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Mesoscale variability in the distribution of krill *Euphausia superba*

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ABSTRACT: Pairs of parallel transects one to the south and the other to east of King George Island (South Shetland Islands) were surveyed in sequence 8 times to determine whether there was any consistency in the pattern of krill distribution and abundance along and between the transects. Vertical migration to the surface at night took krill out of the acoustically sampled layer and caused underestimation of abundance. Krill patches were carried passively along the transects in the main current. There was no evidence for krill becoming concentrated in a large eddy at the eastern end of the area.

INTRODUCTION

Interest in the living resources of the Southern Ocean has increased in recent years due to the establishment of a fishery based on Antarctic krill *Euphausia superba*. Concern has been expressed because krill are at the centre of the Southern Ocean food web, and over-exploitation could have drastic effects on dependent species (Laws 1985). Considerable interest has therefore focused on estimating the abundance and productivity of krill. Abundance over large areas has been estimated using hydroacoustics (BIOMASS 1985), but surveys of this type provide only a single point estimate even though they may take several days or weeks to complete. The purpose of this study was to determine to what extent krill distribution patterns were consistent in a region over a short period of time and how distribution was related to water movement in the area.

MATERIALS AND METHODS

The site chosen for the study was off the south-eastern corner of King George Island, South Shetland Islands (Fig. 1) in an area where an eddy had been detected on a previous study (Heywood 1985) and krill had been recorded during the preceding fortnight. The initial stage of the study was an oceanographic survey of the area to detect water movement, identify water type and quantify chlorophyll and primary production (Heywood & Priddle in press).

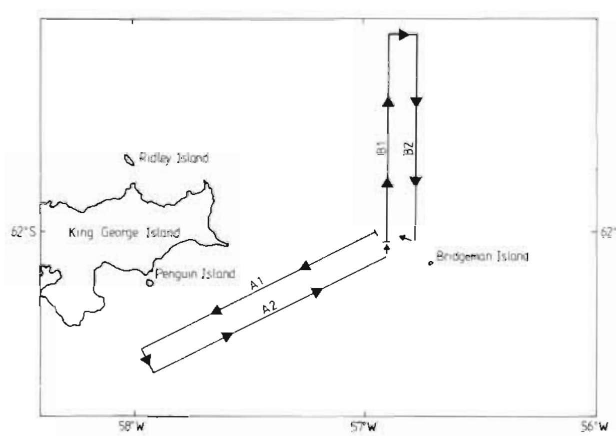

Fig. 1. Location of the 4 study transects

Four transects were chosen and designated A1, A2, B1 and B2. Transects A1 and A2 were 40 n mile long, parallel, 3 n mile apart, and ran along the lines of water flow as determined during the initial survey. A1 ran more or less along the shelf break while A2 was totally in deep water. Transects B1 and B2 were 25 n mile long, parallel and 3 n mile apart, and ran north/south across an eddy identified during the initial survey.

The transects were surveyed in sequence A1, A2, B1, B2, at a nominal and constant speed of 10 kn 8 times during a 5 d period commencing on 11 Feb 1985. One complete pass along all 4 transects was estimated to take 15 h, which, providing the vessel maintained

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speed, would mean that each transect would be surveyed at a different time of day on each pass.

Krill were detected and quantified using a SIMRAD EK400 echosounder. The instrument settings were as follows:

Operating frequency	120 kHz
Source level	115.2 dB
Pulse duration	1 ms
Voltage response	0 dB
Calibration constant 'C'	−47.0 dB
Range	0 to 250 m

The echosounder was interfaced to a SIMRAD QD digital integrator with the 8 surface-referenced layers set to 5 to 15, 15 to 35, 35 to 55, 55 to 75, 75 to 95, 95 to 110, 110 to 145 and 145 to 195 m. The hull-mounted transducer was at 5 m depth, hence the true depth of the layers was 10 to 20, 20 to 40 m etc. The mean echolevel was recorded as the acoustic parameter Mean Volume Backscattering Strength (MVBS). Data were recorded onto a microcomputer at 1 n mile intervals.

