Krill population dynamics in the Scotia Sea: variability in growth and mortality within a single population

K. Reid [a,*], E.J. Murphy [a], V. Loeb [b], R.P. Hewitt [c]

[a]*British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK*
[b]*Moss Landing Marine Laboratories, P.O. Box 450, Moss Landing, CA 95039-450, USA*
[c]*National Marine Fisheries Service, Southwest Fisheries Science Centre, P.O. Box 271, La Jolla, CA 92038, USA*

Abstract

Understanding the demographics of Antarctic krill over large scales may be complicated by regional differences in the processes that govern population structure. The influence of regional differences in growth and mortality on population size structure was examined using data on the length–frequency distribution of krill in the Scotia Sea using samples from the South Shetland Islands and South Georgia collected annually from 1991 to 2000. A correction function, which took account of the higher growth rate at South Georgia, produced a consistent similarity in the position of the modal size classes that was not present in the raw data. Optimising the mortality rate, to minimise the differences in the growth corrected length–frequency distribution, suggested a higher mortality rate at South Georgia that the South Shetlands. The intra-specific variations in growth and mortality rates are consistent with published values and with other Euphausiids species. Having accounted for the demographic plasticity, it is apparent that strong recruitment of the smallest size class of krill is represented in both populations simultaneously. It appears that first-year krill are advected into different regions of the Scotia Sea where the resultant population size structure is determined by regional differences in growth and mortality. The majority of the commercial harvest of krill in the Antarctic occurs in a relatively small number of regional fisheries within the Scotia Sea and is managed using population models based on a single set of demographic parameters. Where substantial differences in these parameters exist between fishing areas, the calculation of catch limits should take these differences into account. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

In the Antarctic a link has been described between a major physical variable, the extent and duration of sea-ice in winter, and the population dynamics of Antarctic krill *Euphausia superba*, a key species in the marine foodweb of the region (Loeb et al., 1997). Variability in the abundance and population structure of Antarctic krill has also been linked with fluctuations in the reproductive performance of krill-dependent predators such as penguins and seals both within the sea-ice zone and in adjacent areas not directly affected by sea-ice (Croxall et al., 1988, 1999; Fraser et al., 1992). To understand the factors controlling the biological dynamics, it is therefore essential to define the scales over which physical and biological varia-

* Corresponding author. Tel.: +44-1223-221607; fax: +44-1223-221259.
E-mail address: k.reid@bas.ac.uk (K. Reid).

bility occurs. Measurement of the extent and duration of sea-ice, particularly using satellite telemetry, is relatively straightforward. Characterising the spatial extent of the biological variability is, however, more difficult and in the case of krill this requires a consideration of the population demography at the ocean basin scale.

Within the southwest Atlantic (Scotia Sea) Sector of the Southern Ocean the major areas of krill spawning are probably in the region near the western Antarctic Peninsula and along the southern Scotia Arc to the South Orkney Islands which are well within the area of winter sea-ice cover (Hewitt and Linen Low, 2000). These areas are believed to be the principal source of the population at South Georgia, where the krill population is thought not to be locally self-sustaining, and which lies to the north of the maximum extent of winter sea-ice (see Murphy et al., 1998). Although some level of concordance is evident in the inter-annual fluctuations in krill biomass across the Scotia Sea, based on data from the South Shetland Islands and South Georgia (Brierley et al., 1999), attempts to show similarities in the presence/absence of individual year classes of krill have proved problematic with strong year classes in one location apparently absent in the other and vice versa (see Murphy et al., 1998). Comparisons of year class strength have been made on the basis of the relative size (length) and strength (abundance), however, these analyses do not take into account the potential for regional differences in the processes governing the structure of the population in the two locations.

