VARIATIONS IN VERTICAL DISTRIBUTION AND DENSITY OF KRILL SWARMS IN THE VICINITY OF SOUTH GEORGIA

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Abstract: Krill abundance and distribution in relation to depth and time of day were investigated by means of a calibrated echo sounder and echo integrator. The study areas were in the Scotia Sea, in the South Georgia area (both on-shelf and off-shelf regions) and a large krill patch close to South Georgia. Comparison of the results from the three areas shows major differences in the diurnal patterns of vertical migration. Mean volume backscattering strength (MVBS) was analysed with respect to size of aggregations. The mean values for day and night were markedly different in the krill patch, the daytime value being higher than expected from concentration effects alone. In the other phases of the study, MVBS and concentration effects appeared to compensate and diurnal variation was less marked.

It has been known for some time that the diurnal vertical migration of krill does not follow a simple pattern with the result that krill swarms are frequently recorded at any depth in the top 200 m of the water column at any time of day. So far, no consistently applicable explanation has been produced for this great variation in behaviour. The results presented in this paper serve to highlight the great differences that are observed between adjacent localities.

The use of calibrated echo sounders has vastly increased the opportunities for behavioural studies as well as giving some insight into the numerical density of krill within swarms. It now appears that the behaviour of krill within swarms does, under certain conditions, vary with time of day in such a way that their target strength is affected (EVERSON, 1982). A major purpose of this investigation was to determine the extent of this variation.

The results presented in this paper were obtained on board RRS JOHN BISCOE during the second cruise of the British Antarctic Survey's Offshore Biological Programme. This cruise was divided into three phases: a "drift station" located north of the South Orkney Islands in the frontal zone between Weddell and Bellingshausen Seas water, a South Georgia zone survey (further subdivided into "on-shelf" and "off-shelf" phases) and a "patch" study.

Methods

A Simrad EKS 120 echo sounder and QM MK II echo integrator were used with instrument settings as in Table 1.

All the echo charts were examined and the size, depth and integrator output of

Table 1.

Pulse length	0. 6 ms
Pulse repetition frequency	50 per min
Bandwidth	4. 9 kHz
Receiver gain	0 dB
TVG	20 log R
Range	0–250 m
Source level	220 dB ref 1 μPa per watt
Voltage response	−107 dB ref 1 volt per μPa

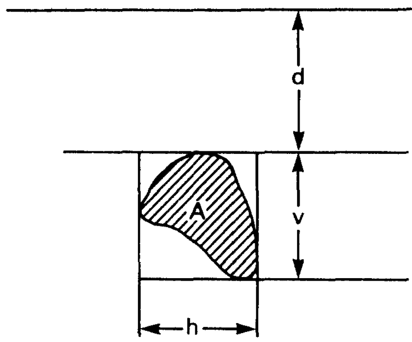

Fig. 1. Diagram indicating the measurements made on each aggregation. d=Depth of swarm (subsequently corrected for transducer depth). v=Vertical extent of swarm. h=Horizontal extent of swarm. A=Area of swarm (shaded). This was computed as $A = v \times h \times P$, *where P is the proportion of the rectangle vh containing krill, as estimated by image analysis of echo integrator traces.*

each aggregation of krill were estimated. The size of each aggregation was estimated using a video TV camera and image analyser. The technique is indicated in Fig. 1. The time (GMT) at which each aggregation appeared on the echo chart was recorded and for all analyses the results were grouped into two hour time intervals beginning at 0000 GMT. Local midnight was approximately 0200 GMT, dawn 0800 and dusk at 2000.

Krill were assumed to be evenly distributed between the upper and lower limits of each aggregation and the integrator output was divided *pro rata* between depth strata which were chosen to be 10 m thick to 50 m, then 25 m thick to 150 m and then 50 m to 250 m depth. The depth range 0–10 m was not sampled acoustically.

Results and discussion

1) Vertical migration

Abundance estimates by depth have been produced for each depth stratum based on unit total abundance for the relevant time period. This was to eliminate variation due to differing amounts of krill being detected at different times of day. The results are shown in histogram form in Fig. 2.

