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Diurnal vertical distribution of krill aggregations in the Western Antarctic

ABSTRACT: On the basis of measurements of the depth of occurrence of 11 000 krill aggregations and the biological analyses of these animals and measurements of some environmental factors the diurnal vertical distribution of aggregations is presented against the background of various environmental conditions. Vertical distribution of aggregations is closely related to the feeding rhythm of krill. Active vertical migrations have been recorded at civil twilight. The increasing and decreasing rate of aggregations in those periods is described.

Key words: Antarctic, krill, vertical distribution

1. Introduction

The vertical distribution of krill aggregations and factors controlling this phenomenon have been frequently discussed in the literature.

Hardy and Gunther (1935) and Marr (1962) have given a diagram of distribution of krill aggregations at different times of day and night in the region of South Georgia. Ševcov and Makarov (1969) have described types of krill distribution in the Atlantic Sector of Antarctic. Pavlov (1974) has shown a diagram of vertical movements of *Euphausia superba* Dana relating this closely to the diurnal feeding rate. Mohr (1976) has described vertical distribution in the region of the South Sandwich against the background of day illumination. Fisher (1976) has described vertical distribution of krill in different regions of Scotia Sea. Kalinowski (1978) has described the distribution of krill aggregations in the region of South Georgia in February and March 1976. Witek et al. (in press) have presented the distribution and characteristics of krill aggregations against the background of environmental conditions in February 1977 in the region of Antarctic Peninsula.

Unfortunately the works cited have dealt with limited amount of material and a relatively narrow range of analysed environmental factors. Thus the result were frequently contradictory and did not allow to draw general conclusions.

Here, the material collected in 1977 and 1978/1979 from the Antarctic to Peter I Island in Bellingshausen Sea up to the South Sandwich Islands on Scotia Sea, is a comprehensive one. Observations and measurements were conducted with regard to hydroacoustic localities of aggregations, solar illumination, thermal stratification and water oxygenation, phytoplankton distribution, characteristics of population and feeding of krill.

The aim was to present the general regularities in diurnal vertical distribution of aggregations and to find factors having a significant effect on the course and rage of vertical migrations of krill.

2. Method and material

Hydroacoustic apparatus on the research vessel "Profesor Siedlecki" was used for studies of vertical distribution of krill aggregations (Burczyński 1973). Water depths were observed by means of a system of diurnal hydroacoustic watch.

The vertical echosounder Simrad EK-120 was mainly used and the cooperating with it echointegrator QMMK II. These apparatus were calibrated before the investigations in acoustic and electrical units. For echosounder EK-120 the following parameters were obtained: working frequency — 120 kHz, source level — 124.1 dB, voltage response — 1.8 dB, pulse power output — 441 W.

In studies for echosounder EK-120 the following settings were used: range — 0—130 m, TVG — 20 log r, recorder mode, normal, pulse duration — 0.6 ms.

The echograms were used to measure, after the method of Kalinowski and Kuptel (1979) the following physical parameters of each krill aggregation: area of recorded aggregation (planimeter), length, depth of upper and lower depth limits of the aggregation, integrator recorder deflection, time.

Diagrams of vertical distribution of krill aggregations were made on basis of measurements of upper and lower depth limits of aggregations in water, using the following method: measured aggregations were arranged in groups according to the time of their occurrence in one-hour intervals in 24 hrs (0—1, 1—2, ... 23—24), water depth was divided into 20-metre depth intervals $A_1, A_2, \dots A_n$. It was assumed that the beginning of the first layer may be 0, 5, 10 m etc. It was determined on the basis of the smallest upper limit of depth — G, e.g., at minimal $G = 8$ m the layers will be: 5—25 m, 25—45 m etc., in layers $A_1 \dots A_n$ one-hour arithmetical means of upper and lower depth limits were counted, mean upper depth limits from A_1 interval and mean lower depth limits from A_n interval were joined by a line. Thus were obtained the diagrams of vertical distribution of krill aggregations. When the differences of mean depths between neighbouring layers were statistically significant the diagrams showed stratification of the occurrence of aggregations.

All calculations were made by means of a digital computer on the research vessel "Profesor Siedlecki".

Measurements of illumination were made every hour all day and night using the luxometer. At civil twilight measurements were made every 10 minutes.

Annals of "The Nautical Almanac" (1977, 1979) were used for reading the hours of sunrise (SR) and sunset (SS) and the civil twilight (CT). Civil twilight is when both the horizon and the brightest stars are visible. The "interim" period should be understood as the period between dawn and sunrise and between sunset and dusk.

Hydrologists made measurements of water temperature and oxygen content. Temperature was measured using the automatic sounder Bisset-Berman, and the oxygen content using the Bisset-Berman sounder or Winkler method from samples taken at standard depths.

Seston (main part of seston was the phytoplankton) was caught by a net of "Copenhagen" type with an inlet surface area 0.2 m^2 and mesh diameter 0.064 mm drawn vertically once from the depth of 100 m to the surface. The phytoplankton amount was determined by measuring the volume of centrifuged deposit (3000 turns per minute during 5 minutes), taking into consideration its hydration which is 2/3 on the average (Wolnomiejski et al. 1977).

Krill catches were made using the net of "Bongo" type or the pelagic trawl with fine mesh insert. The body length of *E. superba* was measured from the tip of rostrum to the end of telson. Maturity was determined after the criteria given by Wolnomiejski, Witek and Czykieta (in press) and by Dzik and Jażdżewski (1978). The following stages were distinguished: adolescent, sub-adult and adult.

Alimentary tract filling of krill was determined in 100 individuals from a sample according to a 5-degree scale (Wolnomiejski, Witek and Czykieta, in press):

1 — lack of alimentary tract content, stomach and hepatopancreas without colour,
2 — food only in stomach, gut empty,
3 — stomach and cephalothorax gut part filled,
4 — faeces in gut reaches less than half of the length of abdomen,
5 — faeces in gut reaches more than half of the length of abdomen.

In order to follow the diurnal feeding cycle, individuals of stage 1 were not taken into consideration because these were as a rule animals after moulting which do not feed till the new carapace hardens (Witek, Soszka and Sołończyk 1979).