The size structure of a population is a function of recruitment, growth and mortality and if these conditions vary geographically this may be reflected in differences in the structure of sub-populations within a wider meta-population. Therefore, it might be unrealistic to track cohorts across large areas only on the basis of size, especially where samples are available from a very limited number of locations. It may be the case that the krill population of the Scotia Sea experiences common recruitment processes, possibly associated with large-scale physical sea-ice processes, but the subsequent regional differences in growth and mortality rates lead to appreciable differences in the size structure of the resulting adult populations. In particular, the position of a mode in the length–frequency distribution that represents a particular year class may

be determined by the growth rate, while the dominance of individual modes will depend upon the mortality rate and relative year-class strength. Given that there is evidence that both the growth and mortality rates of krill at South Georgia are higher than the overall population estimate (Reid, 2001; Murphy and Reid, 2001), accounting for differences in growth and mortality may help resolve the extent to which there are common recruitment processes acting across the population of the Scotia Sea.

The aim of this paper is to take the krill length–frequency distributions from the South Shetland Islands and model the effects of regional differences in rates of growth and mortality to generate expected length–frequency distributions, and compare these with the observed length–frequency distributions from South Georgia. Long-term monitoring data on the population size structure of krill at the South Shetland Islands and South Georgia each year from 1991 to 2000 was used to examine: (a) the level of overlap in the position of the modal size classes when the effects of the higher growth rate at South Georgia were applied to the length–frequency distribution of krill from the South Shetland Islands, (b) the effects of the differences in mortality rates on the relative magnitude of modal size classes, and (c) the implications of these results both in terms of the presence of common recruitment events and inter-annual variation in the size structure of the adult population.

2. Methods

2.1. Data sources

In order to consider the connection between krill populations at the South Shetland Islands and South Georgia we have used the two longest annual time-series of krill population size structure from the Scotia Sea from 1991 to 2000. Data for the South Shetland Islands comes from the US Antarctic Marine Living Resources monitoring programme (see Hewitt and Demer, 1994) and that from South Georgia come from the measurement of krill in the diet of lactating female Antarctic fur seals (*Arctocephalus gazella*) at Bird Island (Reid and Arnould, 1996; Reid et al., 1999). Critical comparisons of the nature of the krill

population as sampled by Antarctic fur seals and net caught samples from the same time and location at South Georgia have shown the utility and suitability of using material from diet samples to examine krill population size structure (Reid et al., 1999; Murphy and Reid, 2001).

2.2. Growth rate function

The consequences of the different growth rate on the length at age of krill was based on a Von Bertalanfy growth curve that has been derived for krill (see Siegel, 1987; Reid, 2001),

$$L_t = L_\infty(1 - e^{-k(t-t_0)}) \qquad (1)$$

where L_t is the length at time t, L_∞ is the maximum size of krill, k is the growth constant.

The difference in length at age between the South Shetland and the South Georgia populations at any age can the be calculated as

$$\Delta L_t = (L_{\infty 2}(1 - e^{-k_2(t-t_0)}))$$
$$- (L_{\infty 1}(1 - e^{-k_1(t-t_0)})) \qquad (2)$$

where $L_{\infty 1}$=63 mm and k_1=0.47, following Siegel (1987) based on data form the South Shetland Islands;

$L_{\infty 2}$=67 mm and k_2=0.75 and for South Georgia (Reid, 2001) and t_0=0.1418. This equation was used to produce a corrected length ($CL1_t$) for each krill sampled at the South Shetland Islands where

$$CL1_t = \Delta L_t + L1_t \qquad (3)$$

and t is the age of each krill as determined by rearrangement of Eq. (1).

