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Vertical Distribution and Diurnal Migrations of Krill – *Euphausia superba* Dana – from Hydroacoustical Observations, SIBEX, December 1983/January 1984

M. Godlewska and Z. Klusek

Department of Polar Research, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny, Poland and
Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, P-81967 Sopot, Poland

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Summary. The depth distributions of krill density with the resolution of 0.435 m has been obtained on the basis of SIBEX hydroacoustic data. Krill was observed to be mainly in a layer from 20 to 100 m with the maximum of biomass migrating from the near surface area at night to greater depths during day. The krill migration pattern can be described by the function: $H(t) = A + B\cos(2\pi t/T + \varphi)$, where H is depth of the mass center of biomass, t-time, A-mean depth of krill occurrence, B-amplitude of diurnal changes, T = 24 h and φ-phase of migration process. The parameters of migration pattern: A, B, T and φ depend on the body length of krill.

Introduction

The phenomenon of krill migrations has been known for a long time. Marr (1962) found that the major concentrations of Euphausia superba occured in the top 100 m, most frequently in the top 10 m. Pavlov (1974) suggested that the period of krill migrations is the same as its feeding cycle, i. e. 12 h. Nast (1979) analysed vertical distribution and migrations for larval and for adult krill pointing out differences between them. The works cited above were based on analysis of net samples. The broad application of hydroacoustic instruments in biological investigations in the seventies provided a new powerful tool, useful for studies of vertical distribution and migrations of marine organisms. Shevtsov and Makarov (1969) and Kalinowski and Witek (1980) by analysing echosounder data determined upper and lower limits of the occurrence of krill aggregations in different regions of the Atlantic sector of the Antarctic. Arimoto (Arimoto et al. 1979) and Tomo (1983) investigated the vertical distribution of krill aggregations in relation to time of day. Witek (Witek et al. 1981), Everson (1983) and Lillo and Guzman (1982) went step further, using results of the echointegrator to estimate the vertical distribution of krill density. They used the assumption that krill is evenly distributed within the swarm. The complex ecological model that linkes feeding, swarming, vertical migration, environmental variables and moulting of krill has been developed by Morris (1985).

In the present work hydroacoustic data were used for the calculations of the depth distribution of krill density as well as parameters of vertical migration such as depths of krill occurrence, period and amplitude.

Material and Methods

While analysing data obtained by downward directed echosounder it should be remembered that this equipment does not provide information about the situation in the upper few meters of the sea. This is a disadvantage of the method, especially in light of the fact that during the night krill may come up to the surface. This problem has not been solved satisfactorily, although theoretically it is possible to do so, by using upward directed transducer.

Krill migration analysis has been carried out, here, on the basis of hydroacoustic data collected during SIBEX in the Bransfield Strait and Drake Passage by the *RV Professor Siedlecki* during the end of December 1983 and beginning of January 1984. Along a series of transects whose total distance was about 2000 Nm, the signal of the envelope from the Simrad echosounder EK-120 was registered on a 4-channel tape recorder Bruel Kjaer 7003. To expand the 38 dB dynamics of the recorder, the signal was recorded on two channels whose amplification differed by 20 dB. This permitted total dynamics of about 60 dB which was usually enough to avoid saturation. The other two channels were used for the pulse trigger and the mile marker. Materials registered on the magnetic tapes have been analysed off line using a HP-9872 A computer. Details of the apparatus and methodology of calculations are in Klusek (1987, in press). The calculations lead to a value for the volume backscattering sound coefficient s_v which is proportional to the density of krill biomass. Because this value varies over a range of orders of magnitude, for diagram presentation we used the volume backscattering strength SV which is expressed as $SV = 10 \log s_v$. For each nautical mile containing krill the depth distributions of SV with the resolution of 0.435 m as well as in 10 m layers were calculated. Parallely, for those miles in which more than 5 swarms were present, the distributions of krill aggregations in 10 m layers were obtained from the echogram paper.

