Krill distributions and their diurnal changes (Elephant Island, South Orkney Islands, December 1988, January 1989)*

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Krill
Migration
Distribution

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Abstract

Krill swarms were recorded acoustically along 2340 NM of the ice edge between Elephant Island and the South Orkney Islands. Depth distributions and migration patterns were different in these three regions. It has been suggested that physical factors are the most important for both horizontal and vertical krill distributions.

1. Introduction

While the large scale circumpolar distribution of krill is well documented in the literature (Amos, 1984; Everson, 1977; Makarov, 1983; Makarov *et al.*, 1970; Marr, 1962; Maslennikov, 1980), the mesoscale horizontal and depth distribution patterns are less evident. The reason for this is that these distributions are variable in time, they depend on hydrodynamic changes, the time of year and also the time of day. Marr (1962) and Everson (1977) assumed that krill might migrate to deeper water layers during the winter. Morris and Priddle (1984) described a scattered vertical distribution in winter down to a depth layer of 500–100 m; however, these samples were very

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small. During a winter expedition Siegel (1986) found that 99% of krill in the water column down to 500 m were confined to the upper 60 m. The latest data (Cuzin-Roudy and Schalk, 1989; Marshall, 1989; Siegel *et al.*, 1990; Śpiridonov *et al.*, 1985) show that krill spend the winter under the ice cover, feeding underneath rather than going to deep water like copepods (Voronina, 1984). Summarizing the widespread acoustic data, we see that the major proportion of krill biomass is concentrated above about 150 m (Arimoto *et al.*, 1979; Daly and Macaulay, 1988; Godlewska and Klusek, 1987; Klusek and Godlewska, 1988; Loeb and Shulenberger, 1987; Shevtsov and Makarov, 1969). It is also evident from the net data that the depths most frequently occupied by krill are confined to the upper layer, although the distributions may differ substantially. According to Marr (1962) krill is most abundant in the upper 10 m (depths not seen by the hydroacoustical equipment) while others (Macaulay *et al.*, 1984; Shulenberger *et al.*, 1984) report the absence of krill at the surface at any time of day. Siegel (1985) and Hosie *et al.* (1988) have observed some krill as deep as 300 m. From the available literature it appears that krill depth distributions depend on the region (Everson, 1983; Kalinowski and Witek, 1985; Loeb and Shulenberger, 1987), season (Godlewska and Klusek, 1988; Siegel, 1988) and the time of day (Everson, 1983; Godlewska and Klusek, 1988; Kalinowski, 1978; Kalinowski and Witek, 1980; Tomo, 1983). There are many factors which may account for this variability: the hydrological regime, amount of light and oxygen level, food availability, distribution of predators, etc. Unfortunately the role of none of them is fully understood at present.

In the following paper we would like to fill this gap, at least partly, by considering data from three different regions (Elephant Island, South Orkney, and the ice edge zone) and analysing in detail how depth distributions change with the time of day.

2. Materials and methods

2.1. Study area

Measurements were performed during the austral summer (25 December 1988 – 17 January 1989) between Elephant Island and the South Orkney Islands along the ice edge, covering 2340 NM of a zig-zag track (Fig. 1). The signal of the EK-120 echosounder (SIMRAD, frequency 120 kHz) was integrated at 1 NM intervals and recorded together with exact time, sea depth and position in a 24-hour watch system. Krill swarms were recorded on an IBM/XT computer, which allowed 0.1 m depth resolution down to 105 m. The description of the data acquisition system is presented in

