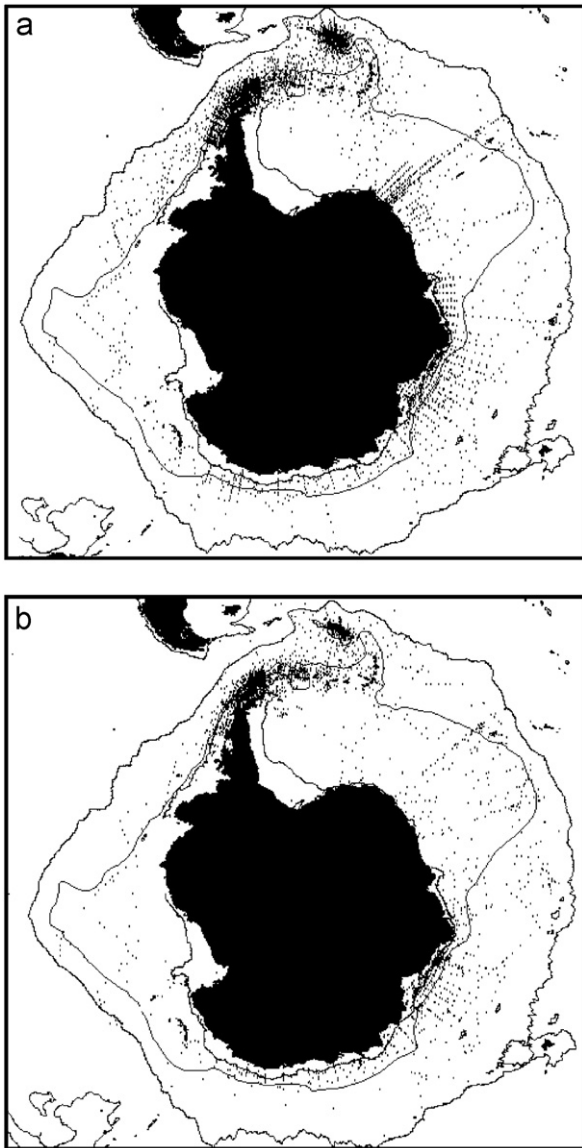


Fig. 1. Sampling coverage in KRILLBASE, with dots showing the subset of stations selected for this analysis. (a) 8137 krill density stations and (b) 5748 stations with length frequency distributions. Fronts shown, from north to south are the Antarctic Polar Front (Moore et al., 1999) and Southern Boundary of the Antarctic Circumpolar Current (Orsi et al., 1995). The 1000 m isobath is also shown.

(Siegel, 1986). This problem varies depending on net type, fishing depth, time of day and season. Second, the recruitment of krill to the postlarval population, coupled to mortality, leads to density fluctuations throughout the season.

We have countered these problems by standardising each of the density values to that from a common sampling method. All data were thus standardised to a nominal 8 m² mouth area net fishing at night from the surface to 200 m on 1 January. This date was selected as when the density of postlarval krill density (of individuals large enough to be retained by the nets) is at its seasonal maximum. Likewise the net type, sampling depth and

time of day were selected as the most efficient method used commonly for scientific net sampling.

The method of standardising each density value is detailed in Atkinson et al. (2008) but is summarised below. The approach was to separate out the relative effects of towing depth, daytime versus night-time sampling, net mouth area and time of year on the measured krill density value. First, by analysis of deep stratified series of nets we determined that 97.3% of the total krill population were located within the top 200 m layer during the summer period. Thus we standardised all data to a sampling depth of 200 m, excepting that this would provide some degree of underestimation. By analysis of 262 stratified net hauls we plotted the cumulative total fraction of total krill abundance in relation to sampling depth, and used this as a basis to “correct” densities from nets fishing to shallower than 200 m. The upward revisions of krill density due to limited bottom sampling depth were, in practice, rather slight because most the net hauls were to at least 100 m depth and hauls to <60 m were in any case automatically excluded (see Table 1).

Time of day had a more severe influence on density values, with night-time catches tending to be substantially larger than those during daytime, probably due to daytime net avoidance. First, all hauls in KRILLBASE were assigned as a nominal “day” or “night” according to a common algorithm (Atkinson et al., 2008). Subsets of data involving many (2595) stations, sampled repeatedly with the same net type and sampling depth within localised geographical areas were then analysed. This reduced the effects of confounding variables and showed that night-time catches were 2.26-fold those made during the day. This factor was used to scale daytime catches up to an equivalent night-time value.

Having adjusted every density value in KRILLBASE for sampling depth and time of day of sampling, we were able to examine the simultaneous effects of net mouth area and time of year of sampling. The frequency distribution of density values showed that the data set was bimodal and highly skewed, so we approached this using logistic binary regression to determine the probability of a non-zero density value and then, for the non-zero component, logging provided the approximation to a normal distribution required for a mixed model. The effects of net mouth area and time of year of sampling were then incorporated by combining the probability value from the logistic regression with the mixed model. Atkinson et al. (2008) provide details of the effects of this standardisation procedure as well as the equations used. However, we present here the results from both standardised and un-standardised data.

2.2. KRILLBASE length-frequency database

This component of KRILLBASE was constructed separately from the density database. Its complete version comprises >1 million krill length measurements, derived from scientific nets, the commercial fishery and predator diets. The length-frequency database was used here to

obtain an overall seasonal picture of the length distribution of krill from which to determine biomass and production values. These data were restricted to those from scientific nets within the same October to April period as the density database (Fig. 1b). Unlike the density database, this data subset (535581 length measurements from 5748 stations) included horizontal and targeted hauls and were taken over the periods 1926–1939 and 1976–2006.

2.3. Determination of total krill abundance

The uneven scattering of the 8137 density stations required a stratification approach to determine total abundance, whereby the whole data set was plotted onto a grid. With the assumption that the mean density of krill from sampling stations in each cell represents the mean density across the whole cell (see Discussion), mean krill densities (no. of krill m^{-2}) per cell and cell areas (m^2) were calculated in ArcGIS 9.1 and exported to Excel for calculation of total krill abundance (no. postlarvae) in each cell. Total abundance N_{total} is calculated by summing all cells, i , with density data D_i :

$$N_{total} = \sum D_i A_i \quad (1)$$

where A_i is the area of cell i (m^2) that is not covered by land/ice shelf and is south of the Antarctic Polar Front. These calculations were done both for the raw (un-standardised) and our standardised density data and for two sizes of grid, namely of 3° latitude \times 9° longitude and of 2° latitude \times 6° longitude (Fig. 2). Each grid was on a South Polar Lambert Azimuthal Equal Area projection to enable faithful representation of areas.

2.4. Determination of biomass: overview

Only a minority of the krill density records had associated length-frequency data, and the latter database comprised many targeted and horizontal hauls. It was therefore not possible to calculate a biomass from the density data on a haul-by-haul basis without losing most of the data from each of the component databases. Instead we used our calculated value for total krill abundance, N_{total} , of 7.8×10^{14} krill, standardised to 1 January and multiplied it by a realistic value for the mean mass of an individual krill at that point in the growing season, as calculated below.

The method of obtaining these mean masses per krill is best illustrated by the actual data, shown in Fig. 3. The length-frequency database for the main growth season is illustrated here; a composite of multiple seasons and regions that nevertheless shows the main trends. The population modes increase progressively in length from October to January, which we define as the somatic growth period. There is much less growth between February and April, but we know that much production occurs then, since this includes part of the spawning period (Quetin and Ross, 2001) and winter lipid stores increase (Hagen et al., 2001). Our estimates of production therefore attempt to capture not only the early season

growth in length but also the period of reproduction and lipid deposition.