2.3. Mortality rate function

The effect of different rates of mortality at the South Shetland Islands and South Georgia were examined according with the assumption of a constant mortality rate

$$N_t = N_0 e^{-Mt} \qquad (4)$$

where N_t is the number of individuals in the population at time t from an initial population N_0. In order to adjust the numbers of krill in each size class given different rates of mortality (M) each age class (t) was converted to an equivalent 2-mm size class according to the growth rate equation (Eq. (1)). The difference in numbers of krill in each size class (S_l) is the ratio of the number of krill in that size class assuming a mortality rate of M_1 (taken here as M=0.6, following Butterworth et al., 1994) compared to the number in
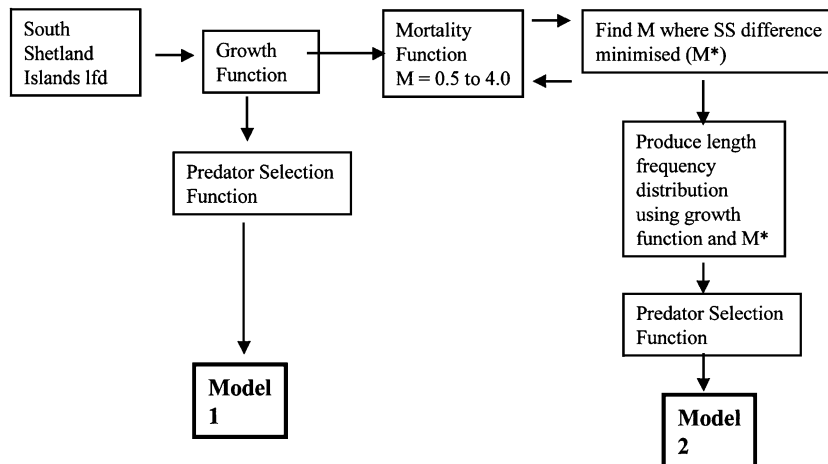

Fig. 1. Flow chart outlining the structure of the procedure used to produce the simulated length–frequency distributions.
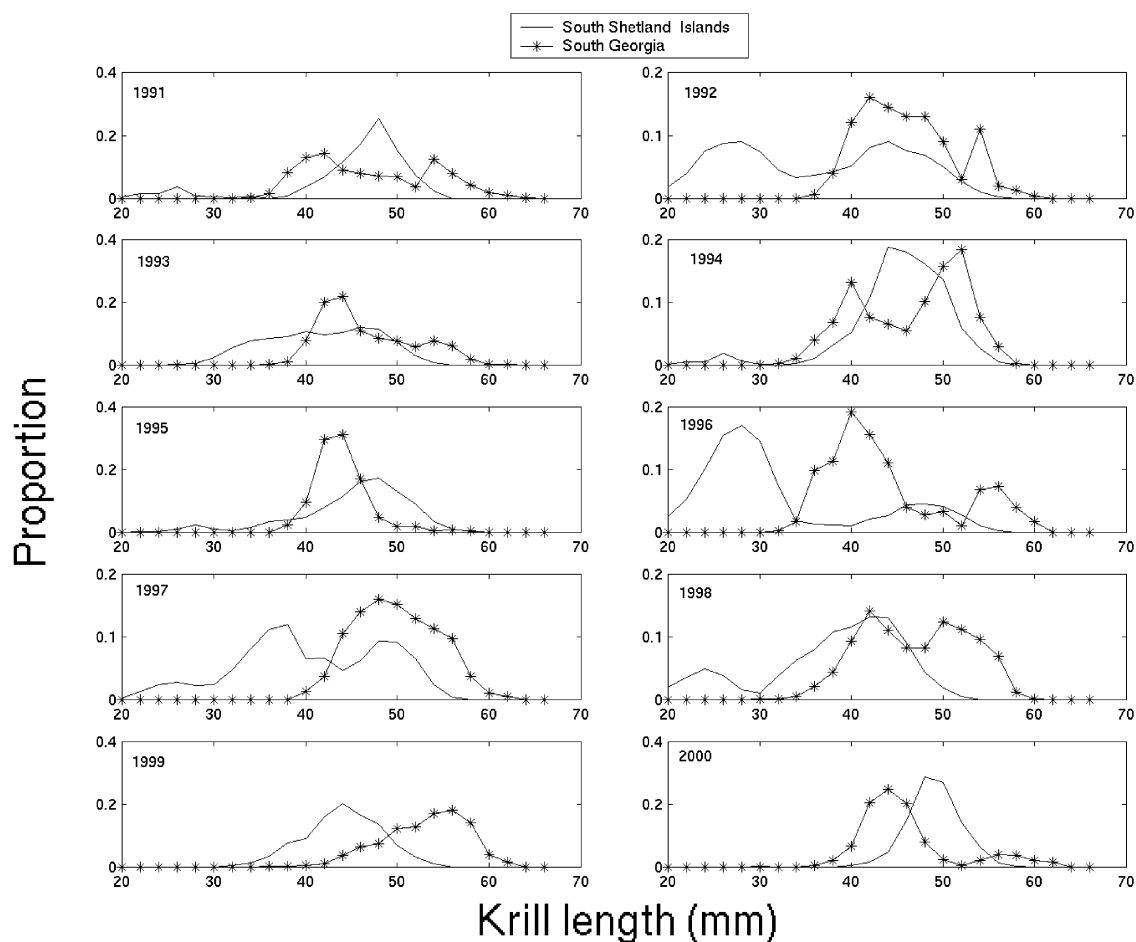
Fig. 2. The length–frequency distribution of krill from the South Shetland Islands (—) and South Georgia (—*—) 1991–2000.