On the drift station (Fig. 2a) there was a regular diurnal migration pattern. During the day the krill were spread out from about 50 m down to about 150 m whilst at night they were close to and at the surface (net hauls at the surface after dark invariably caught large amounts of krill). The drift station was located in the frontal zone be-

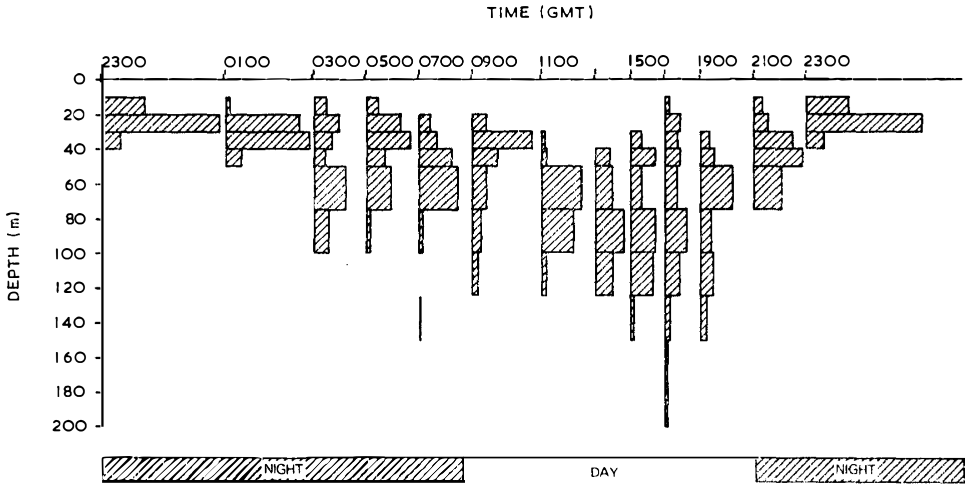

Fig. 2a.

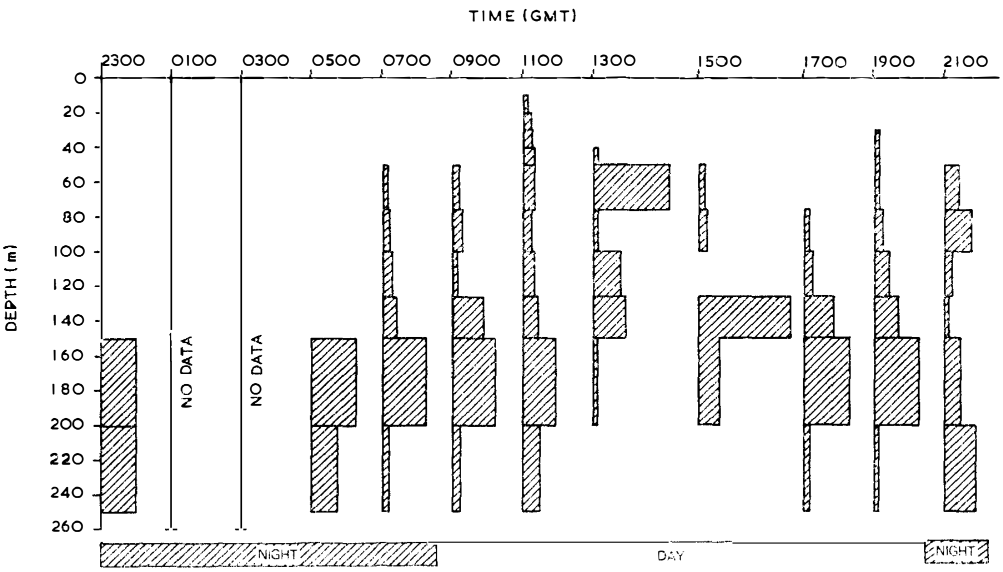

Fig. 2b.