3. Results

3.1. Vertical distribution of aggregations against the environmental conditions

The studies covered a large area (Fig. 1), differentiated as regards topography, hydrological characteristics, phytoplankton density and krill population composition. Because of considerable time during which the observations

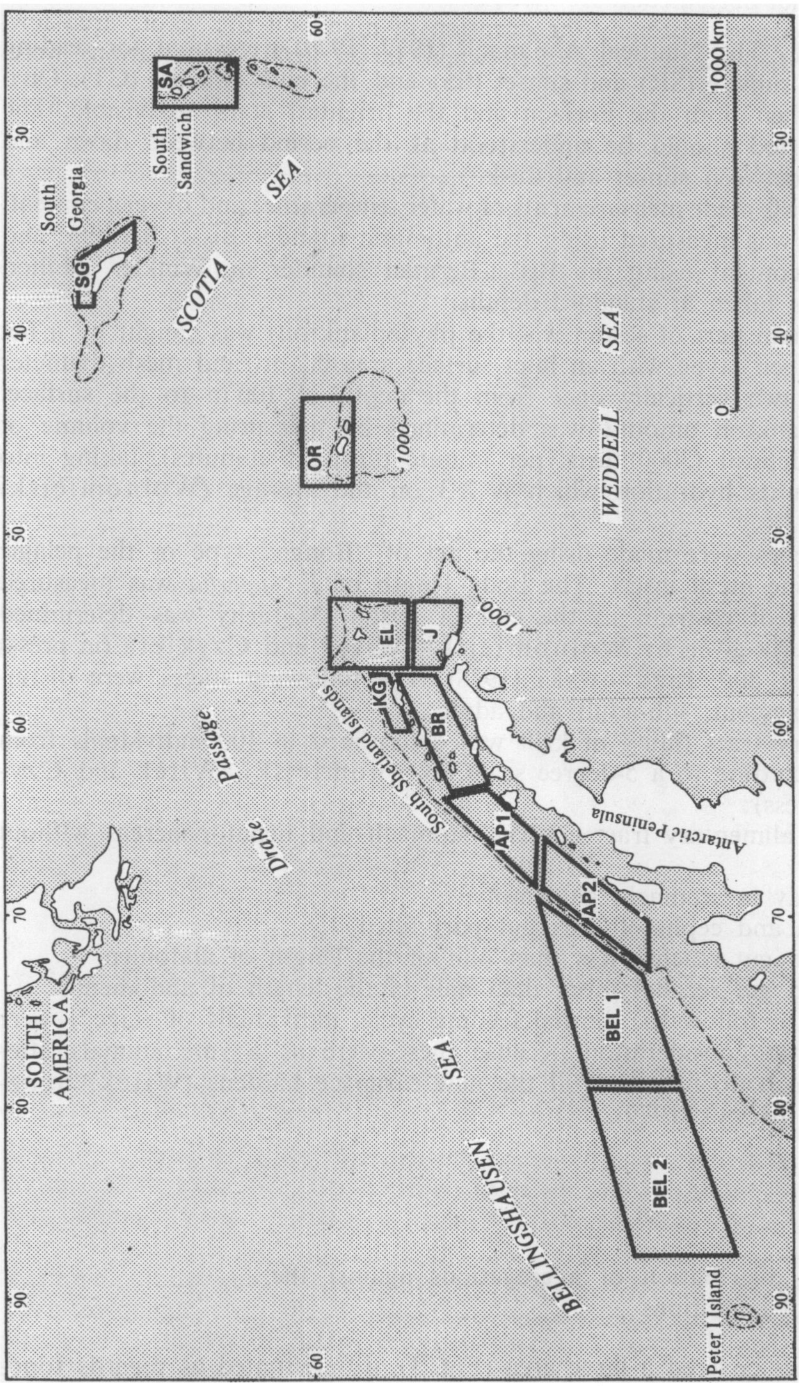

Fig. 1. Distribution of research regions

BEL_1 — eastern part of Bellingshausen Sea, BEL_2 — western part of Bellingshausen Sea, AP_1 — northern part of Antarctic Peninsula, AP_2 — southern part of Antarctic Peninsula, BR — Bransfield Strait, KG — King George Island, EL — Elephant Island, J — Joinville Island, OR — South Orkney, SA — South Sandwich, SG — South Georgia.

were made (from December to March) and because of various latitude zones, particular pariods of investigations varied also as regards characteristics of illumination and especially the duration of night. Of the whole area few regions were distinguished (Table I), where larger krill concentrations were

Table I

Research regions and characteristics of collected material

Region	Month and year	Number of observation days	Number of recorded krill aggregations	Number of krill samples analysed	Number of sites
South Orkney	Dec. 1978	3	1197	3	11
South Sandwich	Jan. 1979	2	337	2	7
Elephant Island I	Jan. 1979	5	1636	4	9
Joinville Island	Jan. 1979	3	713	2	9
Bransfield Strait	Jan., Feb. 1979	4	535	2	12
Antarctic Peninsula I	Feb. 1979	5	1490	3	11
Antarctic Peninsula II	Feb. 1979	3	1046	2	7
Bellingshausen Sea I	Feb. 1979	3	808	3	5
Bellingshausen Sea II	Feb. 1979	3	896	3	6
King George Island	Feb. 1979	4	777	1	6
Elephant Island II	Feb. 1979	3	278	3	5
South Georgia	Apr. 1977	13	1478	22	14

found (> 1000 tons·NMile^{-2}) and which had quite similar characteristics of environment and *E. superba* populations occurring there. Diurnal vertical distribution of krill aggregations in particular regions varying as regards environmental conditions was different (Figs. 2—10). Some of these regions, although not much differentiated in biotope, because of their vastness, were not homogenous from the point of time zone and the duration of night and day, and thus required a division into sub-regions. Illustrations of vertical distribution of krill aggregations include typical for the given region diagrams of water temperature and data of water oxygenation whenever available (Figs. 2—10) and also phytoplankton density in particular regions (Table II).

Studies on the South Orkney were carried out at the turn December 1978. Night were short — 2.5 hours and not very dark. Minimal luxometer

Table II

Seston density in the layer 0—100 m in particular regions

Region	Seston volume ($ml \cdot m^{-2}$) mean	Standard deviation
South Orkney	1.8	±3.3
South Sandwich	85.3	±28.2
Elephant Island — January	4.3	±6.8
Elephant Island — February	0.8	±0.6
Joinville Island	6.7	±5.2
Bransfield Strait	1.3	±1.4
Antarctic Peninsula northern part	28.9	±27.2
Antarctic Peninsula southern part	30.7	±16.4
Bellingshausen Sea eastern part	3.8	±1.6
Bellingshausen Sea western part	11.4	±20.4
King George Island	0.5	0
South Georgia	1.7	±2.0

indications were about 1 lx. Large part of the water surface area was covered with ice, especially the shelf waters. The water was poorly stratified thermally and the surface layer was mixed down to the depth of 80 m and even deeper. High water oxygenation exceeded 80% even at the depth of 200 m. Phytoplankton was scarce, usually less than 1 $ml \cdot m^{-2}$. Adult krill 40—50 mm in length occurred here as well as juvenile krill 20—35 mm in length. At night the krill occurred in a narrow surface layer 20 m deep. At dawn the upper limit of aggregation occurrence decreased to the depth of 40 m, whereas the lower one exceeded 100 (Fig. 2A). After noon some aggregations moved towards the surface to the depth of some 10 m, whereas other remained in deeper parts of water. At sunset other aggregations moved up towards the surface and remained in the 20 m layer.

