Spatial variability of Antarctic krill in relation to mesoscale hydrography

P. N. Trathan[1], J. Priddle[1], J. L. Watkins[1], D. G. M. Miller[2], A. W. A. Murray[1]

[1]British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom
[2]Sea Fisheries Research Institute, Private Bag X2, 8012 Rogge Bay, South Africa

ABSTRACT: To examine the mesoscale distribution of Antarctic krill *Euphausia superba* Dana, length frequency and maturity stage data were subjected to multivariate analysis. The results showed that the population was heterogeneous with respect to size and maturity, with small immature krill found primarily inside the Bransfield Strait and large mature krill mainly north of the South Shetland Islands. Multivariate analysis of hydrographic data collected at the same stations revealed that the oceanography corresponded to previous classifications of the area, with Weddell Sea water in the southeast and east and South East Pacific water in the northwest. Further multivariate analysis using both krill variability and hydrographic data showed that a strong correlation existed between the krill distribution and the oceanography. Several hypotheses to explain the observed distribution of krill are discussed. It is judged that neither simple processes, such as growth during the sampling period, nor processes whereby krill are advected passively through the area by water movement, can completely explain the observed distribution. Instead, it is concluded that the observed gradient of krill size and maturity probably arises, at least in part, from an active ontogenetic migration.

INTRODUCTION

Recognition of the crucial importance of Antarctic krill *Euphausia superba* in the food web of the Southern Ocean, together with concerns over the possible impact of developing fisheries, has highlighted our ignorance regarding several aspects of the species' life history. It is only within the last decade that the complexity of the life-cycle of krill has been appreciated, yet the factors underlying their mesoscale distribution are still not fully understood (Miller & Hampton 1989). As such it is not known to what extent adult krill are passively carried by the prevailing currents, or to what degree their behaviour must also be taken into account. This problem is not new and some time ago was considered by Marr (1962) who examined the possible effects of vertical migration in relation to the prevailing ocean currents and concluded that such interactions could have a major effect upon the dispersion and distribution of Antarctic krill.

The interaction between passive advection and behavioural factors may be complex and will vary depending upon particular conditions. Priddle et al.

(1988) describe the interannual changes in krill abundance at key sites and attributed the large fluctuations to mesoscale hydrographic variation, thus leading to the suggestion that animals may act as passive tracers of the circum-Antarctic circulation. In contrast, several recent descriptions of krill aggregations (Kalinowski & Witek 1985) and breeding (Siegel 1988) suggest that behavioural factors are also very important and that krill are capable of altering their geographic position over spatial scales from hundreds of metres to hundreds of kilometres (Kanda et al. 1982). Watkins et al. (1986) studied krill swarms in a restricted area of the Bransfield Strait and found that the composition of individual swarms did not reflect random sampling of the local population. On a larger scale, Siegel (1988) proposed a pattern of ontogenetic migration in the vicinity of the Antarctic Peninsula, based on the spatial and temporal segregation of different life-cycle stages.

This paper addresses the relationship between a passive and a behaviourally moderated existence and seeks to examine the complexity which underlies the mesoscale dispersion and distribution of Antarctic krill. Mechanisms which may be involved in the mesoscale

distribution of krill and which are considered in this paper include: the advection of developmental stages by ocean currents; subdivision of the krill population into separate subpopulations; and active migration by different life-cycle stages. The first 2 of these factors require no active behavioural component from the krill and hence may be considered as passive mechanisms and therefore amongst the simpler explanations possible. Conversely, the latter hypothesis considers the distribution of krill in relation to an active behavioural element and is therefore more complex.

To explore these factors, data collected from the Bransfield Strait are examined. This area is known to

be one of the principal spawning and feeding grounds for Antarctic krill (Marr 1962) and in addition, is one where the physical oceanography has recently been re-examined (BIOMASS 1987). The present analysis takes data from one of the BIOMASS (Biological Investigation of Marine Antarctic Systems and Stocks) SIBEX (Second International BIOMASS Experiment) cruises undertaken in the Bransfield Strait and South East Pacific Ocean and relates the observed patterns of krill distribution to hydrographic variability.

HYDROGRAPHY OF STUDY SITE

The BIOMASS SIBEX research grid near the Antarctic Peninsula consisted of 53 standard stations (Fig. 1a) within the Bransfield Strait and the adjacent area of the South East Pacific Ocean (southern Drake Passage) (BIOMASS 1982). The hydrography of the area is complex, with input from the Pacific Ocean, the Weddell Sea and the Bellingshausen Sea (Clowes 1934, Heywood 1985, BIOMASS 1987, Stein 1988, Hunt et al. 1990). Analysis of the physical oceanographic observations from the SIBEX programme showed that the varying contributions of different water bodies to the area were likely to be dependent upon the effects of atmospheric forcing on an area southwest of the South Shetland Islands (BIOMASS 1987).