The changes in mean krill mass throughout the season are central to our biomass and production calculations. To convert from length, L (mm) to wet mass W (g) we used first a single length–mass regression for all months of the year, based on Morris et al. (1988)

$$W_{overall} = 3.85 \times 10^{-6} L^{3.20} \quad (2)$$

We also used a series of length–mass regressions (Siegel, 1992) specific to the relevant month (Table 2). From these equations we calculated the mean wet mass of krill for each month (for example December) as $W_{Dec-mean}$ based on the calculated wet mass W_l of each length class, l , the total number of krill of this length counted in that month c_l and the total count in all length classes, c_{all} :

$$W_{Dec-mean} = \sum (W_l c_l) / \sum (c_{all}) \quad (10)$$

This approach is analogous to pooling all krill sampled in a particular month into a massive virtual haul and obtaining a mean krill mass as the total krill mass divided by the total number of individuals.

Fig. 4 shows the results of these calculations. The trend using a single length–mass regression (dotted line) is a general increase in krill mass due to growth in length with superimposed predation effects. But being a single regression it does not account for any seasonal fattening of the krill with lipid, eggs or sperm. By contrast the solid line in Fig. 3 shows also the effects of increasing length of krill in the population, but it also accounts for spawning and then fattening for winter. We have used primarily these month-specific equations to better capture the processes of spawning and lipid build-up in addition to somatic growth. These predictions of mass per krill thus allow us to calculate biomass from abundance.

2.5. Calculation of total biomass averaged over last century

The abundance values N_{total} from Eq. (1) were from sampling adjusted to 1 January. Therefore we calculated total biomass B_{total} (tonnes) by multiplying this value by the average of the monthly mean wet masses of the individual krill from December and January:

$$B_{total} = N_{total} 10^{-6} (W_{Dec-mean} + W_{Jan-mean}) / 2 \quad (11)$$

where 10^{-6} converts grams to tonnes.

2.6. Calculation of total biomass in Jan–Feb 2000

The above calculations are based on multi-season composite data, and they provide a biomass averaged over 40 years of last century. This may not be representative of modern times. For an estimate in a recent year we used an alternative approach, combining nets and acoustics. Onto the $2^\circ \times 6^\circ$ grid map of mean krill density (Fig. 2b) we superimposed the boundaries of the CCAMLR 2000 Synoptic Survey (Hewitt et al., 2004). By summing individual grid cells as described in Eq. (1), we calculated the fraction of the total circumpolar krill population located inside this $2.065 \times 10^6 km^2$ survey area. Where

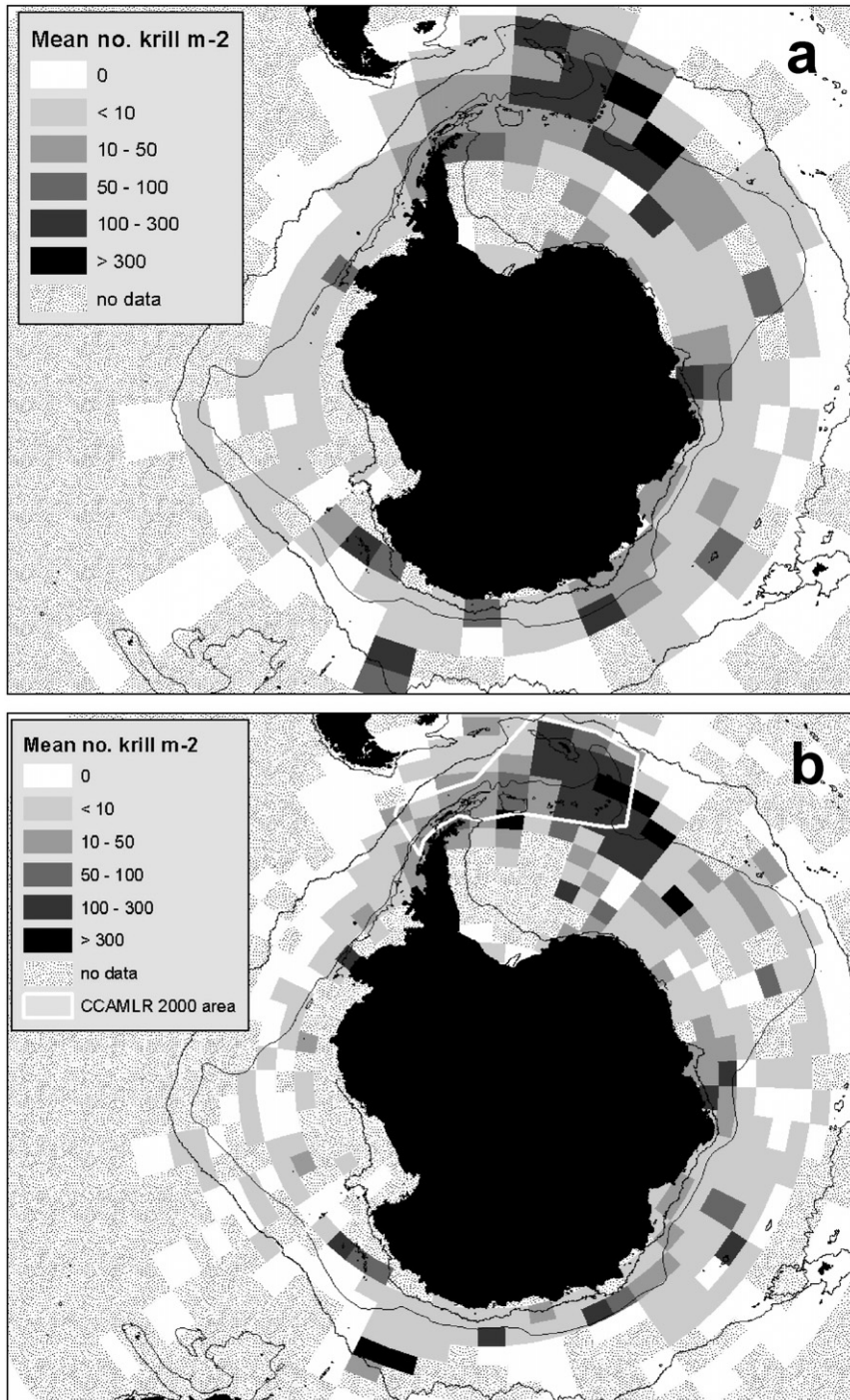


Fig. 2. Circumpolar distribution of mean krill density per grid cell (standardised densities) based on (a) a 3° latitude × 9° longitude grid, and (b) a 2° latitude × 6° longitude grid, with the boundaries of the CCAMLR 2000 Synoptic survey superimposed. Fronts and bathymetry as in Fig. 1.

this boundary crossed a grid cell, abundance inside and outside of it was calculated pro-rata according to area (i.e. assuming constant krill density across the cell).

The most recent acoustic estimate of total krill biomass within this Synoptic survey area, and that currently

accepted by CCAMLR, is 37.3×10^6 t (Demer et al., 2007). We divided this biomass by the fraction of the total population calculated to be within its boundaries (0.28) to estimate total circumpolar biomass for the summer of 2000. In essence this estimate uses nets to provide the

circumpolar picture of relative krill density and acoustics to provide the absolute biomass within a defined portion of the total habitat.