Aimed net hauls were made at krill swarms using an Institute of Oceanographic Sciences (IOS) pattern 8 m^2 Multiple Rectangular Midwater Trawl (RMT8M) (Roe & Shale 1979). Krill size frequency distributions from these net hauls were used to determine target strength (TS) using the target strength-to-size relations derived by BIOMASS (1985). MVBS values were converted to density using the derived TS value.

A Magnavox satellite navigator was used to provide position fixes at irregular time intervals and continuous dead reckoning position estimates in between.

Data were analysed on Honeywell mainframe computer using the statistical package GENSTAT.

RESULTS

Physical environment

The physical oceanography survey (Heywood & Priddle in press) confirmed the anticipated pattern of water movement in the region. To the south of King George Island along Transects A1 and A2 the flow was parallel to the coast whereas along Transects B1 and B2 it formed into a wide meander between King George and Elephant Islands. The rate of flow along Transects A1 and A2 was so strong that, because they were surveyed in opposite directions, it caused major differences in the distances the ship travelled through the water along these transects even though they were of the same nominal length. Differences between satellite fixes and dead reckoning estimates of position at the time of the fix provide estimates of the resultant vector of wind speed and current acting on the ship. The effect of the wind is dependent on the ship's heading relative to the wind direction and velocity. The effect of these factors is impossible to resolve with the dataset available. However, at the speed of the survey (10 kn) the ship's master considered that the wind would have a much smaller effect than the current on the ship (Capt. C. R. Elliott pers. comm.). No definitive data are, however, available to confirm this observation. The differences between satellite fixes and dead reckoning positions have therefore been used to provide rough estimates of the velocity of the surface current. These have been plotted (Fig. 2) and summarised in Table 1 for all pairs of fixes obtained between the start and end time of each pass along each transect, i.e. only pairs of fixes where the ship was sailing at constant speed in the same direction have been used.

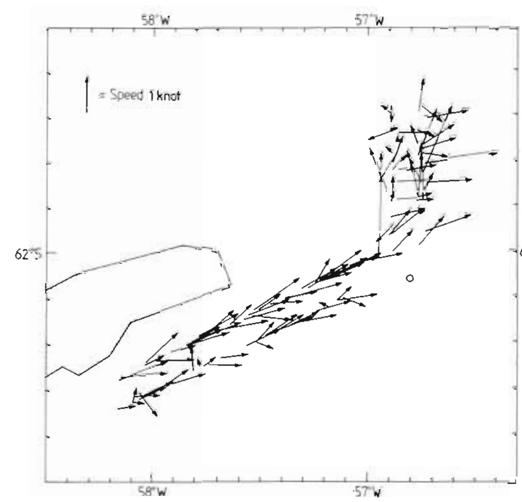


Fig. 2. Estimated surface current speed based on analysis of ship's set and drift information

Table 1. Mean speed and direction of surface current estimated from differences between satellite fixes and dead reckoning. Mean direction and standard deviation (SD): calculated according to formula recommended by Batschelet (1981)

Transect	Mean speed (kn) ± SD	Mean direction (degrees)	SD
A1	1.31 ± 0.27	67	1.8
A2	0.87 ± 0.28	68	4.4
B1	0.75 ± 0.31	38	7.0
B2	0.96 ± 0.50	43	5.4

With a nominal transect length of 40 n mile a single patch of krill would, if carried passively, remain on the transect for about 30 h and thus only be present for, at