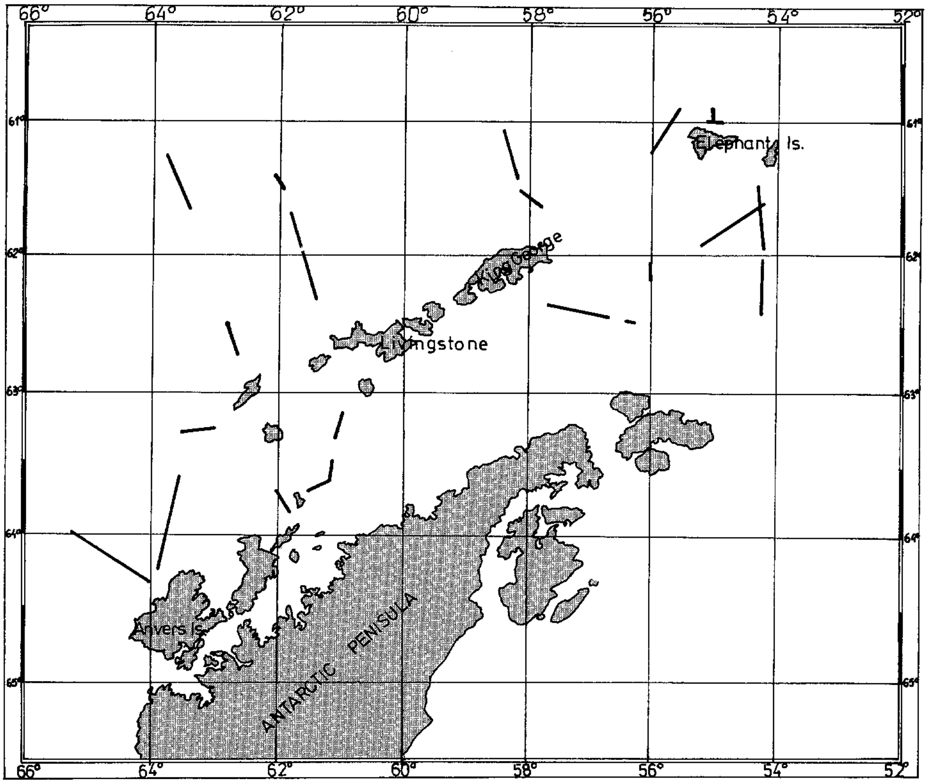

Fig. 1. The area of krill occurrence – bars are along the fragments of the track containing krill

To make the picture of diurnal migrations as clear as possible the depth of the mass center of biomass distribution for every two hours was calculated according to following formula:

$$H = \frac{\int_{H_{min}}^{H_{max}} \langle s_v \rangle dz}{H_{max} - H_{min}} \qquad (1)$$

where H_{max} – maximal depth of krill occurence, H_{min} – minimal depth of krill occurence, $\langle s_v \rangle$ – volume backscattering sound coefficient averaged over all nautical miles in which krill were recorded within 2 h intervals.

Accordingly with the observations that krill goes up to the surface during the night and descends during the day we assumed that this migration process has a periodicity of 24 h. Changes of H with time were approximated by a simple periodical function in a form of:

$$H(t) = A + B\cos(2\pi t/T + \varphi) \qquad (2)$$

where: A – mean depth of mass center, B – amplitude of diurnal changes, T – period of changes, assumed to be 24 h, φ – phase of the process, t – time.

To approximate experimental data (mean for two-hour intervals from all non zero measurements) by the theoretical curve 2 we used least square method. The parameters of equation 2 were calculated by the method of nonlinear regression (Marquardt 1963). Values of SV were recalculated to krill density assuming the target strength of krill TS in accordance with (Anon 1986).

Results

During the second BIOMASS experiment, SIBEX, in the Bransfield Strait and in the Drake Passage very little krill was observed (Fig. 1). The density of krill was greater than zero in only 431 Nm out of 2000 Nm surveyed. Usually, it had a value of less than 10 g/m² and only in a few cases exceeded 100 g/m². Nevertheless, the data received lead to some general conclusions about vertical distribution and migrations of krill. In a layer 20 to 100 m there was substantial amount of krill independently of time of day. Fig. 2 presents krill density distributions during the day (from 4 to 20 h) and during night (from 20 to 4 h). It is clear that the major portion of krill migrates from a nighttime area close to the surface to some greater daytime depths. The migration pattern can better be seen from 2 h interval diagrams. Analysing Fig. 3 we notice that during 0–2 h the maximum of krill density is near