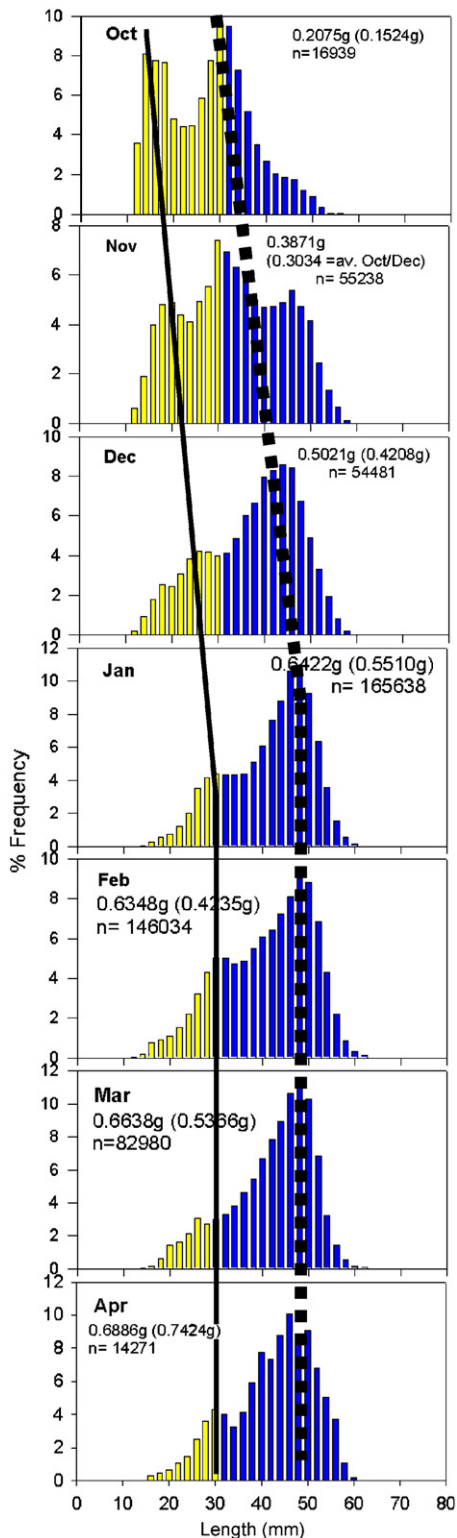


Table 2

Equations specific to a particular month to derive krill wet mass, W from length, L taken from Siegel (1992).

Month	Krill condition	Equation (equation number)
October	Resting stage	$W_{Oct} = 2.36 \times 10^{-6} L^{3.251}$ (3)
December	Gravid	$W_{Dec} = 8.6 \times 10^{-7} L^{3.551}$ (4)
January	Gravid-spent	$W_{Jan} = 2.05 \times 10^{-6} L^{3.325}$ (5)
February	Gravid	$W_{Feb-gravid} = 8.3 \times 10^{-7} L^{3.561}$ (6)
February	Spent	$W_{Feb-spent} = 1.65 \times 10^{-6} L^{3.380}$ (7)
March	Spent	$W_{March} = 1.93 \times 10^{-6} L^{3.325}$ (8)
April	Probably spent	$W_{April} = 1.70 \times 10^{-6} L^{3.433}$ (9)

2.7. Calculation of total gross production: overview

Rather than attempting to calculate net production, which reflects both growth and mortality operating together, we have separated the two processes by calculating gross production. This is the theoretical increase in mass of the krill population over the growing season due to growth, egg production and lipid build-up, and in the absence of mortality. This facilitates estimation and allows comparison of growth and mortality values.

We used three separate methods to estimate growth in krill length. Firstly a predictive growth model (Atkinson et al., 2006) using the instantaneous growth rate (IGR) method (Quetin and Ross, 1991) was used to provide a circumpolar-scale prediction of daily growth rates in mm d^{-1} based on ambient food, temperature and krill length. Second, we used another recent IGR-based model (Kawaguchi et al., 2006; Candy and Kawaguchi, 2006) but converted to a seasonal growth trajectory. The third and simplest approach uses our series of composite monthly length-frequency data from KRILLBASE (Figs. 3 and 4) as an index of growth. All of these methods provide a series of increasing lengths of krill throughout the growing season. These are converted to masses as above, and thence to biomasses by multiplying by total krill abundance (N_{total}).

2.8. Calculation of total gross production: Method 1

To predict daily growth rate DGR (mm d^{-1}) we used the empirical model of Atkinson et al. (2006) based on krill length, L (mm), SeaWiFS-derived food, F ($\text{mg Chl } a \text{ m}^{-3}$)

Fig. 3. The composite percentage length frequency distribution for the main growth season of October–April. For clarity krill are plotted in 2 mm increments with the portion <30 mm long with lighter shading. The main modal peaks are connected by eye to show the rapid growth in the early part of the season compared to that after February. The smaller mode (solid line) probably represents 1-year old krill, whereas the larger mode (broken line) represents probably multiple cohorts. Mean krill masses for each month are based first on Eqs. (2) and then in brackets the equivalent values for month-specific length-mass regression (Eqs. (3)–(9)). N is the number of krill measured in each month.

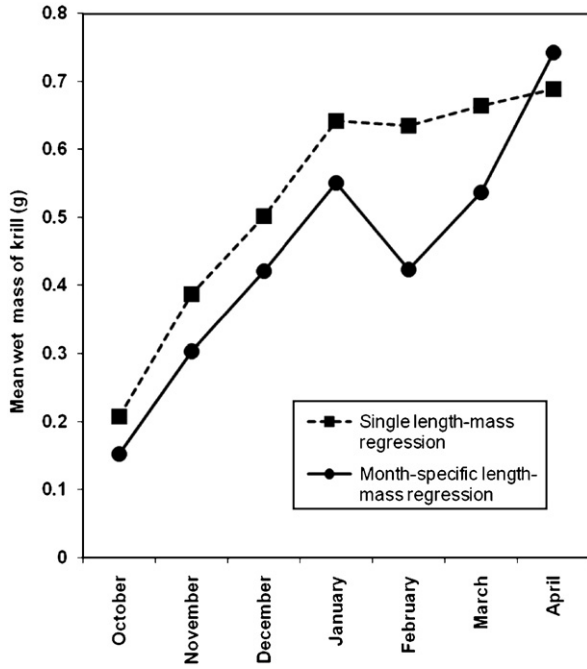


Fig. 4. Increase in mean mass of krill in the population during the main growing season, reflecting somatic growth, reproductive output and lipid deposition. The dotted line reflects somatic growth only (Fig. 3), as it is based on the single length–mass regression of Morris et al. (1988) in Eq. (2). The solid line incorporates the seasonal change in condition as well as somatic growth, being based on the month-specific regressions of Siegel (1992) using Eqs. (3)–(9). Masses for November were calculated as the mean result of the regressions for October and December, and those for February were calculated as the mean of results for gravid and spent individuals for that month (Eqs. (6) and (7)).

and sea surface temperature, T ($^{\circ}\text{C}$):

$$DGR = -0.066 + 0.002L - 0.000061L^2 + 0.385F/(0.328 + F) + 0.0078T - 0.0101T^2 \quad (12)$$

This model is based on data from the SW Atlantic sector during two January–February field seasons. It is designed for use with satellite-derived Chl a inputs, and is based on the IGR method, which is considered to reflect *in situ* growth (Ross et al., 2000; Kawaguchi et al., 2006; Tarling et al., 2006).

We first gridded the monthly SeaWiFS chl a data and MODIS temperature data onto a circumpolar 0.5° latitude \times 1° longitude grid, using the zonal statistics of Arc GIS 9.1 to compute mean pixel values for each grid cell. These monthly specific cell values were then used to drive a spatial grid model of krill growth potential throughout summer. We did not include advection in this model, which is designed to represent spatial locations that are favourable to growth. Model outputs are illustrated in Atkinson et al. (2008).

Since daily growth rates depend on krill size, the empirical model run was repeated with 4 starting sizes of krill, namely 20, 30, 40 and 50 mm. The model was run for 4 months from 1 December, using Eq. (12) for each of the 43,200 grid cells. Thus we based our daily growth

calculation on final krill length from the previous time step and the relevant month’s satellite-derived temperature and food indices. For any of the grid cells, absent temperature or Chl a data within any of the months precluded calculations—extrapolated values were not used. We grew krill for the 4-month period over each of the 7 summers between 1997/1998 and 2003/2004 and calculated the mean of these. If one or more of the years returned absent data for a particular cell for the reason above, values were averaged for the remaining years.

We converted DGR from units of krill length L , to dry mass, M , by applying length–mass regressions that were derived from the same krill used to construct the empirical growth model (Atkinson et al., 2006):

$$\log_{10}M = 3.89 \log_{10}L - 4.19 \quad (13)$$

In this way we could calculate a Gross Growth Potential GPP for each grid cell, i :

$$GPP_i = M_{31st\ March} / M_{1st\ Dec} \quad (14)$$

where $M_{1st\ Dec}$ is the predicted mass of the initial krill predicted from Eq. (2), and $M_{31st\ March}$ is its final predicted mass after 121 days of growth. We stress that this calculation is not analogous to a P:B ratio since it specifically excludes mortality—it is our best estimate of the mass increase that a krill in each grid cell could achieve if it remained alive.