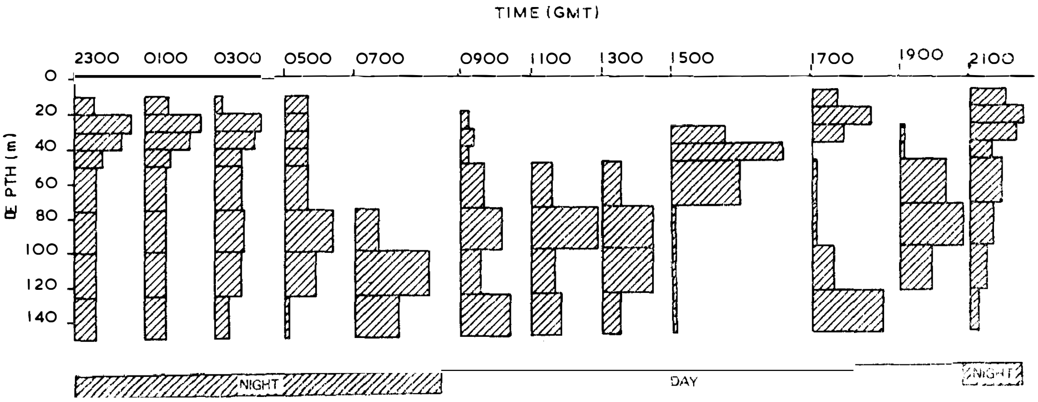

Fig. 2c.

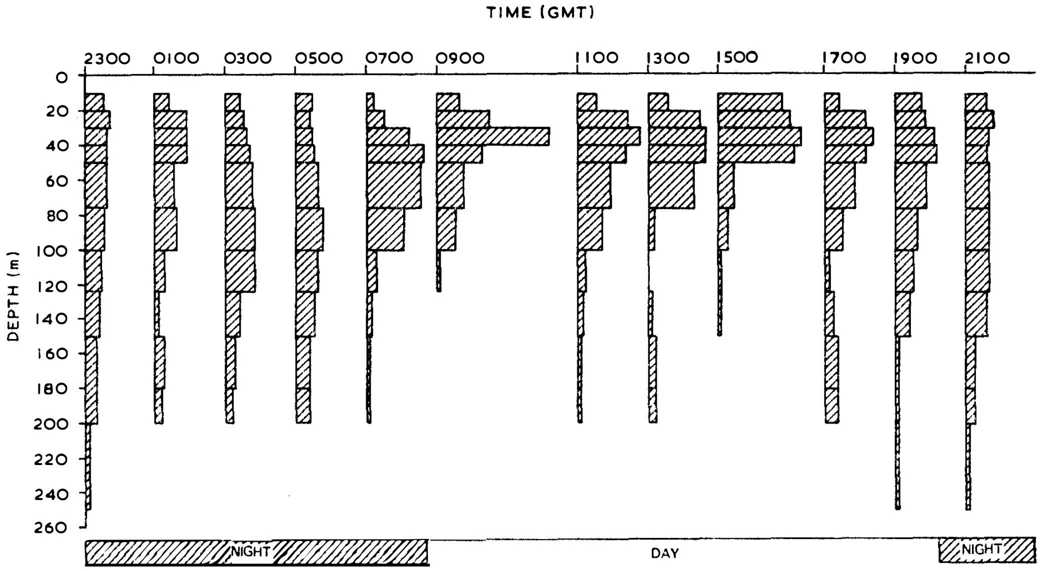

Fig. 2d.

Fig. 2. Relative abundance of krill by depth for: a) "Drift Station", b) "Off-shelf" phase of South Georgia survey, c) "On-shelf" phase of South Georgia survey, d) "Patch" study.

tween Bellingshausen and Weddell Seas water to the north of the South Orkney Islands between 60°S 46°W and 59°00′S and 42°50′W. Surface temperatures ranged from 0.52°C to 1.48°C and salinities from 33.94‰ to 34.08‰ and the depth of thermocline varied from 30 m to 60 m (HEYWOOD pers. commun.). This suggests that the thermocline had little effect on vertical migration. The frontal zone, although containing more krill than most other parts of the Scotia Sea, contained much less krill than the South Georgia region. The pattern of migration was very similar to that reported by KALINOWSKI and WITEK (1980) for the South Sandwich Islands region. During the 21 day period of the drift station the study area moved from the north of the South Orkney Islands towards the South Sandwhich Islands, so the results might be expected to be similar.