The SIBEX cruise of the RRS 'John Biscoe' started on 16 January and continued until 6 February 1985. During this period, the hydrographic structure was relatively well-defined (BIOMASS 1987). The outer stations lay mostly within South East Pacific Basin Water. Some of this water entered the Bransfield Strait at the southwestern end of the South Shetland Islands, around Smith and Low Islands, to flow along the South Shetland Islands shelf. Water from the Weddell Sea entered the Bransfield Strait around the tip of the Antarctic Peninsula and flowed southwestwards, and mixed with South East Pacific Basin Water near Brabant Island (Fig. 1). In the southwestern part of the study area, the influence of Bellingshausen Sea water could be identified (BIOMASS 1987). Thus the major hydrographic classification of the study area during the period could be summarised as follows: Weddell Sea water in the southeast and east, Pacific Ocean water in the northwest, with properties of the water
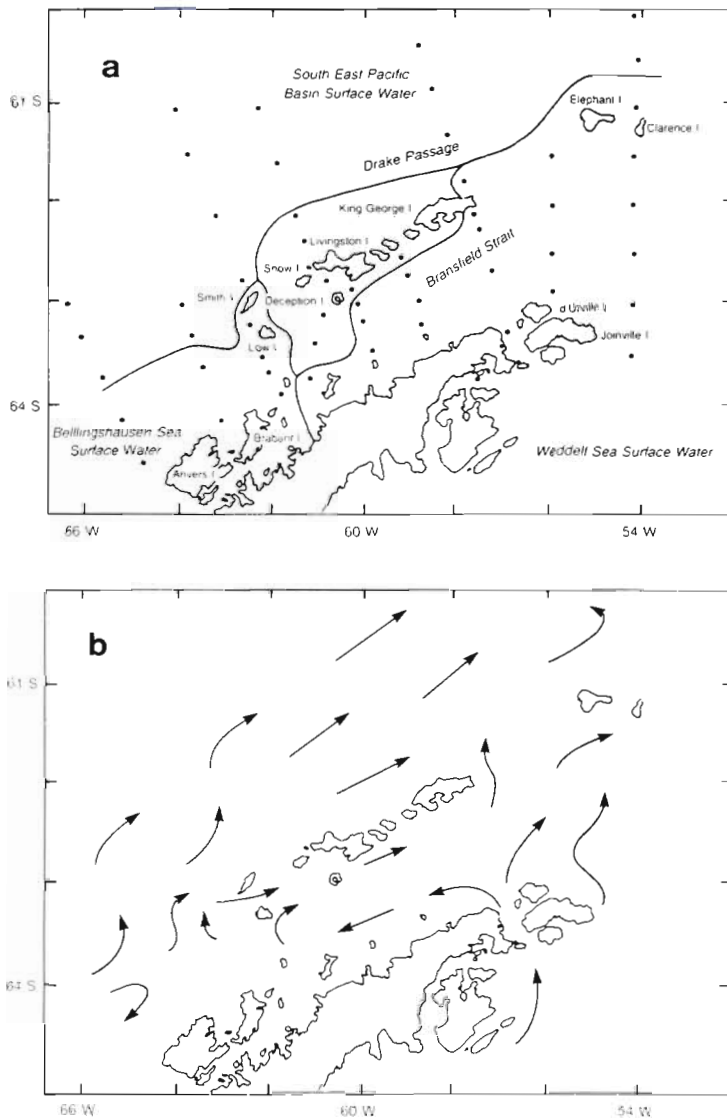

Fig. 1. (a) Map of the study area centred on the Bransfield Strait region of the Antarctic Peninsula. The 53 hydrographic stations in the SIBEX grid are shown as are the major watermass classifications from Hunt et al. (1990). (b) Major directions of water movement (based on geopotential topography from Heywood & Priddle 1987)

in the Bransfield Strait resulting primarily from a mixture of the 2 water types (BIOMASS 1987).

METHODS

The present analysis seeks to link krill characteristics and hydrographic variables for the majority of the hydrographic stations in the study area. The 2 sets of data were explored with a range of multivariate techniques prior to a single combined multivariate analysis using both sets of data.

Sampling. Data were collected from each of the 53 stations in the SIBEX grid. Each station was sampled for krill using a multiple rectangular midwater trawl with a mouth opening of 8 m^2 (RMT 1+8M; Roe & Shale 1979). Unless restricted by bathymetry, the RMT fished the depth range from 5 to 260 m with an oblique tow. A rectangular net with a mouth opening of 1 m^2 (FNET) was towed from a foredeck boom so as to fish at the surface in undisturbed water outside the ship's wake. Mesh sizes were 4.5 mm for the RMT and 5.0 mm for the FNET. The ship maintained a speed of 2.5 to 3.0 knots in order to optimise the mouth opening of the nets. The net trajectories passed through the position of the associated hydrographic station.

Vertical profiles of temperature and salinity were obtained at each station using a Neil Brown Mark 3 CTD. Water samples for nutrient analysis (nitrate, silicate and phosphate) were taken from standard depths using 2.5 dm^3 Niskin bottles on a General Oceanics rosette. Methods and analytical precision for these measurements are described by Heywood & Priddle (1987) and Whitehouse & Woodley (1987). Data from 3 standard depths (50, 100 and 150 m) have been used in this paper. Where the actual sample depth did not coincide exactly with the standard depth, linear interpolation was used to estimate a value. The depth of an interpolated value was never more than 10 m from an observed data point.

Measurements of krill variability. From each krill sample the lengths of up to 100 specimens were measured and rounded down to the nearest millimetre (Morris et al. 1988). The standard length measurement from the anterior margin of the eye to the tip of the telson (Morris et al. 1988) was used. Individual krill maturity stages were classified according to the scheme proposed by Makarov & Denys (1981), using the coding of Morris et al. (1988) and Watkins et al. (1992).

For the statistical analyses, individual krill were assigned to 5 mm length classes and to a grouped maturity stage classification as follows: juveniles (J); sub-adult males (MS1, MS2 and MS3); adult males (MA1 and MA2); immature females (FS and FA1); mature females without spermatophores (FA2); gravid

females (FA3 and FA4); and spent females (FA5). Very few specimens were unclassified for maturity stage and these were only included in those parts of the analysis where knowledge of maturity stage was not necessary.

For comparative purposes, all counts from the various length classes and maturity stage classes were transformed into percentage frequencies in order to avoid problems associated with variable fishing time and differences in the total number of krill sampled from each haul.

Statistical analyses. A range of multivariate techniques were used to analyse both the grouped krill data and the oceanographic data. All analyses were performed using GENSTAT 5.2.2 (Payne et al. 1989). A hierarchical cluster analysis was carried out on the grouped krill data. The clustering technique used was based on the similarity matrix derived from Euclidian distances. The clusters were subsequently formed using an agglomerative furthest-link method of clustering. A principal component analysis (PCA) of the grouped krill data was also carried out. The analysis used the correlation matrix derived from the grouped maturity stages and 5 mm length classes. A similar PCA for the oceanographic data was also carried out, using the correlation matrix derived from the hydrographic variables at the 3 standard depths. Finally, a canonical correlation analysis (CCA) was carried out using the station scores from both of the principal component analyses. The first 6 axes from each of the PCAs were used in the canonical correlation.