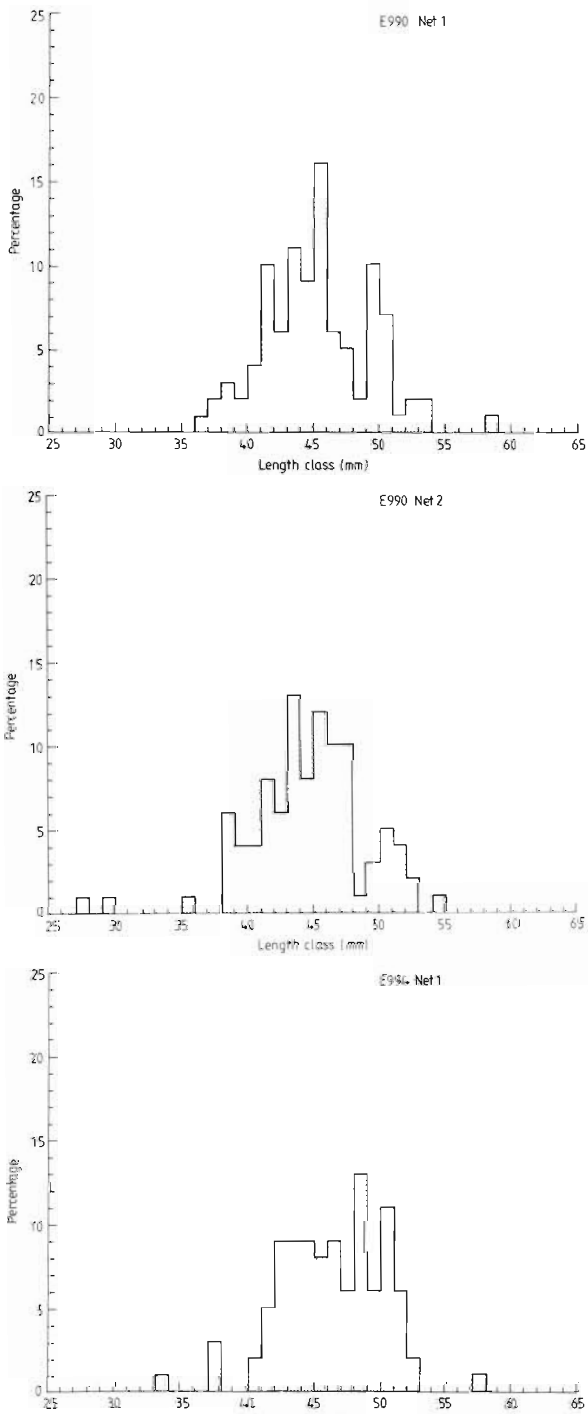


Fig. 3. Size frequency distributions of krill caught in the region. n = 100 for each sample

the most, 3 passes. The eddy across which the 'B' transects were sited means that the residence time of a patch in the area might be longer but there is less likelihood of the patch being present on only one of the transects.

Krill catches

Aimed net hauls were made on krill swarms detected close to the transects at the end of the survey phase. Three samples of krill were obtained whose size frequency distributions are shown in Fig. 3. The size frequency distribution has been used to estimate the target strength (TS, dB) of krill using the formula:

$$TS = 20 \log(\text{length}) - 97.2 \quad \text{(BIOMASS 1985)}$$

where length = total length in mm. A mean TS weighted by the frequencies in the krill size frequency distribution was used. This gave a mean TS of −62.7 dB.

The characteristics (size, sex, maturity stage) of krill caught were essentially the same as those reported by other workers in the region (e.g. Siegel 1982, 1986, Wolnomiejski et al. 1982) suggesting that the situation in the area was not abnormal.

Acoustic data

Eight passes were made along each transect as originally planned. Delays due to inclement weather, temporary equipment failure and a detour to investigate a floating lifejacket meant that the planned 24 h coverage for each transect was not achieved. The pattern of coverage is indicated in Fig. 4.

All MVBS values above threshold were checked against the appropriate point on the echo chart to confirm that they could be reasonably attributed to krill swarms. No swarms were detected in the 2 deepest surface-referenced layers (VII & VIII) and these have been excluded from the subsequent analyses. Layer I, the near-surface layer, frequently had a high MVBS which could be attributed either to krill swarms or to surface aeration. In moderate weather conditions surface aeration did not cause spurious echoes above the threshold, however when the windspeed was greater than Beaufort 5 spurious echotraces were produced which erroneously elevated the MVBS levels. Most of the transects were surveyed in weather of Beaufort 5 or greater and consequently data from the surface layer

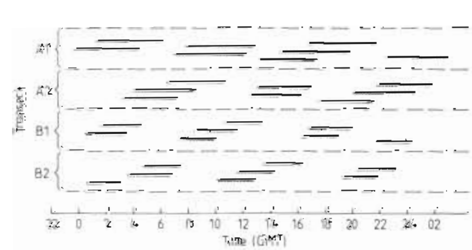


Fig. 4. Daily coverage of sampling along the transects. Horizontal lines: single passes along a transect. Shaded areas: times of day when some sampling took place along a transect

are unreliable and have not been used in these analyses.