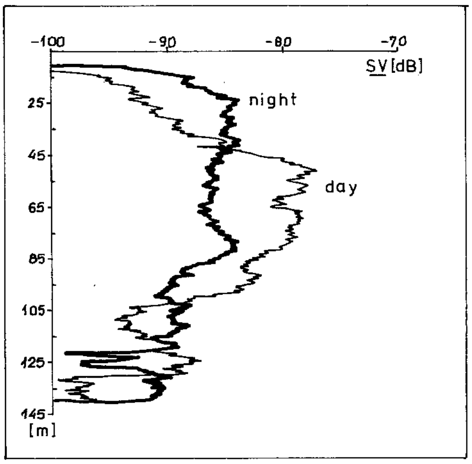

Fig. 2. Vertical distributions of volume backscattering strength SV for day and night. Day: 4 h–20 h, night: 20 h–4 h, local time

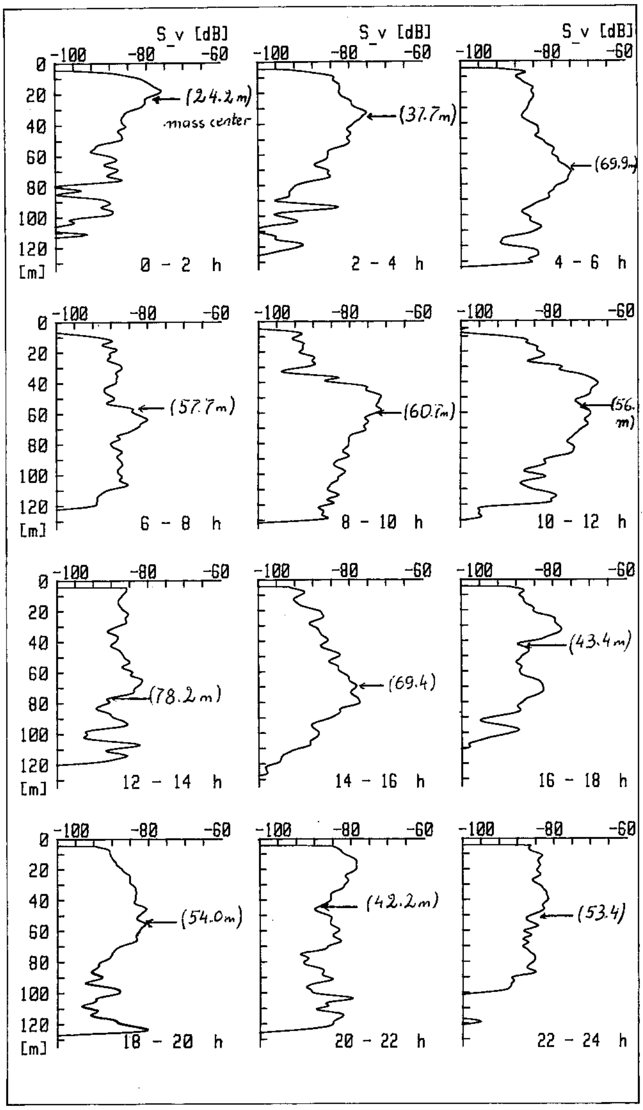

Fig. 3. Vertical distribution of volume backscattering strength of krill in two-hour intervals, local time. The curves were smoothed with a 21 elements low-pass Spencer filter

