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A COMPOSITE RECRUITMENT INDEX TO DESCRIBE INTERANNUAL CHANGES IN THE POPULATION STRUCTURE OF ANTARCTIC KRILL AT SOUTH GEORGIA

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Abstract

A composite recruitment index based on density data derived from acoustic surveys and on length-frequency data obtained from either target or station net hauls is described. This composite index is compared with an index where density and length data are derived from standard station net hauls only. Comparison of these indices showed substantial differences, due in part to bias arising from a large number of krill in just one of the station net hauls. Therefore, when the number of station net hauls is limited, bias is likely to be reduced if target net haul data can be included by using the composite recruitment index. This index is used to describe the population structure of krill around South Georgia during seven cruises between 1989 and 1998. Before 1994 the number of 1+ krill found around South Georgia was very low (proportion of 1+ krill <7%), while between 1994 and 1998 the number of 1+ krill found in the population increased with a very successful recruitment year due to krill spawned in 1994/95.

Résumé

Description d'un indice composite de recrutement fondé sur les données de densité dérivées de campagnes d'évaluation acoustique et sur les données de fréquence de longueurs obtenues à partir de chalutages ciblés ou effectués aux stations. L'indice composite est comparé à un indice pour lequel les données de densité et de longueurs sont dérivées uniquement de chalutages standard effectués aux stations. Cette comparaison met en évidence des différences importantes, dues en partie au biais provoqué par le grand nombre d'individus de krill dans l'un des chalutages effectués aux stations. Ainsi, lorsque le nombre de stations de chalutages est limité, le biais est susceptible d'être réduit si les données de chalutages ciblés peuvent être incluses en utilisant l'indice composite de recrutement. Cet indice sert à décrire la démographie du krill autour de la Géorgie du Sud lors de sept croisières menées entre 1989 et 1998. Avant 1994, le nombre d'individus de krill d'âge 1+ trouvés autour de la Géorgie du Sud était très faible (proportion de krill d'âge 1+ <7%), alors qu'entre 1994 et 1998, il a augmenté dans la population, et grâce au krill pondu en 1994/95, on a vu une année de recrutement particulièrement réussie.

Резюме

Рассматриваемый в статье комплексный индекс пополнения основан на данных по плотности, полученных по акустическим съемкам, и на данных по частотному распределению длин, полученных в результате целевого траления или траления по станциям. Проводится сравнение этого комплексного индекса с индексом, где данные по плотности и длине получены только в результате тралений по стандартным станциям. Сравнение выявило существенные различия, отчасти из-за смещения оценки, возникшего при большом улове криля только за одно траление на станции. Таким образом, когда число тралений на станциях ограничено, смещение можно уменьшить за счет включения данных целевых тралений, используя комплексный индекс пополнения. Этот индекс используется для описания структуры популяции криля около Южной Георгии во время 7 рейсов, проведенных с 1989 по 1998 г. До 1994 г. количество криля годового класса 1+ у Южной Георгии было очень низким (доля криля 1+ <7%), с 1994 по 1998 г. количество криля годового класса 1+ в популяции увеличилось в результате очень успешного пополнения криля за счет нереста 1994/95 г.

Resumen

Este trabajo presenta un índice compuesto del reclutamiento basado en los datos de densidad de las prospecciones acústicas y en los datos de frecuencia de tallas de arrastres dirigidos o de estaciones. A continuación se hace una comparación de este índice con uno para el cual los datos de densidad y tallas se estiman de los arrastres de estaciones solamente. Dicha comparación mostró grandes diferencias debidas en parte al sesgo producido por la gran cantidad de kril encontrado en una estación de arrastre en particular. Por lo tanto, cuando haya un limitado número de estaciones de arrastre, el sesgo se puede reducir incluyendo los datos de arrastres dirigidos utilizando el índice compuesto del reclutamiento. Este índice se utiliza para describir la estructura de la población de kril alrededor de Georgia del Sur durante siete campañas efectuadas entre 1989 y 1998. Antes de 1994 el número de kril de 1+ años alrededor de Georgia del Sur fue muy bajo (proporción de kril de edad 1+ <7%), mientras que entre 1994 y 1998 esta misma clase de edad aumentó en la población y alcanzó un año de reclutamiento muy bueno debido al kril desovado en 1994/95.

Keywords: *Euphausia superba*, population structure, recruitment, South Georgia, CCAMLR

INTRODUCTION

Information on krill abundance and population structure is required to understand the dynamics of krill populations and to provide data for input to management models (Butterworth et al., 1991). Descriptions of population parameters including krill density, proportional and absolute recruitment and biomass for the Antarctic Peninsula region have been presented in a series of papers by Siegel and coworkers (Siegel and Loeb, 1995; Siegel et al., 1997, 1998). For the South Georgia region estimates of krill biomass derived by acoustic techniques have recently become available (Brierley et al., 1999). In addition, qualitative descriptions of population structure have been obtained from krill eaten by predators at the western end of South Georgia (Reid et al., 1999) and some estimates of proportional recruitment index have been obtained from the commercial fishery (Kawaguchi et al., 1998). However, to date there has been no information on the year-to-year changes in population structure and recruitment indices derived from scientific cruises within the South Georgia region.