The region of South Sandwich was penetrated in the first days of January 1979. The night was dark and lasted 4.5 hours. The luxometer deflections at the time was below 0.1 lx. The water was visibly stratified

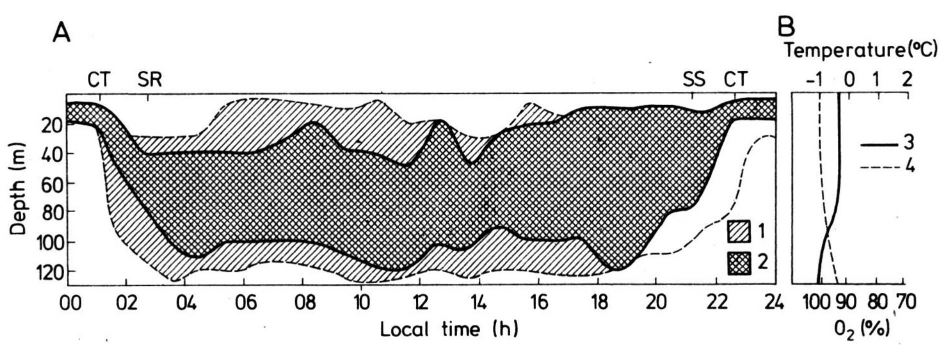

Fig. 2. Vertical distribution of krill aggregations (A) water oxygenation and temperature (B) in the South Orkney region

1 — area of recorded krill aggregations, 2 — area of recorded krill aggregations over 100 kg of weight, 3 — water oxygenation, 4 — water temperature, CT — civil twilight, SR — sunrise, SS — sunset.

although differences in temperatures between the surface layer of summer and winter modifications and the deep layer were not great (Fig. 3B). The surface layer was mixed down to some 20 m. Phytoplankton occurred abundantly, in some places more than 100 ml·m^{-2}. The krill in this region was exceptionally big — 50—60 mm in length. Adult females with ovaries full of eggs dominated. At night krill aggregations were in the 20 m layer. At the morning "interim" period the lower limit of occurrence gradually decreased to 120 m and the upper one to 60. During day time above 60 m no aggregations were found. At dusk the lower limit of occurrence was again 20 m, but this was happened quicker than the morning decrease (Fig. 3).

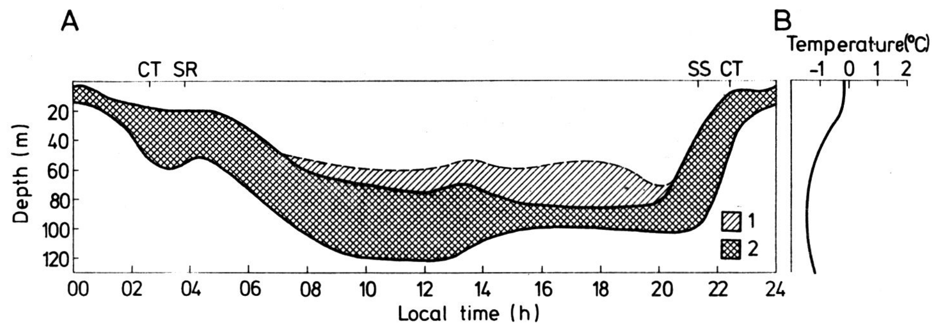

Fig. 3. Vertical distribution of krill aggregations (A) and water temperature (B) in the region of South Sandwich
For explanations see Fig. 2.

In the region of Elephant Island studies were carried out twice: in the third decade of January and in the third decade of February 1979. At the first date the 4-hour night was relatively clear with minimum illumination about 1 lx. At the second date the night was dark and much longer — 8.5 hours. The illumination at night was less than 0.1 lx. This area was not homogenous as regards thermal stratification. Surface water was in general warmer than deeper layers, but the thickness of mixed layer varied between 20 and 50 m and even 70 m (Fig. 4B). Still, warmer deep water was only discovered on sites beyond the shelf on the side of Drake Passage. In the shelf zone there was less than 1 ml·m^{-2} of phytoplankton, beyond the shelf — from several to 20 ml·m^{-2}. Here were also aggregations of adolescent krill of body length 40—50 mm, and of adult krill of body length 40—45 mm. In January the contribution of adolescent krill was higher than in February. In January at night the krill occurred in a layer down to 40 m, at dawn this decreased to 90 m (lower limit), whereas the upper limit did not decrease more than by 25 m. After noon the aggregations occurred from 10 to more than 120 m of depth. At dusk the aggregations moved upwards to the lower limit of 40 m. In February the reaction of aggregations to light was rather similar, but because of a longer night they remained longer in the surface layer. During the day, between 10 a.m. and 2 p.m., in February the upper limit of occurrence of the majority of aggregations took place deeper than in January — about 70 m (Fig. 4A).

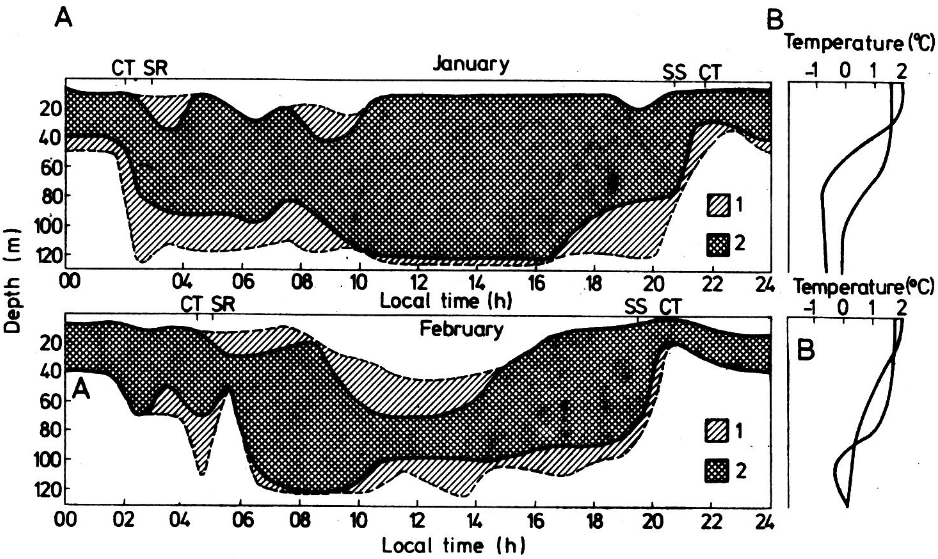

Fig. 4. Vertical distribution of krill aggregations (A) and temperature of water on different sites (B) in the region of Elephant Island
For explanations see Fig. 2.

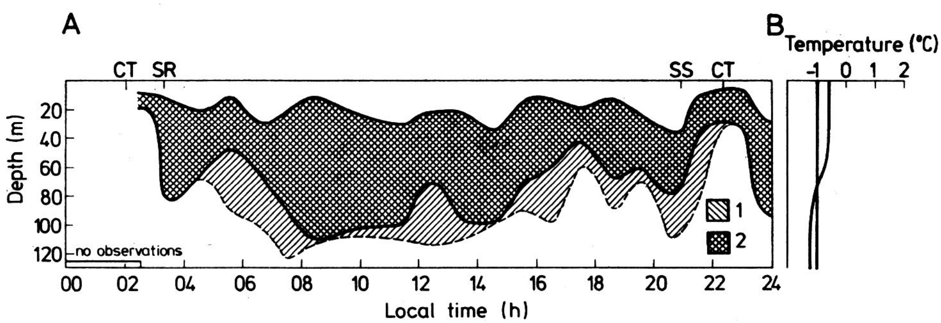

Fig. 5. Vertical distribution of krill aggregations (A) and temperature of water on different sites (B) in the region of Joinville Island
For explanations see Fig. 2.

