Modelling Southern Ocean krill population dynamics: biological processes generating fluctuations in the South Georgia ecosystem

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ABSTRACT: Variability is a key feature of the pelagic ecosystems of the Southern Ocean and an important aspect of the variation is fluctuation in the abundance of krill *Euphausia superba* Dana, the major prey item of many of the higher predators. Direct impacts of variability in the large-scale physical environment, such as changes in ocean circulation, have been suggested as the main factor generating the observed fluctuations. So far, however, there has been little quantitative assessment of the importance of krill population dynamics in the observed variation. Here, analyses of a model of krill population development and predator diet data from South Georgia have been used to examine seasonal changes in the population structure of krill. The krill population model was combined with a size-based selection function and used to generate expected length-frequency distributions in the predator diet through a summer season. Comparison of the model solutions with the predator diet data indicates that the model can reproduce the observed pattern of variation and emphasizes that adult population changes are a key aspect of the interannual fluctuations observed during some years. Low krill abundance was associated with reduced representation of the 3+ age group (3 to 4 yr old), whereas when krill were abundant the 3+ age class was the major age group present. The seasonal changes in the population structure in the predator diet involve a complex interaction of relative year class strength, timing of immigration, fluctuations in growth rates and dynamic predator-selective effects. Development of the model to examine the interactive effects of changing krill growth and mortality rates will be a valuable next step. The dominance of the changes in krill population age structure underlines the fact that to understand the variability of the South Georgia ecosystem we must identify the major factors generating variability in population dynamics throughout the Scotia Sea.

KEY WORDS: Ecosystem · Krill · Ocean · Model · Population dynamics · Predators · Diet data · Interannual · Variability · Allochthonous · Southern Ocean

INTRODUCTION

Variability of physical and biological systems in the Southern Ocean is currently a major focus of research (see for instance Murphy et al. 1995, 1998, White & Peterson 1996, Loeb et al. 1997, Brierley et al. 1999). Much of the variability in the food-web is associated with changes in the distribution and abundance of Antarctic krill *Euphausia superba* Dana (Priddle et al. 1988, Murphy et al. 1998). Krill are the major prey item in the diet of a wide range of predators in the area, including many of the penguin, seal and whale species (Croxall et al. 1988, Priddle et al. 1988). Variation in the abundance of krill within the predator foraging regions affect the foraging and breeding performance of the predators and are associated with changes in the plankton community composition and dynamics (Croxall et al. 1988, 1999, Atkinson et al. 1999). One of the key regions where variability has been noted is around

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South Georgia, on the northern edge of the Scotia Sea (see Fig. 1), where there is an extensive krill-centred food-web. South Georgia was an area where, at the start of the last century, the great whales occurred in large numbers and data from the extensively studied predator colonies give a long-term view of the variability in the ecosystem (Croxall et al. 1988, Priddle et al. 1988).

The Island of South Georgia occurs in the path of the Antarctic Circumpolar Current and as such is strongly influenced by polar waters from further south (see Fig. 1). Krill around South Georgia are on the northern edge of their distribution and the stock is thought to rely on immigration associated with the regional current systems (Marr 1962, Mackintosh 1972, 1973, Murphy 1995). There does not appear to be much separation into sub-populations in the region, although the evidence from genetic analyses is equivocal (Fevolden & Schneppenheim 1989, Zane et al. 1998). The krill in the South Georgia area are considered, therefore, to be part of a larger-scale Scotia Sea population. The Antarctic Peninsula and northern Weddell Sea regions probably form the centre of the population, acting as a source for the areas further north and east (Hofmann et al. 1998, Murphy et al. 1998).

Interannual fluctuations in krill abundance at South Georgia were first noted in the early part of the twentieth century during the whaling period (Priddle et al. 1988). There appear to be 2 to 3 years in each decade where the abundance of krill at South Georgia is low, the predator foraging and breeding performance is reduced, and the krill fishery reports reduced catch levels and rates (Croxall et al. 1988, Priddle et al. 1988, Fedulov et al. 1996, Brierley et al. 1997, Everson et al. 1997, Murphy et al. 1998). These fluctuations are well documented and also highlight that the years of low density (below about 10 g m^{-2}) tend to be followed by years in which krill abundance recovers back to higher values (greater than about 25 g m^{-2}) (Brierley et al. 1999, Reid et al. 1999a).

Lack of adequate within- and between-year sampling of population structure and difficulties in attributing age to krill mean that simple analyses of population age structure have not been possible. This has meant that it has been difficult to distinguish changes within the population from gross changes in overall abundance. Until recently, emphasis was on the large-scale physical factors that may generate shifts in population distribution, particularly at the edge of the species distribution around South Georgia (Priddle et al. 1988, Murphy et al. 1998). However, long-term monitoring programmes have shown that reproductive recruitment strength varies between years (Siegel & Loeb 1995, Loeb et al. 1997, Watkins 1999) and that changes in adult population size structure may reflect changes in age structure (Murphy et al.1998, Reid et al. 1999a). Further clarification of the biological influences on the ecological variation at South Georgia requires a quantitative assessment of the impact that population changes can have on the population structure of krill.

Comparisons of the size of krill caught in pelagic nets with samples from predator diets have shown that the krill consumed by the predators is closely related to that in the local pelagic population (Reid et al. 1996, 1999a). The diet analyses are, therefore, providing valuable insight into the variation in the size of krill consumed by the predators within and between years (Reid 1995, Reid & Arnould 1996, Reid et al. 1999a). We have shown (Reid et al. 1999a) that there were consistent changes in krill length and that gross qualitative comparisons indicated that changes in population age structure were likely to be important. Here, we develop a model of the changes in population structure to test those ideas.

Major revisions in the view of the life history of krill made during the last 10 to 20 yr have not yet been fully included in population models (Miller & Hampton 1989, Pakhomov 1995). The approach used in this study is to model krill population development in conjunction with a predator selection/prey availability function to generate expected length-frequency distributions in the predator diets throughout a summer season. The key question examined is whether the development and fluctuations in size structure can be explained by the population demography. To determine the effects of recruitment failure on population structure, the model was run with particular age classes absent. Comparisons with the predator diet data support the suggestion that krill population changes are important in generating the observed variation in abundance of krill at South Georgia.

MATERIALS AND METHODS

As noted above, the interannual fluctuations in the abundance of krill *Euphausia superba* Dana at South Georgia are well documented and years of low abundance tend to be followed by years in which the krill are abundant. In this study we focus on: (1) the 1993/94 season, in which krill density was low at <7.5 g m^{-2} and predator breeding performance was very much reduced, and (2) the 1994/95 season, when the krill abundance was adequate to maintain the predator breeding performance (Brierley et al. 1999, Reid et al. 1999a). There is no krill density estimate available for the 1994/95 season, but the situation for that season is considered to be similar to that in the 1991/92 season, when the density was >90 g m^{-2}, following a year of

low density (<6.5 g m^{-2}) in 1990/91 (Brierley et al. 1999, Reid et al. 1999a). The breeding performance of the predators and the size structure of krill in their diet showed a pattern of fluctuation in 1990/91 and 1991/92 very similar to that in 1993/94 and 1994/95 (Reid et al. 1999a).

Fur seal diet data. As part of long-term studies of the controls on breeding success of land-based predators, data on the diet of fur seals at Bird Island, South Georgia (Fig. 1), has been gathered by analysing scat samples collected during the lactation period (December to March), as described by Reid & Arnould (1996). These data provide information on the size of krill eaten by the fur seals each week through the summer period. Data have been pooled for each month for 1993/94 and 1994/95.

Development of the krill population model. A number of attempts have been made to synthesize the wide range of information available on krill biology (Marr 1962, Miller & Hampton 1989). Some of the early attempts to develop models of krill population development foundered on the interpretation of data on growth and longevity (Mackintosh 1972, 1973). Here, we combine the current views of krill population dynamics.