The data used by Siegel et al. (1998) have been obtained from large net sampling survey grids with frequently over 70 independent, non-targeted, station net hauls. Such net hauls are used to estimate length-density distributions which are standardised to the number of krill per length class per 1 000 m^3 water filtered. These length-density distributions are then used to calculate recruitment indices (de la Mare, 1994). In this paper I consider a series of British Antarctic Survey (BAS) cruises around South Georgia between 1989/90 and 1997/98. Since 1995/96 the BAS Core Programme has carried out systematic net hauls at up to eight stations within each of two boxes on the north side of South Georgia (Brierley et al., 1997; see also Figure 1). A number of additional net hauls aimed at acoustically detected targets were also carried out. In most cruises prior to 1995/96 there was no plan to sample krill at predefined stations to study population structure, and so samples of krill have been obtained from net hauls carried out for a variety of other purposes such as studying behaviour, validating acoustic transects and collecting live krill for experimental studies. To use such data to calculate recruitment indices requires firstly that the samples can be considered representative of the local population and secondly that representative krill length-density distributions can be derived. In comparison to the surveys carried out by Siegel et al. (1998), the number of station net hauls during the cruises described here is very restricted (Table 1). To be able to maximise the number of krill length-frequency distributions used in the analysis, and so increase the likelihood of obtaining a representative population structure (Watkins et al., 1986, 1990), it is deemed advantageous to include targeted net hauls even though such hauls cannot be considered as true random samples. However, valid net density estimates can only be calculated from station net hauls because targeted hauls, by their very nature, do not provide a measure of average krill density. In this paper I therefore first introduce a composite method to derive the length-density distributions. In this case the density of krill is derived from spatially more extensive concurrent acoustic survey data and this is then used to weight the length-frequency distributions obtained from net hauls. I then use this composite recruitment index to describe interannual changes in the population structure of *Euphausia superba* around South Georgia.