that size class assuming a rate of M_2 given the same initial population size such that

$$S_l = e^{(-M_1+M_2)}t \qquad (5)$$

from which the corrected number of krill in each length class CN_l was calculated as

$$CN_l = N_l S_l \qquad (6)$$

where N_l is the original number of krill in each size class.

2.4. Predator selection function

Antarctic fur seals take relatively few krill of less than 36 mm therefore, in order to account for the

Table 1
Modal size of krill in the population at South Shetlands, South Georgia and Model output

Year	South Shetland		Model 1			Model 2		South Georgia	
1991	26	48		40	58	40	58	42	54
1992	28	44		42	56	42	54	42	56
1993		40	48		58	44		44	54
1994	26	46			58	38	58	40	52
1995	28	48			58	40		4	
1996	28	46		42	58	40	58	40	56
1997	26	38	50	40	50	62	40	50		48
1998	26	42		40	58	40	48	42	50
1999		42			56		56		56
2000		48			60	42	58	44	58

Fig. 3. The length–frequency distribution of krill from the Model 1 output (—) and South Georgia (—*—) 1991–2000.

potential under-representation of smaller krill, a logistic selection function, based on comparison of length–frequency distributions of krill from Antarctic fur seals and simultaneous net samples (Murphy and Reid, 2001), was applied:

$$P_l = \frac{1}{1 + e^{-a(l-b)}} \tag{7}$$

where P_l is the proportion of each length class l that is consumed by Antarctic fur seals. The parameter values applied in the function ($a = 1$, $b = 40$) represented

a strong selection effect close to 40 mm, however the results of the following analyses are not sensitive to changes in the parameterisation. To calculate the number of krill in each size class expected in the length–frequency distribution of krill in the diet of Antarctic fur seals (N_l) prior to comparison of the length–frequency distributions with that actually observed in the diet of Antarctic fur seals at South Georgia, the number of krill in each size class L_i was multiplied by P_l such that

$$N_l = P_l L_l \tag{8}$$

2.5. Model structure

2.5.1. Model 1

In order to produce an 'expected' length–frequency distribution based on the South Shetland Islands data taking account of the different growth conditions between the two regions the growth correction function (Eq. (2)) was applied to the length–frequency distribution from the South Shetland Islands. This produced a new length–frequency distribution, which was compared with the length–frequency distribution from South Georgia after the application of the predator selection function (Fig. 1).