The first step was to set up an initial population age structure based on a constant mortality rate (M) and a time interval (δt) of 1 yr. Thus:

$$K_{i,t+1} = K_{i,t} \, e^{-M \delta t} \qquad (1)$$

where $K_{i,t}$ is the number of krill in age class i at time t. To allow examination of the general effects of changes
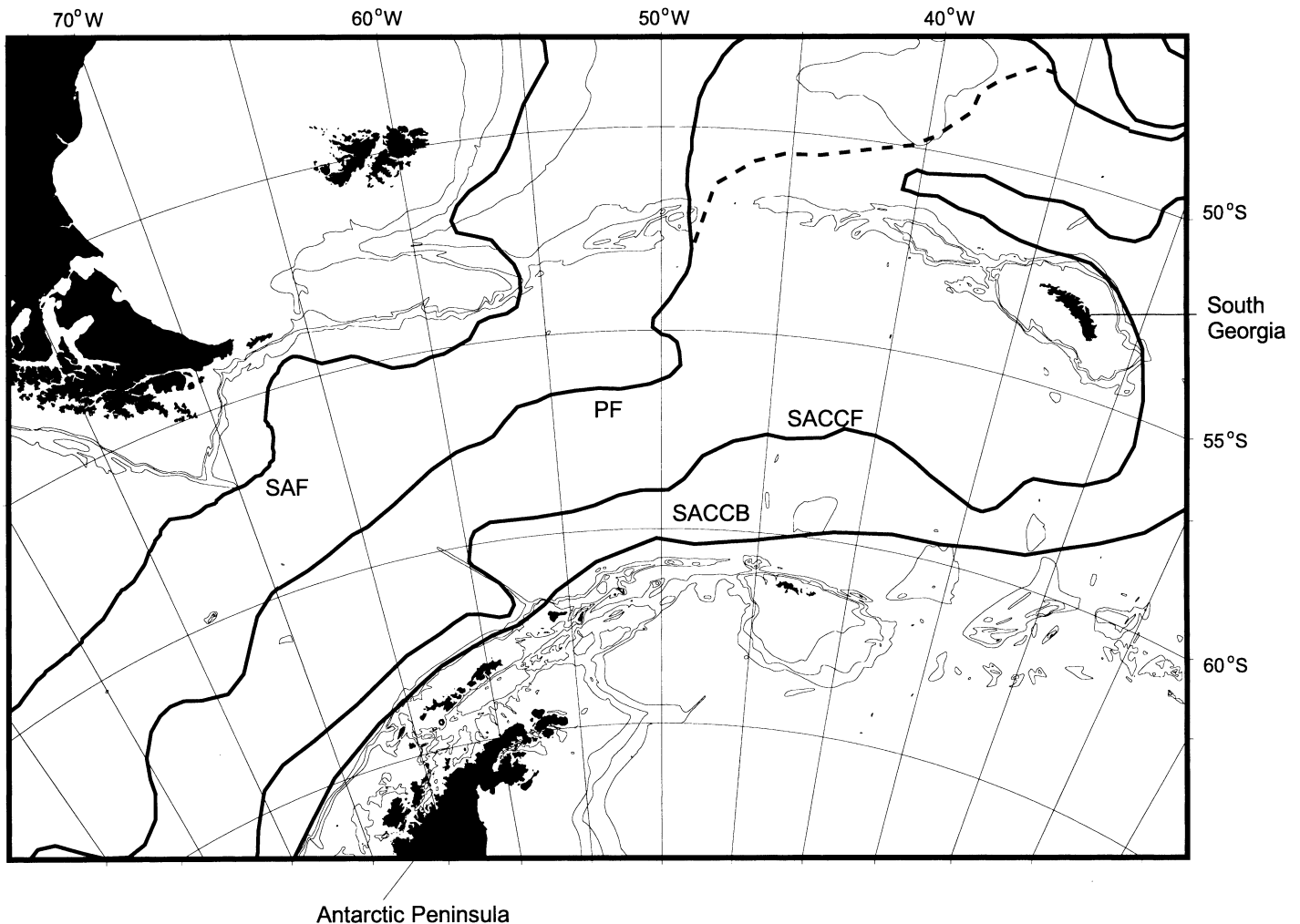

Fig. 1. Scotia Sea region showing South Georgia and the climatological ocean frontal regions (modified from Orsi et al. 1995). SAF: Sub-Antarctic Front; PF: Polar Front (dashed line indicates the position of the Polar Front, from Trathan et al. 1997); SACCB, SACCF: Southern Antarctic Circumpolar Current Boundary and Front, respectively. The general pattern of the surface current flow in the Scotia Sea is from west to east in line with the major ocean fronts. The study area, Bird Island, is located at the western end of South Georgia

in age structure, a constant value of the mortality rate for each age class was assumed. The consequences of varying the mortality rate as a function of size are discussed in the 'Discussion'.

The first age class (<1 yr old) does not to be encountered in large numbers in the South Georgia area (Marr 1962), and it has not been included in the model. To simulate a complete recruitment failure of a year class, the numbers in a particular age group were set to zero. The model was used to follow relative change in age and size structure within a season. The development of the population age structure was tracked through the summer season (December to the beginning of April) with a 1 mo time step. The mean size of krill of a given age was determined by the use of a seasonal form of the von Bertalanffy equation. The distribution of sizes within an age class was based on a normal distribution with a constant standard deviation. The length distributions for all age classes were then summed to give the overall length-frequency distribution at any time.

The relative proportion of krill of each size class that would occur in the fur seal diet was determined by the application of a proportional selection function. The following sections describe key aspects of the model development and parameterization in more detail. All model calculations were carried out using the Mathematica system (Wolfram 1999).

Mortality. Estimates of the instantaneous rate of natural mortality of krill were reviewed by Siegel & Kalinowski (1994), who suggested that a range of values between 0.66 and 0.92 yr^{-1} would be appropriate but noted that some estimates were substantially greater than 1.0 yr^{-1} (see also Pakhomov 1995). Butterworth et al. (1994) utilized a value of 0.6 with a range of between 0.4 and 1.0 yr^{-1}.

To further consider the best estimate of mortality rate, the model-generated length-frequency distributions were compared against the distributions obtained using pelagic research nets in independent surveys (Reid et al. 1999a). The net data were collected throughout the austral summer, but mainly between the beginning of December and the end of January. The net data were compared to the model-derived data for 1 January to examine the effects of changing the mortality rate. The expected length-frequency distribution was generated for 3 mortality rates ($M = 1$, 1.25 and 1.5 yr^{-1}). To allow comparison, the net data were scaled so that the peak at 40 mm was assumed to be a fully representative sample of the population.

Growth. The current view of krill growth suggests a 5 to 7 yr lifespan (Rosenberg et al. 1986, Siegel 1987, Pakhomov 1995). Rosenberg et al. (1986) used historical data from the 'Discovery' period (1930s) to estimate
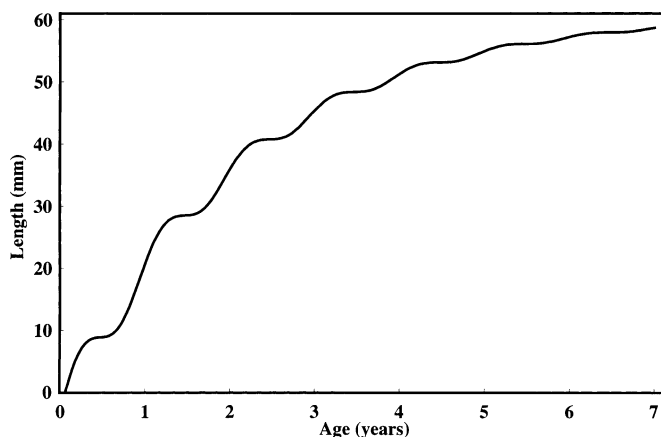