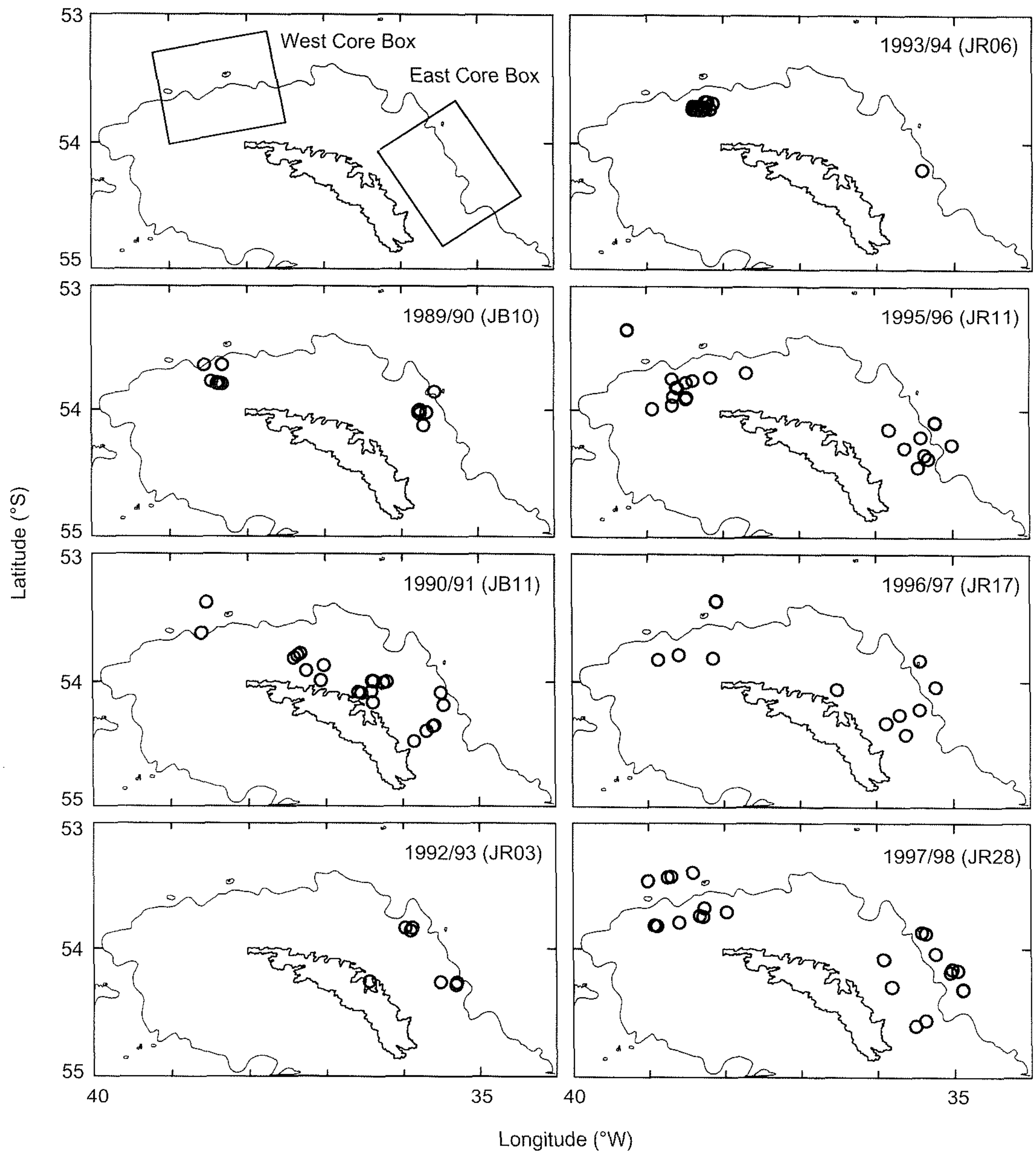

Figure 1: Location of net hauls undertaken in the South Georgia area during cruises between 1989/90 and 1997/98. The location of the British Antarctic Survey Core Programme survey boxes is shown at the top left. The bathymetric contour represents 1 000 m.

Table 1: Number of net hauls used for calculation of recruitment indices in each cruise. Mouth area for each type of net and the maximum number of individual nets within a haul are shown at bottom of table.

Cruise	RMT	FNET	MNET	VKSS	LHPR	RMT25	Total
JB10	10	1	0	6	0	0	17
JB11	20	1	0	0	0	0	21
JR03	1	0	5	0	0	0	6
JR06	0	9	1	0	0	5	15
JR11	18	2	1	0	2	0	23
JR17	10	2	1	0	0	0	13
JR28	19	4	0	0	0	0	23
Mouth area (m^2)	8	1	2	4	0.1	25	
Max. nets/haul	3	1	9	9	60	2	

MATERIALS AND METHODS

Length-frequency data for all cruises between 1981 and 1997 were summarised by Watkins et al. (1997), while those cruises which contained samples from both the eastern and western ends of South Georgia were selected for further analysis by Watkins et al. (in press). The data presented in those papers are used as the basis for the present analysis. The positions of net hauls used in the analysis are shown in Figure 1. Different nets were used at different times in different cruises (Table 1). In many cases a haul with a multiple net may have resulted in several discrete samples of krill. In such cases, or where more than 100 krill from a haul have been measured, these have been combined to provide a single-percentage frequency distribution for that haul. In contrast, where less than 100 krill per haul have been measured the numbers were left as raw numbers.

Here I consider two methods for obtaining acoustic estimates of krill density that can be used to transform the length-frequency data into length-density data. (i) In some cruises acoustic data were collected during each net haul and so it is possible to estimate the total quantity of krill in the water column during the entire net haul. This quantity of krill was used to weight the length-frequency distribution of krill for each haul. The resulting distribution will be referred to as an **acoustic-net** length-density distribution. (ii) Brierley et al. (1999) presented acoustic density estimates (as g m^{-2}) for cruises between 1981 and 1998. In many cases these density estimates are divided into separate estimates for the eastern and western survey areas carried out during the Core Programme (see Figure 1). Using the combined length-frequency distribution for all nets in an area I calculate the absolute number and weight of krill in each size class that contributes to the observed density. This distribution will be referred to as the **acoustically weighted** length-density distribution. The derivation of this latter distribution essentially assumes that the size of krill within a swarm is not related to the density of krill within the swarm, an assumption that is supported by the work of Ricketts et al. (1992). A comparison of these methods with the classical approach adopted by Siegel et al. (1998) has been carried out on data from cruise JR17 (1996/97).

The length-density data obtained from the combination of acoustic density and net length frequency were analysed using the programs LSMIX and MLMIX which generate an overall cruise length-density plot and derive the proportion of krill in each putative year class (de la Mare, 1994).