RESULTS

Krill variability analysis

The mean length of the krill population within the study area was 45.0 mm and was composed of 46.3 % females and 47.6 % males with 68.6 % adult, 25.5 % sub-adult and 5.9 % juvenile. It is evident from the cluster analysis that most stations displayed a high level of similarity since they all fell within a single group at the 85 % level of similarity (Fig. 2). At a higher level of similarity (87 %) stations separated into 2 large groups, apart from a single station (Stn 6) which remained separate.

Frequency plots of sex, length and maturity stage indicated that despite the high level of similarity, the 2 groups identified by the cluster analysis were different (Fig. 3). The first group (Group 1) comprised stations where the individuals tended to be immature and relatively short in length (mode 45 mm) (Fig. 3). The second group (Group 2) contained stations where the individuals were more mature and longer (mode
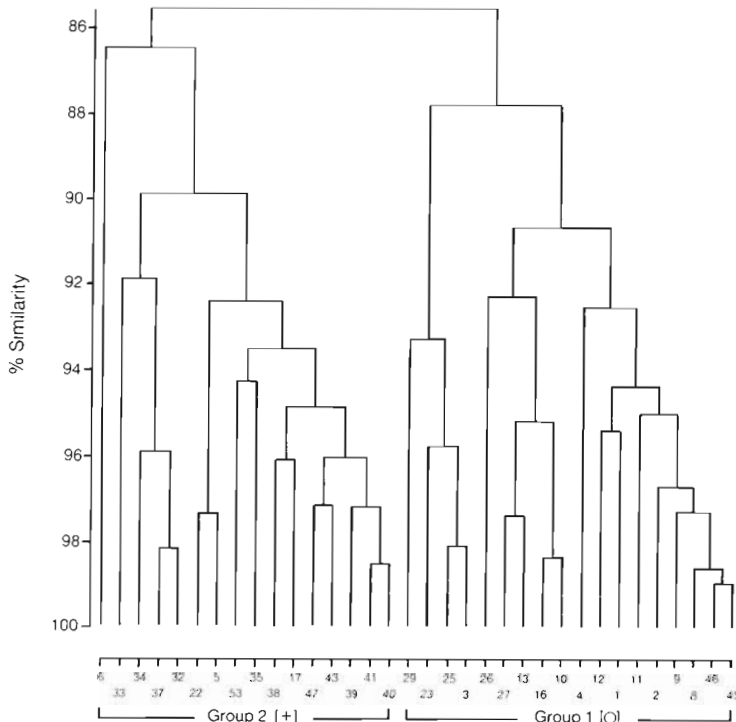
Fig. 2. Dendrogram from furthest-neighbour hierarchical cluster analysis of grouped krill data (Group 1 [O]; Group 2 [+]) for stations within the study area

50 mm). The mean length and standard error for the 1703 kril in Group 1 was 42.9 ± 1.0 mm whilst that for the 1056 krill in Group 2 was 48.5 ± 1.0 mm. The 2 groups were also different in terms of their sex ratios; the first group contained more males, whilst the second contained many more females. A map of the stations showing the 2 groups from the cluster analysis (Fig. 4) indicates that the 2 large groups generally lie within 2 regions of the study area. The first region comprises the Bransfield Strait and the area around the South Shetland Islands, whilst the second region comprises the deeper oceanic area of the Drake Passage. These 2 regions are essentially comparable with those reported by Siegel (1988, 1992) and BIOMASS (1991).

Two well-defined groups of krill are also clearly evident from the PCA of the grouped krill data (Fig. 5). This is not unexpected, however, due to the underlying similarity in the 2 methods. The PCA produced principal components where the first few axes each explained only a relatively small amount of the prevailing variation. The first 3 axes explained 15.9, 10.2 and 8.8 % respectively. Latent vector loadings indicated that the first axis was equally dominated by both maturity and size differences. This produced an ordination where stations with small juveniles and small sub-adults exhibited strong positive scores and stations with large mature individuals displayed strong

negative scores. Latent vector loadings for the second axis indicated that it was largely dominated by size differences and produced an ordination where stations with small animals had negative scores and stations with large animals had positive scores. The first and second axes each produced a separation of stations based upon the differences between the krill inside the Bransfield Strait and those north of the South Shetland Islands, although the station groups produced by each axis were somewhat different.

The plot of the first 2 axes from the PCA (Fig. 5) shows that although the station groups produced by the cluster analysis are well defined, they actually exhibit some degree of overlap. An index of the station score from the first PCA axis, dividing the stations into 3 almost equal-sized groups (Fig. 6a), indicates that this region of overlap occurs right across the study area, along the line of the South Shetland Islands. The general picture from the PCA, showing smaller krill inside the Bransfield Strait and larger krill outside the Strait, but with some degree of overlap, agrees well with the plot of krill mean length (Fig. 6b).

The high degree of similarity between stations suggests that there were no major differences in the krill present in the area. However, on the basis of multivariate techniques, the region could be sub-divided into 2 quite distinct assemblages of animals with an area of overlap between the 2 groups.

Hydrographic analysis

It is apparent from the hydrographic PCA that there was evident separation between the different water bodies in the study area. The separation agrees well with the hydrographic analysis of the full RRS 'John Biscoe' SIBEX data carried out by Hunt et al. (1990). The separation is clearly shown by labelling stations on the plot of the first and second PCA axes (Fig. 7) with the watermass classification of Hunt et al. (1990). Only stations considered to be unambiguous and typical of core Weddell Sea water, South East Pacific water and Bellingshausen Sea water are identified; intermediate stations are not labelled. Intermediate stations resulting from the mixing of water bodies tended to show as intermediate on the PCA plot. As a result of this mixing it was not possible to classify all stations or to identify clear boundaries to the water bodies, even though the water bodies themselves were quite distinct.