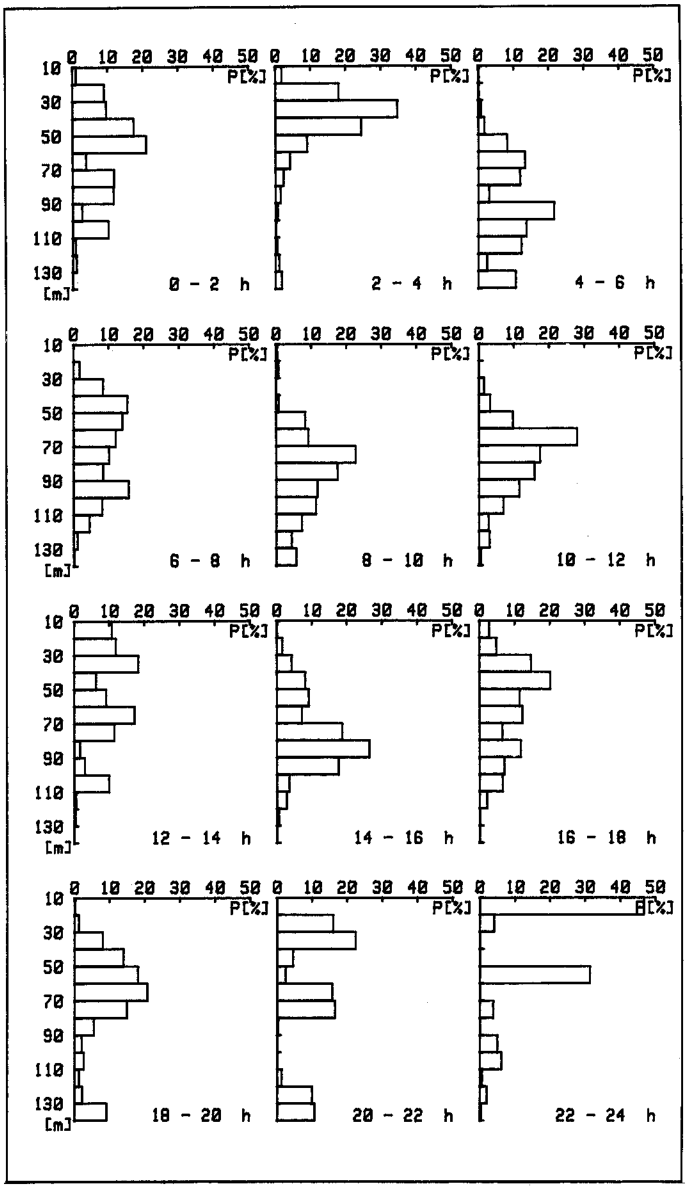

Fig. 4. Vertical distribution of krill density in two-hour intervals and 10 m layers in the Drake Passage. The krill biomass under 1 m^2 within the observed depth range and a given time interval is assumed to be P = 100%

the surface (about 20 m), for the next two intervals it descends to about 80 m, than we observe something like a sum of two processes: part of the biomass is staying at the greater depths, while the other part is returning to the surface; after reaching a depth of about 45 m at 10–12 h it than again descends. The next ascent is observed between 16–18 h, again extending up to a depth of 45 m. We think that the presence of juvenile krill is responsible for this additional periodicity of about 6 h and its small amplitude. This hypothesis is in agreement with Fig. 4 and Fig. 5, where the krill depth distributions for the different regions are presented. Fig. 4 is for the Drake Passage, where mature krill dominates and Fig. 5 is for the eastern part of the Bransfield Strait, where in addition to mature krill, adolescent krill were also present in a large quantities. Not only 6 h periodicity is more clear in Fig. 5 than in Fig. 4, but also the shapes of distributions are different. The distributions from the Bransfield Strait are vertically narrow, while the distributions for the Drake Passage are relatively wider. We think this is due to differences in the developmental stages of krill between these areas (Fig. 6).

Another way to investigate migration pattern is to analyse time dependence of the position of the biomass mass center, as described above. For the 24 h period, parameters of equation 2 calculated on the basis of all data are following: A = 53.6 m, B = 13.86 m, $\varphi = 0.88$ h.

The theoretical curve and the experimental mean values for two-hour intervals, as well as consecutive means for three intervals $\left(\text{i.e. } \bar{H}(t_n)=\frac{H(t_{n-1})+H(t_n)+H(t_{n+1})}{3}\right)$ are presented in