At the coarser grid scale of Fig. 2a, initial biomass values in cell i , $B_{i\ 1st\ Dec}$ (tonnes wet mass) were obtained as

$$B_{i\ 1st\ Dec} = D_i A_i M_{1st\ Dec} 4 \times 10^{-9} \quad (15)$$

where D_i is the mean krill density (no. m^{-2}) in cell i (see Fig. 2a), A_i is the area of water in cell, between and Antarctic coast/ice shelf and the APF (m^2), M_{start} is the predicted dry mass per krill of the starting 20, 30, 40 or 50 mm population, the value of 4 is a conservative factor relating dry mass to wet mass (Morris et al., 1988) and 10^{-9} converts mg to tonnes. Final biomass, $B_{i\ end}$ in the cell was obtained from its overall GPP value:

$$B_{i\ 31st\ Mar} = GPP_i B_{i\ 1st\ Dec} \quad (16)$$

and gross total production in the cell, P_i , then calculated

$$P_i = B_{i\ 31st\ Mar} - B_{i\ 1st\ Dec} \quad (17)$$

Thus total gross production P_{total} , was obtained by summing across grid cells:

$$P_{total} = \sum P_i \quad (18)$$

Total production was thus calculated for 4 sizes of krill, in other words assuming that the entire krill population comprised, in turn, individuals of 20, 30, 40 or 50 mm. This approach was adopted both for simplicity and transparency of method, and to compare production of radically different sizes of krill.

2.9. Calculation of total gross production: Method 2

In common with Method 1, Method 2 is based on the IGR method. However, the experiments were done mainly in the Indian sector not the Atlantic sector, and the growth

model was obtained in an entirely different manner (Kawaguchi et al., 2006; Candy and Kawaguchi, 2006). These authors plot the seasonal growth trajectories in scenarios of winter shrinkage and no winter shrinkage for juveniles and mature males. The model incorporates krill 2 years old starting their third growth season, plus successive seasons thereafter. We have extracted their growth increment data from the beginning and end of the growth season for the 3rd, 4th and 5th seasons of growth and converted them to equivalent wet masses for the year class n ($M_{n-start}$ and M_{n-end}), using Eqs. (3) and (9) respectively. For simplicity and comparison between year classes we calculated total gross production potential of each year class n (P_{totaln}) as if it comprised the entire population:

$$P_{totaln} = (N_{total} M_{n-end}) - (N_{total} M_{n-start}) \quad (19)$$

2.10. Calculation of total gross production: Method 3

This is an alternative approach to estimate the change in mean mass of krill in the wild population from the beginning of the growth season to the end. The start is characterised by lean krill from the end of winter and small animals recently moulted from larvae, and the end by longer animals after a season's growth, with large lipid stores in preparation for winter. The mean mass of the population in October and April are calculated using Eqs. (3), (9) and (10) and these values are converted to

biomass, from which total production is calculated as

$$P_{total} = (W_{Apr-mean} N_{total}) - (W_{Oct-mean} N_{total}) \quad (20)$$

3. Results

3.1. Total range of krill

We define here the potential habitat of krill as the total ocean and shelf area between the APF and the Antarctic continent. Of this $29.8 \times 10^6 \text{ km}^2$, 12.8% comprises the shelf/slope habitat, defined by water depth $< 2000 \text{ m}$ (Table 3) and 19% was not sampled, based on the $3^\circ \times 9^\circ$ grid cells in Fig. 2a. The cells not sampled comprised mainly those near the APF where krill are rare or absent, plus parts of the Ross and Weddell Seas. These are not generally considered major population centres (but see Azzali and Kalinowski, 2000) so were conservatively assumed to have no krill.

Of the total area south of the APF, we calculated positive krill densities in nearly two-thirds of it: $19 \times 10^6 \text{ km}^2$. This is defined as the total range of krill, accepting that densities are low across parts of it, and that Fig. 2 is a composite of multiple months and years.

3.2. Total krill abundance

The Southern Ocean is too large for sampling within a single season, so we need to use the 1926–2004 data set to

Table 3

A variety of methods of calculating habitat area, density and total abundance of krill, based on standardised densities.

Region	Definition of region	Area of region ($\times 10^6 \text{ km}^2$)	Mean krill density in region (no. m^{-2})	Total krill abundance in region ($\times 10^{14}$ krill)	Explanation
Total potential shelf and slope habitat	Total area between ice sheet edge/coast and 2000 m isobath	3.8	60		Mean krill density presented, by averaging across all 3845 shelf/slope stations (not stratified)
				1.0	Total abundance obtained by stratifying only the shelf cells sampled (un-sampled ones are assumed zero density)
Total deep ocean potential habitat	Total area of water deeper than 2000 m south of APF	26.0	36		Mean krill density is presented here, by averaging across all 4338 deep ocean stations (i.e. not a stratified estimate)
				6.8	Total abundance obtained by stratifying only the deep ocean cells sampled (un-sampled ones are assumed zero density)
Total area south of APF	The two habitats above combined	29.8 (but grid cell area sampled is 24.2)	23.2		Mean density obtained here by averaging the cell densities derived for the 216 cells sampled Total abundance obtained by summing the above two rows
				7.8	

The stratified estimates (whereby the data were first gridded) were based on the 3° latitude \times 9° longitude grid of Fig. 2a. Results based on the finer scale 2° latitude \times 6° longitude grid are presented in the text for comparison.

determine the distribution pattern. However, a previous analysis (Atkinson et al., 2004) failed to find convincing evidence that the distribution pattern of krill had changed within that period, so this approach is reasonable.

Overall, we derive a total krill abundance of 7.8×10^{14} krill, based on standardised densities (Table 3). This calculation clearly depends on our stratification method and issues of sampling a patchily distributed population, so we have repeated our calculations with a series of methods. By stratifying on a finer, $2^\circ \times 6^\circ$ grid (Fig. 2b) density is slightly higher: 8×10^{14} krill. The highest sensitivity of this estimate is associated with cells where calculated krill density is high, but which contain relatively few stations. The two cells with greatest influence on our results were the two with mean estimated densities of >300 krill m^{-2} (the black cells in Fig. 2a). If the densities in these are replaced with dummy values of 36 krill m^{-2} (the mean from all 4338 oceanic stations) the total abundance is reduced to 5.4×10^{14} krill. The high densities in these areas reflect the chance event of catching dense swarms of krill and the relatively few sampling stations within each of these cells. There is no reason to suggest that these high values were erroneous so they cannot justifiably be removed as outliers. Cells with few hauls which happened to miss the schools would tend to compensate for them.

3.3. Total krill biomass

Table 4 shows a variety of ways of calculating total krill biomass, using combinations of net- and acoustics-based methods and integrating over different time periods. We combined the total abundance value, N_{total} , of 7.8×10^{14} krill with a mean wet mass of 0.486 g krill $^{-1}$ using Eq. (11) to derive a total circumpolar biomass of 379 Mt. This is

based on standardised densities, and the corresponding figure for un-standardised data is 117 Mt, still a surprisingly high value considering that it is based entirely on net sampling.

These values are based on data averaged over the period 1926–2004. An alternative calculation, combining nets and acoustics, is possible to determine a biomass value at the end of last century. The most recent, CCAMLR-approved biomass estimate for the 2 million km^2 area of the CCAMLR Synoptic Survey area is 37.3 Mt (Demer et al., 2007). Based on our calculation that 28% of the global krill stock lie within the boundaries of this survey area, we calculate pro-rata that the global stock in January–February 2000 was ~ 133 Mt.