Latent vector loadings indicated that Axis 1 was largely determined by a positive association of salinity

GROUP 1 GROUP 2

Sex distribution

Length frequency

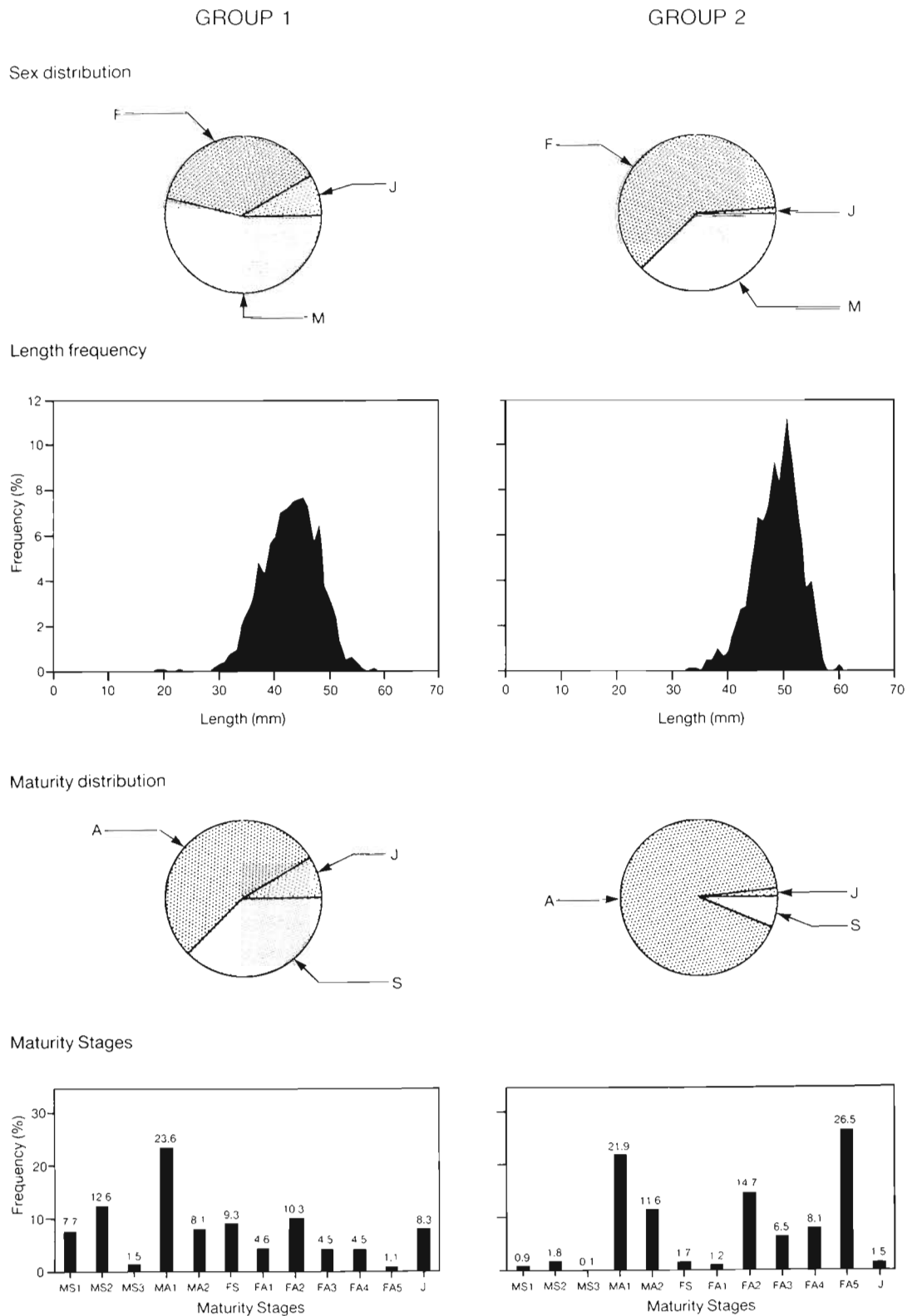Maturity distribution

Maturity Stages

Fig. 3. *Euphausia superba*. Frequency plots of sex, length and maturity stage of groups determined by the cluster analysis. A: Adults; S: sub-adults; J: juveniles; M: male; F: females; individual maturity stages follow Morris et al. 1988
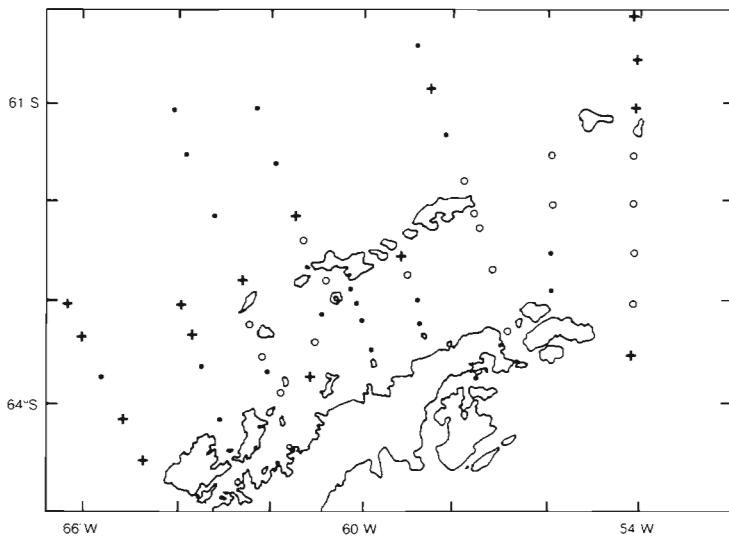
Fig. 4. Map of the study area with the groups determined by the cluster analysis also shown. (o) Group 1; (+) Group 2; (•) no krill or not clustered at 86 % level of similarity
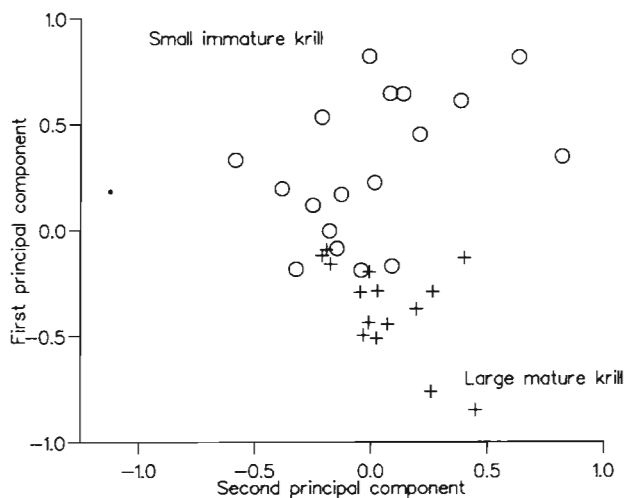