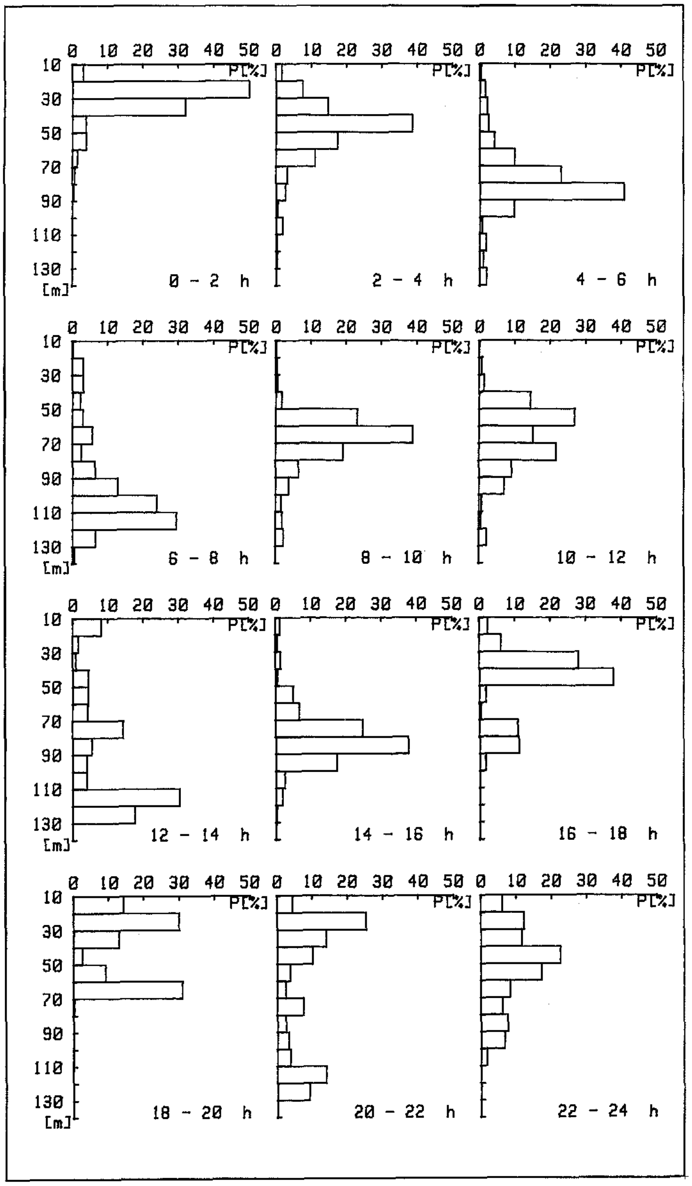

Fig. 5. Vertical distribution of krill density in two-hour intervals and 10 m layers in the eastern part of the Bransfield Strait. The krill biomass under 1 m^2 within the observed depth range and given time interval is assumed to be P = 100%

Fig. 7. Although the mean values are quite scattered, the points of consecutive means fit the theoretical curve fairly well.

Discussion

Our results confirm a general conclusion of other investigators, that krill migrates near to the surface during the night and descends to greater depths during the day. There is less agreement among investigators about the range of depths which krill occupy. According to Lillo and Guzman (1982) biomass of krill was greater in the 110–220 m layer than in the 10–110 m stratum. From our measurements the main concentrations of krill were in the upper 100 m, and below this layer krill were encountered only occasionally. The results of Kalinowski and Witek (1980) were similiar to ours.

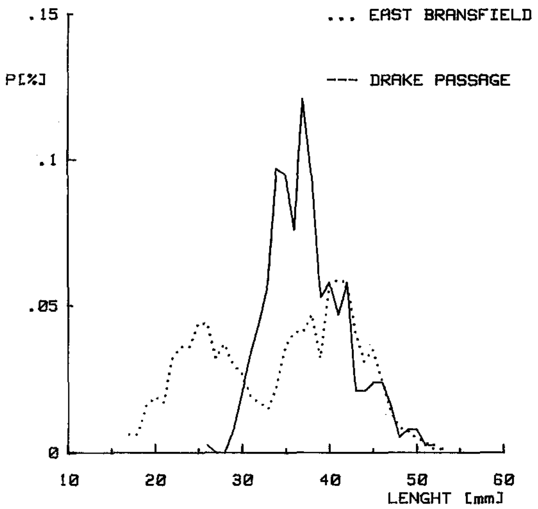

Fig. 6. Krill length distributions for the Drake Passage and for the Bransfield Strait

Comparison of vertical distributions of krill cited by different authors is difficult, if at all possible, because of qualitative differences in ways used to present results. Distributions of krill density can be substantially different from distributions of krill aggregations (Arimoto et al. 1979; Tomo 1983). An example of these two presentations adopted for the same nautical mile is shown in Fig. 8. The difference is not surprising as the first presen-