In the shelf region of Joinville Island, closed from the south by an ice border, the studies were conducted at the end of January 1979. The 4-hour night was relatively clear and the illumination was about 1 lx. Water having a negative temperature was either poorly stratified thermally or there was no stratification at all down to the bottom (Fig. 5B). Phytoplankton occurred up to a dozen or so ml$\cdot$m^{-2}. Krill aggregations consisted of adolescent individuals, mostly 32—45 mm in length. Also juvenile krill 20—30 mm in length was observed. The night observations of aggregations were not complete. At dawn the lower limit of occurrence decreased at first to 80 m and at 8 a.m. down to 100 m (Fig. 5A). The upper limit during the day was 20—30 m. After noon the aggregations remained closer to the surface in the layer

20—60 m. At the evening the lower limit increased up to 40 m. At dusk aggregations were found even at the depth of 90 m.

The waters of Bransfield Strait were penetrated at the turn of February 1979. Night in this region lasted 4.5 hours and was clear. Illumination was about 1 lx. Surface water was mixed to the depth of 20—30 m (Fig. 6B). But below this layer only a slight drop in temperature was observed. Phytoplankton occurred in small quantities, usually below 1 ml$\cdot$m^{-2}. The krill occurring there was adolescent, the majority of species measuring 40—50 mm, At night the krill occurred mainly in the layer down to 30 m (Fig. 6A). In the morning the lower limit decreased at first down to 80 m and then at 8 a.m. down to 120 m. The upper limit during day time was at the depth of 20 m. In the evening the aggregations gradually moved upwards staying in the 30 m layer.

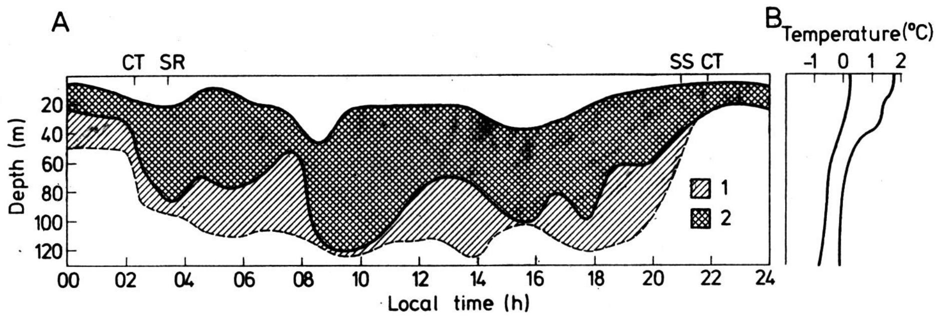

Fig. 6. Vertical distribution of krill aggregations (A) and temperature of water on different sites (B) in the region of Bransfield Strait
For explanations see Fig. 2.

Northern part of the vast shelf region of the Antarctic Peninsula was investigated twice: in the first days of February 1979 and a fortnight later, whereas the southern was investigated only in the first decade of February 1979. The night in the northern part lasted 6.5 hours, whereas in the southern part — 4.5 hours. Illumination at night in the northern part was 1 lx and in the southern part — 0.5 lx. From the hydrological point of view these waters were quite homogenous. Layers of surface water of winter and summer modifications were very distinct which means that they were not mixed much. The thickness of mixed surface layer was about 30 m in the northern part and about 50 m in the southern part (Fig. 7B). Surface water of the winter modification was characterized by very low temperature -1.3 to -1.8°C. Another distinguishing feature of this area was a fast, as compared with other regions, decrease in water oxygenation with the increasing depth. Oxygenation less than 80% was already recorded at the depth of 70—100 m (Fig. 7B). Phytoplankton occurred in quite large quantities, usually several tens of ml$\cdot$m^{-2}. Krill aggregations, both at night and days, occurred in a layer of almost identical thickness and at a relatively small depth not exceeding 60 m (Fig. 7A). The reaction to illumination in the "interim" periods was slight and concerned only the lower limit of aggregations range: 30 m at night and 60 m during the day.

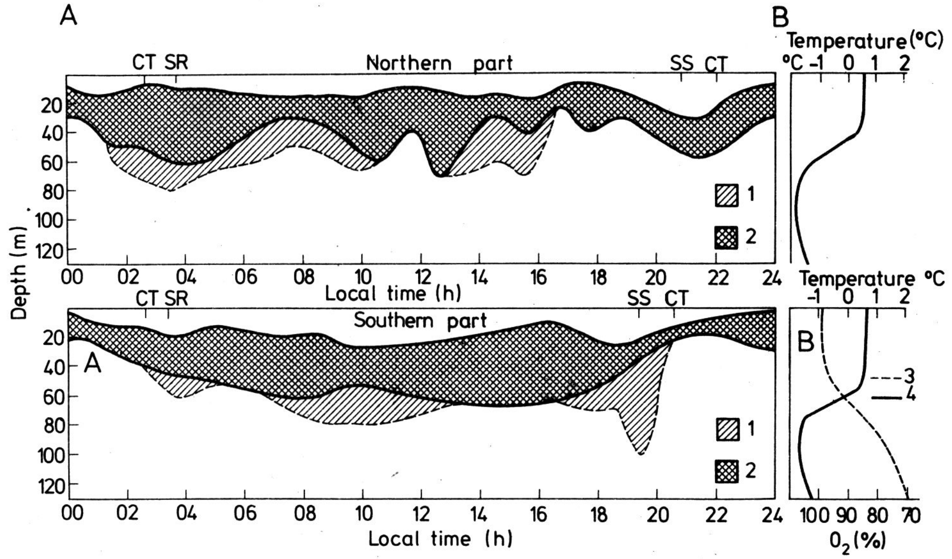

Fig. 7. Vertical distribution of krill aggregations (A), water oxygenation and temperature (B) in the region of Antarctic Peninsula
For explanations see Fig. 2.

In the deep waters of the Bellingshausen Sea the investigations were conducted in the second decade of February 1979. The nights were clear and lasted 5.5 hours in the eastern part and 0.5 hour less in the western part. Illumination at night was about 1 lx. Similarly as in the region of