Fig. 5. Plot of the first and second axes from the krill variability PCA showing the groups determined by the cluster analysis. (O) Group 1; (+) Group 2; (•) not clustered at 86 % level of similarity (Stn 6)

Axis 2 tending to separate Weddell Sea water from the mixed water around the South Shetland Islands (represented by unlabelled points to the upper left of Fig. 7). Axis 2 is mainly determined by nitrate and phosphate, with Weddell Sea water having high phosphate (mean of 5 typical stations is 2.24 mmol m^{-3} at 100 m) and high nitrate levels (29.44 mmol m^{-3} at 100 m), whilst mixed water from around the South Shetland Islands has lower phosphate (2.17 mmol m^{-3} at 100 m) and lower nitrate levels (27.34 mmol m^{-3} at 100 m).

The first 3 axes from the PCA each explained a relatively large amount of the total variation; 41.5, 24.0 and 14.8 % respectively. Thus, even though the study area has been shown to be hydrographically complex (for example Stein 1988), the prevailing hydrography can essentially be characterised by a small number of axes which each explain a large amount of the variability. The most important of the components, Axis 1, primarily provides a summary of the prevailing hydrographic conditions across the study area. This axis effectively separates Weddell Sea water and the waters around the South Shetland Islands from South East Pacific and Bellingshausen Sea waters and in essence is comparable with the broad picture presented by BIOMASS (1987).

Synthesis of krill variability and hydrographic results

From the krill variability analysis it is apparent that there were distinct groups of krill in the study area, and that these were separated by an area of overlap. The hydrographic analysis also showed that the study area could be divided into separate regions and that these largely corresponded to the areas found by the krill variability analysis. A more formal correlation of the populations and the water bodies is provided by the CCA.

The first 6 axes of the krill variability PCA together explained 55 % of the total krill variation and the first 6 axes of the hydrographic PCA together explained 94 % of the total hydrographic variation. The CCA between these 2 sets of pseudo-variables produced strong correlations which also explained a large amount of the total variation (Table 1).

Although the study area contains a wide variety of hydrographic conditions, as shown by the hydrographic PCA, it is essentially an area where 2 major water bodies converge (Stein 1988). In addition, as
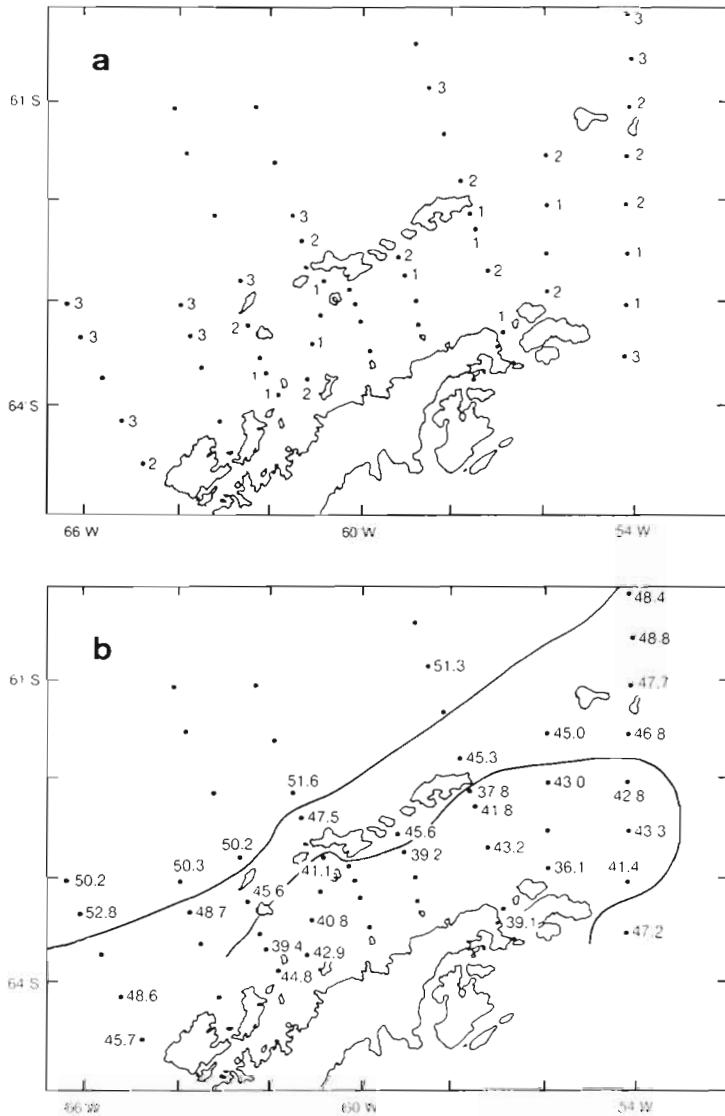
and silicate. From the PCA, Weddell Sea water is characterised by a high silicate content (mean of 5 typical stations is 86.82 mmol m^{-3} at 100 m) and a high salinity (34.44 psu at 100 m), while South East Pacific water is characterised by a lower silicate content (46.82 mmol m^{-3} at 100 m) and a lower salinity (34.05 psu at 100 m). These results accord well with the salinity and temperature description for the fuller SIBEX RRS 'John Biscoe' oceanographic analysis (Hunt et al. 1990).

The less important PCA axes reflected some of the complexity found within the Bransfield Strait, with

Fig. 6. (a) Index of the station scores from the first axis of the krill variability PCA. (1) Station score > +0.2; (2) +0.2 > station score > -0.2; (3) -0.2 > station score. (b) Mean length for krill measured at the hydrographic stations

DISCUSSION

The data from the RRS 'John Biscoe' provide a picture of distinct groups of krill which appear to occupy separate parts of the study area. The geographic ranges of the groups correspond well to the pattern of hydrographic variability, based both upon an objective oceanographic description of the study area and on a multivariate description. Finding such a marked correlation raises the fundamental question: How did the observed distribution originate? Essentially, we are faced with a number of plausible interpretations of the data and here we examine 4 possible alternatives. The various hypotheses are illustrated in Fig. 8.