The mean density at each reset for each pass along each transect is shown in Fig. 5. The data have been arranged so that all 'A' transects go from west to east across the page (the sequence in Transect A1 has therefore been reversed) and the 'B' transects go from south to north across the page (Transect B2 reversed). The arrows link the positions at which a freely drifting particle at any depth might be found assuming water movement along the transects at speeds indicated in Fig. 2 and Table 1.

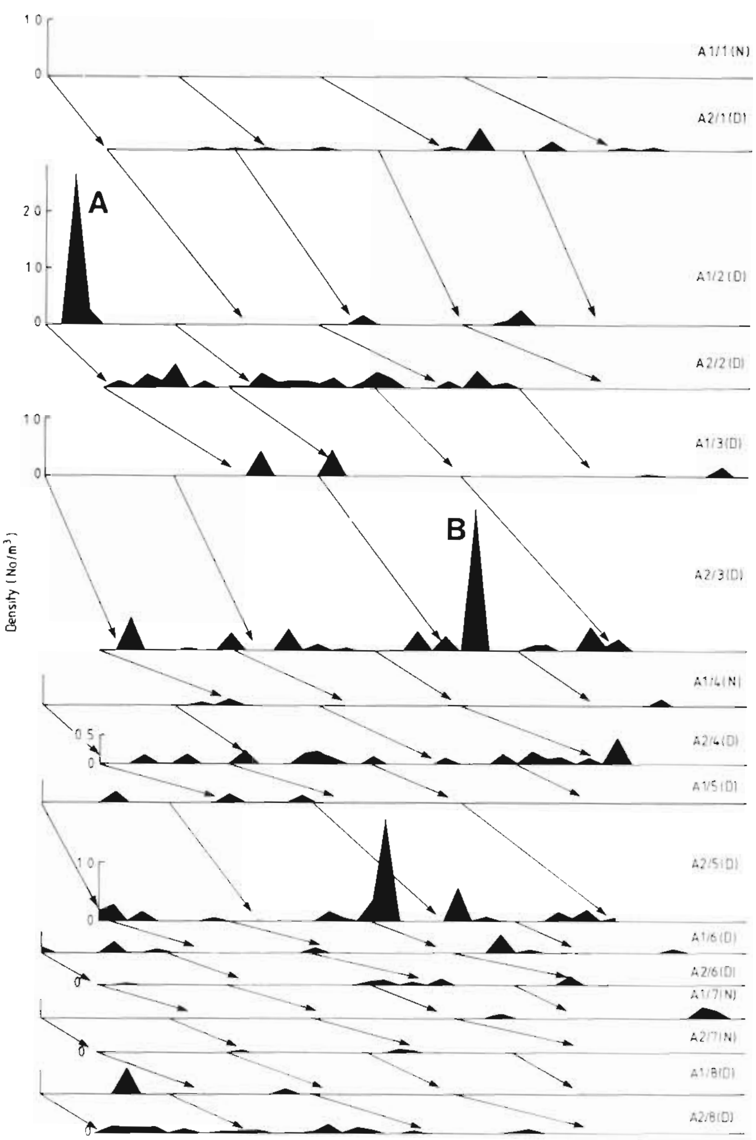
Data analysis

The design of this study has permitted analysis of the data on several spatial and temporal scales. These range from the coarsest scale, where data from the pairs of transects are grouped (e.g. A1 & A2) and mean densities for each pass are compared, to the finest scale, where individual mile resets are compared.