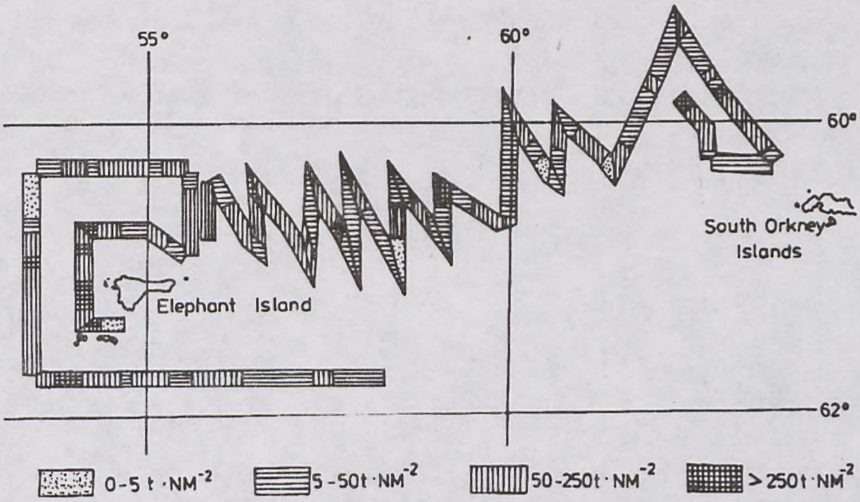

Fig. 1. Krill biomass distribution along the track of the ship. 0–5 $t \cdot NM^{-2}$, 5–50 $t \cdot NM^{-2}$, 50–250 $t_2 \cdot NM^{-2}$, > 250 $t \cdot NM^{-2}$

Godlewska *et al.* (in press). Three different regions can be clearly distinguished in the investigated area on the basis of hydrological (Tokarczyk *et al.*, in press) and biological data (Kittel and Siciński, in press). The western part of the research area – the Elephant Island region – was occupied by surface waters originating from the Bellingshausen Sea, flowing through the Drake Passage and the Bransfield Strait. Krill in this area had a mean body length of 40.3 mm and sexually mature individuals predominated in the population (55.5%). The central and eastern parts of the study region were occupied by surface waters of Weddell Sea origin. East of 49°W – the South Orkney region – the surface layer (down to 45 m) contained relatively warm water of low salinity due to ice melting. Beneath, there was typical Weddell Sea water, the same as in the central area at the ice edge. Krill in the South Orkney Islands region had a mean body length of 41.2 mm and sexually mature individuals were clearly dominant (72.5%). In the central region – the ice edge zone – the water masses were relatively homogenous, the proportion of juveniles was much larger (50%) and the mean length was only 31.9 mm. Hydroacoustic observations showed that these three regions also differed – in the Elephant and South Orkney Islands regions densities of krill were high, while at the ice edge they were about ten times lower.

2.2. Data analysis

Detailed analysis of the acoustic data followed the methods recommended by BIOMASS (1986). Measurements of the returned voltage were made for every 0.1 m, then squared and summed into 10 m depth intervals and averaged for every 1 NM.

For biomass estimates the target strength expression was used in the form (Anon, 1991)

$$TS = -127.45 + 34.85 \log L, \tag{1}$$

and the weight of krill was calculated from the equation (Rakusa-Suszczewski, 1981)

$$W = 0.0018 L^{3.3831}, \tag{2}$$

where

L – length of krill [mm],
W – wet weight of krill [mg],
TS – target strength of krill [dB].

In order to analyse the diurnal changes the data set was divided into 12 time intervals of 2 hours each. The biomass of krill in each of the intervals was taken to be 100%. This was intended to eliminate variations due to differing amounts of krill detected at different times of the day. For each of the intervals the biomass mass centre was calculated according to the formula

$$\overline{H}(t) = \frac{\int_{H_{\min}}^{H_{\max}} H(z) z dz}{\int_{H_{\min}}^{H_{\max}} H(z) dz}. \tag{3}$$

All the analyses were performed separately for the three regions.

3. Results

3.1. Horizontal distribution

The spatial distribution of krill and its abundance along the track of the ship were highly variable (Fig. 1). In the region of Elephant Island, especially north-west of the island, large swarms were dominant. In this area the largest biomass of krill was about 6×10^5 tons (Kalinowski, pers. comm.). The mean density was 101.25 $\mathrm{t \cdot NM^{-2}}$, and the range 2.5–195 $\mathrm{t \cdot NM^{-2}}$. Apart from krill, salpa was also very abundant in this region.