2.5.2. Model 2

The output from Model 1 (without the predator selection function applied) was then subjected to a mortality rate that was allowed to vary over the range $M=0.5-4.0$ (increments of 0.1); for each value of M a length–frequency distribution was produced. For each realisation of M, the sum of squares of the difference between the resultant length–frequency distribution (with the application of the predator selection function) and the length–frequency distribution from South Georgia from the same year was calculated. The optimum value of M for each year (M^*) was taken as that which minimised the sum of squares of the difference. The resultant length–frequency distribution, using the South Shetland Islands data with the growth function applied, a mortality function based on M^* and a predator selection function was then calculated for each year (Fig. 1).

All analyses were carried out using Matlab v.5 (The Mathworks — , www.mathworks.co.uk).

3. Results

Comparison of the raw length frequency distributions from the two regions shows there was little overlap in their relative size and position of the modes (Fig. 2). After the application of the growth rate correction function to the krill length frequency distribution from the South Shetland Islands there was a greater overlap of the modal size groups with those in the distributions from South Georgia (Table 1; Fig. 3). However, there were considerable differences in the relative magnitude of the modes which resulted in an over-representation of krill in the larger size groups such that the proportions of large krill in the Model 1 distributions consistently exceeded that in the South Georgia population (Fig. 3).

The optimisation of mortality rates (Model 2) produced a mean overall rate of $M=1.9$ (range 0.7–2.8) (Table 2). The application of the year-specific mortality rates reduced the number of krill in the larger size classes in each year and hence there was an increased frequency of the smaller size classes in the proportional length–frequency distribution; the overall effect was to produce a congruence in the number, position and relative magnitude of modes in the Model 2 and South Georgia length–frequency distributions (Fig. 4). The highest mortality rates occurred in 1995 and 2000, both years in which the dominant modal size class of krill at the South Shetland Islands exceeded that at South Georgia. There was a significant reduction in the sum of squares of the differences comparing the South Georgia data with the Model 2 output compared to the length–frequency distributions based on the raw data (*t*-test for matched pairs $T=4.11$ $p<0.01$). Overall, the application of the growth function synchronised the position of the modal size classes and the optimised mortality rate reduced the differences in the relative proportion of krill within each mode when compared between the

Table 2

Mortality rate and difference in population structure between South Shetlands, South Georgia and Model output

Year	Difference 1	M^*	Difference 2
1991	0.0919	1.9	0.0266
1992	0.0659	1.2	0.0182
1993	0.0583	2.2	0.0459
1994	0.0634	2.3	0.0433
1995	0.1252	2.4	0.0972
1996	0.1792	0.7	0.0562
1997	0.0819	1.2	0.0089
1998	0.0572	1.9	0.0241
1999	0.1693	1.3	0.0140
2000	0.2076	2.8	0.0491
Mean	0.1100	1.8	0.0384

Difference 1 is the sum of squares of the differences between the South Shetlands and South Georgia.

M^* is the rate of mortality as fitted by the optimisation procedure (see Fig. 3).