RESULTS

Comparison of JR17 Length-frequency Distributions Scaled by Acoustic and Net Density Estimates

For the 1996/97 JR17 cruise the **acoustically weighted** length-density distribution, the **acoustic-net** length-density distribution and the **net-weighted** length-density distribution are compared. In the **net-weighted** length-density distribution the length frequencies are weighted by the total number of krill per unit volume of water filtered in each net; this is the classic length-density distribution as described by de la Mare (1994) and used by Siegel et al. (1998). The composition of net hauls making up this test dataset is shown in Table 2. The length-density distributions derived by the three methods are different both in terms of the overall shape of the distributions and the proportional recruitment indices (Figure 2). The **net-weighted** length-density distribution (from nine net hauls; Figure 2a) is dominated by three net hauls; the haul with the highest density (E279; density >270 krill m^{-2}) contained mainly large krill (mean length 43 mm), while two other hauls (E177 and E257; densities of 135 and 60 krill m^{-2} respectively) contained small and large krill (mean length 27.5 and 49.2 mm respectively). All other net hauls contributed little to the overall density distribution with densities <2 krill m^{-2}. A quite different result is obtained if the net catches are weighted according to the acoustic biomass observed throughout the water column during the net haul (the **acoustic-net** length-density distribution; Figure 2b). In this case it is possible to incorporate the target net hauls and so the combined distribution is now made up from 13 net hauls. In this case the contribution of the net hauls is more even, with four nets having a density in the range of 100 to 350 krill m^{-2} and another five nets with densities in the range of 10 to 100 krill m^{-2}. The **acoustically weighted** length-density distribution (Figure 2c) is more similar to the **acoustic-net** length-density distribution (Kolmogorov–Smirnov $D_{max} = 0.06$, $p >> 0.05$) than either of these distributions are to the **net-weighted** length-density distribution ($K - S$ $D_{max} = 0.23$ and 0.19, $0.05 < p < 0.1$). The **acoustically weighted** distribution is weighted at two spatial scales. First, each survey region is

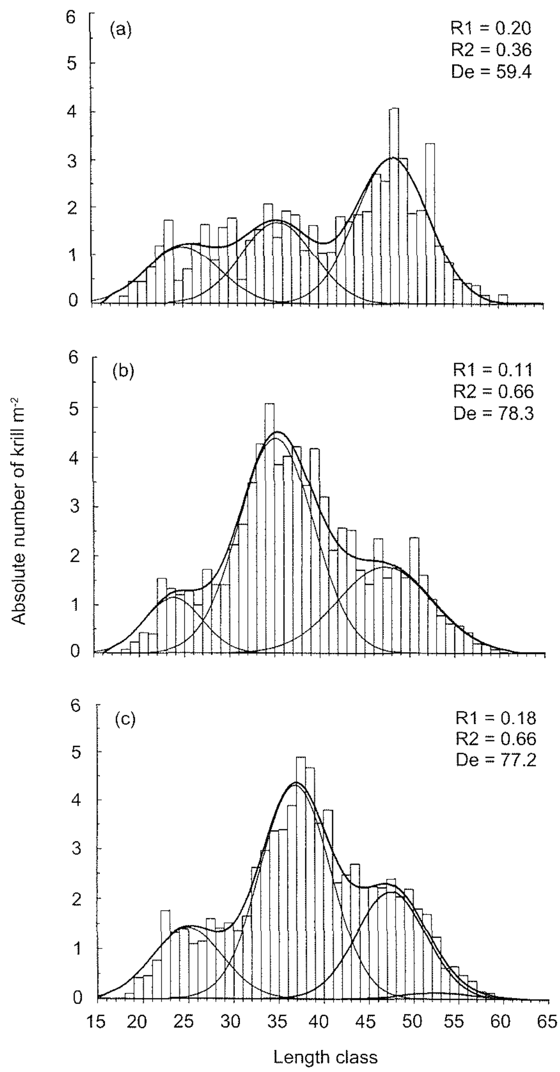

Figure 2: The observed length-density distribution (histogram), fitted length-density distribution (thick line) and the fitted year-class distributions (thin lines) for the JR17 (1996/97) test dataset where overall length density calculated as (a) **net-weighted** length-density (b) **acoustic-net** length-density and (c) **acoustically weighted** length-density distribution. R1 – calculated proportional recruitment index for year class 1+, R2 – calculated proportional recruitment index for year class 2+, De – overall density (krill m^{-2}).

Table 2: Description of net hauls used to compare JR17 length-density distributions.

Event No.	Net Type	Deployment Mode	No. Krill in Net	Net Weighted	Acoustically Weighted	Acoustic-net
E177	FNET	Station	702	Y	Y	East
E184	MNET	Station	1	Y	Y	East
E193	RMT	Station	111	Y	Y	East
E202	RMT	Station	45	Y	Y	East
E207	RMT	Target	>40 000	N	Y	East
E227	RMT	Station	12	Y	Y	East
E233	RMT	Station	8	Y	Y	East
E243	FNET	Target	525	N	Y	East
E244	RMT	Target	>5 000	N	Y	East
E257	RMT	Station	2 800	Y	Y	West
E279	RMT	Station	14 000	Y	Y	West
E288	RMT	Target	2 000	N	Y	West
E291	RMT	Station	7	Y	Y	West

weighted by the mean acoustic density. Second, within each region the nets are weighted to a certain degree by catch density within a haul. Thus, if less than 100 krill are caught then the weighting depends on the number of krill caught. Once more than 100 krill are caught all nets are treated equally. Because acoustic density estimates are not available for some of the net hauls in the earlier cruises, the **acoustically weighted** density distributions have been used in the comparisons presented in the rest of the paper.