Fig. 2. *Euphausia superba*. Seasonal form of the von Bertalanffy growth curve, based on Siegel (1987)

the form of the growth curve, while Siegel (1987) used data from the Antarctic Peninsula region from the 1980s. Both authors emphasized the seasonal nature of the growth of krill and produced empirical estimates of the form of fitted curves. Here, we adopt the seasonal von Bertalanffy growth curve derived by Siegel (1987) and illustrated in Fig. 2. The equation uses a simple sinusoidal change in the seasonal growth rate to reproduce the change in krill length:

$$L_t = L_\infty\left[1 - \exp\left(-k(t - t_0) + \frac{ck\sin[2\pi(t - t_s)]}{2\pi}\right)\right] \quad (2)$$

where L_t is the krill length at time t and L_∞ is the maximum size of krill. Equation constants are $t_s = -0.0272$, $t_0 = 0.1418$, $c = 0.9598$, $L_\infty = 61$ mm and $k = 0.4728$, based on those of Siegel (1987). The analyses of Rosenberg et al. (1986) gave a range of possible growth curves dependent on the length of the growing season. Analyses of length-frequency data from South Georgia indicate that the modal size of particular age classes varies between years (Watkins et al. 1999). There are indications that krill growth rates may be enhanced in this region compared with those of krill in areas further south, on which the growth curve was based. However, the magnitude of any effect is unknown, so we have maintained the parameter values generated by Siegel (1987) as the standard values. The mid-point of the growing season was assumed to occur on 1 January (Fig. 2).

Length-frequency generation. The distribution of krill size in each age class was assumed to follow a normal distribution, with a standard deviation of 3.0 mm based on the analyses of Watkins (1999). The von Bertalanffy growth equation was used to calculate the mean size of each age class at any time in the year. The
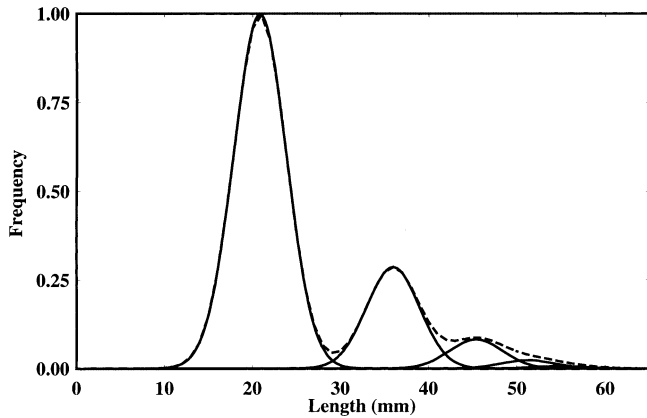
Fig. 3. *Euphausia superba*. Model form of the proportional length-frequency distribution on 1 January based on the seasonal growth curve, an instantaneous natural mortality rate of 1.25 yr^{-1}, and an age class standard deviation in length of 3 mm

model was run assuming there were 7 age classes in the population. The 0 to 1 yr old class is referred to as the 0+ age class, the 1 to 2 yr old class is referred to as the 1+ age class and so on for each age group. The overall model length-frequency distribution for 1 January is shown in Fig. 3.

Predator selection/availability function parameterization. Through active or passive (lack of availability) selection, the smallest size classes are not represented in the diet of fur seals. In the following, the term 'selection' is taken to cover both active selection and availability effects. To reproduce the general form of the length-frequency samples of the fur seals, it is necessary to apply a selection function to the model length-frequency. To produce this effect within the model, a logistic selection function was adopted:

$$P_l = \frac{1}{1 + e^{-a(l-b)}} \tag{3}$$

where P_l is the proportion of krill in each 1 mm length class that is consumed by the predators. The parameter b is the length at which 50% of the class is consumed by the predators and the parameter a determines how steep is the selection function with changing size. The logistic function was fitted to a derived selection function. The derived selection function was based on the calculated ratio of the observed frequency to the expected frequency in each size class from the population model. The value of b, the length when the function is 50% selective (P_l = 0.5), was estimated by linear interpolation. The logistic function was then fitted to the data below this size, with the assumption that the function is symmetrical and the data are most likely to be representative over this section of the curve. The selection function was derived using a composite data set based on all

available years and the data for the last 2 mo of the 1993/94 and 1994/95 seasons. The sampled data were based on 2 mm size classes (Reid et al. 1999a). The robustness of the conclusions to the model parameterization was examined.

To calculate the relative number of krill ($N_{(l,t)}$) of each size class (l) in the predator diet at time t the model krill length-frequency distribution describing the number of krill present in each size class (l) in the population at time t ($K_{(l,t)}$) was multiplied by the size-based selection function. Thus,

$$N_{(l,t)} = P_l K_{(l,t)} \tag{4}$$

RESULTS

Krill length-frequency development from fur seal diet data

In a year of relatively low *Euphausia superba* abundance (1993/94), large individuals with a modal size of 58 mm initially dominated the length-frequency distribution, while later during January and February the distribution was bimodal (Fig. 4a, Table 1). Towards the end of the season, the length-frequency distribution was dominated by individuals in the 35 to 45 mm size range, with a single mode of about 40 mm. The change in length-frequency distribution of krill obtained from scat samples between December 1994 and March 1995 was very different from that seen in 1993/94 (Fig. 4b, Table 1). The krill abundance was adequate for good predator breeding performance (Reid et al. 1999a), and there appeared to be little or no growth in the modal size of the sampled population over the summer season (Table 1). The modal size started at about 42 mm in December and then increased to 44 mm during January and February. Towards the end of the season (April) the peak size decreased to 42 mm.

Mortality rates

The composite data from net hauls in the South Georgia area indicates an under-representation of older age groups in the net samples collected in the area in comparison to that predicted by the model (1 January) with a mortality rate of $M = 1.0$ (Fig. 5a). A value of M of 1.25 yr^{-1}, or approx. 71% mortality each year, gives a better representation of the local population structure (Fig. 5b). Too high a mortality rate ($M = 1.5$ yr^{-1}) produces a model frequency distribution with too few large individuals compared with that sampled by the nets (Fig. 5c). The standard natural mortal-
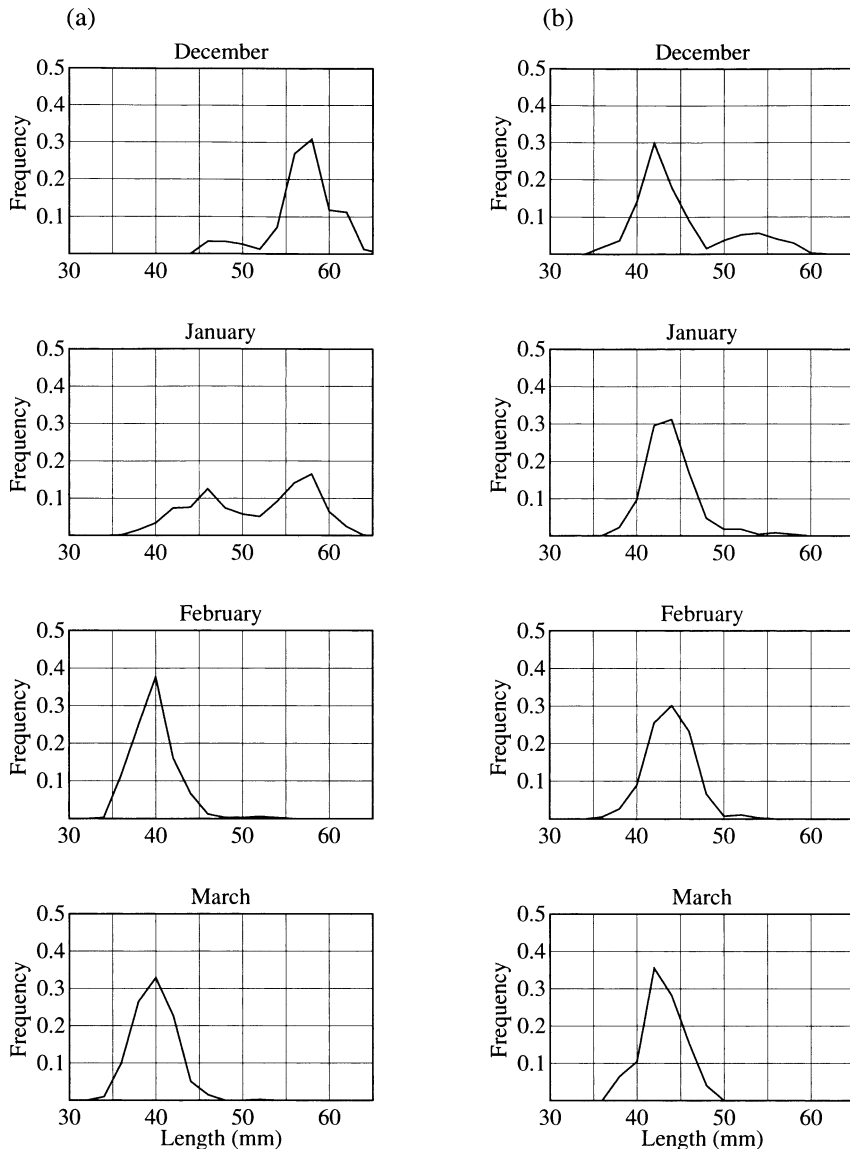
(a)