Intuitively one might expect the results from off-shelf phase of the South Georgia zone survey (Fig. 2b) to be similar to those from the drift station. In this region the bulk of the krill were concentrated deeper than 150 m for most of the day although during the hours of daylight they tended to come nearer to the surface. By comparison, the results of the on-shelf phase of the survey (Fig. 2c) were quite different. Krill tended to be deeper than 75 m during the day and in the late afternoon two distinct concentrations of abundance were recognizable which amalgamated and spread out at dusk. Krill were present from the surface to about 150 m during the night. The structure of the surface water around South Georgia, like that of the drift station, was also complex, reflecting the different characteristics of the water masses reaching the island from the Bellingshausen Sea (Drake Passage), Scotia Sea and Weddell Sea. The depth of the thermocline varied from 20 m to 120 m in both on-shelf and off-shelf phases (HEYWOOD pers. commun.) although this feature alone seems to have had little influence on migration patterns.

The patch study results (Fig. 2d), particularly at night, are very similar to the on-shelf phase of the zone survey. During the day, however, the main concentrations of krill were much nearer to the surface.

In comparing the results from the four regions (Fig. 2a–2d) it is clear that there are major differences between them, thus confirming the great variation in migration pattern described by MARR (1962). Physical, chemical and biological variables associated with krill vertical migration have been reviewed by EVERSON (1977) while more recent information is contained in KALINOWSKI and WITEK (1980). Further analyses are in progress on oceanographic data obtained during this study which may throw some light on possible cause and effect.

2) Analysis of aggregations

The krill patch proved an interesting part of the study for several important reasons:

a) It remained virtually stationary from April 9 until at least April 15, 1980 when the study was terminated.

b) It contained by far the highest concentration of krill in comparison to other areas around South Georgia. Also, the krill went through a regular cycle of condensation into dense swarms by day and dispersion into large low density aggregations by night (Fig. 2d).

The continuous presence of the patch permitted day/night comparisons to be made over a period of five days. In terms of mean abundance, defined by the acoustic parameter Mean Volume Backscattering Strength (MVBS), EVERSON (1982) noted an 8 dB difference between day and night values. This difference was attributed to different orientation behaviour by day and night. Such a difference would introduce a very large error into abundance estimates if its effect were not fully taken into account. It is therefore necessary to determine the precise nature of the variation during the patch study and to see to what extent the results apply to the South Georgia zone survey.

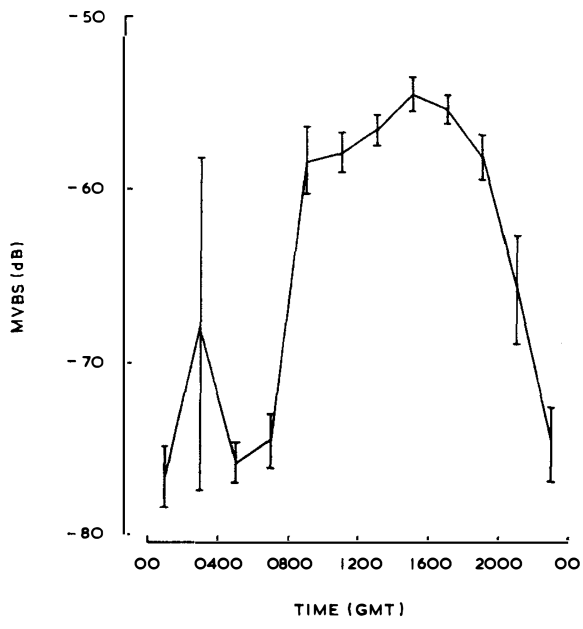

Fig. 3. Mean values of MVBS ± one standard error for all data from the patch study grouped into two hour time intervals.

To achieve this, the results have been investigated in terms of size of swarm and MVBS. In this context the size of the swarm is taken as the area of the swarm as seen on the echo chart; it is therefore a vertical section through the swarm.