In considering the 4 different hypotheses it must be remembered that the present study involves a single cruise which cannot provide answers to all of the questions. It does, however, provide sufficient information to examine many of the problems involved. One of the underlying assumptions used to differentiate between the 4 hypotheses is the expected distribution of krill in the Bransfield Strait. In appraising the various hypotheses the observed distribution of krill is used as a test against which the expected distributions generated by the 4 hypotheses are compared.

Hypothesis 1: Distribution generated by sampling sequence. The first hypothesis (Fig. 8a) considers that the observed distribution of krill may have been generated as an artefact of the sampling series employed by the RRS 'John Biscoe'. Krill growth rates are extremely variable, however, according to the review of Quetin et al. (1993), krill of length 42.9 mm, the mean size from Group 1, have a maximal growth rate of 0.05 mm d^{-1}. This suggests that krill in Group 1 would take in excess of 112 d to reach 48.5 mm, the mean size of krill in Group 2. As the cruise was completed in 21 d, which is significantly shorter than the calculated development time, it is unlikely that the distribution could have resulted simply from sequential station sampling.

Hypothesis 2: Distribution generated by advection of developmental stages. The second hypothesis (Fig. 8b) considers that the observed distribution may have been brought about by advection or physical transport of developmental stages within the study area. Further, that because krill continue to grow all the while, the differences between krill at any 2 points on the path should be related to the length of time that it takes

shown by the krill variability PCA, the study area can also be categorised into separate regions each with its own particular group of krill. It is therefore interesting to note the strong correlations between the krill variability data and the oceanographic variables, shown by the CCA. The CCA pseudo-variables are actually scores of PCA scores and it is therefore not particularly useful to attempt to interpret them; however, the high correlations and relative levels of variation explained by the pseudo-variables are of interest. These results suggest that there is a strong relationship between the hydrographic variability measured and the observed distribution of krill.
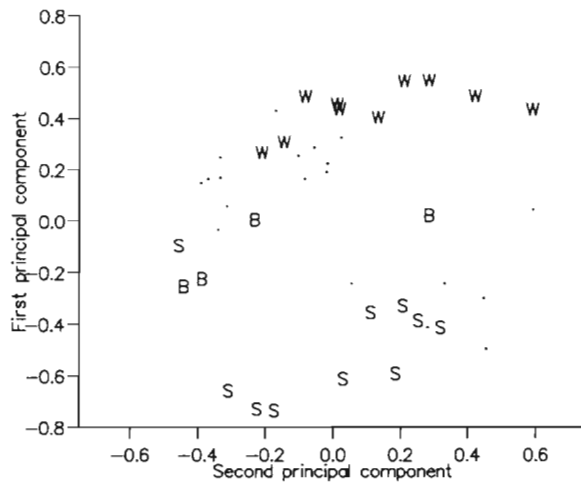
Fig. 7. Plot of the first and second axes from the hydrographic PCA with stations that are typical of a particular watermass also shown. S: South East Pacific water; W: Weddell Sea water; B: Bellingshausen Sea water. Watermass designations are based on conservative criteria following the classification by Hunt et al. (1990)

to move between those 2 points. Hence, this hypothesis requires that water currents in the study area should move at certain speeds and in directions which account for the size differences between the 2 groups.

Current velocities estimated for the region range from under 0.1 to 0.5 knots (4 to 20 km d^{-1}) (Stein 1988). Given the 112 d development interval identified above, these estimated current velocities could involve a transport distance of between 450 and 2500 km. Although the lower estimate is similar in size to the distance across the study region, the upper estimate is greatly in excess of it. Given our present knowledge of the complexity of the circulation in the vicinity of the Antarctic Peninsula, these estimates of distance may be entirely compatible with the hypothesis that a complex circulation and advection path could generate the observed distribution. However, 2 factors provide strong evidence against this explanation.

Firstly, the index of station scores from the PCA of the grouped krill data (Fig. 6a) shows a predominantly onshore-to-offshore gradient (southeast to northwest), as does the average length for krill (Fig. 6b). This does not agree well with the general pattern of water movement (Stein 1988), which might be expected to carry the majority of krill in the Bransfield Strait with the

current to the northeast, that is across the krill development gradient.

Secondly, the season during which krill develop and mature is unlikely to much exceed 112 d (Miller & Hampton 1989). It is questionable therefore, whether there would be sufficient time within a single season for Group 1 krill to mature into Group 2 krill and consequently these groups may represent different year classes. If so, then the difference between the 2 groups may be in excess of 112 d, so even with the lower estimates of current velocity it seems unlikely that the distribution could have arisen simply from advection within the depth range over which krill occur, even if a plausible trajectory could be found.

Hypothesis 3: Distribution generated by distinct populations. The Bransfield Strait is not the only spawning region for krill and groups may be transported in from other areas. This leads to the third hypothesis (Fig. 8c), which supposes that different populations, or stocks of krill, may occupy the 2 main water bodies in the study area and that this could have brought about the observed distribution. Hence, if the krill are simply carried along in the current, then groups of krill will remain separate so long as the currents also remain separate. Where the currents converge, groups of krill will be brought into close proximity and population differences will be more apparent. Thus, differences between populations should be very obvious especially over short distances and for a period of time, at least until mixing occurs.

The observed distribution could have arisen if small krill had entered the study area from the east and large krill from the west; the correlation with hydrographic variability certainly lends some credibility to this. The 112 d size difference between the 2 groups of krill identified above implies that there is a substantial divergence between the krill inside the Bransfield Strait and those outside, or at least that there exists a segregation of age groups, or of cohorts from separate spawning events (for example Miller & Hampton 1989, Siegel 1992). In spite of this, the gradient shown by the index of station scores from the PCA of grouped krill data (Fig. 6a) and the gradient of mean length (Fig. 6b) both extend throughout the region, and show little evidence of large differences over short distances. Obvious population differences may not be apparent however, due to mixing between the water bodies in the

Table 1. Canonical correlation analysis for the krill data and the hydrographic variables

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
Canonical correlation	0.92	0.58	0.57	0.33	0.24	0.02
Percent variation	34.77	21.75	21.27	12.39	9.07	0.74

region. Evidence of mixing is clearly provided by the hydrographic PCA presented above, as well as from previous studies (BIO-MASS 1987). However, given the directions of water movement reported for the region (Stein 1988), together with the distance that the gradients in krill variability extend (up to 350 km), it seems unlikely that the observed distribution could have been generated merely by distinct krill stocks existing in separate water bodies.