(b)

Fig. 4. *Euphausia superba*. Proportional length-frequency of krill measured each month in fur seal scat samples for the period December to March during (a) 1993/94 and (b) 1994/95

Model-derived length-frequency development

The model-based length-frequency development through a year with no selection and a mortality rate of $M = 1.25 \text{ yr}^{-1}$ is illustrated in Fig. 6. The model emphasizes that with the 3 mm standard deviation of size within each age class there is some separation of the peaks of the distribution. In this case the 1+ age class dominates the model sequence. The next stage in developing the comparison of the model-derived length-frequency distributions with the predator diet data requires the inclusion of the predator selection function.

Selection function

The logistic function (Eq. 3) fitted to the lower half of the derived selection data for all years produced an estimate of the 50% selection size (*b*) of 39.57 mm and a rate estimate (*a*) of 0.903. The fit of the function to the data was highly significant ($p \ll 0.0001$), with 95% confidence intervals for the rate parameter of 0.767 and 1.038. The selection curve has a strong effect with increasing size, with just over 10% of the 37 mm size class taken and just less than 90% taken at 42 mm. Repeating the calculations for the last 2 length-frequency distributions (February and March) in each of the 2 years shown in Fig. 4 produced a range of estimates of *b* from 38.15 to 40.93 and values for the parameter *a* from 0.61 to 2.28. An estimate based on a mortality rate of $M = 1.5 \text{ yr}^{-1}$ generated a value of $a = 0.87$ and $b = 39.82$. For comparative purposes, a value of $a = 1$ and $b = 40$ mm was adopted and the effects of changes in the parameter values were examined. The selection model was next applied to the population model to generate the development in population structure throughout a season.

Standard year model with selection applied

The form of the development of the length-frequency distribution throughout the year produced by the model with the selection curve applied is shown in Fig. 7a for a mortality rate of $M = 1.25 \text{ yr}^{-1}$. There

ity rate was therefore taken to be $M = 1.25 \text{ yr}^{-1}$. This value of *M*, which is most appropriate based on the comparison of the model and net size distributions, is sensitive to changes in the standard deviation of the size distribution within an age class used in the model. A broader range of size within a class leads to higher mortality rate estimates; for example, an estimate of $M = 2 \text{ yr}^{-1}$ is obtained, with a standard deviation of 5 mm. It should also be noted that the fit of the model-derived length-frequency distribution to that obtained in the nets is sensitive to the form and parameterisation of the growth curve.

is relatively little change in the mode of the length-frequency distribution through the season (Table 1). For the mortality rate $M = 1.25$ yr^{-1}, the mode starts at 44 mm, increases to about 45 mm in January and then reduces to 41 to 42 mm by the end of the season. With a lower mortality rate of $M = 0.6$ yr^{-1} the mode increases and remains large (47 mm) into February. A high mortality rate ($M = 2.0$ yr^{-1}) produced an earlier shift to the smaller size mode. The proportion of the distribution that is less than 40 mm long increases through the summer. Comparing these model scenarios with the fur seal diet data in Fig. 4b

shows that the model reproduces the general pattern of little change in the modal length over the season seen in 1995. The modal size was larger in the model by 2 mm at the start of the season and reduced in January to February, whereas the diet data indicated a larger mode throughout February (Table 1). Although the general pattern of change is reproduced, 2 related points are important: Firstly, there were very few krill longer than 50 mm in the predator diets throughout the season, whereas, even with a mortality rate of $M = 1.25$ yr^{-1}, there was a significant proportion of individuals greater then 50 mm in length in

Table 1. *Euphausia superba*. Mode with mean (SD) of krill length-frequency distributions in the fur seal diet data for 1993/94 and 1994/95 along with the modal values of the various model-derived distributions. Diet data relate to the whole of the month, while model values were calculated for the first day of the month. For the model analyses, values in parentheses give the second mode of any bimodal distributions. All values are in millimetres. M: mortality rate (yr^{-1})

Data / Model		Dec	Jan	Feb	Mar	Apr
Fur seal diet						
1993/94	Mode	58	58 (46)	40	40	
	Mean	55.9 (3.6)	50.3 (6.3)	39.1 (2.6)	38.9 (2.2)	
1994/95	Mode	42	44	44	42	
	Mean	44.1 (5.3)	43.0 (3.0)	43.0 (2.6)	42.2 (2.3)	
Model without selection						
	$M = 1.25$	18	21	24	26	27
Model with selection: mortality rate varies						
	$M = 0.60$	45	46	47	42	42
	$M = 1.00$	45	46	41	41	42
	$M = 1.25$	44	45	41	41	42
	$M = 1.50$	44	45	41	41	42
	$M = 2.00$	44	40	41	41	42
Model with selection: selection function parameter values vary						
$b = 40$ mm						
$a = 0.5$	$M = 1.25$	45	46	40	41	42
$a = 1.5$		45	45	41	41	42
$a = 1$						
$b = 44$ mm	$M = 1.25$	46	47	47	47	47
$b = 41$ mm		45	46	42	42	42
$b = 39$ mm		44	40	40	41	42
$b = 36$ mm		37	38	39	39	40
Model with selection: growth rate coefficient (k) in the von Bertalanffy equation varies						
$k = 1.1 \times 0.4728$	$M = 1.25$	46	41	42	42	43
$k = 0.9 \times 0.4728$		43	44	44	41	41
Model with selection and failure of 3+ class: mortality rate varies						
	$M = 0.60$	52 (40)	53 (42)	53 (41)	41 (54)	42 (54)
	$M = 1.00$	51 (40)	40 (52)	41 (53)	41 (53)	42 (54)
	$M = 1.25$	51 (40)	40 (52)	41 (53)	41 (53)	42 (53)
	$M = 1.50$	40 (51)	40 (52)	41 (52)	41 (53)	42 (53)
	$M = 2.00$	40 (51)	40 (52)	41 (52)	41 (53)	42 (53)
Model with selection and failure of the 3+ , 4+ and 5+ classes						
	$M = 1.25$	40 (57)	40 (57)	41 (57)	41 (58)	42 (58)