3.4. Gross production: Method 1

This calculation differs from the other two in that it only uses part of the growing season, in order to avoid excessive seasonal extrapolation of the IGR data (from January and February) and to avoid excessive absent data early and late in the season due to ice cover. The production is calculated for different starting sizes of krill, for example, that of 20 mm krill was calculated as if the entire starting population (7.8×10^{14} individuals) were of this size at the start of the model run. The main result (Table 5) is that the GGP of the small krill is much higher than those of the larger animals, in other words they increase in mass throughout the growth season proportionately more than the larger krill. However, for a given number of krill in the Southern Ocean at the start of the model run, production of our populations entirely 20 and 50 mm long differ surprisingly little, between 342 and 536 $Mt yr^{-1}$. This reflects the fact that production is a product of biomass and growth, and the higher biomass of

Table 4

A variety of methods for estimating total biomass (fresh mass) of krill in the Southern Ocean using a combination of acoustics and net-based methods.

Biomass (million tonnes)	Integration period	Method summary	Method details
117	1926–1939, 1976–2004	Actual (unadjusted) densities (no. m^{-2}) from nets, and using net-derived mean mass per krill	Unadjusted net sampling estimates yield an N_{total} of 2.4×10^{14} krill. This is based on summing the product of krill density per 3° latitude \times 9° longitude grid cell and its water area, with the conservative assumption that the 19% of grid cell area south of the APF with no data has zero krill. Krill numbers converted to biomass (wet mass) using a December–January mean value of 0.486 g ind^{-1} (Eq. (1); see Methods)
379	1926–1939, 1976–2004	Same as above but using the standardised net-derived densities.	Standardised density estimates (Table 3) yield an N_{total} of 7.8×10^{14} krill. These converted to biomass as above using 0.486 g ind^{-1} as above
133	January 2000	Using the latest, CCAMLR 2000 survey acoustic biomass estimate, scaled up to the Southern Ocean based on the proportion of total krill abundance within this survey area.	Based on Fig. 2b, we calculate that 28% of the total krill in the Southern Ocean are within the CCAMLR 2000 boundary. Acoustic biomass density recalculated from CCAMLR 2000 was 37.3×10^6 tonnes (Demer et al., 2007) so this value is divided by 0.28 to estimate circumpolar biomass

Table 5Calculated total gross krill production, P_{total} , over a 4-month summer (1 December–31 March).

Krill length (mm)	Wet mass ind ⁻¹ (g)	Initial biomass used in model on 1 Dec (Mt)	Final biomass/initial biomass (GGP, no units)	Total gross production, P_{total} (Mt yr ⁻¹)
20	0.0484	38	10.0	342
30	0.169	132	3.68	353
40	0.483	377	2.3	490
50	1.127	879	1.61	536

These calculations (see Methods) are performed for 4 starting sizes of krill, whose equivalent wet masses are shown. Thus separate model runs were made with the entire population, N_{total} (i.e. all 7.8×10^{14} individuals) of 20, 30, 40 or 50 mm at the start on 1 December. For this reason the total Gross Production P_{total} of the circumpolar stock is estimated here to be in the range 342–536 Mt yr⁻¹ rather than the sum of the respective values for each of the selected krill lengths.

Table 6

Total gross krill production potential using Method 2: the growth curves of Candy and Kawaguchi (2006).

Year class	Length (mm)		Initial biomass (Mt)	End krill mass/start krill wet mass	Production (Mt yr ⁻¹)
	Start	End			
1+	28 (28)	42(41.5)	94 (94)	5.29 (5.08)	402 (384)
2+	42 (41)	49 (49)	349 (322)	2.41 (2.61)	492 (518)
3+	49 (46.5)	53 (51.5)	575 (485)	1.91 (2.05)	523 (512)

Values are available from their calculated lengths at the start and end of the growing season for age classes 1+, 2+ and 3+ in their 3rd, 4th and 5th years of growth. As in Method 1, production is calculated as if the whole population (7.8×10^{14} individuals) were comprised of each of these three cohorts in turn, so total production is within the range of values for 1+, 2+ and 3+ and not the sum of each of their values. Values are illustrated in the two alternative scenarios, first including winter shrinkage and secondly excluding winter shrinkage in brackets.

Table 7

Calculation of gross production potential using Method 3: the seasonal change in mean mass of krill in the population.

Length mass regression used	Mean wet mass (g)		Initial biomass (Mt)	End krill mass/start krill wet mass	Production (Mt yr ⁻¹)
	October	April			
Regression specific to month (Siegel, 1992)	0.152	0.742	119	4.88	462
Single regression value (Morris et al., 1988)	0.208	0.689	162	3.31	374

The initial biomass is calculated as a product of the mean mass in October and the total abundance, N_{total} (7.8×10^{14} individuals). The production calculations are repeated using two approaches to length–mass conversion.

the bigger krill more than compensates for their relatively small proportional increase in mass.

3.5. Gross production: Method 2

The production estimates from this method (Table 6) are similar to those from Method 1, both in their values (402–523 Mt yr⁻¹) and in the fact that the lower mass-specific growth rates of the older krill cohorts is largely compensated for by their high biomass.

3.6. Gross production: Method 3

This alternative, in situ method returns a gross production of 462 Mt yr⁻¹ (Table 7), again within the range of the other methods. In common with the other methods this is based on a standardised abundance of 7.8×10^{14} krill at the start of the model run. Using instead

the single length–mass conversion of Morris et al. (1988), the production is slightly lower.

4. Discussion

4.1. Krill biomass

The total biomass of krill derived from this net sample database is surprisingly high. Indeed, our values of 117 Mt (un-standardised data) and 379 Mt (standardised data) are within the range of acoustics-based estimates of 60–420 Mt (Nicol et al., 2000; Siegel, 2005). Net sampling has been suggested to yield orders of magnitude underestimates of density due to escapement (see Watkins et al., 2000; Hamner and Hamner, 2000), so there is a conundrum: have we calculated biomass correctly? Or is the agreement between nets and acoustics coincidental,

with both yielding major underestimates? Or is net sampling not so inefficient as we thought?

To examine the calculation of total biomass (Eq. (1)), we will examine its two components, abundance and mean mass per krill, separately. Taking abundance first, the data were first stratified onto a grid. This requires sampling to be random, so that the stations within a cell provide an unbiased density estimate for its whole area. The patchy distribution of krill means greater imprecision for sparsely sampled cells, and two such cells returned very high krill densities (See Results). While these should not be excluded for statistical reasons, the total biomass is 259 Mt even without them. All hauls targeted on krill swarms were expressly excluded from the density component of KRILLBASE, but if mesoscale surveys target known krill-rich areas such as shelf breaks, there may be an element of non-random sampling within some of the grid cells. However, this bias is minor because only 13% of the total krill stock live over shelf/shelf break areas (Atkinson et al., 2008). Fig. 2b shows that most of the krill population (and grid cells) are remote from shelves.

The other issue in the calculation of total biomass is the use of a single mean mass per krill to convert abundance to biomass. It could be argued that a single value could lead to bias, if for instance the largest krill catches comprised very small krill. However, our averaging method accounted for this by calculating the total wet mass of all krill caught in a particular month divided by the number caught. Our length-frequency database is large, seasonal and circumpolar and we have used a mean mass per krill of 0.486 g for the middle of the growth season (Figs. 3 and 4), corresponding to a ~40 mm krill, about 2–3 years old and half way through its potential lifespan.

Since this mass component is reasonable, what are the factors leading to the high biomass calculated? Our mean density estimates per cell (Fig. 2) are not unrealistically high, being comparable, for instance, to a mean of 48 g wet mass per m^2 (~100 krill m^{-2}) from a series of acoustic surveys within the Scotia Sea area (Brierley et al., 1999). Instead, the high biomass reflects a massive distributional range. Spanning $19 \times 10^6 km^2$, this is much larger than that of recent estimates of $8 \times 10^6 km^2$ (Nicol et al., 2000) and $12 \times 10^6 km^2$ (Siegel, 2005). Krill are scarce over much of this, but they are abundant over large areas previously assumed to contain a small part of the stock, notably between $30^\circ W$ and $30^\circ E$. Thus the CCAMLR 2000 Survey would have sampled only 40% of the main Atlantic population from 0° to $90^\circ W$.