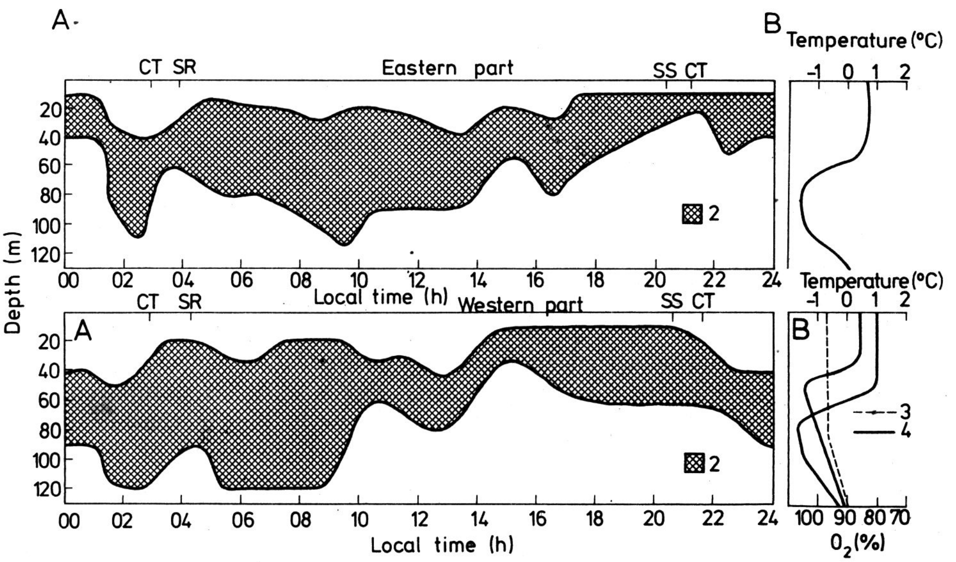

Fig. 8. Vertical distribution of krill aggregations (A), water oxygenation and temperature (B) in the region of Bellingshausen Sea
For explanations see Fig. 2.

the Antarctic Peninsula the thermal stratification of water was very distinct and the water was not mixed much beyond the 20—50 m surface layer (Fig. 8B). Oxygenation in the western part of the region dropped below 80% only at the depth of 180 m. The phytoplankton on the major part of the area remained on the level of several ml·m^{-2} and increased near Peter I Island. The krill here was adolescent, subadult and adult within the length range 42—55 mm. Frequent presence of eggs in females, but not too abundant, indicated that this was a population before reproduction. In the eastern part of the region the krill at night occurred in the layer down to 40 m (Fig. 8A). After the sunrise with the increasing illumination the lower limit moved downwards to 80—100 m and moved again upwards at noon hours. The upper limit of occurrence of aggregations at day time was 20—40 m, whereas in the evening and at night it was getting closer to the surface. In the western part of the region the aggregations at night occurred relatively deep, between 40 and 90 m (Fig. 8A). In the morning they occupied a broad layer from 20 to 120 m. In the afternoon krill usually occurred at the depth of 10—60 m.

Small, shallow water region of the King George Island was investigated in the third decade of February 1979. The night was dark and lasted 8 hours. Illumination was below 0.1 lx. Mild temperature drop from the surface down to the bottom indicated deep water mixing (Fig. 9B). Phytoplankton occurred in amounts smaller than 1 ml·m^{-2}. Adolescent krill, 40—50 mm in length, occurred there as well as juvenile krill of a body length 25—35 mm. At night krill aggregations occurred in a broad layer from 10 to 80 m, in the morning down to 120 m (Fig. 9A). The aggregations did not react specially to daylight, only the upper limit decreased to the level of 20—40 m. About 7 a.m. the limits of occurrence became stratified and this lasted till 11 a.m. The upper limit was 30—60 m and the lower one — 90—120 m. In the afternoon aggregations were observed again from 20 to 110 m of water depths. In the evening the lower limit of occurrence of aggregations increased for a short time, but at night they became more scatterred at greater depths.

South Georgia region, extremely interesting as regards the occurrence of krill, was investigated three times in 1978/1979 and only the last time in March 1979 the krill was found in large quantities. Unfortunately the

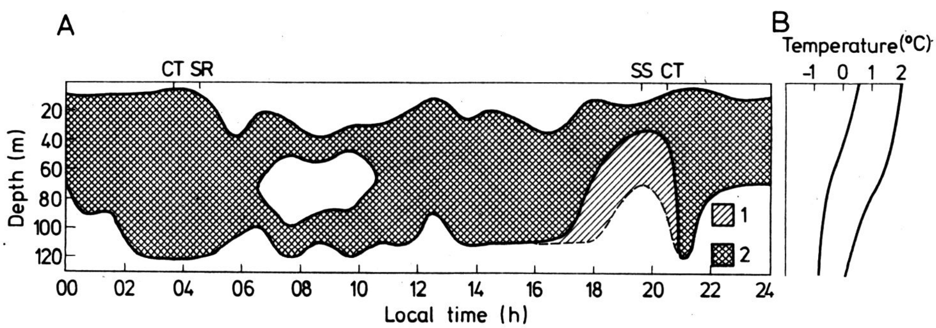

Fig. 9. Vertical distribution of krill aggregations (A) and temperature of water on different sites (B) in the region of King George Island
For explanations see Fig. 2.

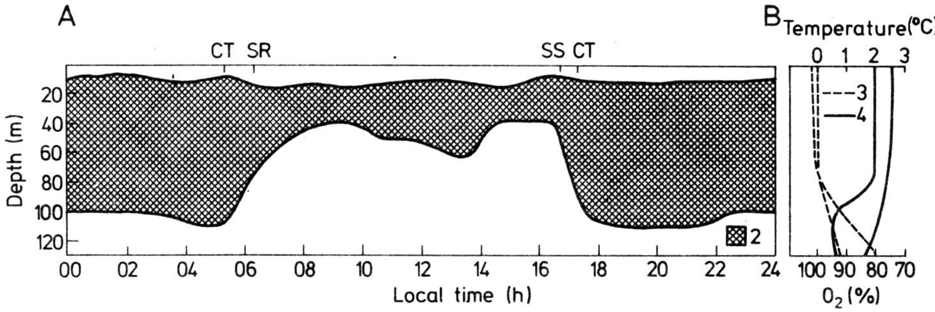

Fig. 10. Vertical distribution of krill aggregations (A), water oxygenation and temperature on different sites (B) in the region of South Georgia
For explanations see Fig. 2.

observations carried out were not sufficient to illustrate fully the diurnal vertical distribution of krill. Thus in order to present the behaviour of krill in the region of South Georgia the data for April 1977 were used. The night then was very long and dark and lasted 12 hours. Illumination was below 0.1 lx. Civil twilight lasted very shortly, up to 40 minutes. The thickness of mixed water layer was 50—100 m and sometimes reached even the bottom of this shelf water area, thus proving higher vertical turbulence (Fig. 10B). Oxygenation of surface waters was high and decreased below 80% only at the depth 130—200 m. Phytoplankton was found in trace amounts below 1 ml$\cdot$m^{-2}. Krill population consisted of adolescent individuals of a body length 35—55 mm. It was characteristic in this region that the krill showed