the model distributions. Thus a single age class (3+) dominated the size structure of the krill in diet samples for much of the year. Secondly, the reduction in modal size of krill at the end of the year in the seal diet probably reflects the selection of larger individua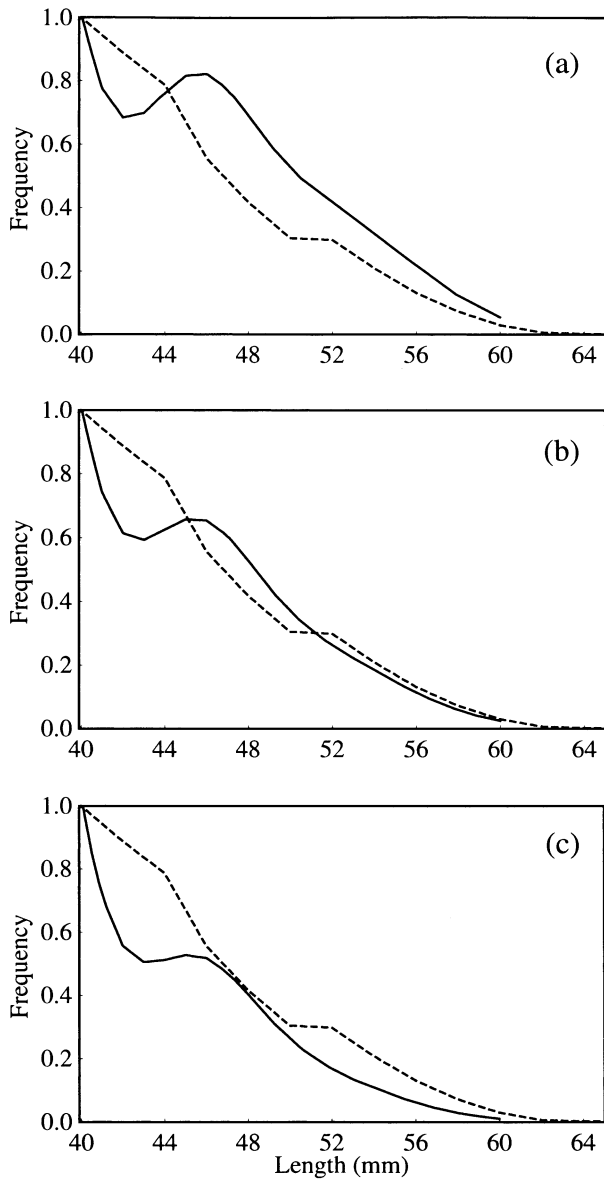ls in the 2+ age class. So in a year in which krill were considered to be abundant there was a strong representation of the 3+ age class. The general pattern of mode changes is robust and is not sensitive to changes in the mortality rate, the growth equation parameters or the selection function parameterization (Table 1). What does change is the timing of the shift

Fig. 5. *Euphausia superba*. Composite RMT 8 net haul proportional length-frequency distribution (dashed line) for all krill collected in samples obtained in the South Georgia area during the period 1982 to 1997 (Reid et al. 1999a) and the model-predicted length-frequency distribution for all year classes at 1 January (solid line). Curves are shown for 3 values of instantaneous natural mortality (per annum): (a) $M = 1.0$, (b) $M = 1.25$, (c) $M = 1.5$. The model and net sample plots have been scaled so that the maximum of the net sampled length-frequency at 40 mm has a value of unity
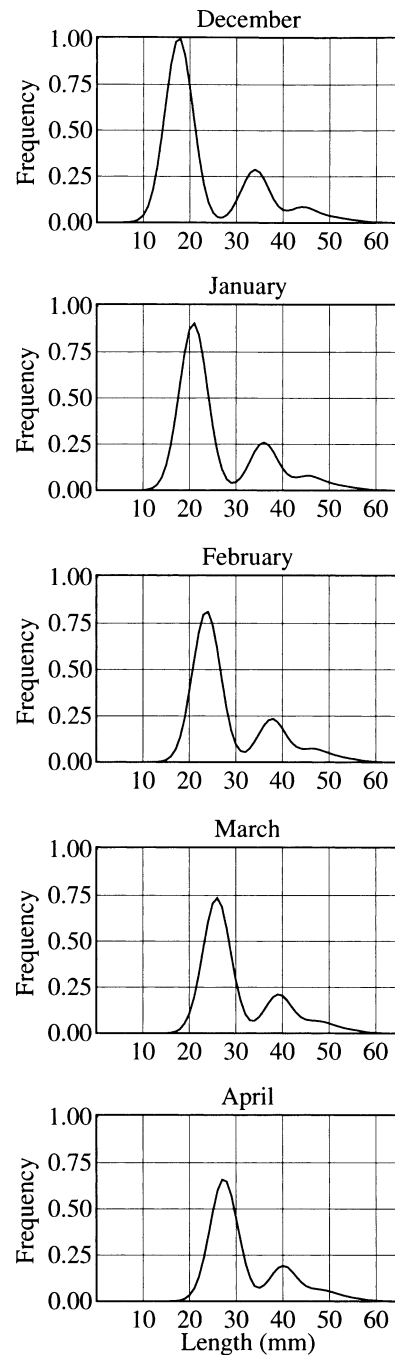

Fig. 6. *Euphausia superba*. Changes in the model-based proportional length-frequency distribution during the summer season with no selection

from large modes, to smaller modes and there is an indication that changes in the model growth rate could give a closer match to the observed changes. However, given the errors inherent in the predator diet sampling, it is unrealistic to expect a perfect sequence of mode changes.
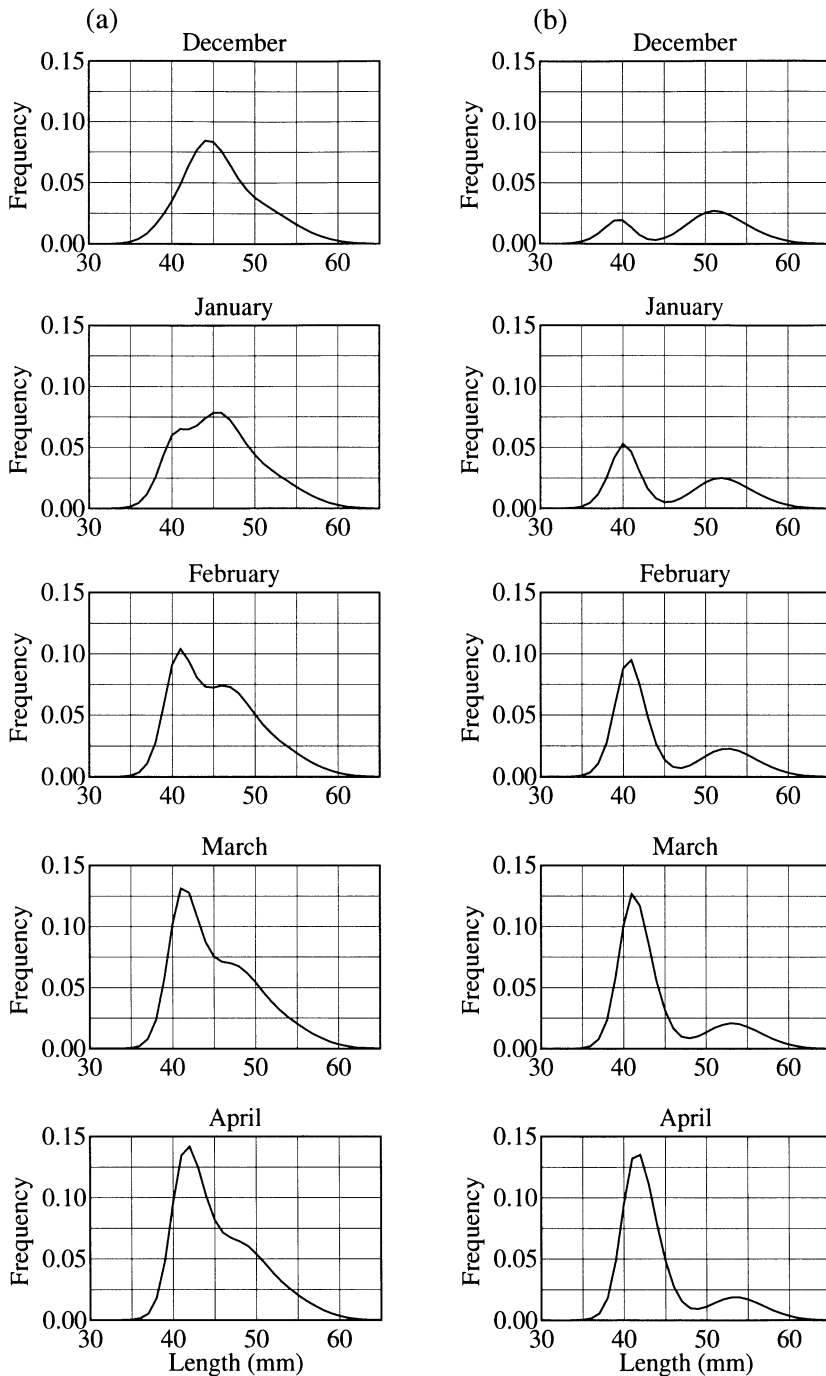