Difference 2 is the sum of squares of the differences between the South Georgia and Model 2 (growth rate $k=0.75$; mortality M^*).
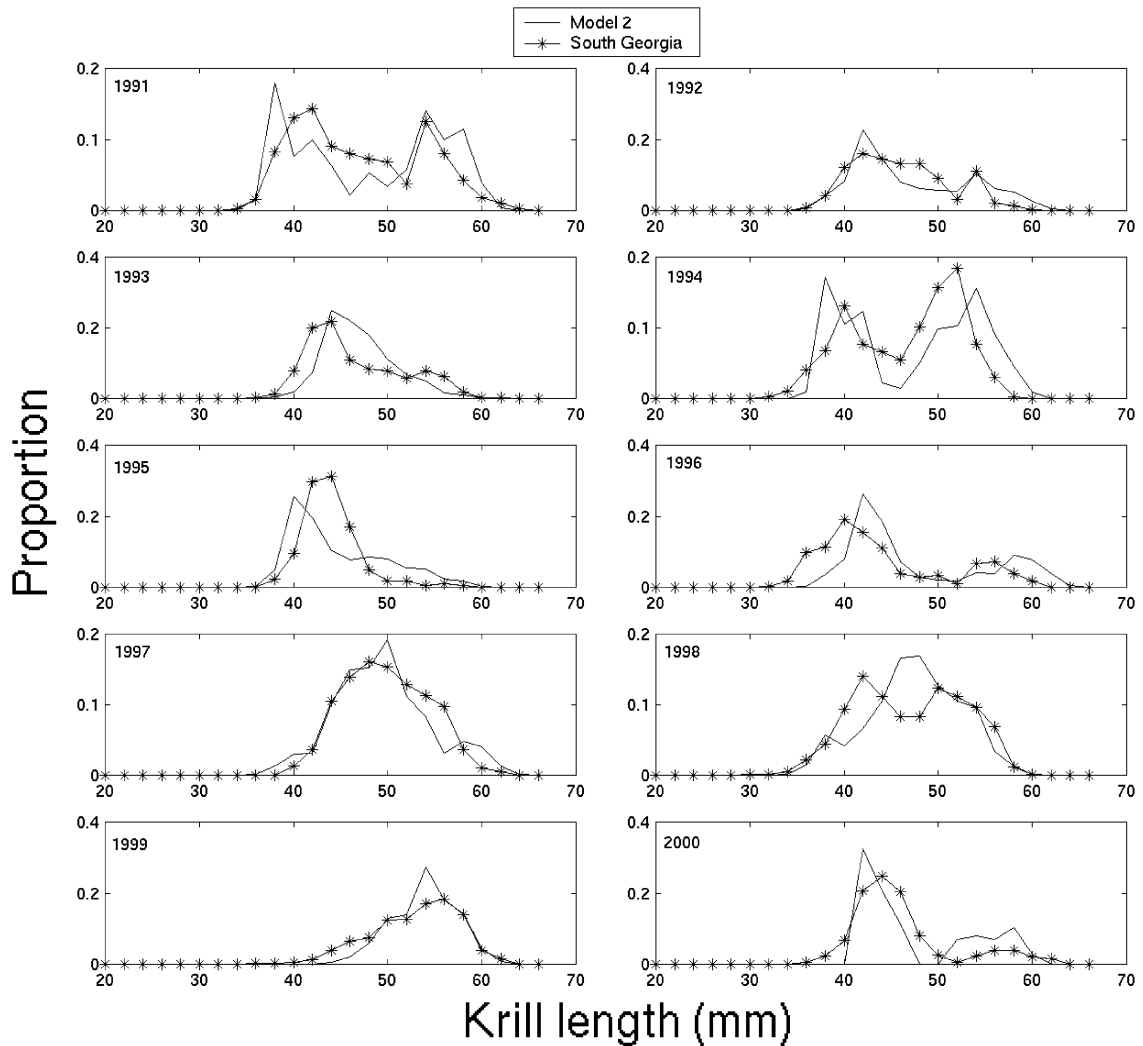
Fig. 4. The length–frequency distribution of krill from the Model 2 output (—) and South Georgia (—*—) 1991–2000.

Model 2 output and the South Georgia length–frequency distributions.

4. Discussion

4.1. Accounting for regional variation in population parameters

In this analysis, we attempted to investigate to what extent the differences in growth and mortality of krill at the South Shetland Islands and South Georgia could explain the differences in the population of krill in those two areas, despite them having a common source region. It is important, however, to avoid a circularity in which the length–frequency distributions from the two locations are made to converge by changing key parameters and then using the overlap in the length–frequency distribution to justify the choice of those parameters. Hence, we maintained fixed growth rates based on published values for krill in the South Shetland Islands and at South Georgia, and utilised a fixed selection function also based on published values (Siegel, 1987; Reid, 2001; Murphy