In the South Orkney Islands region salpa was absent and krill was present exclusively in dense compact swarms. Although the overall biomass of krill in this area was smaller than in the Elephant Island region, the densities here were the highest. The mean density was 136.5 $\mathrm{t \cdot NM^{-2}}$ and the range 2.5–1869.0 $\mathrm{t \cdot NM^{-2}}$.

The area between Elephant Island and the South Orkney Islands along the ice edge was the poorest in *E. superba*. Krill occurred mainly in irregular forms, loosely defined layers and small swarms. Salpa was quite

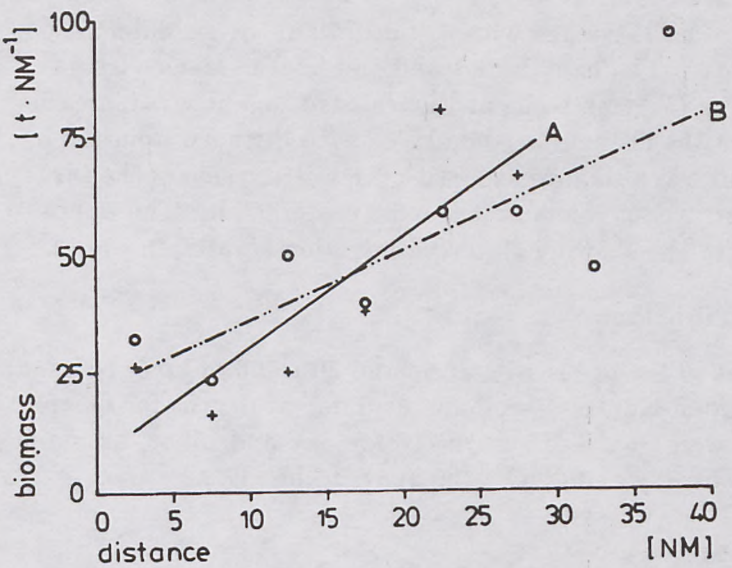

Fig. 2. Regression lines for the change in krill abundance with distance from the ice at the ice edge zone: a – for the meridional segments – B [t · NM^{-2}] = 7.3 + 2.3D [NM], b – for the sloped segments – B [t · NM^{-2}] = 21.4 + 0.85D [NM]

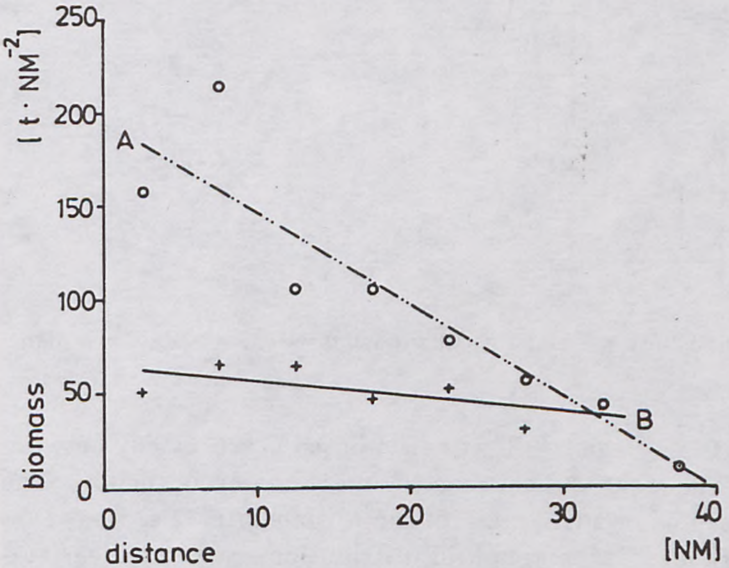

Fig. 3. Regression lines for the change in krill abundance with distance from the ice: a – Elephant Island area – B [t · NM^{-2}] = 195.5 – 4.9D [NM], b – South Orkney Islands area – B [t · NM^{-2}] = 65.0 – 0.85D [NM]

numerous, especially at the stations most distant from the ice border. The mean density of krill was 32.7 t $\cdot$ NM^{-2}.