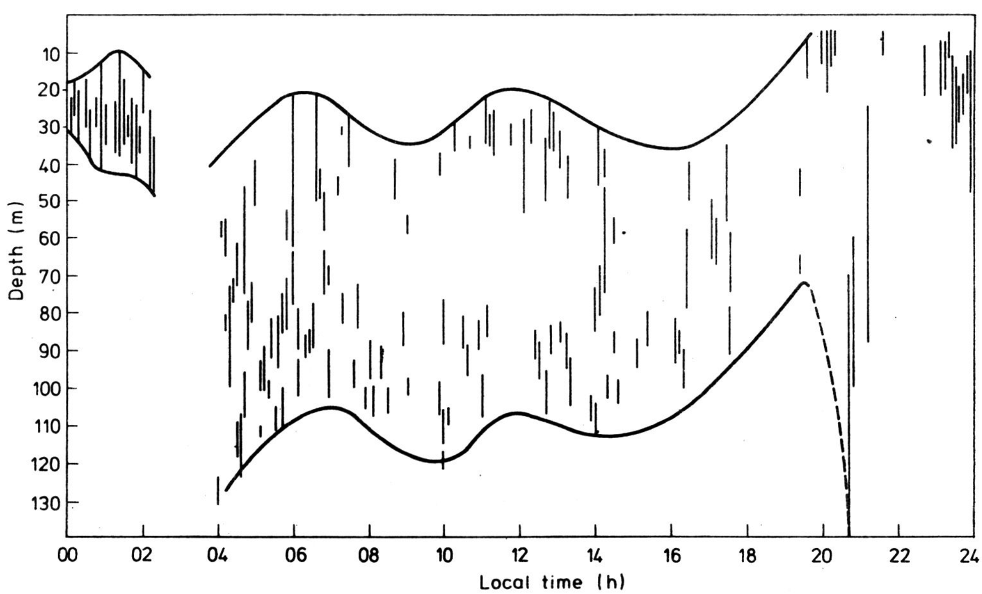

Fig. 11. Vertical distribution of krill aggregations on February 19, 1979 in the region of King George Island
Thick line — limits of occurrence of all aggregations, vertical lines — particular aggregations.

dispersed occurrence from the surface down to the depth of 120 and more, and this began at dusk and lasted till dawn (Fig. 10A). At day time the majority of aggregations occurred in the upper water layer, from several metres to 40—60 m. In the region of South Georgia the krill aggregations occasionally observed were exceptionally high, much higher than anywhere else. This phenomenon took place in the same small water area to the north of Clercke Rocks in April 1977 and in March 1979. This aggregation covered several nautical miles and almost the whole water depth, from the bottom at the depth of 250—300 m almost to the surface, regardless of the time of day. Mean density of aggregations was 500 $g \cdot m^{-3}$, i.e., it contained a large amount of crustaceans — some several hundreds of thousands tons.

Not many observations were made for a longer time in one place as to allow to trace the vertical spreading of the same aggregations. Still, e.g., in February 19, 1979 during 12-hour observation on similar positions on the Drake Passage and to the north of King George Island (61°49—59′S, 59—60°W) cyclic fluctuations of the lower and upper depth limits of occurrence of aggregations were observed (Fig. 11). A characteristic of these fluctuations of an amplitude of 15 m and during 5 hours allows to assume that this was caused by inner wave motion.

3.2. Rate of vertical migrations of krill aggregations

The analysis of this phenomenon, usually observed during the "interim" periods of dawn and dusk, is shown in Figure 12. From diagrams of the mean occurrence of krill aggregations (H) and corresponding in time diagrams of illumination (log I) the ratios $\Delta H/\Delta t$ and $\Delta \log I/\Delta t$ were determined for particular days. ΔH — change of depth of aggregation occurrence (at Δt time) $\Delta \log I$ — change of illumination (at time Δt). Thus a set of points was obtained which characterized the mean rate of vertical migrations of aggregations depending on the rate of illumination changes in the morning and evening periods (Fig. 13). The rate of changes of the depth of occurrence increased with the rate of illumination changes. But this depended on the difference of depth at which the aggregations occurred day and night. The mean rate of subsidence of aggregations was 0.4—1.0 $m \cdot min^{-1}$, of rising 0.01—0.7 $m \cdot min^{-1}$. The described vertical migrations took place at illumination changing from 1 to 1000 lx.

3.3. Diurnal feeding rhythm of krill

The analysis of alimentary tract filling of krill caught at different times of day (Table III) shows that the most intense feeding occurred at night when the krill was in the upper water layer. The lowest alimentary tract filling was observed in krill caught during the day, especially before noon. In the afternoon the degree of alimentary tract filling increased gradually which proved that part of the population at least began feeding around noon.

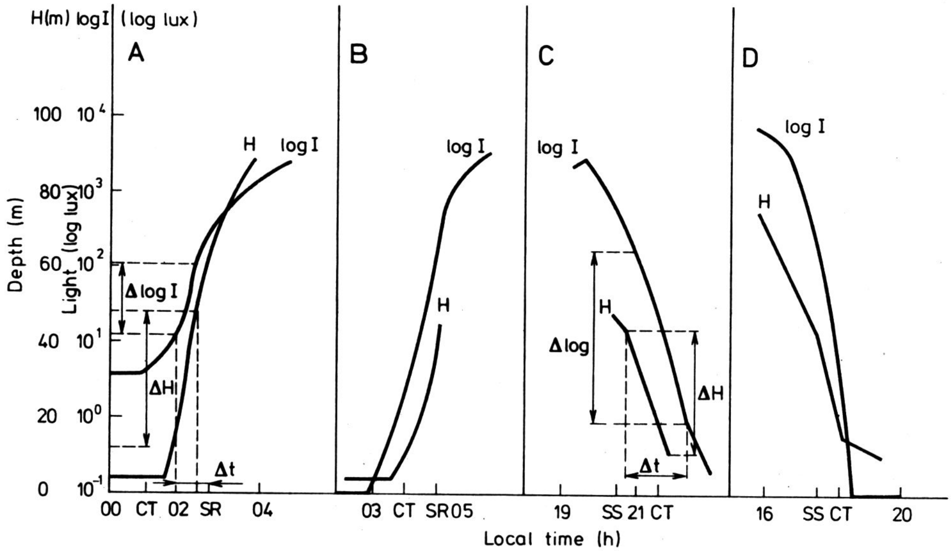

Fig. 12. The rate of changes of the depth of krill occurrence on particular days A — 31 Dec. 1978, $\Delta H/\Delta t = 0.69$ m·min^{-1}, $\Delta \log I/\Delta t = 0.029$ log lx·min^{-1}, B — 24 Feb. 1979, $\Delta H/\Delta t = 0.78$ m·min^{-1}, $\Delta \log I/\Delta t = 0.33$ log lx·min^{-1}, C — 22 Jan. 1979, $\Delta H/\Delta t = 0.48$ m·min^{-1}, $\Delta \log I/\Delta t = 0.02$ log lx·min^{-1}, D — 15 Mar. 1979, $\Delta H/\Delta t = 0.61$ m·min^{-1}, $\Delta \log I/\Delta t = 0.057$ log lx·min^{-1}. CT — civil twilight, SR — sunrise, SS — sunset. Detailed explanations in the paper.