While we find no obvious biases in our calculation method, the broad agreement between net-based and acoustics-based biomass estimates is no guarantee that either are correct. However, if both methods were yielding gross (order of magnitude) underestimates, then from our calculations total production would be around 5 billion tonnes per year, i.e. about $5 \times 10^{14} g C yr^{-1}$. This is over 10% of the primary production estimate for the entire Southern Ocean (estimated as $43.71 \times 10^{14} g C yr^{-1}$; Arrigo and Thomas, 2004). Since protozoans, copepods plus salps outweigh krill in their grazing and production (Calbet and Landry, 2004; Voronina, 1998; Shreeve et al., 2005) this

would clearly be unsustainable. Such calculations support the prevailing view that an average krill biomass tenfold that of the current values is unsupported (Voronina, 1984; Tseitlin, 1989; Priddle et al., 1998).

While nets certainly do underestimate krill density, the error must be much less than tenfold. This might appear surprising, given the extensive discussion of serious net avoidance in the krill literature. However, the few studies of avoidance for *Euphausia superba* are almost without exception at the extremes of the sampling inefficiency spectrum: small nets 1 m diameter or less (Wiebe et al., 2004), samplers with towing gear directly in front (Hamner and Hamner, 2000), daytime observations (Hamner and Hamner, 2000), the relatively rare surface schools (Marr, 1962; Godlewska, 1996), or combinations thereof. Without doubt these do lead to avoidance, evidenced in our data set by the threefold increase in biomass after standardisation. The only avoidance study of *Euphausia superba* using our standardised, RMT8-size net fishing at night, reported only “limited” avoidance (Everson and Bone, 1986).

The surprisingly high krill biomass revealed by RMT8-type nets is not without precedent (e.g. Kasatkina et al., 2004) and demands an explanation. One possibility is that the high packing density of krill within schools prevents most from avoiding a large net (Everson and Bone, 1986). Most of the krill biomass is thought to reside in schools, which are large relative to nets (Witek et al., 1988; Ross et al., 1996). Hamner and Hamner (2000) described these schools as containing extremely closely spaced individuals whose escape response to a sampler towed at the speed of an RMT8 is a poorly orientated tail flipping, which is presumably constrained if within a compact school. Indeed, the high total abundance calculated from KRILLBASE reflects the frequency of catching krill schools and the densities therein, and not the densities of non-schooling “background” krill.

This highly aggregated distribution pattern of krill, with most of the biomass in schools, means that a net sampling survey must sample a representative number of schools (Watkins et al., 2000). The largest such survey of recent years, CCAMLR 2000, comprised 119 un-targeted RMT8 hauls, which returned a biomass of 38 Mt (Kasatkina et al., 2004; Siegel et al., 2004) similar to the current acoustics-derived estimate for this area of 37 Mt (Demer et al., 2007). The size of KRILLBASE is a key advantage, because its 8137 stations average schools and zero catches. Clearly any sampling programme, whether nets or acoustics, misses some of the population residing near the seabed (Gutt and Siegel, 1994; Clarke and Tyler, 2008) or right at the surface. However, we suggest that KRILLBASE provides a valid estimate of average total biomass.

All estimates of circumpolar krill biomass are based on composites of data collected over multiple seasons. However, both regional monitoring (e.g. Loeb et al., 1997; Siegel, 2005) and basin-scale analyses (e.g. Atkinson et al., 2008) show that krill density can vary by an order of magnitude between consecutive years. A series of studies also suggest a decline in krill within the SW Atlantic sector during the last two decades of last century (Loeb et al.,

1997; Reid and Croxall, 2001; Fraser and Hofmann, 2003; Atkinson et al., 2004). We could not standardise the circumpolar data to a particular year because there was insufficient inter-annual coverage outside the SW Atlantic sector, but almost certainly the circumpolar stock size will fluctuate substantially between years.

Nevertheless, our attempts to estimate a mean biomass, based on krill positively identified from nets, is timely given the fivefold range in acoustic estimates for the CCAMLR 2000 survey (Hewitt et al., 2004; Demer and Conti, 2005; Heywood et al., 2006; Demer et al., 2007). Net sampling and acoustics are complementary methods, each with strengths and drawbacks. Although acoustics is often preferred for absolute estimates of biomass, modern surveys cover <25% of krill's habitat, much of which visited only once (Nicol et al., 2000; Siegel, 2005). This has forced their combination with net-based data to calculate total biomass (Voronina, 1998; Nicol et al., 2000). Further, net-derived krill length frequencies are needed for the acoustic estimates. Likewise, we have combined methods to estimate a total biomass of 133 Mt for January–February 2000. Rather than arguing for or against nets or acoustics, these points argue for their closer integration in future.

4.2. Total gross production

Measures of growth and production provide insights into the turnover rate of the krill biomass, the amount available to predators and man. We define net production here as the increase in biomass between two time-points, plus that eaten or otherwise dying within this period. Since net production is impossible to measure directly, two main indirect approaches have been used, namely crude energy flow considerations based on primary production and estimates from predator consumption. Ross and Quetin (1988) reviewed the order of magnitude variability between these production estimates and suggested a narrower range of 100–500 Mt yr⁻¹. They emphasised the great uncertainties involved, for example in the proportion of primary production cropped by krill, and the abundance, seasonal diet and feeding rates of each krill predator (Mori and Butterworth, 2006).

Our approach differs because we estimate the growth of krill that do not get eaten to derive gross production (i.e. the theoretical production in the absence of mortality). The first two methods are based on IGRs, with Method 1 using satellite-derivable indices of chl *a* and temperature to capture the diversity of growth habitats across their range. However, this estimate does not include the first two months of the growth season. By contrast Method 2 includes more of the growth season, but does not account for environmental variation. It is based mainly in the Indian sector, which may not fully reflect the growth rates in the more productive Atlantic sector. Method 3, unlike the IGR models, is based on field-derived length-frequency data. However, mortality rates of older krill may increase (Basson and Beddington, 1989; Pakhomov, 2000), leading to an underestimate of gross production with this method.

While each method may give a conservative estimate of total annual production, they all converge on values of 342–536 Mt per growing season. Since they are all based on the same numerical abundance of krill, the agreement is over the growth rate. Our conversions of IGR measurements of growth in length to units of mass are plausible, fitting into a realistic energy budget. For instance the overall GGP value of 3.6 for a 30 mm krill (Method 1) means a growth of 0.1 mm d⁻¹, which is within the range of observations of wild populations (Rosenberg et al., 1986; see Siegel and Nicol, 2000 and Fig. 3). This equates to a mean growth in mass of 1% per day, a reasonable value given a maximum ration of 13–26% d⁻¹ (Clarke et al., 1988; Perissinotto et al., 1997).

The broad agreement between the three production estimates is not simply because they all basically capture the krill growth process. An additional factor is krill size, since small and large krill have greatly differing growth rates. Methods 1 and 2 examine this by comparing production for different sizes of krill. Both methods concur that, for a given number of krill, gross production is similar whether they are small or large. The smaller krill have much higher mass-specific growth rates, but in the production calculation this is offset by their much lower biomass for a given population size. Because of this compensation, the production estimate is surprisingly insensitive to the underlying size distribution of the krill population.

Given that all three methods may be conservative, our main result is that gross annual production, 342–536 Mt, slightly exceeds the biomass of 379 Mt estimated at the start of January. This turnover rate is lower than that of Antarctic copepods (Shreeve et al., 2005) but it is still substantial for a polar species that grows to 6.4 cm. Krill appear to be a species of high energy throughput for their size (Quetin et al., 1994).