The abundance of krill changed with distance from the ice differently in the three regions. Near Elephant Island and the South Orkney Islands it was clearly decreasing (Fig. 2), while at the ice edge zone it was increasing (Fig. 3). Apart from the changes in abundance with distance from the ice, an east-west gradient was also apparent, with the western side of the survey area having a higher average biomass than the eastern side. The opposite trend was observed in the chlorophyll *a* concentration (Lipski, in press).

3.2. Vertical distributions

In all three areas krill was distributed in the 20 to 90 m layer (Figs. 4, 5, 6), but the maximum biomass was found at different depths for different regions. The data were analysed separately for day and night, assuming 0400–2200 hours to be day and 2200–0400 hours to be night.

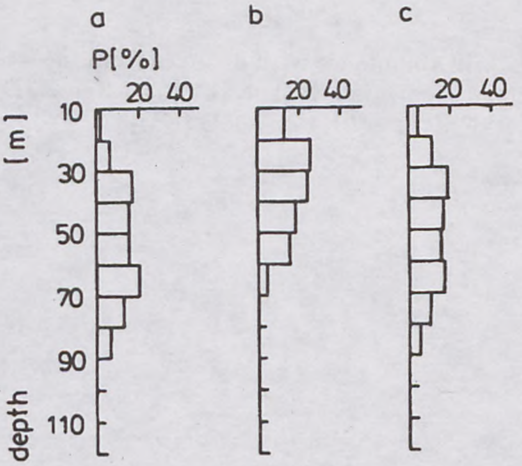

Fig. 4. Krill depth distributions in the Elephant Island area: a – day, b – night, c – total

In the Elephant Island region krill was distributed nearly evenly between 20 and 60 m during the night and between 40 and 80 m during the day. The depth of the biomass mass centre (mean of the 12 time intervals) was 47 m.

In the South Orkney Islands area krill distribution reached a clear maximum between 20 and 40 m, during both day and night. The depth of the biomass mass centre was only 32 m, much shallower than in the Elephant Island region.

In the ice edge zone krill depth distributions were very similar during the day and at night. The biomass gradually increased with depth reaching a maximum at about 40 m, then decreasing again to become negligible below 90 m.

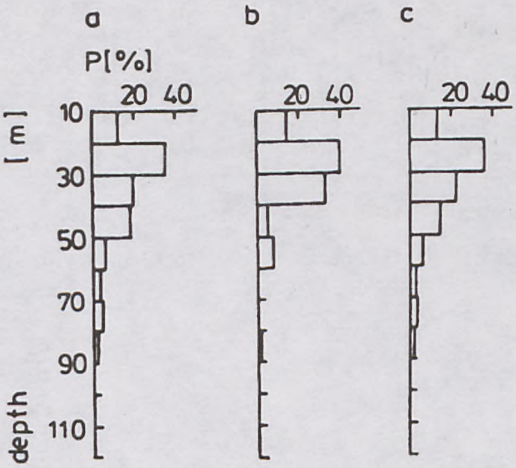

Fig. 5. Krill depth distributions in the South Orkney Islands area: a – day, b – night, c – total

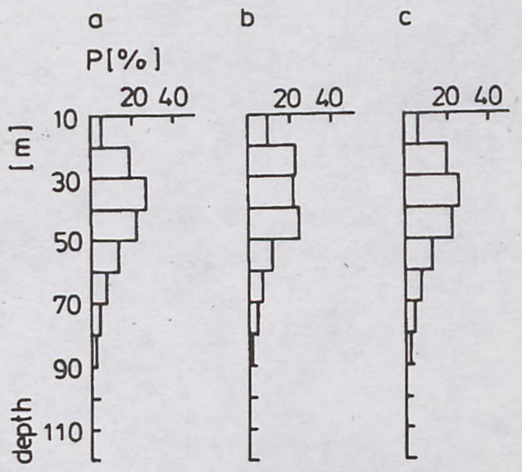

Fig. 6. Krill depth distributions in the ice edge zone: a – day, b – night, c – total