and Reid, 2001). Our growth function, when applied to the length–frequency distribution of krill from the South Shetland Islands, produced a similarity in the position of the modal size classes of krill at the two locations that was not apparent in a comparison of the raw length–frequency distribution data. Despite overlap in the modal position there were still considerable discrepancies in the relative magnitudes of these modes, with fewer large krill than expected at South Georgia, assuming the same mortality rate at the South Shetland Islands. Setting the rate of mortality to that which minimised the differences in the proportion of krill in each mode, suggested a much higher mortality rate at South Georgia relative to the South Shetland Islands. This is consistent with the mortality rates indicated by Murphy and Reid (2001) for South Georgia. The rates we have used for growth and level at which mortality was optimised are consistent with the levels of intra-specific demographic plasticity shown by other euphausiid species (e.g., *Meganyctiphanes norvegica* and *Thysanoessa inermis*; see Siegel, 2000).

Comparison of the relative magnitude of individual year classes between different areas across the Scotia Sea is complicated by the inability to characterise absolute abundance. However, the absence, or presence as a very small component of the population, of a year class may be easier to detect, particularly in the first year (overlapping sizes of older aged krill may prohibit the identification of individual year classes). At South Georgia, analysis of the population dynamics has shown periodic failure of the youngest age class to enter the population leading to a much reduced biomass of krill in the following year (Reid et al., 1999). Such 'recruitment failures' occurred in 1990, 1993, 1997 and 1999 and in each of these years the smallest mode of krill at the South Shetland Islands (ca. 28 mm) is either absent or forms a very small proportion of the population. The 2 years in which this smallest mode dominated at the South Shetland Islands, 1992 and 1996, were the years in which the smaller mode (ca. 40–42 mm) dominated at South Georgia and the differences between the Model 2 output and South Georgia length–frequency distributions were the smallest. The dominance of small krill at South Georgia in both years is also apparent in penguin diet samples and net samples from those years (Reid et al., 1999). Thus, the impacts of both

good and bad recruitment appears to be reflected in the population size structure of krill in both the South Shetland Islands and at South Georgia simultaneously. This would indicate that it is a failure of the 1+ age class to enter the South Georgia population that is responsible for a low biomass in the following year, rather than the 2+ class as was previously considered (Reid et al., 1999; Murphy and Reid, 2001).

4.2. How do regional conditions influence patterns of inter-annual variability?

Hewitt and Linen Low (2000) suggest that the krill population at the Antarctic Peninsula is maintained by occasional strong year classes, such as in 1991 and 1995, which appear as the smallest size class of krill in the population in the following year. These strong year classes are also apparent at South Georgia in the same years, i.e. 1992 and 1996. However, as a result of the higher mortality rate at South Georgia, they persist for a much shorter time in the population. Thus, the strong 1991 year class formed the dominant mode at the Antarctic Peninsula from 1992 until 1995, but only until early 1994 at South Georgia. Similarly, the 1995 class persisted from 1996 until 2000 at the Antarctic Peninsula but only until 1998 at South Georgia.

Brierley et al. (1999) indicated that the inter-annual variation of krill biomass at South Georgia was greater than might be expected from a multi-year age-structured population, and that the amplitude of variation was much greater than that seen at the Antarctic Peninsula, although the relative change in biomass between the two locations showed a high level of concordance. One plausible explanation for this, based on the above analyses, is the effect of a much higher mortality rate at South Georgia, which effectively means that the krill population there has fewer year classes in the same age-structured population, and is therefore under a much greater influence of variability in recruitment.

In both 1995 and 2000, the dominant mode from the South Shetland Islands was larger than that from South Georgia, although the dominant mode at South Georgia is present in the Model 2 population, albeit as a small component. The most straightforward explanation for this is that the larger mode represented in the Model 2 output simply no longer existed in the South

Georgia population, presumably, because the higher mortality rate has led to its much earlier removal from the population. The optimised values for mortality in these years are the highest values for all years, however, they are a function of the cumulative mortality over the preceding 2 years rather than a point measure of the mortality within that year, especially with respect to the older age classes.