After the length-frequency distributions within an area have been combined and weighted by the average krill density for each core box area derived from acoustic surveys (Brierley et al., 1999), the resulting area length-density distributions have been combined using the LSMIX and MLMIX analyses.

Recruitment Indices for Cruises between 1989/90 and 1997/98

Length-density plots for each cruise with the relative contributions of the different year classes are shown in Figure 3. The initial year-class limits used were based on values used by Siegel (1987) for populations of krill found in the Antarctic Peninsula and Weddell Sea areas. These values used four year classes with the mean size of 1+ krill occurring between 24 and 30 mm (Table 3). However, for the 1997/98 season it was necessary to increase the size limits of this 1+ group to 34 mm (Table 3). Subsequent inspection of the mean sizes of the year classes from the BAS Core Programme indicated that in several other cruises (JB11, JR03, JR06) the size of the 1+ group was constrained by the maximum permitted size (30 mm). Therefore all analyses were rerun using five year classes with a mean size for the 1+ krill between 24 and 33 mm (Table 3). The mean size and standard deviation for each year class in each cruise are shown in Table 4. Small 1+ krill were found in the 1995/96 and 1996/97 seasons, while large 1+ krill were found from 1990/91 to 1993/94. There was generally a good separation between the 1+ and 2+ krill sizes in any one year (with the exception of 1997/98), however when comparing between years there was sometimes little difference between the sizes in adjacent year classes (cf. 2+ in 1995/96 and 1+ in 1993/94). The resulting proportional recruitment index (R1) for each cruise is shown in Table 5. In the cruises prior to 1993/94 this R1 index was very low, R1 increased dramatically in 1995/96 and then fell for the final two cruises, however the values still remained from 2 to 20 times higher than those observed prior to 1994.

The proportional recruitment indices for year classes 1+ and 2+ have been related to the year of spawning to show which years might be considered as good or bad spawning years (Table 6). On the basis of the combined R1 and R2 indices the 1994/95 season stands out as a very good spawning year. Note that in other years in which the R2 index shows a high value (particularly 1988/89 and 1991/92) the R1 index shows poor recruitment. The proportional recruitment indices may be misleading in that high recruitment in a low biomass year is unlikely to result in significant numbers of juveniles recruiting into the adult population. To overcome this, the absolute density of krill in each year class and its proportion of the total density in that year are shown in Table 7. The 1994/95 season is once again identified as a good spawning year because large numbers of 1+ and 2+ krill (observed in 1995/96 and 1996/97 respectively) would have been spawned in this year. However, it is also apparent that several other years are also characterised by consistently high numbers of krill. Thus, for instance, the high numbers of 2+ krill in 1995/96, 3+ krill in 1996/97 and 4+ krill in 1997/98 imply that the 1993/94 season was a good spawning year. Similarly, the high value of 3+ krill in 1992/93 implies good spawning in 1989/90.

DISCUSSION

Problems of Growth and Effect of Methodology on Recruitment Indices

The recruitment index is dependent on the separation of krill into year classes. This is not an easy task and an inspection of Table 5 and Figure 3 reveals some of the problems. In 1995/96 (JR11) there was a large number of small, mainly juvenile krill assumed to be 1+ (nearly 70% of the population classified as 1+). This unimodal group was resolved into 1+ and 2+ krill with mean sizes of 26.4 and 34.0 mm respectively. In 1996/97 these 1+ krill had grown to form the large mode at 37 mm which is likely to represent 2+ krill, a much smaller peak of 1+ krill (mean size 25.4 mm) was also observed. By 1997/98 (JR28) the first peak of krill observed (1+ krill mean size 32.3 mm) was somewhat larger than the 1+ krill seen in the previous two years but the 2+ krill (mean size 34.2 mm) were small. It is, therefore,