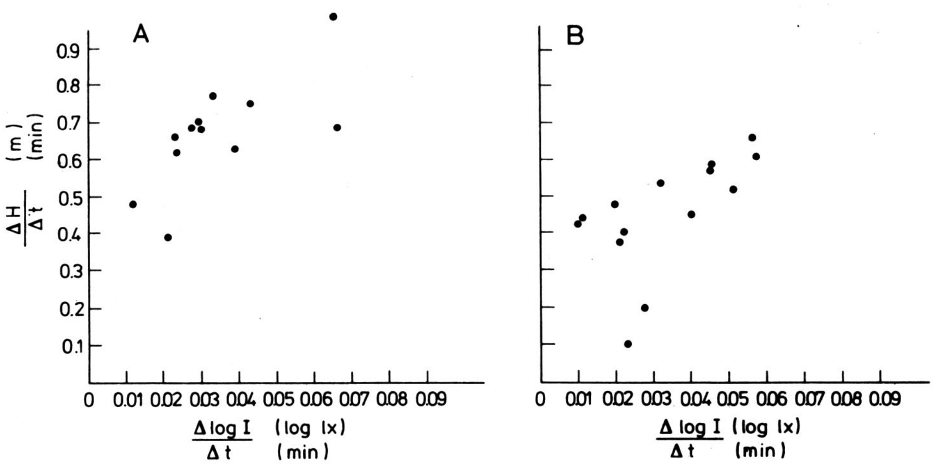

Fig. 13. Relation between the rate of changes of aggregations occurrence (Y-axis) and the changes in illumination (X-axis)
A — at dawn, B — at dusk

4. Discussion

Krill aggregations occurred within the area of Antarctic Surface Water in layers of summer and winter modification, usually down to the depth of 100—120 m.

Table III
Mean alimentary tract filling of krill depending on the time of day and night
acc. to observations in 1978/1979

Hours of observation	Mean alimentary tract filling	Standard deviation
00—04	4.46	±0.28
04—08	4.32	±0.26
08—12	3.94	±0.43
12—16	4.25	±0.38
16—20	4.29	±0.45
20—24	4.47	±0.11

The data confirm Pavlov's (1974) opinion that diurnal vertical krill migrations are directly connected with the feeding of these animals. Feeding takes place first of all at night and for this period krill moves to a layer with higher phytoplankton density. Observations of vertical seston distribution, where phytoplankton is the main component, in the regions of Antarctic Peninsula and South Georgia in 1976/1977 have been carried out by Fischer (1977). A comparison of these data with the hydrological situation shows that where the water stratification is present the algal suspension concentrates in the upper layer of waters of summer modification or sometimes in the thermocline layer. In water mixed at great depths, as for example in the region of the shelf of South Georgia, the seston was quite evenly distributed in water depths. As it can be easily noticed, the behaviour of krill at night was similar. In waters with developed layer of surface heated waters the krill fed in a relatively narrow layer at the surface (regions of North Sandwich, Elephant Island, Bransfield Strait, Antarctic Peninsula, eastern part of the Bellingshausen Sea) or on the level of thermocline (western part of the Bellingshausen Sea). In water strongly mixed vertically (regions of King George Island and South Georgia), where phytoplankton did not occur abundantly, the krill occurred at night in a wide range of depths, although its first reaction to lower illumination at dusk was the movement of aggregations to the surface. During the day krill aggregations were usually deeper than at night, but in many cases part of the population, especially in the afternoon, remained in the upper, more abundant in phytoplankton, layer thus having a possibility of feeding at this time of day also. Therefore the range of occurrence depth of aggregations during the day was usually greater than at night. The exception were regions with high phytoplankton biomass (South Sandwich, Antarctic Peninsula) where animals easily fulfilled their food requirements at night and they did not need to feed additionally during the day. General regularities as regards the diurnal vertical distribution of krill aggregations are shown in Table IV. Vertical migrations of krill aggregations, and thus the beginning and breaks in feeding by the majority of population, were directly connected with the change of illumination and took place at civil twilight. The depth of upper limit of occurrence of aggregations during the day was the highest in the South Sandwich region,

Table IV

Behaviour of krill day and night

Time of day and night	Vertical distribution	Feeding	Escape reactions
Night	in the layer of phytoplankton accumulation (usually upper water layers)	yes	low
Day before noon	in lower and middle water layers	no	high
Afternoon	in lower, middle and upper water layers	no or possibly yes for part of the population	high

where in previous years great transparency of water had been observed (Wensierski and Woźniak 1978). Still, in this region the krill was very big and it had the highest passive subsidence rate because of its body weight. The rate of morning subsidence of krill is definitely higher than the evening rising rate and thus indicates that it is a least partially a passive movement and may explain the earlier in the day occurrence of bigger individuals at greater depths than the smaller ones (Wolnomiejski, Witek and Czykieta in press).

The Antarctic Peninsula waters was the one where the krill aggregations remained practically day and night in the near to surface layer 60 m deep. According to observations in this region the decrease of water oxygenation was exceptionally fast with the increasing depth. With consideration to results of Kils (1979) a conclusion may be drawn that low water oxygenation made it impossible for krill to stay in deeper parts. Still during investigations conducted in the same region of Antarctic Peninsula shelf in February 1977, regular occurrence of aggregations was recorded at depths at which, similarly as in 1979, the oxygen contents were low (Witek et al., in press).

Another interesting phenomenon, observed in the South Georgia region, as the limited lower limit of aggregations occurrence only to the depth 50—60 m, at day time, whereas at night krill reached even the depth of 100 m. Such behaviour of aggregations was not exceptional as it had been observed earlier (Kalinowski 1978). Perhaps this was due to the escape from fish living in the shallow shelf of this region, much more distinct during the day than at night (Witek, Soszka and Sołończyk 1979). The most common fish species there: *Notothenia rossi marmorata* Fischer, *N. gibberifrons* Lönnb., *Pseudochaenichthys georgianus* Norm. and *Champsocephalus gunnari* Lönnb in 1976/1977 fed mainly on krill (Wolnomiejski et al. 1977).

It is known that the fishing grounds of South Georgia are the most abundant in the Antarctic. The above mentioned fish species have been frequently found in seine nets drawn for krill.

The rules of vertical distribution of aggregations have proved to be the same for adolescent and subadult krill and for a population of adult individuals but not during reproduction. The juvenile krill found in some regions was only a very small part of the population. In the material of Polish Antarctic Expeditions there are data on the vertical distribution of krill during reproduction and on migrations of aggregations consisting of juvenile individuals which prove something slightly different and should be elaborated separately.

The depth of occurrence at various times of day and night is one of the most frequently discussed in literature aspect of vertical migrations of krill. Hardy and Gunther (1935) and Marr (1962) have recorded the occurrence of krill during day down to he depth of 160 m, whereas at night — down to 70 m, but main concentrations at day time occurred between 10 and 40 m and at night in sub-surface layers. Ševcov and Makarov (1969) have described vertical distribution of krill aggregations in different regions of the Atlantic Sector of Antarctic. They have observed that both at night and during the day the range of occurrence was similar and did not exceed 70 m, but during the day the krill concentrated at the water surface. Pavlov (1974) has described a diurnal cycle of movements of krill aggregation against the feeding process. He has pointed out the 12-hour periods in vertical distribution. At the subsurface zone krill occurred between 10 p.m. to 2 a.m. and between 10 a.m. and 2 p.m. for feeding, and apart from this it aggregated at depths 20—70 m. Fisher (1976) has found krill mainly down to the depth of 50 m and sometimes even down to 80 m in the region of South Georgia, South Orkneys and South Shetlands. Mohr (1976) described the reaction of krill aggregations to day illumination in the region of South Sandwich which was a strong one only at dawn. At night krill concentrated at the surface down to the depth of 20 m, in the morning when illumination changed from 0.1 to 1000 lx it quickly subsided down to the depth of 110 m. During the day krill slowly moved to the surface attaining the subsurface layer in the afternoon when the illumination was still quite high.