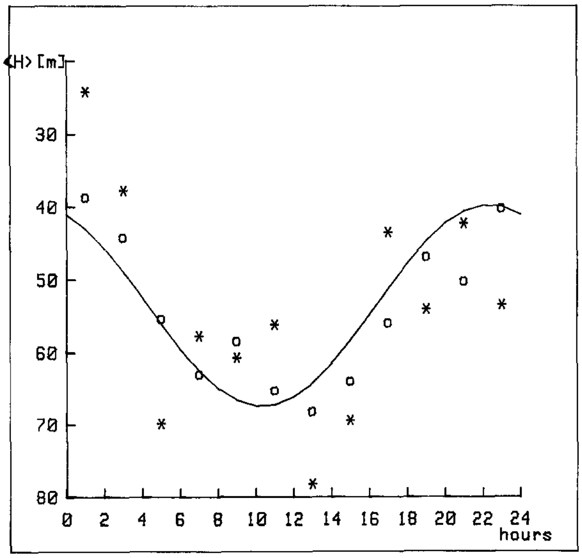

Fig. 7. Time dependence of the depth of mass center of krill biomass. Theoretical curve is described by the function: $H(t) = A + B\cos(2\pi t/T + \varphi)$, where $A = 53.6$ m, $B = 13.86$ m, $T = 24$ h and $\varphi = 0.88$ h. * the experimental points, mean for two-hour intervals; ○ consecutive mean i.e. $\bar{H}(t_n) = [H(t_{n-1}) + H(t_n) + H(t_{n+1})]/3$

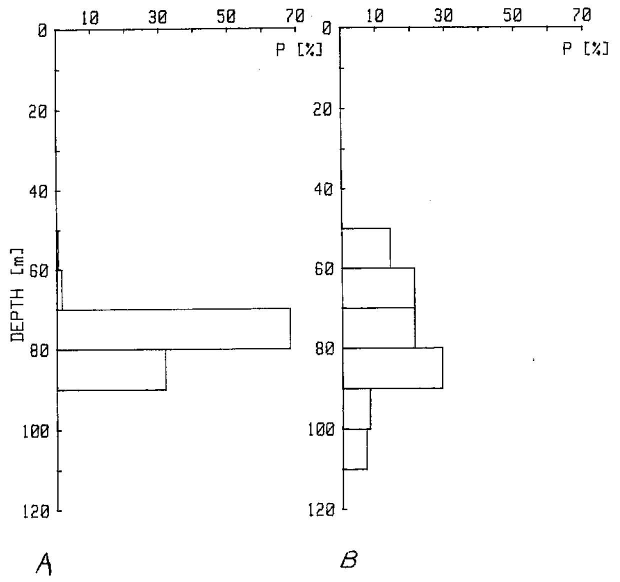

Fig. 8 A, B. Vertical krill distributions for the same nautical mile. **A** for the krill density, **B** for the krill aggregations

tation reflects amounts of krill on different horizons, while the second is related to swarming behaviour of krill.

Kalinowski and Witek (1980), Everson (1983), Lillo and Guzman (1982) and Croxall et al. (1985) all presented distributions of krill density using the assumption that krill is evenly distributed within the swarm. As can be seen from Fig. 9 the distribution of krill within the swarm is not homogeneous in any direction and our results obtained without use of this assumption can not be profitably compared with those cited above.

Now let us examine differences among reported krill migration patterns. The most detailed data are those of Nast (1979). If we calculate parameters of equation 2 on the basis of the 5 points given in Table 4 of Nast (1979), we obtain the following values: $A = 71.4$, $B = 58.0$, $\varphi = 1.3$, total krill, $A = 65.0$, $B = 54.5$, $\varphi = 1.3$, juvenile krill. These values differ significantly from our results. But it should be remembered that Nast collected data from a time station near Elephant Island and all were related to swarms in the same area, while our data were collected along 431 Nm and are mean values for hundreds of swarms from different environmental conditions. Also some difference may be due to the fact, that the Nast values are mean depths of krill occurence while ours are depths of mass centers of the biomass. It is probable that migration pattern differs from place to place depending in part, on amount of light and environmental conditions. Everson and Ward (1980), on the basis of Pavlov's (1974) result that migration of krill is related to its feeding cycle, concluded that smaller krill will tend to go through a cycle of feeding and swarming more rapidly than larger krill. It will also sink to lesser depths than larger krill. Thus the vertical extent of migration and its period depend on size of krill. Our results support well this hypothesis (Figs. 4 and 5). Also in Nast (1979) data the general trend is similiar, although the differences between the results for juvenile and total krill are not large.