Mean MVBS values for two hour periods during the patch study are shown in Fig. 3. These results demonstrate the pronounced difference between swarm density by day and night. By contrast, the South Georgia zone survey, for both on-shelf and off-shelf phases, demonstrated little variation throughout day and night although there is a peak soon after local noon (Fig. 4). This would appear to indicate that there was not much difference between the densities within aggregations in the smaller swarms.

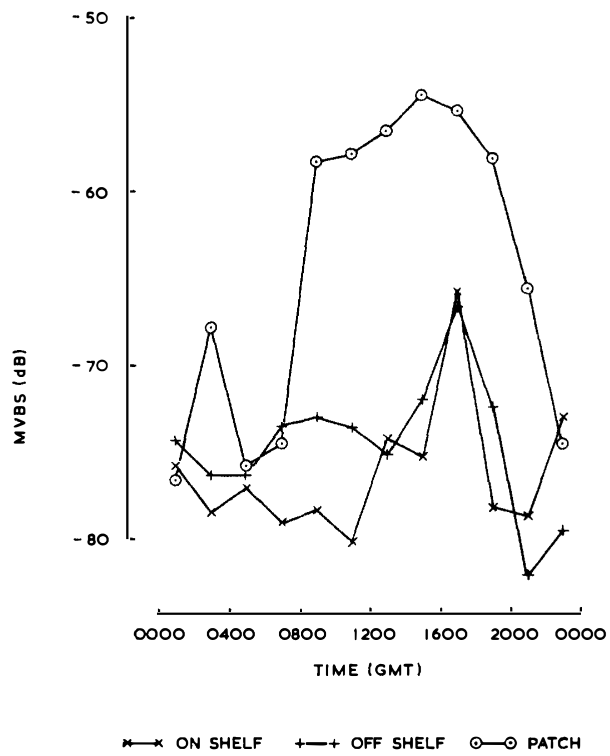

Fig. 4. Mean values of MVBS from the patch study and South Georgia zone survey grouped into two hour time intervals.

The patch study involved a series of repeated acoustic transects over what appeared to be a large, more or less static krill aggregation. Thus, the total biomass appeared roughly constant from day to day although the diurnal variation of the size of the constituent swarms was very great. In this situation the daytime increase in MVBS would be expected to be accompanied by a decrease in the size of the swarms and vice versa. This effect is shown in Fig. 5 for the patch study although such a difference was not present during the other phases of the study (Fig. 6).

A direct comparison may be made between differences in MVBS and differences in swarm size by converting the latter to decibel notation using the formula:

$$(\text{Area ratio})\ \text{dB} = 10 \log_{10} \frac{(\text{mean area by day})}{(\text{mean area by night})}.$$

Bearing in mind the obvious differences between day and night values on the patch it is convenient to group results, with the exception of the transitional dusk period,

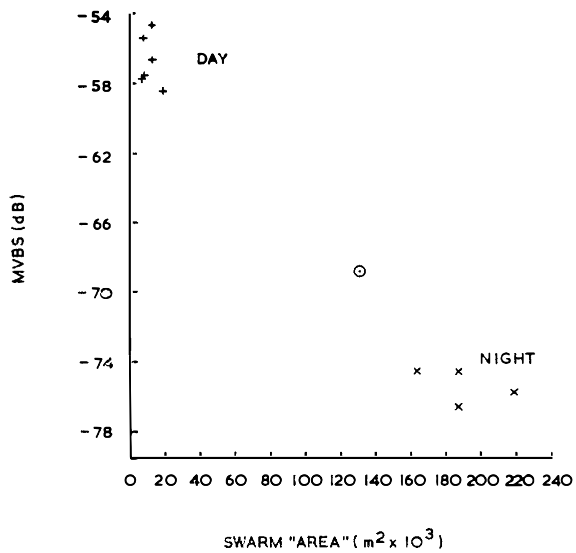

Fig. 5. *Relationship between size of swarms and MVBS on the patch study. + Daytime, × Nighttime, ⊙ Dusk.*