3.3. Diurnal changes

Diurnal changes in krill distribution are different in the three regions. In the vicinity of Elephant Island krill clearly undergoes diel vertical migrations with a periodicity of about 24 hours. Krill is closest to the surface at night (30 m) and deepest about noon (70 m) (Fig. 7). In the ice edge region only minor differences are observed at different time intervals (Fig. 8). At any time, most of the krill occupies depths between 20 and 50 m. A slight

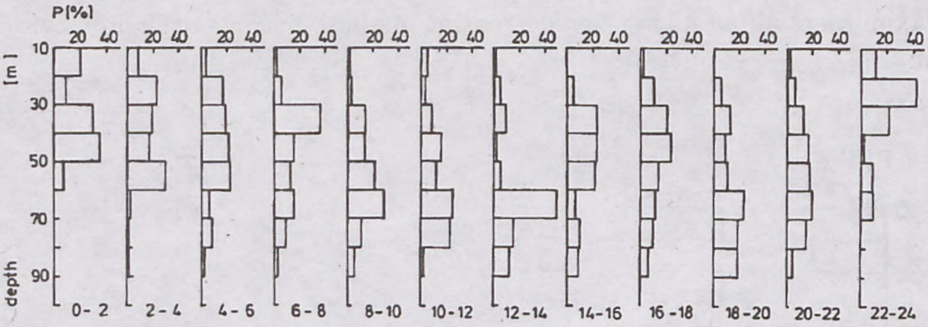

Fig. 7. Histograms of krill depth distributions at 2-hour (local time) intervals in Elephant Island region

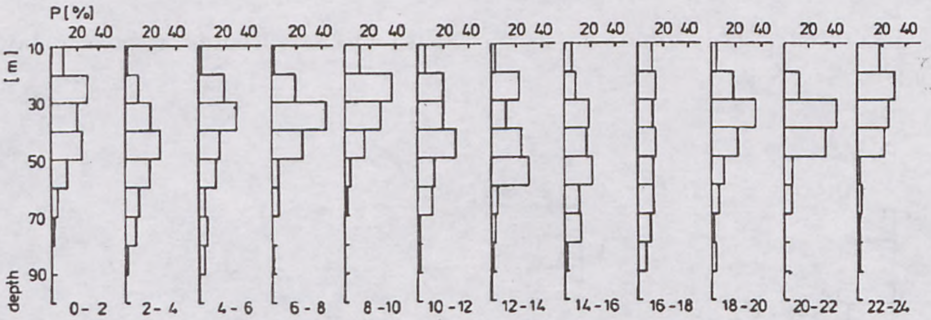

Fig. 8. Histograms of krill depth distributions at 2-hour (local time) intervals in the ice edge zone

Fig. 9. Histograms of krill depth distributions at 2-hour (local time) intervals in the South Orkney Islands region

ascent to the surface is observed twice in a diel cycle, about midnight and just before noon (Fig. 8). This explains the similarity of the day and night vertical distributions (Fig. 6). The range of migrations in the ice edge zone is smaller than in the Elephant Island area, and the periodicity is smaller by half. The krill distribution in the South Orkney Islands region is much shallower than in the other two areas, and the migration pattern is less clear (Fig. 9). The majority of krill occupies depths of 30–40 m, regardless of the time of day, the only exception being 0800–1000 hours.

4. Discussion

In the Elephant Island region krill was distributed between 10 and 90 m with the biomass maximum moving slightly from the greatest depth at noon (70 m) to the shallowest at night (30 m) (Fig. 4). Krill concentrated in swarms was clearly undergoing diel vertical migrations.

In the ice edge region only minor differences were observed at different time intervals (Fig. 8). At all times krill occupied depths between 20 and 40 m. A slight ascent to the surface was observed twice in a diel cycle, about midnight and just before noon. This 12 hour period may be related to the predominance of adolescent krill at the ice edge. The krill distribution in the region of the South Orkney Islands was much shallower than in the other two, and the migration pattern was less clear (Fig. 9). The majority of krill occupied depths of 30–40 m regardless of the time, day or night. It should be noted that the amount of data in this region was much smaller than in the two other regions, especially in the evening and night hours (from 1600 to 0400).