Hypothesis 4: Distribution generated by active migration. The final hypothesis supposes that the observed distribution represents active behaviour such that the distribution was determined by an ontogenetic migration of the type postulated by Siegel (1988) (Fig. 8d). Siegel (1988) suggests that at the onset of the spawning season gravid and spawning adults migrate from neritic areas to the continental slope and oceanic waters, sub-adult krill stay in the Bransfield Strait and close to the coast, whilst juvenile krill are limited to the coastal shelf waters. This theory requires that krill are capable of escaping from their planktonic mode and swimming large distances, with the natural consequence, that a gradient in size and maturity develops. This hypothesis also requires that the deeper waters of the Drake Passage are preferred as spawning grounds by mature individuals.

Krill have been reported to be able to swim at mean speeds of ca 15 cm s^{-1} for sustained periods (Kils 1979, Hamner 1984) even in the face of moderately high current speeds and over distances in the order of hundreds of kilometres (Kanda et al. 1982). Therefore to migrate from inside the Bransfield Strait, past the South Shetland Islands and into the Drake Passage (a distance of approximately 450 km) would take an individual swimming at 15 cm s^{-1} about 35 d. During the time interval for the present study (21 d), krill may have actually moved as much as 275 km as a result of active migration. Clearly the distances involved are not a limitation

Prior to migration, krill within the study area may include a number of different age groups and it is only the older more mature individuals which would be expected to migrate offshore, leaving the smaller more immature individuals to dominate in the Bransfield Strait (Siegel 1988). If ontogenetic migration is an important factor, then a spatial succession of krill sizes and maturity stages should be apparent. This succession should be obvious from shortly after the
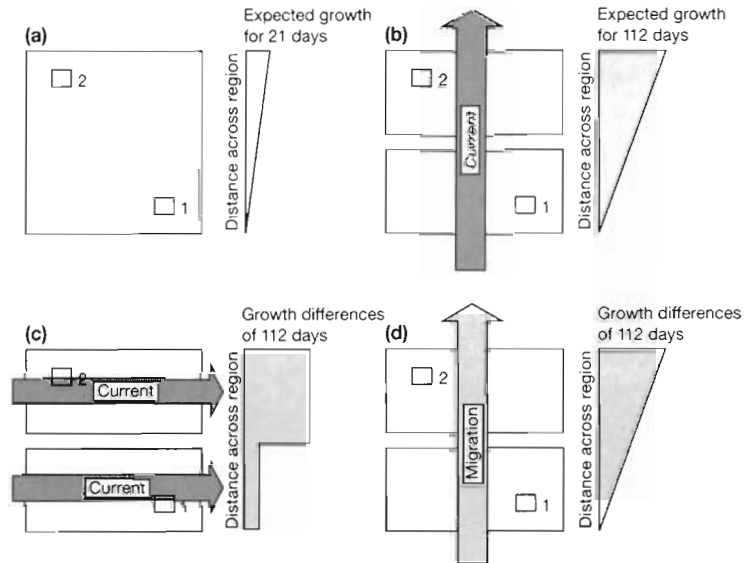

Fig. 8. (a) Hypothesis 1: a single uniform population exhibiting positive growth for 21 d. The early part of the cruise in the south (Stn 1) and the latter part of the cruise in the north (Stn 2) are indicated. The plot of expected growth (or length) vs distance north/south across the region is shown on the right. (b) Hypothesis 2: advection carrying the population for 112 d such that the expected growth differences between 2 sub-areas relates to the length of the advection path. The plot of expected growth (or length) vs distance (or time) along the advection path is shown on the right. (c) Hypothesis 3: 2 populations occupying 2 separate water masses each with a particular length frequency and maturity stage structure. The differences between the separate populations may produce an abrupt interruption in the plot of expected growth (or length) vs distance north/south across the region similar to that shown. (d) Hypothesis 4: a single population showing a breeding migration and forming separate sub-populations. The plot of expected growth differences (or length) vs distance north/south across the region is shown on the right

migration begins, until shortly before the majority of krill have finished migrating. Previous studies, over a number of years, have found a spatial succession in the Bransfield Strait (Siegel 1988, 1992, BIOMASS 1991). Similarly, in the present study, mean krill length shows a clear spatial succession (Fig. 6). This is strong evidence that a behavioural component is involved in producing the observed distribution. The strong correlations with hydrographic variability also adds weight to this hypothesis, if, as presumed, mature krill have a preference for a particular water type.

Summary

From the above discussion it is clearly difficult to entirely refute all of the proposed hypotheses. The strong correlations with hydrographic variability lead us to suggest that it is difficult to distinguish between 2 of the hypotheses (3 and 4 above). Hypothesis 3 pro-

poses that separate water bodies exist and that these contain separate krill populations, whilst Hypothesis 4 suggest that separate water bodies exist and that prior to spawning, adult krill have a preference for one water body and so migrate towards it. This implies that the observed distribution is closely associated with the oceanography of the area, regardless of whether it is generated by either a passive mechanism or an active process.

One reason that may contribute to our inability to refute the various hypotheses could be that the observed distribution is the result of a number of different processes acting in concert. Clearly the area has a complex hydrography and bathymetry and it would be naive to assume that advection paths would be so similar that all krill with a given start point would also have the same end point after a period of 112 d. Equally, growth could not be expected to be uniform over the whole region and must be related to the available food supply, the individuals' age, environmental temperature or other factors (for example see Quetin et al. 1993). Marr (1962) indicated that the underlying processes involved in the distribution of krill were complex and that processes operating at one scale, for instance vertical migration (e.g. Miller & Hampton 1989), may interact with processes acting at a different scale, for instance water movement, to produce a complicated pattern of distribution. Our results suggest that the interpretation of the observed mesoscale distribution of krill is complex, and that a large number of factors must be considered.