4.3. Is there a single krill population in the Scotia Sea?

The optimised mortality rate is a measure of how much correction has to be applied to the growth incremented length–frequency distribution from the South Shetland Islands; the years with the smallest correction were when the smallest size class of krill dominate the length–frequency distribution at the South Shetland Islands (e.g., 1992, 1996), whereas the largest correction was applied when the bigger size classes dominate (1995, 2000). This suggests that while the smallest size class of krill enter the population at the two locations at the same time while the larger size classes are not entering the South Georgia population in the same way. It would appear from this that the movement of krill from the spawning region to South Georgia may not involve a cross-section of the whole population but that only the smallest size class is advected. Evidence from krill energetic modelling suggests that it may only be the smallest size classes that are able to cope with the relatively low food availability in the open ocean (Fach et al., submitted).

It would appear from the results presented here that within the Scotia Sea there is a single krill population in which the recruitment processes are potentially driven by the large-scale physical processes of sea-ice extent and variability in the region of the Antarctic Peninsula and Southern part of the Scotia arc. The first year krill produced each year are advected into different geographical regions within the Scotia Sea where they experience different conditions of growth and mortality. Thus, the physical impact of variability in sea-ice is transmitted well beyond its geographical boundaries by the biological consequences of that variability.

Previous attempts to reconcile the differences in the population structure have suggested that while

krill at both sites share a common source region there may also be additional krill at South Georgia that originate in the Weddell Sea region (Murphy et al., 1998; Watkins et al., 1999). Initial studies of the population genetics of the krill stocks in Antarctic Ocean suggest that significant genetic differences may exist between the krill populations at South Georgia and the Weddell Sea (Zane et al., 1988), however, Zane and Patarnello (2000) suggest that *E. superba* is characterised by weak genetic differentiation. The results of the current study, which explicitly account for the impact of regional conditions on the length– frequency distribution of krill, indicate little evidence of a substantial component of the krill population at South Georgia that is not represented in the Antarctic Peninsula population. This suggests that if krill at South Georgia are indeed a mixture of krill from two source regions then the krill population in the Weddell Sea has the same recruitment patterns as the Antarctic Peninsula, or that krill originating in the Weddell Sea are equally represented in the population at the Antarctic Peninsula and at South Georgia, or that krill from the Weddell Sea do not make a large contribution to the krill stocks at South Georgia.

We have undertaken this analysis using the most complete datasets available for this region, however, it is important to recognise that these represent two sampling points in a large-scale, highly dynamic system. The level of congruence in the length–frequency distributions in any year is dependent upon the cumulative, multi-year influence of differential growth and mortality. Therefore, not only have we examined the influence of differential demographic processes in each year we have shown that these processes are consistently reflected in the year-to-year population dynamics. The level of natural heterogeneity and the limitations of sampling substantially limit the interpretation of data from individual years and emphasises the importance of long-term studies in examining large-scale marine systems.

4.4. Implications for management

The commercial harvest of Antarctic krill is managed by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), which takes an ecosystem approach to resource management. Within the Antarctic the majority of krill

harvest is taken from the SW Atlantic (Statistical area 48) and within this area from three sub-areas in the vicinity of the South Shetland Islands (sub-area 48.1), South Orkney Islands (sub-area 48.2) and South Georgia (sub-area 48.3). Calculation of the catch limits for krill are based on a population model that includes simulation of the effects of different catch limits based on a defined range of recruitment, growth and mortality conditions; the outcome of these simulations is then used to set a catch limit for the whole of the statistical area (Butterworth et al., 1994). Clearly where pronounced regional differences in key population parameters exist, this suggests that the development of ecosystem based management measures, which account for the demands of predators with highly restricted foraging ranges, will need to take account of the geographic variation.

Acknowledgements

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