Our main conclusions are the following:

1. Krill vertical distributions usually extend from about 20 m to 100 m depth, although sometimes small amounts of krill were observed considerably deeper (we exclude the upper 10 m layer from analysis).

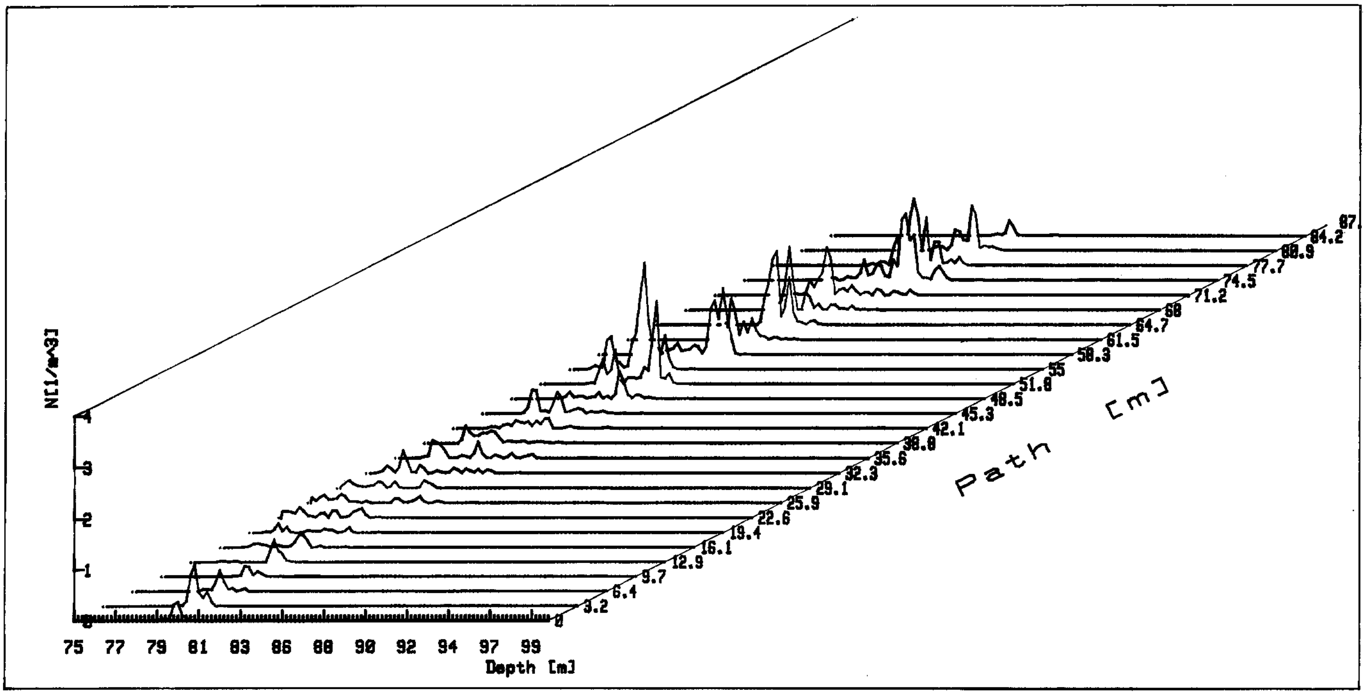

Fig. 9. The two-dimensional structure of krill density within the swarm

2. The maximum of krill density clearly migrates from a near surface area during the night to greater depths during the day.
3. The krill migration pattern can be described by the function $H(t) = A + B\cos(2\pi t/T + \varphi)$, where H – depth of a mass center of krill biomass, A – the mean depth of mass center, B – the amplitude of diurnal changes, φ – the phase of the process.
4. Parameters of the krill migration pattern depend on such factors as developmental stage (body length) and probably light conditions and region of occurrence.

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