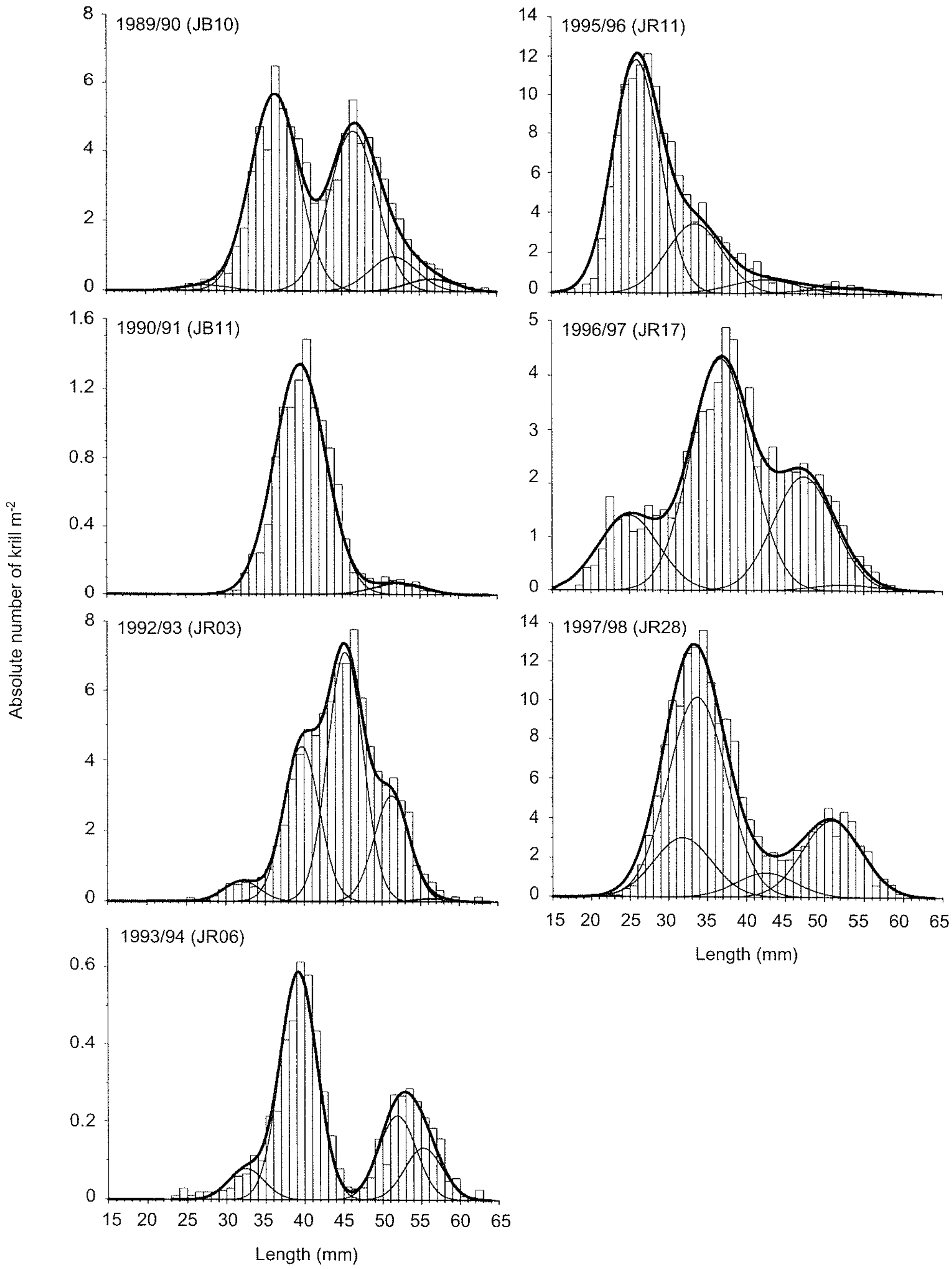

Figure 3: The observed length-density distribution (histogram), fitted length-density distribution (thick line) and the fitted year-class distributions (thin lines) for the cruises between 1989/90 and 1997/98 where overall length density is calculated as an **acoustically weighted** length-density distribution.

Table 3: Year-class boundaries used in LSMIX and MLMIX analyses.

Cruises	Year-class Boundaries (mm)				
	1+	2+	3+	4+	5+
JB10 – JR17	25–30	33–40	41–48	50–56	-
JR28	25–34	35–40	41–48	50–56	-
All cruises	24–33	33–43	43–49	49–53	53–57

Table 4: Mean size and standard deviation of year classes derived by LSMIX and MLMIX analyses.

Cruise (Year)	Mean Sizes (mm) ± SD				
	1+	2+	3+	4+	5+
JB10 (1989/90)	28.1 ± 3.02	36.9 ± 3.02	46.9 ± 3.02	52.1 ± 3.02	57.0 ± 3.02
JB11 (1990/91)	32.9 ± 3.29	40.1 ± 3.29	43.6 ± 3.29	52.9 ± 3.30	53.1 ± 3.30
JR03 (1992/93)	32.5 ± 2.26	40.2 ± 2.26	45.8 ± 2.26	51.7 ± 2.26	56.9 ± 2.26
JR06 (1993/94)	32.9 ± 2.29	39.7 ± 2.33	43.3 ± 2.35	52.4 ± 2.41	55.8 ± 2.43
JR11 (1995/96)	26.4 ± 3.00	34.0 ± 3.57	43.0 ± 4.25	52.9 ± 5.0	54.5 ± 5.12
JR17 (1996/97)	25.4 ± 3.86	37.3 ± 3.87	47.9 ± 3.88	53.0 ± 3.89	55.4 ± 3.88
JR28 (1997/98)	32.3 ± 3.75	34.2 ± 3.75	43.0 ± 3.75	51.4 ± 3.75	53.1 ± 3.75

Table 5: Proportional recruitment index R1 and standard error for all cruises.