Fig. 7. *Euphausia superba.* Changes in the model-based proportional length-frequency distribution during the summer season with the selection function applied, with (a) no 3+ age class and (b) all classes fully represented

Modelled recruitment failure with selection

To examine the effect of failure of a single year class to recruit to the local population, the number of krill in the 3+ age class at the start of December was set to zero. The development of the length-frequency distribution is shown in Fig. 7b for a mortality rate of $M = 1.25$ yr^{-1}. At the start of the season the large size classes with a merged mode of 51 mm dominate the length-frequency distribution (Table 1). This reduces in January to a main mode of 40 to 42 mm, but the secondary mode is still present between 52 to 53 mm. The 40 to 42 mm mode becomes an increasing proportion of the length-frequency distribution through the season. Changing the mortality rate in the model again mainly affects the timing of the shift from the large size mode to the smaller size mode (Table 1).

Comparison of the model data for recruitment failure with the data in Fig. 4a suggests that the model has reproduced partially the observed development of the krill length-frequency distribution for a year of low krill abundance. The growth into the population of the 2+ age class generates a small size mode (Fig. 7b). The mode of the length-frequency distribution in the model was only slightly larger than the 40 mm mode observed in the diet data. However, there are a number of important differences that centre on the observation that at the start of the season the modal value is much greater than that predicted by the model. The small size mode enters the distribution much early than expected at the start of January rather than between January and February. This is the same effect as was seen in the previous analyses, i.e. the 2+ age class entering the diet too early. Reducing the model growth rate has some effect, but generally the small size group enters the population earlier than expected.

The model did not predict the complete dominance of the very small size mode at the end of the season observed in the fur seal diet data. The lack of a mode at approximately 50 to 52 mm at the start of the season in the fur seal diet data and the dominance of the small mode at the end of the season both indicate that there were many fewer larger krill in the size range 45 to 55 mm than would have been expected from the failure of only one age class (3+).

This indicates that the 4+ (and probably 5+) age classes were also largely absent from the seal diet samples. Thus, late in the season, the incoming 2+ age class probably came to dominate the length-frequency distribution because there were very few older krill in the area. This 2+ age class was the same year class that developed into the 3+ age class in the following year and dominated the length-frequency distribution in the 1994/95 season (Fig. 4b).

This effect of the absence of multiple year classes is illustrated in Fig. 8a, where the number in the 3+, 4+ and 5+ age classes in the model was set to zero to sim-
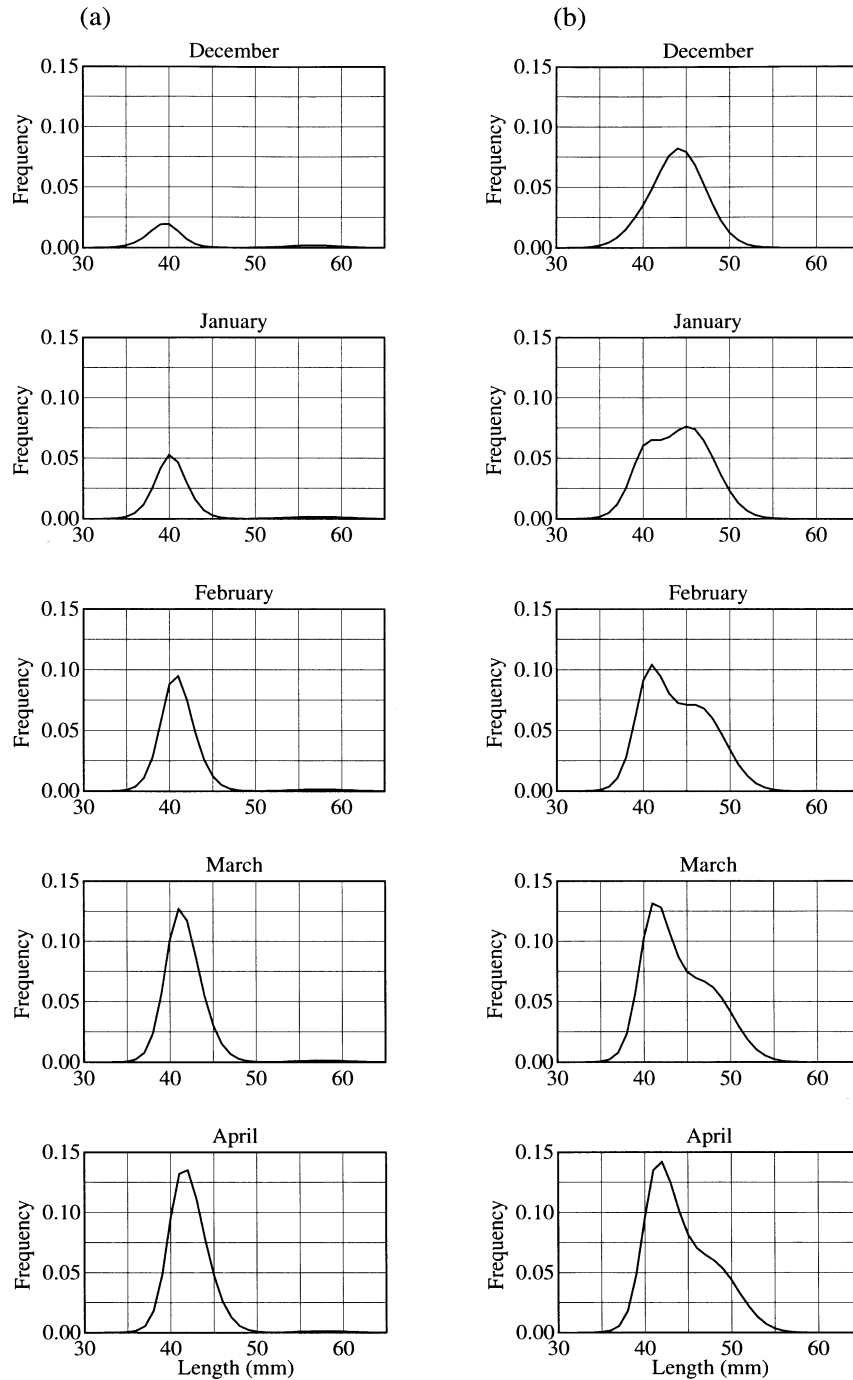

Fig. 8. *Euphausia superba*. Changes in the model-based proportional length-frequency distribution during the summer season with the selection function applied, with (a) no 3+, 4+ or 5+ age classes and (b) no 4+, 5+ or 6+ age classes

ulate the failure of 3 classes. With a value of $M = 1.25$ yr^{-1}, a sequence similar to that in the diet data during 1994 is observed, with the secondary mode at the start of the season at 57 mm although again the small mode at 40 to 42 mm developed earlier than expected in the distribution (Table 1). With a value of $M = 1.25$ yr^{-1}, there are so few krill left in the >5+ age groups that the low numbers of small krill passing through the selection function dominate the whole season. Following the effect through into the next year with the influx of the 2+ age class (Fig. 8b) gives a better representation of the observed changes (compare Figs 4b & 7a), but there are still too many large krill in the distribution compared with the diet data.