Gross comparison of Transects 'A' and 'B'

During the study the hours of darkness were approximately from midnight GMT until 0600 hr GMT. These times have been used to give a broad division of the data into day and night values. Differences between days and transects were explored using a 2-way analysis of variance on log-transformed densities. There were statistically significant differences between both time of day and transects (F test, $p < 0.01$).

Mean krill density on each of the transects during night and day periods is shown in Table 2. In each case the mean night-time density is less than that during daytime.



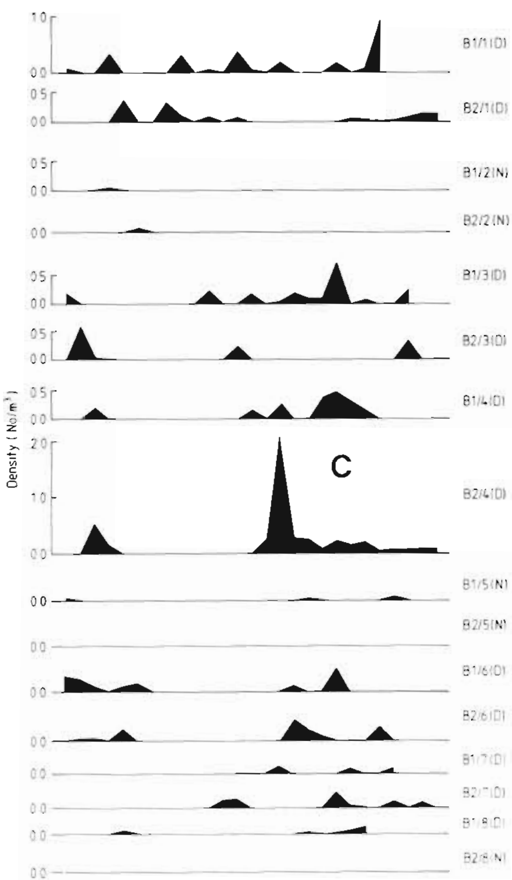


Fig. 5. Mean abundance along each transect (left: Transects A1 and A2; right: Transects B1 and B2) for each pass (1 to 8). A, B, C identify density peaks (see p. 59). D: transect surveyed mostly during daylight; N: mostly at night

Table 2. Mean densities of krill (ind 1000m^{-3}, untransformed, for each mile) along the pairs of transects SE: standard error

Transects	Time of day					
	Day			Night		
	Mean	N	SE	Mean	N	SE
A1	28.9	260	11.0	6.9	109	1.5
A2	62.8	262	12.9	22.4	42	8.7
B1	55.3	140	10.7	9.3	51	2.8
B2	53.2	163	13.9	1.7	29	0.3

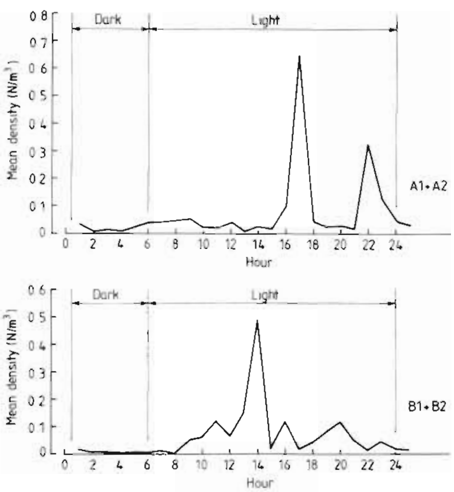


Fig. 6. Mean density values at different times of day

Density estimates for each hour of the day have been plotted for the combined data from A1 and A2 in Fig. 6 (upper) and B1 and B2 in Fig. 6 (lower). The majority of values are low, generally less than 0.1 krill m^{-3} The greatest variation and the highest values were present during daylight. The timing of the peak daytime values was not coincident suggesting that they are not related to time of day. The consistently low night-time values may be due to migration out of the sampled layers or an apparent change in density due to variation in TS with time of day (Everson 1982).