Cruise	Cruise Year	R1	SE
JB10	1989/90	0.013	0.045
JB11	1990/91	0.007	0.338
JR03	1992/93	0.038	0.033
JR06	1993/94	0.075	0.458
JR11	1995/96	0.682	0.038
JR17	1996/97	0.179	0.049
JR28	1997/98	0.164	0.090

Table 6: Relative recruitment indices for animals in year classes 1+ and 2+ each year of spawning. For each year of spawning, R1 is calculated as the proportion of 1+ animals in the total population in the year after spawning, R2 as the proportion of 2+ animals in population of 2+ and older in the second year after spawning.

Year of Spawning	Relative Recruitment Index	
	R1	R2
1987/1988		0.49
1988/1989	0.01	0.95
1989/1990	0.00	
1990/1991		0.30
1991/1992	0.04	0.62
1992/1993	0.08	
1993/1994		0.75
1994/1995	0.68	0.66
1995/1996	0.18	0.66
1996/1997	0.16	

Table 7: Absolute density in krill m^{-2} (percentage of total density) of each year class in each cruise year (i.e. 1+ sampled in 1997/98 were spawned in the 1996/97 cruise year, 2+ sampled in 1997/98 were spawned in the 1995/96 cruise year).

Cruise Year	Year Class				
	1+	2+	3+	4+	5+
1989/90	1.2 (1.3)	43.1 (48.3)	34.8 (39.1)	7.3 (8.3)	2.6 (3.0)
1990/91	0.0 (0.0)	11.1 (94.8)	0.0 (0.0)	0.0 (0.0)	0.6 (5.1)
1991/92					
1992/93	3.3 (3.8)	24.9 (28.9)	40.4 (46.9)	17.0 (19.8)	0.5 (0.6)
1993/94	0.5 (7.5)	3.5 (57.5)	0.0 (0.0)	1.3 (21.6)	0.8 (13.4)
1994/95					
1995/96	89.2 (68.2)	31.1 (23.8)	7.2 (5.5)	3.3 (2.4)	0.1 (0.1)
1996/97	13.7 (17.7)	41.8 (53.9)	20.9 (26.9)	1.2 (1.5)	0.3 (0.0)
1997/98	28.3 (16.4)	95.5 (55.5)	11.7 (6.8)	36.6 (21.3)	0.0 (0.0)

difficult to know to which year classes these krill belong. The results of the modelling undertaken by Rosenberg et al. (1986) show that there is considerable overlap in the sizes of the different year classes. The growth rates and sizes of the year classes of krill sampled by Siegel (1987) at the Antarctic Peninsula tend to fall within the lower half of the growth range. However, krill that are sampled at South Georgia may have experienced very different growth conditions from those around the Antarctic Peninsula. Water temperatures are likely to be higher at South Georgia and this may result in higher growth rates with a corresponding increase in sizes for a given year class. Such additional factors provide an extra level of complication when deciding on the appropriate year classes.

The acoustically weighted recruitment index used here weights the krill length frequencies by the mean density in a specified area. For such a technique to work, it is important that the krill population structure within the area can be considered homogeneous. Analysis of the length-frequency distributions for individual net hauls along the north coast of South Georgia (Watkins et al., 1997 and in press) shows that this is frequently the case, especially within the area of the eastern core box. In the Antarctic Peninsula region there are considerable changes in population structure with large krill found offshore and small krill found on the shelf. Such separation of age classes has not generally been apparent in the regions sampled in this study. Note that in 1997/98, however, large krill were only found in offshore waters at the eastern end of the island. The calculation of recruitment indices from acoustic-net and net-weighted density distributions might be considered to be most comparable given the similar spatial and temporal scales over which the data are collected. However, the problems inherent in using these techniques for small numbers of net hauls have been illustrated in the comparison of JR17 data presented earlier.

Population Structure around South Georgia

The analysis of Watkins et al. (in press) revealed that there were differences in the population structure between the east and west ends of South Georgia. In a number of years small krill tended to dominate the distributions at the eastern end of the island, while in contrast large krill, when present, tended to occur at the western end of the island. In general, the combined distributions appeared to be dominated by one or two year classes and seem unlikely to represent a population composed of all year classes. In two seasons (1993/94 and 1997/98) a bimodal distribution was seen with no krill around 45 mm. Reid et al. (1999) observed that during most seasons there was a marked temporal change in the size of krill taken by land-based predators foraging in the vicinity of Bird Island (at the western end of South Georgia); this trend was particularly marked in the two years identified above. It is probable that the temporal variability observed in the Bird Island region is a result of the spatial variability of the population structure apparent during net sampling along the northern coast of South Georgia. Thus small krill occurring at the eastern end of the island early in the season are likely to be transported westward in the prevailing currents (Brandon et al., 1999).