The estimated consumption of krill is frequently reported to be large, compared to their biomass (e.g. Boyd and Croxall, 1996; Miller and Hampton, 1989; Nicol et al., 2000). At regional scales this apparent mismatch can be explained in terms of advection from upstream within the Antarctic Circumpolar Current (Boyd and Croxall, 1996; Atkinson et al., 2001; Murphy et al., 2007). However, at circumpolar scales the system is closed so advection cannot be invoked (Nicol, 2003). Present (albeit crude) best estimates of total predator consumption range from 128 to 470 Mt yr⁻¹ (Mori and Butterworth, 2006), which is in the lower part of our range for gross production. Thus the often-reported discrepancy between estimates of krill biomass and predation loss can be resolved by inclusion of krill growth.

The current krill fishery is a minor predation loss at present, operating well short of its total allowable catch of 5 Mt yr⁻¹. However, its expansion is predicted for the near future as market forces change (Kawaguchi and Nicol, 2007). CCAMLR are currently developing small-scale management units (for example around islands) to reduce future competition between locally concentrated fishing and land-based foraging predators. However, given the potential fluxes of krill at the ocean-basin scale (Hofmann and Murphy, 2004) circumpolar-scale estimates of biomass and production are also relevant to management.

Acknowledgements

We thank all those who sent krill length-frequency data to form the database, including Kendra Daly, Roger Hewitt, Sanae Chiba, So Kawaguchi, Boris Trotsenko, Rong Wang, James Clark, Javier Quinones and David Ramm. Jon Watkins, Geraint Tarling and Andrew Hirst provided advice for the compilation and analysis of the length-frequency data and Pete Rothery provided statistical advice. Simeon Hill, Jon Watkins and three anonymous reviewers provided constructive comments on the manuscript. This is a contribution to the Discovery 2010 Programme of the British Antarctic Survey.

References

- Arrigo, K.R., Thomas, D.N., 2004. Large scale importance of sea ice biology in the Southern Ocean. *Antarctic Science* 16, 471–486.
- Atkinson, A., Shreeve, R.S., Hirst, A.G., Rothery, P., Tarling, G.A., Pond, D.W., Korb, R.E., Murphy, E.J., Watkins, J.L., 2006. Natural growth rates of Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. *Limnology and Oceanography* 51, 973–987.
- Atkinson, A., Siegel, V., Pakhomov, E.A., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432, 100–103.
- Atkinson, A., Siegel, V., Pakhomov, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A., Fleming, A.H., 2008. Oceanic circumpolar habitats for Antarctic krill. *Marine Ecology Progress Series* 362, 1–23.
- Atkinson, A., Whitehouse, M.J., Priddle, J., Cripps, G.C., Ward, P., Brandon, M.A., 2001. South Georgia, Antarctica: a productive, cold water, pelagic ecosystem. *Marine Ecology Progress Series* 216, 279–308.
- Azzali, M., Kalinowski, J., 2000. Spatial and temporal distribution of Krill *Euphausia superba* biomass in the Ross Sea (1989–1990 and 1994). In: Faranda, F.M., Guglielmo, L., Ianora, A. (Eds.), *Ross Sea Ecology*. Springer, Berlin Heidelberg, pp. 433–455.
- Basson, M., Beddington, J.R., 1989. Preliminary analysis of growth and mortality rates of Antarctic krill (*Euphausia superba*) from length frequency samples. *Antarctic Special Topic*, 51–55.
- Bodungen, B.v., 1986. Phytoplankton growth and krill grazing during spring in the Bransfield Strait, Antarctica—implications from sediment trap collections. *Polar Biology* 6, 153–160.
- Boyd, I.L., Croxall, J.P., 1996. Preliminary estimates of krill consumption by Antarctic fur seals and macaroni penguins at South Georgia. Document WG-EMM-95/96. CCAMLR, Hobart.
- Brierley, A.S., Demer, D.A., Watkins, J.L., Hewitt, R.P., 1999. Concordance of interannual fluctuations in acoustically estimated densities of Antarctic krill around South Georgia and Elephant Island: biological evidence for same-year teleconnections across the Scotia Sea. *Marine Biology* 134, 675–681.
- Calbet, A., Landry, M.R., 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnology and Oceanography* 49, 51–57.
- Candy, S.G., Kawaguchi, S., 2006. Modelling growth of Antarctic krill. II. Novel approach to describing the growth trajectory. *Marine Ecology Progress Series* 306, 17–30.
- Clarke, A., Quetin, L.B., Ross, R.M., 1988. Laboratory and field estimates of the rate of faecal pellet production by Antarctic krill, *Euphausia superba*. *Marine Biology* 98, 557–563.
- Clarke, A., Tyler, P.A., 2008. Adult Antarctic krill feeding at abyssal depths. *Current Biology* 18, 282–285.
- Constable, A.J., de la Mare, W.K., Agnew, D.J., Everson, I., Miller, D.G.M., 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES Journal of Marine Science* 57, 778–791.
- Constable, A.J., Nicol, S., Stratton, P.G., 2003. Southern Ocean productivity in relation to spatial and temporal variation in the physical environment. *Journal of Geophysical Research Oceans* 108 art. no. 9079.
- Demer, D.A., Conti, S.G., 2005. New target-strength model indicates more krill in the Southern Ocean. *ICES Journal of Marine Science* 62, 25–32.
- Demer, D.A., Cossio, A.M., Reiss, C.S., 2007. Section 3.21 of SC-CAMLR—XXVI, Report of the 26th meeting of the Scientific Committee, Hobart, Australia, 22–26 October 2007.
- Everson, I., 2000. Distribution and standing stock—The Southern Ocean. In: Everson, I. (Ed.), *Krill Biology, Ecology and Fisheries*. Blackwell, Cambridge, UK, pp. 63–79.
- Everson, I., Bone, D.G., 1986. Effectiveness of the RMT8 system for sampling krill (*Euphausia superba*) swarms. *Polar Biology* 6, 83–90.
- Fraser, W.R., Hofmann, E.E., 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series* 265, 1–15.
- Gutt, J., Siegel, V., 1994. Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctica). *Deep-Sea Research I* 41, 169–178.
- Godlewska, M., 1996. Vertical migrations of krill (*Euphausia superba* Dana). *Polish Archives of Hydrobiology* 43, 9–63.
- Hagen, W., Kattner, G., Terbrüggen, A., Van Vleet, E.S., 2001. Lipid metabolism of the Antarctic krill *Euphausia superba* and its ecological implications. *Marine Biology* 139, 95–104.
- Hamner, W.M., Hamner, P.P., 2000. Behavior of Antarctic krill (*Euphausia superba*): schooling, foraging, and antipredatory behaviour. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 192–202.
- Hewitt, R.P., Watkins, J., Naganobu, M., Sushin, V., Brierley, A.S., Demer, D., Kasatkina, S., Takao, Y., Goss, C., Malyshko, A., Brandon, M., Kawaguchi, S., Siegel, V., Trathan, P., Emery, J., Everson, I., Miller, D., 2004. Biomass of Antarctic krill in the Scotia Sea in January/February 2000 and its use in revising an estimate of precautionary yield. *Deep-Sea Research II* 51, 1215–1236.
- Heywood, B.G., Brierley, A.S., Gull, S.F., 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.
- Hofmann, E.E., Murphy, E.J., 2004. Advection, krill, and Antarctic marine ecosystems. *Antarctic Science* 16, 487–499.
- Hopkins, T.L., Ainley, D.G., Torres, J.J., Lancraft, T.M., 1993. Trophic structure in open waters of the Marginal Ice Zone in the Scotia-Weddell Confluence region during spring (1983). *Polar Biology* 13, 389–397.
- Kasatkina, S.M., Goss, C., Emery, J.H., Takao, Y., Litvinov, F.F., Malyshko, A.P., Shnar, V.N., Berezinskiy, O.A., 2004. A comparison of net and acoustic estimates of krill density in the Scotia Sea during the CCAMLR 2000 Survey. *Deep-Sea Research II* 51, 1289–1300.
- Kawaguchi, S., Candy, S.G., King, R., Naganobu, M., Nicol, S., 2006. Modelling growth of Antarctic krill. I. Growth trends with sex, length, season and region. *Marine Ecology Progress Series* 306, 1–15.
- Kawaguchi, S., Nicol, S., 2007. Learning about Antarctic krill from the fishery. *Antarctic Science* 19, 219–230.
- Lancraft, T.M., Relsenbichler, K.R., Robinson, B.H., Hopkins, T.L., Torres, J.J., 2004. A krill-dominated micronekton and macrozooplankton community in Croker Passage, Antarctica with an estimate of fish predation. *Deep-Sea Research II* 51, 2247–2260.
- Loeb, V., Siegel, V., Holm Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., Trivelpiece, S., 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387, 897–900.
- Mackintosh, N., 1973. Distribution of post-larval krill in the Antarctic. *Discovery Reports* 36, 95–156.
- Marr, J.W.S., 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Reports* 32, 33–464.
- Miller, D.G.M., Hampton, I., 1989. Biology and ecology of the Antarctic krill (*Euphausia superba* Dana): a review. *BIOMASS Scientific Series* 9, 1–66.
- Moore, J.K., Abbott, M.R., Richman, J.G., 1999. Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *Journal of Geophysical Research Oceans* 104, 3059–3073.
- Morris, D.J., Watkins, J.L., Ricketts, C., Bucholz, F., Priddle, J., 1988. An assessment of the merits of length and weight measurements of Antarctic krill *Euphausia superba*. *British Antarctic Survey Bulletin* 79, 27–50.
- Mori, M., Butterworth, D.S., 2006. A first step towards modelling the krill-predator dynamics of the Antarctic ecosystem. *CCAMLR Science* 13, 217–277.
- Murphy, E.J., Watkins, J.L., Trathan, P.N., Reid, K., Meredith, M.P., Thorpe, S., Johnston, N.M., Clarke, A., Tarling, G.A., Collins, M.A., Forcada, J., Shreeve, R.S., Atkinson, A., Korb, R., Whitehouse, M.J., Ward, P., Enderlein, P., Hirst, A.G., Martin, A.R., Hill, S.L., Staniland, I.L., Pond, D.W., Briggs, D.R., Cunningham, N.J., Fleming, A.H., 2007. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill-centred food web. *Philosophical Transactions of the Royal Society Series B* 362, 113–148.