Mean values of krill depth and density from each reset have been calculated for each transect summing over all passes. On the A transects (Fig. 7A) there was no clearly discernible pattern in depth distribution, the mean depth fluctuating from 40 to 60 m. Depth distribution on Transects B1 and B2 indicates a marked diurnal pattern with krill nearer to the surface by night (Fig. 7B). On these transects the bulk of the krill were probably in the depth range 0 to 20 m from the surface at night. The layer from 0 to 10 m could not be sampled with the hull mounted transducer while the 10 to 20 m layer has been excluded due to the problem of surface aeration described above.

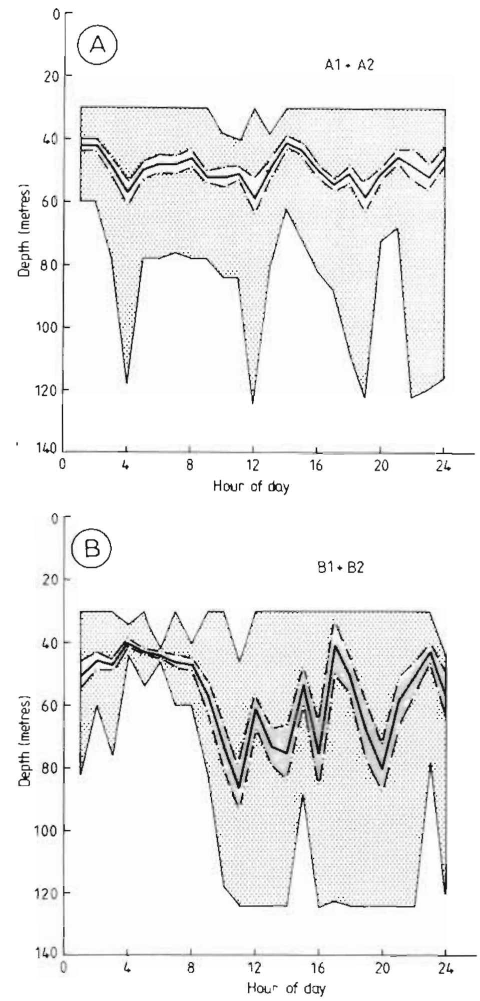


Fig. 7 Depth distribution of krill throughout the day. (A) Transects A1 and A2; (B) Transects B1 and B2

Depths have been calculated based on the mean depth of each integrated layer. The shallowest layer used is Layer 2 whose mean depth is 30 m; this is therefore the minimum estimated depth, although krill swarms were present in shallower depths than this. Comparison of daytime and night-time mean densities indicates a significant reduction in mean biomass within the 20 to 250 depth layer after dark. The evidence from the depth distribution indicates that this is largely due to vertical migration. In common with the B transects the estimated density was lower at night than by day (Table 2).

Vertical migration towards the surface at night is therefore the most likely cause of the night-time reduction in density noted in Table 2. The mean density in each hour of the day fluctuated far more during daylight than after dark (Fig. 7). Night-time values are underestimated due to vertical migration, as indicated above. Daytime values, since they are a result of sampling the full depth range of krill at that time of day, are more representative of natural variation in abundance.