Taking into account the gradients found for krill size, the strong correlations with hydrographic variability and the general direction of water movement in the region (Stein 1988), we suggest that active migration is likely to contribute to the formation of the observed distribution. That krill are able to migrate such large distances implies that a gradient exists which they can follow. This gradient may be regular and continuous, or patchy and discrete; whichever, it must lead the mature krill to the deeper waters of the Drake Passage away from the richer feeding grounds of the Bransfied Strait (Huntley et al. 1991). Water depth is one gradient that krill could follow and the observation that mature krill have been found over the deep central basin of the Bransfield Strait (Siegel 1988) lends some support to this.

Whatever the environmental gradient that krill follow, it is as yet unclear how (or whether) krill return to the Bransfield Strait in order that they may migrate again the following season. Certainly eggs and early planktonic stages could not migrate against the prevailing circulation pattern yet they somehow get into the shallow coastal waters of the Bransfield Strait.

LITERATURE CITED

BIOMASS (1982). Technical Group on Programme Implementation and Coordination. BIOMASS Rep. Ser. 29: 1–28

BIOMASS (1987). SIBEX Physical Oceanography Workshop, Cambridge, UK, 9–27 March 1987. BIOMASS Rep. Ser 62: 1–38

BIOMASS (1991). Non-acoustic krill data analysis workshop, Cambridge, UK, 29 May–5 June 1991. BIOMASS Rep. Ser. 66: 1–16

Clowes, A. J. (1934). Hydrology of the Bransfield Strait. 'Discovery' Rep. 9: 1–64

Hamner, W. M. (1984). Aspects of schooling of *Euphausia superba*. J. crust. Biol. 4: 67–74

Heywood, R. B. (1985). Environmental conditions in the Antarctic Peninsula area of the Southern Ocean during the Anglo-German Joint Biological Expedition, February 1982. Meeresforsch. 30: 220–239

Heywood, R. B., Priddle, J. (1987). Retention of phytoplankton by an eddy. Cont. Shelf Res. 7: 937–955

Hunt, G. L., Heinemann, D., Veit, R. R., Heywood, R. B., Everson, I. (1990). The distribution, abundance and community structure of marine birds in southern Drake Passage and Bransfield Strait, Antarctica. Cont. Shelf Res. 10: 243–257

Huntley, M., Karl, D. M., Niiler, P., Holm-Hansen, O. (1991). Research on Antarctic Coastal Ecosystem Rates (RACER): an interdisciplinary field experiment. Deep Sea Res. 38: 911–940

Kalinowski, J., Witek, Z. (1985). Scheme for classifying aggregations of Antarctic krill. BIOMASS Handbook 27. SCAR (Scientific Committee on Antarctic Research), Cambridge

Kanda, K., Takagi, K., Seki, Y. (1982). Movement of the larger swarms of Antarctic krill *Euphausia superba* population off Enderby Land during 1976–1977 season. J. Tokyo Univ. Fish. 68: 25–42

Kils, U. (1979). Swimming speed and escape capacity of Antarctic krill, *Euphausia superba*. Meeresforsch. 27: 264–266

Makarov, R. R., Denys, C. J. (1981). Stages in sexual maturity of *Euphausia superba* Dana. BIOMASS Handbook 11. SCAR (Scientific Committee on Antarctic Research), Cambridge

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

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

Morris, D. J., Watkins, J. L., Ricketts, C., Buchholz, F., Priddle, J. (1988). An assessment of the merits of length and weight measurements of Antarctic krill *Euphausia superba*. Br. Antarct. Surv. Bull. 79: 27–50

Payne, R. W., Lane, P. W., Ainsley, A. E., Bicknell, K. E.,

Digby, P. G. N., Harding, S. A., Leech, P. K., Simpson, H. R., Todd, A. D., Verrier, P. J., White, R. P., Gower, J. C., Tunnicliffe Wilson, G. (1989). GENSTAT 5 Reference Manual. Clarendon Press, Oxford

Priddle, J., Croxall, J. P., Everson, I., Heywood, R. B., Murphy, E. J., Prince, P. A., Sear, C. B. (1988). Large-scale fluctuations in distribution and abundance of krill – a discussion of possible causes. In: Sahrhage, D. (ed.) Antarctic Ocean and resources variability. Springer-Verlag, Berlin, p. 169–182

Quetin, L. B., Ross, R. M., Clarke, A. (1993). Krill energetics: seasonal and environmental aspects of the physiology of *Euphausia superba*. In: El-Sayed, S. Z. (ed.) Southern Ocean ecology – the BIOMASS perspective. Cambridge Univ. Press, Cambridge, p. 165–184

Roe, H. S. J., Shale, D. M. (1979). A new multiple rectangular midwater trawl (RMT1+8M) and some modification to the Institute of Oceanographic Sciences' RMT1+8. Mar. Biol. 50: 283–288

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

Siegel, V. (1992). Assessment of the krill (*Euphausia superba*) spawning stock off the Antarctic Peninsula. Arch. Fisch-Wiss. 41: 101–130

Stein, M. (1988). Variation of geostrophic circulation off the Antarctic Peninsula and in the south-west Scotia Sea, 1975–1985. In: Sahrhage, D. (ed.) Antarctic Ocean and resources variability. Springer-Verlag, Berlin, p. 81–91

Watkins, J. L., Buchholz, F., Priddle, J., Morris, D. J., Ricketts, C. (1992). Variation in reproductive status of Antarctic krill swarms; evidence for a size-related sorting mechanism? Mar. Ecol. Prog. Ser. 82: 163–174

Watkins, J. L., Morris, D. J., Ricketts, C., Priddle, J (1986). Differences between swarms of Antarctic krill and some implications for sampling krill populations. Mar. Biol. 93: 137–146

Whitehouse, M. J., Woodley, V. R. (1987). Automated seawater nutrient analysis. British Antarctic Survey, Cambridge

This article was submitted to the editor