- Nicol, S., 2003. Krill and currents—physical and biological interactions influencing the distribution of *Euphausia superba*. *Ocean and Polar Research* 25, 633–644.
- Nicol, S., Constable, A.J., Pauly, T., 2000. Estimates of circumpolar abundance of Antarctic krill based on recent acoustic density measurements. *CCAMLR Science* 7, 87–99.
- Orsi, A.H., Whitworth, T., Nowlin, W.D., 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Research I* 42, 641–673.
- 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. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 68–90.
- Perissinotto, R., Pakhomov, E.A., McQuaid, C.D., Froneman, P.W., 1997. In situ grazing rates and daily ration of Antarctic krill *Euphausia superba* feeding on phytoplankton at the Antarctic Polar front and the marginal ice zone. *Marine Ecology Progress Series* 160, 77–91.
- Riddle, J., Boyd, I.L., Whitehouse, M.J., Murphy, E.J., Croxall, J.P., 1998. Estimates of Southern Ocean Primary Production—constraints from predator carbon demand and nutrient drawdown. *Journal of Marine Systems* 17, 275–288.
- Quetin, L.B., Ross, R.M., 1991. Behavioural and physiological characteristics of the Antarctic krill, *Euphausia superba*. *American Zoologist* 31, 49–63.
- Quetin, L.B., Ross, R.M., 2001. Environmental variability and its impact on the reproductive cycle of Antarctic krill. *American Zoologist* 41, 74–89.
- Quetin, L.B., Ross, R.M., Clarke, A., 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, pp. 165–184.
- Reid, K., Croxall, J.P., 2001. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proceedings of the Royal Society of London Series B* 268, 377–384.
- Rosenberg, A.A., Beddington, J.R., Basson, M., 1986. Growth and longevity of krill during the first decade of pelagic whaling. *Nature* 324, 152–153.
- Ross, R.M., Quetin, L.B., 1988. *Euphausia superba*: a critical review of estimates of annual production. *Comparative Biochemistry and Physiology* 90B, 499–505.
- Ross, R.M., Quetin, L.B., Lascara, C.M., 1996. Distribution of krill and dominant zooplankton west of the Antarctic Peninsula. *Antarctic Research Series* 70, 199–217.
- Ross, R.M., Quetin, L.B., Baker, K.S., Vernet, M., Smith, R.C., 2000. Growth limitation in young *Euphausia superba* under field conditions. *Limnology and Oceanography* 45, 31–43.
- Shreeve, R.S., Tarling, G.A., Atkinson, A., Ward, P., Goss, C., Watkins, J., 2005. Relative production of *Calanoides acutus* (Copepoda: Calanoida) and *Euphausia superba* (Antarctic krill) at South Georgia, and its implications at wider scales. *Marine Ecology Progress Series* 298, 229–239.
- Siegel, V., 1986. Untersuchungen zur Biologie des antarktischen Krill, *Euphausia superba*, im Bereich der Bransfield Strasse und angrenzender Gebiete. *Mitt Inst Seefisch Hamburg* 38, 1–244.
- Siegel, V., 1992. Review of length-weight relationships for Antarctic krill. *SC-CAMLR Selected Scientific Papers* 9, 145–155.
- Siegel, V., 2005. Distribution and population dynamics of *Euphausia superba*: summary of recent findings. *Polar Biology* 29, 1–22.
- Siegel, V., Kawaguchi, S., Ward, P., Litvinov, F., Sushin, V., Loeb, V., Watkins, J., 2004. Krill demography and large scale distribution in the southwest Atlantic during January/February 2000. *Deep-Sea Research II* 51, 1253–1273.
- Siegel, V., Loeb, V., 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Marine Ecology Progress Series* 123, 45–56.
- Siegel, V., Nicol, S., 2000. Population parameters. In: Everson, I. (Ed.), *Krill Biology, Ecology and Fisheries*. Blackwell Science, London, pp. 103–149.
- Tarling, G.A., Shreeve, R.S., Hirst, A.G., Atkinson, A., Pond, D.W., Murphy, E.J., Watkins, J.L., 2006. Natural growth rates in Antarctic krill (*Euphausia superba*): I. Improving methodology and predicting intermolt period. *Limnology and Oceanography* 51, 959–972.
- Tseitlin, V.B., 1989. Biomass and production of the Antarctic krill. In: Ponomareva, L.A. (Ed.), *Complex investigations of the Southern Ocean pelagic zone*. IORAN Publishing Office, Moscow, pp. 118–122 (in Russian).
- Voronina, N.M., 1984. *Pelagic Ecosystems of the Southern Ocean*. Nauka Press, Moscow (in Russian).
- Voronina, N.M., 1998. Comparative abundance and distribution of major filter-feeders in the Antarctic pelagic zone. *Journal of Marine Systems* 17, 375–390.
- Watkins, J., Macaulay, M., Everson, I., 2000. Sampling krill. In: Everson, I. (Ed.), *Krill Biology, Ecology and Fisheries*. Blackwell Science, London, pp. 8–39.
- Wiebe, P.H., Ashjian, C.J., Gallager, S.M., Davis, C.S., Lawson, G.L., Copley, N.J., 2004. Using a high-powered strobe light to increase the catch of Antarctic krill. *Marine Biology* 144, 493–502.
- Willis, J., 2007. Could whales have maintained the high abundance of krill? *Evolutionary and Ecological Research* 9, 651–662.
- Witek, Z., Kalinowski, J., Grelowski, A., 1988. Formation of Antarctic krill concentrations in relation to hydrodynamic processes and social behaviour. In: Sahrhage, D. (Ed.), *Antarctic Ocean and Resources Variability*. Springer, Berlin, Heidelberg, pp. 237–244.