These results therefore reveal distinct area-dependent differences in horizontal and vertical distributions of krill. When comparing results from four regions, Everson (1983) also found major differences between them, confirming the great variation in the migration pattern described by Marr (1962). Kalinowski and Witek (1985), who have collected the largest amount of data on krill in Western Antarctic, distinguished 18 regions in which the depth distributions of krill were different. Although the authors tried to investigate the influence of light, water stratification, level of oxygen saturation, feeding conditions and the avoidance of predation on krill distribution, they did not come to any consistent conclusions. The present results do not allow us to solve this problem either. On the contrary, they add one more factor on which the depth distributions may depend – namely the dimensions of krill. It seems from our present and previous results (Godlewska and Klusek, 1987), as well as from other data (Brinton *et al.*, 1987; Everson and Ward, 1982) that small young krill is distributed less deeply than are adults. Moreover the period of migrations is shorter for smaller animals, with a consequent change in the depth distributions. The South Orkney Islands data do not support this hypothesis, but the hydrological regime in that region was found to be very specific and we believe it could affect the distribution pattern.

It follows from the shallower krill distribution at night than during the day (Figs. 4–6) (Kalinowski and Witek, 1985; Miller and Hampton, 1989), and from the shallower distribution patterns during winter and spring than in summer (Klusek and Godlewska, 1988; Siegel, 1989) that light plays an important role in the behaviour of krill. However, it is not the most influential factor, since in the South Georgia region krill consistently behaves in a way opposite to that which would be a consequence of light dependence – that is, a shallow distribution in poor light, and deep distribution in strong light (Everson, 1983; Kalinowski, 1978). Kalinowski and Witek (1980) suggest that this could be related to the avoidance of predation by benthic fishes. Such behaviour for other species has been reported in the literature (Gliwicz, 1986; Zaret and Suffern, 1976).

Feeding conditions do not seem to be the deciding factor either. In the Elephant Island area, feeding conditions are always very poor (little phytoplankton (Lipski, 1982) and the krill are in a bad physiological condition (Dric and Semenova, 1989). Nevertheless, this region is already reputed to be one of the richest in krill (Godlewska and Suszczewski, 1988). In our opinion, although not yet fully documented, they are the physical factors that are the most important for both horizontal and vertical distributions of krill. It has been shown by Everson and Murphy (1987) that krill is carried passively by the current through a region. Maklygin (1986a) has also found a close relationship between the wind drift and migrations of krill aggregations. Hence, the depth distributions of krill should be analysed in correlation with the water mass distribution in a given area (Makarov *et al.*, 1988). In the frontal zones, where deep mixing of water occurs, krill is also distributed in deep layer. In this study, krill north of Elephant Island was distributed nearly evenly down to 80 m (Fig. 4) and during FIBEX down to 250 m (Kalinowski, 1982; Loeb and Shulenberger, 1987; Macaulay *et al.*, 1984).

In the South Orkney Islands area there was a clearly-marked thermocline at about 40–50 m separating two water masses (Tokarczyk *et al.*, in press). Nearly all the krill in this area was confined to the upper 50 m, both day and night. In other years, when the hydrological structure was different, krill was frequently recorded much deeper in this area, undergoing diurnal vertical migrations (Everson, 1983; Kalinowski and Witek, 1985; Maklygin, 1986b).

Our hypothesis is also confirmed by the data of the First Polish Expedition in 1976/77. Comparing the hydrological results (Chłapowski and Grelowski, 1978) with krill distributions (Rakusa-Suszczewski, 1978) we can see that in the Palmer Archipelago region, where there was a distinct thermocline at about 75–100 m separating the different water masses, krill was found only to a depth of about 80 m, while in the King George area and in the Scotia sea, where one type of water mass extended down to 100–150 m, krill distributions was also deep.

Clearly, further studies on the relation between krill depth distributions and hydrology are needed.

During FIBEX in the Palmer Archipelago region the thermocline was very weak and krill was distributed down to 10 m (95.6% of the krill biomass). On the other hand, in the Drake Passage there was a thermocline at a depth of about 75 m and 94% of krill was distributed in the top 80 m.

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