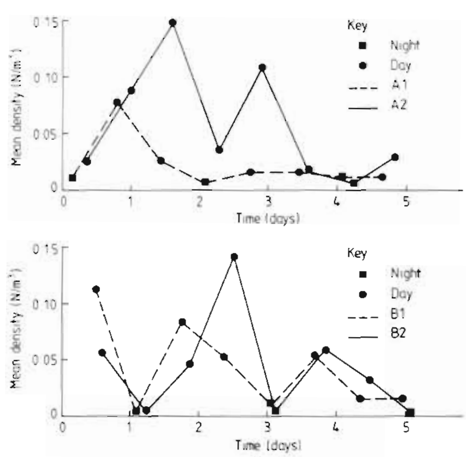


Fig. 8. Mean density for each pass along each transect

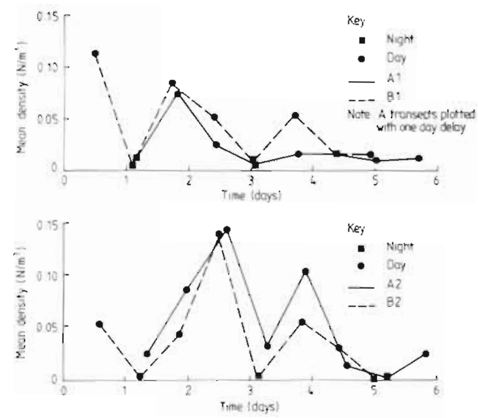


Fig. 9. Mean density for each transect. Transects A1 and B1 plotted together with a 24 h time delay to A1 data. Similarly for A2 and B2

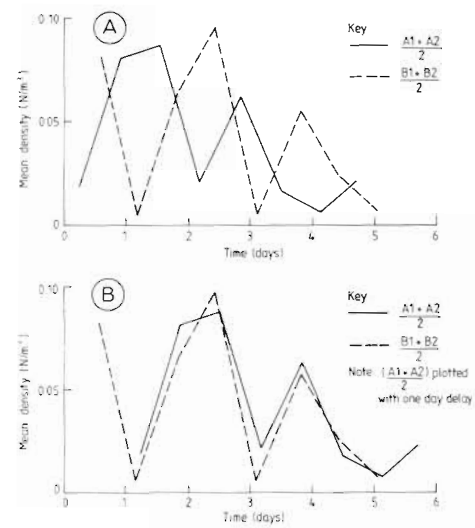


Fig. 10. Mean values (A) for A and B transects plotted together; (B) as for (A) but with 24 h time delay to A data

Krill are known to undergo diurnal vertical migration (e.g. Marr 1962, Kalinowski 1978, Kalinowski & Witek 1980, Everson 1984) which brings them near to the surface at night. The conclusions presented above are in accordance with these findings. They further confirm that abundance estimates based on night-time values will give underestimates. Daytime estimates will be more accurate, but even so there is still the likelihood that a proportion, less than at night, will remain unsampled in the near-surface layer.

Comparison of mean density per pass

Mean density of all resets has been calculated along each transect for each pass. These mean densities have been plotted in Fig. 8 against the time at the mid-point of the transect at each pass. Wide fluctuations are present. In some cases the troughs are due to the night-time problem of underestimation described above but even allowing for this there are still wide fluctuations with some minima occurring in daytime. There is some similarity between the patterns within each pair although it is not as close as might be expected bearing in mind the length of the transects (40 n mile for A1 and A2, and 25 n mile for B1 and B2) in relation to their proximity (3 n mile between pairs). The A transects, being aligned along assumed lines of water movement, are more likely to be different because if the krill are carried passively they would not, in theory at least, be sampled on both transects. The B transects, on the other hand, are aligned across an eddy and hence there is a greater chance that krill would be sampled in both B1 and B2. This may explain the greater similarity between the B than the A transects.

Alignment of transects means that krill present along A transects are likely to have been carried northeastwards and thus to be present on B transects some time later. This would mean that the pattern of abundance on A transects might be repeated on B transects following a delay dependent on the rate of water movement. A delay of 24 h to A1 and B2 data results in a close match to B1 and B2 data respectively. This is demonstrated in Fig. 9. The match is not as good between A1 and B2 or between A2 and B1 suggesting a greater affinity within than between the '1' and the '2' transects. If this assumption is correct it indicates that water which flows along a 40 n mile transect has more similarity with water along a line going 25 n mile north from the eastern end than with water 3 n mile to one side.

Even knowing the directions of flow the probability of selecting transect lines having these properties is very slight and it is therefore more realistic to expect similar patterns between the mean value for each pass on A and B transects. These values are plotted in Fig. 10 both in terms of actual time and also allowing for a 24 h delay for A transects. With the 24 h delay the congruence between patterns is surprisingly good. The congruence does not just apply to the patterns but also to the actual abundance levels, demonstrating that peak values present in A transects follow 24 h later in B transects. The peaks in the distributions occur at approximately 2 d intervals and last for about 2 sampling periods or ca 30 h. Assuming that the flow is along the 40 n mile of transect, pulses of krill would need to be carried through within the 30 h cycle. There is no way to determine whether this is true with the available data set, but to achieve this flowthrough would require a velocity of 1.33 kn (40/30 n mile h^{-1}). This estimated velocity is in reasonable agreement with the value estimated in Table 1.