Comparison of our results to the literature data shows that:

— in the majority of regions krill occurred at the surface, but during the day it frequently exceeded the depth of 100 m. This is consistent with conclusions of the majority of authors, but differs slightly from the description given by Ševcov and Makarov (1969),

— surface aggregations as described by Ševcov and Makarov (1969) and Pavlov (1974) were not observed,

— no regular 12-hour rhythm both of vertical migrations and feeding, as described by Pavlov (1974) were not observed,

— change in the depth of diurnal occurrence of aggregations, especially in the morning, was caused by a change of illumination. A similar phenomenon was described by Mohr (1976).

5. Conclusions

1. Krill aggregations occurred within the Antarctic Surface Water usually down to 100—120 m.

2. Vertical migrations of krill aggregations were controlled by diurnal light cycle and were connected with the feeding rhythm of these crustaceans.

3. Feeding took place mainly at night and additionally in the afternoon.

4. Distribution of krill at night depended on the vertical distribution

of phytoplankton which depended considerably on the mixing intensity and stratification of water.

5. Distribution of krill during day time depended on the degree of satisfying the food demands during night feeding, on the size of individuals, direction of effect of stimuli resulting in escape reaction and perhaps also on the transparency of water and its oxygenation.

6. The rate of vertical migrations of krill aggregations depended on the rate of illumination changes at civil twilight.

7. The morning subsidence of krill was deeper and had partly a passive character.

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6. Summary

During the IV Polish Marine Antarctic Expedition in 1978/1979 in the sector of Antarctic, from South Sandwich in Scotia Sea to Peter I Island in Bellingshausen Sea, complex research and measurements were carried out as regards the hydroacoustic location of krill aggregations, changes in diurnal illumination, thermal stratification and water oxygenation, phytoplankton distribution, feeding and composition of krill population.

The studies were carried out in order to describe general regularities of diurnal vertical distribution of krill aggregations and to point to these environmental factors which decide about the course and range of vertical migrations.

The results allowed to confirm a close relation between the rhythm of vertical migrations and feeding of krill. Krill as a rule fed at night (Table III) remaining in the zone of highest phytoplankton concentration. During the day the lower limit of aggregation occurrence usually decreased down to 100—120 m, whereas the upper limit frequently, especially in the afternoon, remained in the zone more abundant in algal suspension. Thus part of krill population could feed additionally during the day which was of great significance in regions poor in phytoplankton or in those where the night was very short.

Vertical migrations of aggregations were directly connected with the change of illumination and occurred at civil twilight (Fig. 13). The mean rate of morning subsidence of aggregations was 0.4—1.0 $m \cdot min^{-1}$ and was quicker than the evening rate for rising (0.1—0.7 $m \cdot min^{-1}$) (Fig. 12).

The character of diurnal vertical distribution of aggregations depended on abundance and distribution of phytoplankton conditioned by the intensity of water mixing. In some situations water oxygenation and pressure of predators feeding on krill could have been of significance.

7. Резюме

Во время IV Польской Морской Экспедиции в период антарктического лета 1978/1979 в секторе Антарктики от Острова Петра I в море Беллингсхаусена до Южных Сандвичевых Островов в море Скотия проведено комплексные исследования в объёмв гидроакустической локализации скоплений крыля, изменений силы дневного света в суточном цикле, термической стратификации, степени насыщенности воды кислородом, размещения фитопланктона, питания и состава популяции крыля.

Исследования проведились с целью описать главные правильности вертикального распределения скоплений крыля в сутки а также указать эти факторы среды, которые существенно действуют на ход и объём вертикальных миграции.

Полученные результаты подтвердили тесную связь ритма вертикальных миграций с питанием крыля. Крыль в основном питался ночью (таблица III) пробывая в это время в зоне большей концентрации фитопланктона. В течение дня нижняя граница выступления скоплений обычно понижалась до глубины 100—120 м, зато верхняя оставалась часто, особенно в вечерных часах в зоне более богатой в взвесь водорослей. Таким образом часть популяции крыля могла добавочно питаться днём. Это имело существенное значение в районах бедных в фитопланктон или там, где ночь особенно короткая. Вертикальные миграции скоплений непосредственно связаны с изменениями силы освещения. Они происходили во время рассвета и заката (рис. 13). Средний темп раннего падания скоплений равнялся 0,4—1,0 м·мин$^{-1}$ и был скорее темпа вечернего подъёма (0,1—0,7 м·мин$^{-1}$) (рис. 12).

На характер вертикального распределения скоплений в сутки влияли богатство и размещение биомассы фитопланктона обусловлены интенсивностью процессов вымешивания воды. В некоторых ситуациях могли проявлять значение такие факторы как насыщенность воды кислородом а также давление хищников кормящихся крылем.

8. Streszczenie

W trakcie IV Polskiej Morskiej Wyprawy Antarktycznej w okresie lata antarktycznego 1978/1979, w sektorze Antarktyki od wysp Płd. Sandwich w Morzu Scotia do Wyspy Piotra I w Morzu Bellingshausena prowadzono kompleksowe obserwacje i pomiary w zakresie hydroakustycznej lokalizacji skupień kryla, zmian natężenie światła dziennego w cyklu dobowym, stratyfikacji termicznej i natlenienia wody, rozmieszczenia fitoplanktonu, odżywiania się i składu populacji kryla.

Badania miały na celu opisanie generalnych prawidłowości pionowego rozmieszczenia skupień kryla w ciągu doby oraz wskazanie tych czynników środowiska, które w istotny sposób oddziaływują na przebieg i zakres zjawiska migracji pionowych.

Uzyskane wyniki pozwoliły potwierdzić ścisły związek rytmu migracji pionowych z odżywianiem się kryla. Kryl zasadniczo żerował w nocy (tabela III), przebywając w tym czasie w strefie największej koncentracji fitoplanktonu. W ciągu dnia dolna granica występowania skupień zwykle obniżała się do głębokości 100—120 m, natomiast górna granica pozostawała często, zwłaszcza w godzinach popołudniowych, w strefie bardziej zasobnej w zawiesinę glonów. W ten posób część populacji kryla mogła dodatkowo odżywiać się w dzień, co miało istotne znaczenie w rejonach ubogich w fitoplankton lub tam, gdzie noc trwała szczególnie krótko.

Pionowe wędrówki skupień bezpośrednio związane były ze zmianą intensywności oświetlenia i przypadały na okres świtu i zmierzchu (rys. 13). Średnie tempo rannego opadania skupień wynosiło 0,4—1,0 m·min.$^{-1}$ i było szybsze od tempa wieczornego wznoszenia się (0,1—0,7 m·min.$^{-1}$) (rys. 12).

Na charakter rozmieszczenia pionowego skupień w ciągu doby miały wpływ obfitość i rozprzestrzenianie się fitoplanktonu, uwarunkowane intensywnością procesów mieszania wody. W pewnych sytuacjach znaczenie mogły mieć takie czynniki jak nasycenie wody tlenem oraz presja drapieżników żerujących na krylu.

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