Heterogeneity of mortality rates of krill in the Scotia Sea

The above analysis emphasizes the uncertainty in the estimates of the overall mortality rates for the population. Size-based variation in mortality rates may be important, but there is also likely to be marked heterogeneity in the rates in different parts of the population range (Everson 1977). Given the occurrence of large, land-based, predator colonies at South Georgia, there are probably areas within the Scotia Sea where the mortality rate will be much greater than the average

population rate. Let us assume that the mean population mortality rate for the Scotia Sea stock is known ($\overline{M}$) and that, for simplicity, there are 2 types of area within the stock: (1) areas of very high mortality rate in the vicinity of the large predator colonies (M_c) and (2) areas of low mortality rate associated with open-ocean regions (M_o). Then the population mortality rate can by represented as

$$e^{-\overline{M}} = (1-\alpha)e^{-M_o} + \alpha e^{-M_c} \tag{5}$$

where α is the proportion of the population exposed to the higher mortality rate. This can be solved for the mortality rate in the open-ocean regions (M_o):

$$M_o = \ln\left(\frac{(\alpha-1)+e^{(\overline{M}+M_c)}}{\alpha e^{\overline{M}}-e^{M_c}}\right) \tag{6}$$

Assuming that in the vicinity of large predator colonies the mortality rate (M_c) is 1.25 yr^{-1}, the plot of the function for different proportions of the stock exposed to the higher mortality rate is as shown in Fig. 9. If 10 to 20% of the stock is exposed to the higher mortality rate (1.25 yr^{-1}), then the mortality rate of the rest of the stock remains between about 0.5 and 0.6 yr^{-1} for an average mortality rate of ($\overline{M}$) = 0.6 yr^{-1}. Maintenance of much larger proportions of the stock exposed to high mortality rates requires very low, and probably unrealistic, mortality rates in the open-ocean regions. For a higher average mortality rate, for example, ($\overline{M}$) = 1.0 yr^{-1}, then
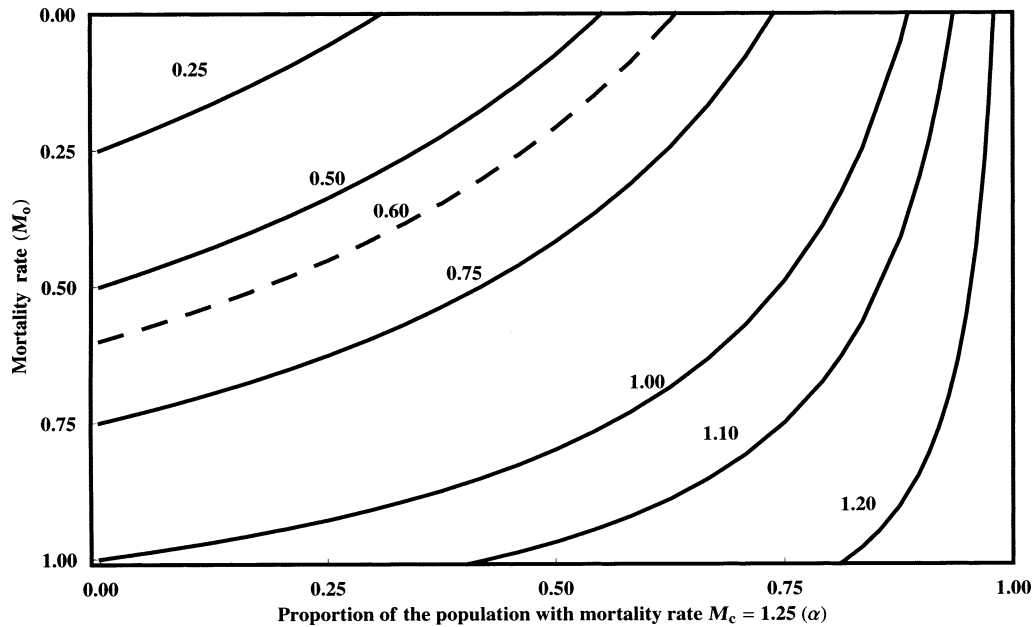

Fig. 9. *Euphausia superba*. Changing mortality rate (M_o) of the open-ocean part of the population with an increasing proportion (α) of the population exposed to an enhanced instantaneous mortality rate of 1.25 yr^{-1} associated with predator colonies (M_c). Note the population average instantaneous mortality rate per annum (M) does not change and is shown next to the isolines for a range of values, e.g., (– – – –) shows changing M_o of the open-ocean part of the population as an increasing proportion of the population exposed to an mortality rate of $M = 1.25$ yr^{-1}; the overall mortality rate is 0.6 yr^{-1}

higher proportions of the population can be exposed to very high mortality rates (M_c = 1.25 yr^{-1}). So approximately 70 to 75% of the population could be exposed to mortality rates of M_c = 1.25 yr^{-1} while the rest experience mortality rates of approximately M_o = 0.5 to 0.6 yr^{-1}.

DISCUSSION

Krill population dynamics

Overall, the *Euphausia superba* population model reproduced the seasonal development of the krill length-frequency distribution in the diet of fur seals. When the 3+ age class is present, mortality and slow growth of the older age groups are offset by the 2+ age class increasing as a proportion of the population structure through growth or immigration; this generates a population structure that shows relatively little change over the season (Reid et al. 1999a). In a year of relatively low krill abundance, the development of the population structure was reproduced reasonably well, with only the removal of the 3+ age class from the model, while removal of further older age classes gave a better characterization of the changes. There were consistent changes in the population size structure and the mean size of krill in the diet of the fur seals over the period 1991 to 1997 (Reid et al. 1999a). Detailed changes in length frequency are shown in Figs 1 to 4 of Reid et al. (1999a) emphasizing that the 2 years considered in this study are part of a consistent sequence and representative of the fluctuations in size frequency observed during periods of high and low krill abundance (see Figs 6 & 7 of Reid et al. 1999b for the sequence of changes in length and Murphy et al. 1998 for a discussion of the impacts of age structure changes on biomass). The consistent changes in population structure represented in the model, and shown in the diet data, emphasize that such fluctuations in krill population structure, with consequent impacts on the regional biomass, do occur around South Georgia.

There are indications that major immigration events resulting in successful recruitment to the krill population around South Georgia occur between periods of low immigration and hence poor recruitment. However, these results require care in interpretation, as changes in year class strength will modify the mortality rates for particular age classes. So, for example, absence of the 3+ age class would mean that there would be greater mortalities of the >3+ age groups and hence reduce their relative representation in the length-frequency distribution in the following year. The outcome of these effects would also depend on the predator responses to the changes in krill abundance.

In the model, we have assumed constant recruitment except in years of complete absence. In reality, the year class strength will vary and produce complex changes in population structure.

The suggestion that variations in year class strength were likely to be important in the observed fluctuations in krill biomass at South Georgia was made by Mackintosh (1972), who noted the irregular occurrence of an intermediate size class in the South Georgia population. However, he was unable to explain the occurrence of the class with the then current views of the age of krill. He did suggest that the number of year classes in the population might not be correct and that there might be variations in the krill growth rates. Based on recent views of krill growth, the model used in the current study indicates that this intermediate class reflects the dominance of the small (2+ age class) size-mode in the length-frequency distribution in years of low krill availability. Mackintosh (1972) noted that these intermediate years tended to occur during years of low krill abundance at South Georgia as characterised by the lack of food for the whales. Such changes are consistent with the population fluctuations revealed in this study during periods of low krill abundance.