Interannual Changes in Recruitment Indices

The relative recruitment index for 1+ animals (R1) shows a clear trend with very low recruitment (<0.04) until 1993/94. In contrast, since 1994 there has been stronger recruitment, with a very high value observed in 1994/95. A similar general pattern has been observed at the Antarctic Peninsula (Siegel et al., 1997). Whether such a change in recruitment is part of a subdecadal cycle or a more permanent shift cannot be deduced from the present dataset. However, high proportional recruitment was also seen in 1981/82 at South Georgia (Watkins et al., 1997), and high proportional and absolute recruitment were observed in this year at the Antarctic Peninsula (Siegel et al., 1997).

The relative recruitment index for 2+ animals (R2) shows much less variation than that for R1. Such a finding is consistent with observations at the Antarctic Peninsula (Siegel et al., 1997). However, in the South Georgia data there appears to be little relation between R1 and R2 (see for example R1 and R2 in 1988/89 and 1991/92). This is unexpected because if a particular year is a very successful spawning year, in contrast to others before and after, then R1 and R2 should be similar (as for example in 1994/95). There could be a number of reasons for such a discrepancy. The 1+ year class could be undersampled in some years, either because of changes in distribution or sampling techniques. Similarly, the larger year classes (3+ and 4+) may be under-represented for the same reasons or because they are eaten preferentially by predators (Reid et al., 1999).

However, it is unlikely that changes in sampling techniques are responsible since techniques have remained broadly similar from year to year and small krill (down to 18 mm) are well represented in several years; similarly, large krill (mean size ~54 mm) dominated catches in 1986 (Watkins et al., 1997). The patterns of distribution around South Georgia seem to be remarkably similar in a number of years. A more probable reason is that krill at South Georgia are likely to have originated from a spawning population located at the other side of the Scotia Sea. Therefore variability is likely to occur because of variation in the transport mechanism as well as the success of spawning. It is noteworthy that in the period before 1994 even in years where krill biomass was high (1989/90, 1992/93) there was little evidence of 1+ krill recruiting into the South Georgia population. While krill may travel across the Scotia Sea in less than six months (Hofmann et al., 1998; Murphy et al., 1998), it appears that high biomass years at South Georgia in 1989/90 and 1992/93 were driven by good spawning years two years previously in the Peninsula region; this therefore implies that krill may have taken two years to reach South Georgia. In contrast, the high recruitment of 1+ krill seen in 1995/96 at South Georgia can be related to very successful spawning at the Peninsula the previous year, implying a much more rapid transport.

The 2+ year class dominates the pelagic population sampled at South Georgia in five of the seven years sampled and the 3+ year class only formed a significant proportion of the population in three of the seven years. This is in contrast to the observations of Reid et al. (1999) where the 3+ year class dominates in predator samples. Such an effect is likely to be a combination of predator selection (Murphy and Reid, submitted) and the presence of samples from the eastern end of the island where large krill are less likely to be found (Watkins et al., in press). However, poor biomass years in 1990/91 and 1993/94 (Brierley et al., 1999) are characterised by a lack of 3+ krill, which confirms the findings of both Reid et al. (1999) and Murphy et al. (1998).

While both R1 and R2 indicate that 1994/95 was a good spawning year, the status of 1993/94 is less certain, because there is no datum for the R1 estimation. Although this was a poor year in terms of biomass surveyed around South Georgia, when we consider the absolute quantities of 2+, 3+ and 4+ krill that must have been spawned in this year, it implies that this was a good spawning year for the population that supplied the South Georgia area. However, according to Siegel et al. (1998), 1993/94 was a poor year in terms of absolute and relative recruitment at the Antarctic Peninsula. Thus it appears that there may be some inconsistencies between the year class structure observed in the Antarctic Peninsula and South Georgia. There is no recruitment data and little information available on the year-to-year variation in population structure in the Weddell Sea. However, it is possible that krill from that region are also transported into the South Georgia region (Mackintosh, 1973; Everson, 1976; Murphy et al., 1998; Watkins et al., in press).

CONCLUSIONS

The composite recruitment index described here maximises the number of net hauls that can be included in the analysis – this is a considerable advantage where relatively few hauls have been taken. However, the calculation of the recruitment index is still dependent on the ability to separate year classes consistently. Around South Georgia the interannual variation in year-class size is sufficient to make the consistent identification of year classes difficult. It is therefore important that more work be carried out on the variability in growth of krill arriving at South Georgia.

The analysis of the recruitment index shows that there is a general concordance in the recruitment patterns seen at South Georgia and at the Antarctic Peninsula. Some of the inconsistencies between these two areas may be due to the influence of krill from the Weddell Sea. To be able to determine the possible effect of this area it is vital that more data be collected on the population structure of krill from the Weddell Sea region.

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