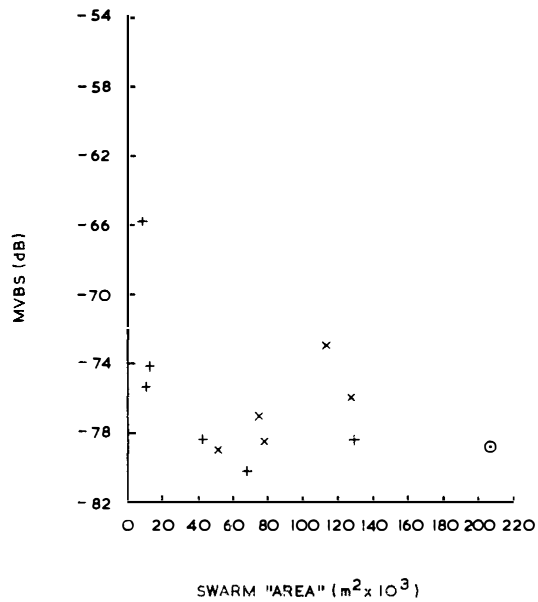

Fig. 6. *Relationship between size of swarm and MVBS during on-shelf phase of the South Georgia survey. Symbols as for Fig. 5.*

Table 2. *Synoposis of aggregation data in terms of MVBS.*

	n	Mean MVBS (dB)	S.D.	Difference (dB)	*t*	Significance level
Patch study						
Day	129	−56.80	5.54			
Night	69	−74.23	6.48			
				17.43	19.87	$p<0.001$
On shelf						
Day	25	−74.92	8.89			
Night	39	−76.14	7.33			
				1.23	0.591	n.s.
Off shelf						
Day	37	−72.75	6.57			
Night	10	−77.30	6.99			
				4.56	0.846	n.s.
Drift station						
Day	12	−58.21	5.92			
Night	7	−57.87	5.31			
				0.335	0.123	n.s.

within these two categories. These results are summarised in Tables 2 and 3.

During the course of the patch study, 61 traverses were made over approximately the same ground during which time there were only minor differences in size of krill. Hence, differences in density of aggregation should be accompanied by equivalent differences in MVBS. The daytime MVBS values are higher (by 6.7 dB) than would be expected from concentration effects alone. EVERSON (1982) discussed this phenomenon

Table 3. Synopsis of aggregation data in terms of swarm area.

	n	Mean area	S.D.	Difference (m^2)	t	Significance level
Patch study						
Day	128	10856	17877			
Night	69	181062	175245			
				170206	10.91	$p<0.001$
On shelf						
Day	25	42837	64305			
Night	39	122600	252513			
				79763	0.968	n.s.
Off shelf						
Day	36	55020	115397			
Night	10	27320	29169			
				27700	0.747	n.s.
Drift station						
Day	12	1900	5214			
Night	7	315.4	263			
				1584.6	0.794	n.s.

and concluded that it was a result of orientation differences affecting target strength.

While there is some evidence for swarms being smaller and more compact by day during all phases except the patch study, the differences broadly compensate when estimated by the two methods. Thus the difference attributed to orientation by EVERSON (1982) in the results from repeat sampling of the patch is not readily discernible in the results from the rest of survey.

This conclusion raises two important and related questions:

a) Does the conclusion give a fair reflection of the real situation? In other words does orientation only affect target strength in regions of high abundance such as patches and superswarms?

b) Is the day/night difference in target strength widespread but undetected due to the lack of repeat sampling?

It is impossible to answer either question with the results available, although, since the area and MVBS results for the survey are broadly in agreement we might tentatively conclude that the day/night difference in target strength is minimal. The fact that the survey MVBS values are broadly similar to the night time patch study results may indicate that orientation is a significant factor at all times in areas of low abundance.

In order to answer these questions there is clearly a need for further study in the following key areas:

a) Repeat sampling in areas of low krill abundance.

b) Further studies on krill patches and superswarms.

c) *In-situ* observations on krill in swarms. Does their orientation vary with time of day?

There are also clear indications that caution should be exercised in analysis of survey data. The key question here is whether the target strength to be applied should be adjusted to take account of time of day, density of aggregations as well as size of krill within the swarms.

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