One of the key features of the model is that the larger krill in the upper tail of the length distribution of the 2+ age class should, on the basis of their size and growth, start to enter the distribution by about December. The appearance of the 2+ age class varies between years in the diet of Antarctic fur seals (Reid et al. 1999a,b). However, the simultaneous appearance of krill from the 2+ age class in the diet of Antarctic fur seals and Macaroni penguins, which are known to take smaller krill than Antarctic fur seals, indicates that krill are being brought in from outside the region. This would indicate that there is relatively little active selection occurring, a point supported by the fact that the outcomes from the model analyses were not sensitive to changes in the parameterization of the selection function. This point is supported by surveys of population size structure, which show that during the summer smaller krill tend to be found in more eastern regions along the northern shelf, while larger krill are found in the west in the main region of Bird Island predator foraging (Watkins et al. 1999). The population size structure of krill occurring in the diet of predators from Bird Island will, therefore, vary not only with any growth-related differences but also with the timing of any advective flux or migration. This emphasizes that the fur-seal diet data give a spatially restricted view of the krill population size changes, and that krill size structure in the area where the Bird Island fur seals forage can be very different from that occurring in other areas where seal foraging is less intense (Watkins et al. 1999).

Mortality rates

The most obvious discrepancy between the model distributions and the observed size structure is that there were many fewer large krill than would be expected from a constant recruitment and mortality model. There is no evidence of any change in activity or distribution of krill that would account for this effect; indeed, the large krill are the main component of the pelagic population taken by the predators in this area (Reid et al. 1996). Although there is a fishery for krill operating in the South Georgia area, this is considered to have only a small impact on the local population (Murphy 1995).

It is possible that adult krill, through active or passive movement associated with the current flow, pass through the area as separate year classes that are not always fully retained. Such an effect would tend to enhance estimates of local mortality rates. However, given the spatial restriction of foraging of the main predators during the land-based breeding seasons, krill mortality rates would be expected to differ greatly within different regions of the Southern Ocean. Analyses of krill populations in the Indian Ocean sector of the Southern Ocean, which derived age-based estimates of mortalities (Pakhomov 1995), obtained some very high values ($M > 2.0$ yr^{-1}). Some of the areas close to Prydz Bay, near the sites on which the analyses of Pakhomov (1995) were based, have large colonies of penguins and seals. We consider that the lack of older age groups in the krill population in the vicinity of South Georgia most likely reflects the enhanced mortality rates that will occur as a result of the high predation impacts.

The model analysis was based on a constant rate of mortality, independent of changes in the size of the population. Alterations in the population size and age structure will generate variation in the mortality rates experienced by different age groups. This would lead to complex changes in population structure within and between years. Developing the model analyses to include changes in the mortality rate associated with changes in population structure and abundance will be an important next step in investigating the long-term population dynamics. Given a high mortality rate of the order suggested, the population effectively consists of the 3+ and 4+ age groups, with very few larger individuals in the 5+ or older age groups. Variations as a result of the absence of the 3+ age class will probably lead to enhanced mortality of older age groups.

Although there is some reasonable information on land-based predators in a few localities, there is little information on the dietary requirements and total demands of pelagic predators. Development of a more detailed model exploring the effects of varying mortality with size will also be useful, although the model general effects are clear from the analyses in this paper. Any increase in mortality rate with increasing size will tend to reduce the representation of larger krill in the length-frequency distribution and more rapidly reduce the upper tail of the distribution. With the Bird Island fur seals feeding mainly on larger krill, this may indicate an increased mortality rate for larger size classes and may help to explain the apparent under-representation of older krill in the diet of fur seals.

Across the Scotia Sea, the proportion of the stock exposed to increased mortality rates is unknown, and only in a few areas can predator demand for prey be even tentatively estimated (e.g. Croxall et al. 1985). The analyses of heterogeneous mortality rates illustrated how enhanced regional mortality rates could be sustained across a population. Such a scenario is reasonable in the Scotia Sea, where the krill are transported over large parts of the open ocean, and where the predator demand for prey is likely to be relatively low compared with the demand in the vicinity of large colonies of land-based predators (Croxall et al. 1988, Murphy 1995, Murphy et al. 1998). One further aspect of the mortality rates is that there may be substantial differences in the mortality rates of males and females that would affect population dynamics. Sexually mature adult females dominate in the diets of the predators at South Georgia (Reid et al. 1996). This would suggest that, at the Scotia Sea population level, the females are exposed to much higher mortality rates than the males. Understanding the interactive effects between changing krill abundance, mortality and size-based mortality will be crucial for understanding the interannual changes in krill biomass around South Georgia.

Age and growth

The model of growth is important in determining the changes observed, and it is critical for further population model development that progress is made on the ageing of krill and defining the limits of size at age. Although the model reproduces the general pattern of the size distribution fluctuation, detailed energetic and age-size modelling will help to define the range of length-frequency distribution fluctuations expected. An important aspect of the fur seal diet data revealed by this model is that the modes are not always age class modes. From the model, the mean size of the incoming 2+ age class will be about 34 to 36 mm (Fig. 6) at the start of the season, whereas the mode of the 2+ age class observed in the diet data is about 38 to 40 mm (Fig. 4b). This is probably a result of the selec-

tion effects and represents the upper tail of the size distribution of the 2+ age class. Later in the season the observed mode is closer to the model mode, but whether it is a good representation will depend on the extent of any selection at that time. This makes it very difficult to use the data to analyse the growth of the krill through the seasonal progression of the modes. An assumption that the mode represents the mean size of an age class would produce an underestimate of the true growth rate. During the early part of the season, when growth rates are likely to be greatest, the progression of the mode of the fully recruited 3+ age group should represent the true growth rate. Later in the season, the increasing representation of the 2+ age group will modify the size progression, and any size-based mortality effects will be increasingly important. Attempts to track growth using larger size modes of the older age groups will not produce good estimates of growth rates, as they will be merged modes of a number of age groups and growth and mortality effects will be confounded. Age and growth rates of krill are a major requirement for modelling population dynamics and the operation of the ecosystem. Developing analyses and models of age and growth is a priority for krill biological research.

Large-scale connections

The fluctuations in the recruitment of krill into the stock around South Georgia will be influenced by the large-scale spatial connections in the population. Murphy et al. (1998) noted that the strength of a given year class at South Georgia could be a result of either changes in the initial reproduction recruitment or fluctuations in the amount of krill transported into the area by the ocean currents. The result of either of these processes would be variations in the level of immigration of different year classes into the South Georgia region (Murphy et al. 1998).

The study has shown that the changes in the population structure of krill at South Georgia are consistent with the population model predictions. At the broader scale, however, the question remains as to what generates the observed variations in year class strength? Fluctuations in the strength of different krill year classes have been recorded in the Antarctic Peninsula region and related to the large-scale physical environmental sea-ice and ocean variability (Siegel & Loeb 1995, Loeb et al. 1997). Recent analyses, which indicate that the biomass of krill at South Georgia appears to fluctuate in concordance with changes at the Antarctic Peninsula, also lend support to the suggestion that there are large-scale coherent fluctuations occurring in the ecosystem (Priddle et al. 1988, Brierley

et al. 1999). Taken together, the studies suggest that large-scale changes in krill age structure across the Scotia Sea produce coherent fluctuations in krill biomass. The fluctuations in krill abundance through population changes examined here will also introduce biological lags into the system dynamics (Murphy 1995, Murphy et al. 1998). This study emphasizes that studies of local food-webs to predict ecosystem responses to change need to include the key processes involved in large-scale ecosystem operation.

Summary

The changes in size structure of krill in the diet of fur seals at South Georgia were consistent with predictions of a population model that included a size-based predator-selection function. The successful recruitment of the 2+ age class into the region is the first indication that it will become the dominant mode as the 3+ age group in the size-frequency distribution of the fur seal diet in the following year. However, the timing of the appearance of the 2+ age class in the fur seal diet within a season is not explained by growth into the length-frequency structure as predicted by the model, but is probably associated with an influx associated with the current systems. Abundance and contribution to the biomass of krill 5 yr of age or older is likely to be low, particularly after years in which the younger 3+ and 4+ age groups were absent. Major recruitment-immigration events appear to occur between periods of relatively low recruitment, but this will be confounded by the interactive effects of changing mortality rates in association with changes in krill abundance and size structure. Understanding the processes generating successful influx, growth and development of the 2+ age class into the east of the South Georgia region during the early part of the season, and refining the estimates of the absolute age of this class, will be a key step in developing large-scale and regional operational models.

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