The same argument cannot be applied to B transects since they are assumed to be sited across an eddy with the main water flow being across the sampled lines. It is not clear how the pattern is controlled by the water movement although the net effect is that the residence time in the area is the same on B as on A transects.

Comparison of density along transects at each pass

Density at each reset along each of the transects has been plotted for each transect (Fig. 5). As mentioned above, the sequence of resets has been reversed in A1 so that all the plots run from the southwest end to the northwest (left to right across the figure). Similarly, B transects are plotted south (left) to north with B2 transects reversed. The diagonal arrows link locations at which a passive particle might be found were it to be carried at the mean current speeds estimated from the data used to produce Fig. 2.

Few very large peaks were present on succeeding passes; the best examples are identified by the letters A, B and C in Fig. 5.

All these peaks are approximately the same density. The spatial and temporal differences between them were:

A–B 27.3 n mile in 18.35 h (mean direct speed 1.5 kn)
B–C 26.3 n mile in 21.15 h (mean direct speed 1.25 kn)

These speeds are sufficiently close to the estimated values of current speed from the ship's set and drift to suggest that the same patch of krill was present at the 3 locations.

DISCUSSION AND CONCLUSIONS

The significant differences due to vertical migration between day and night estimates of krill abundance demonstrate that echosounders using hull-mounted transducers are only sampling adequately by day. This is an important consideration for acoustic surveys of krill abundance.

The main conclusion from a sequential analysis of the replicate passes is that krill are moving along the transect at approximately the same speed as the surface current. This conclusion is reached by reference to the overall mean values as well as by examination of individual reset values. This would indicate that krill are being carried passively in the current through the region. The eddy across which the B transects were sited had no apparent effect in concentrating krill. It may, however, have caused the krill to remain in the area slightly longer because its more variable direction would carry passive particles along a longer track.

Vertical migration patterns on A transects were different from those on B transects. The only major difference between the environments in which the 2 sets of observations were made is that the flow was more or less straight along A transects and in a meander across B transects. There was also a local increase in abundance of phytoplankton at the southern end of B transects (Heywood & Priddle in press). The vertical migration pattern may therefore be a response to locally favourable feeding conditions. There is no way of testing this suggestion with the present data set although it may provide a fruitful line for future studies.

In a wider geographical context the conclusions noted in this paper indicate that in an area such as the Bransfield Strait, krill could potentially pass completely through within 1 or 2 wk. Conventional surveys to estimate abundance do, of necessity, take about this amount of time to complete. Whilst such surveys provide reasonable estimates of abundance over the whole region they are less satisfactory for studying distribution. This distinction is particularly important when considering the availability of krill to predators. Those predators that are restricted in their foraging range, such as penguins feeding chicks ashore, require regular and predictable supplies of food. On the assumption that krill are carried in the surface current then a series of repeat transects across the current upstream of the foraging zone will give a much better indication of food availability than a single broad scale survey of the same duration. Thus, in terms of monitoring krill for a predator/prey study within a defined rectangle, it might be more appropriate to replicate a transect on the upstream edge even though this may be geographically remote from the actual predator foraging region.

The observations presented here indicate a strong current-borne movement of krill. The presence of 'super-swarms' in limited geographical locations for periods of days or even weeks (Macauley 1983) demonstrates that this is not always the case. Clearly, another mechanism must operate in such regions. Whether this is because krill actively adapt their behaviour so as to remain in a favourable location or because they are held temporarily in an eddy or some other feature must remain conjectural. Super-swarms, being foci for predators and fishing activity, are clearly worthy of considerable study particularly since the factors determining their formation and persistence cannot be explained by studies such as the one described in this paper.

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